X-ray microtomography of two Late Carboniferous whip scorpions (Arachnida, Thelyphonida): *Geralinura britannica* and *Proschizomus petrunkevitchi*

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SI Figures
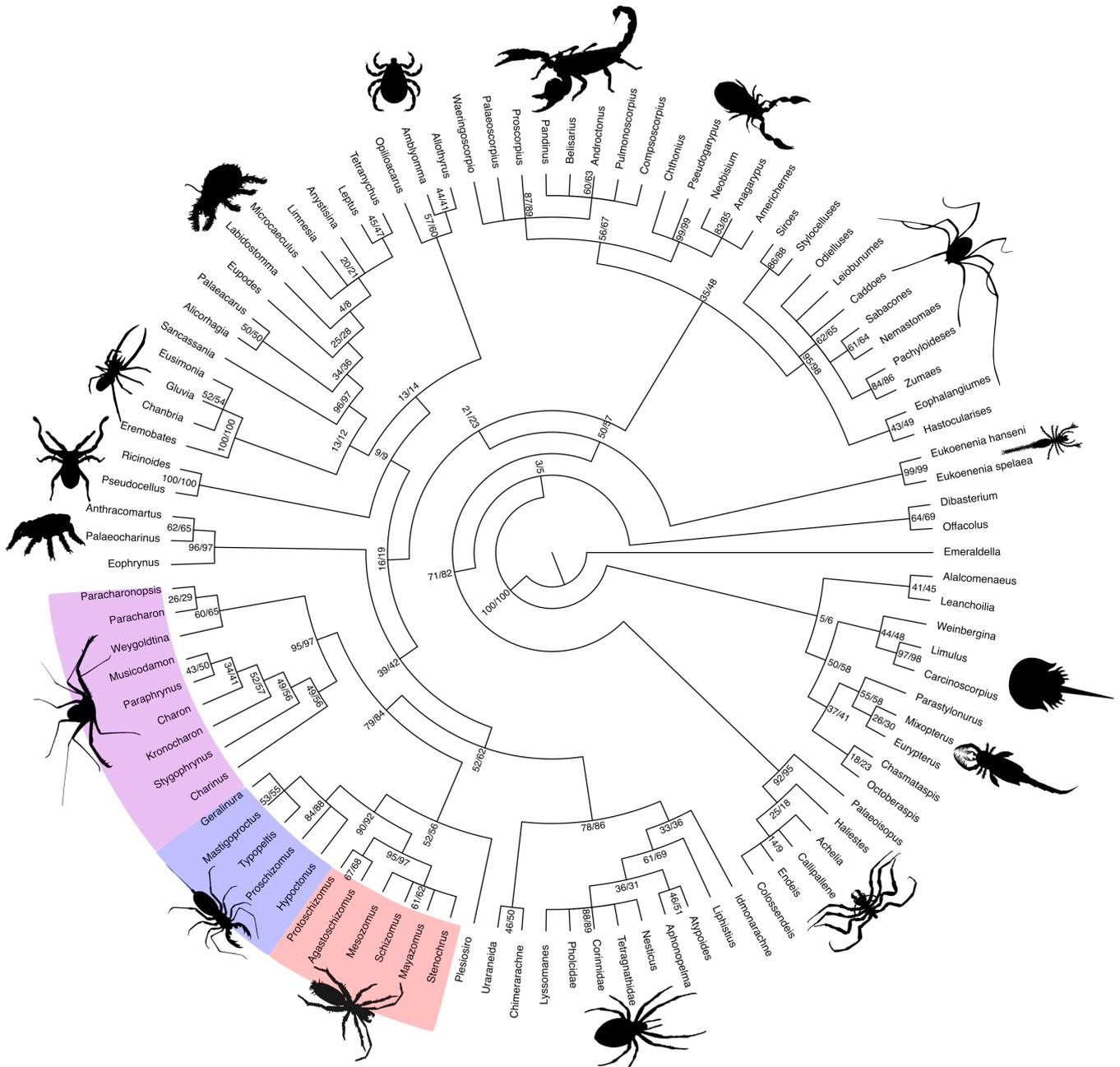
SI Figure 1 - Phylogeny of the arachnid orders, resolved based on the characters and matrix reported herein, and analysed using equal weights parsimony.
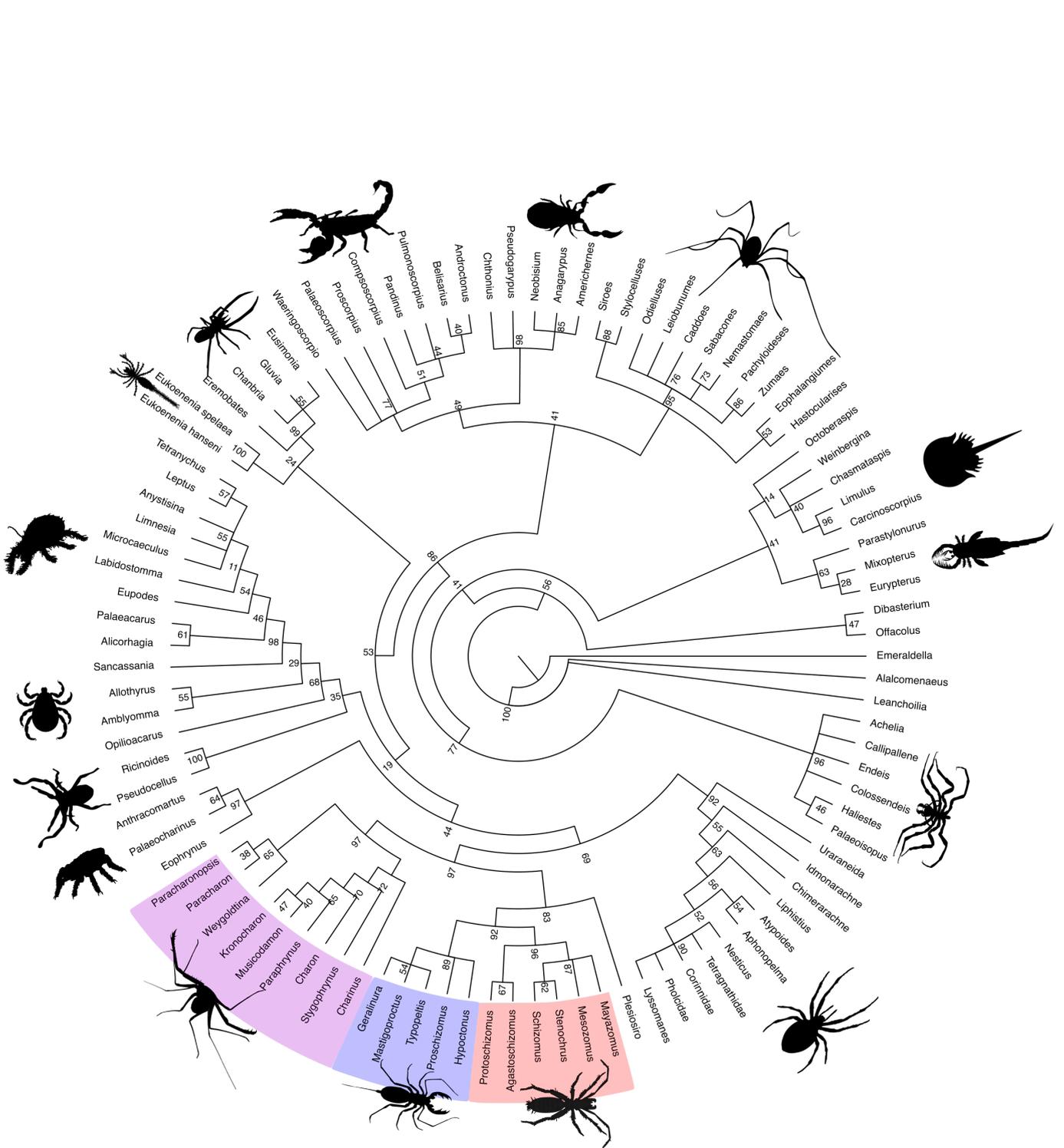
SI Figure 2 - Phylogeny of the arachnid orders, resolved based on the characters and matrix reported herein, and analysed using implied weights parsimony (k = 3).

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Character List

Introduction

Here we present character statements for the current analysis, modified after Pepato, da Rocha & Dunlop (2010), Garwood & Dunlop (2014a), Garwood et al. (2016), Garwood et al. (2017), and Wang et al (2018). Many of the characters have been drawn from previous analyses of arachnid phylogeny: in particular, we note Giribet et al. (2002), and Shultz (1990, 2007) to whom we are indebted for a number of characters. We also note that a modified version of the Garwood et al. (2017) matrix was presented by Huang et al. (2018), which primarily differs in coding the uraraneid terminals *Permarachne* and *Attercopus* individually, and that characters from this and other matrices were included in the total evidence analysis of Ballesteros et al. (2021).

Since the publication of Wang et al (2018), we have added a number of characters to explore the groups of interest herein, and also to allow future development of the matrix and its application to other aspects of arachnid phylogeny. In particular, we have added for resolution within the Schizomida:

- Character 14 - seta at base of anterior process of propeltidium
- Character 36 - dorsal depressions on male flagellum
- Character 37 - number of annuli of the female flagellum

The following characters were added to clarify relationships within the Ricinulei:

- Character 43 - Presence of accessory tooth
- Character 116 - The presence of a median sulcus
- Character 141 - For those taxa with vestigial eyes, whether these are unmodified or diffuse

Furthermore, as part of continued development of this analysis, descriptions for a number of characters have been modified for clarity and to reflect developments from the literature, and coding for some characters has been modified to better reflect uncertainty. Of particular relevance to this study, based on the Coal Measures taxa described in the associated paper and the new taxa included, we have clarified coding for:

- Characters 15 - prosomal dorsal shield with keels
- Character 60 - the nature of the palpal apophyses
- Character 61 - Male patellar apophysis modified

Character List

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 in Garwood & Dunlop 2014) 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.   *Ozophores* (0 = absent; 1 = present).

In opilionids, members of the family Cyphophthalmi have the openings to their prosomal repugnatorial glands on a raised cone-like structure, termed an ozophore. This character is also present in the fossil opilionid *Hastocularis* (Garwood et al. 2014a). This character is inapplicable to taxa lacking prosomal repugnatorial glands.

7.   *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.

8.   *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.

9.   *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.

10.   *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.

11.   *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.

12.   *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.

13.   *Anterior median projection of prosomal dorsal shield* (0 = absent; 1 = present)

Numerous taxa have an anterior median projection of the prosomal dorsal shield. The anterior margin of the propeltidium part of the dorsal shield in schizomids bears an anterior median process or projection (Cokendolpher & Reddell 1992: character 2). Based on figures in Rowland & Cooke (1973: fig. 2) the same character state can be scored for the prosomal dorsal shield of *Hypoctonus* among the whip scorpions. The same projection can also be seen in *Proschizomus*. A similar projection can be seen in some Palaeozoic scorpions, but not among the taxa presently scored in the analysis. Other taxa, such as the trigonotarbid arachnids, have a clypeus, which can manifest as a pointed projection (see e.g. *Eophrynus*, Garwood et al. 2009, Dunlop & Garwood 2014) or more rounded projection (e.g. *Trigonotarbus*, Jones t al. 2014). Where projecting, such as these trigonotarbids, this character is coded as present, but absent in taxa such as e.g. spiders, where there is no distinct projection.

14.   *Seta at base of anterior process of propeltidium (0=absent; 1=present)*

The family Protoschizomidae possess a pair of setae at the base of an anterior propeltidial process that is absent

in the family Hubbardiidae, and the whip scorpions (Cokendolpher & Reddell 1992: character 18; Monjaraz-Ruedas et al. 2017: character 7) . Scored as inapplicable to taxa lacking an anterior propeltidial process.

15.   *Trapezoidal projection of anterior prosomal dorsal shield margin* (0 = absent; 1 = present)

In basal Amblypygi, specifically the genera *Paracharon*, *Graeophonus* and *Paracharonopsis*, the anterior region of the prosomal dorsal shield projects notably forwards, effectively forming a trapezoidal anterior projection bearing the median eyes and between the the lateral eye tubercles in at least *Graeophonus* and *Paracharonopsis* (*Paracharon* is blind, but the projection is in the same place). This character differs from, say, the clypeus of trigonotarbids which is a projection in front of the median eyes, from the tiny spine-like anterior projection in some whip scorpions and in schizomids and from the hood of trogulid harvestmen. Modified from Weygoldt (1996, character 28).

16.   *Prosomal dorsal shield with keels between the median and lateral eyes* (0 = absent; 1 = present).

Rowland & Cooke (1973) proposed dividing the whip scorpions into two families based on the presence (Thelyphonidae) or absence (Hypoctonidae) of distinct marginal keels on the prosomal dorsal shield running between the median eyes and each set of lateral eyes. While their family division was not accepted by later workers, their character state of keels being present or absent remains a useful character for providing some resolution within the whip scorpions. Inapplicable in taxa lacking median and lateral eyes. This is present in the fossil taxon *Geralinurus*, but not *Proschizomus*.

Mouth and pharynx

17.   *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.

18.   *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 dependent on the form and orientation of the proboscis (see above).

19.   *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 the pedipalp (Winkler 1957).

20.   *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.

21.   *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.

22.   *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.

23.   *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 *Sidneyia*; 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 specialized 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).

24. *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).

25. *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.

26. *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).

27. *Intercheliceral epipharyngeal sclerite* (0, absent; 1, present).
Coding follows Shultz (2007, character 191).

28. *Epipharyngeal sclerite large, projecting posteriorly* (0, absent; 1, present).
Coding follows Shultz (2007, character 192). Inapplicable to taxa lacking an epipharyngeal sclerite.

Segmentation, tagmosis and telson

29. *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.

30. *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.

31.   *Metasoma length* (0 = pygidium; 1 = five segments; 2 = nine segments).
In Palpigradi, Ricinulei, Trigonotarbida, Haptopoda, Amblypygi, Thelyphonida and Schizomida the last three segments are essentially ring-like and either two or all three of them project out posteriorly. In ricinulieds they can also telescope out. This character state has been called the pygidium and reflects the 'Arachnida Micrura' concept of Hansen & Soerensen (1904). This character is inapplicable for taxa which do not express a metasomal tagmosis. In Scorpiones and Eurypterida the metasoma has five segments, in Chasmataspidida it has nine segments.

32.   *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.

33.   *Flagellate telson* (0 = absent; 1 = present).
In Palpigradi, Thelyphonida and (albeit in a shortened form) Schizomida, among the extant orders, and now Uraraneida, 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).

34.   *Telson with vesicle and aculeus* (0 = absent; 1= present).
This feature is regarded here as an autapomorphy of Scorpiones.

35.   *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.

36.   *Dorsal depressions on male flagellum* (0=absent; 1=present).
Some genera within the schizomid family Hubbardiidae possess depressions on the dorsal surface of the flagellum. Coding follows Monjaraz-Ruedas & Francke (2016: character 68) where taxa overlap. Inapplicable for non-flagellate taxa, and those without sexually dimorphic flagella.

37.   *Number of annuli in the female flagellum* (0=four; 1=three; 2=two).
The number of annuli of the female flagellum (or flagellomeres; Monjaraz-Ruedas et al. 2016), is phylogenetically informative within the Schizomida (Cokendolpher & Reddell, 1992). Coding follows Monjaraz-Ruedas & Francke (2016: character 84) where taxa overlap. Inapplicable for non-flagellate taxa, and those without sexually dimorphic flagella. Coded as polymorphic for Schizomus where it varies within the genus.

Chelicerae or deutocerebral appendage

38.   *Number of chelicerae 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.

39.   *Basal suture in proximal cheliceral segment* (0 = absent; 1= present).

Haupt (2009) and Krüger (2011) note a suture towards the base of the proximal chelicera in both the Schizomida and Thelyphonida. Haupt (2009) further reports musculature associated with the cuticle proximal to the suture, on which basis this could be considered a separate segment, and the chelicerae of these taxa three-segmented. Pending further studies or lines of evidence of the nature of this region, however, we have chosen to include the suture as a separate character.

40.   *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.

41.   *Cheliceral teeth* (0 = four; 1 = three)

In Amblypygi the specific number of internal cheliceral teeth on the basal element opposing the fang is phylogenetically significant. In early branching taxa, including the fossil *Graeophonus*, there are four teeth. In

more derived taxa this is reduced to three. Derived from Weygoldt (1996, character 1).

42.   *Distal-most cheliceral tooth* (0 = one cusp, 1 = two cusps)

A further refinement of the character above recognises that the distal-most tooth has only one cusp in the basal genus *Paracharon* and the fossil *Graeophonus*, whereas in all more derived taxa in our analysis the distal tooth is bicuspate. Derived from Weygoldt (1996, character 2). This character is inappropriate for non-amblypgid taxa.

43.   *Accessory tooth* (0 = absent, 1 = present)

The genus *Ricinoides* possesses an accessory tooth at the base of the fixed finger, which is not present in the other ricinuleid genera coded in this analysis. This is inapplicable to all taxa with more than two cheliceral segments.

44.   *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.

45.   *Cheliceral fang* (0 = chelate; 1 = clasp-knife type; 2 = Prostigmata styliform or *Anystis*-like chelicerae.

So-called clasp-knife chelicerae, *sensu* Shear *et al.* (1987), in which the apotele forms a fang rather than the movable finger of an explicitly chelate claw, are found in Araneae, Uraraneida, Amblypygi, Thelyphonida, Trigonotarbida and Schizomida (see also Kraus 1976). The chelicerae of Ricinulei also approach this condition (see e.g. Dunlop 1996, fig. 11) with a longer 'fang' articulating against a shorter fixed tooth and are thus scored 0/1 here for this character. Several Prostigmata also have the fixed digitus reduced, but the movable digit is ventral and the condition is clearly non-homologous to the condition observed in Tetrapulmonata and is scored separately here.

46.   *Diaphonous cheliceral teeth* (0=absent, 1 = present).

Dyspnoid harvestman are in part defined by the presence of small regular teeth on the opposing margins of the cheliceral fingers, called diaphonous teeth (Garwood et al 2011).

47.   *Angle of cheliceral articulation* (0 = parallel to sagittal plane; 1 = oblique to sagittal plane; 2 = parallel to transverse plane; 3 = parallel to coronal plane).

A character to reflect the plane of action in which the chelicerae principally move or bite. For taxa with clasp-knife chelicerae, when viewed from above (i.e. looking dorso-ventrally), the chelicerae can bite parallel to the sagittal plane. This is seen in trigonotarbids (palaeognath in orientation; Dunlop 1997, Garwood & Dunlop 2011) and those spiders with an orthognathous bite (Mygalomorphae; Zonstein 2003). In some taxa, when viewed from above, they bite oblique to this plane – a situation seen in mesothele spiders, and termed

plagiognathy by Kraus and Kraus (1993). In contrast most Araneomorphae possess labidognath mouthparts, where the bite is orthogonal to the sagittal plane. This character is coded as unknown for Uraraneida to reflect situation where the chelicerae are not labidognath (Eskov and Selden 2005), but their exact orientation is not known. This character is coded, where possible, for taxa with three-segmented chelicerae. In these taxa, the plane of motion of the cheliceral bite is coded as for those species with clasp-knife chelicerae for characters 0 – 2, but with the addition of character 3 for taxa such as scorpions. In these groups the projecting chelicerae bite within the coronal plane. This character is coded as inapplicable in pycnogonids which have a greater variability in the orientation of their chelifores, and in arachnid taxa with elbowed chelicerae which also display variability in the angle of their cheliceral motion. For the same reason, this character has been coded as inapplicable in mites, where the chelicerae are part of a mobile gnathosoma.

48.   *Chelicerae project beyond anterior prosomal shield margin* (0 = absent; 1 = present).
In the majority of arachnids, the chelicerae project beyond the anterior margin of the prosomal shield margin, and so are visible when the animal is viewed from above. This is not the case, however, in some marine chelicerates, such as Xiphosurans and Eurypterids, and in some arachnid orders including Ricinulei (where they are obscured by the cucullus), and Haptopoda, Trigonotarbida, and the Phalangiotabrida (where they are situated ventrally, posterior to a clypeus). This character is scored as inapplicable in mites, where the incorporation of chelicerae into the mobile gnathosoma means that they project, or not, depending on the position of the gnathosoma. Also inapplicable in taxa lacking chelicerae/chelifores.

49.   *Naked cheliceral fang* (0 = absent; 1 = present).
Selden, Shear & Sutton (2009) suggested that the loss of setae (or other similar sorts of projections) on the cheliceral fang was an autapomorphy of Araneae. Selden, Shear & Bonamo (1991) and Selden, Shear & Sutton (2009) demonstrated a naked fang in *Attercopus*; i.e. this character would support (Uraraneida + Araneae). The fang (or movable finger) in other arachnids seems usually to be setose and/or dentate. The condition observed in some mites is not considered as primarily homologous to this character.

50.   *Plagula ventralis* (0 = absent, 1 = present).
This specific small sclerite between the fang and the basal segment of the chelicera has been proposed as a synapomorphy of Araneae, Amblypygi, Thelyphonida and Schizomida (Homann 1985).

51.   *Cheliceral venom gland* (0 = absent; 1 = present).
Traditionally treated as an autapomorphy of Araneae, venom glands opening through the movable finger (or fang) of the chelicerae are present in all the spiders scored here. Venom glands are also absent in the ingroup spider family Uloboridae (not scored here) and while there have been claims that they are absent in the basal Mesothelae spider clade, this proposal has since been refuted. As a result of the observation of a venom gland in *Attercopus*, this character also supports a (Uraraneida + Araneae) clade.

52.   *Endocephalic spinning apparatus* (0 = absent; 1 = present).
The endocephalic spinning apparatus, together with its associated spinnerets or galea, is an autapomorphy of

Pseudoscorpiones (Harvey 1992). Whether these glands – which open on the movable finger of the chelicerae (Weygoldt 1969) – are homologous with the venom gland of spiders is unclear.

53.   *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 Pseudoscorpiones (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).

54.   *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).

55.   *Mesal fusion of chelicerae* (0 = absent; 1 = chelicerae proximally fused).
Mesal fusion of the chelicerae is seen in mites of the following groups: Tetranychoidea, Raphignathidae, Caligonellidae, Tarsonemina, 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.

56.   *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, Smariididae, 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).

57.   *Cheliceral serrula* (0 = absent; 1= present).
The serrula are modified setae on the free finger of the chelicerae seen in whip spiders and schizomids, but not in whip scorpions Cokendolpher & Reddell (1992: character 15).

58.   *Cheliceral serrula morphology* (0 = rounded; 1 = tooth-like, hyaline).
In those taxa where serrula are present, i.e. whip spiders and schizomids, the serrula are more knob-like in whip spiders and the two genera of the Protoschizomidae. The Hubbardiidae uniquely have a true serrula composed of a row of hyaline teeth though to act as a cleaning organ (Cokendolpher & Reddell 1992: character 15). Inapplicable for taxa lacking a serrula.

59.   *Cheliceral brush* (0 = absent; 1 = present)
A distinct brush of setae is present on the fixed digit of the chelicerae in the family Hubbardiidae among the

schizomids (Cokendolpher & Reddell 1992: character 16). This brush is not known from immediate outgroups such as whip scorpions.

Pedipalps or second head appendage

60.   *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).

61.   *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.

62.   *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 Rhagidiidae by Zacharda (1980) although the structures observed in Rhagidiidae 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.

63.   *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 (Dunlop et al. 2009; Garwood & Dunlop 2014b). 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.

64.   *Apophyses on patella and tibia of pedipalp* (0 = absent, 1 = present).

The raptorial pedipalps of the Mesozoic and Recent Thelyphonida additionally have a distinct set of apophyses projecting inwards from the patella and tibia which give this structure a more subchelate morphology. These specific apophyses are absent in Schizomida, and Tetlie & Dunlop (2008) argued that they are also absent in Coal Measures whip scorpion genera (*Geralinura*, *Prothelyphonus* and *Parageralinura*) too; Garwood and Dunlop (2022) demonstrate that these are, in fact, present in the Coal Measures taxa.

65.   *Modified patellar apophysis of male pedipalp* (0 = absent, 1 =present).

One of the four extant subfamilies of Thelyphonida, the Typopeltinae, was diagnosed by Rowland & Cooke (1973) as having a modified male patellar apophysis. This character state is found in *Typopeltis* and *Hypoctonus* in our analysis (Rowland & Cooke 1973) .

66.   *Plane of motion of pedipalps* (0 = vertical, 1 = horizontal).

In most arachnids the pedipalps are largely pediform and move primarily up and down in a vertical plane. In several taxa (Scorpiones, Pseudoscorpiones, Thelyphonida and most Amblypygi). The pedipalps move primarily from side to side in a horizontal plane, associated with sweeping movements to embrace and grab prey.

67.   *Pedipalp trochanter with a prominent flange* (0 = absent, 1 = present).

In Thelyphonida the pedipalp is modified into an anterior-mesally directed flange ornamented with several spines or teeth. Prey items can be pulled against these teeth to kill or immobilise them.

68.   *Dorsal row of femoral spines* (0=absent, 1=present).

A number of Amblypygi bear a prominent row of dorsal spines on the palpal femur.

69.   *Ventral apophysis on palpal trochanter* (0=absent, 1=present).

The trochanter of Amblypygi bears a ventral spined structure, or apophysis, which is not seen in other arachnids or outgroups.

70.   *Ventral apophysis present as a spine* (0=absent, 1=present).

In most amblypygids this apophysis is present as a row of spines. In contrast, in the Apulvillata clade, this is a prominent single spine. After Weygoldt (1996).

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

This specialized 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).

72.   *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.

73.   *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). Furthermore, we note that derived amblipygids within the Unidistitarsata clade possess a secondarily fused palpal apotele and tarsus (Weygoldt 2000). This is coded as inapplicable in Thelyphonida as it is unclear whether the group's lack of apotele reflects a loss or a fusion.

74.   *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).

75.   *Dorsal row of spines on pedipalp patella* (0 = absent; 1 = present).

Amblypygid palps possess a prominent row of sharp, dorsal spines on the patella associated with prey capture. In some groups – such as the Phrynidae and in the Charontidae – they form a catching basket, whilst the Phrynichidae have a prehensile hand.

Note: Weygoldt (1996, 2000), and a number of other authors, use a naming scheme in which the amblypygid palp lacks a patella. In contrast, we follow Shultz (1999) in using more conventional article series: trochanter, femur, patella, tibia, tarsus and apotele.

76.   *Three principal spines with spine 1 large* (0 = absent, 1 = present).

In the majority of extant, and some amber, amblypygid species, the spine row coded in the previous character has three principal spines, with the distal-most being enlarged. Modified after Weygoldt (1996), character 8; we note that *Paracharon*, originally coded as having two spines, there are actually three, furthermore it is unclear whether the original character referred to dorsal or ventral spine rows.

77.   *Patellar spines decrease in length proximally* (0 = absent, 1 = present).

In some amblypygid taxa the spine row on the pedipalp patellar decreases sequentially in length towards the proximal end. After Weygoldt (1996), character 10.

78.   *Reduced proximal spine from three-spined palpal patella* (0 = absent, 1 = present).

In some of the whip spiders with three main patellar spines, including *Muscidamon* in our analysis, the most proximal one is notably smaller than the two distal ones; the latter in some groups contributing towards the so-called 'hand'. In the amber genus *Kronocharon* the proximal spine is also smaller. Inappropriate for taxa which

do not have this three-spined morphology. After Weygoldt (1996) character 11.

79.   *Spines form a distal catching basket* (0 = absent, 1 = present, 2 = phrynicid hand)

In some species this spine row is large, and – coupled with ventral patellar spines – forms a structure known as a catching basket, as highlighted above, to help with prey capture. In whilst the Phrynichidae (i.e. *Musicodamon* in our current analysis), proximal spines are reduced, and this structure approaches a prehensile catching hand, sometimes termed the phrynicid hand.

80.   *Spines on palpal tarsus* (0=absent, 1 =present).

The amblypygid palpal tarsus is generally spine free; however, a limited number of taxa (in this analysis *Paracharonopsis*, *Paracharon*, and *Charinus*) possess spines on the palpal tarsus; presumably an adaptation towards prey capture.

81.   *Palpal tibia and tarsus* (0 = unfused, 1 = fused).

The tibia and tarsus of the pedipalp appear to be fused into a single element in Ricinulei, forming an element called the tibio-tarsus. This character state is present in at least the amber and Recent ricinuleds (e.g. Dunlop et al., 2009), but is largely equivocal for the Carboniferous fossils.

Ovigers and legs

82.   *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).

83.   *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.

84.   *First leg elongate used as a tactile limb* (0 = absent; 1 = present).

This modification of the first limb was proposed by Shultz (1999, character 16) as a putative synapomorphy of Pedipalpi. Additionally, Solifugae and Palpigradi also effectively walk hexapodally and probe ahead with the first leg and are scored 1 for this character too. We can also infer this character state as being present for Haptopoda, in which the first pair of legs are somewhat longer and have an annulate tip which lacks a claw.

85.   *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.

86.   *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 are 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.

87.   *Leg 1 tibia* (0 = unmodified, 1 = 16 segments; 2 = up to 23 segments; 3 = 25 segments; 4 = more than 25 segments).

Amblypygi achieve their antenniform leg 1 partly through the subdivision of the tibia into multiple elements. In outgroup taxa the tibia is not modified. Within whips spiders there are increasing numbers of tibial segments which are potentially phylogenetically informative. The number of segments is unknown in the fossil *Graeophonus*, but can be scored for the amber genus *Paracharonopsis*. Although it was equivocal in the original description of *Kronocharon* by Engel & Grimaldi (2014), a second species, which might even be conspecific, was later described (Wunderlich 2015) and implies the presence of character state 4. After Weygoldt (1996, character 18).

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

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

89.   *Coxa 2* (0 = unmodified; 1 = enlarged).

In extant Ricinulei the coxa of leg 2 is noticeably larger than the adjacent leg coxae. This enlargement is absent from fossil taxa, which nevertheless have an elongate leg two. This shows that this coxal development is independent from an enlarged second leg within Ricinulei.

90.   *Exopods* (0 = retained on more than one prosomal limb; 1 = on sixth prosomal limb, 2 = lost/not present).

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.

91.   *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.

92.   *Divided femora in legs 3 and 4* (0 = present; 1 = lost).
Shultz (1989, 1990 character 25) discussed previous interpretations of this additional 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.

93.   *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.

94.   *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.

95.   *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.

96.   *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. [01]

97.   *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.

98.   *Metatarsus which is at least 1.5 x tarsus length* (0 = absent, 1 = present).
Of those taxa with a divided tarsus in the walking legs, the majority possess a metatarsus of equal or lesser length than the tarsus. *Idmonarachne brasieri* and the Araneae posses a metatarsus significantly (>1.5 times) longer than the tarsus. Inapplicable to taxa with no metatarsus, and coded as [01] for taxa where the metatarsus:tarsus length varies significantly between legs, such as *Chimerarachne*.

99.   *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.

100.   *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 Eurypterida, *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).

101.   *Onychium /pretarsal plate bearing the claws* (0 = absent; 1 = present).
Of those taxa with claws, some have a pretarsal plate (termed a onychium in spiders), bearing the claws: this is true of spiders, the fossils *Idmonarachne* and *Chimerarachne*, and a most mite taxa. In contrast other taxa have claws that attach directly to the distal tarsus. Inapplicable for taxa with an apotele comprising simple cone or blade.

102.   *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. This character is coded as equivocal in the fossil amblypygid *Graeophonus*.

103.   *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.

104.   *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.

105.   *Single tarsal claws on legs 1 and 2, double tarsal claws on legs 3 and 4* (0 = absent; 1= present).

The Laniatores family of the opiliones are unique within the arachnids in having single tarsal claws on the anterior two walking legs, but double claws on the third and fourth (Pinto-da-Rocha, Machado, Giribet 2007).

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.

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

Weygoldt & Paulus's (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 (?).

107.   *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 specialized 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.

108.   *Number of body segments* (0 = twenty or more; 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 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 *et al.* 2006). For a full treatment of this character we direct readers towards Dunlop and Lamsdell (2016).

109.   *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 seventh and eighth 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 Chasmataspidida, 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).

110.   *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, and chasmataspids, and also coded as present in the Haptopoda on the basis of Dunlop (1999) and Garwood & Dunlop (2014a). This character is treated here as distinct from the specially modified locking ridge seen in Ricinulei and Trigonotarbida.

111.   *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.

112.   *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.

113.   *Opisthosomal sternite 1 triangular in form* (0 = present, 1 = absent)

In Haptopoda, Thelyphonida and Schizomida the first opisthosomal sternite is quite large and distinctly subtriangular in shape, sitting between the fourth leg coxae. In the older literature this structure was thought to be part of the sternum and was sometimes called the metasternum. Schultz (1993) demonstrated that it is actually an opisthosomal element based on the internal musculature. Inapplicable to those taxa lacking a distinct opisthosomal sternite 1.

114.   *Fused opisthosomal sternites* (0 = present, 1 = absent)

The majority of arachnids retain sternites (i.e. sclerotised plates on the ventral opisthosoma). Some groups have lost these, and instead have a smooth ventral surface: present in Acariformes, Parisitiformes, spiders, and some harvestmen.

115.   *Locking mechanism between opisthosoma and prosoma* (0 = absent; 1 = present).

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).

116.   *Opisthosomal median sulcus* (0=absent, 1=present)

The Carboniferous Ricinuleid genera *Curculiodes* and *Amarixys* have a median sulcus longitudinally dividing the opisthosoma, making the animals superficially beetle-like in appearance. This character is absent in other ricinuleids, and the majority of other arachnids.

117.   *Opisthosomal tergites 7-10* (0 = separate; 1 = fused into a single plate)

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.

118. *Opisthosomal tergites trilobate (with a distinct axial region)* (0 = absent; 1 = present).
State 1 is found in some 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. Coded as absent in *Poliochera cretacea* and carboniferous *Poliochera* species on the basis of a lack of distinct lateral plates, despite raised opisthosomal margins in the amber specimen.

119. *Posterior opisthosomal tergites divided* (0 = absent; 1 = present)
In the subfamily Thelyphoninae of the Thelyphonida the posterior tergites of the opisthosoma are medially divided (Rowland & Cooke 1973). This is not a strong division, but can be seen as a median line on the tergites. It is not seen in other whip scorpion subfamilies and applies to *Theylphonus* only in the present analysis.

120. *Opisthosomal tergites fused* (0 = absent; 1 = present)
In a number of arachnid groups the opisthosomal tergites are fused to form a dorsal opisthosomal surface that lacks obvious external segmentation. This character is scored as absent in those taxa where individual tergites are present, and also those in which segmentation is apparent in the form of dorsal opisthosomal ridges. The character is thus scored as present in some ricinuleids, opisthothele spiders, and also in many mites, including those where the original segmentation is only revealed through patterns of setae. All of the coded Opiliones have visible segmentation.

121. *Fused opisthosomal tergites medially divided* (0 = absent; 1 = present)
In some Carboniferous Ricinulei the fused opisthosomal tergites are sagittally divided, creating an opisthosoma dorsally reminiscent of beetle elytra. Not applicable to taxa lacking fused opisthosomal tergites.

122. *Diplotergites* (0 = absent; 1 = one present; 2 = more than one present)
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). Coded as absent in those ricinuleids with longitudinally fused tergites.

123. *Fused opisthsomal segments* (0 = absent; 1 = buckler; 2 = thoracatron).
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 thoracetron or tergum sensu Shultz (2001). In chasmataspids three tergites are fused into a structure conventionally called the buckler (Dunlop, Anderson & Braddy 2003).

124. *Appendages on opisthosomal segment 1* (0 = present; 1 = lost).
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 in 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.

125. *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; there is some debate in the literature concerning its gender assignment and precise function.

126. *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 or genital operculum.

127. *Embryonic appendages on seventh segment* (0 = present; 1 = absent).

Scorpiones and Solifugae clearly retain limb buds on the seventh (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.

128. *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).

129. *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). They are also present in *Chimerarachne*, but cannot be resolved in *Idmonarachne*.

130. *Epiandrous spigots* (0 = absent; 1 = present).

Spiders and *Chimerarachne* possess epiandrous spigots : structures used by male spiders to weave a sperm web prior to transferring the sperm to palps. These are coded as inapplicable for taxa which do not possess spigots on the assumption that they are homologous with the spigots found in Uraraneida and on the spinnerets of spiders, rather than a novel character.

131.   *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), but are seen in *Chimerarachne.*

132.   *Anterior median spinnerets articulated* (0 = absent; 1 = present).

The anterior median spinnerets of spiders are articulated with the ventral opisthosoma. This is not the case in *Chimerarachne*, where they are continuous with a sternite: presumably the plesiomorphic condition for spiders.

133.   *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. *Note: Ventral sacs occur on the second opercular segment in* Palaeothele *and* Heptathela, *but not Liphistius, and were considered to be tracheae by Yoshikura (1954). See Selden 1996.*

134.   *Pygidial defensive secretions* (0 = absent; 1 = present).

Thelyphonida have long been known to use defensive secretions of acetic/caprylic acid, leading to their 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).

135.   *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 95) 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).

136.   *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.

137.   *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.

Sensory systems

138.   *Lateral eyes* (0 = absent; 1 = present).

Lateral eyes are absent in Opiliones – except for members of the suborders Cyphophthalmi and the extinct Tetropthalmi (Garwood et al. 2014) – and Pycnogonida.

139.   *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; 5 = no lenses).

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, except extant Ricinulei and cyphophthalmid harvestmen, which have lateral light sensitive areas without lenses. Inapplicable in those lacking lateral eyes. This is coded as unknown in *Chimerarachne* as the exact number of lenses is unclear.

140.   *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.

141.   *Vestigial lateral eyes* (0=unmodified; 1 = diffuse).

Ricinulei lack lateral eye lenses, but have translucent, light sensitive areas that are lighter in colour, and situated where lateral eyes are found in other arachnid taxa. These are typically found near the second legs, at the edge of the carapace and are relatively small, but in the genus *Pseudocellus* (in this analysis), these are larger, diffuse, and extend further dorsally (Platnick 1980).

142.   *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 & 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.

143.   *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.

144.   *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.

145.   *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.

146.   *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 inapplicable for taxa which lack trichobothria (see previous character).

147.   *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.

148.   *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 second (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; see, for example, *Proscorpius* (Dunlop, Tetlie & 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 euchelicerate opisthosoma.

149.   *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).

150.   *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 next character follows Shultz (2007a, characters 149, 150).

151.   *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.

152.   *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).

153.   *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.

154.   *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 acariform naso.

Respiratory system

155.   *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 Tetrapulmonata 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.

156.   *Book lung/gill on second (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.

157.   *Book lung/gill on third (i.e. postgenital) opisthosomal segment* (0 = present; 1 = absent).

A lamellate respiratory organ has been retained on this segment in modern Xiphosura, the fossil horseshoe crabs Weinbergina, Dibasterium, and Offacolus, in Trigonotarbida, and in Tetrapulmonata. They have been lost in segment 3 in Scorpiones (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 homoplastic with respect to other euchelicerates.

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

A lamellate respiratory organ has been retained on these segments in modern Xiphosura, 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 114–116 are related to the transformation of book gills into book lungs, thus they are again coded only for taxa fundamentally bearing lamellate respiratory organs.

159.   *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 118.

160.   *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).

161.   *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.

162. *Prosomal 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 & Coons 1999). Most Astigmata 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.

163. *Opisthosomal spiracles* (0 = absent; 1 = paired ventral stigmata on genital segment; 2 = paired ventral stigmata on third and fourth 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 fifth 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.

164. *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 (Kühl et al. 2012).

Digestive system

165. *Postcerebral crop and proventriculus* (0 = absent/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).

166.   *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

167.   *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, in which 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".

168.   *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).

169.   *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

170.   *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.

171.   *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.

172.   *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).

173.   *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, although one is present on the coxa of leg III in *Eurypterus tetragonophthalmus* (Selden 1981).

174.   *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 onychophoran 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.

175. *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

176. *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.

177. *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

178. *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.

179. *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.

180. *Paired muscle arising from posterior margin of anterior carapace 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

181. *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.

182.   *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.

183.   *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).

184.   *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).

185.   *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).

186.   *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).

187.   *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

188.   *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.

189.   *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.

Leg musculature

190.   *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.

191.   *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.

192.   *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.

193.   *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.

194.   *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.

195.   *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.

196.   *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.

197.   *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.

198.   *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.

199.   *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 Pseudoscorpiones.

200.   *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.

201.   *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.

202.   *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 Shultz (1989, 1990 character 36).

203.   *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

204.   *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.

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

206.   *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

207.   *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.

208.   *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.

209.   *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.

210.   *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).

211.   *Open gonopore* (0 = present; 1 = absent)

Within the harvestman there are two forms of genital opening (gonopore). The Cyphophthalmi and Tetrophthalmi possess a ring-like cuticular hole, whilst in the Palpatores clade this opening is covered with a plate, the genital operculum (Pinto-da-Rocha, Machado & Giribet 2007).

212.   *Intromittent penis* (0 = present; 1 = absent)

Within the harvestmen the male genital appendage is used as a spermatopositor within the Cyphophthalmi, and as an intromittent organ within the Palaptores. Whilst some fossil taxa (e.g. *Hastocularis*, *Eophalangium*) have a clear male organ preserved, how this was used is not clear, and so is coded as unknown.

213.   *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 here.

214.   *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 in Astigmata, Cheyletidae, Tetranychoidea and Stigmaeidae are scored as "2".

215. *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 male uraraneid palp is unknown, but this is present in *Chimerarachne*.

216. *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.

217. *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 espermdactly insemination or transfer the sperm employing the chelicerae. The exact mechanism of sperm transfer in Opilioacariformes and Holothyrida remains unknown.

218. *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.

219. *Testis* (0 = glandular area unspecialized; 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.

220. *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.

221. *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

222. *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.

223. *Sperm cells coiled* (0 = present; 1 = absent).

This character is inapplicable for taxa without a flagellum.

224. *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 Tetrapulmonata (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.

225. *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). Pseudoscorpiones were 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.

226. *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).

227. *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.

228.   *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).

229.   *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).

230.   *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).

231.   *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

232.   *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. Yoshikura (1975) related this reduction to ovoviviparity and viviparty in scorpions and the laying of eggs in a brood pouch in pseudoscorpions, both of which consequently reduce the reliance on yolk.

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

Anderson (1973) and Yoshikura (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).

234.   *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.

235.   *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.

236.   *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

237.   *Heteromorphic parasitic larvae* (0 = absent; 1 = present).

This specialized life cycle with an obligatory parasitic larva is a putative apomorphy of the Parasintegona group among prostigmatid mites.

238.   *Hypopi* (0 = absent; 1 = present).

The deutonymphal stage in Astigmata has reduced mouthparts, provided with a posterior clasping or sucking device related to dispersal by phoresis. This trait is exclusive to Astigmata (*Sancassania* and *Rhizoglyphus* among the taxa sampled in this study) among the mites.

239.   *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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