Asia–Gondwana connections indicated by Devonian fishes from Australia: palaeogeographic considerations

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Abstract
Middle Palaeozoic vertebrate fossil occurrences are summarised for Australia, with reference to faunal connections between Asia and East Gondwana, as first indicated by fish distributions of Lower Devonian fossil sites. Major endemic groups discussed are pituriaspid (Australian) and galeaspid (Asian) agnathans, wuttagoonaspids (Australian) and antarctaspid (Antarctic, Australian, Asian) arthrodires, yunnanolepid and sinolepid antiarchs (South China, Indochina terrane, Australia), and early tetrapodomorphs (South China, Australia). More widespread groups that lived in shallow marine environments (lungfishes, buchanosteid arthrodires, antiarch Bothriolepis) also show species groups shared between South China and East Gondwana. Exchange of continental facies fishes (e.g. tristichopterid tetrapodomorphs) may have been interrupted by marine transgression in the Frasnian, but were restored in the late Famennian with the appearance of Grenfellaspis in eastern Australia, the only sinolepid antiarch known from outside Asia. The hypothesis of Gondwana dispersion and Asian accretion, to explain the collage of geological terranes forming modern east and southeast Asia, implies increasing dissimilarity with increasing age, but the Siluro-Devonian early vertebrate evidence is inconsistent with this. Previous cladistic analysis of Asian terranes predicted galeaspid agnathans on the Indochina terrane, and their subsequent discovery at Ly Hoa, Vietnam, confirms that Indochina and South China had come together across the Song Ma suture by Middle Devonian time.

Keywords: Devonian, Palaeogeography, Biogeography, Vertebrates, East Gondwana, South China, Indochina terrane

1 Introduction
The Devonian Period is widely known as the ‘Age of Fishes’, because for the first time in the fossil record there were abundant and diverse remains of early vertebrates. In fact, it was an isolated scale of the Upper Devonian lobe-finned fish Holoptelus, identified by Louis Agassiz in 1840 from supposedly ‘Silurian’ strata in Belgium (later described by Agassiz 1844), that proved decisive evidence for correlating between marine strata in Devon, England, and the well-known ‘Old Red Sandstone’ of Scotland (Rudwick 1985). This and other evidence led to Sedgwick and Murchison (1839) erecting the Devonian System, to fill a gap in the stratigraphic succession above the Silurian of Murchison (1839) and beneath the Carboniferous of Conybeare and Phillips (1822) for the British ‘Coal Measures’, which then also included the Devonian Old Red Sandstone. In the subsequent 180 years, Devonian fish fossils have been found in sedimentary rocks throughout the world, in a wide range of lithologies representing all habitable aquatic environments, from marine to estuarine, fluviatile and lacustrine.

First discoveries in the Southern Hemisphere included bones (probably belonging to the antiarch placoderm Remigolepis) from Twofold Bay on the coast of southeastern Australia (Clarke 1860; Young 2007), a skull from Burrimjuck, New South Wales, and fish scales and bones from Antarctica collected on Scott’s 1910–1913
South Pole Expedition (Woodward 1916, 1921). Today these sites are among numerous Devonian fossil fish localities representing the East Gondwanan region (Australasia–Antarctica). In Asia, Mansuy (1907, 1915) first recorded Devonian fish remains from China and northern Vietnam respectively, now extensively documented in the Siluro-Devonian of the South China Block (Zhao and Zhu 2010) as one of the three greatest endemic biological radiation episodes in the entire evolutionary history of the vertebrates (e.g. Zhu et al. 2009, 2013, 2016).

This paper presents an overview of Middle Palaeozoic vertebrate fossils from East Gondwana that provide evidence of faunal connections with the various Asian palaeo-blocks and terranes identified for the Silurian-Devonian. Figure 1 summarises 44 generalised Devonian fish localities for Australia-Antarctica (see also Burrow et al. 2010, fig. 4, for localities represented by Devonian vertebrate microfossils). Zhao and Zhu (2010, fig. 1) provided a comparable summary of 74 Siluro-Devonian fish localities across China, and Wang et al. (2010a, fig. 1) showed 18 fish localities across southeast Asia.

In general terms, the vertebrate fossil record from the Ordovician to the Devonian is concerned with two major aquatic groups: the fish-like agnathans (jawless vertebrates), and fishes with jaws (primitive gnathostomes). This evolutionary phase ended with the emergence of terrestrial vertebrates, for which a minimum age of Early Devonian is provided by the fossil record (both tetrapod body fossils, and trackway evidence). Other evidence (e.g. diversity modelling of genus-level preservation rates; molecular data) does not exclude an even older (Silurian) age for tetrapod origins (Friedman and Brazeau 2011; George and Blieck 2011), as had been previously suggested from phylogenetic and trace fossil considerations (Chang 1991; Young 2006). The aquatic habitat of fishes, which are tied to environments of deposition rather than erosion, gives them a better chance of preservation as fossils than terrestrial vertebrates. The robust bones of the most diverse Devonian group, the extinct placoderm or ‘armoured fishes’ (Young 2010a), provides a highly complex data set such that their distributions in time and space can be applied to questions of Middle Palaeozoic palaeogeography (e.g. Zhu and Young 2010).

Thus, the dispersal capabilities of Devonian fishes have been widely considered regarding reconstructions of past geography, in particular how to distinguish between two groupings: i) ‘primary division’ fishes (entirely restricted to freshwater), and ii) fishes with some tolerance of marine environments, or which entered the sea during parts of their life cycles. Detailed analysis of depositional environments has not resolved this problem; even if adults of certain fossil species are only found in marginal marine or non-marine deposits, the dispersal capacity of larval forms cannot be known. These are questions about processes, which are difficult or impossible to deal with in historical science as testable hypotheses. Yet the same difficulties apply to experimentation on living fish species, for example to establish saltwater tolerance and dispersal capabilities to explain disjunct distributions (e.g. dispersal history of modern galaxiid fishes across the southern continents).

An alternative approach concerns analysis of pattern, whereby two ecological groupings of fishes are considered relevant to biogeographic studies (Rosen 1974): ‘continental’ (freshwater, marginal and shallow marine forms of continental shelves), and ‘oceanic’ (pelagic forms of the open oceans). These are identified by biogeographic analysis of distribution patterns in relation to phylogeny. From this perspective, some compelling inferences can be drawn from the global distribution patterns of major fish taxa recorded from Devonian rocks. Thus, Young (1981) identified five faunal provinces based on the presence or absence of major groups: Cephalaspis Province (Laurussia), Amphiaspid Province (Siberia), Tannuaspis Province (Tuvan massif), Galeaspis-Yunnanolepid Province (South China), and Wutta goonaspis-Phyllolepid Province (East Gondwana). The last two provinces and their inter-connections are the topic of this paper.

Regarding palaeogeographic connections between East Gondwana and other areas, Middle Palaeozoic vertebrate evidence has highlighted two major data conflicts. Strongly endemic Early Devonian faunas in East Gondwana indicate isolation, but with increased cosmopolitanism during the Middle Devonian, and strong evidence by the Late Devonian of faunal exchange with the Laurussian palaeocontinent (e.g. antiarch placoderms such as Bothriolepis widespread across both regions; the arthrodire Greelandaspis antarctica occurring in non-marine deposits in both Greenland and Antarctica). This is contradicted in some palaeomagnetic reconstructions that indicate just the reverse; i.e. proximity between Gondwana, Laurentia, and Baltica in the Early Devonian, and Gondwana widely separated from Laurussia by an equatorial ocean in the Late Devonian (e.g. McElhinney et al. 2003, fig. 6f-h).

The second issue concerns Gondwana dispersion and Asian accretion (e.g. Metcalfe 1996a, 1996b, 2013), also
supported by some palaeomagnetic (e.g. Zhao et al. 1996; Yang et al. 2004) and other data (Wang et al. 2010b; Duan et al. 2011). This proposed that South China, and perhaps North China and various parts of south-east Asia, were attached to the northern Gondwana margin in the Early Palaeozoic, but by the Mid-Late Devonian had separately moved away, to eventually form the collage of geological terranes making up modern Asia. Under that scenario, the further back in time, the greater should be dissimilarities between the Asian tectonic blocks and terranes. However, as previously noted by Young and Janvier (1999), Siluro-Devonian distribution patterns for fossil vertebrates across Asia suggested the opposite, being more consistent with modern geography than with the model of widely dispersed Asian terranes. Zhao and Zhu (2010, figs. 2, 6) show various Asian blocks and terranes closely associated or connected from the Silurian onward, together representing a ‘Pan-Cathaysian landmass’ defined by galeaspids (jawless vertebrates). This issue is further considered below, following a brief overview of Gondwana vertebrates relevant to connections with Asia in the Siluro-Devonian. Some galeaspids and placoderms are illustrated in Figs. 2, 3 and 4, and the temporal-spatial distribution of selected placoderm groups is summarised in Fig. 5. Osteichthyans are illustrated in Figs. 6 and 7 and

Fig. 1 Generalised Devonian vertebrate fossil localities for East Gondwana (updated from Young et al. 2010, fig. 1). a Australian localities numbered from the southeast in an anticlockwise direction; b Devonian reconstruction of Australia, East Antarctica and New Zealand showing additional localities in New Zealand (44) and southern Victoria Land, Antarctica (45). Abbreviations for regions, Australian states, etc. are: MBL = Marie Byrd Land (West Antarctica); NNZ = New Zealand north island; N.S.W. = New South Wales; N.T. = Northern Territory; Qld = Queensland; S.A. = South Australia; SNZ = New Zealand south island; Vic. = Victoria; W.A. = Western Australia; Tas. = Tasmania. Abbreviations for Australian geological provinces and sedimentary basins (shaded areas) are: AB = Amadeus Basin; ADB = Adavale Basin (subsurface Devonian); BPB = Bonaparte Basin; BrR = Broken River Province; BT = Bancannia Trough (subsurface Devonian); BuB = Burdekin Basin; CB = Canning Basin; CAB = Carnarvon Basin; DB = Darling Basin; DrB = Drummond Basin; GB = Georgina Basin; LFB = Lachlan Fold Belt; OB = Officer Basin; THB = Timbury Hills Basin (subsurface Devonian). For details of all localities see Young et al. (2010). Details for localities discussed or mentioned in this paper (shown in bold) are: 2, Buchan/Bindi, Gippsland, Victoria; 4, Twofold Bay, NSW south coast; 5, Taemas/Wee Jasper (Burrinjuck) limestones; 9, Grenfell-Bumberry syncline area; 12, Gunderbooka/Cobar; 13, Wuttagoona/Tambua/Mt. Jack; 20, Toomba Range/Cravens Peak; 21, Dulcie Range; 24, Mount Winter; 40, Munyarai 1 well, Officer Basin; 41, western Darling Basin (Barrier Range, Mutawintji); 42, Grampians, western Victoria; 45, Aztec fish assemblage, Skelton Neve and Cook Mountains areas, Transantarctic Mountains, southern Victoria Land.
the temporal-spatial distribution of some stem-tetrapods is summarised in Fig. 8.

2 Biogeographically significant Devonian vertebrate groups of East Gondwana

2.1 Agnathans: pituriaspids

Three major groups of jawless vertebrates are highly diverse and widespread in Siluro-Devonian continental deposits of other regions, but unknown in Gondwana (e.g. Young 1981, 1990, 1993, 2003). Heterostracans (over 120 genera) and osteostracans (over 60 genera) are distributed across Laurussia, Siberia, and Tuva. The galeaspид agnathans (at least 50 genera), first formally described by Liu (1965), occur only in Asia. The total absence from East Gondwana of Devonian heterostracans and osteostracans, common in the Siluro-Devonian of Laurussia, indicates some sort of significant barrier or isolating mechanism. If this was an oceanic barrier it must have been of considerable extent, perhaps 750–1000 km wide. It would need to have been comparable to or wider than the Uralian seaway (see Young 2003, p. 177), because in Laurussia there are many armoured agnathan occurrences in shallow marine deposits.

In contrast, only two Devonian armoured agnathans are known from Gondwana (Pituriaspis and Neeyambaspis; Young 1991). Both come from the Wuttagoonaspis assemblage in the Georgina Basin of central Australia (Young and Goujet 2003), and show a distinctive morphology, with long rostral processes (Fig. 2). They are poorly known from only a small number of specimens preserved as impressions in sandstone. Pituriaspids have been interpreted as endemic at high taxonomic level (in their own Class Pituriaspida), with a possible close relationship to osteostracans and stem gnathostomes.

Fig. 2 The only armoured agnathans known from Gondwana (a-e) compared with some from Asia (f and g). Pituriaspis (a, b right side, d and e) and Neeyambaspis (b left side, c), as described by Young (1991) from the Georgina Basin (localities 20–21, Fig. 1); c and d reconstructions of Neeyambaspis (c) and Pituriaspis (d) in dorsal view (d based on e); f and g comparison with two galeaspids from South China, Sinoszechuanaspis yanmenpaensis (f) and Asiaspis expansa (g), reconstructions based on Pan et al. (1975, fig. 5) and Pan (1992, fig. 29). Reconstructions and images not to scale. Abbreviation: mdo= median dorsal opening
This would imply derivation from an unknown, presumably pre-Devonian widespread agnathan ancestor (note that Ordovician agnathans are mainly known from marine beds). However, there is a striking superficial resemblance to some South Chinese galeaspid agnathans with long rostral processes (Huananaspidiformes), such as Asiaspis or Sinoszechuanaspis (Fig. 2f-g). In addition, Neeyambaspis (known from a single skull impression, but clearly different from Pituriaspis) partly preserves a galeaspid-like median dorsal (nasohypophysial) opening (Fig. 2b-c).

Galeaspid agnathans first appeared in the Early Silurian of Asia, and became highly diverse in Asia from the Early Devonian. In South China, the Huananaspidiformes with pronounced rostral processes first appear in the Xitun fauna of Pragian age (Zhao and Zhu 2010; vertebrate assemblage III of Zhu et al. 2000), and older representatives (Sanqiaspis; Lochkovian) are recorded from northern Vietnam (Janvier et al. 2009), whereas the pituriaspids of central Australia are somewhat younger (Emsian-Eifelian). Assuming the striking resemblance to huananaspid galeaspids is valid, the appearance of pituriaspids in East Gondwana can be attributed to range...
enlargement (‘dispersal’) from China during the faunal exchange of the E’Em bio-event (Pragian-Emsian boundary), identified by Zhu et al. (2000) as the first faunal exchange between China and Australia (event A1, Fig. 5).

2.2 Placoderms: wuttagoonaspid, phyllolepid

*Wuttagoonaspis* gave its name to the East Gondwana Province first proposed by Young (1981), based on the diverse placoderm assemblage in sandstones of the Mulga Downs Group (Darling Basin, localities 12, 13, 41, Fig. 1), named after the highly distinctive endemic genus described by Ritchie (1973). However, apart from groenlandaspid arthrodires (Ritchie 2004), much of this assemblage remains undescribed. Presumably it had comparable diversity to that documented from the Dulcie Sandstone and Cravens Peak Beds of the Georgina Basin (Young and Goujet 2003). Including the pituriaspids discussed in the previous section, the Georgina Basin *Wuttagoonaspis* assemblage comprises at least 16 genera in 11 families, placed in at least six orders and four classes (Agnatha, Acanthodii, Placodermi, Osteichthyes). There is a second (larger) species of *Wuttagoonaspis* (*W. milligani*; Fig. 3a-b), and a diversity of arthrodires with seven new genera erected. Biogeographically, these form two groups: i) probably more primitive arthrodires (antarctaspids) that show Chinese affinities (see next section), and ii) genera referred to more widely distributed actinolepid, phlyctaenid and groenlandaspid arthrodire families, that have long been recorded from Laurussia (e.g. central Europe, western USA, Spitsbergen, Severnaya Zemlya).

Fig. 4 Placoderm fishes suggesting shallow marine (a–c), possibly marginal marine (d and f), or continental (g–i) faunal exchange between east Gondwana and east Asia. a Skull of the arthrodire *Kweichowlepis* from the early Emsian Duyun Assemblage of South China (after P’an et al. 1975, pl. 9, 10, fig. 1) re-interpreted as a buchanosteid; b Skull of the Australian Emsian arthrodire *Buchanosteus* (after Young 1979); c Buchanosteid skull (cf. *Enrolasteus*) with ridged ornament (Wee Jasper, NSW; locality 5, Fig. 1); d and f, Skulls of the bothriolepid antarctarch *Bothriolepis* with a pentagonal preorbital recess; d, *Bothriolepis shaokuanensis* (Eifelian, Guangdong, China; modified from Chang 1963 and Liu 1973); e *B. karawaka*, and f *B. pontalesis* from the Aztec sequence (Middle-Late Devonian), southern Victoria Land, Antarctica (from Young 1988); g–i Australian sinolepid antarctarch *Grenfellaspis branagani* (Upper Devonian, Lachlan Fold Belt; locality 9, Fig. 1); g Reconstruction based on the only known articulated specimen (from Young 1999); h and i Articulated specimen in ventral view (h, showing the unique ventral fenestra) and dorsal view (i, skull only). Images not to scale. Abbreviations: f.ven= ventral fenestra, Nu= nuchal plate, orb= orbit (eye socket), orb.f= central opening for eyes, pro= preorbital recess.
The age range of the *Wuttagoonaspis* assemblage has been unclear due to the dearth of marine fossils providing external age control, and the fact that many localities are in isolated sandstone outcrops with no stratigraphic context. A post-Pragian to Eifelian age range was suggested for the Cravens Peak Beds by Young and Goujet (2003), probably partly overlapping but perhaps younger than the type area in the Mulga Downs Group of
western New South Wales (to explain the different Wuttagoonaspis species). An extension higher into the Middle Devonian (Givetian) for some sites is supported by similarities in Groenlandaspis arthrodire remains from the Antarctic Aztec sequence (Young and Long 2014).

Across eastern and central Australia, younger (Late Devonian) strata in these non-marine sequences are characterised by a Bothriolepis-phyllolepid fish assemblage. Phyllolepid placoderms (Fig. 3c-e) are the second group used by Young (1981) to define the East Gondwana Province. The documented range of phyllolepid placoderms in Gondwana is Emsian-Famennian, with their greatest diversity in the Givetian-Frasnian (Fig. 5), yet very rare in lowest and highest horizons (evidently small species as an insignificant part of these fish assemblages). In the youngest Australian horizons with placoderm bones (e.g. latest Famennian assemblage with the giant sarcopterygian Edenopteron keithcrooki; Young 2007; Young et al. 2013) phyllolepid plates have not been found. They are shown disappearing just before the D-C boundary (Fig. 5, E-N Gondwana column).

As discussed by Young (2005c), phyllolepid placoderms demonstrate the greatest time/space disjunction of any group of Devonian vertebrates. Agassiz (1844) erected the genus Phyllolepis for a highly distinctive isolated bone with sinuous ridged ornament from the ‘Old Red Sandstone’ of Scotland. Subsequently, 170 years of European research produced nine species within this one genus, all in Famennian strata of Laurussia. In contrast, three decades of research on the phyllolepid placoderms of East Gondwana (Long 1984; Ritchie 1984, 2005; Young 2005b, c; Young and Long 2005) documented five genera: Austrophyllolepis, Placolepis, Cobandrahlepis, Yurammia, and Cowralepis. The first four are represented by several species in eastern Australia and Antarctica. On the Australian craton, different species of Austrophyllolepis and Placolepis have been recorded in the Georgina and Amadeus basins (localities 21, 23, Fig. 1). The first Gondwanan appearance of phyllolepid sensu stricto (Emsian) is based on the oldest Placolepis (and phyllolepid) in the Jauf Formation of Saudi Arabia (Placolepis n. sp.; Lelièvre et al. 1999, fig. 3C). Thus, a Gondwanan origin for the group is strongly indicated, supported by a close relationship to Wuttagoonaspis as proposed by many authors (e.g. Miles 1971; Young 1980; Long 1984; Young and Goujet 2003). In contrast, possible precursors of both Wuttagoonaspis and phyllolepids have been suggested from the Early Devonian of China (Dupret 2008; Dupret and Zhu 2008), but based only on single incomplete skulls, neither of which shows the distinctive and characteristic ridged ornament of wuttagoonaspid and phyllolepid (Fig. 3a-c). Ridged ornament remains are more likely to be observed by field geologists, even as fragmentary bones (Fig. 3d-e). These are a very common component in all Devonian fish assemblages of East Gondwana, but neither wuttagoonaspid nor phyllolepid is known from the diverse younger Devonian fish assemblages in Asia. A new phylogenetic analysis (Hunt and Young 2011) failed to recover the sister group relationship between Wuttagoonaspis (Australia)
and Yiminaspis (China) proposed by Dupret (2008), the resemblances residing mainly in primitive arthrodire skull characters (discussed further in the next section).

2.3 Placoderms: arthrodires

As noted above, the diverse arthrodires documented from the Wutttagoonaspis assemblage of the Georgina Basin by Young and Goujet (2003) included some evidently more primitive forms suggesting Chinese affinities (Fig. 3f-h). Toombalepis from the Cravens Peak Beds (Fig. 3f) was assigned to the actinolepid family Antarctaspidae, other members being Antarctaspis (Antarctica) and Yujiangolepis (South China; Fig. 3b). All of these share a large nuchal plate in the centre of the skull that carried converging sensory grooves. However, this is a general resemblance residing mainly in primitive arthrodire skull characters, being also seen in many other groups, including wutttagoonaspids and phyllolepids (Fig. 3a-c), and petalichthyids (e.g. Eurycaraspis from China). Some Laurussian actinolepid arthrodires (e.g. Aethaspis) have a similarly elongate nuchal plate (Hunt and Young 2011, fig. 7). The incomplete skull of the Chinese ‘wutttagoonaspid’ Yiminaspis Dupret (2008) preserves the same general feature (other supposed resemblances to Wutttagoonaspis are mainly non-preserved and shown as dashed lines). A large nuchal plate with converging sensory grooves is displayed in the skull of Edgellaspis from the Hatchery Creek Group (Fig. 3g).

The Hatchery Creek Group is an alluvial fan deposit with abundant fish and plant remains (Hunt and Young 2011, fig. 7). Osteichthyan fishes suggesting shallow marine (a), or marginal marine/continental (b-i) faunal exchange between East Gondwana and South China. a Restoration (by R.E. Barwick) of the Early Devonian lungfish Speonesydrion from Burrinjuck (locality 5, Fig. 1); b-e cf. Kenichthys (previously ‘Gyroptychius australis’) from Hatchery Creek parietal (b and c, dorsal and ventral) and post-parietal (d, dorsal) skull shields, and right lower jaw (e, external view); f Kenichthys from South China, parietal shield in ventral view; g Muranjilepis from central Australia, parietal shield, dorsal view; h and i Tungsenia (South China) parietal shield, dorsal view (h) and CT scan image showing brain cavity (i). a-e from locality 5, g from locality 24 (Fig. 1); f, h and i from Yunnan Province, in the Pragian of Zhaotong (Tungsenia) and Emsian of Qujing (Kenichthys). Images not to scale. Abbreviations: cv= brain cavity, f.pin= pineal opening, nas.c= nasal capsule, orb= orbit (eye socket), Psp= parasphenoid bone in palate, re.pin= recess for pineal and para-pineal organs.
2012), about 1800 m thick and conformably overlying the Emsian marine limestones at Wee Jasper (locality 5, Fig. 1). The fauna includes early tetrapodomorphs indicating Chinese affinity as discussed below. The parallel-sided skull of *Edgellaspis* is another highly unusual feature seen in placoderm outgroups (Hunt and Young 2011), whilst the tubercular ornament shows a strong tendency to alignment, as in some primitive phyllolepids (e.g. Young et al. 2010, fig. 4d). These early arthrodires from China, Australia and Antarctica show a range of primitive characteristics never seen in the much better studied arthrodire faunas of Laurussia, and thus are interpreted to have had limited dispersal capacity. They can be explained by palaeogeographic connections resulting in faunal exchange related to the E’Em bioclastic event approximating the Pragian-Emsian boundary (Zhu 2000).

A more widespread arthrodire group are the buchanosteids, which are diverse in the Burrinjuck marine limestones underlying the Hatchery Creek Group just discussed (locality 5, Fig. 1). The type area is Buchan, Victoria (locality 2, Fig. 1), which produced the original specimen named *Buchanosteus* (Hills 1936; Stensiö 1945) from equivalent limestones of Emsian age. The

![Fig. 8 a Disparate stratigraphic ranges for some major stem-tetrapod fish groups between Asia, Gondwana, and Laurussia (Europe-America); b Summary of relevant stem-tetrapod distributions and possible dispersal episodes on a Devonian palaeomagnetic reconstruction (Li and Powell 2001; for fossil locality details see Young 2003, fig. 1)](image-url)
buckanosteids are primitive brachythoracids characterised by a rostral capsule separate from the rest of the skull and braincase (Fig. 4a-c), a feature never recorded in the brachythoracids of Laurussia. The most diverse assemblage is from Burrenjiuck (genera *Parabuckanosteus*, *Errolosteus* and *Richardosteus*; Long et al. 2014). Young and Janvier (1999) first noted that a Chinese Emsian arthrodire skull *Kweichowlepis* (Fig. 4a) shows close resemblance to *Buckanosteus* from Australia (Fig. 4b). Wang (2005) summarised the range of *Buckanosteus* in China, extending down to the early Lochkovian (Yulin, Guangxi Zhuang Autonomous Region; Zhao and Zhu 2010). Again, an ‘out-of-China’ origin at the Pragian–Emsian boundary as part of the E’Em bio-event (Zhu 2000) can be suggested, perhaps related to marine transgressions in the early Emsian documented for both South China (Ma et al. 2009) and eastern Australia (Young 1996; Mawson and Talent 2003). These shallow marine fishes were widespread along the northern Gondwana margin, up the Uralian seaway (*Uralosteus*; Mark-Kurik and Young 2003), and in Severnay Zemlya (*Urvaspis*; Long et al. 2014). As biogeographic/palaeogeographic indicators with different marine tolerance, they show quite different distribution patterns compared to the primitive non-brachythoracid arthrodires (*Edgellaspis*, *Toombalepis*, *Yujiangolepis*) just discussed.

### 2.4 Placoderms: antiarchs

The yunnanolepid antiarchs, together with galeaspid agnathans, gave the name for the Yunnanolepid/Galeaspid Province of Young (1981), which was renamed the ‘Pan-Cathaysian Galeaspid Province’ by Zhao and Zhu (2010). The diversification of these groups in the Silurian–Early Devonian of China (e.g. Zhao and Zhu 2007) represents one of the most dramatic endemographic radiations in vertebrate evolutionary history. Of over 40 antiarch genera recognised in the most recent phylogenetic analysis, eight genera are yunnanolepids (Wang and Zhu 2018). This highly endemic group is only known from Asia. First formally documented from Yunnan Province of South China by Liu (1963), fragmentary remains had much earlier been collected from northern Vietnam by Mansuy (1915). Many new localities in this area (e.g. Racheboeuf et al. 2005) lie north of the Song Ma suture (see Wang et al. 2010a, fig. 1), and thus represent an extension of the South China Block. The discovery of yunnanolepid remains in Vietnam south of the Song Ma suture, on the ‘Indochina terrane’ (Tong-Dzuy et al. 1996), provided the first clear evidence of close faunal (and therefore palaeogeographic) connection with the highly endemic yunnanolepid-galeaspid fossil fish of the South China Block.

At the other extreme is the antiarch *Bothriolepis* (Fig. 4d-f), the most widespread Devonian fish. It is known from all regions of the world preserving Upper Devonian strata, with over 60 species recognised world-wide. Traditionally, *Bothriolepis* was typical of non-marine ‘Old Red Sandstone’ deposits, from which it was first described (Famennian of Russia; Eichwald 1840). Subsequently a small number of occurrences have been demonstrated in calcareous beds associated with marine invertebrates, indicating that these species at least had a tolerance of salt-water. Such a widespread form therefore seemed unlikely to contribute much to considerations of biogeography and palaeogeography.

In the Southern Hemisphere, *Bothriolepis* was first identified from the Aztec sequence of Antarctica by Woodward (1921), and considered sufficient to demonstrate a Late Devonian age based on occurrences in Europe and North America. Exhaustive studies of the species *B. canadensis* by Stensiö (1948) seemingly left little to be discovered regarding morphology. However, in a detailed study of very extensive Antarctic material, Young (1988) identified a new type of preorbital recess of the skull in three Antarctic species (*B. portalensis*, *B. karawaka*, *B. macphersoni*; Fig. 4e-f). Remarkably, this structure was otherwise only known in two Chinese species: *B. shaokuanensis* (Fig. 4d) and *B. niushoushanensis*. Both are of middle Eifelian age, in the Tiaomajian Assemblage of South China and the Shixiagou Assemblage of Ningxia (North China Block; Zhao and Zhu 2010). This indicates faunal exchange between these regions in the Middle Devonian for this species group, to the exclusion of other areas. Another significant aspect relative to palaeogeography was a demonstrated temporal discordance in China compared to the Late Devonian age assumed by European researchers, first noted by Wang (1943), but dismissed for decades. *Bothriolepis* is first recorded in the late Emsian Chuandong Assemblage of Yunnan Province (Zhao and Zhu 2010), whereas its European first occurrence (late Givetian of the Baltic region) indicates a range enlargement episode from China-Gondwana near the Middle–Late Devonian boundary (B2, Fig. 5).

The Asterolepisiformes is the second major European grouping of antiarchs, based on *Asterolepis* Eichwald (1840) from the Frasnian of the Baltic. Previous evidence suggested the group was absent from the Early Devonian of Asia, with the later appearance of endemic Middle Devonian (e.g. *Hunanolepis*), and cosmopolitan Upper Devonian forms (*Remigolepis*; Pan et al. 1987). Note that ‘*Asterolepis*’ *sinensis* Pan (1964), based on material from the Wutung Group near Nanjing, was shown by Zhang and Liu (1991) to be congeneric with *Jiangxilepis*, a bothriolepid antiarch. Recently, Pan et al. (2017) suggested that *Luquanolepis* (Emsian, Yunnan Province) could belong in this group (previously interpreted as a
probable bothriolepid; Zhang and Young 1992). However the skull of *Luquanelolepis* is not known, so this result is very provisional (and not supported in the analysis of Wang and Zhu 2018). Asterolepid affinity is anomalous given that all other Chinese antiarchs (except *Hunanolepis, Remigolepis*) are yunnanolepids, bothriolepids, or sinolepids. Janvier et al. (2003) suggested some ornamented fragments from Tra Ban Island, Vietnam, could also indicate an asterolepid antiarch, but such tuberculate ornament is seen in a majority of placoderm groups, so better evidence is needed.

Currently there is no clear indication of asterolepids in the Early Devonian of Asia. In contrast, the Early Devonian of Gondwana has produced acid-prepared remains of an unnamed asterolepid (Young 1984) from the Cravens Creek fish assemblage at Wee Jasper, associated with the primitive arthrodire *Edgellaspis* (discussed above), and basal tetrapodomorphs close to the Chinese *Kenichthys* (see next section). In summary, these data suggest that asterolepiform antiarchs were present in East Gondwana as early as, or earlier than, in Laurussia, even if the typical Middle Devonian radiation of species of *Asterolepis* is not evident.

The antiarch family Sinolepididae (Liu and Pan 1958), as the name suggests, is a distinctive Asian taxon showing clear distributional evidence for Chinese origins. Sinolepids have a highly unusual morphology with a large rectangular opening or fenestra in the ventral trunk-armour (Fig. 4g-h), a structure unknown in any other placoderm group. The genotype of the family (*Sinolepis*) has its type area in the Wutung Group near Nanjing (Famennian Leigutai Assemblage of Zhao and Zhu 2010). Other sinolepids (*Liujiangolepis, Dayoshania, Xichonolepis*) range right through the Devonian of China, and possibly in the Early Devonian of northern Vietnam (*Vanchienolepis*). A Late Devonian range enlargement into Gondwana (event ‘D’, Fig. 5) was demonstrated by the discovery of the genus *Grenfellaspis* Ritchie et al. (1992) in the Lachlan Fold Belt of eastern Australia (locality 9, Fig. 1). The late Famennian age of the *Grenfellaspis* assemblage of East Gondwana was confirmed with the discovery of a single articulated specimen (Fig. 4h-i) high in the Hervey Group sequence of central NSW (Young 1999). Sinolepids have also been found at other localities in the late Famennian of central NSW (e.g. Bumberry syncline; Young et al. 2010, fig. 8F-G).

Other fossil groups support a faunal connection across the Devonian-Carboniferous boundary (e.g. Ritchie et al. 1992; Webb 2000).

### 2.5 Osteichthyes: dipnoans

The diverse Early Devonian lungfish fauna of southeastern Australia (Fig. 7a) has been documented in numerous publications. From the Pragian-Emsian limestone sequence of Burrinjuck, five species are assigned to four genera (*Dipnorhynchus, Speonesydrion, Cathlorhynchus, Placorhynchus*; see Campbell et al. 2009). Wang et al. (1993) had already described *Sorbitorhynchus* from the Emsian of Guangxi Zhuang Autonomous Region, noting the close affinity with *Dipnorhynchus* from Burrinjuck. From the Pobjiao Formation (early Emsian) of Wenshan, Yunnan Province, Chang and Wang (1995) described the dipnoan *Erika jarviki* (*Dipnorhynchidae*). Recently Qiao and Zhu (2015) recorded from Guangxi Zhuang Autonomous Region a new species of the Burrinjuck genus *Cathlorhynchus*. Qiao and Zhu (2015) noted a widespread (‘trans-Panthalassic’) Early Devonian distribution for the *Dipnorhynchus* lineage. As discussed above for the arthrodire *Buchanosteus*, this would be expected for shallow marine tropical environments. However, the more closely related taxa (species) between China and Australia may be considered an indicator of geographic proximity. Again, given the slightly older age of the Chinese occurrences, faunal exchange related to the E’Em bio-event of Zhu et al. (2000) can be proposed.

### 2.6 Osteichthyes: tetrapodomorphs

The origin of land animals from fishes was one of the major events in vertebrate evolutionary history, which has fascinated scientists and the general public since before the time of Charles Darwin (e.g. Lu et al. 2016). Where and when the first tetrapods (land vertebrates) evolved is still shrouded in uncertainty. However, the traditional morphological gap between fishes and amphibians has been partly closed by a wealth of fish-like fossil ‘stem-tetrapods’, many discovered since the mid 1980s. These represent the more advanced part of the stem-tetrapod lineage, and mainly come from the Laurussian palaeocontinent (Europe or North America).

Over the last 15 years, various extinct lobe-finned fishes (sarcopterygians) have been discovered in the remarkable fossil fish assemblages of South China, some of which represent the basal part of the tetrapod stem-lineage (Fig. 6, in red). The oldest and basal-most stem-tetrapod so far known is *Tungsenia* Lu et al. (2012) from the Pragian (Lu and Zhu 2008), and the next most basal is the Emsian *Kenichthys* Chang and Zhu (1993). Both come from South China (Fig. 6), and examples are illustrated in Fig. 7f, h-i. Close resemblances between *Kenichthys* and Australian material from the Hatchery.
Creek Group (locality 5, Fig. 1) was noted over 20 years ago by Chang and Yu (1997). Initially this material (Fig. 7b-e) was provisionally referred to the Laurussian genus *Gyroptychius* (Young and Gorter 1981), but most recently several closely related forms are recognized including one listed as cf. *Kenichthys* (Hunt and Young 2012). Another closely related stem-tetrapod is *Muranjilepis* (Fig. 7g) described by Young and Schulzle (2005) from the Amadeus Basin of central Australia (locality 24, Fig. 1). The detailed relationship between these Australian forms and other Chinese basal stem-tetrapods (e.g. from Wuding, referred to the Laurussian taxon *Thursius*) is ongoing research by the authors. All these taxa (names in red in Fig. 6) are strong indicators of faunal exchange between South China and East Gondwana in the Early Devonian.

Figure 8 summarises the Devonian time-space distribution for major tetrapodomorph groups and related sarcopterygians. Until a decade ago it was argued that overwhelming fossil evidence showed the 'fish-tetrapod transition' (F/T, Fig. 8a) had occurred on the Laurussian palaeocontinent during a 10 million-year time interval of the Late Devonian (~ 372–382 Ma; Ahlberg and Clack 2006; Clack 2007; cf. Young 2006). Then a discovery in Poland of much older possible vertebrate trackways and footprints (Niedźwiedzki et al. 2010) implied that animals with limbs had already evolved before the Middle Devonian. Similar trackways from Australia (Warren et al. 1986) had previously been dismissed as too old, because of a long gap before the first occurrence of tetrapod body fossils (rare examples in the Upper Devonian of Laurussia and Australia). The older Australian and Polish trackway evidence is controversial (e.g. Lucas 2015; cf. Friedman and Brazeau 2011). However, other Middle Devonian trackways still imply that previous assumptions about the fish-tetrapod transition occurring in the Late Devonian is an artefact of an incomplete fossil record from one palaeocontinent (Laurussia). The new trackway evidence focussed attention on regions of the world less investigated than Europe and North America, such as Asia and Gondwana. Gondwana was the largest landmass of the Devonian, but its fossil record remains poorly known.

In Laurussia, tetrapodomorph fishes only occur in strata of Middle Devonian age or younger (Fig. 8a). The oldest tristichopterids (e.g. *Tristichopterus* from Scotland, *Eusthenopteron* from Canada) occur near the Middle-Late Devonian boundary (previously considered good supporting evidence for Late Devonian tetrapod origins in Laurussia). The Pragian-Eifelian age range now established for the genera *Kenichthys*, *Tungsenia*, ‘*Thursius*’, and related forms from South China, and ‘*Gyroptychius*’, cf. *Kenichthys* and *Muranjilepis* from Australia (Fig. 6), makes them older than any tetrapodomorphs from Laurussia. Thus, earlier interpretations that they were ‘migrants’ from a European evolutionary centre are no longer tenable. The older age and basal phylogenetic position indicates instead dispersal or range enlargement to Europe, the most direct route on palaeogeographic reconstructions being along the northern Gondwana margin (‘South Route’ of Zhao and Zhu 2010, fig. 6B).

Similarly, tristichopterids were considered of northern origin, with Australian and Antarctic representatives interpreted as more derived, having dispersed from the north into East Gondwana (Ahlberg and Johanson 1997; Johanson and Ahlberg 2001). The underlying assumption is that basal taxa, or stratigraphically older taxa, or both, indicate the centre of origin for the group concerned (Young 2010b; Young et al. 2010). However, alternative interpretations, of endemic tetrapodomorph subgroups (e.g. Canowindridae, Mandageriinae) in Australia-Antarctica (Young 2008; Young et al. 1992, 2013, 2019) are consistent with the placement of the only Australian taxon (*Marsdenichthys*) in the analysis of Lu et al. (2012, fig. 6), resolved as the sister-group to all other tristichopterids.

Nevertheless, given the diverse basal tetrapodomorphs in the Lower Devonian of China, it is surprising that tristichopterids have not been found in the Frasnian (Fig. 8a, left column), at a time when they are most diverse in both East Gondwana and Laurussia. This seems only explicable by palaeogeographic change. One possibility is that increasing sea-level during the Frasnian, leading to the global maximum transgression near the Frasnian-Famennian boundary (e.g. Young 1996; Mawson and Talent 2003), may have isolated continental areas and prevented dispersal of fishes with limited marine tolerance, perhaps including tristichopterids.

### 3 Discussion

#### 3.1 A key Devonian vertebrate site: Toomba Range-Cravens Peak, Georgina Basin

The area occupied by the *Wuttagoonaspis* assemblage, from western NSW and across central Australia, covers about 1 million km² of the Australian craton (Young and Goujet 2003). In the Georgina Basin of central Australia it extends from the east, in the Toko Syncline area of western Queensland, to the Dulcie Range in the Northern Territory (localities 20–21, Fig. 1). To the west it occurs in equivalent strata along the MacDonnell Ranges of the Amadeus Basin, being identified in the upper part of the Mereenie Sandstone at Mt Winter (Young and Turner 2000; Young and Schulzle 2005; locality 24, Fig. 1).

This highly diverse assemblage represents the first vertebrate fauna to occupy the Australian continent (as
opposed to marine forms in the shallow seas of the Ordovician). The containing strata represent the upper part of thick non-marine clastic sequences characterising the Early-Middle Palaeozoic of central Australia, with an age range from Ordovician to latest Devonian/Early Carboniferous. These were laid down following regression of the Early Palaeozoic ‘Larapintine seaway’ (which bisected the continent from east to west until the Late Ordovician). It is noted that the Palaeozoic in both the Amadeus and Georgina basins is either producing (Mereenie Oil and Gas Field) or being actively explored for hydrocarbons (see Ahmad and Munson 2013; current projects of Central Petroleum; http://centralpetroleum.com.au). In the southern Georgina Basin, Cambrian marine sediments are considered the likely source rocks (e.g. Ayling et al. 2016), and the overlying clastics (including Siluro-Devonian with fossil fish remains) as potential reservoirs.

In the 1970s a new limestone outcrop was found beneath the Devonian Cravens Peak Beds. It is very isolated (locality 20, Figs. 1 and 9a), at the southern end of the Toko Syncline and on the edge of the Simpson Desert, in an area where lack of outcrop but possible petroleum prospects had long been recognized (Sprigg 1963). The outcrop was sampled for microfossils on the assumption it would be either Cambrian or Ordovician, the typical age of marine limestones in this region. Surprisingly, it contained Devonian ostracods and thelodont agnathans (Turner et al. 1981), the first Devonian occurrence in central Australia to produce fossils indicating marine to marginal marine conditions.

Since then, a diverse fish assemblage has been documented from this limestone. In addition to the first-discovered thelodonts (Turner 1995, 1997), it contains asterolepid antarichs (Young 1984), the ‘notidanid’ shark *Mcmurdodus* (Turner and Young 1987; Burrow et al. 2008), various acanthodians (Burrow and Young 2005), and osteolepid, holoptychiid, dipnoan, and onychodontid osteichthyan remains (Young and Schultze 2005). Several new groups are not yet described. Generally, the described assemblage shows little affinity to that of South China, in contrast to the associated ostracods (very close or identical to *Healdianella subdivisita* from the late Emsian Sipai Formation of Guangxi Zhuang Autonomous Region; Wang 1983). The thelodont *Turinia* is widely distributed across Gondwana, but also known from Asia (west Yunnan, part of the Shan-Thai Terrane, and also South China Block), and evidently was able to disperse in marine environments. The shark *Mcmurdodus* seems clearly a Gondwanan form (first described from Antarctica). Chondrichthyans are generally poorly represented in Siluro-Devonian fish faunas of South China; they have been suggested as a vertebrate equivalent of the cool-water Malvinokaffric biogeographic province for Siluro-Devonian invertebrates (e.g. Young 1995a). The only suggestion of a possible South Chinese element from the Cravens Peak limestone fish concerns unusual ‘osteolepid’ scales with posterior serrations described by Young and Schultze (2005), noted by Friedman and Brazeau (2010) to resemble in some respects the scales of the early osteichthyan *Guifu* Zhu et al. (2009) from the Silurian (Ludlow) Kuanti Formation of Yunnan Province.

### 3.2 Palaeogeographic setting and map representation

Without the discovery of Devonian microfossils, the Cravens Peak outcrop would have been readily assigned to Cambro-Ordovician marine limestones that are widespread in this region. Based only on lithofacies, the new site would have had little palaeogeographic significance. Biostratigraphic age control is a key contributor to palaeogeographic map reconstruction, by correlating...
relevant facies in different stratigraphic sections. With the new age assignment based on marine-marginal marine microfossils, the Cravens Peak limestone acquired new significance regarding Devonian palaeogeography for central Australia.

There has been some discussion about the validity of basing palaeogeographic maps on modern geography, or whether they should also take account of plate tectonic reconstructions, or detailed consideration of interaction of terranes in mobile orogenic belts (e.g. orogenic palaeogeography; Feng et al. 2012). Terranes (‘geodynamic units’ of Verard et al. 2015) are assumed to have had separate palaeogeographic histories, and in some regions (e.g. the geological composite of eastern Asia), it seems necessary to take them into account for palaeogeographic map compilation. For Palaeozoic Australia, the Lachlan Fold Belt in the east may have involved separate terranes (e.g. McElhinney et al. 2003). However, for the craton at least it seemed reasonable to base a series of palaeogeographic maps on modern geography, as in the Australian Government ‘Palaeogeographic Maps Project’ (Struckmeyer and Totterdell 1990).

However, the example of the Cravens Peak limestone reveals difficulties with that approach. To explain its palaeogeographic setting, a long marine extension from the southwest (Fig. 9a) was proposed for the relevant Early Devonian time-slice (Wilford and Olissoff 1990; Walley and Cook 1991, fig. 9). This evidently relied upon a single well producing similar thelodont fish scales in the Officer Basin (Long et al. 1988), rather than hypothetical marine extensions either from the northwest (Canning Basin) or from eastern Australia, both of these areas having thick sequences demonstrating marine Devonian (arrows, Fig. 9a). Walley and Cook (1991) gave two objections to the western connection to the Canning Basin, which was first proposed by Turner et al. (1981): drill hole data in the Canning suggested a topographic high to the east, and the Devonian in the Amadeus Basin was entirely non-marine. However, extensive limestone outcrops (mostly undated) have been noted in the western Amadeus Basin by Young and Turner (2000) and Young and Schultzze (2005). To the east of the Toko syncline, Devonian marine sedimentary rocks are widespread throughout Queensland, the relevant sedimentary basins (e.g. Adavale, Drummond, Burdekin; Fig. 1) considered structural remnants of larger sedimentary provinces (McKillop 2013). Emsian-Eifelian allochthonous limestones adjacent to the Drummond Basin (‘Ukalunda Shelf’; Henderson et al. 2013) may extend into the subsurface Belyando Basin (Draper 2013). To the west, in the subsurface Adavale Basin (that hosts the Devonian Gilmore gas field; Randall 2013), subsurface Devonian may extend into the poorly known Warabin and Barrolka troughs (McKillop 2013), which lie about 400 km south-east of the Toko syncline, but with no intervening Devonian outcrop. Similarly, there is no outcrop into the north-western part of New South Wales, where an extensive but poorly dated Devonian succession occurs in the subsurface Bancannia trough (BT, Fig. 1). In outcrops of the adjacent Darling Basin, Early Devonian marine transgressions are dated as Lochkovian (wuschmidtii and pesavis conodont zones; Mawson and Talent 2000), but given the highly similar Devonian fish assemblages (see above) a marine connection to the Toko syncline is also possible (DB, Fig. 9a).

Using a Gondwana reconstruction with Antarctica and Australia juxtaposed (Fig. 9b) makes the southwestern Devonian marine extension proposed in Wilford and Olissoff’s (1990) Early Devonian palaeogeographic map very improbable. The adjacent region of Antarctica is an igneous/metamorphic terrain, which was cratonic for most of the Palaeozoic (e.g. Boger 2011, fig. 13), so the possibility of corresponding unknown marine Devonian strata is extremely unlikely.

The reconstruction of Li and Powell (2001, fig. 12) has Australia placed on the eastern Gondwana margin between 10°S and 40°S, with the North and South China blocks above the equator and off the northern Gondwana margin at similar palaeolatitudes. By the Late Devonian, the South China Block had crossed the equator to have the same southern palaeolatitude as eastern Australia. Based on Chinese Cambrian and Silurian palaeomagnetic data, and an assumed correspondence in the apparent polar wander paths for South China and Australia/East Gondwana, Yang et al. (2004) also showed South China attached to northwestern Australia. Zhao and Zhu (2010, fig. 6) show combined South China, North China and Tarim blocks in this position (their ‘Pan-Cathaysian Galeapid Province’). The palaeoclimatic data maps of Boucot et al. (2013) again show all the Asian blocks and terranes attached to the northwest margin of Australia through the Silurian-Devonian time interval. Thus, given these various reconstructions, an assumed marine incursion from the Canning Basin (CB, Fig. 9a) would represent a direct connection with the Siluro-Devonian vertebrate assemblages of Asia. In contrast, an incursion from the east would be less direct (perhaps more consistent with the minimal Asian affinities on the Cravens Peak limestone fish assemblage).

However, the assumption that juxtaposition of palaeo-blocks on a plate tectonic reconstruction means a palaeogeographic connection is greatly oversimplified. Sea-level fluctuations would dramatically change connections or barriers between areas (discussed below). Other problems include the difficulty of accommodating tectonic deformation, stretched continental margins, compression in highly deformed fold belts representing collision zones, and lost ocean floor sediments with
oblitration of former oceans. All are long recognised issues preventing more realistic palaeogeographic reconstructions using palinspastic base maps (e.g. Ziegler et al. 1985). These issues indicate some of the limitations to standard map representations for palaeogeographic data. It is noted that in the most recent palaeogeographic maps based only on palaeomagnetic constraints (Huang et al. 2018), the South China Block and various south-east Asian terranes are shown closely juxtaposed to the western Australian margin in the Silurian, but drifting away to the west during the Devonian. This is completely the opposite to what is indicated by the highly endemic Devonian fish assemblages of the ‘Pan-Cathaysian landmass’ of the Late Silurian-Early Devonian (Zhao and Zhu 2010).

3.3 Alternative representations of palaeogeographic data

The reconstruction of past geography, like most aspects of historical Earth Science, relies on a range of geological, geophysical, and biological empirical data. How disparate data sets can be integrated, to produce a coherent and testable hypothesis of changing geography through time, has remained elusive and controversial. An oversimplification of the data integration problem is to distinguish between qualitative and quantitative evidence, the latter component (primarily palaeomagnetic data) considered superior because they can be represented as numbers. The standard representation of palaeogeographic data in map form ideally represents a synthesis of all available evidence bearing on the palaeogeography of an area for a particular interval of geological time.

There is no question that map representation is the primary tool for palaeogeography (e.g. Feng 2016; Feng et al. 2012). However, complementary to a palaeogeographic map can be an analytical representation of certain palaeogeographic data sets, to expose particular data in a clearly testable way, and provide a guide to new empirical observations required to resolve data conflicts. An example of such representation is the standard ‘Apparent Polar Wander Path’ (APWP) for palaeomagnetic data, whereby new measurements are tested by the degree to which they conform to a previously established linear pattern (apparent polar wander path).

Quantitative palaeomagnetic data provide evidence of palaeolatitude, as do other qualitative data, for example palaeoclimatic evidence, which could be tested against palaeomagnetism when represented in the same way (first done by Scotese 1986). Palaeobiogeographic data may also provide evidence for palaeolatitude, through recognition of cold and warm assemblages, latitudinal diversity gradients, etc., and would also be best analysed using an APWP representation. An early example of this approach was comparison of labyrinthodont amphibian abundance and diversity gradients versus palaeomagnetism as indicators of palaeolatitude for the Late Palaeozoic and Triassic (Irving and Brown 1964).

However, palaeobiogeographic data may also provide a completely different type of evidence, not concerned with palaeolatitude, but instead with the connections or barriers between regions. This is the predominant approach in preceding discussions of this paper. This information has hierarchical structure, and can be analysed ‘cladistically’; i.e. using branching diagrams or cladograms (Young 1986). Hierarchical structure is not a special attribute of biogeographic data; rather, it is imposed on the empirical evidence to facilitate analysis and testing of competing hypotheses. The same applies to a range of geological data concerning, for example, past distributions of land and sea, palaeocirculation patterns, or many of the criteria used by geologists to work out a history of accretion for allochthonous terranes, as discussed by Young (1990, 1995b, 2010b).

The evidence of past sea-level fluctuations illustrates how the same data can be represented to facilitate either non-hierarchical or hierarchical analysis (Fig. 10). The primary evidence of past sea-level fluctuations derives from lithofacies mapping to distinguish between areas of land and sea for a particular geological time interval (e.g. Feng 2016). However, identifying second- and third-order sea-level changes, and distinguishing local (uplift or subsidence) from global effects requires the most detailed biostratigraphic control (e.g. for the Devonian, using conodonts; Mawson and Talent 2000, 2003). Like the curved lines of a palaeomagnetic ‘apparent polar wander path’, linear (non-hierarchical) representation is standard for a transgression-regression curve (Fig. 10a). But this evidence has implications for reconstruction of barriers or connections between areas (Fig. 10b), and the same information can be transformed into a hierarchical data set, which is then amenable to cladistic analysis (Fig. 10c-d).

Cladistic methods have been applied to analysis of relative timing of collision sequences for palaeocontinental blocks and terranes in the geological past. The first representation of a converging area cladogram in the geological literature (Young 1986) concerned the collision sequence for continental components that came together during the Middle-Late Palaeozoic to form Pangaea. The fusion history of four areas (Laurentia, Baltica, ‘Armoric’, and Gondwana) was considered as three competing hypotheses, based on a range of geological and geophysical data. It was noted that a similar analysis of four taxa in phylogeny could produce 15 fully resolved and 10 partly resolved cladograms, but for the formation of Pangaea only three out of 25 possible hypotheses of collision history had been considered in the geological literature. The complexity was such that
competing hypotheses could not be adequately represented as maps, but most effectively as six different converging cladograms (Young 1986, fig. 8).

A much more complex collision sequence concerns the collage of geological terranes making up modern Asia, and hypothesised to have originated from Gondwana according to a range of geological and geophysical evidence. Young and Janvier (1999) summarised fossil evidence from some 14 terranes or micro-blocks assumed to have had separate histories according to geological or geophysical evidence. Data from Siluro-Devonian vertebrate distribution patterns across the region were integrated and summarised as three converging area cladograms (Young and Janvier 1999, fig. 8). The evidence indicates that the Tarim and South China blocks had come together by the Early Silurian, followed by North China and the Indochina terrane by the Middle Devonian (relative timing unresolved), and then connection with East Gondwana by the Early Carboniferous. The distribution of three key endemic Asian vertebrate groups (galeaspid agnathans, and yunnanolepid and sinolepid antiarchs) represented on the cladogram

![Fig. 10 a-d](image)

**Fig. 10 a-d** Alternative representations of a transgression-regression pattern (sea-level curve), using the Early-Middle Devonian (Emsian-Givetian) as an example. **a** Linear representation (standard sea-level curve); **b** Marine barriers between three hypothetical continental areas X, Y, Z, and dispersal events resulting from sea level fall and rise (letters A-E correspond to positions on sea-level curve in a); **c** Hierarchical (cladistic) representation of a vicariance (splitting) pattern in continental faunas resulting from the successive marine barriers; **d** Converging (dispersal) pattern in continental faunas resulting from disappearance of marine barriers; **e** Summary of Siluro-Devonian vertebrate evidence for collision histories of Asian terranes, updated from Young and Janvier (1999). For more detailed discussion see Young (1995b, 2010b) and Young and Janvier (1999)
Devonian marine limestones. Nevertheless, the possibility of integrating global sea-level (transgression-regression) curves for the Middle Palaeozoic with changing distribution patterns in Siluro-Devonian fish groups is an area to be explored in future research.

Abbreviation
APWP: Apparent Polar Wander Path

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Authors’ contributions
JL provided text and figures on the osteichthyans; GCY provided text and figures on agnathans, placoderms, biogeography and palaeogeography. Both authors contributed to the final version of the manuscript. The authors read and approved the final manuscript.

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Availability of data and materials
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Competing interests
The authors declare that they have no competing interests.

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