

Segmentation and tagmosis in Chelicerata

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ABSTRACT

Patterns of segmentation and tagmosis are reviewed for Chelicerata. Depending on the outgroup, chelicerate origins are either among taxa with an anterior tagma of six somites, or taxa in which the appendages of somite I became increasingly raptorial. All Chelicerata have appendage I as a chelate or clasp-knife chelicera. The basic trend has obviously been to consolidate food-gathering and walking limbs as a prosoma and respiratory appendages on the opisthosoma. However, the boundary of the prosoma is debatable in that some taxa have functionally incorporated somite VII and/or its appendages into the prosoma. Euchelicerata can be defined on having plate-like opisthosomal appendages, further modified within Arachnida. Total somite counts for Chelicerata range from a maximum of nineteen in groups like Scorpiones and the extinct Eurypterida down to seven in modern Pycnogonida. Mites may also show reduced somite counts, but reconstructing segmentation in these animals remains challenging. Several innovations relating to tagmosis or the appendages borne on particular somites are summarised here as putative apomorphies of individual higher taxa. We also present our observations within the concept of pseudotagma, whereby the true tagmata – the prosoma and opisthosoma – can be defined on a fundamental change in the limb series while pseudotagmata, such as the cephalosoma/proterosoma, are expressed as divisions in sclerites covering the body without an accompanying change in the appendages.

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1. Introduction

Chelicerata are one of the principal divisions of the Arthropoda. In addition to the largely terrestrial Arachnida, this clade also includes two extant marine groups: Pycnogonida (sea spiders) and Xiphosura (horseshoe crabs). It also includes the extinct marine-freshwater Eurypterida (sea scorpions) and the little-known and probably marine Chasmataspidida. Furthermore, several Palaeozoic fossils (e.g. Briggs and Collins, 1988; Orr et al., 2000; Chen et al., 2004) have been proposed either as taxa belonging to the chelicerate stem-lineage or as early branches within the chelicerates. Indeed Lamsdell (2013) proposed that some fossils traditionally assigned to horseshoe crabs may in fact belong to the stem-lineage of other chelicerate clades (see 3.4). Chelicerates can be united by the synapomorphy of the first pair of head appendages being modified into chelate or clasp-knife structures usually referred to as the chelicerae or chelifores. Most chelicerates are predators – although mites express a much

wider range of feeding ecologies – and the short, raptorial limbs associated with the first somite are almost invariably used to grasp, tear, pierce, or otherwise manipulate food. Compared to mandibulate arthropods, chelicerates have marshalled far less of their anterior appendages exclusively for food-gathering and can effectively be said to “walk on their heads” (Dieter Waloßek, pers. comm. to JAD; see also remarks in Averof (1998)).

Traditionally, textbooks recognised a basic division of the chelicerate body into two functional units. The first six somites, bearing six corresponding pairs of appendages, form a prosoma which is largely responsible for feeding, locomotion and acquiring sensory information. Sense organs include the eyes, although these are reduced or lost in some groups, as well as a preponderance of cuticular structures such as mechano- or chemoreceptive setae or the slit sense organs of many arachnids. The remaining somites – up to thirteen in number – form the opisthosoma which primarily hosts the digestive and, usually, the respiratory system, the heart (if present), as well as the gonads. In arachnids and horseshoe crabs the genital opening is invariably on the underside of the second opisthosomal segment (somite VIII): a useful landmark for assessing segmentation patterns. The opisthosoma of horseshoe crabs bears a flap-like genital operculum,

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plus five pairs of gill opercula. The arachnid opisthosoma is largely devoid of external appendages, although may retain them in a highly modified form (Shultz, 1993; Thomas and Telford, 1999; Damen, et al., 2002; Pechmann and Prpic, 2009; Pechmann et al., 2010; Farley, 2015). Examples here would include gonopods or papillae flanking the genital opening, ventral sacs in groups like whip spiders, book-lungs and their associated covers, and the spinnerets of spiders.

Pycnogonids deviate from this simple prosoma/opisthosoma pattern (Winter, 1980; Villpoux and Walošek, 2003) and do not really have an opisthosoma equivalent to that of arachnids and horseshoe crabs. Some living genera, such as *Decolopoda* Eights, 1835 and *Dodecolopoda* Calman and Gordon, 1933, have one or two additional pairs of legs. There are also fossils like *Weinbergina opitzi* Richter and Richter, 1929 which also appear to have an 'extra' pair of prosomal legs. This species was originally interpreted as a horseshoe crab, but is now considered to be at a more basal grade of organisation (Lamsdell, 2013). In a similar vein we should note the embryological observations of Scholl (1977) on modern horseshoe crabs – confirmed morphologically by Shultz (2001) – which showed that in this group some opisthosomal segments are incorporated into the prosomal head shield. We should also note several arachnids where the prosoma/opisthosoma division is less obvious. Instead we may see division into a gnathosoma/idiosoma (i.e. two somites, plus the rest of the body) in groups like mesostigmatid mites and in ticks, or a proterosoma/hysterosoma (four somites, plus the rest of the body) in many acariform mites. Lamsdell (2013) elaborated the concept of functional pseudotagmata to accommodate such patterns, and these divergent body plans and the notion of pseudotagmata are reviewed in the present study.

Our aim in the first instance is to document segmentation patterns in all major lineages (orders) of Chelicerata, homologising segments as far as possible and exploring the data to try to recognise key innovations in chelicerate evolution relating to segmentation or the appendages they bear (Table 1). A segment-by-segment comparison of horseshoe crabs and scorpions was fundamental to Lankester's (1881) classic demonstration that Xiphosura are closer to Arachnida than to Crustacea. We also draw on historical (Pocock, 1893; Börner, 1904; Petrunkevitch, 1922; Millot, 1949; Zachvatkin 1952) and contemporary (van der Hammen, 1989; Kraus, 1998; Villpoux and Walošek, 2003; Lamsdell, 2013; Lamsdell et al., 2015a) accounts of segmentation patterns across groups, and expand these here to include data from several recently described fossil taxa which appear to reveal key stages in the early evolution of the chelicerate body plan and limb arrangement.

2. Materials and methods

Data were largely drawn from the primary literature, including the authors' own studies, and citations to relevant papers for individual taxa are provided in the Results section below.

Extinct taxa are indicated by a †.

2.1. Terminology

Comparative studies of arthropods can suffer from inconsistencies in terminology. In the worst-case scenario these translate into erroneous character scores for phylogenetic analyses. Occasionally the same term has been used for what are evidently non-homologous structures. A case in point would be the carapace (= prosomal dorsal shield) of arachnids and the carapace of crustaceans. Alternatively, potentially homologous elements can be masked by the use of long-standing, group-specific

terminologies. An example here would be the cephalosoma of pycnogonids and the proterosoma of certain mites; both of which essentially refer to a distinct body region bearing the first four pairs of appendages. Mites are a particularly problematic group in that morphological terms can be taxon-specific, or even differ between authors of different nationalities. Throughout we try to unify the terminology wherever possible, but also to cross-reference our descriptions to alternative and/or traditional names in the literature.

2.2. Segments and somites

Of particular relevance to the present review is the need to be clear from the outset about the difference between segments and somites. Here, somites refer to the fundamental metamerous units which make up the arthropod body. They are numbered using Roman numerals (Figs. 1–5). We also assume the presence of an ocular somite (labelled 0). A discussion of its serial homology can be found in, e.g., Scholtz and Edgecombe (2006: Fig. 3) who referred to this as the ocular/protocerebral region. Segments refer to the external expression of these somites through discrete plates such as tergites or sternites. Somites often match segments – particularly in the arachnid opisthosoma – but mismatches may occur when adjacent segments fuse. Fusion may affect the whole segment or only the dorsal or ventral part. For example, many of the extinct trigonotarbid arachnids have fused tergites 2 + 3 into a single, larger diplotergite.

A detailed account of the developmental genetics underlying somite/segment formation in chelicerates is beyond the scope of this review, but Damen, (2010) provided a valuable overview. Damen et al. (2005, and references therein) documented several genes which operate according to a so-called pair rule to create repetitive, metamerous stripes and thus contribute towards somite formation in the wandering spider *Cupiennius salei* (Keyserling, 1877). In brief, these authors recognised three distinct gene groups. The genes *even-skipped* and *runt-1* are associated with the posterior end of the growth zone, but do not reach the anterior end. *hairy* and *pairberry-3* also begin in the posterior zone, but continue into the anterior zone. Finally *odd-paired*, *odd-skipped-related-1* and *sloppy paired* are restricted to the anterior growth zone. Damen et al. (2005) further noted that, in contrast to mandibulate arthropods, the gene *fushi tarazu* appears not to be involved in somite formation in chelicerates. This is consistent with the hypothesis that chelicerates are sister group to mandibulate arthropods and that somite formation in mandibulates involves some derived gene mechanisms as compared to chelicerates. Note that Telford (2000) cloned *fushi tarazu* in mites and argued that its ancestral function was patterning the anterior–posterior axis. Only later did it shift to being a segmentation gene, presumably the derived character state, in insects like *Drosophila*.

Studies of gene distribution in other chelicerates include the sea spiders *Endeis spinosa* (Montagu, 1808) and *Nymphon gracile* Leach, 1814 (Manuel et al., 2006) as well as the spider *Tegenaria saeva* [now *Eratigena atrica* (C. L. Koch, 1843)]. Among scorpions *Euscorpius flavicaudus* (DeGeer, 1778) was studied by Simonet et al. (2006), *Mesobuthus martensi* (Karsch, 1879) by Cao et al. (2013) and Di et al. (2015), and *Centruroides sculpturatus* (Wood, 1863) by Sharma et al. (2014a); see also Sharma et al. (2015) for an overview and expansion to a wider range of scorpion taxa. There has been work on the harvestman *Phalangium opilio* Linnaeus, 1761 (Sharma et al., 2012a, b), the oribatid mite *Archegozetes longisetosus* Aoki, 1965 (e.g. Barnett and Thomas, 2012, 2013a, b) and the spider mite *Tetranychus urticae* Koch, 1836 (reviewed by Grbic et al., 2007). Results from these papers are noted below for the relevant taxa, but for the horseshoe crabs and the remaining

Table 1

Key morphological innovations in the evolution of Chelicerata, with special emphasis on segmentation, limb morphology and tagmosis. Traditional orders in bold. See text for details.

Chelicerata	Appendages of somite I become chelate
Pycnogonida	Groundplan of eleven somites or less
Pantopoda	Somites beyond VIII reduced to a stub
Euchelicera	Appendages of somite VIII–XIII plate-like
Prosomapoda	Appendages of somites II–V lose their exopods
Xiphosura	Appendage VII reduced to chilaria
Xiphosurida	Opisthosomal tergites fuse to form a thoraceton
Planaterga	Opisthosomal tergites lose their axial nodes
Dekatria	Groundplan of 13 opisthosomal somites
[†] Chasmataspida	4 + 9 tagmosis of the opisthosoma
Sclerophorata	Spermatophores; loss of exopod on appendage VI?
[†] Eurypterida	Appendages VIII + IX fuse into genital operculum
Arachnida	Unpaired gonopore on somite VIII
Scorpiones	Telson modified into a sting
Opiliones	Body reduced to 15 somites?
[†] Phalangiotarbita	Tergites VII–XII abbreviated; dorsal anal operculum
Palpigradi	Somites IX, X and XII bear ventral sacs
Pseudoscorpiones	Retractable anal cone (somite XVIII)
Solifugae	Malleoli acquired at base of appendage VI
Acariformes	Genital acertabula (absent in some groups)
Parasitiformes	[no obvious autapomorphy relating to segmentation]
Ricinulei	Cucullus; appendage IV used for sperm transfer
Panitetrapulmonata	Appendage I a clasp-knife chelicera
[†] Trigonotarbita	Somites VIII and IX with a diplotergite?
[†] Uraraenida	Somites XI and X with silk glands?
Araneae	Somites XI and X acquire spinnerets; appendage II used for sperm transfer
[†] Haptopoda	Appendage III elongate and probably tactile
Pedipalpi	Appendage II semi-raptorial, appendage III antenniform
Amblypygi	Appendage II (pedipalp) with cleaning brush
Thelyphonida	[no obvious autapomorphy relating to segmentation]
Schizomida	Male telson modified into a club-like structure

arachnid orders comparative gene data on segmentation are currently lacking.

2.3. Tagmata and pseudotagmata

In most arthropods somites are organised into clear functional units, traditionally referred to as tagmata. However, there has been some debate (reviewed by Lamsdell, 2013) as to what precisely constitutes a tagma, and whether tagmata should be defined by visible demarcations along the trunk or by functional divisions relating to the limb series. Drawing on an older concept developed by van der Hammen (1963) for mites, Lamsdell (2013, p. 4) proposed adopting the term ‘pseudotagmata’ for units defined by differentiation of the tergites or sternites without an associated change in form or function of the appendages. By contrast true tagmata would be defined as regions of functional specialization, which in arthropods is predominantly mediated through modification or suppression of the appendages. Applying this concept to Chelicerata we can argue that the prosoma and opisthosoma represent true tagmata because there is a fundamental split (Figs. 2–5) between the feeding and locomotory limbs of the prosoma and the flattened genital/gill opercula of the opisthosoma in horseshoe crabs or the largely suppressed or highly-modified appendages of the opisthosoma in arachnids. Structures such as the proterosoma, encompassing the first four somites of certain mites, would be pseudotagmata in this scheme because there is no associated change in the limb series, which continues with two further leg pairs on the next two somites (Fig. 4). As noted by Lamsdell (2013), there can, however, be notable modification of the limbs close to tagma boundaries. An example would be the small, limb-like chilaria at the front of the opisthosoma in modern horseshoe crabs (Fig. 2). Thus one of the main aims of the present paper is to highlight and document these sometimes significant zones of transition.

3. Results

3.1. Putative stem-taxa

The origins of Chelicerata remain uncertain. Older schemes deriving them from within Trilobita (e.g. Lauterbach, 1983) have largely been abandoned, and seem to rely on superficial similarities between trilobites and horseshoe crabs (critiqued by Scholtz and Edgecombe, 2006). Instead, two alternative hypotheses have emerged in recent years which recognise either the Cambrian fossil *Sanctacaris uncata* Briggs and Collins, 1988 as a *bona fide* member of Chelicerata, or several Cambrian fossils assigned to a (paraphyletic?) Megacheira group as potential stem-group chelicerates. Since this issue remains unresolved, representatives of both models are included here as comparative illustrations.

3.1.1. *Sanctacaris*†

Sanctacaris uncata (Fig. 1) from the Burgess Shale of Canada has been interpreted as a basal chelicerate on the grounds that it expresses a head shield (probably) associated with six pairs of biramous appendages, potentially positionally homologous with those of the chelicerate prosoma (somites I–VI). A pair of stalked lateral eyes are also present. The trunk (or opisthosoma) in *S. uncata* is composed of eleven somites (VII–XVIII), the first ten of which bear biramous limbs composed of a short, segmented inner ramus and a broad, lamellate outer ramus fringed with setae. The telson is wide and spatulate. However, there are inconsistencies in the literature with regards to the interpretation of the limb series. In Briggs and Collins' (1988) original description the prosoma bore six pairs of limbs, but first of these belonging to somite I was described as non-chelate. For this reason there was a reluctance to formally include *S. uncata* within Chelicerata. This is reflected in several cladistic analyses (summarised by Legg, 2014: Fig. 1) in which *S. uncata* did not resolve especially close to the chelicerates. Authors such as Budd (2002) interpreted the entire anterior limb assemblage as an

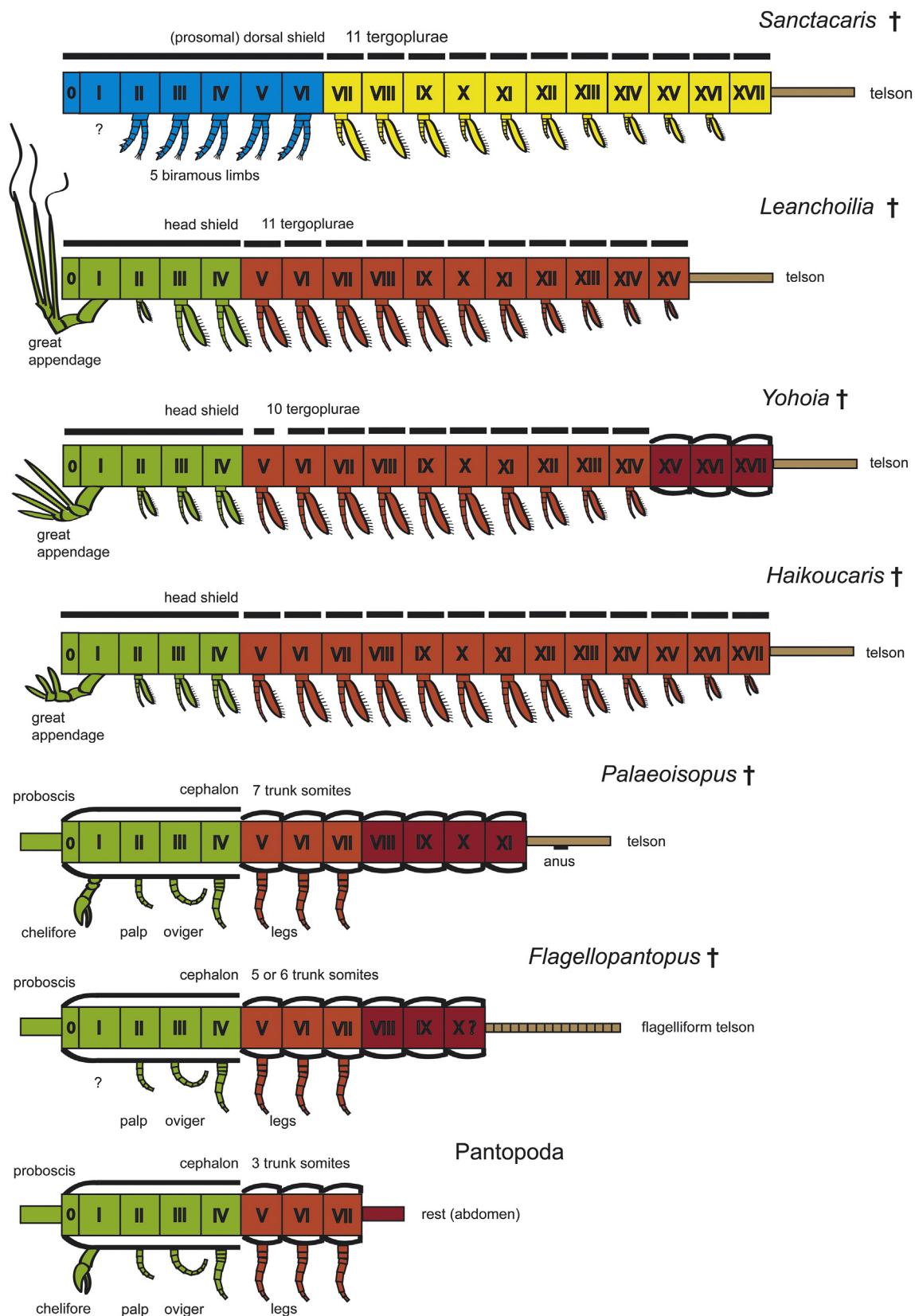


Fig. 1. Schematic model of segmentation in selected putative stem-group Chelicerata and in stem- and crown-group Pycnogonida. Somites numbered with Roman numerals. Extinct taxa indicated by a †. Blue indicates the putative prosomal region, yellow the putative opisthosoma, green the cephalon, orange trunk segments bearing appendages, red ring-like trunk segments without appendages, brown the telson. Not to scale. See text for details.

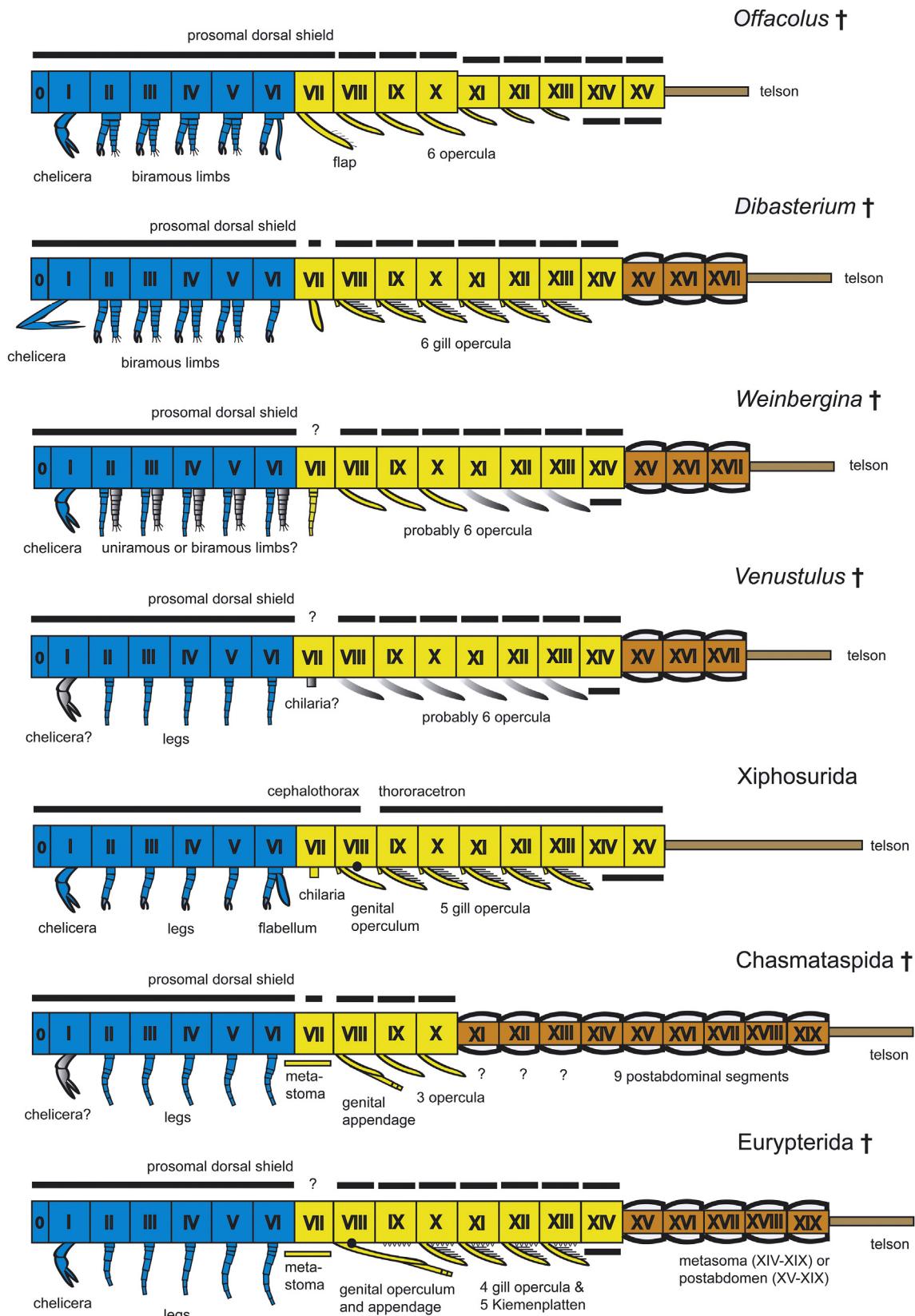


Fig. 2. Schematic model of segmentation in Euchelicerata (excluding Arachnida). Extinct taxa indicated by a †. Blue indicates the prosoma, yellow the opisthosoma, orange ring-like postabdominal segments, brown the telson; equivocal or hypothesised elements greyed out. Black circle indicates the position of the gonopore (where known). Not to scale. See text for details.

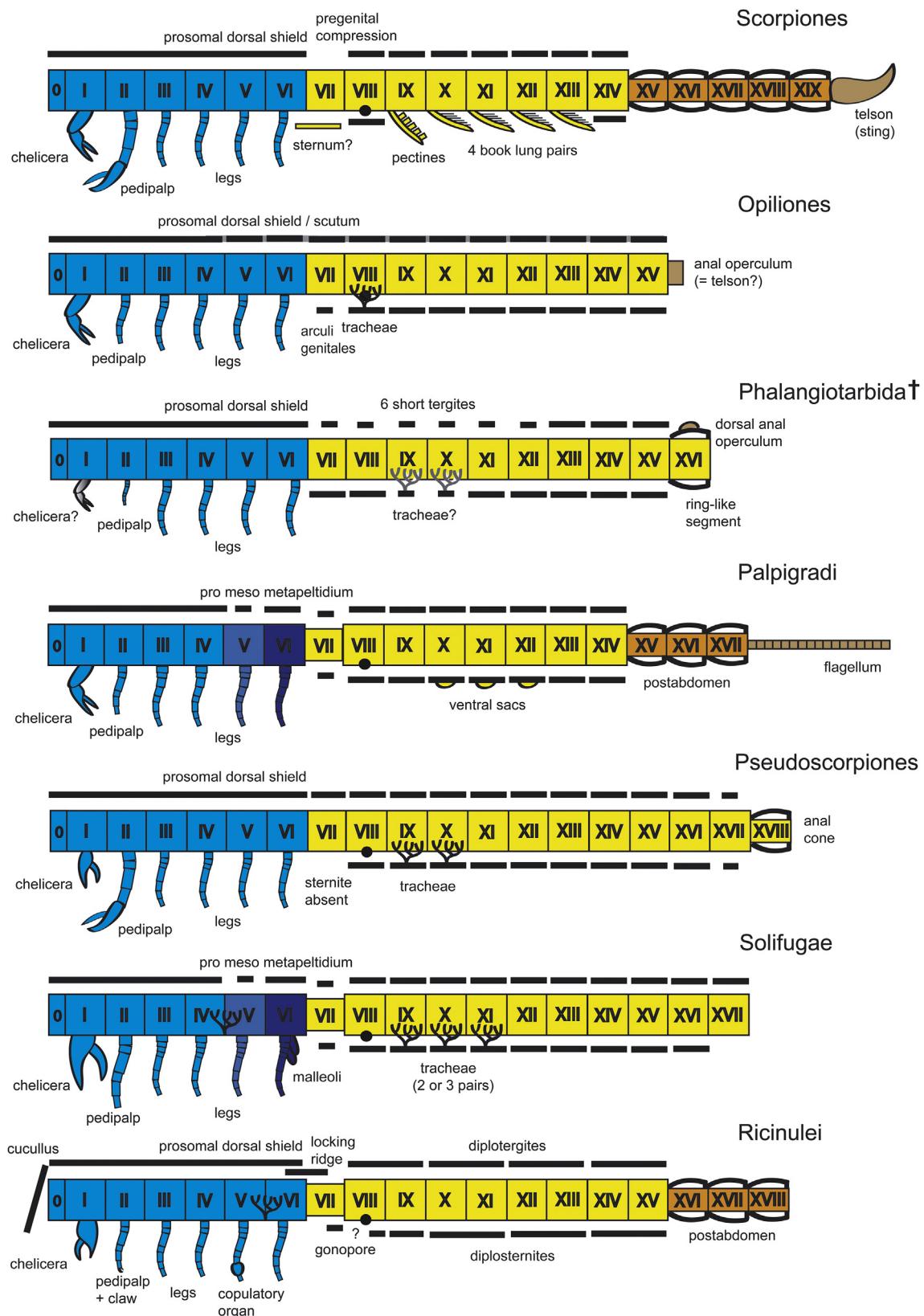


Fig. 3. Schematic model of segmentation in Arachnida: part 1. Extinct taxa indicated by a †. Colour coding as in Fig. 2, with successively darker blues where prosomal somites are associated with a separate meso- and metapeltidium. A narrow somite VII indicates a constriction between the prosoma and opisthosoma. Black circle indicates the position of the gonopore (where known). Not to scale. See text for details.

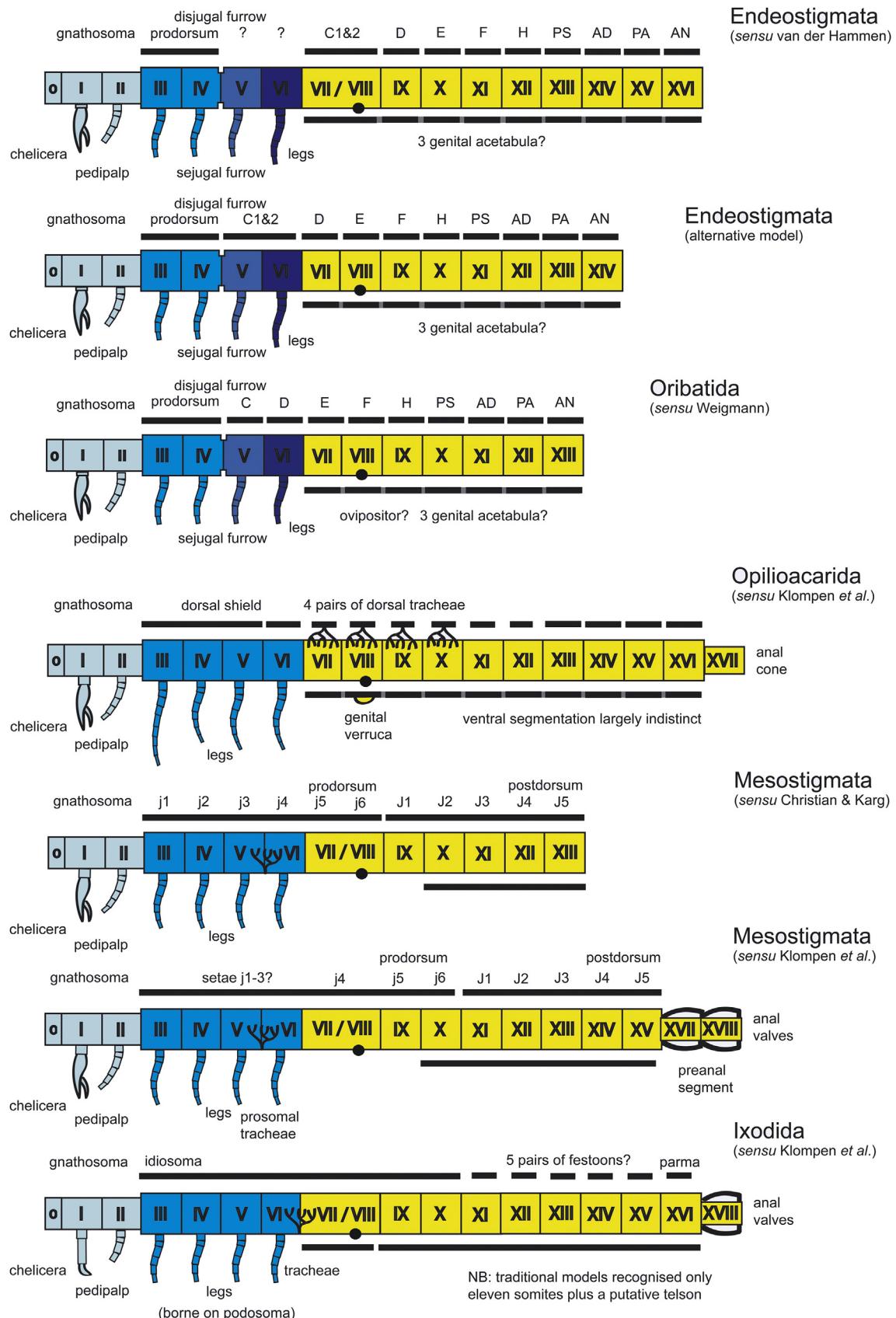


Fig. 4. Schematic model of segmentation in Arachnida: part 2. The mite clades Acariformes and Parasitiformes. Given the divergent opinions in the literature about segmentation in both clades, several alternative models are offered here for comparison. Colour coding as in Fig. 2 with light blue indicating the gnathosoma. A constriction between somites IV and V in acariform mites indicates the dorsal disjugal and ventral sejugal furrows respectively. Not to scale. See text for details.

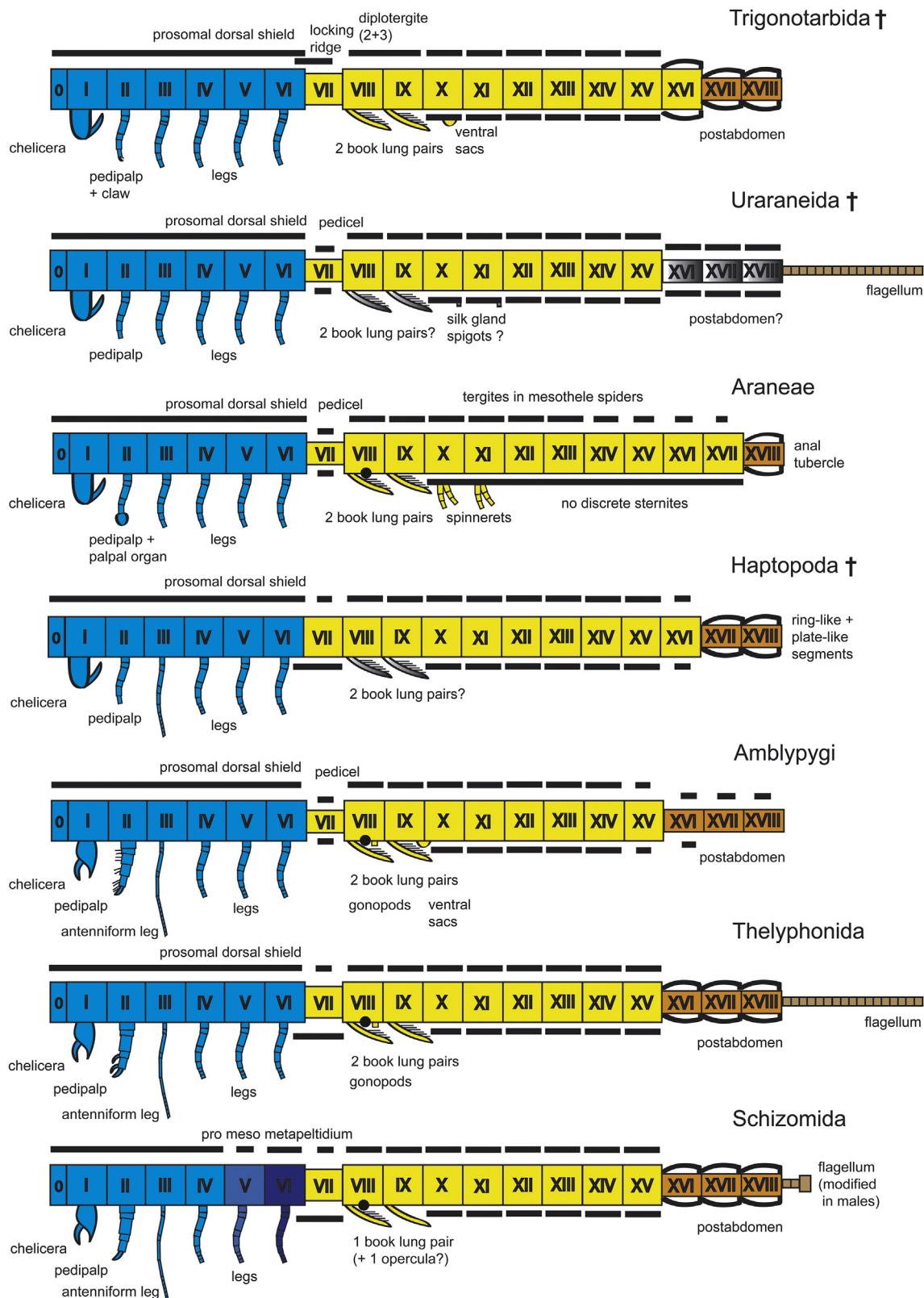


Fig. 5. Schematic model of segmentation in Arachnida: part 3. The Pantetrapulmonata, encompassing spiders and their relatives. Extinct taxa indicated by a †. Colour coding as in Figs. 2–3. Not to scale. See text for details.

expression of a single, multi-branched appendage or limb-basket. More recently, Legg (2014) rejected the limb-basket interpretation and restated the case for treating *S. uncata* as a chelicerate. Note that in Legg's revised scheme – which forms the basis for our

model – the condition of the first head appendage is unknown and the first visible appendage was thus interpreted as limb II. Prosomal limbs II–VI of *S. uncata* were interpreted as biramous, with a more pediform endopod and a more filiform exopod. The endopod of

limb II was described as having five articles; those of limbs III–VI seven. The tips of the exopods bear clusters of setae. The opisthosomal appendages are also biramous, with a short, more or less leg-like endopod of uncertain article number and a flap-like exopod fringed with setae.

3.1.2. *Megacheira*[†]

Several Cambrian fossils have been referred to as short great-appendage arthropods, or Megacheira. Some authors interpreted them as putative members of the chelicerate stem-lineage. Examples figured here (Fig. 1) are *Leancoilia superlata* Walcott, 1912 and *Yohoia tenuis* Walcott, 1912 from the Burgess Shale, plus *Haikoucaris ercaiensis* Chen et al., 2004 from the Maitianshan Shale of China. In all these animals a short head shield covers somites I–IV and is associated with four pairs of limbs and stalked lateral eyes. Key to the Megacheira/Chelicerata hypothesis is the fact that the first head limb (from somite I) is enlarged and either bears long filaments and terminates in a distal tiny claw (*L. superlata*, redescribed by Haug et al., 2012a) or is to a greater or lesser extent raptorial (*Y. tenuis*, *H. ercaiensis*). This enlarged, uniramous first head limb has been homologised with the chelicera/chelifore of the Chelicerata and interpreted as its immediate precursor. A possible scenario is that the ‘great appendage’ became shorter, compacter and more explicitly chelate (e.g. Størmer, 1944: Fig. 24; Chen et al., 2004: Fig. 5; Haug et al., 2012b: Fig. 11). This hypothesis is also supported by the presence of median eyes in megacheirans which have been shown to be homologous to the median ocelli of chelicerates (Tanaka et al., 2013); structures that appear to be absent in *Sanctacaris uncata*.

The next three head appendages in megacheirans are all biramous. Note that in *L. superlata* limb II is especially small and that Liu et al. (2016: Fig. S4) recently suggested that, at least in this species, there were four pairs of biramous head appendages behind the great appendage. Further investigations into this (and other) megacheirans could thus modify the patterns presented in Fig. 1 to include an extra head limb. Similar to *Sanctacaris uncata*, the biramous limbs in megacheirans comprise a pediform endopod. In most taxa the number of articles in the endopod is uncertain but seven (plus the basipod) have been described from *L. superlata*. Again the exopod is flap-like and fringed with setae. The same biramous limb morphology continues along the trunk, which in the examples figured here varies in length from 11 to 13 segments. In *L. superlata* and *H. ercaiensis* all the trunk segments bear tergopleurae; essentially tergites plus their lateral extensions. In *Y. tenuis* there are only 10 tergopleurae and the last three trunk segments are more ring-like and lack appendages. The body of all three figured examples here ends in a telson which can be either styiform (*L. superlata* and *H. ercaiensis*) or spatulate (*Y. tenuis*).

3.2. Chelicera

The name Chelicera, or “claw-bearer”, was introduced by Heymons (1901) and can be defined as arthropods with raptorial appendages on somite I. Traditionally the chelicerae were assumed to belong to somite II and in this scenario Chelicerata originally had, but subsequently lost, antennae on somite I. The important studies of Damen et al. (1998) and Telford and Thomas (1998), summarized by Averof (1998), revealed that the chelicerae in fact belong to the first somite and are homologous with the (first) antennae of mandibulate arthropods. Chelicerae can be fully chelate structures, as in scorpions or harvestmen, or else they resemble a clasp-knife in groups like spiders in which a moveable fang articulates against a basal element, sometimes called the pautron. Some mites show further specialisation of the mouthparts into stylet-like structures depending on their feeding ecology. Retention of three

cheliceral articles – termed the coxa, deutomerite and apotele by, e.g., Shultz (2000) – is widely accepted as the plesiomorphic character state for chelicerates. Sharma et al. (2012b) demonstrated that in harvestmen the most proximal article (the coxa) is associated with expression of the *dachshund* gene. Barnett and Thomas (2013a) provided evidence that acariform mites also retain three cheliceral articles, although only two are clearly visible externally, again with *dachshund* expression in the most proximal article. At least in spiders, *dachshund* suppression correlates with the reduction to only two articles: in this scenario the deutomerite/pautron and the apotele. Further comparative data are needed to test whether all arachnids with only two cheliceral articles utilise the same developmental mechanism.

In the original concept Chelicerata did not include Pycnogonida. The position of the sea spiders has long proved controversial: as either basal chelicerates or basal arthropods (reviewed by Dunlop and Arango, 2005). Most authors now treat sea spiders as chelicerates based partly on the presumed homology between the chelifores of Pycnogonida and the chelicerae of Euchelicerata. Both appear to be uniramous, chelate appendages associated with the deutocerebrum; a result supported by gene distribution (Manuel et al., 2006) and neuroanatomy (Brenneis et al., 2008). Molecular data have also supported chelicerate affinities for sea spiders (e.g. Regier et al., 2010; Campbell et al., 2011).

3.3. Pycnogonida

Comparisons between Pycnogonida and the remaining Euchelicerata are hampered by the unusual morphology of the sea spiders. It is important to recognise from the outset that the four walking legs in sea spiders (on somites IV–VII) do not belong to the same somites (III–VI) as the four walking legs of arachnids (Figs. 1, 3–5). Pycnogonids have undergone several reductive trends, such that the trunk behind the legs in modern taxa is reduced to a vestigial posterior element while the gut and reproductive organs have become partially displaced into the legs. Extinct taxa offer a better guide to the pycnogonid groundplan, expressing a longer trunk behind the last pair of walking legs and retaining the telson. For this reason we figure the body plans of two Devonian fossils, as well as a living representative belonging to the crown-group which is often referred to in the literature as Pantopoda (Fig. 1). It is also important to stress that some extant (and fossil) taxa have further lost the chelicerae, pedipalps and/or ovigers. Furthermore, as noted above a handful of recent genera have either ten or twelve legs rather than the usual eight. Why they have these extra limbs and how this relates to the basic segmentation and groundplan of the sea spiders remains uncertain.

3.3.1. *Palaeoisopus*[†]

The remarkable Hunsrück Slate fossil *Palaeoisopus problematicus* Broili, 1928 is clearly a pycnogonid, but differs significantly from living species. The schematic model presented here (Fig. 1) is based on the redescription of Bergström et al. (1980) and the comparative figure of Villpoux and Waloszek (2003). Anteriorly *Palaeoisopus*, like all other sea spiders, has a cephalosoma. This tube-like body tagma bears the proboscis and the eye tubercle with four eyes. This proboscis appears to be a unique apomorphy of the sea spiders and cannot be easily matched to any particular anterior somite. It is constructed from three antimeres (e.g. Winter, 1980), but attempts to homologise all or part of the proboscis anatomy with the labrum of other arthropods and/or elements of the anterior limbs have been rejected on embryological grounds (Brenneis et al., 2011).

The cephalosoma represents the first four somites and is associated with the chelicerae (limb I), palps (limb II), egg-carrying ovigers (limb III) and the first pair of walking legs (limb IV). This

is followed by three trunk segments (somites V–VII) each associated with further pairs of legs. Beyond this, there are four additional ring-like trunk segments (somites VIII–XI) without appendages. The body terminates in a styliform telson; whereby it is interesting to note that in *Palaeoisopus* the anus opens midway along the telson (Fig. 1), and not at the base of the telson as in euhelicerates. The chelicerae in *Palaeoisopus* have been interpreted as having had five articles (Bergström et al., 1980) and thus to some extent bridge the gap between the megacheiran condition (3.1.2) and the three cheliceral articles of euhelicerates (3.4).

3.3.2. *Flagellopantopus*[†]

In the contemporary Hunsrück sea spider *Flagellopantopus blocki* Poschmann and Dunlop, 2006 there is an obvious trend for the trunk behind the last pair of legs to become shorter and more compact (Poschmann and Dunlop, 2006). Chelicerae in *F. blocki* are either not preserved or are genuinely absent (Fig. 1). As in *P. problematicus* the cephalon of *F. blocki* bears the palps (limb II), ovigers (limb III) and first pair of legs (limb IV). The first three trunk segments (somites V–VII) bear the remaining three pairs of legs. These are followed by two or three short, limbless ring-like segments (somites VIII–?X). The terminal telson is not styliform. Instead it is elongate and flagelliform, and hints at a high diversity of body plans among the Devonian sea spiders compared to living species; none of which retain a telson.

3.3.3. *Pantopoda*

The crown-group Pantopoda are similar to the two previous fossil examples in possessing a cephalosoma (somites I–IV) bearing the chelicerae, pedipalps, ovigers and first pair of walking legs; followed by three more leg-bearing trunk somites (V–VII). As noted above, Pantopoda show the most extreme reduction of the trunk to a small, vestigial element behind the last pair of walking legs. None of the extant species retain a telson. The chelicerae are usually reduced to three articles, but four have been recorded in the literature (Helper and Schlotte, 1935: Fig. 22) and, as noted above, in several living genera the chelicerae have become further reduced or lost completely.

3.4. Euhelicerata

The name Euhelicerata was introduced by Weygoldt and Paulus (1979) and defined as chelicerates possessing plate-like opisthosomal appendages. These are clearly seen in, for example, the genital and gill opercula of horseshoe crabs and eurypterids. They are also seen, albeit in a modified form, in the sclerites covering the book-lungs of arachnids. In an important study of skeleto-muscular anatomy, Shultz (1993) demonstrated that what were traditionally called opisthosomal sternites 2 and 3 in whip scorpions (Thelyphonida) are actually the modified appendages (or opercula) bearing the lungs. These opercula cover the highly reduced true sternites of somites VIII and IX respectively, which can still be identified based on the attachment sites of dorso–ventral muscles.

In its traditional sense, Euhelicerata encompassed the horseshoe crabs, eurypterids and arachnids. Recently, several fossil taxa have been resolved towards the base of this clade, thereby resolving as part of the euhelicerate stem lineage. These include two Silurian examples which still retained biramous limbs on the postcheliceral prosomal appendages.

3.4.1. *Offacolus*[†]

Offacolus kingi Orr et al., 2000 is an interesting fossil from the Silurian Herefordshire Lagerstätte of England (Fig. 2). In overall appearance it resembles a small – less than 5 mm long – eyeless horseshoe crab with a somewhat truncated opisthosoma. Its

detailed three-dimensional morphology was reconstructed by Sutton et al. (2002) by grinding away the matrix and imaging the fossil along successive slice planes. *O. kingi* has a prosomal dorsal shield, albeit associated with somites I–VII (i.e. one more than in arachnids). Sutton et al. thus reported seven pairs of prosomal appendages. The appendages of somite I are a uniramous pair of chelicera. Significantly, the appendages of somites II–V are biramous. The endopod is pediform and ends in a terminal claw; the exopod is also essentially pediform, but terminates in a brush of setae. The appendage of somite VI has a similar endopod, but here the exopod is tendril-shaped. The appendages of somite VII are uniramous and form a pair of flap-like structures bearing several marginal setae. Sutton et al. tentatively homologised the tendril on somite VI with the flabellum of modern horseshoe crabs and the flap-like appendages on somite VII with the chilaria (see below). The opisthosoma of *O. kingi* is divided into a mesosoma of three somites (VIII–X) and a metasoma of five somites (XI–XV). All three mesosomal somites and the first three metasomal somites bear flap-like opercula: the euhelicerate synapomorphy. Sutton et al. homologised these six opercula in *O. kingi* with the genital operculum plus five gill opercula of living horseshoe crabs; although actual gills could not be unequivocally resolved in the fossil. The opisthosoma of *O. kingi* terminates in a styliform telson potentially with a distal bifurcation.

3.4.2. *Dibasterium*[†]

The Herefordshire Lagerstätte has also yielded *Dibasterium durgae* Briggs et al., 2012 which was reconstructed from serial slices using the same methodology as above. Again this ca. 23 mm long fossil looks like a small horseshoe crab and was formally described within Xiphosura. According to Briggs et al. (2012) the prosomal dorsal shield of *D. durgae* lacks any evidence for eyes and appears to be associated with somites I–VI. The appendages of somite I are a uniramous pair of chelicerae. They are unusually long in this fossil and curve back under much of the prosoma. As in *O. kingi*, the appendages of somites II–V are biramous. Both the endo- and exopod are largely pediform; the endopods terminating in a claw and the exopods in three spines. Note that Briggs et al. argued that the endo- and exopod in both *D. durgae* and *O. kingi* were separated at the base, and speculated that this positional separation of the limb bases represented a stage towards the loss of the biramous limb. The appendages of somite VI are apparently uniramous – which is in contrast to the presence of a flabellum in modern horseshoe crabs – and non-chelate. The opisthosoma consists of eleven somites (VII–XVII). The first tergite of somite VII is narrow and partly concealed under the prosomal dorsal shield. The appendages of somite VII are relatively small and flap like; somewhat similar to the chilaria of horseshoe crabs. Opisthosomal somites VII–XIV constitute a preabdomen, and the tergites of XIII–XIV have marginal spines or pleurae. Somites VIII–XIII bear gill opercula, whereby in *D. durgae* the lamellate nature of the book gills can be resolved. Interestingly, the operculum of somite VIII apparently retains a gill. In modern horseshoe crabs this is the genital operculum and the associated respiratory organs have been lost. The last pre-abdominal somite (XVII) lacks appendages. Somites XV–XVII are more ring-like, lack plurae and form a small postabdomen. The opisthosoma terminates in a styliform telson with a possible distal bifurcation.

3.5. Prosomapoda

The name Prosomapoda was introduced by Lamsdell (2013) and defined as Euhelicerata in which prosomal appendages II–V lack

exopods in the adult instar. Thus by this grade of organisation the fully-developed prosomal exopods seen in fossils such as *O. kingi* and *D. durgae* have been lost. Exopods are retained as the flabellum on limb VI of modern horseshoe crabs (see also 3.6.1). The basal part of the Prosomapoda clade encompasses several taxa traditionally referred to as synziphosurines. These animals were treated by, e.g., Anderson and Selden (1997) as a stem-lineage towards the modern horseshoe crabs. Lamsdell (2013) proposed that synziphosurines in fact comprise a paraphyletic assemblage of early euhelicerates; some closer to horseshoe crabs and others to the lineage leading towards eurypterids and arachnids. As noted by Briggs et al. (2012) most synziphosurines are only known from their dorsal anatomy, which can make placing them correctly difficult. Two fossils in which appendages are known are included here as comparative examples.

3.5.1. *Weinbergina*[†]

Weinbergina opitzi (Fig. 2) from the Devonian Hunsrück Slate of Germany is an important species, fossils of which reveal the underside of the body and its appendages. Detailed redescriptions were offered by Stürmer and Bergström (1981) and Moore et al. (2005a). *W. opitzi* may have 17 somites, dorsally with a clear 6 + 11? division into a putative prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). There is no evidence for any eyes. Limb I is small and has been interpreted as the chelicera, but details are lacking. Significantly, *W. opitzi* has six additional pairs of legs corresponding to somites II–VII. In other words, the limb belonging to somite VII is a fully developed leg, similar to the condition in sea spiders (see 3.3.), and is not a reduced element like the chilaria on this somite in modern horseshoe crabs (see 3.6.1). None of these legs were demonstrably biramous in the available descriptions, and Moore et al. (2005a) also commented on the fact that the podomere count of the legs was more like the eurypterid/arachnid condition than the legs of modern horseshoe crabs. It should, however, be noted that Selden et al. (2015) suggested that the limbs of *Weinbergina* may in fact be biramous; referring to several published figures in support of this interpretation. Further study of the available specimens of *Weinbergina* is needed to ascertain the veracity of these suggestions, however if they are accurate this would suggest that *Weinbergina* has a closer relationship to *Offacolus* and *Dibasterium* than to Prosomapoda, and would be considered a derivative of the euhelicerate stem lineage. This scheme may also result in the apparent limb of somite VII instead being the uniramous limb of somite VI.

The opisthosoma of *W. opitzi* reveals 10 segments, but there is debate in the literature about whether an additional microtergite – corresponding to somite VII – was present. Moore et al. (2005a) found no evidence for a microtergite but conceded that somite VII is either not expressed dorsally or corresponds to the (large) first tergite. We have assumed here that there was an element in front of the first visible opisthosomal tergite which is not clearly expressed, as this brings the distribution of the ventral opercula in line with both modern horseshoe crabs and with other basal euhelicerates (Fig. 2). Ventrally, in *W. opitzi* at least three pairs of opercula can be recognised (Moore et al., 2005a) and while some striations are implicit of the lamellae of book gills it is difficult to match operculae unequivocally to somites. For this reason we cannot say, for example, whether the opercula revealed evidence of biramy, or if gills were present on somite VIII given that they are lost here in modern horseshoe crabs. Stürmer and Bergström's (1981: Fig. 3) reconstruction included a total of six pairs of opercula; an interpretation we follow here. They further interpreted the last three segments as ring-like forming a weakly off-set postabdomen. The opisthosoma ends in a short, styliform telson.

3.5.2. *Venustulus*[†]

A similar synziphosurine fossil preserving appendages, albeit perhaps expressing a more derived grade of organisation, is *Venustulus waukeshaensis* Moore et al., 2005 from the Silurian Waukesha Lagerstätte of the USA. Described in detail by Moore et al. (2005b) the body may have 17 somites, dorsally with a clear 6 + 11? division into a prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). There is no evidence for any eyes. Limb I appears to be the chelicera and is followed by limbs II–VI. Thus in contrast to the condition in *Weinbergina opitzi* there is no walking leg on somite VII, although neither is there any obvious evidence for the transformation of these limbs into chilaria as in modern horseshoe crabs. The opisthosoma expresses 10 segments, but again it is not clear if there was originally a microtergite and/or if this has already been incorporated into the prosomal dorsal shield (see 3.6.1). As with *W. opitzi*, assuming a suppressed somite VII brings the body plan into line with several other taxa and has been tentatively assumed in Fig. 2 here. The nature of any opisthosomal opercula is equivocal. The last three segments are ring-like, forming a postabdomen. The opisthosoma ends in a short, styliform telson.

3.6. Xiphosura

In Lamsdell's (2013) scheme the true horseshoe crabs (as Xiphosura) are more restricted in scope and were redefined as euhelicerates with a partially reduced tergite of somite VII (sometimes called the microtergite), appendages of somite VII reduced to chilaria, an opisthosoma broadest anteriorly, a cardiac lobe extending onto the anterior half of the prosomal dorsal shield and ophthalmic ridges which merge anteriorly with median ridge to form double arch. Note, however, the debates above about whether some basal euhelicerates also had a short tergite VII or microtergite.

3.6.1. Xiphosurida

Within this wider Xiphosura clade the derived horseshoe crabs (Xiphosurida), which includes the four living species, are further defined by the fusion of the dorsal tergites into a single, rigid plate. Its evolution, and criteria for recognising it in fossils, was discussed in detail by Anderson and Selden (1997). Classic accounts of modern horseshoe crab morphology include Lankester (1881), as well as more recent studies such as Shultz (2001) and Mittmann and Scholtz (2003). The latter authors confirmed, morphologically, the hypothesis that the chelicerae belong to the first somite, not the second as had been traditionally assumed (see 3.2). An important contribution towards understanding horseshoe crab segmentation was the embryological study of Scholl (1977), who showed that in modern horseshoe crabs the first opisthosomal tergite (somite VII) and the medial tergal elements of the second segment (somite VIII) are integrated into the dorsal shield; see also Shultz (2001). Again, to what extent this applies to fossil horseshoe crabs is difficult to test empirically, but the possibility of a similar fusion should be borne in mind when interpreting segmentation in extinct taxa.

Xiphosurids thus have at least 15 somites (Fig. 2), the anterior ones belonging to what Shultz (2001) termed a cephalothorax. This consists of the prosomal dorsal shield covering somites I–VI, plus the additional dorsal elements from somites VII and (in part) somite VIII. The cephalothorax bears median ocelli and compound lateral eyes, including also several vestigial eyes detailed by Batelle (2006). Limb I is a chelate chelicera with three articles; limbs II–VI act as legs. In mature males of *Limulus* limb II is modified into a clasper which is used to hold onto the female during mating; in *Tachypleus* and *Carcinoscorpius* limb III is a clasper too. Limbs II–V are subchelate or chelate at the tip: the exact pattern depends on

the genus. Limb VI is modified into a pusher which can splay out at the tip and provides greater purchase on the substrate. Limb VI is also biramous, with a small projection from the coxa (an exopod) usually referred to as the flabellum or epipodite. Between the coxae there is a small postoral sclerotized element, the endostoma (Shultz, 2001: Fig. 2), which could be homologous to the arachnid labium and/or sternum. The ventral appendages of somite VII are present as a small pair of limb-like projections called chilaria. Like the dorsal expression of this somite, these ventral elements are functionally part of the cephalothorax and create a water current for moving food along the adjacent gnathobases of the leg coxae.

Dorsally the opisthosoma presents a solid plate, which is usually called the thoracetron or tergum (Shultz, 2001). Patterns of muscle apophyses indicate that the thoracetron includes seven somites (VIII–XIV), with internal evidence in terms of a further muscle attachment site for at least somite XV too. Whether somites beyond XV are part of the thoracetron too is difficult to assess from the available morphology (see also Shultz, 2001: Fig. 3B). Ventrally, somites VIII–XIII all bear opercula. That of somite VIII is the genital operculum. It bears paired gonopores, but lacks respiratory organs. The next five (somites IX–XIII) are gill opercula bearing lamellate book gills. The opercula are all effectively biramous (see e.g. Legg, 2014: Fig. 4). The putative endopod is a small finger-like projection on the median side, albeit absent on the genital opercula of the subfamily Tachypleinae. The exopod bears the gills on the relevant somites. The opisthosoma terminates in a long styliform telson, often referred to as the tail spine.

3.7. Planaterga

The name Planaterga was introduced by Lamsdell (2013) and defined as euhelicerates which lack axial nodes on their opisthosomal segments. In other words the tergites covering the dorsal surface are usually smooth and the raised nodes seen in, for example, horseshoe crabs are absent (although a number of taxa reverse this condition). This grade of organisation encompasses several former synziphosurine taxa, as well as the chasmataspidids, eurypterids and arachnids, essentially representing Dekatriata and the paraphyletic grade leading to it.

3.8. Dekatriata

The name Dekatriata was introduced by Lamsdell (2013) and defined as euhelicerates having, at least in their ground pattern, an opisthosoma with 13 segments. This condition can be recognised in chasmataspidids, eurypterids and scorpions. However, we should note that all other arachnid orders have, in this scenario, reduced their counts to 12 or less (see below). Recently, Lamsdell et al. (2015b) described an intriguing fossil, *Winneshiekia youngae* Lamsdell et al., 2015, from the Ordovician Winneshiek Lagerstätte of the USA as a member of the Dekatriata clade. It preserves a combination of xiphosuran-like features, such as a semicircular head shield with ophthalmic ridges, together with a 13-segmented opisthosoma. Limbs are, unfortunately, unknown; thus it is not included in the comparative figures here.

3.8.1. Chasmataspida[†]

Chasmataspidids (Chasmataspida) are a rare group of ? Cambrian–Devonian euhelicerates, some of which were originally interpreted as unusual horseshoe crabs. A summary can be found in Marshall et al. (2014). Of the eleven known species, the Ordovician *Chasmataspis laurencii* Caster and Brooks, 1956 (family Chasmataspidae) expresses a horseshoe crab-like head shield complete with genal spines (Dunlop et al., 2004). Younger fossils (family Diploaspidae) tend to be more eurypterid-like in

appearance, in some cases with a genital appendage and metastoma plate covering the coxal region (Dunlop, 2002; Tetlie and Braddy, 2004). This divergent morphology led some authors to question the group's monophyly (Tetlie and Braddy, 2004; Shultz, 2007a). Despite this, Chasmataspida can potentially be defined on an obvious tagmosis apomorphy (Marshall et al., 2014), namely somite VII retained as a dorsally visible microtergite; tergites of somites VII–X forming a preabdomen and somites XI–XIX forming a long postabdomen. This 4 + 9 tagmosis of the opisthosoma is unique among chelicerates. Note that none of the species described to date have a complete limb series, thus the description below is something of a composite from the better-known taxa.

Chasmataspidids have 19 somites (Fig. 2) with a clear 6 + 13 division into a prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). This bears both median ocelli and (probably compound) lateral eyes. Limb I is equivocal but presumed to have been a chelate chelicera. Limbs II–VI form the legs, whereby limb VI of most diploaspidid genera is modified into a swimming paddle. A disarticulated limb of *Chasmataspis laurencii* appears to be biramous (Dunlop et al., 2004: Figs. 5–6) with a projection similar to the flabellum on limb VI of horseshoe crabs (see 3.6.1), but it is unclear whether this is typical of all taxa and/or all appendages in the limb series. The chasmataspidid opisthosoma has 13 somites. Tergite 1 (somite VII) is short and ventrally there is a plate-like metastoma presumed to be the modified appendages of this same somite. The tergites of somites VIII–X are fused into a buckler in *C. laurencii*, but seem to be separate from one another in younger fossils. Ventrally there are three opercula corresponding to somites VIII–X; VIII bears the genital appendage alluded to above. The presence of gills on one or more of these opercula is equivocal. Intriguingly, there are Cambrian resting traces of a Chasmataspis-like animal (Dunlop et al., 2004, Figs. 9–10) which seem to show at least three further small opercula apparently on the first three postabdominal segments (i.e. somites XI–XIII). This would yield a total of six opercula, as per the genital operculum and five gill opercula of horseshoe crabs. The opisthosoma in chasmataspidids terminates in a styliform or spatulate telson which is usually quite short in diploaspidids.

3.9. Sclerophorata

The name Sclerophorata was introduced by Kamenz et al. (2011) for Eurypterida and Arachnida and defined as euhelicerates which transfer sperm via a spermatophore, as opposed to just releasing their sperm into the water as per horseshoe crabs. Note that several arachnids – e.g. spiders, ricinuleids, most harvestmen, and some mites – have taken this a stage further and use direct methods of insemination. The likely mode of sperm transfer in eurypterids was revealed thanks to some exceptionally preserved fossils showing a 'horn organ' in the genital region (e.g. Holm 1898: pl. 3, Fig. 24–25) which was interpreted by Kamenz et al. (2011) as a sclerotized precursor to a spermatophore. The mode of sperm transfer in chasmataspidids is unknown although as noted above at least some taxa also have a eurypterid-like genital appendage (see 3.8.1), albeit without obvious horn organs. It is thus conceivable that Sclerophorata could be equivalent to Dekatriata. The name Sclerophorata is also largely equivalent to the Metastomata clade of Weygoldt and Paulus (1979). Their defining character of a plate-like metastoma on somite VII may have a homologue in the scorpion sternum (see 3.10), but is not demonstrably present in other arachnids; hence the proposed name change to Sclerophorata.

3.9.1. Eurypterida[†]

Eurypterids were an Ordovician–Permian group with around 250 described species. They exhibited a range of body plans and some grew to more than 2 m long. Traditionally, eurypterids could be defined by the presence of a genital appendage on the underside of the opisthosoma and a plate-like metastoma on somite VII. Like the chilaria of living horseshoe crabs, the eurypterid metastoma was apparently functionally integrated into the prosoma, covering the posterior gnathobases of the prosomal limbs. The discovery of both a genital appendage and a metastoma in chasmataspids (see 3.8.1) undermined these traditional defining characters. Lamsdell (2013) thus redefined Eurypterida on the apomorphy of a genital operculum which appears to be derived from two elements; the modified appendages of somites VIII and IX respectively. An additional potential autapomorphy is the possession of enlarged, robust coxal teeth on limb VI (JCL, pers. obs.). Eurypterid morphology has been studied in detail by, e.g., Holm (1898) and Selden (1981).

Eurypterids apparently have 19 somites – the Dekatriata synapomorphy – with a clear 6 + 13 division into a prosoma and opisthosoma (Fig. 2). Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). This bore both median ocelli and compound lateral eyes. Limb I is a chelate chelicera with three articles. Limbs II–VI act as legs whereby some taxa show modifications of the posterior limbs into swimming paddles. Similar to modern horseshoe crabs, there is a small endostoma (Selden, 1981: Fig. 2), between the leg coxae which could be homologous with the labium and/or sternum of arachnids. The eurypterid opisthosoma has 13 somites, but only 12 segments can be clearly recognised. Whether the first tergite is expressed is a contentious issue. Dunlop and Webster (1999: Figs. 2–3) offered evidence that it may be retained as a weakly sclerotized region in a fold behind the prosomal dorsal shield and further specimens may also provide evidence for this tergite (JCL, pers. obs. on a *Buffalopterus* from the Peabody Museum), however Haug et al. (2012c) suggested that valley folds may be secondarily sclerotized and not represent true tergites. The unusual mycteroptid eurypterids fuse the tergite of somite VIII to the back of the prosomal dorsal shield. Tagmosis within the opisthosoma can be a source of confusion. As summarised by Lamsdell (2011), some eurypterids have a rather scorpion-like habitus in which the last five opisthosomal segments are noticeably narrower. Several authors thus divided the opisthosoma into a seven-segmented preabdomen (somites VIII–XIV) and a narrower five-segmented postabdomen (somites XV–XIX). However, in other eurypterids the opisthosoma tapers smoothly towards the back and the point of pre- and postabdominal contraction is ambiguous. Lamsdell (2011) preferred a more natural division into a six-segmented mesosoma (somites VIII–XIII), all of which retain ventral opercula, and a six-segmented metasoma (somites XIV–XIX) on which appendages are completely lacking.

As noted above, somite VII bore the metastomal plate, interpreted as highly modified and fused appendages. Somites VIII–IX were covered ventrally by a single large genital operculum which bore a median abdominal (or genital) appendage associated with the paired gonopores. Four more plate-like appendages occupy somites X–XIV. These opercula are sometimes referred to as Plattfüße: literally ‘plate-feet’. Braddy et al. (1999) offered evidence that there were four pairs of lamellate respiratory organs, presumably also belonging to somites X–XIV. In addition to these presumptive book gills, eurypterids have five pairs of gill tracts; oval areas of spongy cuticle with downward-hanging spines on the underside of somites IX–XIV which have been interpreted as having a respiratory function too (reviewed by Manning and Dunlop, 1995). As noted above, the metasoma lacks appendages and the opisthosoma terminates in a telson. This is usually styiform, but can be spatulate in some genera.

3.10. Arachnida

Arachnids are, by some measure, the most diverse chelicerates today with more than 100,000 described living species and perhaps up to a million based on estimates of the number of undescribed mites (Krantz and Walter, 2009). Historically, there has been debate about whether they are monophyletic; in particular whether scorpions might be more closely related to eurypterids than to other arachnids (e.g. Braddy et al., 1999). Cladistic analyses usually recovered a monophyletic Arachnida (Weygoldt and Paulus, 1979; Shultz, 2007a; Pepato et al., 2010; Regier et al., 2010; Garwood and Dunlop, 2014a; Sharma et al., 2014b), although a stable phylogeny based on morphological and/or molecular data has not been forthcoming. Most arachnids are terrestrial and caution is needed to tease out potential autapomorphies for the group from homoplastic response to life on land. For example tracheal systems for terrestrial respiration appear to have arisen on multiple occasions, with spiracles opening on different somites in different arachnid taxa (Figs. 3–5). In terms of defining apomorphies, arachnids can potentially be characterised by a (1) reduced head shield lacking a cardiac lobe, (2) an anteroventrally directed mouth with no proventricular crop, (3) a single genital opening rather than a pair of openings, and (4), at least in adult instars, loss of appendages on the first opisthosomal segment (somite VII).

However, the last point has to be qualified by noting that there is embryological evidence for a transitory pair of appendages on segment VII of scorpions (see 3.10.1), and there is also a hypothesis that the scorpion sternum could be homologous with the eurypterid metastoma (Jeram, 1998: p. 27). Observations on scorpion development by Farley (2005) further suggested that the scorpion sternum is derived from both the first opisthosomal segment – although it is unclear whether this is from the limb buds or from the sternite – as well as medial, bilateral lobes derived from coxae of the third and fourth walking legs.

3.10.1. Scorpiones

Scorpions (Scorpiones) were often treated as sister group to all other arachnids (e.g. Weygoldt and Paulus, 1979), perhaps in part due to their resemblance to eurypterids. Alternatively they have been grouped close to harvestmen (Shultz, 2000) or with the other lung-bearing arachnids (Sharma et al., 2014b). Details of scorpion morphology can be found in, e.g., Shultz (2007b). A long-standing debate has been whether scorpions have twelve or thirteen opisthosomal segments. Twelve are clearly visible externally, but early work by Brauer (1895) observed the transitory pair of pregenital appendages in scorpion embryos noted above. This observation forces the recognition of an additional opisthosomal somite, although authors such as Weygoldt and Paulus (1979) suggested that the pectines could belong to the genital somite, which would return the total count to twelve. The gene expression data of Simonnet et al. (2006) confirmed both the presence of a pregenital somite (VII), and that the pectines belong to a separate, postgenital, somite (IX). An opisthosoma with thirteen somites was also documented morphologically by Shultz (2007b), who proposed a pregenital compression hypothesis in which somite VII became longitudinally shortened and in which the muscles of somites VII and VIII have been brought into close proximity to one another to form a diaphragm which largely separates the scorpion prosoma internally from the opisthosoma. In some respects this is similar to the pedicel of spiders and their relatives in which there is an external constriction between the two main body tagmata; in scorpions it is an internal constriction.

Scorpions thus have 19 somites – the groundplan for Dekatriata – with a clear 6 + 13 division into a prosoma and opisthosoma (Fig. 3). Similar to the eurypterid condition, somite VII is poorly

expressed externally such that 12 opisthosomal segments can be seen. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). Scorpions have a pair of median eyes and groups of lateral eyes with up to five lenses. Note that some extinct scorpions retained fully compound lateral eyes with more than 30 lenses. Limb I is a chelate chelicera, limb II forms the chelate pedipalps and limbs III–VI act as walking legs. Unlike other arachnids with a sternum, the scorpion sternum (see above) sits behind – rather than between – the leg coxae which further supports the idea that these sterna are not homologous. However scorpions also have a tiny and thus often overlooked anterior postoral sclerite (Shultz, 2007b) between the leg coxae, which could potentially be homologous with the endostoma of eurypterids and horseshoe crabs and/or sternum of other arachnids.

The opisthosoma has thirteen somites. As noted above, the first is not expressed dorsally and is only seen ventrally as embryonic appendages, which may or may not eventually form the sternum. The opisthosoma is divided into a mesosoma (somites VII–XIV) and a metasoma (somites XV–XIX). Somite IX bears the pectines; somites X–XIII bear the four pairs of book lungs. Based on what we know about tetrapulmonate arachnids (Shultz 1993) the sclerites covering these book lungs may also be highly modified appendages and fossil scorpions are also typically described as having opisthosomal opercula (e.g. Jeram, 1998). There is considerable debate in the literature about whether these somites in early fossil scorpions bore lungs or gills (see e.g. Dunlop et al., 2008). Compared to the opisthosomas of other arachnids, there is a very marked differentiation in both structure and function between the mesosoma of scorpions and the more slender metasoma. The mesosoma contains various internal organs while the segments of the metasoma are ring-like and form a highly maneuverable tail allowing the animal to sting its prey. Sharma et al. (2014a, 2015) proposed the duplication of a specific set of Hox genes – specifically the neofunctionalization of several Hox paralogs – as a mechanism by which this differentiation may have been achieved. Finally, the telson is uniquely modified into a sting, composed of a more rounded vesicle and sharply tapering aculeus. The vesicle contains a pair of venom glands which open near the tip of the aculeus.

3.10.2. Opiliones

Harvestman (Opiliones) external anatomy has been studied by, e.g., Hansen and Sørensen (1904) and more recently by Shultz (2000) and Shultz & Pinto-da Rocha (2007). Harvestmen are traditionally interpreted as having sixteen somites; although in the scheme of Shultz (2000) the anal operculum was homologised with the telson of other arachnids in that it is a single postanal plate without division into tergites and sternites. The Hox gene data of Sharma et al. (2012a: Fig. 9) also recognised fifteen somites and this is the count adopted here in the present review. Harvestmen express a range of dorsal fusion patterns (see below) which makes it difficult to select a ‘typical’ segmental morphology for the group. Opiliones (Fig. 3) thus have 15 somites with a clear 6 + 9 division into a broadly joined prosoma and opisthosoma. Somites I–VI are usually covered by a unitary prosomal dorsal shield (or carapace), although in some taxa the posterior two somites (V and VI) may be differentiated with separate tergites. The dorsal shield can bear lateral eyes (some cyphophthalmids) or median eyes in the three suborders making up the Phalangida clade. The extinct suborder Tetrophthalmi shows evidence for both median and lateral eyes, and gene expression data in living species support the notion that both types of eyes were present in the harvestman groundplan (Garwood et al., 2014). The ventral margin of the harvestman dorsal shield accommodates the pleural ozopores, which are connected to repugnatorial glands. Limb I is a chelate chelicera, limb II forms the pedipalps, which can be raptorial in the suborder Laniatores, and

limbs III–VI act as walking legs. In the non-cyphophthalmids limb IV (the second walking leg) is longer and used as a tactile device. Usually there is no sternum, except in some cyphophthalmids.

Dorsally the tergites of somites VII–XV show a range of fusion patterns: In the *scutum laminatum* condition all opisthosomal tergites are free, in the *scutum parvum* the first five tergites (VII–XI) are fused, in the *scutum magnum* these five fused tergites are further fused to the carapace, and in the *scutum completum* the carapace and tergites together form a unitary dorsal shield (Shultz & Pinto-da Rocha, 2007: Fig. 2.4). Ventrally, the gonopore in harvestmen has been displaced forwards between the leg coxae. The first sternite of the opisthosoma (somite VII) are the small *arculi genitales* which form the anterior border of the pregenital chamber. In cyphophthalmids and Tetrophthalmi the gonopore is open in adults (it is closed in juvenile cyphophthalmids), but in other harvestmen the second sternite (somite VIII) contributes to a genital operculum which covers this opening. Male harvestmen have a spermatopositor (cyphophthalmids) or a penis (all other suborders) and females have an ovipositor. Previous studies (e.g. Shultz 2000) did not treat them as appendage derivatives. Somite VIII also bears the spiracles for a pair of tracheae. As noted above, the anal operculum may effectively represent the telson.

3.10.3. Phalangiotarbida[†]

Phalangiotarbids are an unusual-looking, extinct order which ranged from the Devonian to the Permian. They have been likened either to harvestmen or opilioacarid mites, but a recent attempt to resolve their phylogenetic position (Garwood and Dunlop, 2014a) was unable to recover a robust position for this group as a number of key characters, such as the nature of the mouthparts, remain equivocal. Accounts of their external morphology can be found in, e.g., Dunlop and Horrocks (1997) and Pollitt et al. (2004). Phalangiotarbids (Fig. 3) probably have 16 somites with a clear 6 + 10? division into a broadly joined prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). This bore a single ocular tubercle with three pairs of lenses. As noted above, the morphology of the chelicerae is equivocal, limb II is a tiny, pediform pedipalp and limbs III–VI act as walking legs. There are four or five small sternal plates between the leg coxae. The dorsal tergites covering the first six opisthosomal somites (VII–XII) are highly abbreviated. A similar abbreviation is seen in opilioacarid mites (see 3.10.8), but in the mites the tergites are not so strongly expressed. Somites XIII–XV in phalangiotarbids were either covered dorsally by three large tergites, or in some taxa these three elements have fused together into a single shield. Ventrally the anterior opisthosomal sternites are similarly short and concentrated like the anterior tergites and there is some evidence for two pairs of spiracles, perhaps opening on somites X and XI (Dunlop and Horrocks, 1997: Fig. 6). A ring-like segment (somite XVI) surrounds the anal operculum. Oddly, the anal operculum of phalangiotarbids is a dorsal structure. If we adopt Shultz’s (2000) argument from harvestmen that the anal operculum lacks tergites and sternites we can potentially interpret the phalangiotarbid anal operculum as a telson too.

3.10.4. Palpigradi

Palpigrades are small, blind, poorly-sclerotized creatures. They have been envisaged by some authors as the most primitive arachnids (e.g. Savory, 1974) in that they appear to express several plesiomorphic character states. Detailed accounts of their external anatomy can be found in, e.g., Börner (1901), Rowland and Sissom (1980) and van der Hammen (1989). Palpigrades (Fig. 3) have 17 somites with a clear 6 + 11 division into a prosoma and opisthosoma and a distinct narrowing of the body at somite VII. There is no unitary prosomal dorsal shield. Instead the first four somites (I–IV)

of the prosoma are covered by an eyeless propeltidium. Somite V is associated with a mesopeltidium divided into two sclerites. This is followed by an undivided metapeltidium covering somite VI. Limb I is a chelate chelicera, limb II is a pediform pedipalp and limbs III–VI are walking legs; whereby it should be noted that in these arachnids the pedipalps are not much differentiated from the legs and also contribute towards locomotion (Rowland and Sissom, 1980). The deuto- and tritosternum of somites II–III are fused and there are three further separate sternal plates associated with somites IV, V and VI respectively. The opisthosoma has eleven segments, the first (somite VII) short and narrow. Ventrally somite VII bears the genital opening. Palpigrades lack respiratory organs, but somites IX, X and XII bear evaginations usually referred to as verrucae (van der Hammen, 1989) or ventral sacs which have been suggested as highly modified appendage derivatives. Somites XV–XVII are narrow, ring-like and form a short postabdomen (or pygidium in some terminologies). The telson is flagelliform. We should, however, note the observations of Monniot (1970) and Rowland and Sissom (1980) who found the cuticle and setae of the first flagellar segment to be more like that of the body than of the rest of the telson. In this hypothesis the basal flagellar segment could actually be a somite (XVIII). This would yield a 12 segmented opisthosoma, but would necessitate a shift of the anal opening back onto somite XVII.

3.10.5. Pseudoscorpiones

Pseudoscorpions (Pseudoscorpiones) superficially resemble scorpions, but have usually been interpreted as the sister-group of Solifugae forming a clade Haplocnemata (but see below). A detailed morphological account can be found in Weygoldt (1969). Pseudoscorpiones (Fig. 3) have 18 somites with a clear 6 + 12 division into a broadly connected prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (a carapace or scutum), although in some taxa (e.g. Weygoldt, 1969: Fig. 1) this may bear two transverse furrows, perhaps reflecting a 4 + 1 + 1 pattern. Limb I is a chelate chelicera with two articles, limb II forms the chelate pedipalps and limbs III–VI act as walking legs. There is a projecting epistomo-labral plate and associated lateral lips, but no sternum. The opisthosoma has twelve segments (somites VII–XVIII). In some species the tergites are medially divided. As noted by Weygoldt (1969: Fig. 11), there are eleven dorsally visible tergites, but the pregenital segment (somite VII) lacks a sternite. Tracheal spiracles open ventrally on somites IX and X. The posteriormost segment (somite XVIII) forms a small anal cone which can be retracted into the previous segment. There is no telson.

3.10.6. Solifugae

As noted above camel spiders (Solifugae) have traditionally been allied with pseudoscorpions, although some data place Solifugae closer to the Acariformes mite clade (e.g. Pepato et al., 2010). A detailed morphological account can be found in Kaestner (1932) and Roewer (1933). Camel spiders (Fig. 3) have 17 somites with a 6 + 11 division into a prosoma and opisthosoma and a narrowing around somite VII. Similar to the condition in palpigrades, the first four somites (I–IV) of the prosoma are covered by a propeltidium bearing median eyes and vestigial lateral eyes. The propeltidium itself is quite complex and constructed from several individual elements (Roewer, 1933: Figs. 13–14) which could potentially reflect the underlying somites. Somite V is associated with a mesopeltidium and somite VI with a metapeltidium. Limb I is a massive chelate chelicera with two articles. Limb II forms the large pediform pedipalps with the unique apomorphy of an adhesive palpal organ at the tip. Limbs III–VI act as walking legs, whereby limb III is often smaller and more slender than the other legs and has a more tactile function. The proximal articles of limb VI uniquely bear sensory

organs called malleoli or racquet organs. There is a projecting epistomo-labral plate and associated lateral lips, but no sternum. The opisthosoma is rather soft and composed of eleven segments (somites VII–XVII). Tracheal spiracles open ventrally between segments IV and V on the prosoma and, as in pseudoscorpions, on segments IX and X of the opisthosoma. In some taxa there are also tracheal spiracles on somite XI as well. There is no telson.

3.10.7. Acariformes

Mites are now conventionally treated as two distinct orders – for which we here adopt the names Acariformes and Parasitiformes – given that there are some quite significant differences in their morphology (Dunlop and Alberti, 2008) and that recent cladistic analyses do not always recover Acari as monophyletic (Shultz, 2007a; Pepato et al., 2010). Some phylogenies grouped mites with ricinuleids (e.g. Weygoldt and Paulus, 1979) based on the presence of a hexapodal instar (the hatching larva has only six legs), although as noted above other data recovered at least the acariform mites as sister-group to camel spiders. Irrespective of their affinities, there is no such thing as a ‘typical’ mite, and caution should be exercised when trying to reconstruct a groundplan either for all mites or for either of the two orders. Their small size and often weakly expressed external segmentation mean that matching the observed morphology to the underlying somites is extremely challenging and often has to be based on inferences of patterns of cuticular structures such as setae or lyrifissures: an acarological term for the slit sense organs. The textbook of Krantz and Walter (2009) noted that counts for mites in general vary in the published literature from 12 to 22 somites, depending on the group being studied and the interpretation of individual authors. It should also be stressed that these animals often add posterior body segments during development, thus the final complement of somites may only be achieved in later instars. Two major lineages of acariform mites can be recognised: Sarcoptiformes and Trombidiformes.

At the base of the sarcoptiform mites are the Endeostigmata; some of which have been referred to as ‘segmented mites’ in that several species retain evidence of external segmentation. One of them, *Alycus roseus*, is something of a model taxon for assessing mite segmentation (Kramer, 1882; van der Hammen, 1989). As in many acariform mites, the principal external division of the body is between the second and third pair of walking legs. This dividing line is known as the disjugal furrow dorsally and the sejugal furrow ventrally. It defines an anterior pseudotagma, usually referred to as the prodorsum, proterosoma or aspidosoma (Fig. 4), which presumably corresponds to somites I–IV (but see below). Somites I and II represent the chelate chelicerae and the pedipalps respectively, which together form the gnathosoma with projecting epistomo-labral plate and associated lateral lips. Note again the data of Barnett and Thomas (2013a) arguing that acariform mites have three cheliceral articles in their ground pattern. The appendages of somites II–VI form the walking legs. It is widely presumed that in adult endeostigmatids there are ten segments behind the prodorsum, the first two of which are interpreted as having fused and the four posteriormost of which are acquired during ontogeny. These segments are conventionally named C (1 and 2), D, E, F, H, PS, AD, PA & AN (e.g. Walter, 2001: Fig. 1), whereby PS is the pseudanal segment, AD the adanal segment, PA the preanal segment, and AN the anal segment (Fig. 4). The real question is how should these be matched to the underlying somites, and in particular what has happened to the dorsal expression of somites V and VI? In van der Hammen's (1989) scheme the anterior division of the body was effectively a true prosoma (somites I–VI) – the prodorsum also bears six pairs of setae – making the 10 opisthosomal somites VII–XVI to yield a total somite count of 16. However, if the first visible segment behind the prodorsum is somite V, then the

remaining segments would represent somites V–XV for a total count of only 14.

The same problem applies to understanding the largest group of sarcophagiform mites, the Oribatida, whereby the Astigmata probably evolved from within the oribatids. [Weigmann \(2001, Figs. 1–2\)](#) critically discussed alternative hypotheses of segmentation in the literature and rejected [van der Hammen's \(1989\)](#) interpretations of a larger number of somites for acariform mites in general in favour of an older scheme, largely based on [Grandjean \(1934\)](#). Here, as above, somites I–II form the gnathosoma with the chelicerae and pedipalps, while appendages III–IV are walking legs and form the propodosoma. The first four somites (I–IV) are covered dorsally by the prodorsum and are separated from the hysterosoma by the disjugal furrow ([Fig. 4](#)). This is hopefully uncontroversial. Appendages V–VI are also legs and constitute the metapodosoma. Critically, and in contrast to [van der Hammen \(1989\)](#), the next dorsal element in Weigmann's scheme – i.e. the first somite of the hysterosoma – is somite V and there is no clear evidence that it is a fused element; as per the C1 & 2 scenario above. Thus in this model the hysterosoma in the groundplan of oribatid mites consists of a total of 9 somites (V–XIII) dorsally labelled C, D, E, F, H, PS, AD, PA & AN, to yield a grand total of only 13.

Another way of looking at the problem is to consider developmental genetics and ventral morphology. [Barnett and Thomas \(2012\)](#) studied the segmentation genes *engrailed* and *hedgehog* and demonstrated that the oribatid mite *Archegozetes longisetosus* patterns only two opisthosomal segments, implying considerable fusion or loss compared to the arachnid ground pattern. Interestingly, the development of the fourth walking leg segment in this species is, uniquely for arachnids, temporally tied to opisthosomal segmentation, although in fairness this has not been tested across a wider sampling of different groups. Other somites almost certainly contributed to the (adult) hysterosoma, but have not yet been demonstrated by these molecular methods (Richard Thomas, pers. comm. 2015). Given that the ovipositor of acariform mites and the three pairs of genital acetabula may be appendage-derived, these also need to be integrated somehow into the segmentation pattern. This is far from being a straightforward process. One model (Richard Thomas, pers. comm) might recognise nine 'opisthosomal' segments: no limb (1), the ovipositor (2–3), the three pairs of genital acetabula (4–6) and the three segments around the anal region (7–9). The problem here is that in the Weigmann model somites V–VI bear walking legs, leaving only seven somites (VII–XIII) to accommodate these nine elements hypothesised above. Removing the ovipositor from the segment count – or treating it as endopod-derived with the genital acetabula as exopods? – could resolve this problem, but clearly further work is required to reconcile the published data into a unified model of acariform mite segmentation.

3.10.8. Parasitiformes

Parasitiform mites (Parasitiformes) encompass the Opilioacarida, Holothyrida, Mesostigmata (predatory mites) and Ixodida (ticks). Three of the four groups are illustrated here. Segmentation in holothyrids has attracted little research. The dorsal surface is covered by a unitary shield and even [van der Hammen \(1989\)](#) was not able to reconstruct a segmentation pattern here. Like acariform mites, parasitiforms have a gnathosoma (somites I–II) as a functional unit bearing the chelicerae and pedipalps. The rest of the body is traditionally referred to as the idiosoma. The hatching larva is hexapodal, as in acariform mites, and the last walking leg (limb VI) is expressed in subsequent instars. Reconstructing segmentation for opilioacarids, mesostigmatids and ticks has also proven problematic. Here, we orientate ourselves on [Klompen et al. \(2015\)](#) who inferred 17 somites as the Parasitiformes groundplan ([Fig. 4](#)).

This translates either into a 2 + 15 tagmosis pattern for the gnathosoma and idiosoma, or a 6 + 11 tagmosis pattern for the prosoma and opisthosoma (but see opilioacarids below). Note that Klompen et al.'s paper counted the ocular somite as number I and we have modified their counts here to make them comparable with our other taxa.

Opilioacarid mites are rare, but are generally assumed to be closest to the original parasitiform morphology in that they express several plesiomorphic characters, including evidence of external segmentation. [Van der Hammen \(1989, and references therein\)](#) summarised their general morphology and recognised 19 somites, of which the pregenital and genital somites (VII + VIII) are dorsally fused, although in some of his earlier studies 20 somites were accepted under the assumption that the anal cone represented two somites. [Klompen et al. \(2015: Fig. 6\)](#) recognised only 17 somites, drawing on interpretations of development and the distribution of rows of lyrifissures and setae. Fusion of somites VII and VIII was not supported, and in their scheme the dorsal shield is not a full prosomal dorsal shield, but corresponds to somites I–V only. Two or three pairs of lateral eyes are present on this dorsal shield. In the gnathosoma limb I is the chelicera – here chelate and unequivocally with three articles – and limb II forms the pedipalps; limbs III–VI form the walking legs. The region behind the dorsal shield includes twelve somites VI–XVII. The first of these (VI) thus effectively belongs to the prosoma. The first six somites (VI–XI) are expressed externally with short segments. The remainder largely has to be inferred, but the anal cone is assumed to represent somite XVII. In this scheme the tracheae open dorsally on somites VIII–XI and the genital opening is flanked by a pair of genital verrucae which could be appendage-derived.

Mesostigmatids are the most diverse parasitiform mites both in terms of their species number and their ecologies. Authors such as [Christian and Karg \(2008\)](#) – drawing on [Coineau \(1974\)](#) – recognised a total of only 13 somites; similar to Weigmann's model for oribatids ([Fig. 4](#)). This implies the loss of several opisthosomal somites compared to the opilioacarid condition and arachnids in general. A gnathosoma bearing the three-articled chelicerae (limb I) and the pedipalps (limb II) are fairly obvious. Mesostigmatids often present two large shields dorsally, although in many taxa they are fused into a single dorsal sclerite. [Christian and Karg \(2008: Figs. 1–2\)](#) used setal patterns to recognise a groundplan condition of a body divided dorsally into an eyeless prodorsum covering six somites (III–VIII), in which the pregenital and genital somites VII + VIII are presumed to be fused, and a postdorsum covering five somites (IX–XIII). Limbs III–VI form the walking legs. [Klompen et al. \(2015: Figs. 8c, 10\)](#) attempted to reconcile these observations with their 17 somite groundplan, but conceded that mesostigmatids were challenging in this context. In their model the anal valves represent somite XVII, there is preanal segment (somite XVI) and five postdorsal segments delimited by the so-called 'J1–J5' setal patterns (somites XI–XV). The prodorsal setae 'j4–j6' may correspond to somites VII–X, again assuming that VII + VIII are fused, and the more anterior 'j1–j3' setae are presumed to correspond to several of the more anterior somites. In the absence of, for example, gene expression data it is currently difficult to say which of these models is correct. Yet as with the ticks below, it poses a fundamental question of whether all parasitiform mites retain the groundplan tagmosis of the order or whether there has been a major suppression and/or loss of the posterior somites *within* the parasitiform lineage, similar to the condition in, say, sea spiders.

A summary of tick morphology can be found in [Sonenshine \(1991\)](#). The gnathosoma is modified for sucking blood. The small chelicerae (limb I) have two articles, the distal one serrated to cut into skin. The pedipalps (limb II) are also small, with only four articles, and both the chelicerae and pedipalps are intimately

associated with a hypostome bearing backward-pointing spines which is inserted into the host. The idiosoma is sometimes divided into a podosoma (somites III–VI) bearing the walking legs, and an opisthosoma comprising the remaining somites (Fig. 4). Dorsally, the idiosoma does not present any external transverse segmentation but forms a continuous integument, often with a distinct plate, the scutum, covering the anterior part. In some genera the scutum bears a pair of simple lateral eyes, but it is difficult to homologise the scutal plate with any given set of somites (Klompen et al., 2015). Ventrally there are several plates, including a pregenital plate, a median plate and an anal plate. The genital opening is thrust forward between the leg coxae and a pair of spiracles open behind the last pair of legs. The traditional model based on embryology (e.g. Aeschlimann and Hess, 1984) recognises only five opisthosomal somites in ticks (VII–XI) for a total of eleven somites, plus the anal valves assumed to be homologous with the telson. However, Klompen et al. (2015) cautioned that segments sometime develop late in embryogenesis and antibody staining by Santos et al. (2013; Fig. 8) found evidence for up to eight (somites VII–XIV). A key question for ticks is whether a series of indentations called festoons around the posterior margin of the body in at least the hard ticks (Ixodidae) are also indicators of original segmentation, as proposed by Schultze (1932). Klompen et al. (2015) assumed this to be the case – although it should be stressed that not all authors accept this interpretation – and reconciled this with their 17 somite groundplan as follows. Somites I–VI form the prosoma (= gnathosoma + podosoma), somites VII–XVII the opisthosoma. Of these, XI–XV correspond to the five pairs of lateral festoons, the central unpaired festoon (or parma) is somite XVI and the anal valves are somite XVII. This scheme of Klompen et al. (2015) is summarised as their Fig. 9.

3.10.9. Ricinulei

Ricinuleids (Ricinulei) are a rare order. Traditionally they have been allied with mites, given that both groups express a hexapodal larva, however ricinuleids also share several characters relating to body segmentation and pedipalp structure with the extinct trigonotarbrids (e.g. Dunlop et al., 2009) which could imply that they are closer to, or even part of, the wider Pantetrapulmonata clade. Detailed accounts of ricinuleid morphology can be found in Hansen and Sørensen (1904). A problem with these animals is that several opisthosomal segments have evidently fused. Certain fossils (Selden, 1992; Fig. 28) reveal two pairs of muscle apodemes on the three largest tergites which is good evidence that these are diplosegments corresponding to two original somites. The question is whether the short tergite in front of these three is also a double segment, as in van der Hammen's (1989) scheme for example. Given the uncertainties in establishing an unequivocal segmentation pattern somite counts of 17–19 can be found in the literature. The scheme presented here is thus somewhat tentative.

Ricinuleids (Fig. 3) are inferred here to have 18 somites (Fig. 5), with a 6 + 12 division into a prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). The front of this shield is hinged and forms the cucullus, a flap-like structure covering the mouthparts. Modern ricinuleids have, at best, only light-sensitive patches laterally, but fossil taxa clearly had two pairs of lateral eyes. Limb I approaches the condition of a clasp-knife chelicera, limb II formed the pediform pedipalp, which terminates in a small chela formed from the tarsus and apotele. Limbs III–VI act as walking legs whereby limb IV is longest and used in a somewhat tactile fashion, while limb V of males bears a sperm-transfer device. There is no sternum. Tracheae open into the prosoma with a pair of spiracles between the third and fourth leg (somites V and VI). Ricinuleids have a complex pedicel region, which is normally concealed because the prosoma and opisthosoma 'lock'

together. Dorsally, the first opisthosomal tergite (somite VII) tucks under the posterior margin of the prosomal dorsal shield as part of this locking mechanism. The next tergite is short but may represent somites (VIII–IX). The remaining tergites are clearly diplotergites and in this scheme represent somites X–XI, XII–XIII and XIV–XV respectively. Ventrally, there are some difficulties in understanding the segmentation. The genital opening – a traditional landmark for somite VIII – is projected forwards and opens on the pedicel. It has two sclerotized lips, but it's not clear if these correspond to somites VI and/or VII. The first visible sternite may thus correspond to somite IX. The next three sternites are large and evidently correspond to the large diplotergites representing somites X–XV in this scheme. The last three opisthosomal segments (somites XVI–XVIII) lack division into tergites and sternites and form a small, retractable postabdomen, or pygidium in some terminologies. There is no telson.

3.10.10. Trigonotarbida[†]

Trigonotarbrids (Trigonotarbida) are an extinct order which ranged from the Silurian to the Permian. A detailed account of their morphology based on exceptionally preserved Devonian material can be found in Fayers et al. (2005), with further details of the limbs in Dunlop et al. (2009) and Garwood and Dunlop (2014b). Trigonotarbrids belong to a larger, widely accepted clade of arachnids known as the Pantetrapulmonata (cf. Shultz, 2007a), all of whom have two pairs of book lungs, at least in their groundplan. Trigonotarbrids appear to have 18 somites (Fig. 5), with a clear 6 + 12 division into a prosoma and opisthosoma. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). This bears both median eyes and in at least some taxa lateral eyes too, consisting of groups of multiple lenses. Limb I is a clasp-knife chelicera, limb II formed the pediform pedipalp, which in at least some species ends in a small chela similar to that of ricinuleids. Limbs III–VI represent the walking legs. There is a labium and a single sternum between the leg coxae. The opisthosoma has 12 segments (somites VII–XVIII); although erroneous counts of 8–11 can be found in the older literature (e.g. Petrunkevitch, 1955). The first tergite (somite VII) was modified into a locking ridge which tucked under the carapace and the first sternite appears to have been absent. In many trigonotarbrids tergites 2 + 3 were fused into a diplotergite. Dorsally, tergites 2 to 9 were characteristically divided into one median and two lateral plates, again similar to the condition in ricinuleids, while in one trigonotarbid family (Anthracomartidae) these tergites were further subdivided to yield five plates per segment. Well-preserved fossils reveal that somites VIII and IX each had a pair of book lungs, and the sclerites covering these lungs were probably modified opercula sensu Shultz (1993). At least somite IX also bore a pair of ventral sacs – similar to their occurrence in whip spiders (see 3.10.14) – and some trigonotarbrids may have borne further ventral sacs on the next couple of somites too. The last three opisthosomal segments lacked division into tergites and sternites and the last two (somites XVII–XVIII) projected slightly as a small postabdomen, or pygidium in some terminologies. There is no telson.

3.10.11. Uraraneida[†]

Uraraneidids (Uraraneida) are extinct, spider-like arachnids known from two fossils from the Devonian of the USA and the Permian of Russia respectively. A recent account was given by Selden et al. (2008). The Devonian fossil is known from cuticle fragments while the Permian fossil from the ventral surface only, thus several aspects of their morphology remain equivocal. From what is known, they appear to have been fairly similar to mesothelid spiders (see below) and we can infer the presence of 18 somites with a 6 + 12 division into a prosoma and opisthosoma. Limb I was

a clasp-knife chelicera; limb II was a pediform pedipalp, and limbs III–VI formed the walking legs. We do not know if males had a modified palpal organ like in spiders. The presence of a labium is equivocal, but there is a single sternum between the leg coxae. Significantly, Uraraneida had spigots on the ventral surface of the opisthosoma for producing silk, but lack the distinct spinnerets seen in spiders. The spigots were borne at the posterior margin of one or more ventral plates. Given the disarticulated nature of the Devonian uraraneids we cannot confirm that the spigot-bearing plates belonged to the same somites (X and XI) as the spider spinnerets, although we consider this plausible (Fig. 5). In uraraneids a flagelliform postanal telson was retained, similar to that of palpigrades and whip scorpions.

Note that Garwood et al. (2016) recently described a Carboniferous fossil which resolved, phylogenetically, between Uraraneida and Araneae. *Idmonarachne brasieri* Garwood et al., 2016 has an essentially spider-like body plan. The flagelliform telson is no longer present, but like the uraraneids this interesting fossil also lacks spinnerets on the underside of the abdomen.

3.10.12. Araneae

The segmentation pattern in spiders (Araneae) is best observed in the suborder Mesothelae, which retains a segmented opisthosoma. Morphological details can be found in, e.g., Haupt (2003). In more derived spiders the opisthosoma is largely soft, but may retain hints of the original segmentation (see especially Crome, 1955). Araneae have 18 somites with a clear 6 + 12 division into a prosoma and opisthosoma (Fig. 5) accentuated by a narrow 'waist' or pedicel. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). Spiders typically have six or eight eyes. Patterning mechanisms of both prosomal and opisthosomal spider appendages were reviewed by Pechmann et al. (2010). Limb I is a clasp-knife chelicera, limb II forms the pediform pedipalps with the unique spider apomorphy of a palpal organ for sperm transfer in males, limbs III–VI act as walking legs. There is a labium and a single sternum between the leg coxae. The opisthosoma has 12 somites. The first is especially constricted as part of the pedicel. Somites VIII and IX bear – at least in the groundplan – the book lungs. In mesothelae these lung pairs are covered by unitary plates, which are probably modified appendages. In more derived spiders these plates are reduced to sclerotized covers over the individual lungs. Most araneomorph spiders have reduced the second lung pair on somite IX and replaced their lungs with tracheae. Given that the tracheae are derived from appendage apodemes (Selden et al., 2008; Pechmann et al., 2010) these structures can also be interpreted as highly derived expressions of the appendages of somite IX.

Segments X and XI bear spinnerets; another key autapomorphy of spiders. Embryologically two pairs on each of these somites develop, but the full complement of eight is only retained in mesothelae (and two of these lack silk-producing spigots), with other spider groups showing alternative patterns of reduction and/or modification. In non-mesothelae spiders the spinnerets have also migrated to a more posterior position, although this does not affect the somites they belong to. Selden et al. (2008) noted that the epiaudacious glands on the genital somite (VIII) may be serial homologues of the silk glands on the next two segments associated with the spinnerets. As discussed by Selden et al. (2008), spinnerets are widely accepted as modified opisthosomal appendages (see also Damen et al., 2002; Pechmann et al., 2010). A walking tarantula spider often moves its spinnerets in time with the pacing of its legs (JAD, pers. obs.). The absence of spinnerets in close relatives of Araneae may imply that spiders (re)evolved these structures by reactivating suppressed genes for appendage development on somites XII and XIII. The ventral opisthosoma behind the spinnerets

lacks obvious external segmentation. The posteriormost segment (XVIII) forms an anal tubercle. There is no telson.

3.10.13. Haptopoda[†]

Haptopoda is an extinct, monotypic order known only from one locality in the Late Carboniferous British Middle Coal Measures. It has tentatively been interpreted as being most closely related to Amblypygi, Thelyphonida and Schizomida as part of a Schizotarsata clade *sensu* Shultz (2007a) defined by subdivided leg tarsi. The morphology of these fossils was most recently summarised by Dunlop (1999) and Garwood and Dunlop (2014a). Haptopoda appears to have had 18 somites (Fig. 5), with a clear 6 + 12 division into a prosoma and opisthosoma, but without a narrow pedicel as in spiders. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). This bears both median eyes and apparent lateral eye tubercles. Limb I was a clasp-knife chelicera; limb II was a small, pediform pedipalp, limb III (the first walking leg) was somewhat elongate and may have been more tactile in life, while limbs IV–VI appear to have acted as the primary walking legs. A labium is equivocal, but there are two sternal elements between the leg coxae. The opisthosoma had twelve segments (somites VII–XVIII), whereby the first segment is rather short. The referral of this group to the wider Tetrapulmonata clade implies that these animals also had two pairs of lungs – and their appendage derived opercula – but this cannot be demonstrated unequivocally in the material available. The last two segments of the opisthosoma are ring-like and plate-like respectively. There was no telson.

3.10.14. Amblypygi

Whip spiders (Amblypygi) have been interpreted either as the sister group of spiders (the Labellata hypothesis) or of whip scorpions and schizomids (the Pedipalpi hypothesis). Detailed morphological accounts of whip scorpions can be found in Börner (1904) and more recently Shultz (1999), supplemented by Weygoldt (2000). Amblypygi (Fig. 5) have 18 somites with a clear 6 + 12 division into a prosoma and opisthosoma, accentuated by an especially narrow pedicel similar to the condition in spiders. Somites I–VI are covered by a unitary prosomal dorsal shield (or carapace). This bears both median eyes and lateral eyes consisting of two groups of three lenses. Limb I is a clasp-knife chelicera; limb II forms the raptorial pedipalps, limb III is an antenniform leg with a largely tactile function and limbs IV–VI act as walking legs. There is an elongate labium (or tritosternum) plus two small sternal elements between the leg coxae. The opisthosoma has twelve segments (somites VII–XVIII). The first is constricted as part of the pedicel. Somites VIII and IX bear the book lungs and their associated appendage-derived opercula (Shultz, 1999). Somite VIII also expresses internal gonopods and somite IX in many species bears ventral sacs, both of which Weygoldt (2000) interpreted as the highly modified endopod ramus of the original biramous limb series. The last three opisthosomal segments form a small post-abdomen, in which somite XVIII is barely visible, but the segments here are still divided into tergites and sternites. There is no telson.

3.10.15. Thelyphonida

Detailed morphological accounts of whip scorpions (Thelyphonida) can be found in Börner (1904) and more recently Shultz (1993). Thelyphonida have 18 somites with a clear 6 + 12 division into a prosoma and opisthosoma (Fig. 5), accentuated by a narrowing similar to the condition in spiders and whip spiders, albeit not to the same extent. Somites I–VI are covered by a unitary prosomal dorsal shield. This bears both median eyes and lateral eyes consisting of two groups of three major and two minor lenses. As in whip spiders, limb I is a clasp-knife chelicera; limb II forms the raptorial pedipalps, limb III is an antenniform leg with a largely

tactile function and limbs IV–VI act as walking legs. There is no labium, but the sternum is composed of a larger V-shaped sclerite between the coxae of appendages IV and a small element between the coxae of appendage V. The opisthosoma has twelve segments (somites VII–XVIII). The first is constricted as part of the pedicel. Somites VIII and XI bear the book lungs, with their associated appendage-derived operculae (Shultz, 1993). Segment VIII also expresses internal gonopods. The last three opisthosomal segments are not divided into tergites and sternites and form a small postabdomen. A flagelliform postanal telson is retained.

3.10.16. Schizomida

Schizomids (Schizomida) are evidently closely-related to whip scorpions and for many years were considered part of the same order. A detailed morphological account can be found in Börner (1904). Schizomids have 18 somites (Fig. 5) with a clear 6 + 12 division into a prosoma and opisthosoma, accentuated by a partial narrowing as per whip scorpions. The prosoma expresses a pseudotagma in the form of a propeltidium covering somites I–IV, plus separate sclerites (the meso- and metapeltidium) for somites V and VI respectively. Many schizomids are blind or have only lateral eye spots, but in a few genera there are lateral eyes with lenses on the propeltidium (Sissom, 1980). As in whip spiders and whip scorpions, limb I is a clasp-knife chelicera; limb II forms the raptorial pedipalps, limb III is an antenniform leg with a largely tactile function and limbs IV–VI act as walking legs. There is no labium, but the sternum is composed of a larger V-shaped sclerite between the coxae of appendages IV and a minute element between the coxae of appendage V. The opisthosoma has twelve segments (somites VII–XVIII). The first is constricted as part of the pedicel. Somite VIII bears a pair of book lungs and is presumably associated with an appendage-derived operculum as per Thelyphonida, but the lungs on somite IX have been lost. We presume that the sclerite here is still appendage-derived. Gonopods have not been reported on the genital somite in the literature. The last three opisthosomal segments are not divided into tergites and sternites and again form a small postabdomen (somites XVI–XVIII). A short, flagelliform postanal telson is retained and in male schizomids it is uniquely modified at the tip into a bulbous or plate-like structure, which the female holds onto during mating.

4. Discussion

4.1. The chelicerate groundplan

The basic evolutionary trend in Chelicerata was consolidation of a functional division of the body into anterior somites specialised for feeding and locomotion and posterior somites specialised for respiration, digestion and reproduction. This is, in essence, the prosoma/opisthosoma tagmosis. Resolving how this body plan was achieved depends to some extent on which fossils we accept as basal Chelicerata, or their immediate outgroup. If Legg (2014) is correct and *Sanctacaris uncata* is a basal chelicerate (3.1.1), then a body divided into a prosoma of six somites covered by a unitary dorsal shield and an opisthosoma of at least eleven somites (Fig. 1) may have predated the acquisition of chelate chelicerae. Recall, though, that in Legg's interpretation limb I is equivocal rather than being demonstrably non-chelate. However, if Pycnogonida are ingroup chelicerates, then in this scenario their tagmosis pattern of a cephalosoma with four somites plus a trunk is implicitly derived.

In the alternative hypothesis megacheirans are stem-chelicerates (Chen et al., 2004). These Palaeozoic arthropods have usually been interpreted (but see Liu et al., 2016) as having had a head shield covering the first four somites – similar to the pycnogonid cephalosoma – plus the longer trunk (Fig. 1). In favour of

this scenario is the fact that the appendage of the first somite in megacheirans is a modified, uniramous limb, for which a putative transition series can be recognised (Haug et al., 2012b), whereby this 'great appendage' becomes increasingly consolidated into a raptorial first head limb similar to the chelate chelicerae of sea spiders, horseshoe crabs, eurypterids and arachnids. In this hypothesis a prosoma was *not* part of the chelicerate groundplan. It presumably evolved later, perhaps at the Euchelicerata grade, by integrating the next two (or three) somites into the head shield or cephalon—a model favoured by authors such as Størmer (1944: Fig. 25) or Winter (1980: Fig. 27). A similar, 4 + 2, tagmosis was envisaged by Kraus (1976: Fig. 7) in his reconstruction of the hypothetical chelicerate archetype.

Of course, a raptorial appendage can evolve quite easily (see e.g. Lamsdell et al., 2013) by developing an apophysis from a preceding limb element to create a simple claw. Thus we must be cautious about assuming that megacheiran raptorial limbs were automatically progenitors of the chelicerae. Essentially, the question we face is whether having an anterior tagma composed of somites I–VI or having a raptorial appendage on somite I is a better guide to the origins and groundplan of Chelicerata. This question is not trivial as it impacts on the polarity of characters used in arachnid phylogeny. For example, is a 'divided carapace' and/or a prodorsal shield an apomorphy in which the original prosomal dorsal shield has become split up, or is it the plesiomorphic retention of (or reversal back to) an ancestral tagmosis pattern, as envisaged by authors such as Kraus (1976).

4.2. Does somite VII belong to the prosoma?

Although the prosoma is traditionally assumed to correspond to the first six somites, we also need to consider exactly where we draw the boundary and whether it is the same across all taxa. Adopting Lamsdell's (2013) argument that tagmata should be defined primarily on the form and function of the limb series, we have to recognise that at least in sea spiders (Fig. 1) and potentially in *Weinbergina opitzi* (Fig. 2) it is somites I–VII which bear the chelicerae and walking legs, and not just somites I–VI. Thus some authors have suggested (e.g. Stürmer and Bergstrom, 1981) that somite VII should also be counted as part of the prosoma in the chelicerate groundplan. Recall that the chilaria on somite VII of modern horseshoe crabs and the metastoma of chasmataspidids and eurypterids may not be legs *per se*, but they do appear to be functionally integrated into the prosoma and play an active role in food acquisition. In euchelicerates somites VIII–XIII are characterised by flap-like appendages, or modifications thereof, often associated with respiration. The tagmosis question is complicated by *Offacolus kingi* and *Dibasterim durgae*. Both these fossils have flap-like appendages on somite VII (Fig. 2). That said, Lamsdell (2013) noted that a flap suggests an exopod ramus. A walking leg here, as in *Weinbergina opitzi*, may be indicative of the original endopod ramus; thus we have to consider the fate of both the endopod and the exopod on somite VII. Note also that the head shield in *Offacolus kingi* has also been interpreted as covering seven somites (I–VII), not six, again raising the question of how many segments are 'prosomal' in the (eu)chelicerate groundplan.

4.3. Transition to uniramous prosomal limbs

In both *Sanctacaris uncata* and the megacheirans the post-cheliceral limbs from somite II backwards all appear to have been biramous (Fig. 1), generally with a leg-like endopod and a more flap-like exopod, which may have functioned as a gill. Sea spiders may be basal chelicerates, but they all have uniramous limbs. Given their many reductive characters, including a foreshortening of the

trunk, sea spiders do not reveal the transition towards the euhelicerate condition of plate-like posterior limbs. Intermediate states are better reflected in fossils like *Offacolus kingi* and *Dibasterium durgae* (Fig. 2) which resemble horseshoe crabs, but retained the exopod on the postcheliceral prosomal appendages (see 3.4.1–2). Note that both these fossils are Silurian in age, contemporary with the oldest arachnids, and thus probably retain an older body plan rather than being directly ancestral to any modern chelicerate group. Today, an obvious prosomal exopod is only retained in horseshoe crabs (Fig. 2) as the flabellum on the appendage of somite VI. Loss of the (adult) exopods from the appendages of somites II–V thus becomes a defining apomorphy of Prosomapoda *sensu* Lamsdell (2013) (Table 1). In *Chasmataspis laurencii* at least one prosomal limb appears to have still been biramous (see 3.8.1), however the limb in question is disarticulated and cannot be placed with certainty in the limb series. Detailed studies of prosomal morphology in eurypterids (Holm, 1898; Selden, 1981) found no evidence for a flabellum/biramy on the appendage of somite VI. Thus loss of the exopod from limb VI could be a further synapomorphy of Sclerophorata (= Euryptera + Arachnida) (Table 1).

However, we should mention that juvenile instars of some arachnids also express vestigial prosomal exopods. The prelarva and larva of many acariform mites bear Claparède organs, a pair of small outgrowths resembling stubby legs which are thought to play a role in osmoregulation. Thomas and Telford (1999: Fig. 5) demonstrated that this structure is unequivocally derived from the base of the limb on somite IV (the second walking leg). These authors further suggested that the Claparède organs are homologous with the so-called lateral organs seen in the same position at the base of the second leg in the larvae of camel spiders, whip spiders and whip scorpions (Yoshikura, 1975; Zissler and Weygoldt, 1975). In the same paper, Thomas and Telford (1999: Fig. 2) documented surprisingly large lobes at the base of the pedipalp in embryos of acariform mites. These can be almost as large as the pedipalp itself at some stages of development and appear to eventually contribute towards constructing the floor of the gnathobase. Thomas & Telford speculated whether these lobes – sometimes referred to as coxal processes or endites – could be another example of a remnant of an originally biramous limb.

4.4. Anterior pseudotagmata

Several arachnids express pseudotagmata *sensu* Lamsdell (2013) towards the front of the body. The most obvious example is the gnathosoma of mites (Fig. 4): a movable, functional unit encompassing the chelicerae (limb I) and pedipalps (limb II), plus the mouth lips. It remains the strongest character in support of a monophyletic Acari, but must have evolved twice if mites are not a natural group; see Dunlop and Alberti (2008) for further discussion and Alberti et al. (2011) for a detailed account of its morphology and evolutionary significance in an oribatid. Acariform mites also often express a proterosoma (somites I–IV) articulating against the remaining somites (the hysterosoma) via the sejugal and disjugal furrows running between the second and third pair of legs (Fig. 4). Essentially the same division is reflected in the propeltidium of palpigrades, camel spiders (Fig. 3) and schizomids (Fig. 5). As noted above, this same unit corresponding to somites I–IV parallels the condition seen in the tagmosis of the megacheiran fossils and in the cephalosoma of the sea spiders (Fig. 1). This cephalosoma (somites I–IV) in sea spiders could also be regarded as a pseudotagma, as the limb series continues behind it with three more walking legs on the next three somites (V–VII). By the same criteria, one could classify the head region/cephalon of megacheirans (somites I–IV) as a pseudotagma as the biramous limb series continues onto and along the trunk without any major change in the structure and function of the limbs.

4.5. Modifications of the prosomal limbs

Lamsdell et al. (2015a: Fig. 26) summarised modifications of the postcheliceral prosomal appendages across various euhelicerates to demonstrate how different limbs in different taxa have been co-opted for: (1) grasping, restraining or otherwise manipulating prey, (2) facilitating reproduction or indirect sperm transfer, (3) sensing the surrounding environment, (4) walking, or (5) even digging or swimming. Depending on which phylogeny one adopts, several of these developments appear to be excellent examples of homoplasy. For example the appendage of somite II (the pedipalp) has often been marshalled for prey capture, becoming subchelate in whip spiders, whip scorpions and schizomids (Fig. 5), and fully chelate in scorpions and pseudoscorpions (Fig. 3). A further modification is the small claw at the tip of the pedipalp in ricinuleids and some (if not all) of the extinct trigonotarbids, and the adhesive pedipalp tip in camel spiders (Figs. 3 and 5). Alternatively, the appendages of different somites may, independently, have come to play a similar functional role. Whip spiders, whip scorpions, schizomids (Fig. 5) and perhaps also camel spiders (Fig. 3) use the appendage of somite III (the first walking leg) to a greater or lesser extent as a tactile appendage probing ahead in search of food or danger. Many harvestmen – and to some extent ricinuleids – use the appendage of somite IV (the second walking leg) in a similar fashion (Fig. 3). Spiders have modified the appendage of somite II (the pedipalp) into a male sperm transfer device (Fig. 5); ricinuleids use the appendage of somite V (the third walking leg) in a very similar way (Fig. 3).

4.6. The prosoma–opisthosoma junction

As noted by Lamsdell (2013), tagmata and their appendages may be modified close to their boundaries and this is particularly obvious at the prosoma–opisthosoma transition. The problem of whether segment VII is prosomal or opisthosomal has been alluded to above. In modern horseshoe crabs the anteriormost opisthosomal somites have been incorporated into the prosomal dorsal shield (Fig. 2). In several basal euhelicerates the tergite of somite VII is reduced to a microtergite. In eurypterids and scorpions somite VII is also foreshortened (Figs. 2–3) and the first opisthosomal tergite is no longer expressed. In ricinuleids and trigonotarbids the first tergite tucks under the posterior margin of the prosomal dorsal shield as part of the so-called locking ridge (Figs. 3 and 5). In several arachnids somite VII is associated with a narrowing of the body, reaching its tightest constriction as the pedicel (or petiolus) of spiders and whip spiders, which divides the prosoma anatomically from the opisthosoma (Fig. 5). It is interesting to speculate why this trend occurred. Perhaps it confers increased motility on the opisthosoma; spiders can move the opisthosoma quite a lot during web building and whip scorpions and schizomids can raise the opisthosoma to appear more scorpion-like in a behaviour called ‘aggressive posturing’. Furthermore the tetrapulmonate arachnids like spiders have certain limb joints which are hydraulic (summarised by Shultz, 1989); expanded by increasing blood pressure rather than muscular activity. A possible advantage of a pedicel in arachnids with hydraulic limb joints is that it physically isolates the opisthosoma from high blood pressures generated in the prosoma during locomotion. Paul and Bihlmayer (1995) studied the circulatory physiology of a tarantula spider. High blood pressures in the prosoma were not transmitted to the opisthosoma, apparently thanks to a (muscular?) occlusion mechanism at the anterior end of the narrow pedicel.

Ventrally, the appendages of somite VII may be functionally part of the prosoma, as with the chilaria of horseshoe crabs, the metastoma of chasmataspids, eurypterids and (perhaps?) the

scorpion sternum (Figs. 2–3). In other arachnids appendages on somite VII have been lost completely, and in pseudoscorpions and trigonotarbrids there is no evidence for a sternite here either (Figs. 3 and 5). Somites VII and VIII may be displaced forwards, as in harvestmen, several groups of mites and in rincinuleids, effectively bringing the genital opening functionally into the prosomal region.

4.7. The opisthosoma

The number of opisthosomal somites in euhelicerates varies from a maximum of 13 down to 9 or even 5, depending on how mites and ticks are interpreted. Whether the total number of somites in individual orders is phylogenetically significant is a moot point, but at least within the Pantetrapulmonata (spiders and their relatives, Fig. 5) there seems to be a stable pattern of 12. Mites remain highly problematic in this context (Fig. 4) and it is difficult to do justice to all the published hypotheses within the present review. In the acariform mites, the main questions seem to resolve around the fate of the dorsal elements of somites V and VI: are they integrated into a prosoma, lost or not expressed, or do they represent the first segment(s) of the hysterosoma? In the latter case, is the first visible segment of the hysterosoma equivalent to one somite (C) or to two (C1 and 2)? Thus, is there a groundplan of 13 or 14 somites in acariform mites, or several more as in van der Hammen's (1989) scheme? The parasitiform mites have been most recently proposed as having 17 somites (Fig. 4), but as noted above there are challenges in reconciling this hypothesis with the observed morphology of mesostigmatid mites and ticks.

4.8. Posterior pseudotagmata

In the megacheiran *Yohoia tenuis* (Fig. 1) the last three trunk segments are slightly offset and ring-like. A number of chelicerates also show a trend towards subdividing the opisthosoma, whereby a pre- and postabdomen could also be regarded as pseudotagmata; here towards the back of the body. Several synziphosurines, including the two figured here (Fig. 2), again have the last three opisthosomal segments as ring-like elements forming a postabdomen. Why they did this is unclear. Perhaps this conferred some motility for the telson if they needed to right themselves? Chasmataspidids have their unusual 4 + 9 tagmosis and several scorpion-like eurypterids have the last five segments offset against the rest of the body (Fig. 2). Among arachnids, the scorpion tail (Fig. 3) is again formed from the last five segments (somites XV–XIX) and this has an obvious functional advantage in conferring manoeuvrability for the sting. In rincinuleids and the pantetrapulmonate arachnids there seems to be a trend towards consolidating their last two or three somites (XVI–XVIII) into a series of short, ring-like segments (a postabdomen or pygidium, Fig. 5). This is also reflected in the 'Arachnida micrura' concept developed by Hansen and Sørensen (1904); however it is important to stress that these are *not* the same three somites which form the postabdomen in synziphosurines (cf. Fig. 2).

4.9. Opisthosomal appendages

Opisthosomal appendages are clearly retained within chelicerates as the gill opercula in horseshoe crabs, chasmataspidids and eurypterids (Fig. 2). As noted above, their flattened plate-like structure defines Euhelicerata. In pulmonate arachnids (Figs. 3 and 5) these opercula are probably retained as the ventral sclerites covering the book lungs (Shultz, 1993, 1999). It is important here to reiterate that scorpions have their book lungs on somites

X–XIII, whereas in pantetrapulmonate arachnids they are in a non-homologous position on the two preceding somites (VIII–IX) instead. In modern Xiphosura there is also no gill on the genital operculum (somite VIII). Thus arachnids and horseshoe crabs must share a distant common ancestor which still had a gill/lung on somite VIII. It is interesting to note that the Silurian fossil *Dibasterium durgae* appears to reflect (or retain) this condition (Briggs et al., 2012), which is consistent with a basal position for this fossil within Euhelicerata.

Other structures in arachnids – ventral sacs, genital verrucae, genital acetabula, gonopods – may also represent highly modified or vestigial opisthosomal appendages. It is not always clear whether these structures ultimately derive from the endopod, the exopod, or even the original basipod. Scorpion pectines represent an interesting case. Their structure, with small platelets borne on a shaft, is somewhat reminiscent of the original gill branch in the biramous limb seen in putative chelicerate outgroups (Fig. 1); see also remarks in Størmer (1944: Fig. 23). Pectine development was studied by Farley (2011), who noted that they appear early in development – before typically terrestrial features like the book lungs – thus he speculated that the pectines may have played a (paddle-like?) role in the original aquatic environment. However, at least some Silurian scorpions appear to have lacked pectines (Dunlop et al., 2008). Either some early scorpions lost their pectines, or perhaps they originated within Scorpiones by reactivating suppressed genes for appendage development on somite IX. This is also the mechanism proposed for the origin of spider spinnerets. Having silk glands opening on movable appendages is clearly advantageous for placing individual threads more precisely. Yet none of the spider's closest relatives (Fig. 5) preserve prominent appendages (with multiple podomeres) on somites X and XI; the closest match being the trigonotarbrids who have ventral sacs shaped like raised pustules on somite X.

4.10. The telson

Finally, a telson evidently belongs to the chelicerate groundplan, being present in all potential outgroups (Fig. 1). It was retained in some fossil sea spiders and in all basal euhelicerates found so far, as well as in horseshoe crabs, chasmataspidids and eurypterids (Fig. 2). At least modern horseshoe crabs use the telson to help right themselves if they get turned over (Vostaka, 1970), and some eurypterids may have used theirs as a rudder (Plotnick and Baumiller, 1988). By contrast most arachnids have reduced or lost the telson (Figs. 3–5). Perhaps dragging a long, rigid telson behind them became more of a hindrance than a help in a terrestrial environment? The telson has been retained in a modified form as the scorpion sting, probably as the anal operculum in harvestmen (and the extinct phalangiotarbrids too?), or as a sensory whip-like flagellum in palpigrades, the extinct uraraneids, whip scorpions and schizomids. As noted above, male schizomids uniquely have a modified flagellum (Fig. 5) which the female holds onto during mating (Sturm, 1958).

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