

Lyriform slit sense organs on the pedipalps and spinnerets of spiders

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Lyriform slits sense organs (LSSO) are a precise assembly of stress detecting cuticular slit sensilla found on the appendages of arachnids. While these structures on the legs of the wandering spider *Cupennius salei* are well studied in terms of morphology, function and contribution to behaviour, their distribution on pedipalps and spinnerets of spiders is not well explored. A study was therefore carried out to observe the distribution of LSSO on pedipalps and spinnerets of some spider species. Haplogyne spiders belonging to family *Pholcidae* have a simple complement of LSSOs represented by one or two LSSOs on their femur. The entelegyne spiders possess a complex assembly of LSSOs on the distal segments of their pedipalps. Various types of LSSOs are found on the pedipalps indicating a capacity for analysis of complex cuticular stress. It is suggested that the complexity of LSSOs on pedipalps of entelegyne spiders relates to courtship and spermatophore transfer and may help in reproductive isolation. Lack of LSSOs on the distal segments of pedipalps leads us to infer that unlike legs, pedipalps are less likely to receive vibratory input through their distal segments.

Spinnerets have a relatively simple complement of LSSOs. One LSSO is found only on anterior spinnerets and it is a common feature observed among spiders, irrespective of the variations in web building behaviour. The orb-weaving araneid *Argiope pulchella*, however, has two LSSOs on the anterior spinneret. As non-web builders and orb weavers do not differ markedly in terms of LSSOs on the spinnerets and LSSOs are simple in nature (type A), it is likely that spinning and weaving are not largely regulated by sensory input from LSSOs on the spinnerets.

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1. Introduction

Animals acquire information about the environment through their sensory systems. Various types of sensory systems are employed for this purpose, depending on the modality of the sensory input, habitat and behaviour of the animal. Some taxa possess unique sensory systems that are specialized in design and function. Such systems, when examined, provide insights into alternate sensory mechanisms of biological significance. The slit sensilla found on the exoskeleton or cuticle of arachnids, is one such example of specialized sensory systems. The arthropod exoskeleton can efficiently transmit mechanical stress generated due to substrate vibration, movements of the animal, and gravitational force. Such stresses are detected by slit sensilla (Barth 1985a). They

appear like slits or clefts, bordered by lip-like cuticle and hence the name. Slits measure between 8 to 200 μm in length and are 1–2 μm wide. They are innervated by dendrites of two sensory neurons. Barth (1978) has carried out a comparative study of slit sensilla on the legs of some arachnids. Detailed morphological, functional and ethological studies have been carried out on the wandering spider *Cupennius salei* (Barth 1985b). Though distributed over the entire body, slit sensillae predominate on the legs. Isolated slits may be distributed all over the body or may occur in deliberate groups. A lyriform slit sense organ (LSSO) is an assembly of two or more slits arranged close together, 5 to 10 μm apart, nearly parallel or at an angle to each other.

Slit sense organs are broadly considered as proprioceptors, responsive to air-borne sound, substrate-borne

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vibrations and cuticular deformities due to muscular activity or haemolymph pressure changes. Thus, slits serve many functions. The transduction properties of the sensory neurons of slits were reviewed by French *et al* (2002). The configuration of slit sense organs and their orientation with reference to the axis of an appendage influence their response characteristics. Vibrations generated by prey caught in the web are detected by the slit sense organs, providing information about the prey's location. The water-dwelling spider *Dolomedes*, precisely locates prey fallen into water (Bleckmann and Barth 1984). Vibratory cues are significant during courtship and each species appears to have its own vibratory 'code'. Spiders appear to depend on lyriform organs for path finding (kinesthetic orientation) (Seyfarth and Barth 1972). The slit sense organs thus serve diverse functions and are of immense significance in the behaviour of spiders. The LSSOs on the legs of the wandering spider *C. salei* have been extensively studied (Barth 2002). A comparative analysis of the distribution of LSSOs on the legs of some spiders has been carried out by Peters and Pfreundt (1986), but their distribution on the pedipalps and spinnerets has not received much attention.

The pedipalps are most anterior pair of appendages in spiders (figure 1a) and serve many functions. They are clawed in some species and some times the claws hold the web while resting. The most striking feature of pedipalps is sexual dimorphism. The tarsus is strikingly complex in males compared to females (figure 3a–d). During courtship pedipalps are used in waving (Bristowe and Locket 1926)

and drumming (Rovner 1975). The male *Lycosa punctulata* – a wanderer, takes the dragline silk laid down by the female in its pedipalps and guides itself to the female (Tietjen and Rovner 1980).

A characteristic behaviour of spiders is production of silk and web-building. While some build webs (web-builders), others do not (wanderers, hunters). However, silk is used for various purposes by all spiders. Webs differ in their geometry and a web design is characteristic to each family. Webs of spiders and the silk used for building it have undergone considerable evolution in relation to their ecology and the behaviour of prey species (Kullman 1972; Craig 2003). Spinning of silk is performed by three pairs of spinnerets (figure 1b) bearing spigots. Each of these three pairs of spinnerets – the anterior, median and posterior, is associated with specific silk glands and the silk of each spinneret serves specific purposes. Spinning silk and its use for various purposes can be expected to require considerable amount of control and co-ordination as spinnerets can be moved independently of each other. Whether LSSOs on spinnerets reflect the complexity of the behaviour, would be interesting to explore. Various spiders that were examined in the present study are listed in table 1. Specimens were collected from the field and fixed in 70% alcohol. The appendages were dissected, dehydrated, cleared in xylene and mounted using DPX. Observations were made using Olympus BX 60 microscope fitted with a camera lucida attachment. Microphotographs were taken using Olympus SC 35 camera.

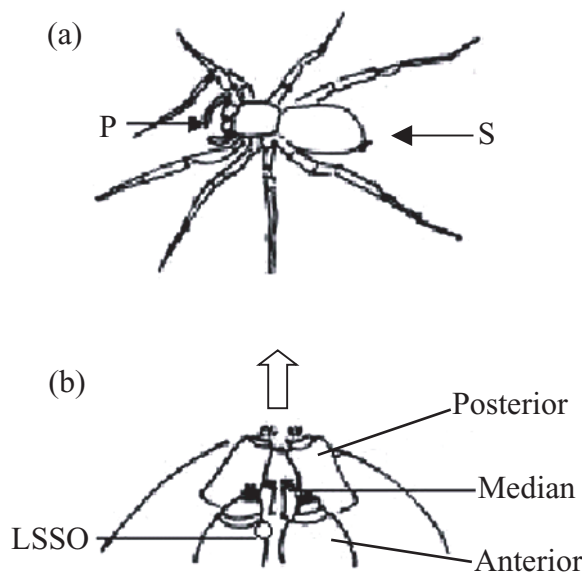


Figure 1. (a) The pedipalps (P) and spinnerets (S) on the spider. (b) The ventral side of a spider showing the three spinnerets – anterior, median and posterior. The location of lyriform slit sense organ (LSSO) on the spinneret is marked by a circle. Arrow in (b) indicates posterior direction.

Table 1. Spiders which have been examined in the present study and their characteristic behaviour.

Family	Species	Behaviour	
Pholcidae	<i>Pholcus phalangioides</i>	Irregular web	P
	<i>Crossopriza lyoni</i>	Irregular web	P
Oxyopidae	<i>Oxyopes shwetha</i>	Wanderer	S
Salticidae	<i>Plexippus paykulli</i>	Wanderer	S
Tetragnathidae	<i>Tetragnatha</i> sp.	Orb (loose)	S
Eresidae	<i>Stegodyphus sarasinorum</i>	Saccular web, social	P+S
Lycosidae	<i>Pardosa</i> sp.	Wanderer	P
Araneidae	<i>Cyrtophora cicatrosa</i>	Dome web	P+S
	<i>Argiope pulchella</i>	Orb web	S

P indicates species whose pedipalps have been examined. S indicates species whose spinnerets have been studied

2. Observations and discussion

The pedipalps have six segments and a metatarsus is lacking. While the distal segment is modified into pincer-like structures in most arachnids, it is not so in spiders. In some spiders the pedipalp has claws at the tip of the tarsus. The pedipalp is sexually dimorphic and helps in courtship and sperm transfer. The male has an enlarged and sometimes complex tarsus in the pedipalp. Spinnerets however, do not show striking sexual dimorphism though orb-weaving females often build a web and males are wanderers in nature. The arrangement of spinnerets and spigots differs among species and is suggestive of different spinning behaviours of the spiders.

Pedipalps are held above the substratum by a spider. The claws on the tarsus are used to hold the silk of the web. Pedipalps are directed anteriorly and bear a dorsal side, a ventral side and inner and outer sides. The LSSOs of spiders are composed of two to many slits that are arranged often at an angle to each other, designated by β (Barth 2002). We have represented the angle between the two outermost slits of an LSSO as β max. β max values of LSSOs on pedipalps are listed in table 2. The value of β max divided by the number of slits in a LSSO roughly indicates the increment of angles between individual slits of a LSSO.

2.1 Slit sense organs on pedipalps

Various types of lyriform slit sense organs were observed on the pedipalps of spiders in the present study. LSSOs of types B1 (figure 2b), B2 (figure 2f), B3 (figure 2a) and C (heart shaped, figure 3c), as classified by Barth (2002) occur on the pedipalps. Another type, which we designate as type D is seen in figure 2c. These types are shown schematically in figure 2 (bottom panel). An interesting feature is the absence of LSSO or groups of slits on the distal segments – tarsus and tibia of the pedipalps in all species

studied. An exception is a two-slit LSSO found at the tip of the tarsus in *Stegodyphus sarasinorum*. Table 2 provides a list of LSSOs found on pedipalps, including some of their features.

2.2 *Pholcus phalangioides* and *Crossopriza lyoni* (Pholcidae)

Members of Pholcidae build irregular webs indoors and several individuals co-exist in a web. They are haplogyne, cribellate spiders. Both male and female *P. phalangioides* have one LSSO having 4 slits (figure 3a). In case of *C. lyoni* (figure 3b), while the LSSO (Fe 1) is arranged perpendicular to the long-axis of the pedipalp in males, it is arranged at 20° to the long axis in the case of females, thus showing sexual dimorphism. The pedipalp of male *C. lyoni* has two LSSOs compared to one in the case of females (figure 3b).

2.3 *Pardosa* sp. (Lycosidae)

Pardosa is a ground-dwelling spider, often seen among grass. This is a wandering spider and the male is known to use its pedipalps to track the female by following the dragline silk of females. Males and females of the species were examined to see whether any sexual dimorphism exists with reference to LSSOs on the pedipalps. A total of five LSSOs were observed (figure 3c, d). The LSSOs on the patella (Pa 1 and Pa 2) are comparable to those of *Cyrtophora* (figure 3f) and occur on a cuticular ridge that is away from the patella-tibia joint. Male and female *Pardosa*, differ from *Cyrtophora* (figure 3f), in the femoral LSSO (Fe 1) occurring on the inner side than on the ventral side. Fe 1 has 7 slits in the case of the male pedipalp while Fe 1 of the female has 4 slits (figure 3c, d). A type C LSSO is seen on the ventral side of the trochanter (Tr 2) and a heart-shaped type D LSSO (Tr 1) consisting of 17–19 slits is seen on the ventral side close to the joint. Notable dimorphism, is that only the male has two groups of slits on the lateral sides of the trochanter (figure 3d, GS 1 and GS2).

Table 2. Slit sense organs found on different segments of pedipalps of the spiders studied.

Segment	LSSO	Type	Number of slits	β max ($^{\circ}$)
<i>Pholcus phalangioides</i> , male, Pholcidae				
Femur	Fe 1	A	4	<5
<i>Pholcus phalangioides</i> , female, Pholcidae				
Femur	Fe 1	A	4	<5
<i>Crossopriza lyoni</i> , male, Pholcidae				
Femur	Fe 1	A	4	<5
	Fe 2	A	5	<5
<i>Crossopriza lyoni</i> , female, Pholcidae				
Femur	Fe 1	A	7	<5
<i>Pardosa</i> sp., female, Lycosidae				
Patella	Pa 1	B2	11	35
	Pa 2	B1	13	20
Femur	Fe 1	A	4	08
Trochanter	Tr 1	C	13	45
	Tr 2	D	17	10
<i>Pardosa</i> sp., male*; Lycosidae				
Patella	Pa 1	B1	11	28
	Pa 2	D	18	35
Femur	Fe 1	B2	7	<5
Trochanter	Tr 1	D	13	46
	Tr 2	C	18	15
<i>Stegodyphus sarasinorum</i> , female; Eresidae				
Tibia	Ta 1	A	2	<5
Femur	Fe 1	B2	11	31
	Fe 2	B2	7	22
	Fe 3	B1	8+2	24
	Fe 4	D	15	<5
Trochanter	Tr 1	D	10	28
<i>Cyrtophora cicatrosa</i> , female; Araneidae				
Patella	Pa 1	B1	15	35
	Pa 2	B2	11	<5
	Pa 3	B1	7	20
Femur	Fe 1	B2	10	20
Trochanter	Tr 1	B1	8	28
	Tr 2	C	11	11

*Group of slits not included.

Type of LSSOs based on Barth (2002). β max ($^{\circ}$) indicates the angle between the two outermost slits of an LSSO.

2.4 *Stegodyphus sarasinorum* (Eresidae)

These are cribellate spiders, often referred to as “social” spiders living as a community, in a saccular nest, constructed of silk. The nests are found on twigs and barbed wires, with a densely woven central core, having tunnel-like formations in which the spiders live. A nest may have as many as 50 spiders of different age groups. They collectively attack prey, caught in sheet-like webs that emanate from the core. The ‘members’ of a colony also co-operate in keeping the nest and web clean of debris. The pedipalp of the female bears six LSSOs (figure 3e), The tarsal tip

LSSO has two slits (figures 2d and 3e; Ta 1). The femur bears four LSSOs. The LSSO designated as Fe 2 is on the outer side close to the patella-femur joint, while Fe 1 and Fe 3 are on the inner side. Fe 2 is composed of 7 slits. Fe 3, which has 7 slits, is associated with two slits forming a LSSO, that is close to Fe 3. We have considered it as a part of Fe 3 and termed it as the “satellite LSSO” of Fe 3. Fe 4 is found on the ventral side of the femur. This has 14 slits and does not conform to any of the types classified by Barth (2002). The trochanter bears a LSSO of type D (Tr 1) with 10 slits on the dorsal side adjacent to the femur-trochanter joint.

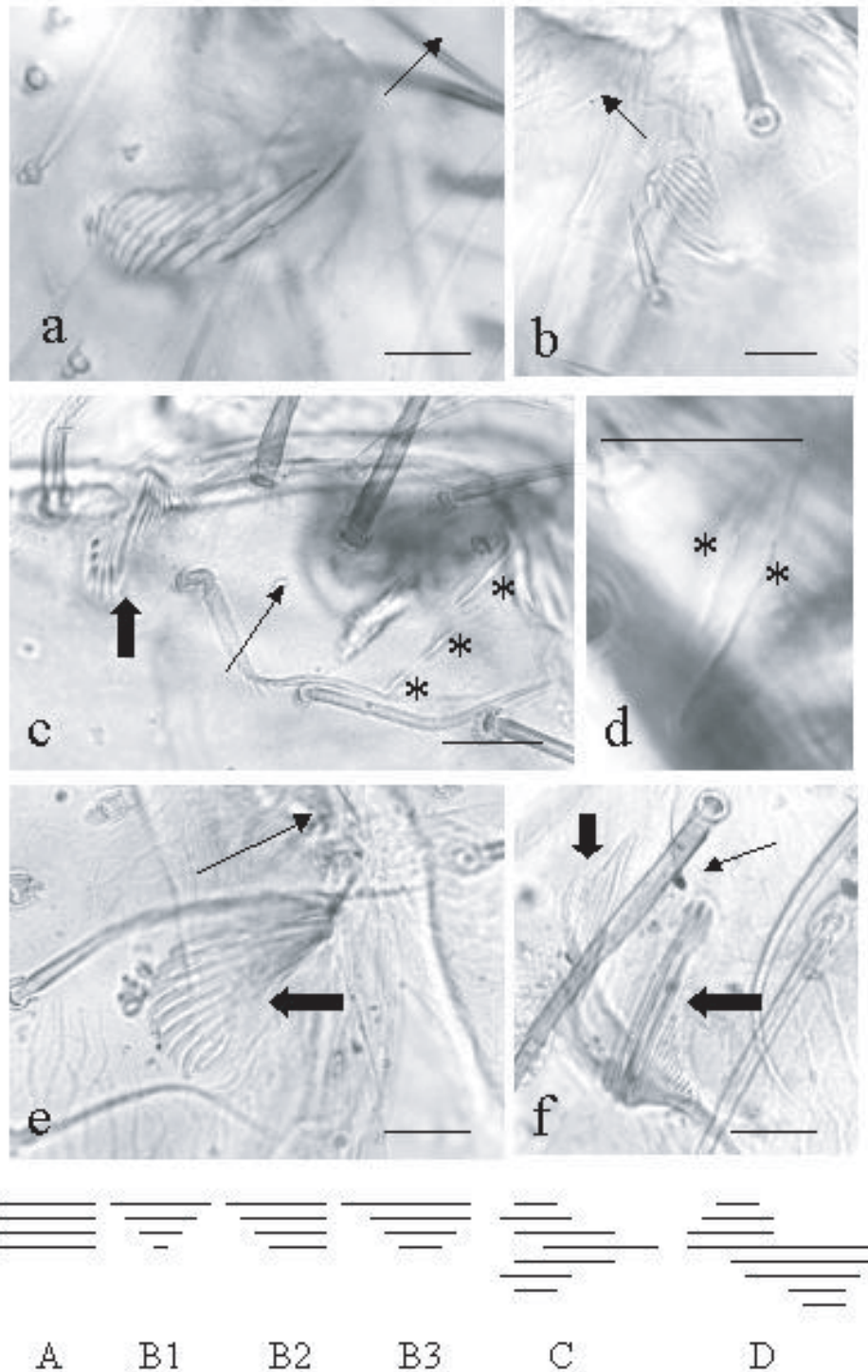


Figure 2. Photomicrographs of lyriform slit sense organs on the pedipalps of spiders. **(a)** Type B3 LSSO (Fe 1 in figure 3e) on the femur of *Stegodyphus sarasinorum* located at the joint. **(b)** Type B1 LSSO (Pa 3 in figure 3f) on the patella of *Cyrtophora cicatrosa*. **(c)** Trochanter of *Pardosa* sp. showing a type D LSSO (thick arrow; Tr1 in figure 3d) and group of slits (each slit marked with asterisk; GS 2 in figure 3d). **(d)** A two-slit LSSO (Ta 1 figure 3e) at the tip of the tarsus of *Stegodyphus sarasinorum*. This LSSO occurs between the two claws of the tarsus. **(e)** Type B3 LSSO on the femur of *Cyrtophora cicatrosa* (Fe1 in figure 3f). **(f)** LSSOs Pa 1 (horizontal thick arrow) and Pa2 (vertical thick arrow) found on a cuticular ridge in the middle of patella of *Pardosa* sp. Thin arrows indicate the long axis of the leg. Scale: **a, c, e, f** 25 μm ; **b** 20 μm ; and **d** 10 μm .

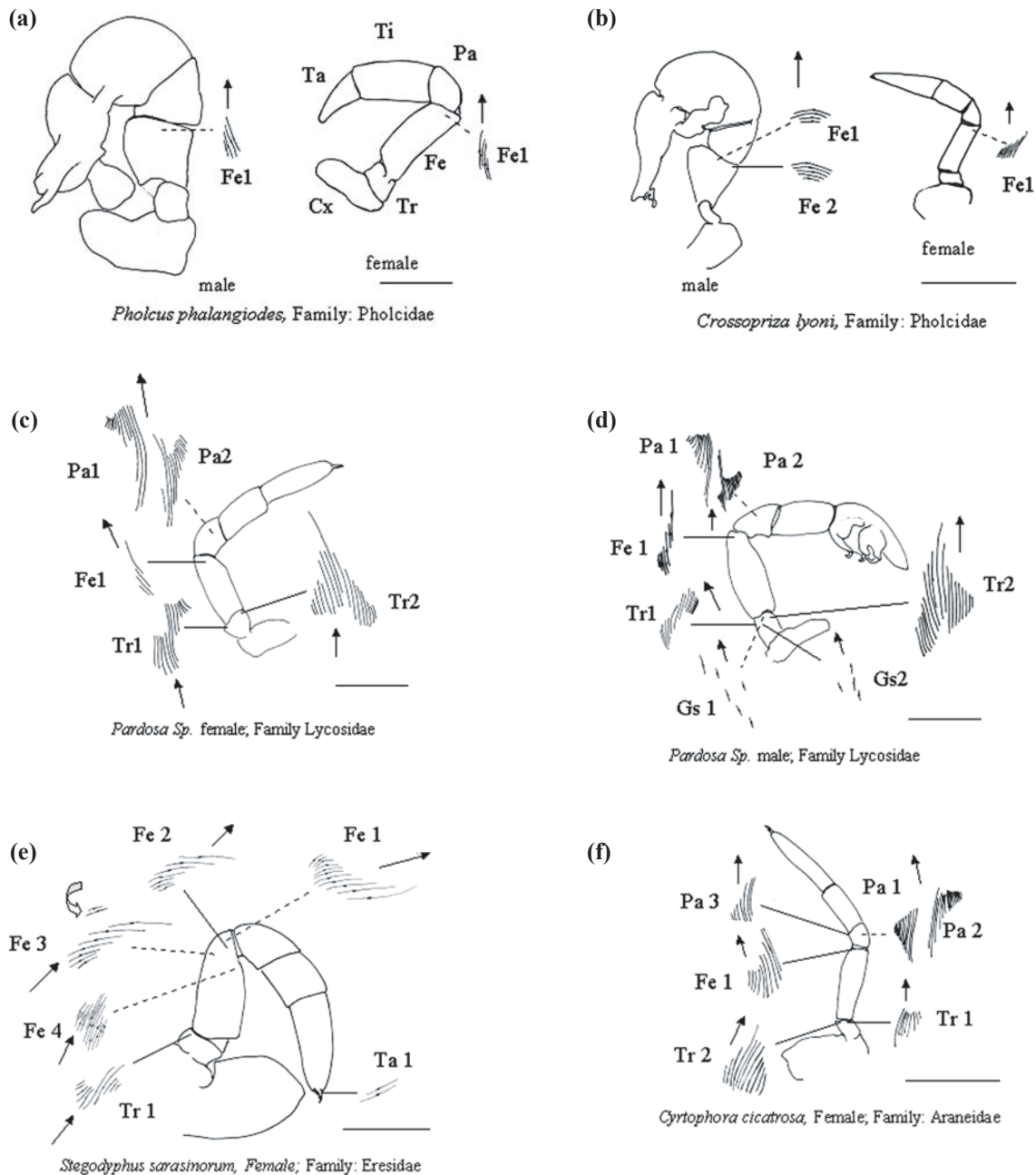


Figure 3. Camera lucida drawings of pedipalps and LSSOs of different species of spiders. Pedipalps are curved appendages and the convex side in the diagrams corresponds to the dorsal surface while the concave side is the ventral side. LSSOs found on the inner surface of the pedipalp are indicated by broken lines, while LSSO on the outer surface are indicated by solid lines. The male pedipalp is larger in pholcids (a and b) and the tarsus is larger and more complex as compared to that of the female. The other segments of the pedipalp are also correspondingly larger in size. The tarsus of male *Pardosa* is complex and the other segments of the pedipalp are slightly larger than that of the female in terms of size. (a) Both male and female *P. phalangioides* have nearly identical LSSOs (Fe 1) on their femur. (b) A clear sexual dimorphism is seen in *C. lyoni*, wherein the male has two LSSOs on the femur (Fe 1 and Fe 2) while the pedipalp of the female bears one LSSO. In case of *Pardosa*, both males (c) and females (d) have five LSSOs and are largely similar, except for the group of slits (GS 1 and GS 2) on the trochanter. (e) *S. sarasinorum* has a LSSO at the tarsal tip (Ta 1). The femur bears 4 LSSOs. One of them (Fe4) is ventral. The trochanter bears one type D (Tr1) LSSO. (f) *Cyrtophora cicatrosa* has six LSSOs. Pa 1, Pa 2 and Tr 2 are comparable to that of *Pardosa* sp. Thin arrows indicate the long axis of the pedipalp in relation to the LSSO. Scale bars for pedipalps are in (a) and (b) 2 mm for males and 1 mm for female. (c) and (d) 1 mm; (e) 2 mm; (f) 1 mm. In all the images scale bars are 100 μ m for LSSOs.

2.5 *Cyrtophora cicutrosa* (Araneidae)

These are solitary spiders. However, a large number of dome-webs (as many 20) built by females, which reside in them, can often be seen together in a suitable habitat such as a *Cycas* plant. Unlike a characteristic araneid orb web, the web of *Cyrtophora* is an exquisitely designed bell-shaped structure with multiple sheets of webs below it, each sheet corresponding to the previous molt. The female hangs upside down at the apex of the bell, which has an opening to escape from, when disturbed. The egg sacs are hung above the bell one below the other. The tarsus and tibia are devoid of LSSOs, while one or two single slits are found near the tip of the tarsus. The patella has three LSSOs (figure 3f). On the ventral side near the tibia-patella joint a type B1 LSSO with 11 slits is found (Pa 3) with β max of 20° . LSSOs Pa 2 (β max $<5^\circ$) and Pa 3 (β max 35°), seen on the inner side of patella are away from the tibia-patella joint, situated on a cuticular ridge. The slits of these LSSOs are

placed very close to each other unlike slits found in other LSSOs. The femur has one LSSO with 10 slits (Fe 1) on the ventral side with a β max of 20° . The trochanter has two LSSOs one of which (Tr 2) is a type D LSSO which is heart shaped, situated on the ventral side while Tr 1 is a B2 type of LSSO situated on the dorsal side.

2.6 Spinnerets

To evaluate the LSSOs on a comparative basis, a variety of spiders such as hunting spiders (*Oxyopes shwetha*, Oxyopidae; *Plexippus paykulli*, Salticidae, *Pardosa* sp., Lycosidae), orb weavers (*Tetragnatha* sp., Tetragnathidae; *Argiope pulchella*, Araneidae) and “social” spider (*Stegodyphus sarasinorum*, Eresidae) were examined. The wanderers use silk for draglines, egg sacs and wrapping the prey. The webs of tetragnathid are more loosely knit compared to araneid orb webs. They also lack a stabilimentum often seen among araneid orbs. In all spiders studied, the

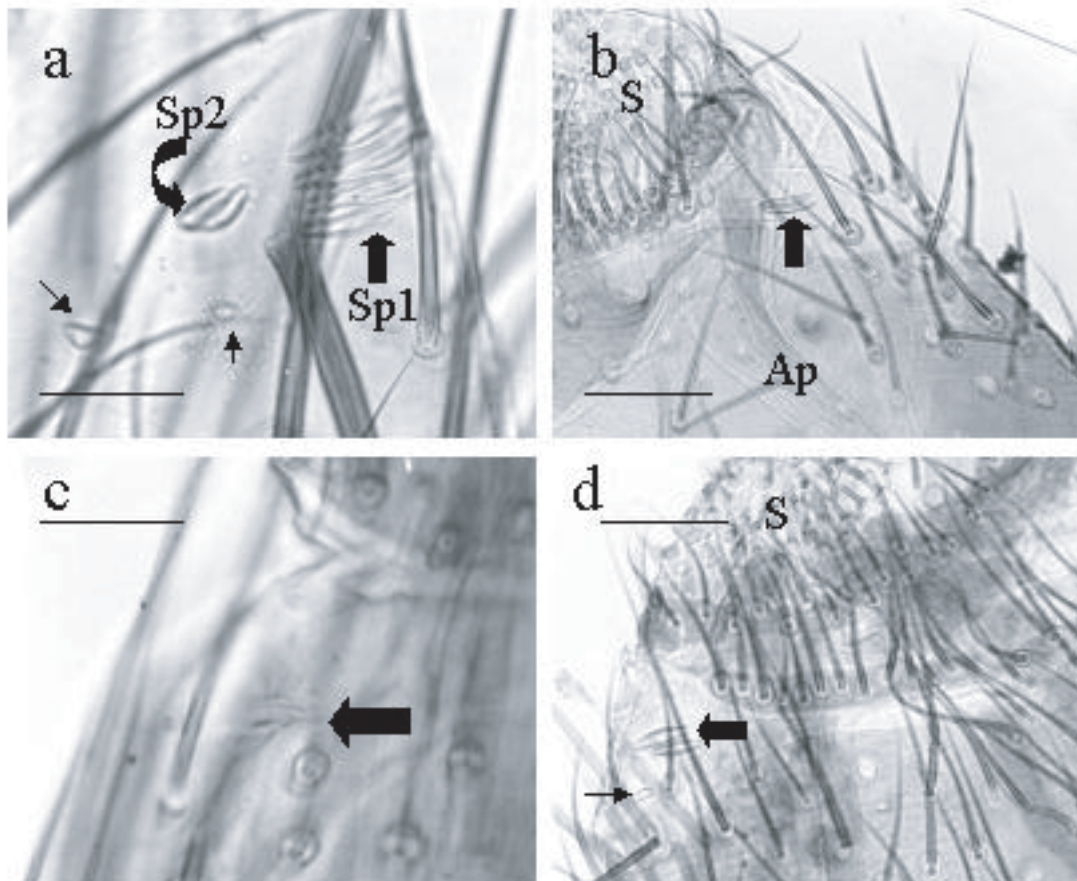


Figure 4. Photomicrographs of the anterior spinnerets of spiders showing LSSOs. A two-slit LSSO (indicated by thick arrows in **b**, **c** and **d**) is a common feature in most spider species. Orb-weaver, *A. pulchella* (**a**) however has two LSSOs, one made of two slits (curved arrow) and the other with four slits (thick arrow). (**b**) *Tetragnatha* sp., (**c**) *S. sarasinourm* and (**d**) *P. paykulli*. All the LSSO are type A. Single slits are seen on the spinnerets and are indicated by thin arrows in (**a**) and (**d**). S, spigots. Scale: **a** 20 μm ; **b** and **d** 50 μm ; **c** 40 μm .

Table 3. Slit sense organs on the anterior spinnerets of spiders.

Species	LSSO/SS	Slits
<i>Argiope pulchella</i> (Araneidae)	LSSO 1	4
	LSSO 2	2
	SS	9
<i>Cyrtophora cicatrosa</i> (Araneidae)	LSSO 1	2
	SS	8
<i>Tetragnatha</i> sp. (Tetragnathidae)	LSSO 1	2
	SS	5
<i>Stegodyphus sarasinorum</i> (Eresidae)	LSSO 1	2
<i>Plexippus paykulli</i> (Salticidae)	LSSO 1	2
<i>Oxyopes shwetha</i> (Oxyopidae)	LSSO 1	2
<i>Pardosa</i> sp., (Lycosidae)	LSSO 1	2

SS, single slits. Numbers indicate the number of slits that constitute a LSSO

All LSSO are type A and their β max is less than 5° .

anterior spinneret has a lyriform organ on the anterior side. Typically it is a two-slit LSSO seen at a specific site close to the apodeme (Ap, figure 4d). All spinnerets have individual slits (e.g. figure 4a, d). *Argiope pulchella* has two LSSOs, Sp 1 and Sp 2 (figure 4a), having four and two slits respectively. They differ in their angle of orientation with respect to the axis and the smaller one is therefore not designated as a "satellite LSSO". Some individuals of *Tetragnatha* sp. (figure 4b) have a LSSO of three slits. All other anterior spinnerets of spiders studied have LSSOs of two slits. These LSSOs are nearly perpendicular to the axis of the spinnerets and are of type A with β max less than 5° . The number of slits on the spinnerets is summarised in table 3. Considerable sexual dimorphism can be seen in terms of organization of spigots (unpublished observations). However, there was no sexual dimorphism in the organization of LSSOs in spider species studied here.

2.7 Types of LSSOs and their functional implications

The implications of the aggregation of slits into deliberate lyriform slit sense organs is extensively discussed by Barth (2002). Aggregation of slits into a LSSO can influence the response properties of individual slits. The slits that occur at the periphery of a LSSO absorb maximum load compared to slits in the middle of the LSSO. Parallel arrangement of slits and varying lengths of slits, which are often gradual, influence the response properties in terms of frequency and amplitude of deflection of slits to which they are most sensitive. The type A LSSO is believed to be suited for sensing stimulus with broad directional range. Type B1-B3 LSSOs are suggested to be capable of range fractionation of stimulus amplitudes. The heart-shaped type C (figure 3c,d) is suited for analysing stress direction. Type D (figures 2c, 3c,

d and e) may have response characteristics comparable to type C LSSO. However, these characteristics for type D LSSOs are as yet unknown. The occurrence of a type C and a type D LSSO on the palpal trochanter of *S. sarasinorum* pedipalps is interesting as they are the most complex of the known types of LSSOs. Such an arrangement may help in accurate analysis of direction of stress. The divergence of slits in a LSSO or β max ($^\circ$) suggests that the slits are sensitive to input from varying angles. Barth *et al* (1984) compares this property to spectral sensitivity of photoreceptors responsible for colour vision, wherein the stimulus components are sensed at the receptor level.

The presence of larger number of LSSO in the proximal segments is suggested to be correlated to the presence of muscles in the proximal segments of the legs (Barth 2002). Spiders do have considerable numbers of LSSOs on the distal segments of legs (Peters and Preufndt 1986). A considerable amount of vibratory input may be received by the distal segments (metatarsus and tarsus), as the legs touch the substratum. As the pedipalps are often suspended in air, stimulus input from the distal end would be least compared to the proximal ends. Pedipalps are not load-bearing structures, and combined with the presence of musculature at the proximal end, these facts may be the reasons for the absence of LSSOs in the tarsus and tibia of the pedipalps. The LSSOs are therefore found on the patella, femur and trochanter of the pedipalps. As in the case of legs, the LSSOs occur at the joints of the pedipalps and often on the lateral sides. The LSSOs on the patella of *Pardosa* and *Cyrtophora* (Pa 1 and Pa 2) occur in the middle of the segment, on a cuticular ridge, which is probably a site for attachment of muscle.

2.8 Analogous LSSOs

The arrangement of LSSOs on the legs is comparable among spiders. A comparative study (Peters and Pfreundt 1986), has shown that spiders follow a general pattern of LSSOs on their leg segments with a few variations between species which can be correlated with their behaviour. The metatarsal organ, a LSSO found on the tibia-metatarsus joint in spiders, is comparable in most spiders. The larger slits of the metatarsal organs are constant and identifiable in all spiders studied (van de Roemer 1980). As compared to this, the LSSO of entelegyne spiders observed in the present study show variations and the haplogyne species are markedly different. While some of the LSSOs (Pa 1, Pa 2, and Tr 1) are comparable in *Cyrtophora* and *Pardosa*, the pattern of arrangement and composition of LSSOs are different among species (figure 3 a-f). *Stegodyphus sarasinorum* has four LSSOs on its femur while most other spiders studied have one LSSO. Similarly, *C. cicatrosa* has three LSSOs on the pedipalp, while *S. sarasinorum* has none.

2.9 Pedipalps in courtship and mating

Pedipalps are used during courtship for sperm transfer. The palp as a whole is used while 'waving' or 'drumming' during courtship. Chemosensory hairs on the palp are used for tracking the female following the female dragline (Tietjen and Rovener 1980). A broad classification of spiders includes haplogyne (simple genital tract) and entelegyne (complex genital tract) spiders. A complex design of the male palp that corresponds to the female epigyne is believed to be the reason for species-specific copulation, but is however, not proven. It would be interesting to observe whether haplogyne and entelegyne traits are displayed in the sensory systems including chemosensory hairs and LSSOs on pedipalps. It is likely that the tarsal (cymbium) structural specialization of the male coupled with a unique LSSO pattern on the pedipalp, which is species specific, contributes to reproductive isolation.

The most striking difference in the distribution of LSSOs on the pedipalps is their absence on the tarsus and tibia, which are the distal segments. A few individual slits are seen at the tip of the tarsus. *Stegodyphus* has a two-slit LSSO that can be considered as a lyriform organ. LSSOs occur on the patella, femur and trochanter. The only previous report on the pedipalp of *Cupennius* (Barth 1985b) showed a type B1 LSSO on the coxa that is made of 6 slits. The present study did not reveal LSSO on the coxa of any of the spiders studied. The entelegyne spiders have 5 or 6 LSSOs on their pedipalps, while the haplogyne species (*P. phalangioides* and *C. lyoni*) have only one or two LSSOs on the femur (figure 3a, b). The complement of LSSOs on the pedipalps matches the complexity of LSSOs on the legs. This is indicative of the rich sensory input that the LSSOs may provide through the pedipalp in case of entelegyne spiders. As the pedipalp is strikingly dimorphic between the sexes, we have compared male and female spiders of three species and we do find some amount of dimorphism. While no striking sexual dimorphism occurs in *P. phalangioides* (Pholcidae), *C. lyoni* (Pholcidae) the male has two type B1 LSSO on the patella that are oriented perpendicular to the long axis of the palp. The LSSO of the female is at an angle of 20° to the long axis of the palp (figure 3b). In case of *Pardosa* a difference exists in LSSO Fe 1 and in the occurrence of groups of slits at the coxal joints, which are absent in the female. Observations in the present study, indicate subtle sexual dimorphism in slit sensilla. However, more data are required to establish it as a significant feature.

The sensory input from the substratum, webs or draglines appear to be less significant as no LSSOs occur on the distal segments of the pedipalps, whereas in the case of spider legs, the tarsus, metatarsus and tibia have a considerable number of LSSOs (Barth 1985b; Peters and Pfreundt 1986). The presence of larger number of LSSO on the distal segments of the leg of web building spiders, led Peters and Pfreundt (1986) to

suggest that the vibratory input from distal parts may be significant for the web builders in prey catching. The presence of slit sense organs on the distal segments suggests that they may provide information about the movements of the palps and the relative positions of the segments of the palps.

There are many hypotheses concerning the complexity of LSSOs and their occurrence on the appendages. The haplogyne pedipalp is simple in structure compared to entelegyne spiders. The pedipalps do not serve a locomotory function. They may receive vibratory input from the silk of the dragline or the web. They serve in injecting the spermatophores. The 'simple' nature of the LSSO complement leads us to suggest that the process of insemination with a simple cymbium in haplogyne spiders (*Pholcus* and *Crossopriza*) requires a simple LSSO arrangement. The complex cymbium and accompanying muscular machinery needed for copulation and injection of the spermatophore among entelegyne spiders may need a complex arrangement of LSSOs. The LSSOs on the pedipalps may also be tuned of the courtship vibratory pattern of the mate.

2.10 Spinnerets

Occurrence of a two-slit type A LSSO on the anterior spinnerets appears to be common feature in all spiders studied. Barth (1985b) reported the presence of a two-slit LSSO on the spinneret of *C. salei*. A deviation from this general pattern towards a degree of complexity was found on the anterior spinnerets of *Argiope pulchella* – a renowned orb weaver, which has two type A LSSOs having 4 and 2 slits respectively (figure 4a). From their structure, their stress detecting capability and directional sensitivity would be weak as they all are type A LSSOs and have a small number of short-length slits. It is therefore likely that a complex behaviour like spinning and web building depends more on strain detectors on the spinnerets described by Gorb and Barth (1996). Apart from LSSOs, single slits are found on the spinneret. They are few in number compared to the density of single slits known to occur on surfaces like the abdomen of spiders and may therefore have a less significant role to play. It is interesting that only the anterior spinneret have LSSOs, whereas the posterior and median do not. The anterior spinneret is served by the piriformes gland, the silk of which is used for spinning the attachment disc and also the ampullate gland that produces the dragline silk and the frame thread of an orb. In spiderlings, the ampullate gland produces the thin gossamer threads (Foelix 1996) that are used in ballooning behaviour for dispersal. Thus specific behaviours, some of which are common to orb weavers and wanderers (attachment disc, dragline and ballooning) are served by the anterior spinnerets. The LSSO on anterior spinnerets may assist such behaviours, that are common to different species.

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References

- Barth F G 1978 Slit sense organs: "Strain gauges" in the arachnid exoskeleton; *Symp. Zool. Soc. London* **42** 439–448
- Barth F G 1985a Neuroethology of spider vibration; in *Neurobiology of arachnids* (ed.) F G Barth (Berlin: Springer) pp 203–229
- Barth F G 1985b Slit sensilla and the measurement of cuticular strain; in *Neurobiology of Arachnids* (ed.) F G Barth (Berlin: Springer) pp 162–188
- Barth F G 2002 *A Spider's World: senses and behaviour* (Heidelberg: Springer) pp 394
- Barth F G, Ficker E and Federle H-U 1984 Model studies on the mechanical significance of grouping in compound spider slit sensilla; *Zoomorphology* **104** 204–215
- Bleckmann and Barth F G 1984 Sensory ecology of the semi-aquatic spider (*Dolomedes triton*) II. The release of predatory behaviour by water surface waves; *Behav. Ecol. Sociobiol* **14** 303–312
- Bristowe W S and Locket G H 1926 The courtship of British lycosid spiders and its probable significance; *Proc. Zool. Soc. London* 317–327
- Craig C L 2003 *Spider webs and silk: tracing evolution from molecules to genes to phenotypes* (New York: Oxford University Press) pp 230
- Foelix R F 1996 *Biology of spiders* (New York: Oxford University Press) pp 330
- French A S, Torkkelli P H and Seyfarth E-A 2002 From stress and strain to spikes: mechanotransduction in spider slit sensilla; *J. Comp. Physiol* **A188** 739–752
- Gorb S N and Barth F G 1996 A new mechanosensory organ on the anterior spinnerets of the spider *Cupennius salei* (Araneae, Ctenidae); *Zoomorphology* **116** 7–14
- Kullman E 1972 The convergent development of orb-webs in cribellate and ecribellate spiders; *Am. Zool.* **12** 419
- Peters W and Pfreundt C 1986 Die verteilung von Trichobothrien und Iyraförmigen Organen und Laufbeinen von Spinnen mit unterschiedlicher Lebensweise; *Zool. Beitr. N F* **29** 209–225
- Rovner J S 1975 Sound production by nearctic wolf spiders: a substratum-coupled stridulatory mechanism; *Science* **190** 1309
- Seyfarth E-A and Barth F G 1972 Compound slit sense organs on the spider leg: mechanoreceptors involved in kinesthetic orientation; *J. Comp. Physiol* **78** 176–191
- Tietjen W J and Rovner J S 1980 Trail following in two species of wolf spiders: sensory and etho-ecological concomitants; *Anim. Behav.* **28** 735
- van de Romer A 1980 *Eine vergleichende morphologisches Untersuchung and dem für die Vibrationswahrnehmung wichtigen Distalbereich des Spinnenbeins*, Diplomarbeit, Universität Frankfurt am Main

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