Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions

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Abstract

The discreteness or otherwise of major Ordovician and Silurian terranes can be recognised by the shallow-water benthic faunas which lived upon them. Their borders are often indicated by the disposition of progressively shallow- to deep-water assemblages at the terrane edge as well as by structural features. Their positions relative to each other in the Early Palaeozoic can be best indicated by a combination of palaeomagnetic and faunal evaluation: the latter is the topic of this paper. Faunal evaluation is now possible quantitatively as well as quantitatively. Global palaeobiogeography is reviewed for the period as deduced from faunal evidence. There was one supercontinent, Gondwana, which stretched from West Gondwana (today's southern Europe and North Africa) at high latitudes to tropical East Gondwana (Australasia and adjacent areas), with intermediate palaeolatitudes in the Middle East and South America. Around Gondwana, especially to its north, were a large number of peri-Gondwanan terranes, particularly Avalonia, Perunica, parts of Turkey and Arabia and Sibumasu. In addition, there were the substantial independent continents of Laurentia, Baltica, Siberia, Annamia, North China and South China. Analysis of the shallow-water benthos, particularly trilobites and brachiopods, provides distinctive signatures for palaeo-position in most cases. Despite a large faunal turnover particularly corresponding with the latest Ordovician glacial event, the progressive evolution of the ecologies of benthic shelly faunas were also much influenced by changing geographies during the 80-Ma period. In the early Ordovician, oceans were at their widest, enabling Baltica and Laurentia to have different signatures from either East or West Gondwana. Siberia in early Ordovician times had faunal contact with Laurentia and East Gondwana, but in the mid-Ordovician, there were more endemics, and by the late Silurian, it was the only continent of substance in the northern hemisphere (hosting the *Tuvaella* Fauna). South China has varied faunal links but seems best treated as at the edge of the peri-Gondwanan collage for most of the period. We show how faunas document the early Ordovician rift of Avalonia from West Gondwana and its movement and subsequent collisions, first with Baltica in the end Ordovician and then with Laurentia in the early Silurian. Faunas also support the postulated movement of the Precordillera of South America from Laurentia in the early Ordovician to intermediate- to high-latitude Gondwana in the Silurian. We examine peripheral terranes bordering Iapetus to demonstrate their pre-collision positions. Analysis of some of the many terranes now forming Kazakhstan and adjacent areas in central Asia today reveals that the benthic faunas there have more

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affinity with Gondwanan and peri-Gondwanan faunas than with Baltica or Siberia, and thereby challenge structural models postulating an Early Palaeozoic Kipchak arc.

1. Introduction

The reconstruction of Palaeozoic palaeocontinents and their peripheral island arcs has attracted considerable interest over the last 30 years or so, ever since the recognition (Wilson, 1966) that plate tectonic models could be applied to continent distributions prior to the assembly of Pangaea near the end of the Palaeozoic. The production of ever more sophisticated atlases of maps of the disposition of landmasses before the end-Palaeozoic has utilised computer-based reconstructions which are of service to many fields of geology, from mineral exploration to palaeoclimatology (Smith et al., 1973; McKerrow and Scotese, 1990; Ross and Scotese, 1997). While post-Pangaea reconstructions are now solidly based on a geophysical framework, there are many areas of uncertainty in older continental configurations for which disparate sources of data in determining continental placement are still relevant. From the first, palaeontological evidence has provided part of the data from which plausible continental arrangements can be derived. Fossil evidence has the advantage that it is decoupled from other physical criteria based on tectonics or palaeomagnetism (Fortey and Cocks, 1986) and thus provides an independent test of configurations derived from different data sources. However, the evidence provided by fossils has often itself been the subject of contention. This is, we believe, at least partly because specialists in different fossil groups do not appreciate the peculiarities of the 'signal' offered by their preferred organisms, or because too much weight is placed on a single occurrence, rather than using a whole fauna as is preferable. In this paper, we attempt to review some of the extensive and scattered palaeontological literature, and explore case histories of the use (and occasional abuse) of fossils in Early Palaeozoic reconstructions to illustrate both the potential of fossils and the pitfalls that may result from their over-interpretation. We will concentrate particularly on the Ordovi-cian and Silurian periods. This is first because we have worked on this time interval, which lasted from 489 to 418 Ma, for more than 30 years. Second, it offers a good test case for reconstruction in general because (a) the Ordovician was a time of wide continental dispersal and climatic zonation, somewhat like the present day, and (b) major changes in continental configuration took place through the interval, thus providing a good paradigm for the shifts in faunal distribution that accompanied the plate movements. Early Palaeozoic world maps have improved progressively over recent years, but there are still published discrepancies between different models involving hundreds, and sometimes thousands, of kilometres of displacement. If properly applied, palaeontological evidence will contribute further towards resolving such ambiguities. In particular, it may bear upon questions of longitudinal position of landmasses which cannot be solved by palaeomagnetism alone. Cocks (2001) and Cocks and Torsvik (2002) have provided summary treatments of Ordovician global geography; the faunal evidence to support these is amplified below.

2. Models relating faunal distribution to continental position

2.1. Characteristics of Ordovician and Silurian sedimentation

The Ordovician and Silurian periods were a time of general continental immersion (Ross and Ross, 1995). Although eustatic cycles are well known for this interval, for the most part, shallow shelf seas covered the stable cratons, and even some regressive intervals are occasionally typified by shallow marine deposits. Freshwater and terrestrial sediments of Ordovician age are virtually unknown, and the latter only appear widely towards the end of the Silurian. The fact of wide epicratonic seas is of particular importance in

understanding Lower Palaeozoic marine biogeography. Faunas adapted to widespread shallow to intermediate shelf conditions include plate-wide endemics which are excellent biogeographic indicators. In some ways, these indicator faunas are more comparable with continental terrestrial faunas at the present day, since they were distributed over far wider areas than are the comparatively restricted modern shelf faunas. In addition, shelf seas left a widespread and often thick legacy of sediments, many of which are little metamorphosed, and from which the majority of fossil faunas have been obtained—they are easily collected, often diverse (more than 20 species per stage), mostly well preserved and have been studied over a long period of time. Extensive marine formations covering large parts of the

North American, Baltic, Australian and Chinese continental interiors are examples. Probably, no geological system other than the Cretaceous compares with the Ordovician for sheer spread of marine facies. Plotting the extensive monographic coverage of such areas as the Ordovician and Silurian Baltic platform reveals a density of sampling sites which would not disgrace a map of living fauna and flora (Fig. 1). Thus, there is likely to be a bias towards collection of widespread faunas which were former inhabitants of the immersed shelves. In that these faunas responded to ambient conditions of temperature, depth and substrate, they are a priori good indicators of geographic entities. Contrariwise, faunas from marginal sites (e.g. island arcs, obducted terranes) tend to be rare, meagre and
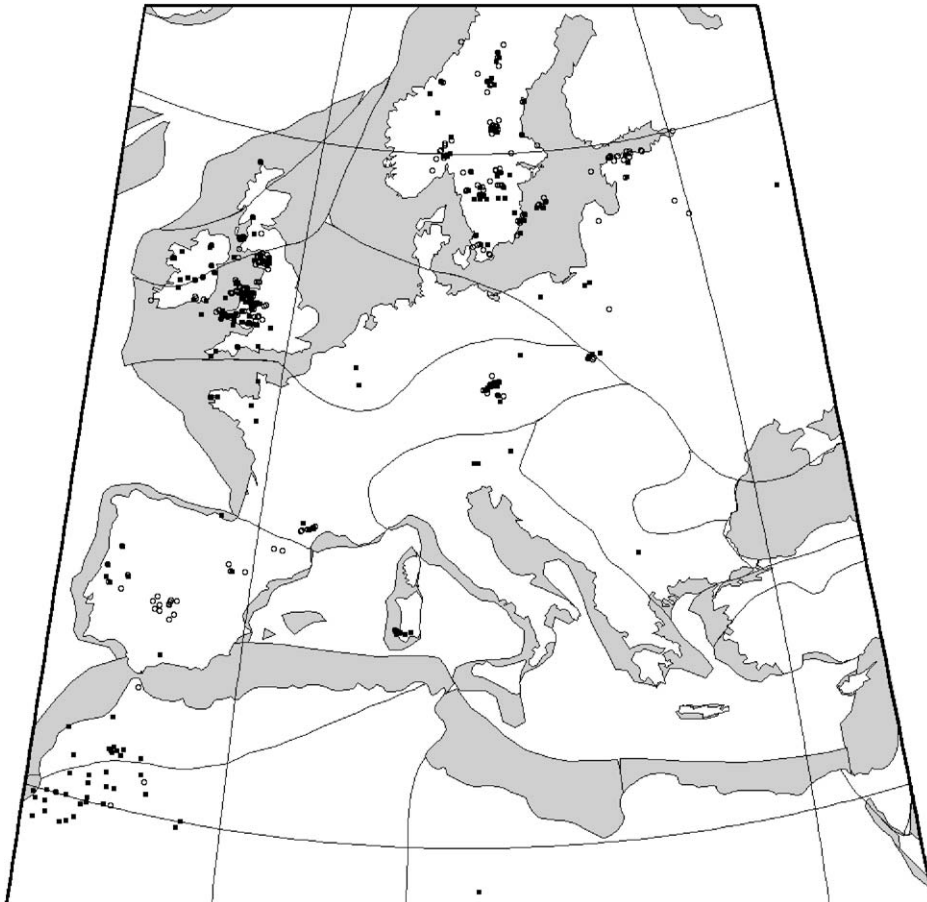

Fig. 1. The distribution of European Ordovician samples in the Lees et al. (2002) database, showing the sampling density available. Black squares are brachiopods; open circles are trilobites.

often subsequently deformed and metamorphosed; in Ordovician Baltica, for example, sites with faunas from Caledonide nappes number no more than eight or so (Bruton and Harper, 1985) compared with the many rich platform occurrences.

2.2. Mapping faunal distributions

Maps of the distribution of fossil faunas and floras are often expressed as envelopes drawn around the known occurrences of a particular taxon, usually a genus. Species-level compilations have been made principally for widespread and distinctive species of graptolites and acritarchs. It is obvious that pandemic forms are biogeographically uninformative, although stratigraphically useful. At the opposite end of the spectrum, endemics known from a single site do not define a geographical entity (although they invite speculation about special evolutionary conditions). Hence, abundant taxa of limited geographic spread tend to be the most useful for palaeogeography. Where a number of taxa share the same envelopes of distribution, this is regarded as evidence that they together comprised a biogeographic entity. The tradition of making such distribution maps applied before plate tectonics made an impact; at that time, the areas so described were usually termed faunal 'provinces'. For example, Whittington (1963, 1966) and Kobayashi (1971) discussed Ordovician and Cambrian trilobite provinces, respectively, Williams (1969), Ordovician brachiopod provinces and Skevington (1969), graptolite provinciality. From the first, there were problems with the objective definition of such 'provinces'—does a subset of coincident distributions merit recognition as a separate province, or a sub-province, and what do such subdivisions mean? It also soon became clear that 'provinces' defined on different groups of organisms did not necessarily coincide with each other (Hughes, 1973; Hallam, 1973).

The liberation from the constraints of present-day geography which followed the plate tectonic revolution immediately opened up the prospect of relating plots of provincial distributions to ancient geographic separations. In his landmark paper, Wilson (1966) originally noted the provincial faunal differences on either side of the palaeo-ocean now known as Iapetus (and then as the 'proto-Atlantic') and used them as prime evidence for the ocean's existence and bounda-

ries in the Lower Palaeozoic. This pioneer work still holds in its essentials today.

2.3. Biofacies and provinces

The next important ingredient contributing to a general biogeographic model for the Lower Palaeozoic was the discrimination of different biofacies within a contiguous geographic area. Such assemblages were originally recognised as depth-related brachiopod "communities" within the Anglo–Welsh Silurian (Llandovery) basin (Ziegler et al., 1968). Each depth zone was typified by an abundant association of distinctive genera. Subsequently, Fortey (1975) and Ludvigsen (1975) specifically associated comparable depth-related trilobite assemblages to Ordovician shelf to slope continent-edge profiles. Previously, Whittington (1966) had reported little association between trilobite faunas and sediment type. Although terminology was initially something of a problem ("community type", "constant generic associations" were used by different authors to mean much the same thing), biofacies has become an accepted term for such ecologically controlled associations of taxa. The term "Benthic Associations" (numbered from BA 1, the shallowest, to BA 6, the deepest) was characterised by Boucot (1975) and his classification is often used in delineating depth-related assemblages. Biofacies have now been almost routinely recognised for all major groups of organisms in the Lower Palaeozoic. For graptolites, depth-controlled zonation in the Silurian (Berry and Boucot, 1972) was elaborated in the Ordovician by Fortey (1984), Fortey and Cocks (1986) and Cooper et al. (1991) who discriminated an oceanic isograptid biofacies from epiplanktic and shelf assemblages. Barnes and Fahraeus (1975) first recognised similar depth controls on conodont assemblages, and biofacies profiles for them are now established through much of the Lower Palaeozoic (Sweet and Bergström, 1984; Bergström, 1990). Brachiopod depth-controlled biofacies at various times in the Ordovician were summarised by Lockley (1983) for Britain and other authors for other areas and for the Silurian globally by Boucot and Lawson (1999).

Since the differences in generic composition between end-member biofacies are at least as considerable as between faunal 'provinces', the question arises

as to how they can be integrated into the biogeographic model. In the first place, deeper water biofacies often include a greater proportion of widespread, or even pandemic taxa (Fig. 2). This is because conditions at depth are generally more uniform with regard to temperature and substrate than in shallow water, where temperature (dependent primarily on palaeolatitude) and substrate type vary enormously. Comparison of a deeper water biofacies with its nearest sibling at generic level can thus prove to be very misleading for palaeogeographic reconstruction if taken literally—they may span a former ocean. This is particularly true for organisms (like conodonts) with good dispersive powers. The North Atlantic conodont 'province' has been regarded as present (Bergström, 1983) on both the Baltica and Laurentian side of Iapetus in the appropriate rocks: taken alone, this might produce an entirely different picture of what-lay-where than if the entire fossil fauna is considered. Rasmussen (1998) has demonstrated that the North Atlantic conodont realm/province as previously understood included a pandemic deep-water biofacies, the *Protopanderodus–Periodon* biofacies. Removing the elements of that biofacies enables discrete provinces on the Laurentian and Baltic sides of Iapetus to be identified. The deep-water Olenid trilobite biofacies is present on both the Laurentian and Avalonian margins of Iapetus when it was at its widest in the early Ordovician (Arenig) (Fortey and Owens, 1978); misjudgement of such

similarity could result in incorrect assumptions about terranes. Hence, shallower water biofacies are, in general, more diagnostic of former continental plates. In Figs. 3 and 4, we provide typical examples of biofacies nomenclature and distribution as regards trilobites and brachiopods for the early Ordovician and Silurian for major biogeographic entities.

On the other hand, deeper water biofacies are useful in discriminating the *margins* of such continents and microplates, and provide evidence of former oceans and deep rifts or aulacogens (Fortey and Cocks, 1986). The graptolite isograptid biofacies was shown to follow Ordovician continental margins very faithfully, almost like ophiolites; for example, a small and structurally isolated sample from Irian Jaya was interpreted as indicating the presence of a former terrane margin there. The presence of deep-water biofacies is invaluable in orientating a former plate with respect to open ocean. As an instance, Fortey and Cocks (1998) could orientate the Sibumasu (Shan Thai) terrane in the Ordovician on account of the eastward (present day) occurrence of the deep-water cyclopygid biofacies. In contrast, deep-water biofacies cannot be 'sandwiched' in the midst of otherwise shallow-water cratonic occurrences without good palaeotectonic reasons. In the Ordovician, the presence of cyclopygid biofaces in the 'Synclinal d'Ancenis' to the south of Brittany, France could be taken as evidence of an aulacogen or narrow ocean there, a
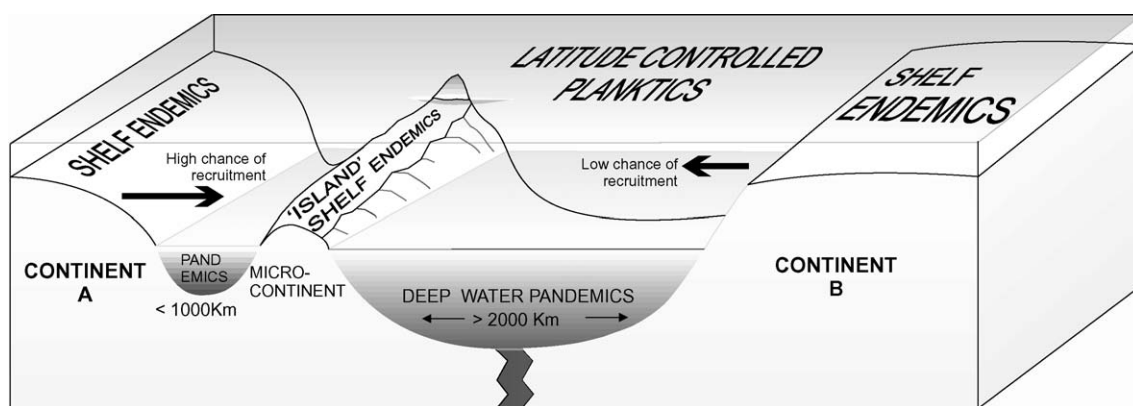

Fig. 2. General model showing control on different benthic faunas in relation to continental separation and recruitment to an intervening microcontinent, developed from Cocks and Fortey (1982, Fig. 1). If continents A and B are at different palaeolatitudes, endemicity differences will be greater. If A and B are at the same palaeolatitude, the differences between shelf endemics will depend on the distance of separation and other barriers to migration. Plankton, being essentially temperature (and thus latitude) linked, will be more different when continents A and B are at different palaeolatitudes.
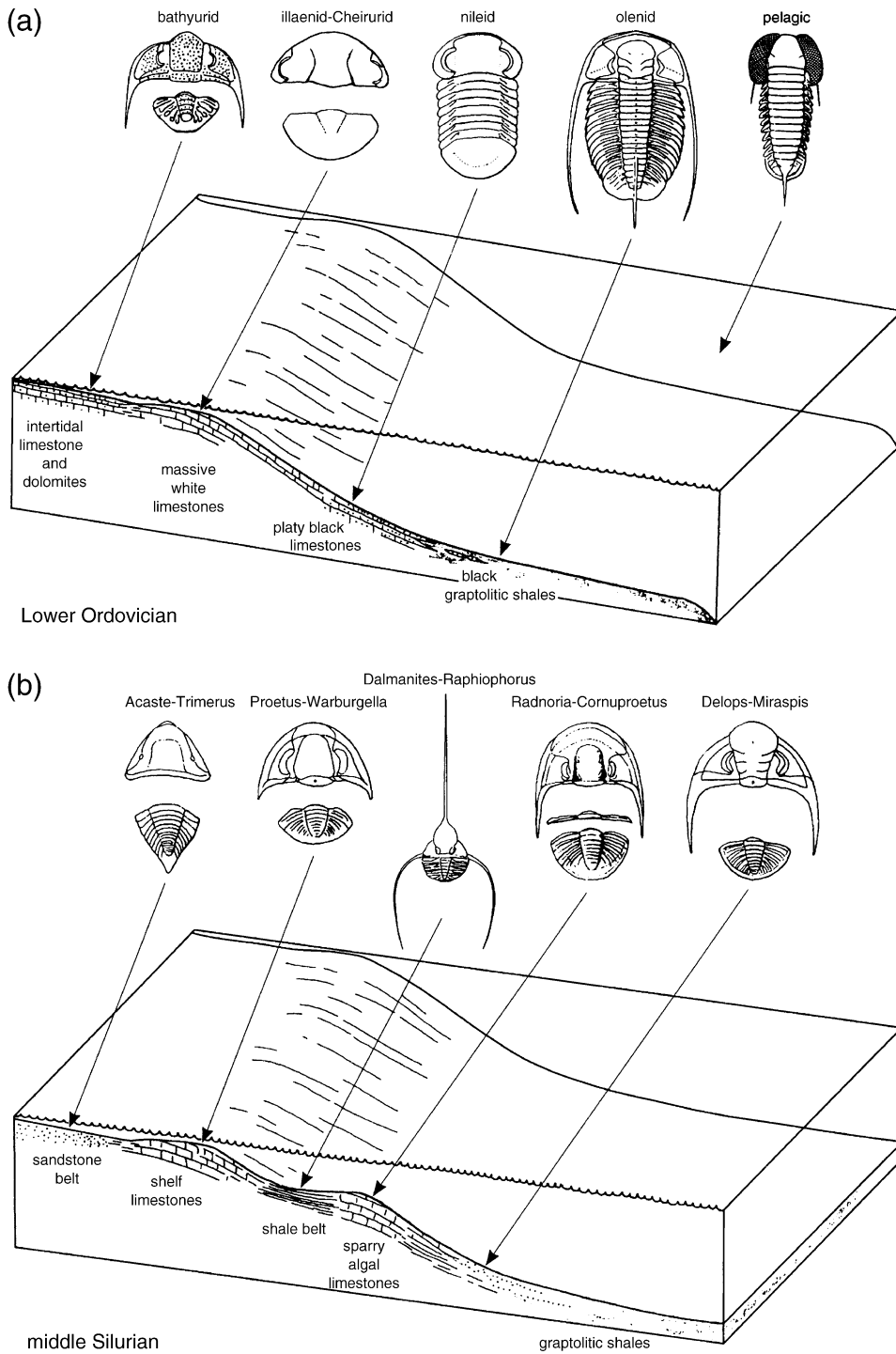
Fig. 3. Biofacies in relation to continental margins: representative shallow- to deep-water biofacies profile for trilobites (a) in the Lower Ordovician (Laurentia) and (b) in the Middle Silurian (Gondwana). From Fortey and Owens (1997, Figs. 204 and 205).
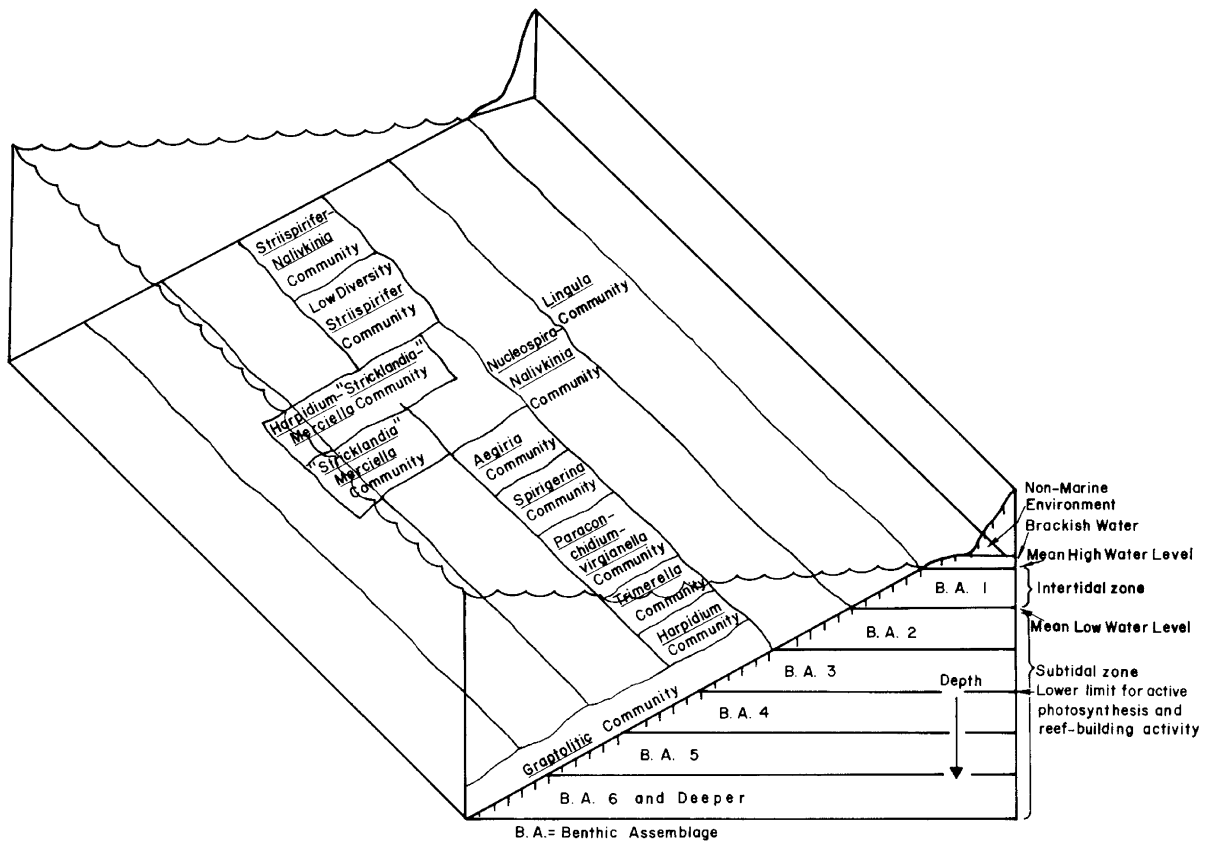
Fig. 4. Block diagram showing Benthic Assemblages (BA) 1 to 6, with the communities recognised in the middle Silurian of South China, from Wang et al. (1987, Fig. 4). Copyright Geological Society of America.

suggestion supported on independent grounds by the presence of serpentinites and metagabbros (Ballèvre et al., 1987). Hence, for objective palaeogeographical reconstructions, deep-water and shallow-water biofacies have complementary roles.

As far as quantitative analyses are concerned, those which factor out pandemic or widespread genera are not overly influenced by the presence of deeper water biofacies: only those elements which are endemic to a particular plate or plates will be emphasized. In the extreme case, deep-water biofacies may be eliminated as uninformative. To properly understand the features of a given continental margin, it is necessary to place such a biofacies in its marginal correct position (on geological evidence) especially being aware of the possibility of aligning it with the wrong continental margin.

2.4. Influence of taxonomic group

The contrasts between different kinds of organisms in giving out a differing biogeographic signal is arguably the most difficult factor to evaluate. Most specialists like to think of their ''own'' organisms as critical—and the present authors are probably no exception. There are few comparative studies of the 'effectiveness' of one Lower Palaeozoic taxonomic group as opposed to another. Fortey and Mellish (1992) attempted to measure success in terms of bootstrap support for cluster analyses based upon a number of Lower Palaeozoic groups. They found that geographical entities based on trilobite or brachiopod clusters were both congruent and had better support than those based upon graptolites or acritarchs. The latter two, being planktonic, are sensitive to palaeo-

latitude particularly, whereas the former pair (especially those forms with direct development as benthos) are a priori more likely to reveal continental configurations. Taxonomy should be consistent, current and critically assessed. The taxonomy of acritarchs has subsequently been much refined and key species of the latter have been postulated as discriminating between palaeocontinents (e.g. Tongiorgi et al., 1995), suggesting that Fortey and Mellish's analysis should now be re-run with more modern taxonomy. However, the same authors (Tongiorgi and Di Milia, 1999), in attempting to define a "Baltic" acritarch province in the Arenig–Llanvirn, recorded "Baltic" faunas from both South China and sporadically from other parts of peri-Gondwana, indicating again that these planktonic microfossils are dominantly latitude- rather than continent-specific (Cocks and Verniers, 2000). Lees et al. (2002) developed a 'goodness of fit' measure that showed that combined databases of brachiopods and trilobites ("total evidence") gave a better statistic than either group taken on their own as applied to Ordovician reconstructions of the North Atlantic region. One probably cannot have too much combined data.

What is clear is that it is unwise to put too much weight on a single common taxon as indicating geographic proximity. For example, Vavrdova (1997) claimed that a single actritarch species in common between the island of Rügen and Baltica was enough to suggest that this terrane had to be off the main Baltic continent in the Ordovician. On the contrary, the widespread (and otherwise pan-palaeotropical) trilobite genus *Carolinites* is known from a single example in the Montagne Noire, France, ostensibly at high palaeolatitudes. Intriguing though this example is, "one swallow does not make a summer," and it would be unwise to allow this one specimen to out- weigh the more pursuasive high palaeolatitude indi- cation provided by the balance of the fauna and also the independent evidence of the palaeomagnetism.

2.5. Families, genera, species

Different levels of endemicity are represented by the different taxonomic categories. In some cases, entire families (or subfamilies) comprising several genera may characterise a geographic entity. In Ordo- vician Baltica, for example, the trilobite subfamily

Megistaspidinae and the brachiopod family Lycophor- iidae are confined to that plate (Section 4.3). The most commonly used 'unit' biogeographically is the genus, largely because there is more often a consensus on recognition and definition of such a category. How- ever, in certain critical cases, species identity can be demonstrated for numerous occurrences and it is reasonable then to 'weight' these similarities in bio- geographic assessment, since close genetic continuity is implied. The Arenig to basal Llanvirn of Avalonia yields the trilobites *Placoparia cambriensis* and *Pri- cylopyge binodosa*—species which are widespread across Germany, France and Spain and may be taken as good evidence that that microcontinent cannot have been greatly separated from the edge of West Gond- wana at that time. Since species definitions are often subject to more disagreement between authors, those distribution examples that are widely accepted can be accorded particular prominence.

2.6. Establishing palaeolongitutude

This is probably the most contentious issue in palaeogeographic reconstructions. In the Lower Palaeozoic, it cannot be claimed that fossils provide an absolute criterion for determining longitude. Loca- tion of a problematic terrane has to be made relative to major palaeocontinents, the position of which is taken as axiomatic. Hence, in the Ordovician, the tropical position of Laurentia and the boreal position of West Gondwana are established (on a variety of good grounds—see below in Section 4.2.1), and the other masses, e.g. Baltica and Avalonia, can be placed relative to them on faunal grounds. Since the palaeo- latitudes are constrained by either faunas or palaeo- magnetism or both, the longitude is only constrained by the kinematic history of the relatively mobile terrane entities. Since the final, or docking, position of a mobile palaeoplate is known, and its 'starting position' can often be inferred, there should be an optimal solution for any intermediate state. However, the assumption is made that the moving plate does so in the most direct way (A to x to B in Fig. 5A). We cannot disprove on faunal grounds a more compli- cated route (A to y1 or y2 to B in Fig. 5A) providing the faunal implications of the intermediate position (y1 or y2) are the same. In the case where the two stable continents are at high and tropical latitudes,
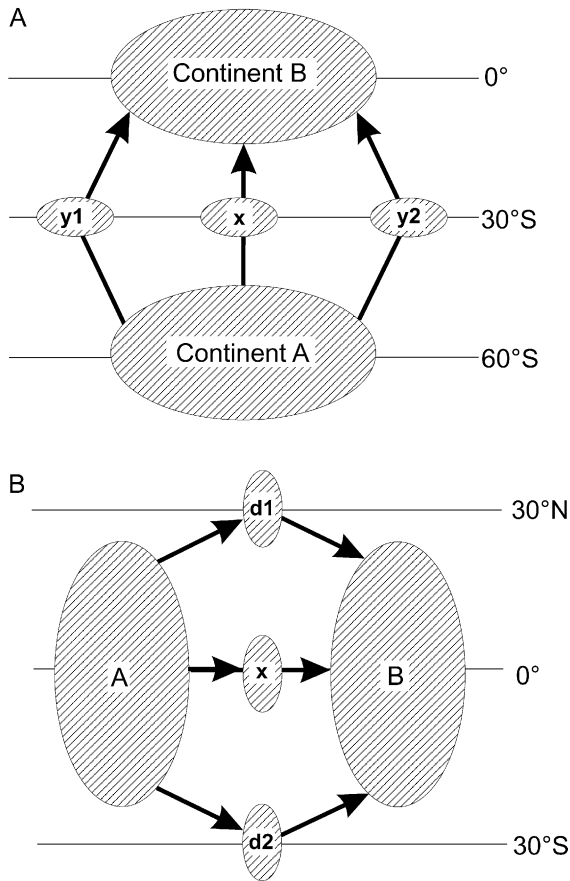
Fig. 5. Theoretical diagram of different faunal migration paths between continents (for discussion see text).

independent of faunal composition, in the form of characteristic volcanic suites, appropriate structural signatures and the like. In the absence of such evidence, the most parsimonious explanation is preferred. This means in effect choosing a simple spreading/docking model, and accepting the palaeolongitude that this implies. For most of the Palaeozoic examples with which we have been concerned, the simple model is sufficient to explain both the faunal observations and geological setting, but it is as well to recognise that future work may well introduce further levels of complexity.

3. Objective methods in reconstructions

Ideally, the same objective methods should be brought to bear on continental reconstructions using faunal evidence in each example. However, there is no general agreement on which method is likely to give best results, and only Lees et al. (2002) have attempted a comparative study of performance of different indices. Methods which factor out, or compensate for widespread taxa will tend to minimise the problems introduced by the different distributions of taxa in biofacies of different depths. Whittington and Hughes (1972) used a variation of the Simpson Index of similarity to compute distances between palaeocontinents. They did not distinguish biofacies. Neuman and Harper (1992), Harper et al. (1996) and Harper and Sandy (2001) used various methods, including correspondence analysis, to assess the relationships of Iapetus terrane faunas from Ireland and elsewhere in the Iapetus mobile belts. Lees et al. (2002) used a measure of Mean Endemicity as the most sensitive approximation to 'real' palaeogeography derived from other methods. This can optimise position in relation to faunal similarity based on shared taxa. In this method, continent positions are assumed for the major continental masses and a mobile terrane is allowed to move to the optimum position suggested by its faunas in relation to those of the 'competing' continents. This method is complex and heavy on computing time, and has only been applied to the microcontinent of Avalonia so far. For most examples mentioned below, assessment of similarity is based upon simple comparisons of the number of endemic, or otherwise subjectively judged significant taxa, shared between

respectively, the possible intermediate positions of the mobile microcontinent, say, would lie on an arc of a small circle. In the case of an intermediate position between two tropical reference continents (Fig. 5B), the options are more constrained, since a longer path (A to d1 or d2 to B) would take the plate at issue to a different palaeolatitude with different consequences for faunal signature. However, these are merely end cases, and real examples will be more complex.

Moving continents, or microcontinents, or terranes also entails the creation and destruction of oceanic basins. A complex dog-leg of the A to y to B variety shown in Fig. 5A would also require the operation of appropriate plate movements—for example, oblique spreading, which then ceases, followed by operation of a transform. This should leave geological evidence

a terrane at issue and one of the major palaeocontinents (e.g. trilobites of the families Asaphidae, Trinucleidae, Pliomeridae, Calymenidae and Dalmanitoidea have proved consistently useful indices). There is not usually a quantified measure of translating difference (or similarity) into distance, although semiquantitative methods have been used (e.g. Havlíček et al., 1994). Provided biofacies considerations have been ruled out, it is reasonable to translate considerable faunal differences into wide geographic separation, and there are usually palaeolatitudinal limits to constrain the answer. Problems arise in assessing the significance of similarities, especially when there are similarities to more than one competing major continent, and even more so if the fauna in question is small, when the addition of a few taxa could make a big difference in geographic assessment. For this review, we cannot pretend that all faunas considered by a multiplicity of authors have been treated in a suitably objective way, and where problems exist we shall note them.

The methods of vicariance biogeography are potentially of use in biogeography in the Lower Palaeozoic. Very few examples have been published (Edgecombe et al., 1999a,b). Initially, a well-supported cladistic phylogeny at species level of a widespread group is required, to which geographical areas can then be matched. At the moment, there are very few trilobite, brachiopod, or indeed other invertebrate phylogenies for which our knowledge has reached a depth suitable for the task. We can identify some groups which would be eminently suitable for this treatment. Trinucleid trilobites, for example, tend to be very endemic. They are also present on interesting terranes and microcontinents, such as the Precordillera of Argentina. It would be highly informative to see if the endemic genera there might relate to its postulated "isolation phase" when it was neither near Laurentia nor Gondwana.

There are, of course, many other factors which determine the differentiation and positioning of biofacies, which are largely outside the scope of this paper. One is the effects of ocean currents: these are notoriously difficult to assess through geological time and can strongly affect the distributions of benthic faunas. However, Christiansen and Stouge (1999) have presented an elegant analysis of early Ordovician biogeography which includes a conceptual oceanographic model.

4. Principal palaeocontinents

The main faunal and floral signatures of the palaeocontinents at a time of wide continental dispersal are determined, as at the present day, by palaeolatitude. There was a strong temperature gradient from pole to equator throughout the Ordovician, as first recognised by Spjeldnaes (1961). Very few taxa outside a minority of planktonic graptolites were truly pandemic. So as to identify the main terranes and continents for discussion, we reproduce here (Fig. 6) a recently published reconstruction (Cocks and Torsvik, 2002) of the early Ordovician (Arenig—480 Ma); however, not all the continents shown are discussed in detail below, and the configuration and positioning of some areas, e.g. those in Central Asia, are modified later in this paper. Before considering terranes, it is necessary to establish the faunal identities and composition of the five major continents (Gondwana, Laurentia, Baltica, Siberia and South China) as the most important areas against which comparative assessments can be made, and these will now be analysed in turn.

4.1. Laurentia

Palaeomagnetic evidence and the widespread occurrence of tropical carbonate sediments firmly place Laurentia as straddling the palaeoequator throughout the time period. It appears to have been the least mobile and therefore most stable continent in its position, and other plate movements are logged relative to it as a fixed reference. Laurentia comprises the main part of the North American continent (apart from the area of Avalonia—see Section 5.1 below), plus Greenland, western Newfoundland (Northern Peninsula), Northwest Scotland, Svalbard and the Arctic Canadian islands. It is bounded to its south by the Ouachita tectonic belt. Laurentia's faunal coherence in the Ordovician has been recognised for a long time (Poulsen, 1951) and has never been seriously challenged. However, there are differences of opinion about the significance of the 'transcontinental arch' that separated what is now the eastern and western seaboards of the USA and Canada (see below).

The definitions of major subdivisions of the Ordovician are as outlined in Webby (1998); otherwise, stratigraphic terminology follows Ross et al. (1997). Whittington (1963) recognised earlier Ordovician Lau-
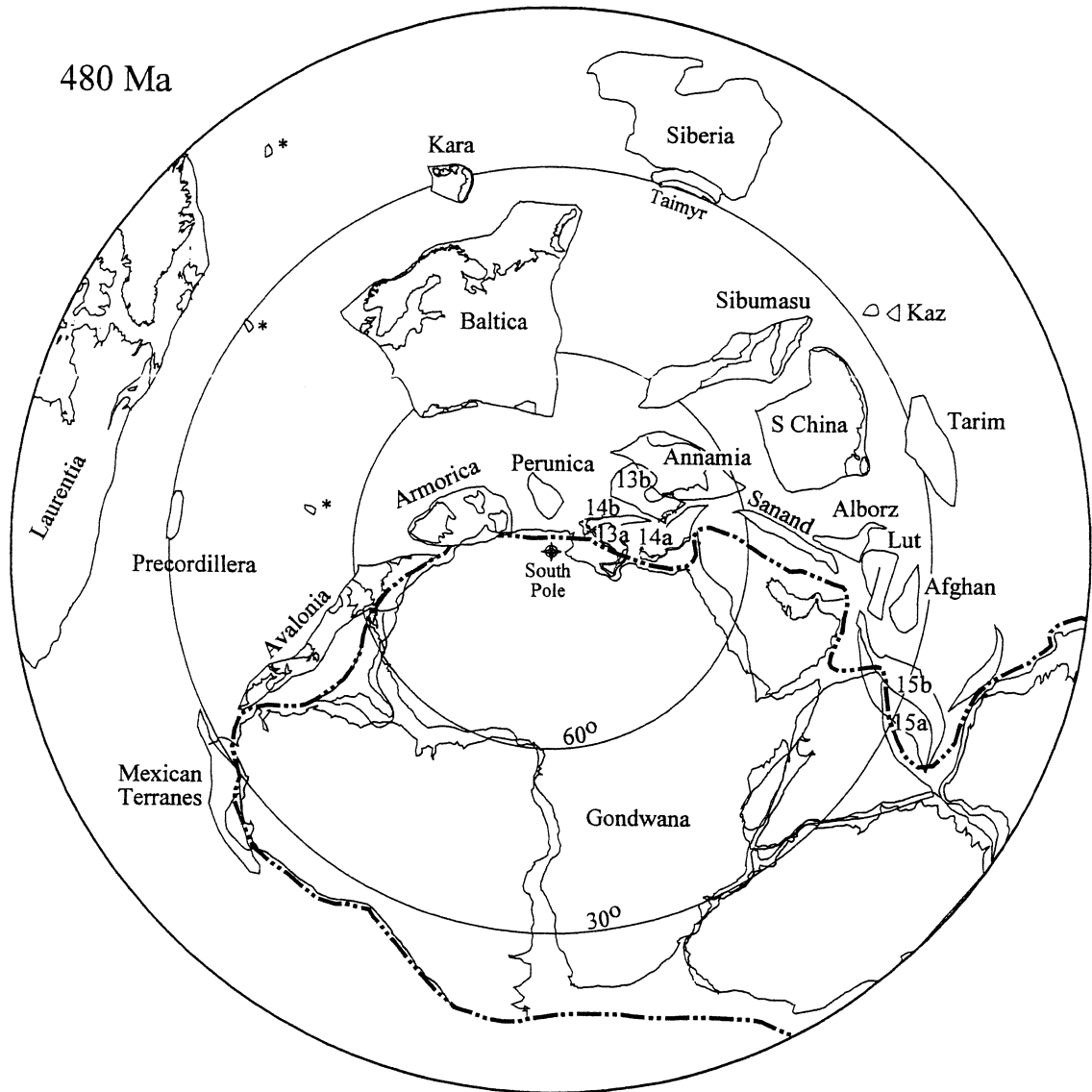
Fig. 6. Positions and names of continents and larger terranes in the early Ordovician (Arenig, 480 Ma), from Cocks and Torsvik (2002, fig. 1). North China was in the northern hemisphere and is thus absent from this figure. The starred small terranes in the Iapetus Ocean are those with palaeomagnetic fixes: the Kazakh terranes (Kaz) are merely two representational triangles. 13a, Apulia; 13b, Hellenic; 14a, Taurides of Turkey; 14b, Pontides of Turkey; 15a, south Tibet; 15b, Qiantang.

rentia on the basis of a review of trilobites known at the time as what he termed the "Bathyurid Province", typified by members of the Family Bathyuridae, most genera of which are confined to the relatively shallow-water carbonate platforms of this palaeocontinent. Subsequent analyses (Whittington and Hughes, 1972; Cocks and Fortey, 1982; Fortey and Mellish, 1992; Cocks, 2001) have all confirmed the distinctiveness of this fauna. In the earlier part of the Ordovician (early Ibexian), bathyurids had not yet diversified, and endemic hystricurids take their place as diagnostic taxa. It is now customary to regard bathyurid- or hystricurid-

dominated assemblages as the most inshore of a series of biofacies belts more or less circumscribing Laurentia. Additional trilobite faunal evidence of endemic Bathyuridae for various parts of the core palaeocontinent have been supplied in scattered monographs and papers in the last 25 years (Fig. 7): on the eastern side on current geography Spitsbergen (Fortey, 1980), Greenland (Fortey, 1986; Fortey and Peel, 1990), North-west Scotland (Fortey, 1992), western Newfoundland (Fortey, 1979; Boyce, 1989), north-eastern North America (Shaw, 1968; Tremblay and Westrop, 1991), Oklahoma (Shaw, 1974) and on today's western side: North-western Canada (Chatterton and Ludvigsen, 1976; Dean, 1989) and the Great Basin (Ross, 1970 and references therein; Fortey and Droser, 1996, 1999). The trilobite faunas are, therefore, generally well known.

Early Ordovician brachiopods were less diverse and also apparently less endemic than the trilobites. Ulrich and Cooper (1938) described many which seem to be pan-tropical in the earlier Ordovician (*Syntrophina*, *Nanorthis* and others). However, among Middle Ordovician brachiopods, also extensively monographed by Cooper (1956), there was a somewhat higher amount of endemism, which persisted to some degree into the latest Ordovician (Richmondian—see below); but

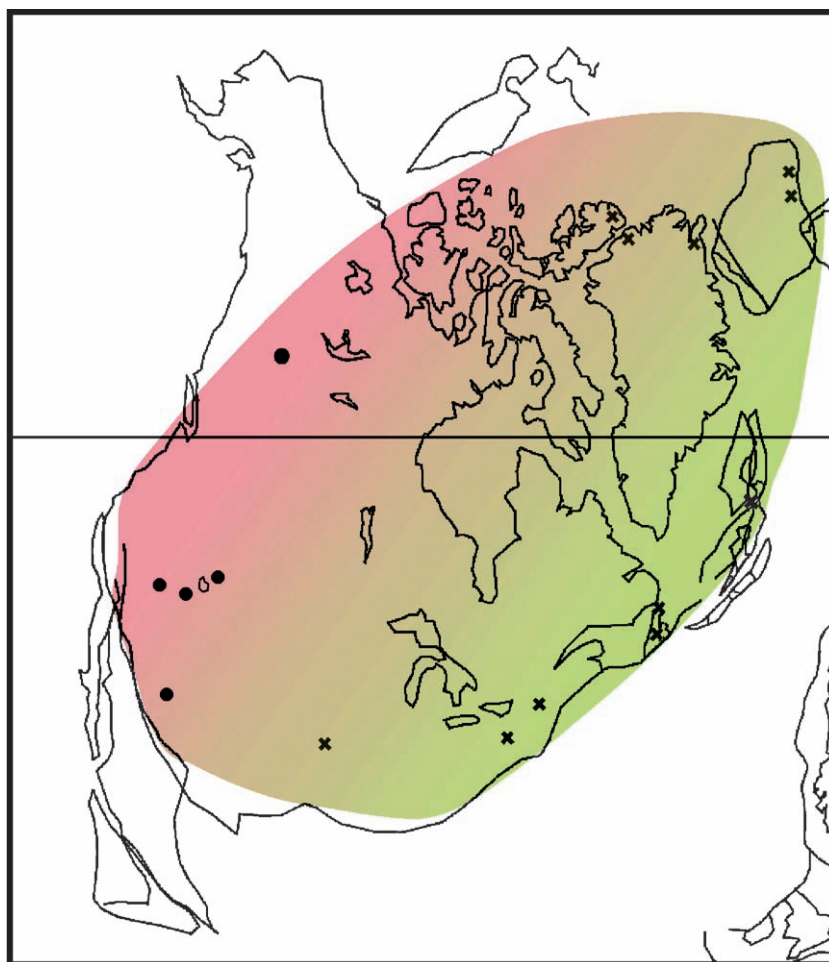Fig. 7. Laurentia, showing the distribution of eastern-style bathyurid and pliomerid trilobites (crosses) compared with western-style asaphid trilobites (e.g. *Aulacoparia, Lachnostoma*) (circles), suggesting some trans-continental differentiation in the early Ordovician. The colour shades show possible differentiation between western (pink) and eastern (green) faunas on either side of the Trans-Continental Arch.

there is no clear division between eastern and western Laurentian brachiopod biofacies.

The differences between eastern and western Laurentian trilobites in the earlier Ordovician (Ibex–early Whiterock) are worth noting, although they have not yet been fully studied statistically. The western faunas include a variety of endemic asaphids that are not recorded further east. Ibexian genera such as *Aulacoparia*, *Stenorhachis* and *Lachnostoma* are very abundant in the Great Basin and extend northwards into Canada (Dean, 1989), but are unknown in apparently suitable limestone strata in western Newfoundland for example. Conversely, the distinctive bathyurid *Bathyurellus* extends from Spitsbergen and Greenland to Newfoundland and New York, but is not yet confirmed among the diverse bathyurid faunas of the West. At the specific level, the differences are more striking. A shallow-shelf trilobite fauna of Arenig (late Ibexian) age includes *Petigurus nero*, *Isoteloides peri*, *Bathyurina timon*, *Punka flabelliformis*, *Bathyurellus* spp., *Ceratopeltis*, *Ischyrotoma anataphra* and *Strotactinus* spp.—most of this fauna being revised from the classical account of Billings in western Newfoundland (St. George Group) by Fortey (1979). Exactly the same fauna, albeit with varying combinations of species, has now been recognised in Spitsbergen (Fortey and Bruton, 1973), Greenland (Fortey and Peel, 1982), western Newfoundland, North-west Scotland (Fortey, 1992) and down into New York State and beyond on the eastern seaboard (Brett and Westrop, 1996). Fortey (1992) noted that on cluster analysis the Scottish faunas were closest to those from Newfoundland (and the identical fauna from Spitsbergen) within Laurentia. Contemporary faunas on the western side of the USA in the Great Basin are often dominated by endemic asaphids, several pliomerids (e.g. *Kanoshia*, *Hintzeia*, *Pseudocybele*) and different bathyurids (*Goniotelina* in variety, *Madaraspis*). It might be contended that these local endemics reflect separation by the transcontinental arch. Ross (1975) invoked differential current gyres on either side of the palaeocontinent. However, there are also many common elements in the shallow water trilobites on both sides of the USA: the pelagic species of *Carolinites* and *Opipeuter*; the ?lecanopygid *Benthamaspis*, the dimeropygids *Ischyrotoma* and *Dimeropygiella*; the pliomerids *Ectenonotus*, *Pseudomera*, and *Pliomerops*; the bathyurids *Licnocephala*, *Acidiphorus*, *Bol-*

bocephalus, *Psephosthenaspis* and *Strigigenalis* (*Petigurus* appears in the West later than in the East); the cheirurid *Kawina*. This long list indicates relatively free passage for some faunas across, or at least around the Laurentian palaeocontinent in the earlier Ordovician. It is possible that the endemics were a product of subtle environmental distinctions. The Great Basin lithologies include a greater proportion of argillaceous and micritic formations, for example, when compared with cyclothemic limestone–dolostone sequences in the east, with abundant sponges and algal packstones. Furthermore, very few of the genera listed above occur outside Laurentia, and they assuredly provide a very reliable signature for shelf faunas of that continental entity.

Marginal faunas of this age are not so widely known around core Laurentia. This is because on the eastern seaboard, in places where they might be expected, the relevant slope sites have largely been obscured by Caledonian (sensu lato) thrust tectonics verging from the east. Comparably, in the West, the marginal faunas were likely to have been part of the allochthon defined by structures such as the Roberts Mountains Thrust of Nevada. Rock units in that region originating from deep-water sites, such as the Vinini Formation, are often more or less graptolitic, and the most marginal trilobite faunas are not preserved. However, we have recently made new collections from the Arenig Al Rose Formation in the White Inyo mountains, California, where an outer shelf/upper slope biofacies is probably equivalent to the Nileid biofacies of Fortey (1975), abundantly represented by raphiophorids unknown in more inshore biofacies. In more inshore regions, brief incursions shorewards of outer shelf biofacies, probably as result of marine transgression, have been recognised by Fortey and Droser (1999) in the Hot Creek Range, Nevada. On the east side of Laurentia, deeper water olenid biofacies are best known from the Olenidsletta Member of the Valhallfonna Formation in Spitsbergen, and the Table Cove Formation of western Newfoundland, where local tectonic conditions have prevented them being concealed and/or metamorphosed. It has been noticed previously that the generic composition of deep-water biofacies includes taxa that are widespread beyond the Laurentian palaeocontinent, and that pandemicity increases with depth. From this fauna, the genus *Hypermecaspis*, for example, has been recognised in

Spitsbergen, Newfoundland, Wales, Argentina, Bolivia, Australia and China across virtually all palaeogeographic boundaries. Thus, that genus is only useful in recognising the proximity of old oceans.

In summary, the distinctiveness of the inshore Laurentian faunas is definitive as a comparative 'base' from which to assess the placement of faunas from marginal terranes in the earlier Ordovician.

Adrain et al. (1998) quantitatively analyzed a comprehensive database of trilobite occurrences worldwide, and identified a change in composition of trilobite faunas at the base of the Middle Ordovician (Whiterockian). Higher level taxa that first appear or diversified rapidly at this level (for example in Laurentian successions) were those that survived the late Ordovician extinction event and populated post-Ordovician faunas (Lichida, Proetidae, Dalmanitidae, Odontopleurida and Calymenidae among them). In Laurentia, first appearances of genera in these families accompany the Whiterock faunal 'revolution'. Its causes are not known in detail, but probably include a regressive–transgressive couplet of some magnitude. Whiterockian and later Ordovician faunas still include Laurentian endemics of the family Bathyuridae (*Bathyurus*, *Raymondites*), Asaphidae (*Stegnopsis*, *Vogdesia*, etc.) and others (Shaw, 1968; Chatterton and Ludvigsen, 1976), while up to half the genera of both brachiopods and trilobites in inshore faunas may be endemic. However, there is a decrease in endemicity at the generic level through the later Ordovician (most recently analysed for trilobites and brachiopods by Lees et al., 2002) accompanying the progressive homogenisation of Baltic, Avalonian and Laurentian faunas. Faunally based biogeographic assessments must be critically evaluated during this period.

In contrast to the differences between the east and west of Laurentia shown by the early Ordovician trilobites, the mid- and late Ordovician brachiopods summarised by Potter and Boucot (1992) show that the two margins of the palaeocontinent carried the same fauna and communities, although they demonstrated that only the shallower water Benthic Assemblage (BA) 2 to BA 3 communities were present on the central Laurentian craton, in contrast to the wider BA 2 to BA 5 range developed on the two margins. In addition, Potter (1990) undertook an elegant analysis of the biogeographical relations of the middle and upper Ordovician brachiopods which he mono-graphed from the Klamath Mountains, California, and concluded that they were most closely comparable to the faunas described from the eastern USA (Virginia, Tennessee and Alabama) by Cooper (1956). Most of the genera and species of the classic latest Ordovician (Richmondian) brachiopod faunas (*Megaamyonia*, *Hypsiptycha*, *Hiscobeccus*, *Lepidocyclus*) found in the Cincinnati area of Ohio and neighbouring states, and also in the Hudson Bay Lowlands (Jin et al., 1997) and as far westwards as the Mackenzie Mountains of Arctic Canada (Jin and Lenz, 1992) and north-eastern British Columbia (Norford et al., 1996) are not to be found on other terranes.

The latest Ordovician (Hirnantian) glaciation influenced marginal North American faunas, as elsewhere, but rare tropical limestone sites, for example in Anticosti Island, Canada, apparently provided refugia for faunas spanning the Ordovician–Silurian boundary. However, even though Laurentia was not apparently glaciated at that time, the brachiopod-dominated community systems there broke down at the end of the Ordovician, with many extinctions within the Richmondian fauna, and their empty niches were filled slowly by more cosmopolitan communities during the first 4 or 5 million years of the Silurian (Cocks and Copper, 1981). The Richmondian fauna did adapt to the changing temperatures in the Ashgill in the development of the Edgewood Fauna, which existed at the same time as the more widespread *Hirnantia* Fauna (Rong and Harper, 1988). These Edgewood brachiopods were monographed by Amsden (1974) and consisted of a mix of older cosmopolitan and Laurentian genera (*Dolerorthis*, *Platystrophia*, *Dalmanella*, *Dicoelosia*, *Cliftonia*, *Leptaena*, *Stegerhynchus*, *Eospirigerina*, *Coolinia*), some elements of the typical *Hirnantia* Fauna (*Hirnantia*, *Eostropheodonta*, *Dalmanella*, *Cryptothyrella*) and some more distinctive new forms (*Biparetis*, *Brevilamnulella*, *Leptoskolidion*, *Thebesia*). However, the last three are now known also from Baltica (Cocks, 1982) and thus, the Edgewood Fauna is now considered as characterising a less distinctive palaeogeographical signal than formerly.

Silurian faunas have recently become better known thanks to recent monographs of the "Arctic" faunas of northern Canada, for example, for the trilobites (Adrain, 1994; Adrain and Edgecombe, 1995; Adrain and Macdonald, 1996) and for the brachiopods systematically described by Lenz (1977) from the Yukon,

Zhang (1989) from Baillie Hamilton Island and Jin et al. (1993) from Hudson Bay and adjacent areas. It is apparent that, even within the context of a relatively uniform and cosmopolitan Silurian fauna, there were a number of Laurentian endemics with potentially useful biogeographic signals, and, as one would expect from a palaeoequatorial position, the overall diversities are very high. Carbonate mound faunas from Greenland (Lane, 1972, 1979; Lane and Owens, 1982) confirm this.

4.2. Gondwana

The main stable "core" of Lower Palaeozoic Gondwana (Cocks, 2001) comprised a supercontinent including Africa, South America, Arabia, the Indian subcontinent, Antarctica and Australia (Fig. 8). Iberia and Armorica in the West, and South China and other terranes in the East are faunally contiguous to various parts of that core, but have been the subjects of several differing reconstructions. There are numerous peripheral terranes all of whose positions require individual evaluation (see below). Throughout the period in question, core Gondwana was a major and varied home for faunal endemics. For this review, we divide the supercontinent into three, West Gondwana, East Gondwana and Intermediate palaeolatitude Gondwana. Benedetto (2001) has analysed the distribution of all the articulated brachiopods during the early Ordovician, and by this means alone has confirmed the previously published (e.g. Cocks and Fortey, 1988) position of the South Pole in North Africa, and shed light on the relationships and relative dispositions of the peri-Gondwanan terranes. We review Gondwana as a whole after South China (Section 4.2.5), with which it was closely faunally linked for much of our period.

4.2.1. West Gondwana

Since the South Pole lay within, or close to, northern Africa throughout the period, the comparatively frigid area of West Gondwana (Fig. 8) had peculiar environmental conditions to which very many endemics were uniquely adapted. This area embraces Armorica, Iberia, North Africa and continental Europe as far east as Serbia (Havlíček, 1989; Gutierrez-Marco et al., 1999). In the earlier Ordovician, the inshore clastic deposits with the trilobites *Neseuretus* and *Ogyginus* (Fortey and Morris, 1982),

and their accompanying trace fossils of the genera *Cruziana* and *Tigillites*, as well as an easily recognised suite of large lingulide brachiopods (*Lingulooglossa*, *Monobolina*, *Ectenoglossa*, *Lingulobolus* and others) are definitive of West Gondwana (Cocks, 2000). Shallow-shelf clastic deposits of Arenig–Llanvirn age are typified by a variety of genera of calymenoid (*Pradoella*, *Calymenella*, *Kerfornella*, *Iberocoryphe*, *Eohomalonotus*, *Salterocoryphe Colpocoryphe*, *Plaesiacomia*) and dalmanitoid (*Zelizskella*, *Kloucekia*, *Crozonaspis*, *Eudolatites*, *Dreyfussina*, *Guichenia*, *Retamaspis*, *Morgatia*, *Ormathops*, *Toletanaspis*, *Eodalmanitina*) trilobites, and the early history of trinucleids is virtually confined there. There are also endemic genera of more widespread families: Asaphidae (*Merlinia*, *Nobiliasaphus*, *Isabelinia*); Nileidae (*Barrandia*, *Parabarrandia*); Illaenidae (*Ectillaenus*); Pliomeridae (*Placoparia*); Cheiruridae (*Eccoptochile*); Lichidae (*Uralichas*); and Odontopleuridae (*Selenopeltis*) among them. The last named gave the label to the "Selenopeltis Province" of Whittington and Hughes (1972), which is broadly equivalent to West Gondwana; other terms, such as "Mediterranean Province" have also been used, e.g. by Havlíček (1989). The development of articulated brachiopods progressed more slowly; in the earliest Ordovician very few colonised these high-latitude areas, with only *Protambonites* and *Poramborthis* endemic to the Tremadoc of West Gondwana, which at that time included both Ibero–Armorica and Perunica. By the Arenig, the combination of *Nocturniella*, *Ranorthis*, *Prantlina* and *Nereidella* is distinctive to the area, and in Llanvirn times *Euorthisina*, *Eodalmanella* and early *Tissintia*. During the late Llanvirn (Llandeilo or Dobrotiva in other stratigraphical terminologies), the province was even more homogeneous, with *Tissintia* and *Tafilaltia* (Cocks, 2000, Fig. 8) ranging as far as Turkey, Shropshire and Bolivia, as well as on the Gondwanan core of North Africa, Ibero–Armorica and Perunica, with *Eorhipidomella*, *Cacemia*, *Appollonorthis* and *Tazzarinia* also abundant at many sites. By Caradoc times, the *Aegiromena–Drabovia* Fauna dominated within the central part of the area (Havlíček, 1989), accompanied by many other orthides, but with strophomenides and rhynchonellides (common in lower latitudes) rare and clitambonitides and pentamerides absent. In later Ordovician (Ashgill) times, the provincial signals
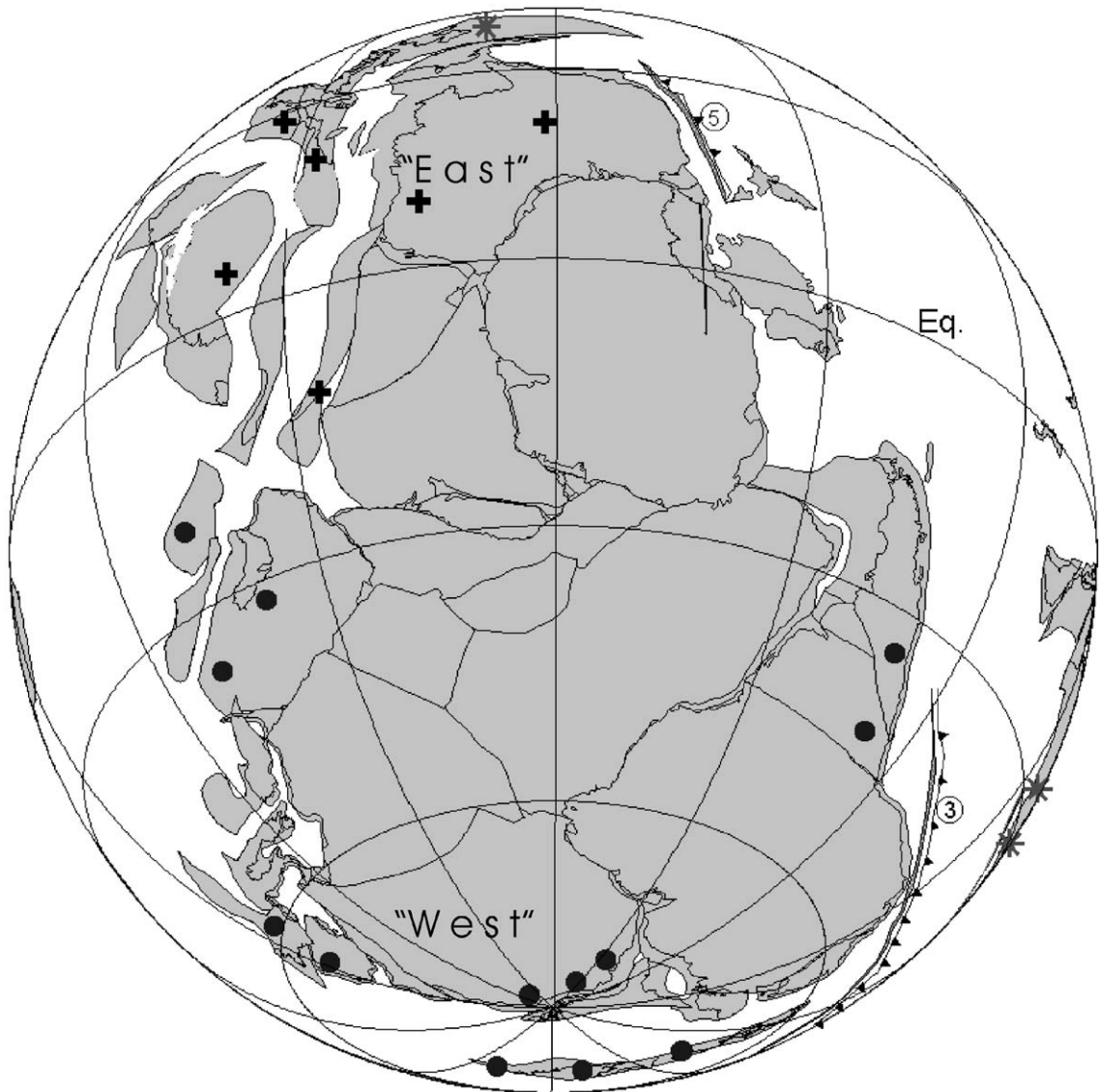
Fig. 8. Gondwana, showing the distribution of key trilobites in the early Ordovician, after Cocks (2001, Fig. 2). Dikelokephalinid fauna (crosses), Bathyurid fauna (stars), Reedocalymenine (=Calymenacean–Dalmanitacean of Cocks and Fortey, 1990) fauna (black dots). Continental distributions modified from C.R. Scotese PaleoGIS for Arcview package: also included are 3—Penobscot Arc (position from Van Staal et al., 1998), 5—south-east Australian Arc (position from Webby, 1992).

weakened, although the largely endemic *Dedzetina* and *Proboscisambon* brachiopod assemblages flourished in places, but by Hirnantian times, only the widespread *Hirnantia* Fauna occurs (Rong and Harper, 1988).

The early history of the bivalves appears to be strongly linked with West Gondwana (Cope, 2000) and there are numerous cool-water endemics (*Redo-*

onia, *Glyptarca* and others). These bivalves are as distinctive as those of contemporary Laurentia, but completely different.

The various trilobites and brachiopods have been described in numerous publications over the last century, of which Dean (1967), Hammann (1983), Havlíček (1977), Henry (1980), Rabano (1990) and

Romano (1982) are merely the most important, and summarize earlier references. The furthest east these faunas extend is to Saudi Arabia (El Khayal and Romano, 1985). Servais and Fatka (1997) have distinguished cool-water Gondwanan from more temperate Baltic and Laurentian acritarchs, the former being typified by *Frankea*, *Dicrodiacrodium* and *Arbusculidium filamentosum*.

Deeper water faunas of the earlier half of the Ordovician include the raphiophorid and cyclopygid biofacies of Fortey and Owens (1987). The olenid biofacies is only developed around intermediate-latitude core Gondwana in Argentina and Bolivia (Harrington and Leanza, 1957; Přibyl and Vaněk, 1980), but it is present also in South Wales, on Avalonia (Fortey and Owens, 1978). Cyclopygid faunas are developed in the Synclinal d'Ancenis, south of Brittany, and in deeper facies of the Montagne Noire, southern France (both in Armorica), which, together with the graptolitic succession of the Pyrenees, may be taken as evidence for a mid-European aulacogen. Armorica has been described as separate from core Gondwana on faunal, stratigraphical and palaeomagnetic grounds during the Lower Palaeozoic by various authors, but is now thought not to have separated from the supercontinent before early Devonian times (Cocks and Torsvik, 2002). In the early Silurian, it was almost entirely submerged deeply enough to carry only graptolites and bivalve and cephalopod molluscs. However, in north Spain, an isolated Llandovery brachiopod fauna is known (Villas and Cocks, 1996) adjacent to contemporary volcanics: this consists of 11 widespread genera, but two (*Asturorthis*, *Viodostrophia*) which were apparently endemic, which was unusual among the nearly cosmopolitan brachiopod distributions of that time (Cocks and Scotese, 1991; Fig. 10 here).

4.2.2. East Gondwana

The Gondwana supercontinent was so extensive that East Gondwana lay in the tropics, and provides an instructive sedimentological and faunal contrast to the polar regions of the same continent (Fig. 8). In the earlier Ordovician, carbonates dominated platform sites in Australia—in some cases these carbonates are lithologically similar to those developed in Laurentia. There is a minority of brachiopods in western Australia that are identical to genera from Laurentia (*Finkelnburgia*, *Eoorthis*, *Syntrophina*) in comparable shallow water carbonates. From the core of East Gondwana the brachiopods are in general rather poorly known, apart from Tasmania (Laurie, 1991), where the early Ordovician genera (*Apheoorthis*, *Nanorthis*, *Tritoechia*, *Syntrophopsis*, *Leptella*, *Archaeorthis* and *Hesperonomiella*) also occur in Laurentia. No endemic genera are known there before the plectambonitoidean *Railtonella* in the Llanvirn. However, in the early Ordovician there is only one trilobite species, the pelagic *Carolinites genacinaca*, in common between Laurentia and East Gondwana (McCormick and Fortey, 1999), although another pelagic genus, *Opipeuter*, is represented by similar species. The Midcontinent conodont fauna is also similar between the two areas, as is the so-called "Pacific" graptolite province (Finney and Chen, 1990). This may be considered a pan-tropical fauna, and represents those taxa with good dispersal ability around the palaeoequator. However, while the presence of common elements is important for stratigraphic correlation, graptolites and conodonts are less important for terrane recognition and palaeogeographic reconstruction.

Benthic trilobites in East Gondwana include a considerable number of endemics of types different from both Laurentia and West Gondwana. These have been reviewed by Wright et al. (2000) for Australia. Among trilobites, one monogeneric family, the Prosopiscidae, is confined there. The probable pliomerid subfamily Hammatocneminae is confined to East Gondwana and peri-Gondwana in the earlier Ordovician (*Pliomerina*, *Ovalocephalus*, *Encrinurella*, *Protoencrinurella*). The Dikelokephalinidae (Fig. 8) are more varied there than anywhere else (some genera extend into South America, Argentina, in intermediate palaeolatitudes; see Section 4.2.3): *Asaphopsis*, *Dactylocephalus*, *Hungioides*, *Meitanopsis*. Trinucleids (*Ichangolithus*, *Ningkianolithus*, *Ceratolithus*) are similar. Whittington and Hughes (1972) combined South America and China into the so-called "Asaphopsis Province" reflecting this distribution. Webby (1971) coined the term '*Pliomerina* Province' for another portion of east Gondwana based upon the occurrence of the eponymous trilobite. The conclusion is that East Gondwana was sufficiently removed from Laurentia to be dominated by endemics among inshore trilobites and brachiopods.

Faunal belts marginal to Australia are sporadically recorded along the Tasman "geosyncline" (Wright et

al., 2000) and include at least one fauna with olenid biofacies (Henderson, 1983).

Among trilobites, inshore Asaphidae have a particular propensity to generate endemic genera, and this is of particular relevance when considering East Gondwana. The same seems to be true of Pliomeridae and Trinucleidae (endemic trinucleids are considered in detail below). Separate basins within the broad East Gondwana realm are typified by asaphids and/or pliomerids that are not generally distributed, but abundant in a given region. In central Australia (Fortey and Shergold, 1984), uniquely tuberculate asaphids of the genus *Norasaphus* are dominant members of the fauna. *Gogoella* and *Pliomeridius* are endemic pliomerids.

4.2.3. Intermediate palaeolatitudes of Gondwana

Since Gondwana was a supercontinent, it stretched over more than 100° of palaeolatitude and thus there were continuous clines between the tropical and polar faunas. This means that the faunas of temperate palaeolatitudes have intermediate characteristics, and there is a complex 'overlap zone' between them. Subsurface Florida has yielded a single early Ordovician trilobite—*Colpocoryphe* (Whittington, 1953)—but one which is diagnostic of Gondwana. The South American portion of Gondwana (excluding marginal terranes such as Precordillera and Famatina—see Sections 5.2 and 6.6) embraces fossiliferous strata especially in Bolivia (Přibyl and Vaněk, 1980) and Argentina (Harrington and Leanza, 1957; Benedetto, 1998). In intermediate-latitude South America (Harrington and Leanza, 1957) distinctive asaphids with denticulate pygidial margins (*Thysanopyge*, *Australopyge*) are abundant in some settings. Deeper water biofacies are present in Venezuela and Peru (Hughes et al., 1980), and widely along the western sub-Andean side of Argentina and Bolivia. In the earlier Ordovician, the olenid biofacies is more widely distributed in this area than anywhere else at that time, but as usual, the taxa are very widespread. Hapalopleuridae seem to be more characteristic of deep biofacies and are widespread. A cyclopygid biofacies has been discovered recently. Among shelf faunas, endemic Trinucleidae include *Famanitinolithus* and *Incaia*. We have mentioned endemic asaphids above, and there are probably more, depending on how the systematics of this complex group is sorted out (*Hoekaspis*, *Branisaspis* and *Kayseraspis* are probably good genera). Among inshore

biofacies, the Gondwana-diagnostic *Neseuretus* is known from Bolivia and the Famanitina Range, Argentina (Section 6.6), and *Colpocoryphe* from Bolivia, the latter genus being more typical of West Gondwana. From the Gondwanan Central Andean Basin of northwest Argentina and Bolivia, Benedetto (1998) recorded a Laurentian/Gondwanan mix of brachiopods—*Hesperonomia*, *Paralenorthis*, *Nanorthis*, *Desmorthis*, *Glyptorthis*, *Euorthisina* and *Camerella*, as well as possible *Pleurorthis* and *Salopia*—from the Arenig, with *Incorthis* as the only endemic. By the Caradoc, in addition to genera of West Gondwanan ancestry (*Desstombesium*, *Tissintia*, *Drabovinella*, *Aegiromena*, *Rostricellula*), there are also migrants from other areas, for example *Oanduporella*, originally from the Baltic. For the earlier Ordovician, therefore, there is evidence of sufficient isolation to develop endemics, and a certain similarity to South China in Argentina, and West Gondwana in Bolivia, but deeper water faunas dominate.

Overlaps are also typical of the earlier Ordovician of the Middle East and Turkey (Section 5.3.6). A few taxa became effectively peri-Gondwanan, and were presumably temperature-range tolerant. The early Ordovician gastropod *Peelerophon* is one example (Jell et al., 1984); the trilobite *Hungioides* (which extends as far west as Thuringia) may be another.

4.2.4. South China

South China is included here as a separate major continent since the palaeomagnetic data (summarised by Cocks and Torsvik, 2002) indicate movements that separate it from Gondwana (Fig. 6), although, as we will review, the South Chinese faunas have much in common with Gondwana. In the earlier Ordovician, carbonates dominated platform sites in both South and North China. Benthic trilobites have been reviewed by Lu (1975). Taihungshaniidae are varied in South China (*Tungtzuella*, *Omeipsis*, while *Taihungshania* itself spread westwards at one level in the Arenig). Leiostegiids are commoner and more varied in this region than elsewhere. The asaphid subfamily Tangyaiinae is endemic to South China and associated terranes; the distinctive asaphid *Birmanites* is widespread in East Gondwana. Shallow- to deep-water profiles have been recognised across the Yangtze platform (Lu et al., 1976; Zhou et al., 2000, 2001) where they trend to the southeast and, as elsewhere, the deeper water faunas, which

include raphiophorids, cyclopygids, shumardiids and nileids, are widespread, and hence provide less geographic signature than the shallower faunas. The distinctive asaphids *Birmanites* and *Tangyaia* are common in South China and associated terranes, where they are associated with *Liomegalaspides*, *Ningkianites* and others. The dikelocephalinids *Asaphopsis*, and *Hungioides* (= *Argentinops* of Přibyl and Vaněk, 1980) are also widely recorded in South China and extend into the main part of Gondwana. *Hanchungolithus* is a trinucleid with a similar wide range from South China to France. Although asaphids are taxonomically difficult, genera named above are among the most distinctive in the family. From the Arenig Dawan and Meitan Formations Xu and Liu (1984) identified five brachiopod assemblages, together constituting a rich fauna of 55 genera, including five endemic orthidines (*Eodiorrthelasma*, *Lepidorthis*, *Metorthis*, *Pseudomimella*, *Xinanorthis*) of which *Metorthis* is the only representative of its family in the *Treatise* (Williams and Harper, in Kaesler, 2000). The Arenig pentameroid *Yangzteella* is abundant and was thought to be endemic to South China until its discovery in the Taurides of Turkey (Cocks and Fortey, 1988), which may have been at a comparable palaeolatitude in the complex array of peri-Gondwanan terranes. The early Caradoc Shihtzupu Formation (Xu et al., 1974; partly revised by Cocks and Zhan, 1998) has 19 brachiopods recorded, many are cosmopolitan, but there is the endemic *Peritritoechia* and also *Saucrorthis*, known elsewhere only from Burma in the Sibumasu terrane (Cocks and Zhan, 1998). The Shihtzupu trilobites (Zhou et al., 1984) include typical Gondwanan endemics (*Birmanites*, *Prosopiscus*, *Calymenesun*), together with a number of more cosmopolitan genera.

In the late Ordovician, there was land (termed Cathaysia by Rong and Chen, 1987) in the south-east part of the South China plate, and this was fringed by a series of shelly faunas. From there, the signals from the brachiopods are not identical to those from the earlier trilobites; for example, studies on early Ashgill faunas (Zhan and Cocks, 1998) show that a quarter of the genera are endemic (*Peritrimerella*, *Wangyuella*, *Rongambonites*, *Fenomena*, *Tashanomena* and others) and there are more genera in common between South China and the Chu–Ili Terrane of Kazakhstan (see Section 6.4.2 below) than there are with North China. The mostly Caradoc Pagoda Formation, widespread in

South China, is a highly diachronous trilobite-bearing unit which includes a number of endemic genera (*Ovalocephalus*, *Paraphillipsinella*, *Elongatanileus*, *Hastiremopleurides*, *Quyania*, *Xuanenia* and others) amounting to about 20% of the fauna (Fortey, 1997). The situation changed as the Ordovician progressed; for example, *Panderia* was earlier a predominantly Baltic endemic but appears abundantly in the later Ordovician of China. From the Upper Ashgill, Rong (1984), in a series of excellent papers, has characterised the Hirnantian brachiopod faunas, largely from shales and thin sandstones (Qian, 1987), and described the different constituents and detailed timing of the varied *Hirnantia* Fauna itself; however, the latter is difficult to use in palaeogeography because of its widespread distribution. Cocks and Fortey (1997) have compared the late Ordovician and early Silurian faunas of South China and Sibumasu and concluded that not only the species from the Pagoda Formation (South China) are essentially identical to those from the Pa Kae Formation (Thailand), but also that the lithological sequences in both areas are extraordinarily similar.

4.2.5. Gondwanan summary

For comparison with marginal terranes in other continents, tropical East and subpolar West Gondwana give good and distinctively separate faunal signatures, particularly in the Ordovician. South China was probably close to East Gondwana and also Sibumasu (Section 5.3.1) and the Himalayan terranes (Section 5.3.3), and is included in this context here. Intermediate-latitude sites are sometimes more ambiguous, but in many instances demonstrate the clines expected at the margins of a large continent with seaboards crossing many degrees of latitude. In the intermediate palaeo-latitudes, there may have been fluctuations between East and West Gondwana faunas at a formation-by-formation level, probably representing climatic shifts which are unrecognisable at higher or lower palaeo-latitudes alone. There is no question that at one or two levels asaphids of Baltic type (Dean, 1973a) made an appearance in the peri-Gondwanan Taurides of Turkey (Section 5.3.6 below), including *Asaphus* itself, one of the most distinctive of normally Baltic forms, and ptychopygids together with a species of *Symphysurus* almost identical to *S. palpebrosus* Dalman, abundant in Sweden during the Llanvirn. This indicates that Baltica must have been sufficiently close to allow relatively

brief colonisation on the appropriate substrate and at the right temperature, but we may also conclude that the independent Taurides terrane may have been further outboard of Gondwana at that time than the rest of the peri-Gondwanan collage.

East and West Gondwana maintained their faunal identity in the later Ordovician. Endemic Calymenoidea and Dalmanitoidea continue to typify the Moroccan later Ordovician but in Spain (Hammann, 1992) endemics such as *Nobiliasaphus* are joined by some trilobites of North American pedigree such as *Heliomera*, as well as a variety of illaenids of ambiguous significance. In Tarim (Section 5.5) and other marginal terranes, extending into South China, distinctive few-segmented raphiophiorids such as *Taklamakania* and *Nanshanaspis* are very abundant in some localities, and confined to this biogeographic region (Zhou et al., 1995). There are a number of endemic asaphids, and *Birmanites* is typical of a wide area. At the same time, there are progressive additions of widespread taxa, or those that have earlier histories in Baltica, reflecting the changes in palaeogeography that progressed during the Ordovician. There is a number of remopleuridid species in common between these two areas.

In the Ashgill, there is some evidence of a westward displacement of Chinese origin faunas accompanying the general homogenisation of trilobite assemblages. *Ovalocephalus* appears in Sardinia (Hammann and Leone, 1997), Spain (Hammann, 1992) and in Poland (called there *Hammatocnemis* by Kielan, 1960). *Josephulus* in the Boda Limestone of Sweden is related. Fortey (1997) considered that *Parvigena* from the same fauna also related to a Chinese proetid. *Amphytrion* is pandemic. These are elements in very diverse and apparently widespread faunas, known also from Avalonia (the Chair of Kildare Limestone, Ireland) and partly from Laurentia (Anticosti Island, Canada). In that the fauna accompanies limestones appearing at relatively high latitudes (and may equate with the bryozoan biostromes at Khabt Lahjar, east of Erfoud, Morocco), it seems reasonable to suppose that there was a climatic warm phase at this time in the mid-Ashgill which spread eastern Gondwana faunas more widely polewards (e.g. Hammann and Leone, 1997; Vennin et al., 1998).

Conversely, the *Hirnantia* fauna of the latest Ashgill is generally considered to be a response to the oncoming of the significant and extensive glaciation which terminated the Ordovician: it has a lower trilobite diversity (Owen, 1986) dominated numerically by the globally distributed *Mucronaspis mucronata*. The then South Pole lay under West Gondwana (Cocks and Fortey, 1988), but the latter had drifted over it during our period, and this is reflected in the faunas. In the early Ordovician, the distribution of the low-diversity brachiopod and reedocalymenid (neseuretid) faunas indicates the Pole's position under North Africa (Fig. 8), but by the Hirnantian, the *Hirnantia* and dalmanitinid faunas present in South Africa (Cocks et al., 1970; Cocks and Fortey, 1986) help to position it under central west Africa, whilst by the end of the Silurian the Pole was probably adjacent to South Africa or east Brazil, as can be seen by the distribution of the high-latitude *Clarkeia* brachiopod fauna discussed below. The Hirnantian brachiopods are more diverse than the trilobites and Rong and Harper (1988) recognised some global biogeographic differentiation within the faunas, with the more typical *Hirnantia* Fauna (*Hirnantia*, *Eostropheodonta*, *Cryptothyrella*, *Dalmanella*, *Leptaena* and others) most widely distributed in Gondwanan and peri-Gondwanan terranes from high (North Africa) to relatively low (Sibumasu) palaeolatitudes, in contrast to the contemporary and somewhat different Edgewood Fauna of Laurentia (Section 4.1). Many authors have written on the major turnover which most invertebrate groups experienced, with many extinctions, at or near the end of the Ordovician.

The Silurian of Gondwana is often somewhat impoverished in shelly faunas in the Llandovery, largely because of the wide spread of clastics with graptolites following the 'rebound' after the glaciation. The Wenlock fauna is rather uniform and diverse, but first Silurian appearances at this horizon suggest that there must have been unknown refugia through the Llandovery for many taxa. This uniformity reflects the change in global geography that had happened by this time, with the major continents separated by much narrower oceans than in the Ordovician. However, in later Silurian times, the distinctiveness of subpolar, high-palaeolatitude faunas is reinforced by the appearance of the restricted *Clarkeia* Fauna, with endemic *Clarkeia*, *Anabaia*, *Australina*, *Castellaroina* and other brachiopods (Cocks, 1972), and with relatively low diversity again

indicating high latitudes, which was established in the subpolar mass of Gondwana (Fig. 10), particularly in Argentina, Brazil, Bolivia, Peru and Paraguay (Benedetto, 1998; Cocks, 2001), together with endemic phacopoid trilobites of the family Calmoniidae (*Andiinacaste*, *Australoacaste*, *Feistia*), dalmanitoids, homalonotids and the proetid *Maurotarion*. By this time, Gondwana had drifted further over the South Pole, which was perhaps under Brazil, and the *Clarkeia* fauna is typical of the South American (Argentina to Bolivia) subpolar sector of the supercontinent in the late Silurian (Edgecombe and Fortey, 2000; Benedetto and Sanchez, 1996).

4.3. Baltica

The modern limits of the ancient Baltica palaeocontinent (Fig. 9) were discussed by Cocks and Fortey (1998), as including the greater part of Scandinavia and northern Europe as far south as the Tornquist line, Russia as far east as the Urals, with a southernmost extension into Kazakhstan and north into Pai Khoi and Novaya Zemlya (and then also Taimyr—but see Section 4.4.2 for the latter). Baltica was the continent that carried the strongest signals of endemicity in the early Ordovician. Torsvik (references in Torsvik and Rehnström, 2001) demonstrated from good palaeo-
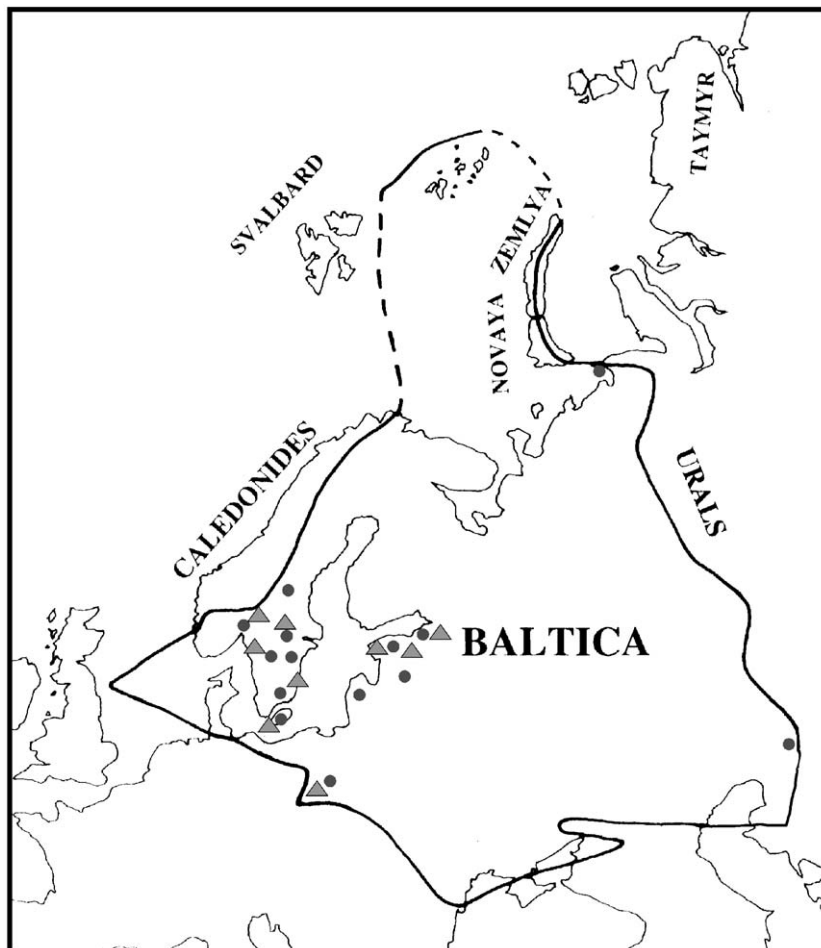

Fig. 9. The outlines of the modern extent of the Lower Palaeozoic Baltica terrane, showing the distribution of Arenig endemic megistaspinid trilobites (circles) and the brachiopod *Lycophoria* (triangles).

magnetic evidence that the continent rotated through more than 90° during the Cambro–Ordovician, but this appears to have had surprisingly little explicit effect on faunal signature. Such rotations are not prima facie determinable from fossil evidence if the reorientation happens within the same climatic zone, and Baltica maintained a generally coherent fauna while rotating substantially. The majority of the marginal biofacies are largely overridden by nappes in the Scandinavian Caledonides and eliminated by strike–slip in the Urals, and are mostly located in boreholes along today's south-western (Tornquist: Trans-European Suture Zone) section. However, within the south-central Urals, Little et al. (1997) have found remarkable Silurian fossils (large inarticulated brachiopods, vestimentiferan worms and other fauna) representing the oldest known mid-ocean ridge hydothermal vent faunas, a "smoking gun" for the edge of an old terrane if ever there was one! Shelf palaeoenvironmental subdivisions have been distinguished as "Confacies belts" by Jaanusson (1984)—these are essentially equivalent to the biofacies recognised as encircling other palaeocontinents. These decrease in depth from the Oslo region, Norway, towards the Russian platform, with the complication of a basin—the Livonian tongue—extending SW–NE in the southern half. The typical Baltic platform succession is extremely condensed, the Ordovician is as little as only a few metres thick in some places. Although much geological time must be unrepresented by strata in these sections, nonetheless, the succession of biozones in a given region is generally surprisingly complete (Dronov and Holmer, 1999). Jaanusson (1973) was the first to point out that the carbonates in the Lower to Mid-Ordovician indicate temperate rather than tropical palaeolatitudes, a fact confirmed as palaeomagnetism came available (Bergström and Noltimier, 1982; other references in Torsvik and Rehnström, 2001). Later Ordovician and Silurian lithologies are typified by tropical-style carbonates, whose deposition resulted in thicker successions. The Lower Palaeozoic fossil fauna of Scandinavia is among the best known in the world. Lees et al. (2002) plotted the faunal data points (Fig. 1) which have a density comparable with those of Recent faunal distribution maps. Trilobites were classically monographed by Schmidt about a century ago, but there have been extensive more recent revisions, of which

Warburg (1925), Öpik (1935), Tjernvik (1956), Owen and Bruton (1980) and Nielsen (1995) are landmarks, and summarize earlier work. Ebbestad (1999) summarized early Ordovician faunas of the deeper biofacies. Brachiopods are in more need of modern revision following the classic works of Schmidt and others in the 19th century and Öpik (1930) in the early 20th, although Holmer (1989) has enabled us to glimpse the diverse variety of inarticulated brachiopods present in Baltica, with 56 species in 29 genera present in the Viru Series (late Llanvirn and Caradoc) of Sweden alone. The global distributions of the 40 articulated brachiopod genera listed by Hints and Rõõmusoks (1997) from the Arenig–early Llanvirn Billingen, Volkov and Kunda Beds of Estonia have been checked using the new *Treatise on Invertebrate Paleontology* (Kaesler, 2000). These reveal that a surprising 17 of them are endemic to Baltica: six of the seven genera of the Clitambonitidae occur there, of which *Apomatella*, *Hemipronites*, *Iru* and *Lacunites* are endemic. Six of the eight Gonambonitidae occur in Baltica and three are endemic (*Estlandia*, *Oslogonites*, *Raunites*). *Orthis*, *Orthambonites*, *Krattorthis* and *Angusticardinia* are endemic Orthoidea, with the last genus part of an endemic Baltic family; within the Strophomenida the early strophomenoid *Panderites* and the plectambonitoids *Plectambonites*, *Plectella*, *Onegia* and *Ukoa* are also endemic. The brachiopod family Lycophoriidae is also endemic to Baltica—*Lycophoria* occurs in rock-forming quantities in Estonia and north-western Russia, and abundantly also in Norway, Sweden and the Holy Cross Mountains of Poland (Fig. 9). *Lycophoria* is not only the sole genus within the family, but that family is morphologically far removed from the others within the Pentamerida (Cocks, 2000, 2002).

Platform successions of the earlier half of the Ordovician are typified by yielding numerous asaphid trilobites—a fact which led Whittington and Hughes (1972) to term what is here called Baltica, the "Asaphid province". This nomenclature was somewhat unfortunate because, as noted previously, every major palaeocontinent had typical endemic asaphids. However, platform Baltica is characterised by an endemic radiation of megistaspinid trilobites (Balashova, 1977), a subfamily unique to Baltica. These are large and conspicuous animals which can be recovered from suitable limestones anywhere in Baltica (Fig.

9). *Ptychopyge* and three or four related genera (sometimes recognised as a subfamily), *Asaphus* itself, *Varvia*, *Lapidaria*, *Pseudobasilicus* and a variety of other asaphid taxa distinguished by Balashova (1977), are equally diagnostic. The asaphids *Niobe*, *Gog* and *Asaphellus* tend to be commoner in outer shelf sites but they are more cosmopolitan. Additionally, inshore taxa belonging to other families are endemic in the Lower to Middle Ordovician, especially cheiruroids (*Pliomera* s.s., *Evropeites*, *Krattaspis*, *Reraspis*, *Cyrtometopus*) phacopoids (*Diaphanometopus*, *Gyrometopus*) and calymenids (*Ptychometopus*). This very strong endemism persisted up to the Llanvirn–Caradoc with, for example, the brachiopod clitambonitoid families Estlandiidae and Gonambonitidae continuing to be known almost entirely only from the Baltic craton.

Other trilobitic elements in the more open-shelf early Ordovician biofacies common in southern Sweden, such as Nileidae (*Nileus*, *Symphysurus*), Raphiophoridae (*Ampyx*, *Lonchodomas*, *Pytine*), Alsataspidinae (*Falanaspis*), Agnostidae (*Metagnostus*, *Arthrorhachis*, *Geragnostus*), Telephinidae (*Telephina*), certain asaphids (*Gog*, *Niobe*) and Shumardiidae (*Shumardia* and allies) are much more widespread, and do not have a specific Baltic 'fingerprint'. They occur in deeper shelf faunas around Laurentia also, like the North Atlantic Province conodont faunas with which they co-occur. This has been attributed to common temperature regimes downshelf in the tropics to those on the outer platform of more temperate Baltica. Later in the Ordovician and in the Silurian (as almost everywhere, but punctuated by the end-Ordovician Hirnantian event), Baltica faunas progressively lose their individual stamp, reflecting the amalgamation firstly with Avalonia and their approach to North America before the Silurian docking. For example, the Caradoc brachiopods and trilobites of the Hadeland area in Norway (Harper and Owen, 1984) demonstrate a mixture of Baltic forms and genera which had originated from Avalonia (Shropshire). However, there is still sufficient 'signal' in the pattern of mutually shared genera to be able to separate these entities on numerical analysis, at least in the late Ordovician (Lees et al., 2002). By the early and mid-Silurian, the combined Baltic, Avalonian and (later) Laurentian faunas are essentially identical, apart from the ostracodes, even at the species level;

for example, the brachiopods (Bassett and Cocks, 1974) from Gotland, Sweden (Baltica), have most of their species in common with the late Llandovery and Wenlock of the Welsh Borderland (Avalonia). However, by late Silurian (Ludlow and Pridoli) times, more endemic brachiopod faunas had evolved, which apparently reflected inhomogeneities across the very substantial Laurussian supercontinent into which Baltica had become subsumed.

Dzik et al. (1994) documented the early and mid-Ordovician platform faunas of the Holy Cross Mountains, Poland, which are tectonically separated from Baltica today and lie south of the important Trans-European Suture Zone (the Tornquist Line). The Holy Cross Mountains are made up of two different blocks, and the main Ordovician sections are in the Małopólska Block. For our period, the faunas there include species-level similarities with Baltica in all groups—ostracodes, trilobites, brachiopods (the particularly distinctive *Lycophoria* and *Antigonambonites*—Cocks, 2000, Fig. 2), including many Baltic endemics. In contrast, the late Cambrian inarticulated brachiopods and trace fossils in the adjacent Łysogory Block had been evaluated as being "Avalonian" in affinity (Belka et al., 2000), but Cocks (2002) reviewed each genus in turn and concluded that they were relatively cosmopolitan and in consequence we place unhesitatingly both the Holy Cross blocks on the margin of the main Baltica continent in the Lower Palaeozoic. This is also supported prior to our review period by the Baltic affinities of the late Cambrian trilobites (Zylínska, 2001). The later Ordovician faunas in the Holy Cross Mountains include only the widespead deeper water *Foliomena* brachiopod Fauna (Cocks and Rong, 1988), the equally widespread trilobites described by Kielan (1960) and the *Hirnantia* brachiopod Fauna (Rong and Harper, 1988), none of which are of much use in assessing palaeocontinental affinity.

4.4. Siberia

Siberia was a substantial and independent palaeocontinent during all of the Ordovician and Silurian. It is considered here under the main part of the continent first, which includes Mongolia, followed by separate sections on Taimyr and Tuva, whose continental identities have been controversial.

4.4.1. Siberian main craton

The main craton comprised the area east of the Urals and north of the Asian fold belts: the latter separating Siberia from the North China terrane of peripheral Gondwana. Palaeomagnetic results from Siberia are considered robust and demonstrate rotation of the palaeocontinent after the Silurian (Smethurst et al., 1998). The continent maintained a tropical position early in the period and became progressively more temperate within the northern hemisphere in the Silurian. Questions arise about its disposition relative to Laurentia and tropical Gondwana, respectively. Earlier (Tremadoc–Llanvirn) Ordovician platform limestones are lithologically similar to those from other palaeotropical regions, and dominated by a shallow-water gastropod/sponge biofacies. Gastropods include such genera as *Ecculiomphalus*, *Ophileta*, *Proplina* and *Archinacella* which are in common with North America, as are leperditiid ostracodes. The brachiopods from the earliest Ordovician, although partly known from a pioneering paper by Nikiforova and Andreeva (1961), require revision, but also suggest Laurentian affinities, although with a few endemics (*Leontiella*, *Rhyselasma*). Trilobites include a number of bathyurids: *Biolgina* (=*Peltabellia*), *Punka*, *Licnocephala*, *Omuliovia* and *Ermaniella* of which the last two named are unknown in North America (Maksimova, 1962; Chugaeva, 1973). Since Bathyuridae are otherwise strongly endemic to Laurentia, the similarities are significant enough to suggest proximity at the time to this continent. However, *Omuliovia* is known from North China (Zhou and Fortey, 1986) but not from Laurentia. There do not appear to be any endemic Siberian asaphids at this time, but other Siberian asaphids have been placed in the North American genera *Isotelus* and *Homotelus*. The pliomerid *Pliomerellus* is confined to Siberia. Another pliomerid described by Chugaeva (1973) as *Pliomera fischeri asiatica* is probably referable to the North American taxon *Perissopliomera* Ross, while *Pseudomera* sp. of Kan'gin et al. (1989, pl. 9, Fig. 5) is very likely another Laurentian genus *Pseudocybele*. This strong overall Laurentian element, and the small number of endemics, is significant enough to suggest that the oceanic separation of the Siberian and Laurentian plates was not considerable in the Early Ordovician. Without an exercise such as that of Lees et al. (2002), we cannot give grounds for an absolute distance figure, but what we know is sufficient to suggest that Siberia should be closer to Laurentia than to North China. This contrasts, for example, with the reconstructions in McKerrow and Scotese (1990).

In the later Ordovician (Caradoc to early Ashgill), however, there was a burst of endemic trilobite evolution in cratonic Siberian sites sufficient to suggest increased separation from Laurentia. In particular, the family Monorakidae is both diverse and confined to Siberia (genera include *Isalaux*, *Isalauxina*, *Monorakos*, *Evankaspis*, *Ceratevenkaspis*, *Parevenkaspis*, *Elasmaspis*, *Carinopyge*). A faint Laurentian connection is represented by a few genera in common (*Ceraurinus*, *Calliops*). The brachiopods from the Caradoc and early Ashgill (e.g. Yadrenkina, 1978, 1982) are once again largely similar to Laurentia, but with some endemics, for example, the strophomenoid *Maakina*, and are notable for the abundance and diversity of the rhynchonelloids, including the endemic *Evenkorhynchia*.

The Siberian Silurian faunas of both Llandovery and early Wenlock age seem to be of the tropical pandemic fauna. However, later in the period a lower diversity endemic brachiopod fauna, the *Tuvaella* Fauna, evolved, dominated by *Tuvaella* itself and associated with *Tannuspirifer*, *Mesoleptostrophia* and *Stegerhynchus* (although the last two also have a more widespread distribution). This is today preserved (Fig. 10) only on the southern margin of Siberia (then facing north and towards the vast Panthalassic Ocean) in the Altai Sayan and Tuva Mountains of Russia and Mongolia and also in northern China (Rong et al., 1995), although the latter does not include the North China terrane (Section 5.4). Thus, this more temperate fauna and associated sedimentary facies reflected the progressive movement of Siberia northwards with time during our period.

Mongolia is another area from which only a few tantalising details are known from the Lower Palaeozoic period. The Cambrian trilobites recorded from earlier beds align it without doubt to Siberia, but few Ordovician faunas have been monographed apart from those from the Upper Ordovician Bayanhongor and Saaltai "zones" described by Rozman (1981) where 19 brachiopod genera are recorded of essentially cosmopolitan faunal affinities apart from *Severginella*, which is also known from Tuva (Section 4.4.3) and the Altai Mountains (Section 6.4.4), and the strophomenoid *Bajanhongorella*, which is endemic (Cocks and Rong,
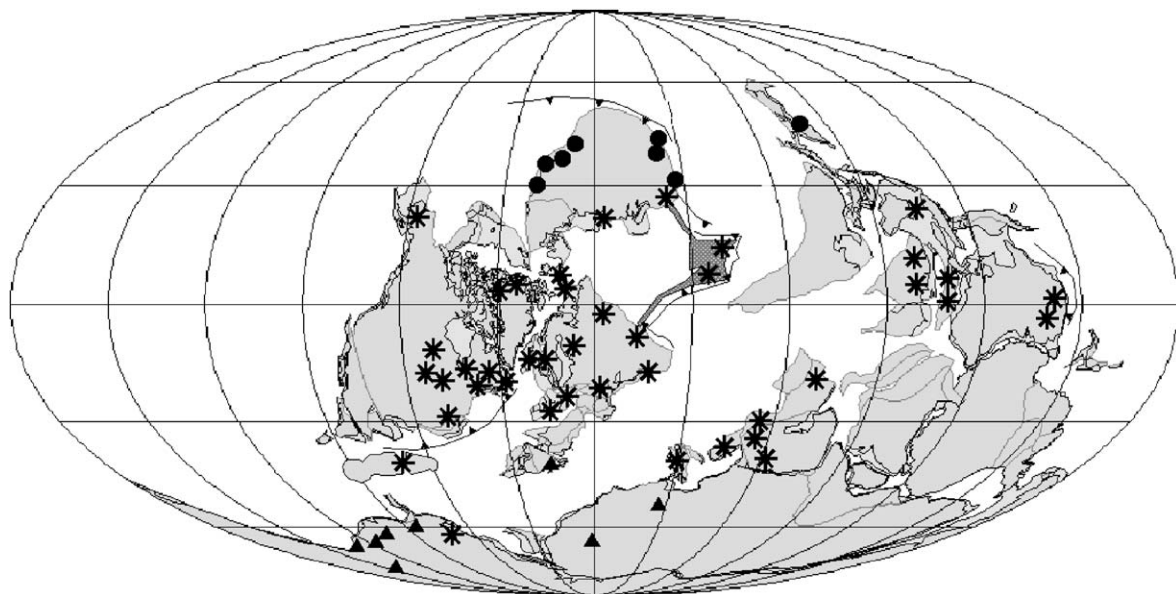
Fig. 10. Global map showing the higher latitude Siberian *Tuvaella* brachiopod Fauna (circles) and the southern hemisphere *Clarkeia* brachiopod Fauna (triangles), as well as the lower latitude cosmopolitan fauna, after Cocks (2001, Fig. 7).

2000). However, as in Tuva, the late Silurian higher latitude *Tuvaella* Fauna is known from Mongolia (Rong et al., 1995), indicating overall that it formed part of the then north of the main Siberian palaeocontinental collage at that time.

4.4.2. Taimyr

Taimyr has a variety of shallow- to deep-water successions of mid-Ordovician and younger age. Deeper water facies are present on the northern side of the Peninsula, where an oceanic style graptolite succession is present (Obut and Sobolevskaya, 1964), but that area, together with Severnaya Zemlya (Rushton et al., 2002), is now considered to have been a separate terrane termed the Kara Block. Cocks and Modzalevskaya (1997) considered later Ordovician (early Ashgill) brachiopod faunas from limestones in central Taimyr as indicating a possible Baltic signature. This opened up the possibility of Taimyr forming part of a microcontinent at some considerable remove from Siberia. Trilobite faunas are known in both deep and shallow biofacies of Caradoc–Ashgill age. The former include widespread taxa of supposed Llandeilan age, such as *Eorobergia*, *Bronteopsis*, *Ampyxina* and *Ampyx*, which are not very different

from coeval faunas on the fringes of Laurentia and Baltica, although there is one endemic form (*Taimyraspis*). Ordovician trilobite faunas in central and southern Taimyr of Caradoc–Ashgill age of shallow-water facies, by contrast, include a whole variety of Monorakidae—the 'fingerprint' endemic taxon (Balashova, 1960) of platform Siberia (*Monorakos*, *Evenkaspis*, *Ceratevenkaspis*, *Carinopyge*). They are accompanied by widespread, pan-tropical genera known from Laurentia and/or late Ordovician Baltica (*Isotelus*, *Stenopareia*, *Selenoharpes*, *Ceraurinus*, *Sphaerexochus*, *Calliops*, *Remopleurides*), which are not biogeographically critical. In our view, the presence of the monorakids is strong evidence that central and southern Taimyr were an integral part of the Siberian plate in the late Ordovician. Two endemic trilobite genera (*Goldillaenoides* and *Taimyraspis*) are hardly sufficient to postulate wide separation. Ashgill brachiopods of Cocks and Modzalevskaya (1997) had interesting similarities with those of the Boda Limestone of similar age in Sweden (Baltica). However, the latter is a carbonate mound fauna (illaenid–cheirurid trilobite biofacies) which does tend to include more widespread taxa (the Boda Limestone is very like the Chair of Kildare Limestone in

Avalonia, for example) which were established in palaeotropical areas wherever the appropriate crypt-algal buildup lithology is found. This Taimyr occurrence may correlate with the warm-water climatic pulse in the early Ashgill noted above under Gondwana (Section 4.2). Thus, in summary, northern Taimyr formed part of the independent Kara Block and central and southern Taimyr were integral parts of the main Siberian terrane (Fig. 6); however, sporadic faunal links indicate that Baltica, Kara and Siberia were not very far from each other during much of the Early Palaeozoic.

4.4.3. Tuva

Adjacent to Siberia today lies the Tuva terrane. There is debate as to whether this was part of Siberia in the Early Palaeozoic or formed an independent terrane. On tectonic gounds, Sengor and Natal'in (1996) show it and Mongolia as forming a separate Tuva–Mongol Arc; nevertheless, Mongolia (see above) was certainly faunally part of Siberia itself. By the end of the Silurian, the *Tuvaella* Fauna was well developed in Tuva, indicating that it was not only of Siberian affinity but that it must have then been on the northern rim of the palaeocontinent, with the main craton between Tuva and the peri-Gondwanan terranes. In the early Ordovician Tarlyk Formation, there are eight brachiopods recorded (Andreeva, 1982, 1985), of which "*Orthambonites*", *Oxoplecia*, *Ingria*, *Isophragma* and *Punctolira* are of Siberian, Laurentian or wider distribution, but there are also the endemic orthoids *Malinella* and *Tuvinia* as well as the early plectambonitoid *Ujukites*, which is only elsewhere known from the Altai Mountains of Kazakhstan (Section 6.4.4). Trilobites are mostly of widespread, deep-water type, but also include the pan-tropical *Carolinites*, and the predominantly Laurentian *Cybelurus*. In the succeeding Malinovskaya Formation, the fauna is not well described apart from two species of a single taxon, the plectambonitoid *Ujukella*, which, although described as endemic by Andreev (1993), was put into the synonymy of *Calyptolepta* by Cocks and Rong (2000), which is itself known only from island arc faunas in Newfoundland and possibly also from South China. The subsequent faunas are unknown until the Ashgill Khondelen Formation, from which Kulkov et al. (1985) described 15 brachiopods including the endemic *Eonalivkinia*, which, however, requires revision amongst the other atrypoids (Popov et al., 2000, p. 863). However, from the Wenlock to Pridoli of Tuva, Kulkov et al. (1985) described not only the relatively endemic and very abundant *Tuvaella* discussed above but also the endemic brachiopods *Tuvaechonetes* and *Tuvaestrophia*, which together reinforce the relative isolation of the area. Thus, in summary, some basic stratigraphic revision of Tuva in its tectonic setting appears timely—the faunas would appear to indicate either an island arc, perhaps in the Ordovician, or integration with the main Siberian continent, the latter might have first occurred at some time within the Ordovician or Silurian. However, provisional palaeomagnetic results by Bachtadse et al. (2000) indicate that Tuva may have amalgamated with Siberia by the early Silurian.

5. Biogeography of microcontinents

In the account above, emphasis has been on conspicuously endemic components of the major palaeocontinents which offer good support for comparison with peripheral terranes or microcontinents in contention. As discussed previously, statistical treatment which takes into account more widespread (but not pandemic) genera does fine-tune the results, but there is a shortage of worked examples. Microcontinents are considered first here, but in practice the distinctions from terranes is arbitrary—and some microcontinents (like Avalonia) are composed of several earlier conjoined terranes. Our definition is therefore a pragmatic one for palaeontology—the term microcontinent is applied to areas large enough to include a range of biofacies including especially shelf faunas developed on cratonic fragments. In addition to the terranes specifically discussed in this paper, there were undoubtedly others present in the Early Palaeozoic, for example, Apulia and the Hellenic Terrane (southern Europe), the Afghan Terrane of central Asia and the Mexican Terranes of central America (Cocks and Torsvik, 2002); however, although diagnostic Ordovician and Silurian graptolite and other faunas are known from them, benthic faunas are not, and thus they will not be considered further here.

5.1. Avalonia

In some ways, this is the classic example of a microcontinent, although sometimes regarded as comprising a number of terranes (Woodcock in Fortey et al., 2000; Armstrong and Owen, 2001). Western and Eastern Avalonia have been treated as separate by some authors; however, not by us—there is no compelling faunal evidence to separate them in the Lower Palaeozoic. Avalonia is composed of Belgium, the Anglo–Welsh area and southern Ireland, eastern Newfoundland, New Brunswick, Nova Scotia and the coastal areas of eastern USA as far south as Cape Cod, MA. Avalonia is underlain by ancient crust of the Midland platform of south-central England, which extended outwards under the Welsh basin; the Iapetus Ocean is presumed to have lain north of the Lake District, represented by a suture line which continues through Ireland. Armstrong and Owen (2001) have

separated the Monian and Lake District terranes (Fig. 11), but for the Ordovician and Silurian, we regard them as part of the Avalonian "superterrane" (Van Staal et al., 1998); we return to this topic below in the discussion of Iapetus terranes (Sections 6.2 and 6.3). A full range of depth-related biofacies is developed across Avalonia. In the Arenig–Llanvirn (Abereiddian), relatively shallow-water faunas in Shropshire are well known (trilobites—Whittard, 1956–1972; brachiopods—Williams, 1974). Trilobites such as *Neseuretus* and *Ogyginus* and brachiopods such as *Monobolina*, *Euorthisina* and *Nocturniella* establish the West Gondwanan signature of this inshore fauna, with *Placoparia*, *Ectillaenus*, *Barrandia* and *Selenopeltis* in more open shelf settings. Fortey and Owens (1978, 1987) documented the generally deeper biofacies in South Wales, including both cyclopygid and olenid biofacies. The latter includes a cosmopolitan fauna, but the cyclopygid biofacies was largely cir-
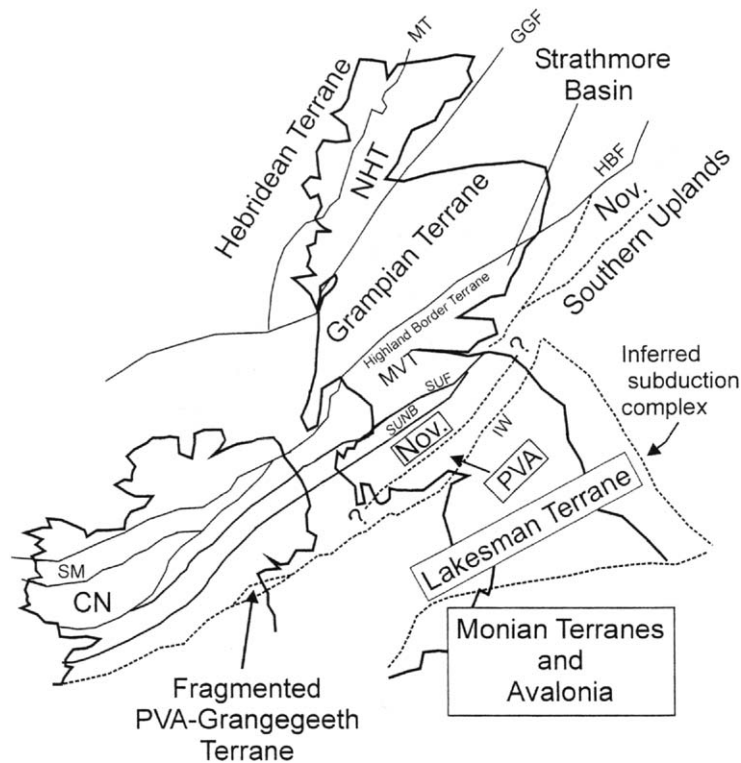

Fig. 11. The Lower Palaeozoic terrane collage on a modern map of northern Britain and Ireland, modified from Armstrong and Owen (2001, Fig. 1). CN, Connemara Terrane; HBF, Highland Boundary Fault; GGF, Great Glen Fault; IW, Iapetus Suture; Nov., Novantia Terrane; NHT, Northern Highlands Terrane; PVA, Popelogan–Victoria Arc; SM, South Mayo Terrane; SUF, Southern Uplands Fault; SUNB, Northern belt of Southern Uplands.

cum-Gondwanan in the earlier Ordovician. The fauna of the Pontyfenni Formation (later Arenig) is identical at generic level to that of the Sarka Formation of Perunica (Bohemia), and includes a number of Gondwanan endemics (*Ormathops*, *Colpocoryphe*, *Ectillaenus*, *Dionidella* and *Dindymene*), as well as some more widespread genera (*Shumardia*, *Ampyx* and agnostids) known from deep-water settings off more than one palaeocontinent. However, the general West Gondwanan signature is clear, and Fortey et al. (1989) showed that this signature applied as far north as the Lake District, thus effectively embracing all the various terranes of which Avalonia was comprised. Cluster analyses of faunal similarity using various methods (e.g. Fortey and Mellish, 1992) objectively confirm this Gondwanan affinity of Avalonia at that time.

This is an important point to establish because there have been various claims about the timing and extent of rifting of Avalonia away from Gondwana and opening of the Rheic Ocean. In the first place, Ordovician faunal data alone is neutral as far as the original location of Avalonia is concerned. Suggestions that it was located off north-western Africa cannot be distinguished from suggestions that it was originally off Armorica, since both would have similar faunal signatures. However, McKerrow et al. (1992), based on the distribution of archaeocyathids and trilobites, have deduced that it probably lay near northern South America and northwest Africa in the early Cambrian. If Avalonia had already rifted away from Gondwana in the late Precambrian, as claimed by Landing (1996), then the close Gondwanan signature in the early Ordovician would be very improbable. Equally, hypotheses invoking a wide ocean south of Avalonia in the early Ordovician (Allen, 1987) can be disproved. The contrary hypothesis that places Avalonia virtually contiguous with Baltica (Pickering and Smith, 1995) in the early Ordovician can also be discounted because there is nothing in common in the platform faunas of the two regions. Neither brachiopod nor trilobite Baltic endemics have been found in the early Ordovician of Avalonia, which is consistent with Avalonia–Baltica oceanic separation by Tornquist's Ocean, as originally postulated by Cocks and Fortey (1982). Similarities in graptolite and chitinozoan (Paris and Robardet, 1990) faunas between these two areas have led to some reconstructions which minimise the Baltica/Avalonia separation; however, those organisms have temperature-controlled

planktonic distribution patterns which are not critical for determining continent boundaries, as explained above (Section 2.4). Like olenids and other deeper water trilobites, and also many inarticulated brachiopods, they can be misleading if interpreted uncritically (Cocks and Verniers, 2000).

Separation of Avalonia from Gondwana as early as Tremadoc, an option reviewed by Prigmore et al. (1997), is difficult to prove on faunal evidence. Tremadoc faunas are rather uniform across much of Gondwana, and those of Wales are very like faunas from the Montagne Noire, France, and many elements extend through to China and Argentina (trilobites: *Macropyge*, *Platypeltoides*, *Asaphellus*, *Shumardia*, *Dichelepyge*, *Apatokephalus*, *Hospes*), accompanying a transgression which seems to have flooded the shelves rather deeply (Shergold, 1988). By the Arenig–Llanvirn, it is possible to argue for separation of Avalonia on the grounds of endemics that appear there, and Gondwana inshore endemics that do not. In the former category are trinucleid trilobites (*Myttonia*, *Stapeleyella*, *Trinucleus*, *Furcalithus*, *Gymnostomyx* and several marrolithines), and in the latter category a variety of dalmanitoids (*Zeliskella*, *Kloucekia*, *Crozonaspis*, *Eudolatites*, *Dreyfussina*, *Guichenia*, *Retamaspis*, *Morgatia*, *Eodalmanitina*) and calymenoids (*Praadoella*, *Kerfornella*, *Iberocoryphe*, *Eohomalonotus*, *Salterocoryphe*) are typical. Only the deeper water genera *Ormathops* and *Colpocoryphe* (and the trinucleid *Protolloydolithus*), and the inshore *Calymenella* and *Neseuretus* are in common in these groups between the two areas. Hence, the Mean Endemicity measure used by Lees et al. (2002) deduced a separation from Gondwana of Avalonia at this time.

The increasing similarity of Avalonian faunas to those of Baltica and North America from the Llandeilo Stage onwards has been documented for brachiopods since Williams (1969) and trilobites since Whittington and Hughes (1972). Schallreuter and Siveter (1985) and Vannier et al. (1989) observed the appearance of Laurentian ostracodes in what would now be regarded as Lower Caradoc limestones (the first Ordovician appearance of such lithologies). The same rocks yield dimeropygid trilobites, a family of Laurentian genesis, and bryozoans with dominant Baltic, but also North American congeners (Buttler, 1997). The inference that Avalonia had attained at least warm temperate palaeolatitudes, and proximity to Baltica, by Caradoc times

is consistent with all this evidence. However, its continued isolation is indicated by retention of a number of endemics among trinucleid trilobites (*Lloydolithus*, *Marrolithoides* and other marrolithines such as *Costonia*, and *Talaeomarrolithus* and *Salterolithus*), and the continued presence of a number of taxa which seem to have closest relatives in Gondwana (the asaphids *Basilicus* and *Nobiliasaphus*, the nileid *Barrandia*—see Hughes, 1979). Hence, in the early Late Ordovician Avalonia had a 'hybrid' fauna consistent with its oceanic position in transit (Lees et al., 2002).

By the Ashgill faunal distinctions had broken down still further, consistent with movement of Baltica equatorwards towards Laurentia, and the approach, if not docking of Avalonia: the increasing exchanges of ostracods between Avalonia, Baltica and Laurentia are documented by Williams et al. (2001). At generic level, trilobites are virtually identical between the Oslo region (e.g. Owen, 1981; Owen and Bruton, 1980) and the north of England (Ingham, 1970–1977; McNamara, 1979). In the endemically inclined trinucleids, this similarity is reflected significantly in common or close species of the genus *Tretaspis* in all three continents, some of which had Laurentian origins (Owen, 1980, 1987). Carbonate mound trilobite and brachiopod faunas in Sweden (Warburg, 1925) and Chair of Kildare, Ireland (Dean, 1971–1978) also include identical species. The Silurian faunas of Llandovery and Wenlock age of Avalonia continue to be as closely related to those of Laurentia/Baltica; for example, the brachiopods from Gotland, Sweden, and the Oslo area, Norway, are largely identical to those from the Welsh Borderland, with numerous species in common (Bassett and Cocks, 1974; Cocks and Worsley, 1993). It was originally from the type Llandovery area in Avalonia that Williams (1951) described and established the evolutionary sequence of the brachiopod *Stricklandia*, which became almost global in distribution except at high latitudes. However, in the Dingle Peninsula, Ireland (Bassett et al., 1976), some endemic brachiopods occur in the Wenlock (the genus *Holcospirifer* and the species *Rhipidium hibernicum*) indicating that all was not uniform across the area. These two Irish endemics are exceptional within the general uniformity of early to mid-Silurian faunas except at the highest latitudes.

Thus, in summary, there is good faunal evidence to deduce the migration of Avalonia from Gondwana northwards over a 55-million-year period from high latitudes as part of West Gondwana in the earliest Ordovician, as an independent Ordovician terrane with the dwindling Iapetus Ocean to its north and the widening Rheic Ocean to its south, and as docking first with Baltica at the end of the Ordovician and later with Laurentia in the mid-Silurian to form a constituent of the new supercontinent of Laurussia. This is confirmed by the statistical faunal analysis of Lees et al. (2002) and by similar movement shown by the palaeomagnetic data.

5.2. Precordillera of Argentina (San Juan Terrane)

The Precordillera of Argentina is almost the reverse case to that of Avalonia. Currently docked with the South American sector of Gondwana, there is good evidence that it was originally part of southeastern Laurentia (Thomas, 1991; Astini et al., 1995). Thus, it drifted from tropical carbonate facies to relatively high-latitude clastic facies during the course of the Ordovician. The faunal history tracks this trajectory in a plausible way, in particular the brachiopods now described in many papers by Benedetto (1998). The microcontinent shows platform environments, and marginal biofacies on both the Cordilleran and eastern side. Cambrian platform trilobite faunas are precisely of Laurentian affinity, even at species level. Ordovician faunas commence in a similar way. In the early Ordovician, the San Juan Formation has yielded bathyurid trilobites including *Peltabellia*, a 'fingerprint' palaeoequatorial taxon (Vaccari and Waisfeld, 1994), from typical platform carbonates, as is *Leiostegium* (Vaccari, 2001), as well as the brachiopods *Syntrophia*, *Leptella* (*Petroria*), *Hesperomena*, *Acanthotoechia* and others, all with a very Laurentian aspect. In the early Caradoc, Ordovician endemicity in the Precordillera was at its highest: nearly all the brachiopod species are of local distribution, and of the genera only *Campylorthis* can be termed Laurentian, but there are seven genera of West Gondwanan or Avalonian aspect, seven cosmopolitan and two endemic (*Oepikoides*, *Ancoramena*). Similarly, the trilobite faunas of the Las Aguaditas Formation (Lanvirn–Caradoc), with magnificent silicified material (Waisfeld et al., 2001 and references therein), include a mixture of faunal signatures compared with the principal palaeocontinents. A suite of endemic genera of trinucleids provide an interesting parallel with Avalonia (Baldis and Pöthe

de Baldis, 1995): *Guandacolithus*, *Australomyttonia*, *Hunickenolithus*, *Bancroftolithus* have been named. Chatterton et al. (1998) have described the endemic *Lasarchopyge* from the same formation. Other trilobite taxa so far described include a minority of pelagic trilobites (*Telephina*, *Carolinites*) of mid- to low-latitude type, and benthic cheirurids, odontopleurids and calymenids. A critical study of the Caradoc odontopleurid *Ceratocara* shows species level relationships with both North America and Baltica (Chatterton et al., 1997), but a cladistic analysis reveals the closest relationship of the Argentine form is still with North American taxa. By contrast, Edgecombe et al. (1999a,b) record the closest comparisons of the Cheiruridae as follows: *Nieskowskia* with Baltic taxa; *Ceraurinella*, *Heliomeroides* and *Macrogrammus* with North American taxa; and *Pateraspis* an otherwise Gondwanan endemic. The calymenid *Flexicalymene* is like *F. cataracti* from Wales (Avalonia). We regard it as significant that the warm-water Gondwanan 'fingerprint' endemic *Prosopiscus* appears in the Precordillera Caradoc, indicating that the drifting microcontinent had by then approached Gondwana, but not at high latitudes, sufficiently for this distinctive trilobite to cross the intervening ocean. Deeper water faunas of the Gualcamayo Formation (Llanvirn) include a biogeographically widespread fauna of Nileid biofacies type (*Nileus*, *Mendolaspis*, *Shumardia* and olenids) which are not critical for placing the microcontinent. The Llanvirn–Caradoc trilobites, therefore, show a remarkable admixture of types, but consistent with drift from Laurentia by way of Baltica palaeolatitudes to approach Gondwana. This admixture of genera is unique to our knowledge. It should provide an ideal case for the utilization of the methods of Lees et al. (2002) to estimate absolute distances. By the end of the Ordovician, contiguous *Hirnantia* faunas between the Precordillera and Argentina to the east indicate the possible docking of the terrane with Gondwana, and the subsequent appearance of the cool water Silurian *Clarkeia* brachiopod fauna in this and adjacent Gondwanan areas in South America testifies to the Precordillera's far removal from the contemporary tropical faunas typical of Laurentia.

Note that the faunal evidence disproves the Lower Palaeozoic reconstruction of Dalla Salda et al. (1992) (see also Dalziel et al., 1994) which abuts Laurentia and South America as a whole. The differences between contemporary Gondwana and Laurentia faunas would be inexplicable on this model, as would the changing affinities of the Precordillera terrane. While the faunas of the terrane were showing their complex mix of endemics and tropical/warm temperate faunas, the part of west Argentina to which the terrane would eventually dock was showing typical Gondwana faunas including the definitive trilobite *Neseuretus* (Vaccari and Waisfeld, 1994; Vaccari et al., 1993). This is a good example where faunas do play a critical role in deciding between tectonic models; thus, the Astini et al. (1995) version is confirmed with some certainty.

5.3. "Cimmeria"

Sengor (1984, 1987) and Sengor and Natal'in (1996) proposed that Turkey, Sibumasu, Annamia (Indochina) and central Asian terranes may have represented a Mesozoic peri-Gondwanan continent termed Cimmeria. This interpretation was principally made on orogenic grounds. Faunal evidence (Zhou and Dean, 1989) can be brought to bear to interpret the original Lower Palaeozoic positions of the Cimmeria segments, and hence the plausibility or otherwise of the existence of this extensive microcontinent as a single entity at that time. We will consider its various terrane components (Fig. 6) in turn.

5.3.1. Sibumasu

This area embraces the western part of the Malay Peninsula plus Thailand and Burma. Fortey and Cocks (1998) reviewed the palaeontological literature bearing on the geographical placing of the Lower Palaeozoic Sibumasu (or Shan–Thai) terrane, which they considered a single entity. They concluded that the earlier platform carbonate Cambro–Ordovician succession had strong similarities to North China and platform central Australia, while the later Ordovician yielded faunas identical even at species level (for trilobites see Fortey, 1997) with South China. There are striking similarities in sedimentary sequence between the succession in NW Malaysia and southern Thailand with that of the Yangtze Platform, notably thick earlier Ordovician shallow subtidal to peritidal carbonates succeeded by a very condensed late Ordovician–Silurian sequence. Cocks and Zhan (1998) have published Burmese brachiopod faunas of Caradoc age which show a modest level of endemism (*Dirafinesquina*,

Bekkerella) and which indicates some separation from South China. However, a close approach in the late Ordovician to South China seems very probable. The present authors are undertaking a further revision of Reed's (1906, 1915, 1917, 1935) Ordovician trilobites and brachiopods from the Shan States, Burma, preserved in the collections of the Geological Survey of India, Calcutta. These include the trilobites *Annamitella*, *Birmanites*, *Encrinurella*, *Liomegalaspides*, *Neseuretus*, *Ovalocephalus*, *Pliomerina* and *Xuanenia*, all of which would be considered typical of South China assemblages in the Middle to Upper Ordovician. The Caradoc brachiopod *Saucrorthis* is also known only from Burma and South China.

5.3.2. Annamia (Indochina)

Separated from Sibumasu by a major fault system, Annamia (or Indochina) has been considered a separate microcontinent (Metcalfe, 1992; Cocks, 2001). The localities have been hard to access in recent years for political reasons and we still rely on old accounts such as Mansuy (1920) for faunal data. Carbonates seem to be rare; early Ordovician trilobites include some widespread taxa (*Annamitella*, *Asaphopsis*, *Asaphellus*) which are scarcely diagnostic but all of which occur also in South and North China. In younger Ordovician faunas are the calymenids *Neseuretinus* and *Vietnamia*; the latter an advanced form which cladistic analysis (Turvey, in press) shows to be allied to *Sarrabesia*, a late Ordovician taxon from Sardinia. *Neseuretinus* is widespread from Sardinia, Turkey, Himalaya and South China. Zhou et al. (1998) have described an Lower to early Middle Ordovician fauna from East Yunnan, China (which formed the northern part of Annamia), which includes the Yangtze endemic trinucleid *Hanchungolithus*, and asaphid *Liomegalaspides*, but also *Neseuretus* and the asaphid *Ogyginus*: the latter more typical of higher latitude West Gondwana (Avalonia, Armorica, North Africa), along with some widespread peri-Gondwanan forms discussed above (*Hungioides*, cyclopygids). Zhou and Dean (1989, p. 435) conclude that "Llanvirn trilobites of the Sibumasu terrane differ markedly from those of the Indochina Terrane suggesting geographical separation" and infer that Annamia may have been in a more westerly (cooler) position. Cope (personal communication, 2001) informs us that the bivalves *Redonia* and *Glyptarca* occur in SW Yunnan, and are also of cool-water

Gondwana type. Hence, a case can be made that in the mid-part of the Ordovician Annamia lay considerably to the west, perhaps as far west as the section of Gondwana which is Turkey today, as shown by Cocks and Torsvik (2002) and Fig. 6 here. Collision with Sibumasu did not take place until the late Jurassic.

5.3.3. Himalaya

The High Himalaya south of the Indus suture include a Lower Palaeozoic succession which is mostly trilobitic, of which the Cambrian is best known: diverse Cambrian faunas were described in a recent revision by Jell and Hughes (1997). They noted that some deep water and more or less pandemic faunas may have accounted for previous ideas of "European" affinities. However, critical examination of the more inshore biofacies emphasises a strong Sino-Australian (East Gondwanan) signature, specifically in Iran and eastwards. There is no reason to suppose that these faunas were other than typically peri-Gondwanan. Ordovician faunas are much less well known, but tentatively point to the same conclusion (some taxa are re-illustrated in Morris and Fortey, 1985). The endemic, blind East Gondwanan trilobite *Prosopiscus*, known otherwise from South China and Australia, is present; *Neseuretus nivalis* is close to the *Neseuretinus* group distributed in Turkey and eastwards, while *Basiliella emodii* is very like a species from Thailand described by Kobayashi and Hamada (1964). A variety of spot Ordovician and Silurian brachiopod faunas have been recorded since the mid-19th century from various parts of the Himalayan region, but no new strong faunal signals may yet be assessed from them. North of the Yarlong–Tsangpo suture with India (Tibet) there are no Lower Palaeozoic fossils known: hence, it is not yet possible to assess whether the Lhasa block was, or was not, contiguous with Burma on fossil evidence. However, Hughes and Jell (1999) have adduced evidence that the Lhasa block may have collided with the Indian margin in the late Cambrian, just prior to the period under consideration.

5.3.4. Central Asia

Evidence for the area south of the Altaid complex of terranes is scattered and sparse. Balashova (1966) noted trilobites from the Pamirs (Section 6.4), which must be reinterpeted from her illustrations. Excluding

widespread taxa, the large asaphid *Pamirotchechites* is assuredly the same as *Nobiliasphus* from Bohemia, and "*Ogygites*" *pamiricus* is almost certainly the East Gondwana endemic *Birmanites*, while it is possible that "*Niobella pamirica*" is a species of the South China genus *Ninkiangites*; the raphiophorid *Raymondella pamirica* is probably attributable to the distinctive S Chinese genus *Taklamakania*. *Synhomalonotus pamiricus* resembles the Vietnam endemic *Vietnamia*. Her pl. 2, Fig. 10 specimen of "*Pamirites pamiricus*" seems to be *Brongniartella*, well known from China and Avalonia. *Dikelokephalina*, a pan-Gondwanan endemic, is correctly identified, as is the similarly distributed *Taihungshania*. The specimen attributed to "*Trinucleus pamiricus*" (ibid., pl. 2, Fig. 20) is like *Ningkianolithus* from South China. Hence, there is a proportion of widely distributed Gondwanan and peri-Gondwanan forms combined with a few known from further west and rather more known from further east, from South China in particular. This is consistent with a position close to where the Pamirs are today, and assuredly close to the Gondwanan continent.

Fossils of Ordovician age from Fergana, Tajikistan (formerly termed Turkestan) are not well known, but include a probable Caradoc species described as *Ampyx bulbifer* by Weber (1932). This is certainly the distinctive raphiophorid *Bulbaspis*, a characteristic endemic of Kazakh terranes peripheral to Gondwana (Section 6.4) and to Tarim (Section 5.6). In Uzbekhistan, an Upper Ordovician trilobite faunas has been described from east of Tashkent in the westward extension of the Chatkal Range (Abdullaev and Khaletskaya, 1970). Although widespread deep-water and pelagic genera predominate (*Cyclopyge*, *Telephina*, *Dionide*, *Trinodus*), there is also *Ovalocephalus* (under *Hammatocnemis*), a probable *Birmanites* (under *Ogygites*) and *Koksorenus* (under *Cybele*), all suggestive of East Gondwana and the related terranes of Tarim and Kazakhstan.

5.3.5. Iran

Various authors have divided Iran into several terranes for structural reasons, and they are shown as the separate Alborz, Lut and Sanand terranes in Fig. 6; however, the Lower Palaeozoic faunas are not yet well enough known from the area to be able to separate these areas on faunal grounds. Bassett et al. (1999) have briefly summarised the area to the north

of the main Zagros Thrust, and list distinctive low-diversity brachiopod associations dominated by *Protambonites* and *Tritoechia* from the Tremadoc, as well as the obolid *Thysanotus*. The common *Drabovia* in the later Ordovician is a distinctive West Gondwanan taxon, but, in contrast, the common rhynchonelloid *Rhynchotrema* and early athyridides are not present in higher latitude West Gondwana. In summary, these terranes carry typical intermediate-latitude Gondwana faunas during the Ordovician: whether they were peri-Gondwanan or structurally part of core Gondwana is uncertain. In the Silurian of Iran (Cocks, 1979), most brachiopods were widespread forms, but there were some endemic species and one genus (*Xerxespirifer*) which Boucot and Blodgett (2001) recognised as defining a possibly distinctive province of their North Silurian Realm.

5.3.6. Turkey

In the south of Turkey, the Lower Palaeozoic faunas are developed on the Arabian plate of core Gondwana (Section 4.2.3 above). Our knowledge of Turkish faunas is due almost entirely to the work of Dean and colleagues over many years. Cambrian evidence was summarized in Dean and Monod (1997) and Ordovician in Dean and Martin (1992), where many of the earlier faunal references are given. South of the Anatolian fault and north of the Arabian plate, in the Taurides Region, the relationships of Ordovician faunas are complex, but might be best summarized as showing a significant component of Baltic influence within a dominantly Gondwanan signature. The trilobite faunas of the earliest Ordovician (Dean, 1982), like those of the Cambrian, are of largely East Gondwanan type. Dean (1971a) described the fauna of the Seydisehir Formation (Lower Arenig) as "mostly of Tethyan type, but some genera from the highest strata exhibit Balto–Scandinavian affinities". The former include Gondwanan endemics such as *Colpocoryphe*, *Neseuretus* and *Taihungshania*, the latter *Symphysurus* and *Ptychopyge* (in our view Dean's *Paramegalaspis* is more like Gondwanan *Asaphellus*). *Neseuretus* and *Taihungshania* are pan-East Gondwana distributed, while *Colpocoryphe* is more West Gondwanan. Brachiopods from the Seydisehir Formation include the pentameroid *Yangzteella* which, until its recognition in Turkey (Cocks and Fortey, 1988), was thought to have been an endemic of South China. Dean (1973a)

showed that the Sobova Formation (Arenig) has a predominantly Baltica trilobite fauna, including the otherwise endemic *Pterygometopus* and *Ptychopyge* along with *Euloma*, *Agerina*, *Metopolichas*, *Niobe*, *Illaenus* and *Panderia* which were all predominantly Baltic at this time. The pelagic warmer water trilobite *Carolinites* is also present. From the Bedinan Formation of Caradoc age, Dean (1967) described a number of trinucleid trilobites which Hughes et al. (1975) redetermined as *Deanaspis*, a genus distributed through northern Gondwana and Perunica. Other Caradoc trilobites (Dean, 1983) include an interesting mixture of taxa, some identified to species level: *Nobiliasaphus* (Gondwanan), *Dalmantina proaeva* and *Colpocoryphe grandis* (both from Perunica), *Calymenella boisseli* (France, Gondwana), *Neseuretinus* (East Gondwana), *Selenopeltis* and *Colpocorpyhe* (West Gondwana), as well as more widespread genera. Similarly, the as-yet unpublished brachiopod faunas show a comparable mix of biogeographical origins. Dean and Zhou (1988) reported a trilobite fauna from the Caradoc–Ashgill boundary which includes a proportion of typical Chinese endemics, such as *Paraphillipsinella*. A younger (Ashgill) fauna from the Antalya nappes (Dean et al., 1999) includes a number of genera which are widespread from southern China to Sardinia (*Ulugtella*, *Cyphoniscus*, *Panderia* and *Hawleia*), of which *Cyphoniscus* and *Panderia* are known also from Baltica. Silurian faunas are all of widespread taxa.

Thus, the predominant Cambro–Ordovician faunal signal from the Taurides is peri-Gondwanan. The mixture, or alternation, of western/northern Gondwana taxa with those from further east, particularly China, is consistent with a Lower Palaeozoic position of this area not far removed from where it lies today, where it might be expected to show such a hybrid pattern, lying as it did at intermediate palaeolatitudes between the boreal and equatorial extremes of the mega-continent (Section 4.2.5). However, the 'incursion' of Baltic faunas at the end of the Arenig is worth remarking particularly. Given the Gondwanan 'fix' of both earlier and later fossil faunas, it is improbable that the Taurides became separated from the main Gondwana continent (and drifted closer to Baltica) during this time period alone. This would imply drifting and re-docking in short order. Rather, as suggested by Cocks and Fortey (1988), it seems more

likely that the temperate palaeolatitudes occupied by the Taurides produced appropriate environments at this time for colonisation from Baltica. From the lithological point of view, in the predominantly clastic sequences the Sobova Limestone is a striking exception. It is possible that a short-lived climatic warming produced calcareous substrates in Turkey that were suitable for Baltic invaders. It is worth noting that at what may be close to the same time a unique carbonate appears on the Saudi Arabian part of the Gondwanan plate (Fortey and Morris, 1982). This is also the time of a global faunal shift as noted by Adrain et al. (1998). Some connections at species level with the independent Bohemia (Perunica) in the Caradoc are not surprising given the similarities of their palaeolatitudes at that time.

North of the Anatolian Fault there is another terrane, termed the Pontides, from which Dean et al. (2000) listed a number of trilobites which indicate a deeper water facies in the late Arenig (including dionidids, cyclopygids and shumardiids) but the endemic components (the trinucleid *Bergamia*, the dionidid *Dionidella*, the bathycheilid *Prionocheilus*) are all of West Gondwanan type and most like Avalonian faunas of that age. Dean et al. (2000) postulated that this Pontide segment originated from further west in the higher latitude part of Gondwana, and we follow them in the reconstructions shown at the end of this paper.

To summarise, there is little evidence to suggest that Cimmeria, as understood in post-Palaeozoic times, existed as a single entity in the Cambro–Silurian, and its various component areas are best considered separately. With the exceptions of Annamia (Indochina) and the Pontides of Turkey, its various subregions fail to present convincing evidence to remove them far from their current positions relative to core Gondwana: with Sibumasu near South China (possibly moving away from North China) and the Taurides of Turkey as a part of intermediate-latitude Gondwana.

5.4. North China

In limestones of North China *Eoisotelus* and *Lonchobasilicus* are nearly as distinctive (Zhou et al., 1989) and quite as endemic as *Birmanites* and *Tangyaia* in the south, implying a faunal separation between the two Chinese terranes which reinforces the

palaeomagnetic evidence for separation (Cocks and Torsvik, 2002). Other inshore endemics include the pliomerid *Koraipsis*, known also from the extension of the North China platform into Korea. The Laurentian family Bathyuridae makes a rare appearance in North China also, and one might infer from this that it was closer to Siberia than South China. Early Ordovician brachiopods are rare, with Xu and Liu (1984) listing only two cosmopolitan forms from the Arenig from North China. From the Caradoc Pingliang Formation (Fu, 1982; revised by Cocks and Zhan, 1998) largely cosmopolitan brachiopod genera have been collected, together with the endemic rhynchonelloid *Longxianirhynchia*; however, the faunal indices calculated indicate that there was some similarity between the fauna and the contemporary Naungkangyi Formation of Sibumasu (Cocks and Zhan, 1998). From the middle Ashgill Beiguoshan Formation (Fu, 1982, revised by Zhan and Cocks, 1998), there are 16 widespread brachiopod genera plus the endemic *Orthocarina* and also *Altaethyrella* and *Ovalospira*, both known elsewhere only from South China and the Chu–Ili terrane of Kazakhstan. However, the comparative similarity indices calculated by Zhan and Cocks (1998) are not very high between North and South China at that time, even though there are several genera (and even one species, *Mimella zhejiangensis*) in common. It is informative to note that the palaeomagnetics (summarised in Cocks and Torsvik, 2002) place North China as one of the few terranes in the northern hemisphere during the early Ordovician, but from the fauna there cannot have been very great distances between it and the neighbouring terranes. However, as the Ordovician progressed, it appears from the faunas that the terrane moved further away from Laurentia and closer to peri-Gondwana, particularly South China and some of the Kazakh terranes (Section 6.4).

5.5. Tarim

Li (in Yin, 1994, ex 1988) treated Tarim (Fig. 13) as a separate biogeographical entity in the Ordovician; in simple cluster analyses, it emerged as related most nearly to North China on the basis of cephalopods and trilobites. If one takes his faunal lists as evidence, there is little reason to separate this region far from the Yangtze block of South China (e.g. 'Middle' Ordo-

vician trilobites: *Ovalocephalus*, *Tangyaia* (= *Lisoogorites*), *Birmanites*, *Calymenesun* and *Kanlingia*). More recent treatments of trilobite faunas have emphasised that in north-west Tarim (Xinjiang) there is a deep-water cyclopygid biofacies (Zhou et al., 1994b) continuing the marginal style of faunas known from the Cambrian of Tien Shan. As is usual, these faunas are informative of direction of open ocean, but uninformative as to terrane affinities. In addition to other widespread taxa such as *Shumardia* and *Nileus*, Zhou et al. (1994a) have described benthic faunas including the endemic and distinctive raphiophorids with reduced thoraces attributable to the genus *Taklamakania*, a genus also recorded from South China, as is the equally distinctive asaphid *Lisogorites*. As we shall see (Section 6.4), these 'fingerprint' trilobite taxa are known also from Kazakh terranes, as are other genera from Tarim (*Ampyxinella* and *Dulanaspis*). In the recent summary of biostratigraphy of Tarim (Zhou and Chen, 1992), additional Ordovician genera such as the South China endemic trinucleid *Xuishuilithus* are listed. The Altun Region to the East of Tarim (Zhou et al., 1994b), and regarded as separate, also includes some deep-water facies with widespread taxa, but in addition the Sino–Australian endemic *Pliomerina*, and North China platform asaphid *Lonchobasilicus*. Although a few brachiopods from Tarim are listed in the substantial biostratigraphical summary of Zhou and Chen (1992), none has yet been systematically revised, but from the lists seem mainly to comprise deeper water forms with little biogeographical signals attached to them. In summary, there is nothing to suggest that the Tarim region was other than close to East Gondwana; the unusual abundance of endemic raphiophorids is a distinctive local feature. There is strong similarity of northern Tarim with South China, and some evidence of eastern Tarim more closely comparing with North China.

5.6. Perunica

This term is applied to the microcontinent which includes the classical Bohemian successions studied by Barrande in the 19th century, now in the Czech Republic (Prague Basin). The adjacent area of Thuringia, which has yielded graptolites and sparse trilobites mostly of the cyclopygid biofaces, was probably marginal. The primary taxonomic literature for Bohe-

mia is vast, and will not be listed here, but a comprehensive Ordovician summary was given by Havlíček et al. (1994), who presented semiquantitative similarity analyses with other areas. Although Perunica was originally regarded as part of Armorica by Cocks and Fortey (1982), there is now good evidence of its independent history, not least because Tait (1999) has shown from palaeomagnetic data that the microcontinent had a different orientation from Armorica by the end of the Silurian and had therefore rotated before then. The time when Perunica separated from Gondwana is open to more than one interpretation. Havlíček et al. (1994) noted that late Mid–early Late Ordovician (Caradoc) was the time of maximum endemicity in Perunica among brachiopods and trilobites, and thus the microcontinent was uncontroversially a separate entity at that time. However, in older rocks there is a very close relationship at species level between the faunas of the Sarka Formation (Llanvirn) of Perunica and the Pontyfenni Formation (upper Arenig) of Wales (Avalonia). Some individual Llanvirn trilobite species (e.g. *P. cambriensis*, *P. binodosa*) extend from Bohemia to Avalonia, Armorica and North Africa and provide a strong Gondwana link (Fortey et al., 1989). The presence at this same time in Bohemia of typical Gondwana endemics such as *Ormathops*, *Colpocoryphe*, *Hungioides*, *Selenopeltis*, *Ectillaenus* and *Prionocheilus* is equally significant. On this evidence, there was fairly free movement of taxa between Perunica and Gondwana in the Llanvirn and in the Arenig before it, as witnessed by the large and distinctive Gondwanan inarticulated brachiopods (Section 4.2.1) present in Perunica. However, even at this time of faunal interchange there were endemic trilobites in Bohemia, such as *Trinucleoides*, and none of the superficially similar-looking endemic Avalonian trinucleid trilobites (*Bergamia*, *Stapeleyella*, etc.) extended into Bohemia despite the otherwise very similar deep basinal facies and faunas: the implication is that Avalonia and Perunica were separate enough to prevent complete homogenisation. One might conclude that, if Perunica had begun its independent history, then it was still close to Gondwana, as was Avalonia. Arenig trilobite faunas, less taxonomically diverse, reveal essentially the same pattern, while the brachiopods from shallower facies listed by Mergl (1995) are without exception of Mediterranean (i.e. West Gondwana) genera.

However, Havlíček et al. (1994; also Mergl, 1984) placed emphasis on the similarities between Baltica and Perunica Tremadoc faunas. This was equated with an indubitably increasing late Caradoc to Ashgill similarity between the faunas of these two plates. The latter is standard, accompanying Tornquist's Sea closure (see Avalonia), and we have nothing new to add here. However, the inference that in the Tremadoc Perunica was similar to Baltica might be taken to imply that at that time the microcontinent was previously closer to Baltica again. In our view this is a misinterpretation. We have seen already how open-shelf Tremadoc faunas are often relatively pandemic. The Avalonian Tremadoc faunas are also generically similar to those of the "Ceratopyge Shale and Limestone" Alum Shale and Bjorkasholmen Formation (Ebbestad, 1999) of Norway, for example. Some of the widespread Bohemian Tremadoc genera (trilobites: *Apatokephalus*, *Symphysurus*, *Ceratopyge*, *Harpides*, *Niobella*, *Proteuloma*) have distributions which are almost uninformative biogeographically—and many extend into the undoubtedly Gondwanan Montagne Noire region of France (Berard, 1986). This is simply a transgression fauna. Where inshore biofacies are preserved on Perunica, which is rare (Treniče Formation, Prague Basin, see Mergl, 1984), a much more peculiar and endemic fauna is present (trilobites: *Holoubkocheilus*, *Holubaspis*, *Eulomina* and *Hemibarrandia* and the early lichid *Holubkovia* are not known from elsewhere). The earliest Tremadoc Leimitzschiefer of Bavaria has endemic *Lichakephalus*, *Leimitzia*, *Kaufmannia* and *Curiaspis* alongside some Gondwana genera such as *Hospes* and *Macropyge* (Sdzuy, 1955). From the immediately succeeding late Tremadoc Vogtendorf beds, Sdzuy et al. (2001) have described brachiopods (*Poramborthis*, *Jivinella*, *Ranorthis*, *Kvania*) and echinoderms of entirely West Gondwanan character, accompanied by equally West Gondwanan trilobites (*Holubaspis*, *Euloma*, *Parapilekia*, *Hemibarrandia*), but with one trilobite, *Agerina*, of normally Baltic provenance. In summary, we believe that Perunica was very close to, although perhaps tectonically separate from, West Gondwana in the Tremadoc, at its greatest oceanic separation in the Caradoc, and closer to (and eventually merged with) Baltica thereafter, finally colliding in the Devonian.

6. Peripheral terranes

The difference between microcontinents and terranes is arbitrary, and we have used the former principally for large geographic entities displaying both platform and marginal biofacies suites. We have followed previous author's usage for terranes, i.e. they are fault- or structurally bounded areas with their own discrete stratigraphy, usually associated with arc settings of one kind or another (''island faunas''). Often the faunas are sporadic and poorly preserved compared with those of microcontinents, which makes for difficulties of interpretation. The principal use of faunal evidence has been to assess the original terrane position relative to their continental neighbours at the time of deposition of their fossil faunas (Neuman and Bruton, 1984). This is clearly geologically important in providing assessment of timing of docking of arcs, and direction of plate movements. One problem is the high proportion of endemics among brachiopod faunas embracing from one to a few terranes. Trilobites (where they occur) seem to relate more generally to a candidate continent at generic level.

There is a problem of biogeographical terminology, particularly in today's North Atlantic area. Williams (1973), in a pioneering analysis of Ordovician brachiopod biogeography, coined the term ''Celtic Province'' for two Arenig-age faunas from Anglesey (Wales) and Tagoat (SE Ireland) to contrast them with faunas from other regions. This concept was expanded by other workers (Neuman, 1984; Neuman and Harper, 1992; Harper et al., 1996) who used the term Celtic Province as an umbrella for a very disparate collection of faunas, largely dominated by brachiopods, in sites ranging from Maine to Argentina and China. Unfortunately, there are no taxa which are common to even a majority of these sites (apart from a few cosmopolitan genera), and thus such a ''Province'' cannot be properly defined as a separate entity. The faunas in question are mostly those inhabiting island arcs and a specific provincial name or identity is mistaken in principle (Cocks and McKerrow, 1993). Nonetheless, the recognition of island-dwelling faunas by Neuman (1972) was an important conceptual breakthrough in the understanding of ancient geographies. It is noticeable too that the diversity of brachiopod genera found at the various sites ranges from 2 to 33, which makes integration difficult within a single scheme. In this section, we treat the various island faunas and terranes within the Lower Palaeozoic Iapetus Ocean in turn in relation to their individual neighbouring larger palaeocontinent, and reject the concept of the Celtic province. However, statistical analysis by Harper et al. (1996) has demonstrated differences between high- and low-latitude intra-Iapetus sites.

6.1. Iapetus terranes—Baltica

The terranes which have been accreted into the Scandinavian Caledonides have yielded sporadic, but important faunas. These have been studied by Bruton (trilobites) and Neuman and Harper (brachiopods) over the last 20 years or so (summaries in Bruton and Harper, 1988; Neuman and Harper, 1992; Cocks and Fortey, 1998). They confirm structural evidence postulating stacking of nappes progressively from the West. The lower allochthon, composed of several nappes, shows a sucession of Cambro–Ordovician faunas which demonstrate that the slices were uncontroversially of Baltic derivation, requiring an original extension of the Baltic shelf westwards (today's geography) by some 400 km. The upper allochthon, by contrast, includes a number of faunas with a different faunal signature. From the Holonda Limestone (Trondheim) Neuman and Bruton (1989) reported 13 genera each of brachiopods and trilobites. The former included seven genera well known from Laurentia (*Aporthophyla*, *Idiostrophia*, *Rhysostrophia*, *Stenocamara*, *Syndielasma*, *Trondorthis*, *Vehnia*), four endemic genera (*Bockelia*, *Chaloupskia*, *Rhabdostrophia*, *Trotlandella*) and two cosmopolitan genera (*Archaeorthis*, *Orthambonites*), although *Trondorthis* (formerly listed as *Ocnorthis*) was subsequently reported from the Montagne Noire in Armorica, *Aporthophyla* from Australia, Kazakhstan and North China and *Rhysostrophia* and *Idiostrophia* from the Baltic. The trilobites include familiar and highly endemic components of Laurentian faunas such as Bathyuridae (*Goniotelina*) and Pliomeridae (*Ectenonotus*), along with a few more widespread genera (*Nileus*, *Illaenus*). There seems little question that this part of the Norwegian Caledonides originated outboard of Laurentia in the Whiterockian (Middle Ordovician), and its insular nature was suggested by association with appropriate volcanic rocks. The endemic brachiopods, with closest Laurentian relatives, suggested to Neuman that separation was

sufficient to induce local evolution, although we are not aware of cladistic analyses that might support this hypothesis. However, the other brachiopods and trilobites are sufficiently Laurentian to indicate that the fauna has to have lived within the palaeoequatorial zone, and hence not more than a few hundred kilometers off Laurentia. Higher in the stratigraphical column, the brachiopods, trilobites and bivalves from the Caradoc–Ashgill Upper Hovin Group of the Trondheim Region (Neuman et al., 1997) have variable affinities which no doubt reflected the approach of Baltica to Laurentia, but appear most similar to the faunas from the Craighead Formation of Girvan, Scotland, then close to or part of Laurentia. The island of Smöla has yielded a platform limestone with bathyurid trilobites and macluritid gastropods which may be a shelfwards equivalent. From the serpentine Otta Conglomerate (Llanvirn), another terrane setting in south-central Norway, a diverse Laurentian-style gastropod fauna was described by Yochelson (1963). Bruton and Harper (1981) analyzed brachiopods and trilobites from the same conglomerate. The trilobites include *Asaphus*, considered a Baltic endemic, and *Pliomera fischeri*, identified with a Baltic species. Additionally, *Annamitella* is a taxon widespread in "island" faunas (see also Section 6.2). Although Bruton and Harper described the brachiopods as of "strong North American affinities", of the two most abundant brachiopods, *Trondorthis* is known also from the Montagne Noire in Armorica as well as Laurentia, and *Neumania* occurs in Norway, Estonia and Ingria (north-west Russia), as well as Laurentia. Of the less common brachiopods, two are endemic (*Ottadalenites*, *Rutrumella*), and all of the other genera with unqueried identifications (*Camerella*, *Orthambonites*, *Palaeostrophia*, *Valcourea*) are also known from a variety of sites from outside Laurentia. Thus, the "Laurentian" identity of this fauna is equivocal—we follow the later opinion of Bruton and Harper (1988) in considering it of mixed Baltic and Laurentian affinity and agree the probability of an original (Llanvirn) position within the body of the Iapetus Ocean, rather than—as in the majority of examples—peripheral to Laurentia. These faunas may have corresponded temporally with a sea level 'lowstand' on eastern Laurentia, and with the approach of island arcs on to the eastern margin of western Newfoundland.

6.2. Iapetus terranes—Scoto–Appalachians

The linear configuration of terranes along the Scottish–Irish–Newfoundland–Appalachian Caledonides was outlined by Harold Williams and others in the late 1970s (see Williams and Hatcher, 1982). Since then, terrane boundaries have been revised, and a complex tectonic history involving the docking of several arcs and putative microcontinents has been elucidated. Tectonic evolution of the British–Irish sector has been recently ably summarized by Armstrong and Owen (2001; Fig. 11 here), who dovetailed the British terranes concordantly with the wider Appalachian interpretation of Williams et al. (1995) and Van Staal et al. (1998). Nomenclature of terranes is as described by Woodcock (in Fortey et al., 2000, Fig. 4). Here we are not primarily concerned with this structural history, but only with the part fossil faunas have had to play in its elucidation.

In Scotland, southwards of the typical early to basal Middle Ordovician Laurentian platform bathyurid trilobite/brachiopod faunas of the Durness Limestone (NW Highlands to Skye), there is no faunal evidence from the Grampian Highlands. From the Highland Border Complex, Ingham et al. (1985) described a Whiterockian silicified trilobite and brachiopod fauna which unequivocally proves Laurentian affinities, including a variety of critical trilobites of Bathyuridae (*Acidiphorus*), Dimeropygidae (*Ischyrotoma*), Pliomeridae (*Ectenonotus*) and others which are related even at species level to endemics of inshore biofacies from Utah and Nevada. This terrane, and its continuation in the Midland Valley Terrane to the south, cannot have been far removed from the Laurentian shelf in the Ordovician. The Midland Valley Terrane extends southwards where it is concealed beneath the northern part of the Southern Uplands. The Ballantrae ophiolite is dated by graptolite faunas, but these are a typical "Pacific Province" type with common deeper water isograptids (Rushton et al., 1996), which are also indicative of tropical palaeolatitudes. This ophiolite was obducted on to the Midland Valley in late Arenig times. The thick cover sequence is also Laurentian-style and has yielded the prolific and well-known fossil faunas of the Girvan district (for many references see Ingham in Fortey et al., 2000). Pebbles from southerly derived conglomerates in the Lower Old Red Sandstone in the Midland

Valley of Scotland and in northerly derived Ordovician conglomerates in the Northern Belt of the Southern Uplands prove that there were shelf limestones present in the southern margin of the Midland Valley from Tremadoc (Rushton and Tripp, 1979) to Middle Ordovician (Armstrong et al., 2000) times. Armstrong and Owen (2001) infer the existence of a southerly arc ("Novantia") which collided with the Midland Valley during the Arenig, thereby causing the obduction of the Ballantrae ophiolite (subsequent Laurentian collision of this amalgamated arc coincided with the Grampian orogeny). South of this amalgamated arc the Northern Belt (Llanvirn onwards) of the Southern Uplands is mostly graptolitic, and conodont faunas are not biogeographically critical, but rare, derived Ordovician shelly faunas (e.g. at Kilbucho with *Palaeostrophomena* and other brachiopods, and trilobites described by Owen and Clarkson, 1992) are still consistent with marginal Laurentia.

These terranes continue into Ireland, where exposure tends to be more piecemeal, or confined to relatively small inliers. Considerable progress has been made in the correlation of these outcrops, and the relationships to other Caledonian terranes clarified (Harper and Parkes in Fortey et al., 2000). The Midland Valley Terrane continues westwards into the Connemara Terrane plus South Mayo Trough. The most diverse faunas of Arenig age confirm the marginal Laurentian position of this terrane. The Tourmakeady Limestone has a rich Ordovician Whiterockian brachiopod (Williams and Curry, 1985) and trilobite (Adrain and Fortey, 1997) fauna, which allows for an objective assessment of affinities. Trilobites are unequivocally Laurentian, including a variety of 'fingerprint' bathyurids (*Acidiphorus*), dimeropygids (*Ischyrotoma*) and cheirurids (*Kawina*), as well as palaeotropical pelagics (*Opipeuter*). There are apparently two trilobite genera so far known only from Tourmakeady. Brachiopods have a higher proportion of endemic genera (8 out of 41), but the majority are again well known from Laurentia. The separation from the Laurentian platform was therefore sufficient to allow for the appearance of local endemics, but assuredly within the palaeotropical climatic regime. The biofacies is an illaenid–cheirurid cryptalgal mound, and contemporary similar occurrences on Laurentia, such as the Meiklejohn Peak 'bioherm' in Nevada, have not yielded the same endemic taxa. The

later Bardahessiagh Formation of Caradoc age in the same terrane whose brachiopods were monographed by Mitchell (1977) is closely similar faunally to contemporary Girvan formations in the Midland Valley of Scotland and equally Laurentian in aspect, and Candela (2001) has analysed the various brachiopod assemblages and their separate environments.

Southwards of the main Southern Uplands–Central Irish–Notre Dame terranes Cocks et al. (1997) linked together the Popelogan–Victoria Arc of central Newfoundland with the Grangegeeth Terrane of central Ireland. The latter is asserted to have rifted from the Gondwana margin and drifted northwards between the mid-Arenig to mid-Caradoc (Van Staal et al., 1998). The faunas are claimed to change from high latitude to "dominantly Scoto–Appalachian". The early Caradoc shelly faunas are, indeed, of particular interest (Owen et al., 1992, Fig. 2 reproduced here as Fig. 12; also Romano and Owen, 1993) but their interpretation is not without ambiguities. There is a case for regarding the Knockerk fauna as one of the rare examples of a genuine provincial "mix". As Romano and Owen (1993) carefully discussed, there are unique co-occurrences in this locality with taxa having a previous Baltic (few), Gondwana (more) or Laurentian (more again) history. The brachiopods (Fig. 12) emphasise the differing earliest occurrences in Laurentia, Grangegeeth and Avalonia. Eliminating cosmopolitan trilobite genera, or those which appeared also in Avalonia at the same time, there is a balance of significant species. We do regard *Birmanites* of significance (contra Romano and Owen, 1993) because, as we have seen already, it is present abundantly in warmer latitude Gondwana; indeed, the group of asaphids to which it belongs is not otherwise known outside Gondwana. *Decordinaspis* is a trinucleid endemic to Grangegeeth (once again this group readily speciates locally), but it is stated that its closest relative is *Nankinolithus*, another 'Chinese' genus, but one which appears in the later Caradoc. The calymenids *Gravicalymene* and *Flexicalymene* have a prior Avalonian history but were already in Laurentia as well as Avalonia and are thus not particularly informative. *Barrandia* is a relatively deep-water taxon, usually of Gondwanan occurrence. The contrast is provided by the cheirurids (*Acanthoparypha*, *Ceraurinella*) with prior Laurentian history, and particularly a similarly related trinucleid, *Tretaspis*, as trinucleids
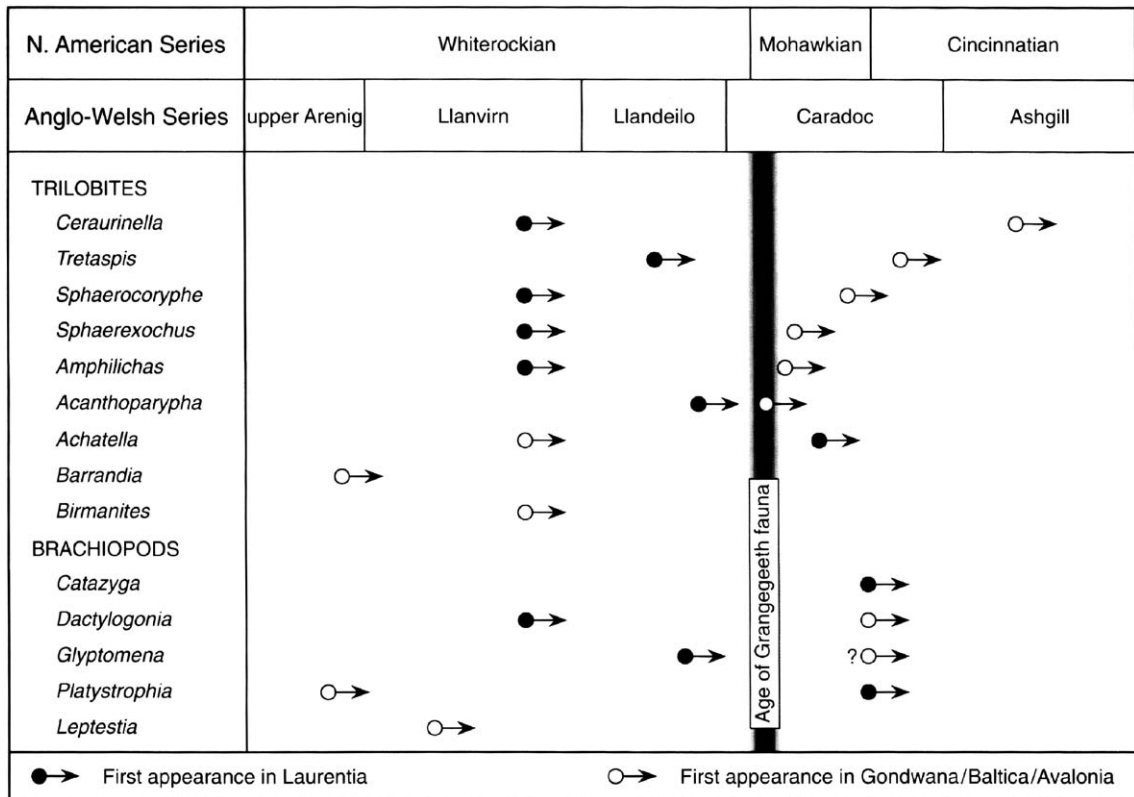
Fig. 12. Middle Ordovician brachiopods and trilobites in the Grangegeeth area, Ireland, showing the ancestry and subsequent appearance of elements of the Grangegeeth fauna in Laurentia and Baltica/Gondwana, from Owen et al. (1992). The Llandeilo is now considered as a stage within the expanded Llanvirn Series (Fortey et al., 2000). Copyright Geological Society of London.

are generally good indicators of endemicity. Romano and Owen (1993, 687) laid particular emphasis on their estimation that the closest related species to eight of the Grangegeeth trilobites were more or less contemporary Laurentian. In detail, the comparisons are mostly with Girvan (Superstes Mudstones and Balclatchie Group) taxa, all of which are preserved in a similar mudstone lithology as compared with the platform limestones typical of Laurentia, and were themselves from marginal sites. This approach also downplays the fact that the Gondwana/Avalonia taxa had their respective closest relatives in those areas. The "Gondwana" affinity of the earlier Slane Formation is based upon graptolites, of which Owen et al. (1992) emphasize the distinctive species *Acrograptus acutidens*. This widespread planktonic species is abundant in Avalonia and southern China. However, at the time in question (Llanvirn) the former had

already rifted from Gondwana and presumably moved to warmer palaeolatitudes, where it may have been commensurate with China (a North American occurrence is dubious): *A. acutidens* may be a mid- to low-latitude plankton. It could be argued that the evidence certainly supports a warm palaeolatitudinal position for the Grangegeeth Terrrane (cf. Mac Niocaill et al., 1997) with commensurate recruitment from Laurentia, but one in which taxa could also be recruited both from China (i.e. warm-water East Gondwana), particularly, and also Avalonia as it moved across Iapetus towards warmer latitudes. The evidence from the faunas alone is not persuasive to the idea of the terrane rapidly 'motoring' across Iapetus.

The southwards continuation of the peripheral Laurentian arc(s) into the Mobile Belt of Newfoundland is documented from a number of mostly brachiopod-rich trilobite-poor occurrences north of the Red Indian

Line. Dean (1970) described a small early Ordovician trilobite fauna from South Catcher Pond in the Notre Dame Subzone of undoubted North American signal (*Ischyrophyma* and *Leiostegium* are both good platform taxa). Continuation of the same terrane further south into New Brunswick and Maine is proved by further spot faunas described in a series of papers by Neuman (summarised in Neuman, 1984), mostly consisting of a small handful of brachiopod genera, but largely without strong palaeogeographical signals. It is a curious fact that the Ordovician trilobite *Annamitella* is often the most common trilobite in insular faunas. It is unknown from platform faunas in Europe and Laurentia, but is found in arcs peripheral to both sides of Iapetus and it seems to have been virtually pandemic in island arc settings, while its only platform occurrences are in eastern Gondwana (China, Australia). From New World Island in the central Mobile Belt, Dean (1971b, 1973b) described two trilobite faunas of Caradoc and latest Arenig/early Llanvirn ages, respectively. The earlier fauna, north of the Cobb's Arm fault, includes an endemic trinucleid genus and the 'insular' genus *Annamitella*; but also *Metopolichas* (which Dean compared closely with a contemporary Baltic species), *Encrinuroides* (compared with a Scoto–Appalachian one of younger age), *Illaenus* (either Baltic or Laurentian at this time), and what Dean determined as *Pseudosphaerexochus* but which is perhaps rather *Mayopyge*, a genus recently described from the Laurentian-affinity Tourmakeady Limestone (South Mayo Trough) of western Ireland (Adrain and Fortey, 1997). Neuman (1976) described a diverse brachiopod fauna from the same New World Island locality, with 27 species present. There are two endemics (*Acanthorthis*, *Guttasella*) and another genus (*Jaanussonites*) known elsewhere only from a similar site in Maine, and *Calyptolepta* is known elsewhere from only Tuva, China and questionably from the Otta Conglomerate of Norway. The bulk of the brachiopods are relatively cosmopolitan, but with a strong Baltic flavour suggested by the five clitambonitoids (*Antigonambonites*, *Atelelasma*, *Jaanussonites*, *Progonambonites* = *Gonambonites* itself, *Tritoechia*) and other orthoids and plectambonitoids also common in Baltica but rare outside that palaeocontinent. These trilobites and brachiopods are not suggestive of any specific connection with Avalonia or Gondwana, but could be taken as indicating inter-

mediate Baltic/Laurentian affinities. They are consistent with a 'mid-ocean' position for this fauna. The Caradoc fauna includes a few pandemic genera, but also *Carrickia*, a Laurentian to warm-water Gondwana pelagic taxon, and a variety of other trilobites from which Dean concludes that although the fauna is predominantly Scoto–Appalachian (i.e. pertains to the arcs off Laurentia) there is "a strong resemblance to Norwegian and Irish faunas". Furthermore, the trinucleid *Bergamia* is otherwise only of common occurrence in Avalonia (although rare in Turkey and Baltica). In short, that fauna is a genuine provincial mix.

An even more questionable emphasis has been placed by Williams et al. (1992) on a small fauna from the central belt of Newfoundland. A late Arenig cyclopygid trilobite previously known from Wales (*Cyclopyge grandis*) suggests an Avalonian, rather than Laurentian position for this terrane to these authors. Determination of cyclopygids is not easy, especially with distorted material. While it is correct to say that in the early Ordovician cyclopygids were mostly peri-Gondwanan, certain species of *Cyclopyge* are known from Scania, Bornholm and elsewhere in Sweden. Assuming the rotation of Baltica is correct (Torsvik and Rehnström, 2001, and references therein), these occurrences were at mid- palaeolatitudes. Cyclopygids were mesopelagic animals, and dispersal in the mesopelagic realm is quite likely. It seems to be putting too much weight on slim evidence to reschedule the tectonic history of the Appalachians on the basis of two pelagic trilobite specimens.

Whilst Cocks and McKerrow (1993) originally postulated largely from the faunas, that there was only a single intra-Iapetus island arc in the early Ordovician, further structural and faunal work (Harper et al., 1996; Cocks et al., 1997; Van Staal et al., 1998) has demonstrated that there were more probably two arcs and hence a variety of terrane collisions as the Iapetus narrowed during the Ordovician, finally closing progressively during the Silurian. It would be desirable to try the method of Lees et al. (2002) to obtain an objective placement of Grangegeeth and the Newfoundland Exploits–Gander terranes at different periods within the Ordovician. For the moment, the provincial mix seems to be a genuine feature, most economically explained by mid-Iapetus positions. However, the evidence for transport of these terranes

from a Gondwanan position to a Laurentian one seem to us to be inadequate. It would not be inconsistent with the faunal evidence to assume a mid-Iapetus position from mid- to late Ordovician. As evidence of Gondwanan origin, the identity of one cyclopygid trilobite seems slim indeed.

6.3. Iapetus terranes—Avalonia and southwards

Neuman and Bates (1978) emphasized the insular nature of a Llanvirn brachiopod fauna from Anglesey. Although Anglesey may well have had an independent history in the late Precambrian and early Cambrian, by the earlier Ordovician it is presumed to have been positioned inboard of the Leinster Lakesman Terrane (Woodcock in Fortey et al., 2000) which, as noted above, had a typically West Gondwana faunal signature in trilobite faunas from Arenig–Llanvirn interval (Fortey et al., 1989). Furthermore, Beckly (1987) has recorded typically West Gondwana genera (*Neseuretus* and *Calymenella*) from immediately on the southern side of the Menai Straits Fault, where Arenig faunas are also exactly comparable (at species level) in most other aspects with South Wales. From both north and south of the Menai Straits Fault the trilobite *Annamitella* is known, which is typical of island faunas throughout Iapetus, and the presence of brachiopods in Anglesey (Neuman and Bates, 1978) known elsewhere only from south-east Ireland (*Rhynnchorthis*, *Treioria*) and Argentina (*Ffynnonia*, *Reinversella*) may suggest a certain measure of separation, but it cannot be considerable or the faunal signature would be more distinctive. However, there is a sliver of deep-water, late Arenig isograptid biofacies graptolite shale along the Menai Strait fault system close to the suspension bridge (Jenkins, 1982) which might suggest the site of a basin. Oceanwards of Anglesey the history of the Leinster–Lakesman Terrane must be pieced together from spot faunas. It was peri-Gondwanan in the Arenig–Llanvirn, as adduced from the Lake District trilobites. Caradoc evidence from the Duncannon Group (Owen and Parkes, 2000) indicates that about one-third of the trilobite fauna "are not known from equivalent or older strata in the Anglo–Welsh region" but are Scoto–Appalachian, that is, peripheral Laurentian. These authors attribute the latter to closure of Iapetus in general combined with precocious 'island hopping' as this marginal

Avalonian terrane drifted northwards. This would also imply a separate drifting/docking history for this terrane, as it would otherwise be difficult to explain the differences from the main body of Avalonia if separations were as short as they are today. By late Caradoc–Ashgill times, trilobite and brachiopod faunas from the Lake District and environs are well known (Ingham and Wright, 1970; McNamara, 1979; Ingham, 1970–1977), and comparable to unified Baltica/Laurentia, as is the Raheen Formation in Ireland (Owen et al., 1986). Close to the northern margin of the Leinster Terrane the Ashgill trilobite faunas of the Chair of Kildare Limestone confirm close Baltic similarity at species level (Dean, 1971–1978) with faunas from the Boda Limestone of Sweden and the Keisley Limestone of north-west England.

The westward continuation of the Leinster Terrane into Newfoundland is recognised as the Avalon Terrane, south of the Dover Fault. Much of the stratigraphy of the Cambrian around St. John's can be matched elsewhere—in Wales, for example. The early Ordovician in this area is platformal, with the Gondwana trilobites *Neseuretus* and *Ogyginus*. The early Ordovician faunas and floras from Random Island (Martin and Dean, 1981) are deeper water, close to the Dover Fault, but are also distinctively Avalonian. This sector continues southwards into New Brunswick and Cape Breton Island, where the successions are very similar to those in Avalonian Wales. RAF has studied the Tremadoc MacLeod Brook Formation which is identical at trilobite species level to the Shineton Shales in Shropshire, England: all these localities being consistent with peripheral Gondwana location at this time.

6.4. Kazakh and neighbouring terranes

Kazakhstan and Northern Tien Shan has been portrayed as a single terrane entity in many treatments of global geography including some recently published (e.g. Seslavinsky and Maidanskaya, 2000). However, it is now clear that the main Palaeozoic region of central Kazakhstan comprises a complex of accreted terranes (Sengor, 1987; Sengor et al., 1993), whose current juxtaposition does not necessarily reflect their original geographic position. As noted above (Section 4.3), that part of the southern Uralian chain located in Kazakhstan (Fig. 13) was part of
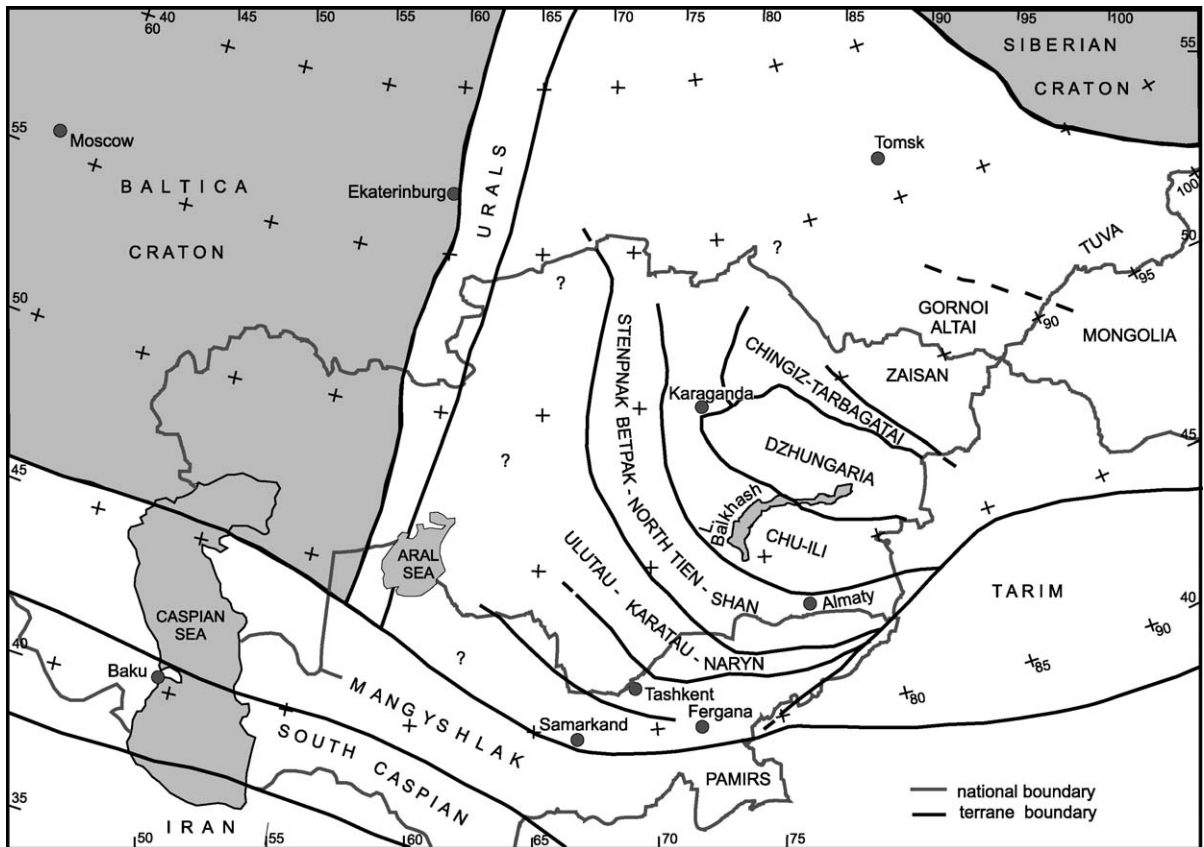
Fig. 13. New map of Central Asia today, showing the boundaries of the various terranes discussed in the text.

Baltica (Balashova, 1961 described Baltica trilobites at species level). The rest of Kazakhstan was not. Sengor et al. (1993) and Sengor and Natal'in (1996) proposed an Ordovician configuration for these Kazakh terranes as strung out in a huge arc, termed the Kipchak arc, (partly refigured here as Fig. 14) stretching from Baltica (their "Russian craton") to Siberia ("Angara craton") in the Ordovician. They postulated that this arc progressively collapsed and telescoped through the Silurian, and did not achieve its present configuration until the Carboniferous. Faunal evidence is obviously germane to establishing the original positions, individuality and developing histories of the Kazakh terranes. Many of them have a Precambrian continental core and might therefore be better regarded as microcontinents, but terrane terminology is customary. That said, the names applied to the terranes are confusing and in part contradictory in

the literature (compare Nikitin et al., 1991; Mossakovsky et al., 1994; Sengor and Natal'in, 1996; Holmer et al., 2001). Furthermore, the terrane boundaries are different according to these several authors.

In this review, we have adopted the nomenclature of Holmer et al. (2001) for south-east Kazakhstan simply because it is the latest (there is no guarantee it will be the last). However, we have extended our newly constructed map (Fig. 13) northwards of that portrayed by Holmer et al. to include northern Kazakh localities. Trilobite faunal lists are scattered, and we have also used data compiled by RAF on a visit to the collections in the Geological Institute, Almaty, made available through the kindness of the late Dr. Apollonov. Brachiopod data includes work in progress by LRMC and Popov. The evidence is considered in more detail below than elsewhere in this review, as it leads to new conclusions. Biofacies ranging from

shallow to deep are found within many of the terranes, which further complicates the biogeographic picture since the deeper water faunas are usually more widespread, and this seems to have led to some confusion. The modern boundaries of the chief Lower Palaeozoic terranes (but probably not all of them) are shown in Fig. 13, with the divisions of Kazakhstan largely following Nikitin et al. (1991). Tuva and Mongolia, although adjacent to the Kazakh terranes, are discussed under Siberia (Section 4.4). We review the most important terranes here, proceeding broadly from southwest to north-east.

6.4.1. Tien Shan

This terrane in the terminology of Holmer et al. (2001) includes the Malyi Karatau and Bolshoi Karatau of previous authors, although Malyi Karatau may have been a separate sea-mount. Sections spanning the Cambrian–Ordovician boundary in southern Kazakhstan have been described by Ergaliev (1983) yielding trilobites that compare exactly with older eastern Tien Shan collections of Troedsson (1937), which in turn are like those from more marginal facies belts in southwest China. Such genera as *Charchaqia*, *Promacropyge*, *Lophosaukia* and *Amzasskiella* are typical, along with species such as the agnostid *Lotagnostus trisectus* and *L. punctatus*. There are more widespread taxa among the pelagic agnostids, and among them deepwater biofacies olenids (*Plicatolina*, *Remizites*) and asaphids (*Niobella*), but these are biogeographically uniformative, except to note that oceanic environments existed SW of Bolshoi Karatau. Apollonov and Chugaeva (1983) described faunas from Malyi Karatau from limestones probably forming mounds over volcanics. These, too, are of dominantly warm-water East Gondwana type with dikelokephalinids, *Proteuloma*, *Troedssonia* (their *Platypeltoides*), *Asiocephalus*, *Saukiella* and *Lophosaukia*; their *Batyraspis* is also recognised in South China. Apollonov demonstrated some endemic trilobites to RAF from this region, which suggests a certain separation, but the evidence is strong at this time that Tien Shan lay close to South China. Claims by Holmer et al. (2001) that inarticulated brachiopods from the Tien Shan terrane are Baltic in character are likely to be the result of the fact that inarticulated genera are more widespread in their planktonic stage than articulated brachiopods, like agnostid trilobites, and the Chinese inarticulated faunas

are not yet well enough known to demonstrate their pandemicity. The only early Ordovician articulated brachiopod they record is *Clarkella*, which is also known from Laurentia and North China (Korea). However, in another paper, Holmer et al. (2000) record late Tremadoc and Arenig faunas of inarticulated organophosphatic brachiopods from Kyrgystan (and part of the South Tien Shan) as possessing Baltic affinities, but the local tectonics are difficult—the early Ordovician carbonates occur only as olistoliths within a Silurian tectonic melange, and thus their relationship to the main Tien Shan terrane must be treated with caution.The 18 articulated brachiopods of the Caradoc Obikalon Beds (Rozman, 1978) are also in the latter suspect terrane, but they are largely widespread genera, although *Ishimia* is known only elsewhere from Chu–Ili, Chingiz and Sibumasu (Cocks and Zhan, 1998), and the polytoechiid *Admixtella* is apparently entirely endemic, as might be the large strophomenoid which is incorrectly referred to *Gunnarella* by Rozman.

A small Tremadoc trilobite fauna from Kendyktas, which is definitely part of the true North Tien Shan terrane, described by Lisogor (1961) is of this widespread type, and it is worth outlining the details briefly as they show how such misapprehensions arise. *Harpides* is a distinctive harpidid originally described from Baltica—and if that were all that were known might be taken to indicate Baltic affinities. However, it is also known from Bohemia (northern Gondwana–Perunica), Argentina (S Gondwana) and western Newfoundand/Quebec (Laurentia), i.e. it is almost cosmopolitan and thus irrelevant to biogeographic reconstructions. Olenids, like agnostids (two poor ones in Lisogor, 1961), have already been noted as independent of biogeography except as indicating deep biofacies. The Kendyktas fauna includes an allegedly endemic olenid *Agalatus*, but this was probably a *Parabolinella* or *Bienvillia* (cosmopolitan). We may repeat the same argument for *Apatokephalus* and *Symphysurus* as for *Harpides*: the type species are Baltic, but they are known from all palaeocontinents. This leaves a balance of a few critical genera. Lisogor erected a genus *Bicornipyge*, which subsequently (Owens et al., 1982) was shown to be the same as an Avalonian (i.e. West Gondwana in the Tremadoc) genus *Dichelepyge*. This in turn is known from Tarim (Zhou and Chen, 1992, p. 114). Another ceratopygid genus *Hysterolenus* is familiar from localities in South

China and Tarim, but also Baltica. An asaphid ascribed by Lisogor to *Kaiseraspis* (sic.) is unidentifiable. Lisogor's '*Bathyurus* sp.' is not a bathyurid (which would be Laurentian in fingerprint), but—like her *Leiostegium* sp.—a leiostegiid, several genera of which are known from contemporary Chinese and Australian strata (but no similar genus is known from Baltica): it could belong to almost anyone. *Hystricurus* is pan-tropical (above). Such detail may be tedious to the non-specialist, but it is important. Despite the several genera in common with Baltica, in the context of widespread Tremadoc faunas only *Dichelepyge* and leiostegiids are significant (Gondwanan) and there is nothing in the fauna to contradict the South China/Tarim signal provided by younger Ordovician faunas.

From the supposed northwards extension of this terrane in NW Kazakhstan, RAF examined a Caradoc collection from the Andreyushenka Formation (Kupriyanovka Village on the River Ishim) which included widespread taxa such as *Nileus*, *Lonchodomas*, *Bronteopsis* and *Sphaerexochus* but also *Pliomerina*, *Koksorenus*, *Trigonoaspis* (= *Tangyaia* in China, also *Lisogorites* in Chu–Ili), *Ampyxinella*. These are definitive taxa for warm-water Gondwana of Chinese type, and indeed some species may be identical with those of Burma and South China. Again, an eastern peri-Gondwanan position is confirmed.

Close to the north-eastern terrane boundary at the Dzhalair–Najman Fault, the fauna of the Karakan Limestone in the Betpak Dala Desert is diverse, and in some respects puzzling. The locality and trilobite fauna was listed by Apollonov (in Nikitin, 1972, p. 54–55), but has only been described in a perfunctory way (Weber, 1948; Keller and Lisogor, 1954). It is probably of early Whiterockian (latest Arenig) age as it includes the pelagic trilobites *Carolinites* and *Telephina* and the graptolite *Pseudotrigonograptus*. The 'island' genus *Annamitella* (under the name *Bathyuriscops*, Keller and Lisogor, 1954) is also present. Examination of a large collection shows that otherwise the fauna is a typical "illaenid–cheirurid" cryptalgal mound biofacies, with a variety of Illaenidae (including the possibly endemic *Bumastides*), Cheiruridae and Pliomeridae, at least one of which is probably a new genus. The Kazakh endemic *Bulbaspis* was noted by Apollonov in Nikitin (1972). *Glaphurus*, *Ischyrophyma*, *Selenoharpes*, *Nanillaenus*, ?*Heliomera*, *Protostygina*, *Leiostegium*, *Cybelurus*,

Amphilichas and *Leiostegium*? have all been associated with mound faunas of Whiterockian (to Chazyan) age but so far mostly in North America, or adjacent terranes (e.g. Whittington, 1963; Adrain and Fortey, 1997). Popov (personal communication) regards the locality as perhaps part of a separate carbonate-topped sea mount. Our contention is that this fauna was much more widespread than previously appreciated in the appropriate circum-palaeoequator habitat, of which the Karakan fauna is a striking example. There are no faunas of this type in contemporary China. The endemic genera provide an indication of its separation from major palaeocontinents, but are in a minority. The other faunas in the terrane entirely rule out any suggestion that Tien Shan might be located close to Laurentia. The most remarkable feature confirming this is that 200 m away from the mound and stratigraphically above it (Apollonov, personal communication, 1998) there is a cyclopygid fauna with *Pricyclopyge* and *Illaenopsis*, both typical of deep water peri-Gondwana sites of Llanvirn age. Although using deeper water faunas can be ambiguous, neither of these genera is known from Baltica or Laurentia at this time.

Thus, we conclude that the Tien Shan Terrane, although most probably an independent terrane, was closer to East Gondwana than to any other large palaeocontinent throughout the Ordovician.

6.4.2. Chu–Ili terrane

This terrane lies north and east of the Tien Shan terrane today (Fig. 13). Trilobites from the Chu–Ili range were described by Chugaeva (1958). The Kopalin and Karakan formations, of probable Late Llanvirn age, represent a somewhat deeper water Nileid biofacies including widespread genera such as *Ampyx*, *Nileus* and *Symphysurus*, but also the genus *Lisogorites* of Chugaeva, which is certainly the same as the genus *Tangyaia* in China, and Chugaeva's "*Ampyxina*" *biloba* is the genus *Ampyxinella* which is also known from Tarim, as is the peculiar *Bulbaspis*. Kolobova (1985) described the characteristic Tarim endemic *Taklamakania* from this area. Hence, the South Chinese affinities are strong even in the deeper facies. However, many of the brachiopods from the richly fossiliferous (more than 20 inarticulated and 30 articulated genera) Uzunbulak Formation (Popov, personal communication), and also of Llan-

virn age, appear to have more in common with Laurentia (plectambonitoids: *Apatomorpha*, *Aportho-phyla*, *Taphrodonta*, *Leptellina*, *Toquimia*), although there are also at least seven undescribed endemic genera of varying superfamilies, and several characteristic peri-Gondwanan forms such as the pentameride *Yangzteella*, all together indicating both low latitudes and links with a variety of terranes. The richest sites are in the Caradoc Anderken Formation, which includes a number of characteristic East Gondwanan endemic trilobites; here *Ogygites almatyensis* is without question a *Birmanites* species; *Pliomerina* is abundant, which, as noted by Webby (1971), is typical of East Gondwana. Raphiophorids are also of Chinese type. Apollonov (1974, p. 65) also records the typically Chinese–Sibumasu genus *Ovalocephalus* from the Anderken. Other trilobite genera are mostly widespread, or are difficult to correctly assign generically (e.g. the asaphid *Isotelus* is probably not that genus, but without further details it is not possible to say exactly which). There are two near-endemics (*Dulanaspis*, and a blind styginid), the former known also from Tarim, China. The Anderken brachiopods are also richly diverse—Popov et al. (2002) have described 62 species within 55 genera and defined six recurrent associations ranging from shallow- to relatively deep-water assemblages. The biogeographic message is mixed—overall there is most similarity between the Anderken and the beds described from North China by Fu (1982), but genera such as *Mabella*, *Dulankarella* and *Teratelasmella* are known only from the Chu–Ili and Chingiz terranes and from the south-east Australian island arcs, and again there are seven endemics (the plectambonitoids *Olgambonites*, *Sortanella*, *Tesikella*, *Zhilgyzambonites*; the spire-bearers *Ilistrophina*, *Nikolaispira*, *Pectenospira*). RAF has examined a trilobite collection from the overlying Dulankara Formation (Late Caradoc–Ashgill), the distinctive elements of which are again Chinese, including the distinctive pliomerid *Parahawleia* (originally named in Lu et al., 1976), *Ovalocephalus* and probably the encrinurid *Koksorenus*. Brachiopods from the Dulankara are partly published (Popov et al., 2000) and partly under revision by Popov and LRMC. Three associations are recognised in the shallower water Otar Member in the middle of the formation, with 21 genera of brachiopod, including two endemics (*Bokotorthis*, *Karomena*). The

fauna is closest to that from South China, but includes two genera (*Phaceloorthis*, *Dulankarella*) yet again only known elsewhere from the island arcs now part of south-east Australia.

A late Caradoc bioherm from the Betpak Dala Desert examined by RAF includes another Illaenid–cheirurid fauna: cheirurids—*Sphaerexochus*, *Hadromeros*; illaenids—varied, but not determined; "isocolids"—*Cyphoniscus* and *Kielanella*; glaphurids—*Glaphurus* and *Glaphurina*; the holotrachelid *Holotrachelus*; the Gondwanan endemic *Pliomerina*. Some of these genera are widespread in the Ashgill in the same biofacies. Overall, this fauna is similar to an undescribed fauna from Iran. From the same locality Nikitin and Popov (1996) and Nikitin et al. (1966) described a rich brachiopod fauna of 23 genera, with the atrypoids *Kellerella* and *Nikolaispira* and the plectambonitoids *Bandaleta* and *Sortanella* endemic to the Chu–Ili terrane (three are also known from the neighbouring Anderken Formation—Popov et al., 2002).

Apollonov (1974) reviewed Ashgill trilobite faunas. A number of deeper water cyclopygids are not informative, and others, such as *Mucronaspis mucronata*, are virtually pandemic associates of the end-Ordovician glaciation. However, his identification of individual Chinese species, such as *Platycoryphe sinensis* Lu, from Chu–Ili is significant even at a time of more generally widespread taxa. Fortey (1997) has noted the similarity of proetids from these faunas to those of Thailand and China. Apollonov reported *Ovalocephalus* from the Ashgill of Chu–Ili; by then it is more widespread than earlier in the Ordovician. Apollonov et al. (1980) reviewed faunas from near the Ordovician–Silurian boundary in this terrane, but apart from an unusually diverse expression of the *Hirnantia* brachiopod fauna, there are few key taxa to shed light on palaeogeography. In the same volume, Rukavishnikova described the single endemic brachiopod *Iliella* as an early spiriferoid from the mid-Ashgill Chokpar Horizon; however, it is now known to be an athyridoid.

The Stepnyak area of northern Kazakhstan has been regarded as a northward continuation of the Chu–Ili terrane by Nikitin et al. (1991), but not, apparently, by Holmer et al. (2001), but we provisionally include it here. The trilobite faunas of the Caradoc sequence are attributed to similar formations

as in more southerly regions of the Chu–Ili terrane, as summarized by Koroleva (1982), who has described many of the trilobites. Although deeper water biofacies, with widespread agnostids and cyclopygid faunas, tend to dominate in this area, virtually the same comments apply as regards the Chinese affinities of those that are more restricted, and further discussion here would repeat that given previously. This area is the type for the genera *Ovalocephalus* and *Koksor-*

enus, for example, and *Trigonoaspis* Koroleva is yet another synonym of the distinctive and relatively restricted Chinese asaphid *Tangyaia*.

Thus, overall the Chu Ili terrane also carries a warm-water Gondwana signature throughout the Ordovician, with strong South Chinese similarities, and also links with North China, Tarim and the southeast Australian arc faunas. In the Silurian rocks, the brachiopods and trilobites found essentially comprise
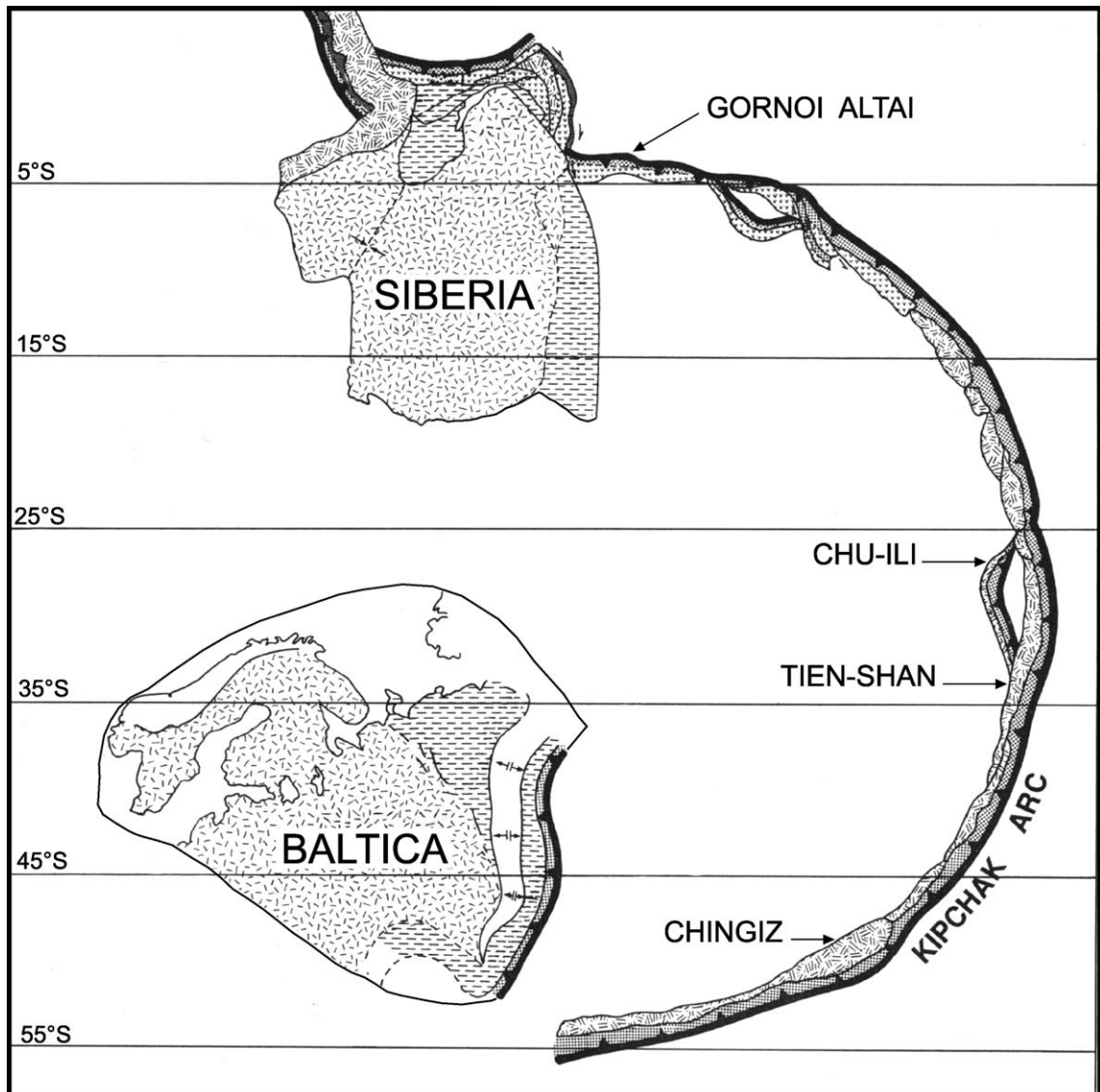

Fig. 14. Palaeogeography of central Asia, showing the Kipchak Arc in Middle Ordovician (458 Ma) times, adapted from Sengor and Natal'in (1996, fig. 21.31), and showing the positions of the Chingiz, Chu–Ili, Gornoi Altai and Tien–Shan Terranes discussed in the text.

part of the very widespread and nearly global cosmopolitan fauna, although some apparently endemic species (not genera) which have been erected require further revision in a global context.

6.4.3. Chingiz–Tarbagatai and Mamat terranes

North-eastern Kazakhstan includes a large terrane (possibly composite) dominated by volcanics and clastics in the Chingiz and Tarabagatai ranges. Trilobite faunas are largely not yet formally described, but RAF has examined extensive collections made by Apollonov. Earlier Caradoc faunas from Karagash Village include a deep-water trilobite fauna with *Dionide*, *Shumardia* (*Shumardella*), *Raphiophorus*, *Oedicybele*, *Eodindymene* and cyclopygids (*Microoparia*, *Cyclopyge*) which is of widespread type, i.e. not diagnostic biogeographically, although it is worth noting that the most similar contemporary faunas are from Perunica (Bohemia), and not from Baltica.

In Chingiz, in the Bestamak Formation at Chagan river (Nikitin, 1972) immediately below the *Nemagraptus gracilis* Zone and thus late Llanvirn in age, the peculiar raphiophorid *Taklamakania* is so prolific as to be a rock former (note that this genus was described under the name *Caganaspis* from this region by Kolobova, 1985). Its associated genus from Tarim *Nanshanaspis* is also present, together with *Dionide*, *Manykaia*, *Birmanites*, *Selenopeltis* and several proetids. All except *Dionide*, which is pandemic, are Chinese (and Tarim) and only *Selenopeltis* is Gondwana-wide (but not outside). From the same formation Klenina et al. (1984) have listed or described 11 inarticulated brachiopods, including the endemics *Ussunia*, the only member of its family, and *Ovidiella*, both of which are among the earliest trimerelloids, and *Nushbiella*, which is only known elsewhere from the Chu–Ili Terrane. There are 22 articulated brachiopods, none of which are narrowly endemic to this terrane apart from the form referred to *Oligorhyncha* which is the subsequently recognised atrypoid *Rozmanospira* of Popov et al. (2000), but *Shlyginia* is known only elsewhere from the Tien Shan and Chu–Ili terranes, *Kajnaria* only from Chu–Ili, the strophomenoid *Esilia* only from Tien Shan, *Ishimia* from Tien Shan and Sibumasu, and *Chaganella* only from New South Wales, Australia, where it was described as *Tylambonites* by Percival (1991). Of the 21 articulated brachiopods from the overlying late Caradoc Taldeboy

Formation, most are relatively cosmopolitan genera, although *Mabella* is only elsewhere known from Chu–Ili and New South Wales. The allegedly endemic atrypoid *Kuzgunia* of Klenina et al. (1984) is probably a synonym of *Shachriomena* (Popov et al., 2000), which in turn is probably the same as the North and South China *Ovalospira* Fu (1982) revised by Zhan and Cocks (1998).

Once again, the evidence supports the Chingiz–Tarbagatai terrane as close to other peri-Gondwanan terranes such as South China, by the Caradoc at least. We do not have good evidence of the earlier Ordovician history and the Cambrian is not the prime concern of this paper. However, from the Selety area, and the Olenty Shiderty area, which may be the northwestwards extension of the Chingiz Terrane, Ivshin (1956) has reported numerous later Cambrian trilobite faunas from tropical carbonates which apparently compare with those of Siberia, rather than China.

Immediately south of the Chingiz terrane, the Mamat area may be a separate area tectonically. The succession of the Mamat Formation of Mamat Mountain spans the lower part of the Ordovician (RAF observations). A probable early Tremadoc trilobite fauna includes *Hystricurus*, *Leiostegium*, *Onchonotellus*, *Nayaya* and ?*Lopeuloma*. This is of interest because the last two named are Siberian platform endemics (Rozova, 1964); one species RAF identified with *Bienvillia tetragonalis* Brøgger, from Norway. From the Upper Tremadoc a small fauna included *Ceratopyge forficula*, ''*Protopliomerops*'' *speciosa* and a *Niobe* species of Scandinavian type. Although the fauna is small, the specific identity of the species does imply a close comparison with Baltica.

6.4.4. Altai–Sayan terrane

The brachiopods in the Gornyi Altai region have been monographed by Severgina and her colleagues in a series of papers (for example, Severgina, 1984; Kulkov and Severgina, 1989). From the Tremadoc Tayanzin Horizon she recovered *Apheoorthis*, *Finkelnbergia*, *Nanorthis*, *Nothorthis*, *Punctolira* and *Syntrophina*, all of which occur in Laurentia and Siberia and in some cases elsewhere, but also the endemic billingselloid *Kozuchinella* and *Akelina*, which may be the oldest member of the superfamily Plectambonitoidea (Cocks and Rong, 1989). Above

this the Arenig Lebed Horizon yielded the widespread *Archaeorthis*, *Diparelasma*, *Finkelnbegia*, *Hesperonomia*, *Nanorthis* and *Tritoechia*, but also the endemic *Akelina* again, the orthoid *Lebediorthis* and also *Rhyselasma* (only known elsewhere from Siberia) and *Ujukites*, only known elsewhere from Tuva, also near the margins of Siberia (Fig. 13). Above this again the early Llanvirn Rydinkov Horizon yielded the relatively cosmopolitan *Archaeorthis*, *Atelelasma*, *Glyptomena*, *Idiostrophia*, *Isophragma*, *Orthidium*, *Plectocamara* and *Trondorthis*, together with the endemic syntrophioid *Talovia*. These early to mid-Ordovician occurrences all add up to a low-latitude series of faunas which have much in common with those from Siberia and to some extent Laurentia, but to a much lesser extent with East Gondwana. However, the many endemic brachiopods present in the Gornoi Altai indicate that the Altai−Sayan terrane was probably some way away from any contemporary large palaeocontinent. In contrast, papers in the volume edited by Sokolov and Yolkin (1978) described the palaeontology of Altai Sayan in the later Ordovician−Silurian interval, and in the Caradoc trilobites the Gondwanan platform signature is strong, with calymenoids *Neseuretinus*, *Prionocheilus*, *Vietnamia* and *Calymenia*, the Dalmanitoidean *Dalmanitina* and the trinucleid *Broeggerolithus*. They are accompanied by more than 30 brachiopod genera in the Caradoc Khankarin Formation (Kulkov and Severgina, 1989) in which there are no new endemics, together indicating progressive nearing of the Altai−Sayan terrane to other low-latitude continents.

6.4.5. Summary of Kazakhstan and adjacent terranes

The evidence is sufficient to falsify the model of Sengor and Natal'in (1996). At least in the later Ordovician it is clear from the Sino-Australian signature of key trilobites and brachiopods that the terranes of the Kipchak Arc were all peri-Gondwanan and not stretched between Baltica and Siberia, as portrayed in their reconstructions. Given the close identity of the Caradoc faunas to those of Tarim, it is likely that there was close proximity with that region. The identity of *Taklamakania* limestones is a case in point. This strange trilobite cannot be confused with any other, so there is no question of muddled taxonomy (although there are plenty of synonyms because of separate taxonomic studies in China and

Kazakhstan, as we have noticed). It seems possible to us that the terranes were distributed alongside Gondwana rather than progressively away from it, or we might expect more differences from the more distant faunas than there actually are.

For the earlier history there are more questions. The control on the earlier Ordovician is not so good, but sufficient to suggest that Tien Shan, Chingiz and Chu−Ili may have been peri-Gondwanan throughout their Ordovician history: the alleged Tremadoc "Baltic" signal is weak, apart from the isolated Mamat Formation fauna (Section 6.4.3). However, for the Altai−Sayan terrane a case might be made for its rapid transport from rifting off Siberia, perhaps in the late Cambrian or early Tremadoc, and moving via temperate palaeolatitudes in the late Tremadoc to attain a final peri-Gondwanan position in Caradoc times. We provide here (Fig. 15) a new palaeogeographical reconstruction for those Kazakh terranes which we have considered above, with the faunal considerations taken into account. In the early Ordovician the four terranes were probably also in the same relative positions as in the Caradoc, but by Ordovician−Silurian boundary times they would have drifted across the palaeoequator into the northern hemisphere.

6.5. New South Wales

To the south-east of Australia, Ordovician faunas are known from two main areas; Tasmania (Corbett and Banks, 1974; Jell and Stait, 1985), which was probably at the margin of core Gondwana (Section 4.2. and Fig. 8 above), and various parts of New South Wales and Victoria (Jell, 1985), formerly termed a "geosynclinal" area. The latter is now known to represent one or more volcanic island arcs (Percival and Webby, 1996), which accreted to the main Australian part of the Gondwanan craton in the late Palaeozoic. Wright et al. (2000) have reviewed the faunas, which are now well known from several sites and horizons, especially from the middle Ordovician. Brachiopods were monographed by Percival (1991): some endemics are known (*Quondongia*, *Molongcola*, *Webbyspira*, *Australospira*), but other genera previously thought endemic [*Tylambonites* (=*Chaganella*), *Wiradjuriella* (=*Mabella*), *Bowanorthis* and *Phaceloorthis* (=*Boonderella*)] are now also known from Kazakhstan (Popov et al., 2002); *Para-*
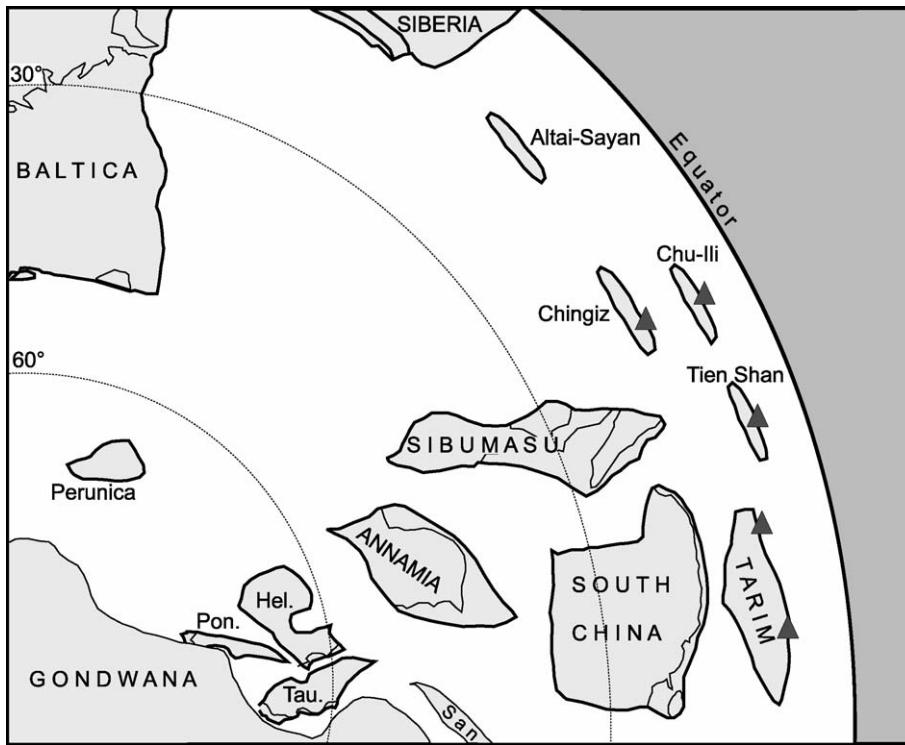
Fig. 15. Our new reconstruction for the Caradoc positions of the Chingiz, Chu–Ili, Altai–Sayan and Tien–Shan Terranes, with base-map of 460 Ma modified from Cocks and Torsvik (2002), but with Sibumasu, Annamia, Tarim and South China moved along palaeolatitude to the east, and with the Chingiz, Altai–Sayan, Tien Shan and Chu–Ili terranes added.

onychoplecia is more cosmopolitan and *Shlyginia* known from both Kazakhstan and Burma (Cocks and Zhan, 1998). Particularly striking in the New South Wales faunas are the shallow-water trimerellide reefs, largely made up of *Eodinobolus*, the earliest such development anywhere, but whose palaeogeographical significance is not clear apart from the fact that were laid down in the tropics. The overall faunal signals reinforce the common identity of New South Wales, Sibumasu and Chu–Ili as terranes fringing Ordovician Gondwana at relatively low latitudes.

6.6. Famanitina

Sandwiched between the Precordillera (Section 5.2) and the main core of Gondwana (there termed the Central Andean Basin), and which includes most of the southern part of today's South America (Section 4.2.3), lies the Famanitina terrane. This is now known to represent an Ordovician island arc (Astini et al., 1995). Only Tremadoc and Arenig age beds yield fossils, but from these Benedetto (1998) has recorded faunas different from those in either the Precordillera (which carries Laurentian faunas) or the Central Andean Basin of intermediate-latitude Gondwana. The Arenig of Famanitina yields the endemic brachiopod *Famatinorthis* and genera such as *Monorthis* and *Fynnonia*, known elsewhere only from peri-Gondwanan islands (and in the latter case only from Anglesey, Wales). However, the typical Gondwanan trilobite *Neseuretus* also occurs, as well as *Merlinia*, *Illaenopsis*, *Hungioides* and *Gogoella*, in addition to the endemics *Famatinolithus* and *Pliomeridius* (Vaccari et al., 1993). All this suggests that in the early Ordovician the Famanitina arc lay not too far outboard from Gondwana at intermediate palaeolatitudes and not so far from the part of core Gondwana with which it later docked at about end Ordovician time.

7. Conclusions

Our review shows that detailed evidence from fossils has been, and continues to be, useful in discriminating Lower Palaeozoic palaeogeographic entities and in suggesting their relationships one to another (Figs. 16 and 17). The data provided by the fossils of shelf benthic groups—trilobites, brachiopods, bivalves and ostracodes in particular—has provided configurations of continents and terranes which have stood the test of time, reinforced as additional palaeomagnetic evidence has accrued. Historically, suggestions made from faunal "fixes" have often preceded other lines of evidence, and a measure of the success of the palaeontological approach is indicated when subsequent field, geophysical or palaeomagnetic evidence
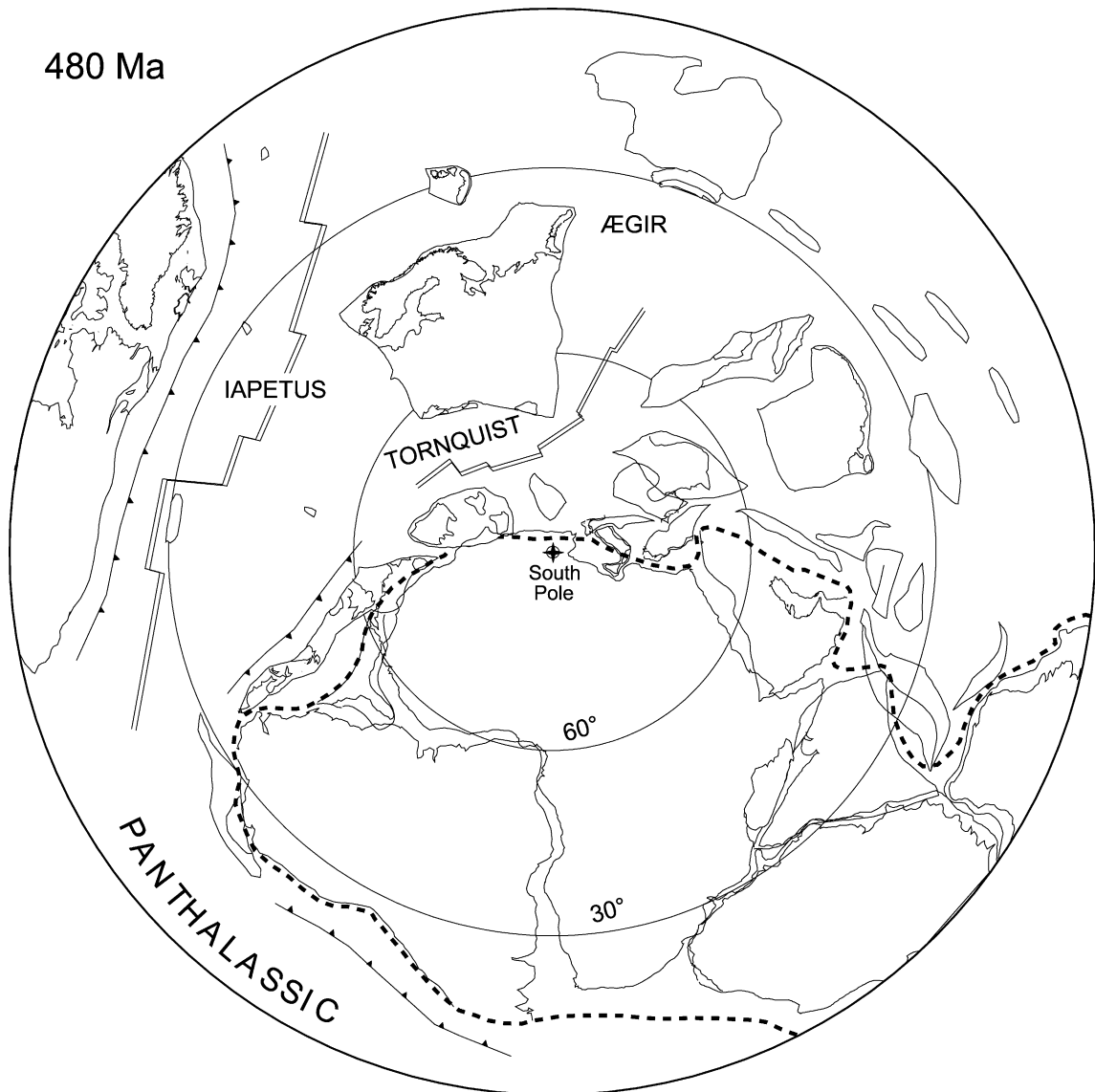

Fig. 16. Global reconstruction in early Ordovician (480 Ma) time, modified from Cocks and Torsvik (2002, fig. 4), and with the Chingiz, Chu–Ili, Gornoi Altai and Tien Shan terranes added as in Fig. 15. North China was in the northern hemisphere and is thus absent.
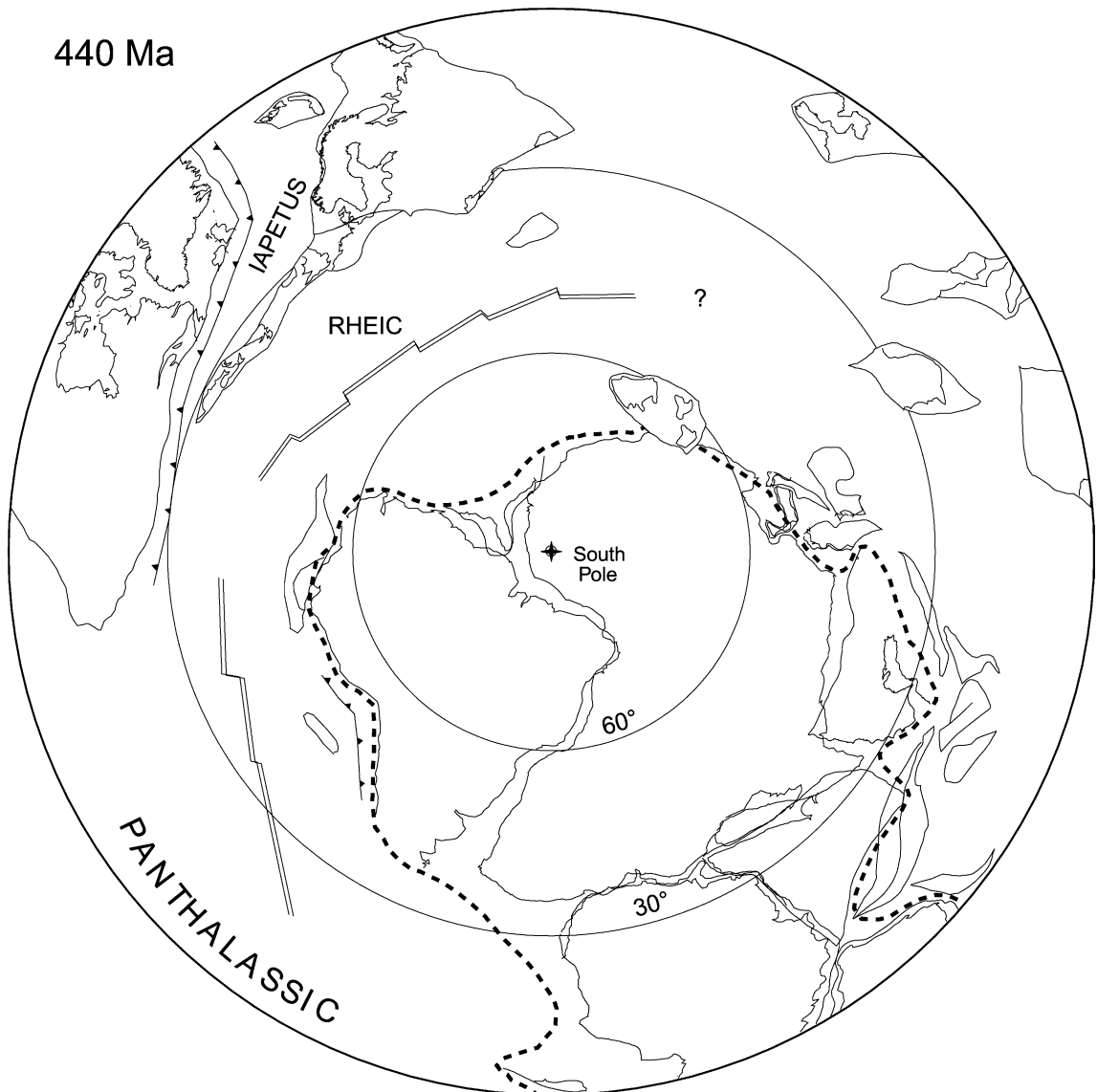
Fig. 17. Global reconstruction at end Ordovician and early Silurian (440 Ma) times, modified from Cocks and Torsvik (2002, fig. 6). Siberia and the Kazakh terranes were in the northern hemisphere at that time and are thus absent from this figure.

confirms the initial hypothesis. The suggestion of a separation of Avalonia from Baltica in the earlier Ordovician first appeared in Whittington and Hughes (1972) and was put on a firmer footing when "Tornquist's Sea" was named, and its extent postulated, by Cocks and Fortey (1982). In the 20 years that followed, its reality has been confirmed by (among other things) deep geophysics recognising the buried

suture, the identification of buried granites and other appropriate rocks connnected with closure, and finer discrimination of marginal terranes. Thus, faunal evidence may lead the way in suggesting hypotheses that can be tested in other fields. However, the fact that Pickering and Smith (1995) could apparently overlook such evidence means that it is continually necessary for palaeontology to reiterate and refine

the basis on which palaeogeographic assignments have been made.

Unfortunately, quantitative methods based upon large databases of fossils are not yet generally applied to palaeogeographic problems, although the methodology is now available (e.g. Lees et al., 2002), from which it is clear that evidence from several fossil groups taken together leads to the best results. Instead, comparisons of the fauna of a terrane in question (for example) is based upon its (subjectively judged) similarity or otherwise to those of contending major palaeocontinents for which faunas are well known. This does lead to defensible results, because palaeocontinents have such distinctive faunal signatures (especially in the Ordovician), and certain critical groups of trilobites and brachiopods are significant indicators of shared endemism. This is clear from the use, for example, of asaphid and trinucleid trilobites in the discussions above. For this reason, we have perforce identified critical faunal elements used in placing controversial terranes relative to the major palaeocontinents. It is encouraging that brachiopods and trilobites so often yield the same "answer". We consider it likely that future application of quantitative methods will further improve the fine tuning of these results, but it would be surprising if they were substantially overturned. One of the interesting conclusions is that the various terranes which today make up Kazakhstan were outboard of greater Gondwana in the Ordovician (Fig. 15), rather than strung out in the hypothetical Kipchak Arc postulated as extending between Baltica and Siberia (Fig. 14). This model clearly has suggestions which should be taken up and tested by geomagneticists and structural geologists.

Fossils may also successfully arbitrate between competing hypotheses. A persuasive example is the suggestion that the Precordillera of Argentina was originally a terrane that separated from Laurentia and eventually docked with Gondwana. Evidence from faunas is quite unequivocal in support of this idea (Astini et al., 1995; Benedetto, 1998) and serves to disprove other theories that place Laurentia and South America in close proximity in the Ordovician (Dalziel et al., 1994).

Where misinterpretations of the meaning of Lower Palaeozoic faunal distribution have occurred, and we identify several cases, this is often because of the different 'signal' provided by planktic, as opposed to benthic organisms. The former (graptolites, acritarchs) are most useful in identifying former latitudinal belts, and hence climatic oscillations, and can be thoroughly complementary to benthic organisms; they do not, however, necessarily provide the best geographic fixes. However, recent work on acritarchs indicates that they, too, may include useful endemic elements, so one must not prejudge what will prove to be useful in future. Deeper water benthic biofacies are also, in general, more geographically widespread, and hence less critical indicators of geographic affinity, but they do have their use in the recognition of continental margins (e.g. Fortey and Cocks, 1986). Biofacies profiles are now known for all the major palaeocontinents in the Ordovician and Silurian, and it should be possible readily to eliminate this element of local palaeogeography from the wider issues of geographical location on a global scale.

Our survey has been necessarily brief, with no pretence of completeness, but shows that fossils are amongst the best tools available for determining the individuality and positioning of old terranes, large and small. In addition to the qualitative presence/absence criteria used in the past, new quantitative treatments of total faunas may provide even more objective results. It is good that fossils provide a completely independent data set from the study of palaeomagnetics. When the two disciplines produce the same answers, then our confidence is much increased: when the two differ, this provides a clear agenda for future research.

Acknowledgements

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