Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders

Arachnids are an important group of arthropods. They are: diverse and abundant; a major constituent of many terrestrial ecosystems; and possess a deep and extensive fossil record. In recent years a number of exceptionally preserved arachnid fossils have been investigated using tomography and associated techniques, providing valuable insights into their morphology. Here we use X-ray microtomography to reconstruct members of two extinct arachnid orders. In the Haptopoda, we demonstrate the presence of ‘clasp-knife’ chelicerae, and our novel redescription of a member of the Phalangiotarbida highlights leg details, but fails to resolve chelicerae in the group due to their small size. As a result, tomographic studies of three-dimensionally preserved fossils now exist for three of the four extinct orders, and for fossil representatives of several extant ones. Such studies constitute a valuable source of high fidelity data for constructing phylogenies. To illustrate this, here we present a cladistic analysis of the chelicerates to accompany these reconstructions. This is based on a previously published matrix, expanded to include fossil taxa and relevant characters, and allows us to: cladistically place the extinct arachnid orders; explicitly test some earlier hypotheses from the literature; and demonstrate that the addition of fossils to phylogenetic analyses can have broad implications. Phylogenies based on chelicerate morphology - in contrast to molecular studies - have achieved elements of consensus in recent years. Our work suggests that these results are not robust to the addition of novel characters or fossil taxa. Hypotheses surrounding chelicerate phylogeny remain in a state of flux.
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Introduction

Arachnids and their relatives (Chelicerata) form a major branch of the arthropods, with around 112,000 living species (Zhang 2011). They also have an extensive palaeontological record, including more than 2,200 fossil species at the time of writing (Dunlop, Penney & Jekel 2014). Chelicerates can be found back into the Cambrian (Waloszek & Dunlop 2002; Dunlop, Anderson & Braddy 2004), although their record through deep time is patchy and tends to be concentrated into windows of exceptional preservation such as the late Carboniferous Coal Measures and various Cretaceous and Cenozoic ambers. Currently, sixteen arachnid orders can be recognised. Twelve have living representatives: scorpions (Scorpiones), harvestmen (Opiliones), pseudoscorpions (Pseudoscorpiones), camel spiders (Solifugae), palpigrades (Palipgradi), mites (Acariformes and Parasitiformes), ricinuleids (Ricinulei), spiders (Araneae), whip spiders (Amblypygi), whip scorpions (Thelyphonida) and schizomids (Schizomida). Four arachnid orders are extinct: trigonotarbids (Trigonotarbida), phalangirotarbids (Phalangirotarbida), haptopodids (Haptopoda) and the spider-like uraraneids (Uraraneida). To this can be added two marine groups with living representatives, the sea spiders (Pycnogonida) and horseshoe crabs (Xiphosura), as well as two extinct groups which were likely to have been primarily aquatic, the sea scorpions (Eurypterida) and the rare chasmataspidids (Chasmataspidida).

Resolving relationships between the arachnid and/or chelicerate lineages remains a challenge. Important cladistic studies include the comprehensive morphological analyses of Weygoldt & Paulus (1979), and Shultz (1990, 2007), as well as numerous applications of molecular data - sometimes with morphology combined (e.g. Wheeler & Hayashi 1998; Giribet et al. 2002; Pepato, da Rocha & Dunlop 2010; Rehm et al. 2011). Few of these include fossil terminals (but see Giribet et al. 2002 and Shultz 2007) - despite the fact that extinct species valuable source of data (Edgecome 2010). Several arthropod-wide analyses - both molecular and morphological - also include chelicerates (Regier et al. 2010; Legg, Sutton & Edgecombe 2013; Rota-Stabelli et al. 2013). Yet, as noted in a recent review (Dunlop, Borner & Burmester 2014), there is still no single accepted phylogeny for arachnids and their relatives, and there are evident discrepancies between trees derived from morphological and molecular data. Dunlop, Borner & Burmester (2014) thus recognised a minimum consensus tree, i.e. supported by various methodologies, of the form (Pycnogonida (Xiphosura (Scorpiones (Araneae (Amblypygi (Thelyphonida + Schizomida)))))). This rather extensively pruned phylogeny still excludes diverse and important groups like mites, harvestmen and pseudoscorpions, and does not place any of the fossil taxa. Xiphosura was recently interpreted as paraphyletic (Lamsdell 2013), at least with respect to Palaeozoic ‘synziphosurines’ which may include lineages eventually evolving into both crown-group horseshoe crabs and, separately, into arachnids.

Fossils have sometimes proved controversial in phylogenetic reconstruction, and for arachnids some authors simply excluded them completely (e.g. Wheeler & Hayashi...
Extinct taxa offer direct evidence of early - and possibly quite different - body plans, but often have large amounts of missing data when compared to living taxa. Furthermore, scoring morphological character states in fossils involves a degree of interpretation, and objective inferences have to be made. Despite the challenges inherent in using fossils in such analyses, recent studies have demonstrated the utility and importance of doing so in a range of different analyses (Legg, Sutton & Edgecombe 2013, Sharma & Giribet 2014). Furthermore, in recent years the level of interpretation required has been reduced through a number of improvements in our understanding of fossil arachnid (and arthropod) data. For example, the application of various techniques such as X-ray computed tomography - especially microtomography (μCT, e.g. Garwood, Dunlop & Sutton 2009) - has allowed the anatomy of some fossils to be reconstructed in unparallelled three-dimensional detail. For a review of such methodologies see Sutton, Rahman & Garwood (2014).

The principal aim of this study is to draw together recently published examples of well-preserved and (where possible) three-dimensionally reconstructed fossils in a phylogenetic analysis, and to augment these with novel data for two extinct arachnid orders: Phalangiotarbida and Haptopoda. Our intention is not to present a fully resolved phylogenetic tree, and we do not consider the topology recovered the sole solution to arachnid phylogeny. Rather, we use it to identify common trends and explore the impact of fossil data on tree topologies when scored into an modified version of a previously published dataset. In addition to twenty-seven newly added fossil taxa, the matrix - which is amended from that of Pepato, da Rocha & Dunlop (2010) - has sixteen new characters to capture the fullest possible range of fossil morphology. This exercise allows us to assess how robust the placement of extinct taxa is, how these impact on the relationships recovered between extant groups, and to explicitly test some earlier hypotheses from the literature. We also hope that our matrix will constitute a starting point for further studies, and provide a useful contribution into which new fossil discoveries can be integrated. Following materials and methods information, we present first the results of our tomographic reconstructions, and then results and discussion for our cladistic analysis. We subsequently discuss the impact of fossils. Character descriptions are included as an appendix.

**Materials and Methods**

**Material and Tomography**

All tomographic reconstructions presented in the current study are based on material from the Coseley Lagerstätte, near Dudley, Staffordshire, UK. They are thus Late Carboniferous, from the *similis-pulchra* zone of the British Middle Coal Measures; Duckmantian in age (ca. 315 Ma; Pointon et al. 2012), or Westphalian B using more traditional terminology. Their preservation is as three-dimensional voids - some partially infilled with kaolinite - within siderite nodules. Scans were conducted at the Natural History Museum, London on a Nikon HMX-ST 225 scanner with a tungsten reflection target.
Two specimens of *Plesiosiro madeleyi* (NHM I. 15899, NHM I. 7923) from the (monotypic) extinct order Haptopoda were scanned. They were selected as the most three-dimensional representatives of all the NHM specimens of this species, and NHM I. 7923 was chosen for subsequent processing as the most complete example. This was scanned at 180kV/175μA, with a 0.25 mm copper filter, and 3142 projections of exposure 354 ms, to provide a reconstructed dataset with a 19.5μm voxel size.

Material from two species of another extinct order, Phalangiotarbida, were scanned. One was not well-preserved enough to justify further reconstruction: *Goniotarbus tuberculatus* (BU 696, Lapworth Museum Birmingham, also Coseley). However, the NHM specimen In 22838, the holotype of *Goniotarbus angulatus*, was better resolved, and revealed important limb morphology. It was last described by Petrunkevitch (1953), whose work has, in the past, necessitated significant revision (e.g. Dunlop 1996a, Garwood and Dunlop 2011). Accordingly this phalangiotarbid specimen was selected for further processing. The scan was conducted at 225kV/190μA, and without added filtration. 3142 projections of exposure 180 ms were collected, and a reconstructed dataset with a 16.0μm voxel size created.

**Digital visualisation**

Both scans were used to create three-dimensional, virtual fossils using the custom SPIERS software suite (Sutton et al. 2012) following the methods of Garwood et al. (2012). The distal limbs of *Plesiosiro madeleyi* were not recovered by the scan where they were truncated by the edge of the nodule. Several of the walking legs of *Goniotarbus angulatus* were absent. Both models were scaled, and then exported to be presented here as VAXML models (SI file 1). SPIERS-generated isosurfaces were then ray-traced in Blender for figures and videos (Garwood and Dunlop 2014) - for *Goniotarbus angulatus* enough of the limbs were preserved to allow missing elements to be manually modelled from those present. This was achieved in Blender, and the added elements are rendered semi-transparent for clarity (Fig. 1).

**Microscopy**

Hand specimen photographs of *Plesiosiro madeleyi* are available in the redescription of Dunlop (1999). No comparable modern photographs of *Goniotarbus angulatus* exist. Accordingly a plate of hand specimen photographs is published herein showing the holotype, and only known specimen (NHM In 22838: Fig. 2). This was studied and photographed using a Leica MZ16A stereomicroscope and incident light. Photographs taken at multiple focal depths were combined using the software CombineZM (see Bercovici et al. 2009). Photographs of the whole fossil - which was too large for the field of view - were created by manually stitching sections using the open source raster graphics editor GIMP 2.8, and figures were assembled in Inkscape 0.48. For comparative purposes specimens of a related species (Petrunkevitch 1949), *Goniotarbus tuberculatus* (NHM In 31249, NHM In 18340, and NHM In 22840), were also studied.
Character coding

The current analysis of 86 taxa and 192 characters is a modified version of ‘Matrix A’ created by Pepato, da Rocha & Dunlop (2010). A particular focus of the previous study was to clarify the position of, and relationships within, the mites. Consequently the analysis had a large number of mite-specific characters. The current study has different goals, and for ease of analysis and clarity we exclude numerous characters which are only helpful for resolving ingroup relationships within one or both of the two major mite lineages (i.e. acariforms and parasitiforms). We remove two further characters based upon the reviews of the current manuscript, which are available with this paper. In addition to these changes, we added 16 characters relevant for fossil taxa, and modified others to make them applicable to newly introduced fossil terminals. Examples of novel characters include: a prosomal shield with a meso- and metapeltidium demarcated; the presence of genal spines; the prosoma and opisthosoma forming a single functional tagma; ‘elbowed’ chelicerae in those taxa with three-segmented chelicerae; a sixth limb modified as a paddle (or pusher); a shortened first opisthosomal tergite; six abbreviated opisthosomal tergites; the absence of a sternite for opisthosomal segment one; fusion of opisthosomal tergites 7-10; a median abdominal (genital) appendage; ventral sacs; a dorsal anal operculum; eurypterid gill tracts; and development with a nymphal stage. Full character descriptions for the updated matrix are included as an appendix. We have also modified a character to explicitly code ingesting solid material, rather than extra-oral digestion. The former is easier to code for fossils, often being apparent from the morphology of mouthparts, whereas the latter is more closely based on behaviour, something which is not typically preserved in fossils. Similarly the presence of opisthosomal venom glands has been altered to code for a telson with an aculeus and vesicle (the ‘sting’), the latter being verifiable in fossil scorpions. Finally, the character recording the number of cheliceral articles now has more than three articles as an option to reflect the state observed in outgroups (Haug et al. 2012a, b; Briggs and Collins 1999), and some fossil horseshoe crabs (Sutton et al. 2002; Briggs et al. 2012).

Taxon selection

As noted above, the focus on mites in Pepato, da Rocha & Dunlop’s (2010) Matrix A differed from the present study. Accordingly there were a large number of acarid terminals, which we pruned for this study. We concurrently added 27 fossil taxa to the matrix. These had on average 59% missing data in comparison to 4% for extant taxa - however we do not consider this problematic on the basis of multiple publications in recent decades demonstrating that this need not result in lack of resolution, and that excluding taxa on the basis of missing data is inadvisable (Kearney & Clark 2003; Cobbett, Wilkinson & Wills 2007; Wiens & Morrill 2011; Weins & Tu 2012). On the basis of the reviews of the current manuscript, the arthropodan Emeraldella brocki, from the description by Stein and Selden (2012) was included as an outgroup. This is has been recovered in the mandibulate stem lineage (Stein and
Selden 2012; Ortega-Hernández, Legg & Braddy 2013), or alternatively as more closely related to the chelicerates (Legg, Sutton & Edgecombe 2013). Two Cambrian arthropods belonging to an assemblage variously referred to as the Megacheira, or the great appendage arthropods, were added to reflect increasing evidence that these fossils may be closely related to chelicerates (e.g. Dunlop 2006; Edgecombe, García-Bellido & Paterson 2011; Haug et al. 2012a, b; but see also Legg 2013). The megacheiran genus *Alalcomenaeus* was coded on the basis of a comprehensive description of *A. cambricus* by Briggs and Collins (1999), and recently reported neural anatomy reported by Tanaka et al. (2013) for *Alalcomenaeus* sp., which minimised the degree of missing data. To assess megacheiran monophyly we added a further fossil, *Leanchoilia superlata*, which was recently redescribed in detail by Haug et al. (2012a).

For analyses of extant taxa only a sea spider (Pycnogonida) was selected as the outgroup as justified in Pepato, da Rocha & Dunlop (2010). To the previously coded pycnogonids we added two well-resolved Palaeozoic fossil examples - the Silurian species *Haliestes dasos* described by Siveter et al. (2004) and the Devonian *Palaeoisopus problematicus* redescribed by Bergström, Stürmer & Winter (1980). The recently discovered species *Pentapantopus vogteli* (Kühl, Poschmann & Rust 2013) resembles *H. dasos* and also some modern pycnogonids - but as highlighted in the original publication - incomplete preservation and a limited understanding of their ontogeny precluded placement of the species. Accordingly we have opted to omit the species from this analysis, as with the fossil of Rudkin et al. (2013), which we consider to be controversial as its incomplete and does not reveal a number of important sea spiders features. As previously noted, Lamsdell (2013) recently challenged the monophyly of the horseshoe crabs (Xiphosura) which have traditionally been interpreted as having a stem lineage (the synziphosurines) leading up to a crown-group Xiphosurida. To test this suggestions we included three of the best preserved putative synziphosurine taxa. From the Silurian we scored *Offacolus kingi* based on the description of Sutton et al. (2002) and *Dibasterium durgae* based on Briggs et al. (2012), as well as the Devonian fossil *Weinbergina opitzi* redescribed by Stürmer & Bergström (1981) and Moore et al. (2005).

Three Silurian representatives of the extinct Eurypterida were scored: *Parastylonurus ornatus* based on Waterston (1979), *Mixopterus kiaeri* based on Størmer (1934) and *Eurypterus* (formerly *Baltoeurypterus*) *tetragonophthalmus* based on Selden (1981). This allowed us to assess the issue of whether sea scorpions are closely related to scorpions; which impacts on the monophyly of arachnids and the likely number of independent terrestrialisation events (Garwood & Edgecombe 2011; Dunlop et al. 2013). From the extinct Chasmataspida we included the Ordovician fossil *Chamataspis laurencii* following Dunlop, Anderson & Braddy (2004) and the Devonian *Octoberaspis ushakovi* after Dunlop (2002). Eurypterids have been recovered as paraphyletic with respect to chasmataspidids in some studies (Shultz 2007), as posited by Tetlie & Braddy (2004). We also wanted to test the impact of fossils on Shultz’s (2000) Stomothecata hypothesis (i.e. Scorpiones + Opiliones) and to this end we coded five Palaeozoic scorpions: the
Silurian *Proscorpius osborni* based on Dunlop et al. (2008); the Devonian *Palaeoscorpius devonicus* based on Kühl et al. (2012); the Lower Devonian genus *Waeringoscorpio*, based on the redescription of *W. hefteri* and description of *W. westerwaldensis* by Poschmann et al. (2008); Lower Carboniferous species *Pulmonoscorpius kirktonensis*, coded from Jeram (1993) with lung details from Jeram (1990); and the Carboniferous *Compsoscorpius buthiformis* based on Legg et al. (2012). Adding the recently described Carboniferous stem mite harvestman *Hastocularis argus* from Garwood et al. (2014) and closely related *Eophalangium sheari* (Dunlop et al. 2003) allowed more robust assessment of the extent to which fossils impact on the proposed sister group relationship between scorpions and harvestmen.

The extinct arachnid order Trigonotarbida has been recovered as sister group to the so-called Tetrapulmonata (i.e. spiders and their closest relatives), but relationships with the rare order Ricinulei have also been suggested in the literature (Dunlop, Kamenz & Talarico 2009, and references therein). For trigonotarbids we scored the Devonian genus *Palaeocharinus* spp. from specimens assigned to *Palaeocharinus rhyniensis* Hirst, 1923 and *Palaeocharinus hornei* (Hirst, 1923) but which we consider to be synonymous. Coding was based on Dunlop (1994a) and Garwood and Dunlop (2014). We also included two Carboniferous species we have previously reconstructed using CT scans, namely *Anthracomartus hindi* based on Garwood & Dunlop (2011) and *Eophrynus prestvicii* based on Dunlop & Garwood (2014). Another extinct (Devonian - Permian) arachnid order, the probably spider-like Uraraneida, was coded on the basis of Selden, Shear & Sutton (2008). Finally, the two remaining extinct arachnid orders were coded based on the digital visualisations presented herein. Characters for the Carboniferous Haptopoda derive from the model of *Plesiosiro madeleyi* and the previously published account of Dunlop (1999). Phalangiotarbida coding was again based on the model presented herein for *Goniotarbus tuberculatus*, plus data from Pollitt, Braddy & Dunlop (2004) for *Bornatarbus mayasii* (both Carboniferous).

**Cladistic Analysis.**

The matrix was analysed with TNT v.1.1. (Goloboff, Farris and Nixon, 2008; made available with the sponsorship of the Willi Hennig Society), using unordered multistate characters, and traditional search options. Searches comprising tree bisection-reconnection [TBR] with 1,000 replicates, saving 100 trees per cycle were conducted on the full matrix (SI file 2), and a pruned version of the matrix excluding fossil taxa (SI file 3). The data matrix is also available in the public database Morphobank (http://www.morphobank.org; Project 1274). For equally weighted analyses (EW) with fossils, TNT was used to create strict consensus trees which were exported as SVGs into Inkscape, and numerous analyses were run to explore the data with differing taxa and characters excluded to explore their impact. Results for equally weighted analyses lacking fossils were exported as .tre files of the strict consensus, and trees collapsed in Figtree 1.4.1 before being exported to Inkscape. Analyses were also run using implied weighting (IW) to assess the impact of
homoplasy on the results. Goloboff (1993) and Goloboff et al. (2008) provide an overview of this weighting scheme, whilst Legg, Sutton & Edgecombe (2013), Legg and Caron (2013) and Ortega-Hernández, Legg and Braddy (2013) provide justification of its use in a palaeontological context. We note, however, the comments of reviewer #1 of the current manuscript - available with the paper - criticizing this weighting scheme; no peer-reviewed contribution discussing these issues is currently available in the literature. Due to a number of difficult to place groups (Phalangiotarbida, Ricinulei, Parasitiformes) and resulting instability, when run with a variety of concavity constants (k = 0.25, 1.0, 3.0, and 10.0) tree topology changed. Here we present a strict consensus of the most parsimonious trees for each concavity constant. For the analyses including fossils, resampling was carried out in TNT: we provide jackknife (Farris et al., 1996; 33% removal probability, 1000 replicates), bootstrap (Felsenstein, 1985; 1000 replicates) and Bremer support (Bremer, 1994) values for the equal weights tree. Nodal support values of the first two of these are shown as absolute frequencies. For implied weights trees we show support through symmetric resampling - chosen because it is unaffected by character weighting (Goloboff et al. 2003) - using a change probability of 33%, and 1000 replicates, and reporting absolute frequencies.

**Tomography Results**

*Reconstruction of Plesiosiro madeleyi*

The digital visualisation of haptopodid *Plesiosiro madeleyi* (NHM I.7923; Figure 1A-D) presented herein largely corroborates previous work on this species (Pocock 1911; Petrunkevitch 1949; Dunlop 1999). Some elements - such as distal limb articles - are not resolved in the CT scan as they run along the crack in the nodule. The most complete leg is shown in Fig.1D. Accordingly we refer the reader to Dunlop (1999) for these details - which include a full description and measurements of the scanned specimen - and focus here on clearly resolved and/or novel anatomical elements. Note that the scanned specimen shows a small amount of distortion due to lateral compression.

As previously reported, the posterior margin of the prosomal shield terminates with a posteriorly directed ridge, obscuring some of tergite one (Dunlop 1999; see SI file 1, animation in SI file 4). Clipping the digital visualisation provides no clear evidence for any kind of locking structure between the prosomal shield and the first tergites, such as is seen in the extinct trigonotarbs for example. Instead the prosoma-opisthosoma junction in *Plesiosiro madeleyi* forms a simple ‘z’-shaped arrangement in lateral section. Median eyes are resolved as depressions either side of a dorsal median ridge on the prosomal shield (Fig. 1A), reflecting the same observation in hand specimens. This is unusual for arachnids - in which the median eyes are normally raised structures - and may be a taphonomic artefact caused by the eyes inverting prior to fossilisation (see also remarks in Dunlop 1999). The lateral prosomal shield tubercles are shown in this specimen to be broader than the rounded structures previously described, being 0.8 mm long latero-posteriorly.
directed ridges, whose dorsal surface projects anteriorly at the anterior prosomal shield margin in parasagittal section. They have been interpreted as possible lateral eye tubercles, but evidence of explicit lenses is lacking. It has also been speculated that Plesiosiro madeleyi was a harvestman (see below), but these lateral tubercles also showed no obvious openings for repugnatorial glands; as would be expected if these structures were raised ozophores similar to the condition in cyphophthalmid harvestmen. Overall, the results of the phylogeny presented herein support Dunlop (1999) in the suggestion that these projections probably represent lateral eye tubercles. Immediately posterior to the tubercles are small depressions.

The ventral prosoma is well-resolved, and confirms the presence of anterior and posterior sclerites in the sternum (Fig. 1C), the former bearing an anterior pair of protrusions. Significantly, the scan unequivocally demonstrates chelicerae of a ‘clasp-knife’ type, comprising a proximal (minimum of 0.7 mm in length) and distal (0.9 mm) article (Fig. 1B). There is no evidence of a third cheliceral article as reported by Petrunkevitch (1949). The chelicerae are ventral to the median anterior projection, their attachment being aligned essentially level with the median eyes. Palpal coxae cannot be resolved due to the crack in the nodule, but the model suggests that the chelicerae were probably tucked between the bases of the pedipalps in life. The chelicerae are preserved with the proximal article dorsally oriented, with a geniculate joint, and the distal article ventrally directed. Thus they probably had something approaching an ‘orthognath’ bite (i.e. hinged so cheliceral movement is parallel to the sagittal plane), similar to the mesothele and mygalomorph spiders (Kraus & Kraus 1993). The opisthosomal segmentation pattern for Plesiosiro madeleyi resolved here - i.e. 12 segments in total - corroborates that reported by Dunlop (1999).

Reconstruction of Goniotarbus angulatus

Digital reconstruction of the holotype of phalangiotarbid Goniotarbus angulatus (NHM In22838) reveals an arachnid with a broad prosoma-opisthosoma boundary (Fig. 1H, 2A, SI file 1, animation in SI file 4). The total body length is 17.0 mm whereby the prosomal shield is 6.5 mm long and 7.1 mm wide at its curved posterior margin. A median bulge causes crowding of - and obscures in part - the anterior-most opisthosomal tergites (Fig. 2D). The prosomal shield has an anteriorly positioned median eye tubercle, however the eye arrangement is not readily apparent - perhaps the reason previous works reported either two (Pocock 1911) or six (Petrunkevitch 1953) lenses. Careful study suggests that are three depressions in a triangular arrangement on one side - a number matching the state observed in other phalangiotarbids (Pollitt, Braddy & Dunlop 2004) - however, this isn’t seen on the opposing side of the prosomal shield, and thus we treat the observation with caution, and discuss the impact of different codings below. The dorsal surface of the prosomal shield is demarcated by three pairs of radiating linear depressions. These are not so clearly visible towards the middle, but become increasingly pronounced laterally (SI file 1). The median prosomal shield bears a subtly raised region with concave lateral margins, widening anteriorly towards the eyes and also posteriorly.
The opisthosoma is 10.6 mm long and maximally 7.5 mm wide. Opisthosomal segments 1-6 are very short and closely spaced, as is typical for members of this extinct order (Fig 1H, 2D). Tergites 1 and 2 express anterior curvature at their edges, accommodating the curved prosomal margin (see above). Tergites 4-6 have straighter margins, and 6 is slightly longer than the five preceding tergites (Fig. 2D). Other data (e.g. Pollit, Braddy & Dunlop 2004) suggest that the phalagiotarbid ground pattern was an opisthosoma with 10 clearly expressed tergites dorsally. In Goniotarbus angulatus and many other species tergites 7-10 appear to be fused into a single dorsal plate covering the back end of the opisthosoma. However, in NHM In 22838 this original segmentation is marked by subtle, v-shaped linear depressions (Fig 2E). The presence of a posterior depression to demarcate the original tergite ten corroborates the observation reported by Petrunkevitch (1953), which was missing in the original description of Pocock (1911). The posterior opisthosoma bears the dorsal anal operculum; marked by a pit in NHM In 22838 with possible discharge visible in the CT scan (Fig. 1H, 2A,E). This might suggest a small degree of decay prior to fossilisation.

The ventral surface is well-resolved (Fig. 1I, 2B). Scans reveal a pronounced anterior median ventral ridge near the expected position of the chelicerae (Fig 1F,I), tucked between the small palpal coxae which are not visible in the hand specimen. The four triangular leg coxae are large, and all abut the sternum. The mesal surfaces of the first coxae (length 2.2 mm) are separated by the aforementioned ridge. Coxal margins otherwise appear to be in contact with the surrounding coxae (Fig. 1I, 2B). The coxae increase in size posteriorly - coxae 4 are 3.2 mm long - but these too abut sternum medially. The sternum itself (Fig. 2C) is subdivided into five plates in a ‘1-2-2’ arrangement from anterior to posterior. The ventral opisthosoma comprises the short sternites 1-4 which are crowded anteriorly between the coxae of leg 4 (Fig. 2B, total length: 1.8 mm). Sternite 5 is significantly longer than the preceding sternites, and all remaining sternites increase in length posteriorly to number 9 (length 3.9 mm). All sternites have straight posterior margins, and are divided longitudinally into three plates by two suture lines running from the distal termination of coxae four, and curving outwards to terminate at the opisthosomal margin towards the posterior end of sternite nine (Fig. 2B). Some previous studies have noted possible openings for (?)tracheal) spiracles among the anteriormost sternites (Dunlop & Horrocks 1997, Fig. 2), but these could not be identified unequivocally here. There are, however, two enigmatic raised structures on sternite 5 whose identity and function remains uncertain.

The preservation of the limbs is patchy. Based on the very small pedipalp size we presume that the phalangiotarbid chelicerae must have been tiny. This would explain their poor resolvability in the current scans. At the anterior margin of the previously described ridge between the first coxae there is a ventrally projecting feature (Fig. 1F). Further details are unrecovered due to lack of resolution, but this could represent a small pair of chelicerae. The pedipalps are also small, hanging ventrally beneath the anterior margin of the prosomal shield; although it should be
noted that the exact prosomal shield margin is hard to differentiate from the crack along which the nodule was split in this specimen, and thus it is possible they projected anterior of the prosomal shield in life. Individual articles in the pedipalps could not be resolved in the CT scan. The first right walking leg is truncated midway along the tibia. All other legs on this side are truncated at the trochanter-femur joint. The legs on the left side are more complete (Fig. 1E,G). On the basis of the preserved articles, leg length appears to increase posteriorly from 1 to 4. Limb article proportions are generally similar throughout - on the most complete leg (left leg 1, Fig 1E) the measurements are: trochanter, 1.0 mm; femur, 1.6 mm; patella, 1.7 mm; tibia, 1.6 mm; metatarsus, 1.1 mm and tarsus, 1.2 mm. Details of any terminal claws (apotele) on the legs are equivocal.

Cladistics Results and Discussion

Analysis using traditional search options (TBR) and equal weights (EW) resulted in 383 trees of 455 steps (average weighted character fit, WCF, 101.5; Goloboff 1993), presented here as a strict consensus (Fig. 3). Using implied weights (IW), results differed with changing concavity constants: $k = 0.25$ resulted in 3 trees of 80.38824 steps (all with WCF = 127.94); $k = 3.0$ in 12 trees of 37.26555 steps (all with WCF = 150.73); and $k = 10.0$ in 6 trees of 16.71747 steps (all with WCF = 171.28). A consensus of the MPTs for each $k$ value is shown in Fig. 4. Without fossil taxa, 40 trees of 384 steps were recovered under the same EW search parameters (average WCF 150.9). In general, several relationships are consistent across all search parameters and our results - and their implications - are discussed in further detail below.

Chelicerata

The two analyses including fossils are rooted on the artiopodan *Emeraldella brocki*. In the EW tree (Fig. 3) the megacheiran taxa form a clade, sister group to (Eurypterida + (Chasmataspida + Xiphosura)). This relationship - defined through the presence of lateral eyes and a pair of median eyes - has essentially no support in the current analysis. In all IW analyses these taxa are found either in a polytomy with all remaining taxa , or as a clade sister group to these (Fig. 4). All IW analyses thus recover Chelicerata (i.e. those taxa which were traditionally assigned to Pycnogonida, Merostomata and Arachnida; Dunlop 2010) - a relationship with stronger support, and in keeping with the idea that *Alalcomenaeus* and *L. superlata* could be considered possible stem-chelicerates in the literature (e.g. Edgecombe, García-Bellido & Paterson 2011; Haug et al. 2012a, b; although see also Legg, Sutton and Edgecombe 2013). We highlight, however, that due to a lack of further Cambrian fossil taxa we do not consider this a robust test of megacheiran relationships. Megacheirans were not our focus group, and study of a range of early Palaeozoic arthropods is needed to resolve the origins of chelicerates and their probable stem-group in detail. We refer to Chen et al. (2004), Haug et al. (2012a, b), Legg et al. (2012), Legg (2013), and Legg, Sutton and Edgecombe (2013) for work in this direction. At the base of the chelicerates in IW analyses we find a clade
comprising *Dibasterium durgae* and *Offacolus kingi* as sistergroup to all other chelicerates. This position for *O. kingi* and *D. durgae* results from their chelicerae, which possess more than three articles, and the presence of exopods on all the postcheliceral prosomal appendages, shared with the Cambrian taxa included, but no other chelicerates. Under EW this clade is sister group to the arachnids and pycnogonids instead: another grouping with essentially no support, in which we place little confidence.

**Merostomata?**

Excluding *Dibasterium durgae* and *Offacolus kingi*, the remaining horseshoe crabs in our analysis resolved in a clade together with the extinct eurypterids and chasmataspidids. In EW analysis, this group is defined by the increase in head shield segments and reduction of cheliceral segments to three relative to the Megachiera and outgroup, whilst with IW these share the synapomorphy of a cephalic doublure (where known). In IW analyses this clade is sister group to an (Arachnida + Pycnogonida) clade (see below), whilst EW analyses have synziphosurine taxa in this position, as previously highlighted. Using EW Chasmataspidida, the remaining Xiphosura, and Eurypterida each form a monophyletic group, with the relationships (Xiphosura (Chasmataspidida+Eurypterida)). Under IW, the position of the synziphosurine *Weinbergina opitzi* is unstable - at high k values (k=3.0, k=10.0) it is sister group to (Eurypterida (Chasmatsapidida (modern Xiphosurida)), whereas at lower values it is resolved as sistergroup to (*C. laurencii* + modern Xiphosurida). At all k values, the eurypterids form a clade, whilst chasmataspids are either split by *W. opitzi*, or form a grade to modern Xiphosura. In an extant-taxa-only analyses under EW and IW, rooted on pycnogonids, Xiphosurida form a monophyletic sister clade to Arachnida.

This overall result with fossils included is interesting in that horseshoe crabs and eurypterids were traditionally grouped together as the class Merostomata; the aquatic counterpart to a largely terrestrial class Arachnida. As argued by authors like Kraus (1976), this is primarily an ecological distinction rather than a phylogenetic one. Previous cladistic studies consistently failed to recover Merostomata and usually placed eurypterids closer to arachnids instead (Weygoldt & Paulus 1979; Shultz 1990, 2007; see also below). We also failed to recover Merostomata in its traditional sense, since our synziphosurines are paraphyletic, with *D. durgae* and *O. kingi* recovered elsewhere. In IW analyses we are, however, left with a monophyletic unit comprising remaining Xiphosura *sensu stricto* (albeit here including the synzophosurine *W. opitzi*; see below), Eurypterida and Chasmataspidida. Were this clade to prove robust - but see Lamsdell (2013) for an alternative model - the name Merostomata remains available for this taxon.

**Xiphosura / Xiphosurida**

Lamsdell (2013) analysed many of the Palaeozoic fossils traditionally assigned to horseshoe crabs, concluding that Xiphosura is not monophyletic and that the fossils...
placed here actually comprise a paraphyletic assemblage of basal chelicerates and
stem taxa for the lineage leading up to modern Xiphosurida. Our taxon coverage
was not nearly as extensive as Lamsdell’s, but in concordance with his study we also
failed to recover a monophyletic Xiphosura. Both here under IW (but not EW, see
above) and in Lamsdell (2013) Offacolus kingi resolved in a basal position among
Chelicerata (Fig. 4). On the basis of our support values, we certainly consider this
the stronger of the two possibilities we present herein. Lamsdell did not score
Dibasterium durgae - the species was described while his paper was in press - but
added a comment in proof addressing the fact that the original description by Briggs
et al. (2012) recovered a monophyletic Xiphosura, a result repeated in Legg, Sutton
& Edgecombe (2013). Lamsdell (2013) questioned a number of the characters in this
matrix. The IW results presented herein agree in part with those of Lamsdell, in
recovering a paraphyletic synziphosurine grade at the base of the chelicerate tree.
Our analysis differs from Lamsdell’s scheme in recovering, at least under some
parameters of analysis, the synziphosurine Weinbergina opitzi in a clade together
with the living horseshoe crabs. In his 2013 paper Weinbergina was part of a newly
formulated Prosomapoda assemblage; essentially comprising the sister group of the
horseshoe crabs sensu stricto, the eurypterids and the arachnids. Lamsdell’s
hypothesis that synziphosurines include basal chelicerates - rather than just basal
horseshoe crabs - has much to recommend it, and the position(s) recovered, but we
also note that whilst two cladistic analyses have now recovered this result, both are
limited in their taxon sampling in comparison to, for example, Legg, Sutton &
Edgecombe (2013). Only through continued analysis and work on fossil chelicerates
can light be shed on this issue. A Xiphosurida crown group - represented here by the
two living horseshoe crabs - was, unsurprisingly, recovered as monophyletic.

Eurypterida

The most recent evidence in favour of eurypterids being the sister group of the
arachnids was published by Kamenz et al. (2011), who identified the enigmatic ‘horn
organ’ in the opisthosoma of an exceptionally preserved eurypterid as a potential
precursor of a spermatophore. Sperm transfer via spermatophores was thus
proposed as a putative synapomorphy for (Eurypterida + Arachnida) and the name
Sclerophorata was introduced by Kamenz et al. (2011) for this clade; nomenclature
also followed by Lamsdell (2013). Despite this, Eurypterida did not resolve in the
present study together with Arachnida, rather they were drawn into the previously
discussed merastomatid clade through their cephalic doublure (a character missing
in Dibastierum and Offacolus, but present in modern xiphosuran taxa), and
‘elbowed’ chelicerae where known. Eurypterids were recovered as monophyletic in
all analyses, with the internal relationships (Parastylonurus ornatus (Eurypterus
tetragonophthalmus + Mixopterus kiaeri)). Until recently there were two very good
synapomorphies for Eurypterida: a median abdominal (or genital) appendage on the
underside of the opisthosoma and a plate-like metastoma covering the back end of
the coxal gnathobases. Both these characters were subsequently identified by
Dunlop (2002) in at least one genus of chasmataspidid (including Octoberaspis), but
the group is defined here by the fusion of the anteriormost abdominal appendages
to form a large genital operculum.

Chasmataspida

In the EW analysis, the chasmataspidids are recovered as monophyletic on the basis of genal spines in both coded species, and this clade is in turn sister group to the eurypterids. The chasmataspidid-eurypterid clade is defined by the combined presence of a metasoma, twenty-segmented body, and presence of a median abdominal appendage. Eurypterids and chasmataspidids also share a very short first opisthosomal tergite. In IW analyses, chasmataspidids are recovered as a grade relative to the extant Xiphosura at higher k values (k=3.0, k=10.0), or split by W. opitzi. Neither IW or EW topologies have strong support. That the group is paraphyletic is in accordance with Tetlie & Braddy (2004) and Shultz (2007), but contra Dunlop et al. (2004). The IW results reflect a fundamental conflict relating to chasmataspidids: in addition to the similarities between some chasmataspidids (e.g. Diploaspis casteri, Octoberaspis ushakovi) and eurypterids, other taxa more closely resemble horseshoe crabs (e.g. Chasmataspis laurencii, which is found as sister group in IW analyses to Xiphosurida). Indeed when Chasmataspis laurencii groups with xiphosurids it does so on the basis of the presence of a cardiac lobe. We note, however, that all chasmataspids described to date share a similar and distinctive body plan in which the opisthosoma consists of a short preabdomen and long nine-segmented postabdomen. These synapomorphies are be outweighed in the IW analysis by those shared with xiphosurans.

Pycnogonida

One result of the present analysis merits particular comment, namely the position of Pycnogonida. The sea spiders usually resolve either as sister group of all other chelicerates - which collectively form the Euchelicerata sensu Weygoldt & Paulus (1979) - or sometimes as sister group of all other arthropods in studies with a broader taxon sampling; see Dunlop & Arango (2005) for a review. In the present study, in the trees including fossil taxa, Pycnogonida are monophyletic. This is to be expected as there are many synapomorphies for both fossil and living sea spiders such as the proboscis used for feeding or the unique oviger appendage. However in the current analysis, Pycnogonida resolved in a more derived position based on our dataset, specifically as the sister group of Arachnida. This result is controversial, but has precedence among some mitochondrial DNA studies (e.g. Podsiadlowski & Braband 2006; Jeyaprakash & Hoy 2009) which also recovered an ingroup position for sea spiders. The work of Simon & Hadrys (2013) makes apparent the problems of using mtDNA for deep divergences in arthropod taxa, and indeed, Dunlop, Borner & Burmester (2014) cautioned that the mtDNA results in question may be an artefact. We strongly suspect that is the case here. The position of of pycnogonids in this study probably results from long branch attraction, coupled with taxon selection. The pycnogonid clade has a multitude of synapomorphies, whilst the effect of the outgroup is to place synziphosurine and merastomatid taxa at the base of the tree. The limited number of completely preserved pycnogonid taxa precludes breaking up
this long branch with such fossils. Rather this issue could be addressed in future studies by adding further outgroup taxa sampling the origins of, and early splits within, the total group chelicerates. These should include a range of Cambrian arthropods. In addition to further megacheirans and xenopods, definitively mandibulate taxa would be beneficial, as could be adding a non-arthropod outgroup, or including novel characters suites to better test the polarity of pycnogonid characters. Within the pycnogonids under EW the fossil taxa are recovered as a grade to a polytomy comprising extant species, whereas in IW fossil taxa are recovered as an internal clade due to multi-segmented chelicerae - the remaining taxa are a polytomy. In extant-taxa only trees Pycnogonids are not monophyletic as we have chosen to root the tree with a single species as the outgroup.

**Arachnida**

The present dataset universally recovers Arachnida as a monophyletic group, sharing the apomorphies across all analyses of lost appendages (at least in postembryonic instars) on opisthosomal segment 1, and a tibial origin of the apotele depressor. In IW analysis this includes the presence of slit sense organs (albeit secondarily absent in Palpigradi). All arachnid orders with more than one taxon included were found to be monophyletic, with a single exception, highlighted below. A monophyletic Arachnida is in concordance with the majority of the published morphological (Weygoldt & Paulus 1979; Shultz 1990, 2007) and molecular (Wheeler & Hayashi 1998; Regier et al. 2010) analyses. However, as outlined below, relationships between the arachnid orders differs between the trees we present are dependent on analytical parameters.

Despite potential synapomorphies for a scorpion + eurypterid clade - such as a five-segmented postabdomen (e.g. Dunlop & Webster 1999) - this was not our most parsimonious result. The similarities between scorpions and sea scorpions would thus be homoplastic. This is supported by the results of the only published eurypterid phylogeny (Tetlie 2007; a tree based on an unpublished phylogeny from the author’s PhD thesis ), who found that the most scorpion-like genera with strongly raptorial forelimbs and curved telsons (Mixopterus, Carcinosoma) resolve in a derived position within Eurypterida; again indicative of convergent character acquisition.

**Opiliones, Pseudoscorpiones, Scorpiones, Phalangiotarbida**

In all analyses excluding IW with low k values (k=0.25, k=1.0), we recover a weakly supported clade of the form ((Pseudoscorpiones + Scorpiones) + (Phalangiotarbida + Opiliones)). With extant taxa only under EW, a clade of the form (Opiliones (Scorpiones + Pseudoscorpiones)) is recovered, whilst in IW extant only analyses and with fossils and low k values, Stomothecata (i.e. Opiliones + Scorpiones) is recovered. In this case the relationship for the other members of the clade is (Phalangiotarbida + (Pseudoscorpiones + (all other non-stomothecata arachnids))). Synapomorphies for ((Pseudoscorpiones + Scorpiones) + (Phalangiotarbida +
Opiliones) include bicondylar femoropatellar articulation, bicondylar patellotibial articulation, and the presence of a cheliceral tergal-deutomerite muscle. We note, however, that these characters are unknown for fossil taxa, including both phalangiotarbid species. In a wider context, the position of Scorpiones has been one of the most divisive issues in arachnid phylogeny. These animals have been variously interpreted as closely related to eurypterids (see above), as sister group to all other arachnids (Pocock 1893; Börner 1904; Weygoldt & Paulus 1979) or more recently as the sister group of Opiliones (Shultz 2000, 2007) based on the shared presence of a preoral chamber formed from projections of the anterior leg coxae (the stomotheca, hence Stomothecata). A recent alternative proposal from Sharma et al. (2014) is Arachnopulmonata - a sister group relationship between the scorpions and tetrapulmonates (spiders and their relatives, a group introduced below). We recover Scorpiones and Opiliones within a clade, but with Pseudoscorpiones and Phalangiotarbida included. The novel clade (Pseudoscorpiones + Scorpiones) is an interesting result, because although scorpions and pseudoscorpions look superficially similar, features like their large pedipalpal claws are generally interpreted in modern analyses as homoplastic. Some (non cladistic) studies did place pseudoscorpions and scorpions together, with Savory (1971) introducing the name Scorpionides for these two orders, but again this was largely based on inferences from gross morphology rather than explicit and testable synapomorphies. Pepato, da Rocha & Dunlop (2010) recovered (Scorpiones + Pseudoscorpions) under some parameters of analysis and indeed our tree builds upon their morphological dataset. In our EW analysis they are united by the nature of their palpal chelae, presence of a patellotibial extensor, ventrally/posteroventrally orientated anterior transpatellar muscle insertion, loss of the posterior patellotibial muscle, and isolecithal/telolecithal eggs.

In most other cladistic studies (Weygoldt & Paulus 1979; Shultz 1990, 2007; Wheeler & Hayashi 1998; Giribet et al. 2002) Pseudoscorpiones were placed as the sister group of Solifugae, together forming the clade Haplocnemata; a name introduced by Börner (1904). Putative synapomorphies identified for Haplocnemata include a very short femur and a correspondingly long patella - in some schemes they were named Apatellata because of confusion about whether these arachnids even had a proper ‘knee’ joint - and two pairs of tracheae opening on the the third and fourth opisthosomal segments. We do not recover Haplocnemata in any of our analyses. A number of morphological characters found in common between Pseudoscorpions and Parasitiformes among the mites do not result in the grouping of these taxa in any analyses. In our low k values (k=0.25, k=1) analyses we recover stomothecata in a form whereby many of the fossil scorpion taxa form a polytomy at the base of a clade comprising the remaining scorpions and the harvestmen. This clade is a polytomy between the fossil scorpion Compsoscorpius buthiformis, the crown group Scorpiones, and the Opiliones. A plesiomorphic scorpion grade leading to crown Stomothecata is novel, but only appears under a limited range of analytical parameters.

Apart from the low k values analyses where they are sister group to the non-
Stomothecata arachnids, the Phalangiotarbida are recovered as sister group to the Opiliones. This grouping has low support, and is supported only by the number of body segments in the EW analysis. Previous hypotheses of relationships with Opiliones were put forward by Petrunkevitch (1948) - and this is the first cladistic support for this hypothesis. Alternatives of close relationships with the Opilioacariformes among the mites (Dunlop 1995) or with the tetrapulmonate arachnids (see below; Pollitt, Braddy & Dunlop 2004) were not supported here. We are cautious of this result however, which we believe lacks stability - in part, we suspect, because of a lack of synapomorphies phalangiotarbid share with other orders. Phalangiotarbs are unusual-looking creatures and preserve a series of novel autapomorphies - short tergites, divided sternites, dorsal anal operculum, etc. - none of which suggest an animal close to the morphological ground pattern of the arachnids. Furthermore, important questions regarding the group’s anatomy remain unclear: for example the nature of their eyes. Many phalangiotarbid taxa possess six eyes located on a median ocular tubercle. Pollitt, Braddy & Dunlop (2004) tentatively identified these as three pairs of lateral eyes. However, phalangiotarbid eyes could equally represent one median eye pair, and two lateral pairs located in close proximity to each other. We have coded the taxa as having the latter - many spiders have a single tubercle bearing two median plus lateral eyes - but note the exact nature of the eyes is impossible to ascertain in extinct groups. If phalangiotarbs are coded as possessing three pairs of lateral eyes, they are recovered under EW in a basal polytomy of non-palpigrade arachnids, along with clades comprising Opiliones, (Pseudoscorpiones + Scorpiones), Pantetrapulmonates, and a clade comprising all remaining taxa (Ricinulei + (Parasitiformes + (Solifugae + Acariformes))). With IW under this coding they match the position seen in the low k values trees presented herein. Unfortunately even tomography could not resolve key features such as the nature of the chelicerae (chelate or ‘clasp-knife’?) that could support a more robust placement. In order to achieve any certainty, widespread application of these techniques to currently known phalangiotarbs, or new fossil discoveries, will be key.

**Palpigradi**

Palpigradi are enigmatic arachnids which appear to retain a suite of plesiomorphic character states, such as chelicerae with three articles, multiple claws on the pedipalp and a telson. Although superficially resembling whip scorpions (Thelyphonida) they are widely perceived as ‘primitive’ arachnids and tend to emerge as an early branching clade. A definitive position is hard to resolve and previous studies showed little consistency in their results. We add no further certainty here: the group resolves variously as sister group to all other arachnids (EW) - reflecting the perception they may be plesiomorphic in their anatomy - but also as sister group to a (Solifugae + Acariformes) clade at low k IW analyses, or at higher k values as sister group to all arachnids minus the ((Pseudoscorpiones + Scorpiones) + (Phalangiotarbid + Opiliones)) grouping. They appear as the earliest branching members of the equivalent clade minus fossils in extant taxa only analyses. The discovery of fossils with a plesiomorphic morphology for the group
(palpigrades’ fossil record is essentially non-existent: the only fossil cannot be identified to family level) could provide key evidence to help move beyond this impasse.

Poecilophysidea

As noted above, Solifugae were traditionally allied with Pseudoscorpiones in most of the recent phylogenetic studies. Authors such as Alberti & Perreti (2002) challenged this proposal and demonstrated similarities, particularly in male genital characters, between Solifugae and the acariform branch of the mites. Two independent studies (Dabert et al. 2010; Pepato, da Rocha & Dunlop 2010) formally recovered (Solifugae + Acariformes) based on molecular and molecular/morphological data respectively. A similar result was achieved molecular in a consensus supertree by Rota-Stabelli et al. (2013). This clade was formally named Poecilophysidea by Pepato, da Rocha & Dunlop (2010) drawing on a historical name used for a solifuge-like mite. Our dataset - which we concede is largely derived from the Pepato, da Rocha & Dunlop characters - also recovers Poecilophysidea under EW and three IW analyses, albeit with low support. The only exception is our IW, k=3.0 tree where we find solifuges as the earliest branching members of a clade also containing mites and the Ricinulei. In extant taxa-only analyses there is little resolution in this part of the tree. Where recovered, Poecilophysidea synapomorphies include a testis with a distinctly larger glandular area, and presence of a nuclear envelope. In analyses including fossils, with EW and IW k=10.0, we recover (Ricinulei + (Parasitiformes + Poecilophysidea)). In IW analyses at low k values (k=0.25, k=1.0), we recover the alternative (Palpigradi + Poecilophysidea); a result from Pepato, da Rocha & Dunlop (2010) upon whose study this matrix is based, and who named this clade Cephalosomata. The recovered clade (Ricinulei + (Parasitiformes + Poecilophysidea)) is a novel result but one, we note, with low support.

Ricinulei, Parasitiformes

A recent topic of debate has been the position of Ricinulei (Giribet et al. 2002; Shultz 2007; Dunlop, Kamenz & Talarico 2009). Traditionally, these rare arachnids were allied to the mites (Acari) on the synapomorphy of a hexapodal larva (Weygoldt and Paulus 1979). The proposal that mites are not monophyletic has challenged this relationship and in some studies Ricinulei were placed as the sister group of the Parasitiformes branch of the mites only (e.g. Shultz 2007). Alternatively, putative synapomorphies have been identified between Ricinulei and the extinct order Trigonotarbida, such as a locking mechanism between the prosoma and opisthosoma, tergites divided into median and lateral plates and a small terminal claw on the tip of the pedipalp (Dunlop 1996b; Dunlop, Kamenz & Talarico 2009). To this we could add the observation of Talarico et al. (2011: fig. 2) that ricinuleids have small filtering projections immediately in front of the mouth remarkably similar to the condition seen in well preserved trigonotarbid arachnids (Dunlop 1994b, fig. 4; Garwood & Dunlop 2010, fig. 6). One of the aims of the present study was to test whether the inclusion of trigonotarbids affects the position of Ricinulei: namely
whether they are closest to one or both of the mite lineages or whether the addition of trigonotarbids modifies their position, bringing them closer to the tetrapulmonate arachnids. The result was not clear cut. With fossils in the EW analyses, and IW K=10 we recover a (Ricinulei + (Parasitiformes + (Acariformes + Solifugae))) clade. In IW, however, at low K-values we find the Ricinulei are recovered as sister group to trigonotarbids, within the Pantetrapulmonata, on the basis of the shared characters already mentioned. In this case parasitiformes create a grade at the base of the pantetrapulmonate/ricinuleid clade, with low support values. For IW k=3.0 we recover a (Solifugae + (Acariformes + (Ricinulei + Parasitiformes))) clade. The groupings we recover comprising Ricinulei, Parasitiformes, Acariformes and Solifugae in various arrangements are poorly-supported, and are defined by the presence of divided femora in legs 3 and 4 (albeit lost in some mite taxa), and a hinged patellotibial articulation.

In a broader sense, our analysis contributes towards the growing support that mites (Acari) are not a monophyletic group. In fact this hypothesis can be traced back to early observations by Grandjean (1935, 1936) that there are numerous fundamental differences in body plan between the acariform and parasitiform mites. Diphyletic origins were formally proposed by Zachvatkin (1952) and were particularly championed by van der Hammen (1989), and references therein. Van der Hammen’s impact was limited by his rejection of cladistics and most of the early cladistic analyses treated Acari as an a priori monophyletic group (Weygoldt & Paulus 1979; Shultz 1990); sometimes simply scoring a generalised ‘mite’ as a terminal taxon. Subsequent studies tried to test mite monophyly by adding in a range of acariforms and parasitiforms as terminals and, as in our scheme, often recovered the two major lineages in divergent positions on the final tree (Shultz 2007; Pepato, da Rocha & Dunlop 2010). All mites share the putative synapomorphy of a gnathosoma - a movable unit including the chelicerae, pedipalps and mouth lips, but this single character is being increasingly outweighed by other data. Acariform mites often resolve closest to camel spiders (Solifugae; as in some trees in this study) while parasitiform mites may resolve close to ricinuleids (this study; see below) or Pseudoscorpionida (Regier et al. 2010).

**Pantetrapulmonata**

Shear & Selden (1986), Shear et al. (1987) and Selden et al. (1991) did pioneering work on integrating the extinct order Trigonotarbia into cladistic analyses of living arachnids. Through identifying characters like the presence of two pairs of book lungs and ‘clasp-knife’ chelicerae where the fang articulates against a basal segment they concluded that Trigonotarbia is the sister group of Tetrapulmonata (see below). Further characters and character states in our analysis derived from recently generated tomographic datasets (Garwood et al. 2009; Garwood & Dunlop 2011, Dunlop & Garwood 2014) continue to support this hypothesis both in the EW and IW trees, with the exception of low K-values where trigonotarbids are sister group to ricinuleids, and this clade is sister group to other tetrapulmonates. There is moderate support for this arrangement, which is otherwise not recovered elsewhere.
Shultz (2007) formally named the (Trigonotarbida + Tetrapulmonata) group Pantetrapulmonata; a name we also adopt here.

Our data also strongly supports Tetrapulmonata (i.e. Haptopoda, Amblypygi, Thelyphonida, Schizomida, Araneae and Uraraneida); an unsurprising result as this is probably one of the least controversial clades within the arachnids (reviewed by Dunlop, Borner & Burmester 2014). An evolutionary lineage including spiders, whip spiders and whip scorpions can be traced back in some form to early studies such as Pocock (1893) and Börner (1904), and is widely recovered from both morphological (Shultz 2007) and molecular (Regier et al. 2010, Sharma et al 2014) datasets.

Our novel tomographic data for Haptopoda is important in that it confirms that these animals had ‘clasp-knife’ chelicerae comprising only two articles (Fig. 1B): a basal paturon and a fang. This in turn reinforces the supposition that Haptopoda belong to Tetrapulmonata, and are not Opiliones (contra Shear & Kukalová-Peck 1990, p. 1812) in which case we would have expected chelate chelicerae with three articles. As per Shultz (2007), Haptopoda resolves in our trees as the sister group of Pedipalpi (see below). This supports his proposed clade Schizotarsata, which as before can be defined on the synapomorphy of walking legs II-IV sharing a specific pattern of three distal tarsomeres.

Amblypygi, Thelyphonida and Schizomida were originally combined as a single arachnid order, Pedipalpi (e.g. Börner 1904). This name is now usually used to recognise a clade of these three taxa. Thelyphonida and Schizomida are unquestionably sister taxa and until 1945 were treated as a single order (e.g. Pocock 1911). There remains debate about the position of the whip spiders (Amblypygi). Pedipalpi has a number of putative synapomorphies including an elongate first pair of legs and the raptorial pedipalps which give the clade its name. To this Shultz (1999) added numerous skeleto-muscular characters; albeit not tested across all Arachnida. The alternative hypothesis is Labellata (Amblypygi + Araneae) whereby whip spiders and spiders share characters such as a narrow pedicel between the prosoma and opisthosoma, a coalescence of the nerve ganglia in the prosoma, and a postcerebral sucking stomach. These two hypotheses and their apomorphies were compared by Alberti & Michalik (2004, fig. 48). Pedipalpi was recovered by Shultz (1990, 2007), Giribet et al. (2002) and Regier et al. (2010). Labellata was supported by Weygoldt & Paulus (1979), Wheeler & Hayashi (1998) and Alberti & Michalik (2004). In the present analysis Pedipalpi resolves as the most parsimonious solution, with the extinct Haptopoda as its sister group as noted above. The divided prosomal shield of Schizomida is thus assumed here to be homoplastic with respect to the Cephalosomata group (see above).
Serikodiastida nom. nov.

This paper builds upon the work of Legg, Sutton & Edgecombe (2013) in formally testing the position of the extinct order Uraraneida. The Devonian genus Attercopus fimbriunguis was initially interpreted as a trigonotarbid (Shear et al. 1987) and was later proposed as the oldest spider (Selden et al. 1991). Subsequently, new Devonian material came to light which - combined with data from a Permian fossil originally thought to be a mesothele spider (Eskov & Selden 2005) - revealed that there was a lineage of Palaeozoic arachnids which resembled spiders, but lacked spinnerets and retained a flagelliform telson rather like a whip scorpion. Selden et al. (2008) redescribed these fossils and proposed a new order, Uraraneida, to accommodate them. They also suggested that uraraneids were probably close to the origins of spiders, sharing with them the presence of silk spigots, but not fully developed spinnerets. Predictably, we recovered (Uraraneida + Araneae) with strong support. Araneae are united in this analysis by the presence of opisthosomal spinnerets, and (Urarineida + Araneae) by silk glands, a naked cheliceral fang and the putative presence of a cheliceral venom gland if there really is a gland pore on the fang of A. fimbriunguis. We propose here the clade name Serikodiastida to formally recognise this relationship. The name derives from the Greek serikodiastes (σηρικοδιαστής) meaning silk worker, reflecting the shared ability of these taxa to produce silk.

Glossary

Chelicerata s.l. - pycnogonids + euchelicerates.
Euchelicerata - xiphosurids, eurypterids + arachnids.
Merostomata - xiphosurids + eurypterids.
Metastomata - eurypterids + arachnids.
Stomothecata - scorpions + opilionids.
Haplocnemata/Apatella - pseudoscorpions + solifugus (widely supported).
Acaromorpha - ricinuleids, acariformes + parasitiforms (widely supported).
Pantetrapulmonata - trigonotarbids + tetrapulmonates
Arachnopulmonata - scorpions + tetrapulmonates
Tetrarulmonata - spiders, amblypygids, whip scorpions + schizomids. This almost certainly includes uraraneids since their publication in 2008 (Selden et al 2008).
Schizotarsata - haptopods + pedipalpids.
Pedipalpi - amblypygids + thelyphonids + schizomids.
Labellata - spiders + amblypygids.
Cryptoperculata - opilionids, ricinuleids + mites.
Dromopoda - opilionids, scorpions + haplocnemataids
Poecilophysidea - solifugus + acariform mites.
Cephalosomata - palpigrades, solifugus + acariform mites.
Serikodiastida - A name coined herein for uraraneids + Araneae.

Impact of fossils
One aim of this study was to include fossils with excellent and (where possible) three-dimensional preservation in a phylogenetic analysis, in order to place extinct arachnid orders. It also allows us to explore the impact their inclusion has on our understanding of chelicerate relationships. A quantitative assessment of this impact is beyond the scope of the current paper, and will be an avenue of exploration for future work. Nevertheless, we believe adding fossils to this matrix has been illustrative. It demonstrates that the addition of fossils breaks up long branches - the most extreme example being the Pedipalpi, which is defined by 28 synapomorphies in the analysis of extant taxa only, but has only three synapomorphies following the introduction of Haptopoia and Trigonotarida. The addition of further crown group members of the constituent clades would not have this effect (see also Edgecombe 2010, Legg, Sutton & Edgecombe 2013). Despite the addition of fossils, long branches remain problematic in some parts of the trees presented herein - most prominently in the pycnogonids. This is an ancient group with a sparse fossil record (Dunlop & Arango 2005, Dunlop 2010) - accordingly the discovery of novel and complete fossil species will be key to the group’s correct placement. Recently discovered species (Kühl, Poschmann & Rust 2013; Rudkin et al. 2013) have proven too incomplete in their preservation for confident placement of species, compounded by poor understanding of their ontogeny. The addition of fossils also results in some changes in tree topology. Stomothecata is present in the IW extant-only analysis - its absence from EW trees suggests the grouping is not stable to the addition of novel characters. With the addition of fossils in IW analyses, it is only recovered at low k values. The lack of support for Stomothecata comes about in part because two fossil scorpions and the tetrophthalmid harvestman *Hastrocularis argus* (Garwood et al. 2014) lack a stomotheca composed of palpal and first leg coxapophyses. Similarly, the addition of fossils - most notably *Offacolus kingi* (Sutton et al. 2002) and *Dibasterium durgae* (Briggs et al. 2012) - results in a paraphyletic Synziphosura as previously discussed (Lamsdell 2013). Such cases suggest the plesiomorphic elements present in fossils’ anatomy appear key to their placement, and this can have significant impact on our understanding of chelicerate evolution. In this example, the addition of fossils (based on IW analyses) would imply a last common chelicerate ancestor that was synziphosurine in form and so directly impacts on our model of chelicerate origins. Finally, the addition of fossils to the current analysis makes the resulting topology better resolved as shown in Figure 3, and adds stability. A strict consensus tree of analyses conducted at k=0.25, 1.0, 3.0 and 10.0 using just extant taxa resolves all arachnid orders in a polytomy, demonstrating the changeability of tree topology with differing concavity constants. The same tree with fossils (i.e. a consensus of analyses with varying concavity constants) in is still largely a polytomy, but there is slightly better resolution - a nested clade appears in the arachnids including all taxa non-scorpion, opilionid and pseudoscorpion taxa.

We believe this study demonstrates fossils’ utility in phylogenetic analyses - as reflected in other works (see overview by Edgecombe, 2010) - even in a group often assumed to have a patchy fossil record. However, we reiterate the caveat that even
with fossils a number of our clades are poorly supported, and indeed there are still significant changes in tree topology between differing analytical parameters.

Conclusion

Adding a small number of fossils to a phylogenetic analysis of the chelicerates changes the topology of the trees recovered, reducing support for several clades, and increasing support for others. Recent decades have seen morphologically-driven cladistic analyses achieve elements of consensus - arguably in contrast to the more variable findings of molecular studies. The skeletomuscular characters of morphological analyses are, in this analysis, not robust to the addition of novel characters and fossil taxa. This instability could result from a paucity of fossils that sample the timing of cladogenesis (Legg, Sutton & Edgecombe 2013), or from the fact that chelicerate origins lie in an ancient rapid radiation, as reported for the insects (Whitfield & Kjer 2008). Whatever the cause, we suggest that chelicerate phylogeny - as molecular studies suggest - remains in a state of flux. Furthermore, we believe the discovery of novel fossils sampling periods closer to both chelicerate and arachnid origins will be integral to changing this.
Figure Captions

**Figure 1.** Digital visualisations of the haptopod *Plesiosiro madeleyi* (NHM I7923; A-D), and phalangiotarbid *Gonioptarbus angulatus* (NHM In22838; E-I). A. Dorsal view of *P. madeleyi*, showing opisthosomal segmentation and prosomalshield architecture. B. Lateral view of the anterior ventral prosoma, nearest limbs and lateral prosoma removed, showing the nature of haptopod chelicerae. C. Ventral view, showing ventral segmentation, and divided sternum. D. Haptopod walking leg. E. First left walking leg of *G. angulatus*, showing typical segmentation. F. Lateral view of the anterior ventral prosoma, showing the small pedipalps, median ridge, and possible chelicerae - below the resolution of the scan. G. Fourth right walking leg. H. Dorsal view showing median eyes and dorsal opisthosomal segmentation. I. Ventral view showing opisthosomal segmentation and coxo-sternal region. Abbreviations: 1-10 - opisthosomal segment number; as - anterior sclerite; ch - chelicerae; cx - coxa; fa - fang; fe - femur; L1-L4 - walking legs 1-4; me - media eyes; mt - metatarsus; pa - paturon; pp - pedipalps; ps - posterior sclerite; pt - patella; ta - tarsus; ti - tibia; tr - trochanter. Scale bars: A,C,F-I = 3mm; B,D,E = 1mm.

**Figure 2.** Holotype and only known specimen of phalangiotarbid *Gonioptarbus angulatus* (NHM In22838). A. Dorsal view, showing prosoma and opisthosoma, and legs 4L and 2L. Proximal portions of Leg 1L are visible at the anterior of the fossil, as are the trochanters of several of the legs on the right. B. Ventral view showing coxo-sternal arrangement and ventral opisthosomal segmentation. Proximal portions of Leg 1L, then 2L 3L and 4L are visible. C. A close up of the sternum, anterior to the leg showing five constituent plates. D. Detail of the anterior opisthosomal segmentation, including the posterior median bulge of the prosomal shield, and associated accommodation in the anterior opisthosomal segments. E. The posteriormost segments (7-10) fused to create a single dorsal plate, with a terminal anal operculum. Scale bars: A,B = 2mm; C-E = 1mm.

**Figure 3.** Results of the cladistic analysis presented herein under equal weights (EW). The trees show the strict consensus of equally weighted analyses of the matrices presented here (SI file 2, morphobank project 1274). A. Tree showing the analysis results with fossils included. Bremer, jackknife and bootstrap support values are provided for each node as shown in the key. B. Tree recovered with fossil terminals removed - ordinal clades are collapsed for clarity.

**Figure 4.** Results of the cladistic analysis presented herein under implied weights (IW). The trees show the strict consensus of implied weights analyses of the matrices presented here (SI file 2, morphobank project 1274). Symmetric resampling support values are provided on the basis that these are unaffected by character weights. A. The topology for concavity constants (k values) 0.25 and 1.0, which are identical. K = 0.25 support value above each node in red, K = 1.0 below in grey. B. Tree for k = 3.0. C. Topology for k=10.0.
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Three dimensional reconstruction and the phylogeny of extinct chelicerate orders: Supplementary Information

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Character statements

Here we present character statements for the current analysis, modified after Pepato, da Rocha & Dunlop (2010).

Cephalic/prosomal region

1. Head shield segments (0 = five [cephalosoma/proterosoma]; 1 = seven [prosomal shield]).

This character refers to the number head segments (or post-acronal segments if the acron existed) included under the anterior prosomal sclerite. Pycnogonida and some Arachnida (in particular Acariformes among the mites, Solifugae, Palpigradi and Schizomida), appear to retain the original euarthropod head sensu Walossek & Müller 1998. We consider the “sejugal furrow” and the gap between anterior coxae I-II and posterior coxae III-IV as evidence for existence of such a separate tagma in Acariformes. We subsume Shultz’s (2007a) character 7 of the presence/absence of demarcation lines between the pro-, meso- and metapeltidium into this character.

2. Ophthalmic ridges (0 = absent; 1 = present)

Extant Xiphosura present a pair of longitudinal crests passing near the region of the lateral eyes or equivalent area when lateral eyes are not evident. Similar structures are present in Plesiosiro (Dunlop 1999, description herein) and ‘non-hypoctonid’ Thelyphonida (Mastigoproctus; Rowland & Cooke 1973).

3. Pleural margin of prosomal shield (0 = absent; 1 = present).

The broad head shield of Xiphosura with its wide pleural margins has traditionally been treated as the plesiomorphic condition relative to arachnids (e.g. Shultz 1990, character 2); although this was largely based on using trilobites and other arachnomorphs as outgroups. If Pycnogonida or indeed megacheiran taxa are used to polarise the character for euchelicerates, the wide head shield of Xiphosura could alternatively be treated as derived.

4. Cardiac lobe (0 = absent; 1 = present).

Extant Xiphosura express a cardiac lobe, a feature shared with several fossil species including members of Weinbergina, Eurypterida, and Chasmataspis.

5. Prosomal repugnatorial glands (0 = absent; 1 = present).

The presence of these glands producing a noxious secretion is a convincing
autapomorphy of Opiliones (e.g. Giribet et al. 2002, character 12).

6. **Cucullus** (0 = absent; 1 = present).

This unique, hinged plate covering the mouthparts but of indeterminate function is a convincing autapomorphy of Ricinulei. Females have been observed using the cucullus to hold their eggs.

7. **Sternal region** (0 = broad; 1 = narrow anteriorly; 2 = narrow posteriorly; 3 = narrow throughout).

Irrespective of whether a sternum is present, chelicerates vary in the degree to which the coxae are consolidated together on the ventral surface of the prosoma. Coding follows Shultz (2007a, character 12), except that the sternal area in all acariform mites should be considered narrow (Alberti 2006). Following Shultz (2007a) we consider the abutting of the coxae themselves and not their endites. The presence/absence of explicit gnathobases is coded as another character.

8. **Prosomal sternum** (0 = undivided; 1 = divided).

The sternum of Palpigradi, Amblypygi, Thelyphonida and Schizomida - plus the extinct pahalgniotarbids and haptopodids - is divided into multiple sclerites. Other arachnids which have a sternum have only a single, undivided sclerite. Not applicable to taxa without a sternum.

9. **Cephalic doublure** (0 = absent; 1 = present).

In many trilobites and other Arachnomorpha, the cephalic exoskeleton continues onto the ventral side as a deflexed rim or doublure. The prosomal shield folds in on itself where the chelicerae emerge in Thelyphonida and palaeocharinid Trigonotarbida. This character is coded as ambiguous for the former.

10. Prosomal shield with lines demarcating meso- and metapeltidium (0 = absent; 1 = present).

Scorpiones and some Opiliones have lines on the prosomal shield demarcating three zones - the pro-, meso- and metapeltidium. This character is not applicable to taxa lacking a prosomal shield.

11. **Genal spines** (0 = absent; 1 = present).

Two non-arachnid chelicerates - Xiphosura and Chasmataspidida - and also Trilobita, possess genal spines. These posteriorly directed lateral extensions of the cephalic region are only seen in marine (usually bottom-dwelling) species.

**Mouth and pharynx**

12. **Proboscis** (0 = absent; 1 = present).

A proboscis formed from three antimere elements terminating in a Y-shaped mouth (Dencker 1974) is autapomorphic for Pycnogonida (e.g. Weygoldt & Paulus 1979, character 58). Attempts to homologise it with arachnid mouthparts have largely
been proved unsuccessful – see comments in Dunlop & Arango (2005) – supporting its interpretation as a unique feeding adaptation for sea spiders.

13. **Mouth** (0 = directed anteroventrally; 1 = directed posteroventrally).
   The mouth of Xiphosura points backward towards the gnathobases. This condition has been interpreted as plesiomorphic for Chelicerata. Several fossils appear to have a similar backward flexure of the digestive tube – e.g. trilobites – as indicated by the backward direction of the hypostome or remnants of the gut contents. Here we score pycnogonids as 0/1, since their mouth orientation is largely dependant on the form and orientation of the proboscis (see above).

14. **Labium/tritosternum** (0 = absent; 1 = present).
   The labium, or tritosternum in some terminologies, is a separate sclerite generally forming the lower lip of the mouth. Shultz (2007a) considered it present in Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida, Trigonotarbida, Ricinulei, and in some acariformes among the mites. In fact, the labium in Palpigradi does not share the same relative position when compared to other Arachnida. Traditional studies of morphology regard the palpigrade labium as a protosternum, i.e. associated with the cheliceral segment (Börner 1902, Snodgrass 1948). Palpigradi is therefore scored 0 here for this character. Pseudoscorpions and Solifugae have a narrow medial sclerite related dorsally to the palpal coxal process. In Pseudoscorpionida, it is known as the so-called lophognath. It is crested and fits in the grooved ventral surface of the epistemolabral plate, or trophognath (Snodgrass 1948). A similar elongated sclerite may be found in some Endeostigmata, e.g. *Orthacarus tremli* Zakhvatkin, 1949 (Bimichaelidae; Jesionowska 2003). Because of its position, this sclerite is regarded as a deuto- or protosternum and thus not homologous to the labium as it is considered here. For a similar reason we exclude a ‘labium’ from phalangid Opiliones (Shultz & Pinto-da-Rocha 2007). We regard this as more likely to be a sternapophysis associated with first leg rather than the pedipalp (Winkler 1957).

15. **Epistomal-labral plate** (0 = absent; 1 = present).
   The labrum is fused to the epistome in Solifugae, Pseudoscorpiones and Acari (see also Snodgrass 1948, contra Shultz 2007a). The whole structure protrudes noticeably between the chelicerae and is flanked by a pair of so-called lateral lips (Hammen 1989; Dunlop 2000a). The plate and lips are here scored together as a single character complex. The plate itself is sometimes referred to as a ‘beak’ or ‘rostrum’, especially in the solifuge literature.

16. **Ventroposterior wall of pre-oral chamber** (0 = formed by labium; 1 = formed by palpal coxae).
   This specific morphology of the epipharyngeal sclerite was proposed by Shultz (1990, character 5) as a putative synapomorphy of Pedipalpi. Its condition in other arachnids without a labium (see previous character) was not discussed and we score such taxa here as (?). This highlights a general problem with many of the putative skeleto-muscular synapomorphies proposed for Pedipalpi, namely that they are
sometimes hard to assess across all arachnids and their outgroups.

17. Stomatheca (0 = absent; 1 = present).

This character was defined by Shultz (2007a) as a preoral chamber formed by the lateral sides of the palpal coxae and ventrally by extensions of the coxae of leg 1 and to a lesser extent leg 2. Shultz treated it as a synapomorphy of Scorpiones and Opiliones, although it has been criticised (Dunlop 2010), not least because it seems to be absent in stem-group (fossil) scorpions in which the coxae lack clearly developed apophyses. Shultz (2007a) speculated that early fossil scorpions may have had a stomatheca formed from soft lips in place of sclerotised projections, but the material available neither supports nor rejects this supposition. This is reflected in the coding of the Silurian species Proscorpius osborni (Dunlop et al. 2008), the Devonian Palaeoscorpius devonicus (Kühl et al. 2012). This character is also coded herein as absent in the fossil species Hastocularis argus (Garwood et al. 2014), which bears small coxapophyses on only the palpal and second walking leg coxae - such growths are entirely absent on leg 1, further supporting a convergent development of this character in Scorpiones and Opiliones.

18. Ingestion of solid material (0 = present; 1 = absent).

Most arachnids do not ingest solid material. Xiphosura possess gnathobases and a muscular gizzard suited for macerating solid food. There is no evidence for liquid feeding in non-arachnid fossils, and it is quite common to observe sediment (Hou & Bergström 1997) and even prey hard parts (e.g. within Sidneya; Bruton 1981) among the gut remains. Pycnogonida have a pharyngeal filter apparatus that certainly precludes the intake of anything larger than subcellular material (King 1973, Fahrenbach & Arango 2007). The latter authors also described 180–220 small salivary glands per jaw of Ammothea hilgendorfi - indicative of primarily liquid material intake. Digestion occurs largely as a result of salivary glands and musculature within the proboscis and oesophagus, and accordingly we have coded ingestion of solid material as absent for extant pycnogonid taxa. Several Opiliones and some mites (Opiliacarida, Oribatida, some Endeostigmata and free-living Astigmata; Pinto-da-Rocha, Machado & Giribet 2007, Walter & Proctor 1998) consume solid particles of food, although all of them have a well-developed preoral chamber so exhibit a certain degree of extraintestinal digestion. All other arachnids are liquid feeders and apparently digest their food preorally, often using specialised filtering devices (see e.g. character 20) to hinder the uptake of particulate matter. Finally, for Paleozoic scorpions this character is uncertain given that they seem to lack a well-developed pre-oral chamber (see above).

19. Palate plate (0 = absent; 1 = present).

This specific modification of the dorsal pharynx wall with fringed platelets used as filters to trap particulate matter from the preorally digested food is an autapomorphy of Araneae; e.g. Giribet et al. (2002, character 159).

20. Filtering preoral setae (0 = absent; 1 = present)

In Ricinulei and in at least Palaeocharinus among the Trigonotarbida there is a
similar-looking filtering structure in front of the mouth consisting of either
downward-pointing setae or platelets. This feature is a potential synapomorphy of
these arachnids.

21. Three-branched epistomal skeleton (0 = absent; 1 = present).
This specific form of the epistome skeleton with three processes for the pharyngeal
dilator muscles was described in detail by Shultz (2000) who proposed it as a
putative synapomorphy of (Scorpiones + Opiliones).

22. Intercheliceral epipharyngeal sclerite (0, absent; 1, present).
Coding follows Shultz (2000, character 191).

23. Epipharyngeal sclerite large, projecting posteriorly (0, absent; 1, present).
Coding follows Shultz (2000, character 192). Inapplicable to taxa lacking an
epiphyangeal sclerite

Segmentation, tagmosis and telson

24. Metasoma (0 = absent; 1 = present).
Cotton & Braddy (2003) defined this character as a “post-abdomen lacking
appendages”. This definition is hard to apply in most chelicerates since some lack
recognizable abdominal appendages altogether (e.g. Palpigradi, Opiliones,
Pseudoscorpiones, Acari). We seek to redefine this tagmosis character here as a
posterior, limbless set of segments, typically with a cylindrical exoskeleton which is,
to a greater or lesser extent, set off from the mesosoma by a narrowing of the body.

25. Prosoma and opisthosoma form a single functional unit (0 = absent; 1 =
present)
In Opiliones and some mite taxa, the prosoma and opisthosoma fuse form a single
unit. After Legg, Sutton & Edgecombe (2013) character 602.

26. Metasoma length (0 = three segments; 1 = five segments; 2 = nine segments).
This character is inapplicable for taxa which do not express a metasomal tagmosis.

27. Well-developed post-anal telson (0= absent; 1= present).
Given that various potential outgroups among early Palaeozoic arthropods have a
post-anal telson, its presence in Xiphosura, Scorpiones, Palpigradi, Thelyphonida and
Schizomida is probably plesiomorphic for Chelicerata. No Recent sea spiders have a
telson, but some fossil taxa do, including Palaeisopus (Vilpoux & Waloszek 2003);
see also Walossek & Müller 1998 for discussions of ground patterns.

28. Flagellate telson (0 = absent; 1 = present).
In Palpigradi, Thelyphonida and (albeit in a shortened form) Schizomida, among the
extant orders, and now Uraaneida, among the fossils, the telson is subdivided into
multiple articles to form a distinctly flagellate, whip-like structure. Not applicable to
taxa without a telson (see above).
29. **Telson with vesicle and aculeus** (0 = absent; 1 = present). This feature is regarded here as an autapomorphy of Scorpiones.

30. **Specialized male postanal flagellum** (0 = absent; 1 = present). This modified male flagellum plays an important role during courtship – the female holds onto the male flagellum and is pulled over a spermatophore – and is widely regarded as a convincing autapomorphy of Schizomida.

**Chelicerae or deutocerebral appendage**

31. **Number of cheliceral articles** (0 = more than three, 1 = three; 2 = two). Solifugae, Pseudoscorpiones, Ricinulei and the Terapulmonata *sensu* Shultz (1990) have only two cheliceral articles. This is widely accepted as the apomorphic condition compared to the three articles seen in other (euchelicerate) taxa. Indeed, gene expression data now suggest that the presence of two articles could have arisen through loss of developmental domains along the proximo-distal axis of the appendage (Sharma et al 2012). Acariformes is scored here as having two articles. Those supporting the hypothesis that Acariformes have a proximal trochanter in the chelicerae argued that the proximoventral region of the fixed digit is a fused remnant of this article. This is based on the attachment of the cheliceral retractor muscles in this region (Evans 1992), and developmental studies support this suggestion in one species (Barnett and Thomas 2013). At least one pycnogonid species has been figured with four cheliceral articles (see e.g. Dunlop & Arango 2005) - including the fossil species included herein. The Megacheiran taxa included in the current analysis both have a deutocerebral great appendage comprising more than three articles (Tanaka et al., 2013; Haug et al. 2012), a state also seen in the synziphosurine taxa *Dibasterium durgae* (Briggs et al. 2012) and *Offacolus kingi* (Sutton et al. 2002). This outgroup choice accordingly implies the possession of more than three articles in the deutocerebral appendage the plesiomorphic state for the chelicerates.

32. **Presence of elbowed chelicerae** (0 = absent, 1 = present). In some taxa with a three-segmented chelicera (e.g. Palpigradi and Opiliones), there is a geniculate joint between the forward-projecting the basal cheliceral element and the distal two elements (forming the claw). This arrangement allows the claws to move in the proximity of the mouth. By contrast, in groups like scorpions all three cheliceral elements simply project forwards. We do not consider the joint in the pycnogonids geniculate: the proboscis limits the required range of motion in the chelifores, which have a greater variability in orientation and podomere proportions than observed in arachnid taxa. Scored as inapplicable for those taxa with only two cheliceral articles, or more than three.

33. **Position of the cheliceral apotele** (0 = articulates ventrally; 1 = articulates dorsally; 2 = articulates laterally). In Solifuges, Pseudoscorpiones and both major groups of Acari the distalmost
cheliceral segment (the apotele) articulates ventrally against the preceding article (e.g. Dunlop 2000). In Tetrapulmonata and Ricinulei it is more or less dorsal (keeping in mind the torsion of the chelicerae in labidognath spiders). Three segmented chelicerae with an ‘elbowed’ articulation, such as in harvestmen and palpigrades, do not fit comfortably into either of these schemes and are tentatively coded as a separated character state.

34. Cheliceral ‘fang’ (0 = chelate; 1 = ‘clasp-knife’ type; 2 = Prostigmata styliform or ‘Anystys’-like chelicerae).

35. Naked cheliceral fang (0 = absent; 1 = present).

36. Plagula ventralis (0 = absent, 1 = present).

37. Cheliceral venom gland (0 = absent; 1 = present).

38. Endocephalic spinning apparatus (0 = absent; 1 = present).
homologous with the venom gland of spiders is unclear.

39. Cheliceral flagellum (0 = absent; 1 = present).

This sometimes complex projection from the dorsal surface of the fixed finger of chelicerae in male Solifugae can take a number of forms, but is (secondarily) absent in the solpugid family Eremobatidae (Punzo 1998). Its precise function in solifuges is not well understood. The character has been treated as an autapomorphy of this order. However, Harvey (1992) regarded the cheliceral flagella of Solifugae and Pseudoscorpionidae (see e.g. Weygoldt 1969, fig. 2) as potentially synapomorphic and this is reflected in the scoring here. Notice that the flagellum occurs on the fixed finger and should not be confused with the galea which is on the movable finger of the pseudoscorpion chelicerae (see previous character).

40. Chelicerocarapacal articulation (0 = absent; 1 = present).

A specific antero-lateral articulation between the prosomal shield and the basal cheliceral article has been described from Solifugae and (most) Pseudoscorpiones, and suggested as a potential synapomorphy for these orders; see e.g. Shultz (1990, character 13).

41. Mesal fusion of chelicerae (0 = absent; 1 = chelicerae proximally fused).

Mesal fusion of the chelicerae is seen in mites of the following groups: Tetranychidae, Raphignathidae, Caligonnellidae, Tarsonomina, and in some Tydeidae and Stigmaeidae (Evans 1992). A similar arrangement can also occur (certainly secondarily) in some spiders such as Filistatidae, but not among the taxa scored here.

42. Movable digit (0 = ‘Anystis’ type; 1 = styliform).

Among those Acariformes with a reduced digitus fixus, two conditions may be observed: the mostly curved, dorsally serrate digits of Trombidiidae, Halacaridae, Trombiculidae, Anystidae and Paratydeidae on the one hand and a smooth movable digit of Erythraeidae, Smaririidae, Cheyletidae and Tetranychidae, suited for piercing, on the other. This character is only applicable to mites without the digitus fixus (cf. character 36, state 2).

Pedipalps or second head appendage

43. Palpal coxae (0 = free; 1 = fused medially).

This is a somewhat problematic character in that it is potentially part of the same character complex which embraces the gnathosoma of mites and, perhaps, ricinuleids (see below). Irrespective of the gnathosoma, a straightforward medial fusion of the pedipalpal coxae is seen in both major groups of Acari, as well as in Ricinulei, Thelyphonida and Schizomida. In the latter two orders it is usually referred to explicitly as a camerostome; see e.g. Yoshikura (1975, table 24) and Shultz (1990, character 18).
44. **Gnathosoma** (0 = absent; 1 = present).

The gnathosoma essentially consists of the fused palpal coxae (see previous character) forming the subcapitulum, plus the chelicerae and mouth lips. All these elements articulate together as a single movable unit against the rest of the body. It has been cited (Lindquist 1984) as one of the most convincing characters for defining mites as a monophyletic group, although its homology was challenged by Hammen (1989) who noted significant differences in the patterns of muscular insertion (see also Alberti 2006). Confusingly, some authors also recognise a gnathosoma as present in Ricinulei; thus essentially the same character has been used by different authors to support either a monophyletic Acari or (Acari + Ricinulei). We find the latter interpretation problematic, and followed here Shultz (2007a) in coding this as ambiguous.

45. **Subcapitular rutella** (0 = absent; 1 = present).

These modified, thickened setae are found in basal members of both Parasitiformes and Acariformes among the mites. Although absent in more derived Anactinotrichida and often cited as lost in prostigmatid mites, they were noted as present in Rhaginiidae by Zacharda (1980) although the structures observed in Rhaediidae and scored here do not resemble the Oribatida or Opilioacarida rutella. Irrespective of ingroup reversals, rutella appear to be one of the more convincing characters defining Acari as a monophylum (Lindquist 1984, character 1). Alberti (2006, and references therein) has, however, questioned how well this character is understood and cautioned about accepting its homology in all groups where it occurs.

46. **Palpal chelae** (0 = leg like; 1 = subraptorial; 2 = chelate; 3 = ‘scorpionid’; 4 = ‘thumb and claw’).

Large, subraptorial pedipalps characterise Amblypygi, Thelyphonida and Schizomida. The pedipalps or equivalent appendages of Xiphosura, Ricinulei and at least Palaeocharinus and Anthracomartus among the Trigonotarbida, end in small terminal claws or pincers in which the apotele opposes a corresponding projection from the tarsus. Scorpiones and Pseudoscorpiones share a specific and potentially homologous ‘scorpionid’ claw morphology involving a large manus, containing a similar musculature, and elongate fingers; see e.g. Shultz (1990, characters 16 and 17) for details. Several Prostigmata among the mites have a strong ‘claw’ (in fact, a hypertrophied seta) in the palptibia which acts against the palpal tarsi. This ‘thumb and claw’ organisation is seen in Tetranychoidea, Stigmaeidae, Cheyletidae, terrestrial Parasintegona, Erythreaoidea, and Anystidae among the taxa scored here.

47. **Palpal cleaning organ** (0 = absent; 1 = present).

This specialised brush of two highly organised rows of tarsal setae (e.g. Weygoldt 2000, figs 133-139) has been called the ‘cleaning organ’ or ‘cleaning brush’. It is one of the few explicit autapomorphies of Amblypygi (Shear et al. 1987).

48. **Pedipalpal venom glands** (0 = absent; 1 = present).

Poison glands within the palpal chelae - which can open in one or both fingers...
(Weygoldt 1969) – represent a convincing apomorphy of the ingroup pseudoscorpion clade Iocheirata sensu Harvey (1992)/Murienne, Harvey & Giribet (2008). It should be reiterated that venomous pedipalpal claws are not an autapomorphy of all Pseudoscorpiones.

49. Palpal apotele (0 = differentiated from tarsus; 1 = not differentiated from tarsus).
Although proposed by Shultz (1999, character 14) as a putative synapomorphy of Pedipalpi only, it is also applicable to the large claws making up the pedipalps of Scorpiones and Pseudoscorpiones too. Apoteles are also absent from the palps of Acariformes and have been convergently lost in at least some Opiliones, such as the genera Nemastoma and Sabacon (Alberti 2006; Giribet et al. 2002).

50. Adhesive palpal organ (0 = absent; 1 = present).
An adhesive structure at the end of the pedipalp (Punzo 1998) is a putative autapomorphy of Solifugae. Given that solifuges do not express a palpal apotele sensu stricto (but see previous character) and that the palpal organ articulates via lateral condyles, it could potentially represent a highly modified claw (Dunlop 2000b).

Ovigers and legs

51. Ovigers (0 = absent; 1 = present).
Modification of the third limb into an egg-carrying oviger is an autapomorphy of the ground pattern of Pycnogonida Giribet et al. (2002, characters 11,40). However, like the chelifores and pedipalps, ovigers are secondarily reduced in some derived ingroup sea spiders – for example Endeis lack ovigers completely – as well as females of Pycnogonidae and Phoxichilidiidae (Arango 2002).

52. Gnathobases (0 = present; 1 = absent).
Among recent Chelicerata, only Xiphosura retains dentate gnathobases along all postcheliceral limb coxae. This is widely accepted as a plesiomorphic mode of feeding. Among fossils they are present in several taxa, including trilobites, eurypterids, various arachnomorphs, and the outgroup taxon - Alalcomenaeus - in the current analysis, which implies that gnathobasal feeding is at some level the original mode of ingestion. Serrula on the pedipalpal coxae (or gnathocoxae) of spiders have to some extent ‘reinvented’ the masticatory function of the gnathobases, but in detail they differ from the dentate xiphosuran/eurypterid gnathobase and are not scored as homologous here.

53. Antenniform first leg (0 = absent; 1 = present).
This antenniform limb was proposed by Shultz (1999, character 16) as a putative synapomorphy of Pedipalpi. Solifugae and Palpigradi also walk hexapodally to some extent and probe ahead with the first leg. However, they do not show the same degree of structural modification of this limb as in Pedipalpi where the antenniform leg pair is markedly different from those used in walking.
54. **Leg 1 sternocoxal articulation** (0 = absent; 1 = present).

This specific pattern of articulation was proposed by Shultz (1999, character 25) as a putative synapomorphy of Pedipalpi.

55. **Apotele of first leg** (0 = present; 1 = lost).

This reduction of the apotele in these antenniform legs was suggested by Shultz (1999, character 17) as a potential synapomorphy of Amblypygi, Thelyphonida and Schizomida. The apotelic claws is retained in Amblypygi, but in a highly reduced form (e.g. Wegoldt 2000, fig. 81). The leg 1 apotele is replaced by a bush of hairs in *some* Solifugae (Roewer 1934) which are here scored 0/1 for this character.

56. **Leg 2** (0 = unmodified; 1 = elongate).

In Ricinulei and most Opiliones – but not in the putatively basal Cyphophthalmi – the second walking leg (or 4th prosomal limb) is noticeably longer and is typically used to probe ahead of the animal (see also Giribet et al. 2002, character 70).

57. **Exopods** (0 = retained on more than one prosomal limb; 1 = on sixth prosomal limb, 2 = lost).

From the original biramous limb, the exopod is retained as the so-called flabellum on the coxa (or basipod in some terminologies) of the last pair of legs in Xiphosura. The exopod on this limb is lost in all Arachnida; see e.g. Giribet et al. (2002, character 110). Dunlop, Anderson & Braddy (2003) reported a dissociated biramous leg belonging to *Chasmataspis* that resembles the flabellum on prosomal limb VI of Xiphosuran. As with most Arachnomorpha, the enigmatic Herefordshire taxa *Offacolus* (Orr et al. 2000, Sutton et al. 2002) and *Dibasterium* (Briggs et al. 2012) retain biramous legs in the prosomal appendages. *Weinbergina* is reported as possessing only uniramous appendages (Stürmer & Bergström 1981; Moore et al. 2005) - although this could be worthy of restudy based on these recent discoveries from Herefordshire.

58. **Coxotrochanteral joint** (0 = simple; 1 = complex).

The coxotrochanteral joint of Araneae, Amblypygi, Thelyphonida and Schizomida has been described as being of a more complex nature - specifically through including so-called intercalary sclerites - compared to the simple bicondylar articulation seen in other taxa; cf. Shultz (1989, 1990 character 24) for details.

59. **Divided femora in legs 3 and 4** (0 = present; 1 = lost).

Shultz (1989, 1990 character 25) discussed previous interpretations of this ‘extra’ limb article which has been variously regarded either as a double trochanter or an extra femur. It was treated by Shultz as plesiomorphic retention of a basi- and telofemur; a character thus retained in Pycnogonida, Ricinulei, Solifugae and Acari. In some schemes (e.g. Hammen 1989) Palpigradi was also interpreted as having two femurs, but this assumption was not followed by Shultz (1989) whose interpretations based on musculature we rely on here for scoring the character.
60. **Femoropatella articulation** (0 = transverse hinge; 1 = bicondylar articulation; 2 = monocondylar articulation).

Interpreted by Shultz (2007a, character 69) as a hinge in most arachnids, the bicondylar condition occurs in Opiliones, Scorpiones and Pseudoscorpiones. A monocondylar articulation here appears to be autapomorphic for Solifugae.

61. **Patellotibial articulation** (0 = monocondylar; 1 = hinge; 2 = bicondylar).

The monocondylar condition of this joint was assumed (Shultz 1990, character 31) to be plesiomorphic, with modification to a hinge in Acari, Ricinulei and Solifugae and to a bicondylar structure with an additional ventral articulation in Opiliones, Scorpiones and early derivative Pseudoscorpiones.

62. **Patellatibial articulation with auxiliary posterior articulation** (0 = absent; 1 = present).

This specific pattern of leg articulation was proposed by Shultz (1999, character 22) as a putative synapomorphy of Pedipalpi. How this relates to the previous character is unclear and these ventral/posterior articulations may turn out to be part of a single character complex; perhaps homologous with the additional ventral articulation alluded to in character state 2 above.

63. **Appendages of postoral somites III–V with fused tibia and tarsus** (0 = absent; 1 = present).

A fused tibia-tarsus is observed in extant Xiphosura, where it forms the fixed finger of the distal claw and articulates against the tarsus as the movable finger. This arrangement is apparently not seen in the Devonian synziphosurine *Weinbergina* (Moore et al. 2005) which seems to retain the tibia and tarsus as separate elements, but is not apparent in the other included fossil taxa.

64. **Tarsus** (0 = tarsus divided into basi- and telotarsus; 1 = tarsus undivided).

The ‘basitarsus’ *sensu* Shultz is equivalent to the metatarsus in more usual arachnological terminology. State 1 occurs in extant Xiphosura (Shultz 1989) and in Acariformes (Lindquist 1984, Evans 1992), with the exception of Erythracarinae among Anystidae; a probable convergence. It also occurs in the anterior two pairs of legs in chthonioid pseudoscorpions, for which the character is coded here as 0/1, and all legs in Feaelloidea (Chamberlin 1931). A circumtarsal ring in Anactinotrichida may represent a joint between a basi- and telotarsus (Evans 1992), however we follow Shultz (2007a) in coding the tarsus as undivided.

65. **Telotarsi of walking legs 2–4 with three tarsomeres** (0 = absent; 1 = present).

This specific pattern of tarsal division was proposed by Shultz (1999, character 18) as a putative synapomorphy of Pedipalpi, but also appears to occur in the extinct order Haptopoda; these together forming a putative Schizotarsata clade Shultz (2007a). Some other arachnids, particularly various long-legged Opiliones, may show numerous tarsomere divisions at the distal ends of their legs; but not the specific arrangement scored for this character.
66. **Apotele** (0 = a simple cone or blade; 1 = a medial piece, comprising a claw or pulvillus, more frequently bearing a pair of lateral claws).

Most Arachnomorpha present a tridactyl terminal piece at the ends of their legs. The main exceptions comprise Euryp terida, *Chasmastaspis*, some fossil scorpions and extant Xiphosura (Dunlop 2002b). For outgroup *Emeraldella brocki*, this is coded as absent as the taxon has a conical, central spine surrounded by possibly movable spines - however, these do not appear to form a claw (Stein and Selden 2013).

67. **Pulvillus** (0 = absent; 1 = present).

A fleshy (?adhesive) pad between the claws of the legs has been variously named a pulvillus or empodium. This structure can be found in Pseudoscorpions, Solifugae, ‘pulvillate’ Amblypygi and Parasitiformes among the mites. When a fleshy structure similar to a pulvillus occurs among the Acariformes sampled, such as *Sancassania* or *Rhizoglyphus*, it is invariably accompanied by a medial claw.

68. **Chelate legs** (0 = absent; 1 = present).

The legs (i.e. limbs III–VI) in extant Xiphosura, *Offacolus*, *Dibasterium*, and *Chasmastaspis* (where known) end in claws formed by the subterminal apotele moving against the tarsus or tibiotarsus. Note that some of the anterior limbs in the Recent Xiphosura from SE Asia are more subchelate in nature.

69. **Divided claws** (0 = absent; 1 = present).

Subdivided claws, or ungues, on the walking legs in which the tips articulate against the rest of the claw (Roewer 1934, Weygoldt 1969, Dunlop 2000b) are a putative autapomorphy of Solifugae.

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**Opisthosoma and opisthosomal appendages**

Incomplete data on the embryology of some arachnid orders makes opisthosomal structure, and its possible appendages, one of least well-understood issues in chelicerate morphology. Almost all structures associated with opisthosomal segments have been argued as limb-derivatives at some stage. Only xiphosuran chilaria, the scorpion pectines, spider spinnerets, the book lungs, book gills, and certain spider trachea can presently be positively identified as appendage derivatives (Damen, Saridaki & Averof 2002). Our coding strategy assumes that these structures are homologous to the posterior limbs of arachnomorph arthropods; probably corresponding mainly to the exopods (but see individual characters like lungs and lung opercula for details). See discussion section of Pepato, da Rocha & Dunlop (2010) for further details of possible leg derivatives.

70. **Plate-like opisthosomal appendages** (0 = absent; 1 = present).

Weygoldt & Paulus’ (1979) defining character for Euchelicerata, these plate-like appendages, or opercula, are not seen in Pycnogonida – not even in fossil forms (e.g. *Palaeoisopus*) which retain a longer trunk behind the last walking leg. They occur as largely gill-bearing structures in Xiphosura and have been demonstrated (Shultz...
1993, 1999) in the lung-bearing somites of at least the tetrapulmonate arachnids. Thus the traditional second and third ‘sternites’ of the opisthosoma are in fact highly modified, lung-bearing appendages. These probably occur in early fossil Scorpiones and may thus contribute to the sternites of modern scorpions (Jeram 2001) - a hypothesis supported by developmental studies (Farley 2005, and citations therein). The character is harder to score for those arachnids which lack lungs as it is unclear whether their sternites in the anterior opisthosomal region are true sternites, sutured on opercula or conceivably combinations of both as per the Jeram (2001) hypothesis for scorpions. Such equivocal taxa are thus scored (?)

71. Limb VI (0 = unmodified; 1 = “pusher”; 2 = paddle)

The sixth limb in arachnids is generally a pediform structure used as a walking leg. In modern xiphosurans the sixth limb has flaps near the distal end which can splay out and, similar to a snowshoe, provide extra traction when the limb is pushed down onto the substrate. It is conventionally called the ‘pusher’ as it helps push the animal forwards. Whilst Dibasterium possesses a specialised sixth limb, this in a single elongate, slender projection and is thus coded as unmodified for this character. In some eurypterids and chasmataspidids the sixth limb is modified into a paddle and presumably enabled the animal to swim.

72. Number of body segments (0 = twenty; 1 = nineteen; 2 = eighteen; 3 = seventeen; 4 = sixteen; 5 = fifteen; 6 = fourteen; 7 = thirteen; 8 = twelve; 9 - 8 segments or less).

Shultz (2007a, character 95) scored the number of opisthosomal segments. This approach works for chelicerates since the prosoma/opisthosoma boundary may be accurately determined by the presence of a reliable marker in the form of the genital opening on 2nd opisthosomal segment, something absent in Pycnogonida. We followed Wills et al.’s (1998, character 41) approach of simply coding the total number of body segments. For Euchelicerata this means adding seven (one limbless plus six appendage bearing prosomal segments) to the number coded by Shultz. Acariformes mites often have some degree of anamorphosis, i.e. the addition of new segments during post-embryonic development. The scoring for them tries to encompass the inside group polymorphism by following Kethley’s (1990) account on this aspect. In Leanchoilid outgroup taxa we have not considered the telson a segment. Scorpions are coded as possessing twenty segments on the basis of evolutionary developmental for an additional segment, lost in adult scorpions (Simonetti 2006).

73. Prosoma–opisthosoma junction (0 = broad; 1 = Xiphosuran ‘cephalothorax’; 2 = narrow, pedicel).

At least the extant Xiphosura seem to have taken the trend of adding segments to the head even further. Their ‘cephalothorax’ sensu Scholl (1977) and Shultz (2001) incorporates dorsal elements of the 7th and 8th somites; a potentially derived condition giving them a longer head shield than that of the arachnid prosomal shield. This character is difficult to assess in fossil xiphosurans where embryological and musculature data are lacking. Note that this specific use of cephalothorax
should be differentiated from its more traditional usage in general arachnological terminology as a synonym of prosoma.

Although some authors previously recognised a simplistic division into ‘Latigastra’, with a broad prosoma-opisthosoma junction and ‘Caulogastra’, with a narrow junction; this character proves to be rather more complex, especially when applied to arachnid outgroups. According to their incipient tagmosis, most Arachnomorpha lacks any sharp distinction between their anterior and posterior trunk segments. In early aquatic Euchelicerata like Chasmataspida, and several Xiphosurida, the seventh tergite, or first opisthosomal tergite is distinctively narrower than the subsequent opisthosomal tergites. In other Xiphosurida and Scorpiones, the ‘broad’ connection between the prosoma and opisthosoma is probably a reversal from state 1, due to loss of most or all of the external expression of the seventh (i.e. pregenital) segment: cf. the xiphosuran microtergite and the incorporation of opisthosomal segments into its ‘cephalothorax’. This condition has been presupposed for eurypterids too (Dunlop and Webster 1999), however in the absence of developmental or muscular evidence, the junction is coded as broad here. The junction between the two body tagma is narrow in Solifugae, Palpigradi, Ricinulei and Amblypygi and Araneae. Some authors (Weygoldt & Paulus 1979) would term it the pedicel and restrict it to Araneae and Amblypygi; others prefer to consider several distinct kinds of ‘pedicel’ (Shultz 2007a, character 97). We acknowledge such difficulties of definition and prefer to recognise a more general narrowing, a probable result of the constriction of the 7th segment that may have affected other segments (e.g. Ricinulei).

74. First opisthosomal tergite (0 = unmodified; 1 = very short)
This character concerns the size of the first opisthosomal tergite in comparison to those immediately posterior. Inapplicable to Pycnogonids where the first ‘opisthosomal’ segment bears a pair of walking legs. In modern Xiphosura segment one is incorporated into the prosoma, and this character has been coded inapplicable, and unknown for fossil taxa where the nature of the first segment is unknown. Present in eurypterids, haptopods, and chasmataspids, and also coded as present in the Haptopoda on the basis of Dunlop (1999) and the current work.

75. Six abbreviated opisthosomal tergites (0 = absent; 1 = present)
The extinct Phalangiotarbida uniquely express a dorsal opisthosomal surface in which the first six tergites form short bands across the back of the animal. The sixth tergite may be a little longer.

76. Opisthosomal sternite 1 (0 = present, 1 = absent)
Assuming that the lung-bearing elements on the ventral surface of Trigonotarbida are (as in Thelyphonida) the anterior and posterior opercula respectively, then studies of well-preserved trigonotarbids suggest that a first sternite is absent here, which seems to be unique for this extinct order.

77. Locking mechanism between opisthosoma and prosoma (0 = absent; 1 =
A specific ‘locking mechanism’ in which a modified first opisthosomal tergite slots into a corresponding fold at the back of the prosomal shield is observed in Ricinulei and Trigonotarbida (Dunlop 1996).

As noted above, all Phalangiotarbida have six abbreviated tergites. Behind this there are either a series of longer tergites (e.g. Bornatarbus) or in some taxa, such as Goniotarbus addressed here, these tergites have fused completely to create a single dorsal plate covering the posterior half of the opisthosoma.

State 1 is found in Ricinulei and Trigonotarbida (Dunlop 1996). Coded as absent in outgroups which lack differentiated median and lateral plates for the tergites, even if trilobate in general form.

Selden (1981) noted that the three large dorsal tergites posterior to the locking structure in the fossil Ricinulei Terpsicroton alticeps are fused together, since they preserve two putative pairs of muscular attachment scars. Fusion of at least the two tergites behind the locking ridge into a single diploterite is a character apparently shared with (most) Trigonotarbida (Dunlop 1996).

In crown-group Xiphosura - but not the fossil stem-assemblage known as synziphosurines (see e.g. Anderson & Selden 1997) - the opisthosomal tergites are fused together into a single, rigid plate termed the thoracatron or tergum sensu Shultz (2001). In chasmataspids three tergites are fused into a structure conventionally called the ‘buckler’ (Dunlop, Anderson & Braddy 2003).

Modern Xiphosura retain this appendage as the chilaria and in some early synziphosurines like Weinbergina it may even have been retained as a fully-developed leg. At least in recent homology schemes (Vilpoux & Waloszek 2003), a limb on the first opisthosomal segment as per arachnids is also present as the last walking leg of sea spiders. Their four pairs of walking legs on segments 4–7 are, in this model, no longer serially homologous with those of arachnids (segments 3–6). Shultz (1990, character 39) proposed loss of appendages on opisthosomal segment 1 as a putative synapomorphy of arachnids, making specific reference to adult instars.

Eurypterids and at least those chasmataspids which are well-preserved ventrally express an often elongate and/or segmented element projecting backwards from the second opisthosomal segment; the putative site of the genital opening. For this

83. Median abdominal appendage (0 = absent; 1 = present).

Eurypterids and at least those chasmataspids which are well-preserved ventrally express an often elongate and/or segmented element projecting backwards from the second opisthosomal segment; the putative site of the genital opening. For this
reason this structure is conventionally referred to as the median abdominal (or genital) appendage, although it has also been referred to as a ‘Zipfel’ in some publications. It presumably plays a role in either mating or oviposition, which some debate in the literature about its gender assignment and precise function.

84. Two anteriormost abdominal appendages fused to form genital operculum (0 = absent; 1 = present).

In eurypterids the first two pairs of mesosomal appendages are fused to form a plate called the Blatfuss/genital operculum.

85. Embryonic appendages on 7th segment (0 = absent; 1 = present).

Scorpiones and Solifugae clearly retain limb buds on the 7th (or first opisthosomal) segment during early embryogenesis (Farley 2005, fig. 1) and there are hints that the scorpion sternum may be derived (at least in part) from elements of opisthosomal segment 1 (Farley 2005, see also the next character). Unknown in fossil taxa.

86. Genital operculum overlaps sternite of third opisthosomal segment (0 = absent; 1 = present).

This so-called ‘megoperculate’ condition is clearly present in Amblypygi, Thelyphonida and Schizomida, whereby the second opisthosomal (or genital) operculum – see above – is quite large and overlaps a largely vestigial ‘true sternite’. This overlap was scored by Shultz (1990, character 42) as present in spiders too, but this is hard to reconcile with the fact that only Mesothelae retain the full genital sclerite (in other taxa it is reduced to a pair of book-lung opercula) and even in mesotheles evidence for the overlap of the third sternite seems to us equivocal. This is, however, tentatively coded as present. Palpigradi clearly lack a ‘megoperculum’, since the unpaired anterior lobe which accompanies the genital opening evidently does not overlap the sternite; contra Shultz (2007a).

87. Opisthosomal silk glands and spigots (0 = absent; 1 = present).

These complex glandular structures, producing silk and opening via spigots are synapomorphic for serikodiastida (Araneae + Uraraneida; Selden, Shear & Sutton 2009).

88. Opisthosomal spinnerets (0 = absent; 1 = present).

Spider spinnerets are appendage-derived opisthosomal structures which represent an unequivocal autapomorphy of Araneae. Specifically, they are not seen in Uraraneida in which the spigots appear to have been loosely distributed across the relevant segments of the ventral opisthosoma (Selden, Shear & Sutton 2009).

89. Ventral sacs (0 = absent, 1 = present).

Ventral sacs are enigmatic structures - possibly highly modified appendages - found on the underside of the opisthosoma in Amblypygi, Palpigradi and Trigonotarbida. Their function is unclear, but there have been suggestions that they play a role in osmoregulation. We score them simply as absent or present here, but note that in
the different groups they occur on different segments which may raise some questions about their serial homology.

90. **Pygidial defensive secretions** (0 = absent; 1 = present).
Thelyphonida have long been known to use defensive secretions of acetic / caprylic acid, leading to the group’s common name ‘vinegaroon’. These secretions are derived from pygidial glands at the back of the opisthosoma. We tentatively score this as present in Schizomida too (as per Shultz 1990, character 46); although we caution that it has only be confirmed in a handful of schizomid species; see e.g. Reddell & Cokendolpher (1995).

91. **Genital acetabula** (0 = absent; 1 = present)
These structures are a characteristic trait of Acariformes among the mites, which usually bear three pairs (but see character 91) probably associated with opisthosomal segments 3–5. It is well-established that they are serially homologous with the Claparède organs or ‘Urstigmata’, sharing the same ultrastructure (Alberti 1977) and function (Bartsch 1973). They are highly likely to be appendage derivatives, judging from evidence concerning the development of the Claparède organs (Thomas & Telford 1999).

92. **Number of genital acetabula** (0 = three; 1 = two; 2 = several)
Among Acariformes the number of genital acetabula may vary in relation to their function in water and ion balance. Freshwater species in particular have an increased number of genital acetabula designed for supplying ions to the hemolymph. Only applicable to acariform mites possessing genital acetabula.

93. **Dorsal anal operculum** (0 = absent; 1 = present)
In Phalangiotarbida there is a round plate located dorsally at the posterior end of the opisthosoma. This has been interpreted as the anal operculum, albeit with some reservations regarding its functional morphology. Nevertheless in well-preserved phalangiotarbids this plate always preserves dorsally and does not seem to be, for example, a ventral structure pushed up through in compression fossils. A dorsal anal operculum would be unique to phalangiotarbids.

1983 **Sensory systems**

94. **Lateral eyes** (0 = absent; 1 = present)
Lateral eyes are absent in Opiliones - except for members of the suborders Cyphophthalmi and the extinct Tetrophthalmi (Garwood et al. 2014) - and Pycnogonida.

95. **Lateral eye lenses** (0 = compound; 1 = five or more pairs of lenses; 2 = three primary pairs [excluding any microlenses]; 3 = two pairs; 4 = one pair)
The eyes of most of Arachnomorpha are compound in nature, as are the eyes of modern Xiphosura. This was apparently also the case in many Palaeozoic
Scorpiones, Eurypterida and Chasmataspidida; although individual facets cannot always be resolved in the fossils. Coding otherwise follows Shultz (2007a, character 140) for arachnids. Extant Ricinulei have lateral light sensitive areas without lenses, thus they are coded as having lateral eyes but with an undetermined lens number. The same approach is adopted for rhagiidids among Acariformes mites. Inapplicable in those lacking lateral eyes.

96. **Lateral eye rhabdomes** (0 = net-like; 1 = star-shaped). The rhabdomes of Xiphosura and Scorpiones share a distinct, star-like shape, whereas those of the remaining arachnids have a net-like arrangement. This star-shape was treated as an argument for a basal position for scorpions by, e.g., Weygoldt & Paulus (1979, character 21). The character is inapplicable to taxa lacking lateral eyes.

97. **Median eyes** (0 = four; 1 = two or three; 2 = absent). Pycnogonida have an ocular tubercle with four eyes and it has been argued (Weygoldt & Paulus 1979) that this is plesiomorphic. All Euchelicerata have either two eyes, or have reduced them completely as in Ricinulei, Pseudoscorpiones, and Schizomida; see e.g. Weygoldt and Paulus (1979, character 14), Giribet et al. (2002, character 1). They can be either present or absent among Acariformes although they are absent in all Anactinotrichida.

98. **Retinula cells of medial eyes** (0 = organized into closed rhabdomes; 1 = organized into a network of rhabdomeres; 2 = disorganized; 3, inverse retina; - = inapplicable due absence of median eyes) Scoring follows Shultz's (2007a) character 137.

99. **Slit sense organs** (0 = absent; 1 = present). These slit-shaped structures function as cuticular strain-gauges. They can be grouped together into so-called lyriform organs in some taxa and are often referred to as lyrifissures in mites. Slit sense organs have been recorded in all Arachnida except Palpigradi; see e.g. Shultz (1990, character 47) and Shultz (2007a, character 142). They could thus be considered a potential arachnid synapomorphy with a presumptive reversal in palpigrades.

100. **Trichobothria** (0 = absent; 1 = present). These sensory hairs set into a specific, cup-shaped socket (the bothridium) detect air vibrations and are a key sensory system in many arachnids for detecting prey or other sources of movement in their vicinity. They are not seen in Pycnogonida and Xiphosura, but apparently occur in all arachnid orders with the exception of Solifugae, Ricinulei and Opiliones (Selden, Shear & Bonamo 1991), and probably Trigonotarbida too.

101. **Tibial trichobothria with 2-1-1-1 distribution** (0 = absent; 1 = present). This specific pattern of trichobothria on the tibia was proposed by Shultz (1990, character 48) as an explicit synapomorphy of (Thelyphonida + Schizomida). It is
102. **Prodorsal trichobothria** (0 = absent; 1 = present)

These specific trichobothria on the prodorsum are a textbook synapomorphy for acariform mites as compared to anactinotrichid species; although they are secondarily lost in several acariform taxa. As with some other ‘mite-specific’ characters, they can be difficult to assess in (the usually much larger) non-acarine taxa.

103. **Pectines** (0 = absent; 1 = present).

These unique structures in Scorpiones appear to be modified appendages, which primarily act as chemosensory organs. Although occurring immediately behind the gonopore, authors such as Weygoldt & Paulus (1979) argued that they belonged to the 2nd (or genital) segment as part of a 12-segmented groundplan for the opisthosoma. Hox gene data from Simonnet, Célérier & Quéinnec (2006) corroborated by morphological data from Shultz (2007b) indicates that the pectines are in fact derived from the 3rd opisthosomal segment as part of a 13-segmented opisthosoma. It is worth noting that recent studies of some early fossil scorpions failed to find pectines, even in well otherwise ventrally well-preserved material - for example see *Proscorpius* (Dunlop, Tethe & Prendini 2008) and *Compsoscorpius* (Legg et al. 2012). It is conceivable that they were genuinely absent in the most basal stem-group scorpions which (if true) would render them no longer synapomorphic for the whole Scorpiones clade. The coding of *Palaeoscorpius* reflects the uncertainty reported by Kühl et al. (2012). See also the section on respiratory organs for an account of the alignment of respiratory organs on the eucaricerate opisthosoma.

104. **Malleoli** (0 = absent; 1 = present).

These unique sensory structures, sometimes called racquet organs, are a convincing autapomorphy for Solifugae, where they occur on the basal articles of the posterior legs (Punzo 1998).

105. **Tarsal organ on leg I** (0 = absent; 1 = present).

The tarsal organs or Haller’s organs occurs on leg I of Opilioacariformes, Holothryda and Ixodida (Klompen 2000), in leg I and II of Ricinulei (Talarico et al. 2005) and in all legs of Araneae and, perhaps, Scorpiones (Foelix 1985). Scoring of this – and the subsequent character – follows Shultz (2007a, characters 149, 150).

106. **Tarsal organ on leg II** (0 = absent; 1 = present).

A tarsal organ, similar to the character above, is present in Araneae and Ricinulei leg II.

107. **Opisthosomal ganglia in adults** (0 = absent; 1 = present).

In some arachnids, such as most spiders and all mites, there is a tendency to consolidate the ganglia of the central nervous system (CNS) anteriorly into the prosoma, effectively forming a unitary ‘brain’. In other taxa ganglia remain along the
length of the CNS into the opisthosoma; the plesiomorphic condition on the basis of outgroup *Alalcomenaeus cambricus* (Tanaka et al. 2013).

108. **Perineural membrane enveloping arterial sinus** (0 = present; 1 = absent).
Firstman (1973) related this membrane structure to the presence of book lungs and it thus scores as present for all (living) lung-bearing taxa.

109. **Intercheliceral median organ** (0 = absent; 1 = present).
This tiny movable structure emerges from beneath the prosomal shield and between the chelicerae of Palpigradi. Whether it represents a modified seta or, conceivably, a vestigial element homologous with some sort of precheliceral appendage is unclear. Van der Hammen (1982) speculated if it could be homologous with the Acariformes naso.

**Respiratory system**

110. **Respiratory organs** (0 = book gills or lungs present; 1 = tracheae; 2 = absent).
In this character, no attempt is made of distinguishing between lamellate gills and lungs. Their differences, as highlighted by Scholtz & Kamenz (2006) are recognized and coded separately below. Although traditionally scored as a ‘lungs absent/present’ character, our revised coding recognises that the ground pattern in the aquatic common ancestor was presumably gills, retained today in Xiphosura. In (modern) Scorpiones and Tetrarapulmonata these have been transformed into lungs. Note that many derived spiders have both lungs and trachea (hence the 0/1 score) while various chelicerates respire only with trachea, have lost the respiratory organs all together, or perhaps never developed such structures at all (Palpigradi, Pycnogonida, some mites?). A simple division into pulmonate and apulmonate arachnids has been criticized in the past and we score this character with reservations given that not all lungs and/or trachea in arachnids open in serially homologous positions. Some of these difficulties are reflected in the characters elaborated below.

111. **Book lung/gill on 2nd (i.e. genital) opisthosomal segment** (0 = present; 1 = absent).
Assuming the plesiomorphic condition was a series of respiratory organs along the trunk/opisthosoma, it is noticeable that in some chelicerates these have been lost on particular segments. As putative basal euchelicerates, *Offacolus* and *Dibasterium* bear a series of flattened appendages along the opisthosoma from the second to the seventh segment, the first to third among them bearing preserved accessory flaps in the former (Sutton et al. 2002), and first to fourth in the latter (Briggs et al. 2012). A similar state is observed in *Weinbergina*. By contrast Xiphosura and Scorpiones are notable for completely lacking a lamellate respiratory organ on the second (or genital) opisthosomal segment.

112. **Book lung/gill on 3rd (i.e. postgenital) opisthosomal segment** (0 = present; 1 =
A lamellate respiratory organ has been retained on this segment in: both modern Xiphosura and the fossil horseshoe crabs *Weinbergina*, *Dibasterium*, and *Offacolus*; in Trigonotarbida; and in Tetrapulmonata. They have been lost in segment 3 in Scorpiones – whereby it is interesting to speculate whether the pectines in this position are homologous appendicular elements – and, perhaps, in Eurypterida too (Braddy et al. 1999). Note that in more derived spiders (Araneae: Araneoclada) the second book lung has almost certainly been modified directly into trachea. This condition is also scored 1 here, but is presumably homoplasic with respect to other euchelicerates.

113. *Book lung/gill on 4th to 7th opisthosomal segment* (0 = present; 1 = absent).

A lamellate respiratory organ has been retained on these segments in both modern Xiphosura and the fossil horseshoe crabs *Weinbergina*, *Dibasterium*, and *Offacolus*; and in Scorpiones. The gill/lung has been (apomorphically) lost on these segments in the Pantetrapulmonata. Note that characters 111–113 are related to the transformation of book gills into book lungs, thus they are again coded only for taxa fundamentally bearing lamellate respiratory organs.

114. *Spiracles* (0 = absent; 1 = present)

Early fossil scorpions do not express ventral spiracles opening within the relevant sclerite. It is possible that the spiracle opening in fossil scorpions was marginal on a segment and concealed beneath a sclerite, rather like in Pedipalpi, but this is difficult to assess from the available material. Marginal spiracles can be clearly seen in well preserved examples of Trigonotarbida. In the coding adopted here, it was assumed that the spiracles of Scorpions and Tetrapulmonata are homologous, a controversial assumption; see also character 117.

115. *Spines on book lung lamellar margins* (0 = absent; 1 = present)

All book lungs express spines from the margins of the lamellae pointing into the atrial chamber which possibly help filter out particles and prevent them from entering the delicate lamellae themselves (Scholtz & Kamenz 2006). These spines are absent in the xiphosuran book gills, and they can be seen in the remarkable well-preserved fossil lungs of the trigonotarbid *Palaeocharinus* (Kamenz et al. 2008).

116. *Shape of pillars of the haemolymph spaces inside the gill/lung lamellae* (0 = at least two perikarya meeting midway in the haemolymph space; 1 = pillars, including a strong axis of microtubules).

State 1 is found in Xiphosuran book gills (Scholtz & Kamenz 2006). This character is inapplicable to those taxa which lack book gills/lungs.

117. *Proosomal spiracles* (0 = absent; 1 = between the coxae of the second and third walking legs; 2 = associated with coxae of third and fourth walking leg; 3 = between cheliceral basis; 4 = brachypyline oribatid tracheal system).

Tracheal openings between coxae II and III (e.g. Giribet et al. 2002, character 25) are a potential autapomorphy of Solifugae. Openings between coxae II and IV are
observed in Ricinulei and are tentatively scored here for Anactinotrichida except
Opilioacarus (see subsequent character). Spiracular openings between the
chelicerae are found in some prostigmatid mites – hence their name – although
further taxon-specific respiratory structures are found among ingroup members
(Evans 1992, Alberti and Coons 1999). Most Astig mata and Endeostigmata lack
respiratory organs. Brachypyline oribatids have spiracles opening in acetabula or
sockets of legs I and II and between legs II and III. Among Oribatida many other
respiratory structures occur, but the details do not seem to be informative for a
higher level phylogeny (Alberti & Coons 1999). This character touches on the
question of whether tracheal systems can be easily reduced to simple
presence/absence characters and/or whether the segment on which the respiratory
organ opens carries as much phylogenetic information as the fact that it is a lung or
a trachea; see also comments below. On current data a simple answer to this
question does not present itself.

118. Opisthosomal spiracles (0 = absent; 1 = paired ventral stigmata on genital
segment; 2 = paired ventral stigmata on 3rd and 4th opisthosomal segments; 3 =
four pairs of dorsal stigmata on the anterior opisthosoma).
Character state 1 is scored for Opiliones. State 2 is scored for Pseudoscorpiones and
Solifugae, although the latter also has an unpaired spiracle on the 5th opisthosomal
segment. State 3 is autapomorphic for Opilioacariformes. If tracheae are derived
from book-lungs it is likely that the positions of the tracheal openings are serially
homologous with the relevant book lungs in other arachnids. In the absence of
unequivocal lung/trachea homology across all arachnids (cf. the prosomal or dorsal
opisthosomal spiracles above) we score these here as independent characters for
now.

119. Kiemenplatten (0 = absent; 1 = present)
Well-preserved eurypterids uniquely possess modified oval areas on the underside of
the body, located within the gill chambers. These are conventionally referred to as
Kiemenplatten or sometimes simply ‘gill tracts’. Assuming that eurypterids retained
lamellate book gills, these Kiemenplatten have been interpreted as an accessory
respiratory system with possible parallels to the branchial lungs of certain modern
crabs which allow these animals to undertake temporary excursions onto land.

Digestive system

120. Postcerebral crop and proventriculus (0 = reduced, 1 = present).
A large crop is associated with the posteriorly-directed mouth in Xiphosura. They
may thus form part of a character complex together. Such a crop is not recorded in
arachnids or pycnogonids and reduction of the crop was proposed as a putative
synapomorphy of Arachnida by Shultz (2007a, character 202).

121. Well-developed sucking stomach (0 = absent; 1 = present).
Clearly present in Araneae and Amblypygi, and treated as a synapomorphy of these taxa by e.g. Weygoldt & Paulus (1979, character 31). Shultz (1990, character 5) noted its vestigial presence in Uropygi and some Scorpiones too, while Shultz (2001) further noted that Xiphosura also have a muscular postcerebral pharynx. Scoring follows Weygoldt & Paulus (1979).

**Endosternite**

122. *Endosternite* (0 = absent; 1 = present).

This structure may be homologous with Dohrn’s septum in Pycnogonida, but it occurs in a specifically plate-like form in Euchelicerata; with the exception of Solifugae. Firstman (1973) gave a detailed account, whereby its absence in Solifugae was considered a secondary reversal. Shultz (1990) also sought to define an endosternite *sensu stricto* as “a broad sheet of non-contractile connective tissue”.

123. *Anterior endosternal horn* (0 = terminating in muscular attachment to labrum; 1 = terminating in muscular attachment to palpal coxa).

This specific morphology of the endosternal horn was proposed by Shultz (1990, character 4) as a putative synapomorphy of Pedipalpi. It is inapplicable to taxa which lack an endosternite (see above).

124. *Fenestrate endosternite* (0 = absent; 1 = present).

This specific form of the endosternite is restricted to Thelyphonida and Schizomida (1990, character 8). It is inapplicable to taxa which lack an endosternite (see above).

**Excretory organs**

125. *Malpighian tubules* (0 = absent; 1 = present).

These excretory organs are another ‘typical’ textbook arachnid character. They have been recorded in all Recent arachnids except Palpigradi, Opiliones, Pseudoscorpiones and most Acariformes; see e.g. Shultz (1990, character 62). Among Acariformes, structures similar to Malpighian tubules have been found in Acaridae, thus they are tentatively scored here as present.

126. *Coxal glands opening on proximal podomere of chelifore* (0 = absent; 1 = present).

Coxal glands are modified nephridia and as such of mesodermal origin. The coxal gland opening is an ectodermal invagination and may not correspond to the segment from which the coxal gland sacculi originate. We prefer a simplified account for the coxal glands considering an anterior and a posterior coxal gland opening as the Bäuplan condition, as has been suggested by Weygoldt (2000). It reflects our poor understanding of the embryology and organogenesis of several orders. Fahrenbach & Arango (2007) described the presence of a pair of coxal glands associated with the *Nymphopsis spinosissima* chelifores – the first occurrence of excretory organs of any kind in Pycnogonida. King (1973) suggested that excretory
organs may be present on other leg bases based on dying techniques, but these results require confirmation. We accept here the existence of this anterior pair of coxal glands, but current data does not rule out the existence of more posterior pairs. Therefore, the following two characters are scored as ambiguous for Pycnogonida.

127. **Coxal glands opening at base of leg 1** (0 = absent; 1 = present).

State 0 is coded here for all living Euchelicerata, except Xiphosurans, Scorpiones, Opiliones and Pseudoscorpiones. Coxal gland openings in this position are thus retained in Acari, Ricinulei, Palpigradi, Solifugae, Araneae, Amblypygi, Thelyphonida and Schizomida (e.g. Shultz 1990, character 64; Shultz 2007a, character 180). Opening of the coxal glands associated with the pedipalps (the second prosomal segment) have been mooted as an autapomorphy of Solifugae (Shultz 1990), but Buxton (1917) described them opening in the same position in Palpigradi. The condition of Solifugae is quite similar to that found in several Acariformes were a cuticle-lined channel lead the fluids of the coxal gland towards the pre-oral chamber. It is worth also mentioning the so-called ‘hatching glands’ associated with the pedipalp in spider embryos (Yoshikura 1975) as well the second ozopore in some opilionids (Hara 2003) could be homologous with coxal glands (Moritz 1959, Yoshikura 1975).

128. **Coxal glands opening on leg 3 segment** (0 = absent; 1 = present).

Coxal gland openings in this position are plesiomorphically retained in Xiphosura, mygalomorph Araneae, basal Amblypygi, Opiliones, Scorpiones and Pseudoscorpiones (e.g. Shultz 1990, character 63). It is scored as ambiguous for the extinct Eurypterida except *Baltoeurypterus* (now *Eurypterus*) where Selden (Selden 1981) reported a pit near insertion of leg III.

129. **Contribution of the coxal gland to saliva** (0 = absent; 1 = Buxton’s group II coxal gland; 2 = coxal glands and saliva converging into the pre-oral chamber through external taenidia or gutters; 3 = podocephalic channel).

The onycophoran salivary gland is a modified nephridium, where a terminal sac lined with podocites is found along with a hypertrophied secretory region (Buxton 1913; Storch, Alberti & Ruhberg 1979). This structure is quite similar to the coxal glands of Palpigradi and Solifugae (Buxton 1913, 1917; Alberti 1979). In Solifugae the putative function of the coxal gland secretion as saliva is congruent with its opening as an excretory organ in close association to the pre-oral chamber. In Palpigradi this relation is not so clear; our coding recognizes the internal structural similarity with Solifugae (*contra* Shultz, 2007a). The condition presented by Parasitiformes approaches that of Solifugae. The so-called podocephalic channel, which leads the coxal gland secretions to the exterior, receives the products from up to three salivary glands and delivers them to the pre-oral chamber (Alberti & Coons 1999). However, each gland has its own distal portion lined by cuticle, being therefore the connection among the podocephalic glands made by an ectodermic structure (e.g. Shatrov 2005). Although functionally very similar, the condition presented by Acariformes apparently evolved from structures of different embryological origins.
and is coded here as a distinct state. Tetrapulmonata, Ricinulei, Holothyrida, and Opiliocariformes present prosomal furrows that lead the product from the coxal glands to the pre-oral chamber where it contributes to the saliva (Shultz 2007a, character 14). Scorpiones, Opiliones, Pseudoscorpiones, Xiphosura, Pycnogonida and ticks have no documented relationship between coxal glands and saliva secretion and are scored as 0.

130. Dorsomedian excretory organ (0, absent; 1, present).
This is a specialized, post-colon, region of the midgut modified for excretion which is present in Prostigmata (Alberti & Coons 1999) among the mites.

Musculature

Pharyngeal musculature

131. Lateral extrinsic precerebral pharyngeal muscle (0 = arising from anterior endosternal horns; 1 = arising from medial surface of palpal coxae; - inapplicable for taxa lacking an endosternite).
This specific arrangement of the pharyngeal musculature was proposed by Shultz (1990, character 6) as a putative synapomorphy of Pedipalpi.

132. Ventral extrinsic precerebral pharyngeal muscle and tergopharyngeal muscle of precerebral pharynx (0 = present; 1 = absent).
A further specific arrangement of the pharyngeal musculature was proposed by Shultz (1990, character 7 and 8) as a putative synapomorphy of Pedipalpi. Shultz (1990) interpreted these two muscles listed above as independent characters, but we prefer to treat them as a single character complex in order to avoid weighting the analysis too heavily towards patterns of individual muscle insertions.

Cheliceral musculature

133. Cheliceral tergal–deutomerite muscle (0 = absent; 1 = present).
Among those taxa whose chelicerae have three articles, this muscle running from the prosomal shield to the proximal margin of the second article (the deutomerite sensu Shultz) has so far only been recorded in Scorpiones and Opiliones (Shultz 2000), for which it was proposed as a putative synapomorphy. It is scored as inapplicable here for taxa with only two cheliceral articles.

134. Lateral tergocheliceral muscle (0 = one head; 1 = three heads).
This specific pattern of tergocheliceral musculature was proposed by Shultz (1990, character 10) as a putative synapomorphy of Pedipalpi.

135. Paired muscle arising from posterior margin of anterior carapodal doublure and inserting on prosomal shield (0 = absent; 1 = present).
Shultz (1990, character 1) described this specific muscle pairing as a putative
synapomorphy of Pedipalpi.

**Endosternal musculature**

136. Posterior oblique muscles of box-truss axial muscle system (BTAMS) of postoral somites I–V (0 = absent; 1 = present in one or more somites).

Shultz (2001) investigated the so-called box-truss axial muscle system in detail. State 0 occurs in Xiphosura, and state 1 occurs in Palpigradi, Araneae, Amblypygi, Thelyphonida, Schizomida and Scorpiones (Shultz 2001; 2007a, character 127). The condition in Acari, Ricinulei, Opiliones and Solifugae is not recorded.

137. Anterior oblique muscles of BTAMS posterior to postoral somite VI (0 = absent; 1 = present).

State 1 occurs in Xiphosura and may represent the primitive condition based on comparison with other arthropods (Shultz 2001; 2007a, character 128). State 0 occurs in all arachnids examined thus far.

138. Intercoxal endosternal extensor muscles (0 = absent; 1 = present).

The presence of these specific muscles was tentatively proposed as a synapomorphy of (Scorpiones + Opiliones) by Shultz (2000).

139. Endosternal dorsal suspensors of somites I and II (0 = present; 1 = absent/detached).

The absence of these suspensor muscles was suggested by Shultz (1990) as a putative synapomorphy of Arachnida; although the possibility that these muscles have become modified in other ways was also discussed; see Shultz (2001, p. 301) for details. Inapplicable to taxa which lack an endosternite (see above).

140. Endosternal dorsal suspensor muscles in somite four with anterolateral carapacal insertion (0 = absent; 1 = present).

The specific insertion of the endosternal suspensor muscles in Palpigradi, basal Araneae, Amblypygi and Uropygi is more posteromedial and often associated with the median prosomal shield depression typically seen in such arachnids (Shultz 1990, character 7). Inapplicable to taxa which lack an endosternite (see above).

141. Endosternal dorsal suspensor muscle of somite five (0 = present; 1 = absent).

This specific pattern of endosternal musculature was proposed by Shultz (1990) as a putative synapomorphy of Pedipalpi. Inapplicable to taxa which lack an endosternite (see above).

142. Ventral endosternal suspensor muscles (0 = attaching primarily to sternum; 1 = attaching primarily to coxa of appendage of anteriorly adjacent somite).

This specific pattern of musculature was proposed by Shultz (1990, character 7) as a putative synapomorphy of Pedipalpi. Inapplicable to taxa which lack an endosternite (see above).

**Pedipalp musculature**
143. *Palpal posteromedial tergocoxal muscle* (0 = present; 1 = absent).
This specific pattern of tergocoxal musculature was proposed by Shultz (1990) as a putative synapomorphy of Pedipalpi.

144. *Palpal posteromedial endosternocoxal muscle* (0 = originates on endosternite, inserts on coxa; 1 = originates and inserts on coxa).
This specific pattern of endosternal musculature was proposed by Shultz (1990) as a putative synapomorphy of Pedipalpi.

145. *Leg musculature*

146. *Intracoxal muscle* (0 = absent; 1 = present).
This specific muscle in the walking leg coxae was proposed by Shultz (2007a, character 54) as a putative synapomorphy of Pedipalpi.

147. *Insertion process of anteromedial tergocoxal muscle* (0 = weakly developed; 1 = large, well developed).
This specific pattern of leg musculature was proposed by Shultz (2007a, character 57) as a putative synapomorphy of Pedipalpi.

148. *Femoropatellar flexor* (0 = symmetrical; 1 = asymmetrical).
The asymmetrical arrangement of this muscle complex in the leg was proposed by Shultz (1990, character 27) as a putative synapomorphy of Pedipalpi.

149. *Pedal anterior femur–patella muscle* (0 = inserting primarily on patellar margin; 1 = inserting primarily on patellar plagula).
This specific pattern of leg musculature was proposed by Shultz (1990, character 27) as a putative synapomorphy of Pedipalpi.

150. *Pedal posterior femeropatella–tibia muscle* (0 = present; 1 = absent).
Absence of this specific muscle in the walking legs was proposed by Shultz (1990, character 33) as a putative synapomorphy of Pedipalpi.

151. *Pedal patellotibia–tarsus muscle* (0 = present; 1 = absent).
Absence of this specific muscle in the walking legs was proposed by Shultz (19, character 29) as a putative synapomorphy of Pedipalpi.

152. *Posterior transpatellar muscles insertion* (0 = dorsoposterior femur/ posterior patella; 1 = distal process of femur; 2 = absent).
Shultz (1990 character 28) regarded a femoral and/or patellar origin of this muscle as the plesiomorphic condition, regarding its specific origin from a distodorsal process as an apomorphy seen in Scorpiones, Opiliones and Pseudoscorpiones. This muscle is absent in Solifugae, Ricinulei and Schizomida, which is interpreted as a further derived state.
152. *Patellotibial extensor* (0 = absent; 1 = present).

According to Shultz (1990, character 29) the posterior transpatellar muscle in Scorpiones and Pseudoscorpiones has a specific dorsal insertion point and appears to act as a patellotibial extensor.

153. *Anterior transpatellar muscle insertion* (0 = anteriorly/anteroventrally; 1 = ventrally / posteroventrally; 2 = absent).

This muscle was reported (1990, character 30) as normally inserting on the anterior margin of the tibia, but as inserting ventrally in Scorpiones, Pseudoscorpions and Solifugae and as being absent in Ricinulei and Schizomida.

154. *Anterior patellotibial muscle insertion on tibia* (0 = anterior; 1 = ventral; 2 = absent).

Shultz (1990, character 32) described this muscle as having a ventral insertion point in Ricinulei, Scorpiones and Solifugae and as (uniquely) being absent in Pseudoscorpions.

155. *Posterior patellotibial muscle* (0 = present; 1 = absent).

This specific muscle was reported by Shultz (1990, character 33) as apomorphically absent in Scorpiones, Pseudoscorpiones, Solifugae and Schizomida.

156. *Origin of apotele depressor* (0 = tarsus; 1 = tibia).

A tibial origin of the apotele (or pretarsus) depressor muscle was suggested by Shultz (1990, character 35) as a possible synapomorphy for Arachnida.

157. *Patellar head of apotele depressor* (0 = absent; 1 = present).

The apotele depressor muscle has a head extending into the patella in Araneae, Thelyphonida, Schizomida, Opiliones, Scorpiones, Pseudoscorpiones and Solifugae.

158. *Patellar head of apotele depressor originates on posterior patellar wall* (0 = absent; 1 = present).

This specific position of the patella head of these depressor muscles was suggested by Shultz (1990, character 37) as a putative synapomorphy for Thelyphonida and Schizomida. It is not applicable to those taxa (see above) that lack a patella head.

**Opisthosomal musculature**

159. *Attachments of opisthosomal posterior oblique axial muscles* (0 = tergal; 1 = pleural).

The pleural attachment of these muscles was suggested as a possible synapomorphy for Arachnida by Shultz (2001). Given the highly reduced trunk in extant forms, all these opisthosomal musculature characters are scored here as inapplicable for Pycnogonida.

160. *Opisthosomal pleural muscle* (0 = continuous dorsoventral sheet; 1 = divided
Division of this opisthosomal muscle sheet was proposed by Shultz (1999, character 28) as a putative synapomorphy of Pedipalpi.

161. **Dorsal and ventral longitudinal muscles** (0 = spanning full length of opisthosoma; 1 = spanning first and, perhaps, last four opisthosomal somites). This specific pattern of longitudinal muscles was proposed by Shultz (1999, character 30) as a putative synapomorphy of Pedipalpi. How this should apply to acariform mites with their rather short ‘opisthosoma’ is unclear and they have been scored (?) here.

**Reproduction**

162. **Internal fertilisation** (0 = absent; 1 = present). Male xiphosurans release sperm directly onto the eggs and thus fertilise them externally (Aberti 2000) – presumably the plesiomorphic behaviour – whereas all arachnids use various mechanisms (outlined as individual characters below) to achieve internal fertilisation. This is a putative synapomorphy of Arachnida. The precise mode of sperm transfer in Pycnogonida is uncertain (Alberti 2000), as is that of various fossil taxa. There is some circumstantial evidence that the extinct eurypterids used internal fertilization too with sperm perhaps being deposited and/or taken up by the genital appendage.

163. **Gonopores** (0 = on limb bases; 1 = on second opisthosomal segment). The genital opening occurs on the second opisthosomal segment in all extant Euchelicerata, whereas Pycnogonida have genital openings on the limb bases. Whether the pycnogonid condition is plesiomorphic or apomorphic is subject to debate (Dunlop & Arango 2005); arguments for both hypotheses can be formulated, such as the displacement of organ systems into the pycnogonid legs.

164. **Gonopores** (0 = paired on second opisthosomal segment; 1 = unpaired on second opisthosomal segment). Consolidation of paired gonopores – as in for example xiphosurans – into a single genital opening has been suggested as a synapomorphy of Arachnida (Shultz 2001). The state of this character in fossil taxa, such as the eurypterids with their median abdominal appendage, is difficult to determine and scored as uncertain.

165. **Anteriorly positioned gonopore** (0 = absent; 1 = present). In Opiliones and Ixodida, the genital opening is thrust forwards into a distinctly anterior position more or less between the leg coxae; see e.g. Giribet et al. (2002, character 165).

166. **Ovipositor** (0 = absent; 1 = present). An ovipositor is present in Opiliones and in some Anactinotrichida – with the important exception of the ticks – as well as Acariformes among the mites sampled.
167. Penis / Spermatopositor (0 = absent; 1= present; 2= acariforme aedagus).
A penis is unequivocally present in Opiliones. A penis-like structure is also seen in
some acariform mites; however in the latter group it is probably better to regard it
as a spermatopositor which has (homoplastically) evolved into a copulatory device
in various ingroup mites. Thus a true penis, as per Opiliones, may not be part of the
acariform mite ground pattern. Anactinotrichid mites do not have a penis at all and
attempts to use a penis to support (Opiliones + all Acari) are misleading. Indeed
among Acariformes the presence of a “penis” has probably evolved several times.
All are scored as “2” here, however, in Astigmata, Cheyletidae, Tetranychioidea and
Stigmaeidae.

168. Male palpal organ (0 = absent; 1 = present).
Direct sperm transfer via the modified palpal organ of mature male spiders is an
autapomorphy of Araneae. The uraraneid palp is unknown.

169. Sperm transfer device on leg 3 (0 = absent; 1 = present).
Functionally similar to the spider palpal organ (see above), a modified organ for
direct sperm transfer on the third leg in mature males is an unequivocal
autapomorphy of Ricinulei.

170. Stalked spermatophore (0 = absent; 1 = present).
Alberti (2000) commented on the possibility that some sort of spermatophore was
part of the arachnid ground pattern, but noted difficulties in defining what exactly
constitutes a spermatophore sensu stricto. Scorpiones, Pseudoscorpiones,
Amblypygi, Thelyphonida and Schizomida transfer sperm via an explicitly stalked
spermatophore; e.g. Shultz (1990, character 57). Among mites most of Acariformes
produces spermatophores while most of Anactinothrichida exhibits espermactly
insemination or transfer the sperm employing the chelicerae. The exact mechanism
of sperm transfer in Opilioacariformes and Holothyrida remains unknown.

171. Spermatophore uptake (0 = without mating; 1 = face-to-face uptake; 2 =
mating parade).
Various arachnids perform ritualised mating behaviours or ‘dances’. In Scorpiones
and Amblypygi the male manoeuvres the female over the spermatophore with the
animals face-to-face. This is often called the ‘promenade-de-deux’ in scorpions and
this face-to-face behaviour is tentatively treated as a potential apomorphy, although
details of courtship may differ between groups. Pseudoscorpiones are more
complex. Some, probably basal, taxa simply leave a spermatophore and do not
strictly speaking mate (Weygoldt 1969; Alberti 2000). Others have a scorpion-like
courtship. We score pseudoscorpions 0/1 here for the character. A specific behaviour
pattern identified for Thelyphonida and Schizomida is what Weygoldt (1978) termed
the ‘mating parade’ (see also Shultz 1990; character 58) in which the female grabs
the male opisthosoma and is pulled over a previously deposited spermatophore with
the animals facing in the same direction. This character is inapplicable for taxa
which do not use spermatophores and the behaviour of Acariformes is too diverse to allow useful coding of this character at this stage.

172. Testis (0 = glandular area unspecialised; 1 = glandular area distinctly larger). Alberti & Peretti (2002) described distinct and potentially apomorphic similarities in the morphology of the testis in Solifugae and Acariformes only among the mites. In detail, they observed that in both groups there is a large glandular area, probably producing secretions needed for spermatophore formation, which has not been observed in other arachnids.

173. Tubular genital accessory glands (0 = absent; 1 = present). These so-called holocrine glands occur among arachnids only within the genital system of Amblypygi, Thelyphonida and Schizomida (Alberti 2000, 2005), and thus potentially support the Pedipalpi clade.

174. Brood sac (0 = absent; 1 = present). Pseudoscorpiones, Amblypygi, Thelyphonida and Schizomida construct a brood sac in which eggs - or in the case of pseudoscorpions, embryos - develop; see e.g. Shultz (1990, character 59) and Shultz (2007a, character 172).

Sperm morphology

175. Sperm cell flagellum (0 = present; 1 = absent). Plesiotypic sperm cells are supposed to be flagellate among animals. Loss of the flagellum is associated with specialization of the sperm transfer mechanisms.

176. Sperm cells coiled (0 = present; 1 = absent). This character is inapplicable for taxa without a flagellum.

177. Microtubule arrangement in axoneme (0, 9 + 0; 1, 9 + 1; 2, 9 + 2; 3, 9 + 3 ) The 9x2 + 3 arrangement of microtubules in the sperm axoneme is widely regarded as a convincing synapomorphy of Tetrarapulmonata (Alberti 2000, 2005 and references therein). Note that some ingroup spiders show further modifications of this pattern (Michalik & Alberti 2005). Inapplicable in taxa without an axonem.

178. Corkscrew-shaped helical nucleus (0 = absent; 1 = present). The specific morphology of a helically-shaped nucleus with sharp edges was suggested by Alberti (2000, 2005) as a potential synapomorphy of (Araneae + Amblypygi). Pseudoscorpion was also noted as having a corkscrew-shaped nucleus, but here derived from a peculiar spiral band. This raises questions about whether it is really homologous with the spider/whip-spider condition and pseudoscorpions are thus scored (?) here for this character.

179. Postcentriolar nucleus (0 = unmodified; 1 = asymmetrical, elongate). The latter condition of the nucleus was suggested as a potential synapomorphy for (Araneae + Amblypygi) by Alberti (2000, 2005).
180. **Implantation fossa** (0 = shallow; 1 = deep).

In arachnids with flagellate sperm the implantation fossa – a posterior part of the nucleus which usually contains the centrioles or their derivatives (Alberti 2000) – is usually shallow, but in many Araneae and Schizomida it is deep and effectively makes the sperm an almost a hollow tube. This character is inapplicable to aflagellate sperm, and only visible in basal Opiliones which develop a transient flagellum.

181. **Manchette of microtubules** (0 = absent; 1 = present).

Alberti (2000) noted that a manchette of microtubules associated with the nucleus – and perhaps related to nuclear shaping – is only seen in Ricinulei and the Tetrapulmonata orders; see also Giribet et al. (2002).

182. **Nuclear envelope** (0 = absent; 1 = present).

A nuclear envelope, which disappears at the end of spermatogenesis, is observed in Solifugae and Acariformes among the mites, although a similar phenomenon may occur in some Xiphosuran (Alberti 1995, 2000).

183. **Persisting flagellar tunnel** (0 = absent; 1 = present).

This tunnel surrounding the axoneme persists throughout spermiogenesis only in Scorpiones and Pseudoscorpiones (Alberti 2000); see also Giribet et al. (2002, character 203).

184. **Vacuolated sperm** (0 = absent; 1 = present).

Alberti (2000, especially fig. 33) described the quite fundamental differences between the sperm types seen in the Anactinotrichida and Actinotrichida groups of mites. He thus concluded that at least the sperm characters offer no characters in support of monophyletic Acari. Vacuolated sperm were suggested as a synapomorphy of Anactinotrichida, with some further modifications to this ground pattern to form ‘ribbon-type’ sperm in the gamasid mites.

**Embryology/Development**

185. **Eggs** (0 = centrolecithal; 1 = isolecithal/telolecithal).

Yohsikura (1975, table 1) described the eggs of most arachnids as centrolecithal. The eggs of scorpions and pseudoscorpions are quite different and show yolk reduction. Yohsikura (1975) related this reduction to ovoviviparity and viviparity in scorpions and the laying of eggs in a brood pouch in pseudoscorpions, both of which consequently reduce the reliance on yolk.

186. **Growth zone** (0 = gives rise to prosoma and opisthosoma; 1 = gives rise to opisthosoma only).

Anderson (1973) and Yohsikura (1975) described a fairly fundamental difference in the way the opisthosoma develops in Xiphosura and Scorpiones, as compared to
non-scorpion arachnids. In the former, the growth zone gives rise to both tagmata, in the latter the prosoma develops directly from the blastoderm (see also Giribet et al. 2002, character 192).

187. **Hexapodal instar** (0 = absent; 1 = present).
An early instar with only six legs is one of the strongest character proposed in support of (Ricinulei + Acari) – see e.g. Lindquist (1984), and Shultz (1990, character 61) – although it should be cautioned that adding limbs during ontogeny could be treated as a plesiomorphic, anamorphic mode of development.

188. **Egg teeth on pedipalpal coxae** (0 = absent; 1 = present).
Yoshikura (1975) observed various serrations in arachnids which probably function to break open the egg while hatching. Of these, a specific pair of teeth restricted to the dorsal surface of the pedipalpal coxae, and which are shed after hatching, was mentioned for Araneae and Amblypygi and is thus a potential synapomorphy of these taxa (see also Wheeler & Hayashi 1998, character 32). It is not clear to what extent this character has been investigated in other taxa.

189. **Lateral organs** (0 = absent; 1 = present).
This is a problematic character, in that the lateral organs seen during development in Solifugae, Amblypygi and Uropygi (Yoshikura 1975) may well be vestigial, plesiomorphic retentions of an exopod from the base of the second walking leg and are probably homologous with the Claperède organ of Acariformes (Thomas & Telford 1999). All four taxa are scored as having this character here. There is a so-called lateral organ in Xiphosura too, but Thomas & Telford (1999) questioned whether it was really homologous with that of arachnids – it does not really occur on the limb base in horseshoe crabs – and this is reflected in the scoring adopted here where its presence is restricted to the above-mentioned arachnids.

Ecology

191. **Heteromorphic parasitic larvae** (0 = absent; 1 = present).
This specialised life cycle with an obligatory parasitic larva is a putative apomorphy of the Parasintegona group among prostigmatid mites.

192. **Hypopi** (0 = absent; 1 = present).
The deutonymphal stage in Astigmata has reduced mouthparts, provided with a posterior clasping or sucking device related to dispersion by phoresis. This trait is exclusive to Astigmata (Sancassania and Rhizoglyphus among the taxa sampled in this study) among the mites.

193. **Anamorphic development with protonymphal stage** (0 = present, 1 = absent)
Pycnogonida show anamorphic development in which the hatching stage, or protonymph, is fundamentally different from the adult in having less segments and appendages. Subsequent segments and limbs are added during development. Xiphosurans and arachnids hatch as miniature versions of the adult, although in
some cases the full complement of limbs is only achieved with later instars (see hexapodal larva).

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Figure 1

Digital visualisations of the haptopod *Plesiosiro madeleyi* (NHM I7923; A-D), and phalangiotarbid *Goniotarbus angulatus* (NHM In22838; E-I)

A. **Dorsal view of *P. madeleyi***, showing opisthosomal segmentation and prosomal shield architecture. B. **Lateral view of the anterior ventral prosoma, nearest limbs and lateral prosoma removed**, showing the nature of haptopod chelicerae. C. Ventral view, showing ventral segmentation, and divided sternum. D. Haptopod walking leg. E. First left walking leg of *G. angulatus*, showing typical segmentation. F. **Lateral view of the anterior ventral prosoma**, showing the small pedipalps, median ridge, and possible chelicerae - below the resolution of the scan. G. **Fourth right walking leg.** H. Dorsal view showing median eyes and dorsal opisthosomal segmentation. I. Ventral view showing opisthosomal segmentation and coxo-sternal region. Abbreviations: 1-10 - opisthosomal segment number; as - anterior sclerite; ch - chelicerae; cx - coxa; fa - fang; fe - femur; L1-L4 - walking legs 1-4; me - media eyes; mt - metatarsus; pa - paturon; pp - pedipalps; ps - posterior sclerite; pt - patella; ta - tarsus; ti - tibia; tr - trochanter. Scale bars: A,C,F-I = 3mm; B,D,E = 1mm.
Figure 2

Holotype and only known specimen of phalangiotarbid *Goniotarbus angulatus* (NHM In22838)

**A. Dorsal view, showing prosoma and opisthosoma, and legs 4L and 2L.** Proximal portions of Leg 1L are visible at the anterior of the fossil, as are the trochanters of several of the legs on the right. **B. Ventral view showing coxo-sterne arrangement and ventral opisthosomal segmentation.** Proximal portions of Leg 1L, then 2L 3L and 4L are visible. **C. A close up of the sternum, anterior to the left showing five constituent plates.** **D. Detail of the anterior opisthosomal segmentation, including the posterior median bulge of the prosomal shield, and associated accommodation in the anterior opisthosomal segments.** **E. The posteriormost segments (7-10) fused to create a single dorsal plate, with a terminal anal operculum.** Scale bars: A,B = 2mm; C-E = 1mm.
Figure 3

Results of the cladistic analysis presented herein under equal weights analysis.

The trees show the strict consensus of equally weighted analyses of the matrices presented here (SI file 2,3, morphobank project 1274). A. Tree showing the analysis results with fossils included. Bremer, jackknife and bootstrap support values are provided for each node as shown in the key. B. Tree recovered with fossil terminals removed - ordinal clades are collapsed for clarity.
Figure 4

Results of the cladistic analysis presented herein under implied weights.

The trees show the strict consensus of implied weights analyses of the matrices presented here (SI file 2, morphobank project 1274). Symmetric resampling support values are provided on the basis that these are unaffected by character weights. A. The topology for concavity constants (k values) 0.25 and 1.0, which are identical. K = 0.25 support value above each node in red, K = 1.0 below in grey. B. Tree for k = 3.0. C. Topology for k=10.0.