

The sejugal furrow in camel spiders and acariform mites

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Abstract: Camel spiders (Arachnida: Solifugae) are one of the arachnid groups characterised by a prosomal dorsal shield composed of three distinct elements: the pro-, meso- and metapeltidium. These are associated respectively with prosomal appendages one to four, five, and six. What is less well known, although noted in the historical literature, is that the coxae of the 4th and 5th prosomal segments (i.e. walking legs 2 and 3) of camel spiders are also separated ventrally by a distinct membranous region, which is absent between the coxae of the other legs. We suggest that this essentially ventral division of the prosoma specifically between coxae 2 and 3 is homologous with the so-called sejugal furrow (the sejugal interval *sensu* van der Hammen). This division constitutes a fundamental part of the body plan in acariform mites (Arachnida: Acariformes). If homologous, this sejugal furrow could represent a further potential synapomorphy for (Solifugae + Acariformes); a relationship with increasing morphological and molecular support. Alternatively, outgroup comparison with sea spiders (Pycnogonida) and certain early Palaeozoic fossils could imply that the sejugal furrow defines an older tagma, derived from a more basal grade of organisation. In this scenario the (still) divided prosoma of acariform mites and camel spiders would be plesiomorphic. This interpretation challenges the textbook arachnid character of a peltidium (or ‘carapace’) covering an undivided prosoma.

Key words: Acariformes, morphology, outgroups, phylogeny, Solifugae, tagmosis

Camel spiders (Arachnida, Solifugae) are a fascinating group of arachnids which, as their name implies, predominantly occur in arid habitats. These fast-moving and voracious predators are also sometimes referred to as wind scorpions or sun spiders. Over a thousand living species are known (HARVEY 2003) and they occur in suitable environments in all subtropical to tropical zones, with the curious exception of Australia. For a summary of their biology see PUNZO (1998). Camel spiders are morphologically and phylogenetically of interest in that they differ in certain key aspects from the typical arachnid groundplan. The best example of this is that the prosoma is not covered by a single dorsal shield. This structure is widely referred to in the arachnid taxonomic literature as the carapace. Strictly speaking – from the perspective of comparative arthropod morphology – the term ‘carapace’ should be restricted to crustaceans and the arachnid structure is better referred to as a prosomal dorsal shield, or (*sensu* BÖRNER 1904) a peltidium.

In camel spiders, schizomids (Schizomida) and pal-pigrades (Palpigradi) the peltidium is not a single plate, but is divided into a series of discrete dorsal sclerites. These are conventionally referred to as the pro-, meso- and metapeltidium. In fact the camel spider propeltidium seems to be even more complex and composed of multiple elements (KÄSTNER 1932, ROEWER 1932).

Authors such as BERNARD (1896, 1897) and KÄSTNER (1932) interpreted this basic tagmosis pattern in camel spiders as plesiomorphic, presumably reflecting a grade of organisation which predates the traditional arachnid prosoma. Other workers explicitly treated a ‘divided carapace’ as a derived character state (WEYGOLDT & PAULUS 1979, SHULTZ 1990, 2007). Irrespective of polarity, the camel spider condition has interesting parallels with certain mites (Acari), which also express a dorsal sclerite again associated with the chelicerae, pedipalps and the first two pairs of walking legs (COINEAU 1974, EVANS 1992, ALBERTI & COONS 1999, WEIGMANN 2001). This whole body region down to the second pair of legs has been termed the proterosoma and the dorsal sclerite covering it is usually called the prodorsum (e.g. WEIGMANN 2001). The name ‘aspidosoma’ can also be found in the literature but, as discussed by WEIGMANN, this term should refer to tergites explicitly associated with the gnathosoma, and there is no evidence that these structures have overgrown the rest of the proterosoma as per the evolutionary scenarios proposed by authors

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such as GRANDJEAN (1969), COINEAU (1974) and VAN DER HAMMEN (1989). In general, issues remain among mites with respect to questions of segmental homology and the use of a standard terminology.

These observations also reflect two recurrent problems in arachnid comparative morphology (see e.g. DUNLOP 2000). The first is the use of divergent terminologies for essentially the same structures in mites and non-mite taxa. The second is the use of the same term, e.g. 'carapace', for non-homologous structures across different arthropod groups. Such discrepancies in nomenclature can mask potential synapomorphies. Here, we draw attention to an older – albeit largely overlooked – observation that camel spiders not only have an obvious *dorsal* division of the prosoma, but also express a distinct *ventral* division (Fig. 1), specifically between the coxae of the second and third pair of walking legs (BERNARD 1896, ROEWER 1932, VAN DER HAMMEN 1989). We believe this character to be of some significance and potentially homologous with the so-called sejugal furrow, which also runs between legs two and three in certain lineages of mites (Figs 2–4).

Several studies either proposed that mites should be split into two distinct clades (e.g. VAN DER HAMMEN 1989, ALBERTI 2006) or did not recovered these two lineages as sister taxa in their cladograms (DABERT et al. 2010, PEPATO et al. 2010, REGIER et al. 2010). These groups are here termed Acariformes and Parasitiformes (= Actinotrichida and Anactinotrichida) and these publications imply that Acari, in its traditional sense, may not be monophyletic. The sejugal furrow is widely cited as a fundamental part of the body plan in numerous acariform lineages only (e.g. COINEAU 1974, ALBERTI & COONS 1999, ALBERTI 2006, DUNLOP & ALBERTI 2008). We argue here that it is present in camel spiders too, and should be scored as such in future cladistic analyses. The sejugal furrow may therefore contribute towards a larger set of morphological and molecular data (ALBERTI & PERRETTI 2002, DABERT et al. 2010, PEPATO et al. 2010, and references therein) explicitly supporting a novel (Solifugae + Acariformes) clade. However, as noted by Bernard and Kästner above (see also Discussion), an alternative interpretation would be that the body region defined by the propeltidium/sejugal furrow is part of an older arthropod groundplan. If so, this would raise questions about the original pattern of anterior tagmosis among arachnids: namely did the first arachnids have a prosoma or a proterosoma?

Historically, KITTARY (1848) differentiated the camel spider prosoma into a 'head' (the propeltidium) and 'thorax' (meso- and metapeltidium) and observed paired spiracles opening ventrally on a membrane between them. The comprehensive study of BERNARD (1896, p. 308) stated that "The Galeodidae show the primitive metamerism of the body more markedly than any other Arachnid". He added (p. 308) "The Galeodidae can bend the body not only between the 6th and 7th segments (at the waist), but also between the 4th and 5th". While Bernard did not explicitly describe the ventral membrane between segments 4 and 5, its presence can be easily inferred from his illustrations (pl. 27, fig. 15, pl. 29, fig. 6). ROEWER

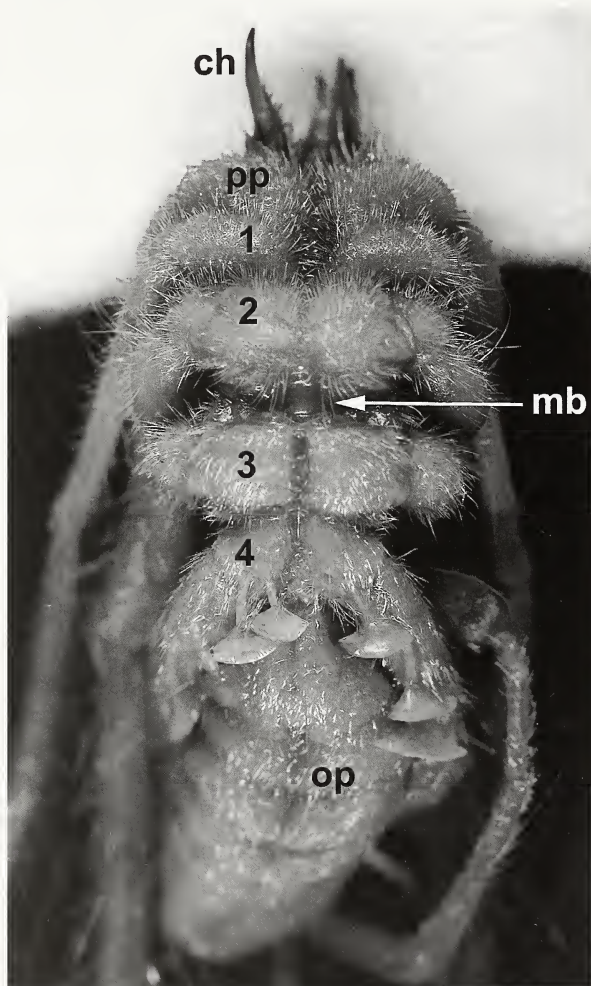


Fig. 1: Camel spider (Solifugae: *Galeodes* sp.) in ventral view. Prosomal region artificially bent slightly backwards to tease out a natural, membranous division (arrowed) between the second and third leg coxae. Abbreviations: ch = chelicerae, mb = membrane (interpreted here as homologous with the sejugal furrow), op = opisthosoma, leg coxae numbered from 1–4.

Sejugal furrow in camel spiders

(1932: 43, fig. 33) explicitly stated for the coxae that "Only these of the 2nd and 3rd walking legs are divided by a wide, soft membrane." [our translation]. KÄSTNER (1932) did not explicitly mention a ventral division, but seems to have been more concerned with the composition of the dorsal prosoma. He did, however, mention structures (also noted by BERNARD 1896) which partly divide the body internally and further help to define and offset this anterior body region. KÄSTNER (1952: fig. 9) seemed to indicate this ventral membrane in a lateral view of a late-stage camel spider embryo. He labelled the region between coxae two and three 'G', but did not define this in the figure legend. It may refer to "Gelenkhaut" [= membrane]. Most recently, VAN DER HAMMEN (1986, 1989: 249), formally stated that for camel spiders "The coxisternal regions of legs II and III (epimera 2 and 3) are transversely separated by the sejugal interval (an intersegmental area of soft skin, which allows of prosomatic articulation)." Here, we confirm these observations and further discuss their potential phylogenetic significance.

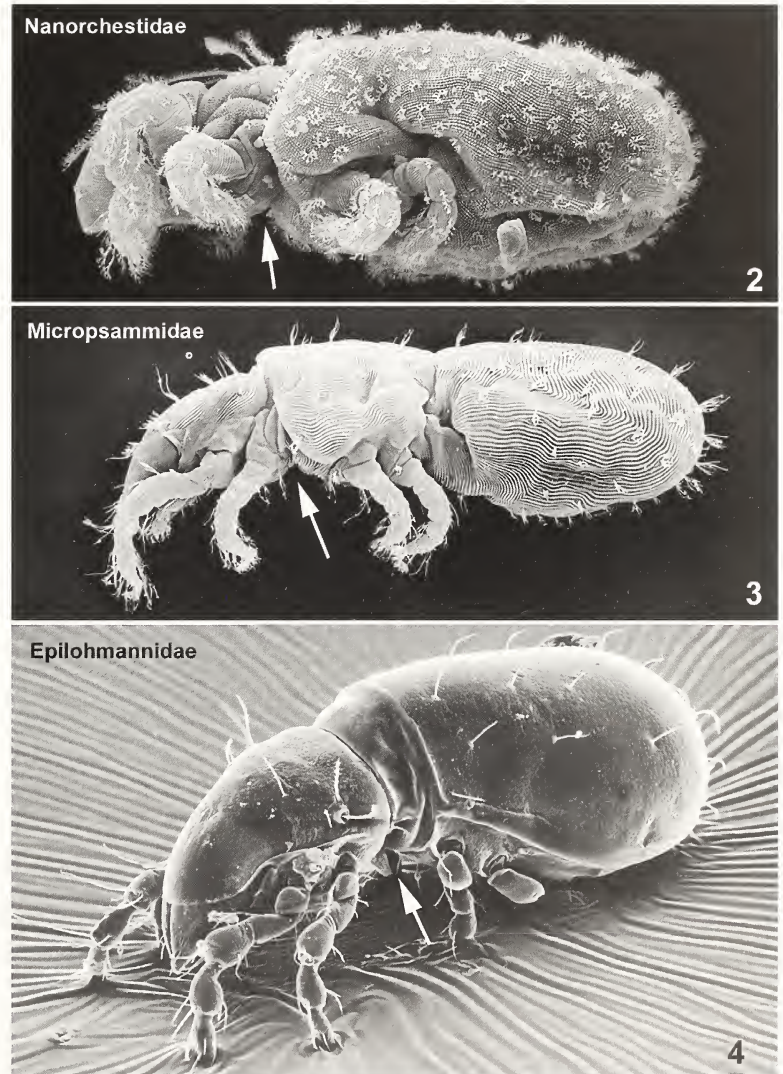
Material and Methods

Camel spider gross morphology was examined under a dissecting microscope. Specimens were carefully bent backwards and/or manipulated with tweezers to investigate where the basic division(s) in the ventral body surface lay. To determine whether the resulting observations were typical for the whole order, representatives of nine of the twelve currently recognised families (cf. Harvey 2003) were examined based on alcohol-preserved specimens in the Museum für Naturkunde, Berlin. Specimens of Melanoblossidae, Mummuciidae and Eremobatidae were not available, but all other families revealed a consistent morphology which we thus presume to be the groundplan character for Solifugae. The ventral prosomal anatomy is easier to resolve in larger

specimens, six of which are illustrated here (Figs. 5–10). Specimens were photographed using a Canon Eos digital camera with either a x1 or a x3 macro lens. The resulting images were cleaned and assembled in Adobe Photoshop. Comparative scanning electron micrographs (Figs. 2–4) of representative acariform mites were produced by GA.

Results

In ventral view, the prosoma of camel spiders from a range of different families (Figs 5–10) presents a fairly



Figs. 2–4: Comparative scanning electron micrographs of selected acariform mites. Note again the principal division between the second and third pair of leg coxae (arrowed); specifically formed here by the so-called sejugal furrow. **2** - *Neonanorchestes ammolitoreus* McDaniel & Bolen, 1981 (Endeostigmata: Nanorchestidae). **3** - *Micropsammus littoralis* Theron & Coineau, 1983 (Endeostigmata: Micropsammidae). **4** - *Epilohmannia cylindrica* (Berlese, 1905) (Oribatida: Epilohmannidae). Not to scale.

compact series of pedipalp and limb coxae. There is no plate-like sternum between the leg coxae, as in spiders (Araneae) for example, nor is there a series of ventral sclerites between the coxae as per Palpigradi. Furthermore, there is no superficial evidence of a 'break' between the successive coxal pairs. In fact the dividing line elaborated here is best revealed by simply taking a specimen and gently bending the prosoma backwards or sideways. The ventral surface naturally opens up between the second and third pair of leg coxae (Fig. 1); precisely because they are separated by a pale, flexible membrane; superficially similar to the pedicel (or petiolus) of a spider. In gross morphology this membrane is similar in form to an arthrodial membrane between adjacent limb articles and does not reveal any embedded sclerites. It forms a distinct narrowing, with a maximum width about a third of the width of the adjacent coxal pairs, and can be followed as a dividing line up the lateral sides of the animal – where it merges smoothly into the dorsal membrane dividing the propeltidium from the mesopeltidium. Significantly, physical manipulation of the prosoma reveals that none of the other coxal pairs can be teased apart in this way to the same extent. In other words, the coxae of the pedipalps, plus legs 1 and 2, essentially form an anterior functional unit. The coxae of legs 3 and 4 form a corresponding posterior functional unit. We interpret this as clear ventral evidence of tagmosis; whereby the soft, membranous suture (Fig. 1: mb) defines an anterior body region bearing the chelicerae, pedipalps and first two pairs of walking legs: the same body region that is dorsally associated with the propeltidium.

Discussion

Here we confirm and illustrate previous observations about the flexibility of the camel spider body between the second and third pair of walking legs. The body region defined dorsally by the propeltidium in Solifugae is also delimited ventrally by a membranous region (Fig. 1), which essentially continues laterally and forms a flexible ring around the animal more or less in the middle of its prosoma. This membrane is, incidentally, also the place where a pair of spiracles opens on the lateral sides of the body. In searching for comparable tagmosis features among other arachnids the most obvious candidate is the sejugal furrow of acariform mites; a character which we reiterate does not occur in the parasitiform lineage. Precise definitions of this character in the literature vary slightly, but to quote some recent authors the sejugal (or

dorsosejugal) furrow:

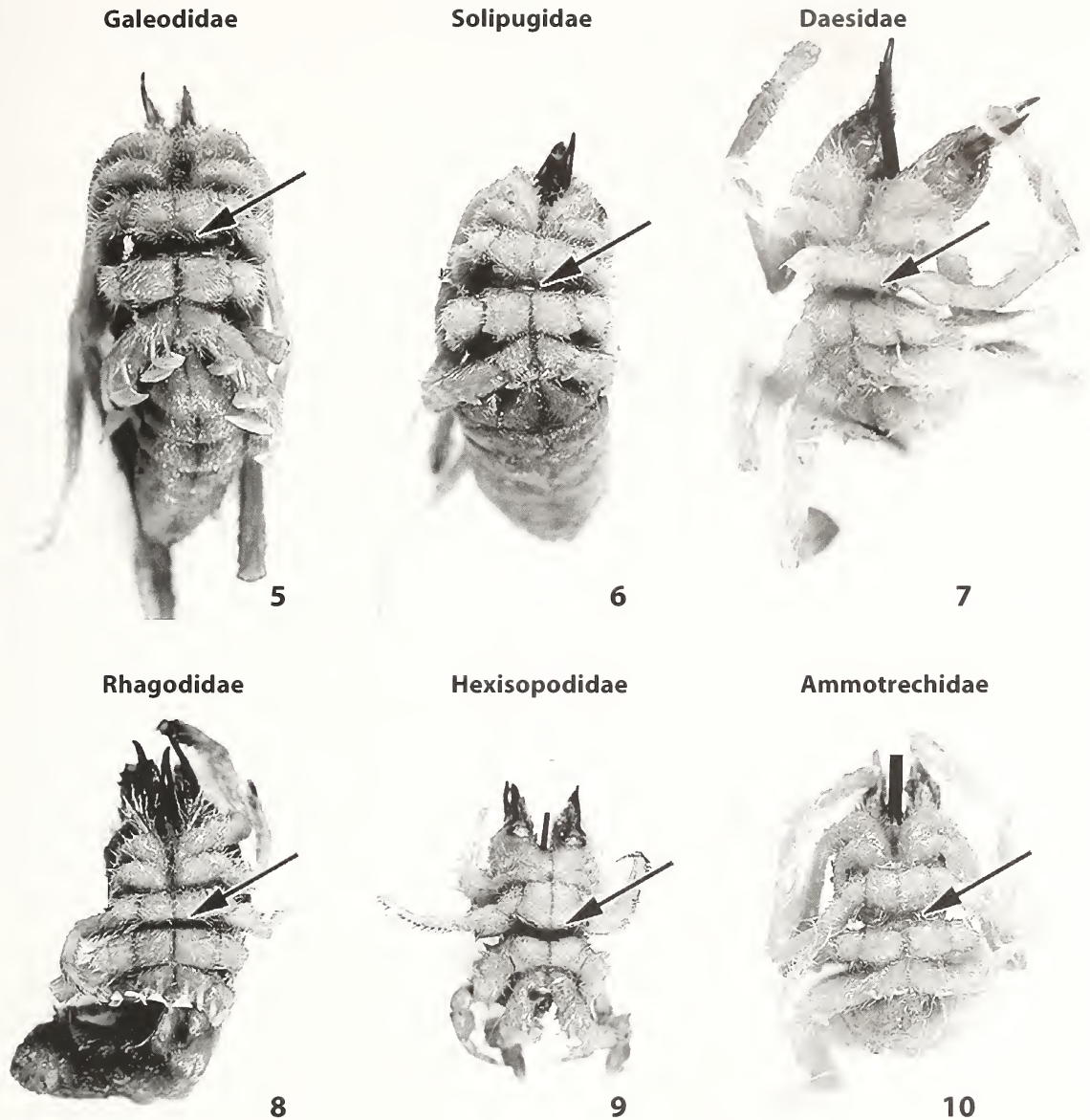
- 1) is "Pertaining to the furrow or interval separating, in Actinotrichida, propodosoma and metapodosoma." (VAN DER HAMMEN 1980: 140),
- 2) is "a transverse furrow running between legs II and III and separating them. This furrow [...] extends dorsally and thus divides the body into an anterior part, the proterosoma and a posterior part the hysterosoma." (ALBERTI 2006: 327),
- 3) is a "circumferential zone of body flexibility that passes between the coxae of legs 2 and 3" (SHULTZ 2007: character 7).

We argue here that on all these criteria a sejugal furrow can reasonably be scored as present for Solifugae too. VAN DER HAMMEN (1989: 249) came closest to this by recognising (and naming) a 'sejugal interval' in camel spiders, but idiosyncrasies in his work have limited the impact of his views. First, he frequently referred to the coxae as 'epimera', as part of a novel hypothesis about coxal origins and evolution. The use of the term epimera – and his general habit of describing all arachnids using mite terminology – tended to marginalise his work. Second, van der Hammen rejected cladistics, and his (sometimes detailed and accurate) observations have been largely overlooked by later authors scoring characters for phylogenetic analyses.

Poecilophysidea

The presence of what we interpret as a sejugal furrow in camel spiders further emphasises their morphological similarity to certain mites (Figs. 2–5) (see also DUNLOP 1999, 2000). Specifically, the sejugal furrow is another potential synapomorphy for a relationship of the form (Solifugae + Acariformes). Most authors have recovered camel spiders as the sister group of pseudoscorpiones (WEYGOLDT & PAULUS 1979, VAN DER HAMMEN 1989, SHULTZ 1990, 2007). Basal (i.e. chthoniid) pseudoscorpions do indeed resemble camel spiders quite closely and this traditional Haplcnemata clade (BÖRNER 1904) is supported by a range of characters such as legs with a very short femur and a correspondingly long patella, two-segmented and chelate chelicerae, and tracheal spiracles opening on the 3rd and 4th opisthosomal segments.

Nevertheless, there is also evidence linking mites and camel spiders; a hypothesis with historical precedent (BANKS 1915). Mites, solifuges (and also pseudoscorpions) have a mouth on a projecting 'beak', or rostrum in some terminologies, and also



Figs. 5–10: Ventral prosomal region in six of the twelve currently recognised camel spider families. Note again in all cases the principal division between the second and third pair of coxae (arrowed); in larger specimens a pedicel-like membranous region here is clearly evident. **5** - *Galeodes armeniacus* Birula, 1929 (Galeodidae: ZMB 17972). **6** - *Zeria keyserlingi* (Pocock, 1895) (Solipugidae: ZMB 15646). **7** - *Biton (Biton) kolbei* (Purcell, 1899) (Daesiidae: ZMB 15517). **8** - *Rhagodocatermes* (Karsch, 1885) (Rhagodidae: ZMB 15642). **9** - *Chelypus barberi* Purcell, 1902 (Hexisopodidae: ZMB 48436). **10** - *Pseudocleobis andinus* (Pocock, 1899) (Ammotrechidae: ZMB 15634). Not to scale.

have chelicerae in which the movable digit articulates ventrally relative to the fixed digit (BERNARD 1896, DUNLOP 2000). Two characters of the reproductive system have been elucidated exclusively for Solifugae and Acariformes (cf. ALBERTI 1980a, b, 2000, ALBERTI & PERETTI 2002, KLANN et al. 2009):

namely simple, aflagellate sperm and a large glandular area of the testis producing secretions. The present tagmosis character of a propeltidium/proterosoma/propodosoma/aspidosoma/sejugal furrow can now potentially be added to this list; although we should caution against the risk of character duplication. For

example SHULTZ (2007) scored the 'divided carapace' and the sejugal furrow as two separate characters. However, but it may be better to treat them as parts of a single character complex relating to tagmosis.

In addition to this morphological data, recent molecular (DABERT et al. 2010) and combined (PEPATO et al. 2010) studies have also picked up a strong molecular signal for (Solifugae + Acariformes). It will be interesting to see whether further investigations of this nature continue to support these results. PEPATO et al. (2010) even went so far as to recognise a clade Poecilophysidea for camel spiders and acariform mites – and a clade Cephalosomata for poecilophysids plus palpigrades. The latter group potentially share the character of a 'cephalosoma'; a discrete anterior body region (see above) covered by the propeltidium and bearing the first four pairs of appendages.

In this context, we should briefly consider whether a sejugal furrow/interval occurs in the other arachnids with a divided peltidium. VAN DER HAMMEN's (1989) account of palpigrade morphology does not explicitly mention such a furrow between leg coxae 2 and 3, and this character is probably hard to test here since the highly flexible body of these animals is only weakly sclerotised. In palpigrades the coxae of the pedipalps and first walking limbs are associated with a sclerite, and each of the successive pairs of limb coxae are associated with a corresponding separate plate (see e.g. BÖRNER 1904: fig. 4). Or to quote ROWLAND & SISSOM (1980: 76), "Following the deutotritosternum and lying between the second, third, and fourth pair of walking legs are the tetrasternum, pentasternum, and metasternum, respectively." Thus in palpigrades leg coxae 2, 3 and 4 are all to a certain extent 'free'. For schizomids, there is again no mention of a specific furrow between legs 2 and 3 in VAN DER HAMMEN (1989). The classic and detailed study of BÖRNER (1904: fig. 2) is likewise circumspect about a specific zone of flexibility here.

A cephalosoma or a divided carapace?

But is 'Cephalosomata' a clade or a grade? We suggest that both acariform mites and camel spiders share an anterior tagma bearing four pairs of appendages which is essentially separated from the rest of the body by a membranous zone for which the mite term 'sejugal furrow' is available and appropriate. WEYGOLDT & PAULUS (1979) and SHULTZ (2007: characters 6–7) interpreted both a divided carapace (in camel spiders, palpigrades and schizomids) and the presence of a

sejugal furrow (in acariform mites) as derived conditions; justifying polarity by using *Limulus* (Xiphosura) – with its large, unitary prosomal dorsal shield and lack of ventral segmental differentiation – as the outgroup.

Further down the euarthropod tree we encounter alternative outgroups such as sea spiders (Pycnogonida) in which the fundamental tagmosis is between a so-called cephalosoma, bearing four pairs of appendages (VILPOUX & WALOSZEK 2003: Fig. 13), and the successive separate segments of the trunk. This cephalosoma is segmentally homologous to the anterior tagma of camel spiders, acariform mites and palpigrades (DUNLOP & ARANGO 2005: Fig. 5). Adopt sea spiders as the outgroup and the 'divided carapace' / sejugal furrow could be interpreted as a plesiomorphic state; retained from an earlier grade of organisation. This is essentially the argument put forwards by BERNARD (1886) and KÄSTNER (1932, 1952) who thought that the divided camel spider prosoma revealed the original arachnid morphology. Authors such as REMANE (1962: 214) have argued that the arachnid prosoma fundamentally consists of a four-segmented head region – bearing the chelicerae, palps and legs 1 and 2 – plus two additional segments bearing leg pairs 3 and 4 respectively. Further discussion can be found in KRAUS (1976), who again favoured the idea that separate prosomal elements reflect a '4+2' arachnid groundplan, or WEYGOLDT & PAULUS (1979) who preferred instead to interpret these divisions as derived and homoplastic features, possibly adapted for increasing prosomal mobility.

Finally, we should mention a series of early Palaeozoic arthropods expressing raptorial anterior limbs – the 'great appendage' arthropods, or Megacheira in some schemes – which some authors interpret as stem-group Chelicerata (CHEN et al. 2004). These fossils also appear to preserve an anterior body tagma bearing four pairs of appendages which authors such as Waloszek and co-workers have termed the 'euarthropod head' (see also REMANE's 1962 hypothesis) and which they interpret as a fundamental part of the body plan in early arthropods (cf. CHEN 2009: Fig. 11). Using megacheirans as an outgroup would again polarise the tagmosis pattern of mites, camel spiders (and palpigrades?) as a plesiomorphic, groundplan, character state for arachnids. In this scenario, a unitary prosomal dorsal shield (or peltidium) emerges as a derived character state; perhaps even homoplastic across Arachnida.

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