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THE EPISTOMO-LABRAL PLATE AND LATERAL LIPS IN SOLIFUGES, PSEUDOSCORPIONS AND MITES

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Abstract

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Solifugae and Pseudoscorpiones are accepted by most recent authors as sister taxa, forming a clade Haplocnemata. The sister group of Haplocnemata is less certain. Most recent authors have accepted Acari as monophyletic and placed them as sister group of Ricinulei, although a (Ricinulei + Trigonotarbida) relationship has also been proposed. In an attempt to resolve some of these phylogenetic questions, the mouthparts of Solifugae, Pseudoscorpiones and Acari were investigated. In these three orders the mouth is covered dorsally by a projecting epistomo-labral plate (a fused epistome and labrum), and ventrolaterally by a pair of finger-like lateral lips, probably derived from the coxae of the pedipalps. This character complex of a epistomo-labral plate + lateral lips is not seen in other arachnids, although similar, and perhaps homologous structures occur in Opiliones. The epistomo-labral plate + lateral lips are interpreted here as a possible synapomorphy for (Acari (Solifugae + Pseudoscorpiones)).

Introduction

On first appearances, solifuges and pseudoscorpions do not appear to be closely related. However, BÖRNER (1904, p. 156) placed both groups together in a taxon he called Haplocnemata, which he considered to be rather primitive arachnids whose legs lacked a patella. Most of the recent studies of arachnid phylogeny have also recognised this (Solifugae + Pseudoscorpiones) clade. VAN DER HAMMEN (1977, 1989) called it Apatellata, also interpreting the patella in both groups as absent based on the principal bend of the leg, or 'knee', in these orders occurring between a 'second femur' and the tibia, rather than the femur and patella as in other arachnids. He further noted that both solifuges and pseudoscorpions had mouthparts consisting of a rostrosoma and a pair of lateral lips (see below).

SHULTZ (1989) concluded that both these orders do in fact have a patella, homologising the musculature of the second femur in solifuges and pseudoscorpions with the patella musculature in other chelicerates. WEYGOLDT, PAULUS (1979), SHULTZ (1990) and WHEELER, HAYASHI (1998) also recognised this (Solifugae + Pseudoscorpiones) clade. The first two authors used Börner's older name, Haplocnemata and identified a number of convincing synapomorphies (Table 1). Haplocnemata therefore appears to be a well-supported group, although in the phylogenetic studies mentioned above there was less consensus about the position of Haplocnemata relative to the other arachnids.

Mites and ticks (i.e. Acari) have proved to be more controversial in studies of arachnid phylogeny. VAN DER HAMMEN (1989) summarised his hypothesis that Acari is diphyletic and consists of two, unrelated orders: Actinotrichida (i.e. 'mites') and Anactinotrichida (i.e. opilioacarids and 'ticks'). All mites have a gnathosoma, or capitulum (see also below). This basically consists of the labrum, epistome (or cervix), chelicerae and fused pedipalpal coxae which together form a movable, functional unit which articulates against the rest of the body, i.e. the idiosoma. VAN DER HAMMEN accepted that both mite groups have a gnathosoma, but noted that the muscles which move it originate in different places. In actinotrichids the muscles attach to an apodeme at the base of the epistome while in anactinotrichids they attach to the base of the gnathosoma. Based on this, VAN DER HAMMEN (1977, 1989) did not accept these gnathosomas as homologous, although it is evident that his conclusions were based primarily on autapomorphies for each of the two main mite lineages. LINDQUIST (1984) reviewed previous models of mite and arachnid phylogeny and concluded that mites are monophyletic and that Ricinulei are their sister group. WEYGOLDT, PAULUS (1979), SHULTZ (1990) and WHEELER, HAYASHI (1998) also regarded Acari as monophyletic, and also supported (Acari + Ricinulei). SHULTZ (1990) used the name Acaromorpha for this clade and presented two synapomorphies: (1) hexapodal larvae and (2) fused palpal coxae.

DUNLOP (1996) proposed two synapomorphies for Ricinulei and Trigonotarbida (an extinct order), namely: (1) opisthosomal tergites divided into medial and lateral plates and (2) a locking mechanism between the prosoma and opisthosoma. These characters have yet to be tested in a parsimony analysis of all arachnids, but provide explicit evidence against the Acaromorpha clade. Acari and Ricinulei both have fused palpal coxae, but then so do other arachnids (e.g. Uropygi). The mobility of the pedipalpal coxae plus the mouthparts as a gnathosoma supports Acaromorpha (e.g. LINDQUIST, 1984), but then coxal mobility is itself a plesiomorphic character state (SHULTZ, 1990). With respect to hexapodal larvae; the recent cladogram of WHEELER, HAYASHI (1998) placed pycnogonids (sea spiders) as sister group to other chelicerates. Pycnogonids show a pattern of development called anamery in which successive larval instars successively add appendages (e.g. BEHRENS, 1984), i.e. juvenile instars have fewer appendages than the adults. Taking pycnogonids as an arachnid outgroup, hexapodal larvae could be interpreted as a plesiomorphic, rather than an apomorphic, state.

Where does this leave the Acari? Most authors support a monophyletic Acari and LINDQUIST (1984, table 8) proposed eleven autapomorphies. A full discussion of all of these

is beyond the scope of this paper. Characters such as lack of well defined opisthosomal tergites and sternites provide strong support for a monophyletic Acari, but others may be symplesiomorphic, e.g. ingestion of solid food, which is also seen in Opiliones and Xiphosura. I want to stress one character in particular, 'A pair of subcapitular, bilobate lateral lips flanking mouth ventrolaterally.' (LINDQUIST, 1984, p. 40). In defence of mite diphyly, VAN DER HAMMEN (1989, pp. 99-100) presented counter-arguments to LINDQUIST's paper, which included the rejection of lateral lips as an autapomorphy of Acari on the grounds that they are present in Solifugae and Pseudoscopiones too. Evidently VAN DER HAMMEN regarded lateral lips as a convergent character (at least in mites), but why is it not a synapomorphy in all the arachnids where it is present? One of the difficulties with identifying the sister group of mites is that arachnology and acarology have developed almost as separate subjects and use different terms for homologous structures. This may conceal potential synapomorphies. In this paper I present a study of the mouthparts in Solifugae, Pseudoscorpiones and Acari in which I have tried to identify homologous elements. Based on this, I propose that all three groups have an epistomo-labral plate, a term used by SNODGRASS (1948) for a distinct, sclerotised projection, formed from a fused labrum and epistome, which is flanked by a pair of fleshy structures called lateral lips by GRANDJEAN (1936), which are derived from coxal endites. This character could be synapomorphic for an (Acari (Solifugae + Pseudoscorpiones)) clade.

Material and methods

Mouthpart morphology was studied in alcohol-preserved specimens. Solifugae were represented by a large specimen, probably of *Galeodes* sp. Pseudoscorpiones were represented by specimens of *Neobisium* (*Neobisium*) *sylvaticum* (C. L. KOCH). Opilioacari were represented by unidentified specimens kindly supplied by Prof. Bill Shear. Specimens were studied under a dissecting microscope and drawings were compared to descriptions in the literature, principally SNODGRASS (1948) and VAN DER HAMMEN (1989), but also PUNZO (1998) for solifuges, WEYGOLDT (1969) for pseudoscorpions and WITH (1904), GRANDJEAN (1936) and EVANS (1992) for mites. In an attempt to standardise nomenclature within this paper, alternative names for homologous structures, or structures interpreted here as homologous, are listed in Table 2 (see also VAN DER HAMMEN, 1980). These are discussed in more detail below.

Results

Solifugae (Fig. 1)

The solifuge mouthparts consist of two massive chelicerae set into a flexible membrane. Each chelicera has an anterolateral chelicerocarapacal articulation, a character SHULTZ (1990) identified as a synapomorphy of solifuges and pseudoscorpions (Table 1). The chelicerae are composed of two podomeres. The fixed ramus is larger, proximally bulbous, but narrows distally. The free ramus articulates ventrally against the fixed ramus. The free ramus

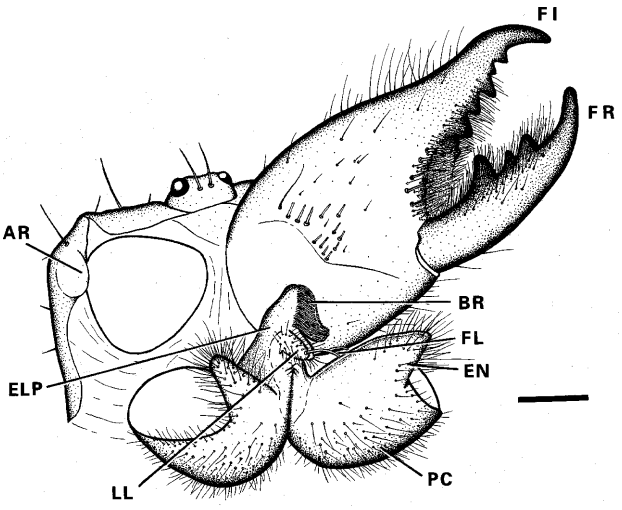

Fig. 1. Mouthparts in Solifugae (*Galeodes* sp.). Pedipalps and one chelicera removed for clarity. Abbreviations: AR- chelicerocarapacal articulation, BR- brush of setae in front of mouth, ELP- epistomo-labral plate, EN- coxal endite, FI- fixed ramus of chelicera, FL- flagellum projecting from lateral lip, FR- free ramus of chelicera, LL- lateral lip, PC- pedipalpal coxa. Scale bar = 2 mm.

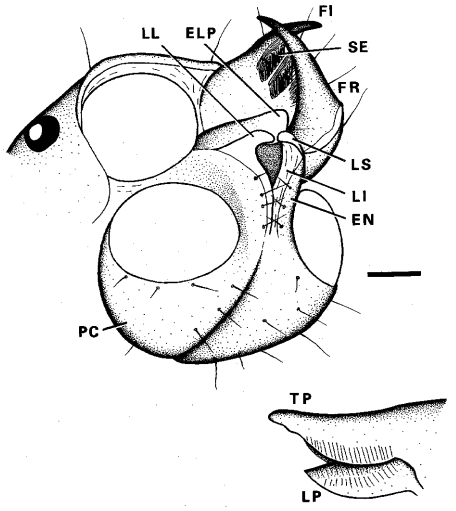

Fig. 2. Mouthparts in Pseudoscorpiones (*Neobisium* (*Neobisium*) *sylvaticum*). Pedipalps and one chelicera removed for clarity. Abbreviations: EN- coxal endite, ELP- epistomo-labral plate (alternatively intermaxilliary jugum), FI- Fixed ramus of chelicera, FR- free ramus of chelicera, LI- lamina inferior, LL- lateral lip (alternatively LS- lamina superior), PC- pedipalal coxa, SE- serrula exterior. Scale bar = 0.2 mm. Inset below: detail of pseudoscorpion epistomo-labral plate in lateral view after SNODGRASS (1948, fig. 12F) showing division into an upper lip, or taphrognath (TP), and a lower lip or lophrognath (LP); not to scale.

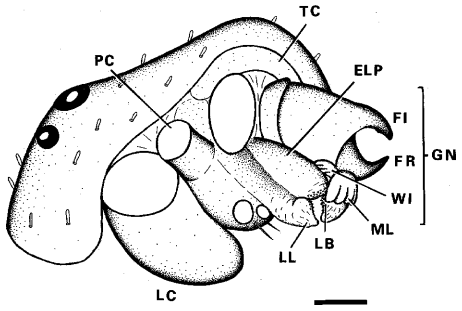

Fig. 3. Mouthparts in Acari (Opilioacarida, undetermined species), partly after GRANDJEAN (1936, fig. 1). Pedipalps, one chelicera and one set of maxilliary lobes and With's organ removed for clarity. Abbreviations: ELP- epistomo-labral plate (alternatively tentorium + subcheliceral plate + labrum), FI- fixed ramus of chelicera, FR- free ramus of chelicerae, GN- gnathosoma, LB- labellum, LC- coxa of first leg, LL- lateral lip, ML- maxilliary lobe, PC- pedipalpal coxa (part of gnathosoma), TC- tectum, WI- With's organ. Scale bar = 0.1 mm.

T a b l e 1. Synapomorphies of Haplocnemata (i.e. Solifugae + Pseudoscorpiones), derived primarily from WEYGOLDT, PAULUS (1979) and SHULTZ (1990).

1.	Two-segmented, chelate chelicerae
2.	A 'rostrum' (see text for details)
3.	An anterolateral articulation between the chelicerae and carapace
4.	Trachea with spiracles on the third and fourth opisthosomal segments

T a b l e 2. Alternative names for structures interpreted here as homologous. Names previously restricted to particular orders are indicated as follows: S- Solifugae, P- Pseudoscorpiones, A- Acari. Where the name refers to a component of the structure it is noted as (in part).

Name adopted here	**Likely synonyms**	**Author**
Epistomo-labral plate	Labrum + Epistome	various authors (e.g. SNODGRASS, 1948)
	Beak [S]	(e.g. BERNARD, 1895)
	Rostrum [S+P]	(e.g. SHULTZ, 1990)
	not Rostrum [A]	(e.g. WITH, 1904)
	Rostrosoma [S+P]	(e.g. VAN DER HAMMEN, 1989)
	Cervix (in part) [A]	(e.g. VAN DER HAMMEN, 1989)
	Intermaxilliary jugum [P]	(e.g. CHAMBERLIN, 1931)
	Taphrognath (in part) [P]	(e.g. CHAMBERLIN, 1931)
	?Lophrognath (in part) [P]	(e.g. CHAMBERLIN, 1931)
	Buccal cone (in part) [A]	(e.g. GRANDJEAN, 1936)
	Subcheliceral plate (in part) [A]	(e.g. EVANS, 1992)
	Tentorium (in part) [A]	(e.g. EVANS, 1992)
Lateral lips	Mouth lobes [S]	(e.g. SNODGRASS, 1948)
	Labium [S]	(e.g. PUNZO, 1998)
	?Hypopharynx [S]	(e.g. PUNZO, 1998)
	Lamina superior [P]	(e.g. SNODGRASS, 1948)
	Pedipalpal processes [S+P]	(e.g. SHULTZ, 1990)
	Maxilliary plates [A]	(e.g. WITH, 1904)
	Malae/Malapophyses [A]	(e.g. EVANS, 1992)

opposes the distal end of the fixed ramus, and together they form a highly sclerotised claw consisting of a number of smaller, opposable teeth. The fixed ramus is highly setose, and both the fixed and free rami have rows of long setae which overlie the distal claw. Mature male solifuges have a dorsal flagellum on the fixed ramus of the chelicerae (not present in the material examined which was presumably female).

An elongate, narrow, sclerotised structure projects between, and just below the chelicerae (Fig. 1). This structure has attracted a number of names (Table 2), although SNODGRASS'S (1948) term epistomo-labral plate is adopted here (see below). In his recent book on Solifugae PUNZO (1998) also referred to this structure as a labrum or rostrum, but labelled it in ventral view as a hypopharynx, while suggesting in the text that the ventral component of this

structure is a labium. SNODGRASS (1948) demonstrated quite convincingly that this structure in Solifugae is formed both from the labrum (the usually fleshy 'upper lip' overhanging the arachnid mouth), and the epistome (an adjacent, sclerotised plate, from which the labrum arises). The arachnid epistome can generally be distinguished from the labrum since the dorsal dilator muscles of the pharynx originate on the epistome (e.g. SNODGRASS, 1948, fig. 2D; SHULTZ, in press, fig. 2), and not the labrum. In Solifugae the labrum and epistome are strongly fused together such that both elements are sclerotised and there is no clear external division between them (Fig. 1), hence SNODGRASS's term epistomo-labral plate (Table 2). At the distal end of this structure, i.e. the labrum, there are two rows, or brushes, of dense setae, which probably filter the preorally masticated food. The mouth opens behind these setae.

Immediately below the labrum are a pair of fleshy projections which SNODGRASS (1948) called mouth lobes (see Table 2 for alternatives), but which I refer to here under GRANDJEAN'S (1936) term lateral lips (Fig. 1). Each lateral lip is highly setose and terminates in a flagellum. These lateral lips show a suture line suggesting fusion both with the palpal coxa and with the epistomo-labral plate and so could conceivably be derived as mesal endites from the palpal coxae. HEYMONS'S (1905) embryological studies showed that these lateral lips develop mesal from the large coxal endites and based on this Snodgrass saw no homology between the solifugae lateral lips and the coxal processes of other arachnids. However, HEYMONS (1905) concluded that the lateral lips, or 'Unterlippe', are derived from the pedipalpal segment and this is consistent with them being mesal palpal endites. VACHON (1958, fig. 3), though, figures these 'processus rostraux' as developing directly underneath the epistomo-labral plate. The palpal coxae are fused medially with a strongly developed and highly setose endite on the mesal surface (Fig. 1), a structure additional to the lateral lips.

Pseudoscorpiones (Fig. 2)

Like Solifugae, pseudoscorpions have chelate chelicerae composed of two podomeres, a fixed ramus and a free ramus. The articulation of the free ramus is primarily ventral, although not to the same degree as in Solifugae. The anterolateral chelicerocarapacal articulation was not strongly expressed in the pseudoscorpion material studied, although an articulation point in the same position as in solifuges was suggested by the way the chelicerae break off from the body during their removal. The free ramus bears a row of plate-like structures, the serrula exterior which is used for grooming (WEYGOLDT, 1969). Although not clearly visible in the preparation (which was not cleared in potassium hydroxide), the free ramus of the chelicera also bears the opening of the silk gland.

As in Solifugae, there is a sclerotised projection beneath and between the chelicerae (Fig 2). This has often been referred to as the jugum (Table 2), but again SNODGRASS (1948) indicated that it is formed from a fused labrum and epistome. I see no reason not to consider it homologous with the Solifugae epistomo-labral plate, as, for example, SHULTZ (1990) did. SHULTZ referred to this structure in both groups as a 'rostrum', but there is

a problem with using this term since 'rostrum' is (a) a crustacean term and (b) widely used for either the rostral tectum *above* the chelicerae in mites and specifically for the leading edge of the prodorsum in oribatids (WALTER, pers. com.). The mite 'rostrum' is clearly not homologous with SHULTZ's 'rostrum' and to prevent further confusion SNODGRASS's epistomo-labral plate is used here as a more neutral term for the projecting upper mouth lip. Some early derivative pseudoscorpions have a relatively long epistomo-labral plate, although HARVEY (1992, character 6), interpreted a long jugum as apomorphic for those taxa where it is present. The material studied here suggested that the distal, labral end of the pseudoscorpion epistomo-labral plate was more fleshy than in solifuges and that a slight demarcation between the labral and epistomal elements is present (Fig 2). There are no brushes of setae at the distal end of the labrum like those seen in Solifugae. Pseudoscorpions do differ significantly from solifuges in one important respect. The anterior part of their epistomo-labral plate can be divided into an upper lip, or taphrognath, and a lower lip, or lophognath (CHAMBERLIN, 1931) (Fig. 2). These elements are ridged, the lower one slots against the upper one and the mouth opens just behind them. There is no equivalent of this structure in solifuges, or in other arachnids, and this taphrognath-lophognath complex appears to represent a pseudoscorpion autapomorphy. Whether this lophognath element is homologous with the labium of other arachnids is not entirely clear and would merit investigation.

Adjacent to the pseudoscorpion epistomo-labral plate are two fleshy lobes, which in this case clearly are derived from the pedipalpal coxae. These coxae have medial flanges, or endites, which bear a number of anteriorly-projecting setae. These sclerotised endites are bordered mesally by more fleshy tissues which form the lateral walls of the preoral cavity (e.g. WEYGOLDT, 1969). These fleshy elements have been referred to as the lamina inferior, the broad ventral part, and the lamina superior, the finger-like dorsal part which lies alongside the epistomo-labral plate (Fig. 2). I suggest that these laminae superior are homologous with the lateral lips of solifuges, although perhaps they show a more plesiomorphic condition in which they are still, in effect, true coxal endites, and have not fused with the epistomo-labral plate directly below the mouth. Although not expressed in cladistic terminology, VAN DER HAMMEN (1989, fig. 118) interpreted both the laminae inferior and laminae superior in pseudoscorpions as lateral lips homologous with those in Solifugae, and treated this as a diagnostic (i.e. synapomorphic) for both orders.

Acari (Fig. 3)

Unlike the previous two orders, where the mouthparts are fairly similar in all members of the group, the variety among mouthparts of Acari can appear bewildering. This is partly due to their unnecessarily complicated terminology and also to specialisations for feeding in certain groups; e.g. parasitism by ticks. Polyphyly among the Acari could also explain this variability. As noted above, all mites have a gnathosoma (Fig. 3). This functional unit is formed from the chelicerae, the pedipalps, the labrum and the epistome. The

palpal coxae are fused to each other and to the labrum/epistome complex; and this whole structure below the chelicerae is usually referred to as the subcapitulum, infracapitulum or hypognathum (e.g. EVANS, 1992).

Oplioacarids are widely accepted as basal mites (e.g. NORTON et al., 1993) and their mouthparts are relatively simple compared to other mite groups. In opilioacarids the chelicerae are composed of three podomeres; a plesiomorphic state in arachnids (e.g. SHULTZ, 1990) compared to the two podomeres in Solifugae and Pseudoscorpiones. The chelicerae originate in a folded membrane and the area above the chelicerae has been referred to as a tectum. This structure forms a sclerotised plate between the carapace and chelicerae seen in some mites (EVANS, 1992) and sometimes referred to as a rostrum (e.g. WITH, 1904, see also above). GRANDJEAN (1936) found no evidence of sclerotisation above the chelicerae in opilioacarids and, although the area in question has been labelled (Fig. 3), the tectum may be absent in this group. The distal podomeres of the chelicerae form a small claw. As in solifuges, the claw has opposable teeth with the free ramus articulating ventrally against the fixed ramus.

As in Solifugae and Pseudoscorpiones, there is a sclerotised plate projecting beneath and between the chelicerae. This has been called the labrum (e.g. WITH, 1904; VAN DER HAMMEN, 1989) and WITH identified both a proximal and distal part. In a diagram of a generalised mite EVANS (1992) called the proximal part the subcheliceral plate and the distal part the labrum. SNODGRASS (1948) pointed out that the proximal part contains the muscles of the pharynx and so must unequivocally be the epistome. Therefore, as in Solifugae and Pseudoscorpiones, we essentially have an epistomo-labral plate (Fig. 3). In other, more derived, mite groups this structure appears to become more complicated as it forms a shelf over which the chelicerae slide, while the proximal region where prosomal muscles attach is often called a tentorium (see EVANS (1992) for a discussion). The distal, labral end of the epistomo-labral plate in opilioacarids appears somewhat fleshy and is ornamented with tiny triangular spines. There are no brushes of setae as in Solifugae.

Immediately below the epistomo-labral plate are a pair of fleshy projections which lie adjacent to it (Fig. 3). The mouth opens at their base beneath the labrum. WITH (1904) and SNODGRASS (1948) called these structures maxillary plates, but both GRANDJEAN (1936) and VAN DER HAMMEN (1989) called them lateral lips; the term adopted here. SNODGRASS felt that these, and the other lobes which develop around the mouthparts in mites, could not be homologised with structures in other arachnids, although he regarded the mouth lobes of pseudoscorpions as at least analogous. The lateral lips of opilioacarids have a distinct dorsal lobe which VAN DER HAMMEN (1989) called the labellum, and which also has small teeth like the epistomo-labral plate (Fig. 3). All authors accepted that these lateral lips in opilioacarids are derived as mesal endites from the pedipalpal coxae. In opilioacarids these coxae are fused together as the ventral part of the subcapitulum and each coxa has a more prominent, articulated, toothed lobe or endite which has variously been referred to as the maxilliary lobe (WITH, 1904), maxilliary organ (GRANDJEAN, 1936) or rutellum (VAN DER HAMMEN, 1989). Immediately mesal to this 'lobe' is a similar projection, usually referred to as WITH's organ. These structures have no obvious counter-

part in Solifugae and Pseudoscorpiones and Evans (1992) noted that they may be setal in origin. The mouthparts of mites are full of complicated, sclerotised projections and a full discussion of their terminology and likely homology with each other is beyond the scope of this paper, although further details can be found in Van der Hammen (1980). More significant is the basic morphology of a projecting epistomo-labral plate and an adjacent pair of lateral lips. This is present in basal mites such as opilioacarids, and can be seen in a modified form in other mite groups (Van der Hammen, 1989, fig. 14; Evans, 1992, figs. 5.1-5.6).

Discussion

Similar mouthparts in solifuges, pseudoscorpions and mites were noted as long ago as 1897 (Bernard, 1897, p. 16). Snodgrass (1948) recognised the basic labrum/epistome morphology in all three orders, but did not regard the various processes, i.e. solifuge mouth lobes, pseudoscorpion laminae and mite maxilliary plates, as homologous. Snodgrass's paper remains the definitive study, with excellent descriptions and constant efforts to standardise terminology. Yet I feel that he tended to use what are essentially autapomorphies of these three orders to reject relationships between them. There are significant differences between the three orders, e.g. fusion of the mouth lobes to the epistomo-labral plate in solifuges, the unfused laminae superior and the taphrognath-lophrognath complex in pseudoscorpions and the complex coxal processes as part of a gnathosoma in mites. However, none of these are clearly synapomorphic with any other arachnid order.

The epistomo-labral plate/lateral lip character identified here needs to be carefully defined. Referring to it as, say, a 'projecting labrum + epistome associated with coxal endites' is too broad and could apply to a number of arachnid orders. By its very nature the arachnid labrum projects forwards to a greater or lesser extent, though not always with a projecting epistome, while there are numerous examples of coxal endites (e.g. in labidognath spiders), not all of which are necessarily homologous with each other. I propose to define this character as: 'Epistome and labrum fused into a distinct, sclerotised projection which bears the mouth. Distal end of this epistomo-labral plate flanked ventrolaterally by a pair of fleshy, finger-like lateral lips derived as mesal endites from the pedipalpal coxae.'

This definition excludes groups such as Uropygi (whip scorpions), which have a large labrum, but which lack lateral lips. Opiliones (harvest spiders) present a more interesting case. Weygoldt, Paulus (1979) placed them close to Acari, while Shultz (1990) recognised a Dromopoda clade of the form: (Opiliones (Scorpiones (Solifugae + Pseudoscorpiones))). One of the characters defining Dromopoda was a stomatheca, a preoral cavity formed dorsally by the epistome and laterally by pedipalpal coxal endites. Shultz (1990) coded the stomatheca as secondarily lost in Haplocnemata, but in his discussion of the 'rostrum' he did note the presence of small processes from the pedipalps (i.e. lateral lips) and speculated that these might represent a highly reduced stomotheca.

The stomotheca has been criticised as a synapomorphy for Dromopoda (e.g. WEYGOLDT, 1998), since coxal endites are absent in early derivative scorpions which implies that the stomatheca is a convergent feature. However, in a recent study of opilionid anatomy, SHULTZ (in press) figured the epistome of a palpatore opilionid as a projecting, sclerotised structure with a small, ventral labrum. This is similar to the epistomo-labral plate as identified both by SHULTZ (1990) and this study. The coxal endites forming the opilionid stomatheca could be interpreted as 'lateral lips' too (WALTER, pers. com.). By contrast, the palpal endites in opilionids are fairly broad and plate-like, and not the finger-like structures identified here. However, these opilionid pedipalpal 'lips' are soft and fleshy SHULTZ (1990), like the lateral lips, and it easy to envisage a series of evolutionary steps by which lateral lips developed as projections from opilionid-like pedipalpal endites. In fact pseudoscorpions show this rather nicely (Fig. 2) with both a broad, fleshy opilionid-like 'lamina inferior' and a narrow, fleshy, solifuge-like 'lamina superior' (Fig. 2).

SHULTZ (1990) did not include Acari in Dromopoda, although on the basis of this study I think his 'rostrum' character (no. 15), i.e. the epistomo-labral plate, should not be restricted to Haplocnemata, but should also be coded as present in Acari; and conceivably in Opiliones too. A number of authors have suggested that mites and solifuges may be related; see EVANS (1992) and DUNLOP (1999) for reviews. Some rahagiid and palaeacaroid mites superficially show a remarkable resemblance to solifuges (DUNLOP, 1999), although LINDQUIST (1984) pointed out that neither group is widely accepted as basal mites and that the resemblance is most likely convergent. As in this present study, GRANDJEAN (1936) noted the presence of 'lèvres latérales' (= lateral lips) in solifuges and opilioacarids and the location of the mouth at the end of a 'rostre' in Solifugae and a 'cône buccal' in mites. GRANDJEAN (1936) mentioned a prelarval organ of Claparéde in actinotrichids and solifuges, although the character is not unique to these groups and may be plesiomorphic (WALTER, pers. com.). Interestingly, ALBERTI (1984) noted similarities in sperm structure between actinotrichid mites and solifuges, to the exclusion of anactinotrichids.

Similarities between mites and pseudoscorpions, other than small size, are less well documented. Acari appear more like Solifugae (Figs. 1, 3) in having a tight grouping of the epistomo-labral plate plus discrete lateral lips around a much more anteriorly located mouth. The lips in pseudoscorpions are less intimately associated with the mouth opening, which is more posterior, and it makes a certain amount of sense to interpret this as plesiomorphic (see above). However, the synapomorphies for Haplocnemata (Table 1), especially two-jointed chelicerae, argue strongly against a (Pseudoscorpiones (Acari + Solifugae)) relationship. Of course this epistomo-labral plate/lateral lips character must be weighed against other phylogenetic evidence and these observations are presented here for further discussion.

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