Character states and evolution of the chelicerate claws

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Abstract
Outgroups of Chelicerata have an apotele in which two smaller claws insert on a larger median claw. A three-clawed plesiomorphic state is retained in basal Pycnogonida and the Palaeozoic xiphosuran *Weinbergina*. Modifications or reductions from this pattern are interpreted here as apomorphic character states. A single apotele element occurs in the crown group Xiphosurida and in the extinct taxa Eurypterida and Chasmataspida. The digitigrade, 'eurypteroid' apotele of *Allopalaeophonus*-like fossil Scorpiones may not be the plesiomorphic condition for the group since the most basal clade, *Palaeoscorpius*, has an apotele more like *Weinbergina* and the outgroups. Among the other arachnids Palpigradi retain the most plesiomorphic apotele morphology with three claws on all postcheliceral appendages. Unequivocal homologies between the claws in different arachnid orders are difficult to resolve, especially in relation to the complex apoteles seen among the Acari. However, further apomorphic apotele states in arachnids include the development of the empodial region between the claws into a pulvillus in adults of basal Amblypygi, in Solifugae and Pseudoscorpiones and among the mites in the (Opilioacariformes + Parasitiformes) clade, but *not* in basal Acariformes.

Key words: Apotele, claw, ungue, empodium, pulvillus, Chelicerata, phylogeny

INTRODUCTION

The terminal element of the postcheliceral limbs in Chelicerata is called the apotele. This apotele has been modified in arachnids to form the claws, while in some taxa (e.g. solifuges, some amblypygids) the membranous region between the claws - the empodium - has been further modified to form a complex, typically eversible structure which is usually called the pulvillus. Chelicerate limb morphology, including apotele character states, has been reviewed by authors such as Barrows (1925), van der Hammen (1989) and Shultz (1989). However, these authors restricted their surveys to Recent euchelicerates and did not consider the basal pycnogonid group (sea spiders), extinct taxa (e.g. eurypterids) or fossil representatives of

scorpions and xiphosurans. Palaeozoic fossils of the latter two taxa preserve character states different from extant forms, which probably better reflect the ground pattern of these clades. The aim of the present paper is to give an overview of apotele morphology which integrates the fossil data and to try and identify potential synapomorphies for clades within the chelicerates.

MATERIALS AND METHODS

Wherever possible specimens of Recent taxa were drawn from life from material in the collections of the Muesum für Naturkunde, Berlin, supplemented by descriptions in the literature as detailed below. Well preserved eurypterids and trigonotarbids from the Natural History

Museum, London were also examined. Terminology generally follows Barrows (1925) and/or Shultz (1989).

RESULTS

Outgroups (Trilobita)

The sister group of Chelicerata (including pycnogonids) has not been satisfactorily established, but Trilobita, and various arachnomorph or trilobite-like taxa, have emerged as potential outgroups for polarising chelicerate characters. Appendage morphology can only be determined with certainty in a few fossils showing exceptional preservation. Studies of *Triarthrus* by Cisne (1975) and Whittington & Almond (1987), of *Agnostus* by Müller & Walossek (1987) and of *Phacops* by Bruton & Haas (1999) consistently show an apotele morphology in which two lateral claws appear to insert into a slightly larger central claw (Fig. 1a). These three apotele structures are potentially homologous with the three claws seen in many chelicerates (see below) and provide a plesiomorphic condition against which the chelicerate apotele can be compared.

Pycnogonida

Most phylogenetic studies have concluded that Pycnogonida are basal chelicerates (Weygoldt & Paulus 1979; Wheeler & Hayashi 1998), representing the sister group of all other chelicerates: the Euchelicerata. The palps (limb II) of Pycnogonida are variable within the group and are reduced or absent in adults of certain taxa. Nevertheless, a distinct apotele in the palp appears to be lacking, at least in adults. By contrast, the oviger (limb III) - also absent in some taxa - ends in a single claw in most groups where it is present (Arnaud & Bamber 1987). The legs of Pycnogonida (limbs IV-VII) typically end in three claws (Fig. 1b): a main claw plus a pair of auxiliary claws (Arnaud & Bamber 1987). The relative proportions of these claw elements can vary, even intraspecifically (e.g. Helfer & Schlottke 1935, fig. 44). The main claw is usually longer than the auxiliary claws, but see e.g. *Ammothea biunguiculata* where the main claw is tiny, and in contrast to the trilobite condition (see above) the auxiliary claws do not insert into the main claw, but arise from the membrane above it (Fig. 1b). The auxiliary claws are lost in more derived clades, e.g. Pycnogonidae.

Xiphosura

Following Anderson & Selden (1997), the class Xiphosura (horseshoe crabs) can be divided into a series of stem group plesion taxa, the synziphosurines, plus a monophyletic crown group, Xiphosurida. Appendages are rarely preserved in Palaeozoic Xiphosura, but significantly the Lower Devonian synziphosurine *Weinbergina opitzi* (Fig. 1c) lacks the chelate postcheliceral appendages with a single apotele characteristic for living species. Stürmer & Bergström (1981) redescibed *W. opitzi* and although there are inconsistencies in their interpretative drawings, their plates (especially their fig. 7a) indicate a trifurcate apotele with all three elements approximately the same size. These three elements appear to emerge adjacent to each other (Fig. 1c) and the lateral elements do not insert on the central one as in the trilobites. By contrast, extant Xiphosura have only a single apotele element in all their postcheliceral limbs which forms the movable finger of a distal chela (Fig. 1d). This apparently apomorphic condition arose in the Xiphosurida by the Carboniferous, having been recently described in the fossil genus *Euproops* by Schultka (2000, pl. 1, fig. 2). In Recent taxa this chela is larger in appendages II-V, but rather small in appendage VI and is essentially subchelate in appendages III and IV of the extant species *Tachypleus tridentatus*.

Eurypterida

In most reconstructions the extinct Eurypterida (sea scorpions) are shown with a trifurcate end to the legs. Jeram (1998) referred to the lateral elements as 'tarsal spurs' and suggested that homologous structures occur in fossil scorpions and that they are in turn homologous with the lateral claws or ungues of other arachnids (see
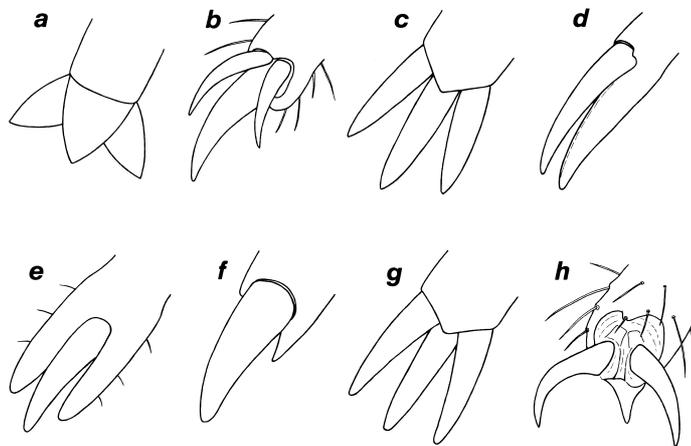
Fig. 1. (a) *Triarthrus* sp. (Trilobita). Ordovician, after Whittington & Almond (1987). **(b)** *Achelia echinata* (Pycnogonida). Recent, from life. **(c)** *Weinbergina optzi* (Xiphosura: 'synziphosurine'). Devonian, after Stürmer & Bergström (1981). **(d)** *Limulus polyphemus* (Xiphosura: Xiphosurida). Recent, from life. **(e)** *Baltoeurypterus tetragonophthalmus* (Eurypterida). Silurian, after Selden (1981). **(f)** *Diploaspis casteri* (Chasmataspida). Devonian, from original material. **(g)** *Palaeoscorpius devonicus* (Scorpiones: stem group). Devonian, after Kjellesvig-Waering (1986). **(h)** *Buthus occitanus* (Scorpiones: Buthidae). Recent, from life. All drawings not to scale.

below). However, when examined in detail - see e.g. Selden's (1981) study of *Baltoeurypterus tetragonophthalmus* - the apotele of eurypterids is represented by a single claw. The spinous elements either side of it, when present, are derived from the *preceding* podomere (Fig. 1e) either as fixed spines (see e.g. Selden 1981, figs. 26-29 for *Baltoeurypterus*) or as socketed spines (see e.g. Clarke & Ruedemann 1912, pl. 28 for *Carcinosoma*) and thus their homology with the ungues of arachnids is questionable. In stylonurid eurypterids, which lack paddles and which probably represent the more basal taxa (S. Braddy pers. comm.), the spines on this podomere preceding the apotele are either absent or only weakly developed; see e.g. Tollerton (1989, fig. 9).

Chasmataspida

Chasmataspida are a rare group of extinct chelicerates. Although initially interpreted as unusual xiphosurans, their phylogenetic position is uncertain (see Anderson & Selden 1997) since they share apomorphies with both Xiphosura and Eurypterida (Dunlop in press). Their appendages are poorly known, but Caster & Brooks (1956) described an isolated limb with chelate, distal podomeres, resembling those of Xiphosurida (see above). A better preserved limb described by Størmer (1972) and Dunlop et al. (2002) ends in a short, slightly curving element with a weakly developed spine on the preceding podomere. As in Eurypterida there is no evidence for lateral claws (Fig. 1f) and Chasmataspida should also provisionally be scored as retaining only a single element in their apotele.

Scorpiones

Among the best known Palaeozoic scorpions are the Silurian *Palaeophonus / Allopalaeophonus* species which have been figured as having crab-like legs ending in a single, large apotele - Pocock's (1901, p. 295) 'clawless terminal segment' - similar to that seen in many eurypterids (see above). However, in the phylogeny of Jeram (1998), the Lower Devonian species *Palaeoscorpius devonicus*, discovered in a marine

palaeoenvironment, emerged as the most basal scorpion taxon. Interestingly, *P. devonicus* has an apotele morphology (Fig. 1g) similar to both the outgroups and *Weinbergina* (see above) with three similar-sized claw elements. Note that the original description by Lehmann (1944) failed to note the middle claw. The lateral elements of the apotele in fossil scorpions have been called tarsal spurs (e.g. Jeram 1998), but in contrast to those of eurypterids (see above) they appear to be post-tarsal, apotele elements and Jeram homologised them with the lateral claws or ungues of Recent arachnids. Extant Scorpiones typically have a median claw shaped like a small, ventrally-pointing spike while the ungues are relatively large and strongly curved (Fig. 1h). A pulvillus-like structure has also been reported between the ungues in at least one buthid scorpion (Millot & Vachon 1949: fig. 191). The apotele of the scorpion pedipalp (limb II) has been lost in the development of the large chela which is formed from the tibia and the tarsus (Shultz 1990).

Other arachnids

Details of apotele morphology in the remaining arachnids can be found in comparative studies, in particular Barrows (1925). Fossils of the remaining orders do not present different character states compared to extant taxa. Barrows (1925) defined the arachnid claw (= the apotele) as the entire terminal segment operated by two antagonsitic tendons. The insertion points of the muscles of these tendons are phylogenetically informative and were detailed by Shultz (1989, 1990). The ventral sclerotised region of the arachnid apotele attached to the flexor tendon was called the tendon plate, the small claw which occurs here in some taxa was called the pseudonychium (other authors have simply called it the onychium or the median claw) and the larger paired claws seen in many arachnids were called the ungues (Barrows 1925); although the less appropriate term 'ungules' has sometimes been used.

Palpigradi / Araneae / Fossil orders

Palpigradi retain three claws on both the pedipalps (limb II) (Fig. 2d) and the legs (limbs III-VI) (Fig. 2e) (see also Hansen & Sørensen 1897). In Araneae (spiders) and the extinct Trigonotarbida (see e.g. Shear et al. 1987) three claws are retained on the legs (Fig 2b), but the pedipalp apotele is reduced to a single claw (Fig. 2a). Barrows (1925) described the development of the male palpal organ (a spider autapomorphy) from a so-called 'claw fundament' on the pedipalp and further noted that some Lycosidae curiously retain additional claw-like structures on the palp of mature males. Apotele morphology is unknown in the extinct orders Phalangiotarbida and Haptopoda.

Amblypygi / Thelyphonida / Schizomida

Shultz (1999, characters 14 and 17) scored Amblypygi (whip spiders), Thelyphonida (whip scorpions) and Schizomida (schizomids) as having synapomorphically fused the tarsus to the apotele in both the pedipalps (limb II) and the first pair of legs (limb III). In fact the pedipalpal apotele is retained as a distinct element both in Schizomida, see e.g. Werner (1935, fig. 26) for *Trithyreus*, and in some Amblypygi such as the basal genus *Charon*, see e.g. Weygoldt (2000, figs. 7-8). In Thelyphonida the pedipalpal apotele is barely discernible as an immovable distal structure (Werner 1935, fig. 27; personal observations). Furthermore, in contrast to Shultz's coding, an apotele *is* retained on leg 1, albeit as a pair of highly reduced claws in some Amblypygi, see Igelmund (1987) and Weygoldt (2000, fig. 81) for details. The remaining limbs (IV-VI) of thelyphonids and schizomids have a spider-like morphology with a small median claw and larger lateral claws. Amblypygids are similar, but in some taxa in place of the empodial claw there is a distinct, fleshy pad: the pulvillus (Fig. 2c). This soft, slightly folded structure presents a flattened, oval, distal face with a slight dorsal indentation in some taxa, and some sclerotised supporting elements in a more proximal position. Weygoldt (1996) interpreted the pulvillus as homologous with the
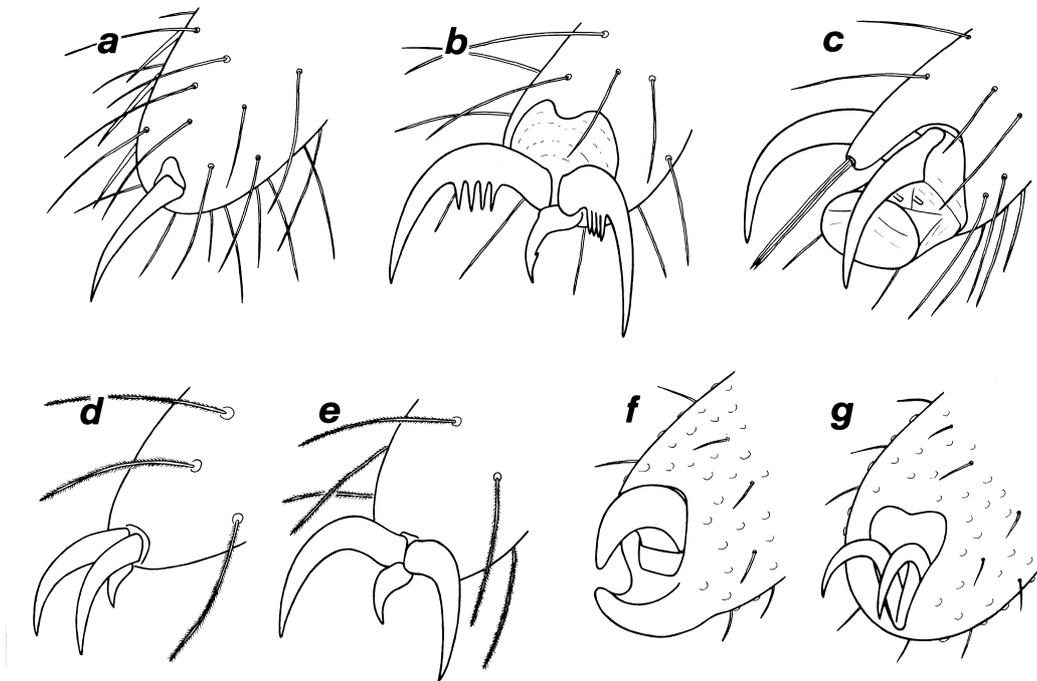
Fig. 2. (a) *Liphistius desultor* (Araneae: Liphistiidae), ♀ pedipalp. Recent, from life. **(b)** Leg of the same. **(c)** *Charon grayi* (Amblypygi: Charontidae). Recent from life. **(d)** *Eukoenenia mirabilis* (Palpigradi), pedipalp. Recent, after Hansen & Sørensen (1897). **(e)** Leg of the same. **(f)** *Ricinoides westermanni* (Ricinulei), pedipalp. Recent, from life. **(g)** Leg of the same. All drawings not to scale.

empodial claw and, since those Amblypygi without a pulvillus also lack an empodial claw, he regarded absence of a pulvillus as apomorphic within Amblypygi and a character defining an Apulvillata clade. Furthermore, Quintero (1981) noted that juveniles of the apullvilate genus *Phrynus* retain a pulvillus-like structure which may help the animal cling to its mother.

Ricinulei / Opiliones

Ricinulei retain a single apotele claw in the pedipalps (limb II) as the free finger of the minute claw (Fig. 2f). In the legs (limbs III-VI) Ricinulei appear to have lost the median claw having only two claws - ?the ungues - which can be withdrawn through a heart-shaped distal opening into a cavity at the tip of the tarsus (Fig. 2g). Basal Opiliones, i.e. Cythophthalmi, have only a single tarsal claw on both the pedipalps (limb II) (Fig. 3a) - where it is highly re-

duced in some taxa Shultz (1998, character 8) - and the legs (limbs III-VI) (Fig. 3b). However, the situation within Opiliones is more complex since the suborder Laniatores is characterised by having a single claw on the anterior two pairs of legs but *two* claws on the posterior two pairs of legs, further modified in other laniatore taxa; see e.g. Giribet et al. (1999, characters 11-12) for alternative character states. Note that some laniatore nymphs have also been described with a pulvillus-like structure in the apotele (Munzo-Cuevas 1971).

Psudoscorpiones / Solifugae

Pseudoscorpiones have lost the apotele on their large, chelate pedipalp (limb II). Pseudoscorpions retain lateral claws on the legs (limbs III-VI), but in the place of the empodial claw there is a fleshy structure (Fig. 3c) which is usually called the pedal arolium; see Harvey (1992) for arolium character states within Pseudoscor-
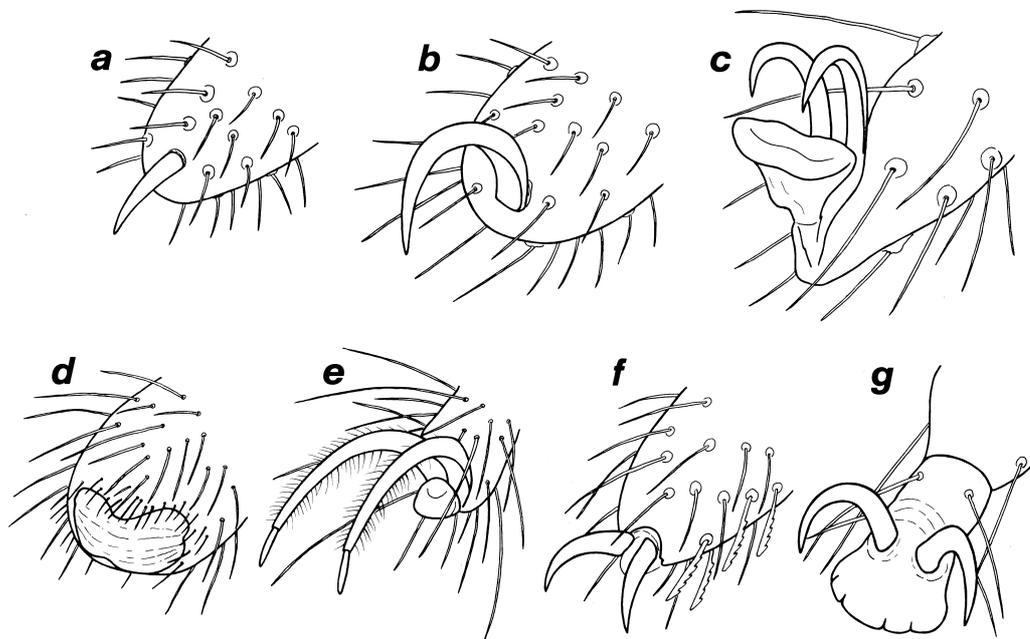
Fig. 3. (a) *Siro* sp. (Opiliones: Cythophthalmidae), pedipalp. Recent, from life. **(b)** Leg of the same. **(c)** *Neobisium* sp. (Pseudoscorpiones: Neobisiidae), leg. Recent, partly after Eisenbeis & Wichard (1985). **(d)** *Galeodes* sp. (Solifugae: Galeodidae), pedipalp. Recent, from life. **(e)** Leg of the same. **(f)** *Opilioacarus texanus* (Acari: Opilioacariformes), pedipalp. Recent, after van der Hammen (1989). **(g)** Leg of the same. All drawings not to scale.

piones. This structure was called the empodium by Shultz (1989, 1990). The pseudoscorpion arolium is basically similar in all taxa (Roewer 1936). It originates from a narrow base below the ungules and widens distally to form a pale, membranous, somewhat funnel-shaped structure with a slightly concave distal face. The arolium is extensible and Roewer (1936) suggested that extension occurs through blood pressure. The arolium functions as an attachment organ and allows pseudoscorpions to walk on vertical surfaces.

The pedipalps (limb II) of Solifugae end in a unique (autapomorphic) structure, the adhesive palpal organ (Fig. 3d). In gross morphology it forms a membranous series of 'lips' at the ventro-distal tip of the tarsus and is probably homologous with the apotele, since Roewer (1934) described articulating condyles between

it and the tarsus. Lateral claws are absent, but vestigial claw bases on the palpal organ were described and figured by both Barrows (1925, fig. 28) and Roewer (1934, fig. 75). Leg 1 (limb III) of Solifugae has all but lost its locomotory function and the claws here are either weakly developed or absent (Roewer 1934). The remaining legs (limbs IV-VI) bear large, curved lateral claws (Fig. 3e) which are uniquely subdivided (an autapomorphy) in all solifuge taxa (Roewer 1934), with the tip of each claw articulating against the rest of the ungue. Highly setous ungues (Fig. 3e) are apomorphic for Galaeodidae only (Roewer 1934) and not Solifugae in general. Like pseudoscorpions, solifuges also have a fleshy structure in place of the empodial claw (Fig. 3e). Roewer (1934) homologised these structures in these two orders and called it the arolium, a homology accepted

by Shultz (1989, 1990) who called it the empodium (see above). In Solifugae this structure is a rounded or distally widening, fleshy organ, divided into two distinct lobes in some taxa (e.g. Roewer 1934). Again extension occurs through blood pressure and an adhesive function has been suggested.

Acari

Acari are widely interpreted as monophyletic (see Lindquist 1984) and are currently divided into three major taxa: Opilioacariformes ('primitive' mites), Parasitiformes ('ticks') and Acariformes ('mites'). Acari show the largest number of empodial character states within Chelicerata and more detailed descriptions can be found in Barrows (1925), Lindquist (1984), van der Hammen (1989) and Evans (1992). It is thus difficult to score a single apotele state as 'typical' for all Acari and to homologise all the various mite structures, some of which may be setal derivatives (Evans 1992), either within Acari or in relation to other chelicerates. Lindquist (1984) tentatively regarded a three-clawed leg as plesiomorphic and this certainly seems to be true for Acariformes, see e.g. van der Hammen's (1989, fig. 49) account of the basal taxon *Alycus*. Three claws occur in many oribatid mites while other Acariformes show quite unique developments such as a single claw on a fleshy caruncle in some Astigmata (Evans 1992, fig. 2.17). By contrast in the Opilioacariformes and the Parasitiformes there is a cushion-like pulvillus between the paired lateral claws (Fig. 3g), similar to the condition seen in amblypygids, pseudoscorpions and solifuges. In Opilioacariformes the pedipalps have two claws (Fig. 3f) and this morphology is seen in many other mites too (Evans 1992).

DISCUSSION

Outgroup taxa (e.g. Trilobita), basal Pycnogonida and fossil examples of basal Xiphosura and Scorpiones all imply that the plesiomorphic apotele condition in Chelicerata was three rather spine-like elements (Figs. 1a-c, g) and not a single terminal segment as assumed by

Barrows (1925) in his otherwise excellent paper written before the discovery of well-preserved appendages in key fossil taxa. Reductions or modifications of this 3-element pattern should be treated as potential apomorphies. Recent Xiphosurida, e.g. *Limulus*, are sometimes used to polarise character states in arachnids, but the fossil *Weinbergina* suggests that the plesiomorphic apotele condition is retained in the ground pattern of Xiphosura (Fig. 1c) and that the reduction to a single apotele element in the Xiphosurida (sensu Anderson & Selden 1987) (Fig. 1d) is apomorphic only for crown group horseshoe crabs. This apomorphic character state can also be scored for the extinct Eurypterida and Chasmataspida (Figs. 1e-f) and represents a potential synapomorphy of these taxa.

In this respect Eurypterida differ from Scorpiones (Figs. 1g-h) which retain all three apotele elements as a central 'claw' plus a pair of tarsal spurs (e.g. Jeram 1998). These spurs are minute in the Silurian *Allopalaeophonus*-like scorpions and some authors have given the impression that these pointed, crab-like, digitigrade legs with a large, central claw are a ground pattern character state for Scorpiones; see e.g. Kjellesvig-Waering's (1986) suggestion that 'eurypteroid' legs in the fossils supported a close relationship between scorpions and eurypterids. However, in the most basal scorpion genus, *Palaeoscorpius*, the tarsal spurs are similar in size to the median element of the apotele (Fig. 1g). Resolving which of these conditions is plesiomorphic for Scorpiones is difficult, but there is an apparent trend in the Siluro-Devonian fossils towards enlargement of the tarsal spurs to form the typical ungues of arachnids and a corresponding reduction of the median, empodial element to form together an apotele essentially similar to that in Recent scorpions (see e.g. Jeram 1998, character 19, fig. 2: node C). This modification of the apotele *within* the scorpion clade is paralleled in the claws of other arachnids.

Although difficult to prove unequivocally, the three claws in the arachnid apotele - the

onychium or empodial claw and its associated tendon plate (see Barrows 1925) plus the paired ungues - are potentially homologous with the three apotele elements seen in the outgroups, e.g. the main claw plus the auxiliary claws in Pycnogonida (Fig. 1b). In this model Palpigradi retain the most plesiomorphic apotele state of any arachnid expressing all three apotele elements on *all* postcheliceral appendages (Figs. 2d-e). Apomorphic apotele states within the arachnids would include the apparent (?homoplastic) loss of the ungues on the pedipalp in most arachnid orders, although as Barrows (1925) and Roewer (1934) noted there are potentially homologous elements associated with the palpal organ (Fig. 3d) of Solifugae, while among the mites Opilioacariformes (Fig. 3f) retain two ungue-like structures on the palp (e.g. van der Hammen 1989, fig. 134).

One of the most interesting modifications of the apotele in the legs of arachnids is the development of the empodial region between the ungues to form a pad-like pulvillus in adults of basal Amblypygi (Fig. 2c), in Solifugae (Fig. 3e) and Pseudoscorpiones (Fig. 3c) and among the mites in the (Opilioacariformes (Fig. 3g) + Parasitiformes) clade, but *not* in basal Acariformes. This character was scored as an 'eversible empodium' by Shultz (1990, character 38) as a synapomorphy for (Solifugae + Pseudoscorpiones). By contrast Weygoldt (1996) used the term 'pulvillus' for all taxa with a modified empodial region and this apomorphic state should probably be scored for all arachnid higher taxa where it is present. When superimposed on the main alternative phylogenetic hypotheses (Weygoldt & Paulus 1979; van der Hammen 1989; Shultz 1990) it emerges as a homoplastic character, probably developing as an adaptation for gripping the substrate (Roewer 1936; Weygoldt 1996).

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