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To cite this article: Emma Randle & Robert S. Sansom (2017) Exploring phylogenetic relationships of Pteraspidiformes heterostracans (stem-gnathostomes) using continuous and discrete characters, *Journal of Systematic Palaeontology*, 15:7, 583-599, DOI: [10.1080/14772019.2016.1208293](https://doi.org/10.1080/14772019.2016.1208293)

To link to this article: <https://doi.org/10.1080/14772019.2016.1208293>



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Exploring phylogenetic relationships of Pteraspidiiformes heterostracans (stem-gnathostomes) using continuous and discrete characters

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(Received 7 January 2016; accepted 20 June 2016; published online 20 July 2016)

Ostracoderms are a paraphyletic group of extinct jawless fishes comprising the gnathostome stem and are fundamental to our understanding of early vertebrate evolution. However, only a handful of these clades have robust phylogenies in place, hindering our interpretation of early vertebrate histories. A new phylogeny is proposed for the Pteraspidiiformes – the largest and most-studied clade of heterostracan ostracoderms. Difficulties such as large amounts of missing data and the limited morphological variability within the group have led us to explore different coding strategies such as the inclusion of quantitative data and implied weighting. We present a new comprehensive data set including all described genera of Pteraspidiiformes (47 taxa) analysed using discrete characters only, a combination of discrete and continuous characters, and gap-coding strategies (transforming the continuous into discrete characters), along with a Bayesian analysis. Two representatives of the Psammosteidae (*Drepanaspis* and *Psammosteus*) are also incorporated within the analysis to elucidate their inclusiveness within the Pteraspidiiformes. Well-resolved trees are only achieved under re-weighted (implied weighting) analyses. Here, we show that many ‘classic’ Pteraspidiiformes clades hold true under our different coding methods, with the implied weighting of discrete characters and inclusion of continuous characters giving very similar topologies. In all instances, the Psammosteidae are found to belong within the Pteraspidiiformes, nested with the Spitsbergen genera *Doryaspis*, *Xylaspis* and *Woodfordaspis*. Gap coding, however, results in a different tree topology to other analyses, perhaps due to the high sensitivity to missing data. Our results indicate that careful consideration and justifications should be applied to quantitative characters when reconstructing relationships of homoplastic ostracoderms. Superfamily Doryaspidae superfam. nov. is introduced.

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Keywords: Heterostraci; Pteraspidiiformes; Psammosteidae; phylogeny; Silurian; Devonian

Introduction

Phylogenetic relationships of fossil jawless vertebrates (Agnatha) are imperative to our understanding of vertebrate evolution. Bony jawless vertebrates (ostracoderms) constitute the majority of the gnathostome (jawed vertebrate) stem group. Jawed vertebrate novelties such as acellular and cellular bone, a bony dermoskeleton, a differentiated gut, a mineralized neurocranium and paired pectoral fins, arose first within the jawless ostracoderms (i.e. heterostracans, thelodonts, anaspids, galeaspids and osteostracans) (Donoghue & Keating 2014). Identification of ostracoderm evolutionary dynamics along with their ancestral morphotypes will greatly improve our understanding of early vertebrate histories and thus the circumstances behind their diversification and the rise to dominance of gnathostomes.

Heterostraci are taxonomically the largest group of stem-gnathostomes and along with other pteraspidiiforms

have been interpreted as the most basal with a bony skeleton (Forey & Janvier 1993; Donoghue *et al.* 2000; Donoghue & Aldridge 2001; Janvier 2001; Donoghue & Keating 2014). In previous analyses they have been recovered as the sister clade to galaeaspids, osteostracans and jawed vertebrates, or as a paraphyletic group leading to these taxa (Donoghue & Smith 2001; Gess *et al.* 2006; Sansom *et al.* 2010; Blom 2012). However, despite being intensively studied over the past 150 years, the evolutionary relationships of the group are poorly understood, impeding our understanding of early vertebrate evolution. A solid phylogenetic framework for the Heterostraci would allow identification of pleiomorphic states and characters, which could in turn elucidate ancestral conditions on the gnathostome stem. Furthermore, a phylogeny would enable the incorporation of ghost ranges to studies of diversity through time (Sansom *et al.* 2015) and a test for scenarios of palaeobiogeography (Sansom 2009; Blicek 2011; Žigaitė & Blicek 2013). Historically, there are five

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major clades within the Heterostraci; Cyathaspididae, Amphiaspididae, Traquairaspididae, Psammosteidae and Pteraspidoformes, along with many *incertae sedis* genera of uncertain affinity (Halstead 1973; Janvier 1996). Only a handful of heterostracan phylogenies have been constructed, most of which concentrate on the ‘higher heterostracans’ – that is, Cyathaspididae and Pteraspidoformes.

Containing over 110 species and 47 genera (Dineley & Loeffler 1976; Elliott 1983, 1984; Blicek 1984; Ilyes & Elliott 1994; Elliott & Ilyes 1996; Elliott *et al.* 2000; Pernègre 2002, 2006; Novitskaya 2004; Pernègre & Goujet 2007; Pernègre & Elliott 2008; Voichyshyn 2011), Pteraspidoformes are the largest and most-studied group of heterostracans. They are relatively morphologically diverse, with a wide palaeogeographical range (Laurussia, Baltica, Kara and Avalonia) and a stratigraphical range from the Late Silurian to the Middle Devonian (Prìdoli-Givetian) (Blicek & Janvier 1999; Elliott *et al.* 2000; Novitskaya 2007; Sansom 2009; Sansom *et al.* 2015). The group is characterized as possessing a separate dorsal spine, a dorsal shield composed of several independent plates (dorsal, pineal, rostral and paired orbital, brachial and cornual plates), ornamentation of the dorsal shield in serrated, concentric rings, and supraorbital canals meeting behind the pineal region (Blicek 1984; Janvier 1996; Pernègre & Elliott 2008; Blicek *et al.* 1991). Within the group is a large variety of forms, some resembling their purported sister group, the cyathaspidids, and others taking more unusual forms such as *Doryaspis* with its ornamented cornual plates and long blade-like pseudorostrum (Pernègre 2002). Anchipteraspididae are the earliest members of Pteraspidoformes, appearing first in the Prìdoli of the Canadian Arctic (Elliott 1984). The latest occurring member of the group is *Helaspis*, found in the Yahatinda Formation of Givetian age in southern Alberta and British Columbia (Elliott *et al.* 2000). Despite being the most heavily studied and numerous heterostracan group, there is yet to be a phylogeny containing all described genera: only subsets of the taxa have been subjected to phylogenetic analyses (Ilyes & Elliott 1994; Pernègre 2002; Pernègre & Goujet 2007; Pernègre & Elliott 2008).

The close affinities of Pteraspidoformes and Psammosteidae have long been recognized, with many phylogenetic reconstructions considering them as sister groups (Halstead 1973; Janvier 1996). Similarities occur in the arrangement of head shield plates, such as separate dorsal, orbital, pineal, rostral, branchial and cornual plates, which are not seen in other heterostracan clades. Also, juvenile psammosteids have been found to possess no fields of tesserae between their plates, thus superficially resembling Pteraspidoformes (Blicek 1984; Janvier 1996). Previous studies have interpreted Psammosteidae as basal or sister taxon to Pteraspidoformes (Blicek 1984; Pernègre & Elliott 2008), while others have recovered them nested well with Pteraspidoformes (Janvier 1996; Pernègre

2002). The uncertainty of their placement means scenarios for heterostracan evolution are somewhat confused. For example, Tarlo (1964) envisaged a transition from tessellated forms such as *Tesseraspis* and *Kallostrakon* to Psammosteidae, with their ‘fields of tesserae’ a vestige of this heritage. If Psammosteidae are found to belong within Pteraspidoformes, then this scenario cannot be corroborated.

Cladistic analysis of Pteraspidoformes is made problematic by similarities in the combination and arrangements of their dermal plates. Many taxonomic distinctions are based on the dimensions of these plates, which are often continuously variable, rather than discrete, states. Anatomical features are often described as short, narrow, elongate, etc., descriptors that without quantification or point of reference are not replicable. One such example of ambiguity is the ratio of dorsal plate width to length, for which 0.7 has been arbitrarily used to distinguish between a broad or narrow dorsal plate (Pernègre & Goujet 2007). Continuous morphological variation such as this is hard to translate into meaningful and discrete cladistic characters and can often lead to uninformative and misleading character coding (Brazeau 2011). Adding to this is the large amount of missing data and poor preservation of some specimens which make the reconstruction of evolutionary histories difficult.

Characters used within phylogenetic analyses are generally discrete; for example, a feature is either present or absent, or is blue or green. There has been considerable debate as to the appropriateness of including continuous characters within cladistic analyses (see Thiele 1993; Rae 1998 for reviews). However, continuous characters can be phylogenetically informative: continuous variation of homologous features meets the requirements of cladistic characters (Thiele 1993; Rae 1998; Garcia-Cruz & Sosa 2006; Goloboff *et al.* 2006; Sansom 2008; Romano & Nicosia 2015). There are different methodologies for treating continuous data (Thiele 1993; Garcia-Cruz & Sosa 2006). Gap coding involves identifying gaps within a data set that represent boundaries between different character states. One example used by Sansom (2008) was to discretize continuous ratio data in his thyeistiid osteostracan phylogeny (another group of jawless vertebrates), identifying gaps in ordered data. These gaps were then translated into changes in character states. However, discretizing continuous data in this manner is problematic as the methods are highly sensitive to missing data and may shoehorn data into evolutionarily uninformative character states. Another method, advocated by Goloboff *et al.* (2006), is to include the raw continuous data within the phylogenetic analysis (this can be implemented in phylogenetic programs such as TNT; Goloboff *et al.* 2008).

Here, we undertake a comprehensive analysis of Pteraspidoformes phylogeny that includes all formally described

genera. Inclusion of Psammosteidae within Pteraspidiiformes is also investigated, with the hope of elucidating the position of this clade. Different coding methods are explored, including analyses with equally weighted characters, implied weighting and inclusion of quantitative data. Quantitative data are further subjected to different treatments including gap coding (transforming continuous data into discrete character states) and using the raw continuous values for taxa. The decision to include quantitative data was made in order to address directly continuous shape variation in Pteraspidiiformes dermal plates, which is often used for taxonomic discrimination. With our novel phylogeny, the stratigraphical and palaeobiogeographical occurrences of the Pteraspidiiformes are reviewed.

Previous phylogenetic analyses

One of the most comprehensive and thorough studies of pteraspidiiform phylogeny and evolutionary history is the monograph of Blicek (1984) in which he systematically described all currently known Pteraspidiiformes and considered their stratigraphical and palaeobiogeographical ranges. Two major groupings of Pteraspidiiformes were recognized based on characters such as the position and coverage of sensory canals, shape and contact of the pineal plate, rostral size and shape and margins of the plates: Pteraspidiidae and Protopteraspidiidae. Blicek (1984) also suggested that Psammosteidae is the sister lineage to Pteraspidiiformes (Fig. 1A). Blicek *et al.* (1991) revised the relationships of the major groupings and placed Pteraspidiiformes (pteraspids and anchipteraspids) with psammosteids in a group labelled 'APP'. APP was defined as having two separate dorsal and ventral plates, pineal and rostral plates and paired orbital, branchial and cornual plates, along with a complete pineal canal, which loops between the two branches of the supra-orbital canal, and three pairs of transverse commissures. However, the pineal canal of psammosteids is unknown, perhaps due to preservation, disarticulated nature of psammosteid fossil material or, as Blicek *et al.* (1991) suggested, migration of the canal from on the plates to the margins between the pineal and rostral plates. The Pteraspidiiformes phylogeny of Janvier (1996) was an amalgamation of evolutionary theories for the group at the time (Fig. 1B). Contrasting with Blicek's (1984) theory of Psammosteidae-Pteraspidiiformes sister group relationships, Janvier (1996) proposed that Psammosteidae is a derived clade within Pteraspidiiformes, with protaspids as a sister group based on the shared possession and arrangement of plates and general similarities to protaspid Pteraspidiiformes.

The first cladistic study to utilize global parsimony in a computerized analysis was undertaken by Ilyes & Elliott (1994). They focused on forms from the western USA

(Fig. 1C), citing concerns of convergent evolution amongst Pteraspidiiformes relating to ecology rather than phylogeny. A second phylogenetic analysis was undertaken by Pernègre (2002) (Fig. 1D) following a redescription of *Doryaspis*. *Drepanaspis* (a psammosteid heterostracan) was included within this analysis and placed as a sister taxon to *Doryaspis* nested well within the Pteraspidiiformes. The analysis included a small sample of Pteraspidiiformes but supported Janvier's (1996) view that the Psammosteidae were derived Pteraspidiiformes. Pernègre & Goujet's (2007) analysis following re-evaluation of *Gigantaspis* included many more characters exploring the variation and differences of Pteraspidiiformes morphology (Fig. 1E). In their analysis, *Gigantaspis* was recovered as the sister group to *Europrotaspis* and protaspid taxa. The most recent study (Pernègre & Elliott 2008) focused on a subset of Pteraspidiiformes taxa that are morphologically well known (i.e. are known from many specimens, are articulated, or a reliable reconstruction can be made). They recognized five major clades within the Pteraspidiiformes: Anchipteraspidiidae, a paraphyletic Protopteraspidiidae, Pteraspidiidae, Gigantaspidiidae and Protaspidiidae (Fig. 1F). *Drepanaspis* was also included in a second analysis (Pernègre & Elliott 2008, fig. 5) and recovered fairly close to the Pteraspidiiformes root, which contrasts with the more derived position recovered by Pernègre (2002). However, when we used the methods and published data matrix of Pernègre & Elliott (2008), *Drepanaspis* was placed outside the Pteraspidiiformes clade, as its sister group. Despite these advances in the systematics of Pteraspidiiformes, there has yet to be a phylogeny including all taxonomically described genera, and the position of the Psammosteidae is still ambiguous.

Methods

Ingroup taxa

All 47 genera described as belonging to the Pteraspidiiformes are included in this analysis (see Supplemental Table 1). This includes all genera outlined in Blicek's (1984) extensive Pteraspidiiformes review, along with newly described, or redescribed, taxa (Elliott 1983, 1984; Ilyes & Elliott 1994; Elliott & Ilyes 1996; Pernègre 2002; Pernègre & Goujet 2007; Voichyshyn 2011). Where possible, the type species of each genus has been used, unless that species is inadequately preserved, the material is missing, or another species from within the genus is substantially better known (see Supplemental Table 1). Character coding is based on the selected species within a genus rather than generalizations for a genus or ambiguity due to intraspecific variation. Two representatives of both *Protopteraspis* and *Zascinaspis* have been included within the study. *Protopteraspis* contains many species, some of

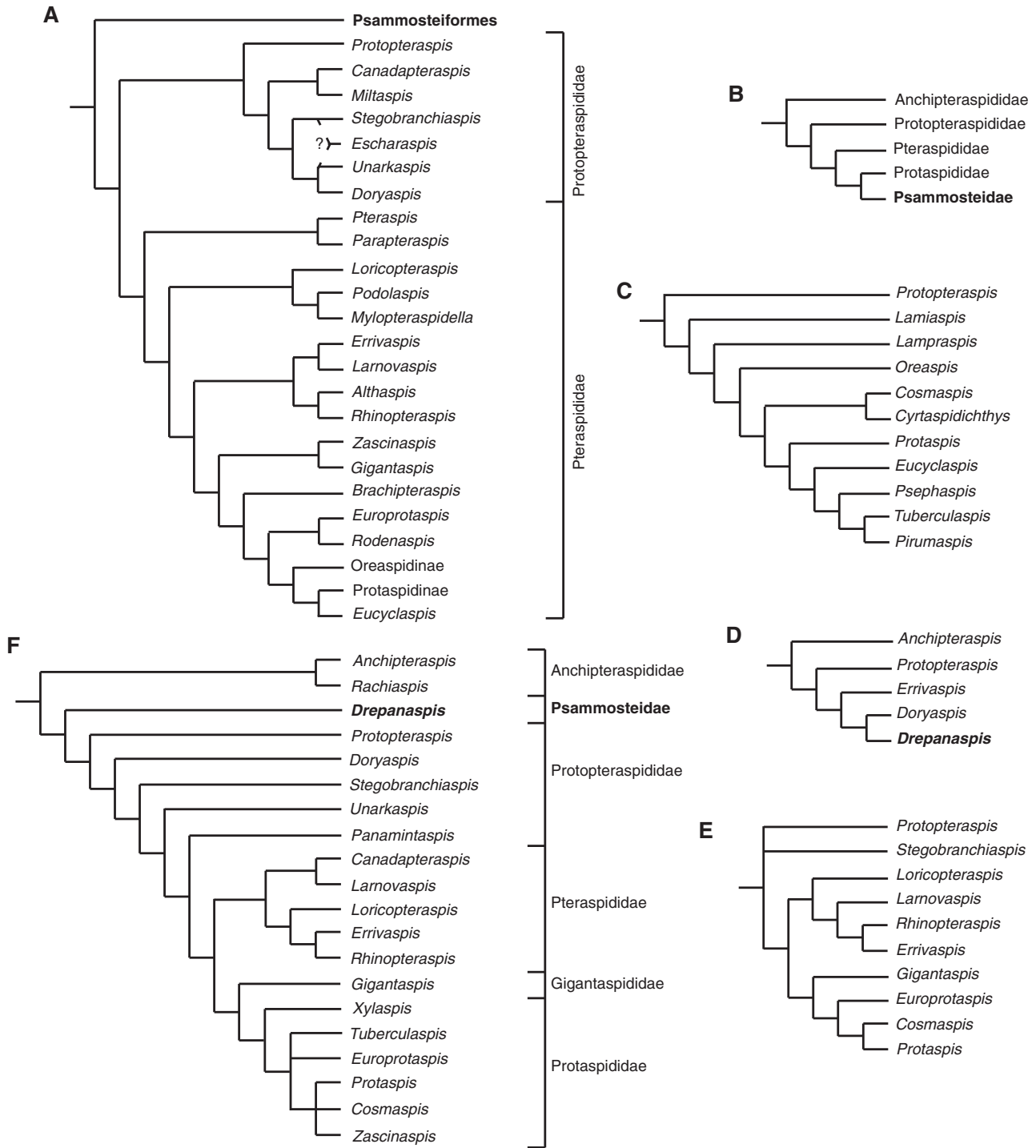


Figure 1. Previous Pteraspidiiformes phylogenies. **A**, Blieck's (1984) Pteraspidiiformes phylogeny for all the then-known taxa. **B**, Janvier's (1996) phylogeny for the major clades of Pteraspidiiformes. **C**, Ilyes & Elliott's (1994) phylogeny for the Western USA taxa. **D**, Pernègre's (2002) phylogeny to determine the position of *Doryaspis*. **E**, Pernègre & Goujet's (2007) phylogeny to determine the position of *Gigantaspis*. **F**, Pernègre & Elliott's (2008) most recent Pteraspidiiformes phylogeny with the identification of major families. The Psammosteidae are highlighted when included in an analysis.

which exhibit notable variation (e.g. presence of internal organ impressions). The two species of *Zascinaspis* (*Z. heintzi* and *Z. carmani*) are also included within the analysis to test the monophyly of the genus. *Zascinaspis*

carmani was first described extensively by Denison (1960) and originally placed within *Pteraspis* but considered an intermediate between *Pteraspis* and *Protaspis*. A re-evaluation by Blieck (1984) noted fundamental

similarities between the overall shape, pineal-orbital belt and oral region of *Z. carmani* and *Z. heintzi*, which he considered enough to include these species within the same genus, *Zascinaspis*. On examination, similarities such as the scale-like dorsal spine, ornamentation pattern and proportions of the dorsal plate suggest that *Z. carmani* perhaps does not belong within the genus *Zascinaspis*; therefore, *Z. carmani* has been included within the analysis to elucidate its classification. *Drepanaspis gemuendenensis* and *Psammosteus megalopteryx* have been chosen as two representatives of the Psammosteidae. These taxa are known from articulated or bountiful material, enabling a clear comparison of the morphology of these forms and the more traditional Pteraspidiformes.

Outgroup taxa

The Pteraspidiformes are often grouped with Cyathaspididae as the ‘higher heterostracans’ (Janvier 1996), the general consensus being that cyathaspidids are the sister group of pteraspids (Elliott 1984; Janvier 1996); they are therefore the logical choice as the outgroup for this analysis. Following Lundgren & Blom (2013), we use *Athenaegis chattertoni* from the Wenlock of the Mackenzie Mountains, Northwest Territories, Canada, and following Pernègre & Elliott (2008) we use *Nahanniaspis mackensiei* from the Lochkovian of the Mackenzie Mountains, Northwest Territories, Canada and *Anglaspis maccoulloughi* from the Prídoli and Lochkovian of the Welsh Borders, UK and the Artois-Ardenne regions of France and Belgium. *Athenaegis* is the oldest heterostracan known from articulated material, and was placed by Janvier (1996) as sister taxon to his ‘higher heterostracan’ clade. *Athenaegis* was originally placed within Cyathaspididae by Soehn & Wilson (1990), but is believed by Janvier (1996) to possess more plesiomorphic characters. *Anglaspis* and *Nahanniaspis* are both known from relatively complete material and share many characteristics and states with some Pteraspidiformes, and are thus very useful in polarizing character states within the analysis.

Characters and coding methods

Characters used in the phylogenetic analysis were obtained from direct observations of specimens, and species descriptions from published literature, and were adapted from the character lists from previous phylogenies (Ilyes & Elliott 1994; Pernègre 2002; Pernègre & Goujet 2007; Pernègre & Elliott 2008). The character list can be found in the Supplemental Material, with Figures 2 and 3 providing visual explanations of selected character codings. Measurements of traits were made using ImageJ (Rasband 1997–2015). Both discrete and continuous characters were used to explore the evolutionary relationships of the Pteraspidiformes. Discrete characters are

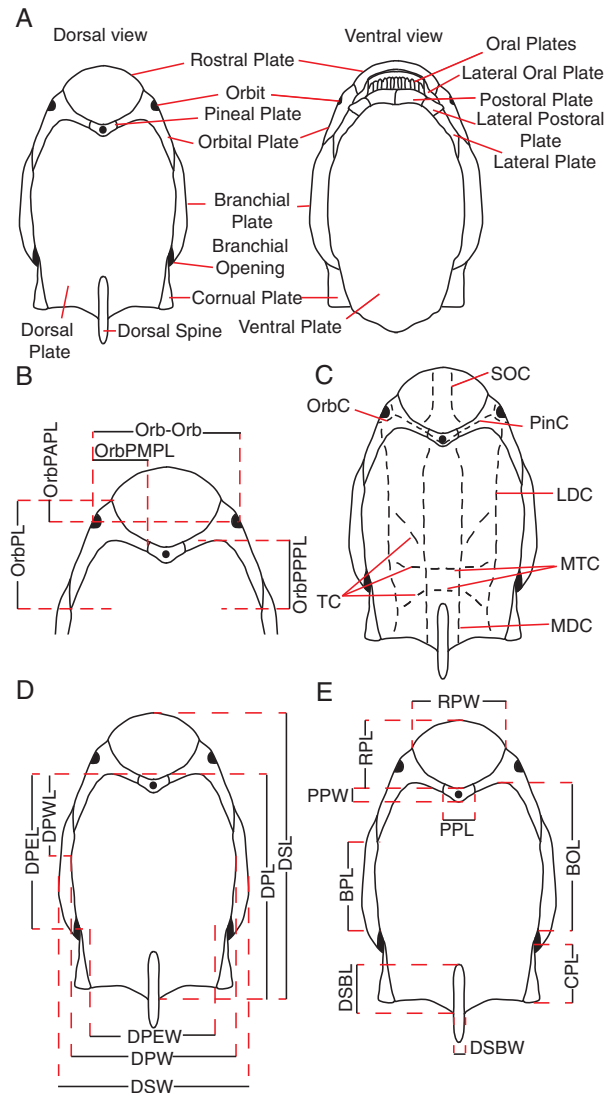


Figure 2. Reconstruction of a hypothetical Pteraspidiformes (adapted from Blicek 1984). **A**, dorsal and ventral view of Pteraspidiformes headshield with plates labelled. **B**, **D**, **E**, measurements used in phylogenetic analysis. **C**, dorsal headshield sensory canals. Anatomical abbreviations: SOC, supraorbital canal; OrbC, orbital canal; PinC, pineal canal; LDC, lateral dorsal canal; MDC, medial dorsal canal; TC, transverse commissures; MTC, median transverse commissures. Measurement abbreviations: DSL, dorsal shield length; DSW, dorsal shield width, not including the cornual plate width; DPL, dorsal plate length; DPW, dorsal plate width; RPL, rostral plate length; RPW, rostral plate width; PPL, pineal plate length; PPW, pineal plate width; BPL, brachial plate length; BOL, brachial opening distance from anterior of dorsal plate; CPL, cornual plate length; OrbPL, orbital plate length; OrbPAPL, orbital plate anterior process length; OrbPMPL, orbital plate medial process length; OrbPPPL, orbital plate posterior process length; Orb–Orb, orbital opening to orbital opening length; DSBW, dorsal spine base width; DSBL, dorsal spine base length; DPEB, dorsal plate embayment distance from anterior of dorsal plate; DPEL, distance to beginning of embayment from anterior end of dorsal plate; DPEW, dorsal plate embayment narrowest width.

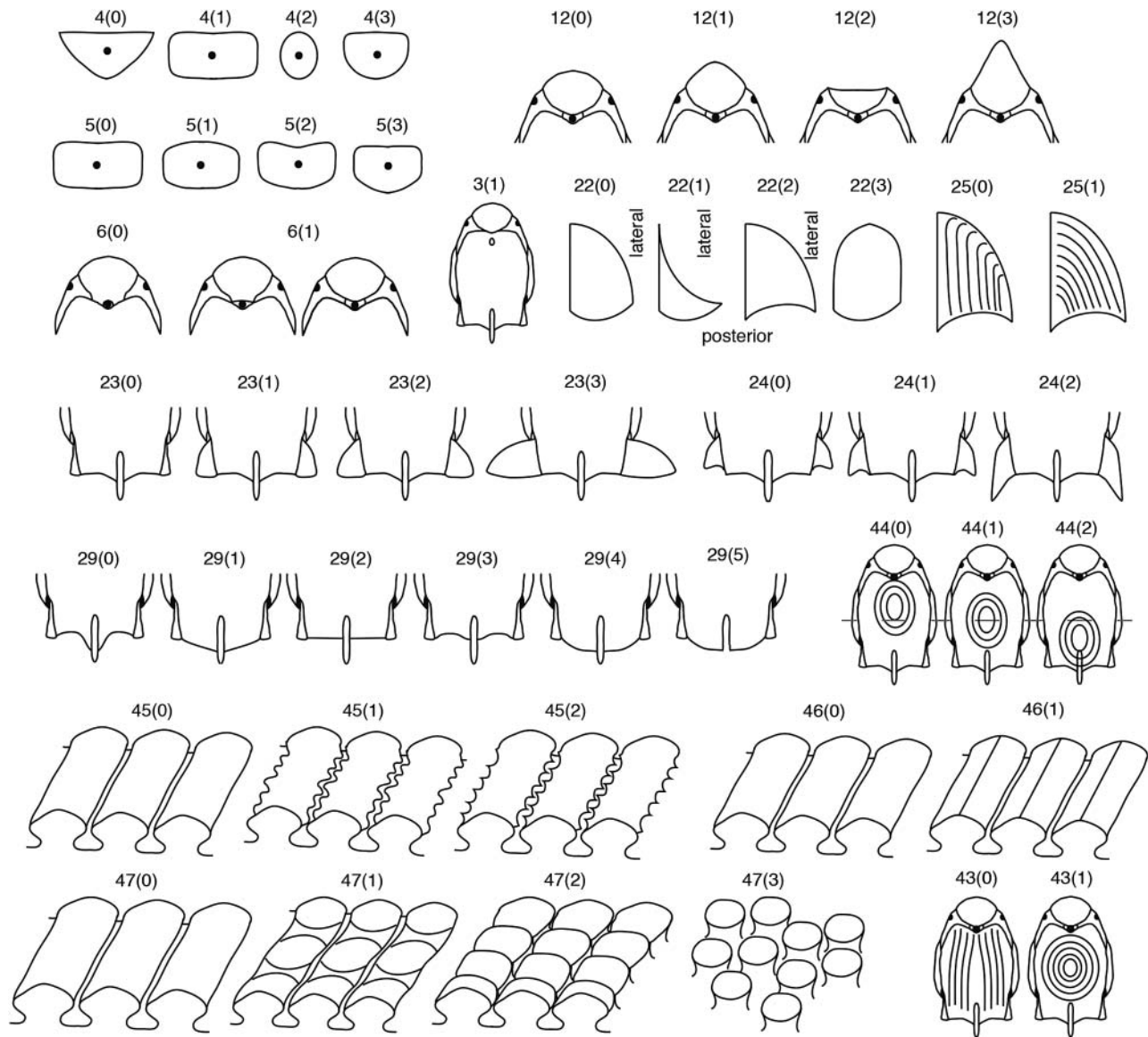


Figure 3. Cartoons of selected characters and character states. Numbers signify characters, bracketed numbers represent character states e.g. 1(0), where 1 is the characters and (0) is the character state.

binary (absent/present) or multistate characters, with some characters contingent on the state of other characters. Sixty-five discrete characters are identified here (see characters 1–65 in the character list). Quantitative or continuous data is seldom used in phylogenetic analysis, although it can be phylogenetically informative (Garcia-Cruz & Sosa 2006; Goloboff *et al.* 2006). Twenty-two continuous characters were used in this analysis in the form of ratio data to standardize for size variation (definitions are given in the character list; characters 66–87). Palaeontological data sets are notoriously difficult for morphological phylogenetic analysis with poor preservation and missing data. Here, different strategies are used to explore the Pteraspiformes data set including equally weighted characters

versus implied weighting (Goloboff 2014), and gap coding to discretize quantitative characters versus inclusion of raw continuous characters (Rae 1998; Wiens 2001; Goloboff *et al.* 2006; Sansom 2008).

Implied weighting is a tool for greater resolution in data sets that contain a large amount of homoplasy and is commonly used in morphological phylogenetics (Dias-da-Silva & Marsicano 2011; Legg *et al.* 2013; Xu & Pol 2014). This method reweights characters based on their homoplasy index (Goloboff 2014), such that highly homoplastic characters are given less weight. However, it has recently received criticism from studies of simulated data, with concerns raised about the increasing amount of error associated with reweighted character analyses compared

to equally weighted characters (Congreve & Lamsdell 2016; O'Reilly *et al.* 2016).

With respect to continuous characters, some morphological measurements are used in multiple characters (often as a reference measurement for a ratio) and this can lead to logical dependence or correlation between characters (Goloboff *et al.* 2006). Therefore, a Pearson's correlation coefficient test was used to identify correlated data (RStudio Team 2015). Significantly correlated characters were removed sequentially, starting with the character with the highest number of correlations. After a character was removed the number of correlations per character was then recalculated, and the highest again removed, and so on. When only single pairs of correlations remained, the character with the least amount of data was then removed, leaving the character with the least amount of missing data. This was repeated until all the remaining characters were uncorrelated and operationally independent.

An alternative strategy to address shape and ratio characters is to discretize them into ordinal character states. This can be done arbitrarily or more formally, for example using gap coding. Traditional gap-coding methods used on neontological data sets (see Garcia-Cruz & Sosa 2006) rely on complete data sets with many replicates of the continuous traits in order to obtain a consensus of the range of variability within a trait, which is not applicable to most palaeontological data sets. The gap coding method used here uses the sequential difference between ordered data points and identifies gaps when the difference is greater than two standard deviations of the gap difference data. This sometimes identified uninformative characters, which were not included within the analysis.

Dermal plates of psammosteids and Pteraspidiformes are treated as homologous following general consensus (Obruchev 1967; Blicek 1984; Blicek *et al.* 1991). It is not clear, however, whether these plates are functionally analogous, or if the quantitative measurements are evolutionary informative (due to the fields of tesserae between the plates of psammosteids). To account for these two possibilities, analyses were conducted with the continuous characters treated as either homologous or inapplicable for psammosteids (see Supplemental Material for analysis of homologous psammosteid data).

Data analysis

Parsimony tree searches were conducted in TNT (Goloboff *et al.* 2008) using a heuristic search method (multiple tree bisection rearrangement) with 1000 replications and space for holding 1000 trees. TNT was the favoured program as it can process discrete and continuous data both separately and together (Goloboff *et al.* 2006). Implied weighting is often used to mitigate the effect of

homoplasy (Goloboff 2014). To investigate this possibility we ran searches with and without implied weighting. There is no general consensus as to which concavity value should be used in an analysis; therefore, the default concavity value ($k = 3$) was implemented (other values for k are presented in the Supplemental Material). Bayesian analysis was performed in MrBayes 3.2 (Ronquist & Huelsenbeck 2003). Priors were kept to their default for standard (morphological) data except the coding function, which was set to 'informative' as the data set used only contains parsimony informative characters. The analysis was run for 2×10^7 generations with samples taken every 1000 generations; the burn-in was set to 0.25.

Results

Searches including all Pteraspidiformes genera recover very little signal, principally due to two taxa (*Mylopteraspis* and *Palanasaspis*) that are very incomplete (95 and 96% missing, respectively), acting as wild cards. These two taxa were excluded from all subsequent analyses.

Heuristic searches using discrete characters only resulted in 275 most parsimonious trees (MPTs; tree length 276), giving a partially resolved strict consensus tree (Fig. 4A). Psammosteidae are placed well within the Pteraspidiformes, in a clade with *Woodfjordaspis* and *Doryaspis*. The anchipteraspid taxa *Rachiaspis*, *Anchipteraspis* and *Ulutitaspis* are recovered in a clade sister to all other Pteraspidiformes (including Psammosteidae). A large number of taxa are in a polytomy within the consensus tree with only one other clade apparent containing *Larnovaspis* and *Unarkaspis*. Of the suspect genera for which two species were included in the analysis (*Zascinaspis* and *Protopteraspis*), neither was found to be monophyletic. Bayesian analysis of the same data set (see Supplemental Fig. 1A for majority rule tree) has better resolution towards the root of the tree, with the *Protopteraspis* taxa and *Stegobrachiaspis* placed as a paraphyletic successive sister assemblage leading towards a large polytomous clade containing the remaining taxa. The Psammosteidae are recovered within Pteraspidiformes but within the unresolved polytomy.

Application of implied weighting ($k = 3$) results in four MPTs with a score of 23.11 (Fig. 4B is the strict consensus). Relationships at the base of the tree are much better resolved than those of the equally weighted analysis. The two *Protopteraspis* taxa along with *Stegobrachiaspis*, *Loricopteraspis*, a clade containing *Gigantaspis* and *Zascinaspis heintzi*, *Escharaspis* and a clade containing *Candapteraspis* and *Miltaspis* all form a paraphyletic assemblage leading to a clade containing the majority of the Pteraspidiformes. Seen within this tree is a dichotomous split between the remaining taxa, with the majority

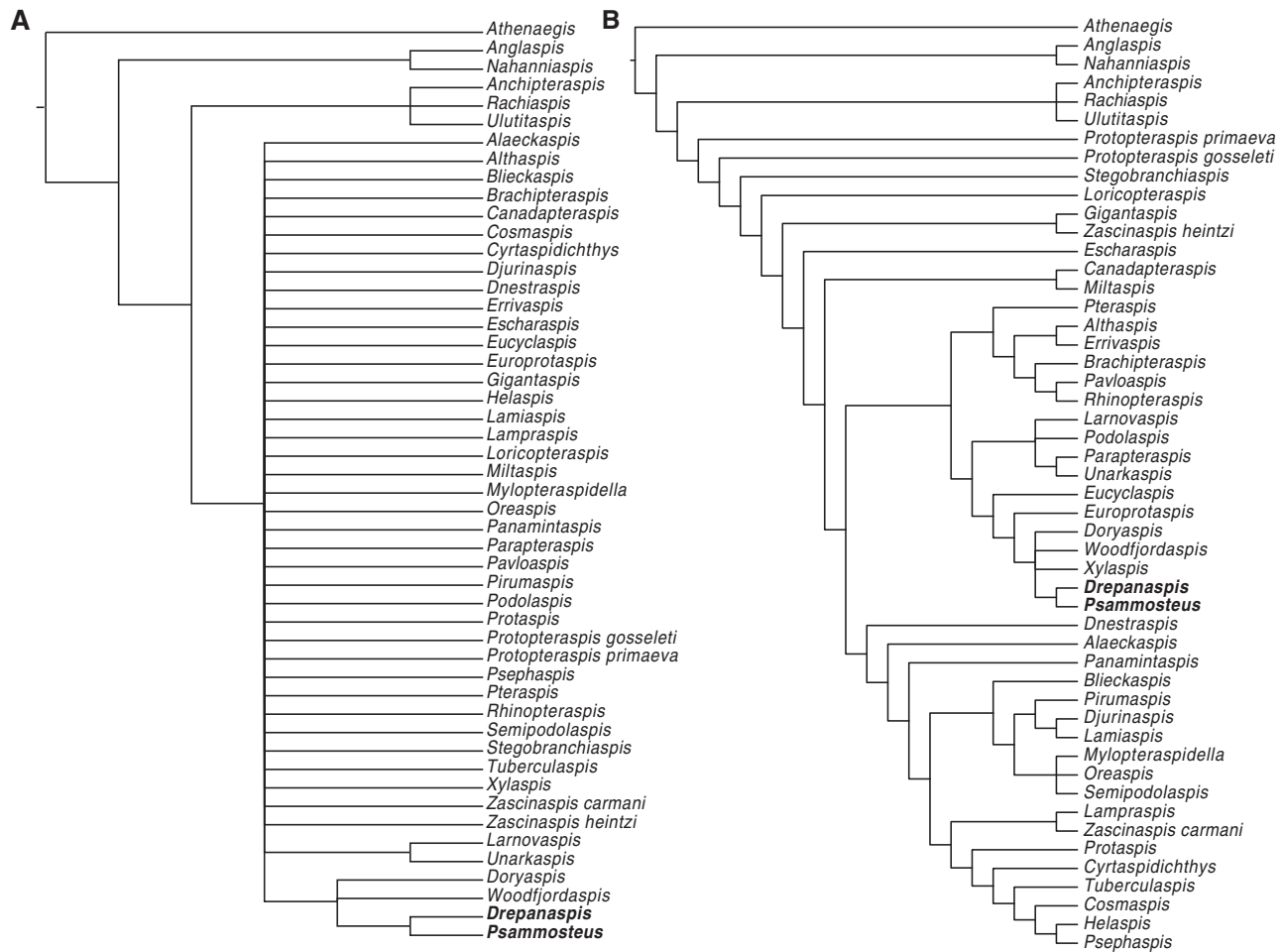


Figure 4. Results from the phylogenetic analysis using discrete data only. **A**, strict consensus of 275 most parsimonious trees with equal character weights; length 276 steps, consistency index (CI) = 0.35, retention index (RI) = 0.59, and rescaled consistency index (RC) = 0.22. **B**, strict consensus of four most parsimonious trees with implied character weighting ($k = 3$) (tree length 23.11). Psammosteidae taxa in bold.

of taxa from the western USA (*Psephaspis*, *Cosmaspis*, *Tuberculaspis*, *Cyrtaspidichthys*, *Lampraspis*, *Zascinaspis carmani*, *Oreaspis*, *Lamiaspis*, *Pirumaspis*, *Panamintaspis* and *Blieckaspis*) in one clade along with *Helaspis* and some Podolian forms such as *Dnestraspis*, *Alaeckaspis*, *Mylopteraspidella*, *Djurinaspis* and *Semipodolaspis*. The rest of the taxa are contained within the other large clade, which includes the psammosteid taxa and classic Welsh-Border-Artois-Ardenne taxa such as *Pteraspis*, *Errivaspis* and *Rhinopteraspis*. Consistent with the equally weighted analysis is the position of taxa in the clade containing the psammosteids with the addition of *Xylaspis*, *Europrotaspis* and *Eucyclaspis*.

The results for the two different methods for including quantitative characters are shown in Figures 5 and 6. Inclusion of the raw continuous characters recovers a single MPT (Fig. 5A). However, this result is dubious as it has a topology very different from all other analyses. In

this tree, taxa that are usually positioned towards the root of the tree (as seen in the Bayesian analysis, Supplemental Figure 1 and the reweighted analyses (Figs 4B, 5B, 6B)), such as *Protopteraspis* and *Stegobrachiaspis*, are replaced by western USA taxa such as *Cosmaspis*, *Lampraspis*, *Oreaspis* and *Eucyclaspis*, which are usually found in a fairly derived position. Application of implied weighting ($k = 3$) also results in a single MPT (tree length 26.53) (Fig. 5B) that compares more favourably with the tree resulting from the implied weighted analysis of discrete-only characters. The majority of the unresolved taxa from the discrete-only analysis with implied weighting (Fig. 4B) are resolved following addition of continuous characters. The composition of the clade containing the psammosteid taxa is unchanged (compared to Fig. 4B) but with much better resolution (Fig. 5B); *Doryaspis* is now placed as the sister group to the psammosteid taxa, with *Woodfordaspis* and *Xylaspis* forming a clade. Of

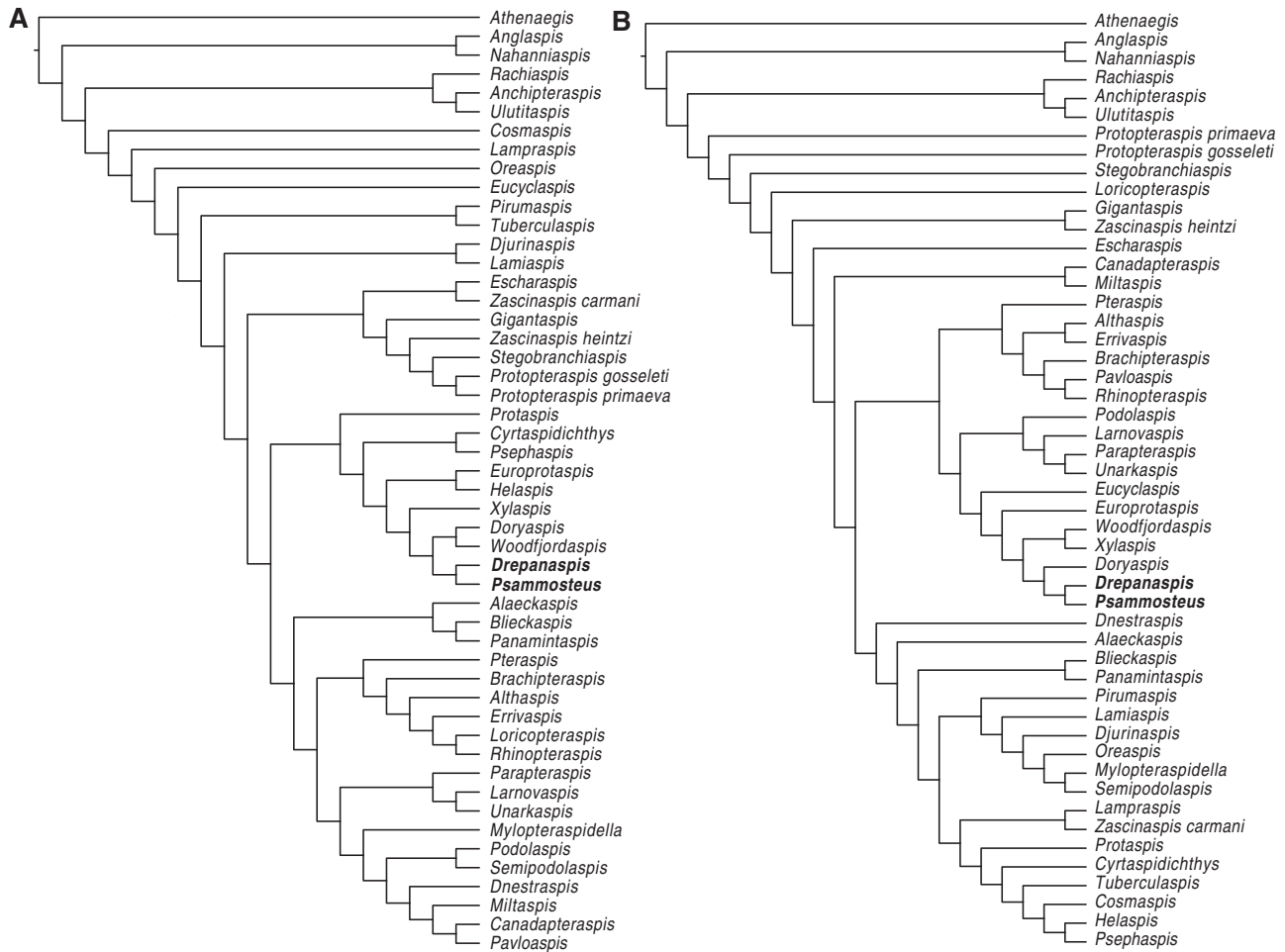


Figure 5. Phylogenetic results from data sets containing discrete (1–64) and continuous (66, 68, 70, 72, 77, 80, 82, 86) characters. **A**, most parsimonious tree with equally weighted characters (tree length 319.36). **B**, most parsimonious tree with implied weighting ($k = 3$) (tree length 26.53). Psammosteidae taxa in bold (for which quantitative characters have been treated as inapplicable, i.e. non-homologous).

differences relating to other taxa, *Blieckaspis* is now placed in a clade with *Panamintaspis* rather than with *Pirumaspis*, *Djurinaspis*, *Lamiaspis*, *Mylopteraspidella*, *Oreaspis* and *Semipodolaspis*.

Discretizing the continuous characters (Fig. 6A) results in a loss of resolution, with many taxa belonging to an unresolved polytomy in the equally weighted analysis, as is also true for the Bayesian analysis of discretized characters (Supplemental Fig. 1B). Application of implied weighting ($k = 3$) results in much better resolution, with one most parsimonious solution (tree length of 27.86) (Fig. 6B). However, the resulting topology is quite different from that seen in the previous two analyses of weighted characters (Figs 4B, 5B). Taxa towards the root of the tree are unchanged in their positions when compared to the other weighted analyses. However, *Miltaspis* and *Canadapteraspis* have migrated towards the root, and occupy a position between *Protopteraspis* and

Loricopteraspis which in previous analyses was occupied by *Stegobrachiaspis*. Similarly to previous analyses, the psammosteid taxa occur in a clade with *Doryaspis*, *Xylaspis* and *Woodfjordaspis*. However, also occurring in this clade are *Pteraspis* and *Escharaspis*, both of which occupied quite different positions in the discrete and discrete-with-continuous analyses. The majority of the derived pteraspidiiform taxa occur within two clades. One contains taxa mainly from the western USA and *Europrotaspis*, whereas the other contains all other taxa. The major difference between the discretized analyses (Fig. 6B) and the discrete-only and discrete-with-continuous analyses (Figs 4B, 5B) is the movement of Podolian taxa along with *Oreaspis*, *Pirumaspis* and *Lamiaspis* from the clade containing the majority western USA taxa into the other major clade with the psammosteid clade, *Rhinopteraspis* clade and other Podolian, Welsh Borders-Artois-Ardenne forms.

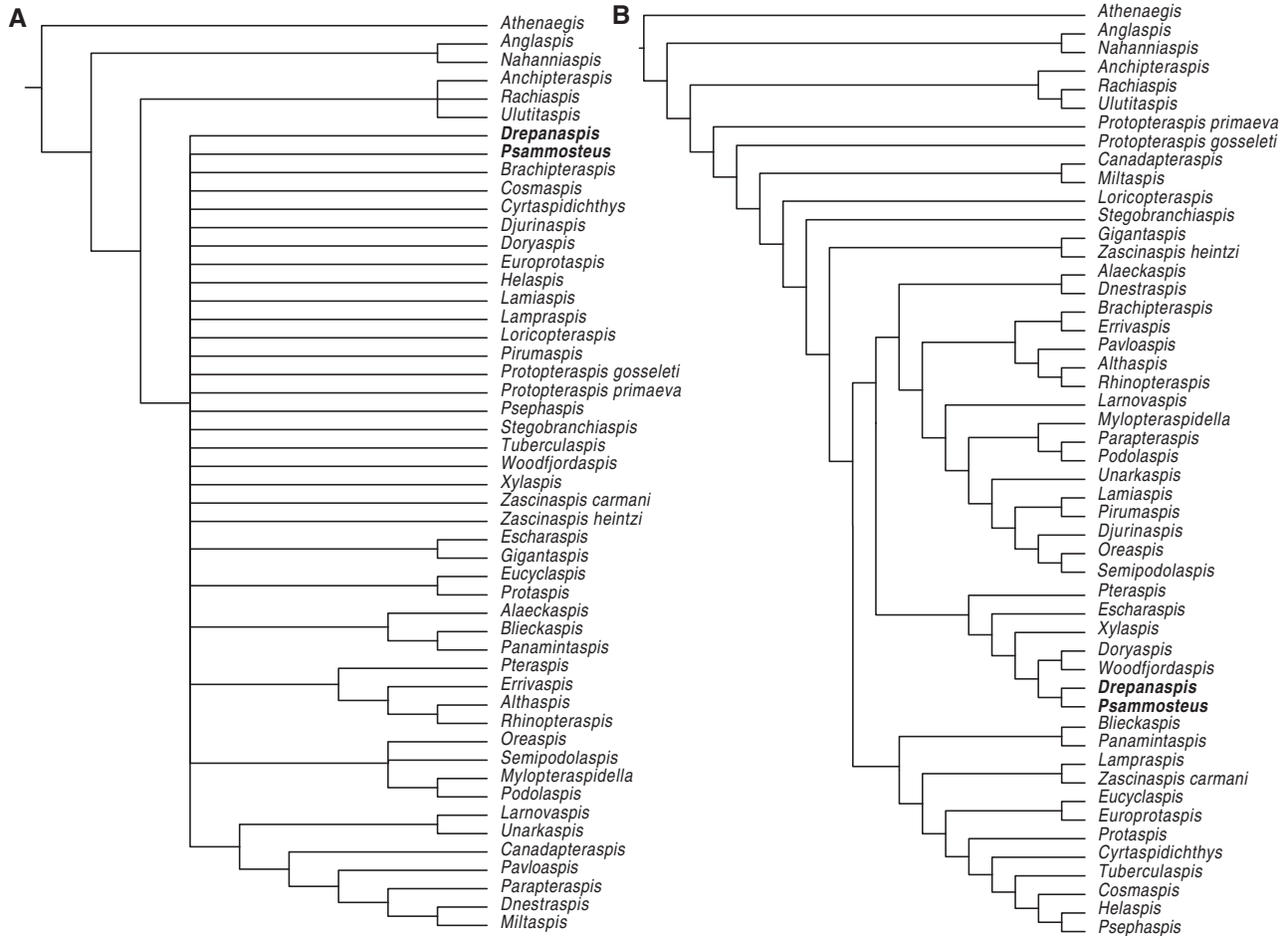


Figure 6. Most parsimonious result from a phylogenetic analysis of discrete (1–64) and discretized continuous characters identified through gap coding (88–100). **A**, strict consensus of 30 most parsimonious trees with equally weighted characters (tree length 346). **B**, most parsimonious solution with implied weighted characters ($k = 3$) (tree length 27.86). Psammosteidae taxa in bold (for which quantitative characters have been treated as inapplicable, i.e. non-homologous).

Discussion

A major issue of contention with respect to Pteraspidiiformes phylogeny is the inclusion of the Psammosteidae. In all instances, *Drepanaspis* and *Psammosteus* fall well within the Pteraspidiiformes clade; thus, our results support the hypotheses of Blicke *et al.* (1991), Janvier (1996), Pernègre (2002) and Pernègre & Elliott (2008) that Psammosteidae do indeed belong within the Pteraspidiiformes. The psammosteids are consistently placed in a clade with the Spitsbergen genera *Doryaspis*, *Woodfjordaspis* and *Xylaspis*. In the discrete-only and discrete-with-continuous analyses (Figs 4B, 5B), the psammosteids are also united with *Eucyclaspis* and *Europrotaspis*. However, in the discretized analysis these two genera move into the clade containing the western USA taxa and are replaced by *Escharaspis* and *Pteraspis*. *Psephaspis* was once believed to belong within the Psammosteidae (Orvig 1961; Tarlo 1964), but was recognized

by Denison (1968) and Blicke (1984) as belonging to the Pteraspidiiformes based on morphological features such as the possession of a free dorsal spine. *Psephaspis* is recovered here as belonging to a clade containing psammosteids but only in the equally weighted discrete-with-continuous analyses; in the remaining analyses it is placed with the western USA protaspids. The position of the psammosteids presented here is most consistent with the tree presented by Pernègre & Elliott (2008). However, it must be noted that under different weighting strategies (i.e. $k = 1$), searches using discrete or discrete plus continuous characters, psammosteids move into a highly derived position within the tree, within the traditional Protaspididae clade, which agrees with the interpretations of Janvier (1996) and Pernègre (2002). This could indicate that the characters supporting the position of Psammosteidae are highly homoplastic. Nevertheless, a pteraspidiiform affinity for Psammosteidae is strongly supported in all analyses.

The Anchipteraspididae (*Anchipteraspis*, *Rachiaspis* and *Ulutitaspis*) taxa are consistently positioned at the base of the tree as sister to all other Pteraspidiformes; this supports the hypothesis of Elliott (1984) that they are transitional forms between Cyathaspididae and Pteraspidiformes. However, this could potentially change with the inclusion of more taxa from other heterostracan clades (i.e. Traquairaspididae) which possess primitive ‘oak leaf’ ornamentation but are similar to the Pteraspidiformes in that their headshield is composed of separate dermal plates (Dineley & Loeffler 1976; Tarrant 1991).

Recovered towards the root in the majority of analyses are paraphyletic *Protopteraspis*, *Stegobrachiaspis*, *Loricopteraspis*, *Zascinaspis heintzi*, *Gigantaspis*, *Escharaspis*, *Canadapterspis* and *Miltaspis*. Exceptions occur in the equally weighted analysis including continuous characters in which these taxa are placed in a clade in a more derived position, and in the implied weighted discretized analysis where the latter three taxa are placed with the western USA taxa. These taxa are in a position analogous to the Protopteraspididae of Blicek (1984) and Pernègre & Elliott (2008). However, Blicek’s (1984) Protopteraspididae (Fig. 1A) also contained *Unarkaspis*, which is recovered in a more derived position in all three parsimony analyses (Figs 4B, 5B, 6B). Also, in Pernègre & Elliott’s (2008) phylogeny, *Doryaspis*, *Unarkaspis* and *Panamintaspis* are within the Protopteraspididae, which is not recovered here. *Gigantaspis* in the majority of other analyses (Fig. 1A, E, F), together with *Europrotaspis*, is recovered as the sister clade to Protaspididae (Pernègre & Elliott 2008), but not in any of our results. *Gigantaspis*, like the majority of the taxa of Protaspididae, is much larger and wider than traditional taxa of Pteraspidiformes, and Pernègre & Goujet (2007) suggested that *Gigantaspis* is perhaps the ancestral morphotype of the Protaspididae.

Other relationships supported by the analyses include a close affinity between *Rhinopteraspis* and *Errivaspis*, which are consistently recovered in a clade often with *Althaspis*, *Brachipteraspis*, *Pavloaspis* and *Pteraspis*, as was suggested by Blicek (1984), Pernègre & Goujet (2007) and Pernègre & Elliott (2008) (Fig. 1A, E, F). This perhaps represents the family Rhinopteraspididae of Novitskaya (2004) and Voichyshyn (2011), which includes *Rhinopteraspis* and *Althaspis*.

Zascinaspis carmani in all instances is placed with *Lampraspis* in a fairly derived position (with the protaspid taxa), which is also supported in analyses using different implied weightings (see Supplemental Figs 1 and 2). The results from these analyses suggest that *Z. carmani* needs taxonomic re-evaluation.

Phylogenetic analyses of equally weighted characters are poorly resolved. Application of implied weighting (default $k = 3$) improves the resolution of all the different treatments (Figs 4B, 5B, 6B). Exploring different levels of implied weighting produced different tree topologies

for each analysis – that is, discrete or discrete and continuous characters (see Supplemental Figs 2 and 3). Trees arising from analyses with the same implied weighting (e.g. $k = 2$) were more similar to each other (compare Supplemental Figs 2A and 3A) than trees arising from the same character treatments with different weightings (compare Supplemental Fig. 2A and B). This indicates that the data sets have a fairly high level of homoplasy. Most notable is the movement of *Drepanaspis* and *Psammosteus* (Psammosteidae) away from the root under higher or more severe weighting ($k < 3$).

Inclusion of the quantitative characters within the analyses consistently improved the resolution. Inclusion of raw continuous characters (implied weighted) resulted in one MPT (Fig. 5B). Poor resolution in some areas of the tree, such as the taxa preceding the protaspid clade, in the discrete-only analysis, is most likely due the homogenous nature of the Pteraspidiformes bauplan. This was also found to be the case within Sansom’s (2009) phylogeny of Osteostraci, in which he stated “the group is diverse in terms of number of taxa yet very few anatomical features can be used to distinguish between them in any character-based analysis” (Sansom 2009, p. 112). This appears to be a common problem within ostracoderms and perhaps indicates the need to explore other methods for distinguishing their evolutionary relationships, such as geometric morphometrics. The resolution of the analysis containing raw continuous characters suggests that this information is phylogenetically informative and suitable for analysis of ostracoderm relationships. Interestingly, the results when including continuous characters ($k = 3$, Fig. 5B) compare closely with the discrete characters only analysis but with improved resolution ($k = 3$, Fig. 4B). Uncertainty in the placing of *Oreaspis*, *Semipodolaspis* and *Mylopteraspidella*, along with *Larnovaspis*, *Podolaspis*, *Woodfjordaspis*, *Xylaspis* and *Doryaspis*, is resolved with the inclusion of the continuous data. It appears that the continuous characters improve the resolution that describes morphological variations used to distinguish different taxonomic genera.

The alternative method of including quantitative characters (i.e. discretizing) was found to perform relatively poorly in the equally weighted analysis (Fig. 6A). Application of implied weighting (Fig. 6B) greatly improved the resolution with one most parsimonious solution. Similar results are seen in the analysis when measurements of Psammosteidae are coded as homologous (Supplemental Fig. 5). Similar to the results of the other analyses (discrete and discrete with continuous characters) is the recovery of a clade containing *Drepanaspis*, *Psammosteus*, *Xylaspis*, *Woodfjordaspis* and *Doryaspis*. The position and relationships of taxa recovered here (i.e. a major split of Pteraspidiformes taxa into two clades) is most similar to that of Blicek (1984), Pernègre & Goujet (2007) and Pernègre & Elliott (2008) (Fig. 1A, E, F). A caveat of

this method is that it is highly sensitive to missing data, which is prevalent in palaeontological data sets. One of the biggest problems is that it is not always clear if a gap is a genuine evolutionary phenomenon (phylogenetically informative), or the result of missing data or poor taxon sampling. One of the few areas of accordance between this method and the others presented here is the relationships of taxa towards the Pteraspidiiformes root. Consideration of *Drepanaspis* and *Psammosteus* continuous measurements in the gap-coding process appears to produce a less-resolved tree (see Supplemental Fig. 5A). Incorporation of their measurements changed the coding states in some of the discretized characters. Inclusion of just two of the 18 described genera of Psammosteidae is not very informative and, as stated previously, the configuration of the psammosteid headshield with its fields of tesserae or platelets means that the continuous character measurements are probably not analogous.

Inclusion of the psammosteid measurements in the discrete and continuous analysis (equally weighted, see Supplemental Fig. 4A) resulted in three MPTs; however, the tree topology and resulting relationships differed from those of all other analyses. This is evident by the psammosteid taxa along with *Doryaspis*, *Woodfjordaspis* and *Xylaspis* being placed in a more derived position within a clade containing western USA taxa, which is only seen in implied weighted analyses with a concavity constant of $k = 1$. Application of implied weighting ($k = 3$) (Supplemental Fig. 4B) resulted in a topology similar to that where the psammosteid measurements were coded as missing (Fig. 5B). This indicates that the psammosteid measurements (i.e. plate dimensions) may not be homologous to those of other Pteraspidiiformes.

Stratigraphical and biogeographical congruence

The trees shown in Figure 5B (implied weighted analysis including continuous characters) and Figure 6B (implied weighted including discretized characters) were calibrated against the stratigraphical and palaeobiogeographical ranges of taxa to explore scenarios of Pteraspidiiformes evolution and assess congruence (Fig. 7). Based on the relationships recovered here, along with stratigraphical and biogeographic occurrences, it is apparent that Pteraspidiiformes did not show strong endemism, unlike other jawless vertebrate clades (i.e. Osteostraci and Galeaspida) (Sansom 2009). It appears that Pteraspidiiformes originated in Laurentia (Canadian Arctic, Mackenzie Mountains, Spitsbergen and western USA localities) and had dispersed to the other palaeocontinents (Avalonia (Welsh Border-Artois-Ardenne), Baltica (Podolia) and Kara

(Severnaya-Zemlya)) by the Early Devonian, a very similar dispersal pattern to that seen in osteostracans (Sansom 2009). However, these similar patterns could be due to inherent biases associated with facies differences and an incomplete fossil record (Sansom *et al.* 2015).

Based on the stratigraphical occurrences and palaeobiogeography of the genera, a more reliable phylogeny – between the discrete-and-continuous phylogeny and the phylogeny resulting from the discretized data – cannot be discerned. There appears to be just as much conflict (based on ghost ranges) and congruence in the two phylogenies (Fig. 7A, B). Palaeobiogeographically, the result from the discretized data appears to be more parsimonious as the majority of taxa from the western USA are placed in one clade, whereas those from Podolia and the Welsh Borders-Artois-Ardenne are placed in another. The discretized phylogeny also has slightly fewer conflicts in terms of ghost ranges and time bins crossed than that from the raw quantitative data. Many forms are common to localities of the Welsh Borders-Artois-Ardenne basin and Podolia, indicating there was faunal exchange between these two palaeobasins, as suggested by Blicek (1984) and Voichyshyn (2011).

The most root-ward and earliest Pteraspidiiformes (Anchipteraspididae) occur in the Pridoli of the Canadian Arctic (Elliott 1984). This first occurrence does not coincide with the first occurrences of other clades of Heterostraci, such as Cyathaspididae, *Tesseraspis* and *Athenaegis*, which are found in rocks of considerable older age (Wenlock and Ludlovian) (Denison 1963; Dineley & Loeffler 1976; Blicek *et al.* 2002; Soehn & Wilson 1990). This suggests either Pteraspidiiformes evolved later than other clades, or their early history is not recorded perhaps due to facies preservational biases (Sansom *et al.* 2015).

The majority of derived taxa in the tree are from western USA localities, most of which are resolved as belonging within the Protaspididae of Pernègre & Elliott (2008). These happen to be some of the youngest members of the Pteraspidiiformes, spanning from the Pragian to the Eifelian, indicating some congruence between this phylogeny and the stratigraphical record of the Pteraspidiiformes. It has long been suggested that the western USA fauna was endemic to this area (Ilyes & Elliott 1994), but our phylogenies indicate that there was some faunal exchange between different palaeobasins (Fig. 7A, B). In the discrete-and-continuous character analysis (Fig. 7A), *Eucyclaspis* is placed in a clade with Spitzbergen forms, and other taxa are interspersed with taxa from Podolia. In the discretized analysis the western USA taxa appear to be less interspersed with other localities and taxa, apart from *Pirumaspis*, *Lamiaspis* and *Oreaspis*, which are nested within a clade containing predominantly Podolian and Welsh Borders-Artois-Ardenne taxa. Alternatively, as Ilyes & Elliott (1994) suggested, similarities in

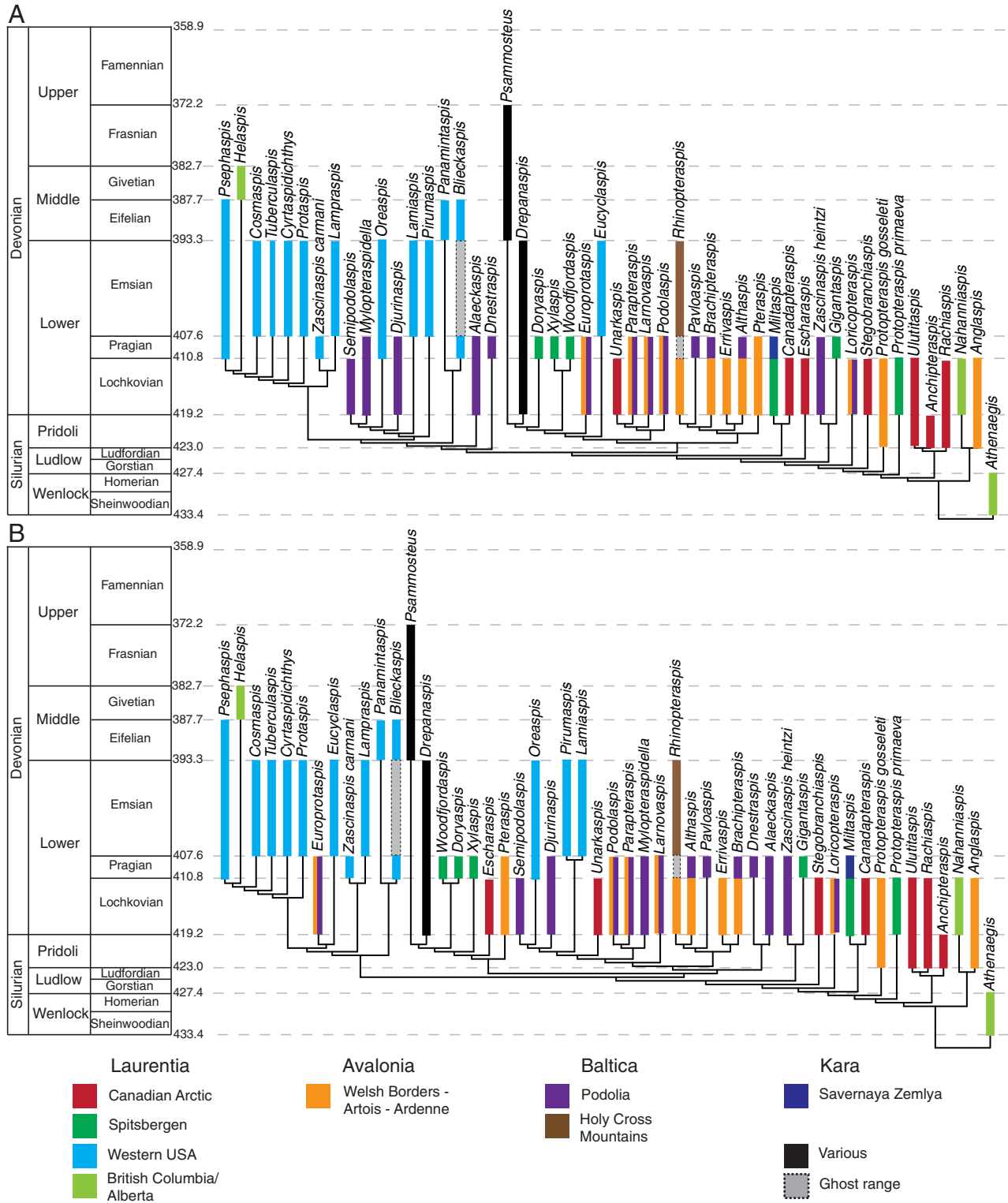


Figure 7. Pteraspidiformes phylogeny with genera plotted against their stratigraphical occurrences. **A**, discrete and continuous character analysis with implied weighting ($k = 3$). **B**, discretized analysis with implied weighting ($k = 3$). Colours relate to palaeobiogeographical provinces.

morphology due to similar environmental pressures could have resulted in their positions within the tree.

The inclusion of Psammosteidae within the Pteraspidi-formes extends the range of the latter by 15 million years; the Psammosteidae are the youngest members of the Heterostraci. *Drepanaspis* is the first Psammosteidae to appear within the fossil record (Lochkovian; Tarlo 1965) with the last occurring just before the end-Devonian mass extinction in the Frasnian (Tarlo 1965; Moloshnikov 2009; Blicek *et al.* 2002; Novitskaya 2004).

Some discrepancies between stratigraphical ranges and phylogenetic positions are apparent, which necessitates long ghost ranges. *Helaspis* from Alberta and British Columbia is the youngest genus of Pteraspidiiformes *sensu stricto*, and the placement of this taxon with *Pesphaspis*, in a clade with protaspids, results in a fairly long ghost range. These are, however, some of the youngest members of the Pteraspidiiformes and this ghost range is most likely due to incompleteness of the rock record (Sansom *et al.* 2015). The relatively early appearance of the psammosteid *Drepanaspis* in the Lochkovian causes many of the ghost ranges seen within the clade containing the psammosteid taxa in both phylogenies. However, the long ghost range of *Psammosteus* is most probably due to poor taxon sampling; inclusion of more representatives of psammosteids in the phylogeny would break up the long branch between *Drepanaspis* and *Psammosteus*. In the discrete and discretized phylogeny (Fig. 7B), *Europrotaspis* potentially causes ghost ranges in the wide-shielded protaspid clade.

Systematic palaeontology

Following the phylogenetic analyses, a new classification is proposed. It must be noted that there is ambiguity in the classification of some Pteraspidiiformes, which reflects instability in our phylogenetic results.

Subclass **Heterostraci** Lankester, 1868
 Order **Pteraspidiiformes** Berg, 1940
 Family **Anchipteraspididae** Elliott, 1984

Genera included. *Anchipteraspis* Elliott, 1984, *Rachiaspis* Elliott, 1984, *Ulutitaspis* Elliott, 1984.

Family **Protopteraspididae** Novitskaya, 1983

Remarks. Paraphyletic grade.

Genera included. *Protopteraspis* Leriche, 1924, *Stegobrachiaspis* Elliott, 1983, *Zascinaspis* Stensiö, 1958, *Escharaspis* Elliott, 1983, *Gigantaspis* Heintz, 1962, *Loricopteraspis* Tarlo, 1961, *Canadapteraspis* Dineley & Loeffler, 1976, *Miltaspis* Blicek, 1981.

Suborder **Pteraspidoidei** (*sensu* Pteraspidina Janvier, 1996)

Family **Protaspidae** (*sensu* Protaspidinae Blicek 1984)

Genera included. *Cyrtaspidichthys* Whitley, 1940, *Cosmaspis* Denison, 1970, *Tuberculaspis* Ilyes & Elliott, 1994, *Helaspis* Elliott *et al.*, 2000, *Psephaspis* Orvig, 1961, *Lampraspis* Denison, 1970.

Lampraspis Denison, 1970

Type species. *Lampraspis tuberculata* Denison, 1970.

Revised diagnosis. A Protaspidae with wide shield and branchial opening in advance of the posterior end of dorsal plate; ornament of undulating tuberculated ridges; pre-oral field which lacks a pre-oral surface; rostral plate with rounded orbital notch; rostral plate well rounded anteriorly and separated from the dorsal plate by an orbito-pineal belt; scale-like dorsal spine and scale-like cornual plates.

Lampraspis tuberculata Denison, 1970

Diagnosis. As for the genus description given by Denison (1970).

Remarks. *Lampraspis tuberculata* has an unornamented pre-oral field rather than the pre-oral surface described by Denison (1970).

Lampraspis carmani (Denison, 1960)

1960 *Pteraspis carmani* Denison: 568, figs 124–141.

1984 *Zascinaspis carmani* (Denison) Blicek: 61.

Diagnosis. As for '*Pteraspis*' *carmani* in Denison (1960).

Remarks. Phylogenetic analyses placed *Zascinaspis heintzi* and *Z. carmani* at different places in the tree (Figs 4–6), indicating they do not belong within the same genus. Blicek (1984) assigned '*P.*' *carmani* to *Zascinaspis* due to similarities in the proportions of the rostral and dorsal plates and the orbito-pineal belt, as well as shared oral region arrangement. In our analysis, '*Z.*' *carmani* falls within the Protaspidae as sister taxon to *Lampraspis* (both recovered from western USA localities). *Lampraspis carmani* also shares with protaspids an ornamentation of undulating ridges and a branchial opening placed towards the posterior end of the dorsal plate, with reduced cornual plates.

Family **Rhinopteraspididae** Novitskaya, 2004

Genera included. *Errivaspis* Blicek, 1984, *Rhinopteraspis* Jaekel, 1919, *Althaspis* Zych, 1931, *Brachipteraspis* Brotzen, 1936, *Pavloaspis* Voichyshyn, 1999.

Superfamily **Doryaspidae** superfam. nov.

Diagnosis. Pteraspidoformes lacking a dorsal spine, with some members possessing a mid-posterior process (posterior medial peak). Some taxa have reduced the rostral plate and have a dorsally orientated mouth.

Genera included. *Xylaspis* Pernègre, 2003, *Woodfordaspis* Pernègre, 2006, *Doryaspis* White, 1935.

Family **Psammosteidae** Traquair, 1896

Genera included. *Drepanaspis* Schlüter, 1887, *Psammosteus* Agassiz, 1845.

Pteraspidoidei incertae sedis

Remarks. The following genera are not assigned to a family: *Europrotaspis* White, 1961, *Protaspis* Bryant, 1933, *Pteraspis* Kner, 1847, *Blieckaspis* Elliott & Ilyes, 1996, *Panamintaspis* Elliott & Ilyes, 1996, *Alaeckaspis* Voichyshyn, 1999, *Dnestraspis* Novitskaya, 1983, *Unarkaspis* Elliott, 1983, *Larnovaspis* Blieck, 1984, *Eucyclaspis* Denison, 1970, *Parapteraspis* Stensiö, 1958, *Podolaspis* Zych, 1931, *Mylopteraspidella* Blieck, 1984, *Semipodolaspis* Voichyshyn, 2011, *Oreaspis* Denison, 1970, *Djurinaspis* Novitskaya, 1983, *Lamiaspis* Ilyes & Elliott, 1994, *Pirumaspis* Ilyes & Elliott, 1994.

Conclusions

The first phylogenetic analysis to include all genera belonging to the Pteraspidoformes is presented here, using different coding strategies to explore morphological shape variations and relationships of the taxa. In all phylogenies resulting from different parsimony coding methods, application of implied weighting gave the most consistent results. The inclusion of quantitative data (i.e. raw continuous characters or discretized characters) led to better resolution relative to searches using discrete qualitative characters only. The implied weighted phylogeny including continuous characters was most comparable to that of the discrete only (implied weighted) phylogeny, whereas discretizing the continuous characters (using objective gap coding) resulted in a different tree topology. Bayesian analyses resulted in similar topologies and resolution to the equally weighted discrete and discretized analyses. In all iterations the Psammosteidae fall within the Pteraspidoformes clade. Congruence between the phylogeny, stratigraphical ranges and palaeobiogeography supports relationships proposed and suggests a Laurentian origin for the Pteraspidoformes.

With regards to the different coding approaches, it is not immediately apparent as to whether raw continuous characters are more appropriate than discretized

quantitative characters for reconstructing ostracoderm relationships. However, we found discretized character analyses to be highly sensitive to missing data, incongruent with the trees using qualitative data only, but marginally more congruent with stratigraphical data than results using continuous characters. In all cases, homoplasy was found to be widespread, mirroring to some degree other clades of ostracoderms. As such, we recommend implied weighting as an objective tool to mitigate this. Furthermore, given the limited number of variable discrete characters within ostracoderm clades and the high degree of shape variation, quantitative characters need careful consideration and explicit justification.


Acknowledgements


We thank the staff at various museums for access to specimens, including Jonathan Clatworthy and Ivan Sansom (Lapworth Museum of Geology, University of Birmingham), Emma Bernard (Natural History Museum, London), William Simpson and Akiko Shinya (Field Museum, Chicago), Kiaeron Sheppard and Margaret Curry (Canadian Museum of Nature), and Lars Werdelin and Jonas Hagström (Naturhistoriska riksmuseet, Stockholm). Charlotte Brassey is thanked for discussion of ideas, methods and coding, along with all others in the palaeobiology and evolutionary biology team at the University of Manchester. Thanks are also given to two anonymous reviewers for constructive feedback on the first draft of this manuscript. This work was made possible by the funding of an NERC studentship (NE/K500859/1) and a Synthesys grant to visit the Naturhistoriska riksmuseet, Stockholm (SE-TAF-3875).

Supplemental material

Supplemental material for this article can be accessed online at: <http://dx.doi.org/10.1080/14772019.2016.1208293>.

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