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The spatial and temporal diversification of Early Palaeozoic vertebrates

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Abstract: Recent discoveries have dramatically altered traditional views of the stratigraphic distribution and phylogeny of Early Palaeozoic vertebrates and permit a reappraisal of biogeographic patterns and processes over the first 120 million years of vertebrate evolution. Stratigraphic calibration of the phylogenetic trees indicates that most of the pre-Silurian record can be inferred only through ghost ranges. Assessment of the available data suggests that this is due to a shift in ecological niches after the latest Ordovician extinction event and a broadening of geographical range following the amalgamation of Euramerica during the early Silurian. Two major patterns are apparent in the biogeographic data. Firstly, the majority of jawless fishes with dermoskeletal, plated 'armour' were highly endemic during Cambrian–Ordovician time, with arandaspids restricted to Gondwana, galeaspids to China, and anatolepids, astraspids and, possibly, heterostracans confined to Laurentia. These Laurentian groups began to disperse to other continental blocks as the 'Old Red Sandstone continent' amalgamated through a series of tectonic collisions. The second major pattern, in contrast, encompasses a number of microsquamous and naked, jawed and jawless primitive vertebrates such as conodonts, thelodonts, placoderms, chondrichthyans and acanthodians, which dispersed rapidly and crossed oceanic barriers to attain cosmopolitan distributions, although many have Laurentian origins. A clear difference in dispersal potential exists between these two types of fishes. Overall, the development of biogeographic patterns in Early Palaeozoic vertebrates involved a complex interaction of dispersal, vicariance and tectonic convergence.

Elliott *et al.* (1991) reviewed pre-Silurian vertebrates, concluding that only six Ordovician genera could be recognized unequivocally, and that none of the reports of Cambrian taxa were sustainable on available evidence. The oldest vertebrates were considered to be *Arandaspis* and the poorly known taxon *Porophoraspis* from the early Llanvirn Stairway Sandstone of central Australia (Ritchie & Gilbert-Tomlinson 1977). In addition, *Sacabambaspis* had been described from the Caradoc of Bolivia by Gagnier *et al.* (1986) and was considered to be closely related to *Arandaspis* (Gagnier *et al.* 1986; Elliott *et al.* 1991). The most diverse vertebrate fauna was thought to be that from the Harding Sandstone (Caradoc) of Colorado, USA, which had been the first locality to yield pre-Silurian vertebrates. Walcott (1892) described three species of fishes from the Harding Sandstone: *Astraspis desiderata*, *Eriptychius americanus* and *Dictyorhabdus priscus*. The last is not now considered to be a vertebrate, although its affinities remain obscure (Sansom *et al.* 2001). A third vertebrate taxon was, however, known from the unit (Denison 1967; Smith 1991) and was subsequently described as *Skiichthys halsteadi* by Smith & Sansom (1997). Of these taxa, only *Astraspis*,

Arandaspis and *Sacabambaspis* were reliably understood in terms of their anatomy and, in phylogenetic terms, Elliott *et al.* (1991) considered *Astraspis* to be the most derived, with *Arandaspis* + *Sacabambaspis* as a sister taxon.

The biogeography of *Astraspis*, *Arandaspis* and *Sacabambaspis* was examined by Elliott *et al.* (1991) in the light of both dispersal and vicariance models. Their dispersal model interpreted the spatial and temporal data rather literally in biogeographic terms, invoking a dispersal route from the older, Australian, locality across Gondwana to Bolivia and thence across an oceanic barrier to Laurentia, amounting to what might be termed an 'out of Gondwana' model. It was recognized that the final trans-oceanic migration was an obstacle to a dispersal model given the apparent shallow-water ecological specialism of these fishes, but it was also noted that a vicariant model was not supported, and that both were in conflict with the palaeocontinental reconstructions of Scotese (1986) and Scotese & McKerrow (1990).

Since the review of Elliott *et al.* (1991), there has been a dramatic increase in the quality of the fossil record of Early Palaeozoic vertebrates which has arisen both through the discovery of

a

b

c
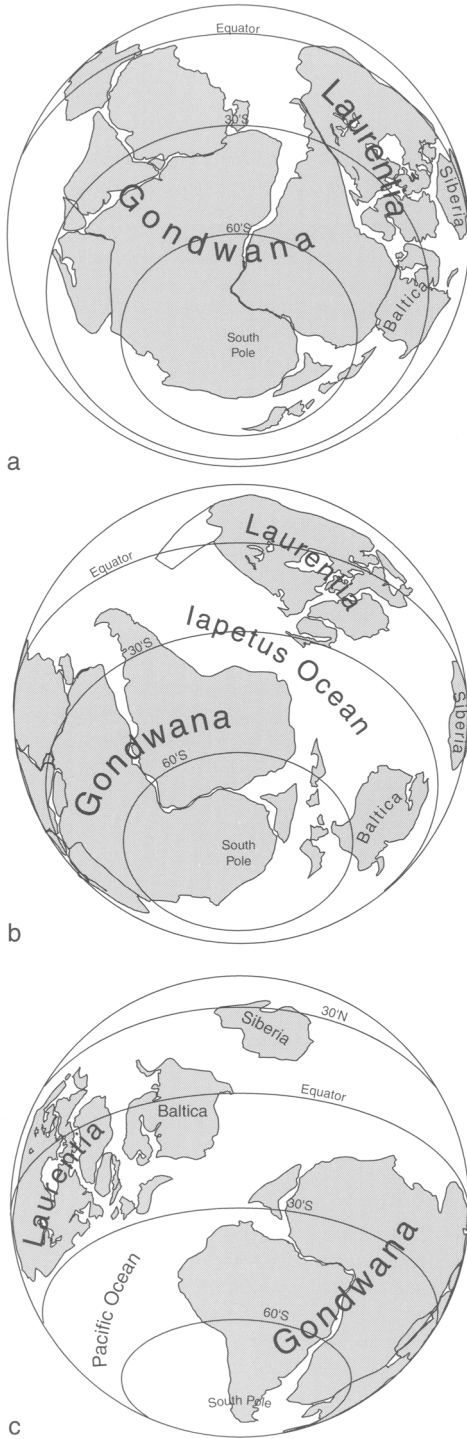
Fig. 1. Palaeogeographic reconstructions. (**a**) Base of Cambrian; (**b**) mid-Ordovician; (**c**) Wenlock. Based on Dalziel (1997).

new faunas and from reappraisals of affinity in well-known faunas. These advances have included the discovery of probable Early Cambrian vertebrates in the Chengjiang Lager-stätte (Shu *et al.* 1999*a*), the recognition of possible vertebrates in the Middle Cambrian Burgess Shale Lagerstätte of British Columbia (Simonetta & Insom 1993; Smith *et al.* 2001), the confirmation of the Late Cambrian–Early Ordovician sclerite *Anatolepis* as a vertebrate (Smith *et al.* 1996, 2001) and the discovery of unanticipated diversity in the Harding Sand-stone of Colorado (Smith *et al.* 1995; Sansom *et al.* 1995, 1996, 2001). Perhaps the most signifi-cant discovery in terms of the biodiversity and geographical range of early vertebrates has been the addition of conodonts to the clade. The presence of preserved soft tissues had already suggested to Aldridge *et al.* (1986) that the affinities of this highly diverse group lay with the vertebrates, and a wealth of new data has now been advanced in support of the hypothesis. These include additional soft tissue finds (Smith *et al.* 1987; Aldridge *et al.* 1993; Gabbott *et al.* 1995), the recognition of vertebrate hard tissue synapomorphies in conodont elements (Sansom *et al.* 1992, 1994; Sansom 1996; Donoghue 1998; Donoghue & Aldridge 2001) and detailed cladistic analysis (Donoghue *et al.* 2000). The inclusion of conodonts as the earliest vertebrates to possess a mineralized skeleton, more derived than either hagfishes or lampreys, increases the generic and specific biodiversity of Cambro-Ordovician vertebrates by two orders of magnitude.

Does the substantial amount of new data acquired subsequent to the review of Elliott *et al.* (1991) permit more detailed and better supported models of Early Palaeozoic vertebrate biogeography?

Early Palaeozoic palaeogeography

The determination of biogeographic trends in Early Palaeozoic vertebrates is highly depen-dent on the accuracy, and choice, of palaeo-continental reconstructions. For Cambrian–Ordovician vertebrates, this is particularly true of the relative positions of Laurentia, Australia and South America, whereas constraints on the timing of collisions that assembled the 'Old Red Sandstone (ORS) continent' are critical for interpretations of Silurian–Devonian bio-geography. To avoid circularity, we have used palaeocontinental reconstructions constructed from palaeomagnetic and tectonic data, and have eschewed those that already incorporate faunal data (e.g. Scotese & McKerrow 1990).

Traditionally, the Iapetan margin of southern Laurentia has been reconstructed as the conjugate margin of NW Africa prior to the opening of Iapetus, following the early reconstructions of Wilson (1966) and an implicit acceptance of an 'accordian style' opening and closure model (Dalziel 1997). However, the evidence for pre-Iapetan juxtaposition of the Laurentian and West African cratons is not strong and evidence has accumulated in favour of a radical alternative which arose out of the 'SWEAT' hypothesis of Moores (1991). Independently, Dalziel (1991) and Hoffman (1991) suggested that, prior to the opening of Iapetus and the final break-up of the Neoproterozoic supercontinent Rodinia, Laurentia was located between East Antarctica–Australia (East Gondwana) and South America (West Gondwana) (Fig. 1a). Following rifting, Laurentia was considered to have followed a clockwise rotating path around the conjoined South American and West African cratons (Dalziel 1991, 1997). Strong supporting evidence comes from the similarities between the fauna, stratigraphy and geological structure of SW USA and the Argentinean Precordillera (Dalla Salda et al. 1992; Astini et al. 1995; Thomas & Astini 1996) and there is now general agreement that the latter terrane originated as part of the Laurentian craton, located within the Ouachita embayment. Opinion differs, however, on the way in which the terrane was decoupled from Laurentia and attached to South America. Dalziel (1997) suggested that it originated as a promontory of Falkland–Malvinas Plateau type whereas Astini et al. (1995) favoured a rifted microcontinent that detached from Laurentia, drifted across Iapetus and collided with the South American margin. This has some relevance to early vertebrate biogeography, as discussed below, but in both cases the conjugate nature of the SE Laurentian and South American margins is implicit. The reconstructions of Dalziel (1997) are used as the basis for our assessments of Early Palaeozoic palaeobiogeography (Fig. 1a–c), although we recognize that not all details of these are universally accepted.

With regard to the assembly of the ORS continent, evidence has mounted to the point where a reasonably well-constrained and consistent model is available. The earliest collisions are of island arcs, with successive terrane accretion events (see van Staal et al. (1998) and Armstrong & Owen (2001) for reviews) serving as a prelude to the assembly of Avalonia, Baltica and Laurentia in mid-Silurian time. On the NE margin of Laurentia, early arc collisions are absent, and the first major assembly event was the collision with Baltica (Elevold et al. 2000). On the basis of palaeomagnetic data and kinematic indicators, it has long been recognized that this collision was oblique to the margins, with a sinistral component. Despite this obliquity, the collision is remarkably synchronous along the entire 2000 km length of this sector of the Caledonides. In NW Scotland, mylonites in the Moine thrust zone were dated by Freeman et al. (1998) as 437–430 Ma (Llandovery) and brittle deformation extends from 430 to 408 Ma (latest Llandovery–earliest Devonian). In comparison, prograde metamorphism in East Greenland has been dated at 435–423 Ma with anatexis at 430–422 Ma (Elevold et al. 2000; Hartz et al. 2001) and in eastern North Greenland, late thrusts truncate earliest Wenlock (425 Ma) foreland basin turbidites (Higgins et al. 2001).

The closure of the Tornquist Sea, between Avalonia and Baltica, probably began in the latest Ordovician by dextral 'soft' amalgamation of the two plates (McKerrow et al. 1991, 2000; Torsvik et al. 1996). Palaeomagnetic data confirm that the sector of Iapetus between Avalonia and Laurentia was also closed, within the limits of palaeomagnetic resolution, by the Wenlock (Mac Niocaill 2000). The location of Siberia during this interval is more open to question. There is good evidence that Siberia was geographically inverted with respect to modern coordinates during the Early Palaeozoic (Torsvik et al. 1995, 1996; Smethurst et al. 1998) and drifted northwards, apparently in tandem with Euramerica (= Laurentia + Baltica + Avalonia) (Smethurst et al. 1998). Rotation of Siberia and collision with Baltica occurred between 360 Ma (earliest Carboniferous) and 250 Ma (end-Permian) (Smethurst et al. 1998), and McKerrow et al. (1991) interpreted Siberia as having an almost juxtaposed relationship with Euramerica during Silurian–Early Devonian time. There is no evidence for collision but there may not have been a significant oceanic barrier separating Novaya Zemlya and the northern Siberian margin. Cocks (2001, p. 199) noted that shelly taxa were mainly endemic at species level, with some endemic genera, indicating that the palaeocontinent was 'not particularly isolated during much of the period'. An additional, and key, component of Siberia from the standpoint of vertebrate biogeography is the terrane of Tuva (Young 1991, 1993), which had amalgamated with Siberia by the early Silurian (Bachtadse et al. 2000) but does contain late Silurian and Devonian endemic vertebrates (Afanassieva & Janvier 1985; Young 1993; Janvier 1996a).

The stratigraphic and biogeographic record

Cambrian vertebrates

Although molecular clock estimates imply an extensive pre-Cambrian history to the vertebrate clade (Kumar & Hedges 1998), at present there are no palaeontological data to support this conclusion. The Cambrian record begins with the Chengjiang Lagerstätte (basal Atdabanian, 530 Ma) which has yielded a number of taxa that have been interpreted as vertebrates. Shu et al. (1999a) described two unmineralized vertebrate taxa, Haikouichthys and Myllokunmingia, from the deposit, which they considered to be closely related to lampreys. Other Chengjiang taxa have also been interpreted as vertebrates. Yunnanozoon and Haikouella were considered to be stem group vertebrates by Chen et al. (1999) and Holland & Chen (2001), but this is not well-supported by the preserved anatomical evidence. Xidazoon was likened to Pipiscius, a jawless vertebrate from the Carboniferous Mazon Creek Lagerstätte of Illinois, USA, by Shu et al. (1999b), but newly discovered material of the latter indicates that it is not a vertebrate (Conway Morris, pers. comm. 2000).

A more equivocal vertebrate record is present in the Burgess Shale Lagerstätte of British Columbia, Canada. Simonetta & Insom (1993) described an unnamed taxon (Smithsonian Institution specimen USNM 198612) and likened the preserved structures in the head region to the cranial cartilages and sensory organ supports of extant lampreys. Testing of this intriguing suggestion probably awaits the discovery of additional material.

The earliest evidence of biomineralizing vertebrates is present in the mid-Late Cambrian where the phosphatic sclerite Anatolepis (Bockelie & Fortey 1976; Repetski 1978; Smith et al. 1996) and euconodonts have an almost simultaneous first occurrence (Smith et al. 2001). The vertebrate character of earliest euconodont hard tissues has been confirmed in a number of studies (e.g. Sansom et al. 1992; Donoghue 1998). If a phylogenetic link with paraconodonts, initially proposed by Bengtson (1976), is demonstrated, then the origin of biomineralizing vertebrates would be extended back to the Middle Cambrian. Euconodonts are cosmopolitan and their first appearance is globally synchronous, at least within the limits of biostratigraphic resolution. In contrast, Anatolepis is entirely confined to the margins of Laurentia. The affinities of Anatolepis have been the subject of some debate, but the presence of dentine indicates that it is a vertebrate (Smith et al. 1996) whilst the presence of dermoskeletal 'armour' (rather than visceroskeletal 'teeth') suggests that it is more derived than conodonts. For ease of reference, groups of jawless fish more derived than conodonts are referred to in this paper as 'ostracoderms', a paraphyletic but nonetheless useful term in this context.

Ordovician vertebrates

In contrast to the six genera, and seven species, recognized by Elliott et al. (1991), the total biodiversity of Ordovician vertebrates is now known to number several hundred species, of which the vast majority are conodonts. However, the recognized diversity of non-conodont vertebrates has also increased significantly. Analysis of the microvertebrate fauna of the Harding Sandstone of Colorado and a number of roughly coeval clastic units in North America has revealed that, in contrast to the three taxa recognized in earlier studies, at least 20 species are present. More remarkably, this fauna contains a large number of first appearances of major clades, including astraspids, thelodonts and chondrichthyans (Sansom et al. 2001). The age of these units is thus critical to accurate constraint of the ghost ranges of vertebrate taxa. Conodonts are present in all units examined and indicate that the Harding Sandstone is of undatus Chronozone age in the graphically correlated stratigraphic framework of Sweet (1984), and that related units with similar vertebrate faunas span the compressa–undatus Chronozone interval (mid-Mohawkian, mid-Caradoc). The chondrichthyan fauna includes mongolepids, which are here considered to be stem-chondrichthyans based on the shared presence of neck canals in the scales, but the absence of other chondrichthyan synapomorphies. In addition to Laurentia, thelodonts are also found in Upper Ordovician localities in Baltica (Timan-Pechora; Karatajūtė-Talimaa 1997) and peri-Gondwanan terranes (Austria; Cocks 2000; Bogolepova pers. comm.).

The application of micropalaeontological methodologies in the Amadeus Basin of central Australia has also revealed more diverse faunas than previously suspected. Young (1997) described microvertebrate faunas ranging in age from early Arenig to early Caradoc. Some of the sclerites are of doubtful affinity, but Apedolepis (Llanvirn) is a probable vertebrate (Young 1997; Sansom et al. 2001) and the range-base of Porophoraspis has been extended from the Llanvirn to the lower Arenig. Pirchanchaspis
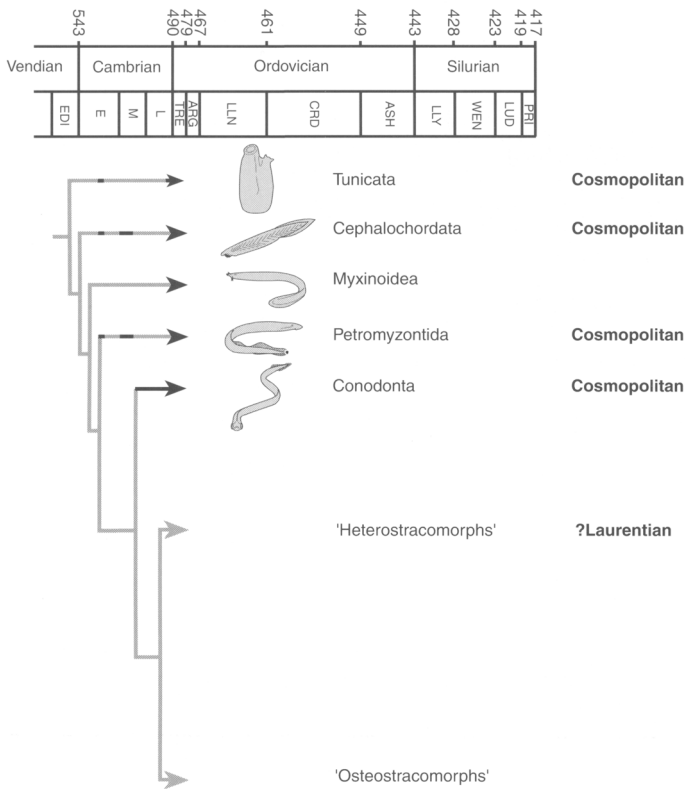
Fig. 2. Stratigraphic distribution and phylogenetic relationships of Cambrian vertebrates, with the biogeographic distribution of each group during this interval indicated. Black bars indicate observed occurrences, grey lines indicate inferred ghost ranges. Phylogenetic tree based on Donoghue *et al.* (2000) and Donoghue & Smith (2001); stratigraphic data from sources in Smith *et al.* (2001); absolute ages of series and system boundaries from sources in Cooper (1999). ARG, Arenig; ASH, Ashgill; CRD, Caradoc; E, Early; EDI, Ediacaran; L, Late; LLN, Llanvirn; LLY, Llandovery; LUD, Ludlow; M, Middle; PRI, Pridoli; TRE, Tremadoc; WEN, Wenlock.

rinconensis, recorded from Bolivia by Erdtmann *et al.* (2000), may represent an additional Gondwanan species.

Euconodonts underwent an explosive radiation at the beginning of the Ordovician, increasing rapidly to a standing diversity of 30–40 genera that exploited a wide range of ecological niches (cf. Aldridge 1988; Sweet 1988). The effect of the latest Ordovician extinction event is dramatic in conodonts, with standing diversity reduced to no more than 10 genera.
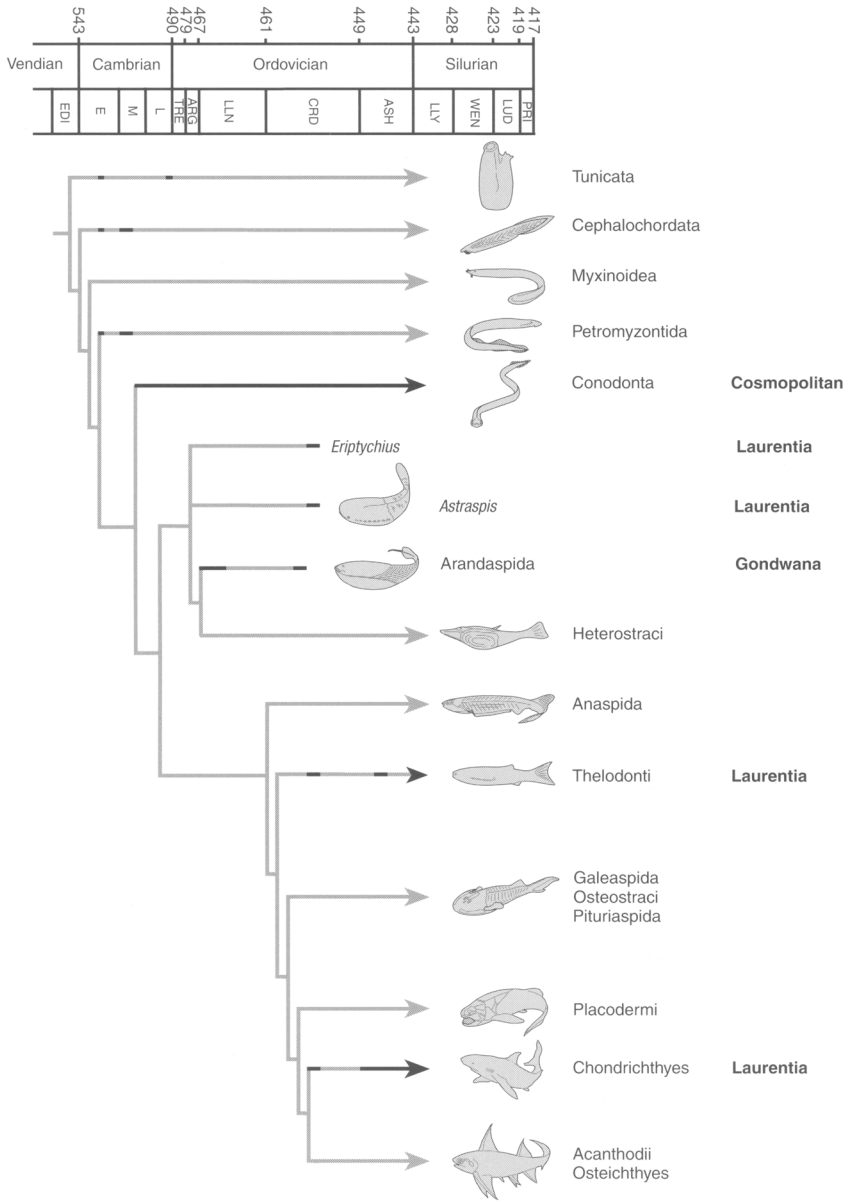
Silurian vertebrates

All the major groups of lower vertebrates are represented in the Silurian, which marks a dramatic increase in the quality and quantity of the non-conodont vertebrate record (extensively reviewed by Blieck & Janvier 1991; Janvier 1996*a*). Conodonts recovered rapidly from their minimum diversity of 10 genera at the base of the Silurian, to reach levels of approximately 20 at the Llandovery–Wenlock boundary. Thereafter, conodonts declined to a standing diversity of approximately 10–15 genera for the remainder of the Silurian (cf. Aldridge 1988; Sweet 1988).

The phylogeny of primitive vertebrates

Donoghue *et al.* (2000) performed a phylogenetic analysis of chordate interrelationships incorporating all of the major groups of extinct and extant jawless vertebrates, including conodonts. The three equally most parsimonious

Fig. 3. Stratigraphic distribution and phylogenetic relationships of Cambrian–Ordovician vertebrates, with the biogeographic distribution of each group during the Ordovician indicated. Black bars indicate observed occurrences, lines indicates inferred ghost ranges. Phylogenetic tree based on Donoghue *et al.* (2000) and Donoghue & Smith (2001); stratigraphic data from sources in Sansom *et al.* (2001) and Smith *et al.* (2001); absolute ages of series and system boundaries from sources in Cooper (1999). Series abbreviations as in Figure 2.
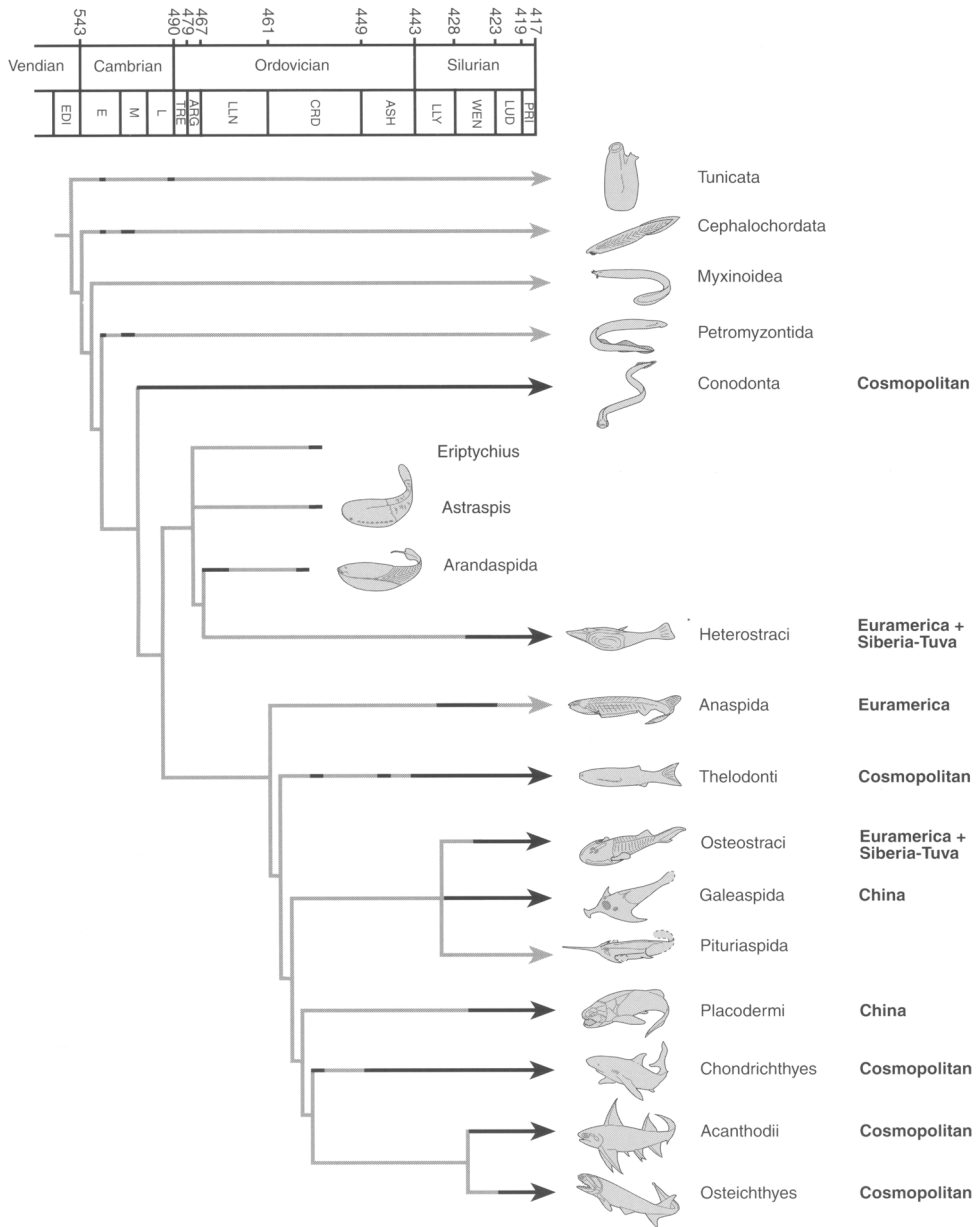
Fig. 4. Stratigraphic distribution and phylogenetic relationships of Cambrian–Silurian vertebrates, with the biogeographic distribution of each group during the Silurian indicated. Black bars indicate observed occurrences, lines indicates inferred ghost ranges. Phylogenetic tree based on Donoghue *et al.* (2000) and Donoghue & Smith (2001); stratigraphic data from sources in Blieck & Janvier (1991), Janvier (1996a), Sansom *et al.* (2001), Smith *et al.* (2001) and other sources discussed in the text; absolute ages of series and system boundaries from sources in Cooper (1999). Series abbreviations as in Figure 2.

trees differed only in the relationship of osteostracans, galeaspids and pituriaspids, which together constitute the sister group to jawed vertebrates. Myxinoids and petromyzontids lie at the base of the craniate/vertebrate clade, with conodonts resolved as the sister group of all other jawless and jawed vertebrates. The relationships of derived jawless vertebrates were further resolved by Donoghue & Smith (2001) who argued that the majority of thelodonts comprise a monophyletic group and constitute the sister taxon to osteostracans, pituriaspids, galeaspids and jawed vertebrates (Figs 2–4).

Ghost ranges and their implications

Calibrating cladograms against stratigraphic range data enables the completeness of the fossil record to be assessed as it provides a means of inferring the existence of unsampled taxa. Such an approach was first adopted by Gauthier *et al.* (1988), and the concept of 'ghost lineages' or 'ghost ranges' was subsequently developed by Norell (1992), amongst others. As useful as ghost ranges are, they are no panacea and require a number of assumptions upon which to base the inference of an unsampled (or unsampleable) fossil record. The most basic assumption requires that the cladogram is at least a reasonable reflection of the true tree of relationships. The second requires that the taxa represented in the cladogram must be monophyletic, since the inclusion of paraphyletic taxa leads to spurious inferences of ghost lineages (see e.g. Wagner 1998).

On the first count, we note that although the tree used is only relatively weakly supported at various nodes (Donoghue *et al.* 2000; Donoghue & Smith 2001), a degree of confidence is provided by the consistency of the signal arrived at following experimentation with the dataset (Donoghue *et al.* 2000) and its congruence with analyses of independent datasets (e.g. Forey & Janvier 1993, 1994; Forey 1995; Janvier 1996*b*). There is also good evidence to support the assumption that the operational taxa are monophyletic given that synapomorphies for each of these groups have been identified through character analysis (see e.g. Janvier 1996*a*) and numerical cladistic analysis of lower rank taxa corroborates this assumption (Donoghue & Smith 2001).

On the basis of these assumptions, it is possible to interpret the stratigraphically calibrated trees presented in Figures 2–4. The trees indicate that although the fossil record of most major groups of lower vertebrates does not begin until the Silurian, all have ghost lineages that extend into the Ordovician, suggesting that the early evolutionary history of these groups is at best unsampled, or at worst unrepresented. In consequence, assessments of diversity change carried out at family level and above (e.g. Benton 1999) cannot be applied with any confidence to the analysis of early vertebrate evolution, since entire orders are missing from the Ordovician record.

Biogeographic trends – patterns and processes

Cambrian–Ordovician

Evidence for the biogeographic distribution of Early and Mid-Cambrian vertebrates is scant and insufficient to derive secure models, other than to conclude that, by the Mid-Cambrian, vertebrates were probably present in both China and Laurentia. It is not until the first appearance of biomineralized vertebrates, *Anatolepis* and euconodonts, in the Late Cambrian, that there are sufficient data to draw firm conclusions regarding biogeographic patterns. As a clade, euconodonts are cosmopolitan and have a synchronous first appearance within the limits of biostratigraphic resolution. At lower taxonomic levels, many euconodont taxa are also cosmopolitan (Miller 1984) although some endemic genera and species are present in the Cambrian, and provincialism develops in the Ordovician between high- and low-latitude faunas (Rasmussen 1998; Armstrong & Owen 2002).

In distinct contrast, the early 'ostracoderm' *Anatolepis* is exclusively circum-Laurentian in its distribution. Indeed, there are no known cosmopolitan 'ostracoderms' during the Cambrian–Ordovician interval, leading to highly regionalized distribution patterns. Many major clades, including astraspids, heterostracans, thelodonts and chondrichthyans have their earliest occurrences in Laurentia, together with a number of plesiomorphic taxa of uncertain affinity, some as yet unnamed (Sansom *et al.* 2001), that are known exclusively from microvertebrate assemblages. That such taxa are exclusively Laurentian in their distribution during the Ordovician is supported by their repeated occurrence in Upper Ordovician deposits throughout Laurentia (Sansom *et al.* 2001, unpublished data) and their absence from coeval microvertebrate assemblages from Gondwana and elsewhere (e.g. Young 1997), which does not seem to be an artefact of sampling (see below). The available dataset thus implies that the latest common ancestor of all

'ostracoderms' and jawed vertebrates was Laurentian, rather than Gondwanan (*contra* Elliott *et al.* 1991).

In this context, the phylogenetic and spatial relationship between the arandaspids and other 'ostracoderms' is puzzling, since the group is entirely restricted to Gondwana (Fig. 3). *Astraspis*, the sister taxon of the arandaspids + heterostracans, is present throughout Laurentia, but endemic to it. In turn, heterostracans have a first record in the Wenlock of Laurentia (Soehn & Wilson 1990) and throughout their stratigraphic range are restricted to Euramerica + Siberia–Tuva. Therefore, despite the strict endemicity exhibited by 'ostracoderm' groups, the presence of arandaspids in Gondwana requires an absence of barriers between Laurentia and Gondwana for at least some of the time interval between the Late Cambrian and earliest Ordovician (Fig. 1a, b), and this biogeographic pattern lends some support to Dalziel's (1997) model for tectonic interaction between Laurentia and South America during the Ordovician.

Most groups exhibit endemicity through to the Wenlock, although significant exceptions amongst the 'ostracoderms' and jawed vertebrates are thelodonts and mongolepid chondrichthyans. The oldest thelodonts are exclusively Laurentian (Sansom *et al.* 2001), but by the end of the Ordovician they had dispersed to Baltica (Timan-Pechora) and peri-Gondwana, and were present in Siberia and Tuva by the end of the Llandovery. A similar pattern is evident amongst the mongolepid chondrichthyans that have a first occurrence in Laurentia (Sansom *et al.* 2001) but which, by the end of the Llandovery, were present in North China, South China and Mongolia (Karatajūtė-Talimaa 1996; Sansom *et al.* 2000).

Silurian

The ghost lineages suggest that the origin of most of the major groups of jawed and jawless lower vertebrates lies within the Ordovician and, thus, that the dramatic change in vertebrate distribution during the Silurian is deceptive. There is, nevertheless, an increase in the biogeographic range, abundance and diversity of all groups during the Silurian.

Blieck & Janvier (1991) recognized four Silurian vertebrate provinces: Euramerica (Laurentia, Baltica, Avalonia plus Kara-Taimyr), Siberia, Tuva and China. Within the Euramerican Province, tectonic convergence in the form of successive terrane and continent–continent collisions led to the assembly of Euramerica. This tectonic setting, with an absence of deep oceanic barriers, enabled 'ostracoderms' to disperse across the range of terranes and continental blocks that made up the ORS continent. The assembly of Euramerica also coincides with the increased abundance of a range of vertebrate clades in shallow marine environments. The timing of dispersal correlates well with dates for the collision events derived from other sources (see above), since none of the elements of the dispersal predate the Wenlock. The assembly of the ORS continent and the dispersal of vertebrates are also coeval with the breakdown of endemism in invertebrate faunas (Hallam 1994).

As noted above, Tuva had docked with Siberia by the early Silurian (Bachtadse *et al.* 2000), but the exact position of Siberia–Tuva and its relationship to Euramerica during the later Silurian and Devonian is the subject of some equivocation (cf. Torsvik *et al.* 1995; Cocks 2001). However, stratigraphic data indicate that osteostracans and heterostracans spread from Euramerica to Siberia–Tuva, suggesting the absence of deep water barriers at that time. Once this initial dispersal had taken place, relatively high levels of endemicity were then maintained between the two blocks during the late Silurian and Devonian, with amphiaspid heterostracans and tannuaspid osteostracans being unique to Siberia and Tuva respectively (Blieck & Janvier 1991; Young 1991, 1993). The presence of the distinctive endemic tannuaspid fauna within the Tuva part of the Siberia–Tuva block (Blieck & Janvier 1991; Janvier 1996*a*) correlates with the development of the endemic *Tuvaella* brachiopod fauna, and may be related to the high-latitude position of Tuva (Cocks 2001).

The Silurian biogeography of vertebrates in China and Vietnam contrasts markedly with that of Euramerica. Osteostracans and heterostracans are absent and faunas are dominated by endemic galeaspids from the Llandovery onwards, together with thelodonts and, from the Wenlock, acanthodians and placoderms (Wang 1995; P'an *et al.* 1996; Thanh *et al.* 1997). The high degree of endemicity is consistent with substantial oceanic separation between China and Euramerica/Siberia, but the palaeogeographic origin of galeaspids is puzzling because their closest known relatives are exclusively Laurentian/Euramerican (Donoghue & Smith 2001). This posits the conclusion that the latest common ancestor of galeaspids and their nearest relatives was, again, Laurentian. The only derived 'ostracoderms' to have dispersed from Laurentia to China were the thelodonts, and

this group may offer a clue to the origin of endemic galeaspids in China.

In Gondwana, 'ostracoderms' disappear from the record after the Caradoc, presumably as a result of glaciation (Elliott *et al.* 1991) and the only reliably documented Silurian vertebrates from Gondwana are conodonts, thelodonts and jawed vertebrates (Blieck & Janvier 1991). Indeed, some parts of Gondwana apparently remained unpopulated until the dispersal of jawed vertebrates during the Devonian. This is demonstrably not a sampling artefact, since conodont faunas from Australia and Laurentia are comparable, but 'ostracoderm' biodiversity is not. By the Early Devonian, an endemic placoderm province (the 'wuttagoonaspid–phyllolepid' province) is recognizable in East Gondwana which began to break down in the Late Devonian (Young 1991, 1993). West Gondwana, in contrast, is relatively depauperate in placoderms and has chondrichthyan–acanthodian-dominated faunas at that time (Young 1993).

The Silurian thus records a complex history of dispersal, vicariance and tectonic convergence. Acanthodians, thelodonts and chondrichthyans continue to be widely dispersed and almost certainly had genuine trans-oceanic dispersal capability (*contra* Blieck & Janvier 1991, p. 377). Heterostracans, anaspids and osteostracans also began to disperse, but only after the tectonic assembly of the ORS continent had removed oceanic barriers. In Siberia, a degree of vicariant endemism is observed after the original input of heterostracans and osteostracans from Euramerica, and in China a significant degree of endemism is also established following initial dispersal.

Where are all the Cambro-Ordovician vertebrates?

One of the most intriguing aspects of this new perspective on Cambro-Ordovician vertebrate biodiversity does not in itself stem from the discovery of vertebrate remains in rocks of this age but, rather, the discovery of significant gaps in the record in the form of ghost ranges. The improved stratigraphic constraints and better understanding of phylogenetic relationships provided by Cambro-Ordovician vertebrates reveal long ghost ranges which imply that most of the major groups of 'ostracoderms' and primitive jawed vertebrates have an evolutionary history that extends into the Ordovician. It is likely that many of the newly discovered Cambro-Ordovician microvertebrate remains of

currently uncertain affinity will fulfil the prediction of these ghost lineages, but there are many more ghost lineages than there are tangible candidates. There are at least three possible, and non-mutually exclusive, explanations for the dramatic improvement in the quality of the vertebrate fossil record during the early–middle Silurian: (a) the increase in the taxonomic diversity and disparity of vertebrate fossil record accurately reflects an early Silurian cladogenic event (cf. Blieck & Janvier 1991) and the inferences of ghost lineages are entirely spurious; (b) Cambrian and Ordovician vertebrates are rare because there is a systematic bias against the preservation of the environments in which they lived; and/or (c) Cambro-Ordovician vertebrates were ecologically distinct from their middle Palaeozoic relatives and their fossil record is either undersampled or the preservation of fossil remains unlikely because of systematic bias.

The fossil record of Cambrian and Ordovician vertebrates (except for conodonts) is so poor that it is not possible to test comprehensively whether or not vertebrates were affected by the latest-Ordovician extinction event. Nevertheless, there is evidence that at least some vertebrate groups were affected. The fossil record of conodonts exhibits a dramatic drop in taxonomic diversity during this event such that the entire clade almost became extinct (Aldridge 1988; Armstrong 1995). However, this model has yet to be tested against phylogenetic trees and it is notable that not one of the major conodont groups became extinct. Furthermore, all of the Ordovician vertebrate remains discovered thus far can be identified either as members of clades surviving into the middle Palaeozoic, or as possible sister taxa to one or more of these clades. Thus, although it is likely that the vertebrate clade as a whole was affected by the extinction event locally, especially at low taxonomic level and in terms of numerical diversity, there is no evidence that any major vertebrate groups arose or met their demise at this time, a pattern mirrored in invertebrate faunas (Droser *et al.* 2000). The absence of extinction in major vertebrate groups indicates that the increase in the quality of the vertebrate record during the Silurian is not the result of major evolutionary turnover at high taxonomic level.

The second possibility, that the fossil record of early vertebrates is poor because of a systematic bias against the preservation of shallow-water nearshore lithofacies, is also doubtful. Such environments are both extensively preserved and crop out extensively throughout the

Ordovician of Laurentia in North America. This interval has been intensively sampled for conodonts, which are abundantly preserved throughout, but the 'ostracoderm' record is confined to specific intervals that seem to coincide with highstand events (Sansom et al. 2001). It is clear, therefore, that although shallow-water, nearshore environments are widely preserved, they contain no record of vertebrates, other than conodonts. Thus, it would appear that the third of the alternatives is worthy of further consideration and investigation, namely that Ordovician 'ostracoderms' were ecologically distinct from their middle Palaeozoic relatives and are preserved in very different facies which are either unsampled and/or systematically underrepresented in the rock record. If this is the case, the two end members that could serve as refugia for Ordovician vertebrates are freshwater and deep marine environments. The former may be excluded. Despite continuing appeals for the freshwater origin of vertebrates (Graffin 1992; Griffith 1994), no Cambro-Ordovician vertebrates are found in freshwater environments and Blieck & Janvier (1991) argued that most or all Silurian vertebrates were marine. To the contrary, Anatolepis occurs predominantly in outer-shelf, circum-Laurentian settings and the Harding Sandstone and Stairway Sandstone faunas may coincide with sea-level highstands (Sansom et al. 2001). This suggests that the missing Ordovician record may be found in deeper-water, outboard settings which, due to their position, tend to be more deformed and metamorphosed than cratonic interiors. Prospecting these areas for vertebrate faunas may provide additional insights into early vertebrate evolution.

What underlies endemism and cosmopolitanism during the Silurian?

There is a notable correlation between the biogeographic distribution of vertebrates during the Silurian and their anatomical design. For instance, thelodonts are the only monophyletic group of 'ostracoderms' to exhibit cosmopolitanism during the Silurian, the other groups being restricted to the margins of Laurentia and, later, Euramerica plus Siberia–Tuva (with the exception of galeaspids, which are restricted to China). In common with the thelodonts and conodonts, jawed vertebrates also exhibit cosmopolitanism during this interval. It is possible that the heavily armoured groups of 'ostracoderms' remained endemic to the ORS continent throughout the middle Palaeozoic because they were constrained against active

swimming in deeper water and/or open ocean environments. Indeed, it has been argued by Gutmann (1967) and Gutmann & Bonik (1983) that, in the absence of a mineralized axial skeleton, the heavily armoured 'ostracoderms' (the Panzerfische of Gutmann) used their extensive dermal skeleton to brace musculature. The mineralized axial skeleton of jawed vertebrates (a synapomorphy of the clade) provides a biomechanically superior structure against which to brace musculature. As part of their 'new head' hypothesis, Gans & Northcutt (1983) noted that the origin of vertebral elements immediately precedes the advent of paired fins, as the final stage of their scenario in which vertebrate evolution was driven by a change in feeding strategies towards active predation. We suggest, therefore, that the heavily armoured dermal skeleton of most pre-jawed vertebrates was a limiting factor in their dispersal. Far from there being a direct competitive link between the 'ostracoderms' and their jawed relatives (see e.g. Purnell 2001), it is possible that the greater dispersal potential of the jawed vertebrates was a significant factor in the longevity of the group, while the 'ostracoderms' underwent a progressive decline to their demise in the Late Devonian. This greater dispersal potential would, in turn, enable the subsequent development of areas of endemism and concomitantly higher levels of global biodiversity which are encountered in Devonian jawed vertebrates.

Conclusions

We began with the 'out of Gondwana' vicariance model of Ordovician vertebrate spatial and temporal diversification (Elliott et al. 1991) and, with the incorporation of new and more complete datasets, conclude with a new model that incorporates a complex interaction of dispersal, vicariance, and tectonic convergence during the Early Palaeozoic. New datasets and the elucidation of existing datasets lead to the suggestion that much of the early evolutionary history of the major early vertebrate clades lies within the Ordovician, or even the Cambrian. Furthermore, it is likely that the record of these events is poor because the organisms were ecologically distinct from their middle Palaeozoic relatives, rather than because of a systematic bias in the preservation of environments typical of these counterparts.

We provide this assessment of the evolutionary palaeobiogeography of Early Palaeozoic vertebrates based on the data that is currently to hand. However, biogeographic analyses based upon historical evidence are, by

their very nature, reliant upon incomplete datasets and it is likely that unexpected discoveries will lead to radical reinterpretation of the data presented herein. Nevertheless, we feel that the database has grown to an extent that we can begin to build testable models with the aim of stimulating the search for new data in both time intervals and palaeoenvironments in which the remains of the earliest vertebrates might otherwise be unexpected and therefore remain unsampled.

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