

REVIEW ARTICLE

Sensory biology of Phalangida harvestmen (Arachnida, Opiliones): a review, with new morphological data on 18 species

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Abstract

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Phalangida includes three of the four suborders of Opiliones (Arachnida): Eupnoi, Dyspnoi and Laniatores. We review the literature on the sensory structures and capabilities of Phalangida, provide new morphological data for 18 species and discuss the 11 sensory structures that have been described in the group. Based on the published data encompassing both behaviour and morphology, three conclusions are apparent: (1) species of Phalangida appear to have limited abilities to detect stimuli at a distance; (2) close range olfaction probably helps to find foods with strong odours, but (3) they appear to be highly dependent on contact chemoreception to detect live prey, predators and mates. We also highlight the fact that legs I in the three suborders and pedipalps in Dyspnoi and Eupnoi are very important sensory appendages, thus legs II should not be called the ‘sensory appendages’ of harvestmen. In conclusion, we highlight the fact that the sensory capabilities, diet, prey capturing and handling ability, and foraging behaviour of species of Phalangida seem to be different from those of most other arachnids. Finally, we suggest future directions for studies in the field of the sensory system of the group.

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Introduction

The input of all environmentally relevant stimuli arrives into an animal’s nervous system by means of sensory structures. These act not only to detect multiple bits of information, but also to filter the relevant ones (Barth 2004). The study of sensory biology allows us to understand what stimuli are important for an animal, and how and why the animals behave the way they do. This is an obvious need when one studies any aspect of behaviour, because it provides important information to understand a variety of behaviours, including navigation, foraging behaviour, mate choice, gregarious behaviour, courtship and predator avoidance.

Among arachnids, spiders have been the most commonly used models in papers on all the aspects of behaviour that directly relate to sensory biology (Barth 2002a). The probable main reason why spiders are currently the most often used

arachnids in such studies is the available frame of reference in this group. Because we know the fundamental aspects of their sensory capabilities and natural history, we are able to test hypotheses and relate their behaviour to broad conceptual theories (e.g. Hebets 2003, 2004), which has not been true for most other arachnids, such as harvestmen (Arachnida, Opiliones). Fortunately, studies on harvestman behaviour and ecology have increased in recent years (Machado *et al.* 2007), and this is greatly contributing to the creation of a basic frame of reference from which behavioural ecologists can work. However, we still lack studies relating to sensory structures and capabilities, and, as mentioned, these subjects greatly help us to understand harvestman behaviour.

In this paper, we review the sensory structures described in Phalangida: the suborders Eupnoi, Dyspnoi and Laniatores of Opiliones, considering studies published from 1890 up to 2007. A review of these structures in the most

basal suborder, the cyphophthalmids, will be presented elsewhere. The first part of the paper is a list of the sensory structures reported in the group, adding new data for 18 species. We discuss sensory capabilities separately per sensory modality, discuss the relative importance of leg II for sensory purposes, relate their sensory capabilities to diet and foraging behaviour comparatively among arachnids, and suggest future directions for studies on sensory structures and capabilities of Phalangida.

Sensory structures

Cuticular ornaments are not considered herein; we encourage the reader to see the papers of Murphree (1988), Kauri (1989) and Pinto-da-Rocha *et al.* (2007), all of which present several scanning electron micrographs of the integument. The glandular capitate and plumose setae (e.g. Wachman 1970;

Shear 1986) and the adhesive hairs of the scopula (Rambla 1990) were not included in this paper.

Except for the eyes, spines, slit sensilla and sensilla chaetica, all other structures mentioned below are, among arachnids, exclusive to harvestmen. The homology between the solenidia of harvestmen and of mites is uncertain. Whenever the structure mentioned has not been reported in the literature, we discriminate it as 'PU' (previously undescribed). Procedures for scanning electron microscope preparation follow the basic protocol described in Willemart and Gnaspi (2003). The species we studied and for which data are presented are listed in Table 1.

Campaniform organs (Table 2)

Campaniform organs have only been reported among Eupnoi: *Caddo agilis* (Caddidae), *Opilio parietinus* and *Phalangium opilio*

Table 1 Species of Phalangida used in this study

Suborder/Family	Species
EUPNOI	
Sclerosomatidae	Unidentified sp. 1 (Gagrellinae)
Phalangiidae	<i>Phalangium opilio</i>
DYSPOI	
Trogulidae	<i>Trogulus nepaeformis</i>
Nemastomatidae	<i>Nemastoma bidentatum sparsum</i>
Ischyropsalididae	<i>Ischyropsalis</i> sp. and <i>Ischyropsalis hellwigi</i>
Dicranolasmatidae	<i>Dicranolasma scabrum</i>
LANIATORES	
Agoristenidae	<i>Trinella venezuelica</i>
Cranaidae	<i>Santinezia</i> sp.
Escadabiidae	Undescribed sp. (Cave Lapa Escondida, Itaete, Bahia, Brazil)
Gonyleptidae	<i>Daguerreia inermis</i> , <i>Goniosoma albiscryptum</i> , <i>Iporangaia pustulosa</i> , <i>Neosadocus</i> sp., <i>Piassagera brieni</i> , <i>Promitobates ornatus</i>
Stygnidae	<i>Stygnus multispinosus</i>
Triaenonychidae	<i>Larifugella afra</i>

Table 2 Sensory structures and hairs described in each group of Phalangida

	Eupnoi	Dyspnoi	Laniatores	Reference
Eyes	X	X	X	e.g. Juberthie 1964.
Campaniform organs	6	—	—	Edgar 1963; this paper.
Double trichomes	1	—	—	This paper.
Dorsal prosomal spines	—	1	—	Lopez <i>et al.</i> 1980; Juberthie <i>et al.</i> 1981.
Falciform setae	—	—	3	Willemart <i>et al.</i> 2007; this paper.
Flat setae	1	—	—	This paper.
Sensilla basiconica	1	—	3	Willemart <i>et al.</i> 2007; this paper.
Sensilla chaetica	X	X	X	e.g. This paper.
General slit sensilla	23	8	14	e.g. This paper.
Paired metatarsal slit sensilla	—	—	16	Hansen 1893; Willemart <i>et al.</i> 2007; this paper.
Spicer's tarsal organ	3	—	—	Spicer 1987; Holmberg and Cokendolpher 1997.
Solenidia	1	3	—	Gruber 1970, 1978; van Der Hammen 1985; this paper.
Spines	X	X	X	e.g. This paper.
Trichomes	X	X	X	e.g. This paper.

The number of species that have been reported to bear these structures are shown in each line. 'X' = all or almost all species have it.

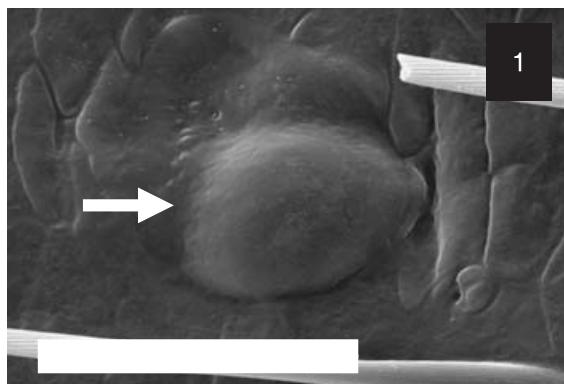


Fig. 1—Possible campaniform sensillum, on the median portion of metatarsus of leg IV in *Phalangium opilio* female, lateral view. Scale bar: 20 µm.

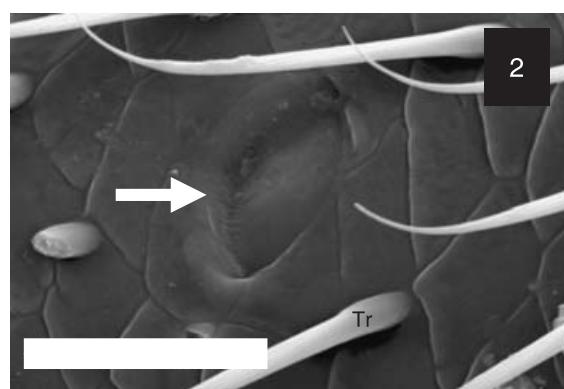


Fig. 2—Possible campaniform sensillum, and trichomes (Tr) on the tarsus of pedipalp, in *Phalangium opilio* male, lateral view. Scale bar: 15 µm.

(Phalangiidae); *Leiobunum calcar*, *L. longipes* and *L. politum* (Sclerosomatidae) (Edgar 1963). In harvestmen, Edgar (1963) made a distinction between slit sensilla and campaniform organs, the former being 'T' or 'L' shaped and the latter being circular. However, Barth and Stagl (1976) did not follow this separation when investigating slit sensilla in several arachnids, arguing that Edgar (1963) did not clearly justify his criteria to distinguish slits from campaniform sensilla. Except according to Edgar (1963) and to Schultz and Pintoda-Rocha (2007), who mentioned such structures on the penis of *L. calcar*, campaniform sensilla have been considered to be typical of insects, analogous to the slit sensilla of arachnids (Pringle 1955; Gnatzky *et al.* 1984) and absent in chelicerates (Keil 1997). They detect mechanical stresses on the cuticle, just like slit sensilla (Chapman 1998).

In *Phalangium opilio*, our observations revealed the presence of circular structures that resemble campaniform sensilla (Figs 1, 2). These were found in males and females, on the prolateral and retrolateral regions of the legs, proximally in the tarsus and metatarsus. A morphological variety was found on the pedipalp of a male (Fig. 2) and on the

penis. Histological studies should be conducted before we can conclude that this is an actual campaniform organ.

Dorsal prosomal spines (Tables 2 and 3)

This pair of spines is situated ~0.5 mm behind the eyes in *Sabaccon paradoxum* (Dyspnoi, Sabaconidae), ~100 µm from one another, and has been called 'dorsal prosomal spines' by Lopez *et al.* (1980) and 'dorso-submedial sensilla' by Juberthie *et al.* (1981). Their length is between 120 and 140 µm with a 50-µm diameter at the base of the shaft, which has a blunt tip and is not inserted in a socket membrane (Lopez *et al.* 1980). Juberthie *et al.* (1981) have shown that the unusually thick walls (between 2 and 4 µm) are perforated and that dendrites occur throughout the shaft, suggesting an olfactory role. The dorsal prosomal spines may therefore be added to the list of arachnid olfactory receptors, which already includes the wall-pored sensilla of Acari, Cyphophthalmi (Opiliones), Ricinulei and Amblypygids (Beck *et al.* 1974; Foelix 1976; Alberti 1998; Talarico *et al.* 2005, 2006).

Double trichomes (PU) (Table 2; Fig. 3)

We found these hairs on legs IV of *Phalangium opilio* males. We failed to find them in females and on legs I, II and III of males. On the tarsus, they are present in low numbers (fewer than six double trichomes) distally on the tarsus (tarsomeres 1–20), and in higher numbers (more than six double trichomes) on the most proximal areas (these numbers of hairs include only those seen on one side of the leg). On the metatarsus they are more abundant on the distal than on the proximal region. This hair is just like two trichomes (see below) fused to one another in appearance, and its function is unknown.

Eyes (Tables 2 and 3; Figs 4–7)

Harvestmen bear two direct eyes though some subterranean species have none (Purcell 1892; Berland 1949; Juberthie

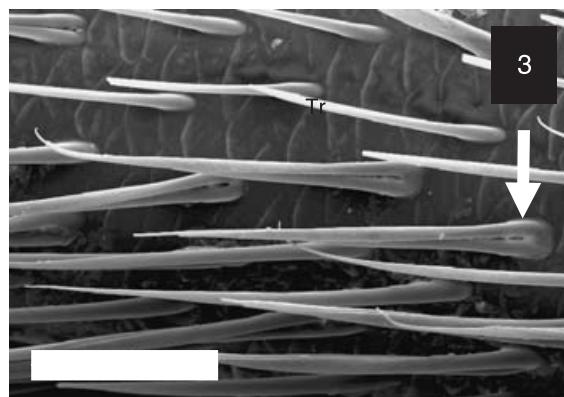


Fig. 3—Double trichomes (arrow) and trichomes (Tr), on the tarsus of leg IV, in *Phalangium opilio* male, lateral view. Scale bar: 30 µm.

Table 3 Sensory capabilities of harvestmen, behavioural (experimental or descriptive) and morphological (external morphology and/or histology) evidence

	Eupnoi		Dyspnoi		Laniatores		Partial reference list
	Behaviour	Morphology	Behaviour	Morphology	Behaviour	Morphology	
Contact mechanoreception	Yes	Yes	Yes	Yes	Yes	Yes	Eisenbeis and Wichaard 1987; Guffey <i>et al.</i> 2000; Willemart and Gnaspini 2003; This paper.
Contact chemoreception	?	Yes	Yes	Yes	Yes	Yes	Immel 1954; Eisenbeis and Wichaard 1987; Guffey <i>et al.</i> 2000; Willemart and Gnaspini 2003; Willemart and Chelini 2007.
Close-range olfaction	?	Yes	Yes	Yes	Yes	Yes	Immel 1954; Eisenbeis and Wichaard 1987; Guffey <i>et al.</i> 2000; Machado <i>et al.</i> 2002; Willemart and Chelini 2007.
Long-range olfaction	?	?	?	Maybe	?	?	Lopez <i>et al.</i> 1980; Juberthie <i>et al.</i> 1981.
Substrate-borne vibrations	No	No	?	No	No	No	Phillipson 1960; Luque 1993; Macíaz-Ordoñez 1997, 2000; Willemart <i>et al.</i> 2007; Willemart and Chelini 2007; Willemart unpublished data; This paper.
Airborne vibrations	No	No	?	No	?	No	Hansen 1917; Santer and Willemart unpublished data.
Slight wind currents	No	No	?	No	No	No	Hansen 1917; Phillipson 1960; Macíaz-Ordoñez 1997, 2000; Willemart <i>et al.</i> 2006; Willemart <i>et al.</i> 2007; Willemart and Chelini 2007; Santer and Willemart unpublished data; This paper.
Photoreception	Yes	Yes	Yes	Yes	Yes	Yes	Pabst 1953; Immel 1954; Clingenpeel and Edgar 1966; Curtis 1970; Muñoz-Cuevas 1978a; Meyer-Rochow and Liddle (1988, 2001); Santos 2003; Pioker 2005.
Hygroreception	Yes	?	Yes	?	Yes	?	Todd 1949; Edgar 1971; Santos 2003.
Thermoreception	Yes	?	Yes	?	Yes	?	Todd 1949; Immel 1954; Clingenpeel and Edgar 1966; Edgar 1971; Santos 2003.

'Yes' = existence of evidence; 'No' = evidence of absence; '?' = no evidence. We defined slight wind current as those produced by prey walking nearby, for example, as opposed to an approaching human. A species of Dyspnoi have dorsal prosomal spines that have wall pores, which could potentially be used for long-range olfaction (see text).

1964; Karaman 2005). In exceptional (teratological) cases, individuals might bear one eye (Cirdei 1955) or none (Juberthie 1963; Holmberg and Kokko 1983). In the three suborders considered here, eyes are located dorsally on the prosoma, the field of view being generally the lateral regions of the harvestmen. They may be on an ocularium (= ocular tubercle) (Figs 4–6) or separated from each other (Fig. 7). An exception to these general rules is found among troglulids (Dyspnoi), in which the eyes are on the hood (= cucullus) (Komposch 2000). The eyes are usually small (see Curtis 1969, 1970), but species of Caddidae are exceptional in that they have large eyes of unknown capabilities (Shear 1975). No evidence exists of any characteristic that would suggest sharp image formation (see below). A general account on harvestmen's eyes can be found in Schultz and Pinto-da-

Rocha (2007). Additional information can be found in Brignoli (1966), Juberthie (1972), Curtis and Pearson (1972), Muñoz-Cuevas (1975, 1978a, 1978b, 1980), and Carricaburu and Muñoz-Cuevas (1978, 1981a,b, 1985).

Falciform setae (Table 2; Fig. 8)

These setae have been described in the gonyleptid (Laniatores) *Neosadocus* sp. and *Iporangaia pustulosa* (Willemart *et al.* 2007). We found it in *Promitobates ornatus* (Laniatores, Gonyleptidae), in which they occur on the lateral region of the most distal tarsomere of legs I and II. They are shorter and thinner than sensilla chaetica (see below), inserted within a socket membrane and the tip is pointed. The function of these setae is unknown.

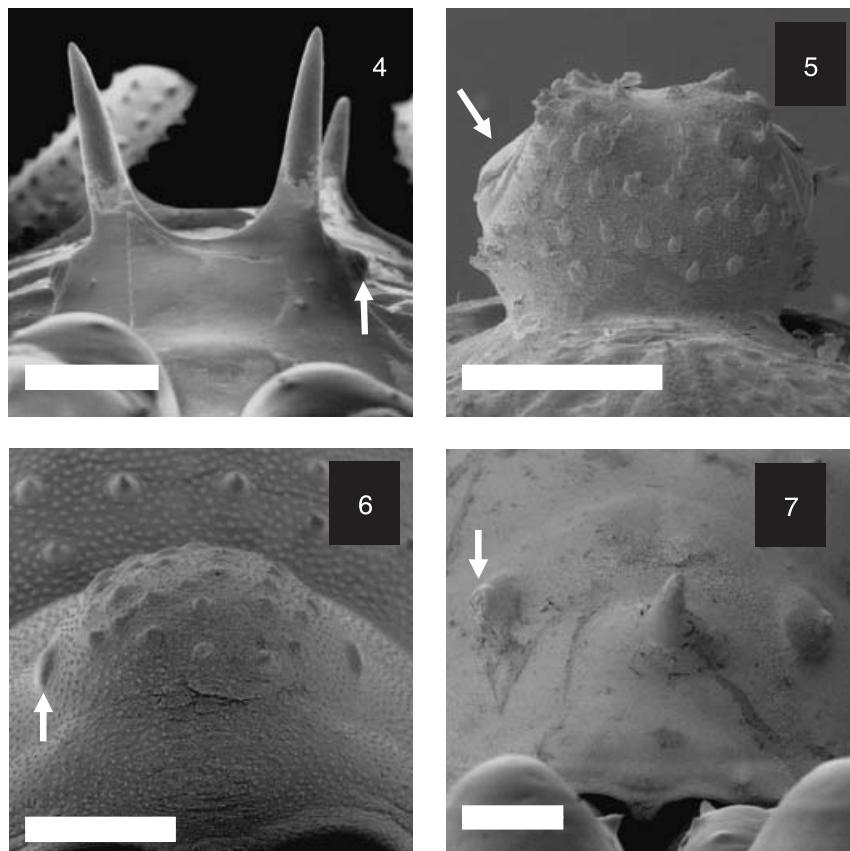


Fig. 4—Ocularium, on the dorsum of the prosoma, frontal view, in *Santinezia* sp. Arrow head = left eye. Scale bar: 1 mm.

Fig. 5—Ocularium, on the dorsum of the prosoma, frontal view, in an unidentified species of Gagrellinae. Arrowhead = right eye. Scale bar: 200 μ m.

Fig. 6—Ocularium, on the dorsum of the prosoma, frontal view, in an undescribed species of Escadabiidae. Arrowhead = right eye. Scale bar: 200 μ m.

Fig. 7—Separated eyes, on the dorsum of the prosoma, frontal view, in *Stygnus multispinosus*. Arrowhead = right eye. Scale bar: 500 μ m.

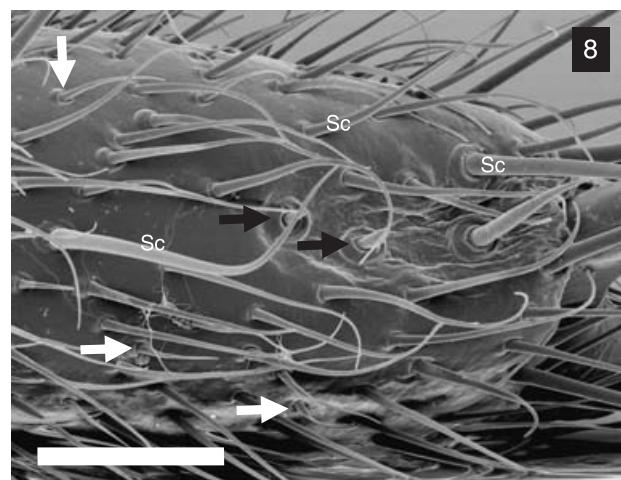


Fig. 8—Sensilla chaetica (Sc), sensilla basiconica (black arrows) and falciform setae (white arrows) on the most distal tarsomere of leg II in *Neosadocus* sp., dorsal view. Note that trichomes are almost absent. Scale bar: 100 μ m.

Flat setae (PU) (Table 2; Figs 9–11)

We found these setae on legs I, III and IV of three *Phalangium opilio* males, but not in all the individuals (legs I and III of one

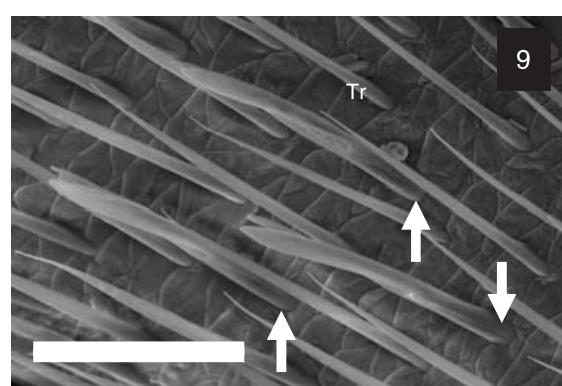


Fig. 9—Flat setae (arrow) and trichomes (Tr), on the tarsus of leg II, in *Phalangium opilio* male, lateral view. Scale bar: 30 μ m.

individual did not have them). We failed to find them in females. On the tarsus, they are present in low numbers (< 10 setae) on the most distal part (tarsomeres 1–25) and in high numbers (> 10, up to 45 setae) on the most proximal ones (tarsomeres 26–40) (these numbers of setae include only those seen on one side of the leg). On the metatarsus they are more abundant on the distal than on the proximal region.

The shaft of the seta is rigid and cylindrical in its proximal portion. More distally, it is usually bifid (Figs 9 and 11),

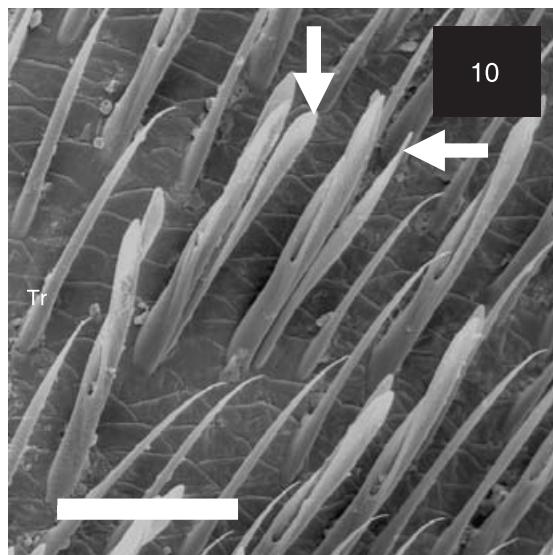


Fig. 10—Flat setae and trichomes (Tr), on the metatarsus of leg I, in *Phalangium opilio* male, lateral view. Arrows indicate ‘accessory setae’ of flat setae. Scale bar: 90 µm.

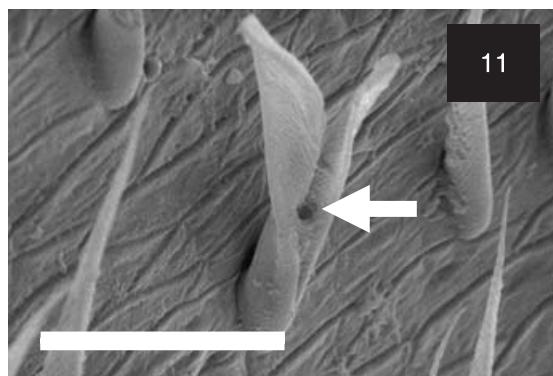


Fig. 11—Flat seta on the metatarsus of leg I, in *Phalangium opilio* male, lateral view. Arrowhead = putative opening. Scale bar: 15 µm.

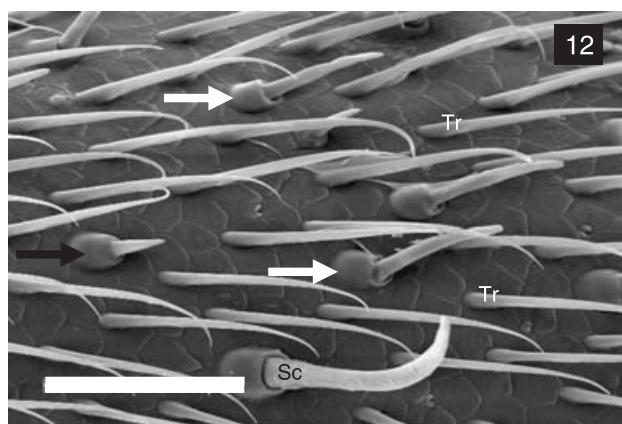


Fig. 12—Solenidia (white arrows), sensillum basiconicum (black arrow), sensilla chaetica (Sc) and trichomes (Tr) on the tarsus of pedipalp in *Phalangium opilio* female, laterodorsal view. Scale bar: 35 µm.

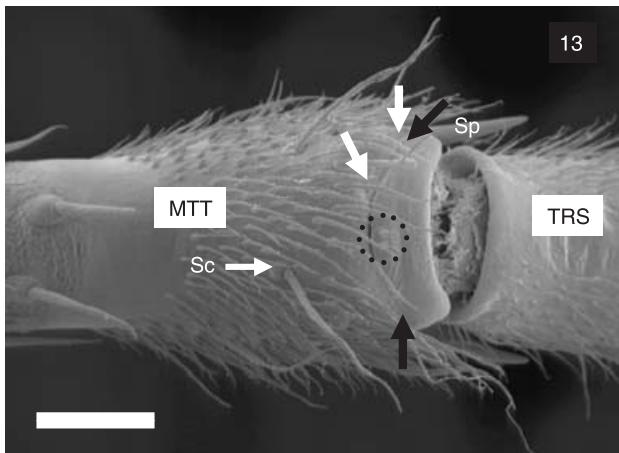


Fig. 13—Metatarsal paired slits, sensilla basiconica (circle), sensilla chaetica (Sc), spines (Sp) and trichomes on the extremity of the metatarsus of leg III, dorsal view, in *Larifugela afra*. TRS = tarsus; MTT = metatarsus. White arrowheads indicate the limits of the proximal slit. Black arrowheads indicate the limits of the distal slit. Scale bar: 100 µm.

bearing two flat portions that surround a circular region where they meet proximally (Fig. 11). Some flat setae have an ‘accessory seta’ (Fig. 10). Neither wall pores nor a pore tip could be detected. Bifid but strikingly different setae have also been described by Juberthie (1970, 1972) on the dorsal region of the metatarsus of the laniatorids *Galanomma microphthalmum* (Zalmoxidae) and *Abasola sarea* (Travuniidae). The function of these setae is unknown.

Sensilla basiconica (Table 2; Figs 8, 12–14)

We found these sensilla in all four legs on the dorsal region of the distal part of the metatarsus (two to four sensilla; Figs 13,14; see also Willemart *et al.* 2007) and in legs I and II on the dorsal region of the distalmost tarsomere (two sensilla), in *Daguerreia inermis* (Laniatores, Gonyleptidae). Willemart *et al.* (2007) also reported them from the latter region in *Neosadocus* sp. (Fig. 8) and *Iporangaia pustulosa*. They seem to open in the apical region by means of a longitudinal aperture. A morphological variety was found at the lateral region of the pedipalp tarsus of female *Phalangium opilio* (Fig. 12). The pointed short shaft inserts in a large socket membrane and has no discernable wall pores. Their function is unknown.

Sensilla chaetica (Tables 2 and 3; Figs 8, 12, 13, 15–19)

These sensilla occur on the whole body of all Phalangida. The angle of insertion of the shaft is between ~50° and 90°. A socket membrane surrounds the proximal part of the shaft. Sensilla chaetica are probably gustatory contact mechano-

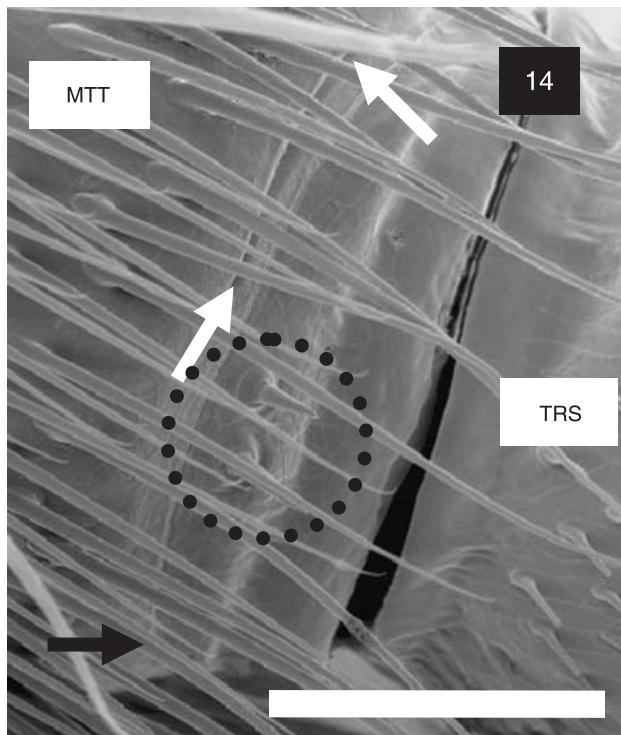


Fig. 14—Metatarsal paired slits and sensilla basiconica (circle), on the metatarsus/tarsus articulation of leg I in *Iporangaia pustulosa*, dorsal view. White arrowheads indicate the limits of the proximal slit. Black arrow indicates the prolateral limit of the distal slit. TRS = tarsus; MTT = metatarsus. Scale bar: 100 μ m.

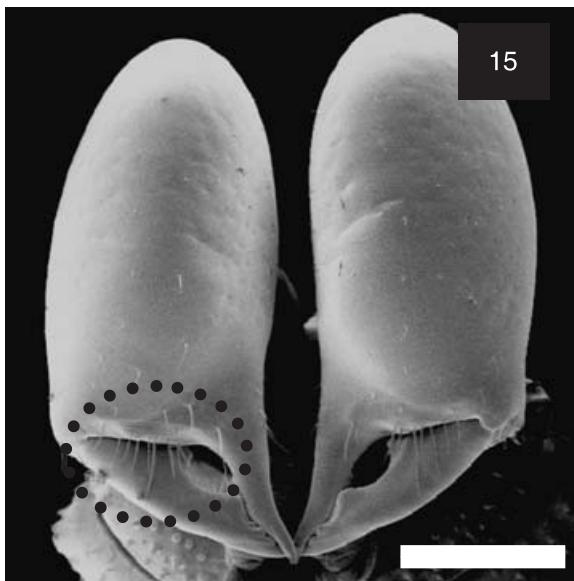


Fig. 15—Sexually dimorphic large chelicerae with sensilla chaetica (circle) on the distal portion of the second segment, frontal view, in *Stygnus multispinosus* male. Scale bar: 1 mm.

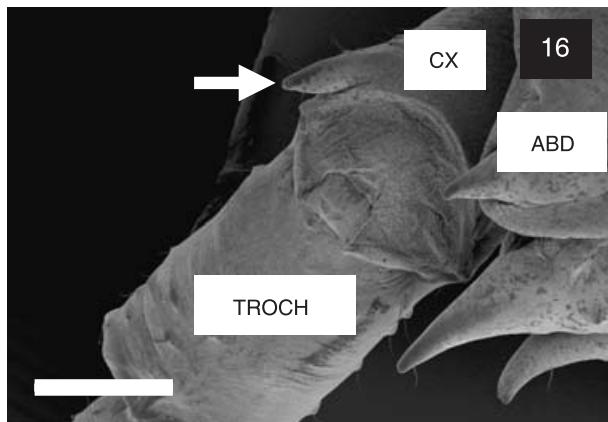


Fig. 16—Coxa-trochanter articulation of leg IV in *Goniosoma albiscryptum* female. Note the small external apophysis (arrow) and the absence of apophysis on trochanter. Abd = abdomen; Cx = coxa; Troch = trochanter. Scale bar: 1 mm.

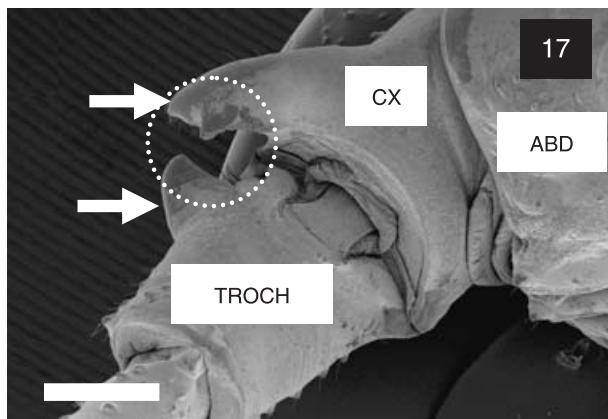


Fig. 17—Sexually dimorphic coxa-trochanter articulation of leg IV in *Goniosoma albiscryptum* male. Note the external apophysis (upper arrow) and apophysis on trochanter (lower arrow) of male coxa. White circle indicates region detailed in Fig. 18. Abd = abdomen; Cx = coxa; fmr = femur; Troch = trochanter. Scale bar: 1 mm.

receptors because they have an internal lumen associated with a pore tip (Willemart and Gnaspi 2003; but see Guffey *et al.* 2000), they overtop the remaining sensilla (Foelix and Chu-Wang 1973; Altner and Prillinger 1980; Foelix 1985), and their histological characteristics (the sheath containing the many dendrites does not attach to the socket membrane; instead, it passes directly through the centre of the setal shaft – Guffey *et al.* 2000) indicate that this may be the case. At the dorsal and lateral regions of legs I and II of laniatoreans, the most distal tarsomere usually bears several sensilla chaetica and few trichomes (Fig. 8), which is not usually the case for legs III and IV (Willemart and Gnaspi 2003). This probably occurs because legs I and II are mostly sensory (see below).

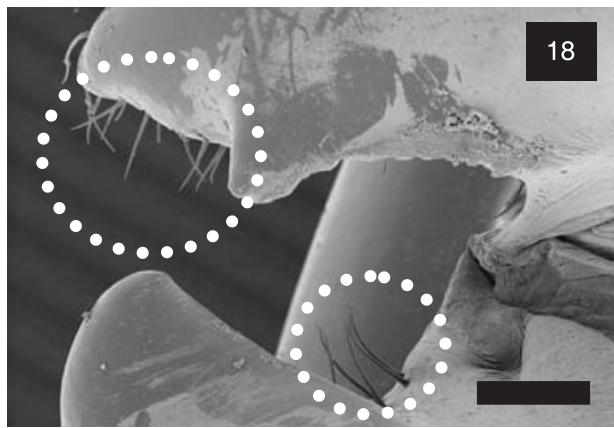


Fig. 18—Coxa-trochanter articulation of leg IV in *Goniosoma albiscryptum* male, detail of Fig. 17, showing mechanoreceptor setae, sensilla chaetica (circles). Scale bar: 250 µm.

In some species that have sexually dimorphic legs IV (Figs 16–18), sensilla chaetica are strategically located below the external apophysis of the male coxa (Fig. 18). When these sensilla are bent, the animal flexes the femur towards the body, which pinches a given offending object between the femur and the apophysis; this behaviour is typically used for defence and in male–male fights (Willemart 2005; Gnaspi and Hara 2007). Finally, because what we are defining as sensilla chaetica includes sensilla of distinct sizes that occur in distinct locations, we cannot rule out the possibility that some of them do not have a pore tip and so act only as mechanoreceptors.

Slit sensilla (Tables 3 and 4; Figs 19–25)

Slit sensilla are cuticular organs exclusive to arachnids, known to occur in all orders except Palpigradi (Millot 1949;

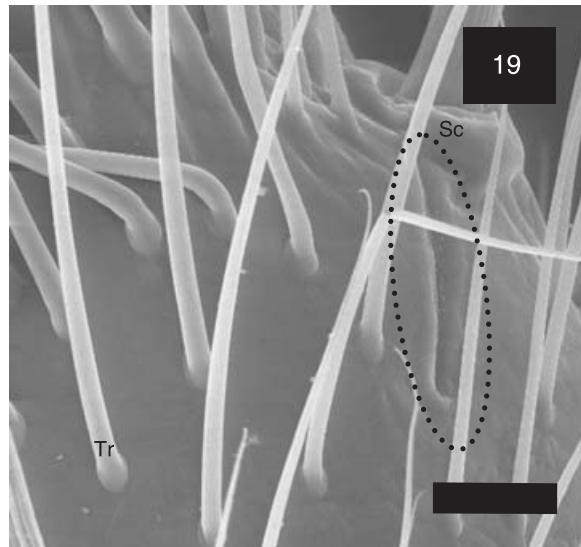


Fig. 19—Slit sensillum (circled), trichomes (Tr) and sensillum chaeticum (Sc) on the most distal tarsomere of leg III in *Promitobates ornatus*, dorsolateral view. Scale bar: 20 µm.

Pittard and Mitchell 1972; Weygoldt and Paulus 1979). In harvestmen, most slit sensilla that have been described are either isolated (Fig. 19) or grouped (Figs 20–25). However, Barth and Stagl (1976) and van der Hammen (1985) have used the term ‘lyriform organs’ for groups of slit sensilla in the trochanter of *Amilenus aurantiacus* and *Paraligolophus agrestis* (Eupnoi, Phalangiidae), respectively (see definitions of ‘isolated’, ‘grouped slits’ and ‘lyriform organs’ in Barth 2002a).

Table 4 shows that slit sensilla can be found in all three suborders, mainly on the appendages. Luque (1993) was the only author to provide histological data on the slit sensilla of harvestmen, and he found that their arrangement was very

Table 4 Slit sensilla in Phalangida; the numbers show how many species in each group have been reported to have slit sensilla in each body region

	Prosoma	Abdomen	Chelicerae	Pedipalps	Legs	Ovipositor	Reference
Eupnoi	1	0	5	4	10	15	Gaubert 1890; Hansen 1893; Hansen and Soerensen 1904; Edgar 1963; Gruber 1969, 1974; Rambla 1975; Barth and Stagl 1976; Muller 1982; Van der Hammen 1985; Eisenbeis and Wichard 1987; Tsurusaki 1987; Holmberg and Cokendolpher 1997; Tsurusaki <i>et al.</i> 2000a,b; Tourinho and Kury 2001; Schultz and Pinto-da-Rocha 2007; this paper.
Dyspnoi	1	3	4	3	6	0	Gaubert 1892; Hansen 1893; Dresco 1952; Juberthie 1961; Gruber 1970, 1978; Lopez <i>et al.</i> 1980; Gruber 1993; Luque 1993; Tsurusaki and Song 1993; Mitov 1995.
Laniatores	0	1	4	2	14	0	Hansen 1893; Hansen and Soerensen 1904; Juberthie 1968, 1970; Van der Hammen 1985; Karaman 2005; Willemart <i>et al.</i> 2007; this paper.

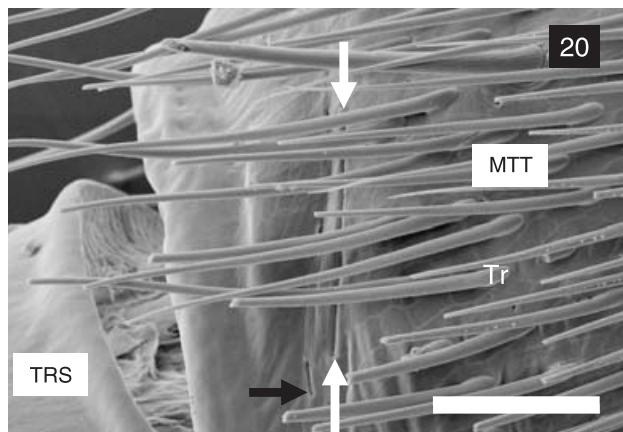


Fig. 20—Metatarsal paired slits on the metatarsus of leg I in *Neosadocus* sp., dorsolateral view. White arrowheads indicate the limits of the proximal slit. Black arrow points to the prolateral limit of the distal slit. Scale bar: 50 µm.

similar to that of spiders, in which they are known to be detectors of mechanical stresses in the cuticle caused by muscular activity, haemolymph pressure and substrate-borne vibrations (Barth 2004). The metatarsal paired slits (Figs 13, 14 and 20) are similar in position to the metatarsal

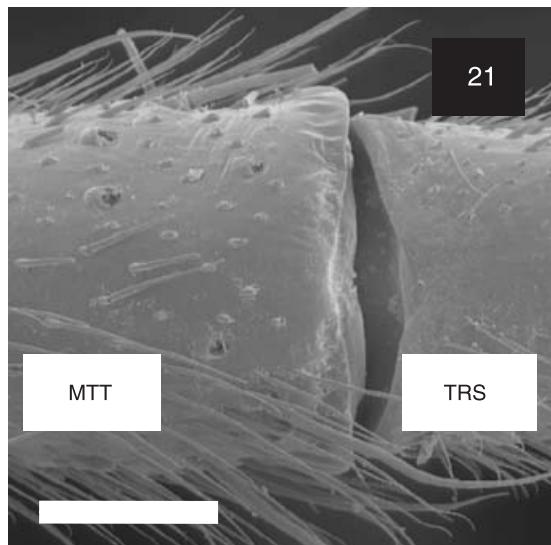


Fig. 21—Distal extremity of the metatarsus of leg III, dorsal view, in *Ischyropsalis* sp., showing the absence of the metatarsal paired slits and sensilla basiconica. TRS = tarsus; MTT = metatarsus. Scale bar: 100 µm.

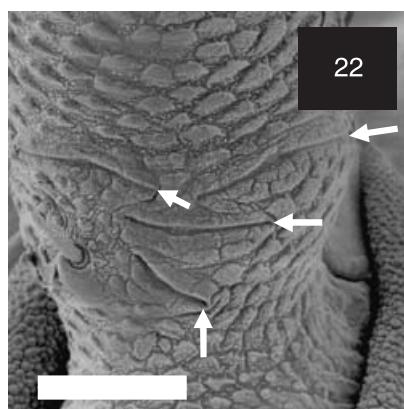


Fig. 22—Group of slit sensilla in the proximal extremity of the femur of leg IV, where it articulates with the trochanter, ventral view, in an undescribed species of Escadabiidae. Arrowheads indicate each of the four slits. Scale bar: 50 µm.

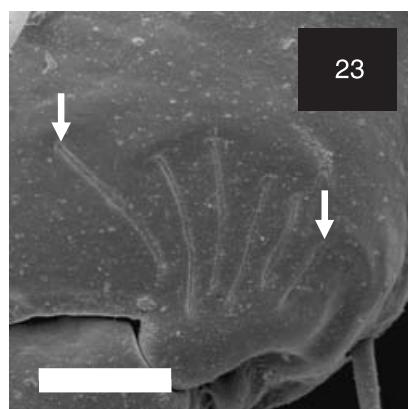


Fig. 23—Group of slit sensilla in the insertion of the movable finger (left chelicera, left side) on the second segment of chelicerae, in an unidentified species of Gagrellinae. Arrows show two of the six slits. Scale bar: 30 µm.

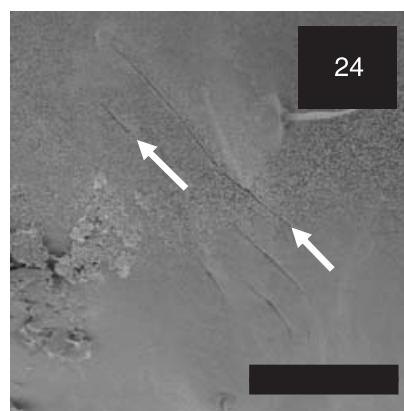


Fig. 24—Group of slit sensilla on the trochanter of leg IV, prolateral view, in *Trinella venezuelica*. Arrowheads indicate two of the five slits seen. Scale bar: 20 µm.

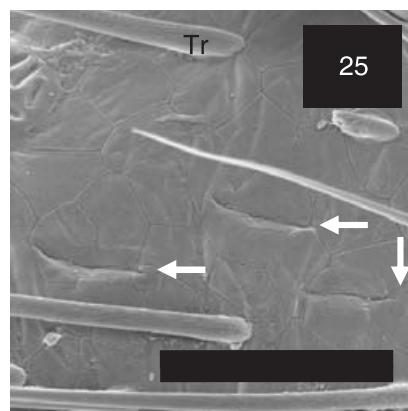


Fig. 25—Slit sensilla and trichomes (Tr) on the distal region of the most distal tarsomere of leg III in *Neosadocus* sp. Arrowheads point to each of the three slits seen. Scale bar: 50 µm.

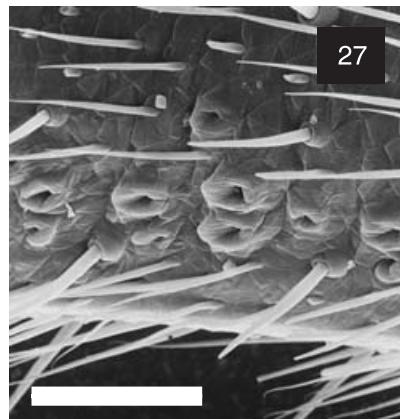
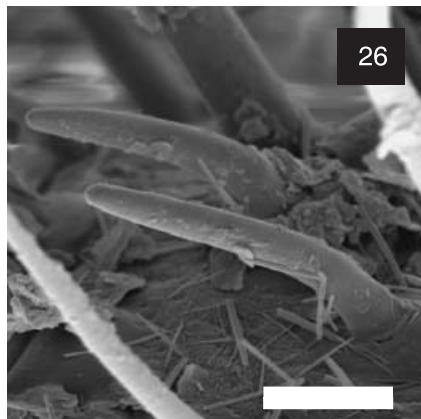


Fig. 26—Two solenidia on the tarsus of *Trogulus nepaeformis*, dorsolateral view. Scale bar: 10 µm.

Fig. 27—Spicer's tarsal organs on the tarsus of the pedipalp, ventral view, in *Togwoteeus biceps* female. Micrograph kindly sent by R. G. Holmberg. Scale bar: 0.05 mm.

organs of whip scorpions, scorpions and spiders (Moro and Geetha Bali 1986; Brownell 2001; Barth 2002b). Though the latter organ is extremely sensitive to substrate-borne vibrations, we know nothing about the sensitivity of the metatarsal paired slits and there is no evidence that species of Phalangida can detect vibrations (see below).

Laniatores is subdivided into two infraorders, Grassatores and Insidiatores (though the monophyly of the latter is uncertain – Kury 2003; other phylogenetic schemes exist – see Giribet and Kury 2007). We studied 13 species of the former and one species of the latter, and all of them have metatarsal paired slits. This sensillum has also been found in *Abasola sarea* (Insidiatores) (Juberthie 1972) and other species of Grassatores such as *Piassagera brieni* (this study), *Pachyloides uncinatus* (Hansen 1893), both in the family Gonyleptidae, *Phalangodes piocardi* (Phalangodidae) (Hansen 1893) and *Galanomma microphthalma* (Zalmoxidae) (Juberthie 1970). Although some studies on the Eupnoi slit sensilla have been conducted (Hansen and Soerensen 1904; Barth and Stagl 1976; van der Hammen 1985; Luque 1993), these conspicuous sensilla have never been reported explicitly. Cyphophthalmids do not have them (R. H. Willemart personal observation). Among Dyspnoi, slit sensilla have never been reported and we did not observe them in any of the examined species, including *Dicranolasma scabrum* (Dicranolasmatidae), *Ischyropsalis* sp. (Fig. 21), *Ischyropsalis hellwigi* (Ischyropsalididae), *Nemastoma bidentatum sparsum* (Nemastomatidae) and *Trogulus nepaeformis* (Trogulidae). Were this sensillum also widespread among Insidiatores and confirmed to be absent in the other suborders, it would be a synapomorphy for Laniatores.

Solenidia (Table 2; Figs 12 and 26)

This name has been borrowed from acarologists, who originally used the term ‘solénidions’ (Grandjean 1935). Though in Acari it has been used to designate setae with very distinct morphologies (see Grandjean 1935), in harvestmen it describes curved setae with short length and obtuse end. These have been reported by van der Hammen (1985) on the

dorsal region of the tarsus of the pedipalps in *Paraligolophus agrestis*. Gruber (1970, 1978) reported solenidia in the pedipalps of *Hesperonemastoma* (Ceratolasmatidae) and in juveniles of *Sabacon* sp. and *Ceratolasma trichanta* (Ceratolasmatidae). Though their external morphology is similar to olfactory sensilla Type 6 in rinculeids (Talarico *et al.* 2006), their function is unknown.

Spicer's tarsal organs (Table 2; Fig. 27)

Hillyard and Sankey (1989) reported that males of Phalangiidae and Leiobunidae (both Eupnoi, the latter family is currently Leiobuninae under the family Sclerosomatidae) have a longitudinal series of microdenticles on the ventral surface of the pedipalps. In both sexes of *Togwoteeus biceps* (Sclerosomatidae) there are pores among this row of denticles, and in *Leiobunum townsendi* of both sexes and *Eumesosoma roeweri* (Sclerosomatidae), at least in males, the whole row is formed by these pores, with no denticles (Spicer 1987; Holmberg and Cokendolpher 1997; R. G. Holmberg personal communication). These pores have been called ‘tarsal organs’ by Spicer (1987). Though dye penetration experiments suggest that there is no innervation in the pore, Spicer (1987) suggested that these organs are olfactory receptors. We cannot follow this suggestion until histological studies are conducted, because they might well be glandular openings, as Spicer (1987) himself noted.

Spines (Table 2; Figs 13 and 28)

Spines occur in pairs, on the lateroventral region of the distal part of the metatarsus of all four leg-pairs, in all Laniatores observed (see also Willemart *et al.* 2007) and in *Ischyropsalis* sp. In *Phalangium opilio*, we found them in the distal region of some tarsomeres. Inserted within a socket membrane, they are easily distinguished from other hairs by their large size and typical position (lateroventral, distally). A similar ventral spine on legs I has been previously described by Hunt (1985). Their function is unknown.

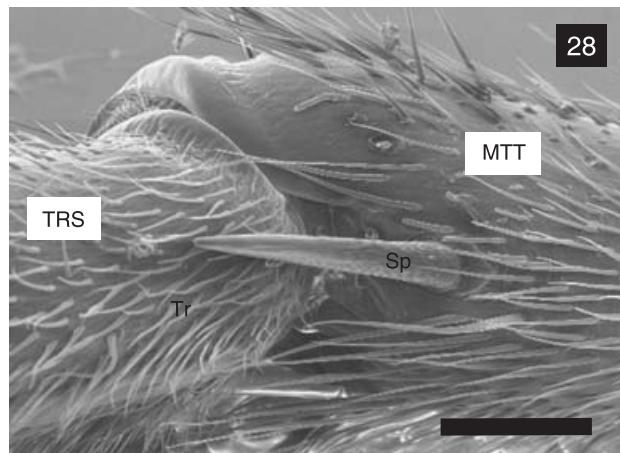


Fig. 28—Spine (Sp) and trichomes (Tr) on the metatarsus–tarsus articulation of leg III in *Daguerreia inermis*, lateroventral view. Most short hairs seen are trichomes. TRS = tarsus; MTT = metatarsus. Scale bar: 100 µm.

Trichomes (Table 2; Figs 2, 3, 9, 10, 12–14, 19, 20, 25 and 28)

These structures have been called ‘false hairs’ by Rafalski (1958), microtrichia or ‘mikrotrichien’ by Gruber (1970) and Shear (1986), ‘faux poils’ (false hairs), ‘chetoïdes’ or ‘chaetoids’ by Juberthie (e.g. 1979, 2000) and Rambla and Lopez (1988), ‘trichomes’ by Foelix (1976) and Willemart *et al.* (2007) and ‘hairs’ by Yigit *et al.* (2007). The same structure has been called ‘sensillum trichodeum’ by Spicer (1987) and followed by several authors (Holmberg and Cokendolpher 1997; Guffey *et al.* 2000; Willemart and Gnaspi 2003; Schultz and Pinto-da-Rocha 2007). However, although sensillum trichodeum has been used across arthropod literature for distinct hairs in terms of form, function and topography (e.g. Lewis 1981; Nichols and Tulloch 1989; Hopkin and Read 1992; Hallberg *et al.* 1994; Amornsak *et al.* 1998; Chapman 1998), it should be restricted to actual sensory structures (‘sensilla’). Because the insertion of this hair is rigid, it is probably not a mechanoreceptor. There are apparently neither pore tips nor wall pores, and broken hairs revealed that there is apparently no lumen, which hampers the possibility that it functions as a chemoreceptor. Therefore, we considered that it should not be treated as a sensillum until histological and physiological tests are made. Trichomes occur on the metatarsus and tarsus of laniatoreans, and metatarsus and tarsus of Eupnoi and Dyspnoi. They may protect the integument, a role that has also been suggested for some beetle hairs (Mustaparta 1973; Faucheu 1989), and help by acting as a brush to clean the body (Willemart and Gnaspi 2003). Indeed, laniatoreans are often seen passing mainly legs I and II over the body and then grooming these legs (R. H. Willemart, personal observations), and brush-hairs have been suggested to occur on the pedipalps of amblypygids (Lawrence 1968). Trichomes also protect

against parasites – McAloon and Durden (2000) showed that mites adhere where these hairs do not cover the integument. Finally Eisner *et al.* (1971) stressed the importance of the hairy tips (the majority of which are trichomes) of the forelegs in *Paecilaema eutypa* (Laniatores, Cosmetidae): this species uses the leg as a brush to administer scent gland secretions to an aggressor.

Sensory capabilities of Phalangida

Hygroreception and thermoreception

It is clear that harvestmen are able to distinguish between dry and humid and between cold and hot. When given a choice, harvestmen choose humidity similar to that from their natural microhabitats and avoid extreme temperatures (Todd 1949; Immel 1954; Clingenpeel and Edgar 1966; Edgar 1971; Santos 2003). In laboratory experiments, the synanthropic species *Phalangium opilio*, which is often found in exposed areas in nature, preferred higher temperatures (27.6 °C), had a higher range of temperature preference than other species and survived longer than non-synanthropic species in dry air (Todd 1949; Clingenpeel and Edgar 1966; Edgar 1971). Laboratory experiments have also corroborated field observations that harvestmen prefer humid environments (e.g. Machado and Oliveira 2002; Novak *et al.* 2004). Such a preference would be necessary because at least one species studied seems not able to close its spiracles, enhancing the need to choose a humid environment (Lighton 2002; see discussion in Santos 2003). Humidity is also important for the eggs: Bishop (1949) reported harvestmen exploring the ground with the tip of the ovipositor before laying eggs. Indeed, there is evidence that harvestmen that lay eggs deep in the soil select humid substrates (Parisot 1962; Savory 1962; Juberthie 1965), suggesting that the ovipositor may bear humidity detectors. We do not know what structures are involved in thermoreception and hygroreception (Tables 3 and 5), but by amputating the pedipalps and the tarsi of *Paranemastoma quadripunctatum* (Dyspnoi, Nemastomatidae), Immel (1954) verified that the treated individuals behaved just like control individuals, choosing a relative humidity close to 100%. Therefore, these species have receptors somewhere else in the body.

Contact chemoreception and olfaction

Chemoreception is a widespread sensory modality among arthropods that has been widely studied particularly in insects (Chapman 1998; Wyatt 2004). The main sensory appendages of Phalangida are the pedipalps (in Eupnoi and Dyspnoi) and legs I and II. These bear contact chemoreceptors (sensillum chaeticum – Table 2) that are assumed to play a major role in food detection (Immel 1954; Willemart 2005; Willemart and Chelini 2007; – Tables 3 and 5). However, contact chemoreceptors also occur in other regions of the

Table 5 Behavioural experiments conducted on harvestmen per suborder; no experiments on mechanoreception have been published

	Eupnoi	Dyspnoi	Laniatores	Reference
Thermoreception	<i>Leiobunum blackwalli</i> , <i>Leiobunum calcar</i> , <i>Leiobunum longipes</i> , <i>Leiobunum politum</i> , <i>Leiobunum rotundum</i> , <i>Leiobunum vittatum</i> , <i>Mitopus morio</i> , <i>Odiellus spinosus</i> , <i>Oligolophus tridens</i> , <i>Opilio parietinus</i> , <i>Phalangium opilio</i> and <i>Platybunus triangularis</i>	<i>Anelasmacephalus cambridgei</i> and <i>Nemastoma lugubre</i>	<i>Acutisoma discolor</i> , <i>Acutisoma longipes</i> , <i>Acutisoma molle</i> , <i>Acutisoma proximum</i> , <i>Acutisoma unicolor</i> , <i>Goniosomatinae undesc. sp.</i> , <i>Goniosoma albiscryptum</i> , <i>Goniosoma spelaeum</i> , <i>Goniosoma varium</i> , <i>Iporangaia pustulosa</i> and <i>Neosadocus</i> sp.	Todd 1949; Immel 1954; Clingenpeel and Edgar 1966; Edgar 1971; Santos 2003.
Hygoreception	<i>L. blackwalli</i> , <i>L. calcar</i> , <i>L. longipes</i> , <i>L. pictus</i> , <i>L. politum</i> , <i>L. rotundum</i> , <i>L. vittatum</i> , <i>Odiellus pictus</i> , <i>O. spinosus</i> , <i>Oligolophus agrestis</i> , <i>Oligolophus hansenii</i> , <i>O. tridens</i> and <i>P. opilio</i>	<i>A. cambridgei</i> , <i>N. lugubre</i> and <i>Paranemastoma quadripunctatum</i>	<i>A. discolor</i> , <i>A. longipes</i> , <i>A. molle</i> , <i>A. proximum</i> , <i>A. unicolor</i> , <i>Goniosomatinae undesc. sp.</i> , <i>G. albiscryptum</i> , <i>G. spelaeum</i> , <i>G. varium</i> , <i>I. pustulosa</i> , <i>Neosadocus</i> sp.	Todd 1949; Edgar 1971; Santos 2003.
Photoreception	<i>L. politum</i> , <i>L. vittatum</i> , <i>Megalopalpis tumida</i> and <i>P. opilio</i>	<i>A. cambridgei</i> , <i>P. quadripunctatum</i> and <i>Trogulus</i> sp.	<i>Hendea myersi</i> ; <i>A. discolor</i> , <i>A. longipes</i> , <i>A. molle</i> , <i>A. proximum</i> , <i>A. unicolor</i> , <i>Goniosomatinae undesc. sp.</i> , <i>G. albiscryptum</i> , <i>G. spelaeum</i> , <i>G. varium</i> , <i>I. pustulosa</i> and <i>Neosadocus</i> sp.	Pabst 1953; Immel 1954; Clingenpeel and Edgar 1966; Meyer-Rochow and Liddle 1988, 2001; Santos 2003; Pioker 2005.
Contact chemoreception	–	<i>P. quadripunctatum</i>	<i>I. pustulosa</i>	Immel 1954; Willemart and Chelini 2007.
Close-range olfaction	–	<i>P. quadripunctatum</i>	<i>G. aff. proximum</i> and <i>I. pustulosa</i>	Immel 1954; Machado <i>et al.</i> 2002; Willemart and Chelini 2007.

body: by amputating the pedipalps and tarsi of all legs, Immel (1954) verified that individuals of *Paranemastoma quadripunctatum* were still capable of distinguishing between distinct stimuli, although they took longer to start feeding. The mouth (with ‘sensory cells’ – Kästner 1969) or their surrounding regions probably played a role in food detection in this case.

Species of Phalangida have also been shown to detect odour molecules, at least in high concentrations. Laboratory chemicals, decaying animals and scent gland secretions might be detected at close range without contact (Immel 1954; Machado *et al.* 2002; Willemart and Chelini 2007; – Tables 3 and 5). Either sensilla chaetica (which might respond to odour molecules if in high concentration – see Chapman 1998) or hairs of unknown function (such as sensilla basiconica, falciform and flat setae, solenidia for example) are probably responsible for this ability. The only olfactory hairs that have been described are the dorsal prosomal spines (Lopez *et al.* 1980; Juberthie *et al.* 1981), and these have only been reported in a single species. The ecological importance of detecting chemicals is clear because an important part of the diet of Phalangida is composed of motionless (which therefore cannot be detected by vibrations

or wind currents) and smelly food items such as dead animals or excrement (see Willemart *et al.* 2007). Machado *et al.* (2002) have also demonstrated that scent gland secretions may act as an alarm pheromone, detected by olfaction.

Concerning mate finding, there is no published evidence of the use of long-range sexual pheromones, and males and females seem to depend on contact to detect each other. However, chemicals left on the substrate may attract conspecifics, as might be the case at least in the species *Prionostemma* sp. (Eupnoi, Sclerosomatidae) (Donaldson and Grether 2007; Grether and Donaldson 2007). Upon contact, *Leiobunum vittatum* and *Phalangium opilio* can usually tell males from females (Macías-Ordóñez 1997, 2000; Willemart *et al.* 2006), and *Goniosoma albiscryptum* (Laniatores, Gonyleptidae) males readily distinguish between conspecific and heterospecific males (Willemart and Gnaspi 2004). Most probably, this recognition is mediated by cuticular chemicals.

Photoreception and scototaxis

Several laboratory experiments have reported that species of Phalangida show negative phototaxis (Pabst 1953; Immel

1954; Clingenpeel and Edgar 1966; Meyer-Rochow and Liddle 1988, 2001; Santos 2003; Pioker 2005; – Tables 3 and 5), and Gnaspi *et al.* (2003) suggested that the light/dark cycle is the major environmental cue to entrain the endogenous clock of the cave species *Goniosoma spelaeum*. Meyer-Rochow and Liddle (1988, 2001) reported that *Megalopsalis tumida* (Monoscutidae, Eupnoi) and *Hendea myersi* (Triaenonychidae, Laniatores) show negative phototaxis towards ultraviolet light and positive phototaxis towards a dim artificial ‘glow-worm’ light. This attraction would help these two cavernicolous species to find their food, because they feed on, among other things, the glow-worm *Arachnocampa luminosa* (Diptera). This is the only study that demonstrated any role of harvestmen’s eyes in prey capture. In other species, such as *Paranemastoma quadripunctatum* and *Platybunus bucephalus* (Sclerosomatidae, Eupnoi), painting the eyes did not affect prey capture (Immel 1954, 1955). Finally, scototaxis (orientation toward dark objects) was tested by Pabst (1953), who showed that when given the choice between a dark and a clear wall in a lighted arena, the animals chose to rest against the dark wall. These behaviours are in accordance with histological data mentioned above, i.e. they both show that the eyes of Phalangida are important detectors of bright/dark. The behavioural importance of telling shaded from lighted places is probably not only for finding shelter but also possibly for avoiding vertebrate predators. Bishop (1949, 1950) reported that an approaching person is readily perceived from a distance of 1 m, though wind currents might well have been the stimulus detected. However, motionless individuals of *Leiobunum vittatum* in closed terraria (with therefore no air displacement) often run if a big object is placed between them (outside the terrarium) and a light source (R. H. Willemart, personal observation), which would suggest that vision is involved. In nature, this would be useful against birds, which are known predators of harvestmen (e.g. Buchanan *et al.* 2006). Because of the contrast between the body of a bird and the sky, harvestmen could potentially detect them with their eyes.

Mechanoreception

Scattered data suggest that harvestmen have limited ability for detecting mechanical stimuli at a certain distance (Table 3). Rüffer (1966) observed that harvestmen do not react to approaching moving tweezers unless they touch the animal, Phillipson (1960) and Willemart and Chelini (2007) reported that *Mitopus morio* and *Iporangaia pustulosa* are unable to detect live prey before contact is established. Macias-Ordoñez (1997, 2000) and Willemart *et al.* (2006) reported that *Leiobunum vittatum* and *Phalangium opilio* do not detect conspecifics unless there is contact. Direct observations under laboratory conditions on *Leiobunum vittatum* standing on leaves showed that they do not react to immature crickets (between 0.006 and 0.01 g) walking on the same leaf even when they are as close as 1 cm from their

legs. After contact was established, they immediately attempted to capture the cricket (R. H. Willemart, unpublished data). *Leiobunum vittatum* also did not respond to a vibrating object in the air at three different frequencies and amplitudes (0.98 Hz; 0.15 mm/9.5 Hz; 0.9 mm/100 Hz; 0.14 mm) as close as 1 cm from its leg II (R. Santer and R. H. Willemart, unpublished data). The typical behaviours of pointing with a leg II or tapping the object (R. H. Willemart, personal observation), were not observed in any of these cases. Finally, these behavioural data are in accordance with morphological data, because harvestmen lack trichobothria (wind detectors) and metatarsal organs (detectors of substrate-borne vibrations). Our literature survey on the location of slit sensilla indicates that maybe apart from the slit sensilla reported in two Laniatores by Hansen (1893) (most probably the metatarsal paired slit sensilla), all the other sensilla have mainly a proprioceptive function. The lack of long-range detection has strong ecological implications when it comes to prey capture, mate finding (discussed in other sections of this paper) and avoidance of invertebrate predators. Detecting the latter only after contact is established implies that these harvestmen may not always be able to flee and therefore often have to rely on chemical defence, autotomizing legs and mechanical defence (pinching with spines on the legs, pedipalps and chelicerae).

Sensory appendages

It is generally agreed in studies of harvestmen that legs II are their sensory legs (Bishop 1949; Savory 1964; Hoenen and Gnaspi 1999; Elpino-Campos *et al.* 2001). Indeed, it is obvious that these legs are always tapping their surroundings and waving around, clearly indicating that they are used as feelers (Comstock 1940; Hillyard and Sankey 1989). Moreover, legs II are usually longer than the others, being more appropriate to make contact with relevant resources. However, this view may be too simplistic and we suggest that it should be reconsidered.

Anuradha and Parthasarathy (1976) noted that legs I are used for sensory purposes and not for supporting the body in *Gagrellula saddlana* (Eupnoi, Sclerosomatidae). Komposch (1992) observed that troglids tap the interior of gastropods with legs I after legs II have detected the food. Canals (1936), Acosta (1983), Mora (1990) and Willemart (2002) reported the sensory use (tapping the substrate) of legs I in gonyleptids, cosmetids and a manaoobiid. Guffey (1999) demonstrated, in *Leiobunum nigripes* and *L. vittatum*, that food recognition appears to be faster when it is touched by legs I instead of legs II. More evidence comes from observations on feeding behaviour: before consuming a food item, laniatorid harvestmen usually tap it repeatedly with legs I and occasionally with legs II (Willemart and Chelini 2007). Morphologically, legs I are similar to the so-called ‘sensory legs’, at least among some of the gonyleptids studied herein (*Iporangaia pustulosa*, *Goniosoma albiscutatum* and *Neosadocus* sp.). Both pairs of legs have more

sensilla chaetica on the most distal tarsomere than legs III and IV. Legs I and II also have a differentiated rough portion on the dorsal region containing a pair of sensilla basiconica (Fig. 8) and have falciform setae, which are all absent in legs III and IV. The latter two have pore openings close to the claws that are absent in legs I and II. We therefore have evidence on the three suborders that, in contrast to legs III and IV, legs I function in a similar way to legs II and have, besides their occasional use for supporting the body, an important sensory function.

The pedipalps are sensory in Eupnoi and Dyspnoi (Berland 1932; Cloudsley-Thompson 1958). Pabst (1953) and Komposch (1992) observed that troglulids use them to touch a food item following detection and before ingestion, which has also been observed in some Eupnoi species (*Phalangium opilio* and *Leiobunum vittatum* – R. H. Willemart, personal observation). Immel (1954) verified that food recognition is slower if the pedipalps of *Paranemastoma quadripunctatum* are removed. In Laniatores they have not been reported to be used for sensory purposes.

The probable reason for the denomination of sensory legs for legs II is because of their conspicuousness, but they should not be considered more important than the pedipalps in Dyspnoi and Eupnoi and than legs I in the three suborders. Instead, it seems that legs I and the pedipalps are mostly used for fine recognition, whereas legs II, because they are longer, are more likely to detect general resources (see Guffey 1999) further from the body.

Phalangida compared with other arachnids

Harvestmen do not have either trichobothria (Hansen 1917) or metatarsal organs, and bear a few slit sensilla (see for comparison with other arachnids: Barth and Stagl 1976; Moro and Geetha Bali 1986; Barth 2002a). Moreover, behavioural evidence shows that they have low ability for detecting prey at a distance, be it by wind currents or by substrate vibrations (Phillipson 1960; Macias-Ordóñez 1997, 2000; Willemart and Chelini 2007). Although some authors have reported that a few species are efficient in capturing living prey (see references in Acosta and Machado 2007), harvestmen clearly do not have the striking ability (rapidity) of some of their relatives, like amblypygids, spiders or solifuges. They lack venom (in contrast with most pseudoscorpions, spiders and scorpions) and most species do not have strong appendages that would allow killing and holding strong living prey, such as the chelicerae of solifuges or the pedipalps of amblypygids, whip scorpions and some scorpions. Even though there is variation between species, an important fraction of their diet is dead prey, decaying material and even plant/fungal matter (see Acosta and Machado 2007), food items that do not move and that therefore require that the animal walk to find them. Indeed, harvestmen spend part of their foraging period exploring the environment (Acosta and Machado 2007; Willemart *et al.* 2007), as opposed to sit-and-wait

predators such as spiders, amblypygids and scorpions (Riechert and Luczak 1982; Benton 1992; Weygoldt 2000). Solifuges, which do not have trichobothria and on which slit sensilla have only been described in chelicerae (Millot 1949; Punzo 1998) (so they should have limited ability to detect prey at a distance by mechanical cues), have been reported to depend on contact to find prey as well, corroborating the notion of having limited ability to detect prey at a distance by mechanical cues. However, unlike harvestmen, they strike very fast and have powerful chelicerae, being able to capture and handle strong and fast-moving prey.

If the features mentioned above are really correlated, one prediction would be that if a harvestman species could (1) detect prey at a distance, (2) move fast enough to capture living prey efficiently, and (3) be strong enough to handle living prey well, one could expect it to be a predator and not an omnivorous species. *Caddo agilis* potentially fits these predictions: they have very large eyes ('excellent vision' according to Shear 1975) that would allow them to detect prey visually; 'agile movements' and spiny pedipalps (an exception among Eupnoi) (Tsurusaki 2003) and do not accept manufactured food or dead prey in captivity, as do other harvestmen. Both Shear (1975) and Tsurusaki (2003) have suggested that *Caddo agilis* is a predator. Further tests with this species and detailed comparative studies on prey detection, capture and handling on selected arachnids could therefore reveal how these characteristics relate to diet. Finally, studies on the feeding behaviour of cyphophthalmids would also provide interesting insights into the evolution of feeding habits in Opiliones because cyphophthalmids constitute the earliest offshoot of harvestmen.

General considerations and future directions

Most of our knowledge on harvestmen sensory structures comes from external morphology. Histological studies have only been made on the eyes, sensilla chaetica, dorsal prosomal spines and slit sensilla (Foelix 1976; Lopez *et al.* 1980; Juberthie *et al.* 1981; Luque 1993; Guffey *et al.* 2000). This scarce knowledge of histological features of the sensilla of Phalangida in addition to the lack of electrophysiological studies hampers inferences about their function and behavioural importance. Since campaniform sensilla have been traditionally considered absent among arachnids, histological confirmation that the structures we reported in *Phalangium opilio* are actual campaniform organs would also be particularly interesting.

Except for thermoreception, hygroreception and photoreception, behavioural experiments on sensory capabilities have only been carried out with three of the almost 6000 species of Phalangida (Table 5). Some specific questions remain unexplored: what is the role of the large eyes in Caddidae; do conspecifics detect the sound produced by species that bear stridulatory organs (e.g. Juberthie 1957, 1968); and the behavioural importance of the dorsal prosomal

spines (the only setae in Phalangida of which histology suggests an olfactory role). It would also be very useful to study in which groups the metatarsal slit sensilla occur because, as previously mentioned, it may be a synapomorphy of the suborder Laniatores.

From our current knowledge, harvestmen have a limited ability to detect long-range mechanical and chemical stimuli. They use their eyes only to detect more or less shaded areas and are therefore highly dependent on contact and close range olfaction to gather information from their surroundings. The world of Phalangida appears to be a near-range one, quite different from a spider's world, because the latter can detect prey walking 50 cm from them and conspecifics signalling acoustically from more than 3 m (Barth 2002a). These harvestmen therefore could be excellent models to understand how evolution has shaped an animal with such limited ability to detect long-range stimuli. Studies on the sensory biology of Phalangida will allow us to better understand their foraging strategies, predator avoidance mechanisms, mate finding strategies and the unexplored field of navigation, because philopatry is high in at least some cave species (Gnaspini 1996; Machado *et al.* 2000; Willemart and Gnaspini 2003). Apart from the studies of Macias-Ordóñez (1997, 2000), there has been no attempt to relate Phalangida's dependence on close-range chemical and mechanical cues to each one of these features. We hope that this review will motivate histologists, physiologists, physicists and behavioural ecologists to give more attention to this fascinating but often ignored group.

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