

ENDEMICITY AND PALAEOBIOGEOGRAPHY OF THE OSTEOSTRACI AND  
GALEASPIDA: A TEST OF SCENARIOS OF GNATHOSTOME EVOLUTION

by ROBERT S. SANSOM

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Bristol BS8 1RJ.

e-mail: r.sansom@le.ac.uk

Currently: Department of Geology, University of Leicester, University Road, Leicester, LE1  
7RH.

**Abstract:** Armoured stem-gnathostomes (jawless vertebrates previously termed ostracoderms) have long been assumed to exhibit strong endemism. This assumption has underpinned their utility in many palaeobiogeographic studies as well as scenarios regarding the evolution and dominance of jawed vertebrates over their jawless relatives. The hypothesis of endemism in stem-gnathostomes is investigated for the first time in light of the phylogeny of the closest relatives of jawed vertebrates – Osteostraci and Galeaspida. Palaeobiogeography of each is reconstructed using Fitch optimisation and modified Brooks Parsimony Analysis.

Palaeobiogeographic distributions corroborate phylogeny. Results, along with consideration of the Heterostraci, enable identification of similar patterns across groups (broad ancestral range, Early Devonian expansion, endemic and pandemic clades within each, and Middle Devonian radiation events) and inferences to the palaeogeographic relationship between major terranes (i.e. Laurentia, Baltica, Avalonia, Kara, Altaids, South China, Tarim). Comparison of basin and terrane level analyses identifies the different palaeogeographic processes responsible for the distributions of each group: sea-level changes in the case of the Osteostraci and rifting in the case of the Galeaspida. The general endemic nature of the Osteostraci and Galeaspida is

confirmed and thus the hypothesis that the demise and extinction of stem-gnathostomes was due to their limited dispersal capacity is supported.

**Key words:** Palaeobiogeography, Osteostraci, Galeaspida, Heterostraci, Silurian, Devonian, Gnathostomata.

JAWLESS armoured fish dominated vertebrate communities during Siluro-Devonian times. These stem-gnathostomes (previously termed “ostracoderms”) are often considered to exhibit strong endemism (Blieck and Janvier 1991; Halstead and Liu 1979; Halstead and Turner 1973; Halstead Tarlo 1967; Janvier and Blieck 1993). The supposed endemism of armoured jawless vertebrates relative to the pandemic nature of their jawed relatives is of significance to two important areas. Firstly, the endemism and limited dispersal capability of jawless vertebrates has been considered as a key factor in an important evolutionary episode - the demise of jawless vertebrates and dominance of jawed vertebrates in a potential competitive replacement event (Long 1993; Smith *et al.* 2002). Secondly, the endemism of these clades has led to the use of their distributions in palaeobiogeographic studies, to the extent that they have been used to define global faunal provinces (Blieck and Janvier 1991; Janvier and Blieck 1993; Young 1981; 1990; 1993).

The endemic nature of these clades however, remains largely untested. Hypotheses regarding the demise of jawless vertebrates, as well as their utility in palaeobiogeographic studies, are thus in jeopardy. Scenarios of biogeographic evolution can only be tested in light of a comprehensive phylogenetic framework for the group. For example, for an endemic fauna to be said to be resulting from single dispersal event, it must be shown to be monophyletic and to have emerged from the supposed area of origin. Whilst advances have been made in phylogenetics of Heterostraci (Blieck *et al.* 1991; Elliott *et al.* 2007; Janvier 1996a; Pernègre and Elliott 2008), thelodonts (Wilson and Märss 2004; Wilson and Märss 2007) and placoderms (Goujet and Young 2004; Brazeau 2009), the frameworks for each are neither comprehensive enough (i.e. all taxa) nor conclusive enough to enable investigations of vicariance and dispersal scenarios. Recent advances in osteostracan (Sansom 2009) and galeaspid (Zhu and Gai 2006) phylogeny, coupled with advances in palaeobiogeographic method (e.g. Lieberman 2000) enable palaeobiogeographic reconstruction. Such reconstructions serve as the first possible test of these

crucial hypotheses of endemism and thus palaeogeography and evolutionary scenarios. As contemporaneous ecological equivalents occurring on opposite sides of the palaeoglobe, the Osteostraci and Galeaspida offer comparable sources of information for the geological processes responsible. Furthermore, palaeobiogeography offers a source of information independent of character homology as a test of the veracity of the proposed phylogenetic frameworks.

The Osteostraci and Galeaspida are characterised by large, fused, cephalic shields which, combined with their shallow marine, lagoonal, estuarine and freshwater environments, gives them a high preservation potential and thus extensive record. The Osteostraci range from the mid-Silurian (earliest Wenlock) to the Late Devonian (Frasnian) and have a range across the Northern Hemisphere (North America, Svalbard, Northern Europe, Eastern Europe and Siberia). The Galeaspida range from the Early Silurian (late Llandovery) to Late Devonian (Frasnian) and are distributed across China and North Vietnam. The Heterostraci have a similar morphology and temporal range to the Osteostraci and Galeaspida (Early Silurian to Late Devonian) and thus offer a comparable source of data. Like the Osteostraci, they are distributed across the Northern Hemisphere, but unlike the Osteostraci, they are also distributed across central and northern Siberia and possibly Spain and north-west Africa.

Phylogenetic investigations of the interrelationships of the fossil jawless vertebrates placed the Osteostraci as sister group to the jawed vertebrates, and the Galeaspida as sister group to the clade [Osteostraci+jawed vertebrates] (Donoghue *et al.* 2000; Donoghue and Smith 2001; Forey 1995; Janvier 1996*a-b*). The Osteostraci and the Galeaspida are therefore stem-gnathostomes. Given their phylogenetic position, they best exemplify the vertebrate condition prior to the origin of jaws, and thus present the most suitable dataset for testing hypotheses concerning the dominance of jawed vertebrates.

## PREVIOUS APPROACHES

On a global scale, Young (1981; 1990; 1993) used armoured agnathans to define Devonian faunal provinces. The Osteostraci define two provinces – the Euramerican ‘cephalaspid’ province and the Tuvan ‘tannuaspid’ province. The Galeaspida defined the South China ‘galeaspid-yunnanolepid’ province, or “Pan-Cathaysian Galeaspid Fauna” of Zhao (2005). An additional Siberian ‘amphiaspid’ province is defined by the amphiaspid Heterostraci. Whilst the monophyly of each of the Osteostraci and Galeaspida is fairly well accepted, the phylogenetic relationship between the tannuaspid Osteostraci (i.e. *Tannuaspis*, *Tuvaspis* and *Ilemoraspis*) and the cephalaspid Osteostraci is not clear (Sansom 2008; Sansom *et al.* 2008) and, therefore, neither is the relationship between their respective provinces.

Within these provinces, biogeographic patterns were observed by Janvier (1985). Certain osteostracan clades are identified as endemic (Boreaspididae and Kiaeraspidida of Spitsbergen, and the Thyestiida of Saaremaa) whilst others are widely distributed (i.e. Zenaspidida and Cephalaspidida). As Janvier noted however, it is not possible to test hypotheses of endemism and dispersal without taking a comprehensive approach i.e. considering all taxa in a clade, and its associated phylogeny. Blicek and Janvier (1999) synthesised data for agnathans to identify palaeocommunities, and subsequently, faunal provinces within Euramerica – North Atlantic, Rocky Mountains, and Arctic provinces in the Devonian and Scoto-Norwegian, Acadian-Anglo-Welsh, and West former USSR provinces in the Silurian. These Silurian provinces were consistent with the thelodont zones of Turner and Tarling (1982). The Chinese province was subdivided into realms by Pan and Dineley (1988), in part on the basis of endemic galeaspid faunas, whilst Wang (1993) reverted to a single undivided province. Pan *et al.* (1996) reviewed the palaeogeography of the Middle Palaeozoic of China and considered three separate units - Tarim, South China (including northern Vietnam) and North China, a scheme followed by Zhao and Zhu (2007).

Fossil jawless vertebrate distributions have been used to reconstruct biogeographic evolution through vicariance and dispersal events. Examples include Halstead Tarlo (1967) and Halstead and Turner's (1973) reconstructions of psammosteid and other heterostracan radiations, Blicek's (1984) reconstruction of pteraspimid palaeobiogeography and Young's (1981; 1993) consideration of placoderm dispersal events. Such scenarios of biogeographic evolution can only be tested, however, in the light of a phylogenetic framework for the group and further data from other clades.

## SILURIAN-DEVONIAN GLOBAL RECONSTRUCTIONS

Palaeogeographic reconstructions produced using palaeomagnetic and faunal data reveal that Euramerica (also known as Laurussia) formed in the Early Silurian (Wenlock) as a result of the collision of Baltica, Avalonia and Laurentia (Cocks and Torsvik 2002; Scotese and McKerrow 1990). These terranes and osteostracan bearing localities are illustrated in Plate 1, figure A1. Whilst confidence is placed upon this fusion and its timing, other aspects of palaeogeography pertinent to the stem-gnathostomes are less certain. During Silurian-Devonian times, the Arctic archipelago of Svalbard (including Spitsbergen) was associated with Greenland as part of Laurentia, whilst Severnaya Zemlya migrated slightly north of Baltica (Cocks and Torsvik 2002; 2005). The majority of Osteostraci and Heterostraci were therefore distributed across the Euramerica continent, which was associated with Kara (i.e. Severnaya Zemlya). The non-Euramerican Osteostraci are from the Tuva and Khakassia Republics, in the south of present day Siberia (Afanassieva and Janvier, 1985; Sansom *et al.* 2008). Interpretations of Tuva and Khakassia Siluro-Devonian palaeogeography vary. They have traditionally been considered as part of the north-east margin of the Siberian terrane which was itself located north-east of Euramerica (Cocks and Torsvik 2002; Scotese and McKerrow, 1990; Young 1990). Yolkin *et al.* (2003) considered Tuva to be part of a separate microterrane – Tuva-Mongolia – located south of

Siberia. The preferred opinion is that of Şengör *et al.* (1993) and Cocks and Torsvik (2007) who considered the peri-Siberian terranes of the Altai-Sayan folded region (including Tuva and Khakassia) as forming a northern island arc, which accreted to the Siberian mainland during the Silurian and Devonian. West-Sayan (including Khakassia, home to *Ilemoraspis*) became accreted during the Late Silurian, whilst Tuva-Mongolia (home to *Tannuaspis* and *Tuvaspis*) became accreted in the Early Devonian. The peri-Siberian terranes are called Altaids. Of the non-Euramerican Heterostraci, the Amphiaspidida were distributed across the terrane of Siberia proper.

The situation for the southern continents is less certain still. Galeaspids would have been distributed across North China, South China and Tarim, yet little consensus exists over the palaeogeography of these terranes during the Siluro-Devonian. Rong *et al.* (2003), Scotese and McKerrow (1990) and Pan *et al.* (1996) agreed that Tarim, North China and South China were separate terranes during the Palaeozoic because of their endemic faunas. South China is reconstructed as being near Australia but North China has fewer palaeomagnetic data and is more difficult to place. Wang (1993) considered the South China continent as being composed of South-eastern China and South China areas and the Qinling-Longmenshan sea (Pl. 1, fig. A2).

The details of the various palaeogeographic reconstructions can vary, for example, the precise locations and orientations of terranes. Confidence surrounds the more basic tenets i.e. the independent nature of the terranes relevant to the ostracoderm faunas during the Silurian and Devonian (as described above). Thus, while the lack of clarity over details is of concern to those unravelling the nature of the tectonic events leading to modern terranes, it is not pertinent to biogeographic scenarios considered here.

## PALAEOBIOGEOGRAPHIC RECONSTRUCTION

In order to reconstruct vicariance and dispersal events within the Osteostraci and Galeaspida, generic level phylogenies are used. Recent analysis of the galeaspids by Zhu and Gai (2006) provided the first phylogenetic framework for the entire group. Thirty-eight terminal taxa were included, representing 49 genera. These groups and genera are shown in Table 1, along with their distribution (basin and terrane).

The phylogenetic analysis of Sansom (2009) provided a comprehensive phylogenetic framework for the Osteostraci. In addition to the 65 terminal taxa (representing 60 genera) of Sansom (2009), "*Cephalaspis*" *novascotiae* Denison, 1955, is included because of its palaeobiogeographic isolation (the only osteostracan known from Nova Scotia, western part of the Avalonia palaeoterrane). Phylogenetic analysis using the criteria and dataset of Sansom (2009), with the addition of "*C.*" *novascotiae* (Appendix) identifies "*C.*" *novascotiae* as a generalised cornuate, in a polytomy with *Zychiaspis* and *Pattenaspis*.

The phylogenies for galeaspids and osteostracans are used as the basis upon which to reconstruct palaeobiogeography. The terminal taxa of the cladograms are substituted with their distributions, once at basin/local region level, and a second time at the level of terrane. The geographic areas of clades and ancestral lineages is then reconstructed using Fitch optimisation (Lieberman 2000; Fitch 1971). The resulting cladograms (Pl. 1, figs B-C) are colour-coded to illustrate the optimised ancestral area(s) of nodes and lineages.

#### *Osteostracan palaeobiogeography*

For the Osteostraci, the palaeobiogeographic reconstructions show the same pattern at both the basin (Pl. 1, fig. B1) and terrane levels (Pl. 1, fig. B2). The ancestral area of the Osteostraci is reconstructed as extending over a large area of Euramerica (Welsh Borderlands/Scotland/Østlandet/Spitsbergen/Nunavut). The Ateleaspididae are restricted to Østlandet (Eastern Norway) and Scotland. The genera *Hemicyclaspis* and *Cephalaspis* are both



widespread. The diversification of the three main orders of Osteostraci (Zenaspidida, Benneviaspidida and Thyestiida) is reconstructed as having occurred in Spitsbergen (Svalbard). The Zenaspidida fauna are known from across Euramerica and are identified as pandemic. Within the Zenaspidida, the Zenaspididae have a Podolian (Ukraine) centre of diversification whilst the Escuminaspidinae represent a separate Middle Devonian dispersal event. Most other clades, with the exception of the generalised cornuates (*Hildenaspis*, *Mimetaspis*, *Pattenaspis*, *Zychaspis* and “*C.*” *novaescotiae*), demonstrate a high degree of endemism such as “unnamed group D” (Sansom 2009, table 3), which is restricted to Laurentia. The Thyestiida consists largely of forms from across Baltica terrane (Østlandet, Baltic and Timan basins). Three dispersal events from the terrane of Baltica to Avalonia are identified for the Thyestiida from the Welsh Borderlands. Within the Thyestiida, the Kiaeraspididae represent a highly endemic clade, being restricted entirely to the Spitsbergen basin. The Benneviaspidida are also highly endemic, restricted almost entirely to the Spitsbergen basin. *Benneviaspis sensu lato* and *Securiaspis* represent exceptions, spreading to Britain, and in the case of the former, Podolia. In the Silurian, tremataspidid (Thyestiida) fauna dispersed to Kara (Severnaya Zemlya) from Baltica, whilst in the Devonian, benneviaspidid fauna dispersed from Spitsbergen, perhaps indicating a shifting position of Kara in relation to these terranes during the Siluro-Devonian. The only other osteostracan from Severnaya Zemlya, the Devonian *Ungulaspis arctoa* (Afanassieva and Karatajute-Talimaa, 1998), does not have enough diagnostic features to ascertain its affinities.

The osteostracans from the Altai-Sayan area of Siberia (*Tannuaspis* and *Ilemoraspis*) represent a conflict between palaeobiogeography and phylogeny (Sansom *et al.* 2008) which is not informed upon here. They have previously been considered as monophyletic (Afanassieva and Janvier 1985; Mark-Kurik and Janvier 1997) yet new anatomical data for *Ilemoraspis* highlighted serious inconsistencies with this relationship (Sansom 2008; Sansom *et al.* 2008). Furthermore, this monophyly is contradicted by parsimony studies including all Osteostraci

(Sansom 2009). Here, two inter-continental dispersal events are necessary from Euramerica to the peri-Siberian terranes (Altaids) which is surprising given not only the palaeogeographic separation between the two but also the absence of Osteostraci from the intervening amphiaspid heterostracan province of continental Siberia. Both of the dispersals to the Altai-Sayan are from northern parts of Euramerica (Timan/Baltic).

A scenario of osteostracan palaeobiogeographic evolution can therefore be proposed. In the Silurian, non-cornuate Osteostraci are known across central Euramerica whilst the Thyestiids are known across Eastern Euramerica (Baltica, and, in the Příklad, Avalonia) and Kara. By the Early Devonian, the non-cornuates are extinct and the Thyestiida have split into the tremataspidids (confined to Timan and Altai-Sayan) and the kiaeraspidids (confined to Spitsbergen). The Zenaspidida are widespread across Euramerica whilst the Benneviaspidida are restricted to East Euramerica/Kara and the unnamed clade D is restricted to west Euramerica. In the Middle/Late Devonian, only the escuminaspidids (Zenaspidida) remain, restricted to central Euramerica. *Ilemoraspis* remains a potential exception (Sansom *et al.* 2008).

#### *Galeaspid palaeobiogeography*

For the Galeaspida, the palaeobiogeographic patterns at the basin and terrane levels show very different patterns. At the basin level (Pl. 1, fig. C1), all Galeaspida appear to be pandemic. The ancestral area is reconstructed as lying across the Chaoxian/Changxing and Kalpin areas. The Silurian Galeaspida (“basal” galeaspids and some Eugaleaspidiformes) show very little consistency with palaeobiogeography and are reconstructed as widespread and pandemic. The Polybranchiaspidida (Polybranchiaspidiformes and Huananaspidiformes) also show little consistency with palaeobiogeography and are reconstructed as diversifying in Qujing, Yunnan. At terrane level (Pl. 1, fig. C2), a much clearer pattern is seen in the Galeaspida. The terranes (Tarim, Qinling-Longmenshan, Southeastern China and South China, here including North

Vietnam) correspond to those considered by Wang (1993). The ancestral area is reconstructed as Tarim/SE China with “basal” galeaspids (Hanyangaspidae, Xiushiaspidae and Dayongaspidae) being present across these two terranes. Silurian Eugaleaspidiformes are present in SE China and disperse to South China in the Devonian. The Polybranchiaspidida also disperse to South China in the Devonian in a single event. The fauna from Qinling-Longmenshan do not display monophyly and represent four separate dispersal events from South China. Given the strong correlation between palaeobiogeography and phylogeny at the terrane level, the sister-relationship between *Geraspis* and *Kwangnanaspis* is called into question. In the Middle and Late Devonian, far fewer galeaspids are preserved, with Polybranchiaspida of uncertain affinities known from Liujiang (South China) and Ningxia (North China) respectively. Galeaspid microremains (e.g. Karatajute-Talimaa *et al.* 2006; Wang *et al.* 2005) are not considered here as they are too poorly characterised to be included in a phylogeny.

#### *Heterostracan palaeobiogeography*

Certain clades of Heterostraci have previously been considered in terms of their palaeobiogeography, but in the absence of a comprehensive generic level phylogeny (Blieck *et al.* 1991; Elliott *et al.* 2007; Pernègre and Elliott 2008), it is not currently possible to reconstruct scenarios for the entire group as is done for the Galeaspida and Osteostraci above. Following the phylogeny of Janvier (1996a), the ancestral area for the Heterostraci could be identified as across Euramerica due to the Welsh Borderlands/North American distribution of the “basal” and problematic genera. The Cyathaspidiformes are a widespread and pandemic group. They are considered as sister group to the amphiaspids, an endemic clade known from across Siberia (Novitskaya 1971) and Severnaya Zemlya (Blieck *et al.* 2002). Blieck (1984) reconstructed scenarios of palaeobiogeographic evolution in the Pteraspidiformes and established a western Euramerican distribution for the Protopteraspididae and an eastern Euramerican distribution for

the Pteraspidae. The Pteraspidae are also present in Taimyr, south (present day north) Siberia. The Protaspidae are an endemic clade restricted to the USA. The Psammosteidae are a large and diverse clade. They are widespread throughout Euramerica in the Early, Middle and Late Devonian. Halstead and Turner (1973; Halstead Tarlo 1967) reconstructed a Baltic centre of psammosteid radiation on the basis of ‘migration’ routes. Overall, the Heterostraci are largely pandemic in terms of their distributions. Exceptions include the endemic amphiaspids and protaspids.

### *Discussion*

In the first instance, palaeobiogeographic reconstruction for the two clades enables a test of the veracity of the proposed phylogenetic frameworks using a data source independent of morphology. For the Osteostraci, consistency between phylogeny and palaeobiogeography (and thus endemicity) is identified in the Ateleaspididae, Benneviastida and Thyestiida. These clades are identified as having strong support from the phylogenetic data matrix in terms of decay indices (Pl. 1, fig. B). Other clades such as the Escuminaspididae, Zenaspididae and generalised cornuates show less consistency between phylogeny and palaeobiogeography. In the case of the Zenaspididae and generalised cornuates, their intrarelationships are the less well supported aspects of the phylogeny. The Escuminaspididae on the other hand are a well supported and stratigraphically consistent monophyletic clade. As such, it is proposed that the Escuminaspididae represent a true expansion of palaeogeographic range, whilst the cosmopolitan nature of the Zenaspididae and generalised cornuates might be an artefact of inexact phylogeny.

Galeaspida decay indices (Pl. 1, fig. C) were calculated from the data matrix of Zhu and Gai (2006). The branches of the phylogeny with the highest support (e.g. Eugaleaspidiformes, Eugaleaspididae, Polybranchiaspidida) occur at times of palaeogeographic transition, further supporting the endemism of these clades. For the clades that show less consistency between

palaeobiogeography and phylogeny (i.e. within “basal” Galeaspida and within Polybranchiaspidida), there is again less phylogenetic support in terms of decay indices. An exception is the Duyunolepididae, which are both widespread in South China and well supported. The monophyly of *Duyunolepis*, *Paraduyunaspis* and *Neoduyunaspis* was assumed however, in the analysis of Zhu and Gai (2006).

Between the osteostracans and the galeaspids, the choice of rank of distributions for the reconstruction has different outcomes. For the Osteostraci, a strong correlation is observed between the phylogeny and palaeobiogeography at both the narrow level (basin/local region) and broad level (terrane), with no significant difference between the approaches. In contrast, the Galeaspida show strong correlation with palaeobiogeography only at the level of terrane and not at the level of basin. Both observations are consistent with current understanding of palaeogeography. The terranes of Baltica, Avalonia and Laurentia are known to have accreted to form Euramerica either at, or before, the first recorded occurrences of Osteostraci (Wenlock). Results here indicate that the barrier to movement between these terranes, within the continent of Euramerica, was no greater than the barrier to movement within the terranes themselves (i.e. between basins). Conversely, in the case of the terranes of South China and Tarim, there was separation throughout the Silurian and Devonian. This is reflected in the marked endemism of galeaspids at terrane level. Movement within these terranes (i.e. between basins) is demonstrated to be common however.

The Heterostraci serve as a comparable source of data to the Osteostraci (above). Both groups show certain similarities in their overall pattern: (1) they have a broad ancestral area across Euramerica; (2) they expand geographical ranges in the Early Devonian with some clades being widespread (zenaspidids and cythaspidids) and some being endemic (kiaeraspidids, thyeistiids, protaspids and amphiaspidids); (3) both have western Euramerican clades (unnamed clade D and protopteraspidids) and eastern Euramerican clades (benneviaspidids, thyeistiids, pteraspidids and

psammosteids); (4) a single family from each survives and radiates in the Middle/Late Devonian (escuminaspidids and psammosteids). Generally speaking, the Heterostraci display less endemism than the Osteostraci.

## PALAEOGEOGRAPHIC PROCESSES

The proposed phylogenies and palaeobiogeographic reconstructions not only enable consideration of evolutionary history of the clades, but also impact upon palaeogeographic considerations. Palaeobiogeographic reconstruction can constrain the timing of the fusion of the major northern continents. The Østlandet/Scotland distribution of the Ateleaspididae suggests that the fusion of Baltica and Laurentia and subsequent closure of the Iapetus Ocean occurred before the Wenlock. Furthermore, the three thyestiid dispersal events from Baltica to Avalonia indicate a close relationship between these terranes before the Wenlock. Data from another group of stem-gnathostomes, the euconodonts, also support the Early Silurian closure of the Iapetus Ocean (Armstrong and Owen 2002). Regarding the minor terranes, the Heterostraci and Osteostraci provide different, but not conflicting, perspectives upon the palaeogeography of Kara (Severnaya Zemlya). In the case of Osteostraci, a shifting association from Baltica in the Silurian (tremataspid fauna) to Laurentia in the Devonian (benneviaspidid fauna) is suggested, whilst heterostracan data support Kara's position as a palaeogeographic "staging-post" for migration between Euramerica and Siberia (Blieck *et al.* 2002). Given the otherwise endemic nature of the thyestiids, the phylogenetic and palaeobiogeographic reconstructions suggest a close relationship between Baltica and Altai-Sayan terranes in the Devonian. Furthermore, the occurrence of the thelodont *Loganellia tuvaensis* in both Tuva and Greenland, a Silurian relationship between Laurentia and Altai-Sayan terranes is suggested (Žigaitė and Blieck 2006). Both would, however, fly in the face of the palaeomagnetic data which indicate that the Altai-Sayan terranes were accreted to the northeast of Siberia, which were in turn northeast of Baltica (Cocks and

Torsvik 2007). Close phylogenetic relationships between *Trewinia* and *Balticaspis*, from the Eifelian of Scotland and the Baltic respectively, support the hypothesis of a faunal connection between these two basins in the Middle Devonian (Newman and Trewin 2008).

In the southern continents, four separate dispersal events are reconstructed as having occurred from the South China terrane to Qinling-Longmenshan. This therefore calls into question the independence of these two regions during the Early Devonian. Furthermore, a close association between Tarim and the southeastern China region is suggested by the reconstructions of the 'basal' galeaspids.

#### *Modified Brooks Parsimony Analysis*

Qualitative observations based on the palaeobiogeographic reconstructions help to understand palaeogeographic processes and constrain the timing of certain events. The palaeogeographic relationships between basins and terranes can be further assessed on the basis of parsimony. A modified Brooks Parsimony Analysis (BPA) (Lieberman 2000; Lieberman and Eldredge 1996) is applied to the phylogenetic and biogeographic reconstructions for the Osteostraci and Galeaspida. Using the phylogenies and Fitch optimisation of geographic areas, vicariance and dispersal matrices are constructed for the Galeaspida and Osteostraci at both the terrane and basin levels (Appendix). These matrices are then subjected to heuristic search methods in PAUP (Swofford 2002). The most parsimonious solutions for relationships between palaeogeographic areas are identified under the criterion of either vicariance or dispersal. The Galeaspida and Osteostraci are considered as ecological equivalents - they both occupied shallow marine, marginal marine and freshwater environments. They are similar in terms of their gross morphology and are hypothesised to be broadly bottom-dwelling filter-feeding benthos/detritophages (Afanassieva 1992; Janvier 1985; 1996a). As such, similar patterns should

be observed in the vicariance and dispersal trees of each, and any differences due to abiotic influences.

*Results.* Strict consensus trees for vicariance and dispersal analyses at both basin and terrane level are shown in Text-figure 1. Datasets have a skew of a magnitude significantly greater than expected by chance at the 0.01 level, as indicated by g1 statistics of random datasets (Hillis and Huelsenbeck 1992), thus indicating a strong biogeographic signal. An exception is the galeaspid terrane level analysis, for which the vicariance dataset skew is significant at the 0.05 level only, and the dispersal analysis, which is not significant at the 0.05 level.

For the Osteostraci, the same pattern is seen for both the vicariance and geodispersal analyses. At the basin level (Text-fig. 1A), close relationships are suggested between the Timan, Baltic and Altaid basins. Furthermore, close relationships are suggested between the central Euramerican basins (Scotland, Welsh Borderlands, Østlandet, Spitsbergen and north Nunavut). The affinity of a number of minor osteostracan localities (Mackenzie Mountains, Severnaya Zemlya and Rhenish Massif) remain unclear. At the terrane level, Laurentia and Baltica form a well-supported sister relationship with Avalonia as outgroup. This outcome is contrary to accepted palaeogeographic reconstructions which consider the fusion of Baltica and Avalonia as having occurred earlier than the fusion of Baltica-Avalonia with Laurentia (Cocks and Torsvik 2005). With movement between terranes having been demonstrated to have been as frequent as movement between basins however, the significance of this observation of a close Baltica-Laurentia relationship is difficult to assess.

For the Galeaspida, a well-resolved pattern of biogeographic relationships is seen in the vicariance analysis at basin level. The basins of the South China terrane (except northern Vietnam) are found to be monophyletic. The affinities of the Yanmenba-Jiangyou (Qinling-Longmenshan) and Xiushui (southeastern China) basins remains unclear. Close relationships



between the Kalpin, Chaoxian/Changxing and Dayong/Xiushan regions are suggested, indicating, along with the terrane analysis, an association between Tarim and southeastern China. The dispersal analysis shows no strong patterns.

*Discussion.* By comparing the vicariance and geodispersal patterns, it is possible to consider the processes involved in the palaeobiogeographic evolution of the clades. In the case of the Osteostraci, strong similarities between the two trees indicate that the same processes that caused vicariance events also caused geodispersal events i.e. a close relationship in the vicariance tree predicts that the barrier between two geographic units was the first to form whilst in the dispersal tree predicts that the barrier was the first to fall (Lieberman 2000). In the case of Middle Devonian trilobites (Lieberman and Eldredge 1996), correlation between vicariance and dispersal trees was suggested to result from cyclic changes such as those due to sea-level transgression and regression events. The same Devonian sea-level cycles (Johnson *et al.* 1985) could well be responsible for the patterns observed in the Osteostraci.

The Galeaspida demonstrate a different pattern to that observed in the Osteostraci. The galeaspid vicariance tree shows a strong pattern whilst the dispersal tree constitutes an unresolved bush. The finding that vicariance is the predominant cause of galeaspid biogeographic distribution indicates that rifting of the Chinese palaeoterranes is the process responsible for galeaspid distributions. A comparable situation is observed in Early Cambrian trilobites (Lieberman 1997), the distributions of which have been suggested to result from vicariance events following rifting of palaeoterranes.

## CONCLUSIONS

In both the Galeaspida and the Osteostraci, a correlation between phylogeny and palaeobiogeographic is observed. As such, a source of information independent of morphology is

used to attach a greater level of confidence to the phylogenies of Sansom (2009) and Zhu and Gai (2006). Furthermore, palaeobiogeographic reconstruction enables investigation of the proposed palaeogeographic events and processes occurring in the Siluro-Devonian. ‘Between basin’ movement and ‘between terrane’ movement occur at a comparable level within the Osteostraci, whilst for the Galeaspida, within terrane movement is far more dominant. This observation supports the concept of separate Chinese palaeoterranes and a fusion of Euramerica prior to the Wenlock. The same pattern is demonstrated by the results of modified Brooks Parsimony Analysis. Differences between the vicariance and dispersal trees of the modified BPA indicate that sea-level cycles are responsible for osteostracan distribution whilst vicariance due to rifting of palaeoterranes is responsible for galeaspid distribution. Further processes may well account for the distribution patterns, namely distribution through time, such as facies bias (Sansom 2008).

Smith *et al.* (2002) suggested that the heavily armoured dermal skeleton of ostracoderm stem-gnathostomes (e.g. Heterostraci, Galeaspida, Osteostraci) limited the dispersal capacity of these clades. A limited role of dispersal in palaeobiogeographic processes and broad endemism identified here are consistent with this hypothesis, and subsequently, the hypothesis that the demise of the Paleozoic jawless vertebrates was due to their limited dispersal capacity in comparison to their jawed ‘competitors’ (Long 1993). Addition of heterostracan and placoderm distributions and phylogenies to the modified BPA will undoubtedly expand the dataset and enable a test of palaeobiogeographic scenarios proposed. Unfortunately, this is not currently possible in the absence of definitive data for these clades.

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## EXPLANATION OF PLATE 1

Palaeogeography and palaeobiogeographic reconstructions of the Osteostraci and Galeaspida.

Fig. A. Middle Devonian palaeogeography as reconstructed by the Scotese Palaeomap project (<http://www.scotese.com>, Scotese and McKerrow 1990) in west sub-equatorial perspective with osteostracan localities and terranes (A1) and equatorial Tethys perspective with galeaspid localities and terranes (A2).

Fig. B. Palaeobiogeographic reconstruction for one of the most parsimonious solutions to osteostracan phylogeny (Sansom (2009) with the addition of "*C.*" *novascotiae* (Appendix)) at basin level (B1) and terrane level (B2). Labelled clades are Ateleaspididae (Ate), Zenaspidida (Zen), Benneviastidida (Ben), Thyestiida (Thy) and Unnamed Clade D (D).

Fig. C. Palaeobiogeographic reconstruction for one of the most parsimonious solutions to galeaspid phylogeny (adapted from Zhu and Gai (2006)) at basin level (C1) and terrane level (C2). Major clades are Eugaleaspidiformes (Eug), Polybranchiaspidiformes (Poly) and Huananaspidiformes (Huan), of which, the later two constitute the Polybranchiaspidida.

Where \* indicates a branch with a decay index (Bremer support) greater than 1 in the comprehensive analysis, and + indicates a decay index greater than 1 in the reduced taxa analysis of Sansom (2009, fig. 6). Palaeomaps by R. Blakey (<http://jan.ucc.nau.edu/~rcb7/RCB.html>).

**TEXT-FIG. 1.** Strict consensus trees of the most parsimonious solutions of relationships between geographic areas as predicted by modified Brooks Parsimony Analysis (Lieberman, 2000) where vicariance analysis is left and dispersal analysis is right. A, Osteostraci at basin level; B, Osteostraci at terrane level; C, Galeaspida at basin level; D, Galeaspida at terrane level.

**TABLE 1.** List of osteostracan (left) and galeaspid (right) genera and distributions at both basin level at terrane level where A is Avalonia, Al is Altaids (Tuva and Khakassia), B is Baltica, L is Laurentia, K is Kara, Ql is Qinling-Longmenshan, S is South China, SE is Southeast China and T is Tarim. North Nunavut includes the osteostracan bearing localities on Somerset Island and Prince of Wales Island whilst Mackenzie Mountains concerns principally the “Man on the Hill” locality. The Østlandet region includes the osteostracan bearing localities in the region of Oslo i.e. Nes, Sundvollen and Jeløya.

OSTEOSTRACI	DISTRIBUTION	OSTEOSTRACI	DISTRIBUTION	GALEASPIDA	DISTRIBUTION
<i>Ateleaspis</i>	Scotland L	<i>Auchenaspis</i>	Welsh B. lands A	<i>Hanyangaspis</i>	Chaoxian/Changxing SE
<i>Aceraspis</i>	Østlandet B	<i>Thyestes</i>	Baltic/Gotland B	<i>Nanjiangaspis</i>	Kalpin T
<i>Hirella</i>	Østlandet B	<i>Witaaspis</i>	Baltic B	<i>Kalpinolepis</i>	Kalpin T
<i>Hemicyclaspis</i>	Welsh B. lands A	<i>Tyriaspis</i>	Østlandet B	<i>Konoceraspis</i>	Dayong/Xiushan SE
	Østlandet B	<i>Aestiaspis</i>	Baltic B	<i>Dayongaspis</i>	Dayong/Xiushan SE
	North Nunavut L	<i>Dartmuthia</i>	Baltic B	<i>Platycaraspis</i>	Kalpin T
<i>Hemiteleaspis</i>	Scotland L	<i>Saaremaaspis</i>	Baltic B	<i>Changxingaspis</i>	Chaoxian/Changxing SE
<i>Cephalaspis lyelli</i>	Scotland L	<i>Timanaspis</i>	Timan B	<i>Xiushuiaspis</i>	Xiushui SE
<i>C. cradleyensis</i>	Welsh B. lands A	<i>Sclerodus</i>	Welsh B. lands A	<i>Microphymaspis</i>	Kalpin T
	Spitsbergen L	<i>Dobraspis</i>	Timan B	<i>Sinogaleaspis</i>	Xiushui SE
<i>Parameteoraspis</i>	Spitsbergen L	<i>Oeselaspis</i>	Baltic B	<i>“S.” xikengensis</i>	Xiushui SE
	North Nunavut L		Sev. Zemlya K	<i>“S.” zhejiangensis</i>	Chaoxian/Changxing SE
<i>Hildenaspis</i>	Rhenish Massif A	<i>Tremataspis</i>	Baltic B	<i>Meishanaspis</i>	Chaoxian/Changxing SE
	Spitsbergen L		Sev. Zemlya K	<i>Anjiaspis</i>	Chaoxian/Changxing SE
<i>Pattenaspis</i>	Spitsbergen L	<i>Balticaspis</i>	Baltic B	<i>Yunnanogaleaspis</i>	Qujing S
	Podolia B	<i>Camptaspis</i>	Utah/Wyoming L	<i>Nochelaspis</i>	Qujing S
	Rhenish Massif A	<i>Didymaspis</i>	Welsh B. lands A	<i>Pterogonaspis</i>	Qujing S
<i>Mimetaspis</i>	Spitsbergen L	<i>Ectinaspis</i>	Spitsbergen L	<i>Tridenaspis</i>	Liujing S
	Podolia B	<i>Escuminaspis</i>	Gaspé L	<i>Eugaleaspis</i>	Qujing S
<i>Zenaspis</i>	Welsh B. lands A	<i>Hapilaspis</i>	Spitsbergen L		Liujing S
	Podolia B	<i>Ilemoraspis</i>	Khakassia Al		Dayong/Xiushan SE
	Spitsbergen L	<i>Levesquaspis</i>	Gaspé L	<i>Polybranchiaspis</i>	Qujing S
	Scotland L	<i>Securiaspis</i>	Welsh B. lands A		N. Vietnam S
<i>Diademaspis</i>	Spitsbergen L		Scotland L	<i>Siyingia</i>	Qujing S
	Podolia B	<i>Spangenhelmaspis</i>	Spitsbergen L	<i>Laxaspis</i>	Qujing S
<i>Machairaspis</i>	Spitsbergen L	<i>Superciliaspis</i>	Mackenzie MTs L		N. Vietnam S
	Podolia B	<i>Tannuaspis</i>	Tuva Al	<i>Damaspis</i>	Qujing S
	North Nunavut L	<i>Tauraspis</i>	Spitsbergen L	<i>Diadongaspis</i>	Qujing S
<i>Tegaspis</i>	Spitsbergen L	<i>Trewinta</i>	Scotland L	<i>Cyclodiscaspis</i>	Guizhou/NE Yunnan S
	Podolia B	<i>Yvonaspis</i>	Gaspé L	<i>Dongfangaspis</i>	Yanmenba-Jiangyou Ql
<i>Scolenaspis</i>	Spitsbergen L	<i>Waengsjoeaspis</i>	Spitsbergen L	<i>Bannhuanaspis</i>	N. Vietnam S
	Podolia B		Mackenzie MTs L	<i>Clarorbis</i>	Liujing S
<i>Zychiaspis</i>	Podolia B	<i>Wladysagiita</i>	Podolia B	<i>Geraspis</i>	Chaoxian/Changxing SE
<i>Stenstopelta</i>	Welsh B. lands A		Welsh B. lands A	<i>Kwangnanaspis</i>	Qujing S
	Podolia B	<i>“Cephalaspis”</i>	Nova Scotia A	<i>Duyunolepis</i>	Guizhou/NE Yunnan S
<i>Ukrainaspis</i>	Podolia B	<i>novaescotiae</i>		<i>Paraduyunolepis</i>	Guizhou/NE Yunnan S
<i>Benneviaspis</i>	Spitsbergen L			<i>Neoduyunolepis</i>	Guiyang S
	Podolia L			<i>Lopadaspis</i>	Liujing S
	Sev. Zemlya K			<i>Zhaotongaspis</i>	Guizhou/NE Yunnan S
<i>“B.” lankesteri</i>	Welsh B. lands A			<i>Wenshanaspis</i>	Qujing S
<i>“B.” anglica</i>	Welsh B. lands A			<i>Antiquisagittaspis</i>	Liujing S
<i>“B.” longicornis</i>	Spitsbergen L			<i>Sanchaspis</i>	Qujing S
<i>Hoelaspis</i>	Spitsbergen L			<i>Gumuaspis</i>	Qujing S
<i>Severaspis</i>	Sev. Zemlya K			<i>Pentathyraspis</i>	Qujing S
<i>Boreaspis</i>	Spitsbergen L			<i>Microhoplonaspis</i>	Qujing S
<i>“B.” ceratops</i>	Spitsbergen L			<i>Sinoszechuanaspis</i>	Yanmenba-Jiangyou Ql
<i>“B.” intermedia</i>	Spitsbergen L			<i>Macrothyrapis</i>	Qujing S
<i>Belonaspis</i>	Spitsbergen L			<i>Lungmenshanaspis</i>	Yanmenba-Jiangyou Ql
<i>Dicranaspis</i>	Spitsbergen L				Guizhou/NE Yunnan S
<i>Spatulaspis</i>	Spitsbergen L			<i>Qingmenaspis</i>	Qujing S

<i>Kiaeraspis</i>	Spitsbergen	L
<i>Norselaspis</i>	Spitsbergen	L
<i>Axinaspis</i>	Spitsbergen	L
<i>Nectaspis</i>	Spitsbergen	L
<i>Acrotomaspis</i>	Spitsbergen	L
<i>Gustavaspis</i>	Spitsbergen	L
<i>Procephalaspis</i>	Baltic/Gotland	B

<i>Nanpanaspis</i>	Qujing	S
<i>Huananaspis</i>	Qujing	S
<i>Asiaspis</i>	Liuqing	S
<i>Sanqiaspis</i>	Yanmenba-Jiangyou	Ql
	Guizhou/NE Yunnan	S
<i>Wumengshanaspis</i>	Guizhou/NE Yunnan	S
<i>Gantarostrataspis</i>	Qujing	S





