Early Palaeozoic Peri-Gondwana Terranes

New Insights from Tectonics and Biogeography

Edited by

M. G. Bassett

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Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography

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EDITED BY

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National Museum of Wales, Cardiff, UK

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Early Palaeozoic peri-Gondwana terranes: new insights from tectonics and biogeography

MICHAEL G. BASSETT

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The Neoproterozoic to early Cambrian breakup of the ancient amalgamated supercontinent of Rodinia spawned a heterogeneous realignment of cratonic masses that involved the construction of the mega-terrane of Gondwana. Such reconfiguration took place from about 650 Ma, mostly via the conjunction of Australasian, Indian, Antarctic, African, South American and some Arabian crustal fragments (e.g. see Cocks & Torsvik 2002, 2006; Pankhurst & Vaughan 2009).

For much of its earliest history, Gondwana formed a non-marine heartland, straddling South Polar environments across northern South America and North Africa through the late Vendian–late Silurian (Cocks & Torsvik 2002, figs 2–8). However, around the margins of this continental core and in relatively adjacent regions, was an assortment of terranes embracing a variety of marine and non-marine environments.

This volume focuses on various aspects of the tectonic and biogeographical evolution around the Gondwanan margin and its adjacent terranes. It is the outcome of a 1 day symposium, under the same title, comprising the annual Lyell Meeting for 2007 held at The Geological Society of London, Burlington House, and organized jointly with The Palaeontological Association. Close to 100 delegates attended. There were 14 presentations at the meeting, plus one paper read in title and abstract only but which is published here in full (Benedetto *et al.* 2009).

Four of the papers presented at the symposium were not submitted subsequently for publication because they were scheduled for publication elsewhere. Nigel Hughes (University of California, Riverside) analysed the complex structural and faunal relationships of the Himalayan margin within the Indian craton and various regions of Tibet, Sibumasu, Indochina and South China. In contrast to some recently published models, there is strong evidence of a continuous passive margin extending from the Indian craton and encompassing all major sectors of the Himalaya during Cambrian time; interpretations are based on new collections of trilobites for biostratigraphical resolution, and on whole-rock neodymium isotope correlations. Hughes and colleagues have recently published an account of the data and results of some of this work in the Society Journal (Torsvik *et al*. 2009).

Jürgen von Raumer and colleagues (Fribourg University, Switzerland) discussed pre-Mesozoic terranes in Central Europe as a key to unravelling the Gondwanan margin. A ribbon-like series of terranes (Galatian and Hun terranes) detached from the Gondwanan margin by the early Devonian, leading to the redistribution of Gondwana-derived microcontinents, which were to form the future Variscan terranes.

The two other contributions not published here both addressed Gondwanan geology in South America. Enrique Díaz-Martínez and Juan Carlos Gutiérrez-Marco (both from Madrid) analysed early Palaeozoic biogeography and geodynamics of the Central Andes, where palaeocontinental latitudinal shifts and related climate changes led to a complex development of both warm- and cool-water carbonates, as well as marine, alpine and continental glaciation. Protracted orogeny along the Gondwanan margin led to complex basin development, with superimposition of magmatic, tectonometamorphic, erosional and depositional events. Stan Finney (California State University, Long Beach) discussed the origin of the Cuyania terrane, which forms the greater Precordillera of western Argentina. This region has been interpreted as a rifted terrane derived from the Ouachita embayment of Laurentia in early Cambrian time, drifting across the Iapetus Ocean as a microcontinent and docking with the proto-Andean margin of Gondwana in the mid- to late Ordovician. From analysis of U–Pb geochronology in detrital zircons, Finney argues that the evidence is not compatible with a Laurentian origin of Cuyania, but is consistent with a parautochthonous Gondwanan origin, suggesting migration along a transform fault from a position on the southern margin of West Gondwana in the mid-Ordovician to its present position outboard of the Famatinian magmatic belt in Devonian time. A full discussion of this controversial issue has been given by Finney (2007*a*, *b*). The model of an

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allochthonous origin from Laurentia has been discussed in detail by Benedetto (2004) and Benedetto *et al.* (2009).

The penultimate paper in this volume (Edwards *et al.* 2009) is the only contribution that was not included in the Lyell Symposium. It is included here to fill an important gap in our knowledge of evolutionary and phytogeographical data on the early history of land plants from high-latitutude Gondwana.

Finally, it is relevant to note that this volume is very much a companion to other recent publications in the Geological Society *Special Publication* series. Those edited by Vaughan *et al.* (2005) and by Pankhurst *et al.* (2008) specifically address ranges of topics covering Gondwanan geology, and the volume edited by Winchester *et al.* (2002) contains a number of contributions relevant to the evolution of Gondwana itself and of Gondwana-derived terranes.

I am especially grateful to The Geological Society of London, the National Museum of Wales, and The Palaeontological Association for their generous financial and logistical support of the 2007 Lyell Meeting. I am also grateful to all the speakers and to a substantial audience for contributing to a stimulating day, of which this volume is a fitting record. Although a few contributors chose eventually not to submit their presentations for publication, their overall input remains important in having provided a well-rounded overview of the early development of peri-Gondwana. All papers in the volume have been subjected to peer review analysis and comment, and for their considerable input to the editorial process I thank the following as referees (some of whom I leaned on more than once!): A. J. Boucot (Corvallis, USA), C. Burrett (Hobart, Tasmania), N. Butterfield (Cambridge, UK), W. G. Chaloner (London, UK), L. Cherns (Cardiff, UK), J. C. W. Cope (Cardiff, UK), D. Loydell (Portsmouth, UK), B. Natalin (Istanbul, Turkey), R. M. Owens (Cardiff, UK), F. Paris (Rennes, France), L. E. Popov (Cardiff, UK), P. Sheehan (Michigan, USA), V. Stepanez (Wilhelmshaven, Germany), C. Wellman (Sheffield, UK) and B. F. Windley (Leicester, UK). One additional referee chose to remain anonymous. My colleague in Cardiff, J. Cope, has been of constant help in discussions and in advising on the editing of some papers. Also at the National Museum of Wales, P. J. Knapman, L. C. Norton and V. K. Deisler gave considerable technical assistance and advice in the preparation of the manuscripts that make up this book.

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The Lower Palaeozoic palaeogeographical evolution of the northeastern and eastern peri-Gondwanan margin from Turkey to New Zealand

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Abstract: In Lower Palaeozoic times, Gondwana was by far the largest tectonic entity, stretching from the South Pole to north of the Equator, and is termed a superterrane. We consider the northeastern sector of the Gondwanan and peri-Gondwanan margin, from Turkey through the Middle East, the north of the Indian subcontinent, southern China and SE Asia, to Australia and New Zealand. There was progressive tectonic activity along some of its margins during the period, with areas such as southeastern Australia undergoing enlargement through the accretion of island arcs as that part of Gondwana rotated. However, most of the area, from the Taurides of Turkey to at least east of India, represented a passive margin for the whole of the Lower Palaeozoic. Other adjacent areas, such as the Pontides of Turkey and Annamia (Indochina), were separate from the main Gondwanan craton as independent terranes. The quality and quantity of available data on Lower Palaeozoic rocks and faunas varies enormously over different parts of this substantial area, and there are few or no detailed palaeomagnetic data available for most of it. Some workers have considered the string of terranes from Armorica to the Malaysia Peninsula as having left Gondwana together in the late Cambrian as a Hun superterrane, leaving a widening Palaeotethys Ocean between it and Gondwana. However, we consider that the Palaeotethys opened no earlier than in late Silurian time (with Armorica and other terranes to its north), and that the Hun superterrane was not a cohesive unity. Other researchers vary in presenting many substantial Central Asian and Far Eastern terranes, including North China, South China, Tarim, Annamia and others, as integral parts of core Gondwana and not leaving it until Devonian and later times. We conclude that North China, Tarim and Annamia, among others, were probably not attached to core Gondwana in the Lower Palaeozoic, that South China was close to Gondwana (but not an integral part of it), and that Sibumasu was probably part of Gondwana. We try to reconcile the very varied published geological data and opinions, and present new palaeogeographical maps for that sector of Gondwana and surrounding areas for the Cambrian (500 Ma), Ordovician (480 Ma) and Silurian (425 Ma).

Gondwana was by far the largest terrane during the whole of Lower Palaeozoic time, and comprised all of South America, Africa, Madagascar, Arabia, India, East Antarctica and Australia, totalling *c.* 95×10^6 km^2; that is, 64% of all landmasses today or 19% of the total Earth surface. However, surrounding it were a whole series of much smaller terranes, many of which originally formed part of the Gondwanan superterrane, and which became separated from it at various times during the Phanerozoic (Fig. 1 shows the modern geography and old terrane boundaries for the western part of the area, and Fig. 2 shows core Gondwana). It is the prime purpose of this review, first, to identify the boundaries of these marginal terranes in the northeastern sector of this superterrane in terms of today's geography, using a digitized database, and, second, to construct palaeogeographical maps of this very substantial area at successive times during the Lower Palaeozoic (Figs 3–5). We have already provisionally attempted this task as part of a global survey (Cocks & Torsvik 2002), but it

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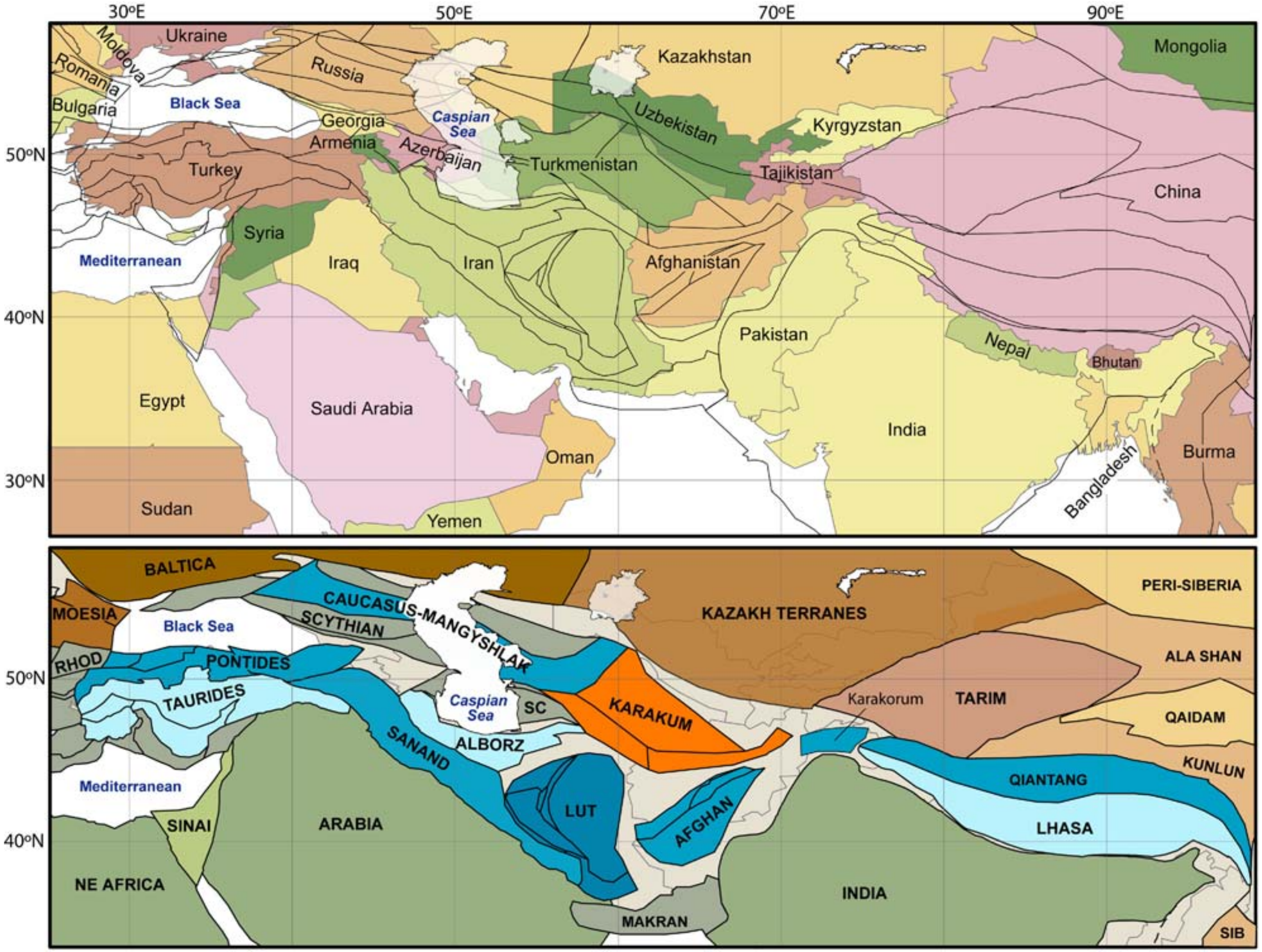

Fig. 1. (**a**) Map of the area from Turkey to Tibet, showing some modern country names and the boundaries of the terranes along the northeastern Gondwanan margin. (**b**) Map of most of the same area as in (a), but with country names deleted and indicating the names of the Palaeozoic terranes, which we discuss here. The light grey areas are Mesozoic to Recent accretionary belts, and the substantial brown area indicates the many Kazakh terranes, which are undifferentiated here. Rhod, Rhodope; SC, South Caspian; Sib, Sibumasu.

seems timely to review the area again in more detail, incorporating some of the large amount of new tectonic, palaeomagnetic and faunal data that have emerged since our previous work. That paper in turn was partially developed from an earlier review of the whole Gondwanan and peri-Gondwanan area in the Lower Palaeozoic by Cocks & Fortey (1988). However, the terrane margins were much more subjectively portrayed in those earlier papers than now, as were also therefore the consequent palaeogeographical reconstructions, and the Far Eastern sector in particular is much revised here.

We have identified two key questions to be considered. They are, first, whether or not many of these peri-Gondwanan marginal terranes were combined in the so-called Hun (or Hunic or Hunia) superterrane, as postulated by von Raumer, Stampfli and their co-authors (e.g. von Raumer *et al.* 2002; Stampfli & Borel 2002, 2004). There is clear consensus on the existence of rifting between core Gondwana and some of its marginal terranes over much of the area to form a widening Palaeotethys Ocean, but when that rifting initiated, and to what extent the peri-Gondwanan marginal terranes were coherent with each other to form a superterrane, is contentious. However, it is agreed by all researchers that the earlier rifting was a clearly distinct series of tectonic events from the subsequent and well-documented late Carboniferous rifting that separated many of the terranes away from core Gondwana to form the Neotethys Ocean in Permian times (Stampfli *et al.* 2001). The second difficult question is the reality or otherwise of the views published by various Australasian workers, particularly Metcalfe (e.g. Metcalfe 2002*a*), concerning the Central and SE Asian parts of the region. They have postulated that an enormous area, including North China, South China, Tarim, Qaidam, Sibumasu, Annamia and others, were unified as an integral part of equatorial core Gondwana throughout the whole of the Lower Palaeozoic, and remained so until the Palaeotethys Ocean opened in (according to them) Devonian times, or even, in the case of some terranes, until the Neotethys Ocean opened in the Permian.

We will first review the relevant parts of core Gondwana, and then each peri-Gondwanan terrane briefly in turn, and then present a short unified outline geological history of the area, accompanied by new palaeogeographical maps for the Cambrian, Ordovician and Silurian. As in our previous papers, we have combined our experience on faunal provinces and palaeomagnetism, together with some consideration of distinctive sedimentary facies, to produce our maps. We must also stress that knowledge and data from the various areas differ enormously, from excellent to pathetic, and the maps we present can only be regarded as provisional.

A note on the terminology of Lower Palaeozoic oceans is relevant. The Panthalassic Ocean was by far the largest, but lay a long way to the north of the area considered here and on the far side of the substantial Siberian terrane (Cocks & Torsvik 2002, 2007). All researchers seem agreed on the term Iapetus for the ocean between Laurentia and Baltica–Avalonia; most are agreed on Tornquist (originally named as a sea) for the pre-Caledonide ocean between Avalonia and Baltica, and Rheic for the widening ocean between Avalonia as it left Gondwana (although different workers have estimated opening and initial spreading times for that ocean varying between late Precambrian and mid-Ordovician), but again all these are topics outside the scope of this paper. For the ocean between Baltica and Gondwana we (Cocks & Torsvik 2005) have used the term Ran (Hartz & Torsvik 2002) from the Cambrian to early Ordovician times (before the rapid rotation of Baltica was complete), although this appears to be a similar oceanic concept to the Prototethys Ocean used by others in a comparable area from the Cambrian to the Silurian (e.g. Stampfli & Borel 2002, 2004). Palaeotethys seems to be consistently used by authors as the name for the ocean spreading from possibly Ordovician, but more probably late Silurian, times onward into the early Mesozoic, between the European and Middle Eastern peri-Gondwanan terranes and core Gondwana itself. However, further eastwards, a rather different concept of the Palaeotethys Ocean is portrayed by other workers, summarized by Metcalfe (e.g. Metcalfe 2002*a*). Also in this Central Asian and Far Eastern region, and adjoining Gondwana and peri-Gondwana to their north, the terms Asiatic and Palaeoasian (or Palaeo-Asian) have been used by various workers, particularly from the Former Soviet Union, for different oceanic areas at various Palaeozoic times. Many of these usages of Palaeoasian Ocean are for eastward extensions of the Ran, Prototethys or Palaeotethys. However, the reconstructions and palaeogeography of the complex area between Siberia and Gondwana, which include the many separate Kazakh terranes (Fig. 1b), are even further from being widely agreed than the region considered here, and will not be discussed further.

Comparably, considering the terminology of orogenies, the terms Caledonide and Hercynian (or Variscide) have been applied by many previous workers to various tectonic events in parts of Asia, both in the Middle and Far East, but those terms should be used only in Western Europe and eastern North America, where they apply to particular orogenic phases in the collision and assembly of terranes there; and thus we do not use them for the eastern and northeastern Gondwana areas discussed in this paper.

The Gondwanan core

All palaeogeographical reconstructions agree that the continents of Africa, Antarctica and Australia and the subcontinent of India were parts of our sector of Gondwana in the Lower Palaeozoic, and most workers also include Arabia. To put the area in larger context, we show the progressive palaeogeographical positions for the whole of core Gondwana in Figure 2. Other regions within the area, which may or may not have been parts of core Gondwana or peri-Gondwana, and whose positions and biogeographical relationships have often been contentious, are treated in the subsequent section. Gondwana is characterized by a series of terrane-distinctive faunal provinces very different from those found in other large contemporary areas such as Laurentia, Baltica and Siberia (documented and reviewed by Fortey & Cocks 2003). Because the old oceans were at their widest in the early Ordovician, those terrane-linked faunas are discussed in the Ordovician section below.

Reviewing the area (Fig. 1) from west to east, although the Sinai area of Egypt and Israel has undergone some Mesozoic to Recent movements, in the Lower Palaeozoic it was unquestionably part of Africa. The Arabia area shown as such in Figure 1, including Saudi Arabia, Yemen, Oman, Lebanon, Jordan and the southern parts of Syria and Iran, as well as the Sinai area, was an integral part of core Gondwana from earliest Cambrian times onwards (Allen 2007). The rest of Iran, particularly the Sanand terrane, is more contentious and is discussed below under ‘Iranian terranes’. Sharland *et al.* (2001) have described the sequence stratigraphy of what they termed the Arabian plate; Millson *et al.* (1996) also reviewed the integrity of the various tectonic components of the area, as did Ruban *et al.* (2007). Fortey (1994) described typically Gondwanan trilobites from the late Cambrian of Oman, as did Fortey & Morris (1982) equally typical Gondwanan *Neseuretus* Fauna trilobites from the early Ordovician (Arenig) of Saudi Arabia, and El-Khayal & Romano (1985) from the middle Ordovician (Llanvirn) of Saudi Arabia. In the Silurian of Saudi Arabia, Al-Hajri & Paris (1998) described widespread deltaic sequences. The main part of the Indian subcontinent was certainly part of core Gondwana, but has relatively few Lower Palaeozoic rocks preserved upon it apart from at the northern margin, which is discussed under ‘Himalayan area’ below.

Between India and Australia today, the Lower Palaeozoic core Gondwana margin has either been subducted or lies beneath the Indian Ocean, and is also complicated by the Mesozoic tectonics of the Sibumasu area (see below). However, it is well exposed in Australia, whose Cambrian, Ordovician and Silurian faunas and biogeography have been reviewed by Wright *et al.* (2000), Webby *et al.* (2000) and Pickett *et al.* (2000), respectively. Li & Powell (2001) described the palaeogeographical evolution of Australasia from the Neoproterozoic onwards, but without many references to the faunas; and Metcalfe, in many papers (e.g. Metcalfe 2002*a*), has also described the Palaeozoic palaeogeography of that area as it developed.

The overall movements of the Gondwanan superterrane during the Lower Palaeozoic (Fig. 2) deserve comment. In the middle Cambrian (510 Ma) the South Pole lay under NW Africa, and Gondwana drifted to the NE in that polar area between then and the early Ordovician (480 Ma). In contrast, between 480 Ma and the middle Silurian (425 Ma), that part of Gondwana drifted to the SW, as can be seen by the Brazilian pole position at 425 Ma. However, the Australian part of Gondwana remained in an equatorial position throughout the entire Lower Palaeozoic; therefore these movements all indicate that the superterrane was in fact slowly rotating during this period, with active margins in the Australian–New Zealand–South American sectors and a passive margin from NW Africa to somewhere east of India.

Terrane review

We now review the areas considered here, progressing from Turkey clockwise round Gondwana to New Zealand. Many (but not all, as discussed separately below) of them were independent terranes at some time in the Phanerozoic. As a starting point we have used modern-day terrane boundaries in a digital form and given by Stampfli & Borel (2004) for the terranes as far east as Afghanistan. The boundaries of the more westerly terranes that we analyse, stretching from Turkey to SW China (Tibet), are shown in newly constructed diagrams (Fig. 1). The remainder, from Burma (Myanmar) to New Zealand, are not shown as a new figure here, but we largely follow Cocks & Torsvik (2002, 2007) and Torsvik & Cocks (2004) in their boundaries.

Pontides terrane

The northern part of Turkey, from just west of the Bosphorus to just south of the border with Georgia, is considered as a single terrane (normally termed the Pontides) by some workers (e.g. Cocks & Torsvik 2002; Ruban *et al.* 2007) and as two or three separate terranes (Istanbul, Zonguldak and East Pontides) by some others (e.g. Stampfli &

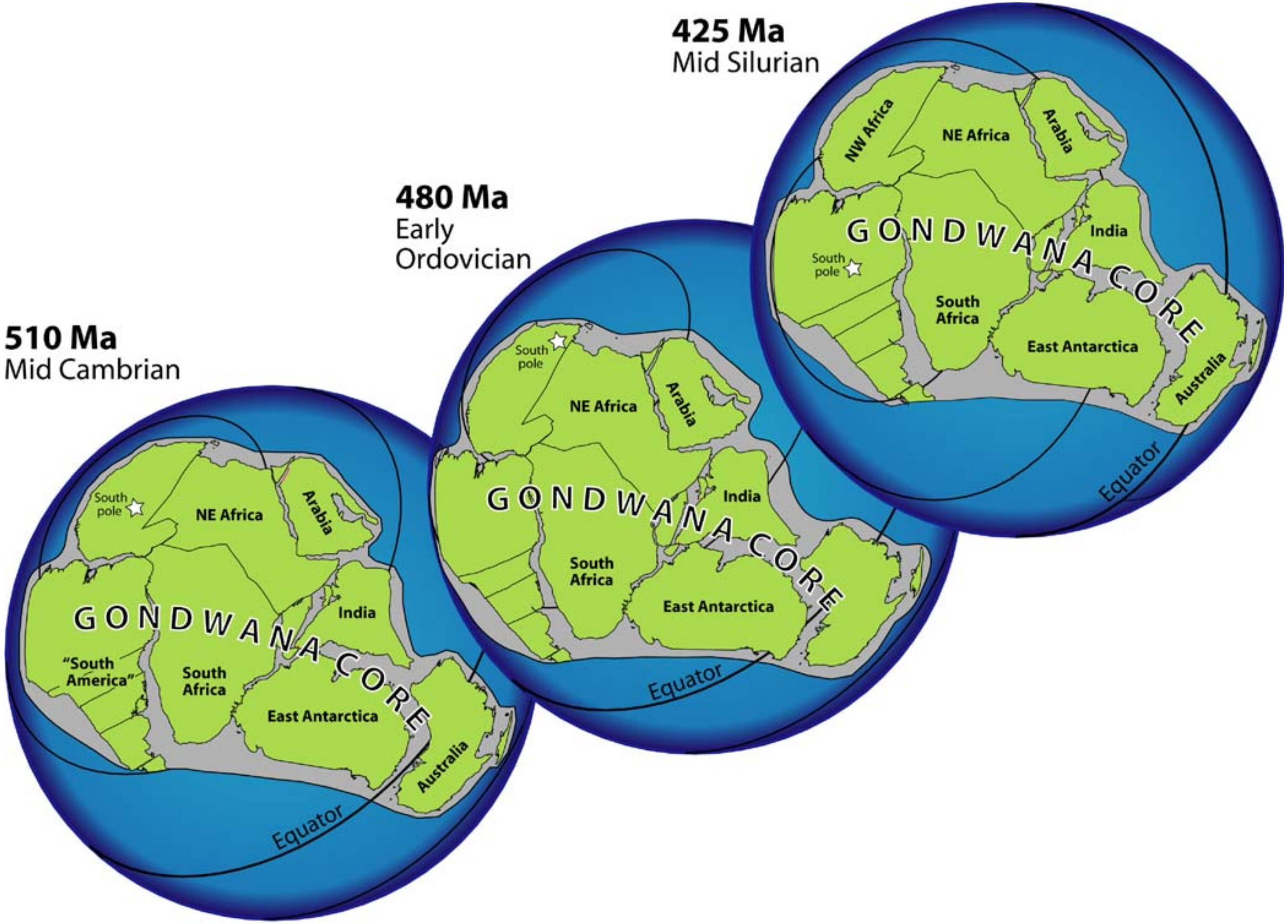

Fig. 2. Reconstructions for the middle Cambrian (510 Ma), early Ordovician (480 Ma) and middle Silurian (425 Ma), showing the palaeomagnetically constrained progressive positions of core Gondwana (Table 1). Many of the peri-Gondwanan terranes discussed in this paper were also probably parts of core Gondwana at these times, but, because their positions are not definitively constrained, they are not included in this figure; neither are the other contemporary terranes around the world.

Borel 2004). Adjoining it to the west lies the Rhodope terrane, which consists entirely of Mesozoic and later rocks, and to its north the Moesia terrane, which has been considered by various workers to have formed part of either peri-Gondwana or Baltica in the Lower Palaeozoic, but whose positioning is outside the scope of this paper.

Dean *et al.* (2000) have described a key early Ordovician trilobite fauna from the Pontus Mountains of northern Turkey, which indicates that the area is of undoubted Gondwanan affinity, as the terrane-specific faunas are very different from those in the substantial Baltica terrane (Cocks & Torsvik 2005), which adjoins the Pontides today. Those Pontide Mountain Ordovician rocks and trilobites, and also the Silurian rocks and brachiopods we have seen in the Istanbul area, contain no substantial carbonates and are, rather surprisingly, very reminiscent of those in the Welsh Borderland, then part of the distant Avalonian sector of peri-Gondwana. Thus we have omitted the Pontides from our maps (Figs 3–5) as its Lower Palaeozoic position is so uncertain.

Taurides terrane

Most of the southern part of Turkey and the NW part of Syria formed a single terrane in the Lower Palaeozoic, although some workers (e.g. Stampfli *et al.* 2001) have divided the area into two separate terranes, the Western Taurides and the Menderas Taurus terrane. Between the Pontides and the Taurides there is a large area within central Turkey that has no Palaeozoic rocks but that we have arbitrarily included within the Taurides in Figure 1b. From the differences between the apparently higher-latitude faunas of the now-adjacent Pontides terrane and the different and apparently intermediate-latitude faunas of the Taurides terrane, we conclude that the Pontides and the Taurides were probably not close to each other in the Lower Palaeozoic, as we also showed earlier (Cocks & Torsvik 2002). The Tauride Ordovician trilobite faunas have been extensively monographed by W. T. Dean (summarized by Dean & Monod 1997), and have been demonstrated to be typically core Gondwanan. However, in Cambrian and earliest Ordovician times, that part of Gondwana was not too far from the Baltica terrane, which lay on the opposite side of a relatively narrow Ran Ocean (Cocks & Torsvik 2005), thus allowing some normally diagnostic Baltic faunal elements, such as the trilobite *Asaphus*, to migrate to the Taurides as rare components of the fauna. In contrast, whereas Baltica carries no trace of the latest Ordovician Hirnantian glaciation, this is well developed in the Taurides (Monod *et al.* 2003). Thus the Taurides terrane is shown as part of core Gondwana on our reconstructions (Figs 3–5) and its later tectonic history was outlined by Okay *et al.* (2006).

Mangyshlak, Caucasus and Scythian terranes

The Caucasus Mountain area of Georgia and adjacent countries has been divided into a northern Greater Caucasus terrane and a southern Lesser Caucasus terrane, both of which lie to the west of the Caspian Sea and are also termed by some the Transcaucasus terrane. To the east of them, and on the eastern side of the Caspian, lies the Mangyshlak terrane, termed by some workers the Kopetdag terrane. Cocks (2000, fig. 6) used the term Mangyshlak terrane (which today adjoins Baltica to its north) to include both the Caucasus terranes and the Mangyshlak terrane. The Lower Palaeozoic faunal signals from these terranes are very inconclusive: there are no rocks older than middle Devonian on the eastern side of the Caspian, and the Silurian cephalopods recorded from the Caucasus are not terrane-specific. There is considerable middle and late Devonian volcanism in the Greater Caucasus terrane; however, Ruban *et al.* (2007), after a review of the published evidence, concluded that the Lesser Caucasus terrane did not leave Gondwana until the Permian, during the opening of the Neotethys Ocean. To the south of the Caucasus terrane lies the Scythian terrane, which was formed only in Mesozoic times by the creation of a Jurassic volcanic arc, and to the south of the eastern part of the Mangyshlak terrane area there is the South Caspian terrane, which is again of Mesozoic origin. Because of the lack of early Palaeozoic palaeogeographical evidence, all these terranes are omitted from our reconstructions (Figs 3–5).

The Kazakh terranes

To the north and NE of the Mangyshlak, Karakum, Karakorum and Tarim terranes lie the many, and as yet poorly defined, terranes, largely today within Kazakhstan, which are termed the Kazakh terrane assemblage. Most did not unite to form a much larger Kazakh (or Kazakhstania) terrane until the Late Palaeozoic. Many of those terranes have Precambrian cores and important and distinctive Lower Palaeozoic successions and faunas, some reviewed by Popov & Cocks (2006) and Fortey & Cocks (2003); but, although some carry faunas that may loosely defined as having some affinities with Gondwana and also with the lower-latitude areas of South China and elsewhere, their history and palaeogeography are outside the scope of this paper. There is no firm proof that any of the

Kazakh terranes lay within the boundaries of our Lower Palaeozoic palaeogeographical maps: some may have done so, but they are not shown in Figures 3–5.

Iranian terranes

In our previous review (Cocks & Torsvik 2002), we treated the Sanand (or Sanandaj–Sirjan), Lut (Central Iran) and Alborz terranes together, although as separate from the main Arabian plate (of which the Zagros Mountains formed part, although these are sometimes represented as a terrane independent from Arabia), following the review of terranes in the area by Millson *et al.* (1996) and Sharland *et al.* (2001). Gondwanan faunas have been reported from the centre of Iran: brachiopods by Bassett *et al.* (1999) for the late Cambrian and early Ordovician, and ostracodes by Ghobadipour *et al.* (2006) for the middle Ordovician and by Schallreuter *et al.* (2006) for the late Ordovician. However, there was some Lower Palaeozoic tectonic activity near that Gondwanan margin; for example, Ramezani & Tucker (2003) have described and dated extensive andesitic and trondhjemitic igneous activity near the western margin of the Lut terrane as occurring from 547 to 525 Ma in early Cambrian times, which is inconsistent with the rest of the neighbouring parts of Gondwana, which apparently formed a passive margin.

Data from the Late Palaeozoic, for example, those given in the paper by Brock & Yazdi (2000), which deals with the palaeobiogeographical affinities of Devonian brachiopods from Iran, indicate close faunal relationships between the Alborz terrane and adjacent parts of the north Gondwanan margin in Afghanistan, Armenia and Pakistan, as well as the Gondwanan cratonic core in northeastern Africa (Libya). Thus we consider these united units as continuing to be an integral part of core Gondwana at that time, and most workers appear to conclude that the Iranian terranes remained part of core Gondwana until the opening of the Neotethys Ocean in the late Palaeozoic, which was the same presumption as that held by us earlier (Cocks & Torsvik 2002). Along the suture zone between the Sanand terrane and the Arabian plate there is an ophiolite of Permian age, indicating their separation as part of the Neotethys opening event. However, Angiolini & Stephenson (2008), after an analysis of terrane-diagnostic Permian (Asselian–Sakmarian) brachiopods and palynomorphs, have concluded that by that later time the faunas in the Alborz Mountains of Iran were more similar to the Uralian sector of southeastern Laurussia (previously Baltica), and bore no resemblance to those from Gondwana, which carried faunas similar to the other parts of the Iranian terrane assemblage. There are few Lower Palaeozoic palaeomagnetic data from this large area, but, as far as can be determined from an analysis of published faunas, all these units were close to each other in Cambrian to Silurian times and formed parts of the Gondwanan passive margin.

The Afghan terrane assemblage

Lower Palaeozoic faunal and palaeomagnetic data are generally rather weak from this substantial area, but these data have been summarized by Talent & Bhargava (2003) and do not appear to include terrane-specific faunas. In contrast, however, there is much more information from Devonian times onwards. Afghanistan and immediately adjacent areas can be divided between a southern Helmand terrane and a northern Farah terrane. To the south of the Helmand terrane is the Makran terrane (Fig. 1b), which is a Mesozoic to Tertiary accretionary wedge, and from which no Lower Palaeozoic rocks are known, and which therefore receives no further mention here. Most workers have concluded that these Afghan terranes remained part of Gondwana until the Neotethys Ocean opened in the late Palaeozoic (mid-Permian), and we follow them.

Karakum terrane

The southern margin of this terrane (sometimes termed the Karaku or Karakum–Turan terrane) is adjacent to and north of the Iranian and Afghan terrane collages. There are no terrane-diagnostic Lower Palaeozoic faunas known from the terrane, and its palaeogeographical positioning is therefore uncertain: it could be either peri-Gondwanan or part of the Kazakh Terrane Assemblage and is thus omitted from the palaeogeographical reconstructions below.

Karakorum terrane

Gaetani (1997) has reviewed this terrane, which lies largely in the NW of Pakistan, from the Ordovician to the Cretaceous. Above a pre-Ordovician crystalline massif of uncertain age lies a succession containing early to middle Ordovician acritarchs and chitinozoans (Quintavalle *et al.* 2000), and Talent *et al.* (1999) have described early Ordovician conodonts from the western Karakorum and the adjacent Hindu Kush area. None of these biota are terrane-specific, and so we simply show the terrane as an outboard part of the core Gondwana passive margin on our reconstructions. The Karakorum terrane was stitched by lavas to the Pamirs to its north by middle Devonian time, but the Lower

Palaeozoic northern Gondwanan margin is difficult to resolve in detail in these areas.

Himalayan area

To what extent any separate and independent terranes fringed the Himalayan part of the Gondwana superterrane in Pakistan and northern India is uncertain, as the northern margin of the Indian plate is considered to have been much foreshortened by its Tertiary collision with China in the Himalayan orogeny, when many Lower Palaeozoic rocks were probably subducted. However, Myrow, Hughes and their colleagues (e.g. Myrow *et al.* 2006*a*, *b*) have ably documented the Himalayan area in the Cambrian and earliest Ordovician, and concluded that the various sections there, many of which have been relocated by subsequent tectonics, represent the Lower Palaeozoic passive margin of the main Gondwana superterrane. The area has been revised for the Ordovician by Torsvik *et al.* (2009*b*). Parcha (1996) has described the Cambrian of Spiti, which is adjacent to the Niti area from which Salter & Blanford (1865) described early Ordovician and other faunas in the pioneering days of the Indian Geological Survey. Those faunas, some of which were revised by Cocks & Rong (1989), are an interesting mix of endemic genera and species and those from elsewhere. There are few data from the succeeding mid- to late Ordovician, as a major unconformity covers much of the area, extending up to the middle Devonian in many places. Talent & Bhargava (2003) have summarized the Silurian data, and concluded that all the preserved rocks and fossils lay on the Indian plate and were thus within core Gondwana when they were deposited: we concur with that assessment.

Tarim, Kunlun, Qaidam, Ala Shan, North China and peri-Siberia

This group of terranes are partly shown in the NE of Figure 1b. We have included the area of the probably independent Gurvanshayan terrane of Mongolia within the Ala Shan terrane in that figure. Some of these terranes, the Qaidam, Kunlun and Ala Shan terranes, have been shown as connected to the Qiangtang and Lhasa terranes in the Lower Palaeozoic; for example, by Metcalfe (2002*a*), who concluded that the large terranes of Tarim and North China were also welded to Gondwana near Australia until the Devonian. However, chiefly from faunal analysis, some summarized by Fortey & Cocks (2003), we do not think that any of them are likely to have formed part of peri-Gondwana, although it must be admitted that their Lower Palaeozoic positions and relations to each other are not well constrained. There are some palaeomagnetic and a great deal of palaeontological data for Tarim, many of these summarized by Zhou & Chen (1992), and also for North China (Zhou & Dean 1996). We have elsewhere reviewed the peri-Siberian terranes (Cocks & Torsvik 2007), and concluded that they rotated with the main Siberian craton in the Palaeozoic, so that the area of peri-Siberia shown in Figure 1b lay on the far side of Siberia from Gondwana in the Lower Palaeozoic.

Tibetan terranes

The modern margins of the various terranes that make up Tibet and immediately adjacent areas in China are shown in Figure 1b; the principal peri-Gondwanan areas of this region are the Qiangtang terrane in the north and the Lhasa terrane in the south. Because the whole Tibetan area was strongly involved in the Himalayan orogeny, there are no good Lower Palaeozoic palaeomagnetic data, and there is some possibility that the Qiangtang terrane might not have formed a single unity in those times. However, there are some useful Lower Palaeozoic shelly faunas, such as the brachiopods described from the early Ordovician by Liu (1976) from near Mount Everest (Mount Jolmo Lungma), which, although many are endemic, nevertheless show some affinity with those in South China. Hughes *et al.* (2002) reviewed a small Middle Cambrian trilobite fauna from the Yunlung collage of the eastern Himalaya and concluded that it represents the most southeastward part of the Qiantang terrane, and that both it and the Lhasa terrane formed parts of the passive margin of core Gondwana in the Lower Palaeozoic.

South China terrane

It is a matter of controversy whether or not the substantial South China terrane area (which is sometimes termed the Yangtze terrane, and which is off the diagram to the NE of Fig. 1b) was an integral part of the core Gondwanan craton in the Lower Palaeozoic, although it has been shown as such by several workers (e.g. Cocks & Fortey 1988; Metcalfe 2002*a*). We did not show it as united with Gondwana in our earlier study (Cocks & Torsvik 2002, figs 3–7).

Blieck & Janvier (1999) have documented the distinctive South Chinese Devonian fish faunas, which were endemic to the area and terrane-diagnostic, and which indicate separation that was probably substantial from both North China and Gondwana. However, in South China, many of the Lower Palaeozoic faunas found there are of the same faunal provinces as those in peri-Gondwana

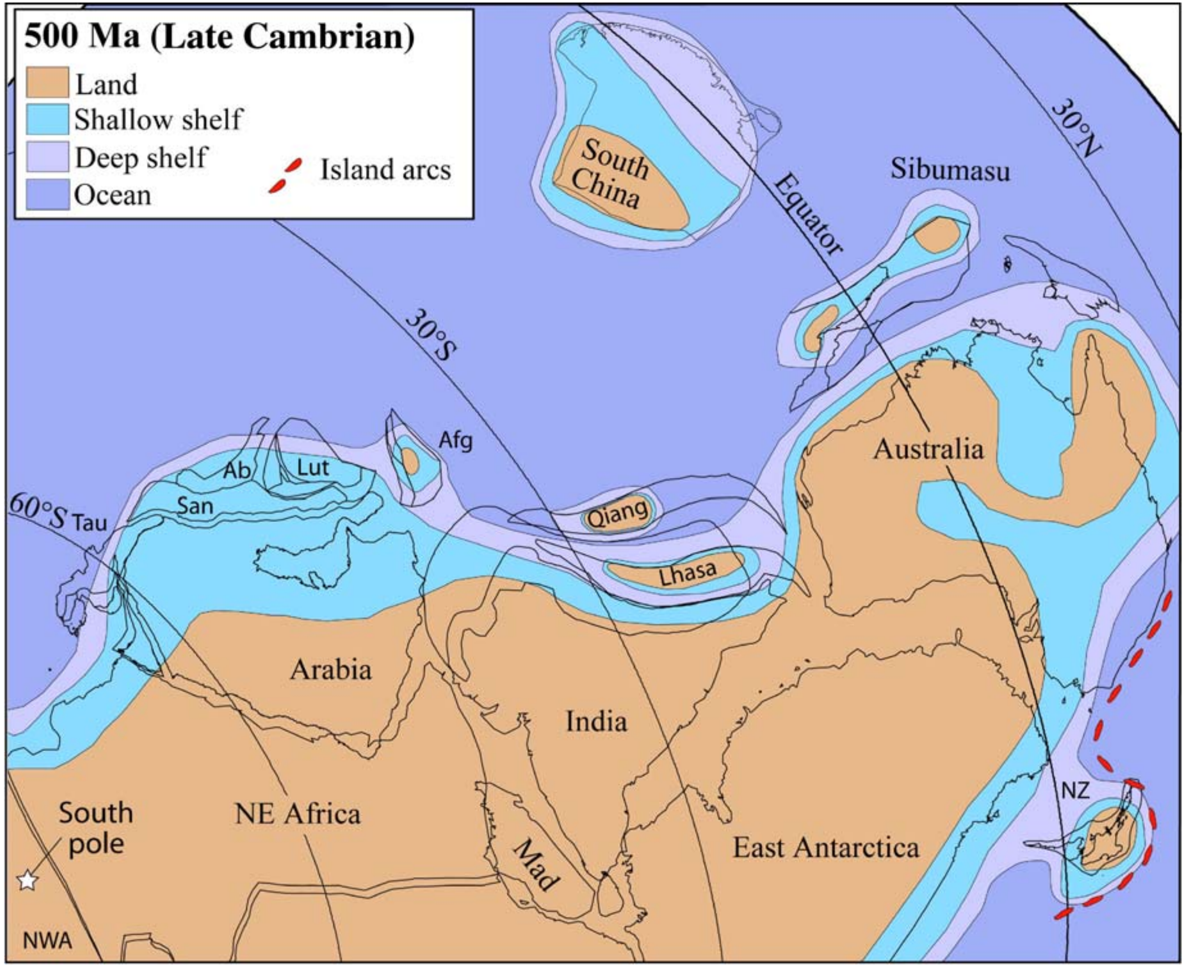

Fig. 3. Palaeogeography of the northeastern and eastern Gondwanan and peri-Gondwanan area in middle Cambrian times at 500 Ma. Ab, Alborz terrane; Afg, Afghan terranes; Mad, Madagascar; NWA, NW Africa; NZ, New Zealand; Qiang, Qiantang terrane; San, Sanand terrane; Tau, Taurides terrane.

and Gondwana. An outstanding example of this is the analysis by Fortey (1997) in which he established that the trilobites found in the late Ordovician Pa Kae Formation of southern Thailand, and the adjacent Kaki Bukit Formation of NW Malaysia, both in the Sibumasu terrane, were identical, even down to the species level, with those from the Pagoda Limestone, which lies in the central part of the South China terrane. In contrast, the South China terrane was probably at a substantial distance from the now-adjacent North China terrane in the Lower Palaeozoic, as the contemporary shelly faunas have little in common, as can be seen from the global provincial analysis of Cambrian trilobites by Shergold (1988). North and South China did not accrete to each other until early Mesozoic times; however, South China had merged with the neighbouring Annamia terrane by the end of the Carboniferous. Unlike most of the other peri-Gondwanan terranes discussed in this paper, South China does have palaeomagnetic data for the Lower Palaeozoic, some of which were summarized by Cocks & Torsvik (2002, table 1). However, since then, Yang *et al.* (2004) have published an important paper with new Cambrian palaeomagnetic data indicating that South China was probably then in the equatorial position that we show in Figure 3, and that agrees with the evidence from the dikelokephalinid trilobites found in both South China and Australia in the Early Ordovician. Yang *et al.* (2004) concluded that South China was attached to core Gondwana, but their new palaeomagnetic data do not constrain that, and we have not followed that part of their conclusions. The late Ordovician and Silurian palaeogeographies (Figs 4 & 5) within the South China terrane follow Rong *et al.* (2003).

Thus we conclude that, although South China appears to have been close to, and in substantial faunal communication with, core Gondwana during the whole of the Lower Palaeozoic, on balance it was more probably a terrane separate from the core. That is supported by an independent tectonic and sedimentary analysis by Allen (2007), which concluded that, whereas South China formed an integral part of Gondwana in the late Neoproterozoic and earliest Cambrian, the two plates evolved separately from early Cambrian times onwards.

Sibumasu terrane

There are diverse and abundant Cambrian to Devonian rocks and faunas in this well-known terrane (sometimes termed the Shan–Thai terrane), whose boundaries stretch today from Sumatra in the south, through the western part of the Malaysian Peninsula and Thailand, to the Shan States of Burma (Myanmar). Unfortunately, the substantial early Mesozoic granites through the spine of most of this terrane have badly distorted and fractured the older rocks, and it is thus difficult to present accurate Lower Palaeozoic palaeogeographical maps of the area. Cocks *et al.* (2005) reviewed the Cambrian to Devonian faunas in the more southerly parts of the terrane, in the NW Malaysian Peninsula and southern Thailand. There, there are extensive Cambrian to mid-Ordovician shallow-water sediments and faunas, which contrast with the turbidites and graptolitic shales of deeper-water, and presumably terrane-marginal, origin seen to the east and south of them in Perak in the Malaysian Peninsula and further southwards. In contrast, in the Silurian there are also thick carbonates of shallow-water origin (now largely dolomitized) in the Kuala Lumpur area in the central part of the peninsula. At the opposite end of the terrane, in the Shan States of Burma (Myanmar), there are extensive

Table 1. *Reconstruction fits for core Gondwana and peri-Gondwana terranes discussed in the text (relative to a fixed South Africa), and the basis for Figures 3–5*

	Euler latitude	Euler longitude	Euler angle
NW Africa	16.5	6.7	−1.15
NE Africa	40.4	−61.4	−0.7
Arabia	30.9	17.5	−6.32
Madagascar	14.8	137.5	−15.4
India, Lhasa	29.8	42.1	−60.5
East Antarctica	10.5	148.8	−58.2
Australia	19.6	117.8	−56.2
Taurides	30.8	17.5	−6.3
Sanand, Alborz, Lut	27.2	18.3	−5.4
Afghanistan	15.8	99.7	16.9
Qiang	32.3	33.2	−52.1
Sibumasu	7.5	91.8	−110.8
North New Zealand	12.9	120.1	−73.5

Based on Torsvik *et al.* (2009*a*) and this study.

Lower Palaeozoic deposits and substantially Gondwanan or peri-Gondwanan terrane-diagnostic faunas, particularly in the Ordovician (Cocks & Zhan 1998). On balance, we now consider that Sibumasu most probably formed part of core Gondwana, as shown by Metcalfe (e.g. Metcalfe 2002*a*) and other workers, in contrast to our previous preliminary conclusions (Cocks & Torsvik 2002).

Annamia terrane

Often termed Indochina, this terrane occupies most of the Indochina peninsula, a portion of adjacent political China, and the eastern part of the Malaysian Peninsula, where it is divided from the Sibumasu terrane by the substantial Bentong–Raub Suture Zone. To the north of Annamia there is a suture with South China, with which it merged before the late Carboniferous (Metcalfe 2002*b*). There are no good palaeomagnetic data, and the Lower Palaeozoic faunas of the former French colonies largely described over a century ago need substantial revision; however, in the Western Yunnan Province of China, Zhou *et al.* (2001) have reviewed the Ordovician (Darriwilian) colder-water trilobite faunas and differentiated between the Sibumasu, Annamian and South Chinese parts of that province, and concluded that the boundaries of Annamia today lie between the Nandinghe–Lanchanfiang Fault and the Honghe Fault in Yunnan. Metcalfe (2002*a*) showed Annamia as adjacent to Sibumasu and as part of core Gondwana in his Lower Palaeozoic reconstruction. However, as reviewed by Fortey & Cocks (2003) and (Cocks *et al.* 2005), although there are some fossils in common between Annamia (on the one hand) and South China and Sibumasu (on the other hand), the dominant impression is that there are rather different Lower Palaeozoic faunas in those terranes, and that Annamia may have been separate and somewhat distant from the other two and situated at higher palaeolatitudes: the shallow-water faunas were certainly very different in the better-documented Upper Palaeozoic. Thus we do not consider it probable that Annamia was part of core Gondwana in the Lower Palaeozoic, and it is omitted from Figures 3–5.

North Borneo

The boundaries of any possible independent Lower Palaeozoic terrane in this area are impossible to define as they are today inextricably involved in the more modern and very complex terrane collage around Indonesia and the South China Sea. However, Fortey & Cocks (1986) documented early Ordovician graptolites from the centre of North Borneo, and it seems probable that those deeper-water rocks represented part of the northern margin of Gondwana. Whether or not they formed a terrane separate from the main supercontinent, or perhaps an offshore mid-ocean basin, is difficult to assess and we do not show it as such in our reconstructions. Talent *et al.* (2003) reviewed more recent discoveries of Ordovician and Silurian rocks, including shallow-water mid- to late Silurian limestones containing corals and conodonts, although the latter have been found only in loose boulders in jungle streams.

Southeastern Australia

Largely today in the states of New South Wales, Victoria and Tasmania, there are the remains of several island arcs and microterrane belts that accreted to Gondwana in the Lower Palaeozoic, partly in the Cambrian but chiefly in the Ordovician. They form the southern part of what is known as the Tasman Orogenic Belt, the northern part of which, extending into Queensland (the New England orogen), is chiefly of Late Palaeozoic age. There is a large body of published data on the area, ably summarized by Gray & Foster (2005), and our palaeogeographical maps are largely drawn from the reconstructions of Metcalfe (e.g. Metcalfe 2002*a*) and Veevers (2004). Nearest the craton, the Delamerian orogen was active from the late Precambrian to the late Cambrian (about 650–500 Ma), and the more outboard Lachlan orogen, the largest in the belt, is largely of Ordovician age, but its final granites were intruded throughout the Silurian and into Early Devonian times. The Lachlan orogen has been revealed by geophysical investigations to continue northwards underneath the much younger surface rocks of the Great Artesian Basin, where it is locally termed the Thomson orogen. The Ordovician and Silurian faunas from both the craton and the arcs, and their palaeogeographical affinities, were summarized by Fortey & Cocks (2003, p. 261) and the correlation of the Lower Palaeozoic sedimentary basins on the adjacent Gondwanan craton was analysed by Jago *et al.* (2002).

New Zealand

Few Lower Palaeozoic faunas are known from this area, which is tectonically very active today; however, Cooper (1989) identified several terranes there. Münker & Cooper (1999) defined a Takaka terrane, cropping out in the Nelson area of northwestern South Island, which consists largely of a mid- to late Cambrian arc complex and which contains characteristic low-latitude Gondwanan Cambrian trilobites, indicating that the terrane may be confidently included within the active margin of

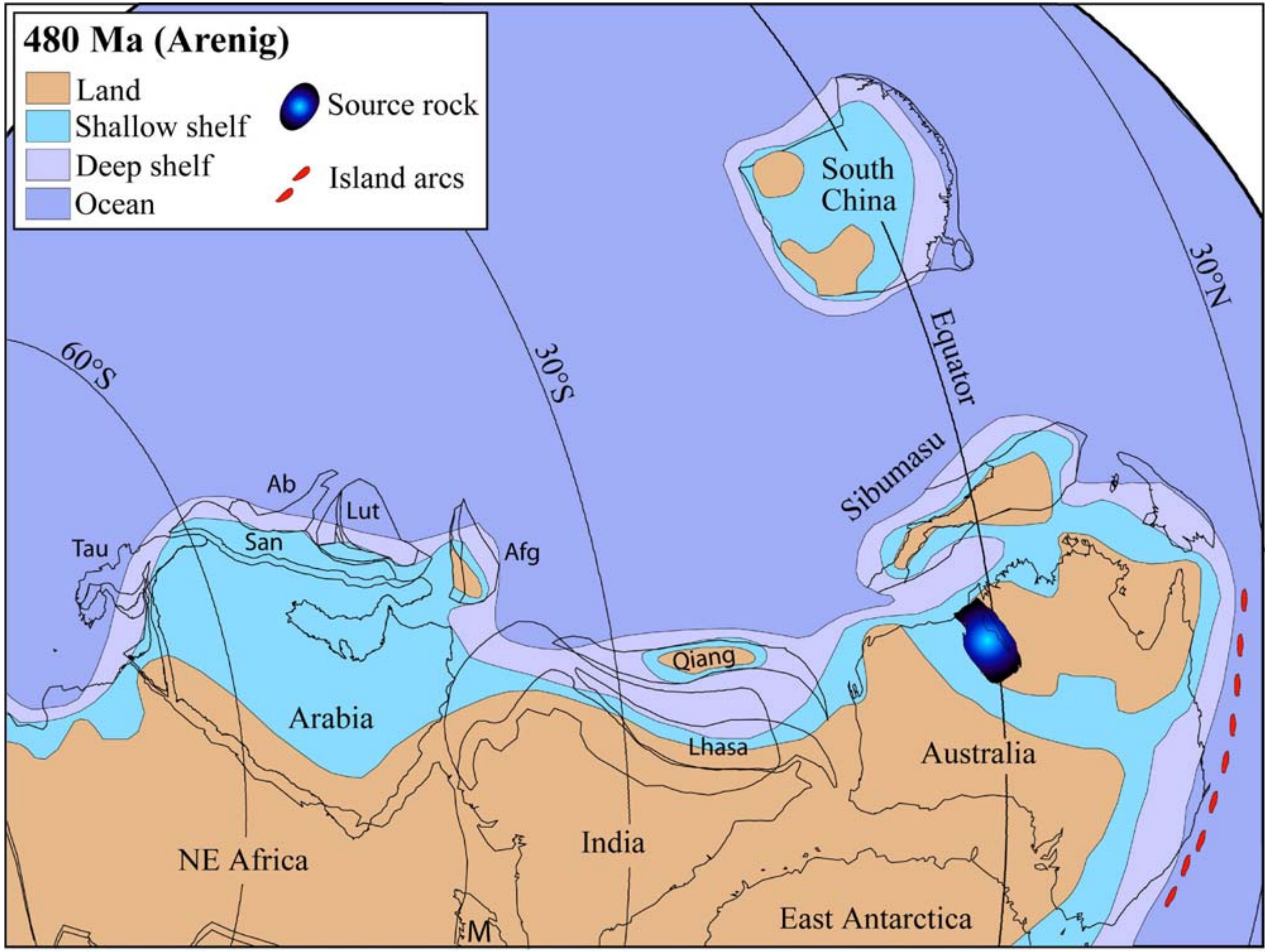

Fig. 4. Palaeogeography of the northeastern Gondwanan and adjacent peri-Gondwanan areas in early to mid-Ordovician (Arenig) times at 480 Ma. Abbreviations as in Figure 3, and M, Madagascar. Petroleum source rock areas are also shown.

peri-Gondwana. Cocks & Cooper (2004) documented a latest Ordovician *Hirnantia* brachiopod fauna within a dominantly graptolitic sequence, also near Nelson.

Geological history

There now follows a series of palaeogeographical reconstructions for the northeastern and eastern parts of Gondwana and their adjacent marginal areas and terranes at three times in the Lower Palaeozoic (Figs 3–5). The reconstructions were made using the digitized modern terrane boundaries outlined above and shown for the more westerly part of the area in Figure 1b, and moving them with kinematic consistency using SPlates, a prototype of Gplates (www.GPlates.org) now being developed by the Geodynamics Group at Trondheim in collaboration with Sydney University and the California Institute of Technology. The palaeomagnetic data for core Gondwana (Table 2) used in the constructions of Figure 2 are largely taken from Torsvik & Van der Voo (2002). As in our previous papers on Baltica and Siberia (Cocks & Torsvik 2005, 2007), we differentiate ocean, deep shelf, shallow shelf and land areas on our maps; however, we do not show mountain ranges or other variations in the land areas. A paramount consideration in our construction of these maps is the need for kinematic continuity between successive reconstructions. There are few palaeomagnetic data for most of the peri-Gondwanan terranes, apart from South China, but the successive palaeolatitudes for core Gondwana are now relatively well constrained (Torsvik & Van der Voo 2002): they are as shown in Table 2. We have also used aspects of the palaeogeographical maps by Veevers (2004) for the whole Gondwanan and peri-Gondwanan region, particularly the Australasian parts, and by Metcalfe (2002*a*) for SE Asia, to assist us in the compilation of our new maps.

Table 2. *Palaeomagnetic South Poles for South Africa and South China*

Age (Ma)	South Africa		South China	
	Latitude	Longitude	Latitude	Longitude
425	−10.2	357.6	−18.4	19.8
480	32.8	6.1	33.2	359.2
510	17.8	1.1	51.3	346.0

For South Africa the mean spline poles of Torsvik & Van der Voo (2002) are used (geocentric axial dipole (GAD)-based model). The South pole for South China is based on a running mean path using the *c*. 510 Ma (Middle Cambrian) Douposi Formation (Yang *et al.* 2004), the *c*. 430 Ma Yangtze Block (Sichuan and Yunnan) pole of Opdyke *et al.* (1987), and the *c*. 422 Ma Daguab–Shiqian pole of Huang *et al*. (2000). The *c*. 478 Ma Yunnan Province pole of Fang *et al.* (1990), which indicates a high latitude for South China, has not been included.

Cambrian

Gondwana was vast, stretching from over the South Pole under NW Africa to as far as 30°N of the Equator in the Australian and North Borneo areas (Fig. 2). Its Precambrian history is largely outside the scope of this paper, but Meert (e.g. Meert 2003) concluded that the formation of the northeastern part of the superterrane was essentially completed during the late Neoproterozoic by about 580 Ma, and that Gondwanan assembly involved the largest known series of mountain-building events in Earth history. In contrast, Allen (2007) concluded that the process was not complete in the Arabian area until earliest Cambrian time, at about 540 Ma. In either case we can assume that the whole cratonic core of the area under review here, from North Africa through Arabia and India to Australia, was a single united terrane well before 520 Ma, still within the early Cambrian. We show a newly reconstructed palaeogeographical map (Fig. 3) of northeastern Gondwana and the peri-Gondwanan terranes there in mid-Cambrian times (500 Ma). Apart from a possible glacial interval near the start of the Cambrian, in general the palaeotemperature and consequently the sea-level stands appear to have been high for much of the period, leading to extensive shallow-water seas flooding many of the Gondwanan craton margins, and the varied niches in those seas probably helped to facilitate the Cambrian faunal radiations.

Allen (2007) has described the substantial belt of early Cambrian evaporites that stretched within the Gondwanan margin, certainly across Arabia and perhaps as far as India. Stump *et al.* (1995) and other workers have identified a ‘Supergroup’ extending from the Middle Cambrian to the Late Ordovician in Saudi Arabia and adjacent areas, which was deposited on a stable continental passive margin in fluvio-deltaic to mid-shelf settings. Comparably, Myrow *et al.* (2006*a*, *b*) have documented the Cambrian and early Ordovician palaeogeography of the Himalayan area and have identified and analysed a Gondwanan passive margin as exemplified in the Zanskar and Spiti valleys. Further eastwards, Cocks *et al.* (2005) have summarized and reviewed the faunas in Sibumasu, in which a thick middle to late Cambrian shallow-water succession in Taratao Island, southern Thailand, carries trilobite and other faunas characteristic of the low-latitude parts of the Gondwanan craton of Australia. In contrast to the reconstructions shown by Cocks & Torsvik (2002), we now show Sibumasu as part of core Gondwana, and South China, although probably a terrane independent of core Gondwana, has new palaeomagnetic data (Yang *et al.* 2004) suggesting an equatorial position, at least from the middle Cambrian onwards. However, to reach that conclusion we have had to discard the data from South China published by Fang *et al.* (1990), whose high-latitude Ordovician positioning of South China contradicts both the faunal evidence and the data of Yang *et al.* (2004).

In the Australian sector, the Delamerian Orogen represents orogenic activity that originated during the late Precambrian and continued through most of Cambrian time, as at least one (and perhaps more) island arcs accreted to the main Gondwanan craton margin. In Tasmania, well-dated mid-Cambrian ophiolite obduction occurred, indicating accretion of an island arc to the Gondwanan margin there (Crawford & Berry 1992). In addition, in the Uluru shelf of central Australia, there was a large igneous province (LIP) tholeiitic eruption at about 510 Ma, termed the Antrim Plateau Volcanics, presumably caused by passage over a hotspot and extending for *c.* 400 000 km^2 (Veevers 2004, p. 113). Wright *et al.* (2000) and Li & Powell (2001) have also presented Cambrian reconstructions of the Australasian area; we differ from the latter in that we do not include the Annamia (Indochina) terrane within the Australasian part of Gondwana. There was an active mid- to late Cambrian island arc complex in New Zealand (Münker & Cooper 1999).

Ordovician

Gondwana and its associated terranes had a series of distinctive shelly faunas in the early Ordovician, which were characterized in detail by Cocks & Fortey (1988) and Fortey & Cocks (2003). These consisted of the Calymenacean–Dalmanitacean trilobite province in the higher-latitude parts of northwestern Gondwana and associated areas such as Avalonia, Armorica and Perunica (Bohemia), which were mostly outside the area treated in this paper apart from the Saudi Arabian occurrence documented by Fortey & Morris (1982); and the Dikelokephalinid trilobite province in the northeastern parts of Gondwana exemplified by Australia and the comparably low-latitude South China terrane. Between these two extremes there stretched a faunal cline through the intervening latitudes of Gondwana, within which were the medium- to high-latitude shelly faunas described from Iran by Bassett *et al.* (1999) and the distinctive early Ordovician (Arenig) brachiopod *Yangzteella* in the Taurides terrane, which also occurs in the lower latitude South China terrane. Stampfli & Borel (2002) stated that their Hun superterrane left Gondwana near the beginning of Ordovician time. However, Robardet (2003) has convincingly demonstrated that the Armorican terrane assemblage (most of France and the Iberian peninsula), which formed the westerly part of the postulated superterrane, carries higher-latitude terrane-diagnostic faunas of many phyla (the Mediterranean Province) which are indistinguishable from those in the main Gondwanan craton in North Africa from the Cambrian until the beginning of Devonian time. These indicate that any possible spreading centre to the south of Armorica could only have opened at an extraordinarily slow rate in the hundred million years after the supposed early Ordovician opening, which we consider unlikely.

In Figure 4 we present a new palaeogeographical reconstruction of the NE parts of Gondwana and the peri-Gondwanan terranes at early to mid-Ordovician (Arenig) times at 480 Ma. Again, this is considerably changed from the palaeogeography published by Cocks & Torsvik (2002), as there is much more now known both on the faunas of South China and Sibumasu and also on the palaeomagnetism of South China, placing both those terranes on equatorial palaeolatitudes and Sibumasu as part of core Gondwana. Part of the main Gondwanan craton in Australia was flooded by the Larapintine Sea, leading to the substantial early Ordovican sequences preserved today in the Canning, Georgina and Amadeus basins of western and central Australia (Veevers 2004), and the island arcs that progressively accreted to Tasmania, Victoria and New South Wales in the Lachlan orogen accommodated a succession of distinctive endemic shelly faunas, including the late middle Ordovician (Caradoc) brachiopods described by Percival (1991). Global eustasy reached a high point in Caradoc times, contributing to marine flooding of many regions in Gondwana and elsewhere.

The very end of the Ordovician saw the well-documented Hirnantian glaciation, which has its maximum expression in the NW African sector of Gondwana near the South Pole, but is also represented by glacial and periglacial deposits in Saudi Arabia and elsewhere in the then more southerly parts of our region. It also contributed to much deeper oxygenation of the oceans than usual, leading to the presence of the coeval and globally widespread *Hirnantia* Brachiopod Fauna even at lower latitudes such as New Zealand, where it is the sole shelly fauna represented in a succession otherwise consisting only of graptolitic shales (Cocks & Cooper 2004).

Silurian

Because most of the major terranes, including much of Gondwana, were at low to intermediate latitudes during the Silurian, which ran from 443 to 416 Ma,

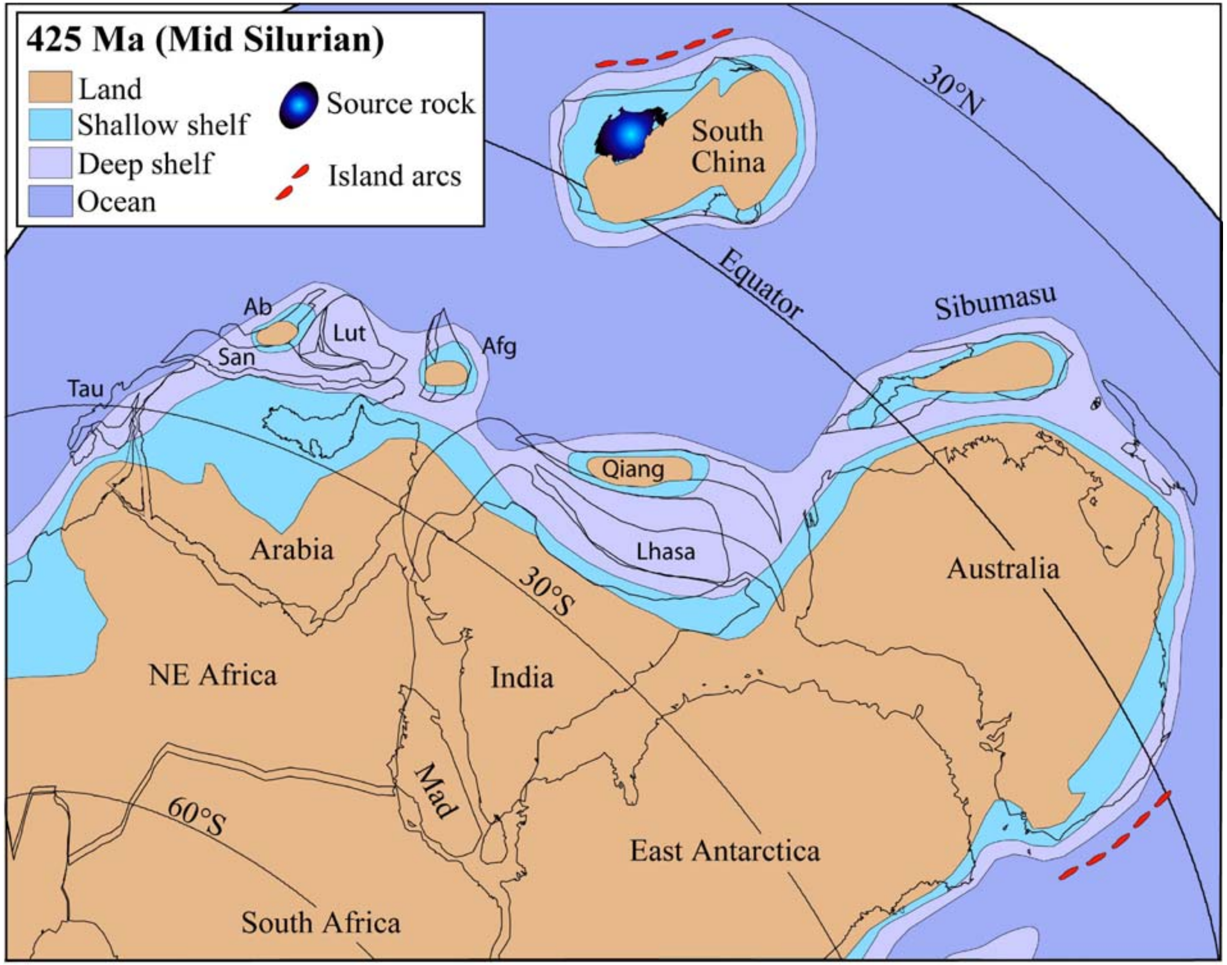

Fig. 5. Palaeogeography of the northeastern Gondwanan and adjacent peri-Gondwanan areas in middle Silurian times at 425 Ma. Abbreviations as in Figure 3.

and were not too far from each other, there were largely cosmopolitan shelly faunas over the whole of the area under consideration here, which are of little use in identifying separations of the various terranes from one another. Gondwana had drifted and rotated so that the South Pole lay under South America rather than NW Africa (Fig. 2). As in the Ordovician, there is a cline seen in the brachiopod and trilobite distributions along the Gondwanan margin, which has been documented for the late Silurian brachiopods by Rong *et al.* (1995). Our palaeogeographical map (Fig. 5) shows NE core Gondwana and the adjacent peri-Gondwanan terranes in mid-Silurian (Wenlock) times at 425 Ma. In contrast to Cocks & Torsvik (2002), and because of the new palaeomagnetic data of Yang *et al.* (2004), South China is shown in a more equatorial palaeolatitude. Sibumasu was a part of core Gondwana adjacent to Australia, as previously postulated by Metcalfe (e.g. Metcalfe 2002*a*).

There are differing opinions as to whether or not the main Australian part of the craton was still crossed by the Larapintine Sea (contrast the various maps of Metcalfe 2002*a*, Talent *et al.* 2003, and Veevers 2004), but we do not show it in Figure 5. In today's SE part of Australia there was substantial orogenic activity, represented by Silurian granites and other intrusions, after the Ordovician island arc terranes in the Lachlan orogen had completed their accretion to the main Gondwanan superterrane, indicating that that part of Gondwana was still an active margin.

Discussion and conclusions

The concept of a Hun (or Hunic or Hunia) superterrane, suggested chiefly by von Raumer, Stampfli and their co-authors (e.g. von Raumer *et al.* 2002; Stampfli & Borel 2002), consists of a large number of peri-Gondwanan terranes all shown as attached to each other in a very elongate ribbon stretching from Armorica to the Tibetan terranes, and all leaving the main Gondwanan cratonic area at the same early Ordovician time. This concept has attractions in that it invokes the parsimonious solution of postulating only a single spreading area within the underlying crust. However, the date of separation of such a superterrane from core Gondwana is contentious. Its western end is said to include the Armorican Terrane Assemblage (chiefly modern France and the Iberian peninsula), but various workers, particularly Robardet (2003), have clearly documented that the Armorican western end of the postulated 'Hun superterrane' remained with faunas identical to those of Gondwana until at least the early Devonian. Unless the sea-floor spreading rate of this Palaeotethys Ocean between the Gondwanan craton and the 'Hun superterrane' was exceptionally slow, it seems that the ocean was unlikely to have opened until, at the earliest, the late Silurian rather than the early Ordovician (Tremadocian) as stated by Stampfli & Borel (2002). Those workers also depicted the Hun superterrane as divided into two in some of their earlier reconstructions, a Cadomian terrane assemblage to the west and a Serindia terrane assemblage to the east; the two displaced from each other by a substantial north–south-trending strike-slip fault system for which we find little evidence.

In the eastern sector of Gondwana, the northeastward drift of the superterrane was fuelled by subduction at that Australian margin, so that consequently island arcs were accreted in the Cambrian Delamerian and the Ordovician Lachlan orogens there. In the northeastern peri-Gondwanan area our reconstructions (Figs 3–5) are different from those previously published (although not for the North Borneo to New Zealand sector), as we do not think that either North China or Annamia (Indochina) were attached to, or even near, core Gondwana during the Lower Palaeozoic. In addition, and with the help of newer and more plausible palaeomagnetic data (Yang *et al.* 2004) than those previously published, we consider South China to have been a terrane independent from core Gondwana but not far from it, and that South China apparently remained equatorial for the whole period. However, we now consider Sibumasu to have formed part of the main Gondwanan terrane in the Lower Palaeozoic, which follows the conclusions of Metcalfe (e.g. Metcalfe 2002*a*) rather than those shown in our previous paper (Cocks & Torsvik 2002).

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Gondwanan faunal signatures from Early Palaeozoic terranes of Kazakhstan and Central Asia: evidence and tectonic implications

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Abstract: Two separate tectonic blocks in the southwestern segment of the Kazakhstanian orogen, the Chu–Ili terrane and the Karatau–Naryn terrane (with particular attention to Malyi Karatau), are selected to illustrate their geological history and major biogeographical signatures from the Cambrian to the early Silurian. Mid- to Late Ordovician brachiopod and trilobite faunas of Chu–Ili show increased endemicity of shallow shelf assemblages, whereas distinct links to equatorial ('east') peri-Gondwanan are more evident in trilobite assemblages of the outer shelf. In the Late Ordovician, strong biogeographical affinities to equatorial Gondwanan faunas became firmly established and they are also traceable into the Silurian. Early Cambrian faunas of Malyi Karatau show remarkable similarity to those of South China. From the Middle Cambrian this region evolved as an isolated carbonate seamount, but until the Early Ordovician links to South China faunas were still evident. Benthic faunas from both regions show weak links to contemporaneous faunas of Baltica and little in common with Cambrian and Ordovician faunas of the Siberian craton. This suggests their location in low southern latitudes, in relative proximity to East Gondwana, which places some constraints on plate-tectonic reconstructions in relation to the southern cluster of Kazakhstanian terranes, including Karatau–Naryn, North Tien Shan and Chu–Ili.

There are many controversies relating to the Palaeozoic geological history of the complex tectonic collage incorporated today within Kazakhstan and Central Asia. In early reconstructions (e.g. Scotese & McKerrow 1990, 1991) Kazakhstan is usually shown as a single plate closely alongside Siberia. However, it can now be postulated with a good degree of certainty that Kazakhstania as an microplate did not exist as a single entity probably until the Mid-Palaeozoic. Nevertheless, the number and origin of Early Palaeozoic terranes incorporated into the Kazakhstanian or Altaid orogen remains a matter of debate (Şengör & Natal'in 1996; Burtman 2006; Windley *et al.* 2007, and references therein). Fortey & Cocks (2003) showed Early Palaeozoic Kazakhstanian terranes as a cluster of microplates situated in low latitudes in relative proximity to Gondwana, mainly on the grounds of biogeographical affinities of supporting faunas, whereas Şengör & Natal'in (1996) proposed a sophisticated model of evolution of the Kazakhstanian orogen from a huge island arc situated between Siberia and Baltica, which they named the Kypchak Arc.

One of the obvious tools to assess the validity of these various, often controversial models is palaeomagnetic studies. However, palaeomagnetic data from the Palaeozoic of Kazakhstan are sparse and at least in some cases they are not always reliable; some data are derived from allochthonous clasts and bear no direct relationship to the palaeomagnetic record of the bedded stratigraphical sequence. An alternative approach is to interpret biogeography. The Ordovician Period is unique in that respect, and not only because of strong global biogeographical differentiation (Fortey & Cocks 2003). This was a time of explosive biodiversication when the Palaeozoic Evolutionary Fauna had emerged (Webby *et al.* 2004). Therefore tracing the locus of origin of numerous newly evolved taxa and entire faunal associations, together with a study of their dispersion in space and time, gives valuable information on the relative position of ancient continents (Bassett *et al.* 2002).

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The first difficulty to overcome is the identification of the Early Palaeozoic terranes. Many papers were published on various aspects of the Palaeozoic geology of Kazakhstan between 1960 and 2000, and the region was mapped at a 1:100 000 scale, but there is still great uncertainty about the number and boundaries of Early Palaeozoic terranes incorporated into the Kazakhstanian orogen. However, only Şengör & Natal'in (1996) acknowledged that they had to deal with secondary orogenic-collage components, and not with primary Early Palaeozoic units. Notable differences in the approach to this problem are evident in comparing Palaeozoic tectonic units recognized by Apollonov (2000) and by Şengör & Natal'in (1996) (Fig. 1). Boundaries of many of these units are defined often not by Palaeozoic sutures, but by strike-slip faults, some of which are currently active. The reason is fairly clear: the Early Palaeozoic sutures are difficult to define and trace if they have been inferred exclusively from existing published data. A significant amount of palaeontological information used for dating single rock units remains unpublished, and in many cases it is ignored if it contradicts the inferred geological position of a particular lithostratigraphical unit based on various earlier concepts. After close analysis of the most important summaries of Kazakstanian geology, including the relevant volumes of the *Geology of the USSR* (Esenov *et al.* 1971), and of currently available geological maps, it becomes immediately clear that in many cases the existing interpretations of the Palaeozoic history of Kazakhstan include many inherited views based on very different theoretical concepts and approaches from those of current application, and there is considerable personal bias. Such data are often of very limited use; for example, in definition of thrust vergence directions and island arc polarity. In addition, the Early Palaeozoic sutures were often reworked in the Devonian–early Carboniferous. To resolve such problems, Şengör & Natal'in (1996) applied the concept of mobile magmatic fronts (Fig. 1), but, as we demonstrate below, the accurate identification of such features depends strongly on the reliability of published data.

Two separate Early Palaeozoic tectonic blocks of Kazakhstan (Karatau–Naryn and Chu–Ili) are selected here to illustrate our current state of knowledge of Kazakhstanian Early Palaeozoic geology, and to typify biogeographical characteristics of the Early Palaeozoic benthic faunas of Kazakhstanian terranes (Figs 1 & 2).

Chu–Ili terrane

The Chu–Ili terrane is selected because it occupies a central position in the Kazakhstanian orogen, and its Early Palaeozoic history is critical for testing and verification of existing models of tectonic development of Kazakhstan through this interval. Its Early Palaeozoic faunas and depositional history are relatively well documented and some useful summaries of Palaeozoic magmatism have been published. Additionally, an analysis of a significant amount of data published on the region make it easier to highlight some substantial problems that still exist in constructing an up-to-date model of the Palaeozoic geology of Kazakhstan.

The Chu–Ili terrane (Figs 1–3), as defined by Popov *et al.* (2002), coincides more or less with the Dzalair–Naiman Unit of the Şengör & Natal'in (1996) model. It is a narrow (up to 150 km wide) belt of the pre-Altaid continental crust, with a Palaeozoic sedimentary cover traceable for almost 600 km length from the Zailiyskii Alatau Range in the SE to the northern Betpak–Dala Desert in the NW, where it is then covered by late Palaeozoic and Mesozoic–Cenozoic deposits. A detailed analysis of the Chu–Ili Precambrian basement, including isotopic ages of some lithostratigraphical units, was made by Kichman *et al.* (in Abdullin *et al.* 1980), Kröner *et al.* (2007) and Degtyarev & Ryazantsev (2007, pp. 63–96, and references therein). General characteristics of the Early Palaeozoic geology are summarized below.

Zhalair–Naiman Fault Zone

In the SW the Chu–Ili terrane is bounded by the huge Zhalair–Najman strike-slip fault complex, including the generally strongly dislocated, mainly northward-dipping homoclinal sequences of latest Cambrian and Early to Middle Ordovician ages; they are mainly siliciclastic slope-rise deposits traceable almost continuously from the town of Otar in the southern Chu–Ili Range to Sortan–Manai in the northern Betpak–Dala Desert (Figs 3–5). These deposits comprise the Dzhambul, Karatal and Kushaky formations (Nikitin 1991).

The Dzhambul Formation (Fig. 6) mostly comprises graded sandstones that are rich in clastic quartz and siltstones, with some horizons of siliceous shales and cherts, and a few units of pebble conglomerates and gravelstones (Avdeev 1991). The only diagnostic fossils reported from the formation are linguliformean brachiopods identified by Gorjansky (Kichman *et al.* in Abdullin *et al.* 1980) as *Broeggeria* cf. *salteri* (Hall), which is elsewhere characteristic of the uppermost Cambrian–Tremadocian units, and *Paterula* sp., which occurs in the uppermost Floian units (*Oepikodus evae* conodont biozone) of Baltoscandia and Iran, but is then widespread from the Middle Ordovician (Mergl 1999).

Important constraints on the age of the Dzhambul Formation have been published by Kröner

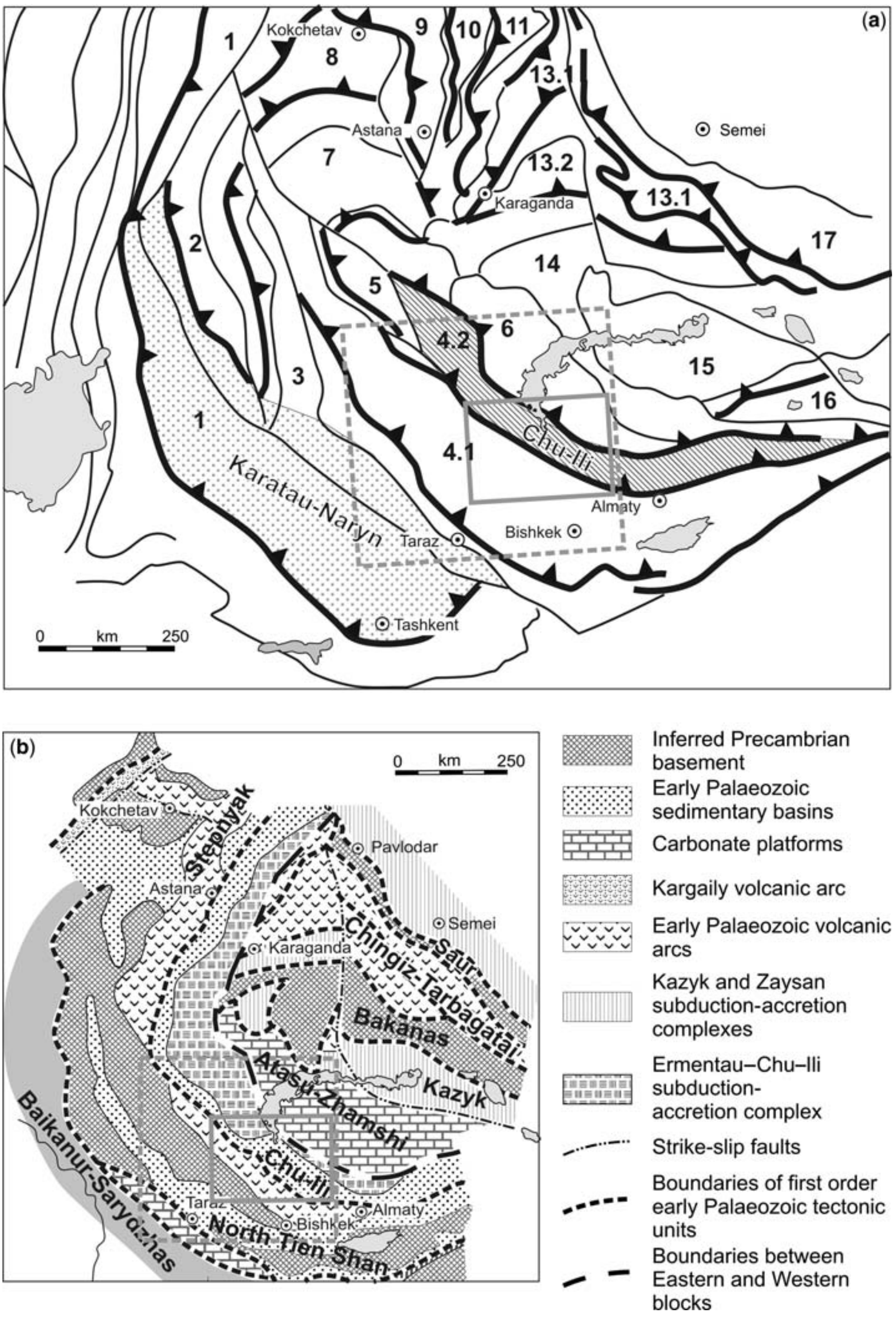

Fig. 1. Generalized maps showing different approaches in subdivision of the Kazakhstanian orogen into different first order Palaeozoic tectonic units. (**a**) Inferred position and polarity of Ordovician magmatic fronts modified after Şengör & Natal'in (1996) in relation to the approximate position of Chu-Ili and Karatau-Naryn terranes as defined in this paper. Numerals denote first order tectonic units recognized by Şengör & Natal'in (1996): 1, Valerianov-Chatkal; 2, Turgai; 3, Baikanur-Taklas; 4.1, Dzhezkazgan-Kyrgyz; 4.2, Zhalair-Naiman; 5, Sarysu; 6, Atasu-Mointy; 7, Tengiz; 8, Kalmykkol-Kokchetav; 9, Ishim-Stepnyak; 10, Ishkeolmes; 11, Selety; 13.1, Boshchekul-Tarbagatai; 13.2, Bayanaul-Akbastau; 14, Tekturmas; 15, Dzhungar-Balkhash; 16, Bortala, 17, Zharma-Saur (Akdym unit is not shown). (**b**) Major Kazakhstanian early Palaeozoic tectonic units after Apollonov (2000). The area indicated by the dashed-line boundaries is the area of Figure 2; the area enclosed by the solid line is the area of Figure 3.

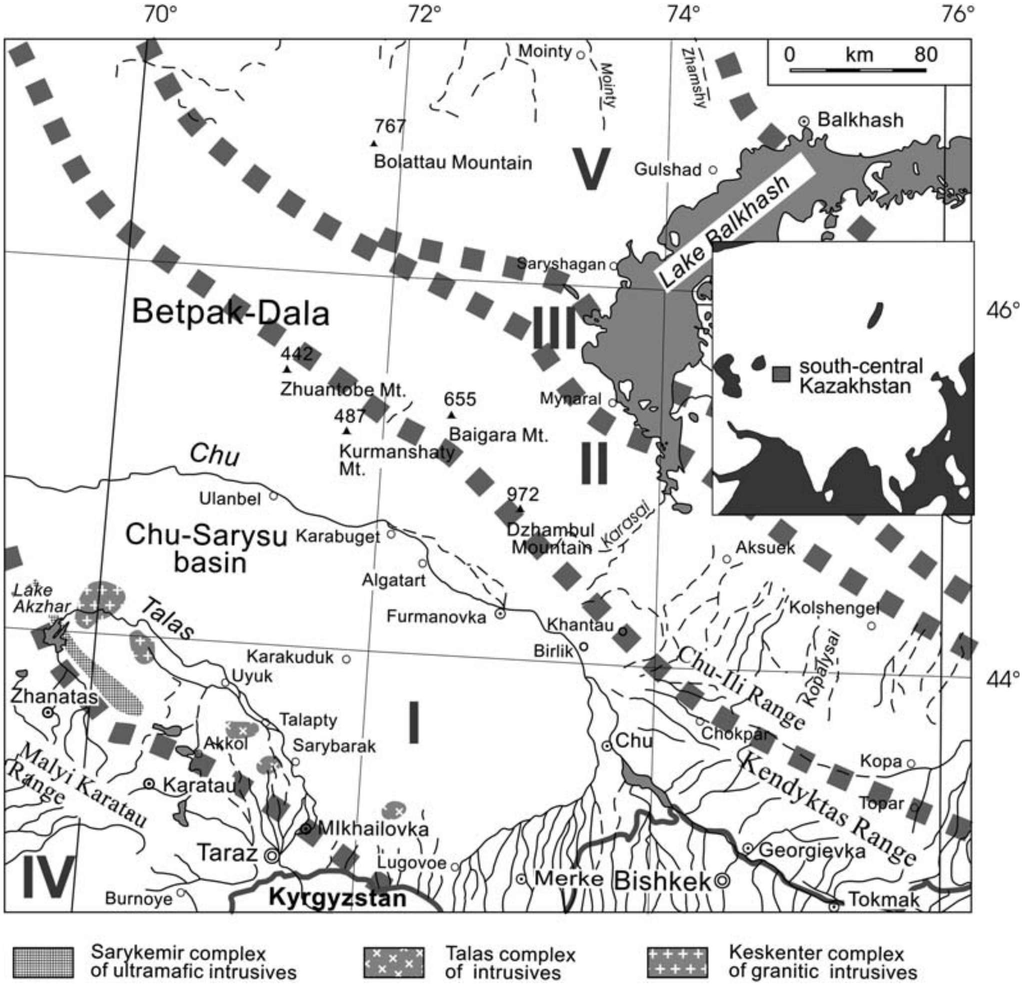

Fig. 2. Geographical map of southern Kazakhstan showing relative position and inferred boundaries of first-order early Palaeozoic tectonic units: I, North Tien Shan microplate: II, Chu–Ili terrane; III, Mynaral–South Dzhungaria terrane; IV, Karatau–Naryn terrane; V, Atasu–Zhamshi microplate. Lithological symbols indicate subsurface location of early Palaeozoic complexes of intrusive rocks along the southern margins of the Chu–Sarysu sedimentary basin (after Sargaskaev in Esenov *et al.* 1971).

et al. (2007). A reported stratigraphical contact between sandstones of the Dzhambul Formation and basaltic pillow lavas and red jaspers underlain by gabbro is of particular significance. Dated zircons from the plagiogranite pods in dykes cutting the gabbro give a ^{207}Pb/^{206}Pb age of 512.6 ± 1.0 Ma for the volcanic rocks, whereas detrital zircon grains from the basal Dzhambul Formation give an early Tremadocian ^{207}Pb/^{206}Pb evaporation age of 489.6 ± 1.0 Ma (Kröner *et al.* 2007). The isotope dating is in good agreement with available palaeontological data suggesting a mainly Ordovician age for the unit (Kichman *et al.* in Abdullin *et al.* 1980). Precambrian dating of some other detrital zircons suggests that the Chu–Ili basement was the most likely source of the siliciclastic rocks. The reported stratigraphical contact of the Dzhambul Formation does not indicate a time of obduction as supposed by Degtyarev & Ryazantsev (2007), but probably relates to the prograded clastic shelf development into a newly formed rift basin, which evolved subsequently into a marginal sea resulting from back-arc spreading. This view is supported by the relatively small difference between the age of the ophiolites and the zircon age from the overlying Dzhambul Formation.

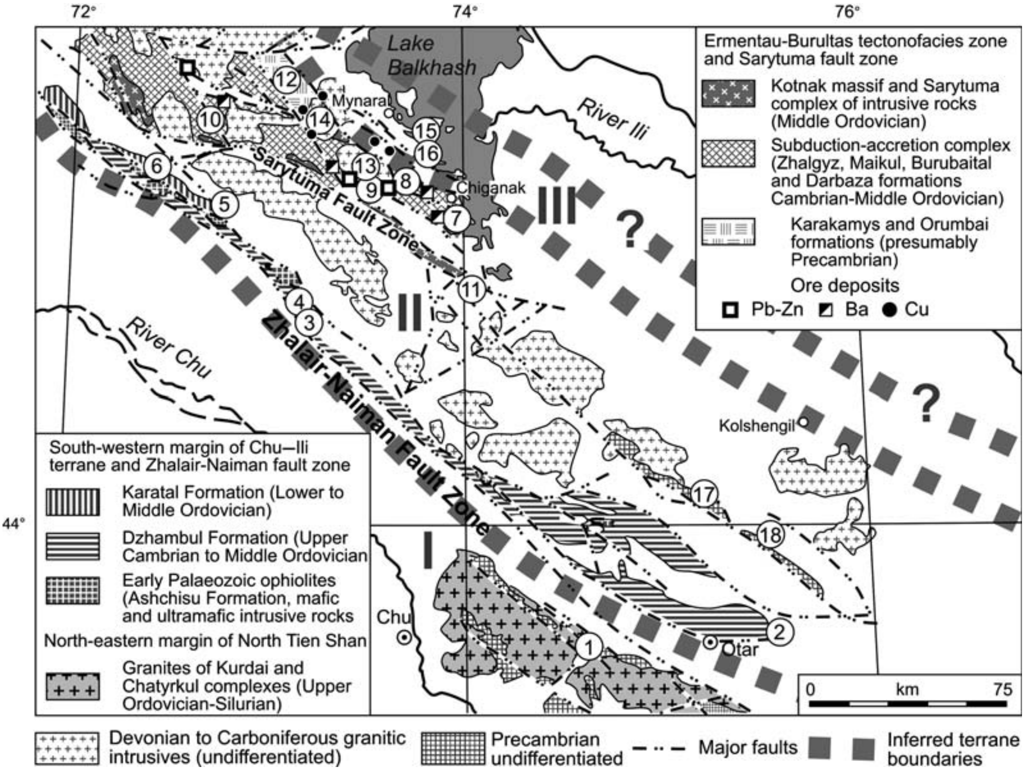

Fig. 3. Simplified map of the Chu–Ili and Kendyktas ranges (see Fig. 2) and the West Balkhash region showing inferred position of boundaries of the Chu–Ili terrane, outcrop areas of Precambrian rocks, siliciclastic turbidites of the Dzhambul and Karatal formations NE of the Zhalair–Naiman Fault Zone, and the geographical distribution of Palaeozoic magmatic and ophiolitic complexes (modified after Abdullin *et al.* 1980). Distribution of massive sulphide and barite ore deposits is after Kazanin *et al.* (1976). Numerals show geographical position of the localities discussed in this paper: 1, Kendyktas Range; 2, Dulankara Mountains and upper reaches of the Ashchisu river; 3, Akzhal Mountains; 4, Dzhambul Mountains and Almalysai; 5, Andasai ophiolitic massif; 6, area SW of Baigara Mountain; 7, location of two overlapping sections of radiolarian cherts (89101 and 9806) in the Burubaital Formation (Tolmacheva *et al.* 2001, 2004); 8, Terenkul valley east of Zhalgyz granitic massif; 9, Burultas area and Shopshoky Mountain south of the Zhalgyz granitic massif; 10, Suukadyr Mountains (locality of Middle Cambrian brachiopods); 11, area SW of Lake Alakul; 12, Orumbai height, outcrop area of the Orumbai and Karakamys formations; 13, Zhalgyz granitic massif; 14, Karakamys granitic massif; 15, Akkerme Peninsula; 16, southern side of Akkerme Gulf; 17, Kopalysai; 18, Kujandysai and Anderkenyn–Akchoku.

If this interpretation is correct, it suggests a relatively late rifting and separation of the Chu–Ili terrane some time in the Mid-Cambrian.

NW of Dzhambul Mountain the Dzhambul Formation is replaced by the Karatal Formation, comprising mainly graded sandstones, siltstones and argillites with units of conglomerates in the lower part and some tuffs in the middle sequence (Figs 4 & 5). The Middle Member of the Karatal Formation contains graptolites, including *Didymograptus* cf. *protobifidus* Elles, *Isograptus* sp., *Phyllograptus anna* Hall, *Phyllograptus typus* (Hall), and *Tetragraptus bigsbyi* (Hall) (Nikitin *et al.* in Abdullin *et al.* 1980), proving an Early Ordovican age (late Floian) and conflicting with a Middle Ordovician (early Darriwilian) age for this unit (Cooper & Lindholm 1990). Further NE, in the northern Betpak–Dala Desert, intercalating fine-grained sandstones, siltstones and siliceous argillites of the Kushaky Formation are exposed almost continuously to the NW of the Zhalair–Naiman Fault Zone. The lowermost part of the formation contains *Tetragraptus approximatus* (Nicholson) (Tsai 1974) characteristic of the early Floian, whereas the upper part of the unit contains such taxa as *Eoglyptograptus dentatus* (Brongniart), *Isograptus victoriae divergens* (Harris) and *Pseudotrigonograptus ensiformis* (Hall), suggesting an

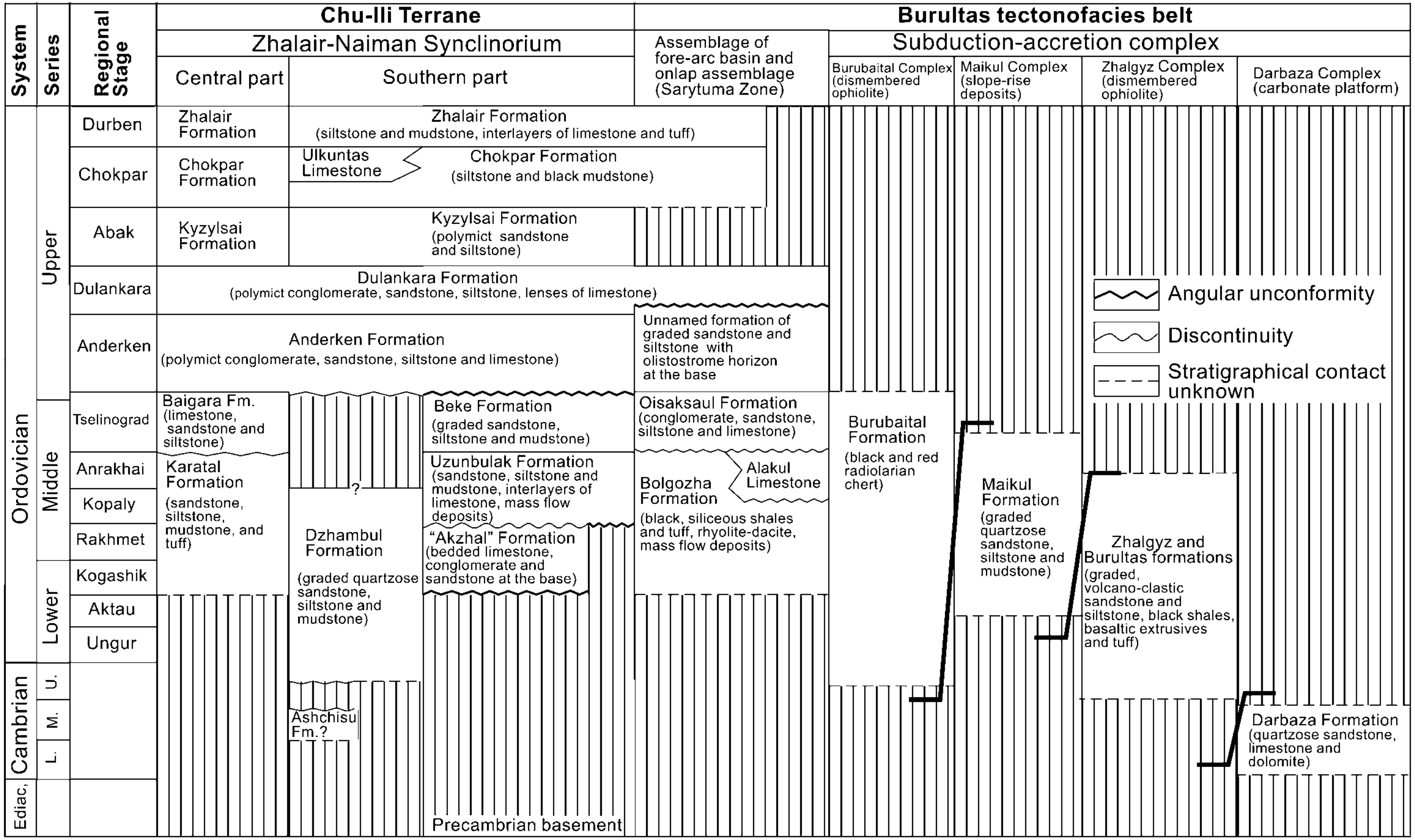

Fig. 4. Correlation of Lower Palaeozoic lithostratigraphical units in the southern part of the Chu–Ili terrane and the adjacent subduction–accretion complex (Ermentau–Burultas tectonofacies belt) (modified after Popov *et al.* 2002).

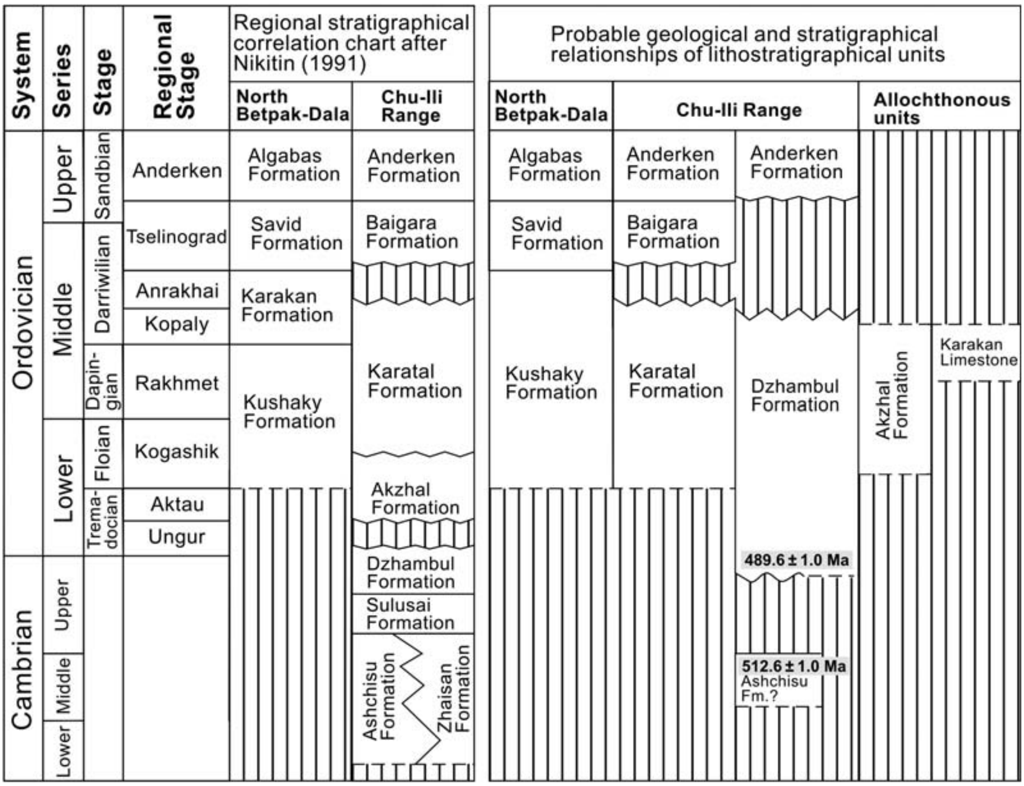

Fig. 5. Interpretation of the subdivision, correlation and relationships of the Cambrian to Middle Ordovician lithostratigraphical units along the Zhalair–Naiman Fault Zone as currently applied from the official geological mapping programme in Kazakhstan (left half of figure, Nikitin 1991), as opposed to a revised correlation of these units based on available published palaeontological and geochronological data (right half of figure, Tsai 1974; Abdullin *et al.* 1980; Danelian & Popov 2003; Kröner *et al.* 2007) and the authors' field observations. The Sulusai Formation is not shown in the chart because it has neither well-documented stratigraphical relationships within the Chu–Ili terrane, nor palaeontological and geochronological age constraints. The Karakan Limestone in North Betpak–Dala has no stratigraphical relationships with fine siliciclastic, graptolite-bearing rocks referred to the Karakan Formation, but according to recently discovered conodonts is of older, late Dapingian to earliest Darriwilian age (Tolmacheva, pers. comm.).

Yapeenian to early Darriwilian age (Nikitin 1972; Cooper & Lindholm 1990). Thin interbeds of pelagic radiolarian cherts in the middle of the formation contain abundant conodonts of the *Oepikodus evae* Biozone. In general, there is continuous development of siliciclastic lithofacies characteristic of submarine fan and slope environments through the Early and Mid-Ordovician along the entire southwestern margin of the Chu–Ili terrane facing the Zhalair–Naiman Fault Zone (Fig. 3). With the exception of several horizons of tuffs in the Middle Member of the Karatal Formation, there are no island arc type Ordovician volcanic or volcanoclastic rocks recorded, and there is no trace of Ordovician or Silurian island arc-related granitic magmatism.

It should be noted that there is some previous misunderstanding of the geological position and age of some units based on inferred geological relationships, which were not supported by biostratigraphical and sedimentological data (Fig. 5). In particular, the age of the Dzambul Formation was usually considered previously as Late Cambrian to Tremadocian (Kichman *et al.* in Abdullin *et al.* 1980; Nikitin 1991) because of inferred relationships with the Akzhal Formation in the Akzhal Mountains, SE of Dzhambul Mountain.

There is also a report of stratigraphical contacts of the Karatal and Akzhal formations south of Baigara, but no detailed sedimentological data or a precise location of that section is available (Kichman *et al.* in Abdullin *et al.* 1980; Nikitin

Fig. 6. Exposure of siliciclastic turbidites of the Dzhambul Formation in Almalysai, Dzhambul Mountains (Fig. 3, locality 4). Photograph by L. Popov.

1991). Field observations in the type area SE of Dzhambul Mountain (Figs 7 & 8) now show that the Akzhal Formation comprises strongly dislocated carbonate turbidites (Danelian & Popov 2003). Pelagic intervals in the Bouma cycles contain a low-diversity radiolarian assemblage, including *Inanihella bakanasensis* (Nazarov), *Inanihella*? *akzhala* Danelian and Popov, *Triplococcus acanthicus* Danelian and Popov, and *Proventocitum* cf. *procerulum* Nazarov, in association with rare conodonts, including *Oistodus lanceolatus* Pander, suggesting an early Ordovician age (Floian). The trilobites *Bumastoides* cf. *betpakensis* Weber, *Lonchodomas* sp. and *Annamitella* (= *Bathyuriscops*) sp. are also reported from the area (Nikitin 1972), suggesting that the upper part of the formation ranges into the Middle Ordovician. However, sparse faunal data show that the Akzhal Formation in the type area formed synchronously with the Karatal and Dzhambul formations in an environment of a deep-water carbonate submarine fan starved of siliciclastic input, which excludes its deposition on the margins of the Chu–Ili terrane, where siliciclastic sedimentation predominated. The so-called 'basal layer of sandstone, conglomerate and sedimentary breccia' (Nedavisin 1961; Nikitin in Abdullin *et al.* 1980) is interpreted here as a tectonic mélange that formed along the basal thrust surface and has no regional sedimentological significance.

Lower to Middle Ordovician basaltic and andesitic volcanic rocks and tuffs similar to those associated with the Akzhal Limestone in the Akzhal Mountains are not reported elsewhere along the southwestern margin of the Chu–Ili terrane (Palets in Abdullin *et al.* 1980). Thus a probable scenario is that limestones of the Akzhal Formation were deposited on the slope of a small carbonate platform formed around an isolated seamount. Their time of obduction onto the Chu–Ili terrane margin is more probably post-Mid-Ordovician, which also places some constraints on the time of obduction of the Zhalair–Naiman ophiolites.

The term 'Akzhal Formation' is also applied currently to several unrelated lithostratigraphical units that formed in different depositional environments and tectonic settings, and in particular to shallow-water carbonates at the base of the Middle Ordovician sequence exposed along the Kopaly river in

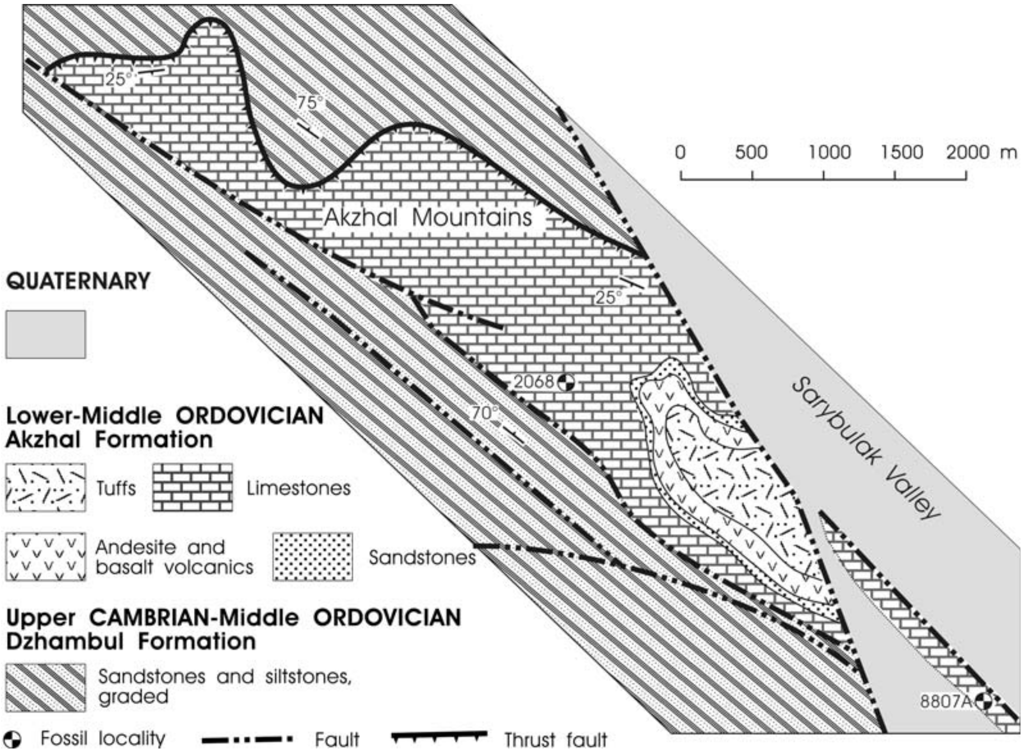

Fig. 7. Schematic geological map of the Akzhal Mountains (Fig. 3, locality 3) showing tectonic relationships of the Dzhambul and Akzhal formations and two currently known fossil localities (modified from Nedavizin 1961; Danelian & Popov 2003).

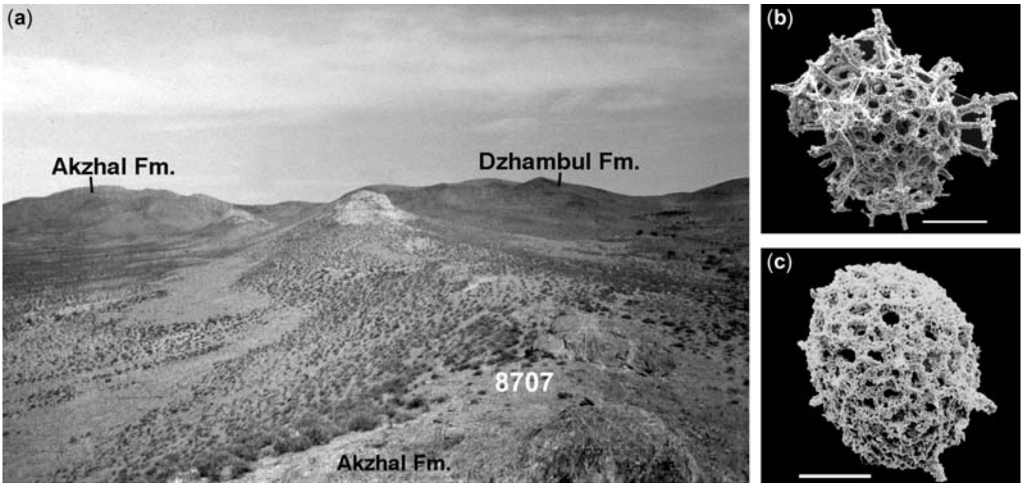

Fig. 8. (**a**) Southeasterly view of exposures of the Akzhal Formation (Fig. 3, locality 4); photograph by L. Popov. (**b**, **c**) Some characteristic radiolarians from the Akzhal Formation (locality 8707); (b) *Inanihella bakanasensis* (Nazarov 1975); (c) *Inanihella akzhala* Danelian and Popov; after Danelian & Popov (2003, fig. 5b and r); all scale bars represent 100 μm.

the central part of the Chu–Ili plate. These carbonates are transgressive across the metamorphic rocks of the Precambrian basement, and are succeeded by the Darriwilian Uzunbulak Foramation (for details see Nikitina *et al.* 2006).

Another lithostratigraphical unit with an obscure geological position, and that is recognized on both sides of the Zhalair–Niman Fault Zone, is the Sulusai Formation. In the Chu–Ili Range it is confined to isolated tectonic blocks that are commonly strongly dislocated and comprise variable fine- to coarse-grained clastic rocks, shales and several horizons of andesite and andesitic basalts and tuffs. It is usually considered to be of Late Cambrian age because of its inferred stratigraphical relationships with the Zhaisan Formation in the Kendyktas Range on the opposite side of the Zhalair–Naiman Fault Zone. However, there is no convincing evidence of stratigraphical relationships with underlying or overlying deposits, nor palaeontological data that could place some constraints on the age and geological position of the unit. Also, the volcanic components of the Sulusai Formation are otherwise unknown in the Upper Cambrian to Middle Ordovician units exposed along the margins of the Chu–Ili terrane; the sequence is more probably allochthonous.

Ophiolites within the Zhalair–Naiman Fault Zone can be traced discontinuously for almost 550 km between Kipchakbai in the NW and the Dulankara Mountains in the SE (Burdynyuk *et al.* in Abdullin *et al.* 1980). They comprise an assemblage of strongly dislocated volcanic and sedimentary rocks known as the Ashchisu Formation, together with a chain of numerous small bodies of mafic and ultramafic igneous rocks (Fig. 3). There are still many unresolved questions concerning the age, tectonic setting of formation, and mechanisms of emplacement of the Zhalair–Naiman ophiolites.

According to Tokmacheva *et al.* (in Abdullin *et al.* 1980) the Ashchisu Formation comprises mainly basaltic pillow lavas classified as spilites, some andesitic basalts, and tuffs. Sedimentary rocks comprise quartzites, siliceous shales, cherts, some dolomites and limestones. The mafic–ultramafic complexes are variable in composition. They consist usually of sheared serpentinite on the basal thrust, layered harzburgites and dunites rich in chromium (about 2000–5000 ppm for Cr in whole-rock analyses according to Burdynyuk *et al.* in Abdullin *et al.* 1980, fig. 46), succeeded by troctolites, norites and gabbro, often serpentinized. Small bodies and dykes of plagiogranites, tonalites and quartz diorites are recorded in the upper part of the sequence. Although not as yet fully adequate, these data may suggest that the Zhalair–Naiman ophiolites were formed probably in a suprasubduction-zone setting.

Burdynyuk *et al.* (in Abdullin *et al.* 1980, p. 179) reported the occurrence of olistoliths and large blocks of siliciclastic rocks derived from the Dzhambul Formation and Upper Ordovician rocks in the tectonic mélange associated with the Andasai Massif of ultramafic intrusive rocks (Fig. 3, locality 5), which suggest a northwestern vergence of thrust building.

Polarity of subduction and age of formation of the Zhalair–Naiman suture. Current data suggest that there is no evidence of Cambrian to Ordovician island arc volcanism and related magmatism preserved along the Chu–Ili margin facing the Zhalair–Naiman Fault Zone (Fig. 3). Instead, there is a relatively well-preserved Lower to Middle Ordovician succession of basin, submarine fan and slope quartz-rich turbidites that suggest a passive margin development at least since the latest Cambrian (Fig. 4). In contrast, widespread andesites, andesitic basalts and less extensive dacitic volcanic rocks and tuffs are characteristic of the Middle Ordovician (Darriwilian) Rgaity Formation and the Upper Ordovician (Sandbian) Keskintas Formation on the opposite side of the Zhalair–Naiman Fault Zone, in the Kendyktas Range (Salin *et al.* in Esenov *et al.* 1971; Nikitin 1972, 1991). There is also extensive Late Ordovician island arc-related granitic magmatism in the northwestern Kendyktas Range and the Chu uplift, SW of the inferred early Palaeozoic suture (Salin *et al.* in Esenov *et al.* 1971; Abdarakhmanov *et al.* in Abdullin *et al.* 1980), which probably continued into the Silurian. According to Ivanov *et al.* (in Abdullin *et al.* 1980), K/Ar ages of the Kurdai and Chatyrkul complexes of granitic intrusive rocks in the northwestern Kendyktas Range (Fig. 4) vary from 466 to 425 Ma.

All these data favour a southwestern direction of subduction (recent coordinates) under the North Tien Shan plate. The presence of Late Ordovician olistoliths in the mélange associated with the Andasai ultramafic intrusive massif suggests post-Ordovician obduction. In the southeastern segment of Chu–Ili (Fig. 4, locality 2, Durben well), the Llandovery and Wenlock rocks of the Zhalair, Betkainar and Koichik formations are involved in tectonic deformation together with Ordovician rocks (Bandaletov & Palets, in Abdullin *et al.* 1980, fig. 28). Therefore the origin of the Zhalair–Naiman suture and associated obduction of the Akzhal limestones and ophiolites on the Chu–Ili margin are definitely post-Mid-Ordovician and may be as late as post-Wenlock.

Sarytuma Fault Zone, Burultas tectonofacies zone and Mynaral–South Dzhungaria terrane

A very different picture emerges on the opposite, northwestern side (present coordinates) of the

Chu–Ili terrane (Fig. 3), which represents an accretionary collage of arc–prism–ophiolite complexes consisting of several tectonostratigraphical units (Fig. 4). Notwithstanding some controversial reports (Kaznin *et al.* 1976; Abdullin *et al.* 1980), none of these can be shown to be in stratigraphical contact with one another.

An important feature of the area is the abundance of radiolarian cherts, which are exposed in a number of nappes incorporated within a tectonic mélange (Fig. 9). The cherts contain diverse conodont faunas, of which the youngest are within the *Pygodus anserinus* Biozone (Koren *et al.* 1993; Popov & Tolmacheva 1995; Tolmacheva 2004). In most cases, fragments of stratigraphical sequences preserved do not usually exceed 10–15 m in thickness and cover stratigraphical intervals corresponding to parts of one to three successive conodont biozones. However, in the southern nappe (Fig. 3, locality 7; Fig. 9a) two overlapping sections preserve an almost continuous sequence from the Upper Cambrian *Eoconodontus notchpeakensis* Biozone to the uppermost Middle Ordovician *Pygodus serra* Biozone (Tolmacheva *et al.* 2001, 2004). Remarkably, the complete sequence, which is about 100 m thick, comprises radiolarian cherts with no significant input of fine clastic material or volcanic rocks. A stable environment in which radiolarites accumulated very slowly and continuously for almost 35–40 Ma is a clear signal of their deposition on an abyssal plain.

Another characteristic tectonostratigraphical unit is a sucession of submarine fan and slope turbidite lithofacies forming the Maikul Formation, which can be interpreted as deposits of a trench fill. Pelagic elements of the Bouma cycles in the Maikul Formation include some thin layers of radiolarian cherts. There are also a few units of chert up to 3 m thick, which contain conodonts varying in age from the *Paroistodus proteus* Biozone (Tolmacheva, pers. comm.) to the *Pygodus serra* Biozone (Nikitin *et al.* in Abdullin *et al.* 1980). Deposits of the Maikul Formation are exposed in a pile of southwesterly deepening nappes without stratigraphical contacts with other units, but often alternating with nappes composed of radiolarian cherts of the Burubaital Formation.

There are considerable massive barite deposits, probably of cold seep origin, which have been assigned usually to the Burubaital Formation (Kazanin *et al.* 1976; Tolmacheva, pers. comm.), but formed in a different tectonic setting on an active continental margin. The Chiganak barite ore deposit, situated about 20 km west of the Chiganak

Fig. 9. Westerly view of Lower Ordovician radiolarian cherts exposed in section 9806 west of Lake Balkhash (Fig. 3, locality 7). Photograph by L. Popov.

railway station (Fig. 3), comprises a lens-like body of barite about 10 m thick and more than 100 m wide, with flank deposits of siliceous siltstones and black cherts containing abundant caryocarid arthropods and ostracodes. It is overlain by a condensed sequence of cherts with units of siliceous siltstones increasing towards the top, dated by conodonts from the Tremadocian to the late Darriwilian (Tolmacheva, pers. comm.).

There are also heterogeneous complexes of volcanic rocks and volcano-sedimentary sequences, which contain some significant bodies of 'Kuroko'-type sulphide deposits (Fig. 3) and are often incorporated in mélange sequences, named the Zhalgyz and Burultas formations (Kazanin *et al.* 1976; Abdullin *et al.* 1980). According to Tokmacheva *et al.* (in Abdullin *et al.* 1980), basalts referred usually to the Zhalgyz Formation are characterized by high TiO_2 content (on average 2.1%). Degtyarev & Ryazantsev (2007) reported the occurrence of picrites with high TiO_2 (up to 6.8%) and high P_2O_5 (1.9%). Available data based on somewhat older whole-rock geochemistry (Kazanin *et al.* 1976) and high titanium content may suggest that at least some of the basalts incorporated into the accretionary wedge in front of the Chu–Ili terrane are superplume-derived oceanic intraplate basalts (W. Stepanets, pers. comm.).

Massive sulphide ore deposits (e.g. Burultas, Chiganak, Takyrnoye, Orumbai) are rich in Zn and Pb, and also yield minor Cu and Ag (Kazanin *et al.* 1976). Burultas galena ore signatures show moderately high radiogenic lead isotope ratios ($^{206}Pb/^{204}Pb = 18.07–18.25$; $^{207}Pb/^{204}Pb = 15.50–15.65$; ^{204}Pb isotope ratio = 1.37 $^{232}Th/^{238}U = 4.24$). Beds of black cherts associated with the Burultas sulphide ore deposits south of the Devonian Zhalgyz granitic massif (Fig. 3, locality 9) contain the lower Darriwilian conodonts *Paroistodus horridus* and *Periodon aculeatus* (Tolmacheva in Degtyarev & Ryazantsev 2007). A nappe of radiolarian cherts of the Burubaital Formation exposed in proximity to the area of the Burultas sulphide ore deposits at Shopshoky Mountain contains abundant Lower to Middle Ordovician conodonts varying in age from the *Paroistodus proteus* to *Baltoniodus navis* biozones (Koren *et al.* 1993).

Another distinctive component of this mélange comprises exotic bodies of massive, laminated and oncolitic dolomites with some quartzites and quartzose sandstones. Mélanges that include boulder- or pebble-sized olistoliths of dolomites and basalts in a fine clastic matrix are commonly referred to the 'Zhalgyz Formation' or described as the separate 'Shopshoky Formation'. Most existing reports of an Ediacarian (Vendian) to Early Cambrian age for these carbonates are based on 'taxonomic identifications' from oncolites (Kazanin *et al.* 1976; Kichman *et al.* in Abdullin *et al.* 1980) and are therefore somewhat unreliable. The only reliably diagnostic fossils are the Middle Cambrian (Amgaian) linguliformean brachiopods *Kleithriatreta najmanica* Imanaliev and *Micromitra semicircularis* Imanaliev and Pelman, dissolved from a carbonate olistolith in a mélange exposed in the Suuk–Adyr Mountains (Fig. 3, locality 10; see also Holmer *et al.* 2001).

The occurrence of conodonts of the *Eoconodontus notchpeakensis* Biozone in radiolarian cherts from the southern nappes indicates a late Cambrian age as the youngest limit for the subducted oceanic crust, whereas the presence of conodonts of the *Pygodus serra* and *Pygodus anserinus* biozones in the Burubaital cherts within both the southern and northern nappes indicates the late Darriwilian as the earliest time of incorporation of these cherts now exposed in the western Balkhash region into the growing accretionary wedge. Because island arc volcanism in Chu–Ili is evident from the Early Ordovician and lasted for at least 30 Ma (Fig. 4), significantly more than 1000 km of Cambrian oceanic crust could have been subducted. This suggests that the interpretation of the Buruntau terrane as an intracontinental rift, as proposed recently by Degtyarev & Ryazantsev (2007, p. 89), is somewhat unlikely.

The anomalous presence of 'Kuroko'-type sulphide ore deposits with Pb isotope signatures suggesting influence of continental crust in front of the Chu–Ili accretionary wedge requires explanation. Degtyarev & Ryazantsev (2007, p. 89) reported tectonic contacts of Burultas sulphide ore deposits with the Zhalgyz and Burultas formations in an area that may suggest their allochthonous nature. The Terenkul and Ortan formations, deposited along the margin of the Mynaral–South Dzhungaria terrane facing Chu–Ili during the Early to Mid-Ordovician, comprise siliciclastic turbidites rich in quartz that suggest passive margin development. If the Mynaral–South Dzhungaria terrane represents the remnant of an ensialic volcanic island arc, this margin might be a likely setting for the formation of the 'Kuroko'-type sulphide ore deposits. Alternatively, the 390–300 Ma U–Pb dating for galena from the Burultas sulphide ore deposits may suggest that they formed later in the Devonian–early Carboniferous, related to back-arc rifting after migration of the magmatic front towards the outer margin of the Mynaral–South Dzhungaria terrane.

It is also probable that olistoliths and large bodies of dolomites and quartzites of the Darbasa Formation incorporated in the mélange, but showing some preserved stratigraphical order (Kazanin *et al.* 1976), were generated originally by gravity sliding into the basin from a collapsed carbonate platform (Koren *et al.* 1993, p. 17); however, none of the Cambrian carbonate deposits are now preserved in the core of the Chu–Ili terrane.

The southwestern margin of the Chu–Ili terrane, known as the Sarytuma Fault Zone, is affected markedly by strike-slip shaving and by significant tectonic deformation related to accretionary events in front of the Chu–Ili terrane at the beginning of the Late Ordovician and in the Early to Mid-Devonian. As a result, stratigraphical relationships between major Lower to Middle Ordovician lithostratigraphical units are mostly destroyed. However, in the area SW of Lake Alakul (Figs 10–12) the Middle to Upper Ordovician section remains undisturbed in significant part (Nikitina *et al.* 2006), which allows the evolution of sedimentary and subsidence history to be reconstructed. This area lies just 20–25 km south of the exposures where the most complete sequence of the Burubaital cherts has been documented (Fig. 3, localities 7 and 11). These data also provide important evidence for the southwestern polarity (present coordinates) of subduction under Chu–Ili during the Early and Mid-Ordovician.

The sequence exposed about 4 km SW of Lake Alakul (Fig. 10) begins with a unit of more than 350 m of coarse, volcanoclastic, subaqueous debris flows containing fragments of rhyolite–dacite lava interbedded with tuffs, siliceous shales and black graptolitic shales, containing graptolites that include *Phyllograptus anna* Hall, *Phyllograptus typus* (Hall) and *Tetragraptus* cf. *bigsbyi* (Hall), together with linguliformean brachiopods and phyllocarid crustaceans (Nikitina *et al.* 2006). Elsewhere this lithostratigraphical unit embraces a variety of siliciclastic and volcanoclastic rocks alternating with andesitic to rhyolitic volcanic rocks and tuffs. The oldest fossils known from the middle part of the formation are trilobites identified as *Kayseraspis* sp., suggesting a late Tremadocian to Floian (early Arenig) age (Kazanin *et al.* 1976). The occurrence of earliest Tremadocian (489.6 ± 1.0 Ma) detrital zircon grains from the basal Dzhambul Formation reported by Kröner *et al.* (2007) may suggest that the active margin of the Chu–Ili terrane and associated island arc volcanism originated by the beginning of the Ordovician.

The top of the Balgozha Formation is at a slight angular unconformity. It is overlain by up to 30 m of polymict conglomerates containing pebbles of chert, siliciclastic and volcanic rocks, followed by 135 m of limestones containing stromatolites, stromatoporoids and a medium-diversity brachiopod assemblage characteristic of the lower Darriwilian *Martellia–Pomatotrema* Association; also present are the trilobites *Annamitella granulata* Weber, *Bumastoides betpakensis* Weber, *Illaenus* sp., and the ostracodes *Coelooenellina inconstans* Melnikova and *Alakolites superbus* Melnikova in the lower unit of nodular argillaceous limestone, about 25 m thick (Nikitina *et al.* 2006). The upper Darriwilian interval comprises a unit of arkosic sandstones and calcareous siltstones up to 80 m thick, forming the Oisaksaul Formation. The biota includes some dasyclad algae and an abundant brachiopod fauna, including *Acculina rgaitensis* Nikitina, *Christiania* sp., *Hesperorthis* sp., *Ishimia* sp., *Isophragma princeps* Popov, *Sowerbyella* sp. and *Strophomena rukavishnikovae* Nikitina, plus rare bryozoans.

The described sequence preserves a record of sedimentation in a forearc basin formed on the growing accretionary complex. It originated from a basinal environment where organic-rich clays accumulated well below wave base, with occasional episodes of mass flows and ash falls from distant volcanic eruptions. By the early Darriwilian the area was raised almost to sea level and a rim of stromatolite-bearing carbonates was formed, bounding a semi-restricted shallow marine basin (Fig. 11) (Nikitina *et al.* 2006).

The succeeding part of the sequence is best exposed in the area about 4 km west of the section described by Nikitina *et al.* (2006). Here the upper part of the Oisaksaul Formation (Figs 11–14a) includes a unit of arkosic sandstone overlain by a nodular limestone unit up to 8 m thick, containing abundant dasyclad algae, calcareous sponges and brachiopods, including *Bandaleta* cf. *bicornigera* (Nikitin), *Essilia* sp., *Glyptorthis* sp. and *Ishimia* sp., indicative of a shallow shelf within the photic zone. The limestone is replaced sharply upwards by 6 m of black, graptolitic argillites containing the trilobites *Ampyxinella* sp., *Taklamakania mira* (Kolobova) and *Telephina* sp., plus the brachiopods *Tenuimena planissima* Nikitina *et al.* and *Chonetoidea* sp.; the graptolites, identified by Tsai (pers. comm.), include *Climacograptus bicornis* (Hall), *Expansograptus superstes* (Lapworth) and *Hustedograptus teretiusculus* (Hisinger), of latest Darriwilian to earliest Sandbian age (see also Kolobova 1986; Apollonov in Kovalevskii & Kotlyar 1991). This unit is followed by siliciclastic turbidites some 135 m thick, with a distinct olistostrome horizon at the base containing large (up to 3–4 m) blocks of massive bioclastic limestones containing the brachiopod *Triplesia* aff. *subcarinata* Cooper (Fig. 13a, c). The clastic matrix also contains redeposited disarticulated shells of the brachiopods *Eodalmanella*? *extera* Popov and *Tesikella necopina* (Popov), characteristic of shallow marine environments of Benthic Assemblage 2 (Popov *et al.* 2002), plus the small plectambonitoidean brachiopod *Kasinella* sp. and the cephalopod *Discoceras kazakhstanense* Barskov. All these taxa are

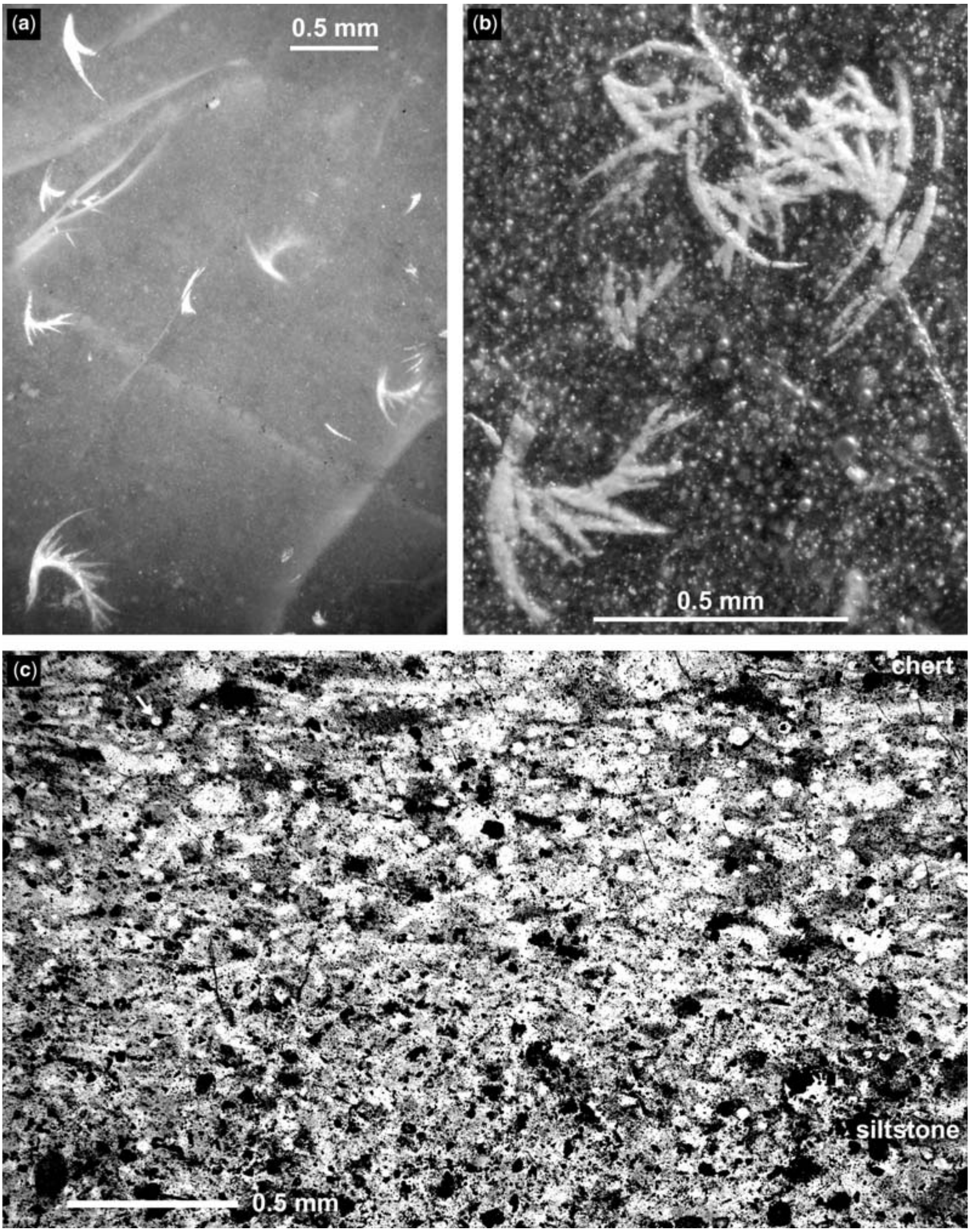

Fig. 10. (**a**) Polished bedding surface of radiolarian chert photographed in reflected light, showing numerous conodont elements mainly of *Paracordylodus gracilis* (Lindström), ×24, Lower Ordovician, *Prioniodus evae* Biozone, locality 9806/19 m, area NW of Burubaital (Fig 3, locality 11; see also Tolmacheva *et al.* 2004). (**b**) Coprolitic element cluster of *Paracordylodus gracilis* (Lindström), ×70, Lower Ordovician, *Prioniodus elegans* Biozone, locality 8927, 1.5 km west of Shopshoky Mountain (Fig. 3, locality 9; see also Tolmacheva & Purnell 2002). Specimens 2008.3G1 and 8, National Museum of Wales. (**c**) Thin section through the uppermost part of a Bouma cycle in the Kogashik Formation (Lower Ordovician, Floian) showing transition from siltstone (below) to a layer of pelagic radiolarian chert (upper 1 mm) with numerous spherical radiolarian tests (some marked by arrow) and poorly preserved elongate sponge spicules. Photograph by T. Yu. Tolmacheva.

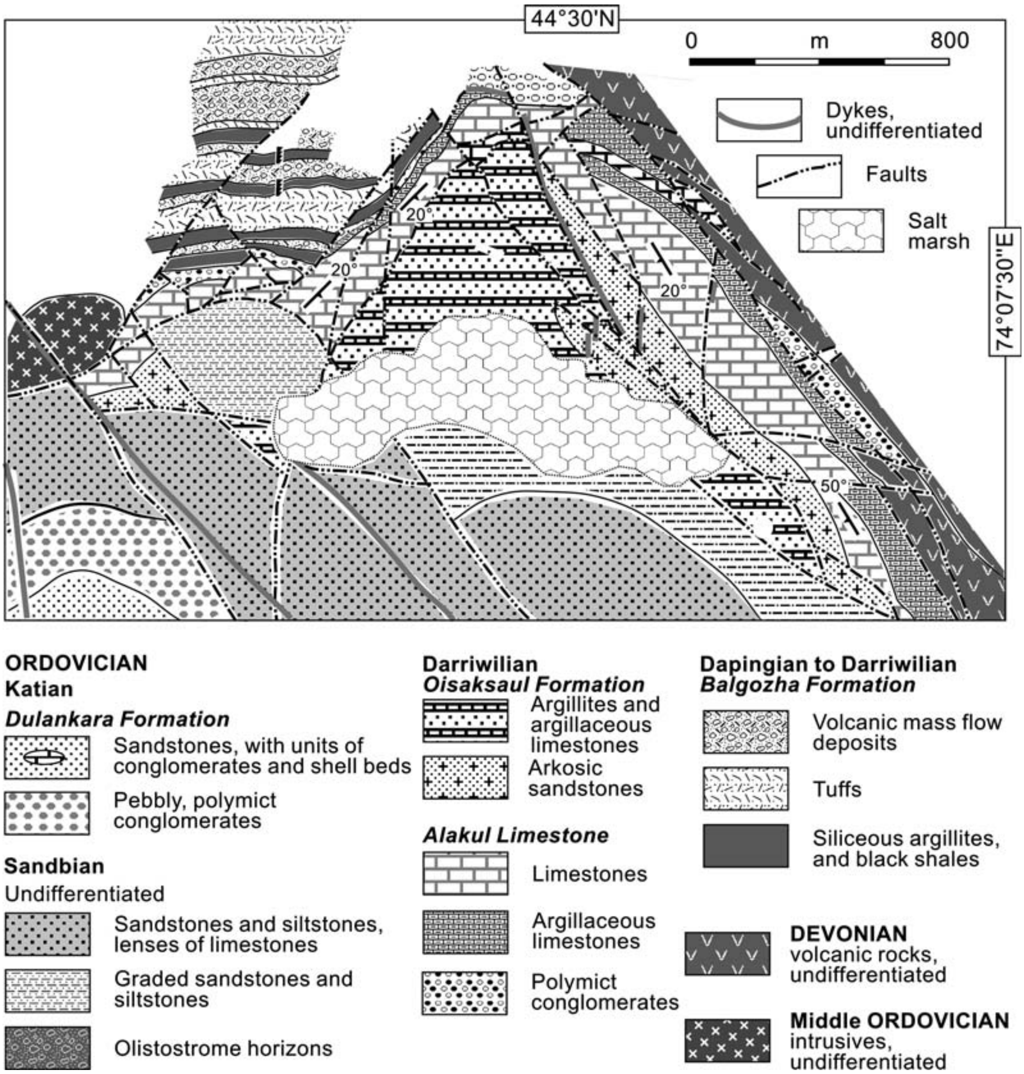

Fig. 11. Geological map of the area 4 km SW of Lake Alakul (Fig. 3, locality 11) showing sedimentary record of a forearc basin. The Balgozha Formation comprises siliceous and black shales with units of volcanoclastic, subaqueous debris flows and tuffs at the base, succeeded unconformably by the Alakul Limestone formed on the rim of a rising accretionary wedge, and shallow shelf calcareous argillites of the Oisaksaul Formation. Modified from Nikitina *et al.* (2006).

characteristic of the Anderken Regional Stage (of Late Ordovician, Sandbian age).

The overlying unit is a second olistostrome, about 18 m thick, comprising polymict conglomerates with a sandy matrix and olistoliths of bioclastic limestone. It is succeeded by units of polymict conglomerates and coarse- to medium-grained sandstones up to 90 m thick, deposited in upper fan and distributary channels, and by a bed of fine-grained sandstone up to 20 m thick with a few shell beds 0.5–1.0 m thick formed in a shallow marine environment. These beds contain an abundant brachiopod fauna that includes *Anoptambonites kovalevskii* Popov, Nikitin and Cocks, *Sowerbyella* sp., *Glyptomenoides* sp., *Ogmoplecia nesca* Popov and Cocks, and *Plectorthis licta* Popov and Cocks (of Benthic Assemblage 3), within the Dulankara Regional Stage (of Late Ordovician, early Katian age).

The upper boundary of the unit is at a slight angular unconformity. Overlying clastic rocks comprise polymict pebbly conglomerates up to 40 m

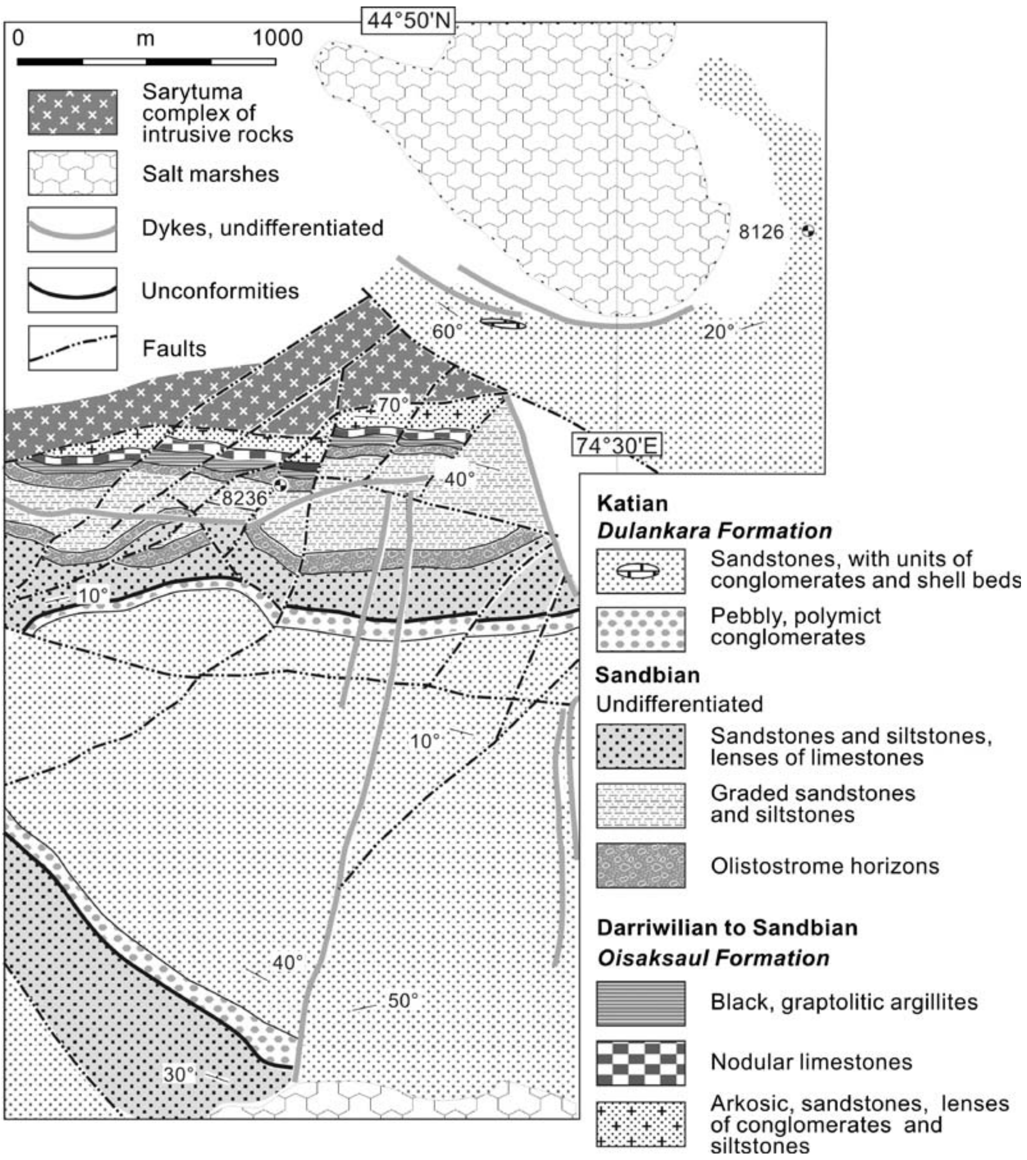

Fig. 12. Geological map of the area 7 km SW of Lake Alakul (Fig. 3, locality 11) showing depositional sequence of a foredeep basin filled with siliciclastic turbidites with a characteristic olistostrome horizon in the lower part. Siliciclastic deposits of the Dulankara Formation were formed mainly in peritidal environments and unaffected by Late Ordovician post-collisional deformation.

thick and then a unit of more than 60 m of sandstone with bidirectional cross-bedding and several coquina storm beds (Fig. 13b). The coquinas contain disarticulated brachiopods, including *Sowerbyella* sp. and *A. kovalevskii*, also characteristic of the Dulankara Regional Stage (Popov *et al.* 1999).

Rapid subsidence recorded through the sequence at the beginning of the Late Ordovician closely followed the termination of subduction in front of the Chu–Ili terrane shortly after the *Pygodus anserinus* Biozone. This resulted in the formation of a foredeep basin, which was filled with almost 250 m of clastic sediment (Fig. 14a). Shallow-water carbonates preserved as olistoliths were deposited almost synchronously, sliding into the basin probably in response to growing thrust systems.

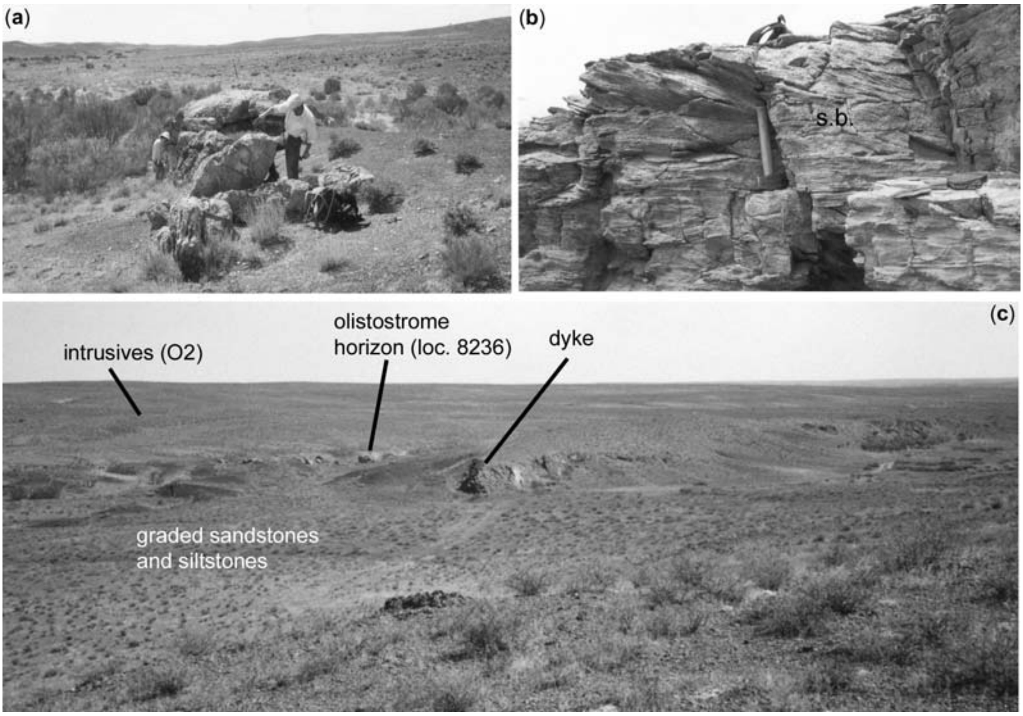

Fig. 13. Outcrop area of Middle to Upper Ordovician rocks in the area about 7 km SW of Lake Alakul. (**a**) Large olistolith (Fig. 12, locality 8236) with stromatolites and the brachiopod *Triplesia* aff. *subcarinata* at the base of a turbiditic unit (Sandbian, Anderken Regional Stage). (**b**) Sandstones with bidirectional cross-bedding and bioclastic limestone storm beds (s.b.), containing disarticulated shells of *Sowerbyella* sp. and *Anoptambonites kovalevskii* (Fig. 12, locality 8126); typical deposits in the upper part of the sequence corresponding to the Dulankara Regional Stage (lower Katian). Photographs by L. Holmer. (**c**) Southern view of the lower part of the Upper Ordovician sequence (see also Fig. 12) with a characteristic olistostrome horizon at the base of a turbiditic unit (Sandbian, Anderken Regional Stage). Photograph by L. Popov.

An unconformity at the base of the Dulankara Formation reflects the last sign of post-collisional deformation, and overlying strata are deformed only slightly, except in areas proximal to post-Ordovician strike-slip faults (Figs 12 & 14a).

Middle Ordovician intrusive magmatism in the Sarytuma Fault Zone comprised mainly diorites and plagiogranites as small plutons referred to the Kotnak and Sarytuma complexes (Toporova *et al.* in Abdullin *et al.* 1980). The mean $^{207}Pb/^{206}Pb$ zircon evaporation ages of 477.7 ± 1.1 and 480.0 ± 1.0 Ma reported by Kröner *et al.* (2007) were probably obtained from the Sarytuma intrusive complex.

Tectonic deformations of the Precambrian core of the Chu–Ili plate in the Early to Mid-Ordovician were extensional in character (Figs 14b & 15). They resulted in the formation of narrow basins in grabens and half-grabens, which underwent several cycles of subsidence and sedimentary infilling. By the late Katian (*Climacograptus supernus* Biozone) most of the Chu–Ili terrane was flooded, with deposition of black graptolitic shales of the Chokpar Formation, probably as a result of thermal relaxation after termination of island arc volcanism, whereas sea-level instability and lithofacies changes across the Ordovician–Silurian boundary were probably induced eustatically in response to terminal Ordovician glaciation (Nikitin *et al.* 1980).

Active subduction under Chu–Ili probably ceased by the beginning of the Late Ordovician as a result of docking of a small terrane of uncertain origin. Its southwestern margin preserves a monotonous, northerly deepening sequence of unfossiliferous, graded siliciclastic rocks referred to usually as the Terenkul Formation. The inferred Cambrian age of this unit is based on supposed stratigraphical relationships with the metamorphic rocks of the presumably Proterozoic Orumbai Formation (Kichman *et al.* in Abdullin *et al.* 1980). However, so-called ‘basal conglomerates’ with ‘cigar-like’ pebbles actually represent a tectonic mélange developed

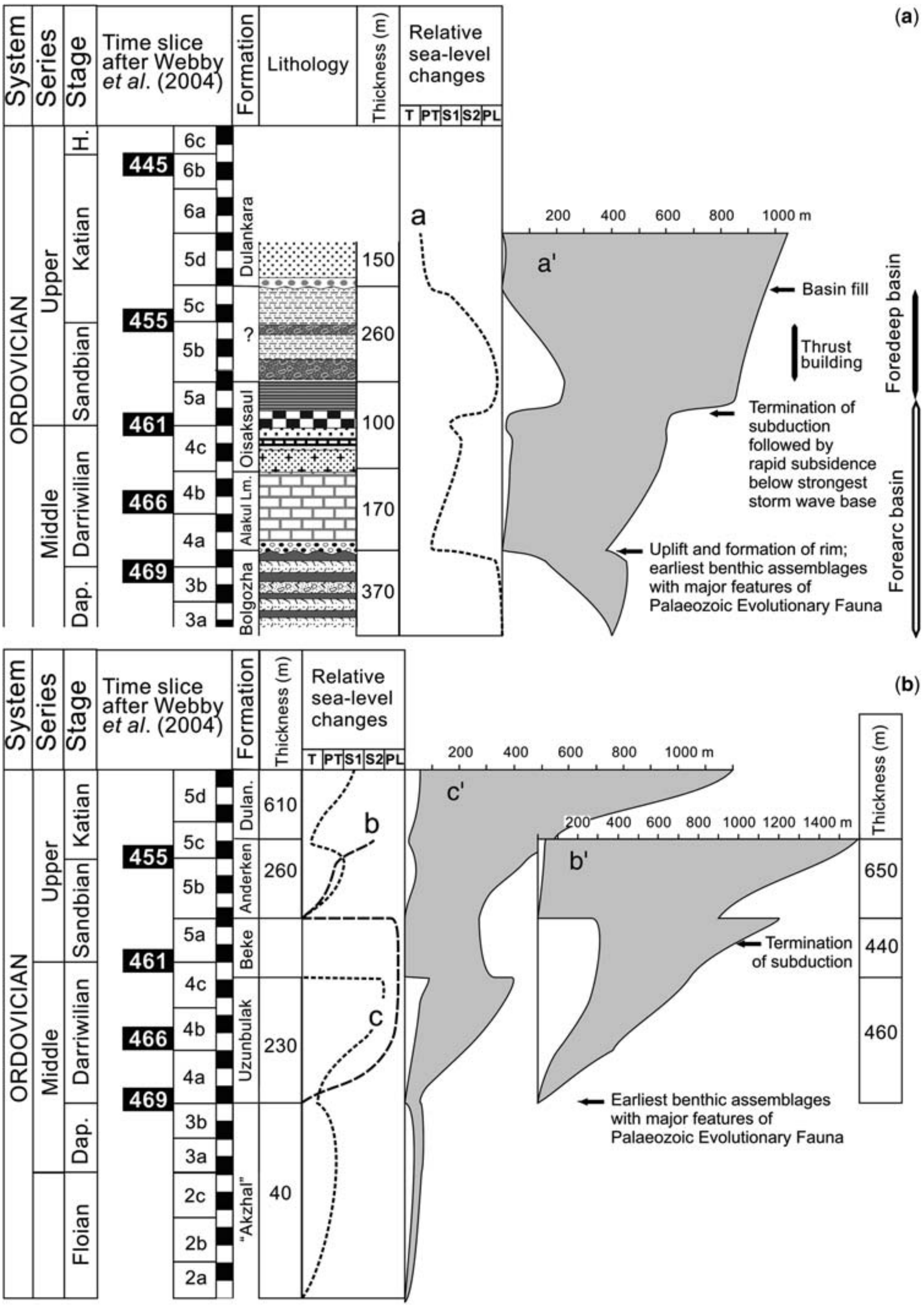

Fig. 14. (**a**) Depositional and subsidence history of the forearc and foredeep basins in front of the Chu–Ili terrane based on two sections exposed SW of Lake Alakul (Fig. 3, locality 11; Figs 10–13). See Figures 11 and 12 for explanation of lithological symbols. (**b**) Depositional and subsidence history of the southeastern sector of the Chu–Ili terrane based on Anderkenyn–Akchoku (b, b′; Fig. 3, locality 18) and Kopalysai (c, c′; Fig. 3, locality 17) sections (Keller 1956; Popov *et al.* 2002; Nikitina *et al.* 2006). Diagrams show Middle to Upper Ordovician stratigraphy, approximate position of the crustal surface with respect to sea level (a′, b′, c′), and cumulative thickness of sediments. T, terrestrial environment; PT, peritidal zone; S1, inner shelf; S2, outer shelf; PL, pelagic zone; Dap, Dapingian; H, Hirnantian.

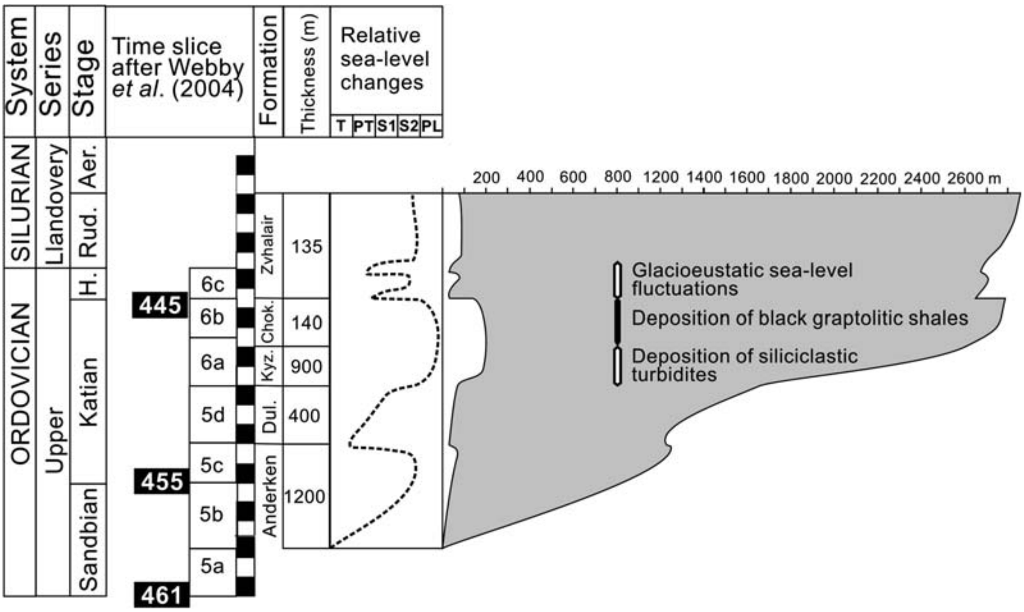

Fig. 15. Depositional and subsidence history in the mid-Ordovician–early Silurian along the western margin of the Chu–Ili terrane, based on the Dulankara section (Fig. 3, locality 2). T, terrestrial environment; PT, peritidal zone; S1, inner shelf; S2, outer shelf; PL, pelagic zone; H, Hirnantian; Rud, Rhuddanian; Aer, Aeronian; Dul, Dulankara Formation; Kyz, Kyzylsai Formation; Chok, Chokpar Formation.

along the basal thrust surface. The rocks were thrust southwards, towards the accretionary prism formed in front of the Chu–Ili terrane. Similar graded siliciclastic rocks, with units of polymict conglomerates and with clear southwestern vergence, are present east of the Zhalgys granitic massif, where they are probably thrust over the subduction–accretion complex. These rocks contain poorly preserved graptolites identified as *Climacograptus* sp. and *Glyptograptus* sp. (Nikitin *et al.* in Abdullin *et al.* 1980).

Another unit of turbiditic rocks formed as facies of an outer fan and fan fringe is the Ortan Formation, exposed near the western coast of Lake Balkhash south of the Akkerme Gulf (Fig. 3, locality 16; Fig. 16). This unit contains Darriwilian graptolites at several levels, including *Cryptograptus* cf. *schauferi* (Palworth), *Dicellograptus* sp., *Expansograptus* sp., *Phyllograptus anna* (Hall), and *Pseudoclimacograptus scharenbergi* (Lapworth) (Nikitin *et al.* in Abdullin *et al.* 1980).

The sporadic occurrence of presumed Precambrian rocks referred to the Karakamys and Orumbai formations along the outer margin of the subduction–accretion complex (Fig. 3, locality 12) requires special attention. Radiometric ages of these units are not known and their Precambrian dating is based exclusively on high-grade metamorphism and inferred affinities with other metamorphic rocks from remote tectonic settings (e.g. Kendyktas and Malyi Karatau), which is not an unusual practice in Kazakhstanian geology (Kichman *et al.* in Abdullin *et al.* 1980). Early acritarch identifications are based on a taxonomy elaborated by Timofeev and certainly require revision. However, a report of the occurrence in the Orumbai Formation of bioclasts, which according to Stukalina (Kichman *et al.* in Abdullin *et al.* 1980, p. 29) may be echinoderm columnals, could well be a sign of an early Palaeozoic age for these supposed Precambrian units. Abdrahmanov & Khokhlov (in Kazanin *et al.* 1976, p. 52) considered that the presumed Precambrian granites and granitic gneisses exposed west of the Devonian Karakamys granitic massif are instead products of high-grade metamorphism of the Ordovician clastic sediments developed in the area.

By Silurian times the magmatic front had migrated about 100 km NE towards the margins of a newly accreted terrane, which coincides more or less with the Mynaral–South Dzhngaria tectonofacies zone of Nikitin (1994, fig. 1). Here, units of andesites and andesitic basalts are reported from the lower part of the Mynaral Group (Llandovery to Wenlock). They are dated as Aeronian because of the occurrence of brachiopods characteristic of

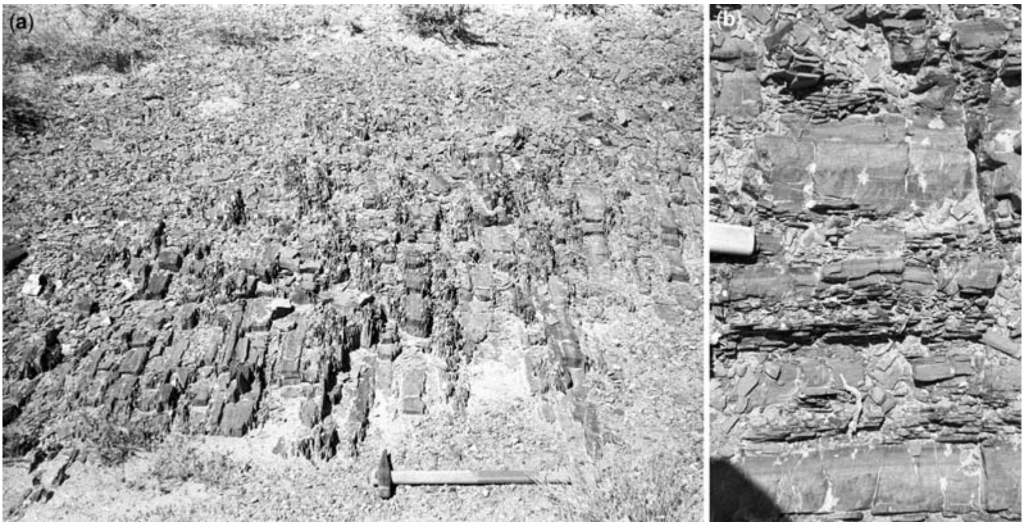

Fig. 16. Exposure of siliciclastic turbidites of the Ortan Formation on the southern side of the Akkerme Gulf (Fig. 3, locality 16). Photograph by L. Popov. (**a**) General view; (**b**) detail showing Bouma cycles.

the *Pentamerus longiseptatus* beds in underlying sedimentary rocks, and by *Octavites spiralis* Biozone graptolites in overlying units (Bandaletov & Palets in Abdullin *et al.* 1980). Intensive island arc volcanism in Chu–Ili took place almost continuously through the Silurian to mid-Devonian (Abdullin *et al.* 1980; Koren *et al.* 2003). The Silurian margin of Chu–Ili was almost completely destroyed in extensive post-Silurian tectonic deformations (Fig. 3, locality 15; Fig. 17).

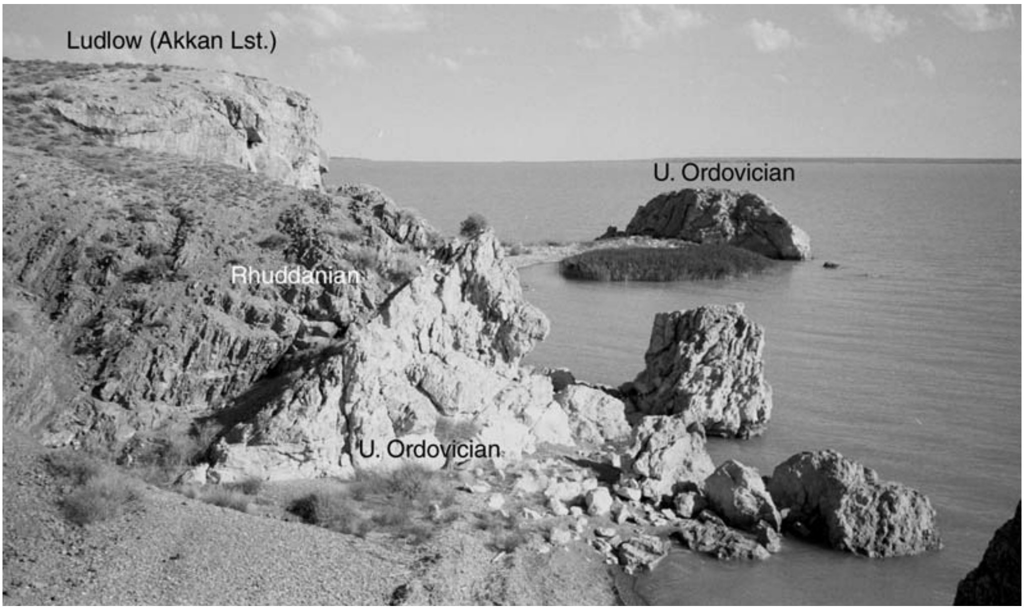

Fig. 17. Exposure of Upper Ordovician and Silurian rocks on the northern coast of the Akkerme Peninsula (Fig. 3, locality 15). Photograph by L. Popov.

Characteristic benthic faunas and their biogeographical signatures

The linguliformean brachiopods *Kleithriatreta najmanica* Imanaliev and *Micromitra semicircularis* Imanaliev and Pelman recovered from an exotic olistolith of Middle Cambrian limestone (Fig. 3, locality 12, Suukadyr Mountains) within the early to mid-Ordovician accretionary wedge of Chu–Ili (Holmer *et al.* 2001) are the only biogeographically informative Cambrian taxa yet known. Both species were described originally from the Kuchek Alai Range in South Tien Shan (Imanaliev & Pelman 1988), where they also occur in olistoliths. Allochthonous Cambrian limestones in the Kuchek Alai Range also contain the protorthide brachiopod *Glyptoria* and the chileide *Chile*, which are known otherwise only from Timna in the southern Negev of Israel (Bassett *et al.* 2002, 2004) and therefore suggest a distinct link with faunas of subequatorial Gondwana. The Order Protorthida is also strictly peri-Gondwanan in the Cambrian (Bassett *et al.* 2002). The acrotretide *Kleithriatreta* was described originally from the Middle Cambrian of the Australian sector of Gondwana (Roberts & Jell 1990). This relatively weak Cambrian link therefore points to subequatorial peri-Gondwanan as a possible original source for the crustal fragment that now forms the Chu–Ili terrane.

The oldest diverse benthic Ordovician fauna known from Chu–Ili is of early Darriwilian age (Uzunbulak Formation and Alakul Limestone). The distinctive brachiopod component of this fauna was described recently by Nikitina *et al.* (2006), and a summary of the Darriwilian trilobites was published by Chugaeva (1958), with ostracodes described by Melnikova (1986). Calcareous sponges (including stromatoporoids) and gastropods are abundant, but not yet monographed, whereas bryozoans and bivalved molluscs are notably absent. Early Darriwilian benthic assemblages of the shallow and mid-shelf are dominated by filter-feeders including rhynchonelliformean brachiopods, pelmatozoan echinoderms (known exclusively from columnals) and calcareous sponges, all characteristic of the early Palaeozoic Evolutionary Fauna (Sepkoski 1981; Sepkoski & Sheehan 1983). Ostracodes are also an important component of this fauna. Because there are no similar contemporaneous or older faunas known elsewhere in Kazakhstan, and almost all rhynchonelliformean brachiopod and ostracode genera are new to the Chu–Ili terrane, their appearance can be attributed to a major immigration event in the region. Thus the biogeographical affinities of the faunas give important clues to the original source of this terrane and its relationships. From the biogeographical analysis of the early Darriwilian rhynchonelliformean fauna of Chu–Ili (Nikitina *et al.* 2006), up to 47% of the total diversity is made up of genera either entirely endemic to the region or genera that make their first appearance in Chu–Ili and later spread across a wider geographical range. The list includes such taxa as *Apatomorpha*, *Christiania* and *Metacamarella* (for detailed discussion see Nikitina *et al.* 2006), which migrated extensively through the late Darriwilian to Floian, but were endemic to the Chu–Ili terrane in the early Darriwilian.

Other important components of the early Darriwilian brachiopod assemblages of Chu–Ili are *Aporthophyla*, *Idiostrophia*, *Leptella*, *Leptellina*, *Neostrophia*, *Taphrodonta*, *Toquimia*, *Trematorthis* and *Trondorthis*, which were considered by Neuman & Harper (1992) as characteristic of the Toquima–Table Head Province. Some of these genera (*Aporthophyla*, *Leptellina*, *Taphrodonta*) occur also in the Darriwilian of peri-Gondwanan (Sibumasu, South China, Tasmania) (Cocks & Rong 1989; Laurie 1991; Fig. 18).

Among other brachiopods only *Martellia* and *Yangtzeella* have a distinct Gondwanan signature (Fig. 18). Both genera are present also in the early Darriwilian of South China (Zeng 1987; Zhan *et al.* 2007). In addition, *Martellia* is reported from Argentina (Benedetto 2002), whereas *Yangtzeella* occurs in the Turkish Taurides and the Alborz terrane of Iran (Cocks & Fortey 1988; Ghobadi Pour *et al.* 2004). More peri-Gondwanan affinities exist according to Fortey & Cocks (2003) in early Darriwilian outer shelf trilobite assemblages. In particular, *Ampyxinella* and *Bulbaspis* are known from Tarim, and *Lisagorites* is reported from South China.

Further constraints on the determination of affinities of newly emergent benthic assemblages in the Palaeozoic Evolutionary Fauna of Chu–Ili can be inferred from their diachronous appearance on major early Palaeozoic continents. As demonstrated by Bassett *et al.* (2002), the main components of these assemblages are rooted deeply in temperate-latitude and subequatorial peri-Gondwana, where their precursors can be traced in the Tremadocian and earlier into the Cambrian. In Baltica the earliest benthic assemblages dominated by rhynchonelliformean brachiopods (including plectambonitoideans, endopunctate orthides, camerelloideans and clitambonitoideans), together with bryozoans and ostracodes, are known from the Billingenian (mid- to late Floian, *Prioniodus elegans* to *Oepikodus evae* conodont biozones), considerably earlier than in the Chu–Ili terrane. By the Darriwilian, the Baltic Ordovician fauna diversified and achieved a high degree of endemism (Harper & Mac Niocaill 2002; Fortey & Cocks 2003; Sturesson *et al.* 2005). The early Darriwilian brachiopod fauna of the Chu–Ili

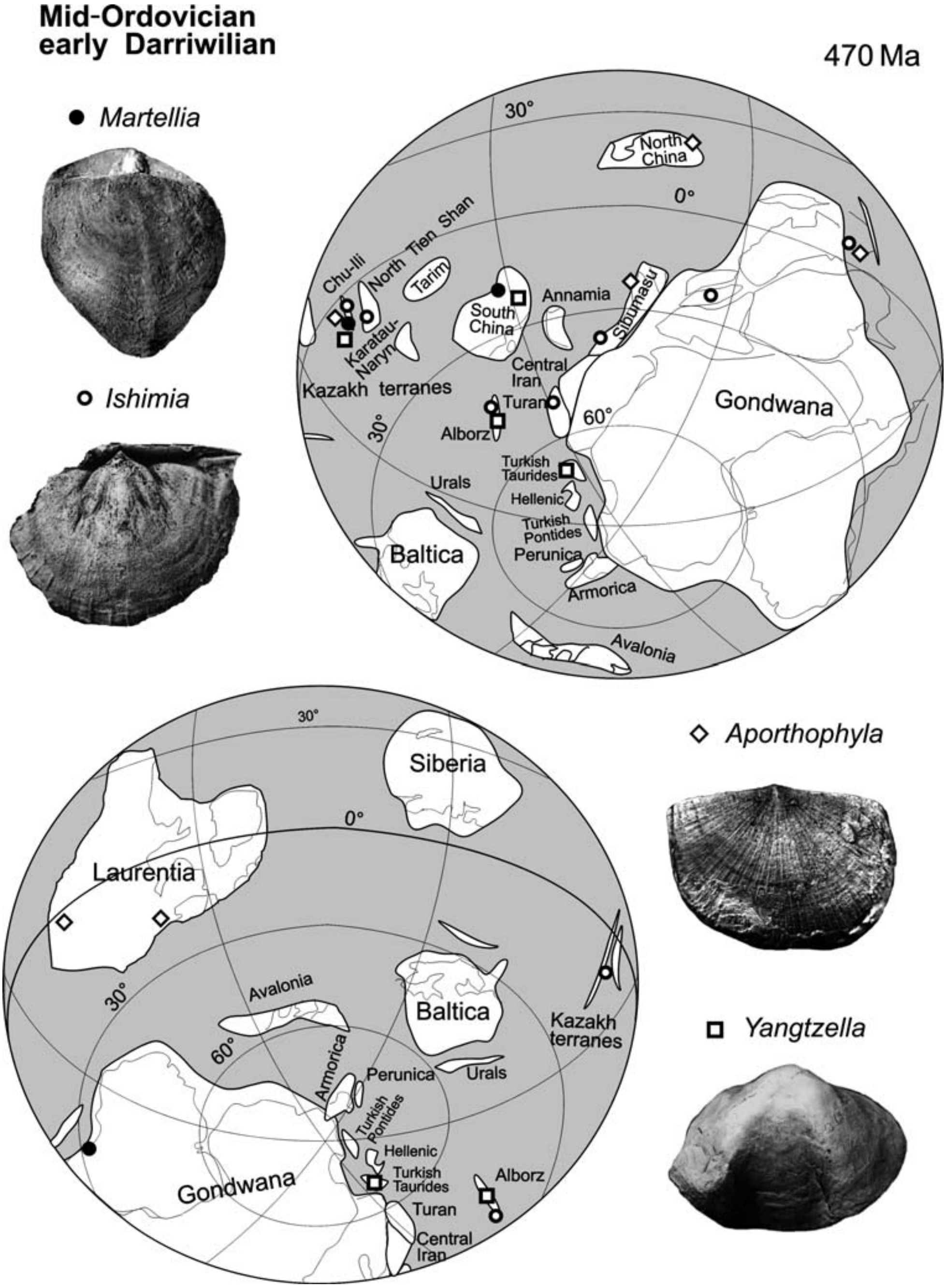

Fig. 18. Global reconstruction of Mid-Ordovician (Darriwilian) palaeogeography showing distribution of some characteristic brachiopod genera from the Uzunbulak Formation of the Chu–Ili terrane. *Martellia* and *Yangtzeella* are common in South China and also spread towards temperate latitudes along the Gondwanan margin; *Aporthophyla* was pantropical, whereas *Ishimia* was confined mainly to low latitudes in 'East' Gondwana. Relative positions of Gondwana, Armorica, Baltica, Avalonia, Laurentia and Siberia are mainly after Torsvik *et al.* (1998). Position of the North China plate in equatorial northern lattitudes and the southern low-latitude position of the Tarim plate are mainly after Zhao *et al.* (1996).

terrane completely lacks endopunctate orthides, clitambonitoideans, the families Porambonitidae and Lycophoridae, and many impunctate orthide genera (e.g. *Orthis*, *Orthambonites*, *Krattorthis*), which form the core of the Baltic Darriwilian assemblages. Baltic bryozoans had diversified already in the Early Ordovician, whereas they arrived in Chu–Ili only in the late Darriwilian (Pushkin & Popov 1993). Trilobites also differ significantly (for details see Fortey & Cocks 2003). Shelf and epeiric seas of the Siberian continent were populated by benthic assemblages displaying major features of the Palaeozoic Evolutionary Fauna only from the beginning of the Late Ordovician (Bassett *et al.* 2002), which suggests a remote location relative to all other early Palaeozoic continents and to the Chu–Ili terrane in particular.

There is a distinct affinity of the early Darriwilian brachiopod faunas of Chu–Ili with contemporaneous faunas of the Whiterockian of Laurentia. However, although fully formed benthic assemblages of the Palaeozoic Evolutionary Fauna were present in Laurentia at the beginning of the Darriwilian (Bassett *et al.* 2002), many brachiopod taxa (e.g. plectambonitoideans, camerelloideans *Camerella*, *Idiostrophia*, *Neostrophia*), as well as bryozoans, have no roots in earlier Laurentian faunas. A possible explanation is that similar Chu–Ili and Laurentian components of the shallow and mid-shelf benthic assemblages were part of a pan-tropical fauna in low latitudes originating from a single source. They possibly originated on the tropical shelf of Gondwana, but current knowledge of the Gondwanan Darriwilian and older faunas is inadequate to provide conclusive evidence.

Ordovician faunas of the North Tien Shan plate are relatively poorly known, but the affinity of the late Darriwilian to early Sandbian brachiopods with those of Chu–Ili is evident, sometimes down to species level (e.g. *Acculina rgaitensis* Nikitina, *Macrocoelia insolita* Nikitina, *Paralenorthis rgaitensis* Nikitina, *Scaphorthis recurva* Nikitina, *Strophomena rukavishnikovae* Nikitina). Both faunas include *Acculina*, which is a Kazakhstanian endemic, and *Ishimia* (Nikitina 1985; Misius 1986), which is characteristic of low-latitude ‘East’ Gondwanan faunas (Australia, Sibumasu, Tibet) (for review see Zhan & Cocks 1998; Percival *et al.* 2001) (Fig. 18).

At the beginning of the Late Ordovician (Sandbian), equatorial peri-Gondwanan links of the Chu–Ili benthic faunas became more evident. In particular, they are expressed in the strong affinity of the brachiopod assemblage from the Jinhe Formation of NW China described by Fu (1982), and brachiopods of the *Acculina–Dulankarella* and *Parastrophina–Kellerella* associations linked closely in Chu–Ili with carbonate mud-mound facies (Popov *et al.* 2002). The precise tectonic setting of that fauna is uncertain, but most probably it inhabited a shelf of the North China plate situated in the Late Ordovician in subequatorial northern latitudes in proximity to the Australian sector of Gondwana (Zhao *et al.* 1996; Fortey & Cocks 2003). Both faunas are characterized by the presence of abundant parastrophinids and paralellasmatids, including some common genera and species (e.g. *Plectosyntrophia*?, *Parastrophina*, *Didymelasma* cf. *transversa* Fu, *Schizostrophina margarita* Fu) together with the early atrypide *Pectenospira* and probably the earliest athyridides. Affinity to subequatorial Gondwana is also accentuated by the occurrence of *Bowanorthis*?, *Dulankarella*, *Mabella*, *Phaceloorthis*, *Shlyginia* and *Teratelasmella*, which occur also in Australia (Laurie 1991; Percival 1991; Percival *et al.* 2001; Popov *et al.* 2002). Similarity to peri-Gondwanan faunas is further evident from some common trilobite genera, such as *Pliomerina* in shallow shelf biofacies, and *Birmanites* and *Ovalocephalus* from the outer shelf, where they occur together with the strophomenide brachiopod *Foliomena* (Nikitin 1972; Popov *et al.* 2002). The latter genus was confined to Kazakhstanian terranes and South China during the Sandbian, and only from the Katian did it achieve an almost cosmopolitan distribution (Fortey & Cocks 2003).

Biogeographical affinities of the Late Ordovician (Katian–Hirnantian) brachiopod and trilobite faunas of Kazakhstan, including those of the Chu–Ili terrane, have been discussed in several recent papers (Fortey & Cocks 2003; Popov *et al.* 1999, 2000; Nikitin *et al.* 2006; Popov & Cocks 2006) and there is no need to discuss the relationships here in detail. These accounts demonstrate that in the second half of the Late Ordovician, brachiopod assemblages characteristic of shallow shelf biofacies in the Chu–Ili terrane and other Kazakhstanian terranes, including North Tien Shan and the Chingiz–Tarbagatai volcanic arcs, show closest similarity to contemporaneous faunas of Tarim and South China, and to a lesser extent to those of the Australian sector of equatorial Gondwana (Fig. 19). Biogeographical links with Baltica faunas increased by the end of the Ordovician, but nevertheless remained relatively weak, whereas affinities with contemporaneous faunas of Laurentia and Siberia were almost negligible (Nikitin *et al.* 2006). Analysis of Late Ordovician trilobite faunas by Fortey & Cocks (2003) demonstrated similar closest similarities of the Chu–Ili biota to equatorial peri-Gondwanan, especially Tarim and South China.

Terminal Ordovician extinction events transformed brachiopod biogeography, which then resulted in the almost cosmopolitan spread of

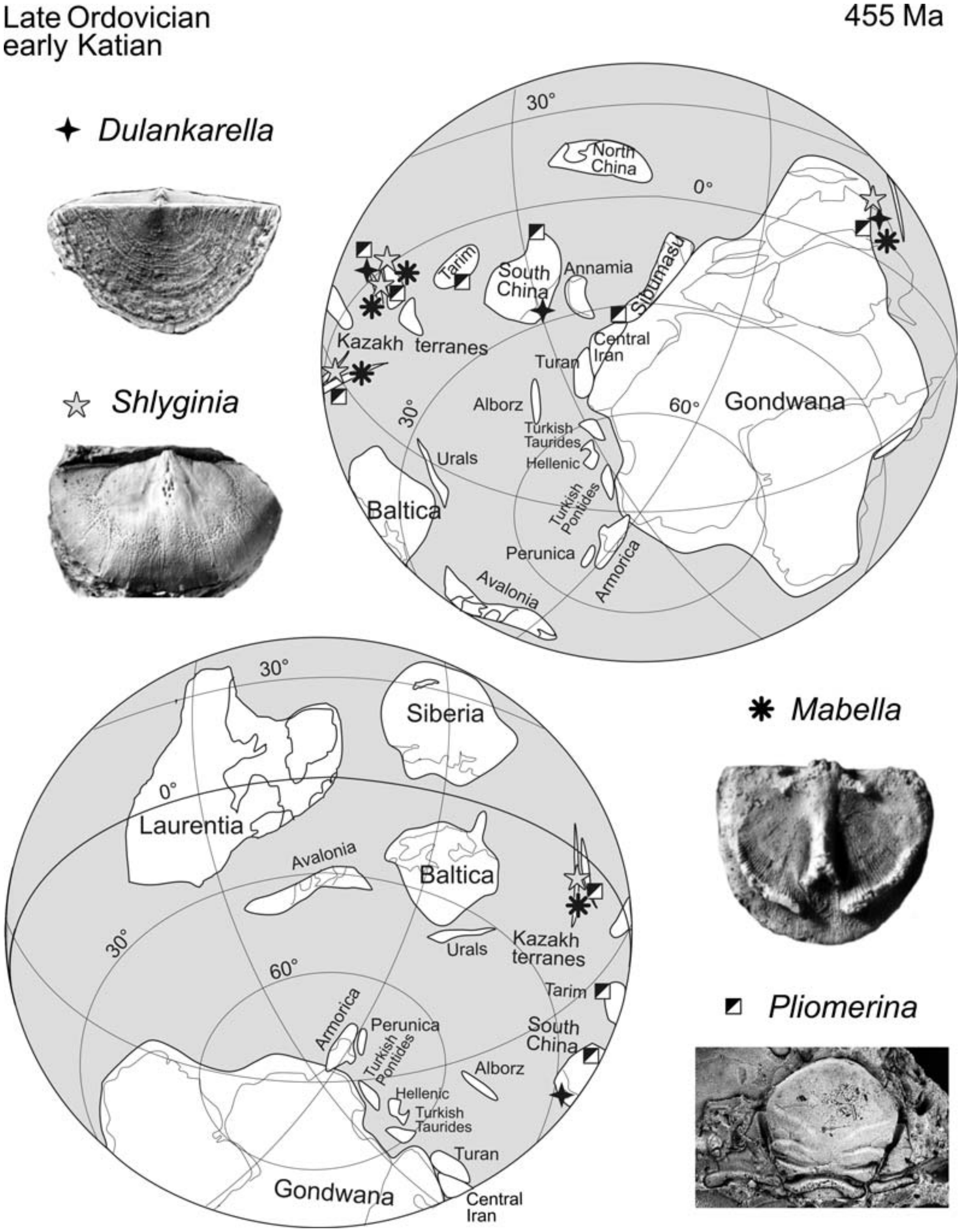

Fig. 19. Global reconstruction of Late Ordovician (early Katian) palaeogeography showing distribution of some characteristic brachiopod and trilobite genera from the Dulankara Formation of the Chu–Ili terrane. The plectambonitoidean brachiopods *Dulankarella*, *Mabella* and *Shlyginia*, and the trilobite *Pliomerina* were widespread in subequatorial latitudes from Kazakhstanian terranes to the Australian sector of ‘East’ Gondwana. This area is confined mainly to the ‘*Pliomerina* faunal province’ of Webby (1971). Remarkably, none of these genera are found in Avalonia, Baltica, Laurentia or Siberia; they are also unknown in temperate- to high-latitude ‘West’ peri-Gondwanan. South China drifted from temperate to low southern latitudes and approached the North China plate by the late Ordovician.

early Silurian (Llandovery) faunas known from low latitudes. However, some important biogeographical patterns are revealed by tracing the diachronous appearances of some distinctive brachiopod groups; in particular, the earliest known spiriferide *Eospirifer* (Fig. 20). As demonstrated by Rong *et al.* (1994) and Rong & Zhan (1996), this genus originated in South China as early as the Late Ordovician (late Katian). By the Rhuddanian, *Eospirifer* spread to the Australian segment of Gondwana (Sheehan & Baillie 1981) and to the Chingis–Tarbagatai group of terranes in Kazakhstan. It occurs in the Chu–Ili terrane from the early Rhuddanian in association with *Stricklandia lens mullochensis* Reed (Modzalevskaya & Popov 1995). The earliest spiriferides in Baltica, Laurentia and Siberia are probably post-Aeronian (Sheehan & Baillie 1981; Rong & Zhan 1996). Thus the position of Chu–Ili in geographical proximity to subequatorial peri-Gondwanan is evident in the early Silurian.

Inferred early Palaeozoic geological history of the Chu–Ili terrane as a test of plate-tectonic models

If the stratigraphical relationship between turbidites of the Dzhambul Formation and underlying mafic volcanic rocks are confirmed, it may suggest that the history of the Chu–Ili terrane as a discrete tectonic unit originated some time in the Middle Cambrian. Passive development of the Zhalair–Naiman margin in the Late Cambrian to Mid-Ordovician finds support from available sedimentological and palaeontological data. This suggests also that the major feature of oceanic development along the Zhalair–Naiman margin through this interval was divergence, and not convergence as in the tectonic model proposed recently by Degtyarev & Ryazantsev (2007). The earliest evidence of island arc volcanism and subduction along the margin of the North Tien Shan microplate facing the Zhalair–Naiman Fault Zone is in the Mid-Ordovician (Nikitin 1972, 1973). By the late Darriwilian, oceanic space separating North Tien Shan and Chu–Ili was sufficiently narrow to allow relatively free exchange of shallow shelf faunas. Thus, following Fortey & Cocks (2003, fig. 2), it is likely that at that time the separation could have been significantly less than 1000 km.

A Cambrian sedimentary cover is not now preserved on the Chu–Ili terrane, but Early to Middle Cambrian carbonates of the Darbaza Formation preserved as olistoliths in the accretionary wedge include oncolitic limestones and laminated dolomites. If one assumes that their original source was a carbonate shelf in the Chu–Ili terrane, it was probably located in low, tropical latitudes. This does not contradict the inferred position of the Zhalair–Naiman Unit (= Chu–Ili terrane) of Şengör & Natal'in (1996, fig. 21.28) on the eastern margin of the Siberian craton in the Ediacarian–Mid-Cambrian. Equatorial Gondwana or its closely neighbouring regions were an equally possible source of Chu–Ili. Because Cambrian data on the Gondwanan affinities of the faunas lack precision, the original source of that crustal fragment can be inferred only from its subsequent Ordovician history and biogeographical connections.

Island arc volcanism, probably in a Japan-type setting (Kröner *et al.* 2007), was probably established some time in the Cambrian and is evident along the northeastern margin (present coordinates) of the Chu–Ili terrane very early in the Ordovician. It terminated by the beginning of the Late Ordovician. A record of continuous sedimentation of radiolarian oozes for at least 35–40 Ma on the subducted slab of the oceanic crust is preserved in the accretionary wedge of Chu–Ili (Tolmacheva *et al.* 2001, 2004). Accumulation of such deposits takes place in narrow belts associated with equatorial divergence or with upwelling systems characterized by high primary biological productivity (Murdmaa 1987). An intra-oceanic position of the Chu–Ili terrane is suggested by high endemicity of the early Darriwilian benthic faunas. This favours its location within a zone of tropical oceanic divergence, so that an oceanic plate subducted under Chu–Ili would have had a strong latitudinal component in its rotation. It also suggests that at the time of subduction of this oceanic slab during the Mid-Ordovician, Chu–Ili was located in the tropics within an oceanic divergence zone, and with an active margin facing east or west. Subduction and associated island arc volcanism in Chu–Ili is evident probably for almost 25–30 Ma from the early Tremadocian to the latest Darriwilian. Significantly more than 1000 km of oceanic crust of Late Cambrian age and older was subducted under Chu–Ili during this time. Benthic faunas inhabiting the Chu–Ili shelf from the Darriwilian to early Silurian show distinct links with equatorial Gondwana, weak links with Baltica, and almost no affinity with Siberia (Fortey & Cocks 2003; Nikitin *et al.* 2006; Nikitina *et al.* 2006). Therefore it is most likely that the active margin of Chu–Ili was facing west during the Early to Mid-Ordovician. This in turn suggests a significant clockwise rotation exceeding 120° from the inferred position of the Chu–Ili terrane in the Mid-Ordovician to its recent position. From the late Mid-Ordovician the North Tien Shan microcontinent was in relative proximity to Chu–Ili, which allowed relatively free faunal exchange, and then collision resulted in amalgamation along the Zhalair–Naiman suture, probably

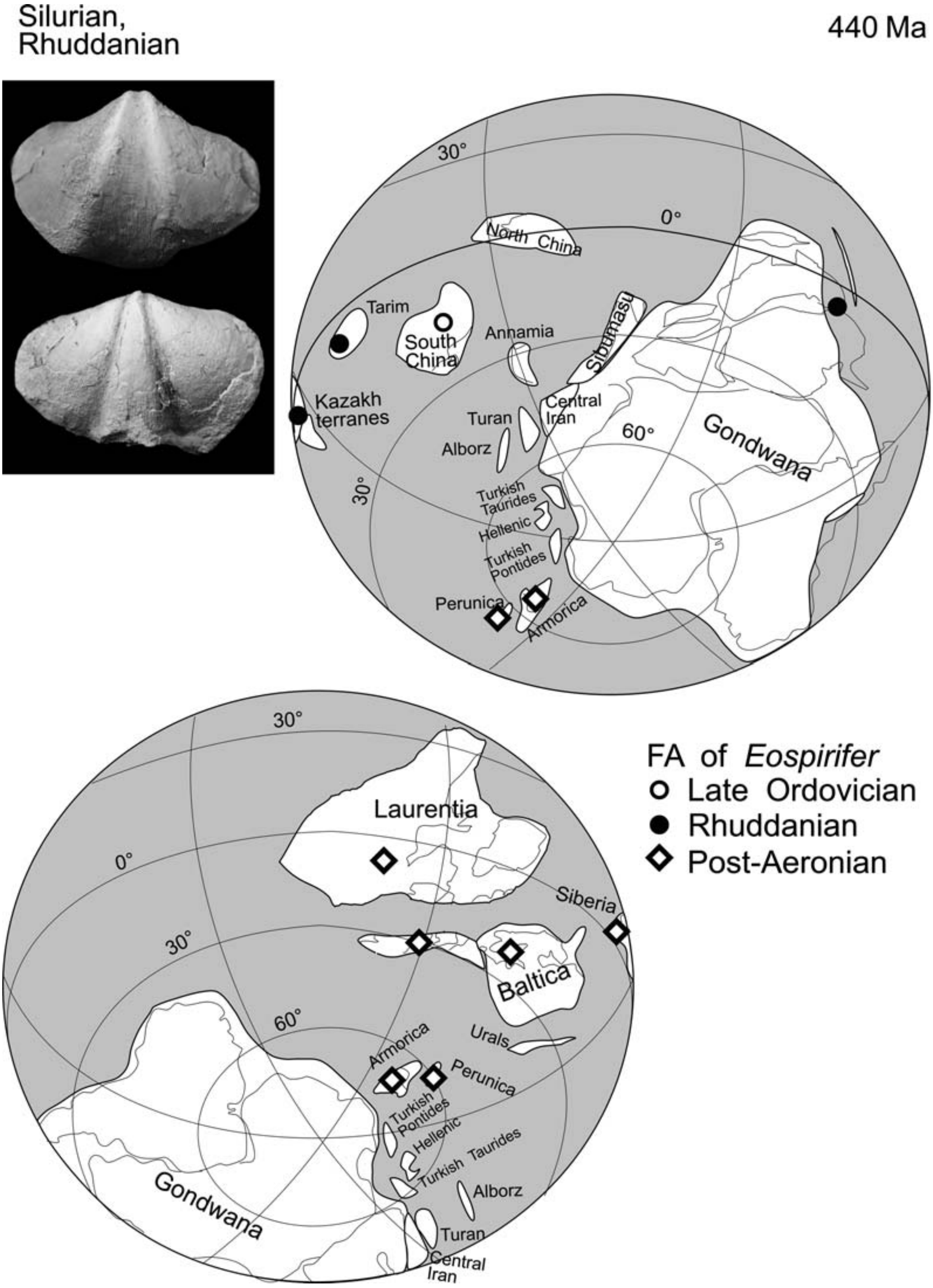

Fig. 20. Global reconstruction of early Silurian (Rhuddanian) palaeogeography showing diachronous first appearance (FA) of *Eospirifer* on shelves of major early Palaeozoic continents.

some time in the late Silurian. Palaeomagnetic data published by Bazhenov *et al.* (2003) suggest that during the Mid- and Late Ordovician the North Tien Shan plate maintained its position in southern subequatorial latitudes without significant latitudinal drift, which is in good agreement with the inferred position of Chu–Ili at that time.

All existing data discussed above suggest that during its entire Ordovician history the Chu–Ili terrane was in relative proximity to the North Tien Shan plate, and there is no evidence that the Zhalair–Naiman suture originated along an early Palaeozoic inter-oceanic transform fault as shown by Kheraskova *et al.* (2003). The most probable alternative is that the Zhalair–Naiman basin was a marginal sea of North Tien Shan, which originated via back-arc spreading and separation of the Chu–Ili terrane some time in the Mid-Cambrian, so that Chu–Ili therefore represents a Japan-type active margin of the North Tien Shan microplate. From the Mid-Ordovician, extensive island arc volcanism became evident along the North Tien Shan margin facing the Zhalair–Naiman basin, and a double volcanic arc had evolved. This model of evolution of the Zhalair–Naiman basin was presented by Şengör & Natal'in (1996), but with one important difference: the polarity of subduction and migration of the magmatic front as inferred here is opposite to that presented in the Kipchak Arc model.

Island arc volcanism and subduction along the Chu–Ili 'western' margin terminated at the beginning of the Late Ordovician following the accretion of a terrane of uncertain origin, corresponding mainly to the Mynaral–South Dzhungaria tectonofacies zone of Nikitin (1994). Some time in the Late Ordovician to Llandovery, the Chu–Ili active margin was reconfigured and the magmatic front migrated towards the newly established subduction zone, in a direction opposite to that predicted by the Şengör & Natal'in (1996) model (Figs 1a & 3). Island arc volcanism and subduction lasted, with only a brief interruption some time in the late Silurian, for an additional 40 Ma until docking with the Atasu–Zhamshi terrane took place (Abdullin *et al.* 1980; Koren *et al.* 2003).

The long history of island arc volcanism and subduction, covering almost 70 Ma, and the continuous sedimentation of radiolarian cherts for 35 Ma together suggest that the Chu–Ili accretionary wedge faced a major oceanic suture. Indeed, ophiolitic assemblages that include Late Cambrian to Middle Ordovician cherts, with mafic and ultramafic volcanic and intrusive rocks, are traceable almost continuously within the so-called Ermentau–Burultas tectonofacies zone (Nikitin 1994; equivalent to the Ermentau–Chu–Ili tectonofacies zone of Apollonov 2000) across Kazakhastan from the Ermentau Mountans in the north to Lake Balkhash and further south in the subsurface to the town of Kolshengil (Tolmacheva *et al.* 2004; Degtyarev & Ryazantsev 2007, fig. 1). These ophiolites cannot be considered as remnants of an early Palaeozoic marginal basin, as suggested by Degtyarev & Ryazantsev (2007). The existence of this vanished early Palaeozoic ocean, with island arc volcanism and associated accretion along its margins, continued until at least the mid-Devonian and probably later, which is strong argument against the stabilization of 'Kazakhstania' as a plate-tectonic unit by the end of the Ordovician (Filippova *et al.* 2001; Bykadorov *et al.* 2003).

Karatau–Naryn terrane

As defined here, the Karatau–Naryn terrane (Fig. 1) includes the southern part of the Valerianov–Chatkal unit and at least a southern portion of the Bailkonur–Talas Unit of Şengör & Natal'in (1996). It occupies a marginal position in the Altaid collage. Biogeographical and sedimentological data from the Karatau–Naryn terrane are important for evaluation of the Kypchak Arc model; this arc, according to Şengör & Natal'in (1996), must have been in proximity to Baltica through the early Palaeozoic.

The Cambrian to Early Ordovician palaeontology and carbonate sedimentology of that region, and especially of the Malyi Karatau Range, is known from much better data than in other parts of Kazakhstan (Eganov & Sovetov 1979; Abdullin & Chakabaev 1984; Abdullin *et al.* 1986, 1990; Cook *et al.* 1991). The Valerianov–Chatkal and Bailkonur–Talas units of Şengör and Natal'in (1996) certainly represent neotectonic units separated by the Karatau and Talas–Fergana strike-slip fault. As demonstrated by Allen *et al.* (2001), the history of reactivation of strike-slip-dominated tectonics within the Karatau fault system is traceable as early as the Neoproterozoic. There is also no convincing evidence of the existence of low-angle Palaeozoic thrust faults in Bolshoi Karatau as depicted in some maps (e.g. Afonichev & Vlasov 1981). According to Allen *et al.* (2001, p. 90), such a model is based mostly on the misinterpretation of Late Palaeozoic sedimentary conglomerates and Mesozoic karstic breccias as being of tectonic origin. These data suggest that Precambrian rocks exposed in Malyi and Bolshoi Karatau more probably form the basement of a single early Palaeozoic tectonic unit, the Karatau–Naryn crustal terrane, whose present boundaries are concealed in the Syr–Dariya, South Turgai and Chu–Sarysu depressions, which represent major sedimentary basins. The southern and partly western boundary coincide with a late Palaeozoic suture (Chatkal and South Fergana sutures after Biske (1996) or the Turkestan suture after Burtman (2006, fig. 2.1)); this remains exposed in the Kurama and Chatkal ranges (Central Tien Shan).

The most comprehensive outlines of Palaeozoic geology of the area are by Biske (1995, 1996) and Burtman (2006), who recognized two major episodes of volcanic activity, in the early Devonian and in the mid-Carboniferous–Permian. The eastern boundary of the Karatau–Naryn terrane is concealed in the subsurface in the Chu–Sarysu depression, where it probably coincides with the Sarykemir complex of ultramafic intrusive rocks that can be traced for more then 100 km via geophysical data (Fig. 2; see also Sargaskaev in Esenov *et al.* 1971). Farther to the SE it is recognized as a suture that originated by the end of the Ordovician after amalgamation with the North Tien Shan microcontinent (the Terskei oceanic suture after Burtman 2006). Mikolaichuk *et al.* (1997) reported the development of an Andean-type magmatic arc on the opposite, southwestern margin (present coordinates) of the North Tien Shan microcontinent between the late Darriwilian and the end of the Ordovician. This incorporated allochthonous thrust sheets comprising Ediacarian to Early Ordovician carbonates derived from the Karatau–Naryn microcontinent, and extensive Late Ordovician to early Silurian granitic magmatism resulted in the formation of the Karakurgur complex of intrusive rocks with ^{206}Pb/^{238}U ages varying from 466 to 438 Ma. The belt of granitic plutons of presumed Palaeozoic age, referred to the Talas and Keskenter complexes, is also traceable via geophysical data in the subsurface of the Chu–Sarysu depression (Fig. 2; see also Sargaskaev in Esenov *et al.* 1971). A northern extension of the Karatau–Naryn terrane cannot be defined at present because little is known of the Early Palaeozoic geology of the 'Turgai Unit' of Şengör & Natal'in (1996), and also because Palaeozoic and probable Precambrian rocks of that region are masked below a thick cover of Mesozoic and Cenozoic deposits. There is also no convincing evidence that the Ulutau–Baikonur region, with its Precambrian and early Palaeozoic rocks, belongs to the same early Palaeozoic tectonic unit as suggested by Şengör & Natal'in (1996).

Aisha–Bibi seamount and its palaeogeographical significance

A unique feature of the Karatau–Naryn terrane among other Kazakhstanian Palaeozoic tectonic units was the extensive deposition of carbonates through two intervals, in the Cambrian to mid-Ordovician and in the late Devonian to early Carboniferous, and there was also extensive deposition of phosphorites in the early half of the Early Cambrian (Figs 21–23).

Cambrian to Middle Ordovician carbonates have been best studied in the Malyi Karatau Range, where they can be traced almost continuously from the Baba-Ata river in the NW to the town of Karatau in the SE (Figs 22–24). Detailed accounts of the Lower Palaeozoic geology, stratigraphy, sedimentology and palaeontology have been given in numerous publications (e.g. Missarzhevsky & Mambetov 1973; Ergaliev & Pokrovskaya 1977; Eganov & Sovetov 1979; Ergaliev 1980; Apollonov & Chugaeva 1983; Cook *et al.* 1991; Mambetov 1993; Dubinina 2001; Holmer *et al.* 2001; and references in these papers). Allen *et al.* (2001) published a most valuable summary of the deformation history of the region. There is evidence of compressional deformation some time in the late Ordovician (Alexeiev & Kraev 1991; Alexeiev 1998), but major tectonic deformation in the region did not occur until the late Carboniferous. There is no strong thermal alteration of carbonate rocks; conodont alteration indices are low and do not exceed CAI 1–2 (Apollonov *et al.* 1988). As with Lower Palaeozoic strata in Malyi Karatau, notwithstanding the existence of several relatively low-magnitude thrust faults, the units are not dislocated strongly tectonically and relationships between major lithostratigraphical units can be traced with a good degree of confidence.

The lowermost fossiliferous Cambrian lithostratigraphical unit recognized in Malyi Karatau is the Kyrshabakty Formation, which discontinuously overlies Precambrian rocks of the Malakaroi Group (Eganov & Sovetov 1979) and comprises siliciclastic deposits with some units of glauconitic sandstone and dolomite with a total thickness up to 160 m (Figs 23 & 24). According to Mambetov (1993), a low-diversity assemblage of anabaritids and the protoconodonts *Protohertzina anabarica* Missarzhevsky and *P. unguliformis* Missarzhevsky are present already in the basal dolomitic conglomerate. These are indicative of the *P. anabarica* Biozone characteristic of the Nemakit–Daldynian (= Manykaian) Stage of Siberia and the Jinningian Stage (*Anabarites–Protohertzina* Biozone) of South China (Peng 2003). A diverse assemblage of small shelly fossils also referred to the *P. anabarica* Biozone occurs in a bed of stromatolitic dolomite up to 12 m thick at the top of the Kyrshabakty Formation, known also as the the 'Lower Dolomite' or Berkuty Formation or Member; in some studies (Eganov & Sovetov 1979; Abdullin *et al.* 1990) this has been considered as the basal unit of the Chulaktau Formation.

Detailed analyses of the Chulaktau Formation have been given by Ergaliev & Pokrovskaya (1977), Eganov & Sovetov (1979) and Mambetov

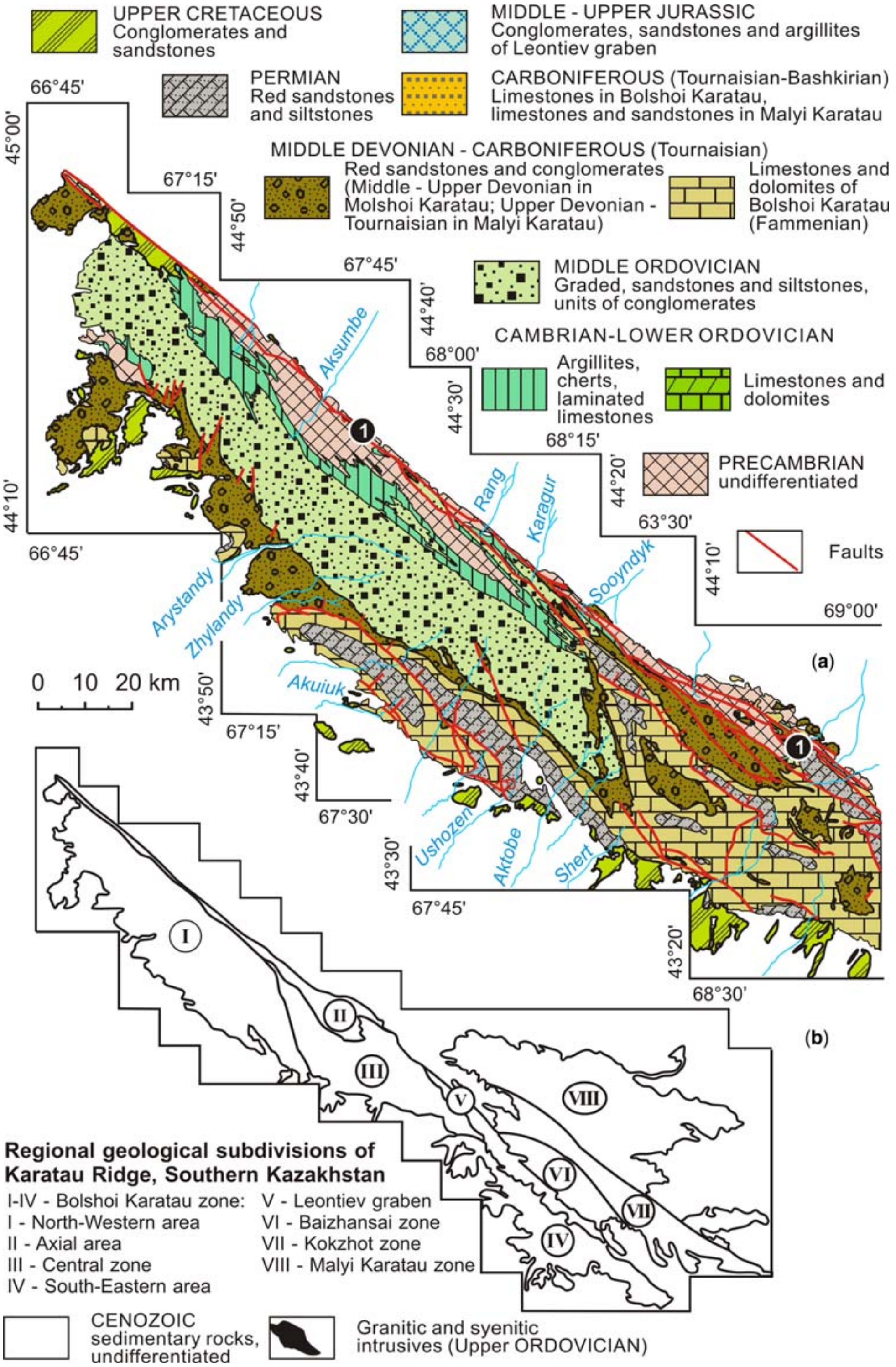

Fig. 21. Geological map of the Bolshoi Karatau Range (**a**), and schematic map (**b**) showing first-order Palaeozoic tectonic units of the Bolshoi and Malyi Karatau ranges. In (a), 1 indicates Karatau and Talas–Fergana strike-slip fault (modified from Allen *et al.* 2001).

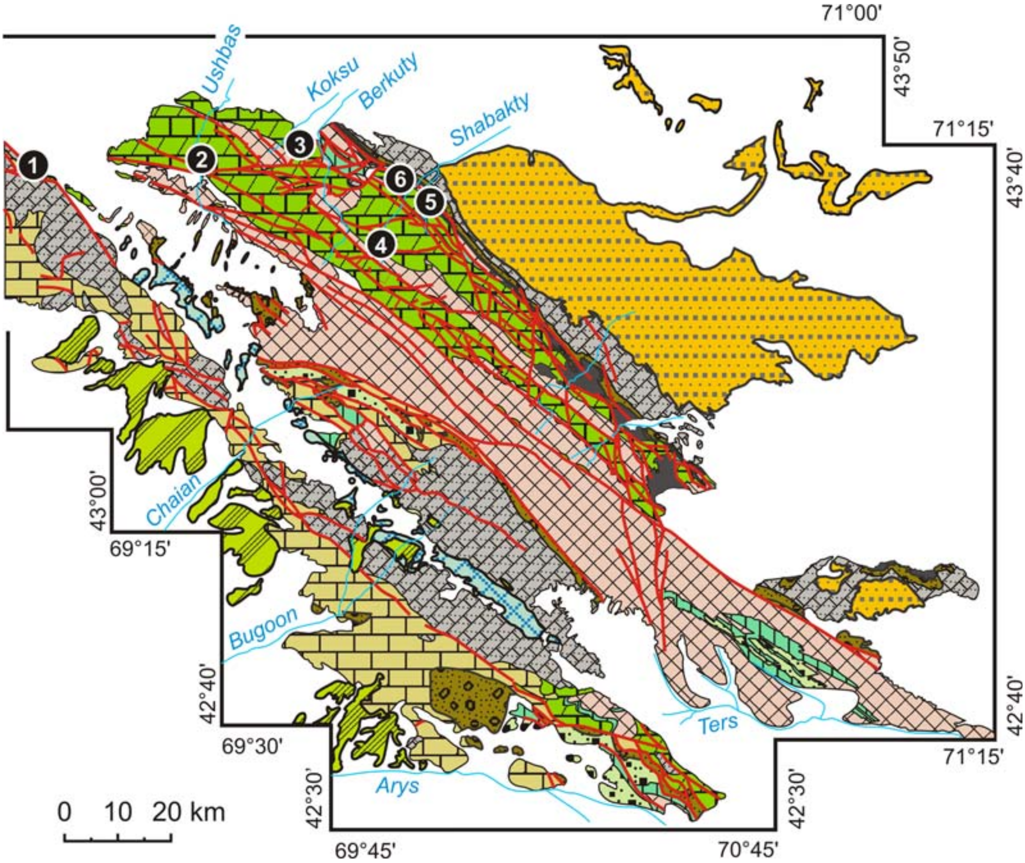

Fig. 22. Geological map of the Malyi Karatau Range; legend as for Figure 21. 1, Karatau and Talas–Fergana strike-slip fault; 2, Ushbas river; 3, east side of Koksu river; 4, Aktogai River; 5, Kyrshabakty section; 6, Batyrbai section (modified from Allen *et al.* 2001).

(1993). This unit discontinuously overlies the Berkuty Member of the Kyrshabakty Formation (Eganov & Sovetov 1979, p. 72). Traditionally the Chulaktau Formation is subdivided into three formal units: the Aksai Member, a bedded chert intercalated with thin beds of argillite and phosphorite, up to 20 m thick; the Karatau Member, comprising ‘lower’ and ‘upper’ phosphoritic beds separated by a unit of argillite and chert, which is about 20 m in total, but may be up to 40 m thick in some sections; the Ushbas Member, comprising a basal bed of conglomerate with a ferromanganese dolomitic matrix and an overlying bed of stromatolitic dolomite, varying from 2 to 5 m in thickness. A Tommotian age of the unit is confirmed by diverse assemblages of small shelly fossils, which belong to the successive *Tiksitheca licis*, *Pseudorthotheca costata* and *Bercutia cristata* biozones (Mambetov 1993).

The overlying carbonate sequence is referred to the Shabakty Group (Figs 23 & 24), of which the lowermost unit is the Dzhylandy Formation, comprising mostly massive dolomites with stromatolitic structures and some units of argillaceous dolomitic limestones up to 250 m thick (Eganov & Sovetov 1979), deposited in shallow marine environments (Cook *et al.* 1991). Missarzhevsky (in Rozanov 1984) and Mambetov (1993) pointed out that the late Atdabanian *Rhombicorniculum cancellatum* Biozone is present only in the Zhaanaryk and Taldybulak members from the northeastern part of the Malyi Karatau Range, whereas the uppermost Geres Member, with a faunal assemblage characteristic of the Botomian *Microcornus parvulus* Biozone, discontinuously overlies the Chulaktau Formation in the SW. Overlying trilobite-bearing Lower Cambrian strata were subdivided by Ergaliev & Pokrovskaya (1977) into the *Hebidiscus*

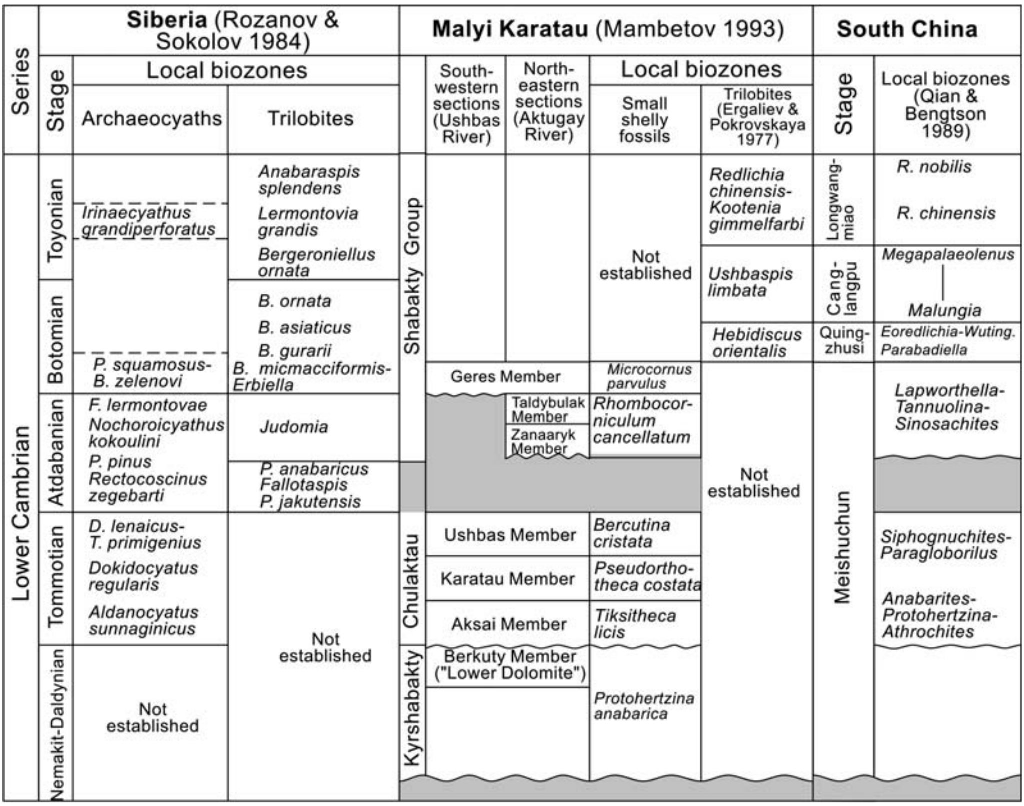

Fig. 23. Lower Cambrian lithostratigraphical and biostratigraphical subdivisions in Malyi Karatau correlated with sequences of Siberia and South China (modified from Holmer *et al.* 2001).

orientalis, *Ushbaspis limbata* and *Redlichia chinensis–Kootenia gimmelfarbi* local trilobite biozones (Fig. 23).

The Early to Mid-Cambrian transition coincides with a significant tectonic reorganization of the northeastern margin (present coordinates) of the Karatau–Naryn terrane, and from that time carbonate sedimentation within the Malyi Karatau Range was controlled by the rifted boundaries of a passive continental margin. From the beginning of the Mid-Cambrian, carbonate deposition took place on an isolated seamount (Fig. 25; the Aisha–Bibi seamount of Cook *et al.* 1991). However, this sequence does not represent carbonate mounds above volcanic rocks as interpreted by Fortey & Cocks (2003, p. 287). The central, flat-topped part of the Aisha–Bibi seamount, corresponding to the Bolshekaroi and Malokaroi blocks (Figs 21 and 22), was flooded by a shallow sea. Significant subsidence of the seaward margins surrounding the mount resulted in the deposition of shallowing-upward and seaward-prograding sequences characteristic of a basin plain and submarine carbonate fan, replaced in the upper levels by lagoonal lithofacies of the seamount interior, which accumulated without significant siliciclastic input during relative separation of significant landmasses (Cook *et al.* 1991). Basinal deposits comprising black argillites, cherts and deep-water carbonates were characteristic of Bolshoi Karatau to the SW, and can be traced also towards the Chu–Sarysu depression in the NE. Carbonate sedimentation in Malyi Karatau was terminated by the Late Ordovician. Folding in Malyi Karatau reported by Allen *et al.* (2001), together with the development of thrust faulting (Alexeiev 1997), may reflect remote collision with the North Tien Shan microcontinent (Mikolaichuk *et al.* 1997). However, the ancient topography of the early Palaeozoic carbonate platform and original distribution of lithofacies belts remains relatively well preserved (Zhemchuzhnikov, unpubl. data; see also Burtman 2006, p. 27).

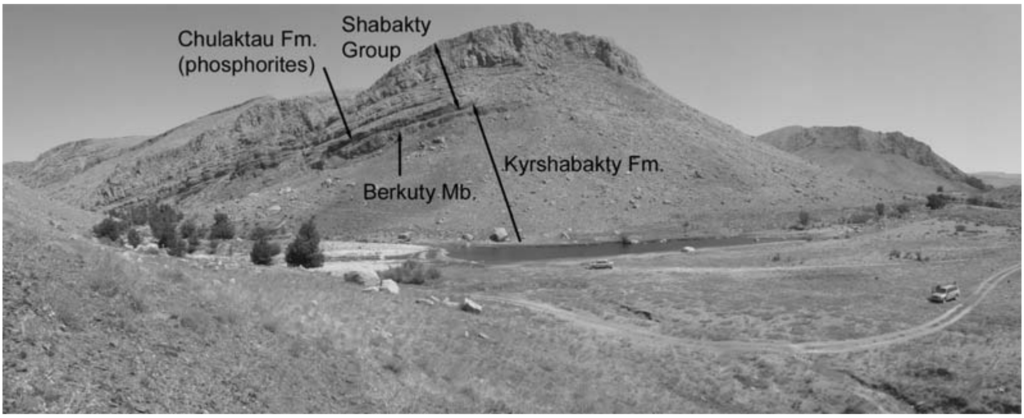

Fig. 24. Aktogai River section, exposing Lower Cambrian deposits of the Kyrshabakty and Chulaktau formations, and the lower part of the Shabakty Group (Dzhylandy Formation, comprising intertidal dolomites). Photograph by V. Zhemchuzhnikov.

Biogeographical and sedimentological signatures of the Karatau–Naryn terrane, and implications for inferred early Palaeozoic geological history

The characteristics of Cambrian carbonate sedimentation in the Malyi Karatau Range contrast markedly with the predominantly siliciclastic shallow marine sedimentation in Baltica, as documented in particular for Baltoscandia (Martinsson 1974; Popov *et al.* 1989) and Novaya Zemlya (Soloviyev 1988, and references therein). As demonstrated recently by Kuznetsov (2005), Lower Cambrian archaeocyath-bearing limestones reported from the South Urals are alien to Baltica; they are preserved as olistoliths incorporated in tectonic mélange only in the Late Palaeozoic. Moreover, palaeomagnetic (Torsvik & Rehnström 2001) and sedimentological data (Cherns & Wheeley 2009) suggest a location of Baltica in temperate to high latitudes through the Cambrian to early Ordovician, whereas the extensive carbonate sedimentation including dolomites, stromatolitic and oolitic limestones that accumulated on the Aisha–Bibi seamount point to a location in low latitudes. This makes the position of the Karatau–Naryn terrane unlikely to be near the margins of Baltica in the Ediacarian–Early Cambrian as predicted in the Şengör & Natal'in model (1996, figs 21, 27 and 28). On the other hand, as pointed out earlier by Rozanov (in Rozanov & Sokolov 1984), the Ediacarian to Lower Cambrian sequences of Malyi Karatau and South China show distinct similarities in characters of sedimentation, in the stratigraphical position of phosphorite and dolomite beds, and in the levels of major discontinuities.

Because of the state of taxonomy, any attempt to establish biogeographical affinities based on small shelly fossils are highly speculative (Bengtson *et al.* 1990). However, the close affinity of Early Cambrian brachiopod and trilobite faunas of Malyi Karatau and South China is well established. The trilobites of Malyi Karatau described by Ergaliev & Pokrovskaya (1977) belong to the typical *Redlichia* fauna, which is characteristic also of South China and the Australian sector of Gondwana (Pillola 1993). The list of common taxa, sometimes down to species level, includes *Redlichia chinensis* Walcott (Fig. 26b), which is widespread in South China (Zhang *et al.* 1980), *Hebediscus orientalis* Chang, known also from the Lower Cambrian Shipai Formation of western Hupei in South China, and *Ushbaspis* Pokrovskaya, 1965 (= *Metaredlichioides* Chien and Yao, in Lu *et al.* 1974), which occurs in both those regions (Fig. 26a). The low-diversity fauna of linguliformean brachiopods also shows affinity with South China down to species level. It comprises mostly cosmopolitan genera, such as *Botsfordia* and *Linnarssonia*, but some species, such as *Palaeobolus liantuoensis* Zeng and *Lingulellotreta malongensis* (Rong), are endemic only for Malyi Karatau and South China (Holmer *et al.* 1997, 2001). The latter species is in the Family Lingulellotretidae, which is unknown outside South China and Malyi Karatau in the Early Cambrian, and from the Mid-Cambrian to Early Ordovician (Tremadocian) it is confined to Malyi Karatau.

Mid-Cambrian to Early Ordovician trilobite and linguliformean brachiopod faunas are relatively well documented, and there is no indication of close faunal affinity to Baltica except in numerous

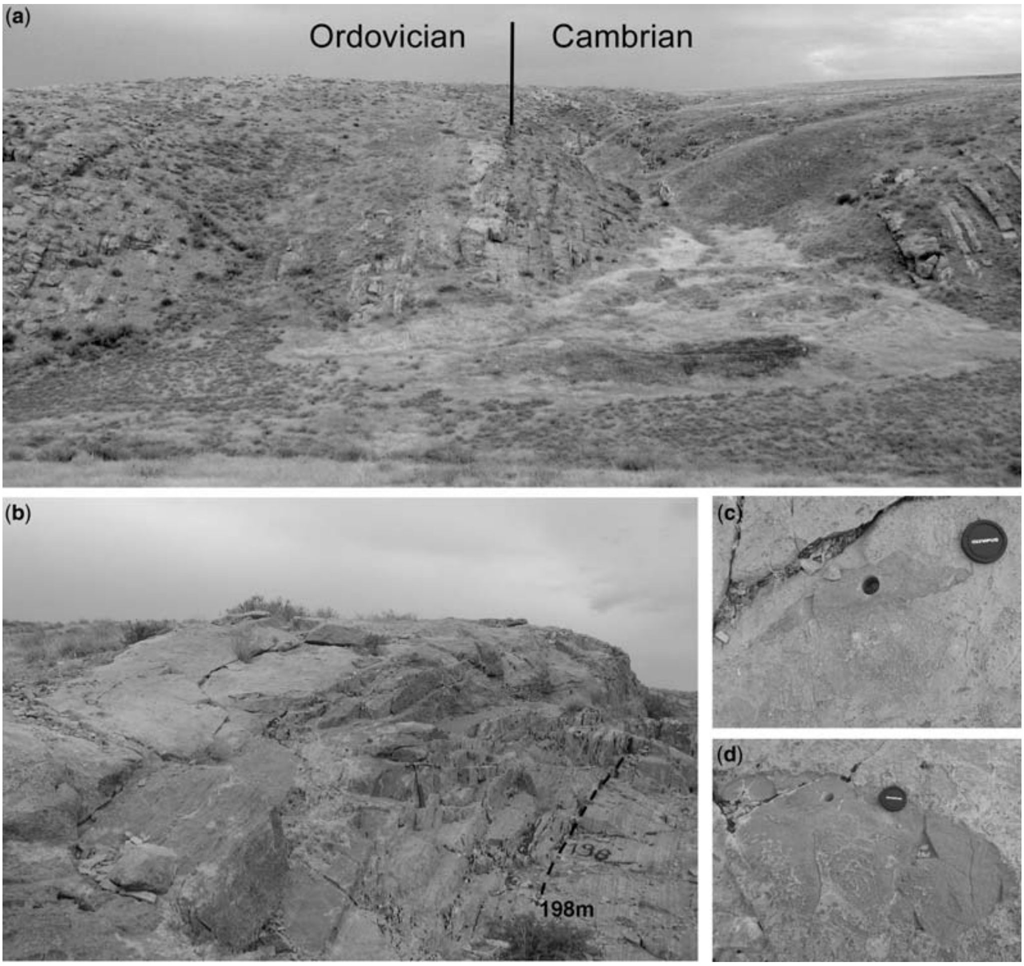

Fig. 25. Batyrbai section in the Malyi Karatau Range (Fig. 22, locality 6). (**a**) Westerly view of Upper Cambrian to Lower Ordovician limestones representing transition from submarine fan to seamount margin lithofacies. (**b**) Position of the Cambrian–Ordovician boundary at 198 m defined by the first occurrence of *Iapetognathus*. (**c**, **d**) Deposits of debris flows with clasts of allochthonous micritic limestone sampled for palaeomagnetic analysis, unrelated to the record from the bedded succession. Photographs by V. Zhemchuzhnukov.

agnostide taxa, which are mostly cosmopolitan and thus do not give a clear biogeographical signature, but serve well for precise biostratigraphical correlation (Ergaliev 1980). As noted by Fortey & Cocks (2003) in their review of south Kazakhstanian trilobite faunas, the Upper Cambrian trilobites of the Kokbulak and Kamal formations in Bolshoi Karatau described by Ergaliev (1983), including such palaeogeographically informative genera as *Charchaqia*, *Promacropyge*, *Lophosaukia* and *Amzasskiella*, closely resemble the fauna of eastern Tien Shan described by Troedsson (1937), and also relate closely to the marginal faunas characteristic of outer shelf biofacies in South China. A closely similar assemblage is known also from the Upper Cambrian (*Hedinaspis sulcata* and *Lophosaukia* beds) of Malyi Karatau (Apollonov & Chugaeva 1983). According to Peng *et al.* (1999), *Taoyuania*, as described originally from South China and also reported from the Upper Cambrian of the Alborz Mountains in Iran, is a senior synonym of *Batyraspis* described by Apollonov & Chugaeva (1983) from the uppermost Cambrian of Malyi Karatau. The list of common trilobite genera endemic for the Karatau–Naryn terrane and South China in the Late Cambrian also includes *Acutatagnostus*, *Ivshinagnostus*, *Acrocephalospina*, *Karataspis* and *Probilacunaspis* (Ergaliev 1980; Peng 1992).

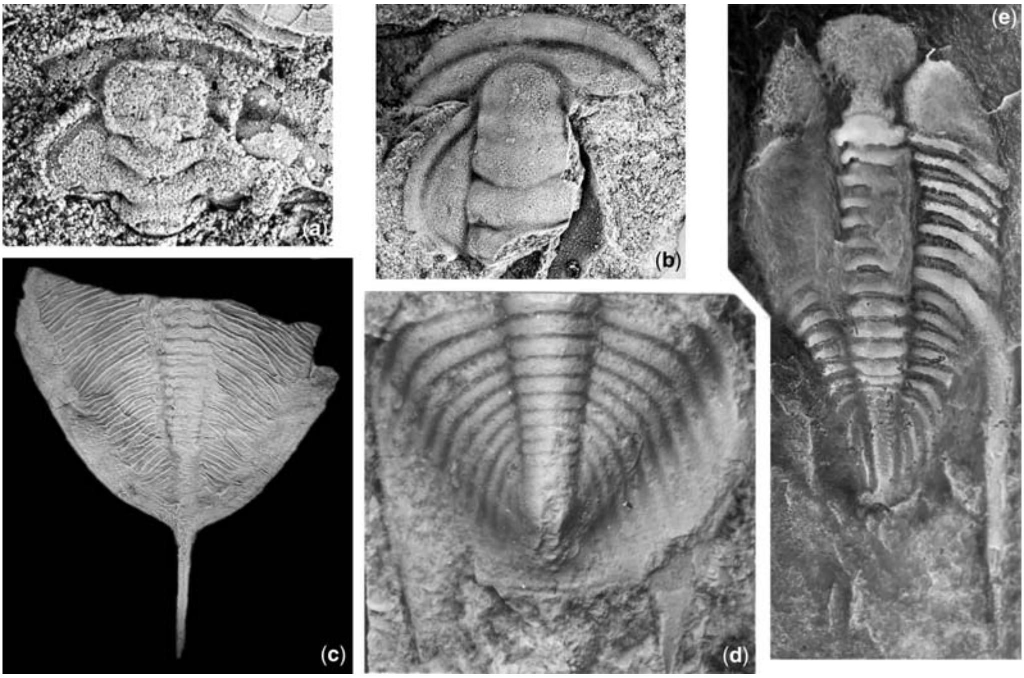

Fig. 26. Selected biogeographically informative Cambrian and Ordovician trilobites from southern Kazakhstan. (**a**) *Ushbaspis limbata*, NMW 2008.3G.2, cranidium, ×6.5, Lower Cambrian, Botomian, *U. limbata* Biozone, locality 1225 (Ergaliev & Pokrovskaya 1977, fig. 2), east side of Ushbas River, Malyi Karatau Range (Fig. 22, locality 2). (**b**) *R. chinensis*, NMW 2008.3G.3, cranidium, ×3, Lower Cambrian, Toyonian, *R. chinensis–Kootenia gimmelfarbi* Biozone, locality 1425 (Ergaliev & Pokrovskaya 1977, fig. 5), Akzhar phosphorite quarry, east side of Koksu River, Malyi Karatau Range (Fig. 22, locality 3). (**c**) *Lisogorites striatus*, NMW 2008.3G.4, pygidium, ×1.2, latex cast of exterior, Middle Ordovician, lower Darriwilian, Uzunbulak Formation, sample 145 (Nikitina *et al.* 2006), east side of Kopalysai, Chu–Ili Range (Fig. 3, locality 18). (**d**) *Taihungshania* sp., NMW 2008.3G.5, pygidium, ×4.3, Lower Ordovician, Floian, Batyrbai, Malyi Karatau (Fig. 22, locality 6). (**e**) *Koksorenus weberi*, CNIGR 60/4263, lectotype, incomplete exoskeleton, latex cast, ×3.6, Upper Ordovician, lower Katian, Besharyk (= Ichkebash) Formation, Dzhebagly Mountains. NMW, National Museum of Wales; CNIGR, Tschernyshew Museum, VSEGEI, St Petersburg.

In the late Early Ordovician (*Oepikodus evae* Biozone), affinity to South China can be illustrated by the occurrences of *Taihungshania* (Fig. 26b) and *Pseudocalymene*, which appear at about the same level in the lower Dawan Formation (Lu 1975; Bruton *et al.* 2004). Both genera are known also in contemporaneous or slightly older deposits in the Alborz and Central Iran (Bruton *et al.* 2004; Ghobadi Pour *et al.* 2007; Turvey 2007), but have never been found in any Kazakhstanian terranes. The only published source on Middle Ordovician faunas of the Karatau–Naryn terrane is the study by Weber (1948), who described a medium-diversity trilobite assemblage from the upper part of the Shabakty Series ('Tamdy Beds'). This small fauna includes mostly endemic species (e.g. '*Apatokephalus' assai* Weber, '*Histricurus' binodatus* Weber, *Ilaenus talasicus* Weber, *Lyralichas bronnikovi* Weber, *Pseudosphaerexohus asper* Weber), but some of the original generic identifications require revision and the data cannot be applied currently with confidence in biogeographical analysis.

Ordovician faunas of Bolshoi Karatau and their affinities

In the Early to Mid-Ordovician, most of Bolshoi Karatau was in a relatively deep-water environment, with predominant accumulation of fine clastic sediments and some units of siliceous shales and cherts with graptolites (Esenov *et al.* 1971; Nikitin 1972, 1991). Only in the Late Ordovician is there a record of low- to medium-diversity shallow shelf faunas, as reported by Kolova (1936) and Misius (1986). Both the trilobite and brachiopod taxa require revision, but by the Late Ordovician an affinity to faunal assemblages in other Kazakhstanian terranes, and especially Chu–Ili, becomes more evident. In particular, the strophomenide brachiopod *Dzhebaglina* was endemic to Karatau–Naryn and Chu–Ili, whereas the trilobites *Birmanites*, *Bulbaspis* and *Koksorenus* (Fig. 26e) were widespread in Kazakhstan, Tarim and South China and are considered to be 'East Gondwanan' (Fortey & Cocks 2003). There are also some features suggesting relative isolation. The early atrypide brachiopod *Nuria* is probably a local endemic and there is no record of the occurrence of *Sulcatospira* and *Sachriomonia*, which are relatively common in the Katian Stage of other Kazakhstanian terranes including the Chingiz–Tarbagatai region and the Chu–Ili terrane, and also South China. *Sulcatospira* (= *Kuzgunia* of Misius 1986) is also present in the North Tien Shan microplate. There is no sedimentary record preserved in the Karatau–Naryn terrane for the Silurian–Early Devonian, and by the time of resumed extensive carbonate sedimentation in the Mid-Devonian–Early Carboniferous it was no longer a separate tectonic unit, but was amalgamated with a group of southern Kazakhstanian terranes (Burtman 2006).

Reconciliation of Early Palaeozoic biogeography and plate-tectonic history of southern Kazakhstanian terranes

Major constraints

As currently understood, existing data on Early Palaeozoic faunas, depositional history, magmatism and plutonism of southern Kazakhstanian terranes and elsewhere within the Kazakhstanian orogen are of markedly varying quality and commonly lack precision. There are significant gaps in knowledge; for example, of Cambrian faunas of the Chu–Ili and North Tien Shan microplates, and of Mid- to Late Ordovician faunas of Karatau–Naryn. Ordovician faunas of North Tien Shan require substantial revision. In contrast, however, data on conodont biostratigraphy of early Palaeozoic ophiolites incorporated into the accretionary wedge of the Chu–Ili terrane (Tolmacheva *et al.* 2001, 2004) are unique in their completeness and have no analogies in other studies of early Palaeozoic ophiolites. Current data suggest that southern Kazakhstanian terranes were amalgamated by the Late Silurian, with the North Tien Shan microplate sandwiched between Chu–Ili and Karatau–Naryn and probably representing a 'host nucleus' (*sensu* Şengör & Natal'in 1996).

According to Mikolaichuk *et al.* (1997), who have given the most detailed available account of the early Palaeozoic geological evolution of North Tien Shan, its southwestern margin (present coordinates) faced a major ocean, and its geological history as a plate-tectonic unit can be traced possibly from the Ediacarian–Early Cambrian. Cambrian biostratigraphy of North Tien Shan relies mainly on sporadic occurrences of conodonts and linguliformean brachiopods (Mikolaichuk *et al.* 1997); however, with a few exceptions many data remain unpublished, and Cambrian trilobite and rhynchonelliformean brachiopod faunas are completely unknown. Thus a peri-Gondwanan origin of the North Tien Shan microplate cannot yet be confirmed, but its Mid- to Late Ordovician brachiopod faunas show strong affinities with those of low-latitude peri-Gondwana, and especially those of the Chu–Ili terrane, South China and Australia (Misius 1986; Nikitin *et al.* 2006).

The Karatau–Naryn terrane was probably a part of South China at the beginning of the Palaeozoic, and probably rifted shortly before the Mid-Cambrian (Holmer *et al.* 2001); its links with contemporaneous faunas of South China remained strong until the Late Ordovician. Then it occupied a marginal position relative to other Kazakhstanian terranes, probably southwards of the Chu–Ili and North Tien Shan microplates, and its Late Cambrian to Early Ordovician faunas include some genera characteristic of temperate-latitude Gondwana, which are missing in other Kazakhstanian faunas. Therefore, if the Chu–Ili and North Tien Shan microplates originated via the break-up of the Gondwanan margin, the source area was probably north of the South China continent. Alternatively, they may have been derived from the break-up of the North China or Tarim microplates, but in the absence of firm faunal evidence and reliable geochemical signatures the entire Cambrian history of these two early Palaeozoic tectonic units remains uncertain.

Mid- to Late Ordovician faunas of Chu–Ili, Karatau–Naryn, North Tien Shan and other parts of Kazakhstan show distinct affinity with those of equatorial peri-Gondwana, and in particular South and North China and the Australian sector of Gondwana (Nikitin *et al.* 2006). There was a clear distinction from contemporaneous Baltic faunas and there were no links with Siberian faunas. As yet incomplete existing faunal and sedimentological data for the early Palaeozoic suggest that a Siberian or Baltic source for the cluster of early Palaeozoic south Kazakhstanian terranes is improbable.

Another conclusion is that the polarity of at least some Kazakhstanian volcanic arcs (in particular, Chu–Ili and North Tien Shan), and the migration of magmatic fronts during the Ordovician–Silurian, are in an opposite direction to that predicted by the Kypchak Arc model (Fig. 1).

Relation to other Kazakhstanian terranes

The evidence of former oceanic separation between the western and eastern groups of Kazakhstanian terranes, along the belt identified by Nikitin (1994) as the Ermentau–Burultas tectonofacies zone, suggests that the source and Early Palaeozoic history of terranes to the eastern side of that suture were distinct from those of the southern cluster of early Palaeozoic Kazakhstanian terranes outlined in this paper. Indeed, with the exception of the Atasu–Zhamshy terrane of Apollonov (2000; equivalent to the Atasu–Mointy unit of Şengör & Natal'in 1996; and Aktau–Mointy unit of Kheraskova *et al.* 2003), which in the Cambrian–Ordovician was a carbonate platform formed on Precambrian basement, the eastern part of Kazakhstan represents a collage of remnants of a number of early Palaeozoic island arcs developed either on oceanic crust or on a heterogenous basement (for summary see Windley *et al.* 2007). The Late Ordovician brachiopod and trilobite faunas of these terranes have strong equatorial peri-Gondwanan signatures (Fortey & Cocks 2003; Nikitin *et al.* 2006), but this does not necessarily imply a peri-Gondwanan origin. Cambrian to early Ordovician brachiopod and trilobite faunas of these terranes have not yet been subjected to detailed biogeographical analysis, although there are clear indications that some of these arcs may have been derived from the detached eastern Cambrian active margin of Baltica (Sturesson *et al.* 2005). In particular, in the Mamat Formation of the Chingiz Range Fortey & Cocks (2003) identified the presence of taxa that imply a close comparison with Baltica, including *Ceratopyge forficula*, '*Protopliomerops*' *speciosa* and a *Niobe* species of Scandinavian type. Popov & Holmer (1994) demonstrated the close affinity of Early Ordovician brachiopod faunas from the Boshchekul region of northeastern Central Kazakhstan with contemporaneous faunas of the Southern Urals.

This mosaic of island arc and continental fragments also included ophiolites dated from the Neoproterozoic to the Early Silurian, associated with sutures, and often strongly reworked since the Early Palaeozoic (Antonyuk 1977; Stepanets 1990; Yakubchuk 1990; Degtyarev *et al.* 1995; Stepanets *et al.* 1998; Degtyarev 1999). The Late Cambrian to Ordovician ophiolites usually contain units of radiolarian cherts, jaspers and siliceous shales with conodonts (for summary see Nikitin 1994), which potentially allows fairly precise age constraints for their formation and time of obduction. Most of these ophiolitic complexes are considered as suprasubductional (Stepanets 1990; Yakubchuk 1990) and there is no good published evidence that some of them were derived from hotspots or as a result of ridge–trench interactions. The inconsistency of these interpretations in relation to possible modern analogues of the Kazakhstanian orogen in the circum-Pacific was pointed out recently by Windley *et al.* (2007).

Another group of early Palaeozoic terranes that require special attention are those of north–central Kazakhstan; for example, the Kalmyk Kol–Kokchetav unit of Şengör & Natal'in (1996) or Shatsk and Kokchetav microplates of Dobretsov *et al.* (2006) and adjacent island arcs (Fig. 1). In various plate-tectonic models they are considered either as separate Early Palaeozoic microplates (Kheraskova *et al.* 2003; Dobretsov *et al.* 2006) or as an integral part of a larger microcontinent that also included North Tien Shan (Apollonov 2000). A recently published account of the Neoproterozoic to Early Palaeozoic history of this north–central sector of the Kazakhstanian orogen (Dobretsov *et al.* 2006) gives sufficient proof that at least by the late Ordovician the various independent Early Palaeozoic units did not interact with the south Kazakhstanian cluster of terranes, based on different polarities of the surrounding Selety and Ishim and Stepnyak volcanic arcs, the duration of island arc volcanism, and the dating of major accretionary events. The Kokchetav microplate is usually considered as being of Gondwanan origin, except by Şengör & Natal'in (1996, figs 21 and 28), who placed it within the Siberian margin in the Ediacarian. It is thus important to note that the brachiopod assemblage from the Middle Ordovician (upper Darriwilian) Andryushino Formation of the Ishim Region (early Palaeozoic Ishim volcanic arc of Dobretsov *et al.* 2006) contains *Ishimia* and *Shlygina*, which are known otherwise mainly from subequatorial peri-Gondwana (Nikitin & Popov 1983, 1985; Fig. 19). Also, the trilobite assemblages contain *Ampyxinella*, *Koksorenus*, *Lisogorites* and *Pliomerina* (Fig. 19), which have a strong Gondwanan signature (Fortey & Cocks 2003). However, there are no good biogeographical or geochemical data that give a reliable link between the Kokchetav microplate and Gondwana, or any other ancient continent, during the Ediacarian to Early Ordovician.

In contrast, Heinhorst *et al.* (2000) noted briefly that gneisses and quartzo-feldspathic schist units of the Kokchetav and adjacent massifs closely resemble those of Baltica, but gave no further supporting discussion. Nevetherless, palaeomagnetic data (Torsvik & Rehnström 2001) indicate that in the Cambrian–early Ordovician, Baltica maintained its position in temperate to high latitudes in close proximity to the North African sector of Gondwana. During that time the oceanic space between equatorial 'East Gondwana' and the eastern margin of Baltica was relatively narrow (Cocks & Torsvik 2002). The Early Palaeozoic history of the eastern Baltica margin is not preserved and thus cannot be reconstructed with any degree of confidence. However, the island arcs obducted onto the Caledonian margin of Baltica in the Early to Mid-Ordovician may represent remnants of the

Cambrian active eastern margin, which then changed polarity of subduction as a result of major tectonic reorganization near the Cambrian–Ordovician boundary, resulting in counterclockwise rotation and rapid northern drift of Baltica in the Ordovician (Torsvik *et al.* 1996), probably involving the origin of a new spreading zone (Sturesson *et al.* 2005). Surprisingly, with the only exception of the model of Şengör & Natal'in (1996), there is no other model of tectonic development of the Kazakhstanian orogen that seriously considers the active eastern margin of Baltica as a probable source of some terranes incorporated into the Altaid collage during the Early Palaeozoic.

Conclusions

The recent review of the evolution of the Kazakhstanian orogen by Windley *et al.* (2007) favoured accretionary models compatible with what is known of circum-Pacific Mesozoic–Cenozoic accretionary orogens. Indeed, the Kypchak Arc model (Şengör *et al.* 1993; Şengör & Natal'in 1996) finds no support from existing data on Ordovician biogeography, which invariably point to strong links with faunas of low-latitude Gondwana for most of the components now incorporated into the Kazakhstanian orogen. The Karatau–Naryn terrane has no sedimentological or faunal links with Baltica in the Early Cambrian. There is also a problem with definition of the polarity of the Early Palaeozoic arcs and direction of migration of the magmatic fronts, at least for the southern cluster of Kazakhstanian terranes.

Also, several recently proposed archipelago-type models (e.g. Mossakovskii *et al.* 1993; Filippova *et al.* 2001; Kheraskova *et al.* 2003) can be considered mainly only as snapshots of the palaeogeographical pattern that emerged during the Late Ordovician–Silurian. Biogeographical data are mostly not considered in all these models, and they do not provide convincing geochemical, biogeographical and sedimentological signatures for an East Gondwanan or Siberian origin of crustal terranes incorporated into the Kazakhstanian orogen. It must be acknowledged, however, that currently inadequate knowledge of Cambrian trilobite and other faunas from most of the early Palaeozoic Kazakhstanian terranes, with the notable exception of the Karatau–Naryn terrane, makes it difficult to apply such data to accurate biogeographical analysis of single tectonic unuts.

There remain considerable unresolved issues with regard to the number and boundaries of first-order Early Palaeozoic units incorporated into the Kazakhstanian orogenic collage, and the age, tectonic setting and nature of emplacement of Early Palaeozoic ophiolites require further study. In many cases, as pointed out, for example, by Windley *et al.* (2007) for ophiolites of the west Jungar region of NW China, situated on a prolongation of the Early Palaeozoic structures developed in the Chingiz and Tarbagatai ranges of Kazakhstan, there are geochemical signatures indicative of an origin in mid-ocean ridges, island arcs and oceanic islands, but almost none have a typical back-arc signature. In contrast, most Kazakhstanian ophiolites are considered as supra-subductional and related to an oceanic core formed in back-arc basins.

Finally, it is important to note that the biogeographical affinities of low-latitude benthic faunas inhabiting Kazakhstanian island arcs and microplates with those of contemporaneous faunas of low-latitude peri-Gondwanan, which are evident in the Late Ordovician, are not always evidence of relative geographical proximity, but a sign of continuity in their geographical distribution. Shallow island shelves of converging island arcs served as 'stepping stones' that allowed benthic faunal assemblages with Gondwanan affinities to spread across significant distances from the Gondwanan margins via narrowing oceanic space. Discontinuity occurred only when oceanic space was sufficiently wide to prevent larval dispersal, because of patterns of oceanic circulation and the limited duration of free swimming stages in planktonic larvae.

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The ‘microcontinent’ Perunica: status and story 15 years after conception

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Abstract: Central Europe consists of a complex mosaic of more or less independent terranes with varying tectonometamorphic histories, usually also of different lithological compositions and protolith, and thus it is reasonable to suppose that the majority of these blocks have experienced somewhat different palaeogeographical evolution. The present terrane juxtaposition has been interpreted in general as a result of the Variscan collision of peri-Gondwanan and peri-Baltic derived terranes, with Gondwana on one side and Baltica and/or Laurentia on the other side. However, reconstruction of the pre-Variscan development and mutual palaeogeographical relationships remains a major challenge of interpretation.

In early Palaeozoic times there was only one supercontinent, Gondwana, and three other major continents, Laurentia, Baltica and Siberia (e.g. Cocks & Torsvik 2002). Numerous smaller but important terranes are supposed to have existed, grouped around the larger continents. The history of Baltica was elaborated in detail by Cocks & Torsvik (2005). The complicated picture of the numerous smaller terranes surrounding Siberia has also been reconstructed recently (Cocks & Torsvik 2007). Similar analyses have been published also for Europe (Cocks 2000, 2002; Cocks & Torsvik 2006) but the complicated geology of southwestern and Central Europe is still a matter of debate (e.g. Robardet 2003), mainly because the poorly defined terranes resulted from the tectonic instability of ‘segments’ incorporated into this area during three major orogenies, the Cadomian, Variscan and Alpine episodes.

For the Variscan orogeny, the decisive role of the Baltic Shield on one margin and Gondwanan Africa on the other side is generally accepted (Fortey & Cocks 2003; but see Landing 2005). However, reconstruction of post-Cadomian and pre-Variscan history of separate European segments is influenced strongly by the reality that both the Variscan and partly also the Alpine orogenies destroyed major parts of the former sedimentary basins, and importantly also altered their relative positions. Consequently, southwestern and central Europe is composed of more or less sharply truncated terranes. Numerous attempts to identify and characterize separate terranes within the Variscan belt, including the Bohemian Massif, have been published (e.g. Franke 1989; Matte *et al.* 1990; Bachtadse *et al.* 1995; Tait *et al.* 1997; Pharaoh 1999; Matte 2001; Winchester *et al.* 2002; Vecoli & Le Hérissé 2004).

In the past 30 years the evaluation of palaeomagnetic data and fossil associations has provided a possibility to establish similarities and differences on a regional scale. Such studies have resulted in the separation and general acceptance of several palaeogeographical domains within Europe, namely, Baltica, peri-Baltica, peri-Gondwana with Avalonia, Armorica and more recently also Perunica, Iberia, and/or an Armorican terrane assemblage (ATA).

Armorica and Avalonia

Armorica was defined originally by Van der Voo (1979) on the basis of palaeomagnetic data. According to that definition it embraced most of western Europe, including southwestern Britain and Wales, various sectors of Variscan Europe south of the British Isles, part of northern Africa, and probably also the Avalon Peninsula of Newfoundland and New England of North America. Since this original definition, the geographical extent of Armorica has undergone several restrictions and redefinitions, resulting in a general reduction of its extent. The first major change was the distinction of Avalonia, which was based first on palaeontological arguments (Cocks & Fortey 1982, 1990), and was supported later by palaeomagnetic data (e.g. Bachtadse *et al.* 1995). Avalonia is geologically well defined, being separated by the two closed Caledonian sutures: the Iapetus Ocean suture separating Avalonia from

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North America, and the Tornquist Ocean suture, part of the Trans-European Suture Zone, marking the boundary with Baltica. The younger Variscan Rheic Ocean suture separates Avalonia from Gondwana to the south. The boundaries of Avalonia were revised and described in detail by Cocks *et al.* (1997), and Avalonia thus now includes a North American sector embracing southern parts of eastern Newfoundland (Avalon), most of the Maritime Provinces of Canada and the eastern US seaboard as far as Cape Cod, Massachusetts, and perhaps southern Carolina, and a European sector with southern Ireland, Wales, England, Belgium, the Netherland and parts of northern Germany, and most probably also northwestern Poland (Pomerania; Cocks *et al.* 1997; Urung *et al.* 1999; Vecoli & Samuelsson 2001; Cocks 2002).

The well-established early Ordovician separation of Avalonia, and its drift across the narrowing Iapetus Ocean associated with opening of the Rheic Ocean to the south, was proposed originally on the basis of palaeontological information (Cocks & Fortey 1982). This scenario has been supported by palaeontogists (e.g. Fortey & Cocks 2003, and references therein) and also by palaeomagnetic studies (e.g. Torsvik *et al.* 1993).

Armorican terrane assemblage and Cadomia

Increasing palaeontological and palaeomagnetic data provided a possibility to evaluate regional as well as local differences in greater detail. This resulted in continual redefinition of the boundaries of separate terranes (Cocks *et al.* 1997; Servais & Fatka 1997; Cocks & Fortey 1998; Moczydlowska 1999; Urung *et al.* 1999). One of most important changes has been the proposal of an Armorican terrane assemblage (ATA) by Tait *et al.* (1994, 1997) and Franke (2000). Originally the ATA included Franconia, Saxothuringia and Bohemia; later Schätz *et al.* (2002) incorporated the Saxothuringian terrane, Teplá–Barrandian region, and Iberian and Armorican massifs. The same terranes were incorporated also in the 'Iberian–Armorican Terrane Collage' of Linnemann & Romer (2002) (Iberia, Armorica, Saxothuringia). Recently, Cocks & Torsvik (2006) incorporated only the Iberian Peninsula and most of France, and separated Perunica from the ATA.

A different approach to distinguishing terranes has been applied by petrologists analysing the age of basements of terranes. In general, the ATA is synonymous with Cadomia, defined as peri-Gondwanan terranes with basement about 2 Ga old. Keppie *et al.* (2003) incorporated the Ossa–Morena and Central Iberian zones of Spain, the French Armorican massif and the Massif Central, and questionably also the Saxothuringian and Moldanubian zones of Germany and the Czech Republic, respectively.

Perunica and its definition

The first attempts to evaluate the history of the Ordovician fauna of the Teplá–Barrandian region, at that time on the basis of only provisional Early Palaeozoic palaeogeography, were published by Havlíček (1976, 1982). However, the earlier establishment of an alternative regional chronostratigraphical scheme by Havlíček & Marek (1973) incorporated an expression of major faunal differences. On the basis of benthic brachiopods, Havlíček & Marek (1973) defined four new stages, Dobrotivá, Beroun, Králodvor and Kosov, for the Middle and Upper Ordovician; thus the paper defining the original concept of the microcontinent Perunica published by Havlíček *et al.* (1994) is essentially only a palaeogeographical expression of the earlier established faunal differences. Havlíček *et al.* (1994) brought together a major part of the Bohemian Massif, involving the Moldanubian, Barrandian and Saxothuringian (Saxothuringian–Lugian) zones, which constituted a separate microplate during the Early Palaeozoic, and for palaeogeographical purposes named it Perunica.

In the last 15 years, some workers have continued to use names such as Bohemia (e.g. Tait *et al.* 1994) or Teplá–Barrandian (e.g. Schätz *et al.* 2002), or even the questionable Barrandian Basin, but the palaeogeographical designation of Perunica has been cited in more than 60 papers dealing with various aspects of palaeontology, stratigraphy or palaeogeography. Numerous new data have been published since the original paper was published, and it now seems appropriate to revise the original definition of Perunica and to bring it in agreement with more recent data.

Paleontology. A majority of papers have focused on systematics and palaeogeography of Ordovician and Silurian trilobites, brachiopods, bivalves and cephalopods. Perunica is employed as a useful designation for a peri-Gondwanan area of species development (for a summary, see Fortey & Cocks 2003).

Palaeomagnetic data. Critical and comprehensive summaries of the earlier palaeomagnetic data from the Teplá–Barrandian region were publisher by Torsvik *et al.* (1990), and were supplemented, discussed and reinterpreted recently by Nysaether *et al.* (2002).

The aim of this contribution is to provide a comprehensive review of available palaeontological data on Neoproterozoic, Cambrian and Ordovician fossils of the Teplá–Barrandian region, complemented by brief remarks on Silurian and Devonian faunas, with the aim of discussing the applicability of existing palaeomagnetic, sedimentological and palaeontological data for reconstruction of the palaeogeographical history of this region.

Teplá–Barrandian region within the Bohemian Massif

The largest exposed area of the Variscan orogen in Central Europe is represented by the Bohemian Massif, which forms a major part of the Czech Republic and adjacent areas in Austria, Germany and Poland (Fig. 1). The Bohemian Massif encompasses three main units in which palaeontologically and geochronologically well-dated Proterozoic to Devonian sequences are present (Fig. 2): (1) Bohemikum, with four main regions: the Teplá–Barrandian region, Železné hory area and Hlinsko Zone, metamorphic islands within the Central Bohemian Granitic Pluton, and the Rožmitál region; (2) the Krkonoše–Jizera Unit; (3) Moravosilesicum, including the Moravian Karst, Velké Vrbno Unit and Drahany Upland. In addition, about 10 geographically very restricted occurrences of palaeontologically dated outcrops of Lower Palaeozoic rocks have been established in various regions of the Bohemian Massif (Fig. 2).

The Teplá–Barrandian region in West Bohemia together with eastern Bavaria and Thuringia represents one of the easternmost segments of the Avalonian–Cadomian tectonostratigraphical belt, which was consolidated between 670 and 550 Ma and was not affected by high-temperature–low-pressure metamorphism during the Variscan orogeny. The basement of these units, if known, is composed of late Proterozoic sediments, including the late Proterozoic flysch and volcanites typical of an arc-related setting. Most of the basement rocks of the region underwent very low-grade to amphibolite-facies metamorphism and deformation at about 550–540 Ma (Zulauf 1997; Zulauf *et al.* 1999). In contrast to other units of the Bohemian Massif, the thickened Cadomian crust collapsed in the Neoproterozoic and allowed deposition of thick sequences of continental clastic deposits in several graben structures; for example, the Příbram–Jince and Skryje–Týřovice basins of the Barrandian area or in the Franconian Forest in Germany. The general evolution of the sequence of sedimentary and volcanic rocks reflects subsidence associated with extension in an intracontinental to passive marginal setting.

Neoproterozoic

Several thousand metres of marine clastic deposits volcanites accumulated in a rapidly subsiding marginal sea bordering the margin of Gondwana, positioned most probably on oceanic crust. The sequence is composed of siliciclastic terrigenous rocks dominated by greywackes, siltstones and shales. Recently two major lithostratigraphical units have been distinguished, the Kralupy–Zbraslav and the Štěchovice groups. A rather monotonous complex of turbidites (greywackes, siltstones) with silicites, volcanites and black shales characterizes the extensive exposures of the Kralupy–Zbraslav Group in Central and West Bohemia (Cháb & Pelc 1973; Cháb 1978).

The volcanites belong to three main series of alkaline, transitional and tholeitic geochemistry, corresponding to volcanic arc and back-arc geotectonic settings (Dörr *et al.* 2002). Neoproterozoic volcano-sedimentary successions belong to an active island arc and sedimentation represents deposition in a back-arc basin until at least 570 Ma. A change in the geotectonic regime from convergence to transtension is indicated by a strong increase in heat flow at around 545 Ma, associated with an angular unconformity between Cadomian basement and Lower Paleozoic sequences near the Precambrian–Cambrian boundary.

Analyses of lithological development of Neoproterozoic rocks support their peri-Gondwanan origin but do not provide any reliable information for more precise palaeogeographical positioning. Fossils are represented solely by organic-walled microfossils, which allow correlation of both groups with the Brioverian of the Armorican Massif and confirm a Late Riphaean to Vendian age (Konzalová 1981; Fatka & Gabriel 1991). However, they do not provide any possibility for palaeogeographical interpretation. The absence of palaeomagnetic data excludes reliable positioning of the Teplá–Barrandian region at this time.

However, analyses of the palaeontological content of the 'lower' Cambrian Paseky Shale and 'middle' Cambrian Jince Formation combined with palaeomagnetic data offer much better datasets for interpretation of possible positioning of the Teplá–Barrandian region during the Cambrian. Such analyses are biased by various factors, but recent evaluation of echinoderm, trilobite and brachiopod assemblages provides a reliable picture of their distribution within the inshore–offshore transect, which could be well used to restore the palaeogeographical position of this area during the Cambrian.

Cambrian

Within the Teplá–Barrandian region, Cambrian rocks are known from three separate areas: the larger and more complete Příbram–Jince Basin, the Skryje–Týřovice Basin and the Železné hory area (Figs 2 & 3). Stratigraphical subdivision of

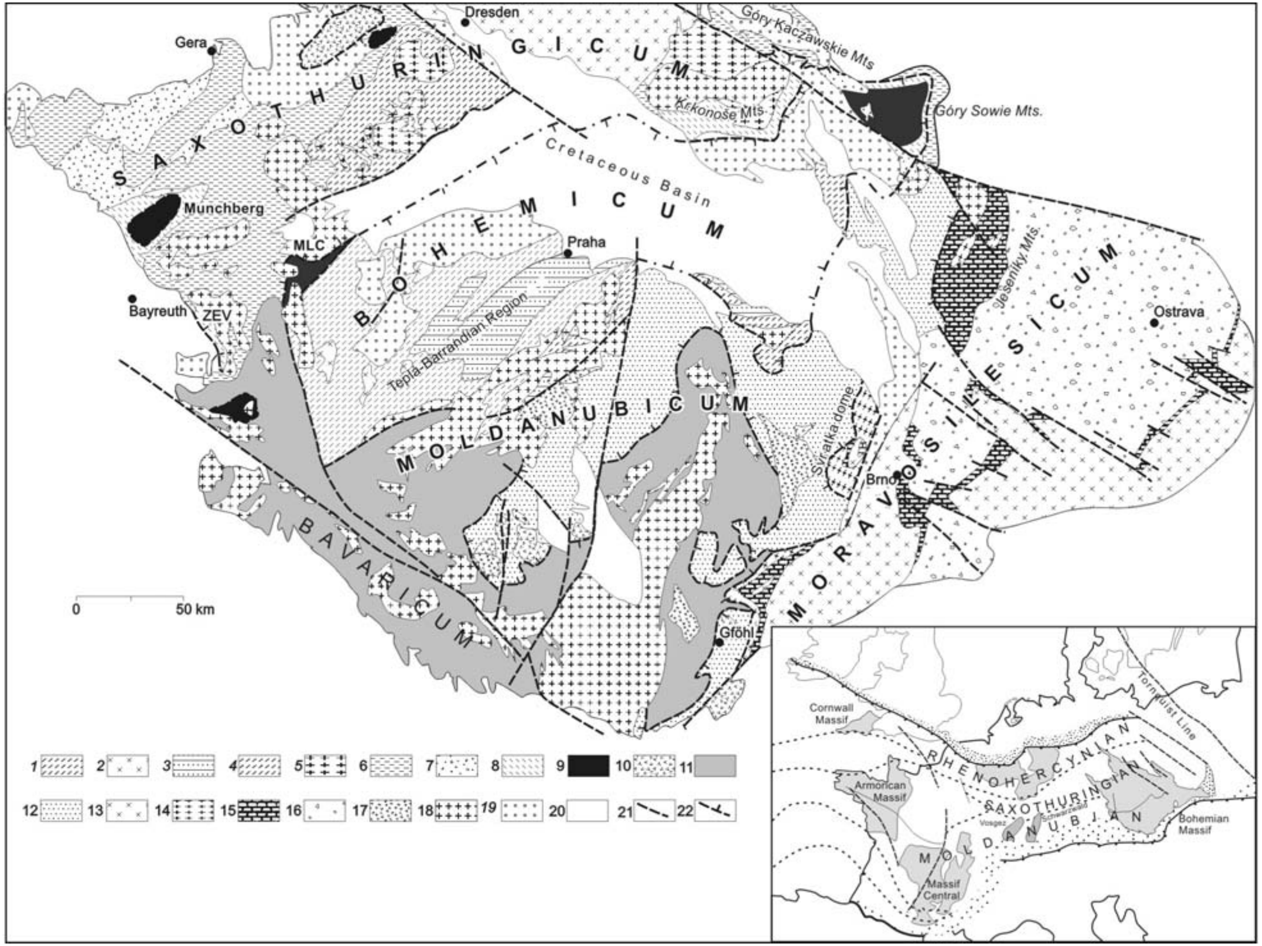

Fig. 1. *Continued*.

Cambrian rocks has been summarized by Havlíček (1971*a*), Chlupáč *et al.* (1998) and Chlupáč (1999*a*).

Příbram–Jince Basin. The Neoproterozoic succession is overlain unconformably by a *c.* 2500 m thick sequence of coarse-grained clastic deposits (conglomerates and sandstones with interlayers of greywackes to shales of the Hluboš–Žitec to Chumava–Baština formations) passing upwards into greywackes and shales of the Jince Formation and then into volcanites. The stratigraphical subdivision, involving a repetition of comparatively fine- and coarse-grained lithotypes, makes it possible to distinguish 13 lithostratigraphical units (Havlíček 1971*a*), grouped into eight formations (Fig. 4). Fossils occur in two levels, in the 'lower' Cambrian Paseky Shale Member of the Holšiny–Hořice Formation, and in the 'middle' Cambrian Jince Formation (Fig. 4).

The Paseky Shale Member. The first reported fossil, the enigmatic aglaspid merostome *Kodymirus vagans* Chlupáč & Havlíček (1965), was described at a time when the Paseky Shale Member was assumed to represent a marginal facies of the younger Jince Formation. The true stratigraphical position of the Paseky Shale, some 800–1500 m below the Jince Formation, was later determined by Havlíček (1968). Investigations at five fossiliferous localities (Chlupáč *et al.* 1996) resulted in an integrated study of various fossil groups and lithology (Kukal 1996). Based on results of these studies, this early Cambrian biota was dominated by the very distinct *Kodymirus*. Association characterized by three genera of non-trilobite arthropods (*Kodymirus*, *Kockurus* and *Vladicaris*; see Chlupáč 1995) associated with diversified trace fossils (?*Rusophycus*, *Monomorphichnus*, *Diplichnites*, *Dimorphichnus* and ?*Bergaueria*; see Mikuláš 1996), macroscopic algae (*Marpolia* Walcott 1919; see Steiner & Fatka 1996), organic-walled microfossils (filamentous microfossils *Rectia* Jankauskas 1989; *Palaeolyngbya* Schopf 1968; *Botuobia* Pjatiletov 1979; *Siphonophycus* spp. and *Polythrichoides* Hermann 1974 emend. Hermann 1976 in Timofeev *et al.* 1976; prasinophyte and acritarch genera *Retisphaeridium* Staplin, Jansonius & Pocock 1965; *Skiagia* Downie 1982, *Adara* Fombella 1977; *Sinianella* Yin 1980 emend. Zang in Zang & Walter 1992; *Leiosphaeridia* spp. and microscopic resting traces, e.g. *Ceratophyton vernicosum* Kirjanov, 1979 in Volkova *et al.* 1979, see Fatka & Konzalová 1996). The distribution of all the taxa recognized from the most fossiliferous locality at Kočka has been summarized by Fatka *et al.* (2004).

The noticeable absence of groups typical of the Sepkoski Cambrian Fauna such as trilobites, echinoderms and brachiopods, combined with the presence of spectacular arthropods and the scarcity of process-bearing acritarchs in the microfossil assemblage, reflects a marginal environment; that is, the biota reflects restricted marine conditions (Fig. 5).

The *Kodymirus* Association inhabited shallow subtidal plains characterized by greywackes to fine shales. Precise dating within the 'early' Cambrian is difficult because of the absence of stratigraphically important taxa. Fatka & Konzalová (1996) reported a rich assemblage of organic-walled microfossils dominated by filamentous cyanobacteria, spherical leiospherids and rare acritarchs, including the occurrence of ?*Volkovia*, which could date the Paseky Shale Member within the *Volkovia–Liepaina* Zone of Moczydlowska (1999); that is, late in the as yet unnamed series of the Cambrian.

The Jince Formation. This unit in the Příbram–Jince and Skryje–Týřovice basins includes the best preserved and most diverse Cambrian faunas in Central Europe, displaying environmentally controlled distribution of assemblages (Elicki *et al.* 2008).

The lower, thick sequence of clastic sediments (over 1500 m) underlying the Jince Formation characterizes the maximum subsidence in the Brdy

Fig. 1. Tectonic sketch map of the Bohemian Massif showing the main terranes (modified after Matte *et al.* 1990). Bohemicum (Teplá–Barrandian Unit): 1, Late Proterozoic volcano-sedimentary sequences; 2, Pre-Variscan (Cadomian granitic rocks); 3, Early Palaeozoic metasediments and volcanic rocks (Cambrian to Devonian). Saxothuringicum: 4, Late Proterozoic metasediments; 5, Cadomian metagranitoids (orthogneisses); 6, Early Palaeozoic metasediments (Cambrian to Devonian); 7, Early Carboniferous diastrophic sediments. Autochthonous units (in Saxothuringicum and Moldanubicum): 8, lower part of allochthonous units consisting of weakly metamorphosed metasediments, basic volcanic rocks and ultrabasic rocks, 9, high-grade rocks (gneisses, metagabbros, eclogites); 10, granulite massifs including eclogites and HP mantle peridotites. Moldanubicum: 11, high-grade gneisses, probably Late Proterozoic to Early Palaeozic in age (Ostrong and Drosendorf groups); 12, allochthonous complexes of the Gföhl Unit with relics of HP rocks. Moravosilesicum (including Brunovistulicum): 13, Cadomian basement of the Brunovistulicum (Cadomian granitic rocks and their metamorphic mantle); 14, Cadomian orthogneisses of the Moravosilesian Units; 15, Early to Late Palaeozoic volcano-sedimentary sequences of the Moravosilesicum (including basement units); 16, Viséan to Namurian diastrophic sediments (Culm facies) in the upper part with transition to weakly deformed sediments of the Variscan foredeep. Variscan granitoids: 17, melanocratic granites and syenites (durbachites); 18, tonalites to granites; 19, Late Carboniferous to Permian clastic sediments and volcanic rocks (epi-Variscan platform sediments); 20, post-Permian cover; 21, major fault zones; 22, thrust, nappe boundaries. (Drawn by V. Kachlík.)

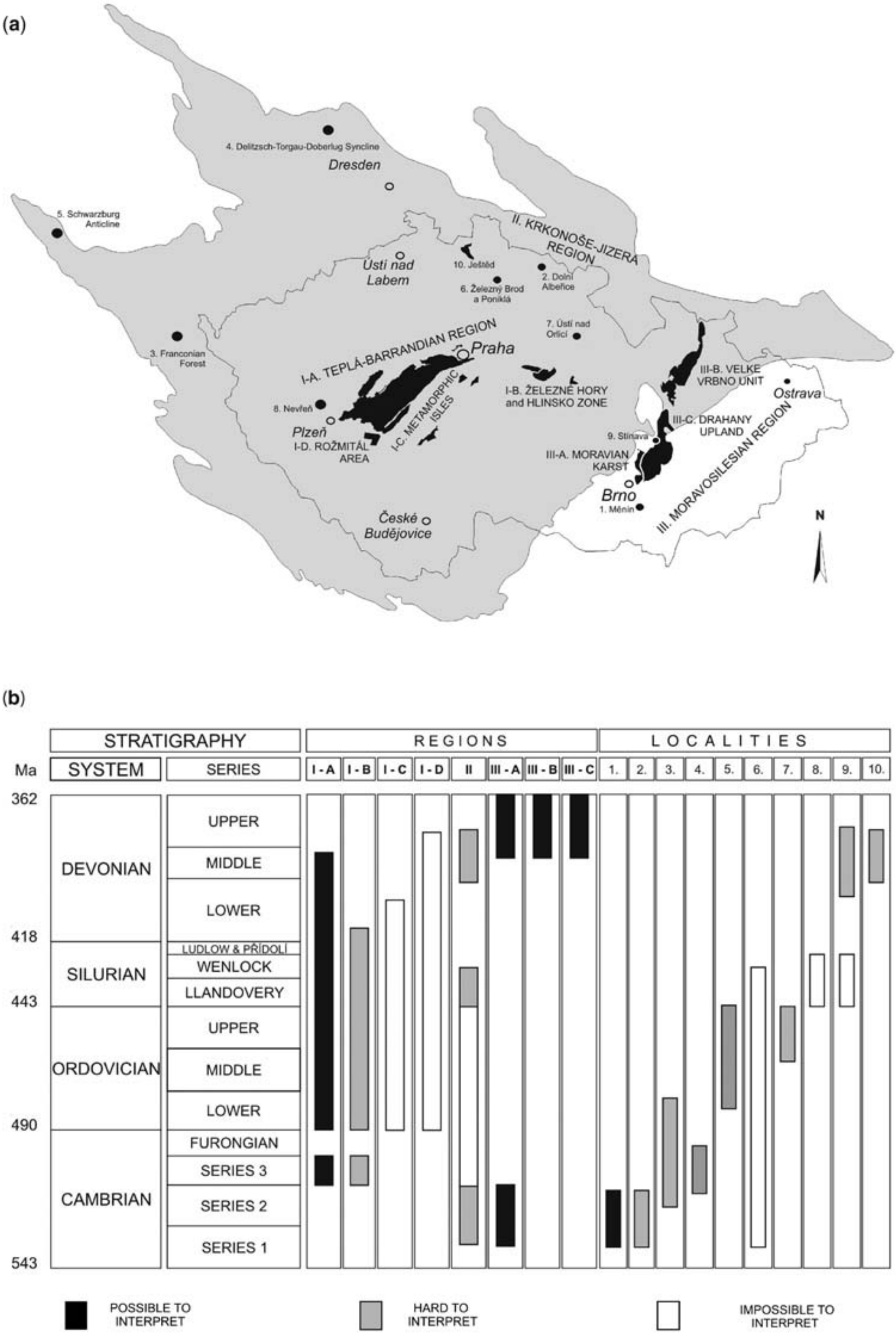

Fig. 2. (**a**) Map of Czech Republic showing regions and localities with Cambrian to Devonian fossils. (**b**) Potential of fossils for interpretation of palaeogeographical position.

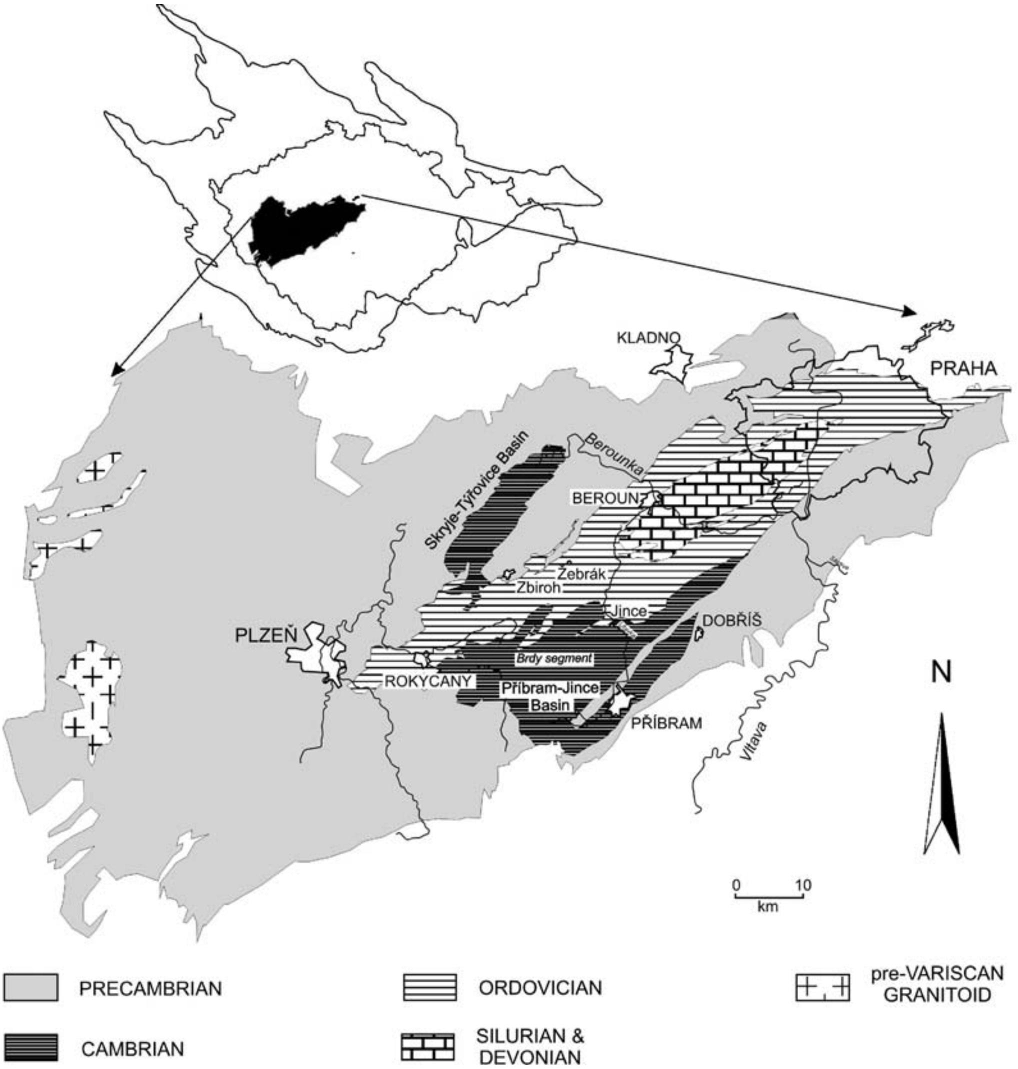

Fig. 3. Geology of the Teplá–Barrandian region with the Cambrian Příbram–Jince and Skryje–Týřovice basins and the Ordovician–Devonian Prague Basin.

area of the Příbram–Jince Basin. An important change in basin geometry is associated with the marine ingression, represented by the 100–450 m thick Jince Formation. At this time the main depocentre shifted eastwards to the Litavka river valley (Havlíček 1971*a*). Within the Jince sequence it is possible to distinguish at least two major facies areas in the basin: a shallower Brdy segment and the deeper-water Litavka valley segment (Fig. 3). For the deepest segment as preserved in the Litavka valley, several bathymetrically controlled associations have been characterized (Fatka 2000). The even distribution of fossil assemblages through the formation in this region is possibly explained by a major transgressive–regressive cycle, with one or two fluctuations associated with pronounced changes in the depositional rate (Fatka 1990, 2000). Analyses of the Jince biota reveal a well-developed bathymetric differentiation. Shallow marine coarser-grained sediments (sandy greywackes and greywackes) are typified by the shallow-water *Lingulella* Biofacies at the base as well as at the top of the formation in the Litavka sequence (Fig. 6a). Slightly deeper-water greywackes to coarse shales are dominated by the Polymeroid Trilobite Biofacies (*Ellipsocephalus*, *Paradoxides*, *Conocoryphe*, *Ptychoparia*, *Acadolenus*, *Litavkaspis*). These two biofacies are predominant in the

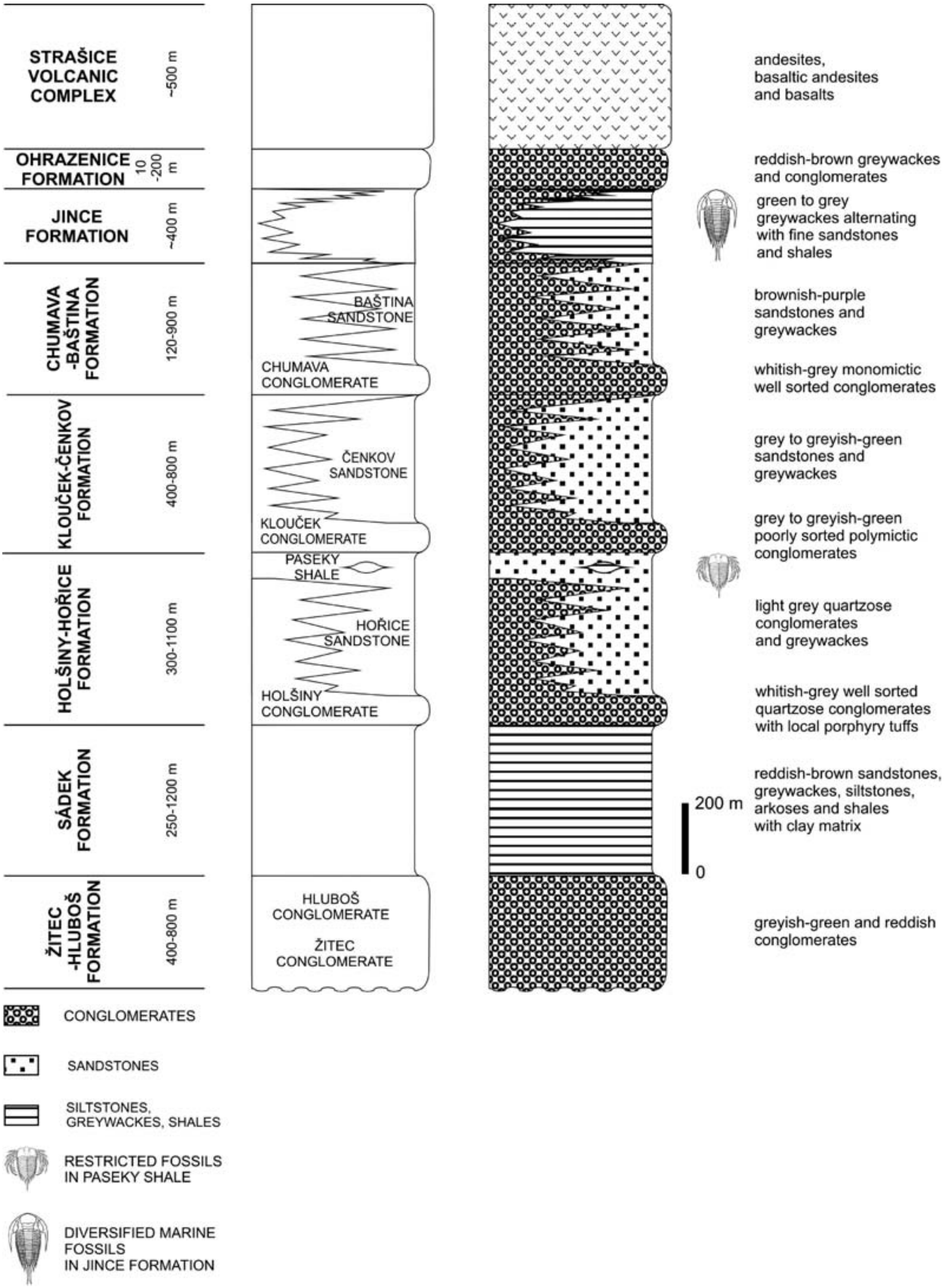

Fig. 4. Cambrian stratigraphy in the Příbram–Jince Basin (adopted after Havlíček 1971*a*; Elicki *et al.* 2008).

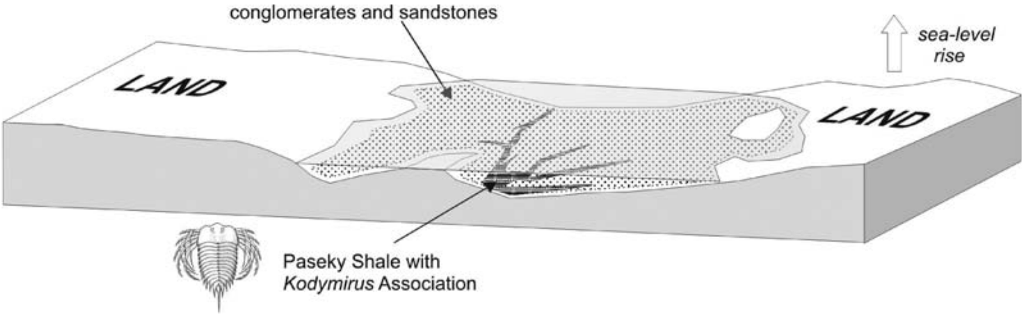

Fig. 5. Diagrammatic history of the Příbram–Jince Basin and the 'early' Cambrian Holšiny–Hořice Formation, with the *Kodymirus* Association in the Paseky Shale.

lower and upper thirds of the Jince Formation in this region, and in the complete thickness of the formation in the WNW area of the Příbram–Jince Basin; for example, in the Brdy segment (Fig. 6b).

Apart from the widely distributed *Paradoxides* and *Ellipsocephalus* and the endemic *Ptychoparia*, the other genera indicate a peri-Gondwanan origin. *Conocoryphe* is widely distributed in southwestern and Central Europe (various areas of Spain, Montagne Noire, Sardinia, Franconian Forest, Skryje–Týřovice Basin and Železné hory area) and Turkey. A typical 'Mediterranean' species is the trilobite *Acadolenus*, as is the cinctan echinoderm *Asturicystis*, which has been reported from the West Asturian–Leonese zone of Spain. The seemingly endemic genus *Litavkaspis* was reported from a similar stratigraphic level in slightly metamorphosed sediments of the Carolina terrane.

In the Litavka valley, the middle part of the formation, comprising mudstones with fine greywackes, is characterized by a dominance of agnostid trilobites of the miomerid Biofacies (Fig. 6c). Three associations can be identified within the transgressive sequence; namely, the relatively shallower *Peronopsis–Phalagnostus* Association, the deeper *Phalacroma–Condylopyge* Association, and the deepest *Onymagnostus–Hypagnostus* Association (Fatka *et al.* 2007).

The *Peronopsis–Phalagnostus* Association contains only the eponymous agnostid genera, associated with common polymeroids of the genera *Ellipsocephalus*, *Ptychoparioides*, *Acadolenus*, *Litavkaspis*, *Ptychoparia* and *Solenopleurina*. In the *Phalacroma–Condylopyge* Association, the eodiscoid *Dawsonia* and the agnostoid *Pleuroctenium* also occur rarely, associated with the common polymeroid genera *Paradoxides* (*Hydrocephalus*), *P. (Eccaparadoxides)*, and *P.* (*Acadoparadoxides*). *Ptychoparioides*, *Ptychoparia*, *Ellipsocephalus*, *Solenopleurina* and *Conocoryphe* also occur, but more rarely. The *Onymagnostus–Hypagnostus* Association incorporates the locally abundant genera *Onymagnostus*, *Hypagnostus*, *Tomagnostus* and *Doryagnostus*. *Peronopsis* and *Phalagnostus* as well as paradoxidid trilobites (*Paradoxides* and its subgenera *Paradoxides*, *Eccaparadoxides*, *Acadoparadoxides*, *Hydrocephalus*). The blind genus *Conocoryphe* and the large bivalve arthropod *Tuzoia* can be present in all three associations. All three miomerid associations are developed only in the Litavka valley; the first association is present also in the central, more western part of the basin, but agnostids are absent in the westernmost sectors of the basin (e.g. in the Brdy segment).

The five cosmopolitan agnostid genera show an unusual pattern of distribution. *Peronopsis* is known world-wide, including southwestern Europe. *Onymagnostus*, *Hypagnostus*, *Doryagnostus* and *Tomagnostus* are known from Baltica but are completely absent from Spain, France, Germany and Turkey, whereas *Condylopyge* is present in Spain and Germany as well as in Britain, Newfoundland and Baltica. *Pleuroctenium* and *Phalagnostus* occur in Germany (Franconian Forest) and Britain, but are absent in southwestern Europe.

At least five substrate and bathymetrically related echinoderm associations can be differentiated in the Příbram–Jince Basin: shallow-water, more or less monospecific *Ceratocystis*, *Asturicystis* and *Stromatocystites* associations, all confined to well-aerated sandy to greywacke, rarely even muddy bottoms, whereas the *Lichenoides–Akadocrinus* and *Etoctenocystis* associations (usually with more or less common eocrinoids *Acanthocystites*, *Vyscystis* and *Felbocrinus*) preferred more quiet, deeper conditions characterized by very fine sandy to muddy sedimentation (Fig. 6d). Echinoderm associations have been observed only in the Litavka river valley.

Ceratocystis has been reported in the Montagne Noire (France) and Baltica, and is most probably present also in the Franconian Forest of Germany. Ctenocystid and cinctan echinoderms appeared in Spain, France, and both the Příbram–Jince and

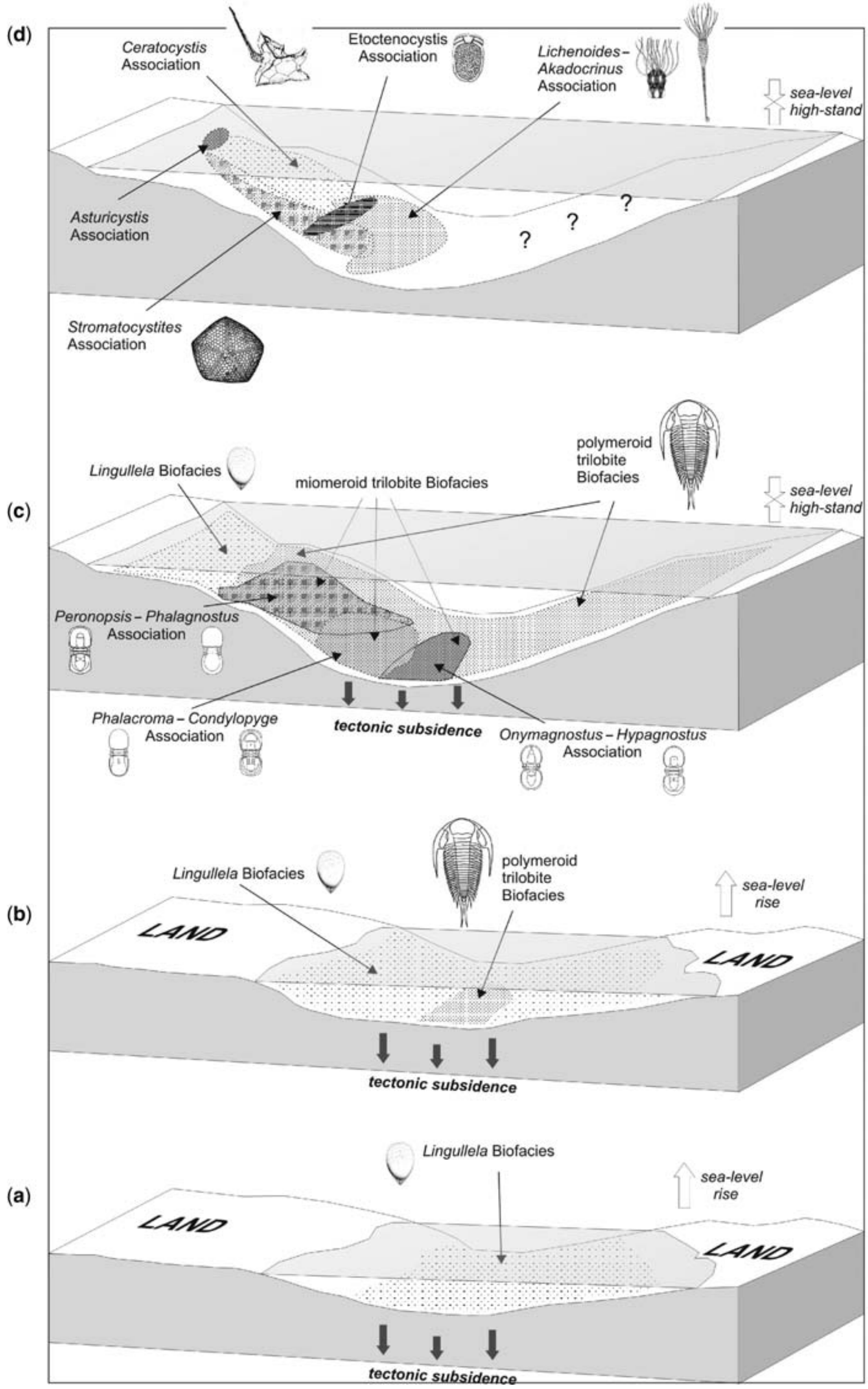

Fig. 6. Diagrammatic history of the Příbram–Jince Basin and its faunal associations in the Jince Formation. Only the left (WNW) slope of the basin is mostly illustrated, for simplification. Palaeoecological terminology is adopted from Fatka *et al.* (2006, 2007). (**a**) Beginning of marine ingression near the base of Jince Formation with the onset of

Skryje–Týřovice basins, as well as in Britain. Cinctans have also been reported recently from Italy (Sardinia) and Siberia, and ctenocystids are known also in Poland (Holy Cross Mountains), Laurentia and Australia (see below). *Stromatocystites* has been established in both the Příbram–Jince and Skryje–Týřovice basins and also in Newfoundland, Baltica and Australia. The eocrinoid genera *Lichenoides*, *Akadocrinus*, *Acanthocystites* and *Felbocrinus* are endemic forms.

The only eodiscid trilobite in the Teplá–Barrandian region, *Dawsonia bohemica*, has been identified recently in two other areas of SW Europe, namely in Sardinia (Elicki & Pilolla 2004) and in the Montagne Noire (Álvaro & Vizcaïno 2000). The cornute echinoderm genus *Ceratocystis* has a similar distribution, whereas the blind polymeroid *Ctenocephalus* cf. *coronatus* is known only from Italy (Sardinia, Cabitza Formation) and the Skryje–Týřovice Basin.

The rich acritarch assemblage of the Jince Formation does not provide any decisive palaeogeographical information (Vavrdová 1974*a*, *b*, 1982; Fatka 1989).

The Skryje–Týřovice Basin

A *c*. 200 m thick succession of Jince Formation in this region (conglomerates, sandstones, greywackes and shales) contains 'middle' Cambrian fossil assemblages (Fig. 7). The Cambrian sequence overlies the Neoproterozoic Kralupy–Zbraslav Group unconformably.

The basal monomict, white to grey Mileč Conglomerate and Sandstone, up to 10 m thick, contain generally fragmentary preserved brachiopods (*Pompeckium*; Havlíček 1970), locally common helcionelloid molluscs (*Helcionella*; Smetana 1918), and polymeroid trilobites (*Perneraspis*, *Germaropyge*, *Ptychoparioides* and rarely *Paradoxides*; Šnajdr 1958) of the *Pompeckium–Germaropyge* Association (Fig. 8a). Kukal (1971) interpreted the high-energy succession as beach coastal barriers and bars, locally with very common brachiopods, the so-called '*Orthis*' sandstone facies.

The Mileč Member is usually overlain by generally darker polymict conglomerates and greyish green greywackes to shales of the Týřovice Greywacke and Conglomerate, commonly containing pebbles of Proterozoic shales and greywackes. More or less fragmentary shells of locally common articulate brachiopods (*Pompeckium* and/or *Jamesella*), helcionelloid molluscs (*Helcionella*) and in some levels spectacular graptoloids and the lightly sclerotized *Wiwaxia* cf. *corrugata* (Matthew) occur (Maletz *et al.* 2005; Fatka *et al.* 2009). Up to 200 m of thick clayey shales and greywackes of the Skryje Shale (including silty and sandy intercalations) are the most widespread lithofacies, containing diverse faunas. The polymeroid trilobite Biofacies [with locally common genera *Conocoryphe*, *Ctenocephalus*, *Luhops*, *Paradoxides* (*Eccaparadoxides*), *P.* (*Hydrocephalus*), *Ptychoparia*, *Sao*, *Agraulos*, *Skreiaspis*, *Jincella*, *Ellipsocephalus* and the rare bivalved arthropod *Tuzoia*] is usually associated with the *Peronopsis–Phalagnostus* Association (Fig. 8a). In higher stratigraphic levels there are locally miomeroid trilobites of the *Phalacroma–Condylopyge* Association, with common *Pleuroctenium*, *Diplorrhina* and *Skryjagnostus.* Early ontogenetic stages of both miomeroid and polymeroid trilobites [e.g. *Sao* and *Paradoxides* (*Eccaparadoxides*)] are dominant, associated with rare brachiopods (*Bohemiella romingeri*) and cinctan, ctenocystoid and eocrinoid echinoderms (Fig. 8a).

Some lenses of fine sandstones occurring in various levels contain specific echinoderm-dominated faunas assigned to the shallow-water

Fig. 6. (*Continued*) *Lingulella* Biofacies (*Lingulella* with the first polymeroid trilobites, e.g. *Paradoxides s.l.*, *Ellipsocephalus*, *Conocoryphe* and the first very rare agnostid *Peronopsis*). *Lingulella* Biofacies shifted to the Brdy segment of the basin, recovering in the Litavka river valley area until the end of sedimentation of the Jince Formation (i.e. after filling of the Příbram–Jince Basin). (**b**) Progressive transgression and deepening of the basin characterized by the first appearance of the later dominant polymeroid trilobite Biofacies (*Ellipsocephalus*, *Paradoxides s.l.*, *Conocoryphe*, *Ptychoparioides*, *Acadolenus*, *Litavkaspis*), associated with the stepwise onset of agnostid trilobites (*Phalagnostus*, rarely also *Phalacroma*, *Condylopyge*, *Pleuroctenium*) and the first shallow-water echinoderms of the *Asturicystis* and *Ceratocystis* associations [see (d)]. The first obvious affinity to Iberian peri-Gondwana is in polymeroid trilobites (*Acadolenus*), and cinctan and stylophoran echinoderms (*Asturicystis* and *Ceratocystis*). (**c**) Deepening and differentiation of the basin with the *Lingulella* Biofacies dominating in the shallow-water Brdy area, followed laterally by diverse polymeroid trilobite Biofacies (with *Jincella*, *Ptychoparia*, *Lobocephalina*) and the offshore miomeroid trilobite Biofacies (*Onymagnostus*, *Hypagnostus*, *Doryagnostus* and *Tomagnostus*). Continuous affinity to southwesten Europe of the polymeroid trilobite is interrupted suddenly by the incoming of miomeroid trilobites unknown in Spain, France or Germany, but typical of Baltic and Avalonian regions (Sweden, Norway, Britain, Newfoundland). (**d**) Substrate-related echinoderm associations occur through a major part of the Jince Formation. The stylophoran *Ceratocystis* is known from Spain and France, as well as from Sweden, whereas the edrioasteroid *Stromatocystites* is restricted to Baltica and Newfoundland. Cinctan echinoderms are known exclusively from Gondwanan Africa, Spain, France, Germany and rarely also in Germany and Britain. The other eocrinoids and the ctenocystid *Etoctenocystis* represent endemic taxa.

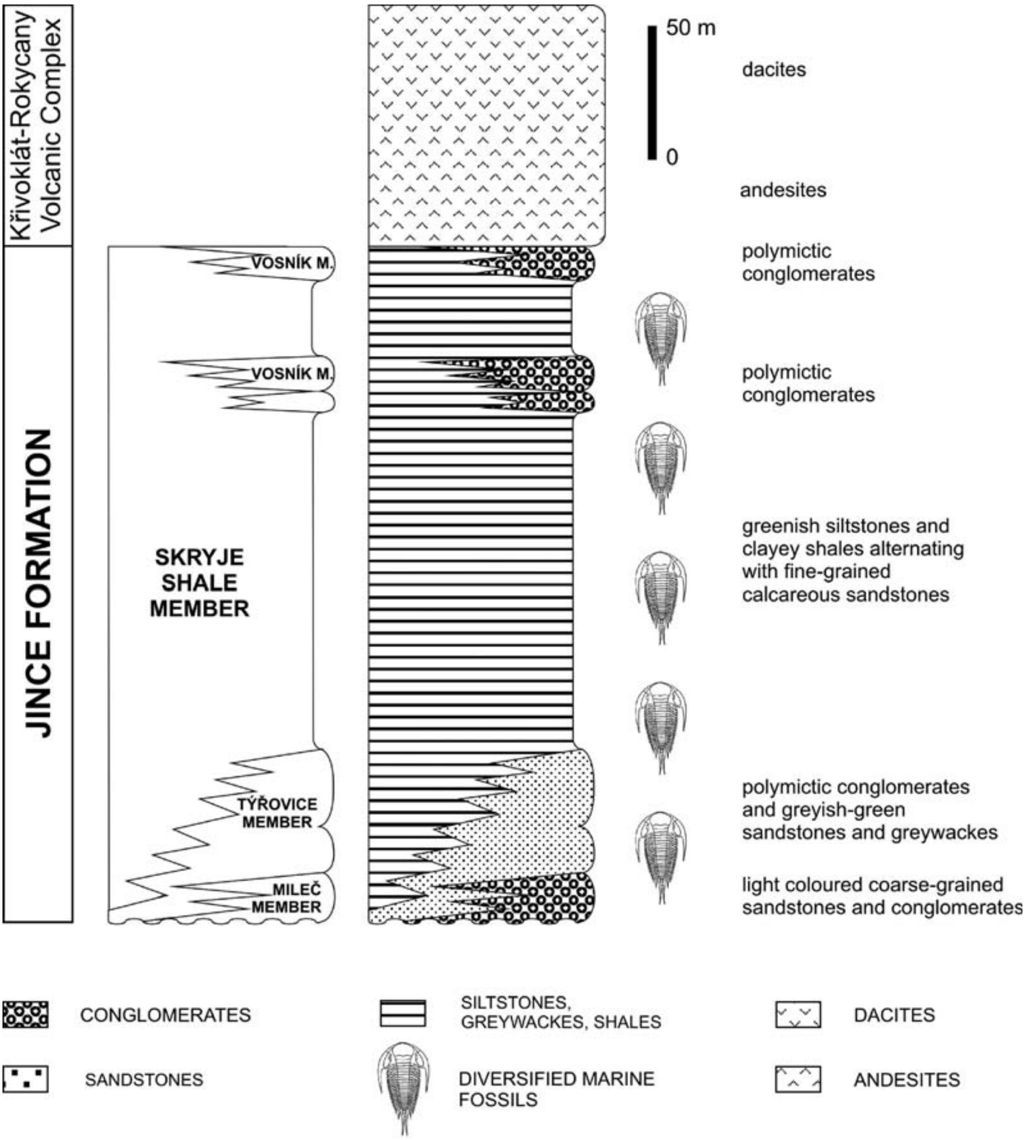

Fig. 7. Stratigraphy of the Cambrian in the Skryje–Týřovice Basin (adopted after Havlíček 1971*a*; Elicki *et al.* 2008).

Ceratocystis Association (commonly with the polymeroid trilobite *Ctenocephalus*) and/or a slightly deeper-water *Stromatocystites* Association (associated with *Ptychoparia* and *Germaropyge*) (Fig. 9). Similarly, very restricted lenses of greywackes to shales can be characterized by the common occurrence of eocrinoids in the *Lichenoides* Association or ctenocystoid echinoderms in the *Etoctenocystis* Association, both associated with common polymeroid trilobites (e.g. *Skreiaspis*, *Paradoxides s.l.*). The fine shales in higher stratigraphical levels of the formation are usually dominated by tests of cinctan echinoderms of the *Trochocystites* Association, usually accompanied by large paradoxidid trilobites, *Conocoryphe*, *Agraulos*, *Jincella*, *Sao*, *Solenopleurina*, occasionally also with the rare eocrinoid *Luhocrinus* (Fig. 8b).

In the northeastern area of the basin, tongue-like bodies up to several metres thick of the polymict Vosník Conglomerate are developed in the upper part of the sequence. Kukal (1971) interpreted the Týřovice, Skryje and Vosník members as deposits

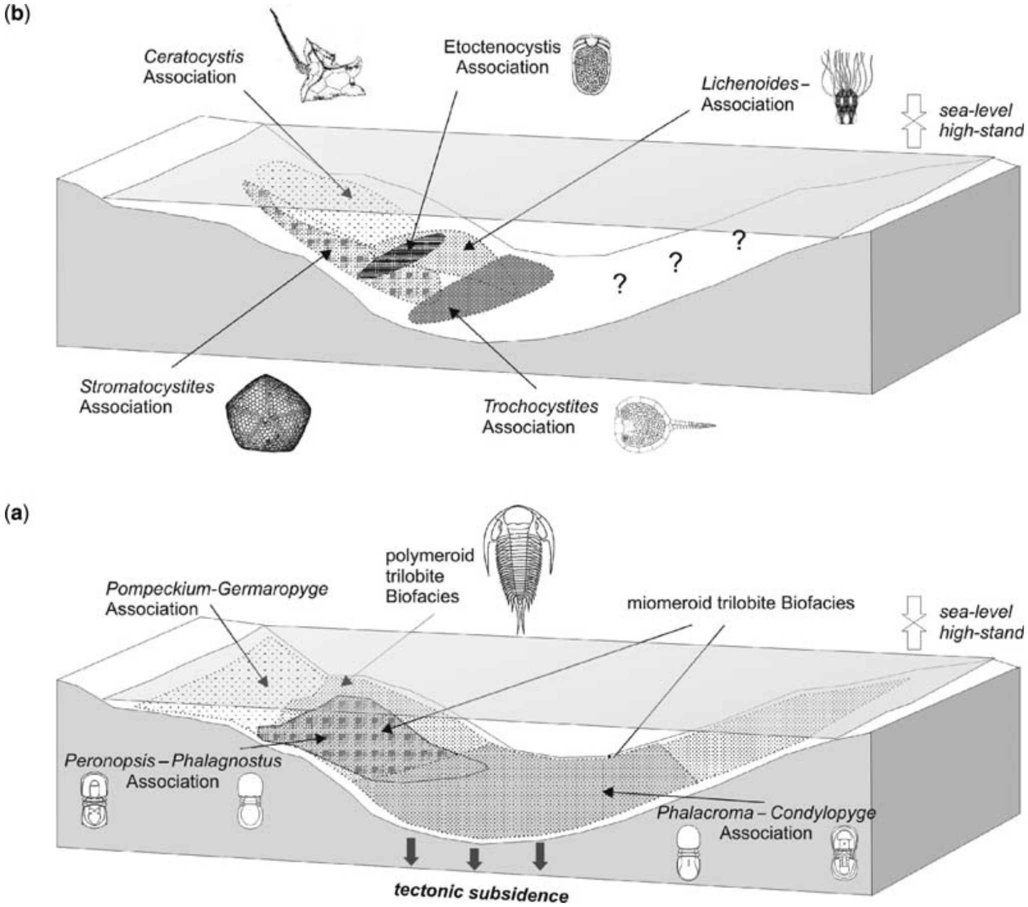

Fig. 8. Diagrammatic history of the Skryje–Týřovice Basin and its faunal associations of the Jince Formation. Only the left (WNW) slope of the basin is mostly illustrated, for simplification. Palaeoecological terminology is adopted from Fatka *et al.* (2006, 2007). (**a**) Beginning of marine ingression near the base of Jince Formation with onset of the endemic *Pompeckium–Germaropyge* Association, followed by progressive deepening of the basin with a stepwise appearance of the polymeroid trilobite Biofacies, associated with the *Peronopsis–Phalagnostus* Association in relatively inshore facies and the *Phalacroma–Condylopyge* Association in the deeper offshore. All the facies were well oxygenated. Numerous trilobite taxa (e.g. *Sao hirsuta*, *Peronopsis umbonata*, *Condylopyge rex*, *Pleuroctenium graulatum*) are common for the Skryje–Týřovice Basin and the Lippertsgrüner Formation of the Franconian Forest as described by Sdzuy (2000). (**b**) As in the Příbram–Jince Basin, echinoderm associations occur through the major part of the Jince Formation and show apparent relation to substrate. The *Ceratocystis*, *Stromatocystites* and *Etoctenocystis* associations are the same as in the Příbram–Jince Basin, being complemented by the *Lichenoides* Association (without any other eocrinoids) and the deeper-water *Trochocystites* Association (locally with the eocrinoid *Luhocrinus*).

related to turbidity currents on steep slopes of the sedimentary basin. Cambrian sediments of the Jince Formation are overlain by extrusive rocks (dacites, andesites and rhyolites) of the Furongian Křivoklát–Rokycany Complex.

The worldwide distributed bivalved crustacean genus *Tuzoia* has an obvious relationship to tropical to warm temperate waters (Vannier *et al.* 2007), as does the enigmatic genus *Wiwaxia* (Fatka *et al.* 2009).

The Cambrian fauna in the Skryje–Týřovice Basin is fairly distinct from that of the Příbram–Jince Basin. It includes several endemic genera of polymerid trilobites (*Ptychoparia*, *Ptychoparioides*, *Solenopleurina*, *Perneraspis*), two miomeroid trilobites (*Diplorrhina* and *Skryjagnostus*; the latter is present also in Siberia; Elicki & Pilolla 2004), and two orthide brachiopods (*Pompeckium*, *Jamesella*). Cambrian hyolithids are too poorly studied to be evaluated in this analysis. The polymerid genera

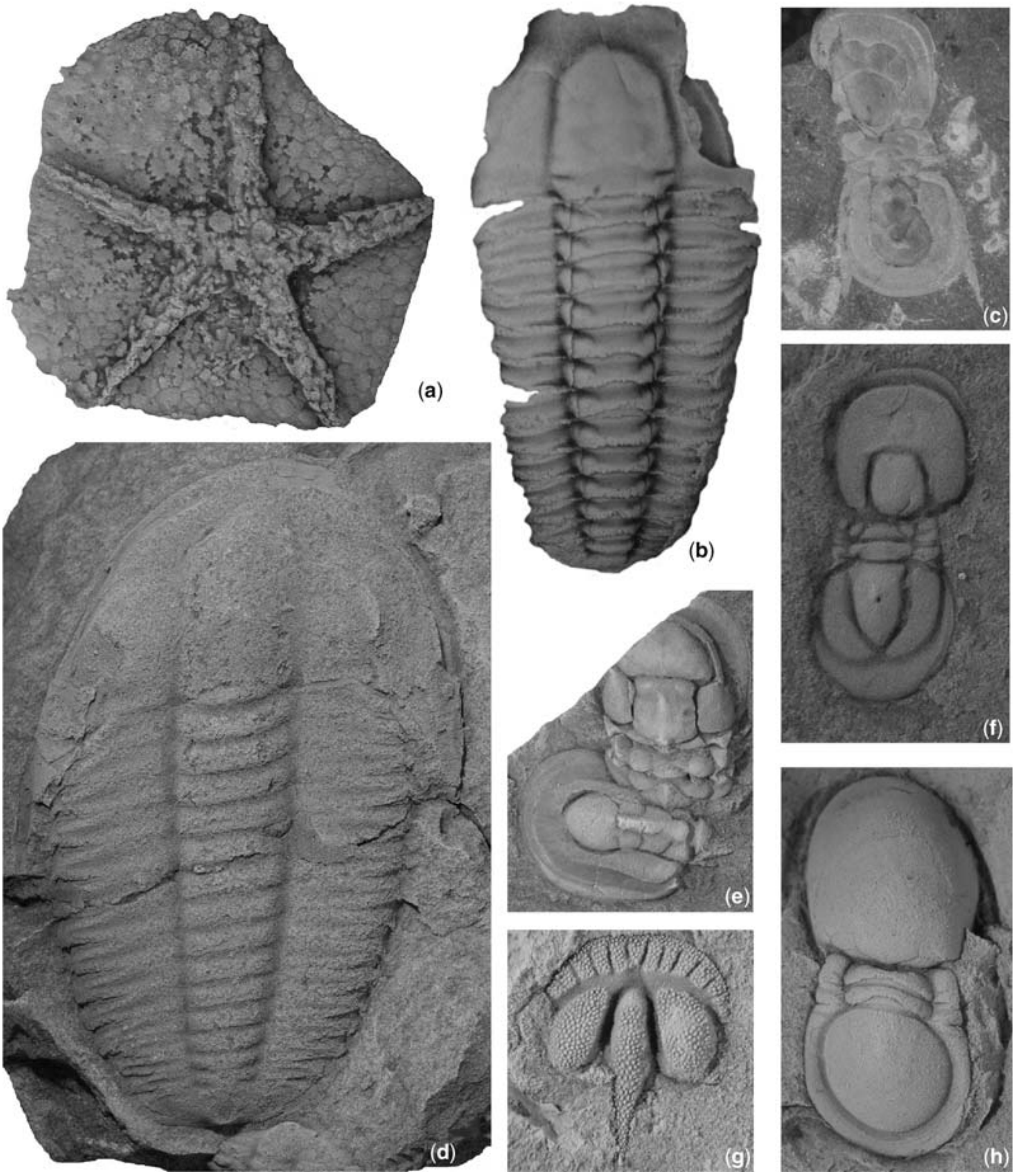

Fig. 9. Characteristic fossils of the 'middle' Cambrian Jince Formation. (**a**) *Stromatocystites pentangularis*; (**b**) *Skreiaspis spinosus*; (**c**) *Pleuroctenium granulatum*; (**d**) *Germaropyge germari*; (**e**) *Condylopge rex*; (**f**) *Hypagnostus parvifrons*; (**g**) *Dawsonia bohemica*; (**h**) *Phalagostus nudus*. (a, f, g) Příbram–Jince Basin; (b–e, h) Skryje–Týřovice Basin, all Jince Formation.

Ctenocephalus, *Conocoryphe*, *Agraulos* and *Skreiaspis* occur in different regions of Iberia, Armorica *s.s.*, Turkey and Avalonia. The genus *Sao* has a typically peri-Gondwanan distribution, being known from the Franconian Forest of Germany and the Ossa–Morena Zone of Spain (Gozalo *et al.* 1994). Similarly, *Jincella* is known from Spain, France and Italy (Sardinia).

Železné hory area

Havlíček (1949*b*), Havlíček & Šnajdr (1951) and Šnajdr (1958) recorded tectonically deformed trilobite fauna from the Senice Shales of the Železné hory area [*Ellipsocephalus*, ?*Paradoxides* (*Eccaparadoxides*), ?*Paradoxides* (*Hydrocephalus*), *Conocoryphe*, *Skreiaspis*, *Lobocephalina*], all known also from the Jince Formation of both the Příbram–Jince and Skryje-Týřovice basins.

In many respects, very similar Cambrian sequences occur in Germany in the tectonically restricted outcrops of the Franconian Forest (Frankenwald in Bavaria) and the subsurface Delitzsch–Torgau–Doberlug Syncline (see below).

Franconian Forest

In this area most of the Palaeozoic succession shows two distinctly different facies developments, designated as the Bavarian and the Thuringian facies. The autochthonous Thuringian Facies has been supposed to represent a large homogeneous basin, whereas the allochthonous Bavarian Facies is interpreted as the remnants of a much more differentiated basin. However, this distinction has not been recognized in the Cambrian (Elicki *et al.* 2008). The six Cambrian formations overlie different Neoproterozoic units disconformably. Trilobites, brachiopods and echinoderms are reported from the lower part of the 'lower to lowermost middle' Cambrian Tiefenbach Formation. An early 'middle' Cambrian (= early Celtiberian) age is proved by trilobites (*Ornamentaspis*, *Kingaspidoides*, *Latikingaspis*, *Parasolenopleura*, *Bailiella*, *Paradoxides*, *Acanthomicmacca* and *Wurmaspis*) associated with echinoderms, brachiopods, hyoliths and trace fossils occurring in the following Galgenberg Formation, about 100 m thick. A similar age is supposed also for the Wildenstein Formation, containing a rich trilobite fauna (e.g. *Paradoxides s. l.*, *Condylopyge*, *Bailiella*, *Parasolenopleura*, *Acanthomicmacca*, *Ornamentaspis*, *Kingaspidoides* and *Dawsonia*) as well as brachiopods, molluscs, echinoderms, sponge spicules and trace fossils. Rare trilobites (e.g. *Conocoryphe* and *Eodiscina*) associated with brachiopods and sponge spicules characterize the sandy to arkosic sediments of the Triebenreuth Formation. Generally rare trilobites (e.g. *Solenopleuropsis*, *Sao*, *Paradoxides*, *Conocoryphe*, *Condylopyge*, *Parabailiella*, *Bailiella*, *Hypagnostus*, *Peronopsis*, *Phalagnostus*, *Ctenocephalus* and *Acontheus*), cinctan and probably also eocrinoid echinoderms are typical for the mid 'middle' Cambrian (late Caesaraugustian) Lippertsgrün Formation. The late 'middle' Cambrian (Languedocian) Bergleshof Formation is estimated to be less than 100 m thick and contains polymeroid trilobites (*Proampyx*, *Parasolenopleura*, *Holocephalina*, *Bailiella*?, *Jincella*, *Peronopsis*) and one miomeroid trilobite (*Leiagnostus*?) as well as brachiopods, hyoliths and echinoderms.

The fauna of the Lippertsgrün Formation shares several trilobite species known from the Skryje–Týřovice Basin and/or from the Ossa–Morena area of Spain (e.g. *Sao hirsuta*, *Peronopsis umbonata*, *Condylopyge rex*, *Pleuroctenium granulatum*).

Saxothuringia–Lusatia and NW Saxony

The 'lower' Cambrian succession in this area differs from the development in Bohemia by an apparent dominance of carbonate sedimentation. However, clear similaries do exist in the Delitzsch–Torgau–Doberlug Syncline, where the 'lower' Cambrian Zwethau Formation (composed of shallow-marine carbonates and siliciclastic deposits) is overlain by the 400 m thick fossiliferous Tröbitz Formation, composed of quartzitic sandstones alternating with micaceous claystones containing trilobites (*Paradoxides*, *Condylopyge*, *Ornamentaspis*). The environment has been interpreted as a quiet siliclastic shelf. The overlying 350 m thick sequence of quartzitic sandstones alternating with micaceous claystones with trilobites (*Paradoxides*, *Ellipsocephalus*, *Bailiella*, *Solenopleura*, *Badulesia*, *Condylopyge*) is assigned to the Delitzsch Formation (Buschmann *et al.* 2006). Trilobite taxa are not decisive from palaeogeographical point of view, as almost all of them occur also in Baltica, Britain, Newfoundland and/or Spain and France.

The 'middle' Cambrian faunas from shallow-marine sandstones, siltstones and greywackes are dominated by poor brachiopod associations and/or by moderately diversified trilobite associations. The oldest assemblages consist of typical Mediterranean-type genera clearly indicating the West Gondwanan affinity, namely to some regions in Spain. In younger levels trilobite taxa characteristic of Baltica and Avalonia appear successively. A similar scheme is known from the Franconian Forest (Elicki *et al.* 2008), whereas in the Delitsch Syncline the poor fossil content excludes discussion of palaeogeographical relationships of this area.

Sources of the Perunica Ordovician fauna

The earliest Tremadocian fauna in the Prague Basin comprises diverse immigrants into the basin. Unfortunately, there is no information about biota from the deeper outer shelf facies surrounding Perunica in this time. The olenid Biofacies is missing in the Prague Basin, and the other deep-water facies of Perunica, most probably present under the Cretaceous in northern Bohemia, are unfossiliferous to very poorly fossiliferous (Fig. 10). In its Ordovician history, the faunas of Perunica were never isolated and never constitute distinctive and endemic and/or clearly different faunas from neighbouring terranes.

Along the West Gondwana periphery, represented mostly by cratonic North Africa, Iberia,

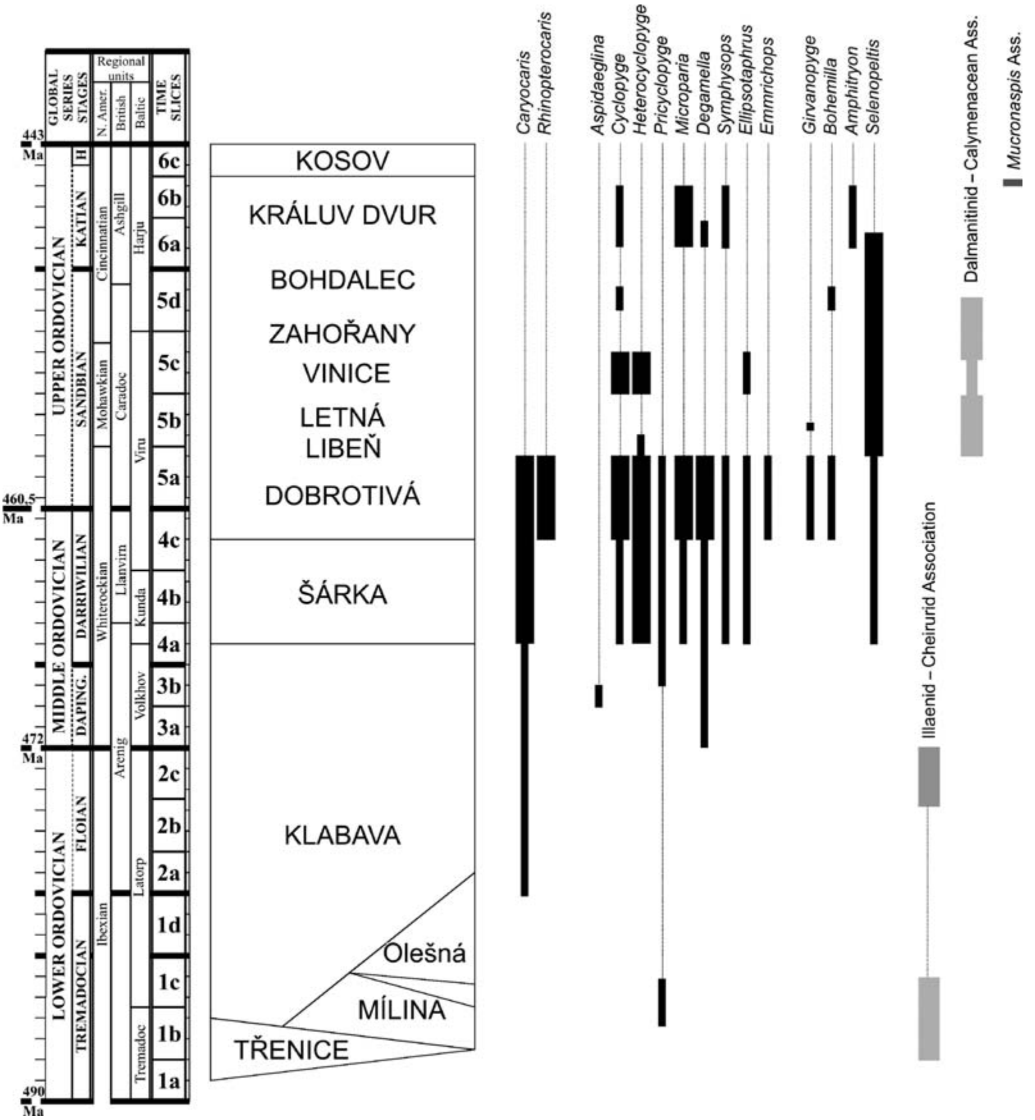

Fig. 10. Stratigraphy of the Ordovician in the Prague Basin (adopted after Havlíček 1982, 1998) with distribution of caryocaridids, supposed nektonic trilobites (cyclopygids, remopleurids, *Bohemilla* and *Selenopeltis*) and range of selected trilobite associations (after Chlupáč 1970 and Marek 1961).

Armorica *s.s.*, Thuringia, Perunica and other suspect terranes, there are only scarce data on late Cambrian and early Ordovician shelly faunas (Bassett *et al.* 2002). The brachiopods *Billingsella*, *Protambonites*, *Poramborthis* and possibly also *Jivinella* and a few trilobites are known in Iberia (Havlíček & Josopait 1972; Hammann 1974; Villas *et al.* 1995). *Billingsella* and *Saccogonum* are reported from late Cambrian sandstones of Morocco (Mergl 1983; Mergl *et al.* 1998) but both taxa have nothing in common with brachiopods of Perunica in the early Ordovician. Early Tremadocian faunas of the Montagne Noire and the Iberian Chains (Courtessole & Pillet 1978; Hammann *et al.* 1982) have olenids, *Angelina*, *Parabolina*, *Triarthrus* and *Shumardia*, which all are missing in Perunica. A small trilobite fauna with *Bavarilla*, *Parapilekia* and *Parabathycheilus* remarkably similar to the fauna of Perunica is reported from Mauritania (Destombes *et al.* 1969). There is increasing evidence that some brachiopods of Perunica had ancestors and relatives in much more distant regions of Gondwana. New records by Benedetto (2007) from the Precordillera of Argentina indicate, together with the older published data (Havlíček & Branisa 1980) that some brachiopods formerly considered to be typical of Perunica (*Apheoorthina*, *Euorthisima*, *Kvania*, *Poramborthis*, *Robertorthis*) have ancestors in this distant region. Rich '*Dalmanella*-shaped small brachiopods' from the Precordillera are representatives of the initial orthide radiation, which took place in a temperate climate and in neighbouring Laurentia. A similar seaway may be proposed for ancestors of other early Ordovician orthid brachiopods of Perunica, namely *Apheoorthina*, *Eoorthis* and the billingsellacean *Protambonites*. Havlíček (1949*a*, 1977) noted that the closest relatives of these genera should be sought among the Late Cambrian brachiopods of Laurentia. Some of these genera (*Jivinella*, *Euorthisima*) reached low-latitude South China as early as in the Arenig.

Large lingulate brachiopods, which are a dominant component of the earliest shallow-water benthic association in Perunica, were probably derived from a low-diversity lingulate fauna in cratonic basins of West Gondwana. Shallow-water lingulate brachiopod faunas of the late Cambrian and early Ordovician in Baltica, containing *Ungula*, *Obolus*, *Schmidtites*, *Helmersenia*, etc. (Popov *et al.* 1989) are very different from the fauna of Avalonia, the ATA, and Perunica, indicating the existence of an ocean barrier wide enough to prevent larval passage and successful settling in this time. The late Cambrian and early Ordovician successions of cratonic West Africa and the ATA contain low-diversity associations with large lingulates, partly reviewed by Cocks & Lockley (1981) and Havlíček (1989). Some of them are probable ancestors of the remarkably rich lingulate brachiopod fauna of Perunica.

A remarkably rich suite of micromorphic lingulate brachiopods appeared in late Tremadocian and early Floian times (Fig. 11b). This fauna, living on fine sands in a subtidal environment, shows remarkably high diversity and is very similar to the *Leptembolon* Fauna reported originally from the St. Petersburg area (Gorjansky 1969) and the Holy Cross Mountains of Poland (Bednarzcyk 1964). Also, some micromorphic brachiopods of the Bjorkasholmen Limestone (*Pomeraniotreta*, *Myotreta*, *Dactylotreta*, *Elliptoglossa, Siphonotretella*, etc.) of south Scandinavia (Popov & Holmer 1994) are common in the *Leptembolon* Fauna of Perunica (Mergl 2002). A fauna with common *Hyperobolus* is also known from slightly younger strata in the South Urals (Popov & Holmer 1994). The geographical distribution of these lingulate brachiopod-dominated faunas indicates easy dispersion of brachiopods, similar climatic conditions and reduction of geographical barriers between Perunica and facing margins of Baltica in the late Tremadocian–Floian interval.

Unlike lingulate brachiopods, the earliest rhynchonelliformean brachiopod faunas of Perunica contain eoorthids of restricted occurrence (*Roberorthis*, Apheoorthina, *Jivinella*), but also early plectorthids that are abundant in the late Cambrian and Tremadocian of Argentina (*Kvania*). Syntrophiids (*Poramborthis*) and billingsellids (*Protambonites*) have relatives in the Iberian Peninsula and South Urals (Popov *et al.* 2001). Other orthid taxa present in Perunica (*Ranorthis*, *Angusticardinia*) are known in younger beds in the Lower Ordovician successions of Estonia and the St. Petersburg area. The similarity is thus merely a mixing of Gondwanan taxa, some of which reached Baltica near the end of the Early Ordovician. The brachiopod fauna indicates a somewhat mild climate in Perunica in the Tremadocian and Floian.

The first Ordovician trilobites appeared in Perunica together with the earliest eoorthids, plectorthids and diverse lingulates in the Late Tremadocian. The illaenimorph *Hemibarrandia*, the large cheirurid *Parapilekia*, and the probable eurekiid *Holubaspis* were dominant in the remarkably diverse trilobite assemblage. Apart from the cosmopolitan *Apatokephalus*, *Ceratopyge*, *Dikelokephalina, Harpides*, *Proteuloma*, *Platypeltoides* and *Geragnostus*, there are genera of likely Gondwanan origin. *Agerina* is known from Argentina, Bavaria and Sweden. *Anacheirurus* has been reported from Bavaria, Spain and England. The endemic Gondwanan *Bavarilla* has been reported from Bavaria and Mauritania, and *Parabathycheilus* is known from Spain, Bavaria and Mauritania, but extended to China in the Arenig. There are only a few truly endemic taxa in Perunica. The orometopid *Celdometopus* is most similar to the rare Baltic *Pagometopus*. The earliest known lichids *Holoubkovia* and *Lichekephalus* are endemic. *Holoubkocheilus* and *Pharostomina* show close affinity to other ancient Gondwanan calymenaceans. In its overall composition the trilobite fauna of the Tremadocian is closely comparable with the illaenid–cheirurid Biofacies of the low-latitude early Ordovician (Fortey 1975), but the *Hemibarrandia–Parapilekia* Association of Perunica is complemented by calymenacean taxa and the earliest cyclopygids. These two latter groups clearly identify the Gondwanan affinity of Perunica trilobite associations, but also the opening of its shelves to incidental immigrants from neighbouring areas (Sdzuy *et al.* 2001).

The Floian and Dapingian brachiopod faunas of Perunica retain some endemic elements (*Jivinella*, *Poramborthis*, *Prantlina*, *Nocturnellia*, *Ferrax*,

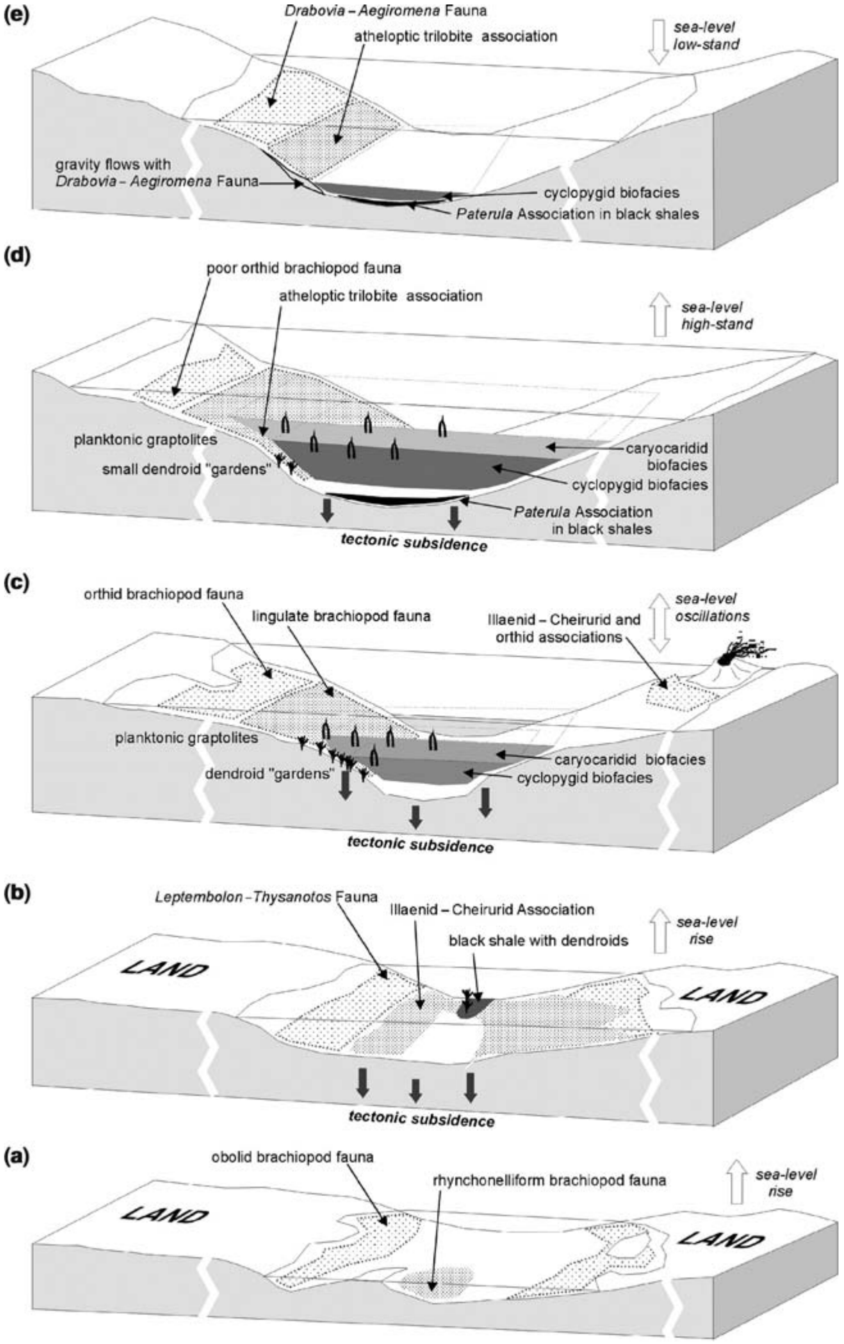

Fig. 11. Diagrammatic history of the Prague Basin and its faunal associations of the Ordovician to early Silurian. Only the left (NW) slope of the basin is mostly illustrated, for simplification. Palaeoecological terminology is adopted from Chlupáč (1965), Havlíček (1982), Štorch & Mergl (1989), Mergl (1999), Štorch (2001) and Mergl *et al.* (2007). (**a**) Early(?) and Middle Tremadocian: Třenice Formation. Transgression with the onset of lingulate brachiopod associations (*Hyperobolus* Community, *Westonisca* Community) and poor rhynchonelliform brachiopod associations (*Poramborthis* Community). Affinity to other Gondwanan faunas. (**b**) Late Tremadocian and Floian: Mílina Formation and Olešná Member of the Klabava Formation. Transgression and deepening of the basin associated with

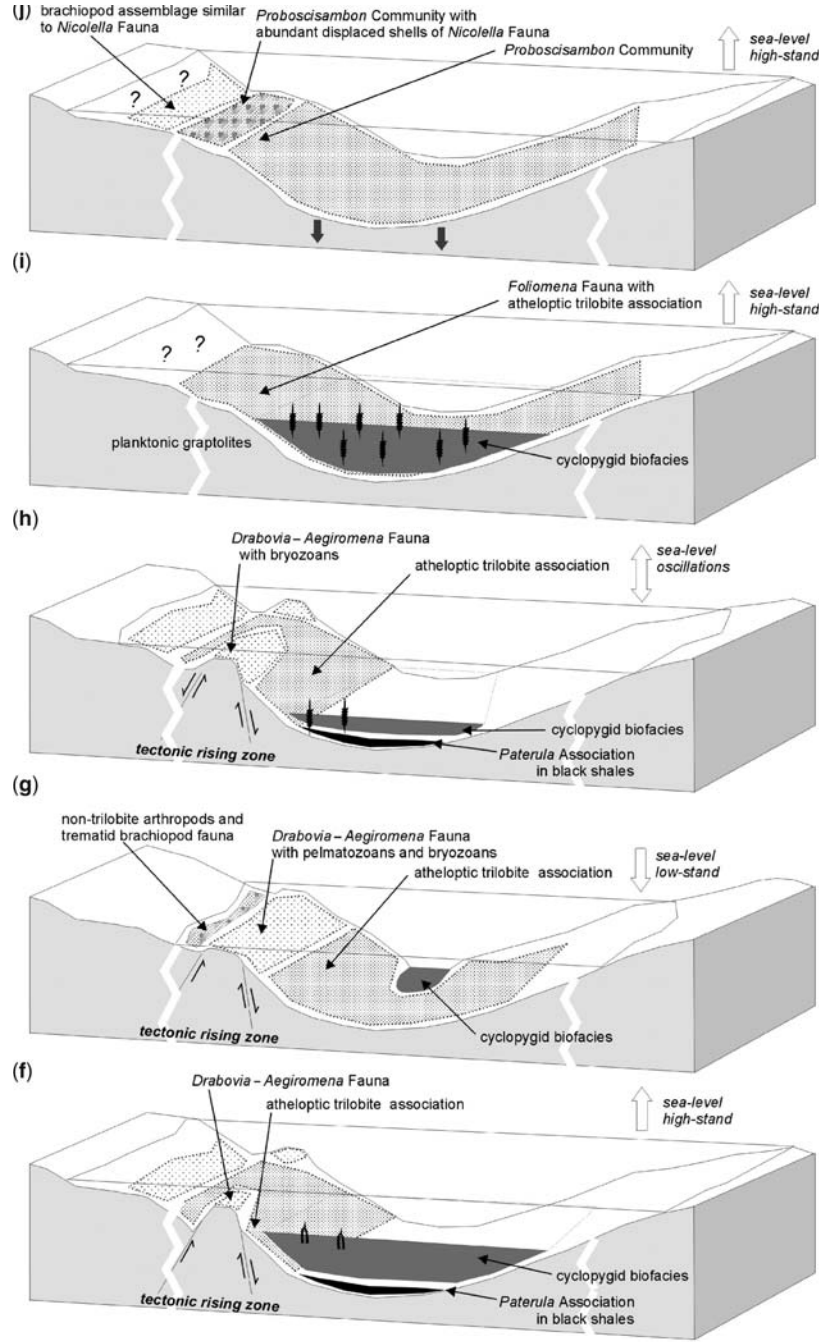

Fig. 11. (*Continued*) diverse lingulate brachiopod associations (*Leptembolon–Thysanotos* Association), diverse trilobite associations (*Hemibarrandia–Parapilekia* Association and a deeper *Proteuloma–Ceratopyge* Association) and black shales with dendroids in NE part of the basin. Affinity both to Baltic and West Gondwanan fauna.
(**c**) Dapingian: Middle and Upper Klabava Formation. Deepening and differentiation of the basin with diverse lingulate and rhynchonelliform brachiopod associations (*Acrotreta* Community, *Rafanoglossa* Community, *Nocturnellia* Community, *Nereidella* Community), diverse trilobite associations (*Pliomerops* Association, Asaphid Association, and the offshore *Euloma* Association); rich benthic dendroid ‘gardens’, diverse planktonic graptolites, and Caryocaridid and

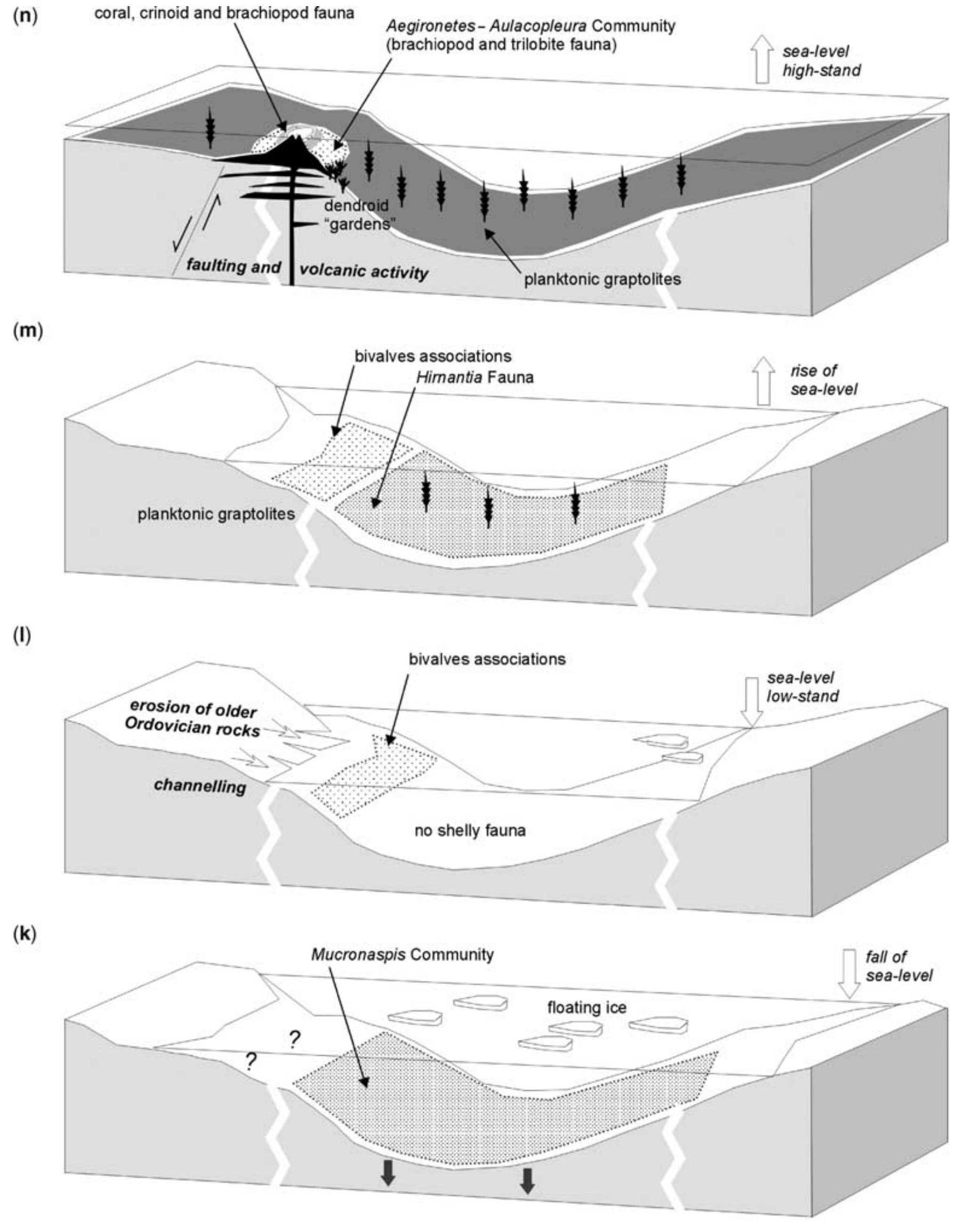

Fig. 11. (*Continued*) Cyclopygid Biofacies. High endemicity and decreasing influence of Baltic fauna. (**d**) Darriwilian: Šárka and Dobrotivá formations. Maximum deepening and differentiation within the basin, with the onset of poorly oxygenated waters. Early *Aegiromena–Drabovia* Fauna with poor 'brachiopod' association (*Tigillites* Community with *Tissintia* and *Tafilaltia*), offshore brachiopod *Euorthisina* Community and *Paterula* Community, atheloptic trilobite association (*Placoparia* Community); poor benthic dendroid 'gardens', poor planktonic graptolites, and peak of both the Caryocaridid and Cyclopygid biofacies. Increasing influence of Gondwanan fauna. (**e**) Early Sandbian: Libeň Formation. Shallowing of the basin, the onset of mature quartzitic inshore sands and poorly oxygenated waters in deep offshore. *Aegiromena–Drabovia* Fauna with rich brachiopod association (*Drabovia* Community) and the inshore trilobite Dalmanitinid–Calymenacean Association, the poor offshore atheloptic trilobite association, and the

Styxorthis), but with an abundance of *Nereidella* and *Ranorthis* in shallow lithofaces, genera described originally from South China and Baltica, respectively, demonstrating a more cosmopolitan character of the fauna. As mentioned above, *Poramborthis* is characteristic of the Tremadocian brachiopod fauna of Perunica but it also persisted to the Dapingian. This genus was described as an aberrant orthid (Havlíček 1949*a*, 1977) but now (unpublished) it is considered to be an early syntrophiid close to *Tetralobula*, which is characteristic of Baltica and Laurentia. The presence of *Protambonites*, early syntrophiids and common taxa of the *Thysanotos* Fauna (including *Leptembolon* and *Thysanotos*, diverse micromorphic brachiopods such as *Dactylotreta*, *Pomeraniotreta*, *Acrotreta*, *Numericoma*, *Elliptoglossa*, the siphonotretids *Eosiphonotreta*, *Siphonotretella*, *Alichovia*, etc.) demonstrate a relationship to the Early and early Middle Ordovician fauna of Baltica, reviewed thoroughly by Popov & Holmer (1994), Egerquist (2004) and others. Stratigraphical records of the *Leptembon–Thysanotos* Fauna in Perunica predate the South Urals and East Baltic occurrences. Perunica seems to have occupied an intermediate position between Gondwana and Baltica in the Early Ordovician. *Thysanotos* and allied faunas probably originated in this peri-Gondwanan area, but *Thysanotos* as well as *Leptembolon* are unknown from the cratonic shelves of Gondwana (exemplified by North Africa) or Armorica. Perunica shelves were sources for later and generally brief passage of this fauna in nearby facing margins (the South Urals), and even more distant parts of Baltica (present East Baltic and the Holy Cross Mountains) and other distant terranes (Iran).

A unique trilobite fauna from the middle part of the Klabava Formation, dated approximately near the Floian and Dapingian boundary, and containing *Pliomerops*, *Ectillaenus*, *Cyrtometopus* and other aberrant but poorly known taxa (*Pseudopetigurus*, ?*Holubaspis*) are also suggestive of temperate illaenid–cheirurid associations (Fig. 11c). However, the faunal similarity between Perunica and Baltica decreased from the beginning of the Middle Ordovician. A rich Volkhov age brachiopod

Fig. 11. (*Continued*) Paterula Community; absence of graptolites and poor Cyclopygid Biofacies. High affinity to Gondwanan fauna. (**f**) Early Middle Sandbian: Vinice Formation. Highstand of sea level and tectonic differentation of the basin, shoals on tectonically rising zones, and poorly oxygenated waters in deeper offshore. A rich *Aegiromena–Drabovia* Fauna (*Bicuspina* Community), less diverse trilobite Dalmanitinid–Calymenacean Association on shoals and atheloptic trilobite association with *Paterula* Community in deeper offshore; poor planktonic graptolites and Cyclopygid Biofacies. High affinity to Gondwanan fauna. (**g**) Early and late Middle Sandbian: Letná and Zahořany formations. Shallowing of the basin, quartzitic sands and greywackes inshore, siltstones offshore. *Aegiromena–Drabovia* Fauna with rich brachiopod associations (*Drabovia* Community, *Bicuspina* Community), non-trilobite arthropods and trilobite Dalmanitinid–Calymenacean Association inshore, and a poor atheloptic trilobite association offshore; rare graptolites and Cyclopygid Biofacies. High affinity to Gondwanan fauna. (**h**) Late Sandbian: Bohdalec Formation. Sea-level oscillations and tectonic differentation of the basin, shoals on tectonically rising zones, and poorly oxygenated waters in deeper offshore. A rich *Aegiromena–Drabovia* Fauna on shoals (*Hirnantia* Community of the so-called Polyteichus facies), less diverse benthic communities in moderately deeper environment (*Svobodaina* Community) with poor trilobite Dalmanitinid–Calymenacean Association and atheloptic trilobite association with *Paterula* Community in deep offshore; poor planktonic graptolites and poor Cyclopygid Biofacies. High affinity to Gondwanan fauna. (**i**) Katian: Králův Dvůr Formation. Highstand of sea level and well-oxygenated waters in deep offshore. Inshore fauna unknown. *Foliomena* Fauna (*Rafanoglossa* Community) and atheloptic trilobite association in deep offshore; abundant planktonic graptolites and rich and latest Cyclopygid Biofacies. Manifestation of the Boda event with the onset of temperate (e.g. Baltic) fauna. (**j**) Late Katian (Rawtheyan): uppermost Králův Dvůr Formation. Initiation of regression, well-oxygenated waters in deep offshore. Inshore fauna unknown, but represented by displaced shelly material. A diversified equivalent of the *Foliomena* Fauna (*Proboscisambon* Community), rich atheloptic trilobite association in deep offshore; absence of graptolites and cyclopygids. Termination of the Boda event combined with a clear affinity to temperate (e.g. Baltic) fauna. (**k**) Early Hirnantian: topmost Králův Dvůr Formation. Rapid regression, well-oxygenated waters in deep offshore. Inshore fauna unknown. Poor trilobite–ostracode fauna (*Mucronaspis* Community) with rare small brachiopods; absence of graptolites and cyclopygids. Initiation of glaciation followed by diamictite deposition, expressed by a cosmopolitan West Gondwana derived fauna. (**l**) Middle Hirnantian: Upper Kosov Formation. Maximum regression, erosion of older Ordovician rocks in coastal area. Inshore fauna unknown except bivalves in sandstones. Maximum glaciation, no palaeogeographical data. (**m**) Late Hirnantian: top of the Kosov Formation. Rapid sea-level rise, well-oxygenated waters in deep offshore. Inshore fauna of bivalves in sandstones. Taxonomically rich *Hirnantia* Fauna (*Hirnantia saggitifera* Community) with trilobites, bryozoans, gastropods etc.; planktonic graptolites rarely present. West Gondwana derived fauna showing affinity to low-latitude palaeocontinents. (**n**) Middle Llandovery: Želkovice Formation. Sea-level fall within general sea-level highstand, with benthic fauna on volcanogenic elevations above surrounding and poorly oxygenated waters of deeper sea. Taxonomically rich trilobite–brachiopod fauna (*Aegironetes–Aulacopleura* Community) with some elements of the *Hirnantia* Fauna, shallow-water crinoids and corals; rich dendroid 'gardens' and abundant and diverse planktonic graptolites in deeper, open-water sites. Probably West Gondwana derived fauna with many new subtropical elements.

fauna of the Baltic area is very diverse and different (Egerquist 2004).

Other evidence relating to the Early Ordovician affinity of Baltica and Perunica can be shown also with other invertebrate groups. Cystoids (*Echinosphaerites*, *Glyptosphaerites*, *Aristocystites*, *Palaeosphaeronites*), the gastropods *Mimospira* and *Modestospira*, the ascidian tunicate *Palaeobotryllus*, trepostomate bryozoans and ostracodes present in Perunica suggest a mild to temperate climate in the Early and early Middle Ordovician. One case of such a rich fossil association, the earliest brachiopod–bryozoan–pelmatozoan association reported from Ejpovice near the top of Dapingian (Mergl 2004), is a remarkable mixture of archaic lingulate brachiopods (e.g. *Orbithele*) with younger elements (bryozoans, hyolith *Quadrotheca*, gastropod *Mimospira*, etc.). At this time these taxa had their relatives in Baltica or other continents of the subtropical zone. In West Gondwana these genera are rare or absent. Palaeolatitudinal data for the late Cambrian and early Ordovician position of Perunica, despite some controversy (Tait *et al.* 1994; Krs & Pruner 1999), indicate low latitude at about 30°S (Krs *et al.* 1986*a*, *b*). Lithological criteria support a temperate climate in Perunica in the Early and early Middle Ordovician (see discussion by Havlíček 1999). Sedimentological data indicate intensive chemical weathering on the nearby land. There are abundant hematite beds in shallow-water sediments, with stromatolitic layers and rapid deposition of immature sands with hematite cement from nearby land. It is notable that rather diverse but as yet unstudied associations of conodonts occur in the Floian deposits of the Prague Basin (Fig. 11b). Younger, early Middle Ordovician rich conodont associations with some Baltica-related taxa (*Barrandegnathus*; Stouge 2005) have been described by Dzik (1983) from beds of late Arenig age (upper Klabava Formation below the late Arenig *Desmochitina bulla* Chitinozoan zone; Paris & Mergl 1984). Early to Late Ordovician chitinozoan assemblages contain typical peri-Gondwanan taxa (Paris 1990; Dufka & Fatka 1993; Fatka 1993). Abundant conodonts in the various lithofacies of the Klabava Formation could indicate mild or temperate climate.

The Mediterranean character of acritarch assemblages has been recognized by Vavrdová (1974*a*, 1997). The diverse late Early to Middle Ordovician acritarch assemblages contain typical peri-Gondwanan taxa (e.g. *Aureotesta* Vavrdová 1972; see Brocke *et al.* 1998; *Arbusculidium* Deunff 1968; see Fatka & Brocke 1999; *Dicrodiacrodium* Burmann 1968; see Servais *et al.* 1996; *Frankea* Burmann 1968; see Fatka *et al.* 1997) known from numerous localities in Gondwanan Africa and peri-Gondwanan Europe, and generally absent in Baltica (Brocke *et al.* 1995; Servais & Fatka 1997; Servais *et al.* 2000).

Middle Ordovician faunal turnover

Turnover of the faunal composition took place in Perunica during the Darriwilian (Šárka and Dobrotivá formations). Above the Šárka Formation, in the Dobrotivá Formation and especially with the beginning of sedimentation of the Libeň Formation, the trilobite and brachiopod faunas show considerable similarity to Armorican and other West Gondwanan faunas. However, the typical shallow shelf Gondwanan *Neseuretus* Biofacies never expanded as far as Perunica.

In Perunica, the first extensive onset of shallow subtidal ferrous sedimentation in the early Darriwilian was followed by sedimentation of mature quartzitic sands in shallow inshore shelf areas. Both lithofacies passed basinwards into thick clay sequences on a deep basinal floor, an environmental equivalent to an outer shelf (Fig. 11d). This situation persisted more or less continuously from the late Darriwilian to the very end of the Katian. During a highstand of sea level, continuous sedimentation of black shales in the basin was interrupted in its later stages by slumps of sands from shoals. The sands brought shelly material from shallower environments into different and often poorly oxygenated deep environments of the basinal floor. In lowstand periods the sandy beaches moved basinwards, and submarine elevations in tectonic-rising zones were eroded and/or formed small shoals suitable for occupation by relatively shallow-water brachiopod–bryozoan–pelmatozoan associations (Havlíček 1982). Sea-level changes were probably controlled by glacioeustasy combined with tectonism during the late Middle and early Late Ordovician, but unambiguous glaciomarine deposits are unknown in Perunica until the Hirnantian (Brenchley & Štorch 1989). Proliferation of the Early Ordovician epibenthic shallow-water lingulate brachiopod associations stopped from the beginning of the Darriwilian. Bivalves became significant at the same time on the shelves of both Gondwana and Perunica (Babin 1993). Such a reorganization of benthic associations is known also in other areas (Sanchez & Waisfeld 1995; Bassett *et al.* 1999; Sanchez *et al.* 1999; Popov *et al.* 2007) but in Perunica it also resulted in dramatic lithological change. The onset of pure quartzitic sands less suitable for infaunal lingulates began at this time. Only the large trematids *Drabodiscina*, *Trematis* and *Ptychopeltis* remained common in very shallow-waters, being often fixed to hard substrates. In the early Darriwilian, rhynchonelliformean brachiopod associations were taxonomically poor, based on immigrants from the West Gondwanan territory. *Eodalmanella* and *Euorthisina* are present exclusively in the deep-water environment of the Šárka Formation. *Brandysia* and *Benignites* are restricted to a similar environment of the Dobrotivá Formation, but the former is reported from deep-water deposits of North Spain (Gutiérrez-Marco *et al.* 1996). *Eodalmanella* was probably derived from the earlier local *Ranorthis*. *Euorthisina* shows much extensive stratigraphical and geographical distributions. It has been reported from the Early and early Middle Ordovician of Bolivia, Avalonia, Iberian Peninsula and cratonic North Africa (Havlíček 1971*b*; Havlíček & Branisa 1980; Robardet & Gutiérrez Marco 2004), but also from South China (Xu & Liu 1984), indicating its restriction to extensive and exclusively peri-Gondwanan regions. *Euorthisina* has never been reported from Baltica or other continents.

In the late Darriwilian and early Sandbian, the benthic faunas of Perunica became dominated by brachiopods of nearby Gondwanan origin. Heterorthids, draboviids, plectorthids and the plectambonitid *Aegiromena* became significant on the shallow shelves. *Tissintia* and/or *Tafilaltia* are reported from the late Darriwilian of more terranes (Armorica, Avalonia, NW Africa, Perunica; Havlíček 1971*b*, 1977; Villas 1985, 1992, 1995; Mélou *et al.* 1999). The next rapid geographical spread of mostly orthid-dominated, and probably cold-water-related brachiopod fauna, in Havlíček's (1989) definition the *Aegiromena–Drabovia* fauna, culminated in the Sandbian Stage. Many genera including the eponymous *Drabovia* and *Aegiromena* became widespread across cratonic West Gondwana and adjacent terranes, extending as far as Argentina and Bolivia (Havlíček & Branisa 1980), indicating a breakdown of geographical barriers. *Chrustenopora*, *Drabovia*, *Drabovinella*, *Gelidorthis*, *Hirnantia*, *Heterorthina*, *Heterorthis*, *Jezercia*, *Onniella*, *Saukrodictya*, *Svobodaina*, *Bicuspina* and *Aegiromena* are among the most significant taxa. These genera are represented in separate terranes and at particular stratigraphical levels by closely related but endemic species to the very end of the Katian. There are, however, genera with closely restricted occurrences and some of them are genuine endemics of cratonic Gondwana or neighbouring terranes in the Middle and early Late Ordovician. The orthid genera *Appollonorthis*, *Atlantida*, *Cacemia*, *Cilinella*, *Crozonorthis*, *Destombesium*, *Irhirea*, *Reuschella*, *Tarfaya* and *Tazzarinia* have very restricted distributions, probably controlled by climatic gradients. Most of these never reached Perunica and only *Cilinella* is endemic in the Prague Basin. In the *Aegiromena–Drabovia* Fauna, other groups of rhynchonelliform brachiopods are less common. There are some rhynchonellids (*Rostricelulla*), triplesiids (*Bicuspina*), plectambonitids (*Urbimena*) and strophomenids (*Rafinesquina*, *Blyskavomena*). The faunas of Perunica lack these taxa, with the exception of the almost cosmopolitan *Rafinesquina*. On the other hand, *Onniella* is unknown from Armorica and cratonic peri-Gondwana but it is common in Perunica and Avalonia. The similar but unrelated *Onnizetina* is present in Perunica and is reported later, in the late Katian, from the Carnic Alps (Havlíček *et al.* 1987).

Records of deep-water brachiopods are generally rare in preserved regions of Perunica, being represented by rare small lingulates among which *Paterula* is dominant, associated with small endemic plectambonitids (*Benignites*, *Urbimena*, *Sentolunia*). The presence of *Paterula* unambiguously indicates a deep, outer shelf environment; it is a genuine cosmopolitan genus, present along margins or in deep intracratonic basins of Laurentia, Baltica, South China, Avalonia and Perunica from the early Middle Ordovician to Middle Devonian (Mergl 1999).

The Middle Ordovician trilobite fauna of Perunica (Figs 12–14) is an example of the Dalmanitid–Calymenacean Fauna (Cocks & Fortey 1988). There are many genera in common with Armorica and cratonic Gondwana, but unlike the latter, trilobites known from the Prague Basin are generally of much deeper, offshore character. For instance, there are no records of the *Neseuretus* Fauna in Perunica. The *Neseuretus* Fauna is a typical inshore peri-Gondwanan fauna, known from a huge area in the late Middle Ordovician (see Cocks & Fortey 1988). A similar fauna is known even from low latitudes (Turvey 2002, 2005). The trilobites of the Šárka and Dobrotivá formations mostly belong to the atheloptic association of a deeper outer shelf (Havlíček & Vaněk 1990, 1996). This fauna has some common elements with an older fauna of the Montagne Noire and Wales (Dean 1966; Fortey & Owens 1978, 1987). Similarity should indicate easy exchange of mobile benthos along deep shelves and an ability to cross narrow barriers between small separate terranes (Avalonia, Armorica, Perunica and margins of cratonic West Gondwana). Migration of shelf biota between Perunica and Armorica has been noted by various workers, and the significance of currents has been emphasized (e.g. Gutiérrez-Marco & Rábano 1987; Gutiérrez-Marco *et al.* 1999). However, there are also significant differences. Apart from the typical and widespread peri-Gondwanan *Selenopeltis* and the genera *Placoparia*, *Ormathops*, *Colpocoryphe*, *Ectillaenus*, *Uralichas*, *Eoharpes*, etc., there are endemic taxa. Of them, the trinucleid *Trinucleoides reussi* is very abundant in the Šárka Formation. This genus is unknown outside Perunica and indicates that there were geographical barriers controlling

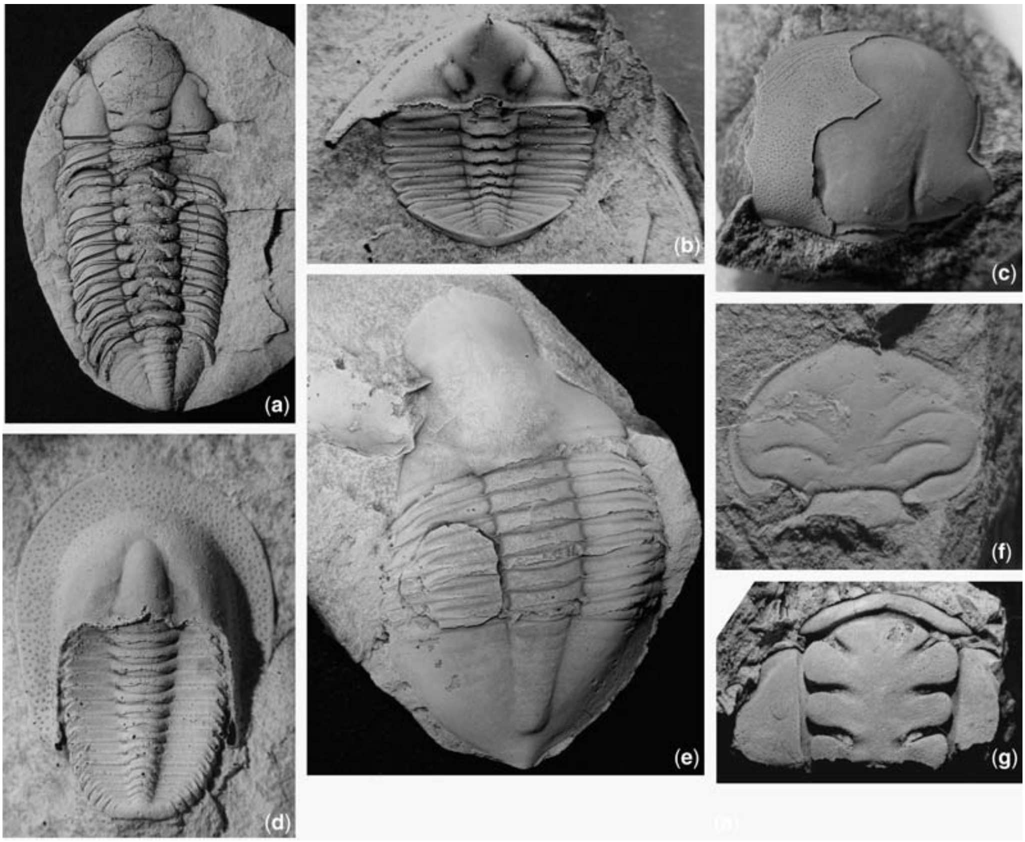

Fig. 12. Characteristic trilobites of the Dapingian (**g**), Darriwilian (**a**, **b**, **d**, **e**) and Katian (**c**, **f**) of Perunica. (a) *Ormathops atavus*, MBH 569, LS = 37 mm; (b) *Trinucleoides reussi* MBH 677, LS = 11 mm; (c) *Stenopareia oblita* PCZCU 1674, LS = 6 mm; (d) *Eoharpes benignesis* MBH 328, LS = 22 mm; (e) *Megistaspis aliena* MBH 9835, LS = 47 mm; (f) *Amphytrion radians* PCZCU 1673, LS = 6 mm; (g) *Pliomerops lindaueri* PCZCU 1672, LS = 15 mm. (a, b, d) Osek; (c) Levín; (e) Šárka; (f) Praha, Rajtknechtka; (g) Hlava u Komárova. LS, length of specimen.

the spread of benthic, deep-water taxa in the Middle and early Late Ordovician. This restriction demonstrates that deeper shelf conditions were not continuous from Perunica toward the margins of the Gondwana landmass, and barriers were effective in controling the spread of at least some deep-water taxa. Because climatic barriers are poorly manifested in a deep shelf environment, deep oceanic currents or a greater geographical distance between Perunica and other peri-Gondwanan terranes can possibly be invoked as a barrier. Typically deep-water outer shelf trinucleids are represented by endemic species in Perunica. The restricted occurrence of the orometopid *Celdometopus klouceki* is known already in the Tremadocian. *Bergamia agricola* and *Bergamia praecedens*, and similarly *Trinucleoides reussi* and *T. hostapulp*, are present in the Darriwilian. *Declivolithus alfredi*, *Marrolithus ornathus* and other species occur in the Sandbian, and *Marekolithus kosoviensis* is restricted in the Katian. High endemicity in species levels also existed among other trilobite groups of Perunica in the Sandbian and Katian (Šnajdr 1955). Shallow-water, sandy subtidal plains had suites of abundant phacopids (*Dalmanitina*, *Ormathops*, *Zeliszkella*), calymenaceans (*Calymenella*, *Colpocoryphe*, *Platycoryphe*, *Prionocheilus*), illaenids (*Cekovia*, *Stenopareia*, *Zbirovia*), cheirurids (*Actinopeltis*, *Eccoptochile*, *Eccoptochiloides*) and locally also trinucleids (*Onnia*) and odontopleurids (*Selenopeltis*, *Primaspis*). Unlike in Armorica and cratonic Gondwana, important shallow-water, inner shelf genera such as *Crozonaspis*, *Neseuretus*, *Eohomalonotus*, *Kerfornella*, *Salterocoryphe*, *Ogyginus*, etc. are absent in Darriwilian and Sandbian of Perunica. Their absence, and the endemic offshore trinucleids in the Prague Basin, indicate that some trilobite groups were not able to cross the barrier between

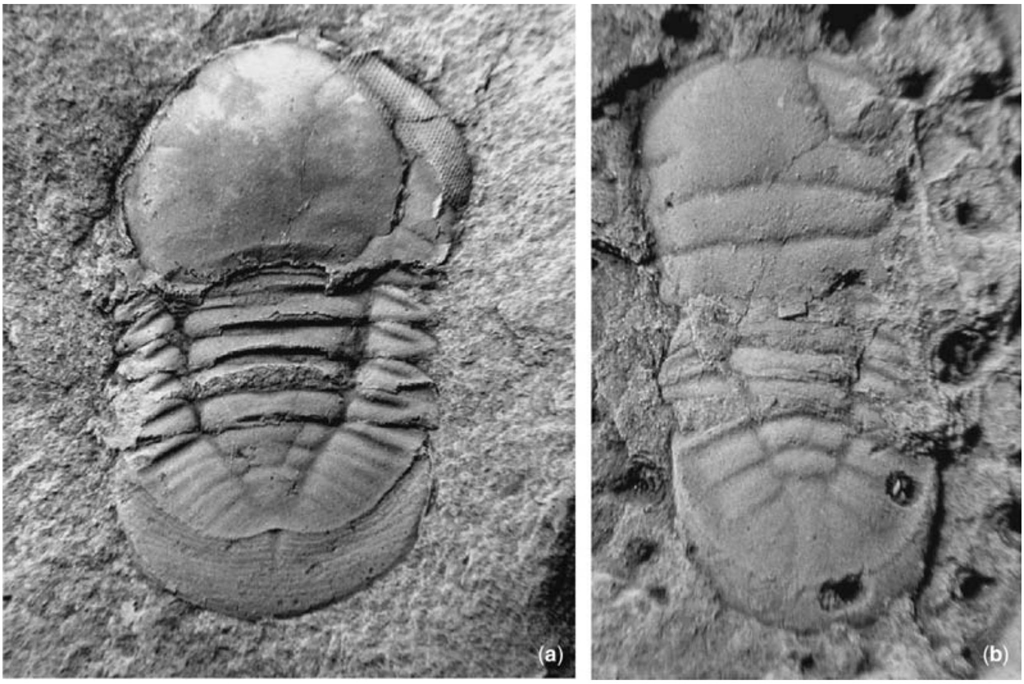

Fig. 13. Cyclopygids of Darriwilian age of Perunica. (**a**) *Microparia brachycephala* MBH 11659, LS = 14 mm; (**b**) *Ellipsotaphrus monophthalmus* MBH 328, LS = 8 mm. Both Dobrotivá Formation, Sedlec (Sutice).

Perunica and cratonic Gondwana and adjacent Armorica. In contrast to the Early Ordovician, the benthic macrobenthos of Baltica is very different from that of Perunica in the Middle Ordovician (see Cocks & Fortey 1998; Fortey & Cocks 2003).

The Boda event in Perunica

A change in the benthic fauna of West Gondwana and Perunica took place following the climatic event in the Katian (near the Caradoc–Ashgill boundary). The warming event in the West Gondwanan area (Boucot *et al.* 2003), also named the Boda event (Fortey & Cocks 2005) brought many shallow-water taxa from the temperate zone southwards towards the landmass of Gondwana. The brachiopods *Cliftonia*, *Dolerorthis*, *Eoanastrophia*, *Hedstroemina*, *Iberomena*, *Leangella*, *Leptaena*, *Longvillia*, *Mcewanella*, *Nicolella*, *Oxoplecia*, *Porambonites*, *Ptychopleurella* and *Triplesia* appeared for the first time in terranes located near or on the platform of West Gondwana (Havlíček 1981; Villas 1985; Mélou 1990; Leone *et al.* 1991). This *Nicolella* Fauna is also rich in other macroinvertebrates, with trilobites, ostracodes, machaeridians, bryozoans, cystoids and other groups. Conodonts are reported from Libya, the Iberian Chains, the Armorican Massif and Sardinia (see Paris *et al.* 1981; Ferreti *et al.* 1998). Trilobites clearly demonstrate climatic amelioration, with the Laurentian genus *Heliomera*, abundant odontopleurids, lichids and proetids (Hammann 1992; Hammann & Leone 1997), but mixed with taxa of Gondwanan origin such as calymenaceans. Bryozoan–cystoid reefs appeared at this time on the northern Gondwana platform (Vennin *et al.* 1998).

The polarward expansion of the low-latitude fauna is manifested also in the deep-water biota. The *Foliomena* Fauna first occurred in the early Late Ordovician in low latitudes (South China, Sibumasu), becoming widespread in the Sandbian and early Katian in deep-waters of temperate and tropical palaeocontinents (Baltica, Avalonia) and extending also to high latitudes (see Rong *et al.* 1999). In West Gondwana, the *Foliomena* fauna is known only from Sardinia (Villas *et al.* 2002) and Perunica; remaining areas of West Gondwana have extensive shallow shelves above the depth occupied by the *Foliomena* fauna. Palaeogeographical relationships of Perunica are thus obscured by differing lithologies and varied depth-related faunas. In Perunica, deep-water sites on outer shelves were first occupied by sparse faunas with *Chonetoidea* and *Cyclospira*, associated with abundant ostracodes and minute lingulaceans. *Dedzetina*, *Foliomena*, *Karlicium*, *Kozlowskites* and

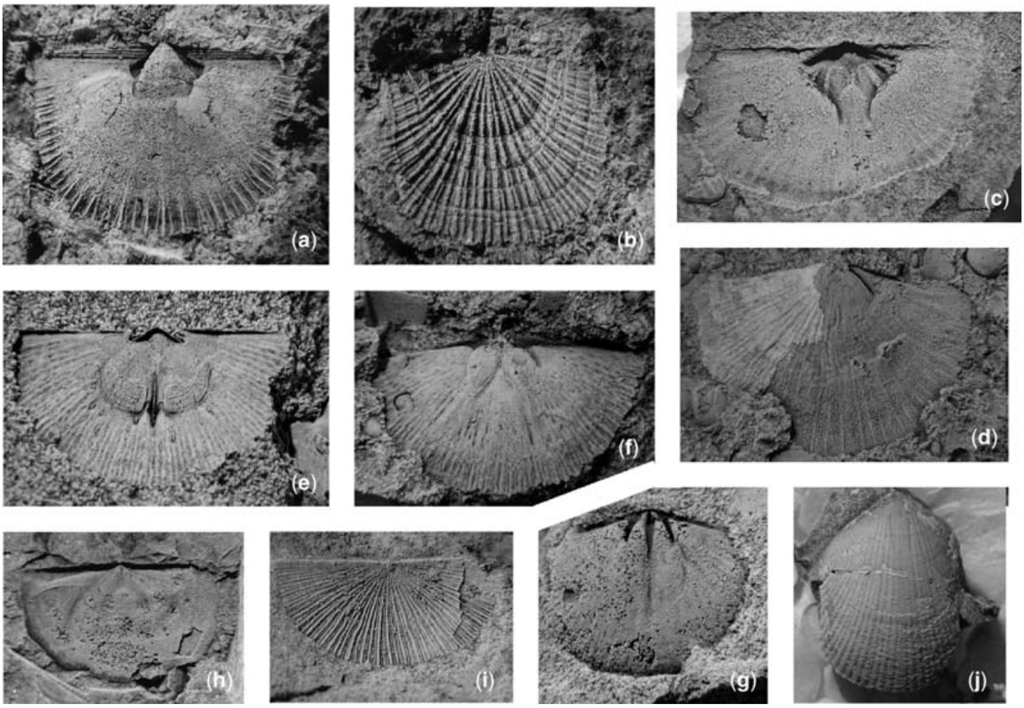

Fig. 14. Examples of endemic, Gondwanan, and cosmopolitan brachiopods of the Dapingian (**a**, **b**) Sandbian (**c**–**g**) and Katian (**h**–**j**) of Perunica. (a, b) endemic *Ferrax ooliticus*, PCZCU 1682, PCZCU 1683, LS = 9 mm, LS = 11 mm ventral valve and exterior of dorsal valve; (c, d) endemic *Blyskavomena blyskavense*, ventral and dorsal valves, PCZCU 1684, PCZCU 1685, LS = 9 mm, LS = 7 mm; (**e**, **f**) Gondwanan *Aegiromena praecursor*, ventral and dorsal valves PCZCU 1686, PCZCU 1687, LS = 6 mm, LS = 5 mm; (g) Gondwanan *Hirnatia kinneloides* PCZCU 1688, LS = 8 mm; (h) cosmopolitan *Foliomena folium*, PCZCU 1689, LS = 5 mm; (i) cosmopolitan *Chonetoidea radiatula*, PCZCU 1690, LS = 3 mm; (j) endemic *Ornothyrella ornatella*, PCZCU 1691, LS = 11 mm. (a, b) Hlava, Klabava Formation; (c–g) Letná F., Loděnice; (h–j) Levín, Králuv dvůr Formation.

Leptestiina appeared at about middle part of the Králův Dvůr Formation (Fig. 14); such taxa provide good correlation with the Boda event. The *Foliomena* fauna in the Prague Basin is less diverse, lacking *Christiania*, *Cyclospira*, *Sowerbyella* and other taxa known elsewhere (see Rong *et al.* 1999; Villas *et al.* 2002). Trilobites accompanying these small brachiopods constitute a typical atheloptic assemblage, with the trinucleid *Tretaspis anderssoni* and abundant, probably pelagic *Amphitryon*. Diverse cyclopygid trilobites are abundant (Marek 1961). Unlike in the earlier Ordovician, there are no records of a shallow-water fauna through almost the total thickness of the Králův Dvůr Formation, and comparison of the Perunica fauna with shallow shelf faunas of neighbouring terranes, including cratonic West Gondwana, is problematical. However, some links can be traced with the deep-water fauna of Baltica, because of the presence of *Tretaspis andersonni*, a common species in the Oslo region and Poland. This similarity is probably a result of climatic amelioration and spread of temperate fauna rather than palaeogeographical proximity of Perunica and Baltica, but some diplacement of Perunica to lower latitude and towards Baltica cannot be excluded.

Near the top of the Králův Dvůr Formation, representing the latest Katian in the Prague Basin, there is a distinct lithological change (Štorch & Mergl 1989). A unique calcareous claystone has yielded an abundant and remarkably diverse benthic fauna (*Proboscisambon* Community; Havlíček 1982) containing the distinctly Gondwanan *Jezercia*, a rare endemic *Boticium*, and with minute-sized and remarkably diverse small dalmanellids and plectambonitids (*Ravozetina*, *Salopina*, *Proboscisambon*, *Anoptambonites*, *Aegironetes* and *Kozlowskites*). Less common are brachiopods displaced from shallower sites (*Leptaena*, *Cliftonia*, *Cryptothyrella*, *Epitomyonia* and *Eoanastrophia*). Trilobites are richly diverse and very different from those in older beds; they include *Actinopeltis*, *Bojokoralaspis*, *Decoroproetus*, *Dindymene*, *Duftonia*, *Gravicalymene*, *Marekolithus*, *Mucronaspis*, *Staurocephalus*, *Stenopareia* and *Zetaproetus*, but *Tretaspis*, *Amphitryon* and cyclopygids are already absent. Although this fauna is of distinctly deep-water character, it provides evidence of a warming event in Perunica. Common proetids, odontopleurids and other peculiar trilobites (*Phillipsinella*, *Trochurus*) are associated with abundant machaeridians, diverse ostracodes, bryozoans, cystoids and other echinoderms (*Mespilocystites*), a hyperstrophic gastropod *Mimospira*, and many other macroinvertebrates. The fauna contains many endemic species and can be considered as a stratigraphically younger and a somewhat deeper-water analogue of the *Nicolella* Fauna of SW Europe. The most diverse assemblages of this fauna in Perunica contain a higher proportion of shallow-water elements (large brachiopods, bivalves), occurring in the NE margin of the Ordovician deposits, indicating the presence of now eroded shallow-water deposits far toward the SE. The *Proboscisambon* Community fauna is the last manifestation of the Boda event in Perunica. The *Foliomena* Fauna reported from Sardinia (Villas *et al.* 2002) above the *Nicolella* Fauna shows some similarity to the *Proboscisambon* Community. In Sardinia, the *Foliomena* Fauna is associated with *Jezercia*, *Epitomyonia* and *Skenidioides*, and is situated directly above the *Nicolella* Fauna and indicates a shoreward position (see Rong *et al.* 1999).

Climatic changes in the Hirnantian

Rapid climatic deterioration, sea-level fall and draining of the shallowest inshore areas drastically affected the fauna in Perunica and neighbouring terranes in the early Hirnantian. A low-diversity *Mucronaspis* Fauna appeared in the Prague Basin (Štorch & Mergl 1989), containing only *Mucronaspis*, *Duftonia* and a taxonomially poor associated fauna. This cool- or cold-water fauna is also known in other palaeocontinents, being reported from cratonic Gondwana, Baltica, South China and the margins of Laurentia (see Owen *et al.* 1991). However, the *Mucronaspis* Fauna is unknown in the ATA. In the Hirnantian the shallow shelves of the ATA were drained and karstification of the Katian limestones took place there. The appearance of the *Mucronaspis* Fauna in the Prague Basin is marked by an increase of bivalves and sudden and almost total disappearrance of brachiopods. Hitherto undescribed minute *Disprosorthis* and *Fardenia* have been recorded. This sparse association is known also in marginal basins of Laurentia (Harper *et al.* 1994) and indicates that Perunica might have been situated in lower latitudes than could be deduced from the presence of diamictites just above the levels with the *Mucronaspis* Fauna. Sedimentation of diamictites had a fatal impact on the biota of Perunica and shelly faunas totally disappeared there (Štorch 1990; Brenchley *et al.* 1991).

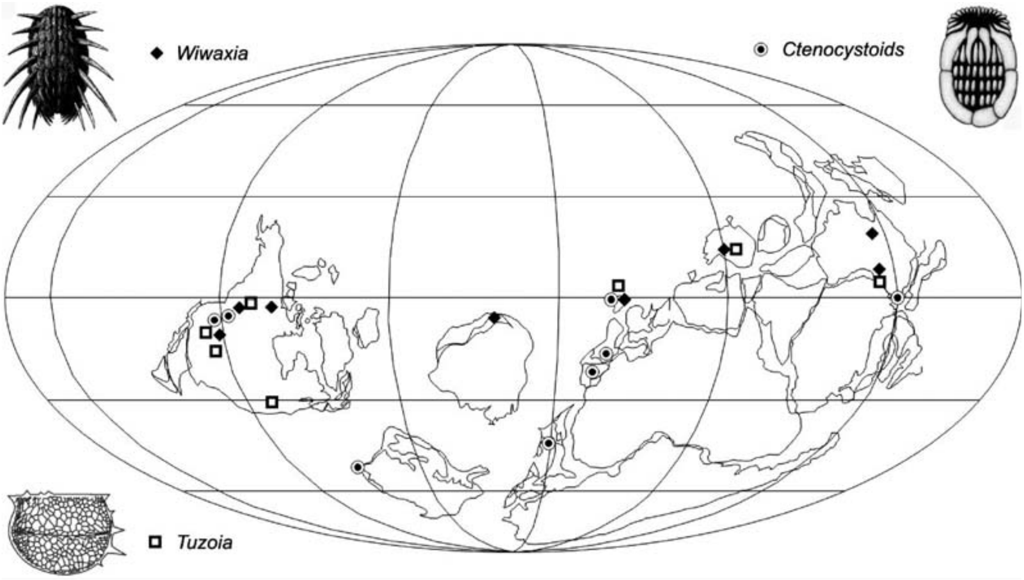

Fig. 15. Palaeogeographical distribution of the enigmatic genus *Wiwaxia*, ctenocystoid echinoderms and the bivalved crustacean genus *Tuzoia* in the 'early' and 'middle' Cambrian (adopted after McKerrow *et al.* 1994; Vannier *et al.* 2007; Fatka *et al.* 2009).

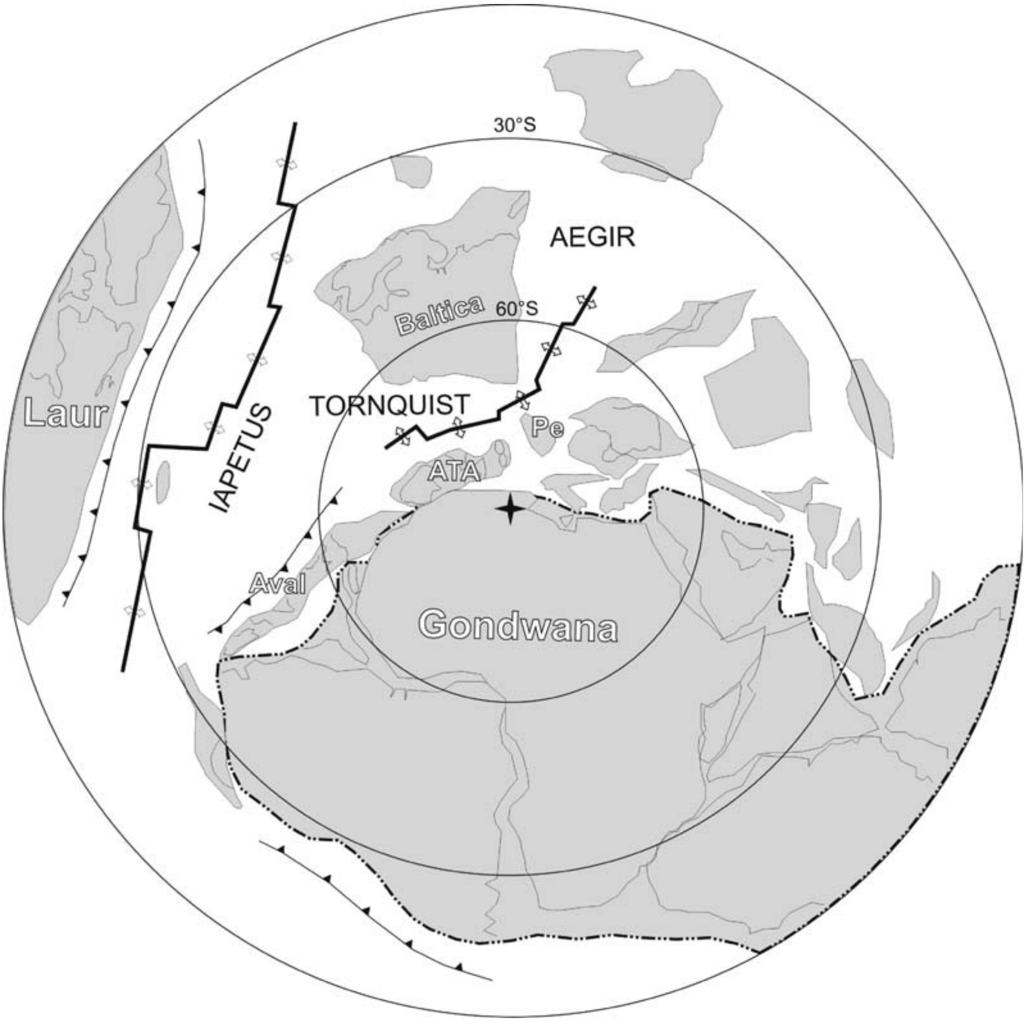

Fig. 16. Late Cambrian palaeogeographical reconstruction of the southern hemisphere modified from Cocks & Torsvik (2002, 2006). Laur, Laurentia; ATA, Armorican terrane assemblage; Aval, Avalonia; Pe, Perunica.

Recovery of the brachiopod-dominated fauna after melting of glaciers in the late Hirnantian is well documented in the Prague Basin (Štorch 1986). Inshore bivalve-dominated sandy beaches are followed by clayey sedimentation with a remarkably rich shelly fauna. Its composition and diversity is comparable with the rich *Hirnantia* fauna of the Kosov Province and is characteristic of the temperate zone, with the most common taxon being *Dalmanella testudinaria*. The fauna of Perunica is more diverse than the coeval poor fauna of the polar Bani province, which is reported from cratonic North African Gondwana and Armorica. Common taxa are *Hirnantia sagittifera*, associated with *Dalmanella*, *Comatopoma*, *Draborthis*, *Giraldibella*, *Kinella*, *Ravozetina*, *Trucizetina*, *Cliftonia*, *Eostropheodonta*, *Leptaena*, *Leptaenopoma*, *Paromalomena*, *Plectothyrella*, *Zygospira*, *Philhedra*, *Sanxiaella*, large glossellids, bryozoans, gastropods, etc. Trilobites are represented by *Mucronaspis*, *Brongniartella* and *Bojokoralaspis*.

The *Hirnantia* Faunas marginal to Gondwana are less diversified than in Perunica. A poor fauna has been reported from western Brittany (Mélou 1987) and in the central Anti-Atlas in cratonic West Gondwana. Taxa include *Hirnantia*, *Arenorthis*, *Destombesium*, *Eostropheodonta*, *Plectothyrella* and *Undithyrella*. *Plectothyrella* is represented by *P. lybica* and *P. chauveli*, which differ from *Plectothyrella crassicostis* in Perunica.

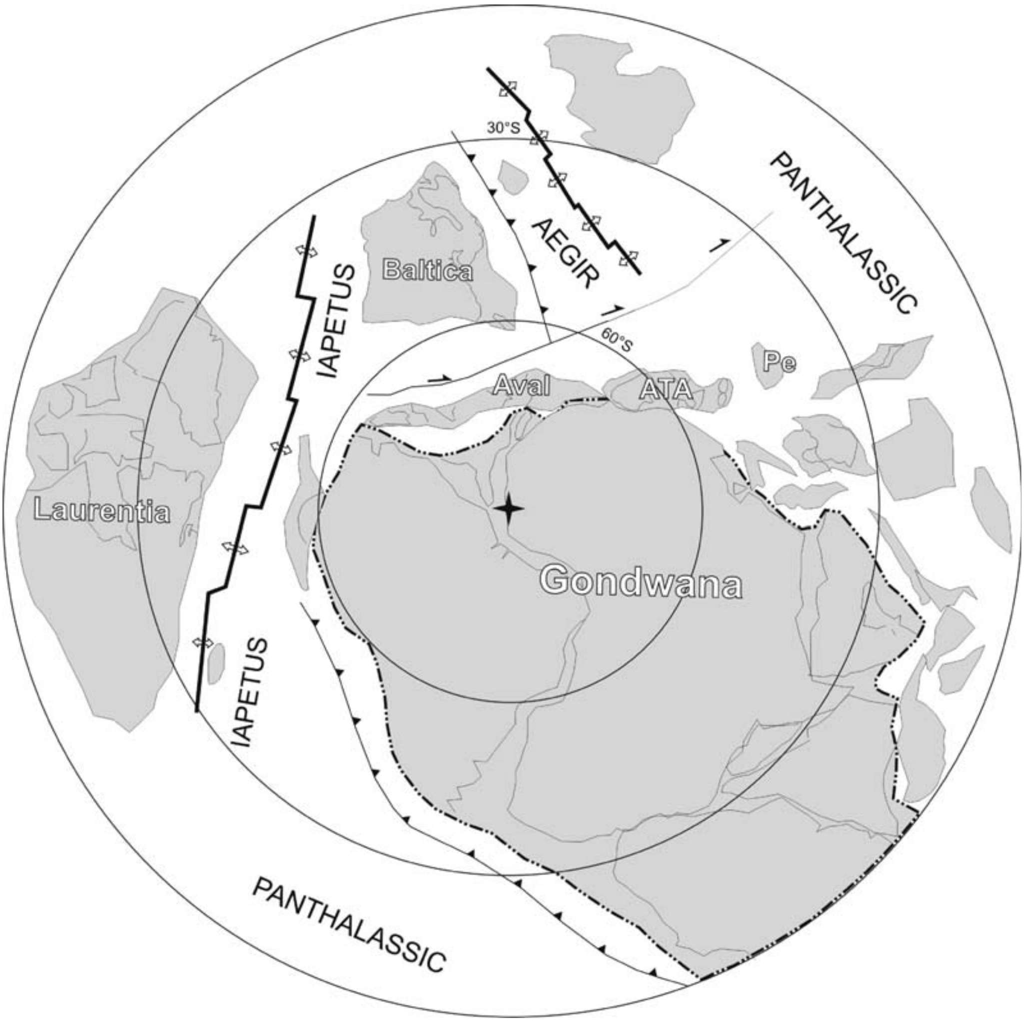

Fig. 17. Early Ordovician palaeogeographical reconstruction of the southern hemisphere modified from Cocks & Torsvik (2002, 2006).

P. crassicostis has been reported from other low-latitude palaeocontinents in the Hirnantian, including Baltica, Avalonia and marginal Laurentia. This led Havlíček (1990) to suggest a fairly temperate climatic position of Perunica in the Hirnantian, contrasting with the more boreal position of cratonic Gondwana and Armorica.

Northward shift of Perunica to low latitudes of the temperate zone, probably starting in the Katian, is evident from the composition of Llandovery (Aeronian) benthic faunas in the Prague Basin (see Štorch 2001). Besides trilobites, in which proetids, harpids, scutellids, lichids and odontopleurids predominate, favositid corals and brachiopods with a significant proportion of plectambonitids, strophomenids, rhynchonellids and atrypids appear. With these brachiopod groups some descendants of the Boda event are also present. *Jezercia*, *Saukrodictya*, *Epitomyonia*, *Hirnantia*, *Aegironetes* and *Proboscisambon* occur together with *Skenidioides*, *Dicoelosia*, *Dolerorthis* and *Stricklandia*. An offshore setting of this remarkable fauna is accentuated by the presence of the lingulate *Paterula*.

Conclusions

Perunica, as with a majority of other small independent terranes, experienced a dramatic paleogeographical history through the Late Precambrian and

Early Palaeozoic. Analyses of palaeontological content of the Cambrian and Ordovician sequences, combined with palaeomagnetic data, provide coherent datasets for possible positioning of Perunica during this time interval. Such analyses are biased by various factors, but recent evaluation of echinoderm, trilobite and brachiopod assemblages has provided a coherent picture of their distribution within inshore–offshore transects, which can be used reliably for restoration of palaeogeographical positions of the region.

In generally accepted reconstructions, the location of Perunica in very low (peri-equatorial) paleolatitudes during the 'early–middle' Cambrian times is clear (Fig. 15). This was followed by very rapid displacement of the terrane to higher, peripolar, latitudes during the late Cambrian (Fig. 16) and early Ordovician (Fig. 17). Such a European peri-Gondwanan story was constrained by the shift and rotation of the whole Gondwanan supercontinent in the southern hemisphere (Figs 16–18). Most areas with trilobite-bearing rocks of the Bohemian Massif were characterized by a gradual transfer from high polar paleolatitudes in the Late Ordovician (Fig. 18), through the cold and warm temperate belts during the Silurian to subtropical and tropical environments in the Devonian and Carboniferous, respectively. These changes had a crucial paleoenvironmental impact on the composition of trilobite assemblages that developed in this region.

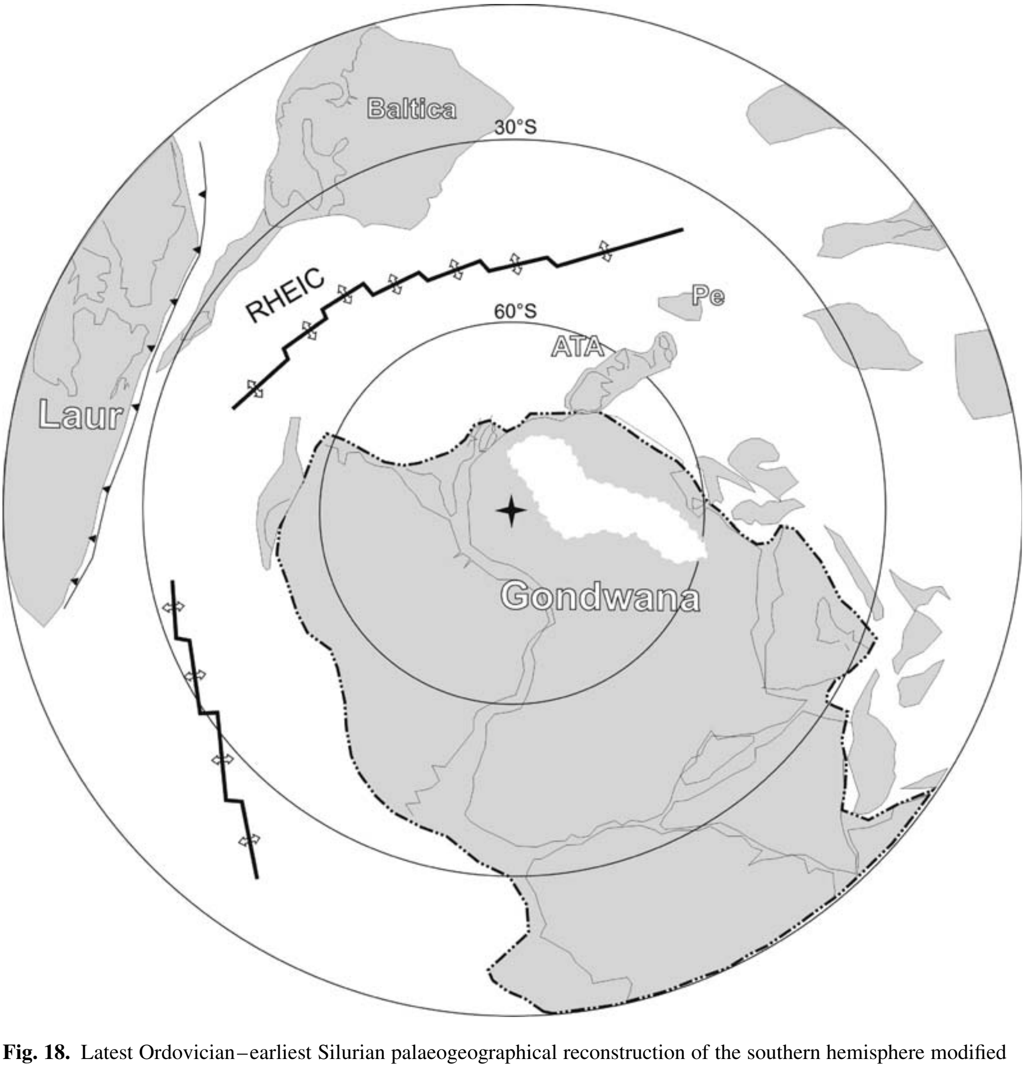

Fig. 18. Latest Ordovician–earliest Silurian palaeogeographical reconstruction of the southern hemisphere modified from Cocks & Torsvik (2002, 2006).

The palaeogeographical path of Perunica traces a shift from tropical to subtropical climate in the 'early' Cambrian to a temperate 'middle' Cambrian, which was followed by transfer to a cooler climate in 'late' Cambrian to Middle and early Late Ordovician times. The absence of Cambrian and Early Ordovician carbonates is consistent with the high imput of various but commonly weathered terrigenous material (as laterites).

Transgressive–regressive cycles make it possible to separate several depth-related assemblages in the Cambrian fauna of Perunica (Fatka *et al.* 2007). It is clear that shallower assemblages of agnostids can be classified as 'Mediterranean' and the deeper assemblages as 'Baltic' *sensu* Sdzuy (1972). Consequently, it is not possible to use such bathymetrically related forms for palaeogeographical interpretation. However, the tropical to subtropical position of Perunica is clearly indicated by the presence of climatically related taxa such as *Wiwaxia*, *Tuzoia* and ctenocystid echinoderms (Vannier *et al.* 2007; Fatka *et al.* 2009; Fig. 15). The absence of 'late' Cambrian faunas combined with shallow-water Tremadocian faunas minimizes any documentation of the following rapid shift to cooler latitudes. However, the comparatively warmest Ordovician climate was in the Floian and Dapingian, when diversity of invertebrates was remarkably high and some groups show a close relationship with Baltica. Climatic deterioration took place via a southward shift of Perunica from the Darriwilian. The generally cold-water character of Darriwilian assemblages is limited by the absence of shallow-water well-oxygenated facies in the basin mainly during Darriwilian and Katian times. The expansion of high-latitude Gondawanan faunas on siliciclastic shoals of Perunica and the generally deeper sedimentary regime with occasional dysaerobic conditions was characteristic until the Late Ordovician. Perunica appeared to be at about 60°S in the Middle Ordovician, but from that time a polarward path was reversed and Perunica began to move northwards. In the Katian, similar faunas to those of Baltica were related to position in a more or less comparable climatic belt and not be geographical proximity. As in other peri-Gondwanan sites, the Boda event led to the immigration of new faunal elements to Perunica. Despite the high-latitude position of Perunica in the Middle and early Late Ordovician, the new immigrants persisted until the drastic cooling at the beginning of the Hirnantian. Rapid melting of the ice sheet by the end of the Hirnantian brought a rich Hirnantian Fauna to Perunica shelves, including bryozoans, odontopleurid trilobites and gastropods. This rich fauna indicates relatively warmer climatic conditions compared with the poorer, more boreal Hirnantian Fauna of other parts of the ATA (e.g. Armorica *s.s.*) and North Africa. This is consistent with movement of Perunica northwards, probably to 50–40°S latitude. A rise of sea level then brought anoxia to Perunica and terminated the expansion of the Hirnantian Fauna. From the beginning of the Silurian, Perunica was flooded by anoxic seas and only some shoals on submarine volcanic elevations allowed the persistence of rich benthic faunas. Corals and rich brachiopod faunas of Llandovery age indicate a mild to subtropical climate, consistent with the continous shift of Perunica toward the Equator.

In general our analyses are in close agreement with Cocks & Torsvik (2002, 2006), but our data do not show any considerable distance from other segments of the ATA (Figs 16–18). Such a scenario is also consistent with the Nd–Sr–Pb isotopic record for Neoproterozoic to early Palaeozoic rocks of Perunica (Drost *et al.* 2004, 2007).

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Avalonia, Armorica, Perunica: terranes, microcontinents, microplates or palaeobiogeographical provinces?

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Abstract: In recent decades various research studies have focused on the reconstruction of Palaeozoic Europe, reflecting the complex geodynamic history related to the formation of the supercontinent Pangaea. It has been demonstrated that Palaeozoic Europe comprises a series of tectonostratigraphical units, or 'terranes', located between the remnants of three major palaeocontinents, Gondwana, Laurentia and Baltica. Some of these 'terranes' have been referred to as 'microcontinents', a typical (palaeo-)geographical term, and as 'microplates', a typical plate-tectonic term, giving rise to misunderstandings and a continuing scientific debate. This confusion is based primarily on an inconsistent use of different palaeogeographical terms by specialists from different scientific disciplines. Whereas large palaeocontinents such as Baltica and Siberia have been named as terranes by some workers, several peri-Gondwanan 'terranes' have been attributed to microcontinents or microplates, without conclusive reasoning. This paper is a critical review of the terminology used for three European peri-Gondwanan palaeogeographical entities: 'Avalonia', 'Armorica' and 'Perunica'. The review indicates that only Avalonia should be considered as a separate (micro-)continent on a separate (micro-)plate. Armorica has many different definitions and is commonly considered to be composed of several terranes. It is, however, not at all evident if Armorica was a separate (micro-)continent and/or an independent (micro-)plate. For Perunica, defined originally as a separate microplate, current evidence demonstrates that it can probably be considered only as a palaeobiogeographical province.

The Palaeozoic geodynamic history of Europe is very complex, resulting in an assemblage of numerous tectonostratigraphical units, or 'terranes', within the various Palaeozoic deformation belts. The reconstruction of the European peri-Gondwanan 'terrane map' is based on research encompassing various geological disciplines, including sedimentology, structural geology, palaeomagnetism and palaeontology.

In recent years, there has been debate on whether or not some of these terranes have been independent (micro-)continents or (micro-)plates. It appears that part of the debate is based simply on terminological misunderstandings between the different scientific disciplines. Terms such as terrane, (micro-) continent and (micro-)plate are used commonly by structural geologists in geodynamic reconstructions, whereas terms such as realm and province are used by palaeontologists in biogeographical reconstructions, describing the geographical distribution of fossil or living organisms. However, the terms microcontinent or even microplate are sometimes also applied in palaeobiogeographical scenarios, based on the spatial distribution of selected fossil groups, but without evidence from structural geology.

The misunderstanding or inadequate use of geodynamic, palaeogeographical and biogeographical terminology led to the interpretation of several 'terranes' as microcontinents or microplates without sufficient conclusive evidence. Most of these interpretations are based on evidence coming from a single discipline, commonly leading to an over-interpretation. In the last few decades, some of these postulated 'microcontinents' have been cited extensively in the literature, and a few even became accepted widely as separate microcontinents or microplates within the main palaeocontinents of Gondwana, Laurentia and Baltica.

This paper aims to review the terminology used in the study of Palaeozoic Europe. Definitions of some of the European peri-Gondwanan terranes, such as Avalonia, Armorica and Perunica, are reviewed. To avoid misunderstandings, each tectonostratigraphical unit should receive its appropriate and sequential terminology: 'terrane', based on tectonostratigraphical evidence, '(micro-)continent', based on palaeogeographical evidence, and finally '(micro-)plate', based on tectonic evidence.

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Basic principles of terminology

Every scientific discipline requires a precise and simple terminology that should be used consistently by all researchers to provide a standardized way of naming the objects of investigation, and to avoid misunderstandings and erroneous interpretations.

Zoologists, for example, use the International Code of Zoological Nomenclature, ICZN (Ride *et al.* 1999), and botanists use the International Code of Botanical Nomenclature, ICBN (McNeill *et al.* 2006). Stratigraphers use the International Stratigraphic Guide (Hedberg 1976) to define and name stratigraphical units. Recently, an attempt has been made to rationalize the nomenclature in marine palaeobiogeographical classification (Westermann 2000; Cecca & Westermann 2003), based on discussions of an international group of specialists in various fossil phyla throughout the Phanerozoic.

So far, no standard nomenclature exists for geodynamic and palaeogeographical terminology. This is because geodynamics and palaeogeography are interdisciplinary sciences, with specialists from various research fields, including palaeogeographers, structural geologists, sedimentologists, palaeontologists, palaeomagnetists and others. These disciplines each use different terms, or they use the same terms but with a different meaning or definition, inevitably leading to confusion and misunderstandings.

Before attributing separate tectonostratigraphical units to independent continents or plates, it is necessary to review the basic terminology used in geography, palaeogeography and plate tectonics. In this paper we focus only on the terminology relevant in the scope of the palaeogeography and geodynamics of Palaeozoic Europe.

Basic terminology in palaeogeography and plate tectonics

Terrane–terrane assemblage

The term 'terrane' has been coined to document the accretionary tectonics of western North America (e.g. Coney 1981). A 'terrane', or more particularly a 'tectonostratigraphic terrane', is defined as a 'fault-bounded package of rocks with a distinct stratigraphy that characterises a particular geological setting' (Howell 1995) and 'that is characterised by a geological history that is different from the histories of contiguous terranes' (Jones *et al.* 1983) or continents. A 'suspect terrane' is a terrane of which the palaeogeographical linkage with adjoining terranes and/or continents is not obvious. Some workers use the term 'composite terrane' to refer to the result of the amalgamation of several terranes. The term 'terrane assemblage', finally, is used to indicate that a group of crustal fragments display broadly the same palaeogeographical history.

Meissner & Sadowiak (1992) noted that the terrane concept is understood as an important extension of plate tectonics, based on the recognition of allochthonous, mobile geological units. Those workers furthermore indicated that the terrane concept is applied successfully to Palaeozoic Europe.

Indeed, the term terrane has become a very popular term used in palaeogeographical reconstructions of Palaeozoic Europe in the past few decades. However, in this context, the meaning of the term has never been defined properly and therefore it used in many different ways. Also the term 'terrane assemblage' has been used commonly (e.g. the Armorica terrane assemblage, the Avalonia terrane assemblage; see below).

Continent–microcontinent–supercontinent

The term 'continent' is used primarily in a (palaeo-)geographical context. A continent is a large, discrete unit, including the continental shelves, founded on continental crust.

Continental crust is the buoyant part of the crust (in contrast to oceanic crust) with an average andesitic composition, resulting from the differentiation process inherent to plate-tectonic processes. Tectonically, most continents consist of a cratonic core surrounded by a 'mobile belt', composing of an orogenic jigsaw puzzle of 'terranes'. A craton commonly consists of old (Archaean and Palaeoproterozoic), thick, cold continental crust and is characterized by a lack of orogenic influence. Orogenic activity is concentrated along the margins of the cratons (i.e. within the 'mobile belt'). If a 'terrane' has a cratonic core, the term 'block' is often used. Continents are surrounded by seas and oceans. In the present-day world, the major landmasses considered as the classical continents are North America, South America, Antarctica, Eurasia, Africa and Australia.

The term 'microcontinent' does not have a proper definition. Typical present-day examples of microcontinents could be Madagascar, Greenland, New Zealand, Borneo, etc. 'Supercontinents' occur when most landmasses are united. The most famous supercontinent is Pangaea (i.e. 'all land' in Greek), defined by Alfred Wegener (Wegener 1915). The assemblage of Pangaea occurred at the end of the Palaeozoic. Other supercontinents are Rodinia, formed at the end of the Mesoproterozoic, and Gondwana, at the end of the Neoproterozoic and during the Palaeozoic.

In the Early Palaeozoic, the principal major landmasses were the three classical palaeocontinents of Baltica, Gondwana and Laurentia. Based on its large size, Siberia can also be considered as a Palaeozoic palaeocontinent (e.g. Fortey & Cocks 2003; Yolkin *et al.* 2003). In some of the most recent Early Palaeozoic reconstructions (e.g. Cocks & Torsvik 2005, 2007), some major palaeocontinents are named terranes, which does not correspond either to the basic definition of the term or to the terrane concept.

Plate–microplate

The terms ‘plate’ and ‘microplate’ refer to the basic entities of the plate-tectonic paradigm. A plate is a relatively rigid piece of the lithosphere, the latter being the outermost part of the Earth that ‘floats’ on the viscous asthenosphere. Such lithospheric plates can consist of both oceanic and continental crust. Some plates are built essentially of oceanic crust (e.g. Pacific plate), whereas other plates consist largely of continental crust (e.g. Eurasian plate). Plates are ‘active’ plate-tectonic entities in the actual plate-tectonic setting of the world. Because of geometrical constraints (i.e. the Euler principle) only three types of plate boundaries exist: divergent plate boundaries (where sea-floor spreading occurs), convergent plate boundaries (where subduction or collision occurs), and conservative plate boundaries (i.e. transform plate boundaries). Where three plate boundaries meet, a triple junction is present. The final result is that the Earth’s surface consists of a jigsaw of connected plates, a basic principle often overlooked in plate-tectonic reconstructions in the past.

‘Microplates’ are small lithospheric plates, smaller than 10^5 km^2 (Howell 1995). They usually occur in complex plate-tectonic settings between major plates in a region of continental convergence. A classic present-day example is SE Asia, where over 60 microplates are recognized between the Indian–Australian, Pacific and Eurasian plates (Hall 1997).

The recognition of a ‘palaeoplate’ or a ‘palaeomicroplate’ is not at all straightforward, primarily because they are largely or even completely consumed by subduction (oceanic part of the lithospheric plate). Only remnants of the continental areas of palaeoplates are preserved. To identify palaeoplates it is necessary to define sutures; that is, linear belts composed of highly strained rocks evidencing the subduction of an oceanic lithosphere (i.e. convergent plate boundary). Typical rocks involved in a suture are ophiolitic material and deep-sea sediments, both remnants of consumed oceanic crust, and tectonic mélanges and blueschists, both the result of a subduction process. Because most of the palaeoplates have been consumed, many palaeoplate-tectonic reconstructions in the past remain highly speculative.

Terranes v. continents v. plates

When reconstructing plate-tectonic configuration in the past, the specific relationship between continent and plate must always be taken into account. This relationship is not at all straightforward. For example, two continental masses can be separated by a sea-way (geography) but situated on the same plate (e.g. Madagascar is part of the African plate). A single continental mass can be formed by units that are juxtaposed but belong to two different plates (California being part of two different plates: the Pacific and the North American plates). Plates exist that contain almost no continental material (e.g. the Pacific plate). Such plates may largely be consumed by subduction, leaving no remains at the Earth’s surface. Thus the orogenic puzzles largely consists of the continental remains that once belonged to a plate. However, the question needs to be asked if remains of all palaeoplates are present in the terrane assemblage.

The strategy in geodynamic research should therefore primarily concern the identification and definition of single ‘terranes’. For each terrane identified, the question needs to be asked if evidence allows us to determine whether or not the terrane is the remnant of an isolated continental mass (palaeobiogeographical evidence), and whether or not the terrane is the remnant of an isolated plate (tectonic evidence).

Basic terminology in palaeobiogeography

Endemism

The basis of biogeographical discrimination is the concept of endemism. An organism has an endemic distribution when it is limited to a specific area. On the other hand, if an organism is not limited to a specific area, but has a wider geographical distribution, it is considered to display a pandemic distribution (e.g. over several continents). If an organism is found across every part of the world, it is considered to have a cosmopolitan distribution.

Provinces, realms, regions or biomes

Most commonly, the endemic distribution of plants or animals often resulted in the definition of ‘provinces’ (i.e. the distribution of restricted geographical areas). However, a range of other biogeographical units have been described, such as ‘realm’, ‘region’ or ‘biome’. The hierarchy of these units was not always clearly defined, and biogeographers studying different geological periods or working on different groups of organisms commonly use different terminologies, or different ranks of the same terms. Kauffmann (1973), for example, noted that neobiogeographers mainly use the following units in decreasing rank: planetary biota (cosmopolitan), realm, region, province or subregion, subprovince, endemic centre and community. Kauffmann

(1973) also noted that some workers abandoned 'realm' or replaced it with 'region'. In addition, he observed that most workers on Late Cenozoic biotas use the same terminology. Kauffmann (1973) also noted that some specialists proposed percentages of endemism to define biogeographical provinces. For Cretaceous bivalves, for example, endemic centres display 5–10% of endemism, subprovinces 10–25%, provinces 25–50%, regions 50–75% and realms >75%.

This terminology is not always followed by palaeobiogeographers. In their survey of faunal distribution to recognize the Iapetus Ocean in the Early Palaeozoic, McKerrow & Cocks (1986), for example, proposed the use of the term 'province' for regions separated by physical barriers to migration and the term 'realm' for climatically controlled faunas and floras. However, as pointed out by Cecca (2002), this proposal has not been widely followed.

Although many workers on Mesozoic biotas attempt to follow the nomenclature in marine palaeobiogeographical classification as proposed recently (Westermann 2000; Cecca & Westermann 2003), most Palaeozoic palaeontologists continue to use terms that are not necessarily accepted generally. For example, the names of many Early Palaeozoic 'provinces' are generally not based on geographical terms, but are taxa-based. Many palaeontologists also use a restricted number of taxa and not the overall endemism of the biota of the provinces. This inconsistent use makes it difficult to compare the provincial distribution of different fossil groups. In addition, some workers consider that only few fossil (benthic) groups are useful for palaeobiogeographical distribution scenarios (e.g. Fortey & Mellish 1992), whereas it is today clear that almost all fossil groups (benthic, planktic and nectic) add useful information in palaeogeographical reconstructions (see discussion by Servais *et al.* 2003, 2005).

Palaeogeographical and tectonic v. palaeobiogeographical terminology

Terranes, continents and plates v. realms and provinces

It is evident that some fossil groups with clear endemism are very useful for the definition of 'provinces', or at a larger scale 'realms'. However, linking provinces to palaeocontinents or palaeoplates is not always straightforward, because palaeobiogeographical entities do not necessarily coincide with palaeogeographical or tectonic units. Present-day examples illustrate this difficulty. Although the island of Madagascar can be considered as an independent biogeographical province for many biotas, it can be considered as a microcontinent. However, it belongs to the same tectonic plate as the African continent (i.e. African plate). On the other hand, most biotas from Baja California (Mexico) are the same as those from the American continent, notwithstanding the fact that both regions are situated on different tectonic plates, the Pacific and North American plates, respectively. One of the best-known examples of the confrontation of biogeography, geography and tectonics is illustrated by the famous 'Wallace line' crossing the Indonesian archipelago. Whereas the archipelago is situated entirely on the Eurasian plate, the 'Wallace line', running between Bali and Lombok, separates the Asian and Australasian zoogeographical zones. The former zone is typical for the Asian continent on the Eurasian plate, whereas the latter is typical for the Australian continent on the Indo-Australian plate.

In ancient reconstructions, provinces and realms may therefore be indicative of different plates or continents, and they may be very useful to detect plate boundaries or different palaeocontinents. However, in many cases, provinces indicate only different palaeobiogeographical habitats (biofacies), which are not necessarily linked to different plate-tectonic configurations or continental distributions. A common mistake is to attribute a palaeogeographical grouping of fossils (a 'province') to a palaeogeographical entity ('microcontinent') or a plate-tectonic entity ('microplate') without sufficient conclusive evidence from structural geology.

Fortey & Cocks (2003), although not following the classical definition of the terms (micro-)continents, plates or terranes, clearly explained how they use the term microcontinent. They noted that 'in practice the distinction from terranes is arbitrary'. They furthermore indicated that their definition of the term microcontinent is pragmatic for palaeontology; that is, applying to areas large enough to include a range of biofacies including especially shelf faunas developed on cratonic fragments. The Fortey & Cocks (2003) microcontinents are thus not necessarily large, discrete landmasses, including continental shelves, founded on a continental crust. They used a 'pragmatic' definition as applied by palaeontologists, not necessarily in agreement with the geographical or tectonic definition. This use of the term microcontinent should thus be avoided, and therefore is not applied here.

'Terrane-diagnostic fossils'?

The term 'terrane-diagnostic fossils', as used by Cocks & Torsvik (2005, 2007), is another example of mixing of terms from geodynamics and palaeontology. 'Terrane-diagnostic fossils' may have some relevance only in the context of an 'exotic terrane' bearing fossil taxa that are strongly different from those of adjacent continents or 'terranes'. Cocks &

Torsvik (2005, 2007), however, named several continents, such as Baltica and Siberia, as 'terranes'. Fossil distributions may be indicative of the margins of palaeocontinents, which bear taxa that are different from those of other continental margins at a sufficient geographical distance. However, in the context of structural geology, the term 'terrane-diagnostic fossils' is difficult to understand and can only be misleading.

Peri-Gondwanan Europe

Following over 30 years of palaeogeographical investigations, which were based initially on palaeobiogeographical (palaeontological) studies (e.g. Cocks & Fortey 1982), recent reconstructions at a global scale include three major palaeocontinents in the Early Palaeozoic: Baltica, Laurentia and Gondwana. Present-day Europe is formed by parts of these three continents, with Baltica forming the cratonic basement of Scandinavia and the East European Platform (including the northeastern part of Poland), Laurentia representing northwestern Europe (including parts of Scotland), and the Gondwanan margin constituted by parts of southern Europe.

Between these three major continents, a large number of terranes located in central and southern Europe have been identified. They mostly have a Cadomian basement, indicating a Precambrian or Cambrian affinity with the margin of Gondwana (e.g. Winchester *et al.* 2002). For this reason these units are usually attributed to peri-Gondwanan 'terranes'.

Palaeozoic palaeogeographical reconstructions are generally in agreement with regard to the position of the major continents. However, there is a continuing debate about the position and palaeogeographical attribution of the numerous smaller 'terranes' at the margin of the major continents, including the European peri-Gondwanan terranes located between Laurentia, Baltica and Gondwana. For some of these terranes, several researchers advanced the hypothesis that these entities represented independent palaeogeographical units, attributed to microcontinents or microplates. In many palaeogeographical maps, several of these terranes are indeed represented as independent islands 'floating' between Gondwana in the high southern latitudes and Laurentia and Baltica in lower latitudes (e.g. Winchester *et al.* 2002, figs 6 & 7; Belka *et al.* 2002, fig. 7; Williams *et al.* 2003, fig. 2).

Gondwana during the Early Palaeozoic: where is North Gondwana?

There is a continuous confusion about the location of West, East, South and North Gondwana, which, similarly to the terms 'terrane', 'continent' and 'province', are terms used commonly, but are rarely defined or explained clearly. Paris & Robardet (1990) and Robardet *et al.* (1990), for example, considered the margin of Gondwana in southern Europe (i.e. the Armorican Massif in Brittany, Spain, Portugal, Sardinia) and North Africa as 'northern Gondwanan regions'. For many researchers who regard Gondwana as a supercontinent in the Late Precambrian, the continent was formed by 'West' Gondwana, composed of South America and Africa, and 'East' Gondwana, composed of India and Australia (e.g. Jacobs & Thomas 2004). 'North' Gondwana is considered to be composed by the Cadomian and Cimmerian terranes during the Late Precambrian.

Figure 1 is a palaeogeographical reconstruction during Early Ordovician times, with the 'supercontinent' Gondwana (Fig. 1b) occupying areas from the South Pole to the northern hemisphere. Most Ordovician and Silurian palaeogeographical maps, such as those by Scotese & McKerrow (1990), Torsvik (1998), Cocks (2001) and Li & Powell (2001), all agree in placing Gondwana in a position with Australia in the north and North Africa in the south. During the Ordovician (Fig. 1b), Australia and North China are located in the northern hemisphere, thus forming the northern margin of Gondwana. Present-day South America was located in the eastern part of the Gondwanan supercontinent, and present-day northern Africa was located near the Ordovician South Pole, forming the southern margin of the continent. Studies of peri-Gondwanan Europe (see below) in the Early Palaeozoic thus clearly concern the southern margin of the continent, although this margin was partly facing north.

Peri-Gondwanan Europe is thus clearly located in the southern hemisphere at high latitudes (Fig. 1) and should be attributed to 'South' Gondwana. The terms 'West Gondwana' (position during the Precambrian) and 'North' Gondwana (because Armorica is located at the northern margin of 'South' Gondwana during the Early Palaeozoic) should be avoided.

Peri-Gondwanan palaeogeography

Many papers have focused on peri-Gondwanan palaeogeography in southern and central Europe, to which several larger international research projects have been addressed. Winchester *et al.* (2002), for example, summarized the results of the multidisciplinary studies undertaken with the EU-funded 'PACE' Network ('Palaeozoic Amalgamation of Central Europe').

There have been numerous papers published on the palaeogeographical affinities of the various peri-Gondwanan terranes. Erdtmann (2000) presented a

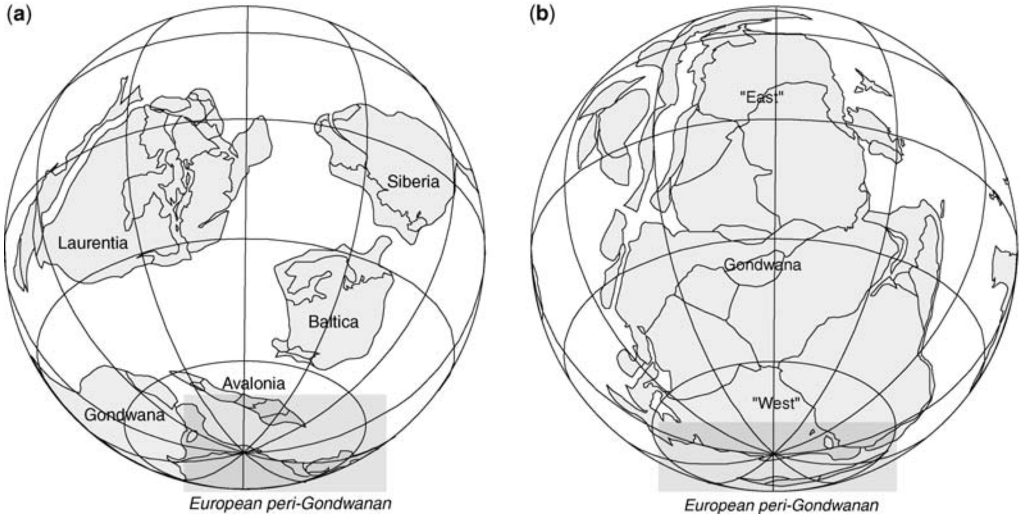

Fig. 1. Early Ordovician (*c*. 480 Ma) palaeogeographical reconstruction modified from C. R. Scotese PaleoGIS for Arcview package, after Cocks (2001, fig. 2). (**a**) Slightly tilted view focused on the three major continents Laurentia, Baltica and Siberia and the 'microcontinent' Avalonia. (**b**) Slightly tilted view focused on the supercontinent Gondwana. European peri-Gondwanan (shaded square) is located around the South Pole and should thus be attributed to 'South' Gondwana.

list of terranes located around Gondwana, which clearly indicates that the discussion about the palaeogeographical affinities of peri-Gondwanan units concerns not only peri-Gondwanan Europe, but also peri-Gondwanan South America, Asia or Australia. A prominent example is the continuing discussion on the affinity of the 'Precordilleran terrane' in South America (e.g. Benedetto 1998; Finney *et al.* 2003; Finney 2007).

It is not the aim of this paper to provide a thorough revision of peri-Gondwanan palaeogeography. It is instead an attempt at a critical revision of the terminology used by various researchers with respect to the most commonly used tectonostratigraphical entities in Palaeozoic Europe: Avalonia, Armorica and Perunica.

Revision of European peri-Gondwanan terranes: sediment packages, terranes, provinces, microcontinents or microplates?

Avalonia: a microcontinent, a microplate

Avalonia is the most widely studied peri-Gondwanan terrane of Palaeozoic Europe. Extensive research has been carried out to understand the palaeogeographical history of this terrane, summarized in geological, geodynamic and palaeobiogeographical reviews (e.g. Winchester *et al.* 2002; Fortey & Cocks 2003).

Avalonia, first defined by Cocks & Fortey (1982), is named after the Avalon Peninsula of Newfoundland. It is composed of present-day eastern Newfoundland, New Brunswick, Nova Scotia and the coastal areas of eastern USA ('West Avalonia') and of the Anglo-Welsh area and southern Ireland, Belgium ('East Avalonia') and parts of northern Germany and northwestern Poland ('Far Eastern Avalonia') (Cocks *et al.* 1997; Verniers *et al.* 2002). In the NW, the Iapetus Ocean is presumed to have been situated north of the Lake District, now represented by a suture that continues through Ireland (Cocks *et al.* 1997). In the NE, the Tornquist Sea, which separated Avalonia from Baltica, was located in the north of Germany, with a suture crossing northern Germany and northwestern Poland (Servais & Fatka 1997). In the south of Avalonia the Rheic suture is difficult to outline and is strongly debated, because of the Variscan overprint.

Avalonia is considered by several workers as comprising several terranes (e.g. Armstrong & Owen 2001) and by others as a single entity (Fortey & Cocks 2003). Keppie (1985) named the terrane the 'Avalon Composite Terrane', whereas Gibbons (1990) called it the 'Avalon Superterrane' and Verniers *et al.* (2002) the 'Avalonia terrane assemblage'.

Based on palaeobiogeographical evidence, mostly data from trilobites (for a summary see Fortey & Cocks 2003), a strong argument can be made to consider Avalonia as a separate microcontinent. These fossils, supplemented with data from other groups (e.g. McKerrow *et al.* 1992), indicate a position of Avalonia close to 'West' Gondwana (northwestern Africa or the northern part of South America) before rifting away from Gondwana and the opening of the Rheic Ocean, which took place during the Early Ordovician, although other workers claim that Avalonia was separated from Gondwana as an isolated continent from late Precambrian times (Landing 1996, 2005). Fortey & Cocks (2003) summarized the palaeobiogeographical arguments in favour of a separation from Gondwana not before the Arenig–Llanvirn (equivalent to the Floian, second global stage of the Ordovician System). Avalonia moved rapidly northwards, with increasing faunal similarities to Baltica and Laurentia from Llandeilo times (equivalent to the late Darriwilian in current global stratigraphy), and reached temperate to warm-water environments in the Late Ordovician (since the Caradoc) before docking with Baltica in the latest Ordovician, as documented by Vecoli & Samuelsson (2001), Samuelsson *et al.* (2002) and others. There is thus good faunal evidence to infer the drift of Avalonia as an independent microcontinent, with a rifting from Gondwana and a northward drift over a 55 Ma period before docking with Baltica in the latest Ordovician, forming Balonia (Baltica + eastern Avalonia) *sensu* Torsvik *et al.* (1993), and collision with Laurentia slightly later (Fortey & Cocks 2003).

The rifting, drifting and docking history of Avalonia is also confirmed by palaeomagnetic evidence (e.g. Trench *et al.* 1992). Trench & Torsvik (1991) first demonstrated that southern Britain had moved northwards away from Gondwana. Torsvik *et al.* (1993) and Tait *et al.* (1997) subsequently reconstructed the palaeogeographical position of Avalonia, with a very high-latitude position in the Tremadocian, *c.* 60°S for Wales. During the Middle Ordovician, a position at about 45°S was estimated. By the Late Ordovician, a position of Avalonia between 30 and 40°S was deduced, and in the Wenlock Avalonia was already located at about 10–20°S (e.g. Torsvik *et al.* 1993; Tait *et al.* 1997).

The paleontological arguments for separation of a microcontinent of Avalonia and its drift history are confirmed by volcanic, structural and sedimentary evidence, as summarized by Verniers *et al.* (2002), who analysed the basin evolution of the eastern (European) part of Avalonia. According to those workers, the history of Eastern Avalonia can be divided into several periods representing very different geodynamic contexts: (1) an early Cambrian to Tremadocian period, with extensional rift basins containing rather thick sediment sequences, along the active continental margin of Gondwana; (2) an Arenig to mid-Ashgill period with shelf basin sedimentation containing moderately thin sequences, when Avalonia was a separate continent; (3) a late Ashgill to early mid-Devonian period, with a shelf and foreland basin development containing thick sediment sequences during the period of docking with Baltica (Verniers *et al.* 2002). The rifting of 'Eastern Avalonia' is also demonstrated by subsidence analysis, indicating that the main separation from Gondwana occurred after the middle Arenig (Prigmore *et al.* 1997).

Although the exact palaeogeographical history of some of the component parts of the 'Avalonian terrane assemblage', such as the Southern North Sea–Lüneburg terrane ('Far Eastern Avalonia', *sensu* Verniers *et al.* 2002), is not yet fully understood, Avalonia is today accepted widely as a microcontinent and a microplate. Avalonia was a small landmass with oceans in the NW (Iapetus Ocean between Avalonia and Laurentia), the NE (Tornquist Sea between Avalonia and Baltica), and the south (the Rheic Ocean between Avalonia and Armorica).

In summary, Avalonia is defined on palaeobiogeographical (palaeontological) evidence. It is now well constrained as a microcontinent and a microplate, most probably composed of several blocks that moved separately with respect to each other.

'Armorica': several definitions and different concepts

Debates about 'Armorica' mostly find their origin in the different concepts of specialists studying the Variscan orogeny; that is, different concepts regarding the tectonic evolution of the Variscan areas in southern and central Europe associated with the closure of the Rheic Ocean.

The question about the meaning of Armorica is a continuing debate. As pointed out by Lewandowski (2003), Armorica had various meanings and definitions according to different groups of workers. Some of the misunderstandings are based simply on the different definitions of the term, and in particular of the concept of the geographical extension of Armorica. The name Armorica is based on the Armorican Massif in Brittany, western France. For some workers, the term Armorica is restricted to the Armorican Massif (and its French and Iberian equivalents; see discussion by Robardet 2002, 2003). However, in the literature, the term Armorica was usually applied to a much larger area. The original definition of the 'microplate Armorica' is based on palaeomagnetic studies (Van der Voo 1979), and included southwestern England and Wales, the various regions of Variscan Europe, and probably also the Avalon Peninsula and New England. Thus, the term originally included various terranes with a Cadomian basement in the

Variscan (and Alpine) fold belts of Europe. It is important to indicate that in this original definition, the 'Armorica microplate' also included Avalonia (Van der Voo 1979). It was only later, with the definition of Avalonia as a separate microcontinent by Cocks & Fortey (1982), that Van der Voo (1988) indicated that the 'Armorica microplate' should be restricted to the Variscan regions of southern and central Europe. At that time, the remaining parts of Armorica then comprised the Ibero-Armorican block and the Bohemian Massif. As pointed out by Tait *et al.* (1997), the name 'Armorica' has been used by palaeomagnetists to refer to the Variscan areas of southern and central Europe (Ibero-Armorican block and Bohemian Massif), the implication being that they formed a coherent microplate, although this has never been fully demonstrated from palaeomagnetic data (Tait *et al.* 1997). The latter workers considered Armorica as comprising 'a number of tectonostratigraphic terranes' and they introduced the term 'Armorican Terrane Assemblage' (ATA), a concept that was subsequently used widely in the literature. According to this concept, the ATA is formed by three constituent massifs (Iberian, Armorican and Bohemian) and includes regions exposed in a series of massifs across much of middle Europe from Portugal and Spain through France, Germany and the Czech Republic to Poland. This 'terrane assemblage' also includes the Bohemian Massif, and several different crustal blocks such as Saxothuringia, Teplá–Barrandia and Moldanubia (and therefore also includes 'Perunica'; see below). Within this concept, 'Armorica' (ATA) can be considered to have been an 'archipelago' of semi-autonomous microcontinents separated by minor oceanic basins on different microplates (e.g. Crowley *et al.* 2002). This concept was also developed by Winchester *et al.* (2002), who considered that the Bohemian and Armorican Massifs (both being parts of the ATA) constituted separate microcontinents, all south of the Rheic Ocean. For other workers (e.g. Cocks & Torsvik 2002), 'Armorica' is limited to the Armorican Massif of Normandy and Brittany (western France), the Massif Central (central France) and the Montagne Noire (southern France), together with various massifs from the Iberian Peninsula. In this view the Bohemian Massif is considered a separate 'microcontinent', named Perunica (see below; see also Fortey & Cocks 2003). Winchester *et al.* (2002) noted that it is likely that the 'Armorican terrane assemblage' comprised several related crustal blocks that migrated together towards Baltica after rifting from their former peri-Gondwanan position. This view can be compared with the palaeogeographical scenario proposed by Stampfli & Borel (2002) and von Raumer *et al.* (2003), who included the southern and central European peri-Gondwanan pre-Variscan elements in their 'European Hunic Terranes'.

From a palaeogeographical point of view, palaeomagnetic data from the 'Armorica microplate' indicated proximity to Gondwana in the Late Proterozoic and Cambrian, and distinct latitudes from Gondwana in the Late Devonian (Van der Voo 1979, 1988). The Ordovician–Silurian history of this 'Armorica microplate' thus allowed various speculations to be made. As summarized by Robardet (2003), some workers considered that Armorica had detached from Gondwana and had drifted northwards, whereas for some others, Gondwana and Armorica had drifted northwards as a whole and joined the southern border of Laurussia (Laurentia + Baltica), before becoming separated, with Armorica holding its position whereas Gondwana retreated southwards. Based on palaeoclimatic and palaeobiogeographical evidence, Paris & Robardet (1990) and Robardet *et al.* (1990) argued that the 'northern Gondwanan regions' (equivalent to the 'Armorican Terrane Assemblage') remained in close proximity of Gondwana during the whole Palaeozoic. This is supported by the studies of Linnemann *et al.* (2004), who presented U/Pb sensitive high-resolution ion microprobe zircon and Nd-isotope evidence that supports a separation of Armorica from Gondwana and that a long drift during the Palaeozoic never took place.

In summary, a first concern should be a proper outline of 'Armorica' or the 'Armorican terrane assemblage'. Moreover, there is seemingly a contradiction between the palaeomagnetic and paleontological evidence. This results in the conclusion of Robardet (2003) that, although maintained repeatedly for more than 20 years, the concept of the 'Armorica microplate' can be considered a fiction. Palaeontologists and palaeomagnetists should thus be careful in using maps that identify an independent microcontinent of Armorica, represented as a 'floating island' between the continents of Gondwana, Baltica and Laurentia. So far there is no hard evidence for a separate microcontinent from Gondwana, although there is evidence for a separate drift history. Most probably a 'Californian scenario' has to be invoked, suggesting that Armorica was part of a separate plate, but that continental separation from Gondwana has never been significant.

Perunica: a palaeobiogeographical province?

Palaeozoic deposits in the Czech Republic and in the Sudetes (western Poland) are interpreted as part of a Palaeozoic 'Centralbohemicum' domain (Franke & Zelazniewicz 2002), which also comprises the Prague Basin of the Teplá–Barrandian area. This latter basin includes the classical Bohemian successions studied by Barrande in the 19th century that led to the definition of 'Perunica'.

A literature review of 'Armorica' indicates that the elements of the Variscan fold belt in the Czech Republic were originally incorporated into this 'microplate' by Van der Voo (1979). After the removal of Avalonia from Armorica (Van der Voo 1988), the terranes from the Czech Republic were still considered parts of Armorica. They also clearly belong to the Armorican terrane assemblage as defined by Tait *et al.* (1997) and used subsequently (see discussion above). Franke (2000), for example, considered the areas of Franconia, Saxothuringia and Bohemia as parts of the mid-European segment of the Armorican terrane assemblage. It is thus important to remember that the Bohemian fossiliferous sequences of the Prague Basin (Bohemian Massif) are considered as a part of 'Armorica' by most geologists.

The creation of an additional palaeogeographical unit, Perunica, was the result of palaeontological studies. Based on the endemicity of some faunas within the Bohemian assemblages, Havlíček *et al.* (1994) proposed Perunica as a separate 'microplate', named after Perun, the god of thunder of Slavic tribes during the early Middle Ages. Havlíček *et al.* (1994) defined the 'Perunica microcontinent' essentially on the basis of comparisons of fossil lists from the Prague Basin with other areas. According to these workers, a maximum provinciality with high endemicity of brachiopod and trilobite genera occurred in the Dobrotivá and Beroun regional stages (equivalent to the latest Middle and early Late Ordovician). The brachiopod and trilobite assemblages were compared with those from the French and Spanish parts of 'Armorica', and with those from Avalonia, Baltica and North Africa ('lingulid domain' and Tindouf Basin). According to the semi-quantitative similarity analyses of the fossil lists, it was concluded that the fossil assemblages of Bohemia included elements from various other areas (considered to be 'separate plates and microplates'), but also including endemic faunas.

Havlíček *et al.* (1994) noted that 'Perunica has many features in common with Armorica' and that 'in some respects the assemblages are similar to those of Armorica and the Tindouf Basin'. They acknowledged the fact that the faunas are not uniform over the whole 'Mediterranean zoogeographic province' (extending over North Africa, and southern and central Europe) as a result of 'latitudinal–climate control, depth control and facies development'. Based on these arguments, it is therefore not clear why Havlíček *et al.* (1994) created a separate 'microplate' because it is not understood if the difference in the faunal lists is the expression of a different palaeogeographical context or of local or regional biofacies changes.

Some recent studies have confirmed the similarities of trilobite faunas between the Prague Basin, the Condroz Inlier in Belgium and other Avalonian and 'Armorican' sequences (e.g. Owens & Servais 2007). According to Owens & Servais, remaining taxonomic questions make it difficult to compare the trilobites from the different areas. In addition, detailed biofacies studies are needed to fully understand the palaeobiogeographical significance of the faunas from the Czech Republic. The differences in taxonomy are most probably a result of different biofacies (including water depth), but not necessarily of a different palaeogeographical setting. In another study focused on Ordovician echinoderms, Lefebvre (2007) also questioned the validity of Perunica, because the compositions of Middle and Late Ordovician echinoderm assemblages from Bohemia and other 'Armorican' areas are closely comparable, and do not provide evidence for a continental separation.

In the original definition by Havlíček *et al.* (1994) the evidence to define a 'separate microplate' is restricted to selected palaeontological data. Detailed comparisons with fossil lists from the neighbouring terranes (of Saxothuringia, Franconia, etc.) are difficult, because all these areas display only a very poor fossil content, compared with the excellent successions of the Prague Basin.

Some palaeomagnetic data for the region (Krs *et al.* 1996, 1997) support the drifting from high latitudes in the southern hemisphere in the Early Cambrian to low northern latitudes in the Late Palaeozoic. These data are broadly comparable with those from other parts of 'Armorica'. Subsequently, Tait (1999) provided palaeomagnetic evidence indicating that Bohemia had a different orientation from 'Armorica' by the end of the Silurian, but data from Lewandowski (2003) do not confirm this.

In the light of the available evidence, there are so far no sufficient arguments to consider that Perunica may have been a separate microcontinent or a separate microplate. Recent sedimentological and structural geology studies indicate that the changing biofacies are probably the expression of the development of a rift-basin structure (Kraft *et al.* 2005).

In a palaeogeographical context the Prague Basin should be considered as a part of the 'Armorican terrane assemblage', as currently considered by most specialists (e.g. Winchester *et al.* 2002; von Raumer *et al.* 2003; Linnemann *et al.* 2004).

In summary, the evidence suggests that Perunica is a part of the Armorica terrane assemblage (see discussion above). At most, Perunica could be considered as a particular palaeobiogeographical province, similar to the Celtic Province for example (e.g. Harper *et al.* 1996). Such a province should be defined in keeping with the marine palaeobiogeographical classification, as proposed recently (Westermann 2000; Cecca & Westermann 2003), and should have a geographically based name.

Conclusions

In this paper an attempt has been made to clarify some terminological misunderstandings with respect to Palaeozoic geodynamics and its consequences in Palaeozoic Europe. This region is indeed composed of an assemblage of peri-Gondwanan terranes, located between the palaeocontinents of Baltica, Laurentia and Gondwana during the assemblage of the supercontinent Pangaea. The terminology of three commonly used palaeogeographical units (terranes), Avalonia, Armorica and Perunica, is reviewed in a historical context.

There is some overall agreement that Avalonia, with its composite regions, is the remnant of a microcontinent that has experienced true continental drift via movement on a separate microplate (Fig. 2).

The terrane 'Armorica' requires a precise definition in terms of its geographical extension. Continuing controversy with respect to the true nature of Armorica is based primarily on seemingly contrasting evidence from palaeobiogeography and palaeomagnetism. The contrasting data may indicate that the continental part of Armorica was never actually separated from Gondwana, but that it was possibly still part of a separate plate; that is, comparable with the current relationship between parts of California and the rest of the North American continent (Fig. 2).

The Teplá–Barrandian area in the Czech Republic, incorporating the classical geological successions of the Prague Basin, might be considered a 'terrane'. For most geologists this entity belongs to the Armorican terrane assemblage. Perunica, as defined by Havlíček *et al.* (1994), is possibly a distinguishable palaeobiogeographical province, similar to the Celtic Province, and also requires clear redefinition. However, there is no sufficient evidence in favour of a scenario with Perunica as a separate microcontinent or microplate (Fig. 2).

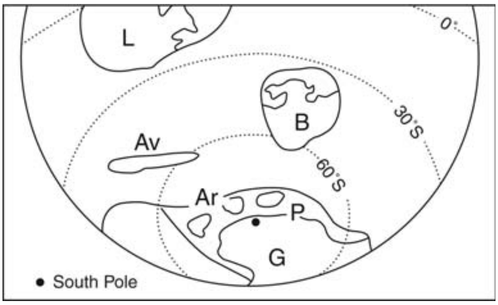

Fig. 2. Tilted Middle Ordovician palaeogeographical reconstruction after Owens & Servais (2007), based on Robardet (2003), placing Armorica (Ar) and Perunica (P) on the periphery of Gondwana (G), and Avalonia (Av) as an independent microcontinent between Gondwana, Baltica (B) and Laurentia (L).

A similar critical assessment, using a precise terminology and revision of palaeontological and geological evidence, should be undertaken for all other supposed peri-Gondwanan terranes. By using a consistent terminology, palaeobiogeographers, palaeontologists, sedimentologists, palaeomagnetists and structural geologists should be able to clarify misunderstandings, not only of terminology, but also of palaeogeographical concepts.

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Late Ordovician carbonate productivity and glaciomarine record under quiescent and active extensional tectonics in NE Spain

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Abstract: Carbonate productivity and glaciomarine deposits of the Ordovician–Silurian transition display different sedimentary architectures in the Iberian and Hesperian Chains of NE Spain, as a result of quiescent and active extensional tectonics on platforms fringing North Gondwana. The late Katian carbonate productivity of the Iberian platform reflects the onset of bryozoan–pelmatozoan meadows and mud-mound complexes throughout an intra-shelf ramp, whereas carbonate nucleation of prominent carbonate factories took place on the top of isolated palaeo-highs in the Hesperian platform. In both cases, the end of carbonate productivity is associated with glacioeustatic regression, subaerial exposure and karstification, pre-dating widespread precipitation of iron ore deposits in the vicinity of palaeo-highs. The Hirnantian glacioeustatic transgression is represented lithostratigraphically by the Orea Formation. In the Iberian platform, the formation consists of two distinct depositional sequences bounded by the progradation of conglomeratic channels, and is dominated by the record of massive and crudely stratified diamictites, with tabular geometries and deposited subaqueously as 'rain-out' facies. In contrast, the Hesperian platform is rich in disrupted diamictites, which form strongly deformed units interpreted as submarine slumps associated with active synsedimentary faults. In both cases, the anomalous occurrence of massive diamictites, rich in boulder- to sand-sized carbonate dropstones, and displaying rapid variations in density and size, suggests that distinct iceberg 'drift lanes' existed, indicating current activity in the open sea.

There is a common consensus in recent literature that grounded ice covered parts of North Gondwana during the Hirnantian (latest Ordovician), as recognized, for example, in Algeria, Mauritania, Morocco, Saudi Arabia and Turkey (see syntheses by Monod *et al.* 2003; Le Heron *et al.* 2006, and references therein). A belt of Hirnantian glaciomarine deposits has also been envisaged surrounding the North Gondwana grounded ice, as described in numerous bordering areas, such as the Iberian and Hesperian Chains (Spain; Carls 1975; Fortuin 1984), Thuringia (Steiner & Falk 1981), the Armorican Massif (Robardet & Doré 1988), Portugal and Bohemia (Brenchley *et al.* 1991). However, it is difficult to discriminate between Hirnantian glaciomarine deposits related to glaciogenic material continuously transported by icebergs and those transported episodically by coastal winter ice (Spjeldnaes 1981). Sediment transported by freezing into seasonally formed river or shore ice is generally characterized by relative sorting and enhanced rounding reflecting the sediment source, which contrasts with the presence of far-travelled, extrabasinal lithotypes, the wide range of clast shapes, and the larger size of rafted boulders transported by icebergs (Gilbert 1990; Eyles *et al.* 1998). Although it is classically considered that ice rafting was probably related to icebergs and transported material further than coastal ice, most Hirnantian ice-rafted material in marine sediments may have been related to seasonal shore ice.

Glaciomarine sedimentation also depends upon the hydrodynamic regime (e.g. frequency and intensity of waves, currents and tides), the proximity of a glacial front, and the depth and geometry of platforms lacking protective rims. These factors directly controlled the Hirnantian sedimentation recorded, for instance, in the Iberian and Hesperian Chains (NE Spain). Their marine strata are comparable with other neighbouring platforms because both were (1) located in similar high-latitude settings, (2) have records of dropstone-rich glaciomarine deposits, and (3) faced the same northern Gondwana margin. However, they differ in their platform geometries (intra-shelf ramp v. irregular shelf characterized by a tectonically induced palaeotopography), and thus represent different hydrodynamic conditions. As a result, offshore ice rafting controlled by relic ice masses developed different glaciomarine facies and facies architecture in these two platforms.

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The aim of this paper is to understand how the geometry of the Iberian and Hesperian platforms affected the nucleation of carbonate productivity and the selective sedimentation of Hirnantian glaciomarine deposits by analysing the facies associations, sequence stacking patterns and sedimentary architecture of two coeval palaeogeographical settings: (1) a proximal intra-shelf ramp, recorded in the Iberian Chains, which evolved under quiescent tectonic conditions; (2) a tectonically active area that led to development of a palaeotopography controlled by faulted blocks, preserved in the Hesperian Chains.

Geological setting and stratigraphy

The pre-Hercynian outcrops of the Iberian Chains (IC) and Hesperian Chains (HC) constitute a relic of the deeply eroded Variscan orogen in NE Spain. The IC exhibit a NW–SE-trending alignment and are divided longitudinally, by the Tertiary Calatayud–Teruel trough, into the western and eastern IC (Fig. 1). Their pre-Hercynian basement consists of a mosaic of crustal elements fragmented and structured during the Hercynian and Alpine orogenies. Their strata were thrust northeastward during the Late Carboniferous (Villena & Pardo 1983) onto a Precambrian continental margin, named the Ebro Massif, which presumably occurs at present under the Tertiary Ebro valley (Carls 1983). The pre-Hercynian basement of the disconnected massifs or inliers that form the HC (named Aragoncillo, Nevera, Sierra Menera and Tremedal) displays similar thrust and faulting systems, also dominated by NW–SE-trending structural alignments (Fig. 1). The Hesperian platform (HC) is considered as the southwestern prolongation of the Iberian platform (IC), although the setting of the land source area of the former is still under discussion. The western margin of the Hesperian platform is not well established, because of the limited exposures of their massifs.

Upper Ordovician sedimentary rocks are known both in the eastern IC and in several massifs of the HC. Previous studies were concerned primarily with regional mapping and stratigraphy, and the glaciogenic character of some strata was first pointed out by Carls (1975) in the IC and Fortuin (1984) in the HC. The two chains have similar stratigraphy, which is known from the studies of Carls (1975), Villena (1976), Hammann (1992) and Gutiérrez Marco *et al.* (2002). Recently, Herranz Araújo *et al.* (2003) proposed a lithostratigraphical revision for the HC, in which they defined new formations based on their lithological characters; this updated stratigraphical sketch is followed below.

This paper is focused on the description and interpretation of five Katian to Llandovery age formations, in ascending order: an 'anomalous' facies association of the uppermost part of the San Marcos Formation (HC); the Cystoid Limestone (IC) and Ojos Negros (HC) carbonate-dominated formations; the diamictites of the Orea Formation (IC and HC); and the siliciclastic Los Puertos Formation (IC and HC).

In the outcrops of the HC where the Ojos Negros Formation is absent, and the Orea Formation overlies the San Marcos Formation unconformably (the name follows Herranz Araújo *et al.* 2003), the uppermost part of the latter contains numerous ferroan-dolostone clasts derived from laterally equivalent dolostones of the Ojos Negros Formation. These are the only outcrops of the San Marcos Formation, a siliciclastic unit, 40–165 m thick, composed of sandstone–shale alternations, which are analysed below.

The Ojos Negros Formation, formerly named El Cabezo Member (Villena 1976), is 0–90 m thick and consists of massive to bedded and lenticular, cream limestones and brownish dolostones, and alternating reddish limestones and shales. Several iron ore quarries are located in the Sierra Menera massif, where the formation displays the thickest outcrops. Thickness is highly variable and the formation can disappear laterally (e.g. in sections PD, Ch_1 and Ch_2; Figs 1 & 2). Herranz Araújo *et al.* (2003) reported the presence of Kralodvorian fossils from the basal marls and the lower part of the formation in the Aragoncillo, Nevera and Tremedal massifs; these include trilobites, echinoderms, ostracodes and conodonts, the last indicative of the *Amorphognathus ordovicicus* Zone.

The Cystoid Limestone of the IC consists of cream limestones, yellow and brownish dolostones and greenish marlstones, up to 50 m thick. Hammann (1992) subdivided the formation into four members. The Rebosilla and La Peña members comprise alternating shales (up to 2 cm thick) and marly limestones (10–25 m thick) deposited under open-sea conditions in an offshore environment characterized by quiet deposition punctuated by storm events. The Ocino Member (0.7–5 m thick) comprises calcareous siltstones and shales deposited under alternations of quiet-water conditions and storm-induced processes with an important fine-grained siliciclastic input. Finally, the Rebollarejo Member (up to 40 m thick) is characterized by the occurrence of pelmatozoan–bryozoan mud-mound complexes, up to 10 m thick and more than 300 m wide; its conodonts suggest a late Ashgill (late Katian) age (Carls 1975), Rawtheyan according to trilobites (Hammann 1992). The sedimentology and sequence framework of the Cystoid Limestone were analysed by Vennin *et al.* (1998), and its facies characterization will not be repeated below.

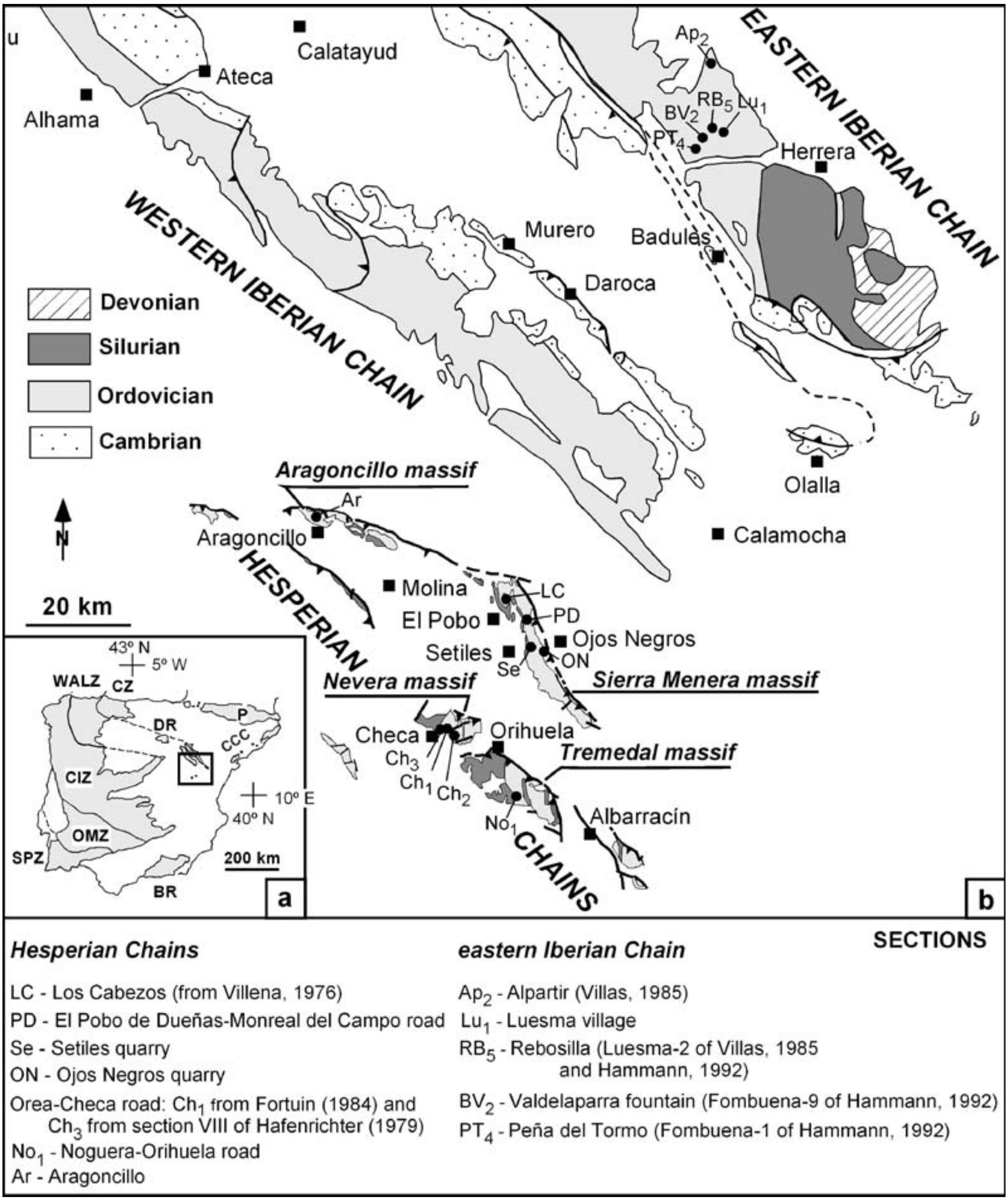

Fig. 1. (**a**) Pre-Hercynian outcrops of the Iberian Peninsula showing the main tectonostratigraphical units: CZ, Cantabrian Zone; WALZ, West Asturian–Leonese Zone; CIZ, Central Iberian Zone; OMZ, Ossa–Morena Zone; SPZ, South Portuguese Zone; BR, Betic Ranges; DR, Demanda Range; CCC, Coastal Catalonian Chains; P, Pyrenees; box indicates area of (b). (**b**) Geological sketch of the pre-Hercynian outcrops of the IC and HC (modified from Álvaro & Vennin 1998; Herranz Araújo *et al.* 2003).

The Orea Formation, 50–80 m thick, comprises impure calcareous sandstones, diamictites bearing dolomite and limestone clasts of various sizes, and centimetre-thick breccias and conglomeratic channels. The formation is classically considered as part of the Hirnantian glaciomarine sedimentation developed widely on the northern Gondwana margin (Carls 1975; Fortuin 1984; Robardet & Doré 1988). In the Nevera massif, carbonate clasts embedded in the Orea Formation have yielded

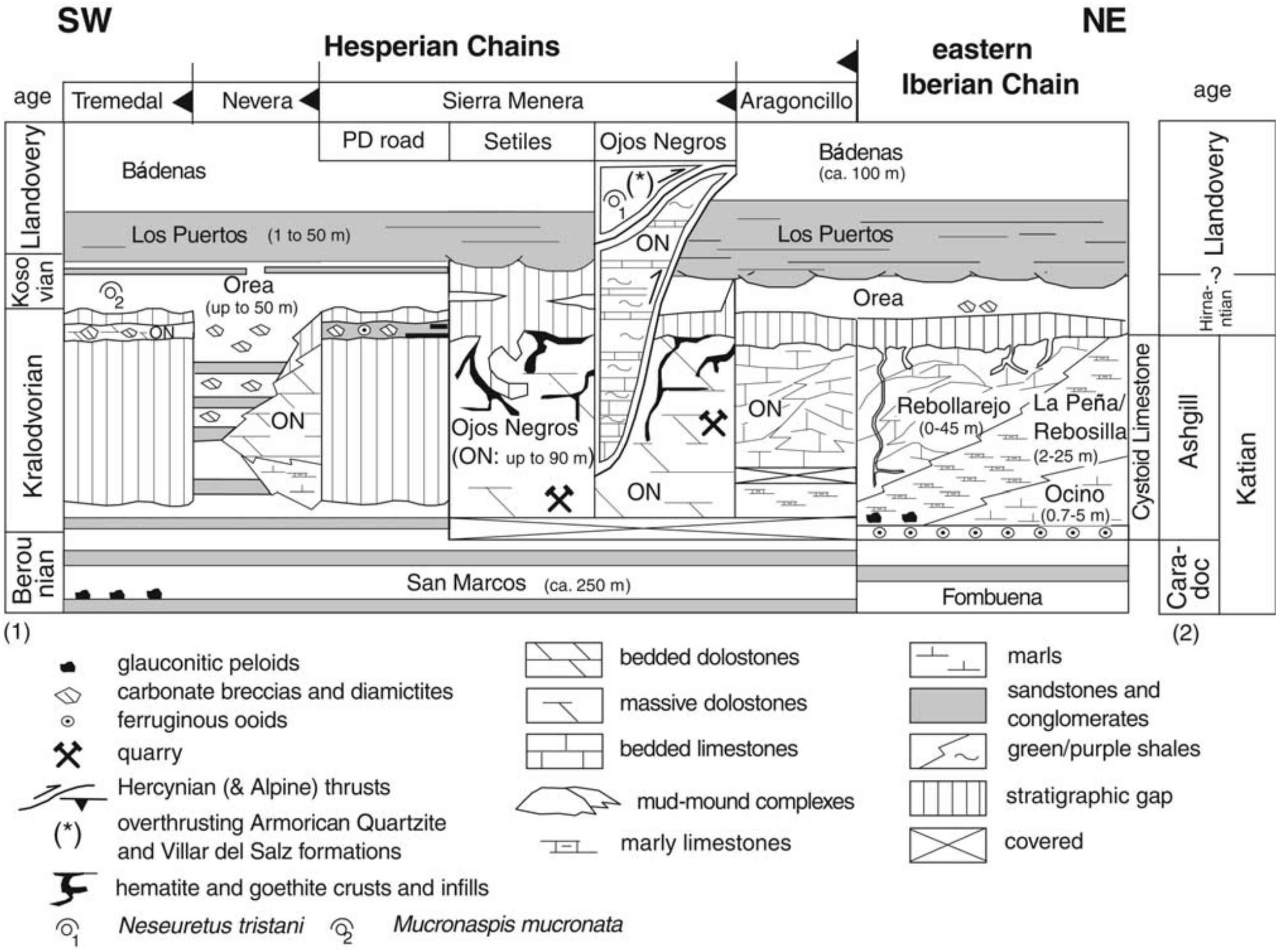

Fig. 2. Stratigraphical chart of the Ordovician–Silurian transition in the IC and HC showing the main gaps and the setting of the Hercynian (and/or Alpine) thrusts in the Ojos Negros quarry; biostratigraphical data after: (1) Gutiérrez-Marco & Štorch (1998); (2) Villas (1985), Owens & Hammann (1990), Hammann (1992) and Vizcaïno *et al.* (2004).

conodonts (Herranz Araújo *et al.* 2003). Vizcaïno *et al.* (2004) also reported the presence of Hirnantian trilobites (such as *Mucronaspis mucronata*) in the Tremedal massif.

Finally, the Los Puertos Formation, formerly named the 'White Quartzite' or 'Valentian Quartzite' in the IC (Carls 1975), is 1–50 m thick and consists of white sandstones and conglomerates with scarce shale intercalations. In the HC, its lower part includes the Ordovician–Silurian boundary interval (Gutiérrez Marco & Štorch 1998), and the formation is overlain by the Telychian black and green shales of the Bádenas Formation (Gutiérrez Marco *et al.* 2002; Herranz Araújo *et al.* 2003).

Facies associations

Thirteen facies associations are recognized in the uppermost San Marcos, Ojos Negros, Orea and Los Puertos formations of the IC and HC. The identification and geometry of their facies belts are illustrated in a north–south to NE–SW transect of the eastern IC (Fig. 3), and a NW–SE transect of the HC (Fig. 4).

San Marcos Formation (HC)

In section PD (Fig. 2), the Ojos Negros Formation is absent and the Orea Formation overlies the San Marcos Formation unconformably. The studied

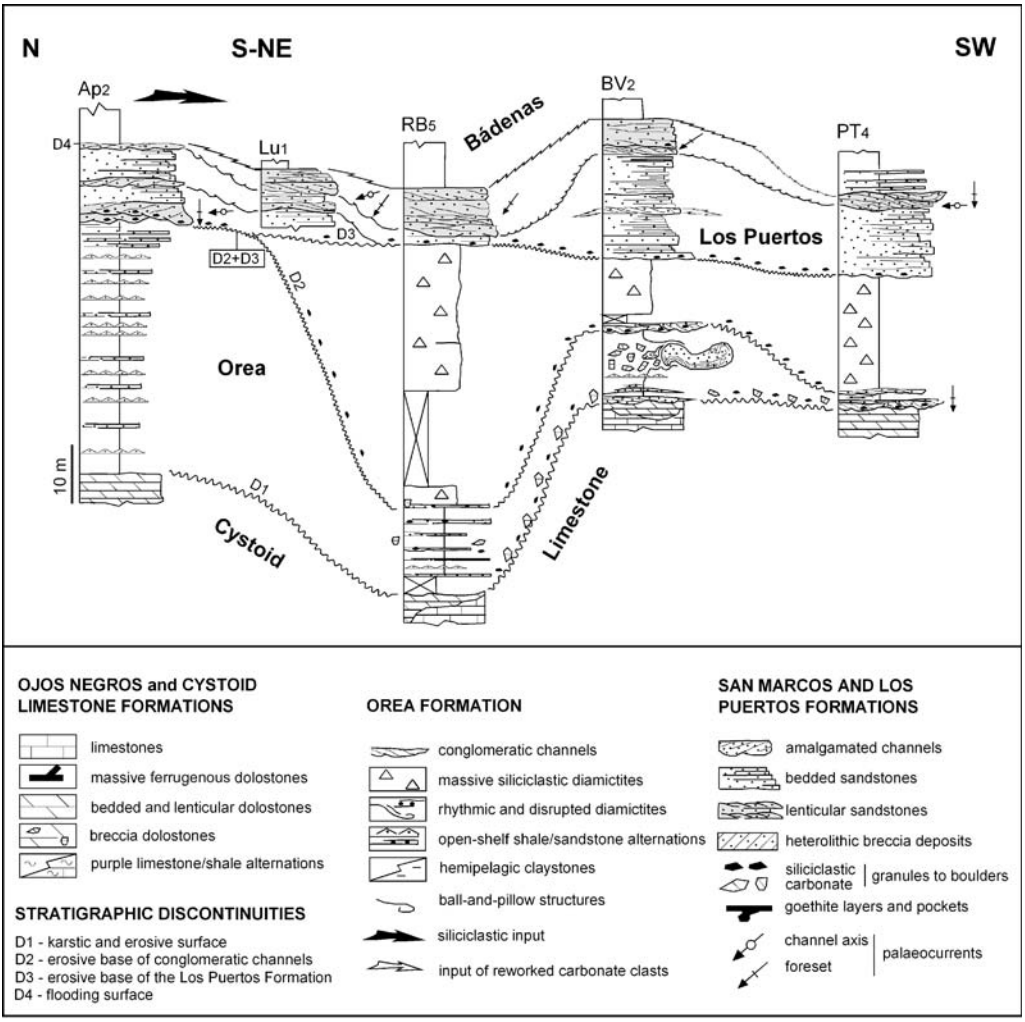

Fig. 3. Measured stratigraphical sections in the IC and correlation of major discontinuities.

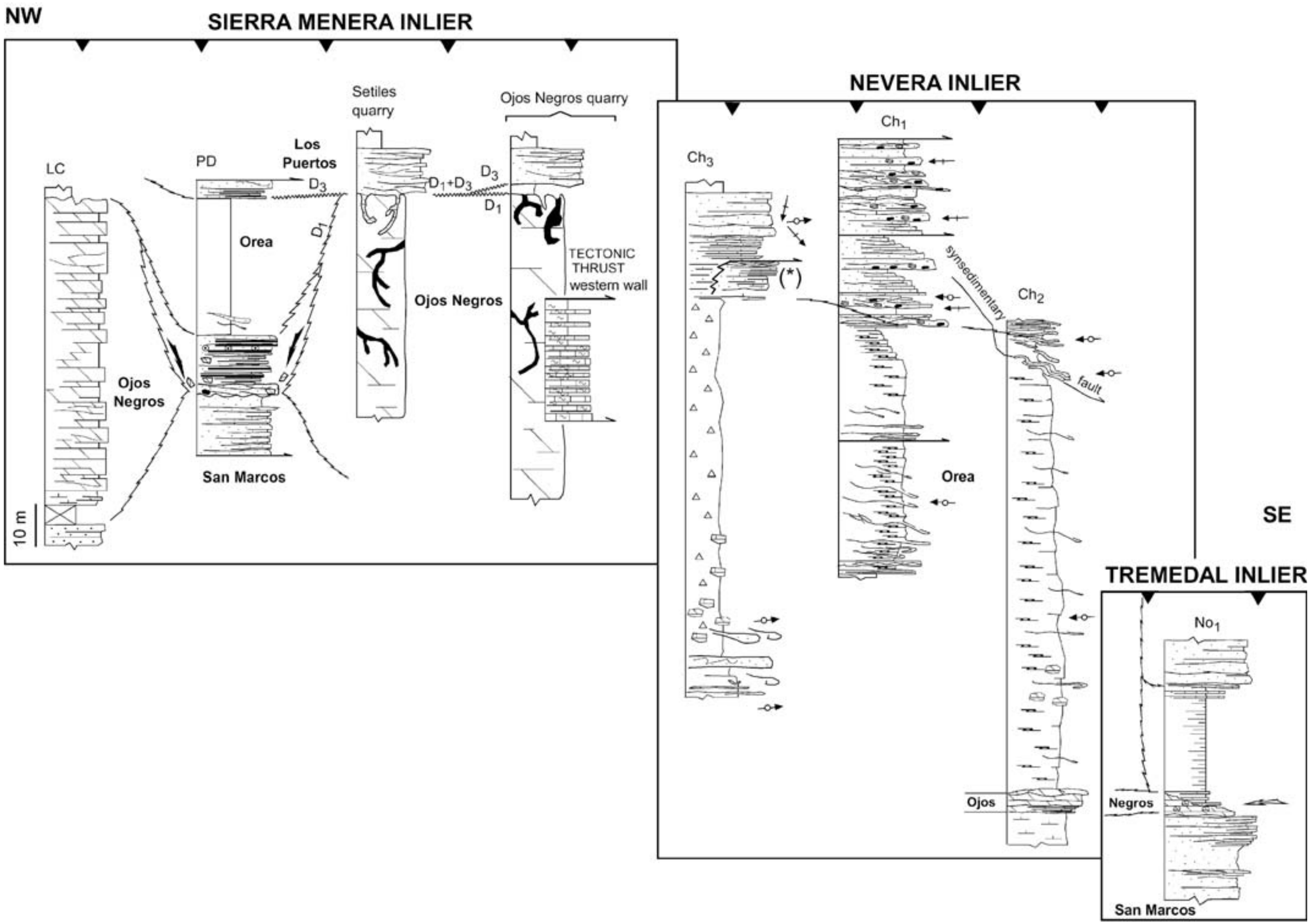

Fig. 4. Measured stratigraphical sections in the inliers of the HC and correlation of major discontinuities; legend as in Figure 3; (*) lowest Silurian graptolites after Gutiérrez-Marco & Štorch (1998).

section, 15 m thick, can be subdivided into two units separated by an erosive unconformity (Figs 2 & 4). The lower unit, 3.5 m thick, displays the typical siliciclastic facies of the formation, and consists of amalgamated lenticular sandstones, punctuated by distinct channelized erosive bases. Several amalgamated, tabular and trough cross-stratified lenses are lined with lags, less than 5 cm thick, of angular to subangular, granule, mono- to polycrystalline quartz and platy shaly clasts (some of the latter dissolved and identifiable by their mouldic porosities). They cover the undulated set bases and are locally imbricated.

The upper 'anomalous' unit is 11.5 m thick, containing millimetre-thick hematite layers that parallel the stratification and foreset tops, as well as numerous ferroan-dolostone clasts. The unit consists of superimposed, thickening- and coarsening-upward parasequences (2.2–4.4 m thick) composed of centimetre-thick shales covered by tabular fine- to medium-grained subarkosic greywackes with parallel- and low-angle lamination, and low-relief trough cross-stratification, better preserved in the thicker beds in which bioturbation can be pervasive. The uppermost part of the parasequences is brownish in colour as a result of the increased content in red-stained hematite. This occurs as thin coatings around grains, authigenic silt-sized crystals, and thin laminae (up to 5 mm thick) of iron oxy-hydroxides encrusting sandstone foresets and bedded laminae (Fig. 5a). The lamination is laterally discontinuous although it can be traced up to 2 m in outcrop. The crusts are opaque or contain identifiable, flattened and distorted (spastolithic) goethite ooids, up to 300 μm in diameter (Fig. 5b); their nuclei show a wide diversity of clasts, such as mono- and polycrystalline quartz, shale and greywacke lithoclasts. Angular to subangular granule clasts occur dispersed in the medium-grained sandstone displaying a wide diversity of lithologies, such as sandstones bearing the above-mentioned authigenic crystals of goethite and hematite, bryozoan debris impregnated and replaced by iron oxides, hematite with and without ooids, and ferroan dolomite.

The upper 'anomalous' unit is arranged in shallowing- and coarsening-upward parasequences, up to 4.4 m thick, which, from bottom to top, display a succession from structureless shales to parallel, low-angle and cross-stratified sandstone sets. The broad, tabular bedding geometries of the cross-bedded sandstones reflect deposition as sheet-like sand bodies, which formed as a result of seaward progradation of sublittoral sand during times of rapid sediment influx. The upward transition from shales to sandstones is gradational, whereas the contact between parasequences is abrupt. Hematite crusts developed during intervals with low rates of siliciclastic influx and minor record of bottom currents, and mark episodic horizons of siliciclastic starvation and iron oxide precipitation capping lenticular foresets. The abundance of ferroan-dolostone clasts suggests deposition of this facies association either coevally or postdating lithification and dolomitization of the laterally equivalent Ojos Negros strata.

Ojos Negros Formation (HC)

Both the Rebosilla–La Peña and Rebollarejo facies types reported in the Cystoid Limestone of the eastern Iberian Chain are recognizable in the exposures of the Ojos Negros Formation located in the Aragoncillo massif (Figs 1 & 2). As their facies associations have been described previously in detail in the IC (Vennin *et al.* 1998), they are not described here.

Massive ferruginous dolostones. These occur in the Sierra Menera massif and display distinct variations in thickness, ranging from 80 m in the Setiles and Ojos Negros quarries to their lateral disappearance in less than 3 km (section PD; Figs 1 & 2). Brownish massive dolostones consist of non-ferroan and ferroan (commonly zoned) dolomite, magnesite, breunnerite, and subsidiary goethite, calcite and quartz [determined by X-ray diffraction (XRD) analysis by Fernández-Nieto *et al.* 1981]. A partial to total replacement of carbonates by goethite has taken place along cleavage planes and crystal walls. Dolomitized skeletons (mainly bryozoans and echinoderm ossicles) are identifiable by their outlines, but their original texture is commonly missing. In both quarries, the top of the massive dolostones displays a great variety of irregular karstic cavities (described in detail below), which are filled with iron oxy-hydroxides, mainly botryoidal goethite (up to 80% based on XRD analyses), gibbsite (15–20%), and minor percentages of hematite, lepidocrocite, pyrolusite, quartz, illite, kaolinite, haloisite (Fernández-Nieto *et al.* 1981), and silt- and boulder-sized angular ferroan dolomite clasts (Fig. 5c).

The biogenic character of the limestones is indicated by the abundance of dolomitized bioclasts, although the frame-building character proposed by Villena (1976) cannot be demonstrated: both the fabrics and the possible development of original build-up geometries are obscured by the massive aspect of dolostones and the intensity of diagenetic processes. The chronology of karst and iron oxy-hydroxide precipitation is discussed below.

Bedded–lenticular dolostones and marls. The Ojos Negros Formation is represented in sections LC and Ch_3 (Sierra Menera and Nevera massifs; Figs 3 & 4)

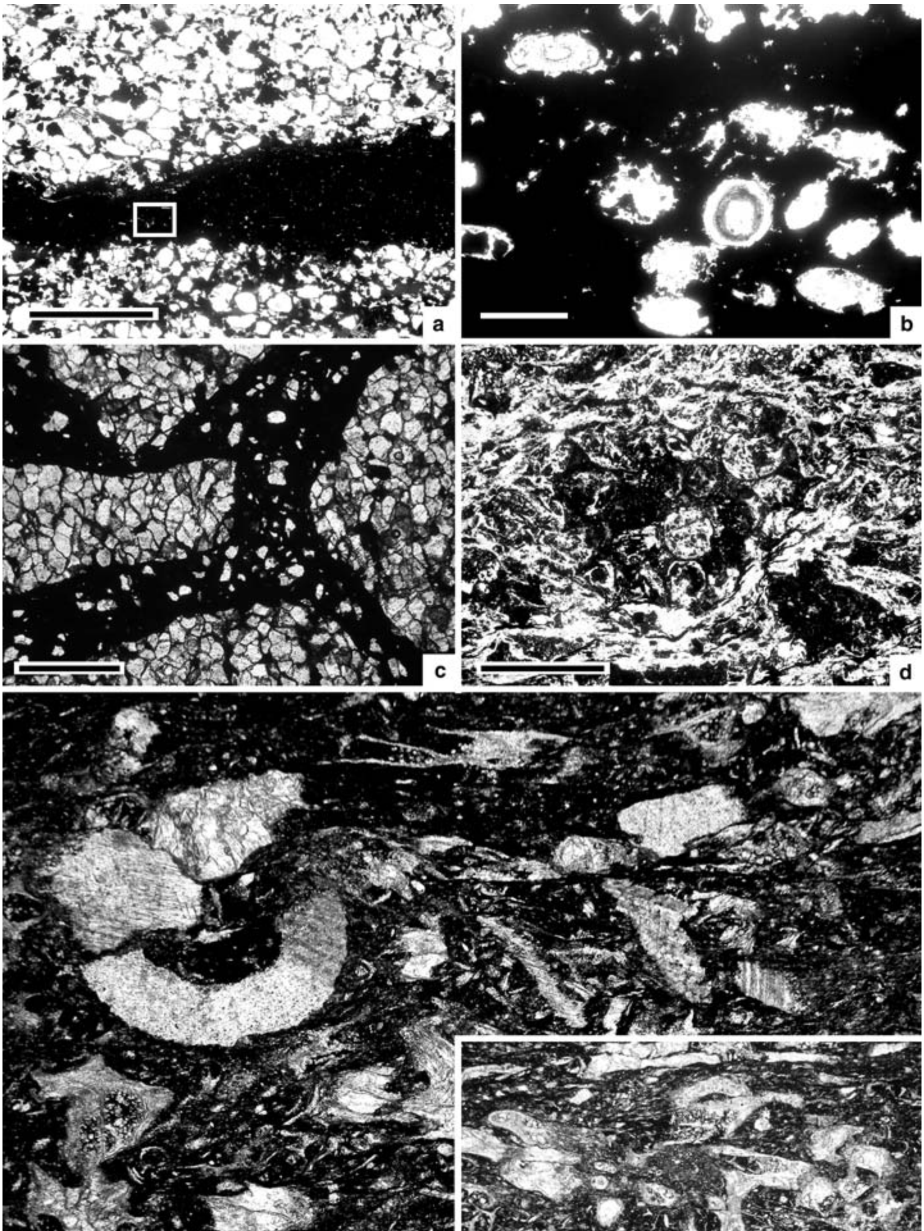

Fig. 5. Photomicrographs of the San Marcos and Ojos Negros facies associations from the HC. (**a**) Millimetre-thick goethite crust embedded in fine-grained sandstone; 'anomalous' uppermost part of the San Marcos Formation in section PD; Sierra Nevera massif; scale bar 2 mm. (**b**) Detail of (a) (boxed area) showing the presence of scattered spastolithic iron-rich ooids with concentric lamellae; scale bar 200 μm. (**c**) Lowermost karstic (breccia) infill of the Ojos Negros quarry (Sierra Menera massif) showing angular clasts of ferroan dolostone embedded in goethite cement; scale bar 1 mm. (**d**) Rounded bryozoan clast (central part) embedded in a mixture of ferroan dolomite–sericite matrix, from the Noguera–Orihuela road, Tremedal massif; scale bar 1 mm. (**e, f**) Bryozoan–pelmatozoan floatstone belonging to the reddish limestone–shale couplets of the tectonic slide found on the eastern wall of the Ojos Negros quarry, Sierra Menera massif; scale bars 1 mm.

by three distinct facies, in ascending order: bedded shales and marls, bedded dolostones and lenticular dolostones. The lowermost calcareous shales and marls, up to 15 m thick, are rich in fragile dendroid–ramose bryozoans, and subsidiary pelmatozoan ossicles and brachiopods. They show common erosive bases and bioclastic grading, and display an upward increase in carbonate content. Upsection, they change into centimetre-thick, laterally continuous, alternating shales and marly dolomitized packstones and floatstones, which are up to 2 m thick, rich in echinoderm ossicles and bryozoans, and have erosive bases. The thickest part of the association, up to 8 m thick, consists of sparry dolostone, with bedded strata ranging in thickness from 10 to 40 cm; its uppermost part is capped by lenticular dolomitized packstones, up to 4 m thick, dominated by echinoderm ossicles, and characterized by large-scale trough cross-stratification, as well as low-angle laminae and common lower and intra-bedded erosive contacts.

Despite modifications of depositional textures by compaction, stylolitization and dolomite replacement, the lower facies was probably deposited in an open-sea offshore environment punctuated episodically by storm events, and represents a 'dolomitized version' of the transition between the Ocino and the Rebosilla–La Peña Members of the IC (see details given by Vennin *et al.* 1998). Frame-building textures (typical of the Rebollarejo Member of the IC) are not recognized. Interpretation of the dolostone beds is difficult because of nearly complete dolomitization of original textures, although the type of stratification and bedforms of the uppermost lenticular dolomitized packstones allow their interpretation as high-energy shoal barriers rich in skeletons, culminating a broad shallowing-upward trend, and mimicking the hydrodynamic conditions that characterize the last episodes of carbonate productivity in the IC (Vennin *et al.* 1998).

Breccia dolostones. One distinct breccia dolostone, up to 2.7 m thick, occurs in section No$_1$ (Tremedal massif; Figs 2 & 4), and is underlain and capped by irregular (erosive) surfaces. The breccia is massive, polymictic, poorly sorted, and is typically disorganized and non-graded. Generally, clasts are randomly oriented, although platy clasts form low-angle laminae. The subangular to rounded clasts, up to 2 cm long, consist of ferroan dolostone, siltstone, claystone, hematite and other opaque minerals, and variable amounts (5–20% in volume) of fragmented to disarticulated echinoderms and bryozoans (Fig. 5d); they are entirely impregnated by iron oxides, and occur 'floating' in a ferroan dolomitized microsparite that changes laterally into sericite, although clast-supported fabrics are also locally recognizable.

Evidence for deposition as episodic mass flows in a slope-related setting comes from the fabric and texture of the breccia: poor sorting, dominantly matrix-supported fabric, polymodal clast size, and subhorizontal orientation of the long axes of clasts.

Reddish limestone–shale couplets. The couplets occur in a tectonic slide recognized on the western wall of the Ojos Negros quarry (Sierra Menera massif), which was thrust northward over the above-mentioned massive ferruginous dolostones, and was itself overthrust and covered by the Armorican Quartzite (Figs 2 & 6). The facies association, up to 30 m thick, consists of alternating centimetre-thick reddish to purple bioclastic limestones and shales, which exhibit an increasing upward shale/carbonate ratio. Thicker (decimetre-thick) limestone beds contain scarce clay seams; upsection, increasingly more and thicker shale strata are interbedded, grading into thick shales with a few isolated or laterally coalescent centimetre-thick limestone to dolostone nodules showing centimetre-scale fining and lower erosive contacts. The thicker limestone beds consist of bryozoan–pelmatozoan floatstones and packstones with variable amounts of calcite-shelled brachiopods and trilobites (Fig. 5e, f). In contrast, the thinner limestone beds and nodules (less than 5 cm thick) are mainly wackestones rich in the same fossil assemblage, in some cases displaying grading, up to 1 cm thick, and local erosive contacts. Shale intercalations are locally burrowed and contain rare bioclasts (mainly bryozoans).

The rhythmic alternation in lithology reflects periodic fluctuations in carbonate productivity and supply of fine siliciclastic sediments, the latter inhibiting the former. The thicker limestone intercalations record the influence of bottom currents and waves (shoreface), whereas the thinner units illustrate quieter conditions interrupted by high-energy, storm-induced pulses (offshore) mimicking the facies of the Rebosilla Member (Cystoid Limestone). A deepening trend is expressed upsection in the decreasing carbonate/shale thickness ratio, reflecting the decreasing effects of reworking by wave action and the increasing record of storm currents in deeper offshore waters. Sedimentary structures, colour and couplet arrangement are similar to the Cambrian 'griotte' facies of southwestern Europe, which represents carbonate productivity on palaeo-highs controlled by a Milankovitch-like cyclicity (for details see Álvaro & Vennin 1997; Álvaro *et al.* 2000).

Orea Formation

The term diamictite used below refers to any lithified, poorly sorted clast–sand–clay admixture

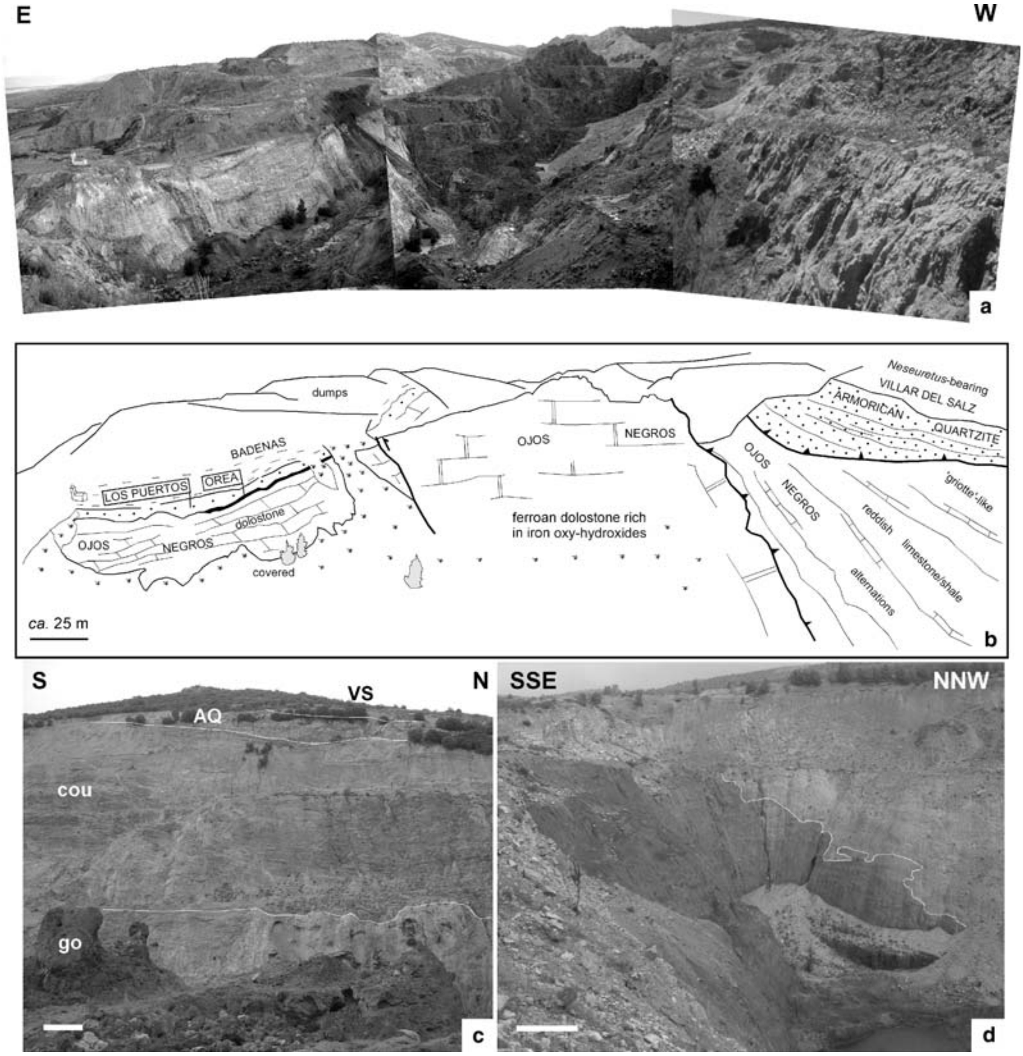

Fig. 6. Field views of the Ojos Negros and Setiles quarries. (**a, b**) East–West transect of the Ojos Negros quarry showing the structural relationships between the facies associations described in the text. (**c**) Western wall of the Ojos Negros quarry showing the superimposition of tectonic slices; go, ferroan dolostones rich in goethite; cou, reddish limestone–shale couplets; AQ, Armorican Quartzite; VS, *Neseuretus*-bearing Villar del Salz Formation; scale bar *c*. 5 m. (**d**) Irregular karstic contact of the Ojos Negros and Los Puertos formations in the Setiles quarry; the Orea Formation is absent; scale bar *c*. 3 m.

regardless of depositional environment (Eyles *et al.* 1983).

Conglomeratic channels and foresets (IC). A set of amalgamated channels (up to 1.4 m thick), which changes upward and seaward into alternations of lenticular trough cross-bedded sandstones and shales (4–8 m thick), occurs in sections RB_5, BV_2 and PT_4 of the IC. The bases of the conglomeratic channels display erosive contacts onto the lower diamictites of the Orea Formation (described below) (Fig. 7a), whereas their tops are gradational into the upper diamictites of the Orea Formation. Each channel is 0.3–0.6 m wide and up to 0.6 m thick; erosive bases are broadly concave-upward and lined with concentrations, less than 10 cm thick, of angular to subangular granules (angularity increases with grain size) rich in mono- and polycrystalline quartz, chert, wholly to incompletely dolomitized packstones to floatstones containing

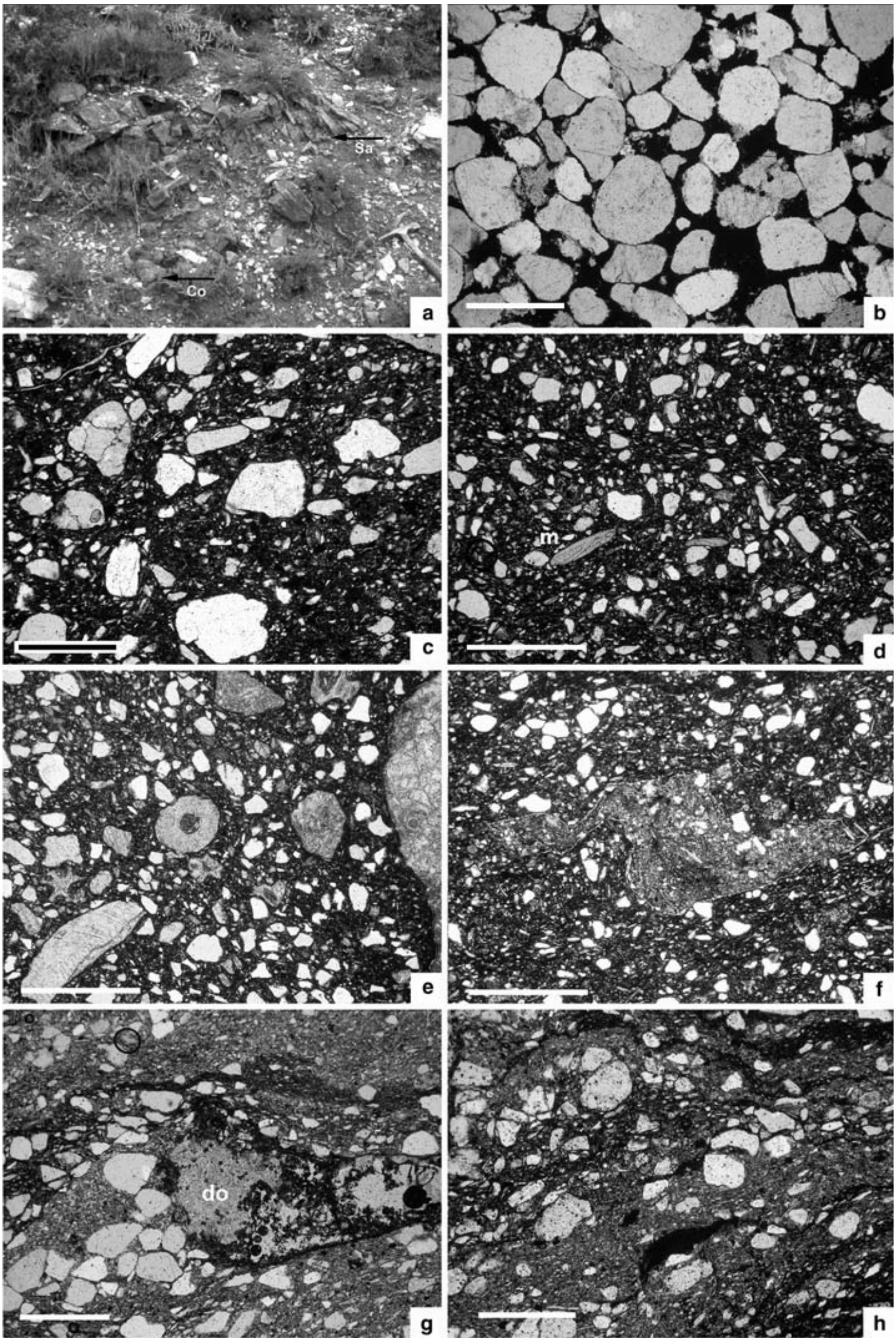

Fig. 7. Field view and photomicrographs of the Orea Formation in the IC and HC. (**a**) Conglomeratic channels (Co) covered by trough cross-stratified foreset sandstones (Sa) from section BV_2, eastern IC; hammer at the lower-right corner indicates scale. (**b**) Quartz arenite cemented by authigenic goethite–hematite sampled in the sandstones shown in (a); scale bar 1 mm. (**c**) Crudely stratified siliciclastic diamictite of section Re_5, eastern IC; scale bar 2 mm. (**d**) Massive siliciclastic diamictite of section Ch_1, HS; m, mica; scale bar 2 mm. (**e**) Massive mixed diamictite showing carbonate clasts and disarticulated and broken echinoderm ossicles and bryozoan fragments; section BV_2, eastern IC; scale bar 2 mm. (**f**) Massive mixed diamictite with a contorted clast (central part) rich in sericite and mica; scale bar 2 mm. (**g, h**) Disrupted diamictite showing contorted contacts of subparallel sets with different concentration of clasts; section Ch_1, HC; do, dolomite; scale bars 2 mm.

bryozoans and echinoderms, and dispersed dolomitized skeletons. The channels consist of clean to slightly calcareous (less than 10% of dolomite microsparite cement), moderately sorted granules fining upward into coarse-grained sublitharenites, with abundant (up to 20%) authigenic, silt-sized goethite and hematite crystals (Fig. 7b). The palaeocurrents of channel axes range from 210° to 270°. Overlying lenticular sandstones are coarse- to very fine-grained quartzarenites to greywackes and locally bear the carbonate clasts mentioned above.

The conglomerates and sandstones were deposited as amalgamated channels filled by intersected cross-bedded sets. The pronounced upward fining displayed by single channels and the unimodal character of their palaeocurrent indicators, along with the absence of lateral accretion surfaces, suggest that these sandstones were deposited in an essentially unidirectional, subtidal channel complex. A broad deepening-upward trend is recorded in the whole facies association, from subtidal coarse-grained channels to finer-grained shoals migrating on a shaly substrate.

Massive and crudely stratified diamictites (IC and HC). The massive diamictites form tabular beds, up to 10 m thick, successively amalgamated with slightly erosive contacts, mostly sharp, planar or gently undulating. They have a chaotic to weakly developed laminated fabric. Scattered outsized clasts are either isolated or chaotically clustered and embedded in a clayey siltstone matrix. The size of the clasts varies from boulder to silt with all intermediate grades represented; finer grains are angular to subangular whereas coarser grains are subangular to well rounded, and their long axes are both randomly oriented and transverse to stratification. Thin (<2 cm) interbeds of laminated claystone and siltstone also occur irregularly, leading to crudely stratified units, which exhibit some degree of textural sorting and stretched or folded claystone–siltstone lenses. The facies association can be subdivided into two types, distinguishable by their clast composition and the related presence or absence of carbonate cement, as follows.

(1) The terrigenous massive diamictite, which occurs in sections RV_5, BV_2 and PT_4 (IC), contains scattered to common, siliciclastic granule- to sand-sized clasts dispersed in a silty claystone matrix rich in authigenic and reworked silt-sized goethite and hematite crystals. Clasts consist of mono- and polycrystalline quartz, chert, siltstone and rare larger clasts of quartz-rich agglomerates, the whole framework commonly coated with hematite films (Fig. 7c, d).

(2) The mixed massive diamictite contains dispersed limestone and dolostone clasts. In the IC, it occurs exclusively in section BV_2, where it is capped by conglomeratic channels and contains dispersed granules to boulders rich in bryozoan–pelmatozoan frame-building limestones (partly or completely dolomitized), and isolated bryozoan, echinoderm, and minor trilobite and brachiopod debris, some of which is coated by sparry calcareous films (up to 50 μm thick). Section Ch_2 of the HC provides a thick (more than 40 m although fining upsection) record of dispersed granule to boulder clasts composed of sparry limestone, ferroan dolomite, siltstone, mono- and polycrystalline quartz, isolated dolomitized and ferruginized skeletons (mainly bryozoans and echinoderms), and sandstones cemented with authigenic hematite, the whole framework immersed in a silty claystone matrix cemented locally with patches of sparry dolostone (Fig. 7e, f).

Outsized clasts are known to be shed from icebergs, partly floating 'glacier termini' and sea ice (Lønne 1995). Massive diamictites most closely resemble 'rain-out' diamicts formed by the settling of suspended fine material and release of coarser dropstones from icebergs in the vicinity of a calving front (Eyles *et al.* 1993). Weakly developed lamination may record episodic current activity that resulted from storm, turbidity or wave-influenced processes. The terrigenous facies form a regionally extensive blanket unit and indicate abundant and relatively homogeneous siliciclastic supply to the platforms, probably from glacial melt-water sources. In contrast, the setting of the mixed facies is selective, occurring in two discrete outcrops of the IC and HC. The presence of common polyphase clasts in some diamictites suggests the onset of 'cannibalistic' processes reworking the 'rain-out' facies downslope. This is probably due either to the outlet of sub-glacial bottom currents scouring former deposits, especially during melt flash floods (IC) or to syntectonic activity (HC).

Rhythmic and disrupted diamictites (HC). These strata occur in sections Ch_1 and Ch_3 of the HC. They vary gradually from those consisting of a chaotic mixture of sandstone and claystone (similar to the massive diamictites), to those having a millimetre-thick, graded siltstone- and claystone-rich couplets with abundant angular intraclasts of laminated silty claystone. The rhythmic fabric, commonly punctured by mostly vertical sand clasts (described in detail below), displays a low-angle and parallel lamination, and widely developed wavy bedding. This facies is locally folded and deformed, and occurs interbedded with disrupted diamictites.

Disrupted diamictites are characterized by a chaotic arrangement of moderately to strongly deformed contorted beds (Fig. 7g, h). Truncation surfaces, some involving sediment thickness of several tens of metres, can be traced laterally up to 10 m, and are revealed by dip discordances bounded above and below by undisturbed sediments. Intraformational slumping has resulted in severe deformation of entrained material, which displays a range of brittle ‘firm’ and soft-sediment deformation, highly contorted and folded. Depending on location, underlying sediments were either lithified (shear beds and laminae, which are sharply truncated and discordant) or unlithified (steeply dipping sediments, up to 50°, which are squeezed and contorted) at the slump interface. On a smaller scale, synsedimentary normal microfaults and sedimentary boudinage have resulted from extensional stresses within poorly lithified to unlithified sediment mass. Palaeocurrents in the measured sections indicate opposite northeastern and southwestern sediment transport (Fig. 4).

Wavy to parallel bedding of the rhythmic facies bearing common claystone pockets and laminae indicates the importance of winnowing and scouring by bottom currents. Graded couplets formed as a result of rhythmically varying sediment input different from slump-triggered (non-rhythmic) chaotic and disrupted facies. Stratified diamictites are typical of stacked subaqueous debris flows resulting from the repeated downslope failure of heterogeneous sediment source areas (distal facies). Chaotic facies indicate deposition extremely close to a coarse-grained and heterogeneous sediment source prone to resedimentation (reworked proximal facies). They probably formed as a result of downslope resedimentation of laminated silts and clays in areas receiving fine-grained sediment from suspension and turbidites; coarser-grained clasts were supplied by floating icebergs.

The rhythmic deposits are interpreted as having formed in response to fluctuations in glacier meltwater discharge. Sandstones and shales were deposited during peak discharge followed by claystone during low-discharge episodes. Disrupted diamictites probably formed as a result of downslope resedimentation of laminated siltstones and claystones in areas receiving fine-grained sediment from suspension. Slumping may have been triggered by rapid sedimentation and the development of high pore-water pressures, deposition on high-relief substrates, oversteepening of depositional slopes, seismic shock or a combination of these processes.

Open-shelf shale–sandstone alternations (IC). These alternations occur directly overlying the Cystoid Limestone in the IC. They consist of non-calcareous silty to sandy widely bioturbated shales. They occur both as thin and discrete beds and lenses and as massive strata, tens of metres thick. Very fine- to medium-grained sandstone intercalations increase in number, thickness and grain size upward to the erosive base of the Los Puertos Formation (section AP_2), whereas they lack any upsection trend in sections RB_5 and BV_2, where the facies alternations are capped by the conglomerate channels of the Orea Formation (Fig. 3). The sandstone beds and lenses are as much as 20 cm thick; they thicken and thin laterally, pinch out over distances of 20 m grading laterally into shales, have sharp bases, and exhibit parallel, low-angle and hummocky-cross lamination, local symmetrical ripples and centimetre-thick graded silty layers. Sandstone strata display sharp bases that can be flat, gently undulating or even widely scoured.

The high abundance of argillaceous sediments indicates an environment where, during ‘fair-weather’ episodes, sedimentation resulted from suspension. There is no evidence of reworking of sediment by unidirectional bottom currents, and the episodic influence of waves is indicated by the presence of symmetrical ripple marks. The environment was probably seaward of the shoreface, but it was sufficiently nearshore to allow the record of episodic reworking by waves. Intercalated lenses of siltstone and sandstone with hummocky bedding and graded silty layers show evidence of proximal and distal storm-induced features. Sandstone–shale alternations were deposited under a wide range of energy levels between fair-weather and storm-wave base. A change in the proximity of the source area is indicated by the upward increase in sandstones, and their change in sedimentary structures.

Grey and black shales (HC). Structureless shales are recognized in sections PD and No_1 of the HC. They are dark coloured, carbonate-free claystones, episodically punctuated by millimetre-thick parallel lamination. Silt content is low (less than 10% in volume), except in the lowermost 4 m of the sections, and the microcrystalline sulphide content (mainly pyrite) is highly variable. Section No_1 has yielded a benthic trilobite fauna of Hirnantian age (Vizcaïno *et al.* 2004), which precludes anoxic conditions. These shales probably originated by the settling of fine-grained sediments from suspension, on a clayey, dysoxic substrate protected from the input of glaciogenic debris.

Los Puertos Formation

As the Hercynian and/or Alpine thrust surfaces of the HC commonly diverge from detachment levels located at the Orea–Los Puertos contact, the lower part of the Los Puertos Formation is highly fractured. As a result, this formation has been studied in detail only in the IC and in the better-preserved outcrops of the HC (sections Ch_1 and Ch_3).

Amalgamated channels (IC). These channels (up to 2 m thick and 1–4.8 m wide), recognized only in the lower part of section Ap_2 (Fig. 8a), are relatively steep-sided, scouring into the lowermost part of the Los Puertos bedded sandstones (described below) and the Orea shales. The channel bases are steeper axially, where they become amalgamated with intra-channel, laterally limited erosive surfaces, which have gradients of 5–10°. The channels are lined with lag deposits of angular gravels, composed of chert, mono- and polycrystalline quartz, and claystone clasts; their orientation is either bed-parallel or relatively random. Generally, above the lags the infill becomes finer upward, changing from well-sorted, very coarse- to fine-grained litharenites widely cemented with silica. Large-scale trough cross-beds, ranging from 1 to 1.4 m in thickness, are pervasive in the lower part of the channels. Foresets show southward dips of 2–25°, tangential, angular or concave-upward, with common reactivation surfaces, and scoured significantly into the underlying sediments. The channels grade upward into current ripples and low-angle to parallel laminae and structureless sandstones. Locally, irregular scour-and-fill features have also been observed. The top of channels is defined abruptly by a direct superimposition of thin-bedded sandstone sheets.

This facies association represents lateral migration, progradation and amalgamation of channels. It occurs only along the northeastern edge of the IC, and a distinction between continental and marine processes is not clear.

Bedded and lenticular sandstones (IC and HC). Beds of this association are dominant in the Los Puertos Formation of the IC and in section Ch_1 of the HC, where two main lithofacies are present: amalgamated tabular sandstones and cross-stratified sandstones. Tabular beds include parallel to low-angle laminated, and plane-bedded sandstones, which combine to form laterally extensive ungraded strata up to 1.2 m thick. Bedded sandstones are incorporated into thinning-upward trends (2–8 m thick), in which low-angle and parallel laminae are better preserved upward. Cross-stratified sandstones are both interstratified with the previous lithofacies and dominant at the upper part of the formation (Fig. 8b, c). They are characterized by large-scale trough cross-stratification, with unidirectional foreset migration directions, which occurs in 0.2–1.2 m thick sets sometimes topped by symmetrical rippled cross-laminae. These lens-shaped units are laterally arranged, from convex- to concave-up morphologies (sigmoidal), where upper and lower bounding surfaces are commonly sharp. The internal cross-laminae are arranged in discrete packages, which are demarcated by reactivation surfaces with a sigmoidal configuration. Cross-stratification and internal reactivation surfaces are flat and subparallel to bedding ($<10°$), and dip toward 260–350°. In places, thin (<5 cm) lags of rounded quartz, shale and chert granules define the erosive base. Both the tabular and cross-stratified sandstones of the HC differ from those of the IC in their clast content, as the former contain numerous ferroan dolomite and goethite-rich granules concentrated as lags in the lowermost part of the thicker beds.

The presence of low-angle cross-laminated and plane-bedded sandstones and the general scarcity of claystones are consistent with facies identified from shoreface to foreshore and coastal-plain deposits (Lindsey & Gaylord 1992). The interbedded, unidirectional, large-scale, cross-bedded sandstones are interpreted as foreshore-ridge runnel and nearshore-bar deposits. Internal reactivation surfaces that bound each cross-laminae set originated from frequent changes in velocity. These nearshore-bar deposits, with inclined bedsets of laminated sandstone and dipping toward the WNW, suggest basinward beach migrating deposits. The absence of shales can be ascribed to a high average energy trend, which allowed the finer sediments to be winnowed away. Tidally induced sedimentary structures are absent.

Both lithofacies are arranged in asymmetrical claystone-free progradational parasequences 0.3–2.2 m thick, with shoal complex lenses capped by coastal-plain strata. The mechanism proposed for this development is somewhat analogous to that of prograding shoreline deposit trends, in which coastal deposition and shoal complexes grew and migrated seaward during times of rapid sediment influx.

Heterolithic breccia and contorted beds (HC). These strata form the lower part of the Los Puertos Formation in sections Ch_1 and Ch_3 of the HC. They consist of bedded sandstones (0.2–0.5 m thick), and channels and trough cross-bedded lenses composed of unsorted litharenites (0.4–1 m thick). Granule to cobble clasts are subrounded to highly angular, polycrystalline quartz, ferroan dolomite and sparry limestone, the last sometimes being dissolved and identifiable by their mouldic porosity (Fig. 8d). Clasts are commonly imbricated, forming low-angle to cross-bedded laminae directed westward. These beds are dramatically slumped and contorted, or even may be arranged into distinct olistostromes in section Ch_3 (Fig. 8e, f), where a synsedimentary fault is marked by an angular discontinuity associated with breccia deposits, slumps, olistostromes, the bases of which are rich in ichnofossil hyporeliefs, and flute and tool marks (Fig. 8g, h). This facies association represents a slope-related shoreface sedimentation reflecting sea-floor instability.

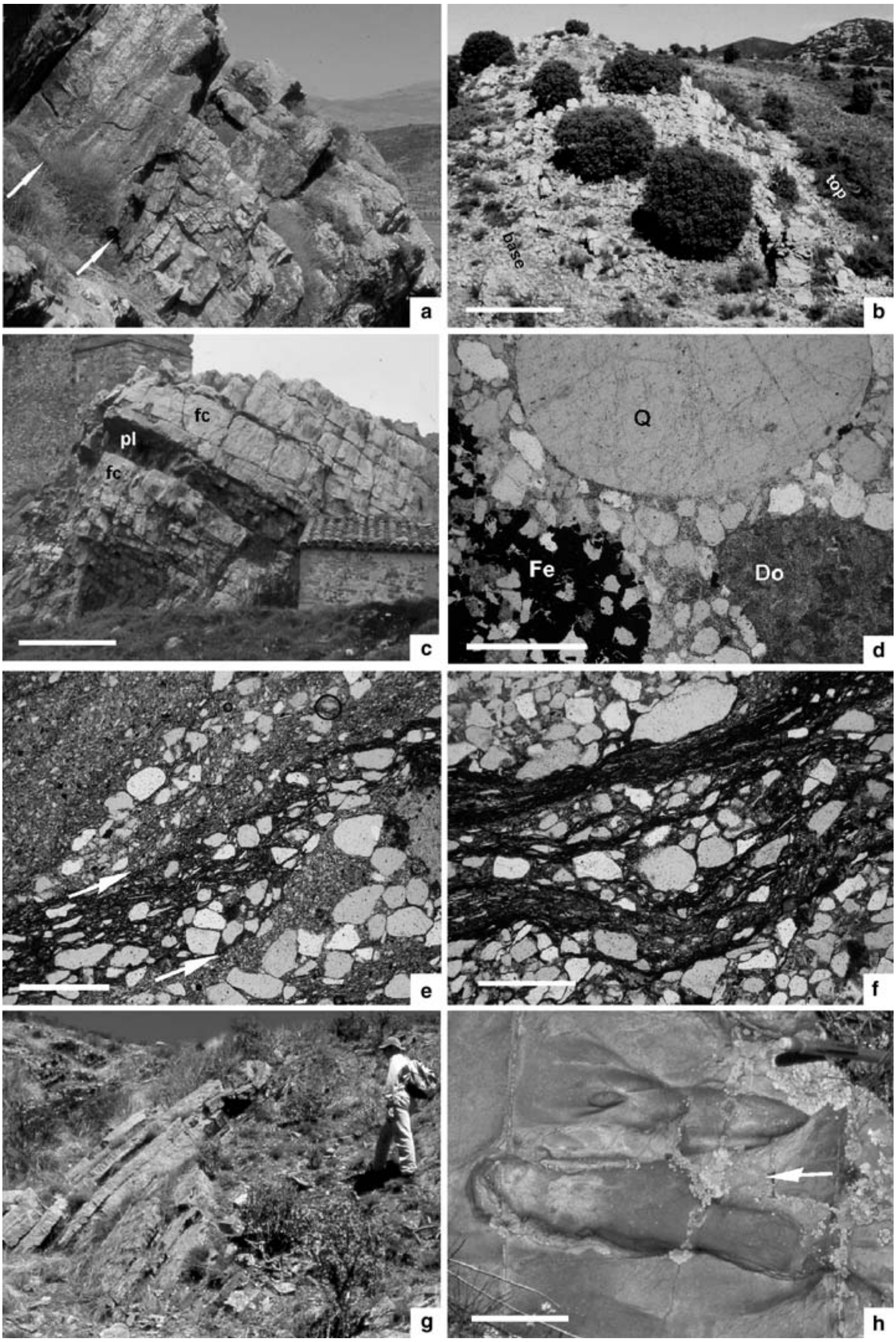

Fig. 8. Field views and microphotographs of the Los Puertos Formation in the IC and HC. (**a**) Amalgamation of channels and foreset sandstones at the base of the formation in section Ap, eastern IC; major erosive surfaces arrowed. (**b**) View of the formation in section BV_2; scale bar 4 m. (**c**) Top of the formation in Luesma showing alternations of foreset complexes (fc) and flat parallel-laminated sets (pl); scale bar 2.5 m. (**d**) Polymictic litharenite exhibiting rounded clasts of quartz (Q), ironstone cemented with goethite (Fe), and dolostone (Do); section Ch_3, Nevera massif; scale bar 2 mm. (**e, f**) Slumped sandstones showing successive onlapping geometries; section Ch_3; scale bars 2 mm. (**g**) Slumping sandstone strata at the contact with a synsedimentary fault; beds on the right are parallel to the base of the picture; top of section Ch_2. (**h**) Flute casts in a slab shown in (g); palaeocurrent indicated by arrow; scale bar 6 cm.

Palaeogeographical features and unconformities

The reconstruction of the main depositional pathways and architectural facies distribution of the Iberian and Hesperian platforms across the Katian–Llandovery transition is based on mapping, palaeocurrent measurements and regional stratigraphical correlation of facies associations and major erosive unconformities (Fig. 9). The sporadic occurrence of biostratigraphically significant Hirnantian fossils (Carls 1975; Herranz Araújo *et al.* 2003; Vizcaïno *et al.* 2004) precludes any biostratigraphical subdivision of the sedimentary packages. According to early Palaeozoic palaeogeographical reconstructions, for example, those made for early–middle Ashgill (late Katian) times (Vennin *et al.* 1998), the NE–SW transect of the IC studied in this work reflects a proximal-to-distal trend.

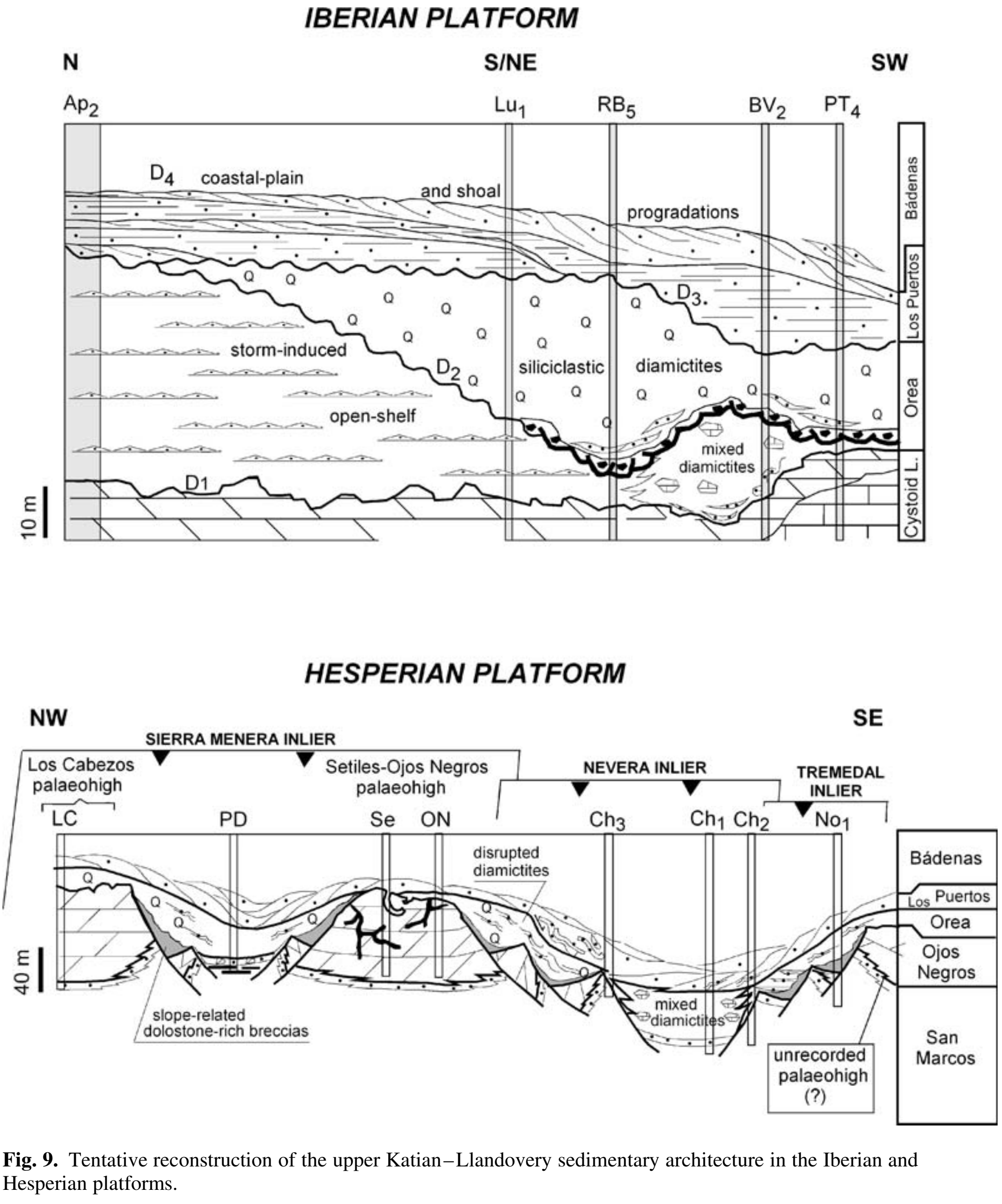

Fig. 9. Tentative reconstruction of the upper Katian–Llandovery sedimentary architecture in the Iberian and Hesperian platforms.

The Iberian intra-shelf ramp under quiescent tectonic conditions

The late Katian episode of carbonate productivity recorded in this Mediterranean region has been associated with (1) the deflection by Baltica (after the accretion of Avalonia) of a warm ocean current toward North Gondwana (Villas *et al.* 2002), and (2) a global warming episode, the so-called Boda event (Fortey & Cocks 2005). The late Katian evolution of the Iberian platform has been described in detail by, among others, Hafenrichter (1979), Hammann 1992) and Vennin *et al.* (1998). The Cystoid Limestone represents the development of pelmatozoan–bryozoan meadows in mid-ramp settings and pelmatozoan–bryozoan mud-mound complexes in outer-ramp environments, under conditions of limited accommodation space. The Cystoid Limestone–Orea contact is marked by an irregular stratigraphical discontinuity (D1 in Fig. 9a). Numerous karstic microcavities, 4–20 mm in size, occur close to the top of the Cystoid Limestone, and are interconnected forming a network capped by D1; these are occluded with admixed clays of the overlying Orea Formation and calcite and dolomite cements (Vennin *et al.* 1998). D1 can be interpreted as a compound erosive–karstic unconformity related to subaerial conditions of the Iberian platform that lasted sufficiently long to allow development of internal karst structures and an eroded palaeorelief. Dolomitization processes are restricted exclusively to the uppermost part of the Cystoid Limestone and to the vicinity of Hercynian faults. The incorporation of partly to completely dolomitized clasts in the overlying Orea Formation indicates an early diagenetic dolomite replacement process.

The Orea Formation can be subdivided into two depositional sequences bounded by a distinct erosive discontinuity (D2 in Fig. 9a) that marks the base of the conglomeratic channels. The diamictites of the lower sequence formed extensive blanket-like sheets that buried the pre-existing karstic palaeotopographies. Proximal outcrops (Ap_2, Lu_1 and RB_5) display offshore deposits that pass basinward into sedimentation of terrigenous massive diamictites (PT_4), punctuated by an isolated wedge of mixed diamictites (BV_2). The latter are associated laterally with intraformational slumps and local synsedimentary bedding distortion (Fig. 10a). The reduced extension of the carbonate–dropstone wedge suggests the underflow action of distinct lanes of iceberg drift.

In proximal outcrops (Ap_2), the upper sequence of the Orea Formation is absent because of erosion, and D2 coincides directly with the unconformable base of the overlying Los Puertos Formation (D3); as a result, the top of the Orea Formation there is a compound erosive unconformity, named $D2 + D3$ in Figure 9a. In central sections (e.g. Lu_1 and RB_5), D2 is represented by an abrupt change from open-sea offshore sediments, laterally recording glaciogenic processes (lower sequence), to conglomeratic channels covered by terrigenous diamictites (upper sequence) indicating abrupt changes in depositional conditions. The conglomeratic channels that rest on D2 wedge out distally (toward the SW), changing into calcareous sandstones rich in limestone and dolostone granules, and limonitized bioclasts composed of disarticulated and broken echinoderm and bryozoan debris. The conglomeratic channels are interpreted as lag deposits rich in siliciclastic and carbonate granule-sized clasts, able to erode the substrate and form cut-and-fill troughs, up to 1.5 m thick. The disappearance of this facies in the proximal part of the Iberian platform, related to the erosive character of the overlying Los Puertos Formation, precludes interpretation of the shallowing associated with the onset of the conglomeratic channels. However, because of its setting separating two glaciomarine deposits, it may represent either the grounding line of an ice-contact submarine fan (Lønne 1995) or the point at which meltwater left confining progradational channels (Dowdeswell *et al.* 1998).

The upper sequence of the Orea Formation consists of homogeneous, terrigenous massive diamictites, which are interpreted as waterlain, so that floating, debris-bearing ice, probably in the form of a discontinuous ice platform, deposited its sediment in areas with little current reworking.

The Orea–Los Puertos contact is marked by another erosive discontinuity (D3). This is related to drastic shallowing, probably related to strong glacioeustatic rebound, which resulted in vigorous bottom current activity excavating the shaly (Orea) substrate and the record of an erosive base level-fall unconformity in proximal outcrops. Deeply incised bedrock troughs in proximal outcrops (Ap_2), with a steepened longitudinal profile, suggest progradational down-cutting: bedded geometries allow an estimate of the lateral truncation developed by discontinuity D3 in the vicinity of Ap_2, as it erodes about 10 m of thickness in less than 50 m. The terrigenous beds of the Los Puertos Formation exhibit a general pattern of southwesterly thinning and diminishing grain size reflecting greater subsidence to the SW, as well as primary northeastern source areas. The Los Puertos Formation is a clastic wedge dominated by coastal-plain and shoreface deposits. They are arranged as three asymmetric claystone-free progradational parasequences, which are 0.3–2.2 m thick: the two first parasequences consist of shoal complex lenses capped by coastal-plain strata, whereas in the third the coastal-plain strata did not prograde. As explained above, the mechanism proposed for this development is somewhat analogous to that of prograding shoreline

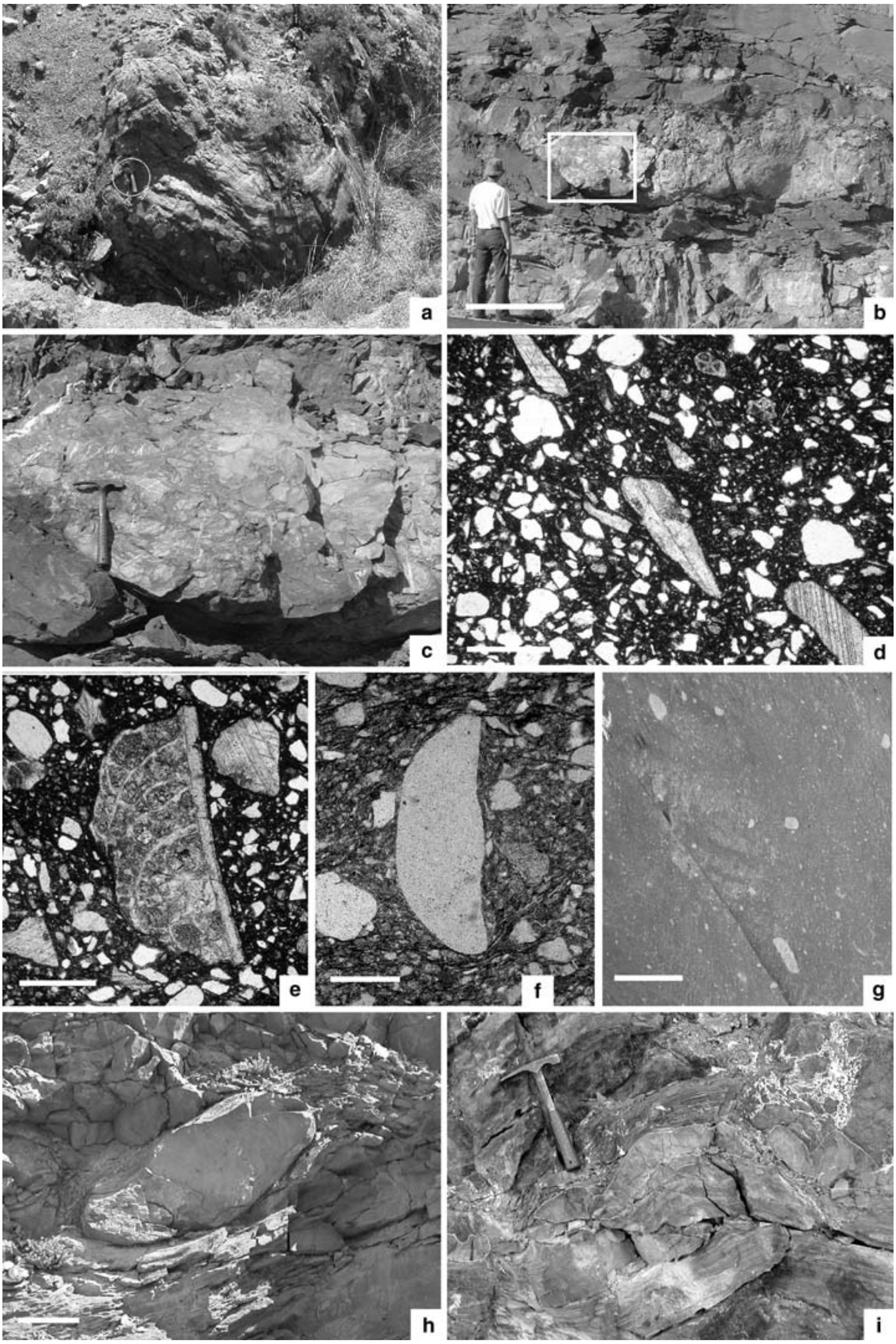

Fig. 10. Key sedimentary structures recorded by the glaciomarine Orea Formation. (**a**) Contorted siltstone and sandstone strata preserved laterally to the mixed diamictite wedge of section BV_2, eastern IC; hammer encircled. (**b, c**) Ball-and-pillow structures, reflecting the onset of fluidification processes, displaying a channelized event embedded in massive mixed diamictites of section Ch_1. (**d–g**) Elongated clasts preserving the high dip of their long axis; scale bars 4 mm (d–f) and 10 cm (g). (**h**) Subrounded siltstone (outsized) clast, *c.* 50 cm across, embedded in the massive diamictites of Ch_2; scale bar 20 cm. (**i**) Contorted siltstone bed embedded in a rhythmic diamictite of Ch_3.

deposit trends, in which coastal deposition and shoal complexes grew and migrated seaward during times of rapid sediment influx. Each progradation terminated in a rapid rise in sea level that flooded the low-lying coastal-plain system and provided the extra accommodation space into which the next parasequence prograded. The low-gradient platform was not covered by water deeper than wave base during the episodes of sharp sea-level rise (with no indicators of scouring or ravinement surfaces), before the shoreface of the next parasequence began to prograde across the inner platform. Comparing the thickest portion of each parasequence and the absence of coastal-plain strata in the third parasequence, it is possible to invoke composite basinward-to-landward-stepping stacking patterns exhibited by the entire formation (Fig. 9). The end of the Los Puertos progradation is marked by another distinct discontinuity (D4). This is sharp in proximal outcrops, where it represents an abrupt flooding of the platform and deposition of deep shales (Bádenas Formation). D4 becomes less clear in distal outcrops, where the Los Puertos–Bádenas transition is characterized by shale–sandstone alternations (PT_4).

The Hesperian shelf under active extensional tectonic conditions

The late Katian carbonate-dominated Ojos Negros Formation displays important lateral variations in thickness and facies reflecting differential fault-induced subsidence, and the development of a major topography of the sea floor. Three prominent carbonate factories were the main production areas in the Hesperian platform, named Los Cabezos, Setiles–Ojos Negros and 'unrecorded' palaeo-highs in Figure 9b. Isolated palaeo-highs or horsts, tens of kilometres wide, were surrounded by deeper-water substrates, where carbonate debris was introduced as winnowed particles. The carbonates of the Ojos Negros Formation were completely dolomitized and their original textures have disappeared, except in two settings: (1) the pelmatozoan–bryozoan meadows and mud-mound limestone complexes of the Aragoncillo massif; (2) the griotte-type, centimetre-thick, limestone–shale couplets preserved in a tectonic slide of the Ojos Negros quarry, in the Sierra Menera massif.

The chronology of the iron-rich ore precipitation is constrained by two sedimentary features: (1) direct iron oxy-hydroxide precipitation took place in the relative palaeo-depressions where carbonate productivity was absent (e.g. PD section; Fig. 7a); (2) hematite clasts derived from the karstic infills are abundantly reworked and deposited in the overlying Orea and Los Puertos formations (Fig. 8d). In the relative palaeo-depressions, goethite and hematite millimetre-thick crusts are also associated with iron-rich ooids. The ooids formed by chemical precipitation of cryptocrystalline iron oxy-hydroxides on available grains on the sea floor. This enrichment could be a result of hydrothermal fluids, volcaniclastic falls into shallow platforms, or rapid glacioeustatic-driven emergence and weathering of fresh volcanic sediments (Sturesson *et al.* 2000; Oggiano & Mameli 2006). The absence of significant ironstones capping the Cystoid Limestone in the IC and the lack of synsedimentary volcaniclastic levels and reworked volcanogenic clasts embedded in the Katian–Llandovery siliciclastic strata suggest a possible hydrothermal origin for the iron, associated with the synsedimentary breakdown of the Hesperian platform. Analysis of fluid inclusions, trace elements and REE, and stable isotope data support this interpretation (Fernández-Nieto *et al.* 2003).

As in the Iberian platform, the end of carbonate productivity was associated with a glacioeustatic regressive maximum leading to widespread emergence of the platform and formation of deeply incised karstic cavities. These structures are evident on the walls of the Ojos Negros and Setiles quarries, where the compound erosive–karstic discontinuity D2 is directly overlain by either the Orea or the Los Puertos strata (Fig. 6d). The karst surface locally exhibits considerable relief related to sink-holes. The fact that Los Puertos strata are preserved within sink-holes confirms the karstic conditions preceding deposition of the Los Puertos Formation: the best example is exposed on the western wall of the Setiles quarry, where the basal fill of the karstic depression includes up to 10 m of brecciated dolostone, which is succeeded by strata more characteristic of the Los Puertos Formation incorporating thin intervals of reworked carbonate clasts (Fig. 8d).

At the beginning of the Hirnantian, the Hesperian platform was still characterized by a series of NW–SE-trending drowning palaeo-highs, which were still able to funnel slope-related currents into deeper parts of the platform. Most of the Orea diamictites close to these palaeo-highs were deposited as debris flows generated by slumping, indicating resedimentation and 'cannibalistic' processes on upper slopes. This also supports the view that the basement lineaments were still active faults at that time. Tectonic movements coeval with the Orea deposition are also suggested by thickness variations of facies associations and the common occurrence of chaotic and contorted bedding (Shanmugam *et al.* 1996). Abrupt vertical and lateral variations are associated with overlying synsedimentary slumped beds, local erosive discontinuities, sedimentary slides, debris flows, associated olistolithic beds and breccia sheets. This suggests the local breakdown and instability of the Hesperian sea floor, and the development of active depositional slopes.

Massive diamictites were deposited subaqueously as 'rain-out' facies, modified locally by resedimentation processes. The 'truly' glacial component of sedimentation was probably restricted to the abundant supply of sediment from incoming melt-water streams and icebergs. The presence of an isolated wedge of mixed diamictites is associated with underlying synsedimentary deformation structures. In this case, broad channels, irregularly filled with ball-and-pillow structures (Fig. 10b, c), reflect the onset of fluidification processes that can be interpreted as the product of melt-out of buried ice blocks (Cheel & Rust 1982; Benn & Evans 1998). Finally, tectonic movements coeval with deposition of the lower part of the Los Puertos sandstones are suggested by thickness variations of facies associations and by the common occurrence of breccias, and chaotic and contorted bedding.

Discussion

Palaeocurrents within the Ordovician strata of the IC show a preferential NE–SW trend, coaxial with the basinward orientation of progradations and retrogradations. This unimodal trend contrasts with the polymodal palaeocurrents in the vicinity of fault scarps related to the terminal Ordovician extensional tectonic regime recorded in the HC, closely controlled by NW–SE-trending lineaments and faults.

During the glacial maximum, the position of ice margins at the time of greatest glacial extent reflects the maximum extension of the oldest glaciogenic erosive unconformity (D1). Its record is related to a general lowering of sea level during glaciation, followed by post-glacial eustatic sea-level rise and widespread deposition of transgressive glaciomarine shales. The Orea transgression was not uniform but punctuated, at least in the IC, by the progradation of either a glacier front or the coastline, as indicated by the onset of the erosive unconformity D2, which passes basinward into shoal complexes. The end of glaciomarine conditions was reached as a result of rapid isostatic rebound and a period of forced regression (late deglaciation).

The glaciogenic character of the Orea diamictites is supported by the active penetration into underlying laminae exhibited by outsized dropstones, observed both at metre- and millimetre-scale (Fig. 10d–g). However, this character is not pervasive because dropstone long-axis fabrics were also influenced by the firmness of the substrate. Where bottom sediments were relatively stiff, but allowed penetration by clasts, they tended to preserve the high dip of angular clasts falling vertically through the water column. Conversely, where bottom sediments were either very soft or compacted, vertically impacting clasts tended to fall sideways (Fig. 10h) because either the sediment could not hold the clasts upright or the clast could not penetrate the sediment, resulting in a girdle fabric (Benn & Evans 1998).

The diamictites of the IC appear to represent deposition under relatively quiescent tectonic conditions. In contrast, in the HC they indicate co-occurrence of glaciomarine and subaqueous mass flows in a platform delineated by NW–SE-trending faults defining the palaeotopography margins and local depocentres. At least three NW–SE-trending areas bounded by fault-controlled lineaments separated two depressions, reflecting an extensional tectonic regime controlled closely by basement lineaments and faults.

In the IC, there is a sharp distinction between the siliciclastic and mixed massive and crudely stratified diamictites. The siliciclastic diamictites are widely dispersed in both depositional sequences of the Orea Formation, whereas the mixed diamictites occur exclusively related to the lower sequence at section BV$_2$. There, the lateral sharp boundary of the mixed diamictite (characterized by the abundance of gravel- and pebble-sized carbonate clasts) indicates open-sea conditions, and outsized clasts are associated with iceberg transport and subsequent melting. Rapid variations in dropstone density and size suggest that distinct iceberg 'drift lanes' existed, indicating current activity in the open sea. The drift lane of the IC did not follow the NE–SW, proximal–distal palaeogeographical gradient, although most of the icebergs had a provenance in the coastal areas of the neighbouring Ebro Massif, where late Katian carbonates under subaerial exposure were widely available. After the onset of the conglomeratic channels related to D2, coarse dropstones in the form of cobbles and pebbles are virtually absent in the whole upper sequence of the Orea Formation. The abruptness of the change in clast composition, size and concentration may be expected in a palaeoenvironment characterized by a widespread and more permanent sea-ice cover, where effects of seasonal variations in sea-ice cover are not observed. The grain size of the transported debris has been invoked as an important tool for distinguishing between sea-ice and iceberg sources. Whereas glacier-derived debris in icebergs is often heterogeneous in particle size, ranging from fine material to boulders (reflecting glacial carrying), much of the debris in sea ice is predominantly fine-grained. However, where icebergs contain silt and clay layers with little coarser debris, or anchor ice entrains coarser debris, in certain shallow-water conditions, a distinction between sea ice and iceberg rafting remains problematic (Kuijpers *et al.* 2003).

In the HC, a discontinuity separating two depositional sequences in the Orea Formation is not distinct. Diamictite facies are broadly interpreted as the product of sediment gravity flows in a glacially influenced marine platform, delineated by NW–SE-trending faults. During the Hirnantian, the Hesperian platform recorded a superimposition of considerable current activity with reworking of the glaciomarine sediment, resedimentation as debris flows and slumping, and iceberg drifting in a distinct lane flanking the Setiles–Ojos Negros palaeo-high. Although sea-ice motion is driven mainly by prevailing (katabatic) winds, deep-keeled icebergs are more probably affected by surface currents. Thus the surface currents within the uppermost several hundred metres must have been largely similar to the reconstructed iceberg drift tracks (Untersteiner 1990).

The presence of abundant strata showing extensive soft-sediment deformation within disrupted diamictite facies suggests episodes of large-scale slope failure, characterized by downslope resedimentation of a variety of semi-consolidated sediment types as slump blocks. The presence of large slump blocks and the wedge-shaped geometry of some disrupted diamictite beds suggest a depositional setting proximal to steep slopes and a relatively short distance of downslope transport for these gravity-derived facies.

An adiabatic glaciation model, involving tectonic uplift and not glacioeustatic lowering (Eyles 1993), could provide a ready explanation for the stratigraphical relationship between dolostone and overlying diamictites in the HC. However, uplift of the basement is not necessarily related to extensional tectonic regimes; the change in lithology of glaciogenic clasts can be interpreted as the result of other causes than unroofing, and glacially influenced sedimentation in the IC is not linked inextricably to the regional tectonic setting.

Finally, a typical feature of former glaciated continental margins and epicontinental seas is a strong glacioeustatic rebound. Rebound has been estimated to result in shallowing and prograding coarse-grained siliciclastic sediments, and may be reflected in the Los Puertos Formation of the IC and HC. This regressive trend has been recorded diachronously in the IC from NE to SW. The diachroneity is also pronounced on the Hesperian palaeo-highs, because the lowest onlapping sandstone–shale alternations of the Los Puertos Formation contain the first Silurian graptolites (Gutiérrez-Marco & Štorch 1998).

Conclusions

Two platforms fringing North Gondwana during the Katian–Llandovery are described in this paper: (1) the Hesperian platform, which represents a heterogeneously subsiding, unstable margin, bordering (2) the relatively stable, Iberian inner platform. Both areas displayed different episodes of late Katian carbonate productivity: the Iberian carbonates reflect the onset of bryozoan–pelmatozoan meadows and mud-mound complexes throughout an intra-shelf ramp, whereas the significant lateral variations in facies and thickness of the Hesperian carbonates allow characterization of prominent carbonate factories on the top of isolated palaeo-highs surrounded by deeper-water substrates, where carbonate debris was introduced as winnowed particles. The end of carbonate productivity was associated with glacioeustatic regression, emergence of both platforms and karstification, predating widespread precipitation of iron ore deposits on the palaeo-highs.

The succeeding transgression, represented by the Hirnantian Orea Formation, was most probably caused by a combination of increased rates of tectonic subsidence and glacioeustatic sea-level rise. In the IC, the Orea Formation is divided into two depositional sequences, whereas in the HC the coeval tectonically induced activity was the primary control on sedimentary architecture, and laterally correlatable erosive unconformities are not observed. The Orea glaciomarine deposits of the IC are dominated by the record of massive and crudely stratified diamictites, with tabular geometries, which were deposited subaqueously as ‘rain-out’ facies. In contrast, the Hesperian platform is rich in disrupted diamictites, which form strongly deformed units interpreted as submarine slumps developed in the vicinity of active synsedimentary faults. In both cases, the anomalous occurrence of massive diamictites, rich in boulder- to sand-sized carbonate clasts, and the rapid variations documented in dropstone densities and sizes suggest that distinct iceberg ‘drift lanes’ existed, indicating prevailing currents and katabatic wind activities in the ice-free sea. Finally, a typical feature of this Gondwana margin is the subsequent glacioeustatic rebound, which resulted in shallowing and prograding, with coarse-grained siliciclastic sedimentation, represented here by the Los Puertos Formation.

This paper is dedicated to the memory of Constanza Fernández-Nieto, one of the pioneers in the study of iron ore deposits in the Hesperian Chains, who died in May 2007. The authors are grateful for field assistance by F. Arabia, E. Blasco, Z. Herrera, E. Villas and D. Vizcaïno, and financial support from project BTE2002-0116 ‘The development of Late Ordovician

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Avalonia: a long-lived terrane in the Lower Palaeozoic?

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Abstract: Avalonia was undoubtedly an independent terrane throughout the Ordovician, merging with Baltica at about Ordovician–Silurian boundary times (443 Ma). We consider it to have been internally unified throughout the Lower Palaeozoic, and not the two independent 'East' and 'West' Avalonian terranes of some authors. In the early Ordovician its faunas were certainly Gondwanan. However, its earlier history is controversial: we discuss whether Avalonia split off from Gondwana in the early Ordovician, or whether it left Gondwana in the late Neoproterozoic. We conclude that the varied basement terranes underlying Avalonia were aggregated to the margin of Gondwana before 650 Ma. Some substantial transform movements occurred along the Gondwanan margin between 610 and 530 Ma, but the Avalonian area remained part of core Gondwana until about the end of the Cambrian (490 Ma), when the rift–drift initiation of the opening Rheic Ocean between Gondwana and Avalonia began.

When plate tectonics were applied to the Palaeozoic for the first time in the classic paper by Tuzo Wilson (1966), he deduced that much of Palaeozoic 'America' was now in 'Europe' and vice versa, thereby correctly concluding that the two were separated by an old ocean, which had preceded the Atlantic and the closing suture of which did not coincide with the line of the modern Atlantic opening. That ocean was originally called the Proto-Atlantic and is now termed Iapetus. However, it was not until the identification of another substantial ocean named Tornquist between Avalonia and Baltica and yet a further ocean (the Rheic) between Avalonia and Gondwana that it was realized that the part of 'Europe' now termed Avalonia was an independent terrane in the Lower Palaeozoic (Cocks & Fortey 1982).

It is the purpose of this paper to review and partly reinterpret the history of Avalonia during the Lower Palaeozoic, with particular reference to some of its contained marine faunas and their relationships to the faunas of the surrounding terranes. Because there is widespread agreement on the faunal identity and geological history of Avalonia during the Ordovician and Silurian, but much unresolved discussion on the Cambrian and earlier periods, we take the unusual course of describing the terrane firstly in Silurian times, then in the Ordovician, and finally in the Cambrian and Precambrian. In particular (and what led to the query in our title), we address the question of whether Avalonia existed as an independent terrane in the late Precambrian and Cambrian, as asserted by some workers, or whether it left the core Gondwana superterrane as late as the early Ordovician.

Our main concern in previous papers has been the utilization of fossil faunal evidence in the positioning of the Avalonian microcontinent relative to the major palaeocontinents of Gondwana, Baltica and Laurentia. It has been repeatedly emphasized by the present authors that faunal difference provides good information for determining separation, especially across latitude, but faunal similarity does not by itself prove 'docking', although it can be germane to suggesting proximity of a given terrane with its closest neighbouring palaeocontinent (Fortey & Cocks 1986). In particular, a terrane might lie at any position within a particular palaeolatitudinal belt if the closely adjacent continent presented a similar temperature and substrate regime: any amount of relative transcurrent movement within the same latitudinal belt is possible without necessarily being reflected in faunal difference (Fig. 1). This is worth emphasizing in the present context, as Avalonia could have lain outboard from one or another part of Gondwana according to the views of different researchers (below), and only subsequently attained its present position. In this case, other evidence deriving from, for example, sediments, sequence similarity or zircon provenance, must be brought in to play to provide a more probable specific 'fix' at a given time.

It is not the purpose of this paper to describe in detail the complex Precambrian and Lower Palaeozoic geology of the various areas of Avalonia, but recent reviews have been given by Brenchley & Rawson (2006) for England and Wales and van Staal (2005) for North America. In addition, van Staal *et al.* (1998) provided a useful summary of Avalonia's part in the Caledonide orogeny as it is

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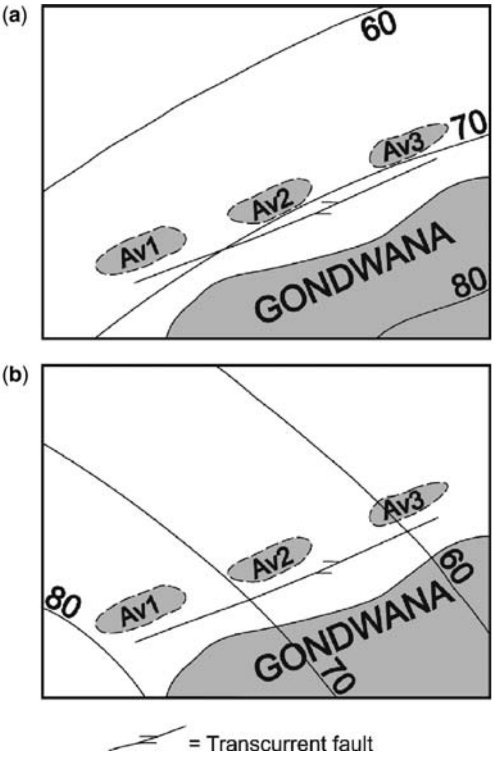

Fig. 1. The Gondwana superterrane, with possible progressive positions (Av1, Av2, Av3) of a terrane such as Avalonia on the margin of it: (**a**) with the Gondwanan margin at a single palaeolatitude; (**b**) with the Gondwanan margin extending across many palaeolatitudes. Faunas should reflect progressive displacement by a transcurrent fault system in (b), but not (a).

seen developed in the mid-Ordovician to Devonian rocks of today's North Atlantic region.

First, a note on terrane terminology is needed. 'Avalonia' is a term used approximately in the same way by most researchers, although its margins differ slightly in different papers, but sometimes it is divided into 'East' and 'West' Avalonia, which we discuss further below. Other southern European terranes have not been so consistently termed. 'Armorica' originally took its name from the Brittany and Normandy areas of France, but the terms 'Armorica' or 'Armorican Terrane Assemblage' have been variably used to include the old Armorica (including the Channel Isles), other parts of France (the Massif Central and the Montagne Noire), the Iberian Peninsula (itself consisting of several terranes), Sardinia (two terranes), Corsica, and sometimes the Apennines of Italy and also Bohemia (also termed the Perunica terrane and now largely within the Czech Republic). In addition, the term 'Cadomia' has also used for many or some of those terranes, but because the late Neoproterozoic Cadomian orogeny also extended to parts of North Africa as well as southern Europe, we do not endorse its use as a terrane term. The varied usages seem irreconcilable, but in this paper we use 'Armorica' to include all of France, the Iberian Peninsula and Sardinia, but not Bohemia (Perunica), which we consider was a separate Lower Palaeozoic terrane. We now agree with Robardet (e.g. Robardet 2003) that Armorica did not leave the North African sector of core Gondwana until the latest Silurian or early Devonian. The margins and concept of Baltica, which includes most of Europe north of the Trans-European Suture Zone (TESZ) and as far east as the Ural Mountains, were discussed by Cocks & Fortey (1998) and Cocks & Torsvik (2005). Laurentia, which includes the bulk of North America, as well as Greenland, northwestern Ireland and Scotland, also varies in concept, but its eastern margin with Avalonia is discussed briefly below. The superterrane of Gondwana is not described in detail here, but its components and margins also differed greatly with time.

The margins of Avalonia

Parts of the old terrane of Avalonia lie on both sides of the modern North Atlantic Ocean. In North America the southern boundary is at Cape Cod, Massachusetts, and it continues northeastwards to include most of the Maritime Provinces of mainland Canada and the eastern part of Newfoundland. The Avalon Peninsula of eastern Newfoundland gives its name to the whole terrane. In Europe, Avalonia includes southeastern Ireland, Wales, England (apart from the southernmost tip of Cornwall), Belgium, the Netherlands, southern Denmark and part of NW Germany. The margins of the terrane were reviewed and summarized by Cocks *et al.* (1997); however, in that study the southeastern boundary of Avalonia was placed at the Elbe Line in Germany; it is now more plausibly extended eastwards to the Trans-European Suture Zone in southern Denmark and northern Germany (Cocks 2002). In addition, various authors, summarized by Verniers *et al.* (2002), have defined the concept of a 'Far Eastern Avalonia' microplate, which comprised the eastern part of Armorica as defined above (eastward of the Brabant Massif of Belgium), but extended even further eastwards to include much of northern Germany and western Poland (Pomerania). They also included the Rügen area of northern Germany, the Early Palaeozoic turbidites of which were probably laid down in an intra-oceanic basin between Avalonia and Baltica (Cocks 2002). However, there are no Lower

Palaeozoic terrane-diagnostic benthic faunas in any part of Far Eastern Avalonia: the arguments for including that area within Avalonia are largely structural, together with broad similarities between igneous rocks in the Rhenish Massif of Germany and those of central England (Winchester *et al.* 2006).

Surrounding the Lower Palaeozoic core, there are a number of old island arcs and other microterranes, mostly situated to today's north of Avalonia, all of which had independent histories within the Iapetus Ocean at various times, many supporting distinctive Ordovician endemic shelly faunas. Those arcs were separately accreted to the northwestern margins of Avalonia at various times in the Ordovician, culminating in the Caledonide orogeny. These small terranes have been reviewed on today's British and Irish side by Armstrong & Owen (2001). On the North American side there were also many peri-Avalonian microterranes, of which some traces are preserved in the Appalachians and northeastward through the Maritime Provinces of Canada and Newfoundland. The suture between peri-Laurentia and peri-Gondwanan (including Avalonia) is now thought to coincide with the Red Indian Line, immediately south of which lie the Bronson Hill and Popelogan island arcs extending northeastwards into the Exploits Zone of Newfoundland (van Staal 2005). To the south of those tectonized rocks, the Central Maine–Aristook Belts and (in Newfoundland) the Gander Zone all lie northwestwards of the 'true' Avalonia, which consists of the Avalon Peninsula and its southwestward extensions as far south as Cape Cod. In addition to Avalonia, eastern Canada also includes the Meguma terrane, which is exposed onshore in southern Nova Scotia, but includes a substantial area offshore. That region consists of a latest Neoproterozoic to Early Ordovician largely turbiditic sequence deposited on a continental rise and outer shelf of a Gondwanan passive margin, overlain by latest Ordovician to Devonian shallow marine rocks. As summarized by Murphy (2007), opinions differ as to whether Meguma was connected to Avalonia during the whole of the Lower Palaeozoic, or whether it did not accrete to it until the Devonian Acadian orogeny: we have nothing new to add to that debate. Another North American terrane that was probably peri-Gondwanan was the Carolina terrane, which lies today to the south of Avalonia and is much altered, as emphasized by its old name of Carolina Slate Belt. That terrane is also tectonically separate from Avalonia, and its Ordovician faunas are largely deeper-water graptolites. However, Middle Cambrian trilobites were described from the Carolina terrane by Samson *et al.* (1990), who concluded that, although they were not strongly terrane-diagnostic, they were not Laurentian in affinity but 'they may be closest to those of Bohemia' (1990, p. 1459). Hibbard *et al.* (2005) reviewed the Carolina terrane, and concluded that, like Avalonia, it was probably Gondwana-derived at some time in the late Cambrian or early Ordovician, but appears on balance to have been separate from Avalonia in its pre-Caledonide history. Hibbard *et al.* (2005) also identified a smaller unit in southwestern Viginia and northwestern North Carolina named the Smith River Allochthon, apparently located today within the western part of the Carolina terrane, but which probably originated in Laurentia.

The identity and unity of Avalonia

Partly because of today's geography, many workers have identified two separate terranes as 'West' and 'East' Avalonia, but we consider them to have been unified as a single Avalonia terrane throughout the Lower Palaeozoic. This is for several reasons. First, significant key faunas are the same in both the west and the east; for example, it has been known for many years (references summarized by Cocks & Fortey 1982) that late Silurian ostracodes are the same across the whole of Avalonia (and into the then-adjacent Baltica), but these are very different from similar-age Ludlow and Pridoli ostracodes in both Laurentia and NW Gondwana (Armorica and Bohemia). This fact was further documented by Berdan (1990), demonstrating that the ostracodes were unable to cross even the small and shallow seas still present on the Laurussia terrane over the site of the old Iapetus Ocean after the latter had disappeared in the Caledonide orogeny. Even before the concept of plate tectonics, it had long been recognized that the Cambrian trilobite faunas of the Avalon Peninsula of Newfoundland are essentially similar to those from Wales, as quoted in the original drift paper by Wilson (1966). Landing (1996, p. 31) analysed the Cambrian to Ordovician sections and sequences from Rhode Island to southern England, and recognized them as 'unified' before the latest Precambrian. Second, Murphy *et al.* (2004, fig. 8) have shown that the palaeomagnetic Apparent Polar Wander (APW) paths of 'West' and 'East' Avalonia were the same from the late Neoproterozoic until the Early Ordovician. Furthermore, van Staal *et al.* (1998, p. 201) have summarized the reasons for identifying both the Appalachians and the British Caledonides as a 'single kinematic entity'. Thus we recommend that the terms 'West' and 'East' Avalonia should be abandoned in all future palaeogeographical reconstructions and paper titles, at least those dealing with the Lower Palaeozoic. Not yet resolved is whether the 'Far Eastern Avalonia' of northern Germany and part of Poland referred to above was a real structural entity; and, if it was, whether or not it formed an integral part of Avalonia during the latter's existence as a separate terrane in the Ordovician. We do not know of strong faunal signals to support either contention, but the overall reasons for believing it to have been part of the independent Avalonia have been summarized by Pharaoh *et al.* (2006) and Winchester *et al.* (2006). However, we do not agree with the analysis and terminology of some workers (e.g. Oczlon *et al.* 2007) who postulated that Avalonia extended even further eastwards so as to include what we term the Pontide terrane in the area of northern Turkey, as well as other terrane units in the eastern Mediterranean and Black Sea.

Methods for assessing palaeogeographical relationships

The two chief methods of assessing the progressive palaeogeography of the Earth in the eons before the Jurassic, from when the oldest ocean floors are known, are by palaeomagnetism and by the analysis of terrane-related faunas, as reviewed in principle by Fortey & Cocks (2003). Palaeomagnetic studies can reveal both the palaeolatitude and the rotation of terranes as long as their palaeomagnetic signals have not been overprinted and erased by later tectonic events, but they give no clue to palaeolongitude. Faunal studies and the identification of provinces give some idea of closeness of faunas in comparable ecological niches of the same age in both latitudinal and longitudinal dimensions, but they are almost invariably subjective. However, a few faunal studies, for example, that by Lees *et al.* (2002) on Avalonia and surrounding terranes in the Ordovician and Silurian, are more quantitatively based and can be used to estimate the relative distances between major terranes. A critical factor in assessing the reality and probability of palaeogeographical reconstructions is whether or not they demonstrate plausible kinematic continuity between successive maps over a substantial period of time. Figure 2 has been constructed from part of a sequence published by Cocks & Torsvik (2002) using both palaeomagnetic and faunal data; it shows the positions of Avalonia and adjacent terranes when Avalonia formed part of the Gondwanan margin in the early Ordovician (earliest Arenig, 480 Ma) and when it was an independent terrane within the Iapetus Ocean during the later Ordovician (early Caradoc, 460 Ma).

Silurian biostratigraphy and palaeogeography

Avalonia includes the global type areas for three of the four Silurian series, the Llandovery (Wales), Wenlock and Ludlow (both Shropshire, England), whose boundaries and rocks have been summarized by Holland & Bassett (1989). The Silurian rocks and margins of Avalonia were reviewed, together with the biostratigraphy and changing sea levels throughout Silurian time of 18 key localities in Canada, Britain and Belgium, by Cocks *et al.* (2003). The British sector of Avalonia clustered around the stable core of the Midlands Microcraton, over which the Early Palaeozoic rocks are essentially undeformed. However, in reality, as the soft oblique docking of Avalonia with Baltica took place at around Ordovician–Silurian boundary time at 443 Ma (Torsvik & Rehnström 2003), Avalonia was not an independent and isolated terrane during the Silurian; although it is often considered separately in review papers. The mid-Silurian also saw the peak of the Caledonide orogeny, when the combined Avalonia–Baltica was accreted to the even more substantial Laurentia terrane to form the superterrane of Laurussia. Cocks & Torsvik (2005, figs 8 & 9) have depicted the palaeogeography both at 450 Ma (the late Ordovician), as Avalonia was approaching Baltica, and also at 425 Ma (Wenlock), after Avalonia had joined Laurussia. Because Laurentia, Avalonia and Baltica were so close to each other in the Silurian, most of the benthic assemblages formed parts of a single lower-latitude cosmopolitan fauna, and cannot therefore be distinguished between those three terrane areas, apart from the ostracodes mentioned above. In contrast, the faunas of Armorica and Perunica (Bohemia) were somewhat different, as reviewed by Robardet (2003).

Ordovician biostratigraphy and palaeogeography

The British part of Avalonia includes the stratotypes for the subdivisions of the Ordovician System traditionally most widely used for correlation, namely Tremadoc, Arenig, Llanvirn, Llandeilo, Caradoc and Ashgill. However, none of these have been accepted as global standards, although the name Tremadocian is preserved, but with its new stratotype in western Newfoundland, which was then in Laurentia. A former stage of the Ashgill, the Hirnantian, is also conserved as a global name, but with its redefined basal stratotype located in China. Following earlier palaeomagnetic work, Torsvik & Trench (1991) and Torsvik *et al.* (1993) were able to estimate that the distance across the Iapetus Ocean between Laurentia and Avalonia was reduced from a possible maximum of about 5000 km in the late Tremadocian (485 Ma) to 3300 km by the end of the Llandeilo Stage at about 460 Ma. Coming to the same question in a different but still quantitative way, Lees *et al.* (2002) were

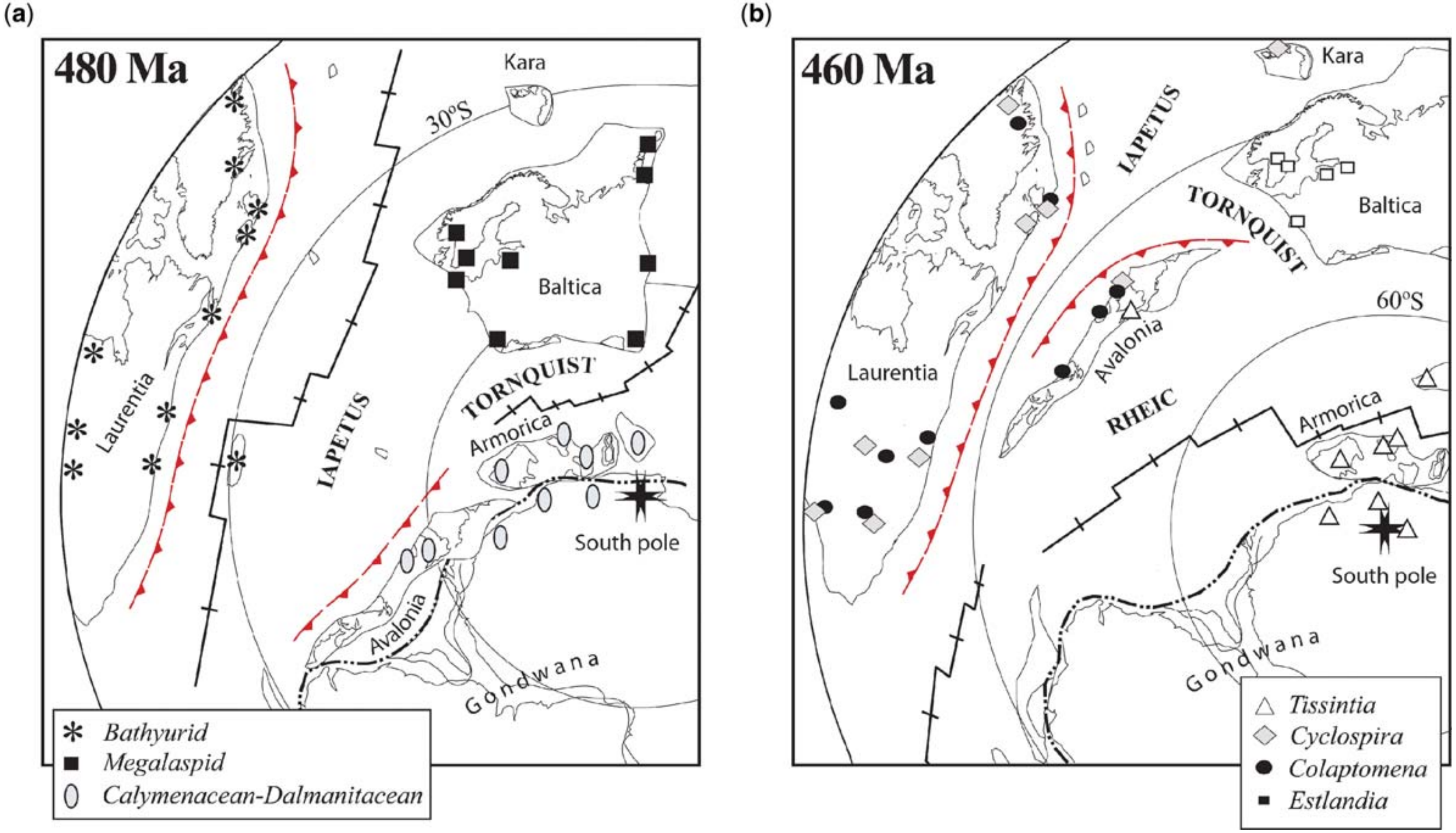

Fig. 2. The positions of Avalonia: (**a**) in the early Ordovician (Arenig, 480 Ma); (**b**) in the middle Ordovician (Caradoc, 460 Ma), based on palaeomagnetic and faunal evidence, and showing trilobite provincialism at 480 Ma and key brachiopod distributions at 460 Ma. Newly drafted by T. Torsvik with data from Cocks & Fortey (1982), Cocks & Torsvik (2002) and Nysæther *et al.* (2002).

able to assess the statistical differences between the brachiopod and trilobite faunas of Avalonia, Laurentia, Baltica and northwestern Gondwana through Ordovician and Silurian time, and to translate these into distances round the spherical globe at successive times in the Ordovician and Silurian. They also demonstrated quantitatively what had been postulated qualitatively by many previous workers, that in the early Ordovician Avalonia was within or very near Gondwana. By the middle Ordovician the Gondwanan faunal signals had become steadily weaker, and from then onwards Avalonia had an increasing stream of generic migrants from both Laurentia and Baltica as the Iapetus and Tornquist Oceans steadily narrowed. This was reflected in all of the benthic biota, including the molluscs (e.g. Cope, in Webby *et al.* 2004), echinoderms and ostracodes, not just the trilobites and brachiopods with which we are most familiar. In addition, the progressive decrease in palaeolatitude while Avalonia was a separate terrane, from high in the latest Cambrian to subtropical in the Silurian (Cocks & Torsvik 2002, 2005), and the consequent greater warmth, also contributed to the increased faunal diversity in Avalonia as Ordovician time went by. Changes in the biodiversity of the various faunal and floral groups have been summarized by many authors in the book by Webby *et al.* (2004).

When Avalonia left Gondwana is postulated as early Ordovician by most workers, but that is not agreed in detail. We originally (Cocks & Fortey 1982) suggested a late Arenig separation date, and that has been followed by, for example, Verniers *et al.* (2002). A variant has been provided by Stampfli *et al.* (2002), who illustrated their interpretation at 490 Ma (Cambrian–Ordovician boundary times) in which a narrow Rheic Ocean existed between Avalonia and Gondwana, although it was so narrow as to not be a hindrance to faunal communication between the benthos on the shelves of the two opposing terranes. Van Staal (summarized by van Staal 2005) has demonstrated that the tectonic characteristics of the Avalon Peninsula of Newfoundland, which consists of a shale-rich platform that includes some rift-related volcanic rocks, also point towards a latest Cambrian and earliest Ordovician time of initial drifting away from Gondwana. The same timing has been endorsed by Murphy (2007), based on data from Nova Scotia. Furthermore, it is clear from the work of Smith & Rushton (1993), and subsequent workers, that from the onset of the Tremadocian various grabens and half-grabens developed across southern Britain prior to the opening of the Rheic Ocean. We contrast this with the work of Landing (e.g. Landing 1996), who postulated a much earlier date for the rifting, as discussed below.

Cambrian biostratigraphy and palaeogeography

In their review of the Cambrian of the world, McKerrow *et al.* (1992) concluded that Avalonia formed the edge of part of the core of the immense superterrane of Gondwana, and was probably situated adjacent to today's north of Brazil (which formed the Proterozoic craton of Amazonia) and Florida, at least until about Cambrian–Ordovician boundary time. Those conclusions have been much quoted; for example, by Fortey & Cocks (2003). According to Brenchley *et al.* (2006) and Murphy (2007), the Neoproterozoic accretion to Gondwana of the various fragments that made up Avalonia was over well before the beginning of Cambrian time, as discussed below. However, the 'Avalonian' area was not tectonically quiescent in the Cambrian; for example, the sediments in the Welsh Basin were deposited in an extensional regime probably formed in response to transtensional movements along the margins of Gondwana (Brenchley *et al.* 2006). That transtensional process was particularly active in the Middle Cambrian (Smith & Rushton 1993). Landing (1996) has also documented how the sedimentary basins in both the North American and Anglo-Welsh parts of the Avalonia area migrated locally with time.

However, the suggestion by McKerrow *et al.* (1992) that Avalonia was part of Gondwana during the Cambrian has been rejected by some workers, principally Landing and his co-workers (e.g. Landing 1996, 2005), who asserted that Avalonia was an independent terrane separate from Gondwana during the whole of the period. Landing has maintained that Gondwana and Avalonia were not only separate from each other in the late Neoproterozoic, but also at greatly dissimilar palaeolatitudes. Landing's assessment is now considered here in more detail, especially as his 2005 paper included 'an obituary' for Avalonia in its title. Landing leant heavily on the evidence offered by the Cambrian sequences in Avalonia, particularly in eastern Canada, and their differences from equivalent-age rocks in southern Europe and NW Africa, and averred that Avalonia had been completely independent from Gondwana since their separation in the Neoproterozoic. He also brought to his aid the conclusions published by Keppie *et al.* (2003). However, in practice Keppie *et al.* (2003, p. 202) endorsed the conclusions of Prigmore *et al.* (1997) that the 'rift–drift' separation of Avalonia from Gondwana occurred in the early Ordovician, even though Avalonia contained originally independent island arcs that had become welded to core Gondwana in the Neoproterozoic.

Landing (1996, pp. 56–58) compared the sedimentary successions of Avalonia with Morocco (NW Gondwana), NW France (Armorica) and Baltica, and correctly concluded that Avalonia was very different from each of the other three, and Pillola's (1993) description of the Armorican and NW African Early Cambrian trilobite *Bigotina* and its relatives supports that.

There is little disagreement between Landing (2005) and the present authors in maintaining an Avalonia that separated from the Gondwanan area in the Early Ordovician; this steadily increasing separation was put on a quantitative basis by Lees *et al.* (2002), a paper not cited by Landing (2005). The critical period is therefore the Cambrian. Fossil evidence is hardly germane to the later Precambrian despite the more widespread discovery of acritarchs in strata of Ediacaran (Vendian) age. The formal base of the Cambrian is, of course, defined in eastern Newfoundland, and in that circumstance Avalonia's whereabouts at the time is important to determine. Landing (2005) took Fortey & Cocks (2003) to task for not considering Cambrian evidence, even though our paper was specifically entitled as pertaining to global Ordovician–Silurian reconstructions, on which the authors could express reasonably authoritative opinions. In the present paper we consider whether the 'faunal evidence on all areas of Avalon through the preceding Cambrian ... prove[s] its isolation from the West African and Cadomian margins of West Gondwana' (Landing 2005, p. 170). Fortunately, there have been a number of recent faunal studies of Avalonian fossil faunas, detailed below, that do indeed contribute something new to the debate. Despite his forthright assertion, none of them is in the reference list of Landing (2005).

As neither of us would claim particular expertise in Cambrian palaeontology, we are obliged to accept the determinations made by the authors of recent studies describing Avalonian faunas. Cambrian terrane-diagnostic faunas in the area are somewhat sparse. Inarticulated brachiopods, which are common, had spat that could have travelled long distances and are therefore of little use in recognizing terrane affiliations. Articulated brachiopods (which would have been more useful) are relatively rare except in lower palaeolatitudes, which included Laurentia but not the Avalonian area of Gondwana. Although there are some diagnostic higher-latitude Gondwanan brachiopods in the early Cambrian, these do not extend far beyond the Middle East (Bassett *et al.* 2002), and those few found in Avalonia are not diagnostic.

The palaeobiogeography of the Cambrian of Avalonia, and indeed of the world, has traditionally been dependent on signals from the distribution of trilobites. This is because they are the commonest fossils and, by and large, among the most distinctive. As far as positioning Avalonia is concerned, we are obliged to examine trilobite evidence in the first place, as most other organisms are either widespread or ambiguous. For example, bradoriid arthropods are virtually cosmopolitan according to the review of Williams *et al.* (2007); and Avalonian Phosphatocopina ostracodes described by Williams & Siveter (1998) are almost all widespread, apart from *Comleyopsis*, which is endemic to the terrane. Neither of these groups provides critical evidence for Cambrian palaeogeography. However, Jefferies *et al.* (1987) described the benthic carpoid *Protocystites menevensis* from the Middle Cambrian of Pembrokeshire, and its closest relatives appear to be from Bohemia, which was probably part of Gondwana at the time.

As the review by Álvaro *et al.* (2003) makes clear, the use of trilobites for the purposes of palaeogeographical reconstruction on the Gondwana margin is not entirely unambiguous for much of the Cambrian, in marked contrast to the Ordovician. In this context, it is particularly important to understand the biofacies distribution of particular trilobites. From their appearance in the Early Cambrian, genera of Agnostida are widespread, probably because they had pelagic or planktonic habits. Many are associated with sites proximal to ancient oceans or in deep-water sediments: it has been known for some time that the same genera can be found in the Taconic region of New York in marginal Laurentia as in such localities as Warwickshire (e.g. Rushton 1966), and it is evident that taxa could cross oceanic barriers. Some workers have noted a degree of endemicity among more platform-living faunas (Fatka & Mergl 2009), but these agnostids are ones with smoothed-out (leiagnostoid) morphology and therefore the least distinctive among the clade. It would be unwise to rely on them. Hence for the purposes of assessing biogeography miomerid (Agnostina + Eodiscina) trilobites are eliminated at the outset herein, even though they are often abundant and varied.

As far as the Late Cambrian is concerned, Avalonian biofacies are also problematical. Thick sequences in Wales and on the Avalon Peninsula, Newfoundland, and somewhat more condensed ones on the margin of the Midland Platform, are dominated by trilobites belonging to the Family Olenidae. It has been recognized at least since the time of Henningsmoen (1957) that these are specialized trilobites adapted to coping with low oxygen concentrations at or near the sea floor. It has been suggested (Fortey 2000) that they may have lived in collaboration with sulphur bacteria, like many living animals adapted to a similar habitat. They are frequently found in species-poor, individual-rich 'stinkstones' and other trilobites (other than presumably swimming agnostids in some cases) are absent in the same beds. The classical development of Olenidskiffer is in Scandinavia. Olenids are also widespread, even at species level. For example, Rushton (1982) recognized species in North Wales identical to those in Norway and Sweden (Baltica), at the top of the Cambrian succession, and olenids also dominated earlier in the Avalonian Late Cambrian of Wales and Canada (Hutchinson 1952; Rushton 1983). Non-olenid trilobites found in the later Cambrian olenid biofacies include other very widespread, non-diagnostic taxa such as *Proceratopyge*, or the probably pelagic *Irvingella.* It is likely that the oceans of the Late Cambrian were exceptionally well stratified, with poor water-mass turnover, which encouraged widespread development of olenid biofacies on all palaeocontinents. The degree of endemicity they display is controversial; for example, Chatterton & Ludvigsen (1998) have recognized new genera apparently confined to what is now the western edge of Laurentia in the usual marginal facies. However, faunas in South America are similar to those of Europe, even though probably far removed geographically. In any case, it would not be correct to use the similarity between Baltica and Avalonia in Olenidae as strong evidence of their close proximity.

There are a few examples of Late Cambrian shallow-water trilobites in non-olenid environments in Avalonia, which may be more diagnostic. For example, Hughes & Rushton (1990) have described the trilobite *Cermatops* from north Wales, a genus otherwise known from eastern Gondwana. The trilobite trace fossil *Cruziana semiplicata* was originally described from Wales and is widespread across Gondwana (Fortey & Seilacher 1997), and not in Laurentia or Baltica, but if it is correctly associated with the trilobite genus *Maladioidella* this is also known from Siberia and China (Rushton & Hughes 1996). A Welsh species described by Salter and named *Richardsonella? invita* by Rushton (1996) is probably better referred to a Chinese genus such as *Yosimuraspis*. Hence what little evidence there is, after subtracting agnostids and olenids, points to Gondwanan affinities for late Cambrian Avalonia, but it is scarcely compelling.

The Middle Cambrian Avalonian faunas present comparable problems. The richest fauna is the classical 'Menevian' one from western Wales near St. Davids, Pembrokeshire. It is matched closely by faunas in eastern Newfoundland and New Brunswick (Álvaro *et al.* 2003). Unfortunately, a comprehensive modern evaluation of the whole fauna is not available. However, an unpublished PhD thesis by Lewis (1987) revised the Menevian faunas on the basis of new collections, and we have drawn on that work here. By going through his systematic descriptions of non-agnostoid trilobites, we have noted in which palaeocontinent the nearest related species to a given Welsh one under consideration is to be found (if equally similar in more than one 'province' we have given a half score to each). In addition we have included smaller Avalonian Middle Cambrian faunas; for example, the Avalonia Newfoundland fauna described by Fletcher (2003). The results (Fig. 3) show that there is no clear affinity signal from the whole fauna in the Middle Cambrian. Although the Baltica similarity is greatest, there are elements from Laurentia and Siberia, as well as endemics within Avalonia. The relatively deep-water fauna of the 'Menevian' clearly includes widespread elements. To take one example, the definitive Middle Cambrian genus *Paradoxides* is well known from both Baltica and Bohemia (Rushton 2006), as well as widely in Avalonia as far south as the Carolina Slate Belt. The 'Paradoxidid realm' does not equate with a geographical entity in any obvious way.

However, it is possible to consider the Middle Cambrian Avalonian faunas a little more critically. Typical of the relatively deep-water fauna is the presence of a number of blind trilobites traditionally classified together in the Conocoryphacea, a group that has now been proved to be polyphyletic (Cotton 2001). Álvaro & Vizcaino (2003) have identified what they termed the conocoryphid biofacies, a typical natural assemblage of trilobites with many blind forms living alongside large-eyed contemporaries. The Menevian faunas are of this type, and there are many other examples from localities in Spain, Bohemia and the Montagne Noire, southern France (Courtessole 1973). Although not all conocoryphid genera are spread throughout the region, five extend into Wales, where they are accompanied

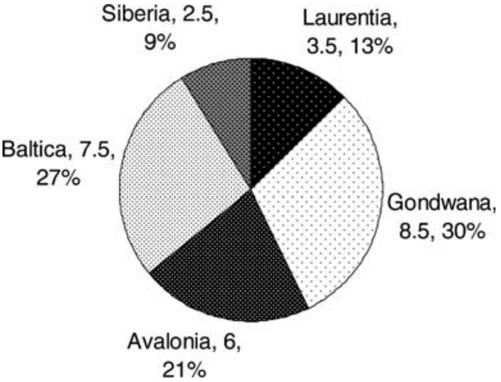

Fig. 3. Percentage distribution of the closest relatives of Avalonian Middle Cambrian trilobite species in other terranes.

by the large-eyed solenopleurid *Solenopleuropsis*, the species of which seems to be almost identical to one from the Montagne Noire (Fig. 4). It might be appropriate to regard the Avalonian faunas as belonging to this Gondwanan conocoryphid biofacies, with the addition of more widespread elements of the Paradoxidid fauna, consistent with their more marginal position at the edge of the Gondwana supercontinent. It would be difficult to conclude from the small number of endemic genera that Avalonia was an independent terrane distant from Gondwana at this time (Landing 2005); although, for reasons mentioned above, neither do the faunas necessarily prove their contiguity.

For the Early Cambrian, Álvaro *et al.* (2000, 2003) have summarized the evidence in detail, noting that the interval as a whole is typified by warmer climate over much of Gondwana, and by a greater degree of regional endemicity than later in the Cambrian. Álvaro and his colleagues concluded that their trilobite cluster analysis suggests a grouping of 'Southern British Isles, Morocco and the Ossa Morena Zone' (Spain), which places Avalonia firmly with Gondwana, but separate from areas such as Sardinia where thick limestone formations were deposited at the time when a condensed sequence was accumulating in central England. If it is correct to assert that the Avalonian terrane lay to the south of its present position, (e.g. in proximity to what is now the northern part of South America; Fig. 2), then it seems probable that is was at substantially higher palaeolatitudes than 'tropical' Gondwana, and that both the similarity to Morocco and differences from other areas of Gondwana could be accounted for simply by difference in palaeolatitude.

This is endorsed by analysis of the archaeocyathids. Courjault-Radé *et al.* (1992) noted that Avalonia lacks Early Cambrian archaeocyathids and substantial carbonate and evaporate sediments, in contrast to northwestern Gondwana, which has both archaeocyathids and tropical sediments at many localities. Courjault-Radé *et al.* (1992) also concluded, correctly in our opinion, that those differences were simply due to different Early Cambrian palaeolatitudes, with the higher-latitude Avalonian area more southerly than the temperate to subtropical regions of northwestern Africa and Armorica (Fig. 5).

Thus, to summarize our conclusions on the significance of the Cambrian faunas in assessing whether or not the Avalonian area was a part of Gondwana or, as Landing (2005) suggested, an independent terrane distant from Gondwana, we believe that Landing has not made his case for separation, and that the overall faunas signal a Gondwanan rather than an independent situation for the Avalonian area.

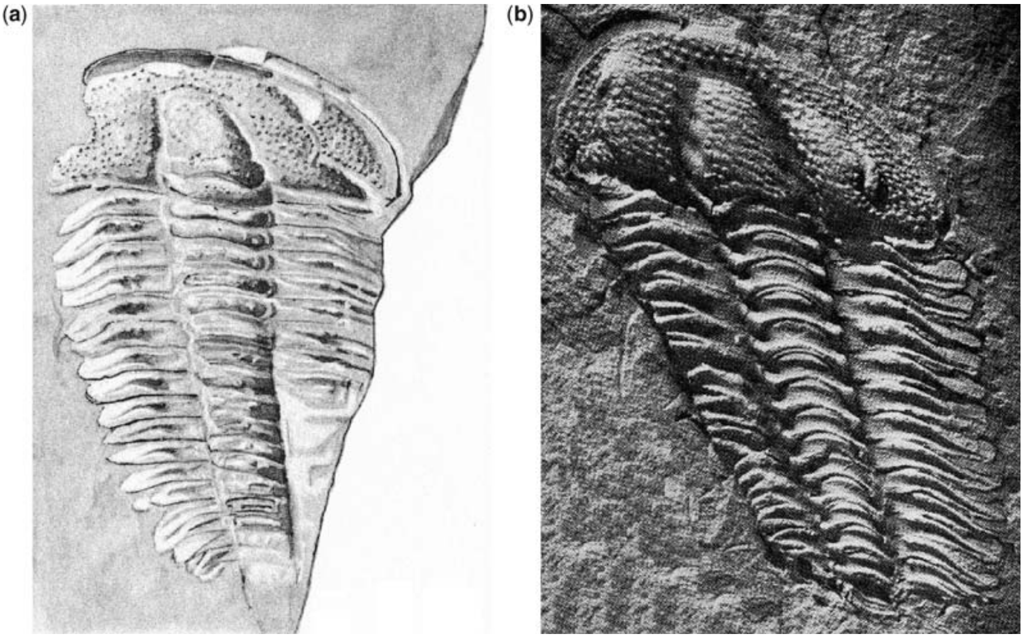

Fig. 4. Middle Cambrian *Solenopleuropsis* from the Gondwanan margins: (**a**) *S. variolaris* (Salter), as figured by Lake (1931) from St. Davids, Pembrokeshire, Wales; (**b**) *S. rouayrouxi* Munier-Chalmas & Bergeron as figured by Courtessole (1973), from the Montagne Noire, southern France.

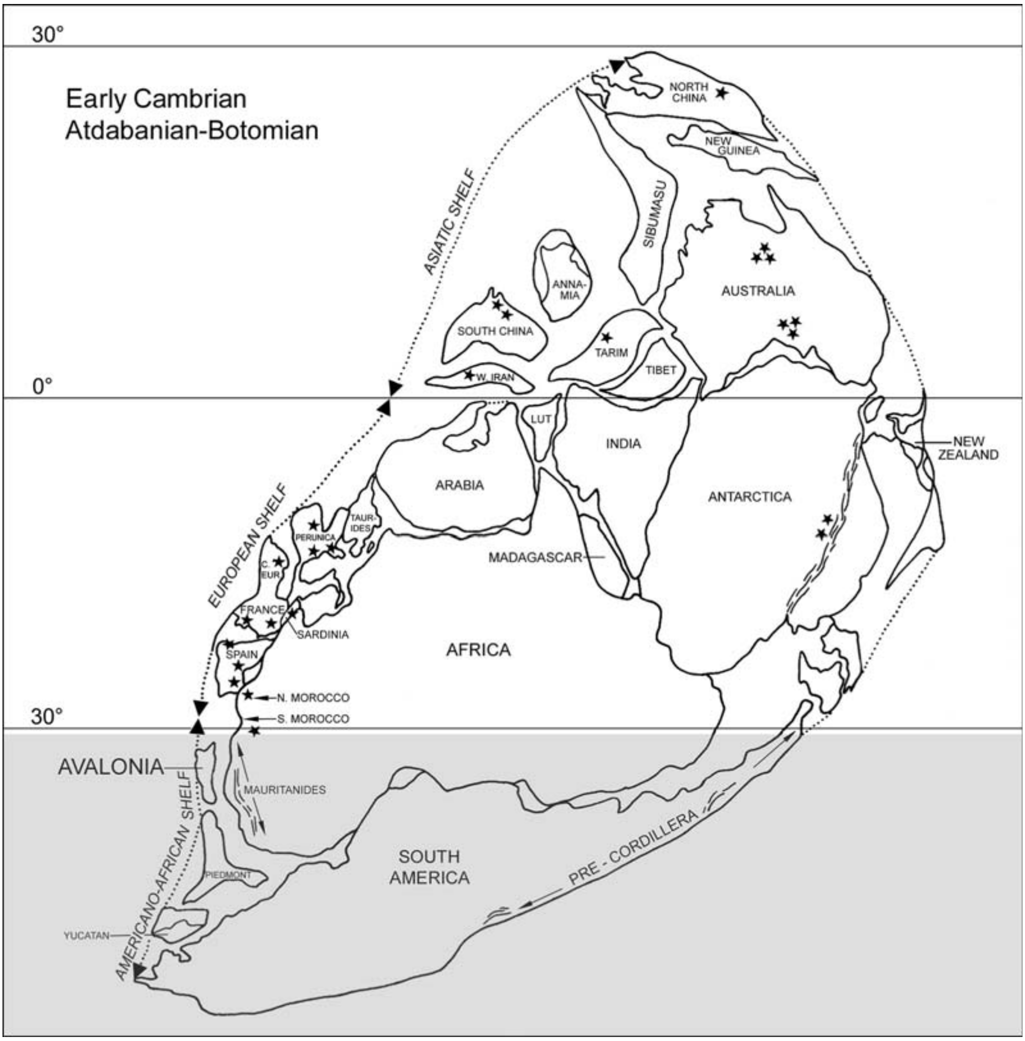

Fig. 5. Early Cambrian archaeocyathid distribution in Gondwana (stars) and surrounding regions. Data from Courjauld-Radé *et al.* (1992). The regions to the south of about 30°S, which is shaded here and includes Avalonia, lack archaeocyathids because they were at higher palaeolatitudes.

Precambrian prelude

The fossils have little to tell us about the position of Avalonia during the Precambrian. The most relevant biota are acritarchs, and their message is the same as that from their Cambrian relatives; that Avalonia was not then close to the Armorican part of Gondwana.

The basement of Avalonia consists of a jumble of old terranes; for example, McIlroy & Horák (2006) have reviewed them for southern Britain and have identified four major terranes, the Cymru, Wrekin, Charnwood and Fenland terranes, all of which have a proven Neoproterozoic history, and a probable Mesoproterozoic basement as well, the latter inferred from the included zircons in the Neoproterozoic rocks. In addition, there is the Monian Composite Terrane Assemblage, cropping out in NW Wales, which they analysed to consist of at least two terranes (Monian and Coedana) with a probable Mesoproterozoic basement, in addition to a Neoproterozoic Aethwy island arc lying on oceanic, rather than continental, basement. There are comparable terranes in the Avalonian basement of eastern Canada.

Various companion papers by a combination of collaborating researchers, particularly Nance *et al.* (2002), Keppie *et al.* (2003) and Murphy *et al.*

(2004, 2006), have ably reviewed the history of several peri-Gondwanan terranes, concentrating particularly on Avalonia, the Mexican terranes, Carolina, Florida (sometimes termed the Suwannee terrane), 'Cadomia' (more usually termed the Armorican Terrane Assemblage) and Bohemia (Perunica). Having reviewed several possibilities, these workers concurred that the most likely model for the early history of Avalonia was that the various integral components of Avalonia started as island arcs between 1.2 and 1.0 Ga, termed by some Proto-Avalonia. Murphy *et al.* (2000, 2006) then described their second phase of development as several mature island arcs developing in separate episodes between 750 to 650 Ma. From 635 to 570 Ma voluminous arc-related igneous extrusions occurred, and together with intra-arc and interarc sedimentary basin deposition, those arcs were accreted first to each other and then to the margins of core Gondwana. Thus the Avalonian area formed part of the vast Gondwanan superterrane off Amazonia for the rest of the Neoproterozoic. This was eventually followed in the latest Neoproterozoic and the earliest Cambrian, from 590 to 540 Ma, by the development of an intra-Gondwanan wrench system, until the rifting off from Gondwana of the mature combined Avalonia, and the initial rift–drift of the Rheic Ocean between Avalonia in Gondwana in latest Cambrian or earliest Ordovician time. Linnemann *et al.* (2007) concluded that the rifting of the Saxothuringian terrane (chiefly in Germany) from Gondwana occurred at the same time (490–480 Ma) and probably as part of the same event.

In contrast, Keppie *et al.* (2006) have described what they interpreted as plume-related 546 Ma dykes in east–central Mexico, and related that tectonic activity to the initial separation of Avalonia from Gondwana. However, we do not think that the varied Mexican terranes formed parts of Avalonia, and thus the Mexican dyke data are not directly related to the Avalonia–Gondwana separation and the opening of the Rheic Ocean.

However, where Avalonia lay within Gondwana during the Neoproterozoic remains unresolved. Most researchers (e.g. Murphy *et al.* 2004; Samson *et al.* 2005) endorse the original suggestion of McKerrow *et al.* (1992) that it lay off Amazonia. There has been substantial geochemical and isotopic work both on the Precambrian rocks of Avalonia and surrounding terranes and on their contained detrital zircons. Samson *et al.* (2005) are among a number of authors who have demonstrated that the detrital zircons of the Armorican terrane assemblage (France, the Iberian Peninsula and Sardinia) are different from those of the Neoproterozoic of Avalonia.

In contrast, McNamara *et al.* (2001) concluded that Avalonia was part of the West African, rather than the South American, part of Gondwana, based on 580–570 Ma palaeomagnetic data from Newfoundland, and Murphy *et al.* (2000) came to similar conclusions based on Sm–Nd isotopic signatures. However, as pointed out by Landing (2005), that would contradict the evidence from the stromatolites. Thus we still think that the original site of Avalonia during the late Neoproterozoic and Cambrian was probably in a position off South America and certainly well to the West of Armorica, whose relationship to northwestern Africa now seems proven.

Conclusions and history of Avalonia as an independent terrane

In contrast to the sections above, we can now approach the history of the Avalonian terrane in a more conventional way, from the late Precambrian onwards until the accretion and combination of Avalonia within the very large Laurussia superterrane in the Silurian (Table 1).

It is clear that the early Neoproterozoic basement of Avalonia is made up of a number of originally separate terranes, many represented today by relatively small fragments. We accept as the most

Table 1. *Summary geological history of the Avalonian terrane area*

425 Ma	Mid-Silurian union of Avalonia–Baltica with Laurentia to form Laurussia
443 Ma	End-Ashgill soft oblique docking of Avalonia with Baltica
490 Ma (approx.)	End-Tremadocian: Avalonia leaves Gondwana margin as an independent unity, with a widening new Rheic Ocean between them
550–490 Ma late Neoproterozoic to earliest Ordovician	'Avalonian' area within Gondwanan margin, but some sporadic transform fault movements
610–530 Ma	Transform system develops along 'Avalonian' Gondwanan margin
635–570 Ma	Island arcs develop progressively (with voluminous volcanic rocks and intra-arc and interarc sedimentary basins), uniting old basement terranes and welding with core Gondwana off Amazonia to form 'Avalonia' area of Gondwana
750–650 Ma	Island arc activity in the 'Avalonia' area
1.2–1.0 Ga	Mesoproterozoic origination of various 'Avalonia' basement terranes

probable the conclusions of Keppie, Nance, Murphy and their colleagues (e.g. Murphy *et al.* 2006) that between 635 and 570 Ma one or more island arcs, including voluminous igneous intrusions and associated intra-arc and interarc sedimentary basin deposition, united the area of what was to be Avalonia and welded it to the main Gondwana superterrane somewhere off Amazonia. From the late Neoproterozoic to the earliest Ordovician there were sporadic and sometimes major transtensional movements along that part of the Gondwana margin, leading to the variable Cambrian and Tremadocian sedimentary basins and unconformities seen over much of the terrane. The off-Amazonian position of Avalonia explains all the differences seen between the Cambrian successions of Avalonia and other marginal areas of Gondwana such as the Armorican terrane assemblage and NW Africa. Avalonia was at an higher latitude than those other areas, explaining the paucity of Cambrian carbonates there, as well as the other dissimilarities. However, we do not concur with the opinion of Landing (e.g. 1996, 2005) that Avalonia was a terrane completely separated from Gondwana during the late Neoproterozoic and Cambrian.

We conclude from a review of all the evidence, faunal, sedimentary, structural and palaeomagnetic, that the most probable time of separation of Avalonia from Gondwana, and the opening of the Rheic Ocean, was at around the end of the Tremadocian. Thus Avalonia had an independent existence as a terrane only during Ordovician time, from about 480 to 445 Ma (Fig. 2). After the end-Ordovician oblique soft-docking with Baltica it became increasingly involved in the successive episodes of the Caledonide orogeny, after which the Avalonian terrane area became an integral part first of Laurussia and eventually, in the Late Palaeozoic, of Pangaea.

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Ordovician life around the Celtic fringes: diversifications, extinctions and migrations of brachiopod and trilobite faunas at middle latitudes

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Abstract: During the early to mid-Ordovician, marine life experienced an unprecedented rise in diversity at the species, genus and family levels that firmly installed the suspension-feeding benthos as the main component of the Palaeozoic fauna. The earlier Ordovician was characterized by a wide dispersal of the continents together with a high frequency of microcontinents and volcanic arcs. Magmatic and tectonic activity was intense, climates were warm and sea levels were high. Central to the entire diversification is the role of gamma (inter-provincial) diversity and by implication the spread of the continents and frequency of island arcs and microcontinents. A disparate group of continental fragments and island arcs loosely assigned to the Celtic province contained distinctive shelly faunas that formed a testable biogeographical unit. The Celtic faunas are characterized by a large number of endemic brachiopod taxa, some cosmopolitan forms, and taxa at the beginning or end of their stratigraphical ranges. The associated trilobite faunas are composed largely of wide-ranging genera, a few genera at the start of their stratigraphical range and some recently evolved taxa extending their geographical range. The Celtic province helped provide a burst of gamma diversity during the early stages of the Ordovician Radiation whereas the timing and position of the archipelagos associated with the Celtic province may have provided a mechanism for the diachroneity associated with the diversification.

Islands are an important part of our planet's ecosystem and have formed the basis for models of biotic speciation. Oceanic islands, related to fracture zones, hotspots, island arcs and mid-ocean ridges, together with islands on rifted fragments of continental crust, litter the oceans today (Ben-Avraham *et al.* 1981). Fossil island complexes are, in contrast, relatively rare, the majority having been subducted or variably preserved within orogenic belts. The latter, where identified, generally contain few fossils, which are commonly poorly preserved and often tectonized. Along the Caledonian–Appalachian mountain belt and in coeval orogenic zones, key palaeontological evidence for an Early Palaeozoic ocean system with diverse and endemic faunas is preserved. The faunas of many of these marginal and oceanic terranes have been associated with a Celtic province, defined largely on the basis of its brachiopod faunas. Trilobites also occur but their biogeographical signal is less clear. The disparate sites, however, of the Celtic province contributed a substantial amount to the Great Ordovician Biodiversification through the delivery of gamma diversity.

The Celtic concept

A number of 19th century palaeontologists, including Nicholson & Etheridge (1878), noted provincial differences between North American and European Early Palaeozoic faunas. Tuzo Wilson (1966), in a benchmark paper, provided an explanation for these differences, based on the existence of a previous Atlantic Ocean, the proto-Atlantic, that divided Europe from North America. Orthogonal opening and closure of this Early Palaeozoic oceanic system formed the basis for the Wilson cycle.

During the late 1960s, a thorough multivariate investigation, using cluster analysis, of all the then-known Ordovician brachiopod faunas confirmed differences between the North American and European biotas but also indicated important

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provincial differences within the European faunas themselves; for example, the Arenig brachiopods of the island of Anglesey could be associated with those from Baltica, in contrast to those from Shropshire, which apparently had affinities with those from the Montagne Noir of southern France (Williams 1969). A later re-evaluation of these data (Williams 1973) indicated the presence of a well-defined cluster, separate from those of Scoto-Appalachia, northwestern North America and the Baltic, characterized by the presence of *Rhynchorthis* but demonstrating close ties with the Baltic province. Williams (1973) considered that this, his 'Celtic province' containing marginal areas of Ireland and Wales, was a distinct biogeographical entity. Williams demonstrated a reduction of provinces during the Ordovician, from five in the Arenig to three in the Ashgill. Moreover, the relative numbers of endemic genera in each province ranged from 80 to 90% during the Arenig and Llanvirn, falling to some 55% during the later Ashgill (Williams 1973, fig. 12).

During the 1970s and 1980s Tuzo Wilson's model was modified to accommodate rates of opening and closure based on faunal data (e.g. McKerrow & Cocks 1976) and a more complex plate configuration (Cocks & Fortey 1982; Fortey & Cocks 1986) involved the interaction of the continents of Avalonia, Baltica, Gondwana and Laurentia. None of these models explicitly indicated the presence of islands; however, Neuman (1984), building on his earlier research on the brachiopod faunas within the Caledonian–Appalachian orogen (e.g. Neuman 1964, 1972), indicated the existence of a group of intra-Iapetus islands in his palaeogeographical reconstructions. A large number of the faunas associated with these island terranes could now be tied to Williams' concept of the Celtic province, suggesting origins seaward of the main continental plates. These faunas, however, presented other characteristic features: they contained a high proportion of endemics, commonly known only from one or two sites, taxa with links to adjacent continents and some taxa that are better known from younger rocks in the adjacent platform provinces.

Multivariate analyses of many of the late Arenig–early Llanvirn brachiopod faunas (Neuman & Harper 1992; but see also Harper 1992) confirmed a discrete and distinctive grouping of both sites and taxa conforming to the Celtic province. This biogeographical unit has been tested with both new data and modern statistical techniques, and its integrity remains reproducible (Harper *et al.* 1996, 2008).

This concept of the Celtic province was, however, challenged by McKerrow & Cocks (1993), who suggested that the term should be abandoned on the basis of the very widespread distribution of its brachiopod genera and the lack of an obvious pool of cross-province endemics. Implicit in their argument was the suggestion that some groups of brachiopods were better biogeographical indicators than others, a concept that has been applied to a number of other fossil groups (e.g. Fortey & Mellish 1992; Servais & Sintubin 2009). This argument was, however, not based on any particular taxonomic groups within the Brachiopoda, rather it was only those associated with the Celtic province that were clearly of limited value as they occurred along the same volcanic arc as localities with the marginal Laurentia Toquima–Table Head fauna. The answer was much simpler. The single Bronson Hill–Tetagouche–Lushs Bight Island arc proposed by McKerrow & Cocks (1993) is in fact at least two separate arcs: one part (with the Toquima–Table Head taxa) was associated with marginal Laurentia, whereas the other (associated with the Celtic province) developed at higher latitudes, within the Iapetus Ocean (Neuman *et al.* 1994). A more detailed analysis of this interpretation and an alternative model was provided by Harper *et al.* (1996) and Williams *et al.* (1996).

More recently, support for the Celtic province has accumulated from three sources of data. First, new faunas particularly from South America, for example, Argentina (Benedetto & Sanchez 2003), Bolivia and Peru (Gutiérrez-Marco & Villas 2007), have provided new occurrences of taxa associated with the Celtic province, supporting its extension along a high- to mid-latitude belt. Second, new data from already well-documented sites such as Otta, central Norway (Harper *et al.* 2008), continue to provide taxa that anchor these faunas within the province. Third, new data from the platform provinces such as Baltica (Harper & Hints 2001; Sturesson *et al.* 2005; Rasmussen *et al.* 2007) and South China (Rong *et al.* 2005; Zhan & Harper 2006) confirm the differences between these faunas and those of the Celtic province. Multivariate analyses consistently identify the Celtic group as distinct from the platform provinces of Baltica, Gondwana and Laurentia, and separate them from the marginal Laurentian Toquima–Table Head realm (e.g. Harper 2006).

Although the Celtic province is primarily recognized on the basis of its brachiopod faunas, reviews of the province have also commented on the associated trilobites (e.g. Bruton & Harper 1981, 1985; Neuman 1984; Neuman & Harper 1992; see also Dean 1974), most of which have been the subject of taxonomic studies. The trilobite faunas are generally of lower diversity and, as noted by Bruton & Harper (1985), their distribution was not influenced by island settings to the same degree as the brachiopods. Endemics (either from one site or several of the Celtic faunas) are extremely rare, whereas many taxa are shared with one or more platform faunas. As a result, the trilobites do not provide a 'signal' that would emerge from the multivariate analyses that so clearly differentiate the Celtic brachiopod faunas from those of the major palaeoplates (e.g. Harper *et al.* 1996). Thus, for example, island faunas lie in the middle of the seriation undertaken by Turvey (2005, fig. 9) to determine the palaeogeographical affinities of Arenig trilobites in South China, reflecting the dominance of taxa shared between the islands and several plates.

Early to Mid-Ordovician palaeobiogeography

Whereas the existence and integrity of the Celtic group of brachiopod faunas has been demonstrated by a range of multivariate statistical analyses, the precise pre-drift positions of the terranes, and by implication the geographical extent of the Celtic province, require a more multidisciplinary approach. Early to Mid-Ordovician palaeogeography has been refined by a series of recent studies based on both palaeontological and palaeomagnetic data (Fig. 1; Harper *et al.* 1996). More recent publications have emphasized again the role of shallow-water, marine benthos in defining provinces; for example, those by Cocks (2000, 2001) and Fortey & Cocks (2003). These workers, although recognizing the existence of marginal and peripheral sites to Avalonia, Baltica and Laurentia, opposed the concept of marginal or oceanic provinces based on a lack of province-wide endemics; nevertheless, they have accepted that these faunas cannot readily be accommodated within the platform provinces associated with major continental plates. Further, modern palaeogeographical analyses (e.g. for Baltica, Cocks & Fortey 1998; Cocks & Torsvik 2005; for Avalonia, Cocks *et al.* 1997; for Siberia, Cocks & Torsvik 2007) have consistently recognized the complexity of Ordovician geography and the existence and location of marginal terranes.

Fig. 1. Palaeogeographical reconstruction for the greater Iapetus and adjacent regions during the mid Darriwilian (after Harper *et al.* 1996 with modifications). Abbreviations: Am, Alpine massifs; Arm, Armorica; ATA, Armorican Terrane Assemblage; Boh, Bohemia (Perunica); Ib, Iberia; M , Meguma; Pc, Precordillera; Approximate positions of the sites clustered on Figure 2 indicated by numbers.

Current palaeogeographical studies have also emphasized the existence and significance of other comparable archipelagos. The Toquima–Table Head province (Toquima–Table Head Realm of Ross & Ingham 1970) includes a number of Laurentian marginal terranes now part of the Caledonian–Appalachian belt. Parts of western Ireland together with SW Scotland and a chain of localities along the eastern seaboard of the USA have also yielded a distinctive fauna with some endemics and very different from the carbonate platform faunas of the adjacent Laurentian craton (Neuman & Harper 1992; Harper & Mac Niocaill 2002). Typical of the province are the genera *Aporthophyla*, *Idiostrophia*, *Leptella*, *Leptellina*, *Neostrophia*, *Taphrodonta*, *Toquimia*, *Trematorthis* and *Trondorthis*.

However, *Aporthophyla* and a number of other typical members of the Toquima–Table Head province are known from outside the margins of Laurentia. *Aporthophyla* occurs together with *Leptellina* in South China, together with a number of endemic taxa such as *Parisorthis* and *Saucrorthis* (Rong *et al.* 2005). *Aporthophyla* apparently had a widespread distribution across broadly low-latitude sites. On the other hand, *Paralenorthis* was widely distributed across higher latitudes. Both taxa occur in terranes from South Kazakhstan, providing an interface between the two provinces (Nikitina *et al.* 2006).

The many terranes associated with central Asia have their own distinctive faunas. For example, the early Darriwilian brachiopod faunas of the Chu Ili range and the West Balkhash region of South Kazakhstan contain some 60 genera distributed across at least five palaeocommunity types. The faunas are highly endemic but show strong links with South China at this time. The early to mid-Darriwilian (late Arenig–early Llanvirn) was an interval of intense magmatic and tectonic activity. This is reflected in the presence of a large variety of island arcs and microcontinents dispersed across a spectrum of latitudes that interacted with a range of oceanic currents (Christiansen & Stouge 1999).

Brachiopods

The brachiopods experienced a marked diversification at the species, genus and family levels during the early and mid-Ordovician (Harper *et al.* 2001, 2004). It is clear, however, that the distributional patterns and ranges of the two main informal groups within the Brachiopoda, the nonarticulated (Bassett *et al.* 1999; Popov *et al.* 1999) and articulated stocks (Harper *et al.* 1999, 2004) developed independently during the biodiversification and, moreover, ecological events within the phylum were not always correlated with taxonomic radiations (Droser & Sheehan 1997; Bottjer *et al.* 2001; Harper *et al.* 2004). Many of the data evaluated here are derived from the distributions of articulated (rhynchonelliform) brachiopods.

Integrity of the Celtic province

Intensive study of sites associated with the Celtic province is relatively recent, essentially since the early 1960s, compared with those of the coeval platform provinces, many of which have been documented since the late 1800s and early 1900s (Harper 1998). This, coupled with the relative rarity of localities and the imperfect preservation of material, has contributed to the difficulties in defining this biogeographical unit. Moreover, a number of the new genera described from this province are difficult to relate to existing taxa because of their poor preservation, lack of some taxonomic information, and their different and distinctive morphologies. Nevertheless, since the 1990s a critical mass of data has been available for analysis. The majority of these earlier Ordovician faunas are developed in relatively shallow-water facies (e.g. Cocks 1996; Lockley 1983) and thus in most cases assemblages from similar depths are compared. Multivariate analyses of large datasets of brachiopod distributions (Harper 1992, 2006; Neuman & Harper 1992; Harper *et al.* 1996, 2008) have consistently isolated a cluster of brachiopods, identifiable as the Celtic province (Fig. 2). About 15 taxa occur at two or more of the Celtic sites; four taxa (*Paralenorthis*, *Productorthis*, *Tritoechia* and *Rugostrophia*) are relatively widespread, whereas some such as *Famatorthis*, *Ffynnonia*, *Monorthis*, *Platytoechia*, *Rhynchorthis* and *Treiroria* are relatively restricted, occurring only at two or three sites. A number of genera such as *Fistulogonites*, *Ottadalenites*, *Rutrumella* and *Schedophyla* are reported only from single sites. Many of these sites have been subsequently amalgamated into allochthonous complexes and thus located in Caledonian or coeval orogenic belts so that today, unlike the coherent platform provinces, they have a very disjunct distribution. None the less, where assembled in their pre-drift positions the majority of sites form a high- to mid-latitude belt marginal or seaward of Gondwana.

Temporal context of the Celtic province

Diversity curves are available for rhynchonelliform brachiopods through the Ordovician (Harper *et al.* 2004) and indicate four peaks of diversification of varying magnitude (Fig. 3). The first peak, which is weaker than the others, coincides with the immigrations into Baltica of a number of brachiopods possibly associated with an earlier phase of arc

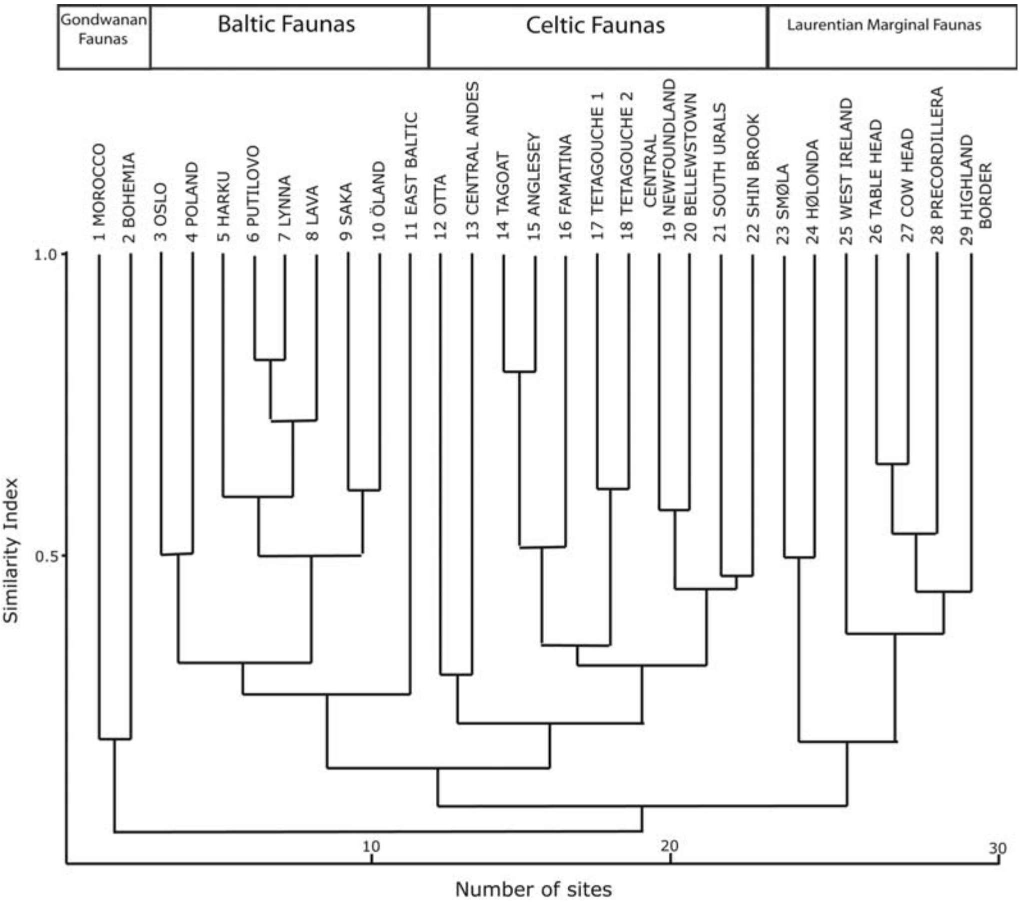

Fig. 2. Spatial cluster analysis of brachiopod distribution data (using the Raup–Crick coefficient, implemented by PAST: Hammer *et al.* 2001) for a number of key sites of Floian and Darriwilian age.

development adjacent to the southern margins of that continent (Sturesson *et al.* 2005). The second, in the early Darriwilian, coincides with the establishment of the Celtic province, its archipelagos and islands, associated with microcontinents and volcanic arcs. The third peak is broader, occupying the Sandbian and the early part of the Katian, whereas the fourth correlates with the Boda Warming Event in the late Katian (Boucot *et al.* 2003; Fortey & Cocks 2005). The third peak has been associated with rampant beta diversity, particularly correlated with the expansion of the benthos into deeper water with the development of a wide range of new communities (Harper *et al.* 2004). The fourth peak, coincident with the Boda Warming Event, may also be associated with a burst of beta diversity associated with new communities in carbonate build-up facies, but the event also promoted local endemism (Cocks 2005*a*; Fortey & Cocks 2005), which supplemented beta diversity.

Re-examination of the database developed for that survey emphasizes a number of clear trends across the two major groups, the orthides and strophomenides. There is a major change in the composition of both brachiopod orders during the mid-Llanvirn (late Darriwilian); those faunas in the lower Llanvirn units being very different from those in the upper part of the series. In both orders, the faunas from 4a and 4b (late Arenig–early Llanvirn) form an independent cluster (Fig. 4), remote from those faunas before and those after. This diversification thus coincides with the peak development of the Celtic province but also of other marginal clusters, such as the Toquima–Table Head fauna around Laurentia (Harper & Mac Niocaill 2002) and those associated with arc systems now located, for example, in Kazakhstan (Bassett *et al.* 2002; Nikitina *et al.* 2006).

The database (Harper *et al.* 1996; Harper 2006) also emphasizes the clear distinction between

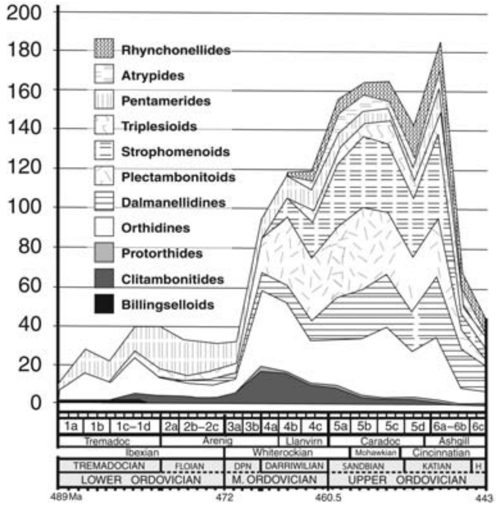

Fig. 3. Diversity curve for rhynchonelliformean brachiopods through the Ordovician Period (after Harper *et al.* 2004).

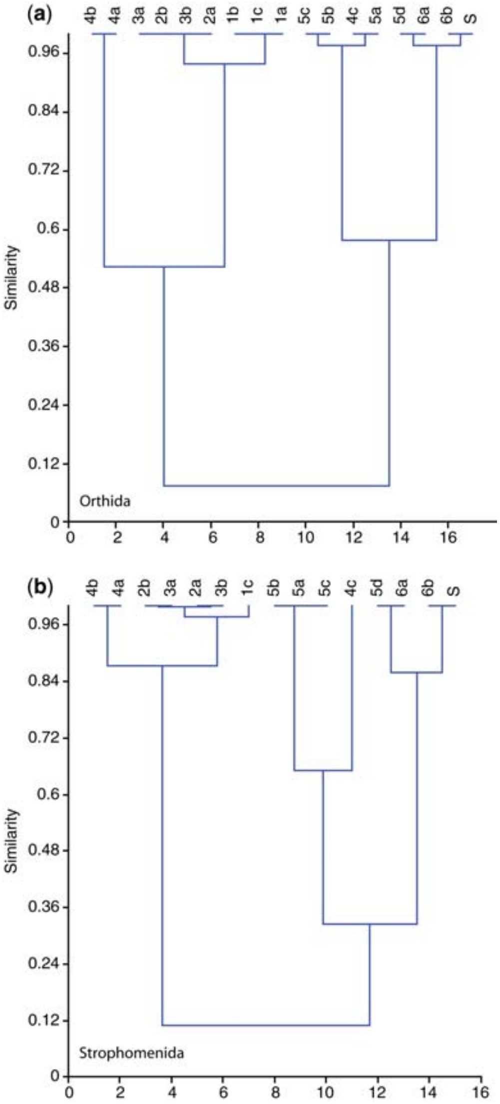

Fig. 4. Temporal cluster analysis using the time divisions and database assembled by Harper *et al.* (2004). Analysis implemented by PAST (Hammer *et al.* 2001) using the Raup–Crick coefficient.

tropical faunas, located on, for example, Laurentia and Siberia, that were dominated by syntrophidines together with specific orthide families (e.g. finkelnburgiids, hesperonomiids and orthidiellids; Patzkowsky 2005) as opposed to the cool-water clastic facies of Gondwana and its margins with nearshore lingulate communities and eoorthids, nanorthids and porambonorthids together with tritoechiids (Benedetto & Sanchez 2003).

Diversity dynamics of the Celtic province

The pivotal temporal position of the Celtic province suggests that it was an interface between two different brachiopod faunas, the lower-diversity faunas of the Tremadocian and early Arenig and the more diverse faunas of the late Llanvirn and younger. Moreover, particular faunas, for example, those of Otta (Norway: Bruton & Harper 1981; Harper *et al.* 2008) and Virgin Arm (Newfoundland: Neuman 1976), have relatively high diversities in comparison with the absolute number of individuals.

Harper *et al.* (1996) and Harper & Mac Niocaill (2002) examined the proportions of endemics together with first, last and mid-range occurrences in the Celtic and Toquima Table Head faunas for the billingsellides (including the clitambonitides) and orthides. Across both marginal provinces about 30% of genera were first occurrences, 25% were last occurrences and about 30% were endemic to these sites. Roles as cradles or museums of taxa were suggested for these marginal and oceanic belts (Harper & Mac Niocaill 2002). Within the Celtic province a number of key billingsellides, orthides, pentamerides and strophomenides have their first appearances. For example, early occurrences of *Orthidiella*, *Platystrophia* and *Valcourea* within the Orthida, *Ahtiella*, *Calyptolepta* and *Inversella* within the Strophomenida and *Camerella* within the Pentamerida signal an early stage in the evolution of these genera, pursued later on the platform provinces; whereas the genera *Famatinorthis*, *Hesperonia* and *Rhynchorthis* are the oldest in their respective families. Last appearances are indicated by the occurrences of *Tritoechia* (billingsellide), *Ranorthis* (orthide) and *Palaeostrophia* (pentameride). Some groups were particularly well represented across the province; for example, the orthids and taffiids.

It is difficult to source the fauna of the Celtic province at present but an origin for many of the taxa at higher latitudes around the margins of Gondwana is a possible and testable hypothesis (Bassett *et al.* 2002; Benedetto 2007).

Celtic province within the Great Ordovician Biodiversification Event

The coincidence between the disparity of the continents and the generation of volcanic arcs and microcontinents with the planet's largest increase in marine biodiversification is not accidental. Gamma or interprovincial biodiversity is an important factor. Williams (1973) demonstrated a decreasing provinciality throughout the period. A brief comparison of available data for the early to mid-Ordovician and late Ordovician faunas confirms this. Jaccard coefficients of similarity between selected sites in Laurentia, Avalonia and Gondwana (L/A: 0.05; L/G: 0; A/G: 0) are lower for the earlier Ordovician (this paper) than for the late Ordovician (L/A: 0.3; L/G: 0.1; A/G: 0.5; see Rong & Harper 1988; Owen *et al.* 1991).

The Celtic province may have been only one of a number of marginal and oceanic belts that helped fuel some of the initial phases of the biodiversification. The Toquima–Table Head province (Ross & Ingham 1970; Harper & Mac Niocaill 2002), which developed around parts of Laurentia, forms a low-latitude counterpart to the Celtic province with similar faunal dynamics. Earlier island arc systems (Tremadocian–Floian) were probably present seaward of the eastern margin of Baltica and combined with fragments of the Uralian margin of Baltica (Sturesson *et al.* 2005) to provide similar but older archipelagos to those of the Celtic province. A number of these terranes are probably now located within the complex orogenic belts of Central Asia and Kazakhstan (Popov & Holmer 1994; Holmer *et al.* 2000). These island complexes may have provided a link between the diverse assemblages of East Gondwana and the early Ordovician immigration and subsequent diversification in Baltica; the rhynchonelliform brachiopods *Apheoorthina*, *Angusticardinia*, *Prantlina* and *Ranorthis* occur at the same level in Baltica as in Bohemia and Morocco (Sturesson *et al.* 2005). There is also evidence for a similar early Ordovician (early Floian) biodiversification on the South China plate (Zhan & Harper 2006) dominated by orthide brachiopods. However, parts of Kazakhstan and South China retained their own endemic faunas through the early Darriwilian with strong ties to the Toquima–Table Head province rather than to the Celtic group of assemblages (Rong *et al.* 2005; Nikitina *et al.* 2006).

New data from some of the marginal terranes to East Gondwana, such as the Alborz Mountains, Iran, suggest early occurrences (Tremadocian) of a number of key taxa that later diversified mainly along the Gondwanan margins and in Baltica (Popov & Ghobadi Pour 2007). The model for the development of the main types of brachiopod assemblages through the Cambrian and into the early part of the Ordovician, documented in detail by Bassett *et al.* (2002), graphically illustrates the diachronism of the Ordovician biodiversification. By the early Floian the Palaeozoic evolutionary fauna was already established on and around Gondwana; different facets of this fauna developed at the same time in Baltica but somewhat later in Laurentia. The diversity of marginal and oceanic sites through the early to mid-Ordovician interval can help provide an explanation and a testable model for the diachronous development of the Great Ordovician Biodiversification. Early Ordovician sites associated with eastern margins of Baltica may have provided an entrance to the Baltic province for Gondwanan elements whereas the Celtic assembly of terranes provided a mid-Ordovician access to Laurentia.

Within the context of the Great Ordovician Biodiversification Event, the Celtic province was one of a series of marginal and oceanic belts of island arcs and microcontinents that, through their disparate brachiopod fauna, contributed gamma biodiversity to the event. However, the Celtic and other similar biogeographical units also had important roles in the delivery of faunas to adjacent continental provinces, sparking changes in alpha and beta diversifications as new community types developed and more species were accommodated into existing community structures (Harper 2009).

Trilobites

Like the brachiopods, trilobites underwent major diversification during the Early and Mid-Ordovician (summarized by Adrain *et al.* 2004) and the global diversity curve is similarly a composite of different regional and taxonomic patterns. However, given the lack of endemic taxa, the question must therefore arise as to whether the 'Celtic' trilobite faunal associations are different from contemporaneous shelf faunas. One way to test this is to take as a 'null hypothesis' the speculation that the palaeobiogeographical make-up of any of the trilobite faunas is similar to that of contemporaneous platform faunas on the palaeoplates to which the supposed island faunas are now attached. In other words, without the brachiopods, might the trilobite faunas have been considered unremarkable? This is best tested in relation to the three most diverse trilobite faunas by dividing the palaeogeographical affinities of their component genera into four categories in comparison with those of the plate to which they are attached, as follows.

(1) Genera already present on the plate or making their first appearance in coeval undoubted platform faunas there.

(2) Genera that without other information indicating an island fauna would be considered as first appearances on the plate.

(3) Genera that without other information indicating an island fauna would be considered unique occurrences on the palaeoplate of genera known from elsewhere.

(4) Endemic genera unknown from elsewhere.

The Otta trilobite fauna

The trilobites from the Otta Conglomerate were described by Bruton & Harper (1981) and recently reassessed by Harper *et al.* (2008). This fauna comprises 10 species assigned to nine genera. Most recently, Holloway (2007, p. 5) has erected the new genus *Cyrtocybe* (type species *Raymondaspis turgidus* Whittington) and included under open nomenclature within it material previously assigned to *Turgicephalus* Fortey and identified as *T.* cf. *turgidus* by Bruton (Bruton & Harper 1981) from the Otta Conglomerate and also *Raymondaspis* sp. of Whittington (Neuman 1964, p. 31, plate 7, figs 8–12) from an insular setting in Maine (see below). Holloway (2007, pp. 5–7) regarded *Turgicephalus* as being a junior synonym of *Raymondaspis* Pribyl and clearly different from his new genus *Cyrtocybe*.

The precise age of the Otta fauna is not known, but an early Llanvirn age seems most likely (Bruton & Harper 1981). If the fauna inhabited part of Baltica rather than the shelf of an intra-Iapetus island, the trilobite genera could be broken down into categories representing their palaeogeographical affinities, as follows.

(1) Genera already present in Baltica (*Asaphus*, *Megistaspis*, *Pliomera*) or making their first appearance in coeval undoubted platform faunas there (*Cybelurus*, *Cyrtocybe*).

(2) Genera that without other information indicating an island fauna would be considered as first appearances in Baltica (*Amphilichas*, *Ceraurinella*). An illaenid pygidium doubtfully assigned to *Stenopareia* may also belong here but is excluded as its generic assignment is equivocal.

(3) Genera that without other information indicating an island fauna would be considered unique occurrences on the palaeoplate of genera known from elsewhere (*Annamitella*).

The equivalent palaeobiogeographical profile for the uppermost Stein Formation and lowermost part of the Elnes Formation (Helskjer Member; lower Llanvirn) in the Oslo region to the south of Otta and undoubtedly part of Baltica (based on Wandås (1984) and Hansen (2009)) comprises the following.

(1) Fourteen genera already present in Baltica comprising seven Baltic endemics (*Asaphus*, *Cyrtometopus*, *Megistaspis* (*Megistaspidella*), *Metopolichas* (which later spread to Avalonia and China), *Pliomera*, *Pterygometopus*, *Volchovites*) and seven that had a wider distribution (*Ampyx*, *Cnemidopyge*, *Geragnostus*, *Illaenus*, *Nileus*, *Niobe*, *Scotoharpes*).

(2) Eight genera making their first appearance in Baltica (excluding Otta). One of these, the epipelagic *Telephina*, was an immigrant, the earliest recorded species of which is from the Arenig of Argentina (Chatterton *et al.* 1999), whereas seven were newly evolved genera (*Atractopyge*, *Botrioides*, *Bronteopsis*, *Ogmasaphus*, *Ogygiocaris*, *Pseuobasilicus* and *Sphaerocoryphe*). [Note that *Ogygiocaris teicherti* Legg from the Arenig of the Canning Basin, Australia, was designated the type species of *Emanuelaspis* Laurie (Laurie & Shergold 1996), and T. Hansen (pers. comm.) considered that *Ogygiocaris araiorhachis* Harrington & Leanza from the Tremadoc of Argentina recently described by Waisfeld & Vaccari (2006) does not belong in this genus.] The ancestry of *Atractopyge* is not clear but may lie within *Cybelurus*. The trinucleid *Botrioides* may have had an Avalonian origin, possibly within *Bergamia*, but the remaining five new genera probably had Baltic ancestors.

(3) Four genera that are unique occurrences at undoubted Baltic platform sites but are known from elsewhere at equivalent horizons (*Cybelurus*, *Cyrtocybe*, *Icelorobergia*? and an indeterminate genus referred to the Elviniidae by Hansen (2009) [= *Carolinites* of Wandås 1984]).

The overall distribution of genera to the three palaebiogeographical groups in the Otta and Oslo region faunas is superficially very similar, comprising a mixture of genera already present on the plate, new appearances and rare unique occurrences. Without the brachiopods, the Otta trilobite fauna might have been considered unremarkable in a Baltic context. However, whereas at least half of the genera in the platform fauna are either Baltic endemics or new taxa with Baltic ancestry, a feature also recognized by Hansen (2009) in considering the history and origins of the species concerned, the underlying biogeographical signal of the Otta trilobites is a much more cosmopolitan one. Teasing apart the three palaeobiogeographical categories, provides further information on the palaeogeographical links of the Otta fauna as follows.

The three genera in the Otta fauna that had an earlier history in Baltica, *Asaphus*, *Megistaspis* and *Pliomera*, are all amongst the Baltic endemics in the Oslo region. Only the record of *Megistaspis* is unequivocal in this respect. As Bruton & Harper (1981) pointed out, some of the Otta material assigned to *Asaphus* (*Neoasaphus*) bears a strong similarity to pygidia of *Priceaspis* Legg (1976) from the Canning Basin in Australia, part of low-latitude Gondwana. The ancestry of *Pliomera* is not clear and the genus appeared in Baltica in the latest Arenig (see Bruton & Harper 1981), not long prior to its occurrence in the uppermost Stein Fm. and Helskjer Mbr of the Elnes Fm. and (if the postulated early Llanvirn age is correct) the Otta conglomerate. *P. fischeri asiatica* Chugaeva from a broadly similar level in eastern Siberia was reassigned to the Laurentian genus *Perissopliomera* by Fortey & Cocks (2003, p. 266).

The two genera that made their first appearance in coeval undoubted Baltic platform faunas, *Cybelurus* and *Cyrtocybe*, are the two named genera that are otherwise unique Baltic occurrences in the Oslo region fauna. *Cybelurus* is palaeogeographically widespread but is at best a paraphyletic grouping of species (Peers 1997) including taxa from the Arenig of Laurentia and so its palaeogeographical signal is not clear. As is discussed below in relation to the island fauna from Maine, *Cyrtocybe* [= *Turgicephalus* of Bruton & Harper (1981) and *Raymondaspis* (*Cyrtocybe*) of Hansen (2009), Wandås (1984) and Hansen (2009)] was short lived and seems to have spread rapidly from its island origins in the late Arenig both to the Oslo region and to Laurentia (*C. turgidus* Whittington from the Table Head Group; see Holloway 2007). Its occurrence in the Otta fauna could therefore be interpreted as compatible with Otta being part of Baltica or an island 'stepping stone'.

The 'first appearances' of *Amphilichas* and *Ceraurinella* at Otta are also the earliest occurrences of both genera, both with probable Laurentian ancestry. *Annamitella* is unknown from Baltica and is discussed in detail below.

The Summerford Group, Newfoundland

There has been taxonomic reassessment of some of the 11 trilobite genera described by Dean (1974; see also Boyce 1987) from the late Arenig–early Llanvirn Unit B of the Summerford Group on New World Island in the Dunnage Zone of Newfoundland. Bruton & Harper (1985, table 3) assigned the indeterminate odontopleurid to *Apianurus*. Owen (1987, p. 94) argued that Dean's *Bergamia*? sp. (reassigned to *Botriodes* by Hughes *et al.* 1975) was too poorly preserved for generic assignment, and Fortey & Cocks (2003, p. 284) suggested that material described by Dean as *Pseudosphaerexochus* (*s.l.*) sp. may be reassigned to *Mayopyge* Adrain & Fortey, otherwise known only from the insular Tourmakeady Limestone fauna of western Ireland. In addition, Adrain & Fortey (1997, p. 104) considered *Ischyrophyma* Whittington to be a junior synonym of *Celmus* Angelin (see also Bruton 1983; Bergström & Suzuki 2005).

The palaeogeographical breakdown of the Summerford Group fauna is as follows.

(1) Genera already present in Laurentia or making their first appearance in coeval undoubted platform faunas there (*Celmus*, *Geragnostus*, *Illaenus*, *Scotoharpes*).

(2) Genera that without other information indicating an island fauna would be considered as first appearances in Laurentia (*Apianurus*, *Encrinuroides*).

(3) Genera that without other information indicating an island fauna would be considered unique occurrences in Laurentia of genera known from elsewhere (*Metopolichas* and, excluding other island sites, *Annamitella*, *Mayopyge*).

(4) Endemic genera unknown from elsewhere (*Paratretaspis*).

The palaeobiogeographical profile of the fauna is far from typical of Laurentia (see, e.g. Whittington 1965; Fortey 1975, 1980). All four of the genera already present in Laurentia also have a history in other palaeocontinents and there are none of the many endemic taxa that are a major component of contemporaneous Laurentian faunas such as the bathyurids (see Fortey & Cocks 2003, pp. 255–258, for summary). The ancestry of *Apianurus* is uncertain, but *Encrinuroides* is known from older Arenig strata in Baltica (see Pärnaste 2006); both genera appeared in undoubted Laurentian settings later in the Llanvirn. *Metopolichas*, an essentially Baltic taxon, is not known from Laurentia, and as noted above the only other record of *Mayopyge* is in an island setting, albeit on the Laurentian side of the Iapetus Ocean. *Annamitella* is not known from Laurentian shelf sites, but also occurs in North America in island faunas in Maine (see below) and in several other sites in the Dunnage Zone in Newfoundland (Boyce 1987; Boyce *et al.* 1988).

The Shin Brook Formation, Maine

The trilobites from these upper Arenig volcaniclastic rocks were described by Whittington (in Neuman 1964) in the first of the succession of papers by Neuman and co-workers documenting the Iapetus island faunas and their significance. Of the eight identifiable trilobite taxa, two have been revised taxonomically: Bruton & Harper (1985) identified Whittington's 'miraspinid gen undet.' as belonging in *Apianurus* and, as is noted above, Holloway (2007) reassigned the *Raymondaspis* sp. of Whittington to his new genus *Cyrtocybe*. The generic assignment of Whittington's '*Hibbertia*? sp.' remains uncertain.

The palaeogeographical breakdown of the Shin Brook fauna is as follows.

(1) Genera already present in Laurentia or making their first appearance in coeval undoubted platform faunas there (*Ampyx*, *Geragnostus*, *Illaenus*, *Nileus*).

(2) Genera that without other information indicating an island fauna would be considered as first appearances in Laurentia (*Apianurus*, *Cyrtocybe*).

(3) Genera that without other information indicating an island fauna would be considered unique occurrences in Laurentia of genera known from elsewhere, excluding other island sites (*Annamitella*).

As with the Summerford Group fauna, the palaeobiogeographical signature of the Maine fauna is unlike that of contemporary Laurentian assemblages. None of the genera with an earlier history in Laurentia were confined to that palaeoplate; all four were virtually cosmopolitan in their distribution. As is noted above, the ancestry of *Apianurus* is uncertain. Its occurrence in the Shin Brook Fauna is the oldest record, slightly predating that in the Newfoundland island fauna. Similarly, the record of *Cyrtocybe* is the oldest known and the genus spread rapidly to Laurentia and Baltica.

The ubiquitous Annamitella

The most remarkable, and widely commented on, aspect of the Celtic trilobite faunas is the widespread occurrence of the leiostegiid genus *Annamitella* (e.g. see Bruton & Harper 1985; Fortey & Cocks 2003; Bruton *et al.* 2004). Amongst these is its presence in the upper Arenig shelly fauna from Anglesey (= *Monella* Bates; see Whittington in Neuman 1972, and subsequent studies), from where the brachiopods formed part of the Williams' original concept of the Celtic province. *Annamitella* also occurs in a comparable fauna in the Bangor area on the north of the Welsh mainland (Beckly 1989). The assignment of the Anglesey and Bangor faunas to an island setting has been controversial (e.g. references in Neuman & Harper 1992), at least in part because of the co-occurrence of trilobites of typical Avalonian–Gondwanan aspect. There is now wider agreement, however, that these faunas occupied island sites marginal to Avalonia (Cocks & Fortey 2003, p. 285; Cocks 2005*b*, p. 122). Significantly, one of the typical Gondwanan taxa occurring with *Annamitella* in the Bangor area is *Calymenella*, which Beckly (1989) noted was the first occurrence of the genus earlier than the Caradoc. Were the fauna to have lived in Avalonia, it would be the only record of the genus there.

Outside island settings, *Annamitella* otherwise occurs in areas that formed parts of mid- to low-latitude Gondwana (Australia, Argentina) together with an array of plates that lay at a range of latitudes at varying degrees of proximity to that margin: Annamia, South China, Sibumasu, Tarim, Kazakhstan (see Fortey & Shergold 1984; Fortey & Cocks 2003; Turvey 2005; Vaccari *et al.* 2006). Significantly, it is not known from undoubted platform successions in Laurentia, Baltica and Avalonia, the plates bordering the Iapetus Ocean, despite its presence in island settings there (e.g. see Fortey & Cocks 2003, p. 284).

The reasons for the absence of *Annamitella* from the platforms around the Iapetus Ocean are not clear, given its widespread distribution elsewhere. Interestingly, the genus may also occur in the volcanic and volcaniclastic rocks containing the blocks of the late Arenig Tourmakeady Limestone in County Mayo, western Ireland (= *Bathyurus*? *reynoldsi* Reed; see Whittington in Zen *et al.* 1968, p. 56). The trilobite fauna of the Tourmakeady Limestone was described by Adrain & Fortey (1997), who considered it to be very close to the illaenid–cheirurid trilobite biofacies of the Laurentian platform. Fortey & Cocks (2003, p. 282) reiterated this strong Laurentian 'fingerprint' but also highlighted the presence of two endemic trilobite and eight (of 14) brachiopod genera (see Williams & Curry 1985, for monographic treatment of the brachiopods). They argued that the fauna represents an insular setting that was sufficiently separate from the Laurentian platform to produce this endemicity but still within the palaeotropics. The absence of *Annamitella* from the Tourmakeady Limestone but its presence in the associated volcanic-related lithology may indicate some sort of environmental rather than strictly palaeogeographical control on its distribution in the Iapetus region. Such a control could not have been simply that of lithofacies. The Mayo example suggests that *Annamitella* could not inhabit Laurentian shallow-water carbonate environments but this does not explain its absence from the volcanic and volcaniclastic successions that abound in the Arenig and Llanvirn of the Welsh Basin in Avalonia. Whatever the reason, *Annamitella* seems to be an important 'marker' for island faunas in the Iapetus region.

Endemic taxa

The monotypic *Paratretaspis* Dean in the late Arenig–early Llanvirn Summerford Group fauna described by Dean (1974) is the only recorded endemic trilobite genus associated with the Celtic brachiopod faunas. Hughes *et al.* (1975, p. 565) noted similarities between this trinucleid and *Decordinaspis* Harper & Romano from the Early Caradoc of the Grangegeeth terrane in eastern Ireland. The associated fauna in Ireland contains a mixture of Laurentian, Baltic and Avalonian taxa. Owen *et al.* (1992; see also Romano & Owen 1993) argued that this indicates a setting within the Iapetus Ocean, which Van Staal *et al.* (1998; see also Armstrong & Owen 2001) subsequently considered may have been part of the Popelogan–Victoria Arc that included elements of the Gander zone and collided with (or even included) the block containing the Summerford Group. Although any direct phylogenetic relationship between *Paratretaspis* and *Decordinaspis* remains to be fully demonstrated, any such link would be evidence of evolution within Iapetus island faunas.

If Fortey & Cocks (2003) are correct in reassigning the cheirurid from the Summerford Group fauna to *Mayopyge*, this too becomes an endemic island trilobite taxon, being restricted to the Newfoundland fauna and the Tourmakeady Limestone in Co. Mayo.

The biogeographical signal in the trilobite faunas

The palaeobiogeographical profiles of the trilobites associated with Celtic province brachiopods are not typical of faunas on the palaeoplates to which they are now attached although they have elements in common. A consistent pattern emerges, as follows.

(1) Endemics are very rare (in marked contrast to the brachiopods).

(2) Some genera may be otherwise restricted to contemporaneous or earlier faunas on a single palaeoplate, which may or may not be that to which the island fauna is now attached. In the latter cases, the islands were acting as biogeographical stepping stones.

(3) Many genera, in some instances a majority, were widespread.

(4) Some genera, notably *Apainurus*, *Amphilichas*, *Calymenella* and *Cyrtocybe*, have their earliest recorded occurrences in these faunas, and like the brachiopods reflect islands as cradles of evolution.

(5) One genus, *Annamitella*, is very widespread and occurs throughout the Iapetus islands, but not the adjacent shelves (compared with widespread occurrences elsewhere). The reasons for this are not clear but do not lie simply in lithofacies or palaeolatitude.

Conclusions

The Celtic province is a testable grouping of brachiopod faunas that developed at higher latitudes, but seaward of the main continents, during the Early to Mid-Ordovician. The Celtic faunas are characterized by a large number of endemic brachiopod taxa, some cosmopolitan forms and taxa at the beginning or end of their stratigraphical ranges. The associated trilobite faunas are composed largely of wide-ranging genera, a few genera at the start of their stratigraphical range and some recently evolved taxa extending their geographical range. The Celtic province helped provide a burst of gamma (inter-provincial) diversity during the early stages of the Ordovician Radiation, whereas the timing and position of the archipelagos associated with the Celtic province may have provided a mechanism for the diachroneity associated with the diversification.

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The tectonic context of the Early Palaeozoic southern margin of Gondwana

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Abstract: The oceanic southern margin of Gondwana, from southern South America through South Africa, West Antarctica, New Zealand (in its pre-break-up position), and Victoria Land to Eastern Australia, is one of the longest and longest-lived active continental margins known. Its construction was initiated in late Neoproterozoic times following the break-up of the pre-existing supercontinent of Rodinia. Gondwana was established by the amalgamation of Australian, Indian, Antarctic, African and South American continental fragments mostly derived from Rodinia. Its 'Pacific' margin continued to develop as the site of the 18 000 km Terra Australis orogen, predominantly facing subducting ocean floor and involving some terrane accretion events, through Palaeozoic and Mesozoic times until, and during, the eventual break-up of Gondwana itself.

Although the exact configuration of Rodinia is debatable, the existence of a Neoproterozoic supercontinent is consistent with the widespread occurrence of orogenic belts in the age range 1000–1200 Ma (Fig. 1); that is, coetaneous with the Grenville Belt, which runs all the way along the present eastern coast of North America (Laurentia in the Precambrian context). These belts have been interpreted as collision zones during the formation of Rodinia (Hoffman 1991). Such belts criss-cross Antarctica (Fitzsimons 2000, 2003; Fig. 1) and together with palaeomagnetic data (Pisarevsky *et al.* 2003) seem to require the conjunction of the East Antarctica, Australia, Laurentia, Baltica, India, Siberia and South China blocks by about 1000 Ma. The exact configuration of Rodinia has been disputed, and Cordani *et al.* (2003), for example, have proposed that some of the cratonic elements now in NW Brazil and West Africa were never part of Rodinia. However, 'Grenville-age' lithological assemblages are now being found in the western Sierras Pampeanas of Argentina (Casquet *et al.* 2005, 2006) and as far north as Colombia (Cordani *et al.* 2005; Fig. 1): they appear to present a conjugate collisional margin with Laurentia, which thus seems to have subsequently split apart along the main axis of this Grenville belt. The timing of Rodinia break-up and the paths followed by the disrupted masses are at present poorly constrained by geochronology or palaeomagnetic studies, respectively. Evidence from igneous activity is rare, but the occurrence of passive margin sedimentary sequences, mafic dyke swarms, alkaline igneous complexes and occasionally ophiolites, in the age range 850–700 Ma in Laurentia (e.g. Heaman *et al.* 1992), Africa (de Kock *et al.* 2000), Australia (Wingate & Giddings 2000) and Brazil (Paixão *et al.* 2008), generally suggests a rifting environment consistent with the predominant presence of intermediate oceanic basins during this interval. Final rifting between Laurentia, Baltica and Amazonia did not occur until about 600 Ma (Pisarevsky *et al.* 2008).

Formation of Gondwana

The cratonic fragments, derived directly from Rodinia or otherwise, were gradually realigned to form Gondwana from about 650 Ma onwards. Interpretations of the stages involved are based on the constraints of palaeomagnetism and the correlation of dated orogenic belts. According to one such model (Boger & Miller 2004), India (and Dronning Maud Land, the region of East Antarctica now nearest South Africa) was accreted to eastern Africa along the Mozambique Belt at 590–560 Ma (the Kuunga orogen of Cawood & Buchan 2007; Fig. 1), followed by the collision of Australia and the bulk of East Antarctica (Mawson craton; Fig. 1) at 535–520 Ma along the Pinjarra orogen (Cawood & Buchan 2007; Fig. 1). These collisions caused the series of orogenies known as Pan-African, often equated with the amalgamation of 'East' and 'West' Gondwana. The main suture is sometimes referred to as the East African or East African–Antarctic orogen (e.g. Jacobs & Thomas 2004). However, the process must have started even earlier in the Neoproterozoic, as the

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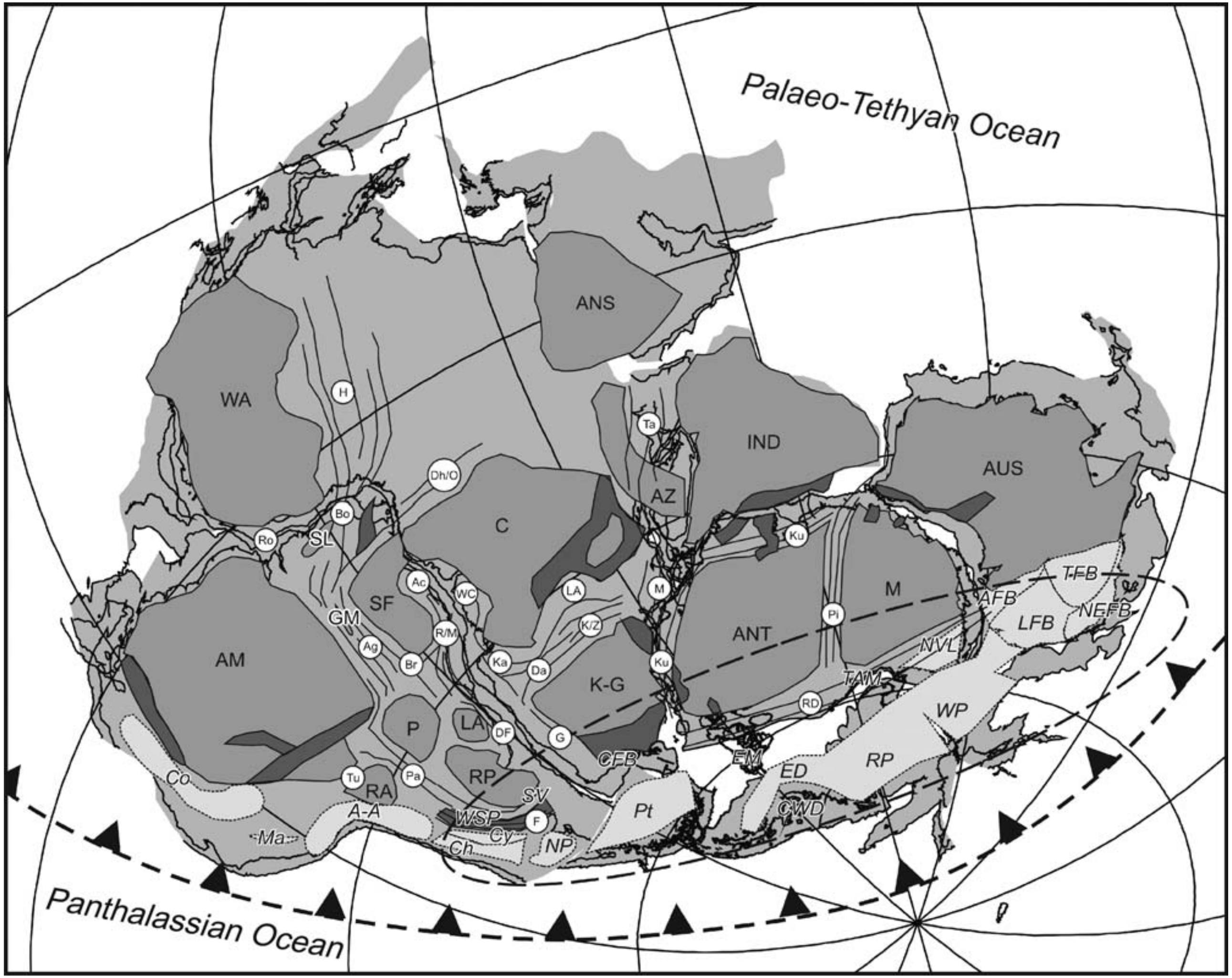

Fig. 1. Reconstruction of West Gondwana after Tohver *et al.* (2006) and East Gondwana after Cawood & Buchan (2007) showing cratonic and Brasiliano–Pan-African–Early Palaeozoic elements. Cratons shown in medium grey: AM, Amazonia; ANS, Arabian–Nubian Shield; ANT, Antarctic; AUS, Australian (including Yilgarn, Pilbara, Gawler and Musgrave); AZ, Azania; C, Congo; GM, Goias Massif; IND, India (including Bundelkhand, Dharwar, Bastar and Singhbhum); K-G, Kalahari–Grunehogna; LA, Luis Alves; M, Mawson; P, Paraná; RA, Río Apa; RP, Río de la Plata; SF, São Francisco; SL, São Lius; WA, West Africa. 1200–1000 Ma 'Grenville' belts shown in dark grey: West Gondwana from Tohver *et al.* (2006) and East Gondwana from Fitzsimons (2000); WSP, Western Sierras Pampeanas. Brasiliano–Pan-African–Early Palaeozoic belts (ringed): Ac, Araçuaí; Ag, Araguaia; Bo, Borborema; Br, Brasilía; Da, Damara; DF, Dom Feliciano; Dh/O, Dahomeides/Oubangides; F, Famatinian; G, Gariep; H, Hoggar; Ka, Kaoko; K/Z, Katangan/

Arabian–Nubian Shield (Fig. 1) was already in place north of the Mozambique Belt, possibly by *c.* 700 Ma. Moreover, West Gondwana includes the South American sector, where a collage of cratonic and accretionary fragments was similarly colliding with the western side of the proto-African continent through closure of the Adamastor Ocean (Brito Neves *et al.* 1999); this occurred from around 600 Ma, producing an equivalent series of Brasiliano–Pan-African orogenies (Fig. 1; see contributions in de Wit *et al.* 2008 for an up-to-date review), which also culminated in the mid-Cambrian. The main elements constituting the southern margin of the new supercontinent were essentially in place by the mid-Cambrian, from which time onwards erosion of the newly formed orogenic belts became a significant and continuous process. However, the tectonic development of the margin was far from over.

Subsequent development of the southern margin of Gondwana

During the early Palaeozoic much of the margin was dominated by successive episodes of subduction–accretion. In Eastern Australia the Neoproterozoic Adelaide Rift system changed into an active, and then collisional, margin during the Cambro-Ordovician Delamerian orogeny, forming the Adelaide Fold Belt (Cawood & Buchan 2007; Fig. 1). Continued accretionary events resulted in the margin stepping out to include the Lachlan and New England fold belts (see review by Glen 2005; Fig. 1). Late Ordovician to Devonian granites dominated the Lachlan Fold Belt, with several deformation phases, the most important being near the Ordovician–Silurian boundary. This is the region in which the concept of I- and S-types granites was established (Chappell & White 1971, 2001), although any inference that the substrate is predominantly (or even partly) crystalline continental basement is now highly contentious. Accretion of already developed magmatic arcs appears the most likely process of continental growth (Gray & Foster 2004). The New England Fold Belt, further outboard and to the north, also consists of accreted sedimentary sequences and copious mica-rich granites, with Late Devonian–Carboniferous deformation, followed by Permian rifting and a Triassic subduction regime.

The Early Palaeozoic margin of Gondwana continued through the Antarctica to South America. Northern Victoria Land and extensive parts of the Transantarctic Mountains (Fig. 1) also record the first of these two events, the Cambro-Ordovician Ross–Delamerian orogeny (Fig. 1), with the intrusion of a widespread suite of granites. The innermost, autochthonous(?) part of Northern Victoria Land, the Wilson terrane, consists of Neoproterozoic crystalline basement, but there are two further accreted terranes of unknown origin (Tessensohn & Henjes-Kunst 2005): the Bowers terrane, which in part has the character of a Cambrian island arc, and the possibly allochthonous Robertson Bay terrane, which consists of an Ordovician turbidite sequence. Remnants of Ordovician turbidites intruded by granites are also found in the Ross Province of Marie Byrd Land (Pankhurst *et al.* 1998*b*; see Fig. 1) and the Antarctic Peninsula (Millar *et al.* 2002) (deformed in the latter case) and these areas constitute the innermost ‘Eastern Domain’ of Vaughan & Storey (2000; see Fig. 1). The outer (Central and Western) domains (Fig. 1) are considered to represent Palaeozoic to Mesozoic accreted oceanic and island arc material. Taken all together they comprise the Terra Australis accretionary orogen of Cawood (2005); the Mesozoic parts were also separately termed the Australides by Vaughan *et al.* (2005).

Similar tectonic elements are recognized at the South American end of the margin, where the Cambrian Pampean orogeny (Fig. 1) occurred with dextral strike-slip along the western edge of the 2200 Ma Rio de la Plata craton (Fig. 1); much of the sedimentary material in the Pampean metasedimentary sequences may be derived from erosion of the Brasiliano–Pan-African collisional orogens (Fig. 1) rather than from cratonic elements of Gondwana (Rapela *et al.* 2007). This was followed by an Ordovician active margin, also with intense granite–rhyolite magmatism (Famatinian; Fig. 1), which is now known to extend from Ecuador to NE Patagonia (Pankhurst *et al.* 1998*a*;

Fig. 1. (*Continued*) Zambezi; Ku, Kuunga; LA, Lufilian Arc; M, Mozambique; P, Paraguai; Pi, Pinjarra; RD, Ross–Delamerian; R/M, Ribeira/Mantequeira; Ro, Rockelides; Ta, Tanzania; Tu, Tucavaca; WC, West Congo. Terranes with Early Palaeozoic elements shown in light grey; Eastern Australia after Cawood & Buchan (2007): A-A, Arequipa–Antofalla massif (Ramos 2008*a*); AFB, Adelaide Fold Belt; Ch, Chilenia; Co, Colombian Terranes (Cordani *et al.* 2005); CWD, Central and Western domains; Cy, Cuyania; Ma, Marañón massif (Chew *et al.* 2007); ED, Eastern Domain (Vaughan & Storey 2000); LFB, Lachlan Fold Belt; NEFB, New England Fold Belt; NP, North Patagonian Massif; NVL, Northern Victoria Land; Pa, Pampia terrane; Pt, Patagonia; RP, Ross Province (Pankhurst *et al.* 1998*b*); TAM, Transantarctic Mountains; TFB, Thompson Fold Belt; WP, Western Province (after Adams *et al.* 2005). Large dashed ellipse indicates area affected by the Terra Australis orogen of Cawood (Cawood 2005): CFB, Cape Fold Belt; EM, Ellsworth–Whitmore Mountains; SV, Sierra de la Ventana.

Chew *et al.* 2007). Since the early tectonic analysis of Ramos (1988), much of the western part of the South American margin has been regarded as composed of exotic or suspect terranes, and these were recently reviewed from a palaeomagnetic perspective by Rapalini (2005); the geology of the northernmost Arequipa–Antofalla and Marañón blocks (Fig. 1) was recently reviewed by Ramos (2008*a*). The best known of these is the Precordillera terrane, or Cuyania (Fig. 1), of central western Argentina. The identification of this terrane is based largely on the deposition of passive margin sediments, including limestones, during the Cambro-Ordovician interval when the rest of the margin was undergoing intense orogenesis. The fauna has been described as showing a Cambrian–Ordovician transition from Laurentia to Gondwanan (Benedetto 1998), and these passive margin sedimentary rocks are overlapped by Late Ordovician and Silurian sandstones of orogenic provenance. This is consistent with a Laurentian origin and mid-Ordovician collision (see Thomas & Astini 2003). However, this scenario was disputed by Aceñolaza *et al.* (2002), who favoured an origin from the Antarctic–South African region of the Gondwana margin itself, an alternative theory that is consistent with the absence of a Grenvillian detrital zircon signature in Cambrian sandstones from the Precordillera (Finney *et al.* 2005). Collision of a further terrane ('Chilenia'; Fig. 1) to the west of the Argentine Precordillera was also inferred by Ramos (1988), principally on the basis of Devonian granite magmatism in the Sierras Pampeanas to the east. In southernmost South America there is very little direct evidence for Palaeozoic orogenesis; the principal deformation and metamorphism registered is of much later age. On the southern edge of the Rio de la Plata craton, the Sierra de la Ventana (Fig. 1) is composed of a sequence of Cambrian(?) to Permian quartz-rich sediments and turbidites (Limarino *et al.* 1999). Some of the folding appears to be of Permian age, but there is also a significant unconformity or structural break in the Mid-Carboniferous (von Gosen *et al.* 1991). Together with the Cape Fold Belt of South Africa (Fig. 1) and the Ellsworth–Whitmore Mountains of West Antarctica, this 'Gondwana fold belt system' seems to represent a passive margin during the Early Palaeozoic, with the accumulation of predominantly reworked continental sedimentary deposits (the 'Samfrau Geosyncline' of Du Toit 1937), and the elements have been grouped into the final stage of the Terra Australis orogen by Cawood (2005) (Fig. 1). The cause of that deformation has long been a mystery. One school of thought favours a far-field effect of subduction at the southern Gondwana margin (Lock 1980; Johnston 2000), although this lay some 1500 km away beyond the landmasses of Patagonia (Fig. 1) and the Antarctic Peninsula. The alternative view is of a Carboniferous collision of such landmasses during ocean closure, albeit with different ideas about the details of the timing, direction of subduction and location of the sutures, and without any evidence of obducted oceanic crust (Ramos 1984, 2004, 2008*b*; Pankhurst *et al.* 2006). The accretionary orogen model of Cawood (2005) may offer a form of compromise between these alternative types of model.

In many of the outer areas, accretion and intense granitic–rhyolitic magmatism continued during the Late Palaeozoic; for example, the New England orogen in Eastern Australia, southern Patagonia and (possibly) Chilenia in the South American–South African sectors, and the Western Province and Median Batholith terranes of New Zealand. The immense rhyolitic large igneous province of southern South America represents a Permo-Triassic switch to extensional tectonics and the establishment of the Andean subduction margin, interpreted by Pankhurst *et al.* (2006) as a response to post-collisional slab 'tear-off'. Elsewhere at this time the margin largely became passive, with terrane accretion continuing in New Zealand, which finally rifted off from the West Antarctic sector of the margin during the break-up of Gondwana in Cretaceous times.

This extended abstract is partly based on a *Gondwana Research* Focus Paper (Vaughan & Pankhurst 2008), to which the reader is referred for more extensive information and bibliography. We are grateful to M. Bassett for the opportunity to contribute to the present volume.

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Enigmatic fossils from the Upper Silurian of Bolivia: evidence for marine productivity in high-latitude Gondwana

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Abstract: Specimens collected recently from the Las Carmelitas facies of the Kirusillas Formation exposed in the Cochabamba area, Bolivia and dated as Ludlow (Late Silurian) by graptolites, show bedding surfaces almost completely covered by coalified compressions and impressions. The majority comprise mixtures of fragmented amorphous, unidentifiable material ('debris'), but some horizons are dominated by well-defined morphological entities with a particular type or combination of types confined to a particular layer. In all, five morphotypes have been circumscribed, but their affinities, based on a comprehensive review of the possibilities, remain conjectural. Algal affinities are suggested tentatively for abundant, unbranched, narrow, strap-shaped fossils lacking any further diagnostic features and the numerous coalified discs or three-dimensionally preserved spheres (?leiosphaerid acritarchs) occurring isolated in the matrix or, less often, in clusters. Following a discussion on the recognition of faecal pellets in the fossil record, it is postulated that elliptical, spiral or simply segmented structures may be the excreta of planktonic or benthic metazoans, although the latter seems less likely in view of the proposed anoxic depositional environment of the shales that lack any bioturbation. Such coalified remains, whether from primary producers or grazers, indicate high productivity at high palaeolatitudes in the late Silurian continental seas in this region of peri-Gondwana.

Assemblages from Bolivia provide the best evidence to date for Silurian land vegetation at high latitudes on Gondwana. Probable Ludlow examples from the Kirusillas Formation exposed at Sella in theTarija area of southern Bolivia (Figs 1 & 2) include taxa (e.g. *Cooksonia*) at a similar grade of organization to those found in coeval strata of Laurussia (Edwards *et al.* 2001), but a more reliably dated and far more diverse Ludlow assemblage (Toro *et al.* 1996) from the more northerly Cochabamba region of central Bolivia is reported to include taxa such as *Rhynia*, *Zosterophyllum* and *Drepanophycus* that occur much later at lower palaeolatitudes. Such a discrepancy in this latter report demanded further investigation and, as part of a collaborative multidisciplinary venture between palaeobotanists and sedimentologists from La Plata, Argentina and Cardiff, UK, new collections of both plant and animal fossils were made at a number of localities to the east of Cochabamba. A major objective of the project was not only to relate the organisms to depositional environments but also to reconstruct communities in (potentially stressed) habitats associated with high latitudes. Coalified axial fossils that could be assigned unequivocally to land plants were found at only one locality in this new area and are extremely fragmentary and sterile. However, at a number of localities in the Ludlow age Carmelitas Facies, bedding surfaces are sometimes almost completely covered by minute thread-like strands, spheres, comminuted debris, and coalified compressions with consistent, but frequently unfamiliar, morphology. Much greater attention has been paid to such morphologies in the Precambrian than in younger rocks (e.g. Butterfield *et al.* 1988; Hofmann 1994), although undoubtedly some of the organisms must have persisted into the Phanerozoic, and may well be present in the Silurian, albeit as members of far more complex ecosystems. Such similarities are

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Fig. 1. Outline locality map of localities in south and central Bolivia from which collections discussed in this paper were obtained.

explored further here as part of a more comprehensive investigation of the entire assemblage.

Stratigraphy, facies and material

All material discussed and described here is from Cochabamba Province in Central Bolivia, and specifically from sections some 15–20 km SE of the town of Cochabamba closely adjacent to both sides of the main road leading eventually to Santa Cruz (Fig. 1).

The regional context and facies relationships of Ordovician–Silurian sequences in the Cochabamba area have been reviewed extensively by various researchers in recent years (e.g. Díaz-Martinez & Grahn 2007) and need not be repeated here. Suffice it to say that, in the context of this paper, there is abundant evidence of glaciogenic-related sedimentation through upper Ordovician to mid-Silurian sequences across the whole region, with implications for cool-water, temperate deposition along the active western margin of Gondwana.

We are currently revising the facies evolution of parts of these sequences, across the Cancañiri, Kirusillas and Tarabucco lithological successions in the region. In the upper part of the Kirusillas Formation, there is a distinctive unit of ‘black shale’ argillites that we refer to here informally as the Carmelitas Facies. This is the unit from which Toro *et al.* (1996) recorded Silurian vascular

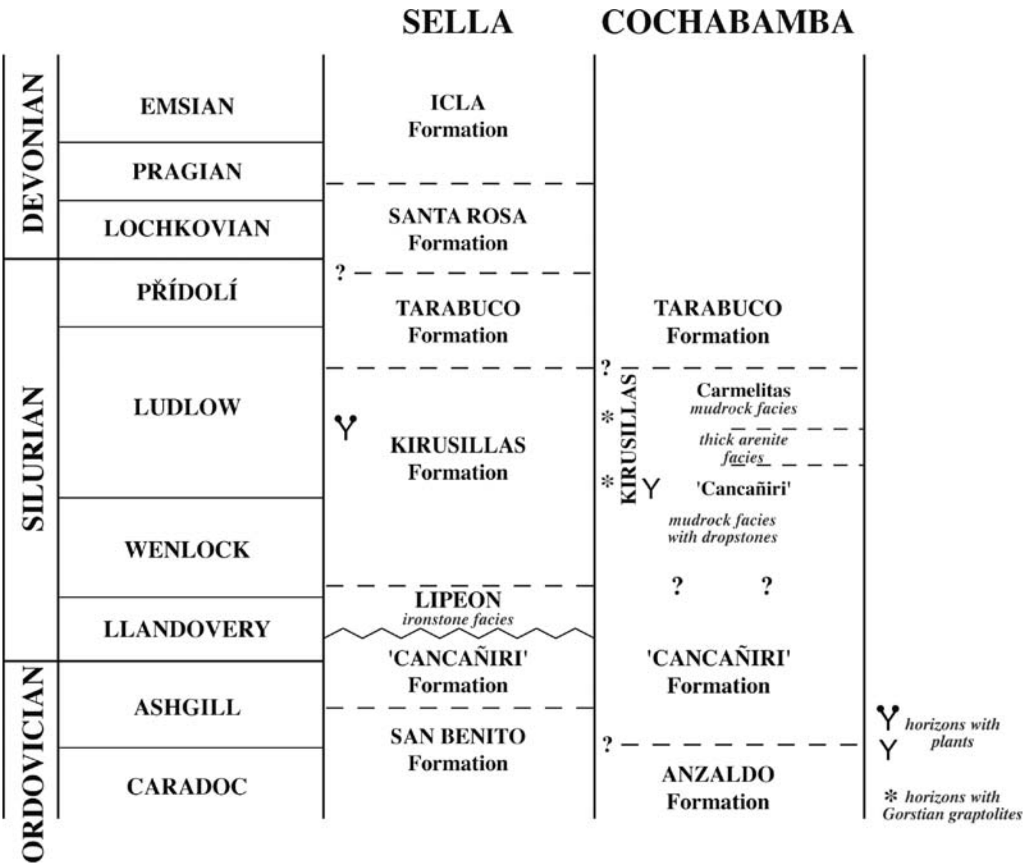

Fig. 2. Stratigraphical successions in the Sella (Tarija) and Cochabamba regions.

plants dated by graptolites as being of late Wenlock–early Ludlow age. The Toro locality was along the old railway track from Mayka Pampa, and high in the valley side above the aqueduct at 17°30′098″S, 066°05′098″W at an altitude of 2741 m; the beds dip at 20° from a strike of N210°. As noted below, we have been unable to examine the original Toro *et al.* material, although we have made comparable collections.

In this paper, we concentrate on a locality in the Carmelitas Facies above the opposite side of the main road in a small, terraced shallow roadside quarry at 17°30′098″S, 66°05′168″W. This is one of the localities from where Maletz *et al.* (2002, p. 330, locality 13) described the early Ludlow graptolite *Saetograptus argentinus*, and confirmed by us via our new specimens. Cuerda (1974) and Cramer *et al.* (1974) also reported Ludlow age graptolites, and chitinozoans and acritarchs, respectively, from this locality.

At Las Carmelitas the beds comprise mainly very fine mudrocks that weather to a mid-grey to whitish colour, but that are dark grey to black in fresh section. Bedding is very thinly laminar, with sub-millimetre lamination within beds and almost no sign of sedimentary structures. X-ray diffraction (XRD) analysis of the sediments indicates an average composition of 37% muscovite, 32% kaolinite, 24% quartz and 7% pyrophillite. The facies are indicative of very low-energy environments with restricted circulation. Trace fossils include *Chondrites* and small ?*Planolites*.

The fossils consist of thin sporadic layers of particulate coalified material covering more darkly stained grey, or very rarely pink rock. A similar colouring is seen on impressions. They encompass a number of well-defined morphologies, frequently crowded on bedding planes. The morphologies vary between layers, with one particular type or combination of types confined to a particular layer (Fig. 3a). In addition, numerous coalified disc-like circular structures are dispersed in the matrix (Fig. 3e), and three-dimensionally preserved spheres of similar size occur isolated in the matrix or

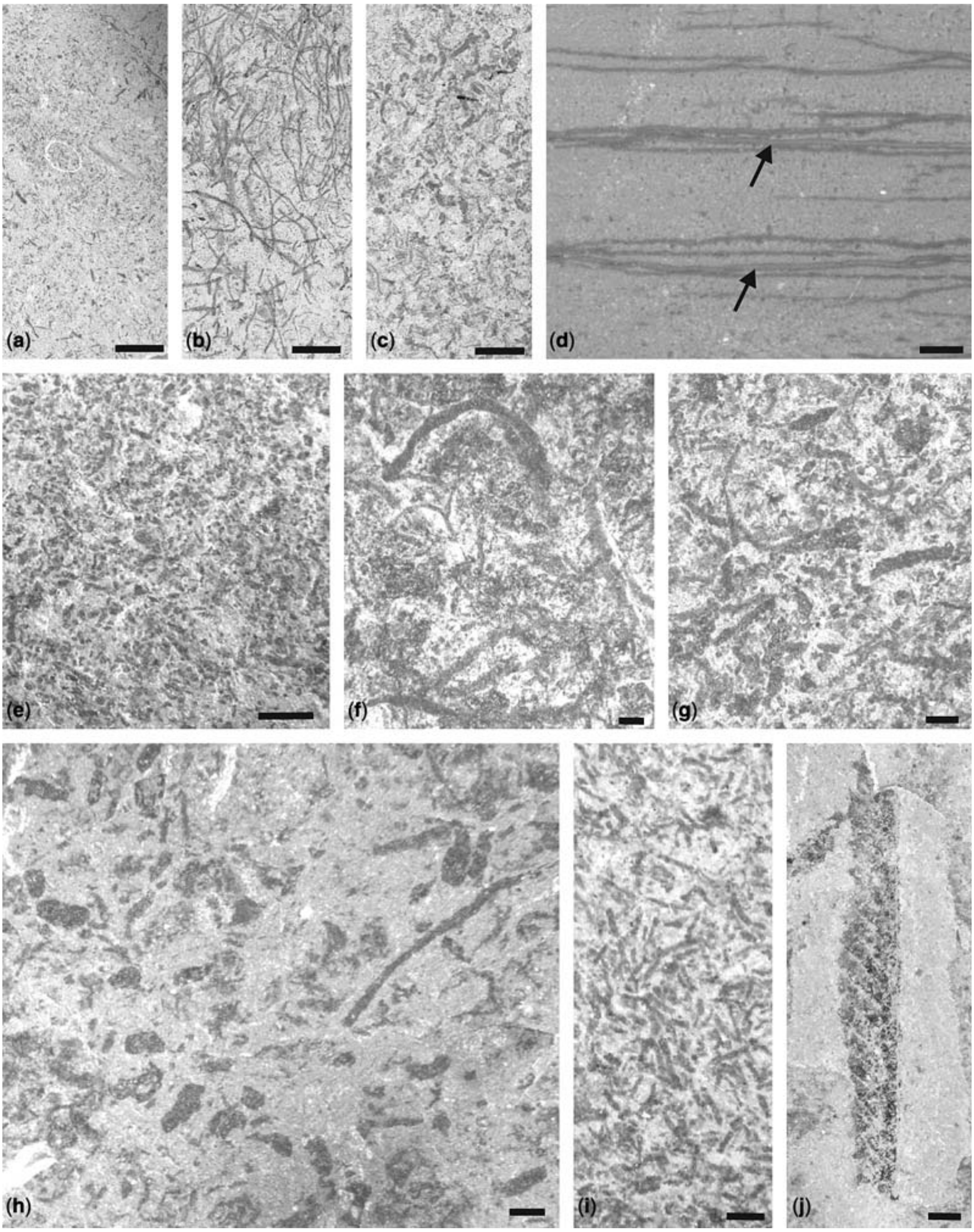

Fig. 3. Ludlow Las Carmelitas Formation, near Cochabamba, Bolivia. (**a**–**c**) Three bedding surfaces from same specimen demonstrating distinctive nature of assemblages separated by millimetres of matrix. NMW2007.26G.1i–iii. Scale bars 5 mm. (**d**) Vertical section showing layers of coalified material corresponding to bedding plane assemblages. Arrows indicate splitting within coalified layers. NMW2007.26G.2. Scale bar 1 mm. (**e**) Heterogeneous coalified material with fragmentary threads and some spheres. NMW2007.26G.3a. Scale bar 1 mm. (**f**) Heterogeneous comminuted coalified material associated with wider forms of morphotype 1. NMW2007.26G.4i. Scale bar 1 mm. (**g**, **h**) Heterogeneous material including some morphotypes. (g) NMW2007.26G.5i. Scale bar 1 mm. (h) NMW2007.26G.6i. Scale bar 1 mm. (**i**) Abundant short lengths of narrow forms of morphotype 1; different bedding surface to top of image comprises heterogeneous unidentifiable material. NMW2007.26G.7. Scale bar 1 mm. (**j**) The graptolite *Saetograptus argentinus* exposed in rock just below bedding surface covered with spheres and unidentifiable fragments. NMW2007.26G.3b. Scale bar 1 mm.

in clusters. Such spheres may be filled with very fine-grained sediment or mineral.

Illustrated specimens are deposited in the National Museum of Wales, Cardiff (NMW).

Techniques

Bedding plane specimens were examined under a Leica MZ16 stereomicroscope and photographed with a Leica DC480 digital camera, and were measured using Leica IM 1000 software. The small size of many of the specimens involved working at the limit of the microscope, and this coupled with irregularity of surfaces made photography difficult. The coalified material was a similar colour to the matrix so the only way to highlight it was with the use of polarizing filters to enhance contrast, and this resulted in long exposure times. Blocks of typical assemblages were viewed uncoated at low vacuum in an Field Electronics and Ions (FEI) (Philips) XL30 ESEM FEG (environmental scanning electron microscope with field emission gun), at an acceleration voltage of 20 kV using both gaseous secondary electron (GSE) and back-scatter electron (BSE) detectors. The BSE detector failed to image the ubiquitous, but obviously very thin films apparent in light microscopy (LM), making location finding a problem in the SEM, but carbon was sometimes detected in the walls of the three-dimensionally preserved spheres. Smaller blocks were mounted on stubs using sticky C tabs and examined uncoated at high vacuum using the secondary electron detector (SE). With the exception of certain sphaeromorphs, the coalified fossils were remarkable in that they exhibited almost no relief.

An Inca Energy X-ray microanalysis system was employed to analyse elements in the matrix, coalified fossils and sphaeromorphs.

Film pulls were prepared by applying successive layers of a solution of cellulose nitrate dissolved in amyl acetate. Following light microscopy these were examined by SEM, but neither procedure revealed any anatomical detail.

Conventional palynological techniques involving hydrofluoric acid yielded small quantities of amorphous coalified residues and rare poorly preserved palynomorphs. The latter were examined by LM and residues scanned using SEM.

Palaeoecological considerations

In situations where assemblages are composed of readily identified organisms the latter can be used in palaeoecological reconstructions. In contrast, in the situation encountered here the nature and affinities of the various coalified remains, be they representative of organisms or even their excreta (e.g. benthic, planktic, etc.), remain conjectural and hence clues to original life styles might be found through deliberations on the nature of the depositional environment; for example, on the amount of oxygen present and, most particularly, water depth related to onshore–offshore gradients.

Depositional environments

Oxygen levels. Although the mudrocks are now weathered to a light greyish white or less typically pink colour, in fresh samples they are typically black, very finely laminated argillites, with the inference that they were deposited in anoxic or dysoxic conditions. Fine lamination in the sediments relating to varying amounts of organic material shows almost no disturbance from bioturbation (Fig. 3d), although this cannot be taken automatically as evidence for no oxygen. Marine benthic communities of detrital feeders (polychaetes, echiuroids and members of minor phyla) that flourish in dysoxic conditions produce numerous very small-scale shallow burrows in fine-grained sediments, but their activities are not visible after compaction (Cuomo & Bartholomew 1991). The presence of well-preserved, discrete coalified morphotypes might suggest preservation *in situ*, as seen in colonization of the benthic realm, in that transport and descent through the water column prior to burial might be anticipated to have produced some degradation. This would have been retarded in cold water, as inferred from high palaeolatitude, although the descent itself could have been protracted by viscosity effects. Moreover, there is no evidence of a shelly benthic fauna. Indeed, the only macrofossils present are planktic graptolites, epiplanktic bivalves and nektic hyoliths, nautiloids and trace fossils. The totality of evidence thus suggests that the sea floor was probably anoxic and inhospitable for aerobic organisms.

Water depth. Graptolites from throughout the section of the Carmelitas facies generally indicate that the sediments were deposited some distance from the coast, although actual water depth is equivocal. Substantial thick mudrocks and arenite facies with shallow-water depositional structures occur below the Carmelitas facies; any subsequent deepening may relate to rises in sea level following deglaciation, there being no evidence for contemporaneous tectonic activity in the area. Indeed, the fact that organic remains have actually reached the sea floor and not been recycled en route could also indicate fairly shallow water (Bishop *et al.* 1977). Should some of the morphotypes be macroalgae, the high quality of preservation would again indicate either an autochthonous origin and hence, if benthic, within the photic zone in a low-energy environment lacking effects of wave action or, if allochthonous, would indicate relatively shallow seas or rapid transport, thus accounting for good preservation of planktonic fossils lacking resilient structural biopolymers. However, overall sedimentology suggests low-energy–low-oxygen environments, which are more usually associated with deeper water. The latter is supported further by the paucity of terrestrially derived palynomorphs in an environment that might be anticipated to enhance fossilization. On the other hand, low-diversity assemblages comprising large numbers of spheroids in the fossiliferous horizons are thought to characterize blooms in near-shore shallow waters in the Precambrian (Vidal & Knoll 1983).

Cramer *et al.* (1974) listed an assemblage of acritarchs probably from the same locality, but not from the beds with the 'mega fossils', which was assigned to the *Neoveryhachium carminae* facies (Cramer 1971). This is a temperate (i.e. cool-water) shelf facies common in the Silurian of North Africa, Arabia and South America. The overall composition of the acritarchs suggests an offshore assemblage, although the material could have been swept over the shallow shelves into deeper water.

Recognition of faecal pellets

Where it is impossible to relate the various morphotypes circumscribed here to known coeval animals and plants, consideration must be given to the possibility that these compressed coalified discrete shapes are not body fossils but coprolites or faecal pellets, the latter term being applied to structures up to 1 cm long (Robbins *et al.* 1996). Several morphotypes fall into this scenario and hence some general issues are debated here before discussion of types. Robbins *et al.* listed four criteria of relevance to the recognition of fossil faeces: morphology, content, chemistry and context. Producers might be crustaceans or extinct arthropods, zooplankton, larvae or fish, and form a starting point in seeking the producers by considering size (Brodie & Kemp 1995) and shape of extant representatives (Fig. 4). In considering the trophic level between primary producers and first-stage carnivores, the majority of herbivores in the planktic realm are small; for example, protozoans and larvae of microcrustaceans, with the dominant copepods producing the largest (ellipsoidal) faecal pellets (<600 μm). Gelatinous zooplankton such as pteropods (<6 mm) and tunicates produce larger faeces with often distinctive shapes. Small clupeoid pelagic fish (e.g. anchovies), and presumably juveniles, are nektic herbivores feeding on phytoplankton and produce either discrete ellipsoidal pellets (e.g. anchovies <2 mm × 1 mm) or faecal ribbons. Discreteness in shape might result from the presence of a peritrophic membrane, sometimes extending beyond the contents. In terms of content, siliceous (e.g. diatoms), calcareous (coccoliths) or organic-walled (dinoflagellate) plankton may be recognizable entities in post-Palaeozoic forms and can also be detected by chemical analyses. In the Recent, for non-skeletonized phytoplankton, residual colour (green or brown) provides evidence based on pigments. Such analyses can be extended into sub-fossil and fossil forms, but for the latter more simple elemental analysis may be more feasible. Thus, for example, in extant forms the ratio of N and P to C is greater in faecal pellets than in body tissues (Porter & Robbins 1981) and this might be useful in their detection. However, N is unlikely to be recorded in such ancient fossils and we lack control from body fossils. Abundance of Al (and sometimes K and Mg) may point to a benthic detritus feeder, although sediment is better detected in three-dimensionally preserved pellets than in compressed examples (Cuomo & Rhoads 1987; Cuomo & Bartholomew 1991; Brodie & Kemp 1995). However, transported pellets collected on the sea floor in coastal waters may also contain a high proportion of mineral material (Dunbar & Berger 1981). Most work on marine faecal pellets has centred on copepods (Honjo & Roman 1978), which are first recorded in the Cretaceous Dichekleshiidae (Briggs *et al.* 1993) and relatively recent phyto- and zooplankton; for example, diatoms, coccolithophores and dinoflagellates, groups that have no representatives in the Silurian, an exception being the dinoflagellate *Arpylorus* (Late Silurian, Ludlow; Sargeant 1978). The broad composition of benthic assemblages (e.g. annelids, gastropods, echiuroids) has changed relatively little since the Silurian, but the period saw major increases in radiation of animals into the planktic zone (Rigby & Milson 1996), although crustaceans were not included among the zooplankton by Rigby (1997).

Descriptions of coalified material

Where bedding planes are characterized by an abundance of organic material, they may be dominated by one of five morphological forms, although others may also occur sporadically. Such morphotypes were collected preferentially. Other bedding surfaces revealed jumbled associations of a wide range of types that varied in quality and extent of preservation and in coverage of the surface (Fig. 3a–c, e–i). In some cases density was so high that it was difficult to discern outlines of individuals; more widely spaced examples proved easier to quantify. In the same hand specimen,

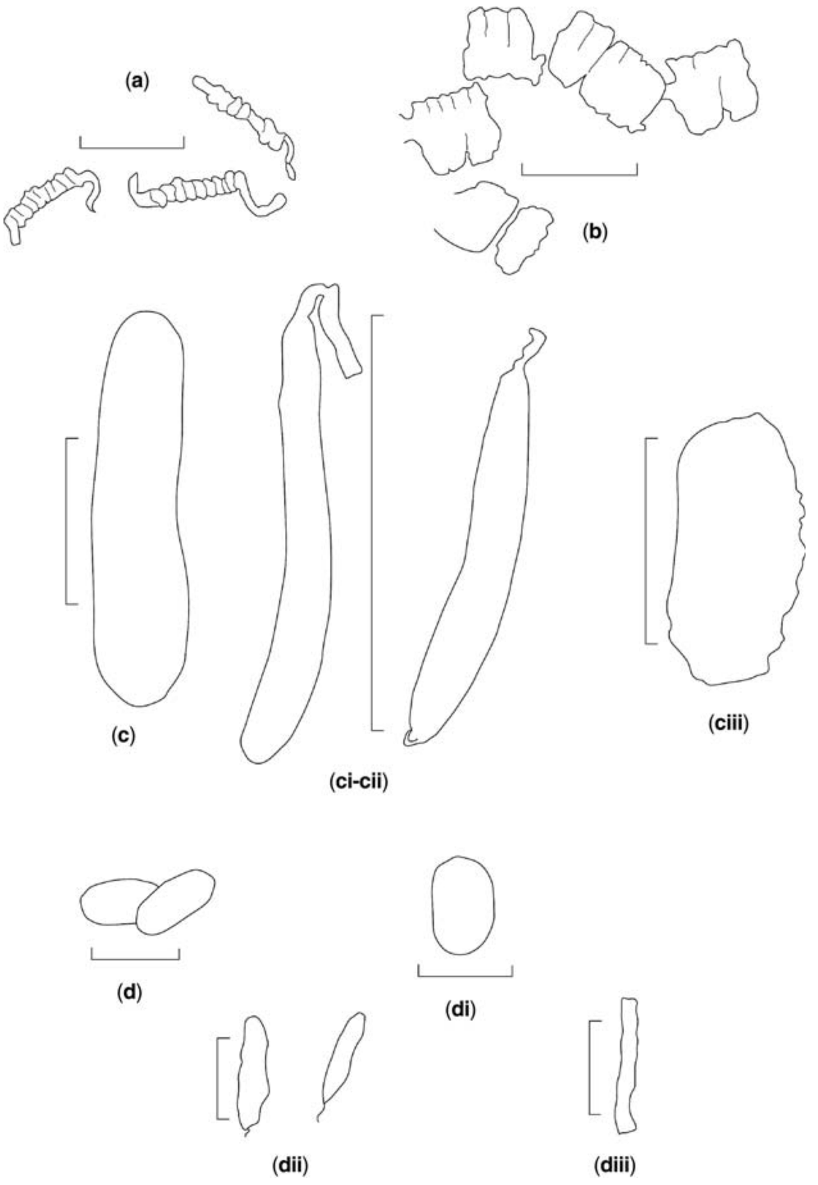

Fig. 4. Outlines of shapes of faecal pellets of extant planktonic crustaceans and benthic invertebrates; (**a**, **b**) from Bruland & Silver (1981); (**c**, **ci**, **cii**, **ciii**) from Honjo & Roman (1978); (**d**, **di**, **dii**, **diii**) from Martens (1978). (a) *Corolla spectabilis* (pteropod). Scale bar 2 mm. (b) *Salpa fusiformis* (salp). Scale bar 5 mm. (c) *Acartia tonsa* (copepod). Scale bar 0.1 mm. (ci, cii) *Calanus finmarchicus* (copepod). Scale bar 0.5 mm. (ciii) Unknown origin. Scale bar 0.1 mm. (d) Maldanid, *Rhodine* sp. (polychaete). Scale bar 0.75 mm. (di) *Syndosmia alba* (bivalve). Scale bar 0.5 mm. (dii) *Centropages hamatus* (copepod). Scale bar 0.1 mm. (diii) *Meganyctiphanes norvegica* (krill). Scale bar 0.1 mm.

changes in composition and quality of preservation are apparent at millimetre-scale vertical separation (Fig. 3a–c), with the intervening matrix commonly characterized by flecks of coalified material identified as palynomorphs (?acritarchs).

Morphotype 1: threads and ribbons (Figs 5 & 6; Table 1)

This morphotype comprises slender unbranched elongate structures of more or less uniform

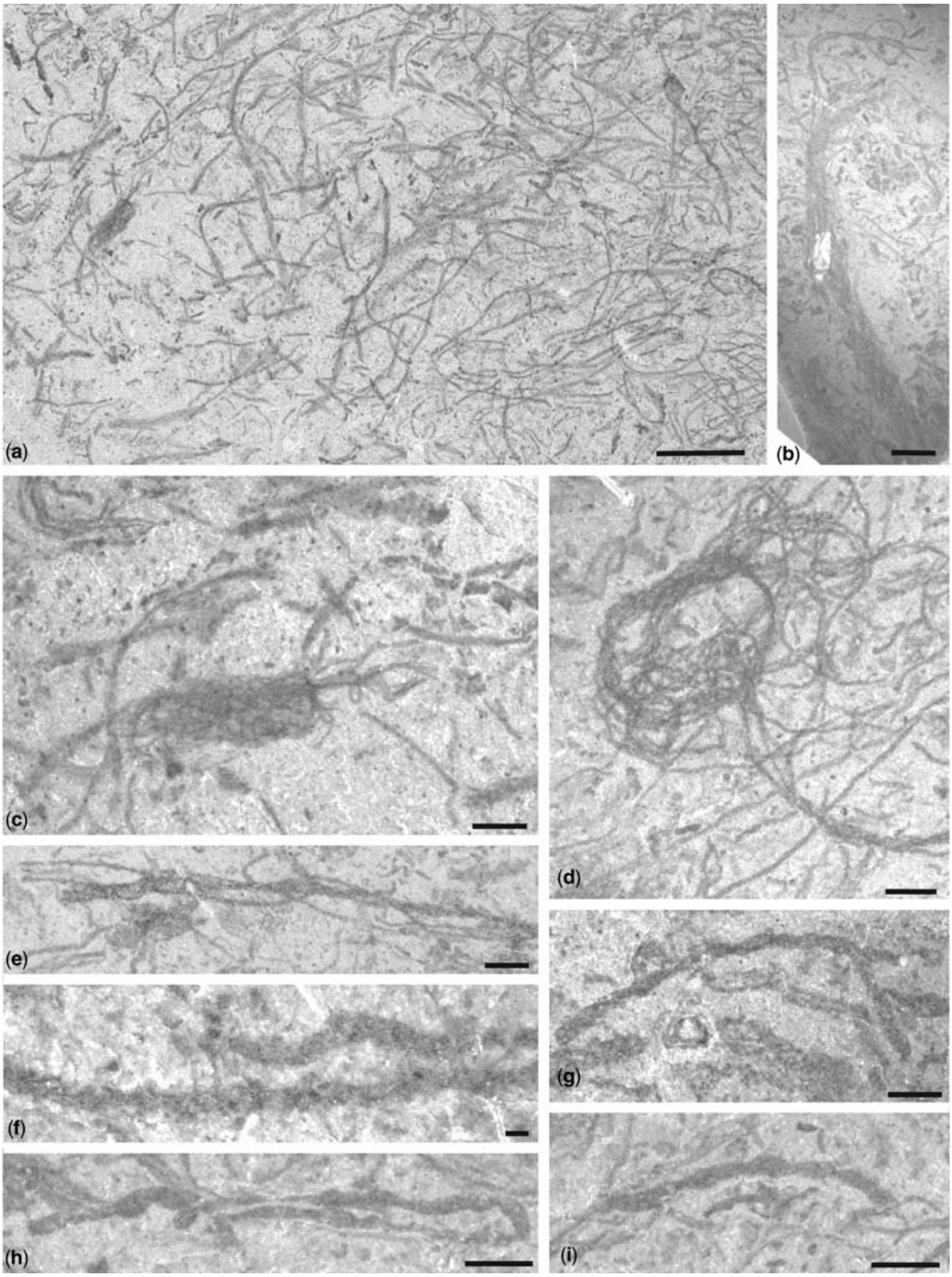

Fig. 5. Las Carmelitas Formation, morphotype 1: threads and ribbons. (**a**) Bedding surface covered by predominantly narrow threads. Black specks here and in other specimens can often be resolved as sphaeromorphs (morphotype 5). NMW2007.26G.1iv. Scale bar 5 mm. (**b**) Numerous aligned and intertwined threads. The characteristic darkening of the matrix towards the edge of the rock should be noted. NMW2007.26G.8. Scale bar 5 mm. (**c**) Part of (a) enlarged showing aggregations of entangled threads. Scale bar 1 mm. (**d**) Entwining and coiling of threads. NMW2007.26G.9i. Scale bar 1 mm. (**e**) Alignment of threads with some loss of identity. NMW2007.26G.10i. Scale bar 1 mm. (**f**) Enlarged typical narrow thread revealing irregular ‘fuzzy’ margin, dark background and sporadic granular coaly material. NMW2007.26G.10ii. Scale bar 1 mm. (**g**–**i**) Wider examples with irregular sometimes lobed, undulating margins. (g) NMW2007.26G.11; (h, i) NMW2007.26G.9ii + iii. Scale bars 1 mm.

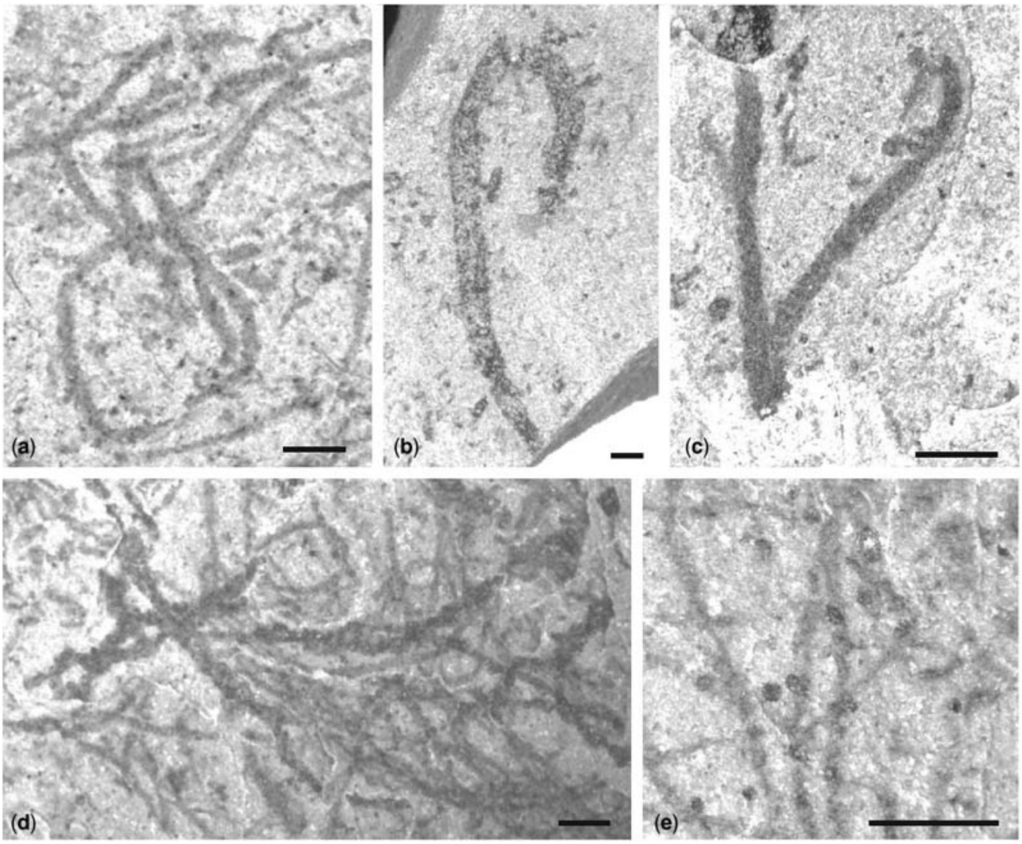

Fig. 6. Las Carmelitas Formation, morphotype 1 (continued): threads and ribbons. (**a**) NMW2007.26G.12. Scale bar 1 mm. (**b**, **c**) Isolated ribbon-shaped structures. (b) NMW2007.26G.13b. Scale bar 1 mm. (c) NMW2007.26G.14. Scale bar 1 mm. (**d**) Threads with very irregular margin possibly comprising small sphaeromorphs. NMW2007.26G.1v. Scale bar 1 mm. (**e**) Larger sphaeromorphs either adhering to threads or fortuitously superimposed on them during compression. NMW2007.26G.1vi. Scale bar 1 mm.

diameter, ranging between very narrow examples resembling threads (minimum diameter 60 μm) to broader ribbons of more variable width but lower frequency. None show any evidence of transverse septation, and tips are difficult to distinguish from broken ends. Detailed measurements of bedding surfaces failed to reveal any distinct size classes. Values show broad overlapping width ranges, although superficial examination appeared to show concentrations of narrower examples. A typical example is illustrated in Figure 5a and c, where the bedding plane shows abundant elongate structures with a very wide size range, but with the vast majority between 70 and 220 μm, and about 8% between 250 and 410 μm. The wider specimens generally have similar appearance to the narrower ones, and because of gradation the latter are not conspicuously distinct. In contrast, NMW2007.26G.4 has 10 examples ranging from 360 to 750 μm ($\bar{x} = 466$), distinct from the very short lengths of threads associated with numerous discs and less well-defined coalified masses that almost completely cover the bedding surface (Fig. 3f).

In Figure 5a the bedding surface is almost completely covered with threads interspersed with rare detritus and numerous small discs (?compressed spheres). There is a hint of alignment, also noted in Figure 5e, where the threads are less frequent but long (<50.4 mm) and straight. In aggregations of long intertwining examples, outlines of single threads may be lost (Fig. 5b, c). Threads may also be curved, bent or coiled around each other (Fig. 5d). The curved examples tend to be the shortest. In most extreme cases, bedding surfaces are covered by minutely comminuted fragments (Fig. 5i). Some specimens show different degrees of fragmentation in successive layers. Narrow threads rarely show well-defined margins (see

Table 1. *Widths of morphotype 1: threads and ribbons (all measurements in µm)*

	Width	Mean	*n*	SD	
NMW2007.26G.1	70–410	172	85	72.36	
NMW2007.26G.4	360–720	466	10	115.97	
NMW2007.26G.8	140–410	261	15	94.18	
NMW2007.26G.9	60–300	140	26	62.00	Maximum length = 1738
NMW2007.26G.10	90–310	153	20	46.69	Maximum length = 5036
NMW2007.26G.11	140–520	282	38	99.45	
NMW2007.26G.12	170–370	251	15	57.05	Maximum length = 4062
NMW2007.26G.13	710, 740	725	2	21.21	
NMW2007.26G.14	250–400	310	4	66.83	
NMW2007.26G.21	180–410	248	24	52.17	
NMW2007.26G.25	240–570	438	8	99.53	
NMW2007.26G.26	80–250	143	40	38.61	Broken up
All	60–740	217	287	116.09	

Figs 5f & 6a) and because of irregular distribution of coalified material sometimes appear beaded, particularly at the upper end of the size range (Fig. 6d). Well-defined spheres appear sometimes aligned in the threads, but may well be superimposed (Fig. 6e). Abundant small coalified discs are present in the matrix.

Broader 'ribbons' (250–740 µm) may be scattered amongst coalified material (Fig. 3f), but rarely in similar abundance to the threads. They sometimes occur in isolation on bedding surfaces more or less devoid of other remains (e.g. Fig. 6b, c). These fall into a more limited size range, but the broadest examples (Table 1) tend to be much shorter, sometimes characterized by a less regular outline (Fig. 5g–i) and occasionally 'containing' circular structures. The latter are, again, perhaps superimposed. In contrast, the more conspicuous isolated examples comprise a uniform band of coalified material (Fig. 6b, c).

Affinities. In gross morphology, the morphotype threads resemble sulphur bacteria, filamentous algae (e.g. Ulotrichaceae) or cyanobacterial sheaths (e.g. Oscillatoriaceae), with diameters exceeding those of all groups although approaching those of the eukaryotic green algae. Unusually large sizes in the Precambrian have been attributed to 'megascopic (morphological) replicates of microscopic organisms' for example from filament to ribbon in aggregations of cyanobacterial strands (e.g. *Trichodesmium* colonies, Capone *et al.* 1997; *Nematonostoc*, Walter *et al.* 1976), and although they could have been produced by eukaryotic metaphytes, the possibility of cell gigantism in cyanobacteria has also been aired (Peat *et al.* 1978; Hofmann 1994, p. 354). The absence of any evidence for either cellular differentiation or branching further precludes unequivocal identity with green algae. *Ulva sensu lato*, with ribbon-like *Enteromorpha* morphology that falls into the size range of wider examples here, can be free floating, but is abundant in saline water only in estuaries and coastal bays, and is considered unlikely to have been transported in such abundance. The extant brown alga *Chorda* is also morphologically similar. We know of no comparable fossils in mid-Palaeozoic or later rocks, but there are similarities to often abundant coalified remains recorded from the Proterozoic and early Cambrian. Thus, should they have been found in the older rocks, they might well have been assigned to *Vendotaenia*, strap-shaped structures <2 mm diameter with fibrous resilient walls showing a particular longitudinal 'microstructure' (Hofmann & Aitken 1979). *Vendotaenia* has been considered variously as a giant cyanobacterium, the sheath of a large sulphur-oxidizing bacterium (Vidal 1989) or an alga, which Gnilovskaya (1979) related to the brown algae. Walter *et al.* (1976) described four types of ribbon-like compression fossils in finely laminated grey shale from the 1.3 Ma Belt Supergroup as megascopic algae. Similar to the narrower forms described here, they are long, narrow, entangled unbranched ribbons (0.1–2.0 mm wide, the majority *c.* 1.3 mm) up to 125 mm long and named *Proterotainia montana* and *P. neihartensis*. Walter *et al.* (1976) compared them with the brown algae *Chorda* and *Scytosiphon*, the red alga *Nemalion* and the green alga *Enteromorpha*, but as in the case of these Silurian examples were unable to decide on affinity. Broad unbranched ribbons were also present, as were loosely and tightly coiled ribbons (0.25–0.75 mm diameter, 13–44 mm long) assigned to *Grypania*. *G. spiralis* (0.7–1.1 mm wide; <90 mm long) from the 2.1 Ga Negaunce Iron Formation, Michigan, was originally considered to be a siphonous alga, and coiling was considered to be either an original feature of the possibly attached green alga or a response to certain environmental conditions (Han & Runnegar 1992). Samuelsson & Butterfield (2001) doubted Han & Runnegar's identification of the specimen as a *Grypania* and hence as a eukaryote, postulating that the wide ribbons might indicate a collection of aligned filaments as Vidal (1989) had suggested for the sulphur-oxidizing bacterium *Thioploca*. However, they illustrated a number of loosely aligned, coiled and tangled filaments (cyanobacteria *Polytrichoides* and *Siphonophycus*) that are remarkably similar to examples of morphotype 1, but are much narrower (<8 μm diameter).

A wide variety of slender thread to ribbon-like coalified structures, interpreted as algae and placed in at least nine genera including *Vendotaenia* (e.g. Xu 2001*a*, *b*, 2002), have been recorded in the Early Cambrian Chengjiang biota, Yunnan, China. More recently, Steiner *et al.* (2005) reinterpreted all but two in this organic hash as coprolites. *Synocylindraena yunnanensis* (0.3 mm wide, <20 mm long: Chen & Erdtmann 1991) resembles the smooth, uniformly wide unbranched Silurian threads from Bolivia described here. Rejected as too large for an oscillatoriacean (Hou *et al.* 2004), it was compared more favourably with the brown alga *Chorda*. Elongate coalified structures considered as faecal strings or ribbons sometimes contained discrete structures interpreted as sediment pellets; for example, the loosely but regularly coiled *Megaspirella houi* (Chen & Erdtmann 1991) <4.8 mm long, gross diameter 3 mm, thread (500 μm), whereas the very tightly coiled *Fuxianospira gyrate* (<1.2 mm wide) has a beaded appearance. Relief, lack of branching and holdfasts, and solitary occurrences were cited as further faecal characteristics, although Steiner *et al.* (2005) did not completely eliminate the possibility of degraded algae. Similar uncertainties emerge in our considerations on affinities. String-like structures (100–250 μm diameter and several centimetres long) containing spheroidal acritarchs were isolated from Middle Cambrian clastic rocks by Butterfield & Nicholas (1996). These were identified as coprolites with contents enclosed in a peritrophic membrane. Their illustrated example has an irregular, slightly lobed outline with a hint of spiralling somewhat similar to a number of the Carmelitas examples (Fig. 7) and also the Chengjiang biota.

The production of the very finely comminuted forms (Fig. 3i) is less easy to explain. There is certainly no evidence of high-energy activity in the depositional environment. This leads to the possibility of decay into smaller lengths of cells in the water column, and hence possibly indicates original segmentation.

If indeed these morphotypes represent photosynthetic organisms, their abundance is suggestive of blooms in the photic zone, which then drifted to the bottom and became entangled or fragmented in the process.

Cyanobacterial blooms occur in marine habitats in the modern tropics, where they are probably stimulated by more eutrophic conditions. They are more rare at higher latitudes, although blooms of *Phormidium* have been recorded in Antarctic lakes (Fritsch 1959).

The abundance of seemingly intact entangled or intertwined specimens at certain horizons in the Carmelitas strata is, however, suggestive of benthic microbial mats (e.g. Samuelsson & Butterfield 2001, fig. 6), which are common in muddy habitats. Such possibilities reduce the value of algae as depth indicators, particularly as there are records of extant (e.g. *Sargassum*; Schoener & Rowe 1970) algae and seagrasses (e.g. *Thalassi*; Menzies *et al.* 1967) on the floor of the deep ocean (Wiebe *et al.* 1976).

In terms of likelihood of fossilization, the cyanobacterial sheath would seem to have greater potential, although the proposed exceptional combination of low temperatures and anoxia may have increased chances of fossilization of cellulose cell walls. Against such a hypothesis is the absence of cross walls in the threads, unless of course the organisms were siphonous (see discussion on *Grypania*).

Morphotype 2: cylindrical lobed structures with extensions (Fig. 7; Table 2)

These are preserved occasionally in heterogeneous assemblages with other morphotypes. The specimens illustrated in Figure 7a show the greatest concentration on any one bedding plane, where they are associated mainly with short lengths of morphotype 1 (narrow threads). Almost all examples are preserved as a sprinkling of coalified material on a grey-stained matrix. They show a range of shapes; most are more or less oblong and have 0.88–1.39 mm maximum width, with lobed or very occasionally straight sides and one or both extremities extended into a strap-shaped region, sometimes curved and with a rounded end. The extensions are usually offset, but occasionally attached centrally. The longest specimen with both extensions is 4.39 mm, but two examples with only one exceed 5 mm. The smallest 'complete' specimen is 3.21 mm. The bases of the lobes (usually 3–8) are 0.34–1.08 mm wide with more or less uniform dimensions in a single specimen. Their number in specimens with two extensions is variable (3–7), but there is no correlation between total length and lobe number. A single specimen (Fig. 7j) detected among more diverse debris is unusual for its small dimensions (maximum length 2.20 mm with one

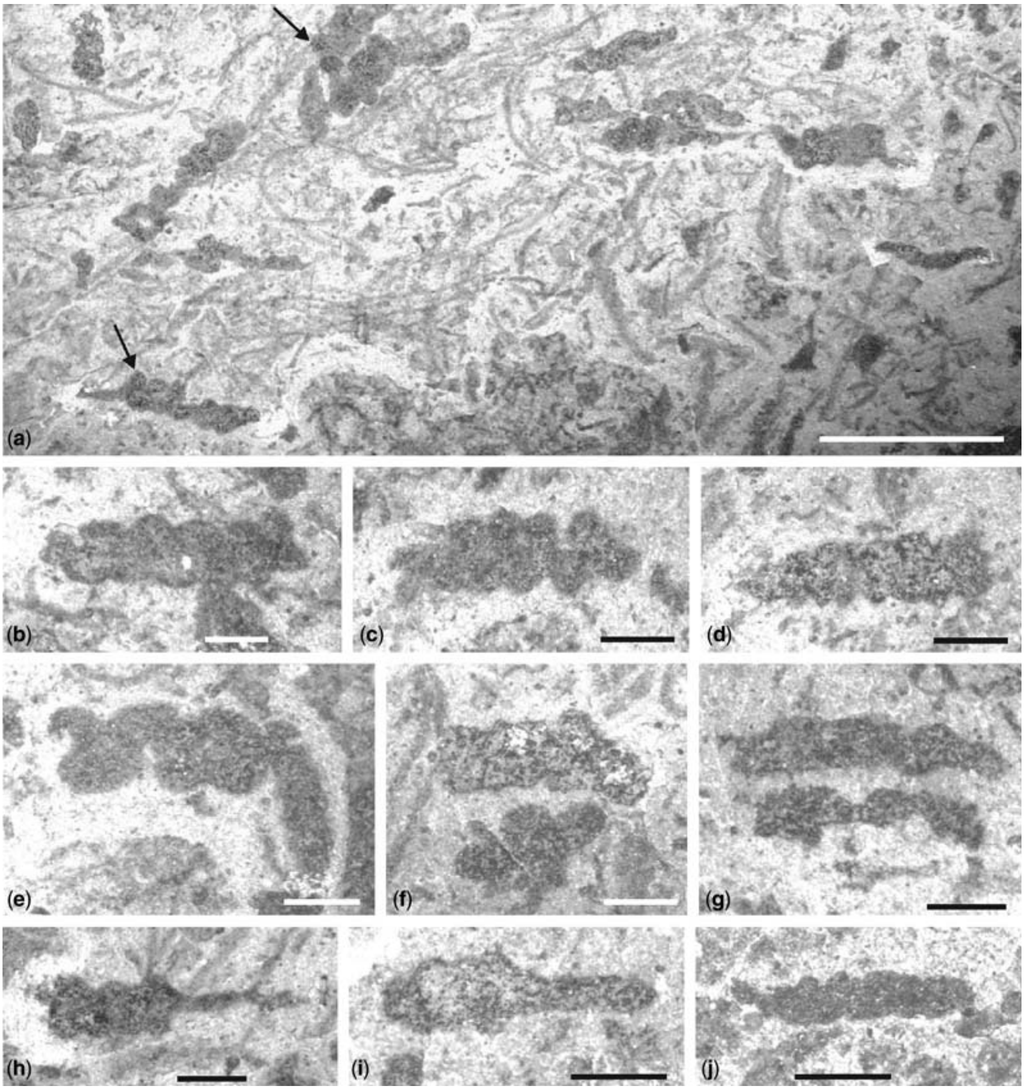

Fig. 7. Las Carmelitas Formation, morphotype 2: cylindrical lobed structures with extensions. (**a**) Bedding plane covered with ?spiralling structures with extensions and thread forms of morphotype 1. Bottom right is at a lower level that lacks morphotype 2. NMW2007.26G.15. Scale bar 5 mm. (**b**–**h**) Further specimens from same bedding surface as illustrated in (a), demonstrating variability within the morphotype. NMW2007.26G.15i–vii. Scale bars 1 mm. (**i**, **j**) Isolated specimens on surface with heterogeneous material. (i) NMW2007.26G.6ii. Scale bar 1 mm. (j) NMW2007.26G.5ii. Scale bar 1 mm.

extension of 0.47 mm, and 0.44 mm wide) and greatest number of lobes (nine).

The marginal lobes are interpreted as indicating a segmented organization with segments usually oriented obliquely to the major axis of symmetry. However, this obliquity plus the 'polar' extensions into a ribbon approximating the diameter of the segments raises the possibility that the morphotype is a compressed coil, the elongate less regular structures representing partial separation of the helix (Fig. 7a). Against such an interpretation is the complete continuity of the compressed coalified material between adjacent segments.

Although examination by light microscopy gives an impression of circular structures within the coaly material, this was not confirmed by SEM or film pulls. Records of large spheres probably reflect fortuitous superimpositioning (arrow in Fig. 7a).

Table 2. *Dimensions of morphotype 2: cylindrical lobed structures with extensions (all measurements in mm)*

	Max. length	Max. width	Extension length	Length between extensions	Range in segment width	Mean width	Range in depth	Mean depth	No. of lobes
NMW2007.26G.5	2.20	0.44	0.47	1.73	0.34–0.49	0.40	0.14–0.22	0.17	9
NMW2007.26G.6	2.69	0.80	1.06	1.63	0.53–0.76	0.69	0.27–0.37	0.31	4
NMW2007.26G.15	2.36	0.88	0.11, 0.3	1.95	0.85–0.86	0.86	0.36–0.37	0.37	2
	4.74	1.35	–	–	0.88–1.35	1.07	0.37–0.55	0.51	7
	5.51	1.13	0.47, 1.5	3.54	0.91–1.17	1.03	0.47–0.76	0.56	5
	5.75	1.99	2.26	3.49	1.53–2.10	1.78	0.64–0.97	0.81	4
	4.39	1.39	1.34, 1.06	1.99	1.32–1.36	1.34	0.64–0.99	0.78	3
	3.98	1.03	0.42, 0.46	3.1	0.76–1.05	0.88	0.28–0.52	0.39	7
	3.93	1.09	0.60, 0.76	2.57	1.02–1.17	1.08	0.53–1.08	0.73	3
	2.75	1.08	0.81	1.94	0.86–1.08	0.92	0.33–0.53	0.48	4
	3.49	1.03	–	3.49	0.81–1.04	0.90	0.35–0.53	0.41	6
	2.79	1.11	–	2.79	0.84–1.10	0.98	0.46–0.50	0.48	5
	3.95	1.19	–	3.95	1.05–1.28	1.12	0.54–0.59	0.56	6
	2.71	1.09	–	2.71	0.90–1.13	0.99	0.45–0.52	0.49	5
	4.31	1.06	–	4.31	0.52–1.05	0.76	0.32–0.50	0.40	8
	3.26	1.24	0.39	2.87	0.75–1.22	1.03	0.47–0.53	0.50	5
	4.11	0.92	0.39, 1.96	1.76	0.85–1.06	0.96	0.33–0.47	0.41	4
	3.3	1.32	–	3.3	1.14–1.33	1.24	0.49–0.69	0.58	4
	3.21	1.29	0.26, 0.64	2.31	0.92–1.36	1.15	0.35–0.46	0.42	5

Affinities of morphotype 2

Algae/cyanobacteria. Coiling and curvature in putative phototrophs has been discussed for morphotype 1 (see above). The same reservations regarding size, particularly in cyanobacteria, apply here (e.g. ?*Obruchevella* sp., diameter *c.* 30 μm; Knoll & Ohta 1988). In much larger Precambrian specimens assigned to *Grypania spiralis* by Han & Runnegar (1992), spiralling is less regular or compact (for further discussion on nature and affinities of *Grypania*, see pp. 186, 187).

Faecal pellets. The polar extensions of the morphotypes show some similarities to the extensions of trophic membranes present around faecal pellets of extant planktonic Crustacea (Honjo & Roman 1978). Segmented pellets characterize those of gelatinous zooplankton (salps or tunicates). (See comments on morphotype 3, below.) However, should the interpretation of the morphotype as a coiled structure be correct, there is a direct morphological comparison with the coiled pellets of an extant pteropod, *Corolla spectabilis*, another member of the gelatinous zooplankton (coils are 0.2 mm in diameter and 6 mm long: Bruland & Silver 1981, fig. 1b), where contents are amorphous, but in living examples coloration (e.g. yellow) indicates a diet of phytoplankton. Pelagic opisthobranchs have a predominantly Mesozoic to Recent fossil record, with the Cylindorbullinidae extending into the Devonian (Benton 1993). Invertebrates with coiled guts (e.g. as in *Vetulicola* in the Chengjiang Biota; Aldridge *et al.* 2007) are an even more speculative and unexplained source.

Morphotype 3, rectangular segmented structures (Fig. 8a–i; Table 3)

Morphotype 3a, impressions or sparingly coalified segmented compressions (Fig. 8a–d; Table 3). A single hand specimen has a bedding surface more or less covered with segmented structures, variously fragmented, with some more irregular fragments and short ribbons. The segmented examples vary in length related to numbers of segments (<12); the latter are of approximately the same size within an entity, but because they are preserved mainly as impressions they are difficult to resolve and hence measure. The structures are more or less parallel-sided but give an illusion of lobing because of the distribution of darker areas, which produce an almost dumb-bell shape in a slightly lighter stained area that in turn remains darker than the matrix (Fig. 8b). They are not bilaterally symmetrical because the segments are very slightly inclined towards the margins. They range in overall length between 1.3 and 4.3 mm, and between 0.4 and 1 mm in width. Segments are *c.* 300 μm long. Some consideration was given to the possibility that these structures were poorly preserved examples of morphotype 2. Indeed, they have a similar maximum length (excluding extensions in morphotype 2), but are generally shorter and

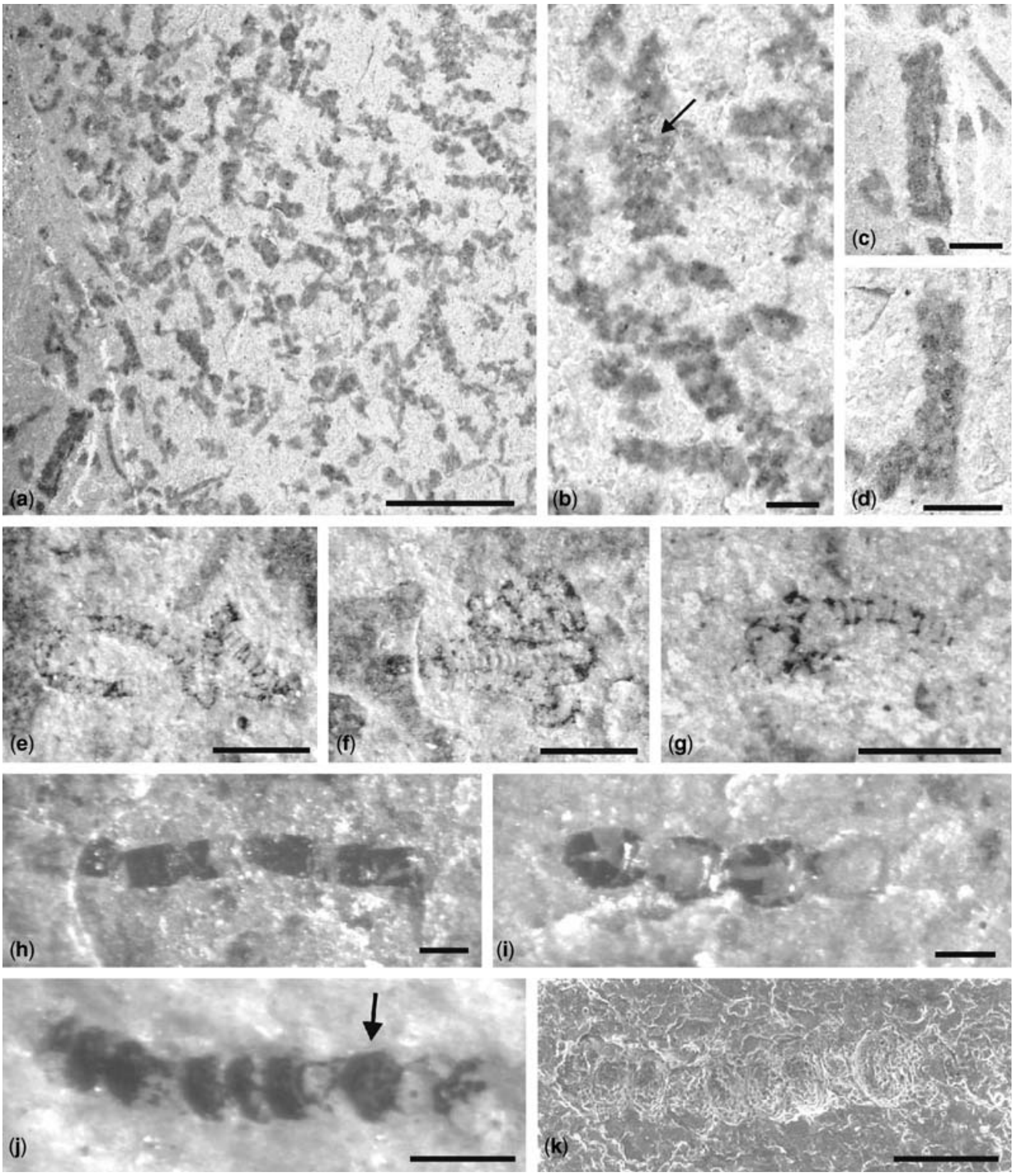

Fig. 8. Las Carmelitas Formation, morphotypes 3a–c: segmented structures; morphotype 5: sphaeromorphs. (**a**–**d**) Morphotype 3a. Bedding surface covered with mainly impressions of segmented structures. NMW2007.26G.16. (a) Scale bar 5 mm. (b–d) Enlargement of parts of (a). Arrow in (b) indicates concentrations of spherical structures. Scale bars 1 mm. (**e**–**g**) Morphotype 3b. Minute segmented structures. (e, f) NMW2007.26G.10iii + iv. Scale bar 0.5 mm. (g) NMW2007.26G.17. Scale bar 0.5 mm. (**h**, **i**) Morphotype 3c. (h) Possible filament with glossy appearance. NMW2007.26G.4ii. Scale bar 0.1 mm. (i) Chain of 4+ cells with preservation similar to (h). NMW2007.26G.3b. Scale bar 0.1 mm. (**j**, **k**) Morphotype 5. Chain of coalified cells under light and scanning electron microscopy. NMW2007.26G.18i. Scale bars 0.1 mm.

narrower. In this they are closest to the isolated specimen of morphotype 2 (Fig. 7j). However, the segments themselves are shorter, and there is never any evidence of extensions. In one ill-defined example there appears to be a linear aggregation of spheres in the central area (arrow in Fig. 8b), but in most cases isolated spheres are superimposed on the segmented structures.

Table 3. *Dimensions of morphotypes 3a–3c: segmented (all measurements in mm)*

	Max. length	Max. width	Range in segment width	Mean width	Range in segment depth	Mean depth	No. of lobes
Morphotype 3a							
NMW2007.26G.16	4.29	0.98	0.68–1.11	0.88	0.26–0.39	0.33	11
	1.18	0.70	0.52–1.11	0.79	0.19–0.39	0.30	4
	No. of segments measured	Range in length	Mean	Range in width	Mean		
Morphotype 3b							
NMW2007.26G.10	8	80–140	100	40–50	45		
	8	80–100	93	30–70	46		
	7	80–130	109	30–60	46		
NMW2007.26G.17	9	70–90	81	40–60	44		
All data	32	70–140	95	30–70	45		
Morphotype 3c							
NMW2007.26G.3	4	130–170	153	110–120	113		
NMW2007.26G.4	4	100–130	115	50–80	65		
	6	80–140	118	80–90	83		
All data	14	80–170	126	50–120	87		

Affinities of morphotype 3a. Superficial observations give an impression of highly compressed, poorly preserved segmented animals (e.g. arthropods and annelids). The absence of terminal parts and appendages argues against an arthropod origin, and the asymmetrical orientation of the segments precludes an annelid derivation. There remains a possibility that these structures are fragmented composite faecal pellets as, for example, are produced by extant herbivorous gelatinous zooplankton (Bruland & Silver 1981). In size and shape there is some similarity to the faecal pellets of salps (tunicates), which comprise abundant organic material including coccolithophores, diatoms and dinoflagellates, although extant forms usually have fewer ‘segments’ (e.g. four in *Salpa fusiformis*). In common with pteropod pellets (see p. 189), they are large and sink rapidly through the water column even though they are of low density (Paffenhöfer & Knowles 1979; Bruland & Silver 1981), and may be far more important participants in the faecal delivery of organic matter to the sea floor than previously thought. Swarms of larger species of salps cover very extensive oceanic areas (e.g. the California Current ($<45\ 000\ \text{km}^2$), and in completely dominating the zooplankton for several months are major processors of the phytoplankton (Bruland & Silver 1981). The pelagic tunicates, including the Salpidae, have no fossil record, although as stem group chordates an extended history might be anticipated (Benton 1993).

Butterfield & Nicholas (1996) described segmented vermiform fossils up to 3 mm long and 0.7 mm wide from the Cambrian of the MacKenzie Mountains, NW Canada, suggestive of annelids, but because of variability and degrees of asymmetry concluded that they were a type of sculpted coprolite. Although the Canadian fossils were preserved in phosphate, there is a general similarity to the less clearly defined ‘segmented’ structures discussed here, which are much smaller.

Morphotype 3b, glossy, more coherent coaly segmented structures (Fig. 8e–g; Table 3). This form shares with morphotype 3a an elongate, presumably segmented organization, but has a different and highly distinctive preservation. Coalified material with glossy rather than matt appearance occurs between segments and tends to be concentrated at junctions, with further accumulations marking the limits of the elongate structure. This produces a ladder-like effect with regions between the ‘rings’ of smoother matrix, which are either slightly depressed or elevated. Some additional coalified material may occur in these areas. The outer limits are more or less parallel, but not of uniform separations throughout. The fossils are sometimes curved, occurring in dense clusters or isolated. The most unequivocally complete example is *c.* 1.35 mm long, but is associated with two folded extensions covering a further millimetre. In all, more than 20 specimens were counted on one bedding surface of a single block, where they occur associated with morphotypes 1 and 4, which comprise more typical granular coaly material or impressions. A single isolated example occurs on NMW2007.26G.17. Measurements proved difficult, but most segments are between 70 and 130 μm wide and 30–70 μm long; the longest example contained at least 50 segments.

Affinities. The difference in appearance of this type (glossy coherent v. matt granular coal) suggests that the original organisms had a different original chemistry rather than diagenetic history, as both types are preserved in the same samples. They are in marked contrast to the threads and broader ribbons of morphotype 1 where there is no evidence of segmentation, and coal is more granular as noted also in the postulated coprolites (morphotype 2). An animal origin thus might be more appropriate.

Morphotype 3c, glossy coalified, well-defined, segmented, bead-like structures (Fig. 8h, i). Two examples on specimens NMW2007.26G.4 and NMW2007.26G.3b are very heavily coalified and consist of segments delimited by constrictions of varying depth. The smaller example has up to four segments ranging in width between 0.05 and 0.08 mm and 0.10–0.13 mm long, and single segments appear rounded (Fig. 8i). In contrast, the second is more strap-shaped with more uniformly wide segments (0.08, 0.09 mm) but varying length (0.08–0.14 mm) (Fig. 8h).

Affinities. Hints of a filamentous nature point to an algal or cyanobacterial affinity, although dimensions are large for the latter. However, the difference in preservation between these and morphotype 1 is striking and again suggestive of a different wall chemistry and possibly increased resilience to decay. Indeed, there is some superficial resemblance to chains of chitinozoans such as the Silurian *Densichitina densa* (*c.* 60 μm diameter: Grahn & Paris 1992).

Morphotype 4, circular to elliptical coalified structures (Fig. 9; Table 4)

Elliptical forms of subtly varying outline occur randomly throughout the assemblages, with concentrations on at least two bedding surfaces (Fig. 9a–g). Figure 9a shows structures associated with short lengths of threads (morphotype 1) plus more comminuted debris, including small spherical structures and one example of a larger 3D sphere (*c.* 150 μm diameter) with fine-grained infill (morphotype 5). Elliptical forms range in length from 0.6 to 1.68 mm ($n = 0.93$ mm) and are 0.32–0.81 mm wide ($n = 0.57$ mm). Their ends are usually rounded but some are more truncated. Outlines are usually well defined, but it is possible that the more extended forms were originally part of longer structures, rounding having occurred during transport. Almost circular coalified forms are rare (*c.* 700 μm diameter). Similarities in diameter of the more circular forms to the lower end of the length range of elliptical ones may indicate a similar origin. Strap-shaped structures associated with spheres, ellipses and cylindrical structures occur on two areas on one specimen (Fig. 9e–g), which is unusual in that the matrix is pink to pinkish grey on weathering, enhancing the contrast with the coalified fossils. The majority are roughly circular in outline. Broad similarities in diameter within the two well-separated clusters and alignment on the bedding plane with ribbon-shaped fragments, which show occasional marginal indentations, suggest that variation results from disintegration of longer strap-shaped structures. Although this morphotype is more heavily coalified, with slightly higher relief then the others, no structure could be ascertained on film pulls or on SEM examination.

Affinities. Lack of any structural information indicating possible contents limits any conclusive discussion. Except where concentrated on bedding planes (NMW2007.26G.19), more than one source is a possibility. Some shapes are reminiscent of spore masses or sporangia but subtending axes are never preserved, and such a source can therefore be discounted. Similar shapes also characterize faecal pellets, as noted for extant examples as well as later examples in the fossil record. These include macro-zooplankton including crustaceans, benthic invertebrates (see shapes illustrated by Martens 1978) and even nektic fish (e.g. anchovies; <2 mm × 1 mm today; Brodie & Kemp 1995). Indeed, in trap experiments on the sea floor, pellets of this shape but consistently less than a millimetre long and usually of uncertain origin dominate the organic material collected (Bishop *et al.* 1977). Approximately coeval representatives of these groups are rare, and possibly confined to benthic annelids. The latter would indicate more or less autochthonous origin, and the aligned spheres and ribbon-shaped structures illustrated in Figure 9a may exemplify this. However, the concentration of organic material militates against a detrital feeding producer, and sizes are perhaps too large for most annelids (see Porter & Robbins 1981; Cuomo & Rhoads 1987; Cuomo & Bartholomew 1991; Brodie & Kemp 1995). Differences in composition also preclude identity with the clastic cylindrical pellets associated with a number of invertebrates in the Ordovician (Bruthansová & Kraft 2003).

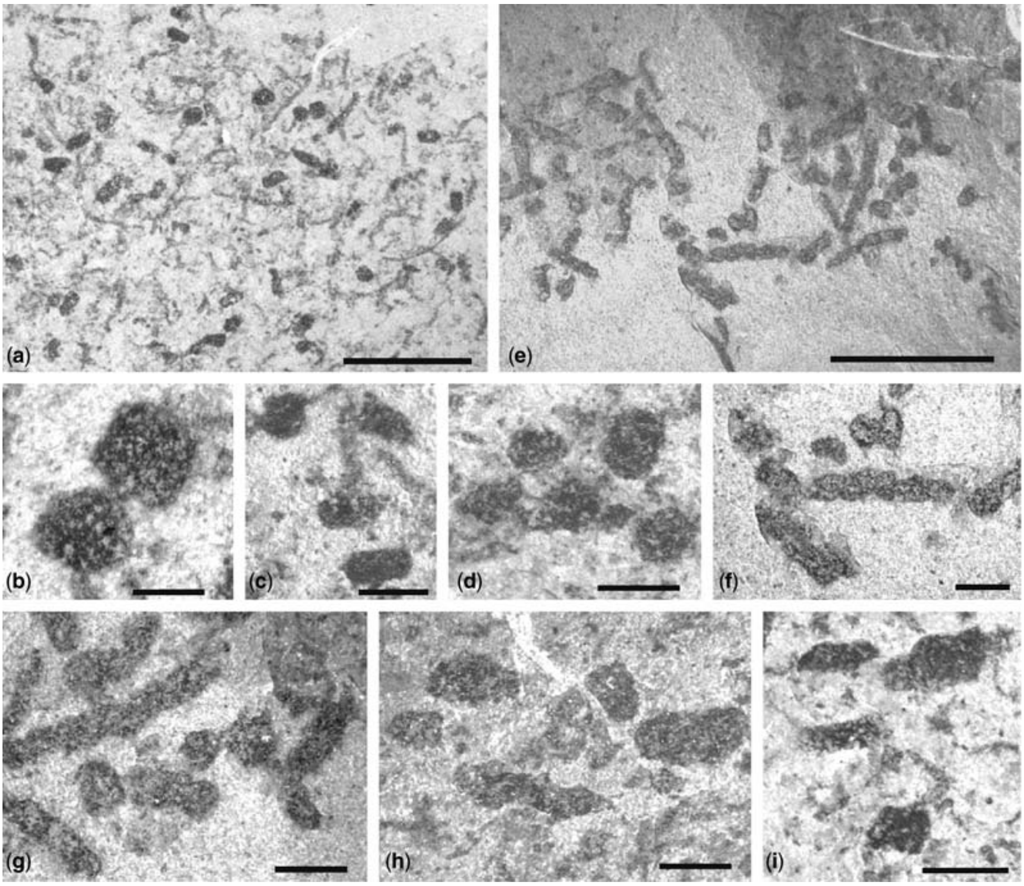

Fig. 9. Las Carmelitas Formation, morphotype 4: circular to elliptical coalified structures. (**a**) Bedding plane covered with circular to elliptical structures interspersed with fragments of morphotype 1. NMW2007.26G.19. Scale bar 5 mm. (**b–d**) Enlargements from (a). NMW2007.26G.19i–iii. Scale bars 0.5 mm (b), 1 mm (c, d). (**e**) Atypical pinkish matrix with broader ribbon-like structures possibly partially disaggregating to form circular and elliptical structures. NMW2007.26G.20. Scale bar 5 mm. (**f**, **g**) Enlargement from (e). NMW2007.26G.20i + ii. Scale bars 1 mm. (**h**, **i**) Isolated discrete elliptical structures occurring in heterogeneous 'debris'. (h) NMW2007.26G.6iii. Scale bar 1 mm. (i) NMW2007.26G.21b. Scale bar 1 mm.

The isolated occurrences of elliptical structures, and in one case (Fig. 9a) accumulations on a bedding plane with fragmentary threads (morphotype 1), suggest vertical transport into the depositional environment and hence, if faecal pellets, the excreta of invertebrates, or even vertebrate grazers on phytoplankton (see table 2 of Brodie & Kemp 1995).

Morphotype 5, sphaeromorphs (Figs 8j, k & 10; Table 5)

These range from three-dimensionally preserved spheres infilled with sediment (usually clays) with little organic material present, to circular coaly discs interpreted as compressed spheres. They occur as individuals dispersed in the matrix where they may cover bedding planes, occur in clusters, in which there is very little additional coalified material (Fig. 10b, i), or are associated with irregular patches of organic material (Fig. 10c, d). Dispersed examples show most variation in size (50–300 μm), with a similar size range recorded on a number of surfaces. Smaller examples were more difficult to measure on the rock. The botryoidal clusters show least variation: the majority are about 200 μm in diameter (Fig. 10b, i) but some are much smaller at *c.* 140 μm. Figure 10a shows a wide array of coalified shapes; clusters of larger spheres are parallel-sided to elliptical and appear to be variants of more consistent shapes in an unusually bleached matrix. Lobed outlines reflect the sizes

Table 4. *Dimensions of morphotype 4: circular to elliptical structures (all measurements in μm)*

	Range of length	Mean	Range of width	Mean	Range in ratio length/width	Mean ratio length/width	*n*
NMW2007.26G.1	630–1750	1057	280–680	382	1.84–5.47	2.9	9
NMW2007.26G.6	710–1580	1200	400–620	500	1.54–3.3	2.41	10
NMW2007.26G.9	490–850	647	200–300	243	2.0–3.7	2.72	3
NMW2007.26G.10	780–2070	1311	550–1130	771	1.26–2.72	1.7	9
NMW2007.26G.19	600–1680	935	320–810	570	1.11–2.47	1.67	45
NMW2007.26G.20*	570–960	744	390–700	492	1.1–2.0	1.55	14
NMW2007.26G.21	560–1430	869	330–670	463	1.1–2.69	1.93	12
NMW2007.26G.27†	840–2720	1518	400–600	480	2.1–4.53	3.04	5
NMW2007.26G.28‡	650–4040	1500	280–1050	629	1.02–7.35	2.61	25
Specimen 17 (missing)	530–1370	964	240–860	430	1.31–4.04	2.37	22
Specimen 18 (missing)	660–1210	953	210–590	373	1.51–3.27	2.69	7
All data	490–4040	1063	200–1130	524	1.02–7.35	2.14	161
Polychaete worm§	400–800		100–300				
Polychaete worm§	120–500		50–200				
Pteropod§	Up to 6000		200				
Copepod§	200–600		40–70				
Anchovy§	Up to 2000		Up to 1000				

*Example where there is possible fragmentation *in situ.*

†Rounded ends, but constant width and variable length.

‡Very varied, similarity with NMW2007.26G.21.

§References given by Brodie & Kemp (1995).

of the single spheres, and there is very little additional coalified material. A bedding surface on NMW2007.26G.18 (Fig. 10c–i), which is remarkable for its clusters of spheres and profusion of isolated perfectly spheroidal structures embedded in a soft matrix, also has a single example of a chain of fractured hollow structures, three-dimensionally preserved but laterally compressed to varying extents, such that single segments appear discoidal (Fig. 8j). The widest approximates to a sphere (arrowed in Fig. 8j). The cavities have a coating of coaly material, which is very similar to that on the surrounding fossils. Its preservation is thus very different from the chain of putative spheres described under morphotype 3c (Fig. 8i). Overall length is 0.41 mm, encompassing six well-preserved structures linked in two cases by coaly material. Measurements of single units are difficult. The diameter of the chain is *c.* 66 μm with five of the units *c.* 35 μm and the longest *c.* 60 μm. These are considerably smaller than the easily recognizable dispersed spheres and those in clusters.

Low-magnification light microscopy studies suggest that the spheres are smooth. Maceration has yielded a few very eroded spheres. The larger size category was examined by SEM (Fig. 10e, g–k). Members are smooth-walled, but the wall itself is rarely present, and then appears to be single. Noteworthy features are the very smooth surfaces of the infill (Fig. 10j) and occasional examples with large-scale gentle folds (Fig. 10k). There is no evidence for excystment structures. In some examples, chemical analyses confirm the presence of carbon in the cell wall at much higher values than in the matrix, whereas the infill and matrix have a somewhat similar signature indicating the presence of clays (with Al, K and traces of Mg and Ti) as well as quartz. The infill appears to be different from the matrix, often displaying a honeycomb structure or minutely perforated sheets. On one surface where three-dimensionally preserved spheres of similar dimensions are bright red (?orange), iron oxides are present.

Affinities

Algae. Such spheres, although rather large, are most probably the remains of planktonic unicellular algae (namely, sphaeromorphic acritarchs). In the Precambrian they have been given a variety of generic names, but are best united as *Leiosphaerida* Timoveev, a form taxon particularly widespread in the Silurian (e.g. Le Herissé 1984), and ranging in diameter between 8 and 440 μm (Lindgren 1981). The larger spheres fall into the lowest part of the size range (100–1000 μm) of Proterozoic spheroidal structures, called, for example, *Chuaria circularis*, but the latter genus is reported to possess very thick walls (Butterfield *et al.* 1994) and concentric wrinkles that might indicate spiralled coiled filaments as in *Nostoc* balls (Hofmann 1994). Returning to the acritarch concept, the vast majority of the spheres occur as isolated individuals in the rock

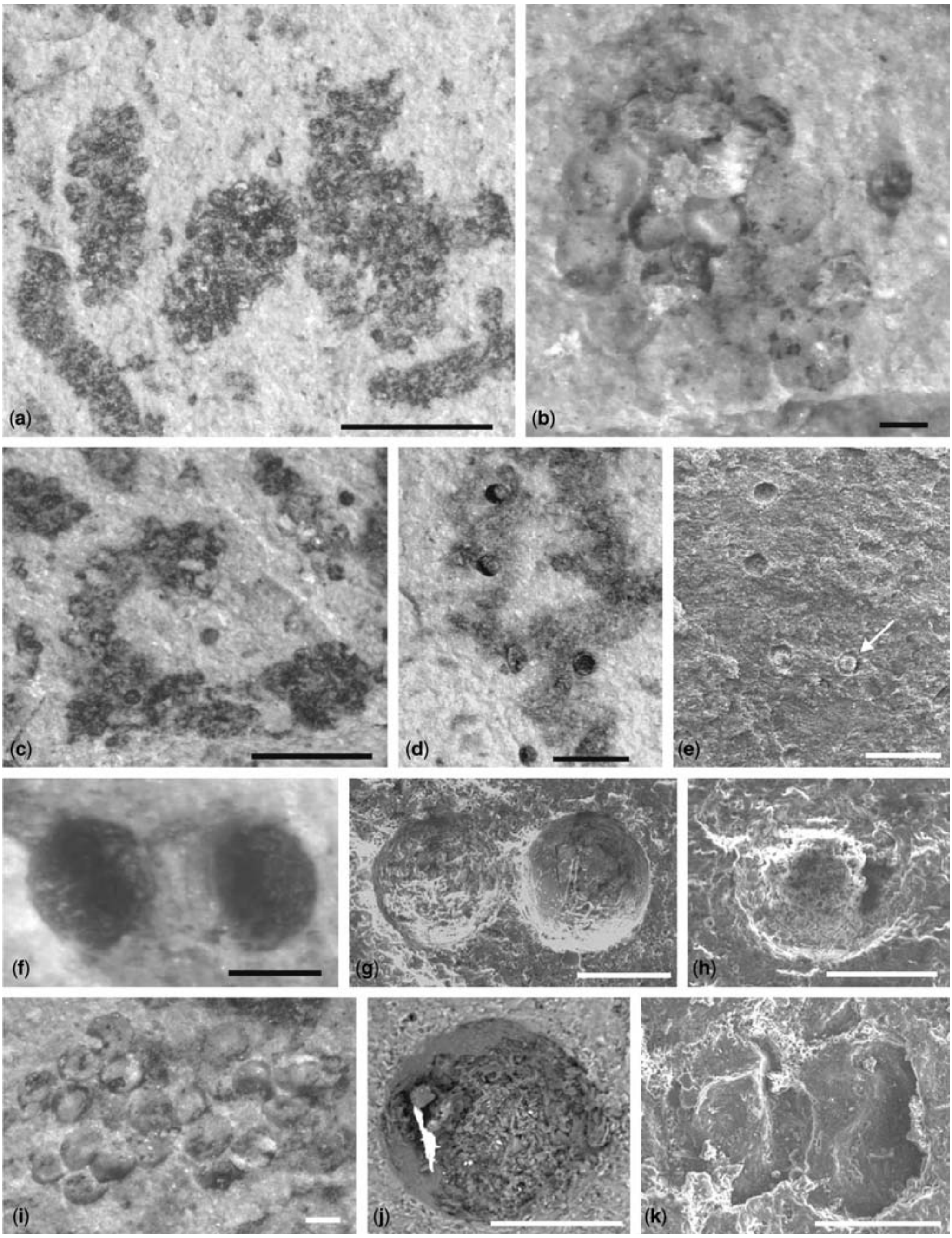

Fig. 10. Las Carmelitas Formation, morphotype 5: sphaeromorphs. (**a**) Variously shaped aggregations of compressed coalified spheres. NMW2007.26G.22. Scale bar 1 mm. (**b**) Cluster of three-dimensionally preserved spheres with fine-grained surfaces. NMW2007.26G.23. Scale bar 0.1 mm. (**c**–**i**) Bedding surface on NMW2007.26G.18. (c) Spheroids associated with irregular patches of sparsely associated coalified material and isolated in the matrix. NMW2007.26G.18ii. Scale bar 1 mm. (d, e) Same area under LM and SEM. The 3D form of the spheres under SEM should be noted. NMW2007.26G.18iii. Arrow in (e) indicates sphere shown enlarged in (h). Scale bars 0.5 mm. (f, g) Isolated spheres in LM (f) and SEM (g) NMW2007.26G.18iv. Scale bars 0.1 mm. (h) SEM detail of sphere arrowed in (e). Scale bar 0.1 mm. (i) Cluster of three-dimensionally preserved spheres with little coal remaining [compare with (b)]. NMW2007.26G.18v. Scale bar 0.1 mm. (**j**, **k**) SEM images of spheres on NMW2007.26G.24. (j) SEM image of sphere with remains of smooth covering (?coalified wall) and fine-grained infill (BSE mode). NMW2007.26G.24i. Scale bar 0.1 mm. (k) SEM image of two adjacent sphaeromorphs with prominent folding on smooth wall. NMW2007.26G.24ii. Scale bar 0.1 mm.

Table 5. *Dimensions of morphotype 5: sphaeromorphs (all measurements in μm)*

		Max. diameter	Mean	SD	*n*	Notes
NMW2007.26G.1		60–130	97	19.99	30	Dispersed but some superimposed on threads
NMW2007.26G.5		90	90	0	6	Botryoidal cluster
NMW2007.26G.9		130, 200	165		2	Dispersed
NMW2007.26G.11		60–220	132	41.94	51	Dispersed
NMW2007.26G.16		90			1	Dispersed
NMW2007.26G.17		150–200	178	17.22	6	Red dispersed spheres
NMW2007.26G.18	(i)	150–210	166	19.96	8	Dispersed but associated with diffuse carbonaceous material
	(ii)	130–260	198	36.02	34	Botryoidal cluster
	(iii)	70–80	72	4.08	6	Spheres in chain (Fig. 8j, k)
	(i) + (ii)	130–260	192		42	
NMW2007.26G.22	(i)	150–300	210	38.69	32	Botryoidal clusters
	(ii)	50–220	146	37.52	23	Dispersed
	(i) + (ii)	50–300	183		55	
NMW2007.26G.23	(i)	120–240	183	36.73	35	Botryoidal clusters
	(ii)	50–220	133	47.16	15	Dispersed
		50–240	168		50	
NMW2007.26G.24	(i)	100–210	168	24.2	28	Botryoidal clusters
	(ii)	120–210	164	24.53	18	Dispersed
	(i) + (ii)	100–210	167		46	
NMW2007.26G.28		200–320	253	41.79	6	Botryoidal cluster
NMW2007.26G.29		180, 190	185	7.07	2	Red dispersed spheres
All data		50–320	159	51.37	303	

matrix, suggestive of a unicellular rain to the sea floor as produced by extant dinoflagellates and other planktonic algae. However, Downie (1973) indicated that smooth spheroids can occur in monospecific clusters or loose chains of varying numbers of individuals. Such aggregations are common in the Precambrian (e.g. Butterfield *et al.* 1994) and Cambrian rocks; less so in the Silurian. Examples with discrete ellipsoidal morphologies were compared with the contents of sporangia, but clustering can occur in extant phytoplankton (e.g. the much smaller haptophyte *Phaeocystis*) resulting from stickiness produced by secretion of extrapolymeric substances (Wassmann 1994). In the haptophyte, aggregations were more common in living rather than senescent forms, and increased sedimentation rates. Aggregations showing discrete shapes (e.g. Fig. 9a) or associated with coalified material may well be the remains of the faecal pellets of primary grazers in the plankton realm. Variations in shape may indicate more than one producer, but they would have been considerably larger than most of the zooplankton known to us, and perhaps derive from swarming (?juvenile) fish. Mullins (2003) also considered *inter alia* a faecal origin for small clusters (2–7) of the Silurian acritarch *Dilatisphaera laevigata*, where radiating processes appear to facilitate the aggregations with less well-differentiated material. Mullins also suggested that the increased size (and presence of processes) in such aggregations could have deterred herbivory of zooplankton.

We have no data to allow further speculation on more detached affinity of the majority of the sphaeromorphs; for examples, prasinophyte, chlorococcacean or even in the red algae lineage. Whether they were vegetative cells or cysts also remains conjectural. The rarity in macerates of sporopollenin-impregnated walls that usually characterize acritarchs (leading to the inference that the latter are cysts) might be taphonomic or point to vegetative cells preserved under exceptional conditions. Indeed, some chlorococcaceans possess resilient wall polymers (e.g. Atkinson *et al.* 1972) and, although large examples are rare, some reach 165 μm in diameter (e.g. *Ankistrodesmus*; Lindgren 1981).

The single filament of presumably coccoid cells, at *c.* 66 μm in diameter, is too large to be cyanobacteria (Fig. 8j, k). Filaments of broadly similar organization recorded in the Cambrian of northwestern Georgia were discovered recently as possibly encrusting coccoidal green alga, but not given a name (Schwimmer & Montante 2007).

Eggs. The possibility that these larger spherical structures are eggs, egg cases or animal cysts cannot be discounted, although records of dispersed eggs in the Palaeozoic are rare. A remarkable exception is recorded in the Lower Cambrian Doushantuo Formation of south China, where single cells and embryos occur within large spinose spherical microfossils assigned originally to an acanthomorphic acritarch genus *Tianzhushania*, now reinterpreted as diapause egg cysts (Yin *et al.* 2007). The abundant zooplankton as evidenced by the proposed faecal pellet record would presumably have produced eggs and, although the resilience of such structures would seem low, there are Recent and Quaternary records of diapausing eggs forming egg banks in sediments (e.g. Bennike 1998; Hairston & Kearns 2002). Almost all of the Recent records refer to copepod crustaceans (e.g. Kasahara *et al.* 1974; Marcus *et al.* 1994), in which single eggs may or may not be surrounded by a resistant coat, with small clutches of eggs enclosed in chitinous sacs or occurring as strings (Poulin 1995). In size, single eggs are broadly similar to those described here, and although the majority are smooth, some have projections and equatorial extensions reminiscent of many acritarchs (Kasahara *et al.* 1974). Their resilient outer coverings can act as protection against decay and predation. Marcus (1984) reported viability after passage through the digestive system of a polychaete and also in small groups interpreted as faecal pellets. Such crustaceans, however, are not recorded before the Mesozoic, although there is always the possibility that zooplankton with similar life histories and ecological niches existed earlier.

Thousands of phosphatized spheres, 85–110 μm in diameter, with weakly textured walls were recovered from the Cretaceous Brazilian Santana Formation, in which ostracodes also occur (Smith 1999). Based on this context and comparisons with extant ostracodes they were assigned to that group, with the tentative suggestion that they were liberated in profusion into sediments. This may not have been the case for the only Silurian record of indisputable ostracode eggs found in brood pouches within carapaces, in which they are guardedly postulated to have developed (Siveter *et al.* 2007).

There are similarly no direct records of planktonic molluscs, although we have discussed the possibility of pteropods having produced some of the faecal pellets described here. Extant forms produce pelagic eggs (Lebour 1937) that float in gelatinous strips (*c.* 2 mm long and 0.6 mm wide) and sometimes appear to be caught in some thread-like structures (Lebour 1937, p. 124) presumably similar to entities described here. However, it should be noted that chances of fossilization of pteropod eggs are rare as they exhibit very rapid embryo development. Prosobranchiate gastropods introduce eggs into the plankton in coastal areas, enclosed in gelatinous masses or strings often with a firm peripheral layer (Lebour 1932), which might, following compression, resemble structures described here. Prosobranchs are recorded in the coeval fossil record, but it seems unlikely that they would have produced such a profusion of eggs. Fish, in contrast, might well have, but Recent records indicate a somewhat larger size even in planktonic eggs (>500 μm; Wickstead 1976), and we know of none in the Silurian. To sum up, the most parsimonious conclusion is that these spheroidal structures should be assigned to the acritarchs/algae, but alternative affinity should not be ruled out completely.

Leiosphaerid acritarch distribution in Ludlow seas

Uncertainties as to the depth of the water column associated with the Carmelitas facies limits sensible discussion as to whether or not the larger leiosphaerid examples could have been benthic or were a component of phytoplankton, but their occurrence throughout the matrix is more indicative of the latter (Strother 1994). Detailed studies on undoubtedly planktic coeval Ludlow acritarchs have been made at comparatively low latitudes in the Anglo-Welsh area, where distribution of leiosphaerids has been related to distance from shore (Dorning 1981), as in other times and regions (e.g. Ordovician, Jacobson 1979; Precambrian, Butterfield & Chandler 1992). Low-diversity assemblages of low to moderate abundances are indicative of both near-shore and deep-water environments, although, in the latter, walls are thicker. The abundance of smooth *Protoleiosphaeridium* in both Silurian assemblages was related to environmental stress; namely, near-shore 'instability' or offshore lack of nutrients (Dorning 1981). The intervening offshore community is characterized by moderate abundance and high diversity, particularly in forms with well-developed processes. Dorning reported low diversity in blooms of these forms on the shallow-water shelf in the Ludfordian of the Welsh Borderland (Leintwardine and Whitcliffe Beds). Thus although the high-latitude Bolivian acritarch bloom contained abundant sphaeromorphs as well as acritarchs with processes (Cramer *et al.* 1974), its cause probably relates to a completely different set of environmental conditions related to high latitudes.

Productivity and carbon sequestration in Silurian seas

The presence of so many bedding planes almost covered by coalified fossils indicates efficient burial of organic matter in sediments and hence ancient sequestration of carbon. The latter derives not only from primary productivity in the form of acritarchs or algae, but also from the excreted products of grazers, which subsequently escaped coprophagy, bacterial and fungal degradation, and consumption on the sea floor. There the presence of clays in the sediment would have produced further barriers to both physical and biological degradation (Butterfield 1990). The abundance of material suggests blooms of phytoplankton presumably stimulated by nutrient enrichment in the photic zone, followed by proliferation of herbivores and accumulations of faecal pellets. The contemporaneous Kirusillas Formation cropping out in the SE of Bolivia is identified as a source rock of oil, and it is tempting to relate this to the fossilized remains described here, the first direct record of abundant biomass in the Ludlow of Bolivia. A similar relationship has been postulated in Pennsylvanian to Miocene strata in the USA, where faecal pellets occur in finely bedded marine and lacustrine black shales associated with oil and coal deposits (Porter & Robbins 1981).

However, palynomorph and associated sapropel maturity indicate that the rock has been heated to at least 240 °C followed by shearing, such that no oil and gas would be anticipated in this area. In this paper, postulated low temperatures and exclusion of consumers in an anoxic depositional environment contribute to sequestration of organic matter in the form of the fossils described here The presence of different associations of morphotypes in submillimetre-scale laminations strongly supports frequent episodic events, although background occurrences of spheres throughout the matrix suggest that phytoplankton flourished over a longer period of time. A combination of environmental factors affecting the water column and sea floor, high productivity, and the large size of the presumed coprolites has resulted in reduction of recycling of organic material and hence its incorporation in the rock record.

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Cambrian and Ordovician biogeography of the South American margin of Gondwana and accreted terranes

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Abstract: Three main geological units were involved in the Early Palaeozoic history of South America: (1) autochthonous intracratonic and pericratonic basins developed around the Gondwana basement (e.g. the Central Andean basin, CAB); (2) volcano-sedimentary basins marginal to Gondwana (e.g. Famatina and Puna volcanic belts); (3) crustal fragments accreted to the Andean margin through the Palaeozoic (e.g. Precordillera terrane). Knowledge of brachiopods, trilobites and bivalves has increased substantially over recent years, leading to the assembly of a more complete dataset. Furongian–Tremadocian trilobites from Famatina, western Puna and the CAB are mostly widespread forms (Olenid Fauna); however, the record of *Amzasskiella* and *Onychopyge* suggests a connection with East Gondwana, Siberia and Kazakhstan. At that time, the Central Andean brachiopods and bivalves show links with Iberia, Bohemia and North Africa. Floian trilobites from these regions show a complex array of endemic and peri-Gondwanan forms, indicative of relatively free migration for some taxa around Gondwana. Coeval brachiopods from Famatina and western Puna volcaniclastic rocks are of Celtic type, having some taxa in common with coeval faunas from south Peru, which would support the existence of a long and nearly continuous volcanic arc marginal to the Iapetus Ocean. Cambrian to Middle Ordovician platform carbonate rocks are confined to the Precordillera basin. Trilobites from the Lower and Upper Cambrian limestones of the Precordillera include key genera indicating Laurentian affinities (*Arcuolenellus*, *Madarocephalus*, *Plethopeltis*). Associated rhynchonelliformean brachiopods (e.g. *Nisusia*, *Wimanella*) are also typical of low-latitude palaeocontinents. Trilobites from the upper Tremadocian–Floian sequences of the Precordillera match those of the Bathyurid Fauna, whereas associated brachiopods include a high percentage of Laurentian taxa. From the Floian, a biotic exchange with Gondwana and Baltica becomes evident in the Precordilleran trilobite faunas. By Darriwilian times, Precordilleran brachiopods form a well-defined low-latitude realm, but numerous Celtic and Baltic taxa immigrated into the basin. By the Sandbian, affinities of Precordilleran brachiopods shift to West Gondwanan (North Africa, Armorica, Perunica and central Andes), probably reflecting the accretion of the Precordillera (Cuyania) terrane to the proto-Andean margin, although some mixed faunas persist. The low-richness CAB brachiopod, bivalve and trilobite assemblages display stronger 'Mediterranean' affinities than those from the Precordillera. In summary, there are abundant palaeontological data supporting the view that the Precordillera is a Laurentian-derived far-travelled microcontinent accreted to Gondwana during the Early Palaeozoic. A new early Middle Ordovician reconstruction of the southern and central proto-Andean margin is based on recently published geological data as well as the new palaeontological evidence summarized in this paper.

The geodynamic history and developing palaeogeography of the southern proto-Andean margin of Gondwana, which today forms the Andean and Subandean ranges of Argentina, Chile, Bolivia and Peru, have been fully addressed in the collections of papers edited by Pankhurst & Rapela (1998), Ramos & Keppie (1999) and Vujovich *et al.* (2004), among others. There is general agreement that three main geological units were involved in the early Palaeozoic history of South America (Fig. 1): (1) autochthonous intracratonic and pericratonic basins developed on and around the Gondwana basement; (2) early Palaeozoic subduction-related volcanic arcs and associated volcano-sedimentary basins marginal to Gondwana; (3) crustal fragments accreted to the Andean margin of Gondwana through the Palaeozoic (Precordillera, Chilenia). Palaeogeographical evolution of the northern segment of the Andes (Ecuador, Colombia, Venezuela) is less well known, but at least two terranes (Mérida and Chibcha) have been recognized (Toussaint & Restrepo 1989; Bellizzia 1992; Bellizzia & Pimentel 1994). The autochthonous 'Caparo Block' is located on the eastern flank of the Venezuelan Andes, adjacent to the Mérida terrane.

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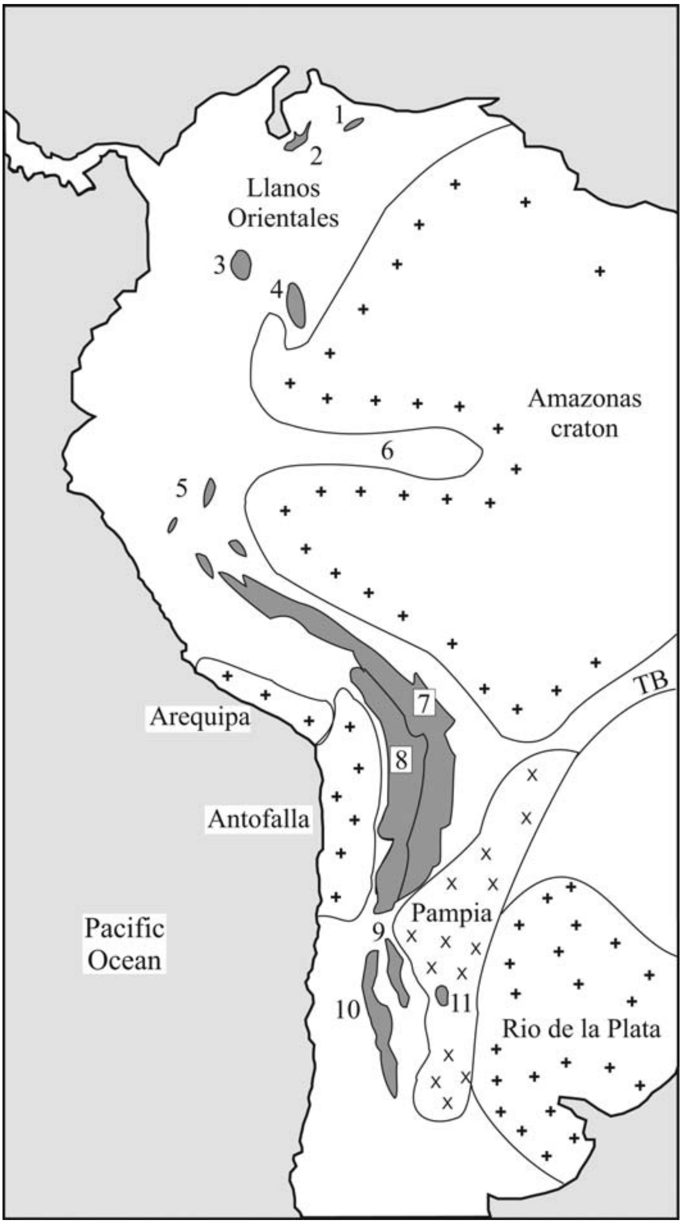

Fig. 1. Map of central–western South America showing main geological units and Cambro-Ordovician sedimentary basins. 1, El Baúl Massif (Venezuela); 2, Mérida Andes, Río Caparo area (Venezuela); 3, Sierra de la Macarena (Colombia); 4, Sierra de Araracuara (Colombia); 5, Contaya (Peru); 6, Solimoes basin (Brazil); 7, Cordillera Oriental and Sierras Subandinas (Bolivia and NW Argentina); 8, Puna region (northern Chile, Bolivia and NW Argentina); 9, Sierra de Famatina (western Argentina); 10, Precordillera (western Argentina); 11, Pampean Ranges (central Argentina); TB, Transbrazilian lineament. (Modified from Benedetto & Sánchez 1996; Ramos & Aleman 2000; Ramos 2008.)

The biogeographical signature of Cambrian and Ordovician faunas has been useful to discriminate the boundaries between such geotectonic units and also for determining the probable origin, trajectory and timing of accretion of the Precordillera (or Cuyania) terrane, which constitutes a major component of the southern proto-Andean margin and is a focal point for understanding the early history of this Gondwana portion (Benedetto 1993, 1998*a*, 2004; Astini *et al.* 1995; Thomas & Astini 1996). As is well known, biogeographical affinities of the Cambrian trilobite faunas (Vaccari 1994, and references therein) are the keystone of the hypothesis supporting the Laurentian derivation of the Precordillera terrane (Astini *et al.* 1995; Benedetto 2004).

By the Ordovician, brachiopods and trilobites, and to a lesser extent bivalves, were common components of carbonate and clastic platforms, and also of volcaniclastic areas surrounding volcanic edifices (Waisfeld *et al.* 2003), and they have been critical in understanding the complex palaeogeography of the South Iapetus Ocean during the early Palaeozoic (Benedetto 1993, 1998*a*, 2004; Astini *et al.* 1995; Benedetto & Sánchez 1996; Waisfeld 1995; Vaccari 1995, 1996; Benedetto *et al.* 1999; Vaccari *et al.* 2006). Other groups, such as sponges and ostracodes, are relatively abundant in the Precordillera basin but they are scarce or poorly known in other South American basins, so they will not be addressed in detail in this synthesis. Biogeography of Ordovician sponges has been analysed by Carrera & Rigby (1999) and Carrera (2003), and ostracodes were addressed by Salas (2002*a*, *b*) and Williams *et al.* (2003).

The main purpose of this contribution is to reassess the biogeographical affinities of the South American benthic faunas in the light of new discoveries and recent advances in the taxonomy of trilobites, brachiopods and bivalves. Within this framework, we discuss in some detail the recent paper by Finney (2007), who argued that available evidence is also compatible with a parautochthonous (SW Gondwana) origin of the Precordillera terrane. Palaeontological data presented in this review are no longer consistent with such a provenance and indicate that the most likely place of origin is Laurentia.

Faunas from each of the above-mentioned geological units are compared with coeval assemblages from Gondwana and other palaeocontinents and microplates. Information is examined for Early Cambrian, Late Cambrian, Furongian–early Tremadocian, late Tremadocian–Floian, Dapingian–Darriwilian, Sandbian–Katian and Hirnantian time intervals.

Cambrian–Ordovician basins of South America

Cambrian–Ordovician biotas are preserved in a wide variety of deposits along the western part of the present-day South American plate (Benedetto & Sánchez 1996, and references therein) (Fig. 1). Lower Palaeozoic fossiliferous rocks in Venezuela form small exposures in the El Baúl Massif and the Mérida Andes (Caparo Block). In the former locality there are Upper Cambrian black shales referred to the Mireles Formation. The Caparo Formation is composed of green siltstone and fine-grained sandstone bearing graptolites, brachiopods and trilobites of Sandbian age (Arnold & Smith 1964). In the Sierra de la Macarena and the eastern slope of the Cordillera Oriental of SE Colombia the Guejar Group consists of calcareous sandstones and limestones of Cambrian age, and sandstones interbedded with dark grey fossiliferous shales that have been correlated with the widespread Ordovician clastic succession lying in the subsurface of the Colombian and Venezuelan pre-Andean plains ('Llanos Orientales') (Ulloa *et al.* 1982; Mojica & Villarroel 1988; Pimentel de Bellizia 1992). In the Central Cordillera of Colombia, Ordovician rocks are represented by the Cristalina Formation in the north and the El Hígado Formation in the south. The latter consists of sandstones, bioclastic lenses and fossiliferous dark shales bearing graptolites and trilobites. The Middle Ordovician (Darriwilian) age of these rocks has been well established recently by conodonts (Gutiérrez-Marco *et al.* 2007, and references therein), but the presence of reworked conodonts of Tremadocian age indicates deposition of older rocks in the area. At the Sierra de Araracuara, near the Guyana shield border, in the SE corner of Colombia, reddish violet conglomerates, sandstones and siltstones yielded *Cruziana*, linguliform brachiopods and acritarchs of Early Ordovician age (Thery *et al.* 1984).

The Lower Palaeozoic succession of Ecuador is almost completely unknown. In the westernmost part of the Amazonas basin of Brazil (Solimoes depocentre) shales and sandstones have been detected in the subsurface, lacking shelly faunas but dated as Early Ordovician by mean of palynomorphs. The Contaya Formation in east–central Peru consists of sandstones and dark shales bearing graptolites, brachiopods and trilobites of Mid-Ordovician age (Hughes *et al.* 1980).

Most palaeontological information from the Lower Palaeozoic sequences of South America comes from the up to 6000 m thick sedimentary successions that are exposed superbly in the Cordillera Oriental (Eastern Ranges) and Sierras Subandinas (Subandean Ranges) of southern Peru, Bolivia and NW Argentina, forming the vast Central Andean basin (Fig. 1). Stratigraphical nomenclature of the Cambro-Ordovician units in this basin varies according to the countries, mountain belts and geotectonic provinces, and their correlation is often difficult in the absence of adequate biostratigraphical markers and accurate palaeontological studies. Some preliminary data from the San José Formation (Lower Ordovician) of the Cordillera Oriental of SE

Peru were published by Chacaltana *et al.* (2004) and Gutiérrez-Marco *et al.* (2004), and brachiopods were described by Gutiérrez-Marco & Villas (2007). Of particular interest for palaeogeographical reconstruction is the volcaniclastic succession that underlies the San José Formation, named the Ollantaytambo Formation, and the correlative Umachiri beds that crop out in the Peruvian altiplano. The Ollantaytambo Formation is a succession of dark shales, quartz-rich graded sandstones and ignimbrites of calc-alkaline basaltic to andesitic composition; this geochemical signature indicates that these rocks formed in a volcanic arc setting. On this evidence, Bahlburg *et al.* (2006) concluded that these volcanogenic deposits were connected to the westward-lying Ordovician granitoids on the Arequipa Massif, and also that this magmatic arc may represent the northward continuation of the Famatina–Puna magmatic arc of northern Chile and NW Argentina.

In the Cordillera Oriental of NW Argentina, the Cambro-Ordovician succession starts with shallow-water, *Skolithos*-rich reddish sandstones and siltstones (Mesón Group) of inferred Early–Middle Cambrian age. Apart from trace fossils, this tidal-dominated succession yielded only scattered linguliformean brachiopods. The Mesón Group is overlain by the Santa Victoria Group, which includes the Santa Rosita Formation (Furongian–Tremadocian), the Acoite Formation (upper Tremadocian–Floian), and the Alto del Cóndor Formation (Dapingian–lower Darriwilian?). However, a varied set of formations has been established to account for the strong lithofacial changes through the Cordillera Oriental and Sierras Subandinas (see stratigraphical chart by Astini 2003). A basin-wide transgressive surface separates this sequence from the overlying open platform deposits of latest Darriwilian–Sandbian age (Capillas or Santa Gertrudis formations). Comparable siliciclastic rocks can be traced northwards into southern Bolivia, where the Cambrian–Lower Ordovician succession is represented by the Sama, Iscayachi, Cieneguillas, Obispo, Agua y Toro, and Pircancha or Sella formations, and the Middle Ordovician by the Anzaldo and San Benito formations. A lithostratigraphical and biostratigraphical scheme of Bolivian units was provided by Suárez Soruco (2000), and basin evolution of southern Bolivia was discussed by Erdtmann & Suárez Soruco (1999) and Egenhoff *et al.* (2004), among others. The Ordovician succession culminates with glacigenic deposits of Hirnantian age, named the Zapla Formation in NW Argentina and Cancañiri Formation in Bolivia.

The Puna region of NW Argentina and northern Chile is characterized by a lower volcanosedimentary succession of Furongian–Early Ordovician age bearing graptolites and scarce trilobites and brachiopods (Las Vicuñas and Aguada de la Perdiz formations). These units are overlain by the up to 3500 m thick 'Puna Turbidite Complex', dated essentially as Middle Ordovician (Bahlburg *et al.* 1990). South of Salar in the Atacama of northern Chile, the volcanosedimentary Cordón de Lila Complex is overlain unconformably by a transgressive, *c.* 1000 m thick marine succession named the Quebrada Grande Formation, containing brachiopods and graptolites (Niemeyer *et al.* 2007; Benedetto *et al.* 2008). Approximately equivalent volcaniclastic rocks (Umachiri beds) are exposed in the southern Peruvian altiplano (Bahlburg *et al.* 2006).

Stratigraphy of the Sierra de Famatina was reviewed by Astini & Benedetto (1996), Mángano & Buatois (1996, 1997), Astini (1999*a*, 2003) and Astini & Dávila (2002). The oldest sedimentary rocks, named the Volcancito Formation, of Furongian–Tremadocian age, consist of calcarenites, marls and laminated dark siltstones deposited on a storm-influenced marine platform (Albanesi *et al.* 2005). The Bordo Atravesado Formation consists of deep-water black shales of late Tremadocian age. The overlying volcaniclastic succession, *c.* 2000 m thick, starts with the Suri Formation, composed of silicified black shales, tuffs, bioturbated siltstones bearing calcareous nodules, and fine-grained green sandstones, and culminates with the Molles Formation, which consists of reddish purple sandstones and siltstones, pyroclastic breccias and tuffaceous dark mudstones. The overall succession displays a shallowing upward trend, evolving from starved-basin graptolitic black shales to storm and tidally influenced shallow-water sandstones. Muddy and silty intervals of both the Suri and Molles formations are rich in brachiopods, bivalves and trilobites. The Floian–Dapingian age of this succession is well constrained by graptolites and conodonts (Albanesi & Vaccari 1994; Lehnert *et al.* 1997; Toro & Brussa 1997).

The Precordillera basin of western Argentina contrasts strongly with other South American geological provinces in the development of a *c.* 2500 m thick succession of Cambrian to Middle Ordovician shallow-water platform carbonates. Its stratigraphy, lithofacies, biostratigraphy, palaeocology, and fossil content have been the target of numerous studies in the last 25 years (summarized by Benedetto 2003*a*). The Cambrian succession is represented, in ascending order, by the Cerro Totora, La Laja and Zonda or La Flecha formations. The Ordovician carbonate units are the La Silla and San Juan Formations (Keller *et al.* 1994; Cañas 1999, 2002). The evaporites, dolomites and reddish clastic deposits of the Cerro Totora Formation have been interpreted by Astini & Vaccari (1996) as recording synrift graben-filling deposits related to the rifting of the Precordillera terrane from Laurentia. These rocks grade upwards into a passive-margin carbonate succession, which represents, according to this model, the rift–drift transition. Along the western Precordilleran belt ('western tectofacies', Astini 2003) Cambrian rocks are preserved as limestone boulders and large olistoliths, including deep-water platy limestone and lime-shale strata, embedded within Ordovician shales. This olistostromic unit, named the Los Sombreros Formation, records deposition in a deep-water slope setting. The San Juan Formation is a widespread, 300–380 m thick carbonate unit dominated by richly fossiliferous limestones deposited on top of an unrimmed shelf, which by the Darriwilian evolved into an homoclinal ramp with a depocentre located to the north of the basin (Cañas 1999). Outer ramp and basinal facies are represented by mixed carbonate–clastic facies and graptolitic black shales, respectively (Gualcamayo Formation). The Middle and Upper Ordovician successions are dominantly clastic and were deposited in a varied set of environments (fan deltas, marine platform and slope, glacigenic) displaying abrupt lithofacies changes and hiatuses, attesting to a strong depositional instability (Astini 2003). According to Benedetto & Astini (1993) and Astini *et al.* (1995), these phenomena may reflect the docking of the Precordillera terrane against the Gondwana margin and subsequent post-collisional extension.

The Pampean Ranges (Pampia terrane) of central Argentina are a series of mountainous ridges uplifted during the Tertiary Andean orogeny, composed largely of polymetamorphic rocks and granitoid plutons of Mesoproterozoic to early Palaeozoic age (Pankhurst & Rapela 1998, and references therein). The first shelly fossils, of Early Ordovician age, were discovered recently in amphibolite-grade metasedimentary rocks (Verdecchia *et al.* 2007).

Data and methods

The brachiopod database for this study includes 117 Ordovician genera and 166 species from various localities of western Argentina. Of these, 80 genera and 97 species come from upper Tremadocian to Hirnantian successions of the Precordillera terrane. The Lower Ordovician assemblages from the Famatina and Puna volcaniclastic rocks are composed of 30 genera and 34 species. The Central Andean siliciclastic rocks of the Cordillera Oriental have yielded 35 species and 29 genera of Cambrian to Sandbian age. Ordovician brachiopods from Chile, Bolivia and Peru are still poorly known, and consequently they are under-represented in our statistical analyses. This should, however, not be relevant to the results because the large Central Andean basin extends into NW Argentina (Salta and Jujuy provinces), where fossil faunas are adequately known (Benedetto 1998*b*). It seems, therefore, that the biogeographical signature of these faunas should not change substantially with new findings.

Multivariate analyses of faunal data were performed using the program PAST, version 1.28 (Hammer & Harper 2004). Cluster analysis was carried out only for brachiopods and bivalves, of which reasonably complete databases are available, whereas principal coordinates analysis (PCO) was applied only for brachiopods. In the cluster analysis, the Dice similarity index by unweighted pair group linkage was used to compare associations. As with other similarity indices, the Dice index ranges from zero (no similarity) to one (identity). Principal coordinates analysis is an ordination method that finds the eigenvalues and eigenvectors of a matrix containing the distances between all data points. It can be used to interpret large multivariate datasets including presence or absence data. The eigenvalues are given for the first and second eigenvectors, and these values are plotted in a coordinate system, graphically showing relationships (affinity) between data points (faunal assemblages). To enhance palaeobiogeographical affinities, both endemic and cosmopolitan taxa were excluded from statistical analyses.

Biogeographical affinities of Ordovician bivalves were evaluated previously by Sánchez & Babin (2003) using the Jaccard index. In the present paper, associations from 12 localities were clustered by using the Dice similarity index. Of the nearly 150 bivalve genera reported globally for the Ordovician Period, only 48 non-endemic taxa have been analysed statistically for two temporal intervals: Tremadocian–early Darriwilian, and Sandbian–Hirnantian.

Early Cambrian

Brachiopods

Rhynchonelliformean brachiopods in the Precordillera terrane are rare and still poorly known. A preliminary survey of the Lower Cambrian carbonate beds indicates the presence of *Nisusia* (probably a new species), *Wimanella* (close to *W. simplex* Walcott), some undetermined obolellids, and probable protorthids and eoorthids (Benedetto 2003*b*) (Fig. 2). *Nisusia* and *Wimanella* are confined to plates located within the equatorial belt (e.g. Laurentia, Siberia, Altay–Sayan, South China), supporting the low-latitudinal position of the Precordillera terrane at that time.

Agmatan

Discovery of the cone-shaped agmatan *Salterella macculochi* (Murchison) in a Lower Cambrian

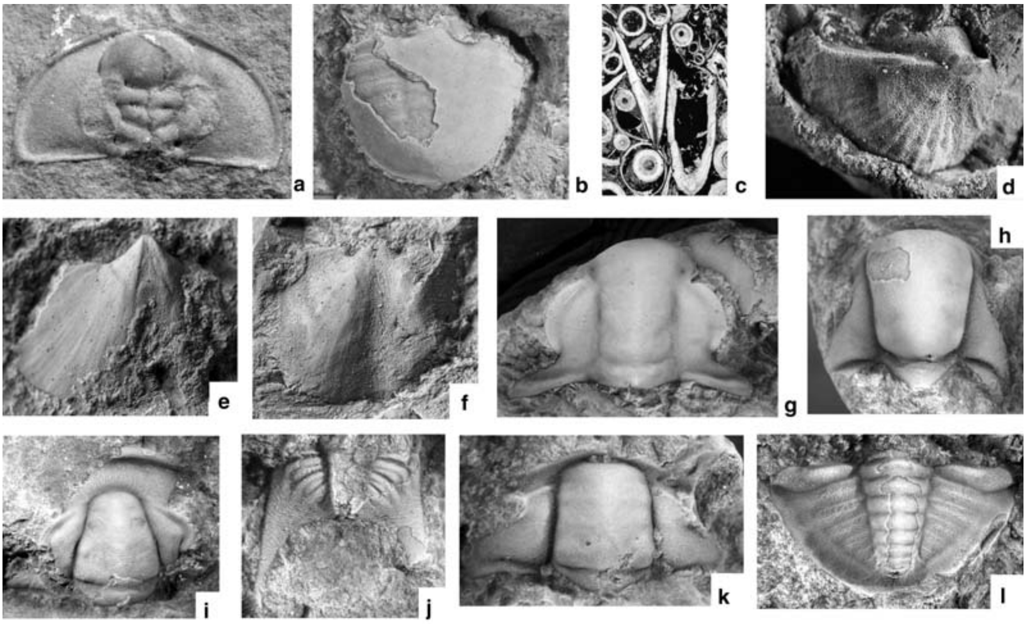

Fig. 2. Selected Cambrian trilobites and brachiopods from the Precordillera terrane. (**a**) *Arcuolenellus megafrontalis* (Vaccari), Cerro Totora Formation, Lower Cambrian; (**b**) *Bonnima* sp., La Laja Formation, Lower Cambrian; (**c**) *Salterella maccullochi* (Murchison), Ancaucha olistolith, Lower Cambrian; (**d**) *Nisusia* sp., Ancaucha olistolith, Lower Cambrian; (**e**, **f**) *Wimanella* sp., La Laja Formation, Middle Cambrian; (**g**) *Glossopleura walcotti* Poulsen, La Laja Formation, Middle Cambrian; (**h**) *Madarocephalus laetus* Resser, La Flecha Formation, Marjuman; (**i**, **j**) *Crepicephalus iowensis* (Owen), La Flecha Formation, Marjuman; (**k**, **l**) *Cheilocephalus brachyops* Palmer, La Flecha Formation, Furongian.

olistolith within the Los Sombreros Formation of the Precordillera is significant, as this species is restricted to North America, Greenland, Scotland and Spitsbergen, and it has never been found anywhere in Gondwana (Astini *et al.* 2004) (Fig. 2).

Trilobites

Borrello (1963) described the first Early Cambrian trilobite from the Precordillera and referred it to *Fremontella inopinata* Borrello. This species is based on poorly preserved material from the El Estero Member of the La Laja Formation (Sierra de Villicum). Later, Borrello assigned to this species an additional specimen from the locality of Zonda (Borrello 1964). Despite the poor preservation of this material it is possible to conclude that it is not conspecific with *F. inopinata*. In the Lower Cambrian units of the Precordillera (Sierra de Villicum) Borrello (1971) identified *Laudonia*, *Olenellus*, *Zacanthopsis*, *Eoptychoparia* and *Kootenia*, and later Bordonaro (1986) described species of *Olenellus*, *Bristolia*, *Bonnia* and *Antagmus.* This material is poorly preserved and many diagnostic features are obscured, precluding reliable identifications. Palmer & Repina (1993) mentioned the occurrence of *Olenellus* (*Mesolenellus*) and *Fremontella* in the La Laja Formation. New extensive trilobite collections from this unit are now under study by one of us (R.F.) and representatives of the Olenellidae, Biceratopsidae, Dorypygidae, Zacanthoididae and Ptychopariidae have been recognized. Initial results (Foglia & Vaccari 2006) indicate the presence of a new species of *Bonnima* Fritz and *Zacanthopsis* (previously reported by Borrello 1971, p. 405). Additionally, following the revision by Lieberman (1999, p. 193), a species of *Bolbolenellus* (Palmer & Repina 1993) close to *B. groenlandicus* (Poulsen 1927) has been recognized. Although the material is still scarce it may prove to be conspecific with *B. groenlandicus*, to which may belong the specimens described by Borrello (1963). So far, *Arcuolenellus megafrontalis* (Vaccari 1988) from the Cerro Totora Formation (Guandacol, La Rioja) is the best documented species from the Lower Cambrian sequences of the Precordillera. It is associated with three additional species of Olenelloidea and a Ptychopariidae. The Lower Cambrian boulders from the Los Sombreros Formation at Rio Ancaucha have yielded at least four species associated with the agmatan *Salterella maccullochi*, two of which belong to *Arcuolenellus* and a third can be referred to *Elliptocephala* Emmons. The fourth species is fragmentary but may belong to *Olenellus* (*Paudemias*). Olistoliths in the Los Túneles section contain *Sombrerella argentina* Vaccari & Bordonaro and fragmentary olenelloidea referred to *Olenellus*? sp. (Vaccari & Bordonaro 1993). Palaeogeographically, it is worth noting that both *Arcuolenellus* and *Bolbolebellus* belong to a clade recorded so far only in Laurentia.

Middle–Late Cambrian

Brachiopods

Some assemblages of lingulate brachiopods from Precordillera were described by Holmer *et al.* (1999). The fauna, composed mainly of acrotretids, comes from Middle Cambrian limestone olistoliths within Ordovician slope deposits named the Los Sombreros Formation. Other samples are from the Middle Cambrian Cerro Pelado Formation and the El Relincho olistolith of Marjuman age. All of the nine genera identified and two of the species are known elsewhere from Laurentia, and *Curticia* represents the first record outside that palaeocontinent. *Picnotreta* is a widespread genus recorded from Australia, Greenland, Kazakhstan and North Tien-Shan (Kirgizia). According to Holmer *et al.* (1999, p. 230), the Cambrian lingulate faunas of the Precordillera demonstrate a consistent similarity to the contemporaneous assemblages of North America. Moreover, they stressed their affinities with Siberian assemblages (e.g. both *Neotreta* and *Hadrotreta* have been recorded from southeastern Siberia).

Trilobites

Middle Cambrian trilobites are under revision; consequently they are not considered herein. Late Cambrian faunas from the Precordillera are derived largely from the La Flecha Formation (Marjuman–Sunwaptan) that crops out in the Guandacol area (La Rioja province) in the north to the Cerro Pedernal (San Juan province) in the south. This unit has been interpreted as a peritidal carbonate shelf by Cañas (1999). Other Late Cambrian fossiliferous localities contain resedimented boulders of the Empozada and Los Sombreros formations in Mendoza and San Juan (Bordonaro *et al.* 1993).

Vaccari (1994, 1995, 1996) recognized in the La Flecha Formation the *Crepicephalus*, *Aphelaspis* and *Saukia* zones. Trilobites from the *Crepicephalus* Zone include species of *Crepicephalus*, *Cosella*, *Pemphigaspis*, *Madarocephalus*, *Wellerаspis*, *Lonchocephalus*, *Kingstonia* and *Komaspidella*. So far, only *Dytremacephalus* and *Cheilocephalus* have been reported from the *Aphelaspis* Zone. An association belonging to the *Saukia* Zone is dominated by plethopeltids, represented by species of *Pletopelthis* and *Stenopilus*, recovered from the uppermost levels of the La Flecha Formation at Gualcamayo, La Silla and La Flecha localities. Boulders of the Empozada and Los Sombreros formations have yielded trilobites of the *Cedaria*, *Crepicephalus*, *Elvinia* and *Saukia* zones (Borrello 1971; Shergold *et al.* 1995; Bordonaro 2003). Reported taxa include widely distributed forms (e.g. agnostids and *Irvingella*), along with the geographically more restricted *Tricrepicephalus*, *Elvinia* and *Hungaia*.

Genera documented in the peritidal carbonates of the La Flecha Formation are overall exclusive to Laurentia (Fig. 2). Moreover, it is remarkable that the occurrence of several Late Cambrian species is shared by Laurentia and the Precordillera, such as *Crepicephalus iowensis* (Owen), *Tricrepicephalus texanus* (Shumard), *Komaspidella laevis* Rasetti, *Madarocephalus laetus* Resser, *Cheilocephalus brachyops* Palmer and *Elvinia roemeri* (Shumard), along with the pelagic trilobite *Irvingella major* Ulrich & Resser. Some of these species (e.g. *T. texanus*, *C. brachyops* and *E. roemeri*) are widely represented in North America (Palmer 1965; Westrop 1986; Pratt 1992; Chatterton & Ludvigsen 1998, among others), whereas others are more restricted. Among them, *M. laetus* was reported from Alabama, Tennessee and Quebec (Rasetti 1946, 1965), and *K. laevis* from Virginia, Missouri and Newfoundland (Rasetti 1961; Lochman 1968; Westrop 1992). Accordingly, Later Cambrian trilobite faunas from the Precordillera belong to the biogeographical province of Laurentia; the greatest affinities are evident with the eastern part of this palaeocontinent. These records strongly support the view that during the Late Cambrian there were no barriers to faunal exchange between the Precordillera and Laurentia.

Furongian–early Tremadocian

Brachiopods

The earliest rhynchonelliformean brachiopod so far published from the Central Andean basin is *Protorthisina simplex* Benedetto, from Furongian dark grey mudstones (Lampazar Formation) of the Cordillera Oriental of NW Argentina and Bolivia. Morphological and stratigraphical evidence suggests that this species is the stem group of both nanorthid and euorthisinid clades and that it gave origin to the genus *Kvania*, which is represented by at least three species in the lower Tremadocian strata of the Cordillera Oriental and western Puna (Benedetto

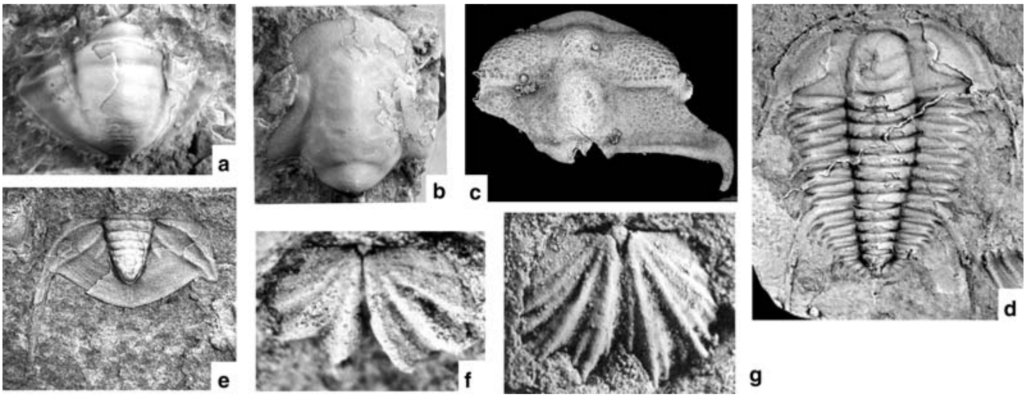

Fig. 3. Selected Upper Cambrian–lower Tremadocian trilobites and brachiopods from the Central Andean basin (CA), western Puna (WP) and Precordillera (P). (**a**, **b**) *Plethopeltis obtusus* (Rasetti), La Silla Formation, Furongian (P); (**c**) *Amzasskiella* n. sp., Las Vicuñas Formation, Furongian, lower Tremadocian (WP); (**d**) *Neoparabolina frequens argentina* (Kayser), Lampazar Formation, Furongian (CA); (**e**) *Onychopyge* sp., Lampazar Formation, Furongian (CA); (**f**) *Protorthisina simplex* Benedetto, Lampazar Formation, Furongian (CA); (**g**) *Kvania*? *primigenia*, Lampazar Formation, Furongian (CA).

2007*a*) (Fig. 3). *Kvania* is known elsewhere from the upper Tremadocian of Bohemia (where the type material come from; Mergl 1984) and NE Bavaria, Germany (Villas, in Sdzuy *et al.* 2001). This record of *Kvania* suggests a migratory route linking the Central Andean basin with north Gondwana, probably along the clastic platforms fringing the North African and Brazilian shields. Accompanying forms are *Apheoorthis*? Ulrich & Cooper and *Finkelnburgia* (Benedetto 2003*a*, plate 21, fig. 13).

In the revised version of the brachiopod *Treatise* the genus *Orusia* Walcott is mentioned as occurring in the Cambrian of Argentina (Williams & Harper 2000). It should be noted, however, that the presence of this genus in the Central Andean basin has not been confirmed. *Orthis saltensis* Kayser, which was reassigned to *Orusia* by Kobayashi (1937), was referred subsequently to *Nanorthis* by Ulrich & Cooper (1938). *Orusia putilliformis* Kobayashi (1937), of early Tremadocian age, was reassigned to *Nanorthis* by Castellaro (1963), but owing to the very limited material on which this species was erected and the lack of types designated, it has been considered a *nomen nudum* (Benedetto 2007*a*). Finally, the mention in the *Treatise* of *Otusia* Walcott for the Upper Cambrian of Argentina is also erroneous.

The Furongian–Tremadocian brachiopods from the Famatina basin are poorly known. Harrington (1938) referred some external moulds from the Volcancito Formation to *Finkelnburgia samensis* Kobayashi. In ornament, these specimens resemble *Kvania*? *primigenia* Benedetto, but because internal features are unknown their systematic position remains uncertain.

The uppermost Furongian–lower Tremadocian assemblages from Andean Gondwana cannot be included easily neither in the *Billingsella* Association nor in the *Huenella* Association recognized by Bassett *et al.* (2002) because of the absence of syntrophioidean pentamerides. Billingsellidines, on the other hand, are represented by a new genus that belongs to a lineage that probably branched off at the base of this clade (Benedetto, unpublished). A distinctive feature of the Andean assemblages, besides their low diversity, is the occurrence of the earliest representatives of the nanorthid clade, which during the late Tremadocian and Floian diversified in shallow shelf environments.

Trilobites

The only trilobite from the uppermost Cambrian restricted carbonate facies (La Silla Formation, Precordillera) is *Plethopeltis obtusus* (Vaccari 1995), a typical Laurentian form. Furongian trilobites are confined to the *Neoparabolina frequens argentina* Zone, both in the Central Andean basin (Lampazar Formation, Casa Colorada Member of the Santa Rosita Formation) and the Famatina Range (Volcancito Formation) (Fig. 3). They have been included traditionally in the 'olenid fauna' known elsewhere from several broadly similar environmental settings in biogeographically disparate regions such as Baltica, Avalonia, Laurentia and Siberia. Olenids are associated with several widespread agnostid taxa. The widespread *Asaphellus* and *Conophrys* are common forms in NW Argentina. Hapalopleurids (e.g. *Hapalopleura*, *Rhadinopleura*) are also common (Waisfeld &

Vaccari 2003); however, considerable generic splitting of the group and the lack of recent taxonomic revisions makes it difficult to assess their biogeographical significance.

Vaccari *et al.* (2006) noted that some lower Tremadocian taxa documented in the Cordillera Oriental suggest East Gondwana connections. *Onychopyge* occurs in the Furongian Volcancito Formation and Furongian and Lower Tremadocian strata of Cordillera Oriental (Harrington & Leanza 1957; Tortello & Esteban 1999). This genus is known from several species in the Furongian of NE China (Lu *et al.* 1986), and it is more widely distributed in the early or middle Tremadocian, with records in Australia, New Zealand, North and South China, and Mexico. The occurrence of the leiostegiid *Brackebuschia* in the lower Tremadocian of the Cordillera Oriental is also remarkable. Although the genus ranges into the early Sandbian (Ludvigsen 1980; Ebbestad 1999; Adrain, in Jell & Adrain 2003), the earliest records are so far restricted to the upper Tremadocian of Scandinavia (Tjernvik 1956; Ebbestad 1999) and the Cordillera Oriental.

Leiostegium, recorded from the lower Tremadocian of the Cordillera Oriental (Harrington & Leanza 1957; Waisfeld & Vaccari 2003) is known elsewhere from Laurentia, the Precordillera, China and Australia. *Australoharpes* occurs in the lower Tremadocian of the Cordillera Oriental (Harrington & Leanza 1957), and it was also reported from Victoria (Australia). Jell (1985) pointed out the affinities of the Victoria and NW Argentina faunas, and Webby *et al.* (2000) also discussed the affinities of the Australian fauna and emphasized the records of *Australoharpes* and *Onychopyge* as good indicators of these connections. The occurrence of *Amzasskiella* in the lower Tremadocian of the Cordillera Oriental reported by Vaccari *et al.* (2006) is also significant because it occurs in East Gondwana (China, Australia and New Zealand), as well as in Siberia and Kazakhstan. Hence, lower Tremadocian trilobites exhibiting restricted geographical distributions support faunal affinities with warm-water settings. Some of these forms are also present in the lower Tremadocian Las Vicuñas Formation (western Puna), where the occurrence of *Amzasskiella*, *Leiostegium* and *Onychopyge* (Vaccari & Waisfeld 2000, 2008) also reveals exchange with low-latitude areas.

Late Tremadocian–Floian

Brachiopods

The Precordilleran assemblages recovered from the lowermost part of the San Juan Formation limestones, of late Tremadocian–Floian age (*P. deltifer*/*O. evae* conodont zones) are moderately diverse and include *Archaeorthis*, *Paralenorthis*, *Orthidium*, *Ranorthis*, *Nothorthis*, *Nanorthis*, *Hesperonomiella*, *Hesperonomia*, *Tritoechia*, *Syntrophia*, *Parallelostrophia*, *Huacoella* and *Leptella (Leptella)* (Benedetto 2001*a*, 2002; Benedetto *et al.* 2003*a*) (Fig. 4). With the exception of *Ranorthis*, which occurs in Baltica, and the endemics *Huacoella* and *Parallelostrophia*, most of these taxa have also been recorded from Laurentia and South China (Zhan & Rong 2003).

In general, brachiopod assemblages recovered from inner to mid-carbonate-ramp settings of the Precordillera terrane may be ascribed to the low-latitude *Clarkella* Fauna (Bassett *et al.* 2002), typified by the co-occurrence of pentamerides, finkelnburgiids, eoorthids and tritoechiids. However, in contrast to the typical assemblages from Laurentia and Central Asian terranes, eoorthiids and finkelnburgiids are absent in the Precordillera, whereas ranorthids and orthidiellids are relatively abundant, as in Baltica (Egerquist 1999, 2004) and northern Gondwana (North Africa, Bohemia; Havlíček 1971, 1977). This is consistent with the mixed Laurentian–Baltic–Gondwanan signature of the Precordilleran benthic faunas noted by Herrera & Benedetto (1991) and supports the hypothesis that the Precordillera terrane was located at that time in an almost equidistant position between Laurentia and Gondwana (Benedetto *et al.* 1999). It should be noted that the *Clarkella* Fauna is unknown from coeval clastic cold–temperate platforms of the Andean region of Gondwana.

The Central Andean assemblages are different from the low-latitude faunas. A distinctive feature of these Andean faunas is the occurrence of the endemic euorthisinids *Notorthisina* Havlíček & Branisa (1980) and *Lesserorthis* Benedetto (2007*a*), and the earliest known enteletacean *Liparnorthis* Benedetto (Harper *et al.* 2004) (Fig. 5). Also notable is the absence of tritoechiids, which were dominant in the north Gondwanan '*Tritoechia–Protambonites* Association' (Bassett *et al.* 2002). The occurrence of *Astraborthis* Williams in upper Tremadocian beds of NW Argentina (Benedetto & Carrasco 2002) is biogeographically significant as it is known elsewhere only from the Welsh Borderland of Britain, although in slightly younger rocks (Williams 1974). The record of *Euorthisina* in Peru (Gutiérrez-Marco & Villas 2009), Bolivia, NW Argentina, Avalonia and South China (Zhan *et al.* 2006) points to a faunal connection along the Gondwana periphery, from intermediate to high latitudes. As noted previously (Benedetto & Sánchez 2003; Sánchez & Benedetto 2004; Benedetto 2007*a*), the autochthonous Andean shelves were the site of the early diversification of euorthisinids, nanorthids and primitive endopunctate orthides, and such a diversification pattern is in striking contrast to that seen in the low-latitude

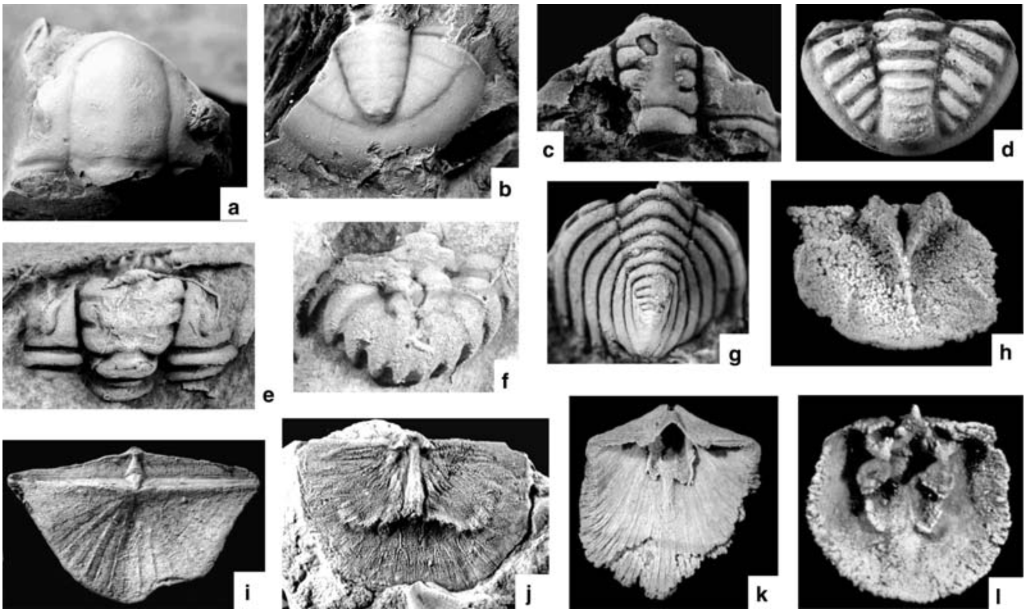

Fig. 4. Selected upper Tremadocian–Floian brachiopods and trilobites from the Precordillera terrane (San Juan Formation) and Sierra de Famatina. (**a**, **b**) *Peltabellia* n. sp., San Juan Formation, upper Tremadocian; (**c**, **g**) *Benedettia niquivilensis* (Harrington & Leanza), San Juan Formation, Floian; (**d**) *Annamitella harringtoni* Vaccari, San Juan Formation, Floian; (**e**, **f**) *Pliomera tmetophrys* Harrington & Leanza, Suri Formation, Floian (Sierra de Famatina); (**h**) *Syntrophia sanjuanina* Benedetto, San Juan Formation, upper Tremadocian; (**i**) *Leptella* (*L.*) *alata* Benedetto & Herrera, San Juan Formation, Floian; (**j**) *Huacoella radiata* Benedetto & Herrera, San Juan Formation, Floian; (**k**) *Tritoechia prima* Benedetto, San Juan Formation, Floian; (**l**) *Orthidium prominens* Benedetto, San Juan Formation, upper Tremadocian–lower Floian.

Laurentian carbonate platforms (Patzkowsky 1995). It is now apparent that the first ‘articulate’ brachiopod radiation on temperate to cold-water Gondwana shelves was not delayed with respect to other continents (e.g. Baltica, Laurentia) but it started before and involved different clades (see Harper 2005).

Bivalves

The lower Floian Precordilleran strata have yielded only two poorly preserved species of bivalves, a modiolopsid (*Modiolopsis*? sp.) and an undetermined ambonychiid. As ancestors of ambonychiids are unknown in Laurentia, and considering that the earliest known member of this family is from the Precordillera, the origin of this group may lie in that terrane. By the Late Ordovician ambonychiids diversified in Laurentia, becoming a characteristic component of its faunas.

In the Central Andean basin of NW Argentina and Bolivia several Gondwanan genera have been recorded (e.g. *Redonia*, *Coxiconchia*, *Babinka*, *Hemiprionodonta*; Fig. 5), supporting closest palaeogeographical relationships with south Europe (Sánchez & Babin 2005). The dendrogram in Figure 6a shows a well-defined Gondwana group embracing Iberia, Armorica and Morocco. By the late Tremadocian–early Floian bivalves underwent a remarkable radiation in the Andean basins of Gondwana including origination of new clades, such as goniophorinids, ucumariids (probably ancestral to the Anomalodesmata), redoniids and cycloconchids (Sánchez & Vaccari 2003; Sánchez 2005, 2006). Some of them dispersed subsequently along the Gondwanan shelves, whereas others became extinct before the end of the Ordovician. It seems likely that the coxiconchins, recently recognized as a clade within the Family Babinkidae (Sánchez 2008), and babinkids, evolved from the late Tremadocian *Coxiconchia babini* Sánchez from northwestern Argentina. Babinkids (including coxiconchins) are typical of Gondwanan and peri-Gondwanan terranes.

Bivalve faunas from Famatina are highly endemic (four of the seven Floian genera are endemic), leading to an inference of some kind of isolation from other basins and/or peculiar environmental conditions (e.g. narrow and unstable platforms peripheral to volcanoes). The Famatinan *Colpomya* is recorded elsewhere from younger

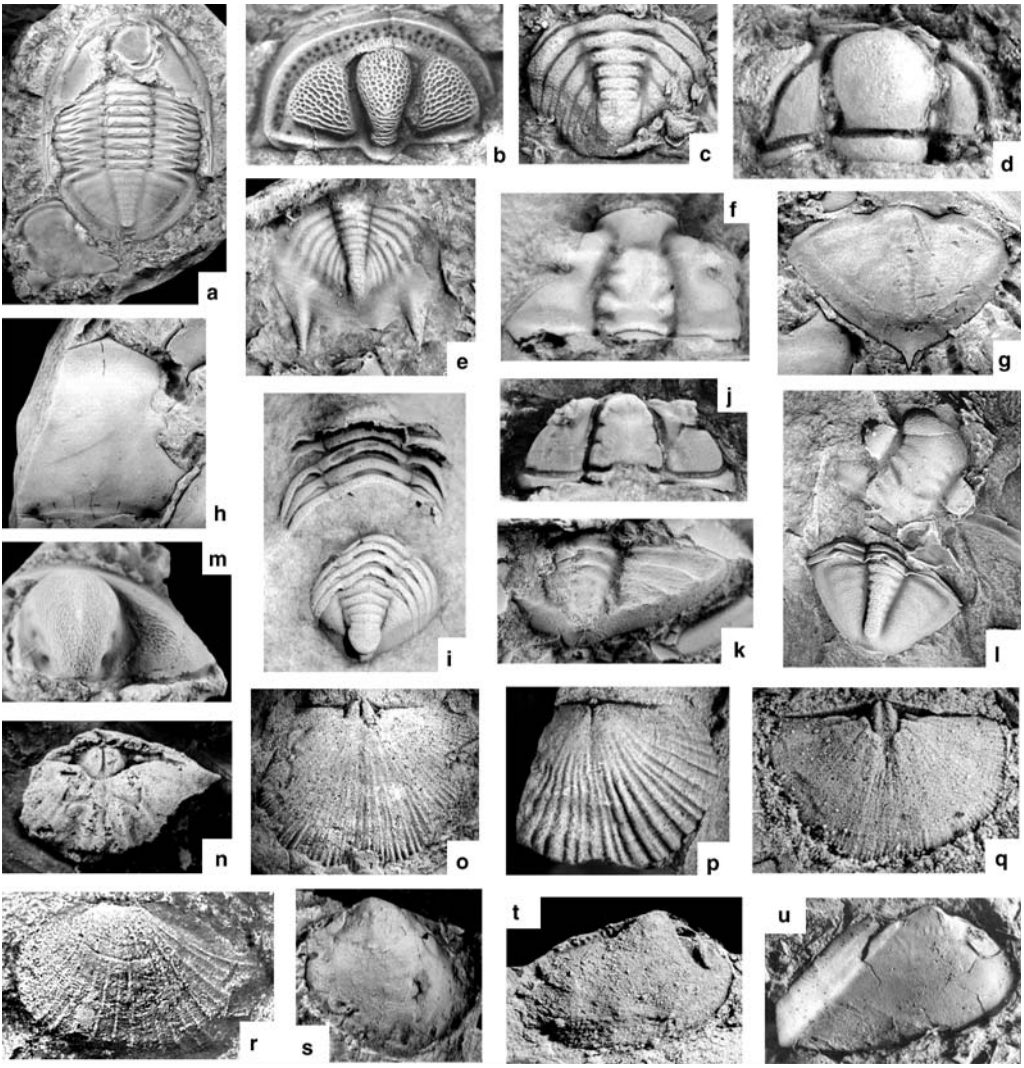

Fig. 5. Selected upper Tremadocian–Floian brachiopods, bivalves and trilobites from Sierra de Famatina (F) and Central Andean basin (CA). (**a**) *Merlinia megacantha* (Harrington & Leanza), Suri Formation, Floian (F); (**b**) *Famatinolithus jujuyensis* Benedetto & Malanca, Acoite Formation, Floian (CA); (**c**, **f**) *Neseuretus* (*N.*) *lipanensis* Waisfeld, Acoite Formation, Floian (CA); (**d**) *Carolinites* sp., Acoite Formation, Floian (CA); (**e**) *Hungioides intermedius* (Harington & Leanza), Suri Formation, Floian (F); (**g**, **h**) *Kayseraspis asaphelloides* Harrington, San Bernardo Formation, Floian (CA); (**i**, **j**) *Pytine wirayasqa* Vaccari, Waisfeld, Chatterton & Edgecombe, Acoite Formation, Floian (CA); (**k**, **m**) *Colpocoryphe perforata* Waisfeld, Acoite Formation, Floian (CA); (**l**) *Branisaspis* n. sp., Acoite Formation, Floian (CA); (**n**) *Astraborthis quebradensis* Benedetto, Coquena Formation, upper Tremadocian (CA); (**o**) *Incorthis* sp., Acoite Formation, upper Floian (CA); (**p**) *Euorthisina* sp., Acoite Formation, upper Floian (CA); (**q**) *Lipanorthis santalaurae* Benedetto, Floresta Formation, lower upper Tremadocian (CA); (**r**) *Ucumaris conradoi* Sánchez, Floresta Formation, lower upper Tremadocian (CA); (**s**) *Babinka notia* Sánchez, Santa Victoria Group, upper Tremadocian–lower Floian (CA); (**t**) *Suria ovalis* Sánchez, Suri Formation, Floian (F); (**u**) *Coxiconcha sellaensis* Sánchez & Babin, Sepulturas Formation, Floian.

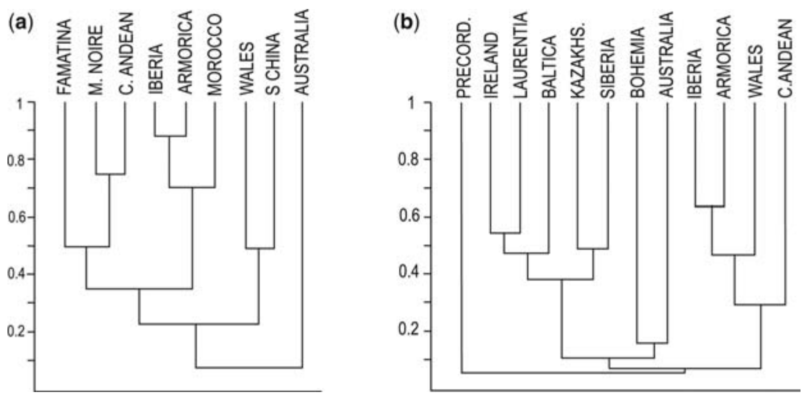

Fig. 6. Dice similarity index dendrograms for (**a**) Early Ordovician bivalves and (**b**) Late Ordovician bivalves.

rocks of Laurentia, *Redonia* from the Central Andean basin and south Europe, and *Goniophorina* from younger strata of China. *Suria*, a typical Famatinan genus, was reported recently by Gutiérrez-Marco *et al.* (2004) from the Ordovician of southern Peru (Fig. 5).

Trilobites

Records from Famatina (Bordo Atravesado Formation, upper Tremadocian) are restricted to deep-water environments, and hence are of little biogeographical meaning. Tortello & Esteban (2003) described an 'atheloptic assemblage' (see Fortey & Owens 1987) from this unit, composed of widespread forms as well as cyclopygids characteristic of peripheral sites marginal to Gondwana. No equivalent assemblage has been reported so far form the Cordillera Oriental.

Late Tremadocian faunas from the Cordillera Oriental include widespread elements (*Conophrys*, *Asaphellus*, *Apatokephalus*, *Parabolinella*, *Leptoplastides*, *Bienvillia*), some endemic asaphids (*Notopeltis*, *Doloreasaphus*, *Mekynophrys*), as well as some forms that are in need of taxonomic revision. Latest Tremadocian to early Floian low-diversity trilobite associations are included in the *Thysanopyge* Fauna (Harrington & Leanza 1957; Waisfeld *et al.* 1999). This fauna exhibited a rather narrow intraregional distribution and developed in relatively restricted, locally oxygen-deficient prodeltaic settings (Waisfeld & Astini 2003; Waisfeld & Vaccari 2008). Several endemic trilobites such as *Thysanopyge* itself, *Australopyge*, *Sanbernardaspis*, *Niobides*, *Zuninaspis* and probably '*Colpocoryphoides*', are associated with widespread forms (*Asaphellus*, *Megistaspis* (*Ekeraspis*), *Ogygiocaris*, *Conophrys*, *Hypermecaspis*, *Bienvilllia*). *Kayserapsis* is otherwise known from the upper Tremadocian of North China (Zhou & Fortey 1986), and lower Floian of Korea (Choi 1998), Australia (Laurie & Shergold 1996) and Kazakhstan (Lisogor 1961). The raphiophorid *Rhombampyx* has been recorded in Spitsbergen, Baltica and South China (Nielsen 1995), and the olenid *Psilocara* is so far known from the lower Floian of Spitsbergen. Although biogeographically sensitive elements are scarce, the records of *Kayseraspis*, *Psilocara* and *Rhombampyx* suggest exchange with warm-water areas. Recently, Waisfeld & Vaccari (2008) interpreted the peculiar biogeographical signature of the *Thysanopyge* fauna as a result of ecological or environmental factors coupled with a particular geodynamic context. Accordingly, restricted circulation and limited connections to oceanic waters might have been linked to the development of a shallow seaway related to an active volcanic arc to the west. In this setting, heterogeneous dysoxic or anoxic conditions, variable in intensity and duration, promoted the establishment of a distinctive trilobite fauna having only weak connections with other peri-Gondwanan regions.

By late early Floian–late Floian times, depositional patterns in the Central Andean basin changed, associated with a remarkable coastal progradation bringing about a complete shift in the array of trilobites. These associations, mostly referred to the *Famatinolithus* Fauna, display higher diversity than earlier Floian counterparts and also include a suite of endemics (*Famatinolithus*, *Pliomeridius*, *Branisaspis*, *Hoekaspis*), as well as widespread forms (*Hypermecaspis*, *Porterfieldia*). In inshore environments the widespread peri-Gondwanan genera *Neseuretus* and *Ogyginus* occur (Fortey & Cocks 1988, 2003). *Neseuretus* ranges into mid-shelf environments (Waisfeld 1995, 1997), where it is associated with *Colpocoryphe* and raphiophorids resembling British representatives of the group (see Fortey & Owens

1987), accounting for a west Gondwanan signature. Interestingly, these forms are associated with *Carolinites*, an epipelagic taxon distributed between 30°N and 30°S (McCormick & Fortey 1999), and *Psilocara* and *Pytine*, recently reported from the lower Floian of the Cordillera Oriental (Vaccari *et al.* 2006; Fig. 5). *Pytine* occurs elsewhere in Spitsbergen, Australia, North and South China, and probably Baltica.

Some members of the *Famatinolithus* Fauna have also been reported from Bolivia (e.g. Sella Formation and equivalents units) by Branisa (1965), Přibyl & Vaněk (1980) and Aceñolaza *et al.* (1999), and recently *Neseuretus*, *Anebolithus* and *Branisaspis* were recorded in the lower part of the San José Formation, southern Peru, by Gutiérrez-Marco *et al.* (2004). *Branisaspis* is an endemic asaphid hitherto known from the Cordillera Oriental of Argentina and Bolivia, and *Neseuretus* is a peri-Gondwanan form, extensively represented in the Cordillera Oriental of Argentina and Bolivia, and also in Famatina.

Unlike the *Thysanopyge* fauna, the *Famatinolithus* fauna has been recorded in widely separate areas of the Cordillera Oriental, and representatives of this fauna were also documented in the Cordillera Oriental of Bolivia (Branisa 1965; Přibyl & Vaněk 1980; Aceñolaza *et al.* 1999), accounting for the regionally widespread nature of this assemblage in the South American proto-Andean margin (Waisfeld 1998). From a biogeographical viewpoint, the Floian trilobite fauna reveals a complex pattern, which is consistent with the position of the South American margin at intermediate latitudes (see Fortey & Cocks 2003). Endemism, mainly in asaphids, supports a certain degree of isolation; meanwhile, provincially significant elements exhibit a mixture of affinities either with warm-water areas or with West Gondwana.

Coeval early and late Floian trilobite faunas from the volcaniclastic successions of Famatina show a mixture of East and West Gondwanan forms (Vaccari 1995; Waisfeld 1998; Fig. 5). Famatina shares with Precordillera mostly widely distributed taxa, and with the Cordillera Oriental, apart from widespread taxa, the endemic genera *Famatinolithus* and *Pliomeridius*. The *Neseuretus* biofacies has been recognized in inshore settings (Vaccari *et al.* 1993). *Neseuretus* is associated with *Merlinia*, otherwise known from the British Floian–Darriwillian (Fortey & Owens 1978; Rushton & Hughes 1981), and *Annamitella*. High-diversity middle-shelf faunas account for an interesting mixing of *Merlinia* and *Salterocoryphe*, of clear West Gondwana affinities, *Hungioides*, widely distributed in disparate peri-Gondwanan areas, and *Pliomera*, *Gogoella* and *Pliomerina*, showing connections with warm-water settings (East Gondwana and Baltica). The occurrence of the epipelagic *Carolinites* and *Oopsites* (Vaccari & Waisfeld 1994) also reinforces these connections. Low-diversity distal shelf faunas are composed of agnostids and olenids (*Porterfieldia*, *Hypermecaspis*).

Affinities of Ordovician trilobites from the Precordillera are particularly interesting as they document a progressive latitudinal change from a tropical position in the Tremadocian to high latitudes in the Hirnantian. A shallow-water assemblage dominated by bathyurids (e.g. *Peltabellia* and *Uromystrum*) and *Leiostegium* occurs at the base of the overlying San Juan Formation (upper Tremadocian) (Fig. 4). In the early Floian (*P. elegans* Zone) the endemic pliomerid *Benedettia*, which is closely linked to the Australian *Canningella*, has been recorded. *Annamitella*, *Illaenus*, *Platillaenus*, *Benedettia* and a new bathyurid species very close to *Petigurus* are present in the *O. evae* Zone. The bathyurid biofacies is characteristic of inshore settings of Laurentian and Siberian carbonate platforms (Fortey 1975; Fortey & Peel 1983). Species of *Peltabellia* occur in Laurentia and Siberia, whereas *Uromystrum* is so far restricted to Laurentia. *Leiostegium*, *Annamitella* and *Illaenus* exhibit a wide geographical distribution. The absence of *Annamitella* in the carbonate platform of North America and Siberia has been interpreted as a result of facies controls (Fortey & Shergold 1984; Webby & Edgecombe in Webby *et al.* 2000). Fortey & Cocks (2003) suggested that *Annamitella* is absent not only in the carbonate successions of Laurentia and Siberia, but also in the siliciclastic platforms of Europe. This pattern is only partially endorsed in Argentine basins. *Annamitella* is lacking in siliciclastic successions of the Cordillera Oriental of Bolivia and Argentina, and it is common in volcaniclastic settings of Famatina and Puna. However, *Annamitella* is the most widespread trilobite in the Floian to Darriwilian carbonate successions of the Precordillera (Vaccari *et al.* 2006), demonstrating that its distribution was not controlled by facies.

Trilobites from volcanosedimentary successions of western Puna (at Vega Pinato, partially equivalent to Aguada de La Perdiz Formation) exhibit interesting biogeographical affinities (Vaccari 2003). Relevant taxa include *Hystricurus* (*s.l.*), a form displaying a pan-Equatorial distribution, *Protostygina*, recorded in Kazakhstan, Bohemia, Spitsbergen and western Ireland, and *Gogoella*, so far known from Australia and Famatina. The record of a dikelokephalinid is also significant. Although representatives of this family exhibit a largely peri-Gondwanan distribution, earlier Ordovician species are restricted to East Gondwana. *Illaenus* and *Annamitella* are widely distributed forms, but in Argentina they are confined to the carbonate and volcaniclastic successions of the Precordillera, Famatina and Puna, and are lacking in the siliciclastic deposits of the Cordillera Oriental. In summary, trilobite faunas from western Puna exhibit a notable influence of East Gondwana elements, showing close affinities with the Famatina assemblages and a sharp contrast to those of the Cordillera Oriental.

Dapingian–Darriwilian

Brachiopods

The time interval analysed here ranges essentially from the *O. triangularis* to *E. suecicus* conodont zones. However, to analyse the affinities of the Famatina and Cordillera Oriental those assemblages from the late Floian *O. evae* have also been included. The dendrogram of Figure 7a shows three main clusters, which coincide largely with the biogeographical units recognized by Williams (1973): (1) low-latitude brachiopod faunas developed on a heterogeneous set of palaeocontinents and microplates; (2) mid- to high-latitude volcano-sedimentary Iapetus Ocean-related settings (the Celtic Realm *sensu* Neuman 1984); (3) mid- to high-latitude Gondwanan and peri-Gondwanan assemblages. It should be noted that the mid-latitude, highly endemic Baltic faunas cluster among the second group because endemic taxa have not been considered. This grouping does not differ substantially from the dendrogram produced by Harper (2005). Perhaps the main difference lies in that in Harper's analysis the Central Andean brachiopods cluster within the Celtic Realm, but this is no longer consistent with the absence of Celtic taxa in the Central Andes of Bolivia and Argentina. Also comparable is the dendrograma produced by Rong *et al.* (2005) in which Celtic, Gondwanan and low-latitude assemblages are clearly separated.

The Precordilleran faunas form a well-defined cluster together with the Laurentian (not differentiated here in 'marginal' and 'intra-plate' faunas) and Irish faunas (Tourmakeady Limestone; Williams & Curry 1985), which in turn are linked with the peri-equatorial carbonate-platform assemblages from South China, Kazakhstan and Altay–Sayan (marginal to the Siberia plate). This ensemble is roughly equivalent to the Toquima–Table Head Realm of Ross & Ingham (1970), redefined later by Neuman & Harper (1992). By Darriwilian time, several Celtic and Baltic genera migrated into the Precordillera basin, giving a mixed 'Laurentian–Baltic–Celtic' signature to these assemblages (Herrera & Benedetto 1991). In the correspondence analysis performed by Neuman & Harper (1992, fig. 2), the Precordillera plots near to the Celtic localities, although closer to the Laurentian faunas than any other Celtic assemblage. The same pattern is shown in the PCO diagram of Figure 8. By the Dapingian–early Darriwilian (*B. navis–L. variabilis* zones) typical Celtic Realm elements such as *Monorthis*, *Ffynnonia*, *Rugostrophia*, *Productorthis*, *Ahtiella* and *Inversella* (*Reinversella*) suddenly appear towards the top of the San Juan Formation, where they constitute up to 40% of the genera (Fig. 9). Except for *Inversella*, all these genera also occur in the Famatina basin, but in slightly older rocks. Increasing similarity between Famatinan and Precordilleran brachiopods can be interpreted as resulting from the final approximation of the Precordillera terrane to the Gondwana margin. It is believed that in such a palaeogeographical configuration, most brachiopods inhabiting the Famatina basin moved into the narrow seaway separating the two crustal blocks and then

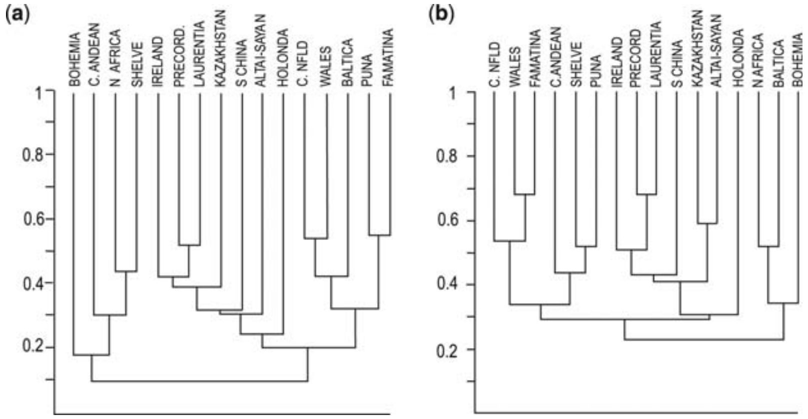

Fig. 7. (**a**) Dice similarity index dendrogram for the late Floian–early Darriwilian rhynchonelliform brachiopods (all orders included); (**b**) similar dendrogram for Order Orthida only.

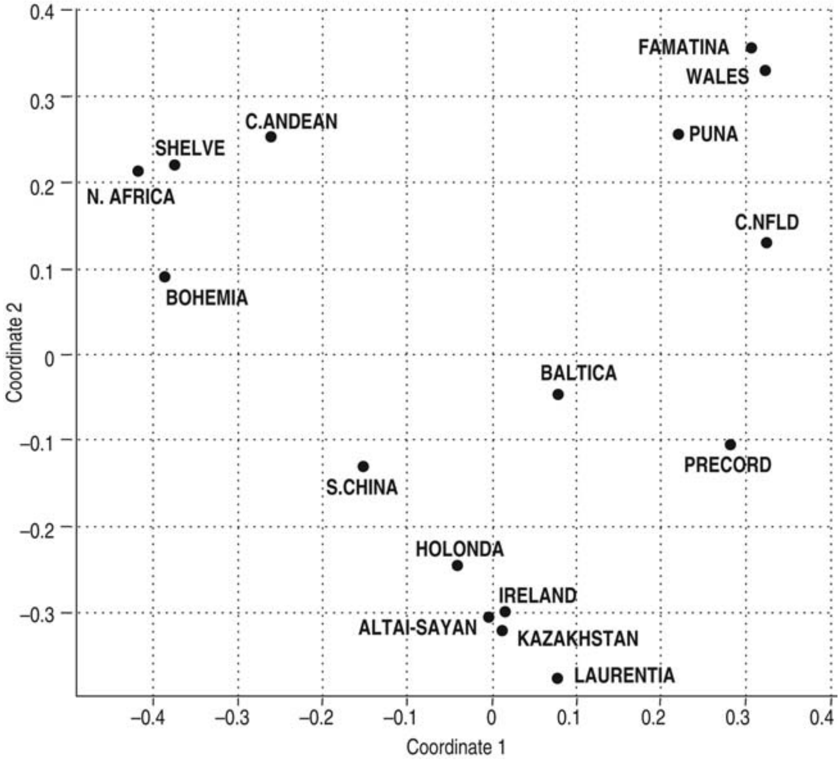

Fig. 8. PCO analysis (Dice similarity index) for the late Floian–early Darriwilian time interval (all rhynchonelliform orders included).

reached the Precordilleran carbonate ramp (Benedetto 2004; Benedetto & Cech 2006). Similarity between the brachiopods from the upper part of the volcanosedimentary succession of Famatina (Molles and Cerro Morado Formations) and the upper San Juan Formation of the Precordillera is particularly strong. The two units share similar species of *Ahtiella* and *Skenidioides*, suggesting that by Darriwilian time the Precordillera lay relatively close to the Famatina volcanic arc (Benedetto *et al.* 2003*b*).

Rhynchonelliformean brachiopods from Famatina, Wales, Central Newfoundland–New Brunswick and western Puna form a statistically significant cluster, supporting the distinctiveness of the Celtic faunas (Neuman & Bates 1978; Neuman 1984; Bruton & Harper 1985; Neuman & Harper 1992; Harper *et al.* 1996). The Celtic signature of the Famatinan brachiopods was confirmed by Benedetto (2003*c*, fig. 3) by using multivariate cluster analysis. In the present analysis, brachiopods from the western Puna volcaniclastic rocks (Benedetto 2001*b*) were included in the data matrix. As dendrograms (Fig. 7) and the PCO diagram (Fig. 8) show, the Puna assemblage clusters close to Famatina. Besides the endemic *Pinatotoechia* and *Trigonostrophia*, these regions share *Hesperonomia*, *Tritoechia* and *Rugostrophia.* The recent discovery of *Monorthis transversa* Benedetto, a typical Famatinan taxon, in the Puna high plateau of northern Chile (Atacama region) (Niemeyer *et al.* 2007), and of *Ffynnonia* in the Pampean Ranges, almost 200 km east of the Famatina Range (Verdecchia *et al.* 2007) (Fig. 10) confirms the wide geographical distribution of these taxa, supporting the existence of a more or less continuous chain of emergent volcanic islands separated by shallow seas along the Andean margin (Benedetto 1998*a*). Strikingly, the Puna brachiopods contrast markedly with those of the neighbouring Cordillera Oriental (Benedetto 1998*b*), which display affinities with the Welsh Borderland, Shelve District brachiopods (Williams 1974). This suggests the existence of a geographical barrier separating the Puna and Central Andean faunas. It appears that the barrier was the deep-water extensional back-arc basin developed behind the volcanic arc, which is well documented by thick turbidite deposits associated with submarine bimodal volcanism (Bahlburg 1990; Coira *et al.* 1999).

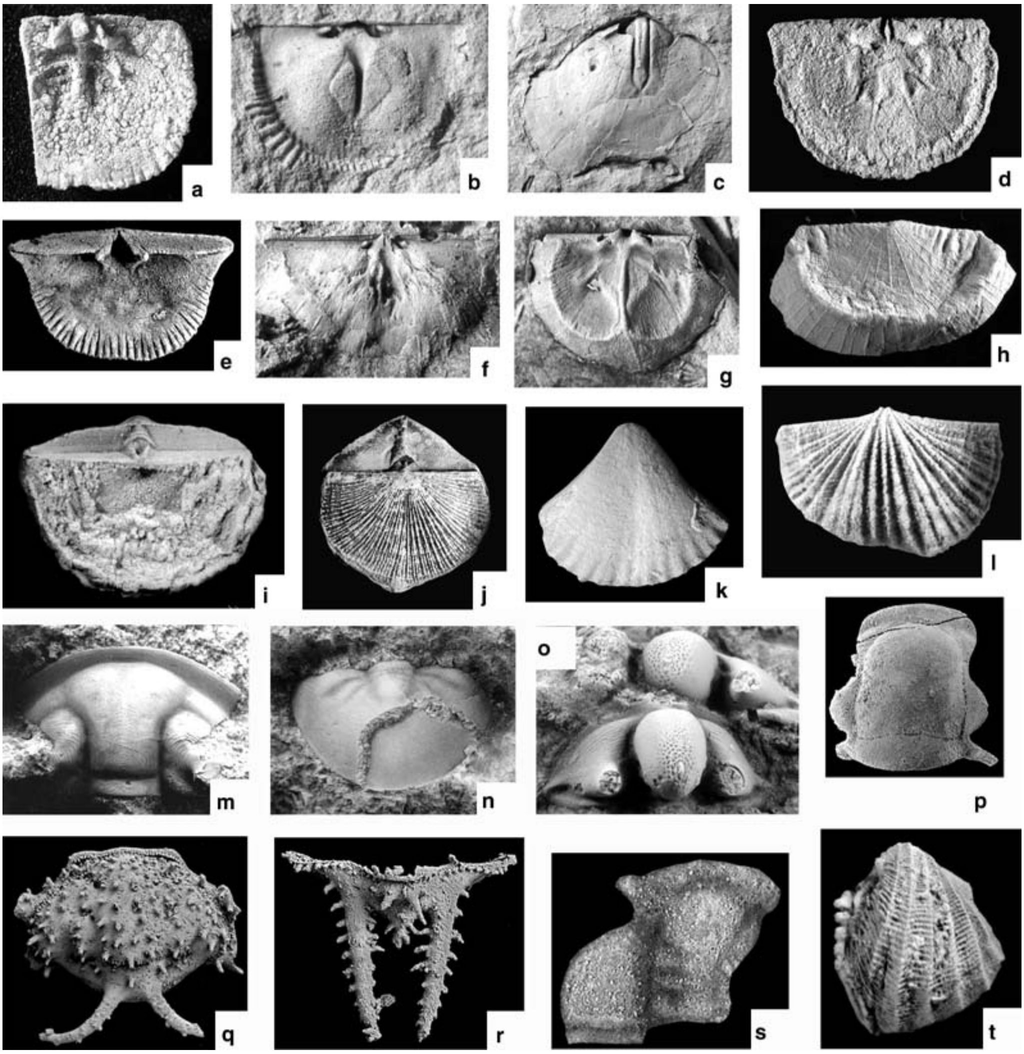

Fig. 9. Selected Dapingian–Sandbian brachiopods, trilobites and rostroconchs from the Precordillera terrane. (**a**) *Productorthis cienagaensis* Herrera & Benedetto, upper San Juan Formation, lower Darriwilian; (**b**) *Orthidium geniculatum* Herrera & Benedetto, upper San Juan Formation, lower Darriwilian; (**c**) *Porambonites* sp., upper San Juan Formation, lower Darriwilian; (**d**) *Taffia anomala* Benedetto & Herrera, upper San Juan Formation, lower Darriwilian; (**e**) *Monorthis cumillangoensis* Benedetto, San Juan Formation, Dapingian; (**f**) *Ahtiella argentina* Benedetto & Herrera, upper San Juan Formation, lower Darriwilian; (**g**, **i**) *Petroria rugosa* Wilson, San Juan Formation, Dapingian–Darriwilian; (**h**) *Inversella* (*Reinversella*) *arancibiani* Herrera & Benedetto, upper San Juan Formation, lower Darriwilian; (**j**) *Martellia talacastoensis* (Benedetto), upper San Juan Formation, lower Darriwilian; (**k**) *Idiostrophia* sp., upper San Juan Formation, lower Darriwilian; (**l**) *Ffynnonia spondyliformis* Benedetto, San Juan Formation, Dapingian–Darriwilian; (**m**, **n**) *Waisfeldaspis beatrizae* Vaccari, upper San Juan Formation, Darriwilian; (**o**) *Lehnertia wawisapa* Vaccari, Waisfeld, Chatterton & Edgecombe, Las Chacritas Formation, Darriwilian; (**p**) *Stenoblepharum astinii* Edgecombe, Chatterton, Vaccari & Waisfeld, Las Aguaditas Formation, Sandbian; (**q**, **r**) *Ceratocara argentina* Chatterton, Edgecombe, Vaccari & Waisfeld, Las Aguaditas Formation, Sandbian; (**s**) *Prosopiscus* sp., Las Aguaditas Formation, Darriwilian; (**t**) *Talacastella herrerai* Sánchez, San Juan Formation, lower Darriwilian.

The Central Andean faunas form, together with the NW African, Avalonian and Perunican faunas, a Gondwana cluster (Fig. 7b), although all these regions share only a few taxa. The genus *Incorthis* (Fig. 5), perhaps one of the most distinctive brachiopods of the temperate to cold-water Gondwanan shelves, has been recorded in Floian strata of NW Argentina, Bolivia and NW Africa (Morocco), but

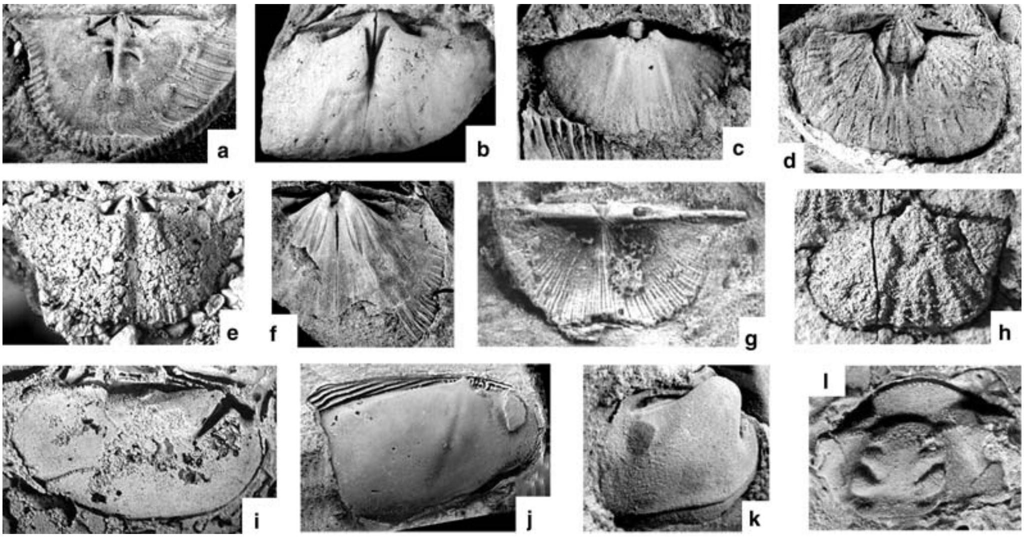

Fig. 10. Selected Floian–Dapingian brachiopods, trilobites, bivalves and rostroconchs from Famatina (F), NW Chile, and Pampean Ranges (P). (**a**) *Productorthis angulensis* Benedetto, Molles Formation, lower Dapingian (F); (**b**) *Famatinorthis turneri* Levy & Nullo, Molles Formation, Dapingian (F); (**c**) *Skenidioides kayseri* Benedetto, Molles Formation, Dapingian (F); (**d**) *Ffynnonia famatinensis* Benedetto, Suri Formation, upper Floian (F); (**e**) *Monorthis* aff. *cumillangoensis* Benedetto, Quebrada Grande Formation, Dapingian, NW Chile; (**f**) *Tritoechia* (*T.*) *mollesensis* Benedetto, Molles Formation, Dapingian (F); (**g**) *Ahtiella* cf. *argentina* Benedetto & Herrera, Molles Formation, Dapingian (F); (**h**) *Ffynnonia* sp., La Cébila Formation, Dapingian–Darriwilian, Pampean Ranges; (**i**) *Ribeira spinosa* Babin & Branisa, Suri Formation, Floian; (**j**) *Catamarcaia chaschuilensis* (Aceñolaza & Toselli), Chaschuil, Dapingian; (**k**) *Redonia suriensis* Sánchez & Babin, Suri Formation, upper Floian; (**l**) *Neseuretus* (*N.*) *chaschuilensis* Vaccari & Waisfeld, Chaschuil, Dapingian.

also in lower Dapingian volcaniclastic rocks of Famatina, indicating a certain degree of admixture between the Famatina back-arc basin and clastic shelves surrounding Gondwanan shields. The recent discovery of *Ahtiella* in the San José Formation (Floian) of Peru (Gutiérrez-Marco & Villas 2007) indicates that faunas of 'Famatinan' signature can be traced far to the north. Other typical Gondwanan genera, but not necessarily restricted to this palaeocontinent, are *Euorthisina*, *Tissintia* and probably *Tarfaya*. The presence of the last, however, needs to be confirmed by further studies (see Villas & Herrera 2004; Benedetto 2007*a*).

The statistical study performed by Tychsen & Harper (2004) was based exclusively on orthides. To compare their and our results, a new data matrix including solely orthid genera was constructed; the resulting Dice index dendrogram is shown in Figure 7a. It is worth noting that it does not differ substantially from the dendrogram depicted in Figure 7b. In the Early Ordovician dendrogram produced by Tychsen & Harper (2004, fig. 3), the Precordillera appears closest to Siberia, and Laurentia groups with 'South America' (probably the Central Andean basin), and by the 'Llanvirn' the Precordillera terrane groups with the Avalonia–South America–North Africa cluster, whereas Laurentia forms a separate cluster with Baltica. This is no longer consistent with the high latitude of NW Gondwana and the low to intermediate latitude of the Precordillera terrane at that time, as extensive carbonate platform demonstrate.

Rostroconchs

In South America, rostroconchs are scarce and almost restricted to the Upper Cambrian and Lower Ordovician successions. The Upper Cambrian and Lower Ordovician genera from the Central Andean basin are widespread forms. It is interesting to note that *Ribeiria spinosa* Babin & Branisa occurs both in the Central Andean basin (Sella Formation of Bolivia and Acoite Formation of Argentina) and Famatina basin (Fig. 10). In the Precordillera terrane *Ribeiria* is represented by a species close to *R. compressa* Whitfield, which is known otherwise from the Lower Ordovician of New York and Vermont. The endemic rostroconch *Talacastella* is restricted to the upper San Juan Formation (lower Darriwilian) (Fig. 9). Although its phylogenetic relationships are unclear, it seems to be related to Tremadocian genera of Manchuria and Laurentia (Sánchez 1986).

Trilobites

Diversity of trilobites from the Precordillera basin increases significantly during the Dapingian–Darriwillian, associated with the record of silicified faunas in the San Juan, Gualcamayo and Las Aguaditas formations. So far, *Annamitella*, *Illaenus*, *Waisfeldaspis*, *Prosopiscus*, *Macrogrammus*, *Pateraspis*, *Pliomerina*, *Carolinites*, *Telephina*, *Chomatopyge*, *Basilicus (Basiliella)*, *Nileus*, *Ampyx*, *Mendolaspis*, *Lehnertia*, *Protoincaia*, *Bancroftolithus*, *Kweichowilla*, *Changchowilla*, *Nieszkowskia*, *Platycalymene*, *Frencrinuroides*, *Lasaguaditas*, *Lasarchopyge*, *Stenoblepharum*, *Ceratocara* and *Porterfieldia* have been recognized. Among them, *Annamitella*, *Illaenus*, *Nieszkowskia*, *Platycalymene*, *Carolinites*, *Telephina*, *Stenoblepharum*, *Basilicus (Basiliella)*, *Nileus*, *Ampyx*, *Mendolaspis* and *Porterfieldia* are widespread taxa. According to Edgecombe *et al.* (1999), trilobites from the Las Aguaditas Formation exhibit two broadly contrasting biogeographical patterns: Laurentian and peri-Gondwanan. Laurentian affinities are phylogenetically supported by the presence of sister species of *Ceratocara* (Chatterton *et al.* 1997), *Stenoblepharum* (Edgecombe *et al.* 1997) and *Frencrinuroides* (Edgecombe *et al.* 1998) in the east of North America. On the other hand, peri-Gondwanan affinities are upheld by key taxa from this paleocontinent, such as *Prosopiscus*, *Pliomerina*, *Pateraspis*, *Lehnertia*, *Kweichowilla* and *Changchowilla* (Fig. 9). The presence of endemic forms (*Waisfeldaspis*, *Protoincaia*, *Bancroftholithus*, *Lasaguaditas* and *Lasarchopyge*) is also remarkable. The same pattern of mixed Laurentian and peri-Gondwanan taxa persists in the Sandbian.

Darriwilian trilobites have been reported elsewhere from Eastern Peru by Hughes *et al.* (1980). The association is composed of *Anebolithus*, *Ogygiocaris* (=*Ogygiocarella*) and *Porterfieldia*. These are widespread forms, except for *Anebolithus*, so far known from the Floian or Dapingian of Wales (Hughes & Wright 1970) and Southern Peru (Gutiérrez-Marco *et al.* 2004).

Sandbian

Brachiopods

No shelly faunas of this age have been encountered either in the Famatina Range or in the western Puna region. In the former there is a stratigraphical gap spanning the Late Ordovician–Late Devonian, whereas in the Puna basin shallow-water volcaniclastic deposition evolved in post-Dapingian time to deep-water turbidites lacking shelly faunas (Bahlburg 1990). In contrast, Sandbian brachiopods are well documented in the Precordillera terrane and the Central Andean basin. Precordilleran brachiopods come from the Las Plantas Formation, a mixed carbonate–clastic succession (Benedetto 1995), and from the almost coeval bioclastic sandstones named La Pola Formation (Benedetto 1998*c*, 2003*d*). The biogeographical signal of these faunas is not conclusive, but could be taken as indicating predominantly Gondwanan affinities. Some components, such as *Tissintia*, *Aegiromena*, *Drabovia*? and *Howellites* cf. *macrostoma* Barrande, are members of the Mediterranean *Aegiromena–Drabovia* Fauna (Havlíček 1989) (Fig. 11). These taxa are associated with the pan-tropical genera *Atelelasma* and *Anoptambonites*, the former having numerous species in Laurentia and the latter in Kazakhstan, Siberia, Australia, Scotland and North America. The fauna from the Las Plantas Formation includes a species of *Campylorthis* (Benedetto 1995) which, until its recognition in the Precordillera basin, was thought to have been an endemic Scoto-Appalachian genus, and *Oanduporella*, known elsewhere from the East Baltic (Hints 1975) and Ireland (Harper *et al.* 1985) (the material illustrated by Havlíček & Branisa 1980, from Bolivia, seems to be closer to *Nocturniella* than *Oanduporella*). *Destombesium*, which occurs in the Precordilleran Trapiche Formation of Katian age, has been recorded elsewhere from Bolivia and Morocco (Benedetto 1999*a*).

A dendrogram resulting from a data matrix of 112 genera (Fig. 12) shows three well-defined clusters. The first encompasses the North African, Bohemian (Perunican) and Armorican brachiopod assemblages, which in turn are linked with the Central Andean and Precordilleran faunas. This grouping is significant because for the first time affinities of the Precordilleran brachiopods shift from Laurentian to Gondwanan, reflecting, in our opinion, the final approximation and docking of the Precordillera terrane against the proto-Andean margin (Benedetto 2004).

The low-diversity upper Darriwilian–Sandbian brachiopods from the Central Andes are almost exclusively of Mediterranean type. Havlíček & Branisa (1980) first reported from Bolivia *Destombesium*, *Drabovinella*, *Eorhipidomella* (probably synonymous with *Crozonorthis*) and *Aegiromena*. The finding of *Heterorthis alternata* (Sowerby) (Havlíček 1990) stressed the similarities to Mediterranean assemblages. New sampling from the Bolivian San Benito Formation cropping out in the Cochabamba area yielded *Drabovinella* cf. *erratica* (Davidson) (Suárez Soruco & Benedetto 1996) and a species closely related to *Rafinesquina pseudoloricata* (Barrande) (unpublished). *Drabovinella*

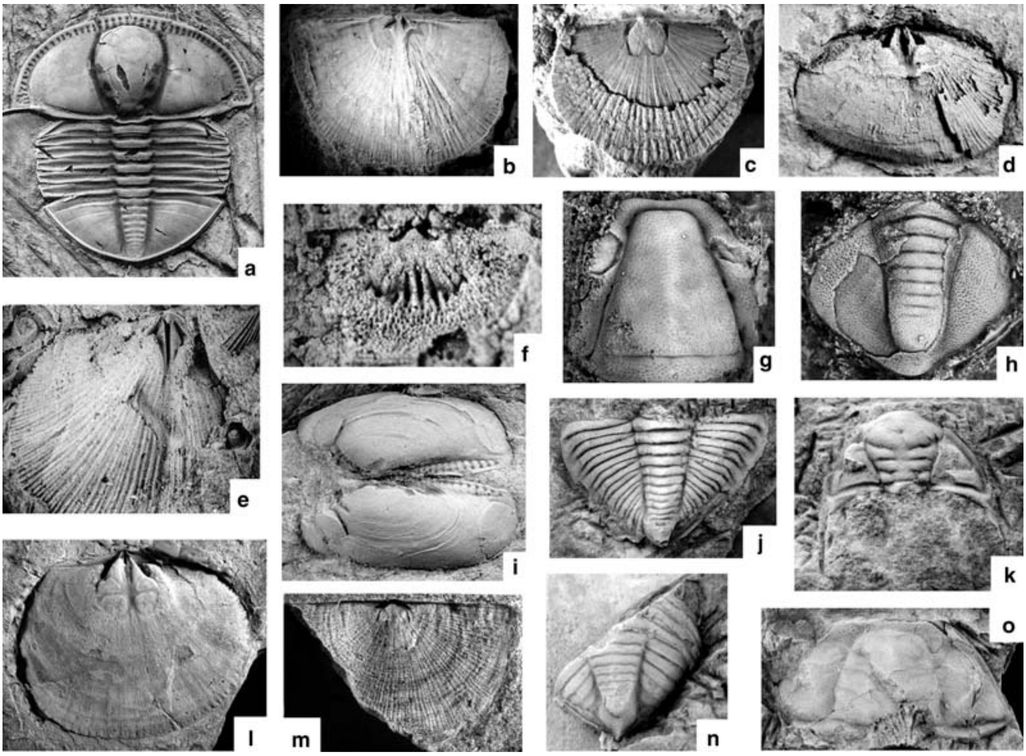

Fig. 11. Selected Sandbian, Katian and Hirnantian brachiopods, bivalves and trilobites. (**a**) *Incaia deormacheai* Baldis & Cabaleri, Las Aguaditas Formation, Sandbian (Precordillera); (**b**) *Tissintia robusta* Benedetto, Las Plantas Formation, Sandbian (Precordillera); (**c**) *Campylorthis gualcamayensis* Benedetto, Las Plantas Formation, Sandbian (Precordillera); (**d**) *Destombesium argentinum* Benedetto, Trapiche Formation, Katian (Precordillera); (**e**) *Drabovinella* sp., San Benito Formation, Katian (Bolivia); (**f**) *Aegiromena glacialis* Benedetto, boulder of Sandbian age from Hirnantian glacigenic diamictite (Precordillera); (**g**, **h**) *Huemacaspis gallinatoensis* Waisfeld & Henry, Santa Gertrudis Formation, Sandbian (Central Andean basin); (**i**) *Cadomia typa* de Tromelin, Santa Gertrudis Formation, Sandbian (Central Andean basin); (**j**, **k**) *Mucronaspis sudamericana* (Baldis & Blasco), Don Braulio Formation, Hirnantian (Precordillera); (**l**) *Hirnantia sigittifera* (M'Coy), Don Braulio Formation, Hirnantian (Precordillera); (**m**) *Paromalomena polonica* (Temple), Don Braulio Formation, Hirnantian (Precordillera); (**n**, **o**) *Eohomalonotus villicumensis* (Baldis & Blasco), Don Braulio Formation, Hirnantian (Precordillera).

mojotoroensis Benedetto also forms monospecific assemblages in the Cordillera Oriental of northwestern Argentina (Benedetto 1999*b*). The sole brachiopod described from the upper Darriwilian Contaya Formation of eastern Peru is *Tissintia* (Hughes *et al.* 1980), which is a common taxa in Bohemia, Spain, Morocco and England, but also in the Precordillera terrane (Las Plantas Formation). The second cluster embraces the Baltic and 'Anglo-Welsh' faunas, reflecting the progressive separation of Avalonia from Gondwana through the Ordovician as the Rheic Ocean enlarged, and its drifting towards Baltica as the Tornquist Ocean became narrower (Cocks 2000). The third cluster is formed by the closely related North American and Scottish faunas (the 'Scoto-Appalachian' province of Williams 1973). They are weakly linked to the NE Chinese and the Kazakhstanian faunas; the former, according to Cocks & Zhan (1998), show some affinity with those from the Sibumasu terrane, not included in our analysis. The Australian (Percival 1991) and Tasmanian (Laurie 1991) brachiopods form an independent pair having low affinity with Laurentia–NE China–Kazakhstan, which form a large low-latitude cluster. The PCO diagram (Fig. 13) also shows a well-defined grouping formed by the Central Andes, Morocco, Bohemia and Armorica, which reaches the highest values on the first eigenvector. This cluster is well separated from the low-latitude faunas, which have much lower scores on the first eigenvector. Both Australia–Tasmania and Avalonia–Baltica are separate from these clusters whereas the Precordillera terrane plots at an intermediate position between

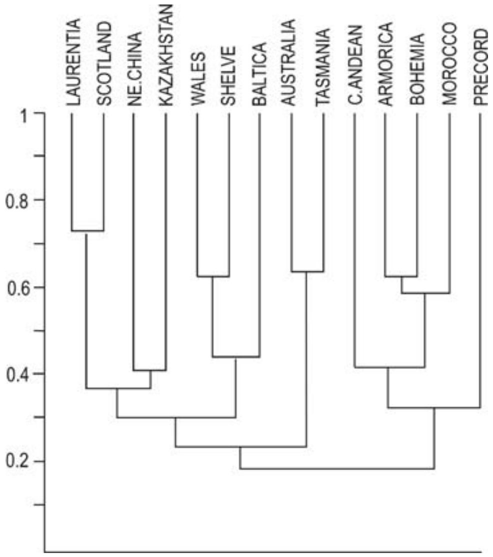

Fig. 12. Dice similarity index dendrogram for Sandbian brachiopod assemblages.

the two main clusters. This is due to the co-occurrence of Mediterranean (the most abundant), Scoto-Appalachian, Baltic and pan-tropical genera, which may be interpreted as evidence of some geographical separation of the Precordillera terrane from Gondwana or, alternatively, as the result of the marginal location of the Precordillera basin with respect to the Gondwana plate. Deposition in the Precordillera of a thick succession of graptolitic black shales punctuated by brachiopod-rich carbonate lenses reflects a major transgressive event that can be correlated with the widespread late Darriwilian–Sandbian Furudal Highstand (Nielsen 2003). Thus, the input of cosmopolitan or widespread brachiopods seems to be closely related to global sea-level fluctuations, the highstand events enhancing dispersal of larvae across tectonic arches (Stigall Rode & Lieberman 2005). As a result, the sea penetrated profoundly into the Gondwana plate where shallow-water sandy deposits (e.g. San Benito Formation of Bolivia; Capillas Formation of Subandean Ranges of NW Argentina) are characterized by nearly pure, low-diversity Gondwanan assemblages.

Bivalves

The Sandbian bivalves so far recorded from the Central Andean basin are the glyptarcoid *Zaplaella* Sánchez, and the palaeotaxodonts *Cardiolaria* and *Cadomia* (Fig. 11). All of them show clear affinities with cold to temperate areas of Gondwana (Sánchez 1986, 2003; Sánchez *et al.* 2003). The species

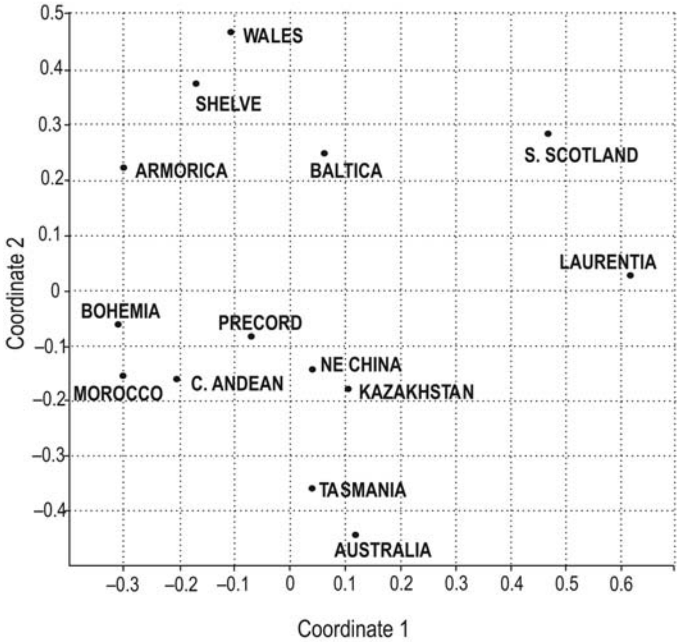

Fig. 13. PCO analysis (Dice similarity index) for Sandbian brachiopod assemblages.

Cadomia typa de Tromelin, recorded in the Santa Gertrudis Formation, was described from Iberia and the Armorican Massif, whereas glyptarcoids are typical of peri-Gondwanan shelves. *Cardiolaria* has been recorded from Morocco, Spain, the Armorican Massif and Wales. The genus *Lyrodesma*, recorded in the Bolivian San Benito Formation (Sánchez & Suárez Soruco 1996), is a widespread genus lacking biogeographical significance.

The Sandbian bivalve fauna recovered from boulders within the Hirnantian glacigenic diamictite (Don Braulio Formation) consists of 10 genera, eight of which are endemic. Strong endemism was interpreted as the result of a local, short-term radiation event followed by extinction, linked to a local climatic warming (Sánchez 1999*a*, *b*). The two non-endemic genera are *Praenucula*, a widespread form, and *Concavodonta*, restricted to Gondwana. The cluster of Figure 6b shows two main groups, a 'Gondwana group', to which the Central Andean bivalves belong, and a 'Northern group', which includes Ireland, North America and other areas from the northern hemisphere.

Trilobites

Sandbian trilobite faunas from the Cordillera Oriental are of low diversity and sparse. The lower Sandbian association reported by Waisfeld (1996) and Waisfeld & Henry (2003) from the Santa Gertrudis Formation is composed of *Neseuretus*, the endemic asaphid *Hoekaspis, Huemacaspis* (the only representative of the Kerfornellinae outside southern central Europe and northern Africa) and *Eohomalonotus*?, also reported from the last mentioned regions (Fig. 11). Similar associations are documented in Bolivia (Přibyl & Vaněk 1980). Thus, available data suggest faunal connections with West Gondwana during Sandbian times.

Katian and Hirnantian

Brachiopods

Katian brachiopods are rare in the Andean basins. They are restricted to the upper part of the Trapiche Formation in the northern Precordillera, which contains *Trucizetina*, *Hotedahlina*? and *Cyphomena*? (Benedetto 1999*a*). No representatives of the deep-water *Foliomena* Fauna have yet been discovered in South America. Typical elements of the *Hirnantia* Fauna are well documented in the Don Braulio Formation of the central Precordillera (Benedetto 1986, 1990; Astini & Benedetto 1992), including most of the taxa that characterize the Kosov Province defined by Rong & Harper (1988) (Fig. 11). Their association with glacigenic rocks indicates conditions of grounded glaciers, and a near shore floating ice shelf supports the high-latitude (*c.* 60°S) location of the Precordillera by the Hirnantian Stage (Astini 1999*b*). A deep-water Hirnantian fauna dominated by *Anisopleurella* and small specimens of *Reuschella* has also been recorded.

Bivalves

Hirnantian bivalves are represented by the widespread genus *Modiolopsis*, which is associated with the shallow-water *Hirnantia* fauna in the Don Braulio Formation, and *Whiteavesia*, from coeval deep-water mudstones. The latter genus has been recorded elsewhere from Laurentia and Siberia (Sánchez *et al.* 1991).

Trilobites

In the Hirnantian successions of the Precordillera a low-diversity trilobite association including *Mucronaspis* and *Eohomalonotus* (Fig. 11) has been reported, both forms having displayed a wide geographical distribution.

The Precordillera terrane: Laurentian or Gondwanan?

Trilobite evidence through the entire Cambrian successions of the Precordillera points to a strong faunal identity with Laurentia, and denotes the absence of faunal exchange with areas of East Gondwana. Essential for paleogeographical interpretation is the fact that Precordilleran trilobites are mostly from shallow-water environmental settings. It is widely accepted that such 'inshore biofacies' tend to be confined to a single palaeocontinent (Fortey & Owens 1978) and, hence, these associations are among the best biogeographical markers. In the parautochthonous model proposed by Aceñolaza *et al.* (2002), and recently reviewed by Finney (2007), the Precordillera terrane (or Cuyania) in the Cambrian is placed adjacent to the Gondwanan margin, close to Antarctica. In such a reconstruction Australia, Antarctica and Cuyania are in a similar latitudinal position, with carbonate platforms developed in continuity in the three areas, without separation by oceanic barriers. Despite such a geographical proximity, no faunal elements of the Redlichiid Realm, which characterizes the Cambrian trilobites of Antarctica and Australia, have been recorded in the Precordillera terrane. On the other hand, in the parautochthonous reconstruction by Finney (2007, fig. 5) a fluid bidirectional faunal exchange between the Precordillera and Antarctica–Australia should be expected. Finney (2007, p. 149) argued that the westward direction of equatorial oceanic currents is responsible for the lack of tropical Gondwanan elements in the Precordillera. However, as stated above, during the Furongian–Tremadocian interval active larval dispersion into the Andean platforms from Australia, New Zealand and South China is well documented by the occurrence of characteristic forms such as *Onychopyge*, *Amzasskiella* and *Australoharpes*, among others (Vaccari *et al.* 2006; Vaccari & Waisfeld 2008). If Cuyania was adjacent to Gondwana, the question that arises is: why are faunal affinities of the Precordillera exclusively Laurentian until the Tremadocian? On the other hand, if Laurentian faunas were carried into the Precordillera by 'west'-flooding equatorial currents (Finney 2007, fig. 10) it is hard to explain why they did not reach the East Gondwanan carbonate platforms. Clearly, the more parsimonious biogeographical interpretation is to place the Precordillera terrane close to Laurentia.

With respect to the questioning of the biogeographical value of olenelloids (Finney 2007, p. 145) and the role of oceanic currents in their dispersal, it is interesting to note that, in the exhaustive study of Lower Cambrian trilobites by Lieberman (2003, and references therein) he found that geodispersal had little influence in radiation and distribution of the olenellids. Instead, observed patterns appear to be mediated mainly by vicariance events associated with continental fragmentation.

The upper Tremadocian–Floian trilobites of the Precordillera belong to the bathyurid fauna, indicating unequivocal affinities with Laurentia (see Cocks & Torsvik 2002, fig. 3), which is what can be expected in the light of the Laurentian signature of the Cambrian trilobites. Most rhynchonelliform brachiopods from this interval are present in Laurentia, but they are also known from other low-latitude continents (pan-tropical taxa). The presence in the Floian–Dapingian of two genera in common with Baltica (*Nothorthis*, *Ranorthis*), together with the appearance of Celtic forms (e.g. *Monorthis*, *Ffynnonia*), strongly suggests a trans-Iapetus trajectory for the Precordillera as depicted by Benedetto (1998*a*) and Cocks & Torsvik (2006), and not a displacement from the southern margin of West Gondwana as Finney (2007, fig. 5a, b) showed in his parautochthonous model.

At that time, the autochthonous Andean shelves were the site of early diversification of euorthisinids, nanorthids and primitive endopunctuate orthides. However, no Gondwanan taxa belonging to these lineages have been discovered in the Precordillera terrane. The Gondwanan diversification pattern contrasts strongly with that seen in the low-latitude Laurentian platforms (summarized by Patzkowsky 1995) and demonstrates that at that time the Precordillera terrane was not attached to Gondwana. Bivalves also underwent a significant radiation in the Andean clastic platforms with the appearance of endemic taxa, but non-endemic forms indicate closest palaeogeographical relationships with Iberia, Armorica and Morocco. No bivalves of such lineages have been recorded in Cuyania, as would be expected in the parautochthonous interpretation.

Although by the Darriwilian the number of taxa (not the percentage) shared by the Precordillera terrane and Laurentia is higher than in previous levels, as Finney (2007) noted, it is important to point out that (1) most of them, if not all, are very widespread taxa, thus having limited biogeographical significance, and (2) the number of taxa shared with Laurentia reached a maximum at that time (*Ahtiella argentina* Zone) because communities were by far the richest of the Ordovician carbonate platform. This does not mean that 'dispersal between Laurentia and Cuyania was far easier and more efficient' (Finney 2007, p. 141) at that time, but rather denotes a change in ecological conditions (Benedetto 2007*b*). More significant for palaeobiogeographical interpretation is the progressive increase of non-Laurentian taxa throughout the Ordovician until the Silurian. This is the reason why we have used in our analyses 'percentage' rather than 'total number' of taxa. We still consider that the best explanation for this change in the biogeographical signal is the drifting of the Precordillera terrane away from Laurentia and its approximation to Gondwana, as proposed previously (see Benedetto *et al.* 1999). The translation of the Precordillera terrane along the Gondwana margin does not account for such an evolving biogeographical pattern.

By the Dapingian–Darriwilian, a well-defined cluster embracing Famatina, western Puna, Wales, Central Newfoundland and New Brunswick assemblages had emerged, supporting the distinctiveness of the Celtic brachiopod realm. Precordilleran faunas are characterized by a sudden increase of Celtic components. Notable also is the presence of species in common with Famatina, suggesting that Cuyania had been located at that time relatively close to the Famatina magmatic arc. The mixed Laurentian–peri-Gondwanan signature of trilobites also indicates approximation of the Precordillera microcontinent to Gondwana. A major incongruence in Finney's (2007) model is the arrival of the Cuyania terrane at its present position during Late Silurian–Devonian time. According to this reconstruction the Precordillera was located by the Early Ordovician at the corner formed by southern South Africa (Kalahari Craton) and southern South America. However, as Benedetto (2004) stated previously, it is well known that both the Cape fold belt and the Malvinas–Patagonia basins lack Cambro-Ordovician carbonates; their first linkage with the Precordillera does not become evident

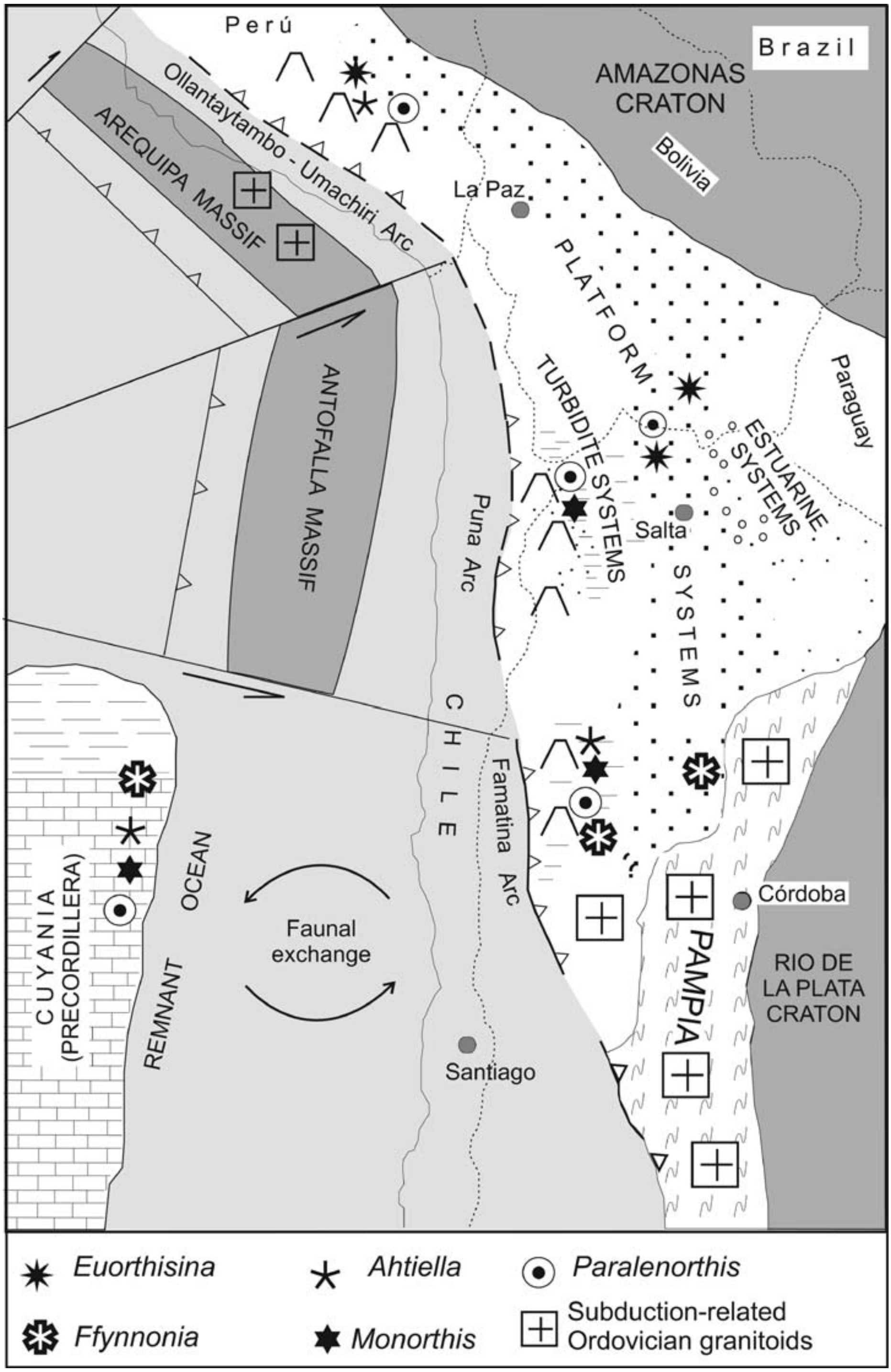

Fig. 14. Palaeogeography of the proto-Andean margin of Central and southern South America showing the volcanic arcs and back-arc basins discussed in the text, and the distribution of key rhynchonelliform brachiopods in Dapingian–early Darriwilian times (compiled from maps by Benedetto 2004 and Ramos 2008; platform system and Rio de la Plata–Amazonas craton boundaries after Astini 2003).

until the Early Devonian, with the appearance of Malvinokaffric Realm faunas in all these regions.

By the late Darriwilian and Sandbian–Katian the Gondwanan signature was stronger than in the preceding faunas, especially in ostracodes, trilobites and brachiopods, marking the onset of the so-called 'pre-accretion stage' (Benedetto *et al.* 1999). The Sandbian scenario was one of more generalized collision, involving the progressive closure of the remnant seaway separating Cuyania from Gondwana. In shallow-water environments highly endemic bivalves and ostracodes flourished, but endemism is also evident in trilobites and, to a lesser extent, in brachiopods.

The precise timing of collision of the Precordillera is still a matter of debate. On the basis of faunal affinities, facies distribution and tectonic data, Benedetto (2004) proposed an oblique sinistral docking against Gondwana that may have begun in the Darriwilian, although sustained collision leading to a climax of deformation, the so-called 'hard collision', may have continued through the late Ordovician and probably the early Silurian, until the remnant ocean between the Precordillera and Gondwana was completely destroyed. We provide here (Fig. 14) a new reconstruction of the southern and central proto-Andean margin during the Middle Ordovician, including new geological data by Bahlburg *et al.* (2006), Rapela *et al.* (2007) and Ramos (2008), as well as the new palaeontological evidence summarized above.

Conclusions

(1) The Early Palaeozoic proto-Andean margin is part of the Terra Australis orogen, which developed along the 'Pacific' margin of Gondwana, from Australia to South America (Cawood 2005). The complex geodynamic history of the Andean segment of this orogen included extension, rifting and subsequent reaccretion of Gondwanan fragments, opening of back-arc basins, development of subduction-related volcanic arcs, accretion of exotic terranes and several phases of deformation and metamorphism. Evidence from different groups of benthic fossils taken together is a powerful tool for determining the origin, trajectory and timing of docking of terranes, and also for arbitrating between contrasting palaeogeographical models.

(2) Palaeontological data from South America are not uniform; the majority of published Cambro-Ordovician fossils are from Argentina and Bolivia; available information from Venezuela, Colombia and northern Peru is still very limited.

(3) Tremadocian–Floian faunas from the autochthonous siliciclastic platforms developed along the periphery of the Brazilian craton include deep-water, widespread trilobites (agnostids, olenids, shumardiids) and inshore faunas displaying Gondwanan affinities. However, the biogeographical signal from the brachiopods and bivalves is not identical to that from the trilobites. Rhynchonelliformean brachiopods and bivalves include typical Ibero-Armorican, Perunican and North African genera, but some trilobites show affinities with warm-water Australasian faunas, which indicates relatively free migration for some taxa around Gondwana. By the late Tremadocian and Floian, a suite of endemic trilobites (mainly asaphids) flourished in the Central Andean basin. Endemism is also remarkable among the bivalves and, to a lesser extent, among the brachiopods. The very low degree of faunal exchange between epicontinental platforms and continental-margin volcanic arcs indicates some kind of barriers to the migration, which would have been the poorly oxygenated, deep-water marginal seas located behind the arc (Fig. 14).

(4) The Ordovician volcanoes and related back-arc basins located outboard from the pericratonic platforms were a major component of the proto-Andean margin from western Argentina to southern Peru. In general, Tremadocian and Floian trilobites inhabiting volcanic settings display mixed West and East Gondwanan affinities. The peri-Gondwanan *Neseuretus* biofacies has been recognized in the inshore settings of both clastic platforms and back-arc basins. Similarity between the Early–Mid-Ordovician brachiopods from western Puna–Famatina, southern Peru and Central Newfoundland–Wales would support the existence of a system of volcanic chains up to 2500 km long and/or microplates marginal to the Iapetus Ocean, which might have played a role in the migrations (Fig. 14). As can be expected in such volcanic settings, endemism was relatively high, in particular among bivalves. As pointed out previously (Benedetto & Sánchez 2003), the mid-latitude volcanic arcs fringing West Gondwanan shelves were the sites of origination and rapid diversification of several clades.

(5) Cambrian to Middle Ordovician platform carbonate rocks are confined to the Precordillera basin. There are abundant geological, palaeomagnetic, palaeoclimatic and palaeontological data to indicate that the Precordillera is a Laurentian-derived far-travelled microcontinent that accreted to Gondwana during the Early Palaeozoic.

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Plant assemblages from SW Gondwana: further evidence for high-latitude vegetation in the Devonian of Argentina

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Abstract: Plant assemblages are described from the Talacasto and Punta Negra Formations, San Juan Province, the Argentine Precordillera. A detailed facies study involving trace fossil assemblages indicates that the plants were buried in shallow low- to high-energy marine environments, but not in turbidites as previously postulated. Apart from a single specimen resembling *Cooksonia* from the Lochkovian Talacasto Formation, the abundant compression fossils consist of short lengths of smooth axes, occasional defoliated lycopod stems, and very rare isolated sporangia. It is thus impossible to assign any to existing taxa with confidence nor are there sufficient distinguishing characters to erect new ones. Although the possible age of the formations in the Precordillera remains conjectural, the fossils themselves, even preserved in such fragmentary states, indicate much lower grades of organization than seen in coeval assemblages elsewhere, particularly on the Laurussian and South China palaeocontinents. Palaeocontinental reconstructions of Gondwana indicate that the localities are within 30° of the palaeo South Pole. Thus a global latitudinal gradient in vegetation is postulated for the Early Devonian with decreasing disparity and diversity at higher latitudes. An explanation for the latter is explored in terms of light regime and temperature in highly stressed environments.

A major constraint to an understanding of the early history of land plants from both evolutionary and phytogeographical perspectives has been the paucity of records from the present southern hemisphere, and more importantly from high latitudes of the palaeocontinent Gondwana. As this supercontinent straddled the South Pole in Mid-Palaeozoic times, it has the potential to provide information on high-latitude vegetation, to some extent realized by descriptions of Silurian plants from Bolivia (Edwards *et al.* 2001*a*) and Lochkovian and later assemblages from Brazil (Gerrienne *et al.* 2001) and Argentina (Edwards *et al.* 2001*b*). Here we provide descriptions of assemblages from new localities in the Argentine Precordillera Lower Devonian units, together with information on their stratigraphic positions and sedimentary environments.

Although very fragmentary fossils ('plant debris') have been found throughout the Precordillera in San Juan Province (Fig. 1), we will concentrate on those localities with distinctive plants, although even here it is impossible to assign them to existing taxa even at generic level. Descriptions of such debris, the latter normally only mentioned in accounts of Devonian plants, are presented here because records of land plants in Lower Devonian rocks of Gondwana are so rare.

Material

For the most part, plant axes are preserved as highly indurated coalified compressions or impressions, sometimes iron-stained. Interspersed with the axes are numerous coalified patches, usually of irregular shape but sometimes circular or resembling isolated sporangia. Apart from occasional coalified longitudinal strands on axes presumably representing remains of cell walls, no anatomy nor *in situ* spores have been detected, although conventional palaeobotanical techniques (maceration, oxidation) were attempted. Dispersed spores sufficiently well preserved to allow identification were not found in the rocks containing the fragments. More detailed accounts will be given for each locality together with the stratigraphical and lithological data (Figs 2 & 3).

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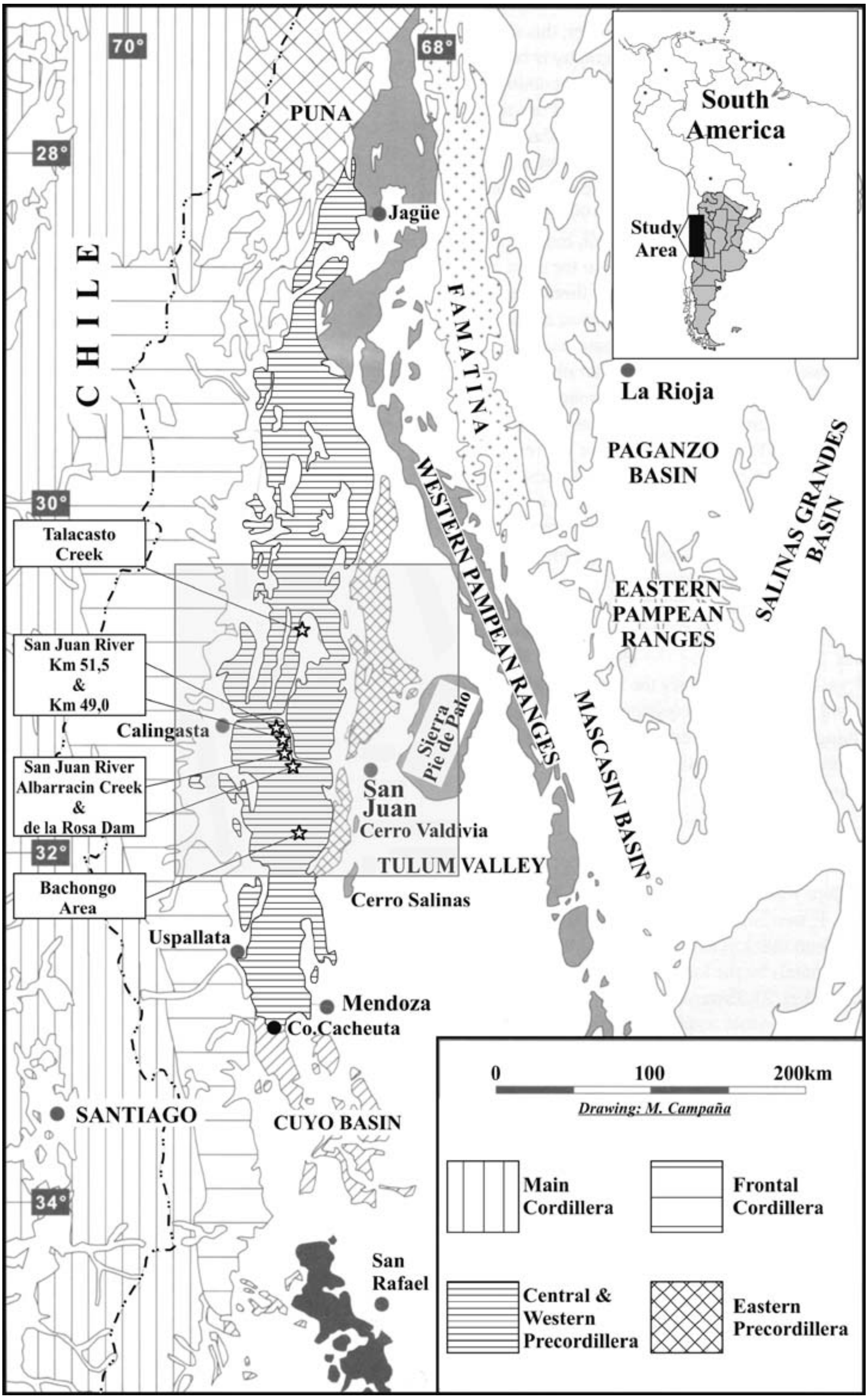


Fig. 1. Locality map for Mendoza, San Juan and La Rioja provinces showing geological outcrops and localities. Modified from Keller (1999).

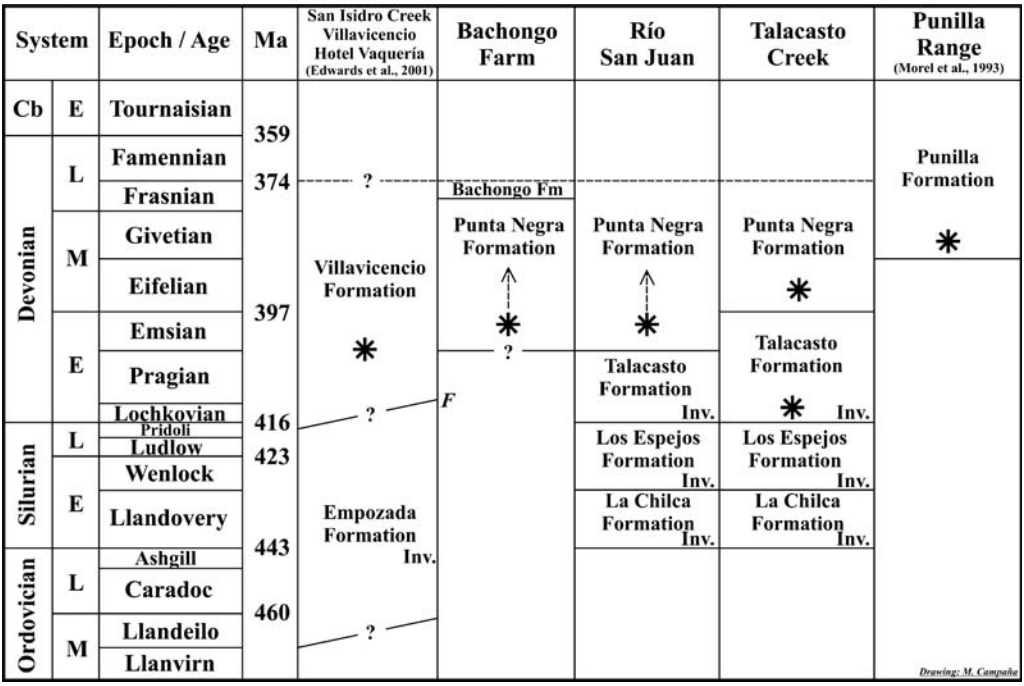


Fig. 2. Stratigraphical columns of localities with plants (indicated by stars) in San Juan and Mendoza provinces. Arrows indicate uncertainties on the precise stratigraphical position of the plants; Inv., invertebrates present within the formation.

Plant assemblages (Fig. 1)

Locality 1, Talacasto Creek, San Juan Province (Figs 1, 3, 4 & 5j, k); 30°59′57″S, 68°48′06″W

The Talacasto and Punta Negra Formations are very well exposed at the Talacasto Creek. The level bearing *Cooksonia* occurs in the lower part of the Talacasto Formation, and several levels with plant debris are present in the overlying Punta Negra Formation.

Road-side exposure of the Talacasto Formation (Fig. 4). The single specimen (Fig. 4a–d) was collected by Z. Herrera and is currently deposited in the collections of P. Racheboeuf at the University of Lyon, France.

Geology. The fossiliferous horizon is *c.* 20 m above the siliciclastic Silurian Tucunuco Group with graptolites and conodonts (Albanesi *et al.* 2006).

Age. The age is Lochkovian (Early Devonian) based on chonetid brachiopods (Racheboeuf & Herrera 1994; Herrera 1995); and on spores, acritarchs and chitinozoans (lower part of Formation at Cerro del Fuerte = upper Lochkovian; Le Hérissé *et al.* 1996). The Los Espejos Formation (Upper Tucunuco Group) is assigned to the Wenlock–Ludlow by conodonts (Albanesi *et al.* 2006).

Facies. The plant material is in a fine-grained facies interpreted as sedimentation in fair weather below wave action on a muddy shelf. (Facies sequence ‘A’ of Astini 1991.)

Description. The single specimen is preserved in part and counterpart, both as impressions with some residual traces of coalified material. The illustrations are taken from latex casts, the specimen being unavailable for direct photography. The fragment on which the surface shows the stem preserved in positive relief is considered the part; its latex cast is illustrated in Figure 4c and d. The isotomously branching axial system is 40 mm long with at least three orders of branching (Fig. 4a, c). One axis terminates in a laterally extended elliptical structure interpreted as a sporangium (Fig. 4b, d). Axis diameter is *c.* 2.0 mm at the base and decreases above each branch point such that it is 0.4–0.6 mm wide distally. The axis surface is not smooth, but bears irregular longitudinal undulations, forming lenticular structures

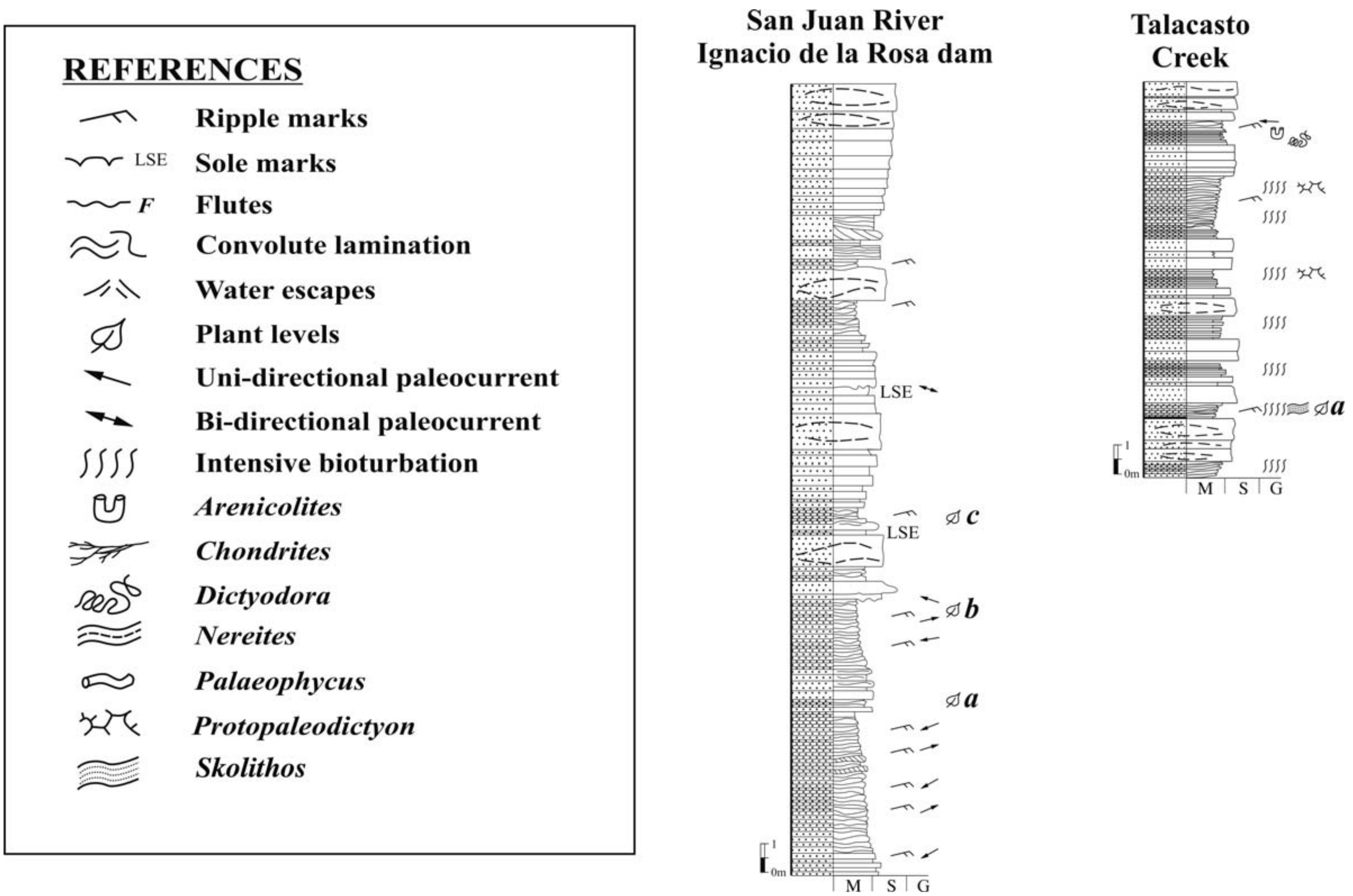
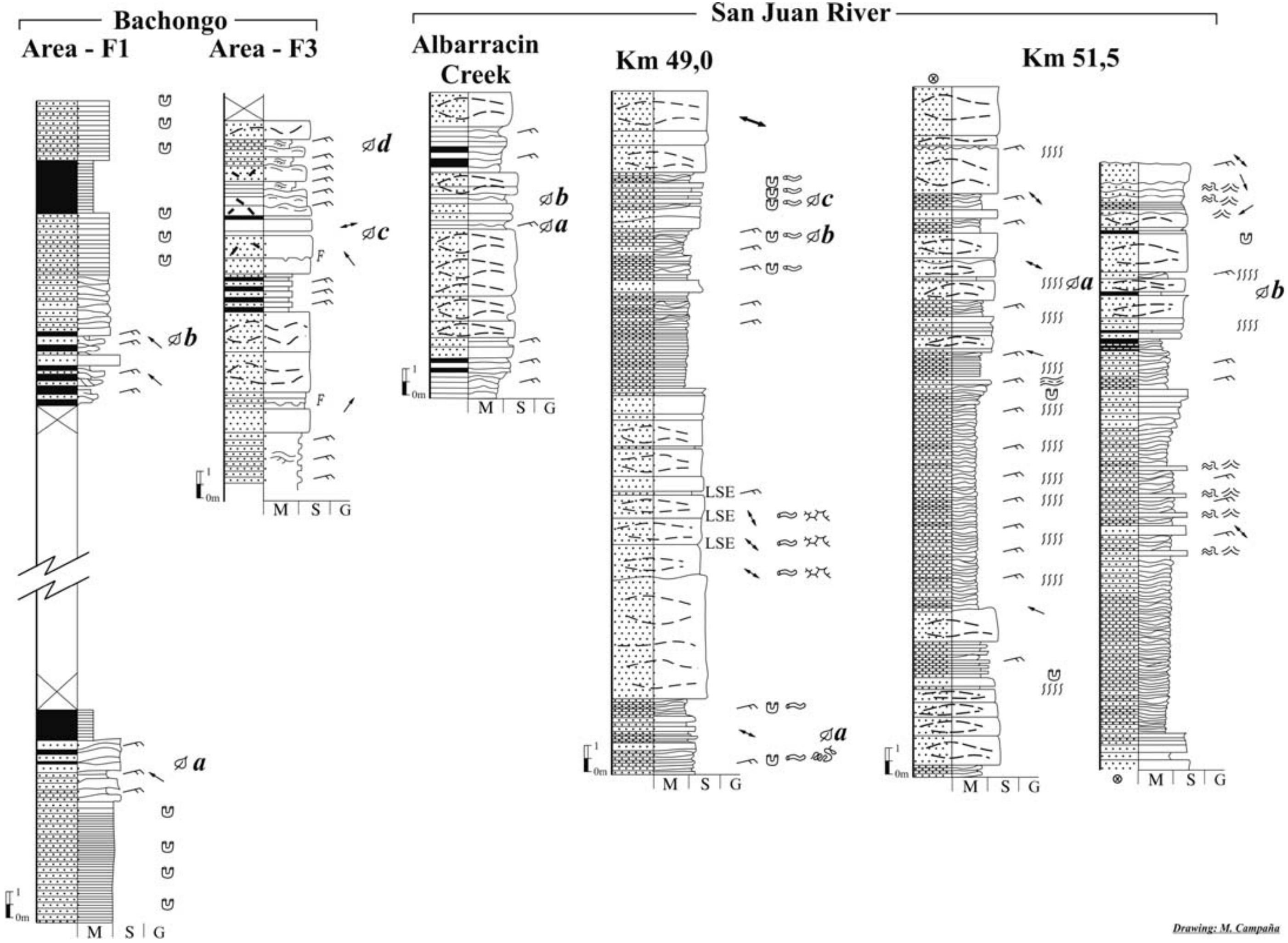


Fig. 3. Sedimentary logs of studied plant-bearing localities in the Punta Negra Formation, Mendoza and San Juan provinces. M, mud; S, sand; G, gravel.



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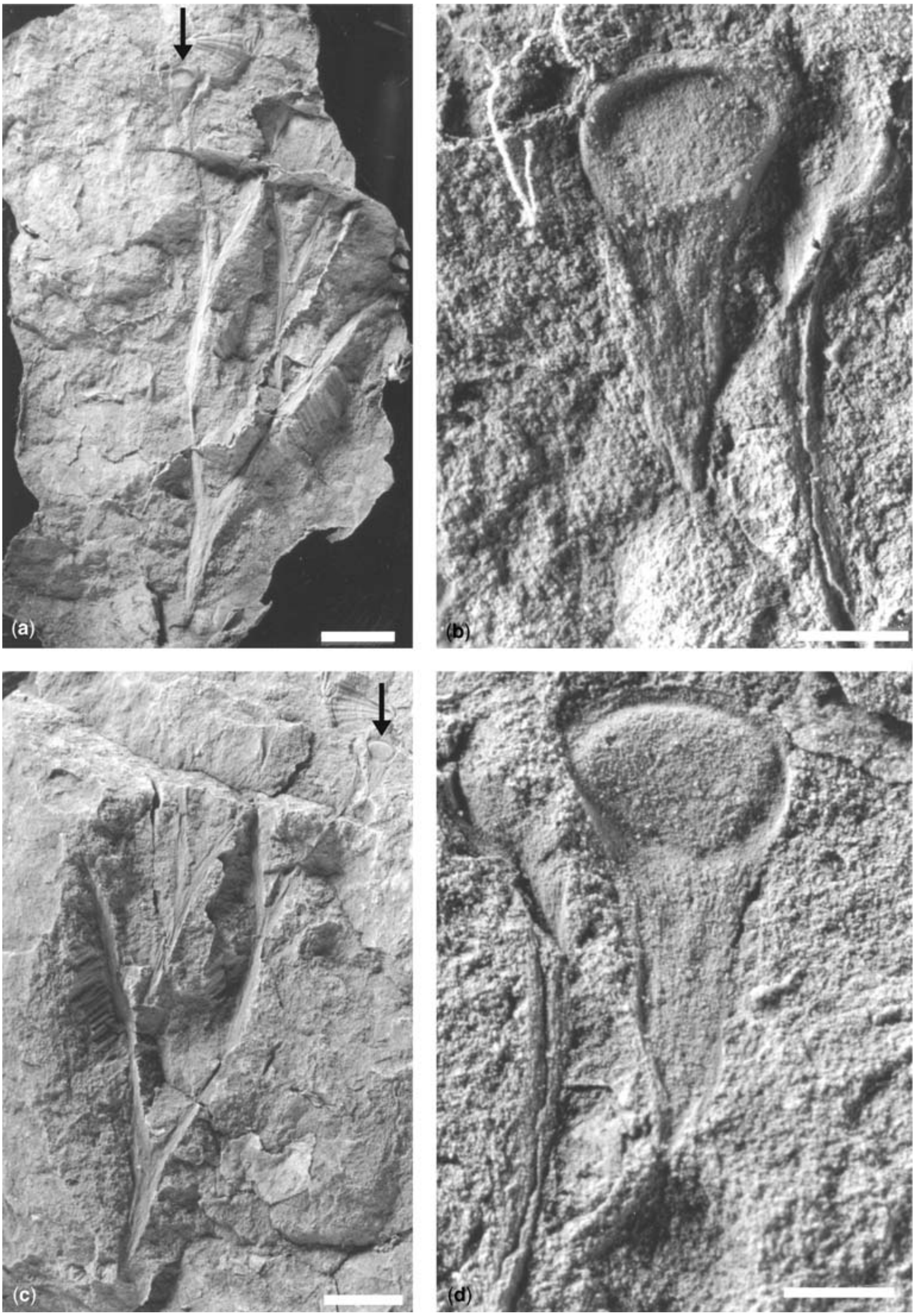

Fig. 4. Latex casts of new cooksonioid (specimen now in University of Lyon). Talacasto Formation, Talacasto Creek, San Juan Province, Precordillera, Argentina: Lochkovian. (**a**) Complete specimen interpreted as counterpart, but, because a latex cast, it shows the appearance of the part. Scale bar 5 mm. (**b**) Complete terminal sporangium from (a, arrowed) and partially preserved example on right. Scale bar 1 mm. (**c**) Part to (a). Scale bar 5 mm. (**d**) Magnification of sporangium on cast of sporangium on part from (c). Scale bar 1 mm.

sometimes accentuated by coalified strands (Fig. 4a, b). The single sporangium is 1.5 mm high and 2.0 mm wide. It has a distinct flat border of consistent width (*c.* 0.2 mm) around the entire convex margin. The border appears continuous with the subtending axis (0.7 mm wide at junction), because the longitudinally orientated microstriations, probably representing the remains of cells on the axis surface, continue uninterrupted into the marginal band (Fig. 4d); however, they end at the base of the presumed area occupied by spores, which is thus smooth and slightly depressed on the part. It becomes more convex distally where it is limited by the distal flattened to raised border.

Comparisons. The terminal short and wide sporangium is characteristic of *Cooksonia*, but the undulating features of the axis are not. There are two Lochkovian species (*C. banksii*, Welsh Borderland, Habgood *et al.* 2002; *C. paranensis*, Paraná Basin, Brazil, Gerrienne *et al.* 2001) where the sporangial cavity appears embedded in the stem apex. However, the sporangial border feature was not recorded in the coalified Brazilian species, in which there are also differences in the attitude of axes and their surface topography. *Cooksonia banksii* has not been recorded as an impression or compression, but as a 3D preserved charcoalified mesofossil, thus making meaningful comparison difficult. In other taxa with terminal, non-sunken sporangia with a marginal feature (e.g. *Renalia*, Gensel; *Uskiella*, Shute & Edwards 1989), the latter clearly represents a region of the sporangium wall associated with dehiscence, and is distinct from the subtending axis. This Argentinian specimen thus merits the erection of a new taxon, but, in view of the lack of information from a single, essentially impression, fossil, whether or not it should be included in *Cooksonia* or a new genus is conjectural. We tend to favour the latter, but more specimens are essential for detailed circumscription.

Road-side exposure of the Punta Negra Formation in Talacasto Creek with abundant plant debris (Fig. 5j–k)

Geology. The horizon is in the first 10 m of the lower part of the Punta Negra Formation.

Age. The age is probably Emsian or younger, based on field or stratigraphic relationships with the underlying Talacasto Formation.

Facies. The plants in the Punta Negra Formation occur in mid- to dark grey, finely laminated siltstones and fine sandstones, with distinctive buff weathering and partings of highly micaceous fine sands in rippled heterolithic sandstones (Fig. 3). They are very abundant, but highly fragmented, and were deposited in a subtidal environment.

Description. The plant material comprises short lengths of smooth unbranched axes randomly interspersed with irregularly defined coalified patches. Axes very rarely extend beyond 2 cm in length, with the longest tending to be wider (30% 1–2 cm long and 1.5 mm wide; 40% 0.5–1.5 cm long and 0.8–1.0 mm wide; the remainder smaller). Among the typical debris is a distinctive irregularly branching, axial fragment *c.* 2 cm long (Fig. 5j, k). The surface of the main axis is marked by coalified strips, and some of the laterals by two pronounced depressions on the main axis (arrow in Fig. 5k), which may mark the departure of further branches.

Comparisons. In its branching pattern and surface features this specimen (Fig. 5k) is unique.

Locality 2, Bachongo Farm, San Juan Province (Figs 1, 3 & 6a–e, g–i)

Outcrops of the Punta Negra Formation occur sporadically in the bed of a dried-up river; the two most productive palaeobotanically occur in the vicinity of Bachongo farm. Of these two outcrops, one (F1, Fig. 3) is more consistently finer grained and contains abundant plant debris at two horizons.

31°55′63″S, 68°53′50″W (F1, Fig. 3)

Geology. No lower contact was observed but the upper part of the formation passes gradually without break into the red beds of the Devonian Bachongo Formation (Cuerda *et al.* 1988). The latter is overlain unconformably by the Upper Carboniferous fluvial Andapaico Formation. The plants occur most abundantly in the upper part of the Punta Negra Formation.

31°54′45″S, 68°49′75″W (F3, Fig. 3)

Geology. The fossils occur in an isolated outcrop with abundant plants at two horizons in the bed of a dried-up river near Bachongo Farm, both from Punta Negra Formation. No contacts were observed. The relationship with the more western Bachongo Farm outcrop (F1) is uncertain because of the strong folding deformation, which has affected the Silurian–Devonian sedimentary succession in the Argentine Precordillera.

Age. There is no direct evidence for age from invertebrates or spores. The top of the underlying Talacasto Formation elsewhere in the south of San Juan is dated as Lochkovian to Pragian from abundant invertebrates (Herrera 1995). This provides a maximum age for the Punta Negra Formation. However, the Talacasto Formation is diachronous, with abundant brachiopods indicating an Emsian age to the north (in Talacasto Creek) and Lochkovian–Pragian (San Juan River) to the south. It thins from the south from the Jachal to the San Juan River

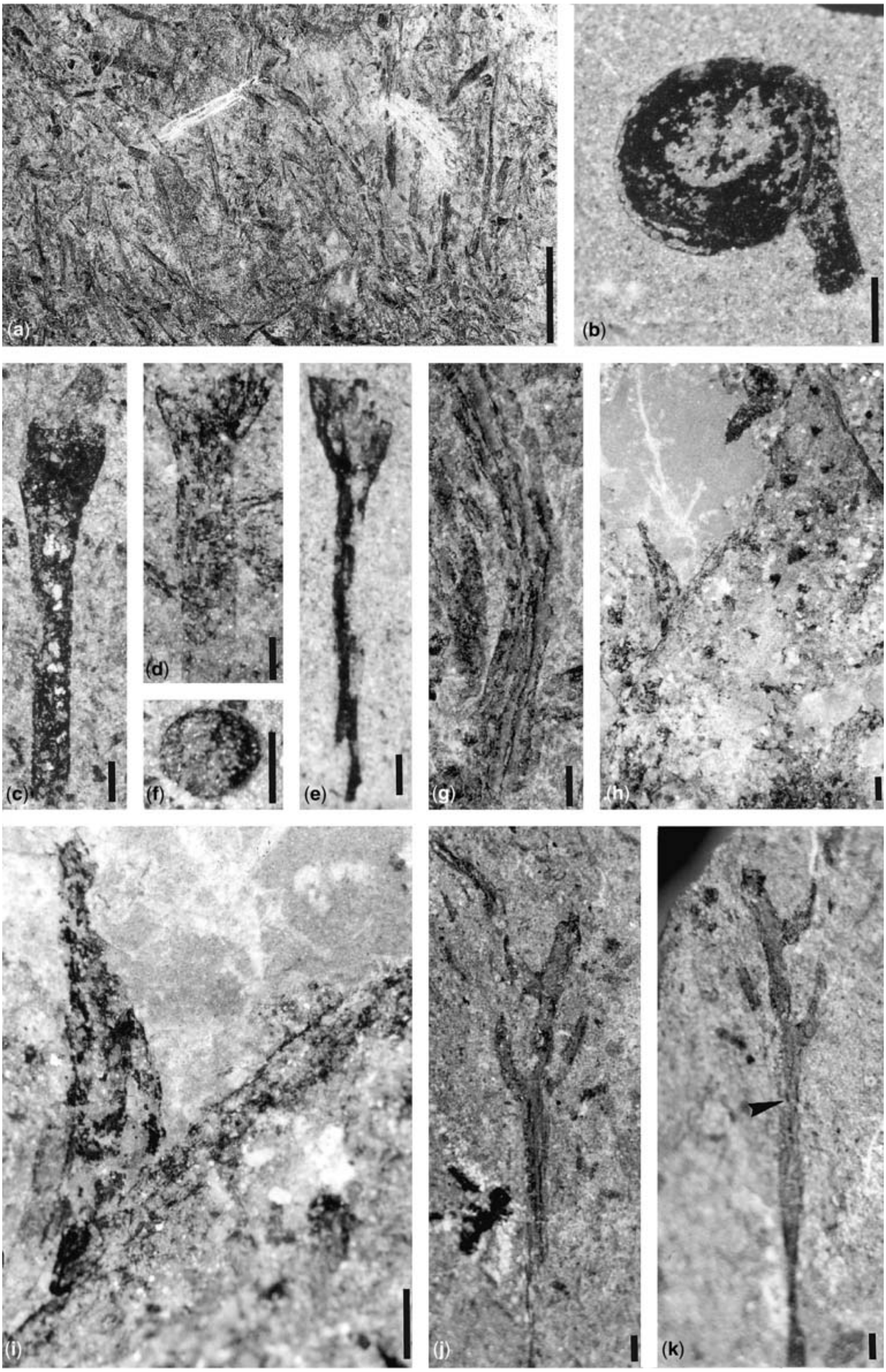

Fig. 5. *Continued.*

(Astini 1991) and there are no further outcrops south of the San Juan River area (Figs 1 & 2).

Facies. These outcrops are of particular interest in that the plants are preserved in mid-grey to buff sandstones and laminated muddy siltstones in rippled and laminated sandy heterolithic facies, which together with abundant *Arenicolites* are indicative of high energy in a shallow marine environment. The overlying Bachongo Formation comprises continental facies.

Description. Axes, including *Hostinella*, are smooth and fragmentary, and occur among masses of coalified patches, a number of which have a well-defined shape, and are probably sporangia.

Axis with ?lateral sporangium LPPB 13260, Figure 6a, b. Associated with minutely disseminated plant debris is a single specimen comprising a smooth isotomously branching axis and a single laterally attached sporangium (Fig. 6a). The latter has a long tapering decurrent subtending axis. The angle of contact might suggest mere juxtapositioning, but more probably the lateral structure is attached to the axis just below its left-hand margin. The axis itself is sometimes represented by a cast covered by rather powdery coalified material. Just above the attachment point there is a small protrusion on the surface of the cast, suggestive of the base of a further sporangium. Similar raised areas, one markedly elongate, are also present elsewhere (arrow in Fig. 6a). The oval sporangium has a very well-defined outline, further distinguished by a narrow band of coalified material. It is 3.3 mm at maximum width, but its height is difficult to determine. The surface of the sporangium has very little coalified material, except at its base where it tapers into the subtending axis (*c.* 1.0 mm wide at its narrowest point). The junction is marked by a convex but irregular line, *c.* 2.9 mm from the distal convex margin.

Comparisons. Laterally attached sporangia with dehiscence around the convex margin indicated by a well-defined border characterize the Canadian Emsian genus *Renalia* (Gensel 1976). However, in the Canadian plant the lateral structures are usually dichotomously branched axes and the sporangia are round to reniform. Thus on the basis of the vertically elongate sporangium shape and the unbranched subtending axis, the Argentine specimen stands apart, but further more complete specimens are required before it can be circumscribed as a new taxon.

Specimen LPPB 13262, BF.1b.5, Fig. 6c, d. Among patches of coalified material and axes in a fine-grained grey matrix is a dichotomously branching axial fragment *c.* 10.5 mm long and *c.* 1.8 mm wide at its base, where the axis looks somewhat frayed. Indeed, the branching axes are not parallel-sided but have undulating margins associated with irregularly and longitudinally striated surfaces. Distally the two outermost axes are of this type with faint indications of a median longitudinal fork. In the left-hand example (Fig. 6c), this produces two parts at different levels on the rock surface. The right-hand branch shows a further division, the inner axis terminating in a pair of poorly defined, almost globular structures just above the branch point (Fig. 6d). These are not clearly delimited from their narrow subtending axes, and there is no direct evidence for their being sporangia. The left-hand termination is *c.* 1.1 mm in diameter and the right *c.* 0.95 mm.

Comparisons. Short and wide sporangia terminating smooth isotomously branching axes characterize *Cooksonia* (Lang 1937), where regularity of branching usually produces sporangia at the same level. It is possible that this latter feature is exhibited by the Argentine specimen with the two outermost branches terminating in sporangia that are compressed at 90° when compared with the more globular structures, but the surface irregularities argue against assignment to *Cooksonia* as currently circumscribed. Longitudinally elongate fusiform structures characterize the isotomously branching axes of *Isidrophyton iñiguezii* from the Pragian (originally thought Lochkovian) Villavicencio Formation at San Isidro Creek near Mendoza, Argentina. This more complete much branched specimen has similar axial and sporangial dimensions to the Bachongo one. The terminal sporangia in *Isidrophyton* are broadly similar in shape, but borne in pairs. Unfortunately, the poor state of preservation of the new material precludes detailed comparison, but there is a strong possibility that they are at least congeneric.

Isolated ?sporangia. Figure 6e, g shows the range in appearance of possible isolated sporangia; for

Fig. 5. Río San Juan (**a**, **b**), Albarracin (**c**–**i**), Talacasto Creek (**j**, **k**), Punta Negra Formation, San Juan Province, Precordillera, Argentina: ?Lower Devonian. (a) Typical plant debris showing current alignment. LPPB 13259. Scale bar 10 mm. (b) Elliptical structure with margin and ?superimposed axis. LPPB 13257. Scale bar 1 mm. (c–e) Axes with terminal truncated expansion. (c) LPPB 13273. Scale bar 1 mm. (d) LPPB 13275. Scale bar 1 mm. (e) LPPB 13270. Scale bar 1 mm. (f) Elliptical body. LPPB 13272. Scale bar 1 mm. (g) Heavily ridged axis. LPPB 13274. Scale bar 1 mm. (h, i) ?Lycophyte. LPPB 13271. (h) Scale bar 1 mm. (i) Close-up of ?leaf. Scale bar 1 mm. (j) LPPB 13252b. Scale bar 1 mm. (k) LPPB 13252a [counterpart of (j)]. Scale bar 1 mm.

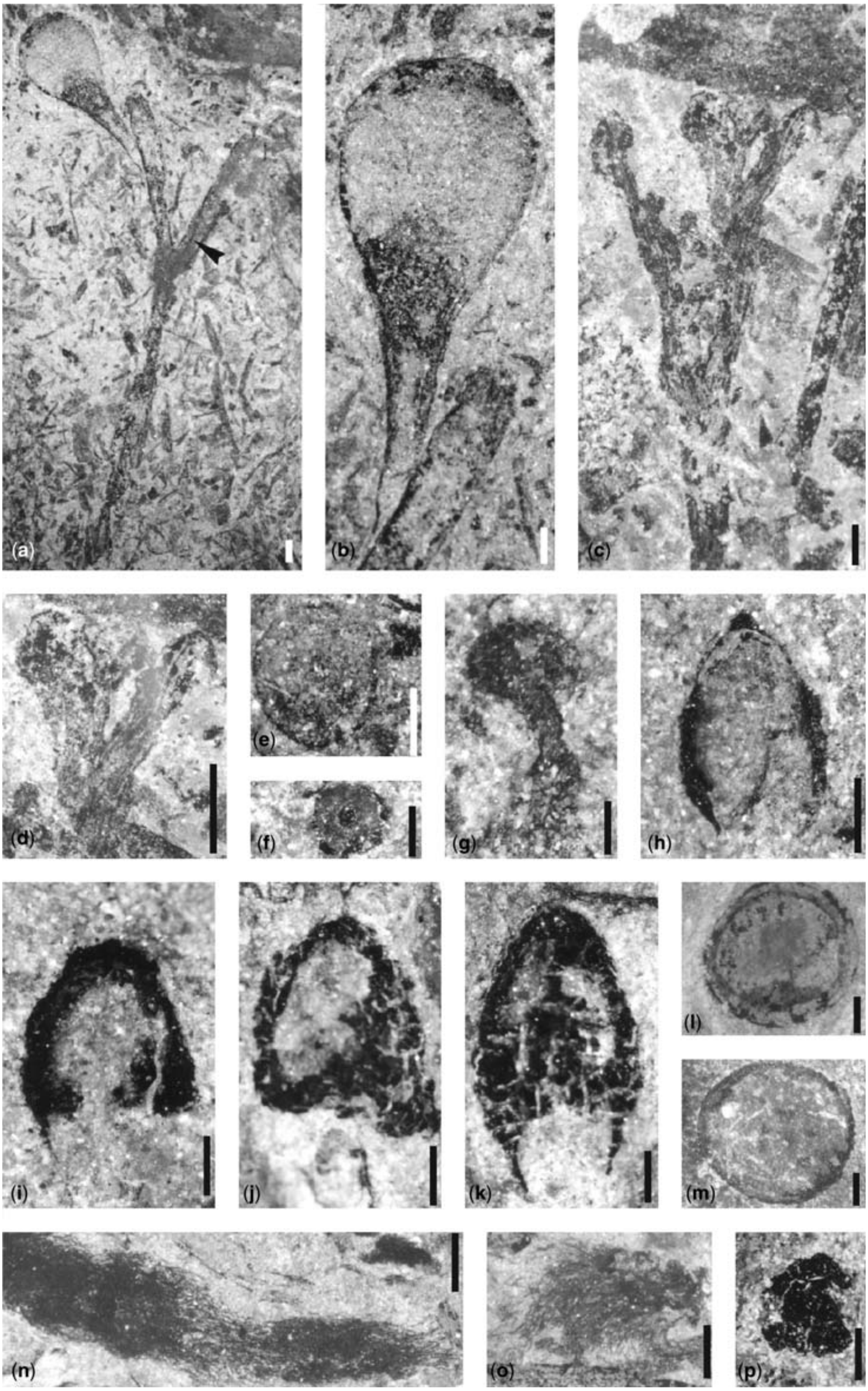

Fig. 6. *Continued.*

example, laterally extended forms attached to short lengths of axis (Fig. 6g, LPPB 13264), whereas others are more or less spherical and completely isolated (Fig. 6e, LPPB 13263). Even more problematic are isolated 'arrowhead'-shaped structures, in which a central convex, fairly elliptical area with little adhering carbon is partially surrounded by a zone of heavily coalified, often glassy carbon forming a V- or U-shape (Fig. 6h, i). We are uncertain as to whether there is a less heavily coalified extension on the remaining margin, because the majority of examples lack this. The two illustrated from Specimen LPPB 13265 (Fig. 6h, i) are 2.3 and 2.4 mm in maximum diameter with a central region 1.5 and 1.3 mm wide, respectively. The border ranges between 0.3 and 0.4 mm.

Comparisons. The ?sporangium (Fig. 6g) subtended by a short stalk has superficial resemblances both to *Cooksonia* and isolated zosterophyll sporangia. The circular structures would require *in situ* spores (not available) to confirm identity. The 'arrowheads' are even more conjectural, although they could represent more heavily coalified sporangia with subtending axes not preserved because they are less robust. Similar morphologies have not been recorded outside the Precordillera.

Locality 3, Albarracin Creek, San Juan Province (Figs 1, 3, 5c–i & 7a–c); 31°31′92″S, 68°50′34″W

The fossiliferous horizons occur in isolated outcrops in a tributary of the San Juan River. The outcrops begin near the bridge over the road and extend for about a kilometre to the south where they are then overlain by Cenozoic rocks. Plants are very abundant at two horizons in sandstones.

Geology. The fossiliferous horizon is part of the Punta Negra Formation (Log $RB_3N237/54$).

Age. There is no direct evidence for age, but elsewhere in the north the underlying Talacasto Formation has abundant Lochkovian invertebrates.

Facies. The very abundant plant debris occurs in thin- to medium-bedded, mid-grey, fine sandstones and siltstones with very sparse mica. Laminae of finer mud rocks make up an overall rippled sandy heterolithic facies indicative of a subtidal environment, where the medium fragmentation of the plants indicates limited transport. Flutes and longitudinal scours in this facies provide evidence of fairly high-energy erosive currents.

Descriptions. Abundant axial debris is associated with coalified patches of varying size and shape in a grey, often fine-grained micaceous matrix, and lacks evidence of marked current alignment. There are no obvious sporangia, but isolated highly coalified elliptical to rarely circular structures are common (Fig. 5f, LPPB 13272), and there are also examples of the 'arrowhead' form recorded from Bachongo. In one example there is a slightly asymmetric terminal expansion of a short length of unbranched axis showing a constriction at the junction. Its discrete shape is strongly suggestive of a sporangium, but it is too incomplete, and lacking in diagnostic characteristics, to allow adequate comparisons. Circular coalified structures, which would probably be assigned to *Pachytheca* had they been in Laurussia, show none of the zonation associated with that genus and no structure when examined by SEM.

Sterile fragments: ridged axes. That illustrated in Figure 5g (LPPB 13274) is 12 mm long, unbranched and *c.* 1.5 mm at its widest point. Its surface is marked by ridges and elongate grooves with further centrally placed elevations or depressions. Well-defined enations are not visible.

Sterile fragments: smooth axes. The majority are unbranched and less than 1 cm long (40% 1.5–2 cm long and 1 mm wide; 40% *c.* 1 cm long and 1 mm wide; 10% 1 cm long and 1.5 mm wide; *c.* 10% are smaller). A few axes show a terminal expansion with irregular or sharply truncated apex. Figure 5c (LPPB 13273) shows a typical highly coalified example, 9.8 mm long, with parallel-sided axis, 0.9 mm wide, and the expansion double that width. In two others of similar relative dimensions,

Fig. 6. Bachongo Farm (**a**–**e**, **g**–**i**) and Río San Juan (**f**, **j**–**p**), Punta Negra Formation, San Juan Province, Precordillera, Argentina: ?Lower Devonian (a, b) New taxon. LPPB 13260. (a) Isotomously branching axis with lateral sporangium among typically fragmentary axial plants. Scale bar 1 mm. (b) Close-up of sporangium with narrow border. Scale bar 1 mm. (c, d) New taxon LPPB 13262. (c) Branching fragment with strong longitudinal lineations. Scale bar 1 mm. (d) Close-up of possible terminal sporangia. Scale bar 1 mm. (e) Elliptical body with well-defined margin. LPPB 13263. Scale bar 1 mm. (f) ?*Pachytheca.* (Note pronounced central coalified region.) LPPB 13259. Scale bar 0.5 mm. (g) Possible terminal sporangium. LPPB 13264. Scale bar 0.5 mm. (h, i) LPPB 13265. Scale bars 1 mm. (j, k) LPPB 13280. Scale bars 1 mm. (l, m) Circular structures with bevelled margin. (l) LPPB 13254. Scale bar 1 mm. (m) LPPB 13256. Scale bar 1 mm. (n, o) Aggregations of longitudinally orientated coalified 'ribbons'. (n) LPPB 13259. Scale bar 1 mm. (o) LPPB 13258. Scale bar 1 mm. (p) Two-zoned coalified structure with irregular outline LPPB 13259. Scale bar 0.5 mm.

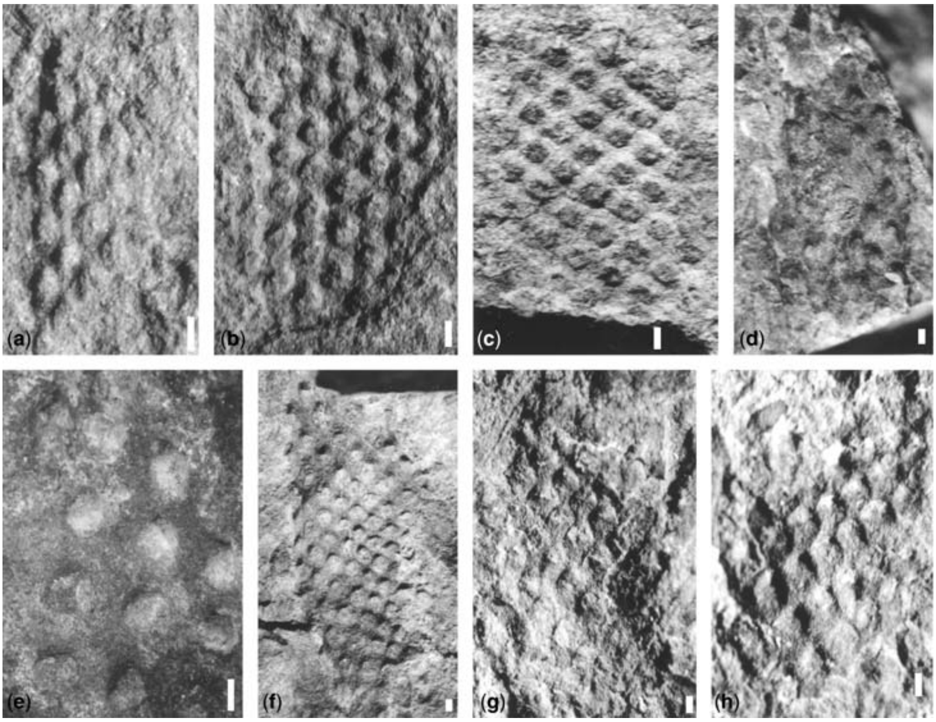

Fig. 7. Lycophyte stems. Albarracin (**a**–**c**), Río San Juan (**d**–**h**), Punta Negra Formation, San Juan Province, Precordillera, Argentina: ?Lower Devonian. (a) LPPB 13268. Scale bar 1 mm. (b, c) LPPB 13267a,b. Scale bar 1 mm. (d) LPPB 13281. Scale bar 1 mm. (e) LPPB 13282. Scale bar 1 mm. (f) LPPB 13286. Scale bar 1 mm. (g, h), LPPB 13284, 13285. Scale bar 1 mm.

the truncated end has a frayed appearance (Fig. 5d, LPPB 13275; Fig. 5e, LPPB 13270). The nature of the terminal expansion, be it the base of a sporangium or incomplete branch point, could not be determined.

Comparisons. The ridged axes are similar to those of *Isidrophyton iñiguezii* from the Villavicencio Formation near Mendoza. The morphologies of the more distinctive smooth axes have not been seen elsewhere.

Lycophytes. Specimen LPPB 13268 (Fig. 7a) is an unbranched (11 mm long and 4 mm wide) cast, which shows approximately vertical rows of projections with diamond-shaped bases resembling small, slightly proximally decurrent, 'volcanic' cones, representing the swollen bases of presumed microphylls. They are 1.1 mm wide and 1.1 mm long. Specimen LPPB 13267a and b (Fig. 7b, c, fossiliferous horizon 2) is also a fragment (9 mm wide × 13 mm long) with non-contiguous leaf bases preserved in part and counterpart, with an estimated six per gyre on the preserved surface. They are essentially rhomboidal with further centrally placed oval or crescentic ridges or depressions marking the sites of the leaf laminae or scars of their abscission. The swollen bases (Fig. 7c) are *c.* 1.5 mm or 1.0 mm wide and 1.2 mm long. Development of the counterpart (with depressions) failed to reveal laminae.

Comparisons. Although lacking leaf laminae, it seems likely that these fossils represent fragments of herbaceous lycophytes originally with persistent leaves. They are comparable in the general appearance of the presumed swollen leaf bases, but differ in their being either tangentially or vertically extended. Whether they derive from different taxa must remain conjectural in view of the variability in shape and arrangement of leaf bases in coeval lycophytes that relate to ontogenetic and taphonomic factors. In the Argentine specimens, the leaves were probably removed on transport. Unfortunately, such lycophytes are usually identified on characteristics of the leaves, with leaf bases of less taxonomic value. Forced to use the latter characters here, we find the Argentinian lycophytes most similar to the recently redescribed *Halleophyton* (Li & Edwards 1997) from the Siegenian of

China, although the Chinese lycophyte has far better preserved leaf bases, showing consistent patterns. Li & Edwards (1997) compared *Halleophyton* with *Drepanophycus gaspianus* from the Emsian of North America, the only member of that genus to show well-defined surface patterning. The Argentine fragments cannot be assigned to far better known Early and Middle Devonian genera such as *Leclercqia*, *Haskinsia* and *Colpodexylon*. Younger Devonian lycophytes include *Malanzania antiqua* (Punilla Formation, Punilla Range, North Precordillera, Morel *et al.* 1993), *Haplostigma furquei* (Chigua Formation, Volcán Range, Río Blanco Basin, North Precordillera, Gutiérrez 1996), *H. baldisii* (locality data as for *H. furquei*, Gutiérrez & Archangelsky 1997) *Haplostigma* sp. [Middle–Upper Devonian northern Antofagasta region (northern Chile), Moisan & Niemeyer 2005] and two unnamed species of *Archaeosigillaria* (Punta Negra Formation, Talacasto Creek, San Juan Province, Gutiérrez 1996). Gutiérrez's *Archaeosigillaria* sp. B has similarities to the specimens illustrated in Figure 7a–c, e, f and was found in the same geographical area. However, if these fragmentary stems do indeed derive from the same taxon, it should not be called *Archaeosigillaria* for the reasons given by Berry & Edwards (1997). Thus we consider it inappropriate to name the lycophyte fragments, although their presence has significance for diversity in land vegetation.

?Lycophyte. This specimen (fossiliferous horizon 1; Fig. 5h, i, both LPPB 13271) contrasts with the two previous examples in that there is no regular arrangement of swollen leaf bases. Instead, a probable stem, at least 10 mm in diameter with a smooth faintly stained surface, is marked by irregularly shaped small areas of coalified material (interpreted as possible leaf attachment sites). At its margin is one triangular outgrowth, *c.* 5.5 mm long with decurrent base. This may be a microphyll, but there is no indication of a vascular strand and its margin is somewhat irregular.

Comparisons. The enation superficially resembles some recorded in certain species of *Drepanophycus* (e.g. *D. spinaeformis*), but more convincing evidence is needed to permit assignation even at a generic level.

Locality 4, roadside exposure, Río San Juan: 49 km marker, San Juan Province (Figs 1, 3, 5a, b & 6f, l–p); 31°31′04″S, 68°56′06″W

This locality is a roadside exposure near Río San Juan, 49 km to the west of San Juan City.

Geology. The fossiliferous horizon is part of the Punta Negra Formation (Log KM 49 $\mathrm{Rb_3N260/70}$).

Age. There is no direct evidence for age. The underlying Talacasto Formation (not exposed at these localities) has abundant invertebrates indicative of a Lochkovian age (e.g. Herrera & Racheboeuf 1997).

Facies. The very abundant plant fragments with a medium degree of fragmentation occur in rippled sandy heterolithic facies with *Arenicolites* (high-energy), *Palaeophycus*, *Dictyodora* and *Protopaleodictyon* (low-energy) trace fossils. In total, evidence indicates deposition in low-transport, coastal shoreline environments (Pemberton *et al.* 1992).

Descriptions. Smooth sterile axes. Figure 5a (LPPB 13259, general view) illustrates a typical surface with short lengths of unbranched axes, in this case showing current alignment. *Hostinella* is rare. No axes are fertile. About 25% of the axes show a central line and are *c.* 1.5 mm wide and up to 2 cm long. Smaller fragments (40%) are 0.8–1 mm wide and up to 1.5 cm long. The remainder are even smaller. Associated with the axes are patches of coalified material, most with irregular outline, but many with discrete circular or elliptical outlines (see below), or the 'arrowheads' described for Bachongo. The latter are particularly common on irregular bedding planes covered with axial plant debris.

Incertae sedis. These consist of collections of ?tubes (Fig. 6n, LPPB 13259; Fig. 6o, LPPB 13258). A fragmentary specimen *c.* 10 mm long and 1.2 mm wide is made up of an aggregation of longitudinally oriented strap-shaped structures of glossy appearance and *c.* 20 μm wide (Fig. 6n). These are particularly evident near the margins and at the frayed ends, where branching of the structures is occasionally observed. They probably represent compressed tubes, although we have failed to substantiate this by SEM. A smaller similarly organized mass of tubes has been recorded on another surface at the same locality (Fig. 6o).

Comparisons. Similar, but much smaller, associations of tubes have been recovered from macerations of Lower Devonian rocks from the Welsh Borderland, where they have been tentatively assigned to the Nematophytales, a group of uncertain affinity (Lang 1937), although Hueber (2001) has recently proposed fungal activities for *Prototaxites* (Hillier *et al.* 2008).

Elliptical structures. Two examples (4.1 mm × 3.6 mm and 4 mm × 3.5 mm) are isolated (Fig. 6l, LPPB 13254; Fig. 6m, LPPB 13256), whereas a third (3.7 mm × 3.0 mm) is associated with a short length of unbranched axis (Fig. 5b, LPPB 13257). All occur in a fine-grained grey matrix in which plant fossils are relatively rare. Both isolated forms are discoidal with a convex surface encompassed by a narrow rim (*c.* 0.4 mm wide), in Figure 6l forming a bevelled edge, but in Figure 6m, a flat one. Such a margin is not present in the third, where the edge curves down into the matrix. Its slightly convex surface is interrupted by a circular and a larger crescentic depression. The axis is probably fortuitously situated, merely lying under the edge of the elliptical structure (Fig. 5b).

Comparisons. These structures differ from compressed *Pachytheca* (Lang 1945) in that they are not circular, nor do they possess indications of a medulla and cortex. Their affinities remain unknown.

Circular structures. Two specimens are more or less circular in outline, and consist of a thick layer of coalified material in which a central circular area is distinguished. In the smaller (1.05 mm diameter), the outer region is mostly missing, and the central area is 0.29 mm in diameter (Fig. 6f, LPPB 13259). The second specimen (1.53 mm) has a much narrower outer zone (0.3 mm) in which radial striations are visible (Fig. 6p, LPPB 13259). SEM examination failed to show any cellular detail or further information on the radiating striations.

Comparisons. The zonation is typical of *Pachytheca* Hooker, a common but enigmatic genus in the Lower Devonian of the northern hemisphere (Lang 1945). Unfortunately, diagnostic cellular detail is not present in the Argentine specimens. However, if substantiated by anatomy, this would be the first record of *Pachytheca* in the southern hemisphere.

Locality 5, roadside exposure, Río San Juan: 51.5 km marker, San Juan Province (Figs 1, 3, 6j, k & 7d–h); 31°31′03″S, 68°56′06″W

This locality is a roadside exposure of sandstones of the Punta Negra Formation, 51.5 km west of San Juan City. The matrix with abundant but fragmentary coalified fossils is very micaceous and hard. Axes were sometimes three-dimensionally preserved with traces of carbon and iron staining.

Geology. The fossiliferous horizon is part of the Punta Negra Formation (Log KM 51,500).

Age. The age is as for locality 4.

Facies. Plants are rare and highly fragmented in the amalgamated sandstone beds, indicative of deposition after considerable transport in subtidal environments. They are more abundant and larger in the rippled sandy heterolithic facies deposited near the coast. Trace fossils are *Arenicolites* and *Nereites* associated with intense bioturbation, water escape structures and convolute lamination.

Descriptions. Sterile axes. All are unidentifiable, being smooth and featureless and lacking branches (53% 1.5 cm long and 1 mm wide; 32% 1 cm long and 1.5 mm wide; remainder are smaller).

Lycophyte stems (Fig. 7d–h). Four impression fossils (one in part and counterpart) consist of fragments of stems with regular surface patterning thought to represent the swollen bases of leaves. Their dimensions and particularly the shape and arrangement of the leaf bases suggest that they belong to the same taxon, although there is some variation in detail. Stem width ranges between 11 and 14 mm and the longest fragment, unbranched, is 45 mm. The leaf bases are all *c.* 1.5 mm wide, but of varying length and hence shape. Stems bear up to eight rows of bases. The latter range from oval (where vertically well separated), to hexagonal, to almost pear-shaped with decurrent base, although here again closely surrounded by six adjacent bases. The moulds of the surface show bases (as depressions) each with a distal crescentic or straight line marking the presumed attachment of the lamina (Fig. 7e, LPPB 13282; Fig. 7f, LPPB 13286). The broad base of the latter is sometimes revealed to the side of or below the stem, but the complete lamina has not been seen. The cast of the surface shows more restricted conical mounds (Fig. 7d, LPPB 13281) in this distal position. The part and counterpart (Fig. 7g, LPPB 13284; Fig. 7h, LPPB 13285) indicate that the leaf bases are basally attenuated and contiguous, but provide little information on the leaf itself.

Comparisons. Absence of information on leaf morphology makes detailed comparisons impossible. The specimens (LPPB 13268, 13267a, b; Fig. 7a–c) from Albarracin Creek are similar in appearance and dimensions, and probably belong to the same taxon. The discussion on their affinities is thus relevant here, with general similarities to the Chinese Siegenian *Halleophyton* (Li & Edwards 1997).

Incertae sedis. Figure 6j, k (both LPPB 13280) shows typical examples of the incomplete elliptical to arrowhead structures recorded at other localities in the Precordillera. All are very heavily coalified and sometimes glossy on the periphery, with varying amounts of coalified material on the acuminate end, which may sometimes be more rounded, and at the other, two extensions of varying length. The central area may lack carbon and have a convex contour, compared with the flattened margin. Examples range between 1.62 and 3.3 mm maximum width and are from 2.0 to 5.52 mm long.

Comparisons. The frequency and consistency in shape of these isolated structures from a number of localities confirm that they were probably dislocated elements of a local flora rather than artefacts. However, in that they have absolutely no equivalents in coeval vegetation elsewhere, their nature and the plants from which they derive remain unknown. Their shape is suggestive of some kind of reproductive structure, probably a sporangium, where proximal parts had poor preservation potential, but this is pure speculation in the absence of spores and anatomy.

Additional Precordillera localities in San Juan Province

Occasional plant fragments occur throughout the Punta Negra Formation at a number of localities. Particularly noteworthy, but not included in the above because all fossils are sterile, is the exposure near the Ignacio de la Rosa Dam (31°31′08″S, 68°48′96″W: Log RB$_3$N66/63, Figs 1 & 3), the type locality for the Punta Negra Formation. Three horizons in the cliff contain abundant but indeterminate plant axes.

Taphonomy and depositional processes

The distribution of the fossil plants in different sedimentary facies provides a guide to recognition and interpretation of the processes developed in this sedimentary succession in the Argentine Precordillera. Thirteen sedimentary facies associations have been differentiated throughout the succession, which is dominated by sandy beds with massive and amalgamated structures and heterolithic facies. Plant debris is particularly abundant in only two of the facies types (Poiré & Morel 1996): (1) massive medium-bedded sandstones; (2) rippled heterolithic mudstone–siltstone–fine sandstone packets. The first is interpreted as a product of storm events on a shallow shelf (Fig. 8b), involving slumping, and the second as fair-weather, subtidal coastal deposits (Fig. 8a). In both cases the plants would have been transported some distance from their presumed coastal and riverbank habitats, for which we have no direct information. Before this facies study, the younger deposits in the Villavicencio, Bachongo, Río San Juan and Talacasto areas had been interpreted as turbidites associated with a deep submarine fan (Gonzáles-Bonorino 1975; Peralta & Ruzycki de Berenstein 1990; Peralta 2005*b*). More recently, some sedimentological studies in Talacasto Creek have suggested deltaic deposits (Bustos 1996; Bustos & Astini 1997). We show here that they are shallow marine deposits formed on the inner shelf and, in the vicinity of Bachongo Farm, shallow into a continental facies. For the first time in the Precordillera, trace fossil assemblages have been used in interpretation of depositional environments. They mainly belong to the *Nereites* ichnofacies but some *Cruziana* and *Skolithos* ichnofacies are also recorded. Such overlapping of ichnofacies demonstrates that environmental energy was variable. In the subtidal coastal zone above the wave base level, moderate- to high-energy habitats are indicated by the prevalence of *Skolithos* and *Cruziana*. Following the rapid deposition of storm and turbiditic currents, the *Nereites* ichnofacies is characterized by low-energy conditions and an abundance of organic material (Pemberton *et al.* 1992).

Comparisons with coeval assemblages

Lochkovian

To date the only unequivocal Lochkovian plants in South America come from the Paraná Basin, Brazil (Gerrienne *et al.* 2001). Among a diverse

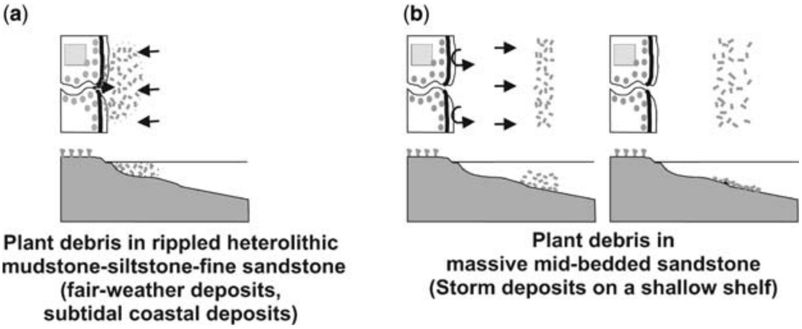

Fig. 8. Depositional environments based on facies studies.

assemblage of rhyniophytoids and more enigmatic plants with terminal clusters of enations and spiny axes, Gerrienne *et al.* described a new species of *Cooksonia*, *C. paranensis*, with sporangia interpreted as partially enclosed within the subtending axes. Although the Talacasto cooksonioid is also thought to have sunken sporangia, the relative dimensions of sporangium and axis, overall sporangial shape and branching attitude are different, eliminating the possibility that the plants are conspecific. The diverse assemblage in the Villavicencio Formation at San Isidro Creek was thought to be Lochkovian when originally described (Edwards *et al.* 2001*b*), but this allochthonous olistostrome (Peralta 2005*a*, *b*) has now been placed in the upper Pragian–lower Emsian on the basis of relatively poorly preserved palynomorphs (Rubinstein 2009) and more precisely correlated with the upper part of the Ems Biozone also found in the Brazilian Amazon Basin.

Lochkovian assemblages outside South America were described in detail by Edwards & Wellman (2001). On Laurussia, and in particular in Britain and Belgium, more precise stratigraphic placement has been possible from use of the spore zones as exemplified by Richardson *et al.* (1984). The South American plants show similar morphological organization to Laurussian ones in the basal Lochkovian apart from the occurrences of *Zosterophyllum* in the latter, with younger strata in southern Laurussia marking a diversification of zosterophylls.

The Lochkovian was possibly a time of very rapid plant diversification and migration: in the most recent estimates of time span it extended for about 2 Ma (Williams *et al.* 2000), thus accentuating the need for precise correlation. Differences in composition have been discussed in terms of evolutionary history, taphonomy and palaeogeography (Edwards & Davies 1990). In relation to the latter, the British and western European floras are representative of the southern margins of the Old Red Sandstone (ORS) continent at a latitude of *c.* 30°S (Fig. 9). More tropical areas of the palaeocontinent are now represented in Arctic Canada and further afield in NE Gondwanan Australia. On Bathurst Island (Gensel *et al.* 2001; Kotyk *et al.* 2002), although there are no records of Lochkovian plants, the presence of a diverse Late Silurian assemblage dominated by zosterophylls, with a new ?*Cooksonia* and plants showing characters typical of both zosterophylls and rhyniophytoids is accompanied by further representatives of zosterophylls (e.g. *Bathurstia* and *Distichophyton*) in overlying Pragian strata. This allows the inference that the vegetation of the region was highly diverse throughout the Lochkovian and thus comparable with that of the uppermost strata in Europe, but not in South America.

A similar analysis of Ludlow to Emsian assemblages in Australia shows that although *Zosterophyllum* itself is the only taxon recorded in Lochkovian rocks (Tyers, Victoria: Tims 1980), the presence of *Baragwanathia longifolia*, zosterophylls and rhyniophytes in Ludlow, Pragian and Emsian strata leads to the most parsimonious conclusion that the plants also existed in the area in Lochkovian times. Such palaeogeographical observations, including those from South America, lead to a hypothesis that in early Lochkovian times, there may have existed latitudinal variation in floras, with highest diversity in the tropics, decreasing towards the South Pole.

Testing of such a hypothesis requires more information from other geographical areas. Very little is known of Lochkovian plants from China, although subsequent highly diverse Pragian assemblages are said to share taxa with Australia (Hao & Gensel 1998). At higher northern palaeolatitudes, analysis is hampered by our lack of familiarity with taxa recorded from the 'Gedinnian' of Siberia (?30°N; Stepanov 1975), although scrutiny of species lists and illustrations indicates that, in addition to *Cooksonia*, the majority of taxa are in the zosterophyll clade and include *Zosterophyllum* as well as a number of endemics. The assemblage would thus seem to have more in common with those of Bathurst Island and the late Lochkovian of South Wales. However, precise and independent controls on the age of the rocks are essential prerequisites to identification of evolutionary and phytogeographical trends.

Correlation based on spore zonations, which in turn result from the distribution of the plant producers, gives confidence only over small geographical areas. On a global scale, especially where information on megafossils, and particularly their *in situ* spores, is rare, the composition of an assemblage may reflect the timing of migrations or local adaptive radiations related to environmental or climate changes. However, there were sufficient similarities between assemblages in the Jutai Formation, Solimões Basin, NW Brazil and those from the ORS continent (Laurussia) to provide a Late Lochkovian age for the Brazilian material, an assignment independently confirmed by chitinozoans (Rubinstein *et al.* 2005). On the other hand, spores from the Furnas Formation in the Paraná Basin are less satisfactory in suggesting an MN zone older age, because this is based on an absence of certain taxa.

In the Precordillera, in the lower part of the Talacasto Formation in the Cerro del Fuerte Section, San Juan Province, spores, acritarchs and chitinozoans indicate a late Lochkovian age (Le Hérissé *et al.* 1996). This imposes a younger age for the Villavicencio Formation with its assemblage

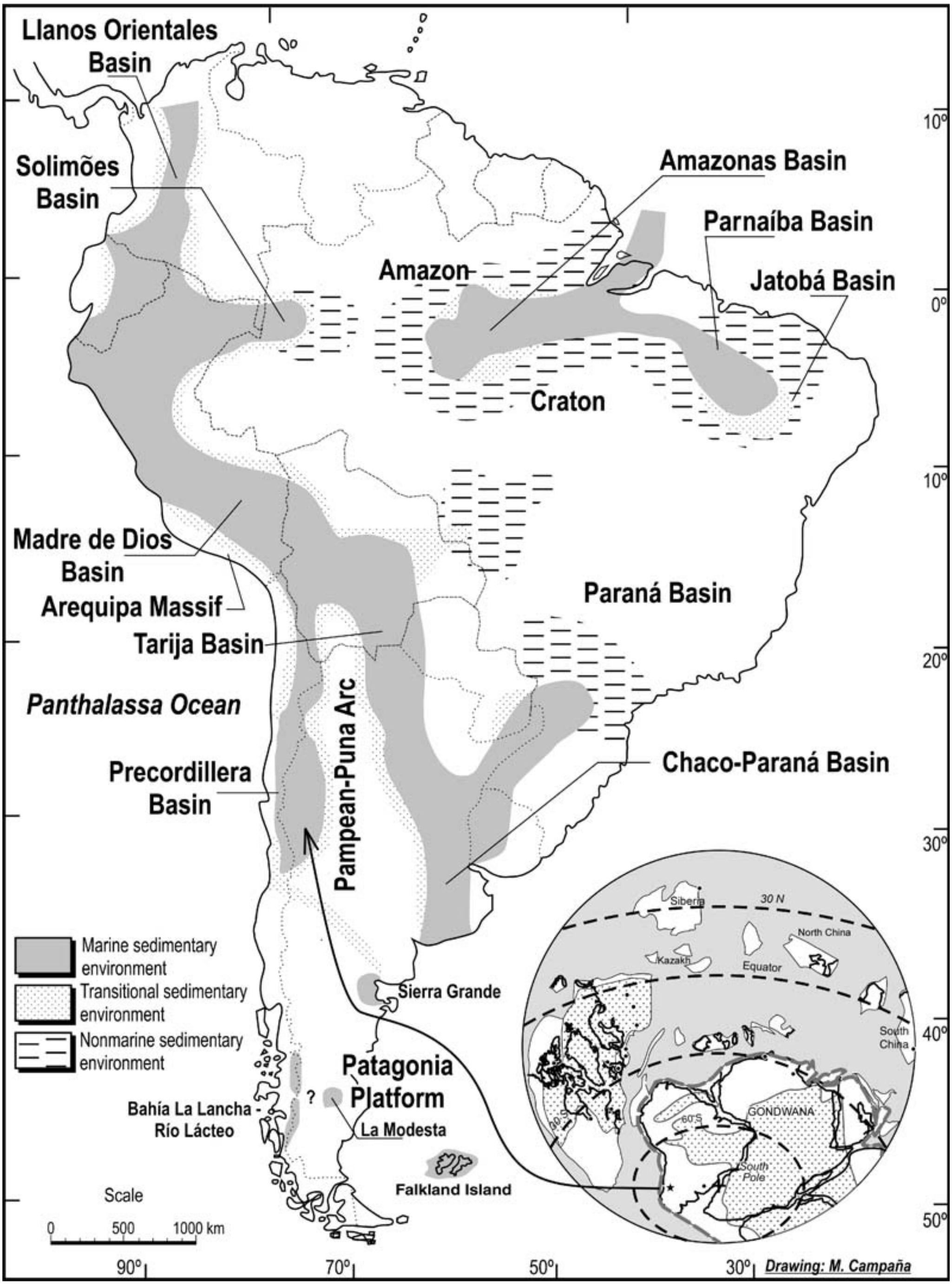

Fig. 9. Postulated land–sea relationships in South America during the Early Devonian based on Melo (1988) and Grahn (2003). Inset indicates global palaeogeography *c*. 400 Ma, based on Torsvik & Cocks (2004). Wide grey line indicates possible extent of the Gondwana supercontinent or plate. Dots indicate localities of selected Early Devonian plant assemblages.

dominated by rhyniophytes (Morel *et al.* 1993). Possible explanations will be considered in the discussion.

Post-Lochkovian comparisons

Detailed comparisons at even the genus level are impossible as the majority of the Precordilleran fossils are fragmentary and sterile, whereas the best preserved and diverse assemblage in an olistostrome recently redated as late Pragian–early Emsian (Rubinstein & Steemans 2007) comprises endemics. These include mainly fertile axial plants with terminal sporangia (rhyniophytoids) and an enigmatic 'leafy' shoot (*Bowerophylloides mendozaensis*) (Edwards *et al.* 2001*a*). The majority of the other fragments are featureless, mainly unbranched axes, of diameter up to 2 mm, with a few isolated taxa (very tentatively assigned to morphotaxa) and lycophytes. The latter, leafless but with swollen leaf bases, may seem to offer the best possibility of more precise identification. Indeed, fragments from the Punta Negra Formation at Talacasto Creek, superficially similar to those described here from Albarracin and the Río San Juan road section and probably the same taxon, were identified as two unnamed species of *Archaeosigillaria* (Gutiérrez 1996; but see p. 244).

Lycophytes also dominate Gondwanan Devonian assemblages of Libya. Originally described as Silurian to Early Devonian on the basis of field relationships and lithostratigraphy, the Acacus and overlying Tadrart Formations are now considered at least of Pragian age, although this is based on the plants themselves (Streel *et al.* 1990). The Acacus plants (Klitzsch *et al.* 1973) included fragmentary, smooth and spiny axes with isolated, elongate, fusiform sporangia named *Dawsonites*, *Psilophyton* and *Steganotheca* as well as abundant lycophytes with swollen leaf bases and leaf scars reminiscent of those from the Punta Negra Formation. These were originally assigned to well-known genera such as *Protolepidodendron* and *Archaeosigillaria*, in addition to endemics *Protosigillaria acacusense* and *Precyclostigma tadrartense* (Klitzsch *et al.* 1973). We concur with Streel *et al.* (1990) that many of these leafless or decorated lycophytes belong to the same taxon, paralleling our conclusion on the identity of the Argentine examples. The overlying Tadrart, Onon-Kasa and Emi Magri Formations, initially dated as Lochkovian–Emsian and also containing abundant fragmentary, sterile lycophytes assigned to *Lepidosigillaria*, *Archaeosigillaria* and *Lepidodendropsis* (Lejal-Nicol 1975), are probably no older than the Middle Devonian (Streel *et al.* 1990). Again, the placement of the poorly preserved, probably decorticated lycophytes in well-defined taxa is unwise. However, Streel *et al.* observed that a few stems had dimensions and leaf base characteristics more reminiscent of later Devonian arborescent forms with abscissed leaves than older herbaceous ones with persistent leaves.

In contrast to the Libyan assemblages, plants from Morocco occur in marine sediments, confidently dated by tentaculitids as Early Emsian. The plants themselves are fragmentary with only small clusters of sporangia assigned to a genus (*Dawsonites*) known elsewhere unequivocally (Gerrienne *et al.* 1999). Cf. *Sporogonites*, cf. *Uskiella* and cf. *Sartilmania* are applied to single sporangia and *Zosterophyllum* sp. to the base of a spike. More abundant axes have unusual small appendages with bifurcating recurved tips and elongate sporangia (*Aarabia brevicaulis*; Meyer-Berthaud & Gerrienne 2001). The single lycophyte has irregularly arranged swollen similar leaf bases and short spine-like triangular leaves. Meyer-Berthaud & Gerrienne thought the north African material closest to that found from the southern margins of the ORS continent on the basis of shared taxa. However, taking into account the uncertainties of identification of isolated sporangial shapes and sterile stems (admittedly with some exceptions), the Moroccan assemblage has much in common with Precordilleran ones; namely, indeterminate sporangia and occasional endemics.

The precisely dated Pragian and Emsian assemblages from the east coast of Gondwana (now Australia) at lower latitudes are dominated by the herbaceous lycophyte *Baragwanathia longifolia*, with persistent leaves (rarely found leafless), zosterophylls (e.g. *Zosterophyllum australianum*) and plants with clusters of terminal sporangia (e.g. *Hedeia* and *Yarravia*) (Lang & Cookson 1935; Tims 1980) but have no genera identical to those of the Argentine material.

Detailed comparisons with numerous and highly diverse assemblages from North America, Europe, Russia and China, where excellence of preservation has allowed detailed morphological and often anatomical studies of the components, are counterproductive. Axes in the Precordillera are of similar widths indicating similar dimensions, but none show the well-defined spines that characterize, for example, *Sawdonia* and certain *Psilophyton* species. There are no trusses or spikes of sporangia, nor axes with unequivocal lateral sporangia. Poor preservation of lycophytes precludes comparison with well-circumscribed taxa such as *Drepanophycus* and *Haskinsia*.

Although the fragmentary nature of the fossils may reflect a highly energetic transport history, it seems unlikely that it would have produced the sorting constancy in composition over a wide geographical area resulting in such reduced diversity and disparity. Although we cannot completely eliminate the possibility that facies bias has produced the differences in composition between the low-latitude assemblages (mainly continental) and Argentina ones (marine), it should be noted that the Moroccan material also occurs in marine rocks and, based on our analyses, also indicates lower disparity. We thus conclude that the plant record, with one exception (San Isidro), indicates abundant land vegetation but of low diversity and probably disparity. Absence of the abundant fertile specimens at a similar grade to lower latitude coeval examples may reflect seasonality in sporangial production, non-coincident with storm events, or alternatively linked with a life-style strategy in which plants remained in vegetative state over long periods. Hotton *et al.* (2001) have, for example, suggested that the rarity of fertile zosterophylls (five localities) in extensive assemblages (60 localities) from the Gaspé, in which abundant vegetative remains are recorded, may relate to such a strategy. The San Isidro assemblage, however, does contain fertile specimens and these endemics are at a simpler morphological grade to coeval specimens at low latitudes.

On such extremely limited evidence we propose that the latitudinal variation noted in the Lochkovian persisted into later times.

Discussion

Parrish (1990, p. 22) commented that 'more confusion has arisen over Devonian plate positions than for any other time'. This has had implications for the position of the South Pole. We may compare, for example, the position used by Gerrienne *et al.* (2001) in NE Brazil, based on Boucot (1999); by Edwards *et al.* (2001*b*), based on Eldridge *et al.* (1996); between South Africa and Southern Brazil, used by Torsvik & Cocks (2004); and in the palaeocontinental reconstruction used here (Fig. 9). Whatever the chosen reconstruction, all Precordilleran assemblages are (preserved) within 30° of the palaeo South Pole and thus plants would have been growing in extended periods of darkness in winter as well as experiencing low temperatures. Just how low these were is conjectural. The postulated high levels of CO_2 in the Early Devonian (Berner 1993) suggests a greenhouse world, confirmed by absence of evidence for glaciation on land or for sea ice (e.g. dropstones) (Caputo & Crowell 1985). However, the position of the pole towards the margin of the continent (Torsvik & Cocks 2004) would allow continental ice sheets even at high CO_2 levels (Crowley *et al.* 1987). In contrast, Worsley *et al.* (1994), using the premises that global CO_2 levels and temperature are directly proportional to average latitude of Earth's land masses and inversely related to total land area, postulated a major decrease in temperature through the Devonian (culminating in Early Carboniferous ice-ages), from a thermal maximum, in terms of average polar temperature, about 425 Ma for the whole of the Phanerozoic. More specifically, they suggested a global polar temperature of *c.* 14 °C and those at the Equator just a little warmer than today with a decrease of *c.* 2 °C in the Early Devonian. However, these temperatures are probably overestimates, as they do not take into account the prevailing decreased solar luminosity. In contrast, Golonka *et al.* (1994) modelled subzero mean annual surface temperatures for southern South America. Low temperatures are inferred from occurrences of Malvinokaffric Realm faunas (Cocks & Torsvik 2002), particularly brachiopods (Boucot & Blodgett 2001), although in the Argentine Talacasto Formation there is some evidence of the presence of exotic 'more temperate' elements (Herrera 1995; Herrera & Racheboeuf 1997).

Parrish (1990) herself, working with a similar Gondwanan reconstruction and palaeopole to Torsvik & Cocks (2004), but based on Scotese & Denham (1988), used their influences on zonal circulation and precipitation patterns to infer that plant localities would have received abundant moisture from westerlies. On balance then, it would seem likely that land vegetation in Argentina would have experienced some freezing temperatures in winter, persistent precipitation (but not prolonged snow cover) and winter darkness, environmental conditions in marked contrast to the equatorial and temperate non-light-limited, humid climates of lower latitudes (Golonka *et al.* 1994).

Gerrienne *et al.* (2001) addressed some of the problems for plant life in very cold climates in relation to the Brazilian Lochkovian assemblages (within 70°S of the palaeo South Pole), and concentrated on morphological adaptations. Thus they attributed the high percentage of taxa with enations or spines not only to light harvesting in connection with poor insolation at high latitudes, but also to protection, particularly of apices, against freezing and wind damage. Sunken sporangia would have provided similar benefits, as would the condensed branching resulting in a shrubby habit. Although similar plants with sunken sporangia (*Cooksonia banksii*) and spines also occur at higher latitudes, they might well have provided the pre-adaptations to colder climates. An abundance of thick-walled tissues noted in Old Red Sandstone plants would have been an advantage, as is exemplified in Arctic plants today (Crawford 1989), although high CO_2 concentrations might have increased sensitivity to freezing, as demonstrated for extant seed plants (Royer *et al.* 2002). The turgid tissues recorded in the Rhynie Chert plants (Edwards 2004) were certainly unlikely to have survived freezing. This leads to speculations on life cycle (ethology). Plants at high latitudes today have to ensure that carbon gain during the growing season must not only allow completion of developmental and reproductive cycles, but also permit the accumulation of sufficient reserves to survive winter and to initiate spring growth. Higher temperatures in winter that stimulated respiration would add to this stress. We know very little about the duration of life cycles of early land plants, although studies such as those on Gaspé assemblages in relation to depositional environments (Hotton *et al.* 2001) and the Rhynie Chert (e.g. Kerp *et al.* 2001) provide some insights. Thus the Scottish *Nothia aphylla* exhibited clonal grown on sandy substrates, with postulated short-lived aerial parts arising from perennating underground rhizomes that possessed an abundance of dormant meristems. Such a life strategy would also be advantageous at high latitudes and was probably adopted by Emsian trimerophytes from the Gaspé, postulated to have exhibited monocarpy in production of sporangia. In contrast, zosterophylls were hypothesized as occupying sites over long intervals in a vegetative state, perhaps comparable with graminaceous plants in the Arctic today and mentioned above as an explanation for the lack of reproductive organs in the post-Lochkovian Argentine assemblages. Thus it seems likely that early land plants could have survived at high latitudes but the record suggests at lower diversity than lower latitude representatives and with less disparity in aerial sporophytes.

In view of Parrish's conclusions on precipitation it seems unlikely that the plants were water-stressed, but they would perhaps have experienced wind exposure and nutrient deficiency. In the present-day Arctic, winds remove decomposing debris from around plants, thus exacerbating nitrogen and phosphorus deficiencies, and minimizing soil development with consequences for poor water retention (Crawford 1989). In contrast, in more temperate realms, accumulation of litter would lead to development of mesic environments, opportunities for successional levels of vegetation, more variability in habitats and hence more diversity.

Finally, the detailed facies descriptions presented here indicate that the plants were preserved in marine settings fairly close to a coastline. Indeed, in the Bachongo area the marine Punta Negra Formation is succeeded by the continental Bachongo Formation. However, we remain uncertain as to how this coastline relates to the palaeocontinent Gondwana; namely, whether the Precordillera localities were on the SW edge of the continental land mass, where Ramos (1988) suggested that the oceanic crust remnant of the nearest Chilenia terrane was subducted below Gondwana and accreted during late Devonian times. Indirect evidence for a coastline is derived from the distribution of marine faunas during this time interval, although their absence cannot always be taken as evidence for existence of a land mass (Fig. 9). Alternatively, should the localities be indeed situated on isolated land masses developed as part of the Tontal arc associated with the development of a forearc basin, they would have been situated some kilometres from the mainland, and thus would still have been at relatively high latitudes, with similar light regimes, but marginally higher temperatures. Thus the discussion on the environmental and physical conditions remains broadly relevant to this island scenario, with perhaps less likelihood of prolonged snow cover. The limited endemism recorded in the assemblages may have resulted from evolution in isolation, but the latter has not resulted in increased disparity, with morphological grades being similar to those elsewhere on high-latitude Gondwana.

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Early Palaeozoic cooling events: peri-Gondwana and beyond

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Abstract: The short-lived end-Ordovician Hirnantian glaciation allied to marine mass extinction is variously considered as a short-lived event or as the peak of long-drawn-out climatic cooling through at least late Ordovician–early Silurian times. Evidence from Early Palaeozoic facies, faunas and stable isotope excursions used to interpret climatic cooling events ranges farther, from late Mid-Cambrian to late Silurian times. Glacigenic sediments, structures and geomorphology provide direct evidence of glacial episodes. Cool-water carbonate deposition, which is particularly widespread during the late Ordovician Boda event in high-latitude peri-Gondwana–Gondwana, and beyond into mid–low palaeolatitudes, is interpreted as indicating global cooling, not warming as has been proposed. Such carbonates also characterize mid-latitude continents widely at horizons earlier in the Ordovician, and more locally in the mid-Silurian in high-latitude Gondwana. Cool-water carbonate mounds have distinctive facies-controlled mound faunas across palaeocontinents. Other facies evidence for palaeoclimates includes black shale deposition, including deglacial organic-rich 'hot shales', which indicate transgression in epeiric seas, and sea-level curves interpreted from facies and faunal successions. Correlation is shown between facies evidence and positive C isotope excursions, from which cyclicities are apparent. The possible interface of orbitally controlled rhythms is considered against evolving palaeobiogeography, and changes in global sea level and in $p\mathrm{CO_2}$. Facies and faunal evidence from peri-Gondwanan terranes (Armorica, Central Europe, Alborz) is assessed with that from Gondwana (mostly North Africa, South America) and correlatives in Avalonia, Baltica and Laurentia to establish a wider picture of early Palaeozoic cooling events.

The late Ordovician Hirnantian glaciation centred on western Gondwana is variously considered as either a short-lived, rapid (1–2 Ma) event closely associated with marine mass extinctions (Brenchley *et al.* 1994, 2001; Brenchley 2004), or as the culmination of a long-drawn-out climatic shift from late Ordovician (Sandbian; early Caradoc) to early Silurian (late Llandovery) times (Saltzman & Young 2005; Cherns & Wheeley 2007; Díaz-Martínez & Grahn 2007). Page *et al.* (2007) suggested that high atmospheric $\mathrm{CO_2}$ levels and episodes of oceanic anoxia characterized a late Ordovician–early Silurian icehouse period of *c.* 30 Ma that included seven glacial maxima.

Here, facies, faunas and isotopic data from peri-Gondwanan terranes, Gondwana and beyond are reviewed to interpret how the waxing and waning of Gondwana-centred glaciations controlled climatic changes through the wider early Palaeozoic geological record. The various strands of evidence are interwoven to suggest that periodic cooling events that came to a climax in the Hirnantian actually spanned a much longer time scale, from at least late Mid-Cambrian to late Silurian times. We consider what might have driven the periodicity of early Palaeozoic climate cooling; in particular, how orbitally controlled rhythms may have interfaced with intrinsic factors such as evolving palaeobiogeography, bathymetry and $p\mathrm{CO_2}$.

The broad changes in palaeobiogeography from Cambrian to Silurian are illustrated in Figure 1 (Cocks & Torsvik 2002, 2004, 2005). The supercontinent of Gondwana stretched in the southern hemisphere from high (West Gondwana–North Africa and southern Europe) to low (East Gondwana–Australia and adjacent regions) latitudes. Around the north of Gondwana the peri-Gondwanan terranes discussed below include Avalonia, Armorica, Perunica and Alborz. Baltica and Laurentia are separate continents, the latter consistently in low latitudes. The Kazakh terranes include parts of Baltica (southern Urals) and the Chu-Ili terrane with warm-water Gondwanan affinities (Fortey & Cocks 2003). In the late Cambrian (Paibian), reconstructions show Avalonia on the northern edge of high-latitude Gondwana, and Baltica (rotated) in temperate latitudes. During the early Ordovician, Avalonia rifted away from West Gondwana and

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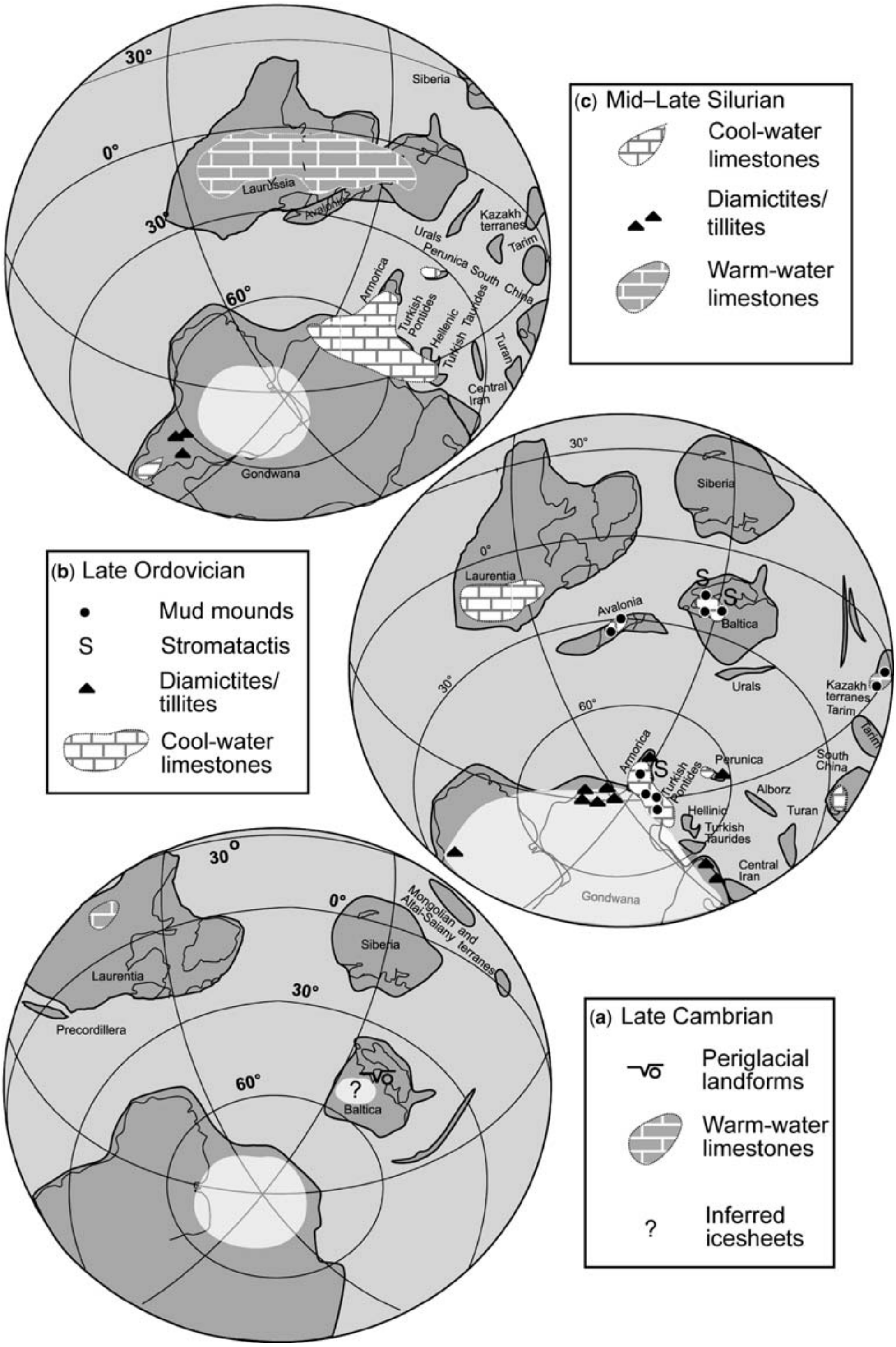

Fig. 1. *Continued.*

drifted north, colliding first with Baltica in mid-latitudes with the closure of the Tornquist Sea in the late Ordovician and then with Laurentia in the early Silurian as Iapetus closed. Faunas support movement of the Precordillera of South America rifting from Laurentia in the early Ordovician to high-latitude Gondwana in the Silurian (Fortey & Cocks 2003; Benedetto *et al.* 2009; compare Finney 2007). The Gondwanan pole wandered from North Africa to the late Ordovician to South America in the early Silurian.

Facies and geomorphological evidence of climatic cooling

Glacigenic deposits and associated structures

Glacigenic deposits and associated features provide direct evidence of continental and marine glaciation. There is widespread sedimentological, glaciotectonic and geomorphological evidence of late Ordovician glaciation as Gondwanan inland ice extended north and northeastwards to a Hirnantian maximum (e.g. Semtner & Klitsch 1994; Hallett 2002; Page *et al.* 2007, table 2; Fig. 1). Indications of sea ice come from glacial diamictites and ice-rafted dropstones in late Ordovician to early Silurian marginal and glaciomarine successions (e.g. Grahn & Caputo 1992; Buttler *et al.* 2007; Díaz-Martínez & Grahn 2007). In North and West Africa, glacigenic deposits widely lie with angular unconformity on older rocks of Precambrian–late Ordovician age, and are overlain by lower Silurian shales. The age of some of the fluvioglacial deposits on the Gondwanan margin is relatively well constrained by intercalated marine successions. From Libya, glacial deposits in the Melaz Shuqran and Mamuniyat formations are dated as early Caradoc to Ashgill (e.g. Hallett 2002), whereas in Algeria the Tamajert Formation is Caradoc–early Silurian (Biju-Duval *et al.* 1981). However, glacial deposits in southern Morocco are restricted to the early Hirnantian (Destombes 1981; Destombes *et al.* 1985; Villas *et al.* 2006). In South Africa (Pakhuis Formation of the Table Head Group), two thin diamictite horizons, the lower one at least a continental deposit, are separated by shallow marine sandstones and overlain by dark marine shales of the Hirnantian Soom Shale or Member of the Cederburg Formation (Young *et al.* 2004). In other areas, glacial deposits correlated with the late Ordovician–early Silurian are more broadly bracketed by under- and overlying successions; for example, Mauritania (Taoudeni Basin; Deynoux & Trompette 1981), Ghana (Talbot 1981), Sierra Leone (Reid & Tucker 1972; Tucker & Reid 1973), west Egypt, Sudan–Chad and northern Ethiopia (Hambrey 1981; Semtner & Klitsch 1994). At its maximum extent in the Hirnantian, the continental ice sheet extended into northern Morocco (Le Heron *et al.* 2007). In North Africa, phases of ice sheet decay are indicated by deeply incised palaeovalleys and glacigenic deposition, whereas ice growth is indicated by deformation and shearing of unconsolidated sediments in subglacial environments (e.g. Ghienne & Deynoux 1998; Hirst *et al.* 2002; Ghienne 2003; Deynoux & Ghienne 2004). Field evidence from North Africa is interpreted as indicating 2–4 cyclic sequences resulting from waxing and waning of Hirnantian ice sheets (Ghienne 2003; Le Heron *et al.* 2005). Sutcliffe *et al.* (2000) recognized two subglacial erosion surfaces within the early Hirnantian (*extraordinarius* Biozone), and concluded that these related to the 100 ka eccentricity cycle.

In Jordan and Saudi Arabia, in high-latitude East Gondwana, two episodes of late Hirnantian glacial incision and deposition are indicated by deep palaeovalleys that have basal coarse deposits of glacially striated and faceted clasts, and further filled with glacio-fluvial to glaciomarine sediments (Armstrong *et al.* 2005, figs 4 & 5). Saudi Arabia at this time lay at the edge of a continental ice sheet, with Jordan on the bordering marine shelf (Turner *et al.* 2005, fig. 3). The basal conglomerates of the upper channel horizon in southern Jordan, and at both levels in Saudi Arabia have been interpreted as tillites (Vaslet 1990). In southern Jordan the first glacial lowstand is marked by incision onto

Fig. 1. Oblique southern hemisphere projection of palaeogeographical reconstructions for (**a**) Late Cambrian, (**b**) Late Ordovician and (**c**) Mid–Late Silurian, showing the extent of the Gondwanan ice cap interpreted from glacigenic deposits (diamictites and tillites) and geomorphology, and coeval marine facies. (a) Late Cambrian (Paibian) at SPICE C isotope excursion, showing periglacial geomorphology resulting from severe permafrost conditions in temperate Baltica, and inferred ice cap on Gondwana (although facies evidence is lacking). The SPICE excursion is known from an extensive shallow carbonate platform in the Great Basin, USA (Laurentia) to Australia (East Gondwana), Kazakhstan and South China. (b) Late Ordovician (Katian–Hirnantian), showing extensive glacigenic deposits in Gondwana and peri-Gondwana, cool-water carbonates from high to low latitudes, distribution of carbonate mounds and stromatactis. (c) Mid- to Late Silurian, showing diamictites and glacial dropstones, and cool-water carbonates (Sacta Limestone) in Gondwana (South America), cephalopod limestone biofacies through peri-Gondwanan terranes, and warm-water limestones in low latitudes (Baltica, Avalonia, Laurentia). C isotope excursions are reported from Laurentia, Baltica, Perunica and East Gondwana (Australia).

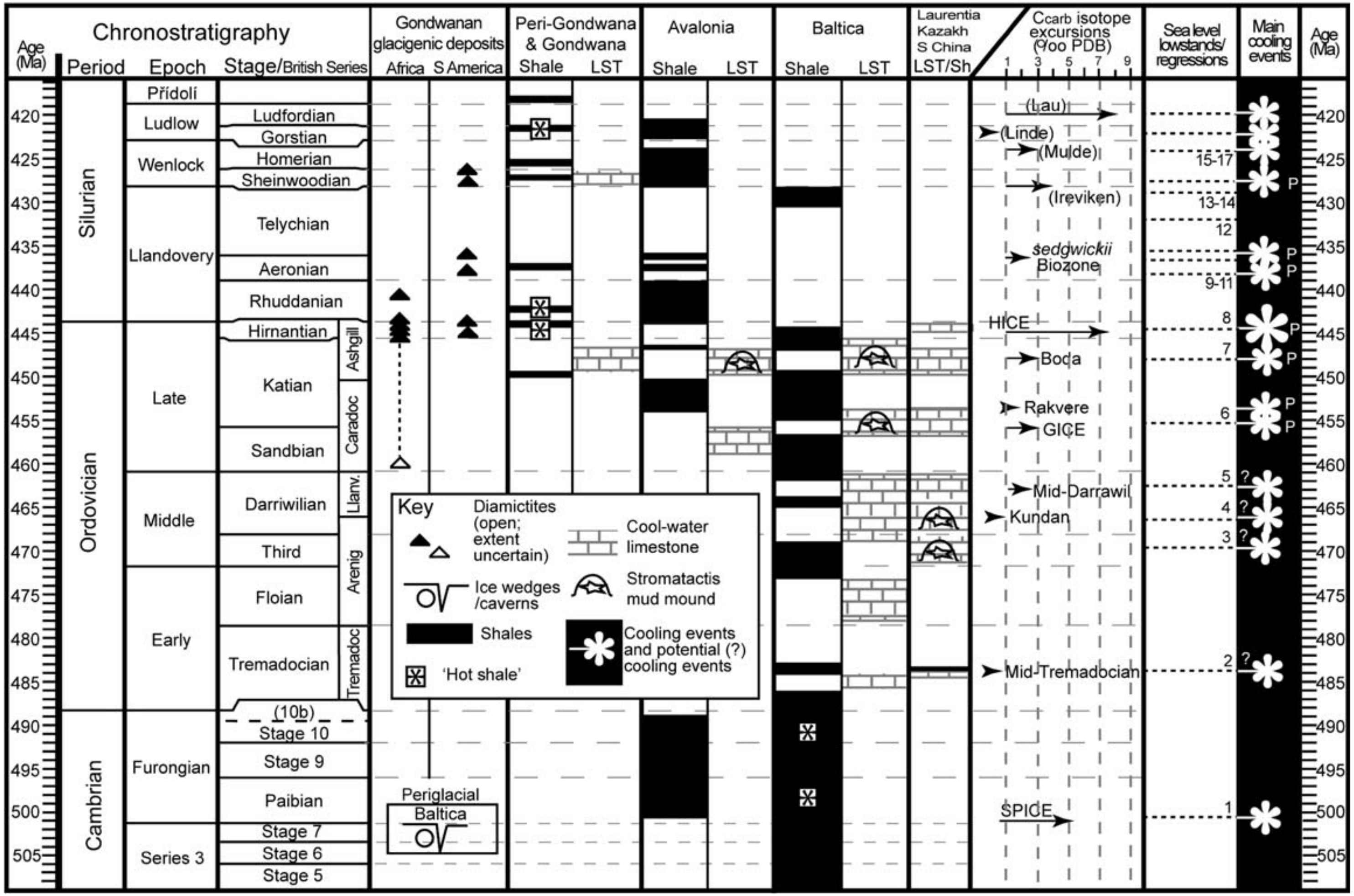

Fig. 2. *Continued*.

shoreface sediments, the second by larger, subglacial tunnel valleys. In southern Jordan in addition, Turner *et al.* (2005) recognized two subsidiary glacial advances between the two major horizons.

In SW Europe, late Ordovician diamictite deposits represent ice-rafted clasts in glaciomarine deposits in the peri-Gondwanan terranes of the Armorican massif, the Iberian peninsula, Central European Thuringia (Robardet & Doré 1988) and in Perunica (Brenchley & Štorch 1989). In the peri-Gondwanan Taurides, glacial features including a glacial pavement and striated dropstones are dated by faunas as Hirnantian (Monod *et al.* 2003).

In the Avalon zone of Newfoundland, diamictites of Caradoc age are reported from the Davidsville Group (W. B. Harland 1981), and of late Ordovician–early Silurian age in the Stonesville Group of the Dunnage Zone (Kennedy 1981). Diamictites in Nova Scotia in the Meguma Zone, where sequences indicate late Ordovician regression (Schenk 1997), have a poorly constrained age range of Early Ordovician–mid-Silurian (Schenk & Lane 1981). These suspect terranes were accreted to the North American margin (Williams & Hatcher 1983).

From the late Ordovician to early Silurian the Gondwanan pole wandered from western North Africa into South America (e.g. McElhinny *et al.* 2003, fig. 5; Díaz-Martínez & Grahn 2007, fig. 14). In the Cape Basin, South Africa, diamictites (Pakhuis Formation) are dated as late Ordovician by overlying Hirnantian shales (Cocks & Fortey 1986; Sutcliffe *et al.* 2001). Glaciations continued into the Silurian in South America (Grahn & Caputo 1992). In South America, late Ordovician glacigenic deposits are documented from Brazil (Paraná Basin) and the Precordillera of Argentina (Grahn & Caputo 1994; Bergström *et al.* 2006; Díaz-Martínez & Grahn 2007). Ordovician–Silurian diamictite-bearing units, including the Cancañiri Formation in Bolivia, which correlates into Peru (San Gabán Formation) and Argentina (Zapla Formation), crop out across an area $>640\,000\ \text{km}^2$, unconformably overlying various upper Ordovician formations (Díaz-Martínez & Grahn 2007). Chitinozoan assemblages confirm an early Silurian, Llandovery age for these diamictites, which include glacially striated and faceted clasts, resedimented into deep glaciomarine settings by gravity flows (Díaz-Martínez *et al.* 2001; Díaz-Martínez & Grahn 2007). A glaciated, tectonically uplifted source area supplied material from the west into a foreland basin (Peru–Bolivian Basin) along the western margin of Gondwana (Sempere 1995). In Brazil, four glaciations were dated from glacigenic deposits between early middle Llandovery and earliest Wenlock times (Grahn & Caputo 1992).

In Bolivia SW of Cochabamba, younger diamictites of the Kirusillas Formation, derived from the north and east, are associated with resedimented limestone slabs of early Wenlock age (Díaz-Martínez 2007).

Glacigenic deposits from early Caradoc (Sandbian) to late Silurian times in high-latitude Gondwana and peri-Gondwanan terranes cover a time span of *c.* 35–40 Ma, with periodicities from *c.* 0.1 Ma to *c.* 8–10 Ma (Fig. 2).

Periglacial features and deposits

Periglacial processes of freezing and thawing form or modify landscapes in cold, non-glacial climates. Late Cambrian Baltica lay in temperate latitudes 40–50°S (Fig. 1). In the St. Petersburg region of the East Baltic, ice wedge casts preserved in the 'Obolus Sands' of mid-Cambrian–early Ordovician age indicate seasonal freezing and severe periglacial environments; that is, permafrost below -15°C and air temperatures below -6°C (Dronov & Popov 2004; Fig. 3). Tapering fissures into the poorly consolidated sands have breccia infills apparently syngenetic with the uppermost Middle Cambrian Rebrovo Member. Cavern collapse

Fig. 2. Summary diagram showing facies evidence and C isotope excursions interpreted as cooling events from late Cambrian to late Silurian times, against regressions in sea-level curves (primarily for Baltica), as discussed in the text. Facies evidence of glacigenic deposits, periglacial geomorphology, black and 'hot' shales, and cool-water carbonates including carbonate and stromatactoid mud mounds are presented for palaeocontinents from high-latitude Gondwana, through Avalonia, Baltica and into low-latitude Laurentia, Kazakhstan and South China. For the positive C excursions, the arrows indicate the maximum $\delta^{13}C_{carb}$ values for named events. In the Silurian, conodont extinction events associated with excursions on Gotland are shown in parentheses. Sea-level lowstand or regressive horizons: 1, SPICE; 2–8, Ordovician (Nielsen 2004) (2, *Ceratopyge* regressive event; 3, Komstad regressive event; 4, Stein lowstand event (basal Kundan); 5, Skärlov lowstand; 6, Frognarkilen lowstand event; 7, Grimsøya regressive event; 8, Hirnantian regressive event); 9–12, Llandovery (Loydell 1998), (9–11, *argenteus*, *sedgwickii*, *turriculatus*; 12, *lapworthi*); 13–17, Wenlock–Ludlow of Gotland (13, 14, *riccartonensis*, *lundgreni*; 15–17, *nassa–ludensis*, *tumescens*, *leintwardinensis*). Cooling and potential cooling events interpreted here are compared with the glacial maxima recognized by Page *et al.* (2007; P in Cooling event column) for the late Ordovician–early Silurian, which is the most widely studied interval. Evidence for glaciation in the period between the SPICE excursion and Middle Ordovician is currently less apparent, which may indicative a relative lull in glacial development.

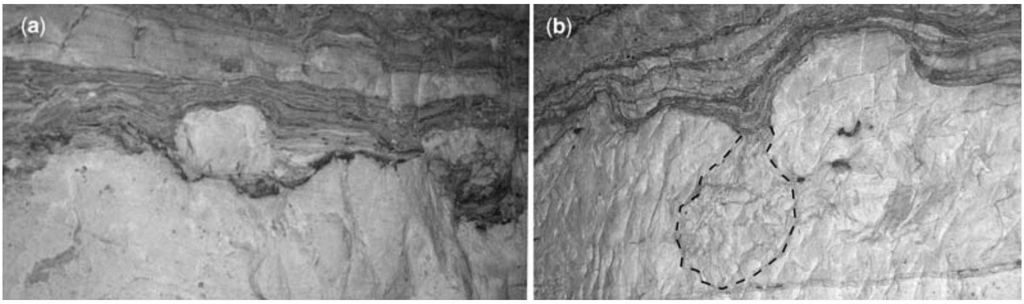

Fig. 3. Periglacial geomorphology, east of Syas River, St. Petersburg region, Russia. (**a**) Irregular contact between poorly consolidated Middle Cambrian *Obolus* Sands and overlying transgressive shales of the late Cambrian (*Agnostus pisiformis–Leptoplastus* biozones) Ladoga Formation, in tunnel section. Detached blocks of 'sandstone' among the basal shales, and in breccia-filled synsedimentary erosion cavities in the *Obolus* sands. (**b**) Irregular breccia-filled erosion cavity (dotted line) in Obolus Sands, interpreted as synsedimentary cavern collapse from ice wedge cast. Structures indicate persistent submarine permafrost (Dronov & Popov 2004; photographs courtesy of those authors).

occurred during late Cambrian (*Agnostus pisiformus–Leptoplastus* biozones) marine transgression, although persistence of permafrost during transgression is indicated by marine sediment-filled lenses within loose sands, possibly representing casts of former ice lenses (Popov, pers. comm.).

In south–central to southern Sweden, collapse structures affect Cambrian rocks in several areas. In Västergötland, the deep (>20 m) Brattefors plugs are cut through the Middle–Upper Cambrian Alum Shale and underlying Lower Cambrian sandstones, and are filled with Alum Shale up into early Ordovician (Tremadoc) sedimentary strata (Teves & Lindström 1988). Breccia-filled structures described from upper Lower Cambrian sandstones of Närke are of late Mid-Cambrian–early Ordovician age (Karis & Magnusson 1972). In Skåne, 'funnel grabens' 5 to >150 m in diameter in Lower Cambrian sandstones are of late Cambrian–early Ordovician age (Lindström 1967). Tectonic uplift may have contributed to rapid changes of sea level of the order of *c*. 50–150 m (Artyushkov *et al.* 2000), but the collapse structures can be interpreted as indicating ice wedge casts formed in severe permafrost environments across southern Baltica in mid–late Cambrian times (Figs 1 & 3).

This horizon correlates with the SPICE (Steptoean) C isotope excursion, and a 2–3 Ma interval documented from Upper Cambrian successions of Laurentia, Kazakhstan, China and Australia that starts (*Glyptagnostus reticulatus* Biozone) with an extinction event affecting trilobites and linguliformean brachiopods (Saltzman *et al.* 2000; see below). Direct evidence for late Cambrian glaciation is lacking, but permafrost across temperate latitudes implies high-latitude ice sheets.

In Baltica, sporadic ice-transported quartz sand grains are found in Lower–Middle Ordovician carbonates of Sweden (Lindström 1972). These may have been derived through pack ice from Late Cambrian glacial complexes in Baltica. In the Urals, glacial deposits of the Asha Formation have a poorly constrained, pre-late Ordovician age (overlain by Caradoc Typel Regional Stage). Although previously assigned tentatively to the latest Proterozoic Ediacaran, a late Cambrian age may be more likely (Popov, pers. comm.).

Deglacial black shales and other epeiric sea black shales

For the last Ice Age, deglaciation at high latitudes is thought to have been initiated by orbitally controlled changes in insolation and increase in $p\mathrm{CO}_2$, with rise in sea level through melting of ice sheets, and reduced ocean circulation (e.g. Rahmstorf 2002). In Lower Palaeozoic successions, sea-floor anoxia resulting from high productivity and eutrophic epeiric seas is represented by deposition of organic-rich black shales (e.g. Page *et al.* 2007). Deglacial shales are additional facies evidence in the rock record for a preceding glacial episode in high latitudes.

An organic-rich 'hot shale' forms a lower Silurian marker horizon overlying glacigenic sediments across the northern Gondwanan margin (Lüning *et al.* 2000; Buttler *et al.* 2007, text-fig. 2). These black shales, rich in radioactive uranium, which form important hydrocarbon source rocks in Arabia and North Africa, indicate post-glacial anoxia in a transgressive marine succession. Source rocks are also developed in the basal Silurian in the Amazon Basin of South America, the Russian Platform and in Laurentia in the Interior basins of the USA (Lüning *et al.* 2000). In southern Jordan, graptolitic black shales overlying Hirnantian glacigenic channel fill sediments were interpreted by Armstrong *et al.* (2005) to represent a deep-water, transgressive to highstand sequence deposited on the maximum flooding surface (Wignall & Maynard 1993; Wignall 1994). They suggested that latest Ordovician (*persculptus* Biozone) ice sheet melting was modulated by obliquity cycles (41 ka), with sea-floor anoxia developed in a salinity-stratified water column. In South Africa, dark 'hot shales' of the Soom Shale, directly overlying the higher of two diamictites, indicate Hirnantian transgression (Young *et al.* 2004). Lüning *et al.* (2000) concluded that the 'hot shales' in North Africa and Arabia representing post-Hirnantian anoxia were restricted to the early Llandovery (Rhuddanian), and that maximum transgression was not until Late Llandovery times. They suggested that post-glacial upwelling of nutrient-rich waters leading to black shale deposition on the Gondwanan shelf was possibly reinforced by oxygen-poor waters resulting from stratification of the water column caused by meltwater influx (Lüning *et al.* 2006; see Armstrong *et al.* 2006; Page *et al.* 2007). A younger, late Llandovery–Early Wenlock 'upper hot shale' in Jordan has a more restricted distribution on the distal Gondwana shelf (Lüning *et al.* 2005, 2006).

In South America, organic-rich shales of the Ludlow 'Carmelitas facies' within the Kirusillas Formation in the Cochabamba region, Bolivia are interpreted as a Gorstian deglacial deposit (dated by graptolites; Edwards *et al.* 2009). Also in Bolivia (Altiplano–Eastern Cordillera), Late Ordovician (Tokochi Formation: ?late Caradoc–?early Ashgill) organic-rich black shales lie unconformably below the early Llandovery Cancañiri Formation diamictites (Díaz-Martínez & Grahn 2007, fig. 4).

Epeiric, relatively organic-lean black shale deposition that occurs widely and repeatedly through the Early Palaeozoic indicates significant periods of sea-floor dysoxia–anoxia during what were typically greenhouse conditions with high $p\text{CO}_2$. Such deposits are also widely associated with transgressions (Wignall 1991, 1994). High sea levels and warm, salinity-stratified oceans caused widespread sea-floor dysoxia (Railsback *et al.* 1990). Increased organic carbon burial is commonly considered the driving factor in positive C stable isotope excursions (e.g. Kump & Arthur 1999; Cramer & Saltzman 2007*a*). Page *et al.* (2007) suggested that the carbon sink represented by these shales acted as a negative feedback mechanism for temperature by drawing down CO_2 levels. Taking the occurrence of black shale deposition as a proxy for glacioeustatic sea-level rise during interglacial periods, Page *et al.* (2007, fig. 2) proposed seven glacial maxima between the mid-Caradoc (early Katian) and early Wenlock (Sheinwoodian); that is, across a time span of *c.* 28 Ma. Evidence for Gondwanan ice from diamictites or tillites is stratigraphically well constrained for the Hirnantian, rather less so for the subsequent early Silurian events.

Cool-water carbonates

Cool-water (non-tropical) heterozoan carbonates are characterized by generally low rates of carbonate production and accumulation, and by a scarcity of framework-building photozoans (colonial corals, stromatoporoids, calcareous algae; James 1997; Pedley & Carannante 2006). Intervals of cool-water carbonate development require well-ventilated and -oxygenated sea floors, suggesting thermohaline circulation and ocean overturn induced by high-latitude glaciation (e.g. Cherns & Wheeley 2007, fig. 5). Although they are most common in mid–high latitudes, cool-water carbonates can also form in low latitudes when conditions are right (e.g. Samankassou 2002). Between cooling events, oceans had sluggish circulation and were salinity stratified. Thick Lower Palaeozoic successions of fine clastic sediments, including intervals of black anoxic shales, were laid down. Development of carbonate mud mounds during limited intervals in previously offshore shelf or mid–outer ramp settings indicates reduced influx of clastic sediment with shallowing, which supports glacio-eustatic sea-level fall.

The pre-Hirnantian Ashgill (late Katian) Boda event involving changes in faunal distributions (Fortey & Cocks 2005) corresponds to a short-lived but extremely widespread facies change to limestones within typically thick successions of fine-grained clastic deposits in high and mid-palaeolatitudes. This interruption to clastic sediment supply affects peri-Gondwanan terranes, the West Gondwanan margin, Baltica, Avalonia, Kazakh terranes and also the stable platform of Laurentia (Boucot *et al.* 2003; Fortey & Cocks 2005; Cherns & Wheeley 2007, fig. 1). Although Fortey & Cocks (2005) proposed this as an episode of global warming, Cherns & Wheeley (2007) interpreted the limestones as cool-water carbonates, which, from their extensive latitudinal range, indicate an episode of global cooling and glacio-eustatic shallowing.

Along the high-latitude West Gondwanan margin *c.* 60–70°S, a shelf-parallel belt of limestones developed across several hundreds of kilometres, intercalated within glaciomarine shales and siltstones. The limestones include deep subtidal, bryozoan mud mound complexes and bryozoan-rich biostromes (e.g. Destombes *et al.* 1985; Álvaro *et al.* 2007; Buttler *et al.* 2007). Associated with the mounds in Libya there are 'microbrecciated facies' recently interpreted as diamictites (Buttler *et al.* 2007). In Armorica, outer ramp mud mound complexes of the Iberian Cystoid Limestone in NE Spain comprise bryozoan–cystoid–pelmatozoan limestones (Vennin *et al.* 1998). The Hirnantian regression led to subaerial exposure, erosion and karstification of these limestones, which are overlain unconformably by Hirnantian glaciomarine shales (Vennin *et al.* 1998). In Avalonia, early–mid-Ashgill carbonate mud mounds of the Kildare and Keisley limestones include the cold-water *Hirnantia* fauna in the top beds (Wright 1968, 1985; Rushton *et al.* 1999). In Baltica, at temperate palaeolatitudes 30–35°S, subtidal carbonate mud mounds developed at this same stratigraphical level are found in south central Sweden (Boda Limestone), in the subsurface of Gotland and the Baltic (Tuuling & Flodén 2000; Bergström *et al.* 2004; Sivhed *et al.* 2004), and in Estonia (Nestor 1995; Hints & Meidla 1997; Harris *et al.* 2004). Offshore carbonate mud mounds also occur in the low palaeolatitude Chu-Ili terrane of Kazakhstan (Kipchak Arc) in the early–mid-Ashgill (*anceps* Biozone) Ulkuntas Limestone (Nikitin & Popov 1996; Nikitin *et al.* 2006).

In the Avalonian Welsh Basin, thin offshore Ashgill limestones developed locally within thick fine clastic successions include phosphate nodules and horizons, cherts and pyrite (Crûg, Sholeshook limestones; Cherns & Wheeley 2007). In Laurentia, comparable carbonate successions with chert and phosphate-rich deposits in the Ashgill upper Montoya Group of south New Mexico and western Texas, USA, were deposited on a deep subtidal ramp in what is interpreted as a vigorous, cool-water upwelling regime (Pope & Read 1997; Pope & Steffan 2003; Pope 2004).

Cool-water carbonates at horizons earlier in the Ordovician provide evidence of additional cooling episodes and glacio-eustatic shallowing. In the upper Caradoc (lower Katian) of Baltica, the Kullsberg Limestone mud mounds of south central Sweden, below the Boda Limestone, developed in comparable, offshore subtidal ramp settings (e.g. Tobin *et al.* 2005). The Kullsberg Limestone correlates with Saltzman & Young's (2005) GICE (Chatfieldian) C isotope excursion accompanying regression in Nevada, which they related to onset of continental glaciation on Gondwana, *c.* 8–10 Ma before the Hirnantian glacial maximum. The Kullsberg carbonate mounds and their shelly faunas contrast with the warm-water limestone coral–stromatoporoid–calcareous algal reefs of the coeval inshore shelf Steinvika and Mjøsa limestones, southern Norway (T. L. Harland 1981; Webby 2002; Tobin *et al.* 2005). The latter developed in very shallow ramp settings, and represent the earliest tropical carbonate reef development in Baltica (Webby 1984, 2002). Local development of warm-water carbonates adjacent to cool-water deposits is reconciled by a temperature-stratified shelf–ramp framework where environmental settings are differentiated by key facies elements (Cherns & Wheeley 2007, fig. 4). In northern Estonia, subtidal small carbonate mud mounds with bryozoan-rich faunas of the Vasalemma Formation are overlain by larger mounds or shoal accumulations with corals and algae in a regressive succession (Webby 2002; Hints *et al.* 2004). There is a hiatus at this time in the succession below Gotland (Nõlvak & Grahn 1993).

In low-latitude Laurentia, there is a transition to cool-water carbonates across a broad tract of eastern North America from Kentucky to southern Quebec in the Chatfieldian (Blackriveran–Trentonian; Brookfield 1988; Pope & Read 1997). In more equatorial central Quebec, a slightly younger, latest Caradoc (Edenian) transition into cool-water carbonate deposition (Lavoie & Asselin 1998) may indicate some palaeolatitudinal diachronism. In North Greenland, Middle to Upper Ordovician carbonate mud mounds with fenestrae developed in shelf margin environments (Hurst & Surlyk 1983), and there are also Caradoc–Ashgill mud mounds in southern Kazakhstan (Nikitin *et al.* 1996).

In Avalonia, locally developed early–mid-Caradoc (Sandbian–lower Katian) limestones of the Welsh Basin (Castell Limestone, upper 'Narberth Group', Mydrim Limestone, upper Llandeilo Flags, Cymerig Limestone, Alternata Limestone; Rushton *et al.* 1999) represent a further cool-water carbonate facies interruption of fine clastic sedimentation. These are approximately equivalent to somewhat older than the Kullsberg or Chatfieldian carbonates.

In Gondwana, the lower Wenlock Sacta Limestone in Bolivia represents a post-Hirnantian cool-water carbonate deposited at 50–60°S (Díaz-Martínez 2007). This relatively thin and local unit is in the lower Kirusillas Formation, above diamictites of the Cancañiri Formation, and below younger glacigenic deposits (see above).

Stromatactis and associated features

Stromatactis and zebra limestone (Fischer 1964) are calcite spar–sediment-filled cavity structures known from a variety of warm- and cool-water carbonates (e.g. mud mounds, bedded micritic limestones, reefs) from Precambrian to Phanerozoic times. The origin of these enigmatic structures is still debated (reviewed by Flügel 2004).

Krause (2001) proposed that the early–mid-Ordovician stromatactis structures in the Meiklejohn mud mound of Nevada, USA, associated with zebra limestone, breccias and fluid expulsion pipes, may have formed through interaction with gas clathrate hydrates. This would have required very cold waters on the shallow tropical Laurentian shelf, possibly sourced from glacial currents. He showed that the stromatactis and associated stuctures found throughout the mud mound resembled frost heave and cryoturbation structures identified in Holocene and Pleistocene cryosols, and could be created in laboratory experiments with advancing freezing fronts in clay sediment. Support for Krause's (2001) proposal comes from the development of cold-water reefs and mounds in association with a shallow gas hydrate reservoir in the Porcupine Basin off SW Ireland, whose evolution has been influenced by changes in temperature of bottom water currents during much younger glacial–interglacial episodes (Henriet *et al.* 1998). Stromatactis-like cavities, tepee structures, layer-parallel sheet cracks and cemented breccias are also known from Neoproterozoic cap carbonates, and may represent the evolution of gas hydrates as glacial conditions ameliorated (e.g. Jiang *et al.* 2006). It is notable that stromatactis carbonate mounds were particularly abundant in the Devonian–Carboniferous icehouse world (Krause *et al.* 2004). Cold-water settings for Mid-Devonian (Givetian) stromatactis mud mounds are interpreted from isotopic compositions of early calcite cements (Wendt & Kaufmann 2006). Furthermore, Li *et al.* (2005) proposed for the Devonian of China that cool-water carbonates (Famennian) rich in stromatactoid or zebra limestone, overlying warm-water stromatoporoid limestones (Frasnian), were influenced by glacially induced southern hemisphere currents.

In Late Ordovician cool-water carbonates, stromatactis-like structures are known from the peri-Gondwanan Cystoid Limestone mounds of Iberia (Armorica; Vennin *et al.* 1998) and the Ulkuntas Limestone mounds of Kazakhstan (Nikitin & Popov 1996; Cherns & Wheeley 2007, fig. 4; Figs 1 & 2). Stromatactis mud mounds are also well developed in offshore settings of the Upper Ordovician Boda (Ashgill; upper Katian) and Kullsberg (Caradoc; Sandbian?–Lower Katian) limestones of Baltica (Figs 1 & 2). In the Boda interval, stromatactis mounds are developed in similar settings also in Avalonia (Figs 1 & 2). For the Kullsberg mound interval, Tobin *et al.* (2005) estimated a decrease in seawater temperature by up to 15 °C. Further examples of cool-water stromatactis are known from the Middle–Upper Ordovician Børglum River Formation 'lime mud mounds with irregular fenestrae' in eastern North Greenland, which were compared with the Meiklejohn stromatactis mound (Hurst & Surlyk 1983). Stromatactis has also been reported from the Middle Ordovician (upper Whiterockian) Table Point Formation mud mounds of Newfoundland (Stenzel & James 1995).

Cool-water offshore carbonate mud mounds with stromatactis and associated structures from peri-Gondwana and beyond support other facies evidence for cooling events (Fig. 2).

Stable C isotope events

Stable isotopes in marine limestones (shells, bulk-rock or marine cement analyses) are widely used as environmental proxies. Positive $\delta^{13}C_{carb}$ excursions, which provide good stratigraphical correlations in the Lower Palaeozoic succession, are thought to be related to increase in burial of organic matter, productivity or weathering of terrestrial carbonates (Berner 1994; Kump & Arthur 1999; Kump *et al.* 1999). Variation between carbonate data and the paired $\delta^{13}C_{org}$ data, proposed as a proxy for $p\mathrm{CO}_2$, may affect detailed correlations between limestone and shale successions (Kump *et al.* 1999; Cramer & Saltzman 2007*b*). Positive $\delta^{18}O$ isotopes have environmental significance for temperature and salinity, although they appear more susceptible to diagenetic overprint.

Isotope studies on Early Palaeozoic rocks initially focused on key biological and regressive events, such as the Hirnantian (e.g. Brenchley *et al.* 1994, 2001; Kump *et al.* 1999). Pronounced C and O stable isotope excursions that correlate with the short-lived Hirnantian glacial climax (HICE) are interpreted as indicating a severe drop in atmospheric $p\mathrm{CO}_2$ (Brenchley *et al.* 1994; Gibbs *et al.* 1997; Brenchley 2004). Global sea levels fell by 50–100 m at the start of the excursion and glaciation (Brenchley *et al.* 1995). The positive $\delta^{18}O$ excursion signifies growth of continental ice and fall in seawater temperatures. This isotope event was recognized initially from low-latitude areas of Laurentia (e.g. Nevada, Anticosti, Arctic Canada) and mid-latitude Baltica (Sweden, Estonia; Marshall & Middleton 1990; Long 1993; Brenchley *et al.* 1994, 1995; Melchin & Holmden 2006; Schmitz & Bergström 2007), and also from China (Wang *et al.* 1997). Marshall *et al.* (1997) recorded a similar positive C excursion from high-latitude Gondwana, in Argentina, confirming the global nature of this event. This event has also been recorded recently from mid-continent North America, where two phases of shallowing were recognized (Bergström *et al.* 2006).

A further isotope event *c.* 8–10 Ma earlier, also recognized globally, is the Guttenberg C excursion (GICE) of the mid-Caradoc (early Katian) Chatfieldian Stage of the USA (Hatch *et al.* 1987; Ludvigson *et al.* 2004; Young *et al.* 2005). In the Great Basin Region, USA, of western Laurentia, the accompanying regression (Eureka Quartzite) was ascribed in

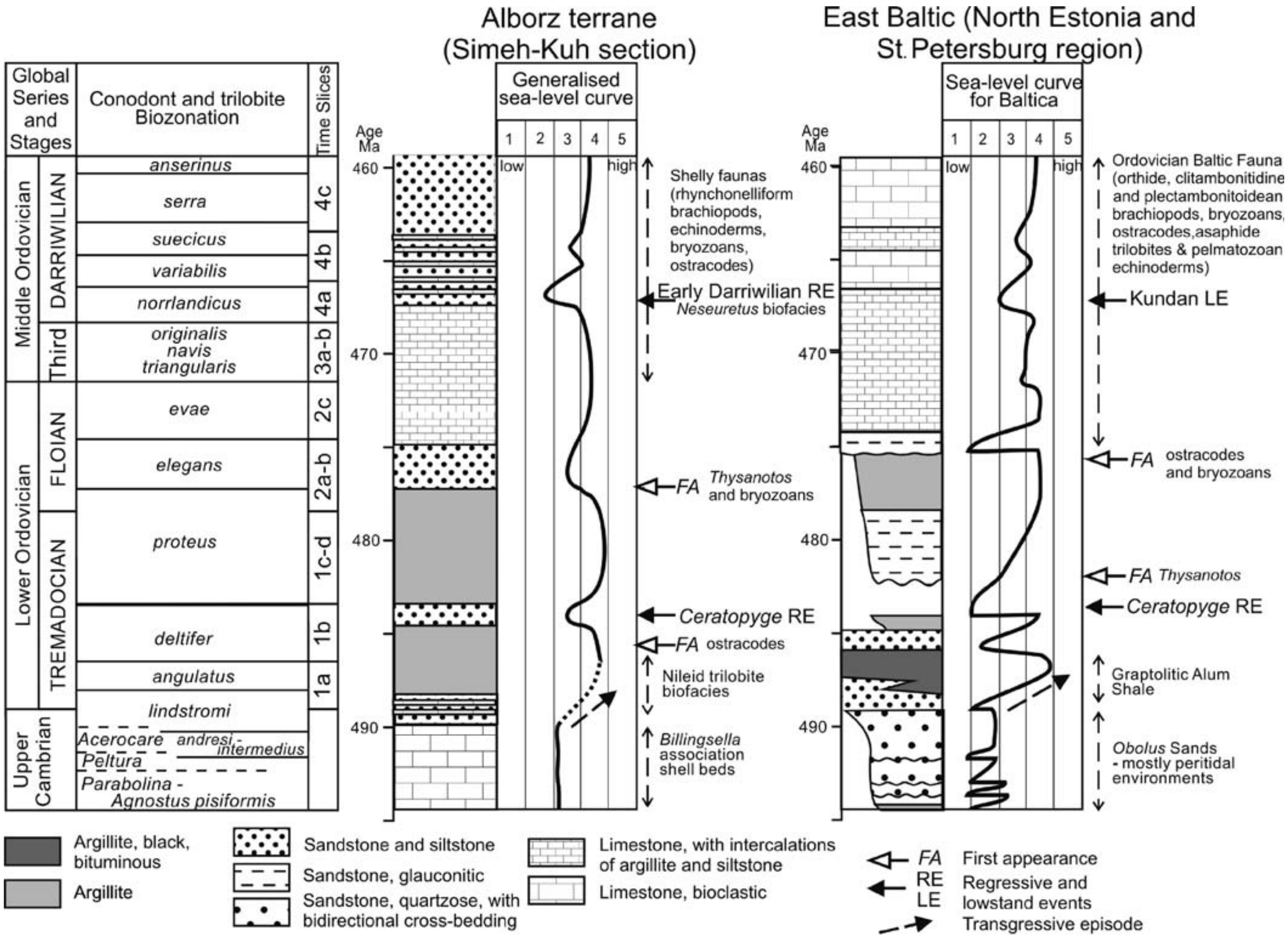

Fig. 4. *Continued.*

part to sea-level drawdown from the initiation of continental glaciation on Gondwana, the excursion signalling lowering of atmospheric $p\mathrm{CO}_2$ to levels near the threshold for ice build-up (Saltzman & Young 2005).

In Baltica, the GICE event correlates with positive C and also O isotope excursions in the Swedish Kullsberg Limestone, which were estimated to indicate decrease in seawater temperature by up to 15 °C compared with pre-excursion conditions, with *c.* 1‰ increase in $\delta^{18}\mathrm{O}_{\mathrm{water}}$ probably attributable to increased salinity rather than to polar ice growth (Tobin *et al.* 2005). A comparable C excursion is recognized in Estonia (Ainsaar *et al.* 1999, 2004).

At the time of the intervening Boda event, Saltzman & Young's (2005, fig. 2) $\delta^{13}\mathrm{C}$ curve for the Ashgill Hanson Creek Formation shows pre-Hirnantian excursions of up to +3‰ in Laurentia, similar in magnitude to the Chatfieldian excursion. Bergström *et al.* (2007) recently noted four minor positive C excursions correlatable between the GICE and HICE in mid-continent USA and Estonia. From a series of seven positive C isotope excursions between the upper part of the Lower and the uppermost Ordovician of Baltoscandia, Kaljo *et al.* (2007) noted a change to events of increasing frequency and magnitude from mid-Caradoc times onwards.

The late Cambrian SPICE C isotope excursion documented from low-latitude Laurentia, Kazakhstan, China and Australia is also interpreted as marking a global glacioeustatic event, and corresponds to mass extinctions among benthos (Brasier 1993; Saltzman *et al.* 2000, fig. 2; Saltzman *et al.* 2004). Runnegar *et al.* (2005) proposed a frequency of minor modulations of the C isotope curve that indicated an eccentricity signal of 400 ka. In Laurentia there is evidence for sea-level fall and erosion of the carbonate platform (e.g. Saltzman *et al.* 1998). Black shale successions indicating increased marine burial of organic matter include the widespread middle Cambrian–lower Ordovician Alum Shale of Baltica, which in the Upper Cambrian has 'hot shale' intervals (deglacial facies, see earlier section; Fig. 2) with enhanced levels of radioactive uranium (e.g. Thickpenny 1987). The evidence from Baltica for severe permafrost conditions in the late Cambrian is outlined above.

Silurian isotope excursions have been associated with both conodont and graptolilte extinction events (reviewed by Loydell 2007; Fig. 2). Baltica and Avalonia had drifted into lower latitudes as Iapetus closed (Fig. 1). Positive C and O isotope excursions documented from the tropical, photozoan carbonate platforms of Baltica (Gotland and Estonia) have been correlated with changing oceanographic conditions and faunal extinctions, with four conodont extinction events (Ireviken, Mulde, Linde, Lau) recognized on Gotland between the late Llandovery and late Ludlow (e.g. Jeppsson 1997, 1998; Jeppsson & Aldridge 2000; Jeppsson & Calner 2003; Munnecke *et al.* 2003; Calner *et al.* 2004, fig. 3). Both the early Wenlock (Sheinwoodian), and the youngest, Ludlow (Ludfordian) excursions are widely recognized beyond Baltica, from mid-latitude peri-Gondwanan Perunica (Lehnert *et al.* 2003, 2007) and the Central European–Perunican Carnic Alps (Wenzel 1997), East Gondwana (Australia; Talent *et al.* 1993; Jeppsson *et al.* 2007), Avalonia (Loydell & Frýda 2007) and low-latitude Laurentia (Saltzman 2001). An earlier, late Llandovery *sedgwickii* Biozone positive C excursion is tied closely with a graptolite extinction event and black shale horizons (Melchin & Holmden 2006; Loydell 2007; Page *et al.* 2007; Fig. 2).

Silurian isotope events correlate with the evidence from diamictites in South America of periodic cooling episodes continuing to Ludlow times. On Gotland, the early Sheinwoodian (*c.* 428 Ma) and Ludfordian (*c.* 420 Ma) isotope excursions are separated by lower magnitude late Wenlock (*c.* 424 Ma) and early Ludlow (*c.* 422 Ma) events (Calner *et al.* 2004).

Cyclic sea-level changes

Sea-level curves based on facies patterns and faunal distributions that are comparable between palaeocontinents or terranes are interpreted as reflecting global eustasy (e.g. Hallam 1992). One peri-Gondwanan example of cyclic sea-level changes comes from the early–mid-Ordovician of the Alborz terrane of Iran compared with Baltica; both lay in mid-palaeolatitudes (Ghobadi Pour *et al.* 2007; Popov *et al.* 2008; Figs 1 & 4). Early Ordovician (Tremadocian) transgression saw a sea-level rise of several tens of metres. From the East Baltic (northern Estonia and St. Petersburg region) across to south-central Sweden (e.g. Siljan region), deep-water black Alum ('*Dictyonema*') shales replaced the peritidal *Obolus* Sands, and in Alborz

Fig. 4. Correlation of the Early–Mid-Ordovician successions of the peri-Gondwanan Alborz terrane and the East Baltic, showing faunal successions and key faunal events (*FA*, first appearances), regional regressive and lowstand events (RE, LE), a major transgressive episode, and interpreted sea-level curves (1, supratidal; 2, peritidal; 3, shallow subtidal above storm wave base; 4, subtidal below storm wave base; 5, basinal). Biozonation for conodonts (continuous lines), Cambrian trilobites (dotted lines); Ordovician time slices (Webby *et al.* 2004). (Figure courtesy of M. Ghobadi Pour.)

deep-water argillites with nileid trilobite biofacies replaced shallow-water *Billingsella*-rich limestones (Ghobadi Pour *et al.* 2007: Fig. 4). Subsequent Early Ordovician regressive episodes in both regions are represented by the *Ceratopyge* Regressive Event (Figs 2 & 4 CRE; e.g. Nielsen 2004, fig. 10.2), which has been proposed as a likely glacial event (Nielsen 2007). The *Thysanotos–Leptembolon* lingulate brachiopod association known from Baltica and Perunica appears in Alborz in the Floian. Temperate Lower Ordovician limestone sedimentation developed across western Baltoscandia and the East Baltic, and also in Alborz. Carbonate sedimentation ended in Alborz with renewed regression in the early Darriwilian (Mid-Ordovician) and invasion of the cold-water *Neseuretus* trilobite biofacies. This level corresponds to a major lowstand traceable widely in the basal Kundan across the East Baltic, indicating a cooling episode and associated glacio-eustatic sea-level fall (Ghobadi Pour *et al.* 2007; Fig. 4). Following the regressive event, the later Darriwilian in Alborz is in quartzitic sandstones with thin bioclastic limestones, and in the East Baltic, bioclastic limestones replace micritic limestones. The transgressive–regressive sedimentation through the two successions shows a eustatic cyclicity of *c.* 8 Ma (Figs 2 & 4).

Faunal distributions

Faunal distributions provide key evidence for establishing palaeobiogeography and the timing of breakdown of barriers to dispersal, particularly for shallow benthic faunas (e.g. Fortey & Cocks 2003). Faunal migrations are used above in interpretation of cyclic sea-level histories (Fig. 4). For peri-Gondwana, Boucot *et al.* (2003, fig. 1) had suggested a warm interval during late Ordovician, pre-Hirnantian times based on brachiopod associations, specifically some warm-water taxa among the widespread cool-water Mediterranean realm faunas (e.g. Villas 1995). For the same interval, (i.e. the Boda event), Fortey & Cocks (2005) and Cocks (2007) pointed to the appearance of low-latitude trilobite and brachiopod faunas in higher latitudes as evidence for climate amelioration. An alternative scenario sees glacio-eustatic shallowing, carbonate sedimentation and increased oceanic circulation as leading to wider dispersal of benthic faunas (Cherns & Wheeley 2007). The rich faunas of carbonate mounds (e.g. Boda Limestone; Cocks 2005; Fortey & Cocks 2005) appear to be facies controlled, with many species in common between mounds in mid-latitude Baltica and Avalonia, low-latitude Kazakhstan, and also in Laurentia (Cocks 2005; Fortey & Cocks 2005; Cherns & Wheeley 2007).

Orbital forcing

The Earth and other planets have elliptical orbits around the Sun, subjected to its gravitational pull, and with much lesser influences from neighbouring planets. These forces produce secular changes in the orbit of each planet. The Earth is affected by four orbital elements: eccentricity, the longitude of the perihelion point (where the Earth is closest to the Sun) with respect to the vernal equinox point, the inclination of the plane of the Earth's orbit with respect to a fixed reference (defined by the orbit of Jupiter), and the longitude of the ascending node (the intersection of the planes of the orbits of the Earth and of Jupiter). In addition, gravitational forces affect the obliquity (tilt) and direction (precession) of the Earth's axis.

Changing orbital parameters control the intensity and timing of incoming solar radiation (insolation) at all points on the Earth's surface, and thus have a significant influence on its climate. Changes on scales of 10^4 years (Milankovitch Cycles) are well established as a driving force for the Pleistocene ice ages (e.g. Hays *et al.* 1976), and are interpreted as responsible for fine-scale sedimentary cycles observed in the late Mesozoic–Cenozoic record (e.g. Hilgen *et al.* 1995; Krijgsman *et al.* 2001; Aziz *et al.* 2003; Dinarès-Turell *et al.* 2003). Although cyclic sedimentary sequences are readily identified in the earlier geological record (e.g. Hallam 1984; Pope & Read 1997; Munnecke *et al.* 2001), determining the cycle frequency and its interpretation are made much more questionable by inaccuracies in the time scale, sedimentary hiatuses, variable sedimentation rates and diagenetic effects (e.g. Mayer 1993; Bohm *et al.* 2003; Westphal *et al.* 2004; Westphal 2006).

Berger *et al.* (1992) and Berger & Loutre (1994) concluded that eccentricity cycles (106 ka and 410 ka) could be considered essentially constant back from the Quaternary through the Phanerozoic, despite shortening of the Earth–Moon distance and day length that changed the obliquity and precession cycles. However, on a time scale above 10 Ma, the eccentricity time series becomes less predictable. Matthews *et al.* (1997) proposed cycles of orbital forcing on a time scale of millions of years, based on calculated modulations in eccentricity (and therefore modulation of the effects of tilt and precession) with nodes around 2.4–2.8 Ma, 4.4–4.8 Ma and 7.2–7.6 Ma. Such predictions of eccentricity time series should be testable against the stratigraphical column.

Discussion

In the Early Palaeozoic, which has conventionally been thought of as a greenhouse world, $p\mathrm{CO}_2$ has been estimated as high (8–18 × present atmospheric level (PAL); Berner 1994) and oxygen levels as lower by around half (Berner & Kothavala 2001). The CO_2 ice threshold of 3000 ppm for the Hirnantian suggested by Royer (2006) is consistent with other estimates (e.g. Herrmann *et al.* 2003, 2004), and represents a drop to close to half of the Ordovician background levels of 5600 ppm (Yapp & Poths 1992, 1996). Mechanisms in the carbon cycle proposed to explain this fall have been carbonate drawdown (Villas *et al.* 2002) and marine carbon sinks for atmospheric carbon represented by black shales (Page *et al.* 2007). Royer (2006) commented on the growing recognition of cool but possibly non-glacial periods identified through the Phanerozoic that are characterized by their short extent, typically <3 Ma.

Global eustasy through the early Palaeozoic is estimated to have been higher (>100 m) than at present, and rose overall through the Cambrian and Ordovician to a Phanerozoic peak in the earliest Caradoc (Sandbian), when sea levels are considered (by Hallam 1992) to have risen by 100–200 m. Broad epeiric seas were maintained for long periods, with those at low latitudes particularly prone to poor circulation and salinity stratification (Railsback *et al.* 1990). Transgressions are commonly indicated by black shale deposition, as shown, for example, by the widespread organic-rich shales of the late Cambrian in mid–high latitudes (e.g. Alum Shales, Dolgellau Formation; Brenchley *et al.* 2006), the late Ordovician (early Katian; Caradoc) *clingani* Biozone following the GICE isotope excursion, and the mid-Llandovery *convolutus* Biozone global highstand (Loydell 1998). The major carbon sinks represented by these shale deposits have been interpreted as controlling temperatures and isotope excursions (Cramer & Saltzman 2007*b*; Page *et al.* 2007). 'Hot shale' intervals may also represent post-glacial peaks in primary productivity.

Positive stable C (and O) isotope excursions correlate closely with episodes of global cooling interpreted from facies indicating glaciation in high-latitude Gondwana (HICE, GICE) and periglacial environments in Baltica (SPICE). These, and also the pre-Hirnantian Boda event bracketed within the stratigraphical interval of glacigenic evidence, correspond to peaks of 3–8‰ (Saltzman & Young 2005, fig. 2; Fig. 2), Three of the four Silurian conodont extinction events (Ireviken, Mulde, Lau) in low latitudes are associated with similarly large positive shifts (Calner *et al.* 2004, fig. 1). The earlier two, and the *sedgwickii* excursion, correlate with Llandovery–Wenlock glacigenic deposits in Gondwana (Fig. 2; also Azmy *et al.* 1998; Kump *et al.* 1999). Additional smaller (1–3‰) Ordovician excursions have been proposed as facilitating correlation across palaeocontinents (e.g. Kaljo *et al.* 2007). Meidla *et al.* (2004) suggested an early Mid-Ordovician (Darriwilian) cooling event in Baltica, which corresponds to Baltoscandian regression (Kunda–Aseri stages; Nielsen 2004; Fig. 2) and to the cooling interpreted from invasion of cold-water trilobite biofacies for the peri-Gondwanan Alborz terrane (Ghobadi Pour *et al.* 2007; Fig. 4, and above). In Laurentia, the Meiklejohn stromatactis carbonate mounds, interpreted as cold-water indicators (Krause 2001), are of early Mid-Ordovician age, and other Mid-Ordovician stromatactoid carbonate mounds are known from Virginia and Newfoundland (Read 1982; Stenzel & James 1995). In general, however, in the Early–Mid-Ordovician the apparently reduced stratigraphical or facies evidence for significant sea-level flux (Fig. 2) might be interpreted as representing a lull in glacial development.

The relationship between palaeoclimate and the Silurian C (and O) isotope excursions is more problematic. Cramer & Saltzman (2007*a*) discussed the apparent contradiction of C excursions correlating with low-latitude carbonate ramp and reef development (e.g. Calner *et al.* 2004) rather than with organic matter sequestration in epeiric seas. The Ireviken conodont extinction event on Gotland corresponds to a facies change from limestone–marl alternations up into limestones with coral–stromatoporoid reefs, which Jeppson (1998) identified as a P–S oceanographic transition (e.g. Calner *et al.* 2004, fig. 2). P states correspond to icehouse conditions with thermohaline circulation, upwelling of nutrients and high nutrient availability in epeiric seas, whereas S states represent greenhouse conditions with reduced oceanic circulation and low nutrient availability on shelves, when tropical carbonate platforms developed on Gotland (Jeppsson 1990, 1998). Bickert *et al.* (1997) and Calner *et al.* (2004, fig. 2) modified the model to infer humid (H)–arid (A) climatic shifts in shallow seas between estuarine and anti-estuarine circulation whereas deep ocean environments remained anoxic. However, in low-latitude Laurentia, the C excursion correlates with transgressive cherts and black shales deposited over a widespread late Llandovery unconformity, interpreted as indicating deep ocean upwelling and high primary productivity leading to anoxia (Saltzman 2001; Cramer & Saltzman 2007*a*). Cramer & Saltzman (2005, 2007*b*) proposed that reduced polar downwelling during deglacial conditions shifted formation of deep-water anoxia to low–mid-latitudes, producing the C excursion, whereas carbonate factories developed and flourished on flooded platforms. Cramer & Saltzman (2007*b*) proposed that pCO_2 remained high during the Ireviken excursion.

In high-latitude Gondwana (Jordan), there are deglacial 'hot shales' across the Llandovery–Wenlock boundary (Lüning *et al.* 2005, 2006). The early Sheinwoodian positive C isotope excursion and Ireviken conodont extinction correlate with temporary cool-water carbonate deposition in South America (Sacta Limestone; Díaz-Martínez 2007). On Gotland this sequence is regressive (Munnecke *et al.* 2003), as is the late Wenlock (Homerian) C excursion and Mulde conodont extinction event (Calner & Jeppsson 2003). There is observational evidence from peri-Gondwana and Arctic Canada for high organic burial during the latter interval (Loydell 2007). The late Ludlow (Ludfordian) C isotope excursion and Lau conodont extinction event on Gotland correspond to wider evidence of regression in Baltoscandia and beyond, in peri-Gondwanan Perunica and in East Gondwana (Australia; Jeppsson *et al.* 2007). There is karst formation locally on Gotland (Cherns 1982) and in the Prague Basin (Požáry section; Lehnert *et al.* 2007). In southern Sweden (Skåne), limestones (Bjärsjölagård Limestone) replace deep graptolitic shales (Wigforss-Lange 1999); continuing, tectonically influenced regression resulted in the spread of Old Red Sandstone (ORS) facies in front of the advancing Caledonian mountains (Bassett 1985). Correlation of the Silurian isotope excursions with global eustatic sea-level falls suggests cooling episodes. Evidence for repeated glacigenic episodes in Gondwana through this period comes from tillites up to early Wenlock times, and a 'hot shale' of early Ludlow age (Edwards *et al.* 2009).

The localized early Wenlock Sacta Limestone of high-latitude Gondwana, and the widespread development of cool-water carbonates from high to low latitudes during the late Ordovician (late Katian) Boda event and earlier (early Katian) Kullsberg–Chatfieldian, show close correlation with C isotope excursions and are interpreted as indicating cooling episodes (Fig. 2). Cherns & Wheeley (2007) suggested that high-latitude carbonate deposition on the Gondwanan margin followed reduction in riverine clastic input resulting from continental ice sheet growth, glacio-eustatic sea-level fall, and onset of thermohaline circulation leading to oceanic overturn. The temporary facies change to carbonates from fine-grained clastic deposits across peri-Gondwanan terranes and the West Gondwanan margin is mirrored in carbonate mound limestones interrupting fine clastic deposition in mid-latitude Baltica and Avalonia, and in the low-latitude Kazakh Chu-Ili terrane (Cherns & Wheeley 2007; Fig. 2).

Even in cool-water carbonate settings it appears that in very shallow and restricted environments the sea temperatures may have risen through insolation. Cherns & Wheeley (2007) outlined an Ordovician depositional ramp profile for the Avalonian Welsh Basin where corals and dasyclad algae characterized the shallowest environments, whereas downslope, upwelling of cool waters is represented by heterozoan faunas and phosphatic nodules and horizons. That model is expanded here to cover different palaeocontinents through the late Ordovician, showing the environmental settings for carbonate mounds and the distribution and warm- and cool-water carbonates across palaeocontinents (Fig. 5). Li *et al.* (2005, fig. 2) documented Hirnantian cool-water carbonate deposition (Kuanyinchiao Bed) interrupting graptolitic shale successions in low–mid-latitude South China, NE of peri-Gondwana, passing up in some limited areas into very shallow warm-water facies (oolites and peloids) during maximum regression. This 'warm-water enclave' is consistent with the pattern seen in Baltica during Kullsberg cooling, when cool-water deposition in offshore settings was replaced temporarily in the shallowest shelf settings by warm-water reefs and mounds (e.g. Mjøsa Limestone, upper Vasalemma Formation).

Periodicities of the palaeoclimatic indicators discussed above are apparent in Figure 2. For the early Palaeozoic, accuracies of absolute radiometric dates are *c.* ±2 Ma (Sadler & Cooper 2004, table 3.1), which does not preclude greater accuracy from relative ages within limited intervals such as the Hirnantian. The timing of late Ordovician–Silurian glacial deposits or erosional morphology is relatively poorly constrained through the early Caradoc–Ashgill (Sandbian–Katian), but from the Hirnantian to the youngest horizon in the Ludlow there are at least eight episodes within *c.* 25 Ma, spaced from <1 Ma within the Hirnantian, to *c.* 8 Ma in the late Llandovery. Even finer cyclicity detected within the Hirnantian in North Africa has been suggested as indicating a 100 ka obliquity signal (see above; Ghienne 2003; Le Heron *et al.* 2007). Black shale deposition was related to late Ordovician–early Silurian transgressive anoxia and glacigenic episodes by Page *et al.* (2007). Their correlation for the Upper Ordovician–Lower Silurian between the Avalonian Welsh Basin epeiric sea and Iapetus trough succession of the Southern Uplands of Scotland (Page *et al.* 2007, fig. 3) demonstrates longer periods of black shale deposition in the Caradoc (late Sandbian–early Katian) and late Hirnantian–early Aeronian, and a shorter interval in the mid-Llandovery *convolutus* Biozone that corresponds to global highstand (Loydell 1998; Fig. 2). The latest mid-Llandovery *sedgwickii* Biozone 'oxic' shales, in contrast, mark a widespread, short-lived regression (Loydell 1998), presumably corresponding to deposition of diamictites in South America. There are continuous black shale intervals in the Wenlock and lower

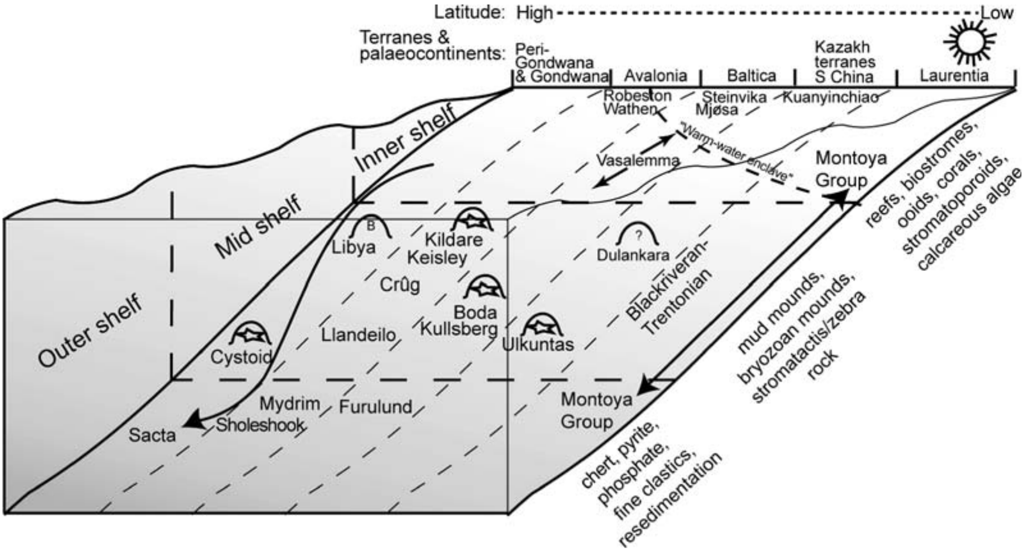

Fig. 5. Cool-water heterozoan carbonates and mound facies on a temperature-stratified shelf model, reconciling the local co-occurrence of warm-water photozoan carbonate facies developed in very shallow and sheltered enclaves (delimited zone within inner shelf and low–mid-latitudes) through insolation and glacio-eustatic shallowing. Palaeocontinents from high to low latitudes include formations or labels as discussed in the text. B, bryozoan mounds; star, stromatactoid mound; ?, ?stromatactoid mound (Dulankara). Key facies and faunal elements are indicated for interpretation of shelf zones.

Ludlow succession of the Welsh Basin. The four major intervals span *c.* 33 Ma (i.e. mean *c.* 8 Ma), with shorter spacing in the Llandovery of *c.* 1–2 Ma (Page *et al.* 2007, fig. 2).

Sea-level curves interpreted from facies and faunal evidence and correlated between palaeocontinents indicate cyclicity of 8–10 Ma for the early Ordovician (see above). This finds support in Nielsen's (2004) sea-level curves for the Ordovician of Baltoscandia, which show six highstand and lowstand intervals through 46 Ma.

Conclusions

From the various lines of facies and faunal evidence presented above, correlated with isotope excursions, a larger picture starts to emerge as cyclicities from <1 Ma to 8–10 Ma suggest possible orbital controls. The proposed cooling events in the Silurian (early Wenlock–Ludlow) are separated by 2–4 Ma. Climate change is typically represented in the Palaeozoic rock record on a scale of millions of years (Matthews *et al.* 1997). Multiple cooling episodes both preceded and followed the end-Hirnantian glacial maximum, between the mid–late Cambrian and late Silurian. Accepting *c.* 0.5% uncertainty for radiometric dating, it is still possible to discern frequencies in the Early Palaeozoic down to 1–2 Ma. For the Cambrian SPICE event, an eccentricity signal of 400 ka has been proposed, and for the extensively studied Hirnantian, even finer cyclicities have been proposed down to obliquity at 100 ka. More thorough analysis remains to be made on the cyclicities recognized here, and on the interrelation of the different indicators of palaeoclimate in the rock record.

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