

The fine structure of scorpion sensory organs.

I. Tarsal sensilla

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Summary

The fine structure of the following sensory organs on the tarsi and basitarsi of scorpion legs was investigated: (1) mechanoreceptive hairs and bristles, (2) slit sensilla, (3) chemoreceptive hairs, and (4) tarsal organs.

The mechanoreceptive hair sensilla are innervated by seven bipolar neurons, the dendrites of which are attached to the hair base. A large multicellular gland underlies the hair socket. The slit sensilla have two neurons each. The first neuron gives off a single dendrite which attaches to the cover membrane of the slit. The second neuron gives rise to two dendrites which penetrate the slit but do not reach the cover membrane. The chemoreceptive hairs are associated with 22-23 neurons; four dendrites end as mechanoreceptive dendrites at the hair base, the other dendrites enter the double lumen of the hair shaft and become exposed to the outside through a pore at the hair tip. The tarsal organ, situated dorsally near the distal end of the tarsus, is a small pit with two pores inside. Six to nine dendrites are exposed at each pore, which implies a chemoreceptive function (olfaction?).

The structure of the various receptors closely resembles that of spider sensilla. In comparison with insect sensory organs, scorpion and spider sensilla are exceptional in always having multi-innervated mechanoreceptive hairs and a higher number of sensory cells per sensillum.

Introduction

Most studies of arthropod sensory organs have focused on insects and this is probably the reason for the general belief that mechanoreceptive hairs are singly innervated whereas chemoreceptive sensilla are multiply innervated (Bullock & Horridge, 1965). However, in some arachnid orders (Araneae, Acari) it has been shown that the mechanoreceptors are always multiply innervated (Foelix, 1970a; Foelix & Chu-Wang, 1973a; Harris & Mill, 1977). In scorpions

'supernumerary' sense cells of apparently purely mechanoreceptive hairs have been reported from morphological and physiological investigations (Venkateswara Rao, 1963; Sanjeeva-Reddy, 1971; Brownell & Farley, 1979a). No fine structural studies exist as yet which demonstrate the exact number of sense cells associated with each mechanoreceptive hair. Furthermore, in scorpions very little is known about the structure of any other receptor types, such as chemoreceptive organs. The aim of the present study is thus to elucidate the morphology of the various sensory organs of scorpions, particularly those situated on the distal segments of the walking legs. These segments (tarsi and basitarsi) are in direct contact with the substrate and should therefore exhibit the greatest variety and highest density of receptors.

Material and Methods

Scorpions mainly of the species *Androctonus australis* (L.) from Djerba (Tunisia) were used for this study. A few specimens of *Euscorpium italicus* (Herbst) (Jugoslavia) and of *Buthus occitanus* (Amoreux) (Tunisia) were also examined for comparison. The distribution of receptor types was determined from whole mounts using the light microscope, and from freshly severed, gold-coated legs using the scanning electron microscope (ISI Super 3A). For transmission electron microscopy distal leg segments were cut off from CO₂-anaesthetised *Androctonus australis* and immersed in cacodylate-buffered 5% glutaraldehyde for six hours. After post-fixation in 1% OsO₄, the leg segments were dehydrated in a graded ethanol series and embedded in hard Epon resin. Sections of 1-2 µm thickness were stained with methylene blue-basic fuchsin for evaluation in the light microscope; 60-80 nm sections were cut with a diamond knife, stained with uranyl acetate and lead citrate and viewed in a Siemens 101 electron microscope.

Results

The most conspicuous receptors on scorpion legs are certainly the *hair sensilla* (Figs. 1, 2). A closer examination under the microscope reveals three different types of hairs: (1) long, straight hairs, (2) shorter, straight 'bristles', and (3) short, curved hairs.

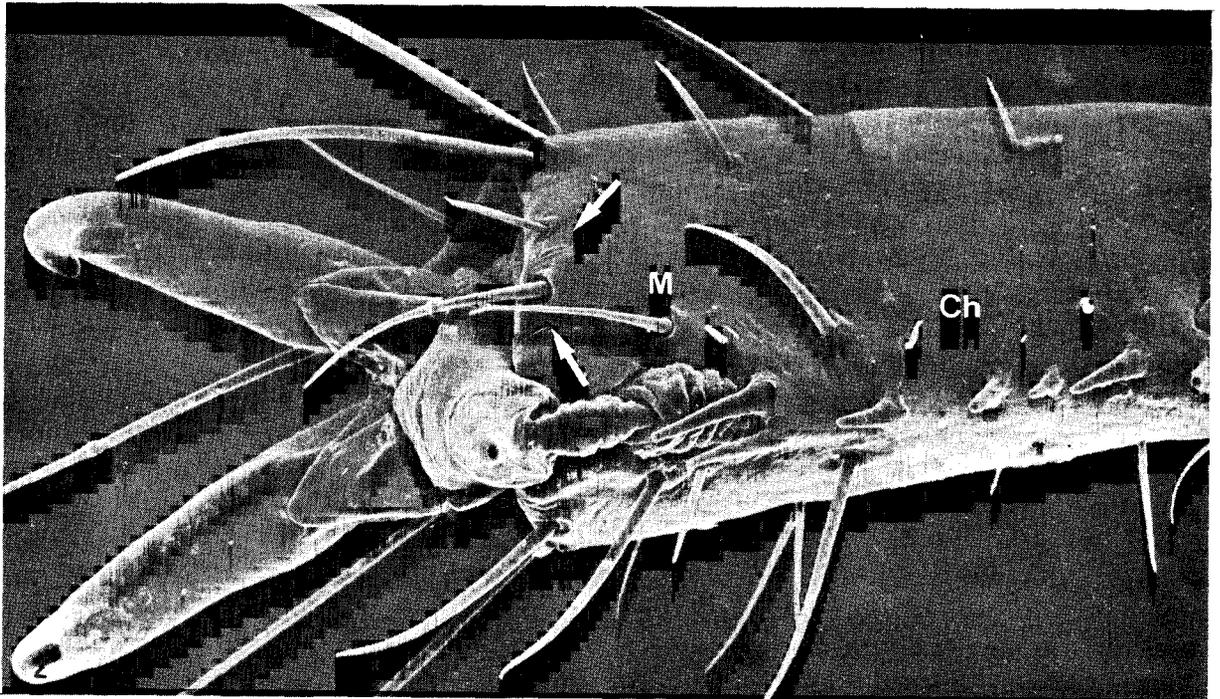
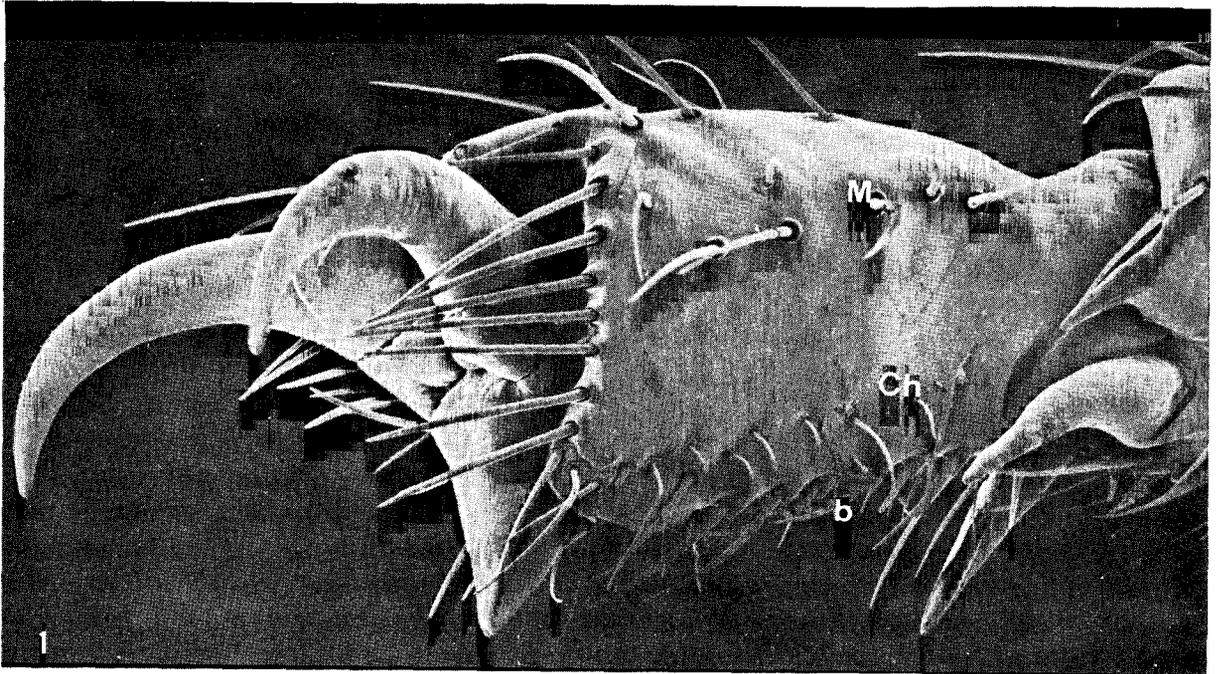


Fig. 1: Tarsus of leg II of *Buthus occitanus*, lateral view. Hair sensilla are mostly arranged in rows. M = mechanoreceptive hairs, Ch = chemoreceptive hairs, b = ventral bristles. x 200.

Fig. 2: Tarsus of leg II of *Euscorpilus italicus*, ventral view. Besides the two types of hair sensilla (M, Ch), two slit sensilla (arrows) can be seen near the insertion of the claws. x 300.

On the basis of a comparison with similar types of hair sensilla in spiders (Foelix, 1970a, b), it seemed likely that the first two types are mechanoreceptive (touch), whereas the third type is chemoreceptive (taste).

Distribution of hair sensilla

The distribution of hair sensilla on the distal leg segments (tarsus, basitarsus) was studied in detail for *Buthus occitanus* and is shown in Fig. 3; an almost identical distribution was found in *Androctonus australis*. Most of the hair sensilla are arranged in longitudinal rows. This is particularly noticeable on the ventral and lateral surfaces of the tarsus and basitarsus, but less apparent on the dorsal side. The highest concentration of hair sensilla occurs on the ventral face of the tarsus (two rows of bristles) and around the insertion of the claws (Fig. 1). The longest hairs stand along a ridge on the lateral side of the basitarsus.

The density of hair sensilla is highest on the first legs and lowest on the fourth legs. This holds true for both the mechano- and the chemoreceptive hair sensilla. Table 1 gives the data obtained from the tarsi (Ta) and basitarsi (Bt) of a female *Buthus occitanus*. Note that the absolute number of mechanoreceptive hairs is about the same on all legs; the density (number/mm²), however, is higher on the front legs, because these are smaller than the hind legs. The chemoreceptive hairs decrease in density and absolute number along the legs from anterior to posterior. Altogether there are about 1,000

mechanoreceptive hairs and 400 chemoreceptive hairs on the distal leg segments of *Buthus occitanus*.

We shall first describe the fine structure of the mechanoreceptors, i.e. the hair sensilla and the slit sensilla. The following discussion of chemoreceptors will cover the taste hairs and the tarsal organ, which, to our knowledge, has not been described in scorpions before.

Mechanoreceptive hair sensilla

The long, straight hairs (250-500 μm long, up to 25 μm in diameter) are basically similar to the shorter 'bristles' (200 μm long, 15 μm diameter), but differ with respect to their sockets. The long hairs have a rather low-rimmed socket which permits the hair shaft to protrude at angles from 45 to 90° from the leg surface. The 'bristles', in contrast, have a narrow socket with an elongated rim on the proximal side (Fig. 4). Consequently, their shafts form a rather flat angle (about 30°) with respect to the leg surface. This obviously limits the range of movement of the bristle shaft, which can only be raised by 15° until it abuts against the extended socket rim. The following description of the fine structure of mechanoreceptive sensilla focuses on hair sensilla but applies to bristles as well.

The hair shaft has a rather thick wall (8 μm) surrounding an equally wide central lumen. The hair base is suspended in its socket by means of a joint membrane. Longitudinal sections show that this membrane is composed mainly of an inner ring of suspension fibres, surrounded by exocuticle (Fig. 8a).

The base of each hair has two distinctive features: (1) it is innervated by seven sensory cells, and (2) it is underlaid by a multicellular gland. The seven bipolar sensory cells lie approximately 100 μm proximad of the hair base. Their offgoing dendrites are initially of equal diameter (1-2 μm) but are constricted to 0.25 μm at the 'ciliary region' (Fig. 6). The outer dendritic segments contain dense aggregates of cross-linked microtubules (Fig. 5, inset), which are called *tubular bodies* (Thurm, 1964). Such structures are a diagnostic feature of mechanoreceptive hair sensilla of arthropods in general (McIver, 1975). In the scorpion hair sensilla these tubular bodies are exceptionally long (about 20 μm) and occupy almost the entire length of the

			Mech.	Chemo.
Leg	1	Ta	59	32
		Bt	63	36
	2	Ta	65	20
		Bt	66	26
	3	Ta	68	18
		Bt	57	27
	4	Ta	67	12
		Bt	55	19
			500	190

Table 1: Number of mechano- (Mech.) and chemoreceptive hair sensilla (Chemo.) on the tarsi (Ta) and basitarsi (Bt) of the right legs of *Buthus occitanus* (♀).

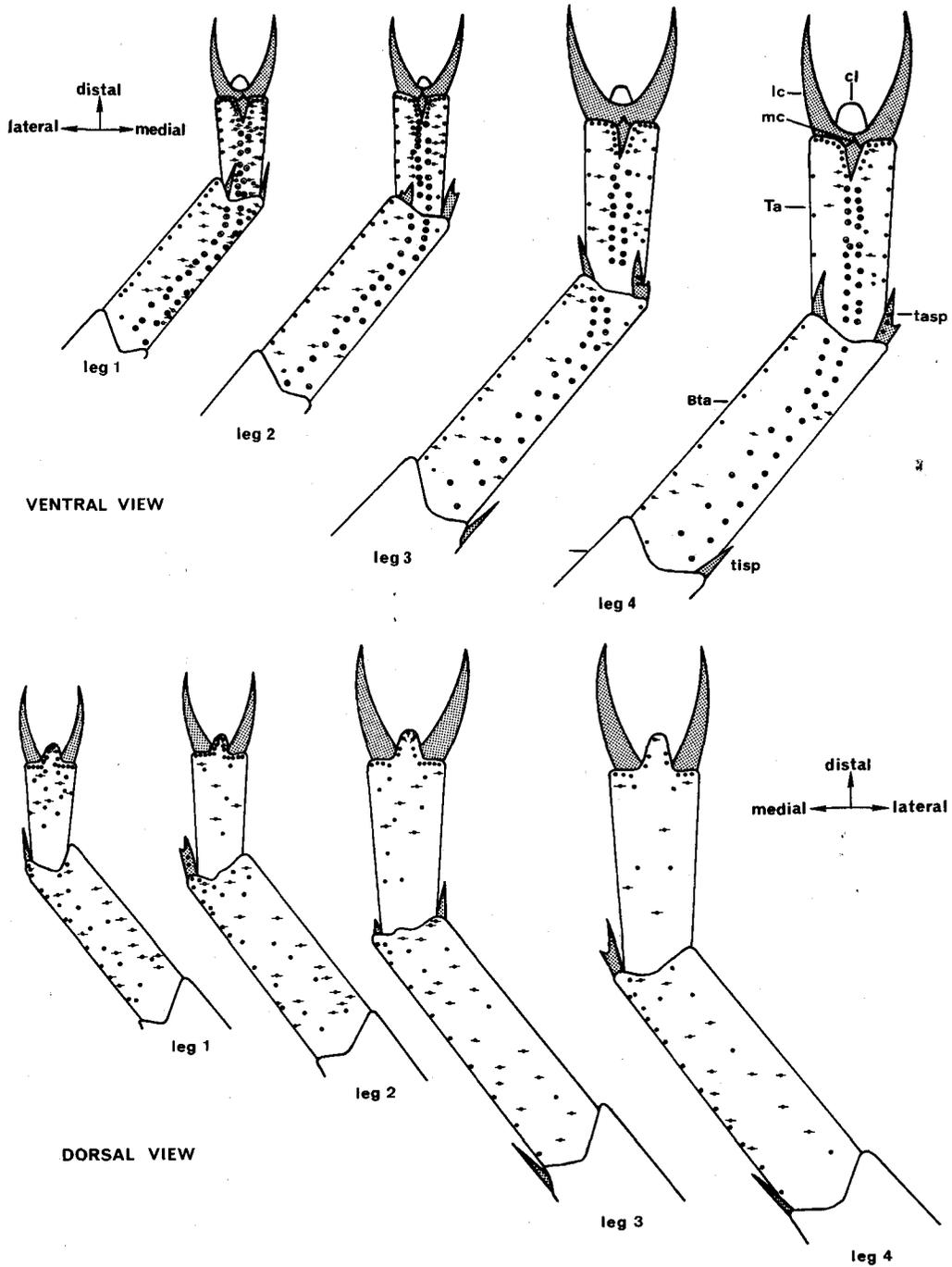
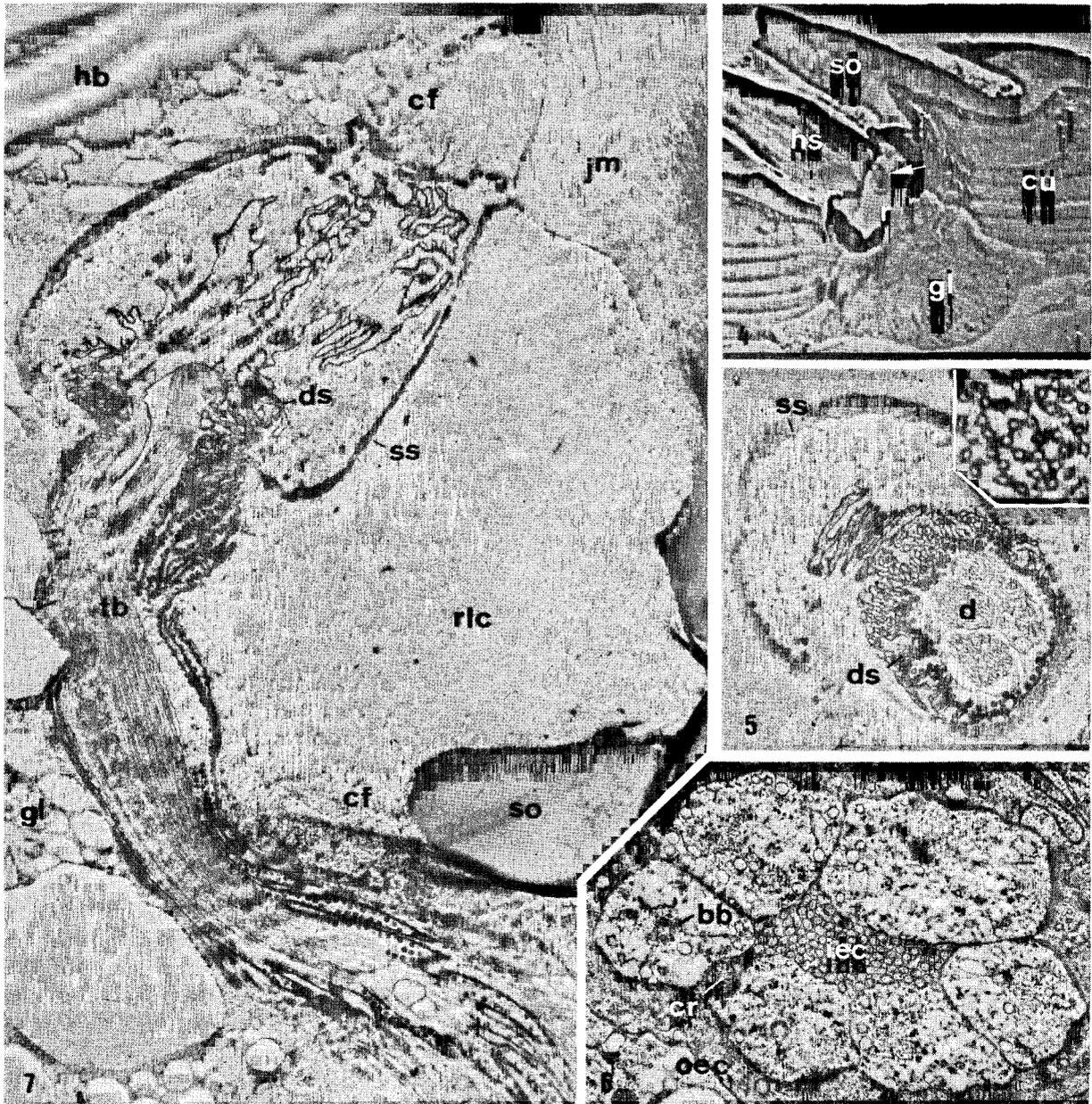


Fig. 3: Distribution of hair sensilla on tarsi (Ta) and basitarsi (Bta) of *Buthus occitanus*. Mechanoreceptive hairs are represented by solid black circles, chemoreceptive hairs by a hollow circle with a horizontal dash, and the ventral bristles by a circle with a central dot. Note the high density of sensilla on the ventral side, especially on the tarsi of the front legs. cl = claw lobe, lc = lateral claws, mc = medial claw, tasp = tarsal spur, tisp = tibial spur.



Figs. 4-7: Innervation of mechanoreceptive hair sensilla. **4** Longitudinal section of a bristle. The shaft (hs) is suspended in a narrow socket (so) of the leg cuticle (cu). The dendritic attachment is indicated by an arrow. A large multicellular gland (gl) underlies the receptor lymph cavity (r). $\times 600$. **5** Cross-section of outer dendritic segments shortly before attachment to the hair base. The seven dendrites (d) are enclosed by the highly folded dendritic sheath (ds) and the socket septum (ss). $\times 11,000$. *Inset*: Some dendritic terminals contain a tubular body which consists of cross-linked microtubules. $\times 80,000$. **6** Cross-section of inner dendritic segments, just before the transition to the outer segments. One dendrite has already narrowed to form a ciliary region ($9 \times 2 + 0$; cr); the neighbouring fibres exhibit basal bodies (bb) which give rise to the ciliary structure. In the centre of the dendrites microvilli of the inner enveloping cell (iec) are seen; the periphery is occupied by two outer enveloping cells (oec). $\times 15,000$. **7** Longitudinal section of the dendritic attachment (cf. Figs. 4, 8). The socket septum (ss) connects via fibres (cf) to the hair base (hb) and to the base of the socket (so). jm = joint membrane, ds = dendritic sheath, ss = socket septum, rlc = receptor lymph cavity, gl = gland cell. $\times 9,500$.

outer dendritic segment (Fig. 7).

The outer dendritic segments traverse the fluid-filled receptor lymph cavity underneath the hair base. They are encased by a double extracellular meshwork: a *dendritic sheath*, and a socket septum which covers the distal half of the dendritic sheath. The inside of the dendritic sheath is lined with cuticular globules (Figs. 5, 7), which often indent the dendritic membrane. The distal end of the dendritic sheath is expanded and highly folded, while its mid-region is surrounded by a delicate fibrous meshwork (Figs. 7, 8b). The *socket septum* is even more complex and consists of a distal *cap* that continues into a fibrous *collar*, which in turn forms a *trough* at the proximal end (Figs. 7, 8). Thin fibres connect the cap to the hair base and the trough to the socket base. The receptor lymph cavity is bordered basally by a multicellular gland which forms a large evagination underneath the hair socket. We did not detect a specific secretory activity of the gland (e.g. whether it contributes to the receptor lymph fluid) and cannot offer any interpretation as to its function.

The somata and the inner dendritic segments of the seven sensory cells are surrounded by three enveloping cells (sheath cells). The arrangement of these cells corresponds to the description given for spider sensilla (Harris & Mill, 1973). The characteristic feature is that the innermost sheath cell penetrates between the inner dendritic segments (Figs. 6, 8b).

Slit sensilla

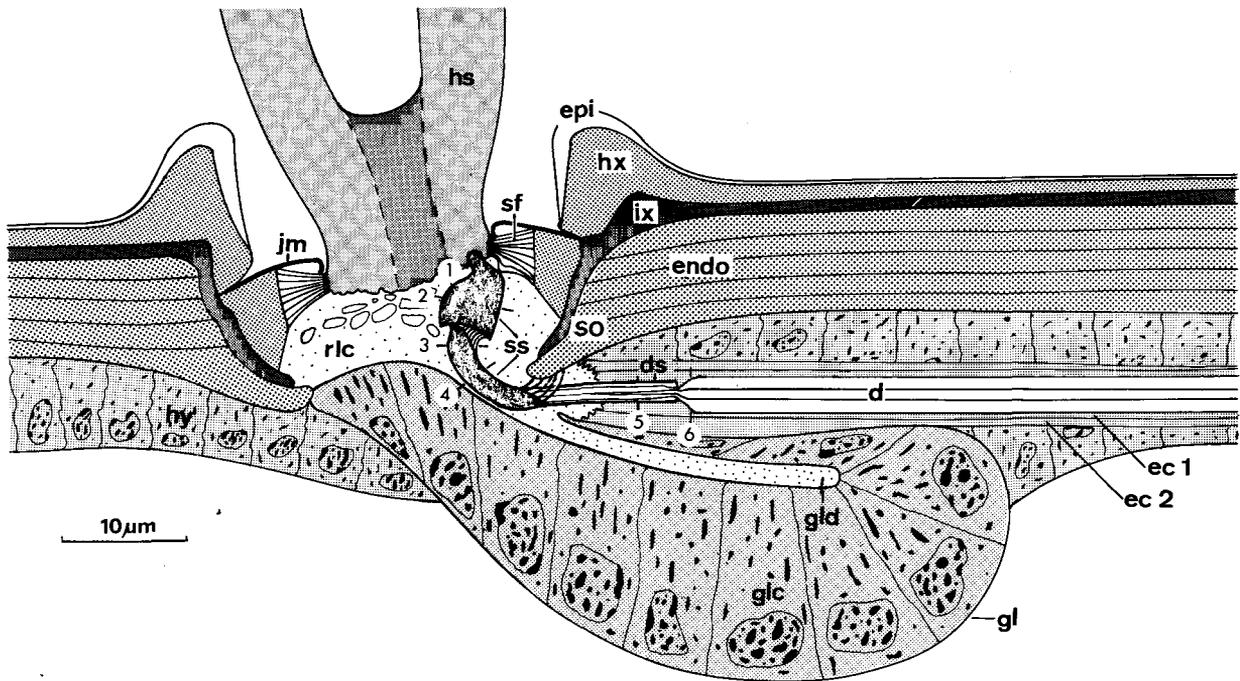
Slit sensilla are mechanoreceptors which are typical of all arachnids. They occur either as single slits or groups of slits (lyriform organs) in the cuticle of the exoskeleton, particularly on the legs. The distribution of slit sensilla has been studied in detail in the scorpion *Androctonus australis* by Barth & Wadeuhl (1975). Since our electron-microscopical investigation dealt with the same species, we can add here some cytological features of these sense organs.

The single slit sensilla are rather inconspicuous, because the cuticular lips bordering the slit are not very prominent (Fig. 2). In some cases, e.g. on the claws, cuticular lips are lacking altogether and the slit sensillum cannot be recognised from the outside, but only in sections or in transparent whole mounts.

The slits on the tarsi and basitarsi are 15-150 μm long and 1-3 μm wide. Each slit is covered by a thin layer (1 μm) of exocuticle (identified from electron micrographs as the laminated layer below the thin layer of epicuticle). The boat-shaped cavity lying underneath this cover widens to a bell shape at the site of innervation. Two bipolar sensory cells supply each slit sensillum, but only one neuron sends its dendrite all the way to the covering membrane. The dendritic terminal contains a typical tubular body (Fig. 11) and ends horizontally within a coarse cuticular membrane (*outer membrane*) lying underneath the exocuticle. The second neuron gives off one dendrite, which has two ciliary regions (Fig. 12) and consequently two outer segments. These two segments end shortly after entering the slit; they also exhibit aggregations of microtubules, yet lack the electron-dense substance typical of the tubular body of the first neuron. All three dendritic outer segments are encased by one dendritic sheath. When this sheath enters the bottom of the slit, it penetrates a fine cuticular membrane (*inner membrane*) and then proceeds vertically towards the outer membrane. The space between these two membranes is filled by a framework of parallel fibres. When it reaches the outer membrane, the dendritic sheath turns abruptly by 90° and then runs within that membrane (Fig. 11). Only its very tip tilts upwards again and attaches to the exocuticular cover. In contrast to the other two dendritic segments (Fig. 10, inset) the dendrite of the first neuron is always in close apposition to the dendritic sheath. This is especially noticeable at the bend, where the dendritic sheath appears corrugated and actually indents the dendritic membrane. This region also demarcates the beginning of the tubular body. The arrangement of the sheath cells and the receptor lymph cavity is similar to that found in other sensilla. This area was not studied in detail.

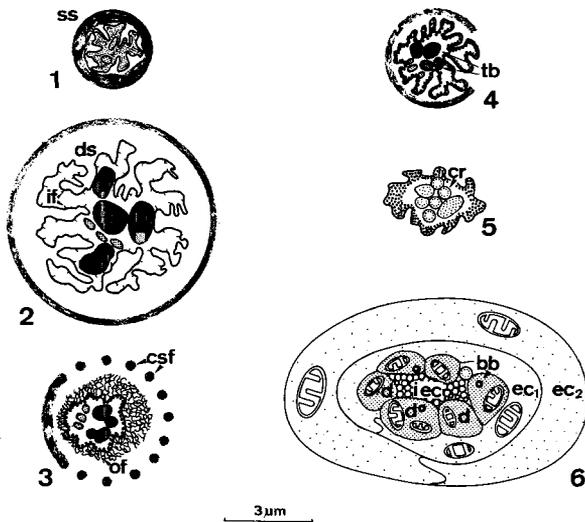
Chemoreceptive hair sensilla

The chemoreceptive hair sensilla are only 100 μm long and 4 μm in diameter and thus much smaller than the mechanoreceptive hairs. The hair shaft is slightly curved and forms almost a right angle with the leg surface (Figs. 1, 2). The tip is blunt and has an opening to the outside. This is barely visible in the light microscope and even under the scanning



10µm

Fig. 8: (Above) Diagrammatic longitudinal section of a mechanoreceptive hair. The hair shaft (hs) is movably suspended in a socket (so) by a membrane (jm) that is reinforced by cuticular fibres (sf). The dendrites (d) narrow at the ciliary region (near 6), then proceed through the receptor lymph cavity (rlc) to the hair base. Their distal part is surrounded by a dendritic sheath (ds) and a socket septum (ss), the proximal part by enveloping cells (ec₁, ec₂). A large multicellular gland (gl) underlies the sensillum. epi, endo = epi- and endocuticle; hx, ix = hyaline and inner exocuticle; glc, gld = glandular cell and duct. The numbers indicate the levels of cross-sections shown below. (Below) Consecutive cross-sections of the innervation. Level 1 (cf. above): Socket septum (ss) and dendritic sheath just below the attachment to the hair base. Level 2: The folded dendritic sheath (ds) encloses three slender dendrites and four large dendrites with tubular bodies. if = internal cuticular fibres. Level 3: The cap of the socket septum breaks up into separate fibres (csf) on its dorsal side. The dendritic sheath exhibits globules on the inside and fibrous extensions (of) on the outside. Level 4: The socket septum has changed into a trough shape. Tubular bodies (tb) are still present in the four large dendrites. Level 5: Ciliary regions (cr) of the dendrites and beginning of the dendritic sheath. Level 6: The inner dendritic segments are surrounded by two outer enveloping cells (ec₁, ec₂); an inner enveloping cell (iec) lies between the dendrites, bb = basal body.



3µm

electron microscope the orifice is usually obscured by dried-up receptor lymph (Fig. 14). The tip region of the hair shaft is cylindrical, but the lower part is flattened with the long axis pointing laterally (Fig. 17). Consecutive cross-sections show a characteristic double lumen as is well known from taste hairs in insects (Zacharuk, 1980) and spiders (Foelix & Chu-Wang, 1973b). The inner, circular lumen (C_1) contains about 20 dendrites, whereas the surrounding crescent-shaped lumen (C_2) is filled with receptor lymph only. A narrow third lumen (C_3), filled with an electron-dense substance, is discernible in the distal half of the hair wall (Figs. 15-17).

Each chemoreceptive hair is innervated by 22-23 bipolar neurons (Fig. 18). Four of the dendritic outer segments are relatively large and terminate at the hair base with typical tubular bodies; the other, slender, dendrites enter the C_1 -lumen of the hair shaft (Figs. 19, 20). The suspension of the dendritic sheath at the hair socket via a socket septum (Fig. 21) is very similar to that described for the mechanoreceptive hairs. The same applies to the structural organisation of the ciliary regions, the sheath cells and the receptor lymph cavity. Some gland cells underly this cavity, but they do not form a sac-like extension as in the mechanoreceptive hairs.

Tarsal organ

Tarsal organs are usually only described for spiders, where they form small sensory pits on the dorsal side of each tarsus. Using the scanning electron microscope we found very similar organs on all scorpion legs, situated dorsally behind the claws. These receptors appear as slight, oval depressions ($16 \times 22 \mu\text{m}$) in the cuticle with two pore openings just inside the cuticular rim. Based on the position and innervation pattern we feel justified in using the term 'tarsal organ' in analogy (or even homology?) to the well-known tarsal organs in spiders (Blumenthal, 1935; Foelix & Chu-Wang, 1973b; Forster, 1980).

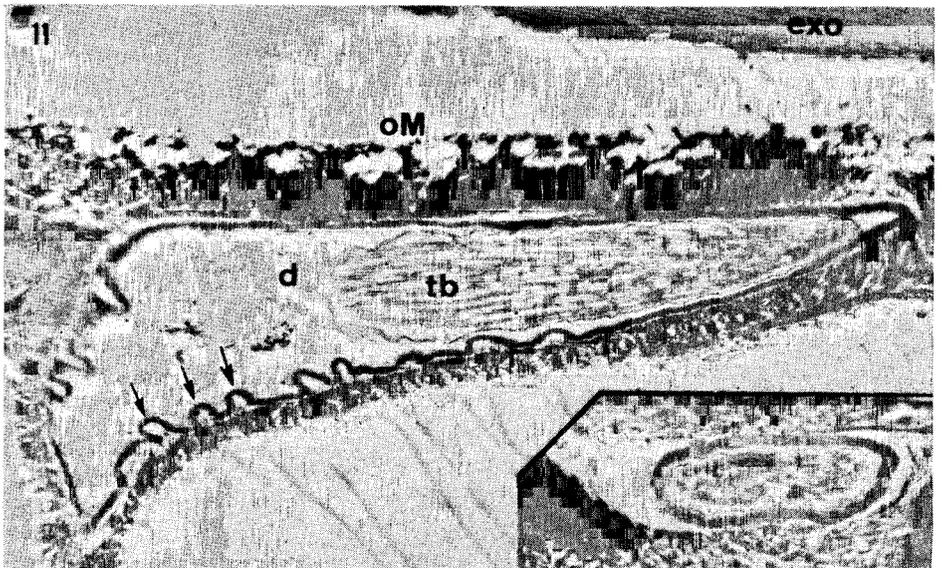
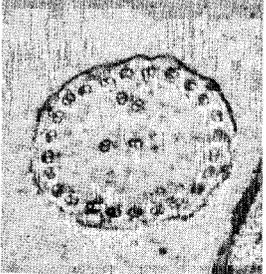
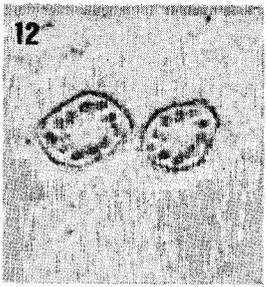
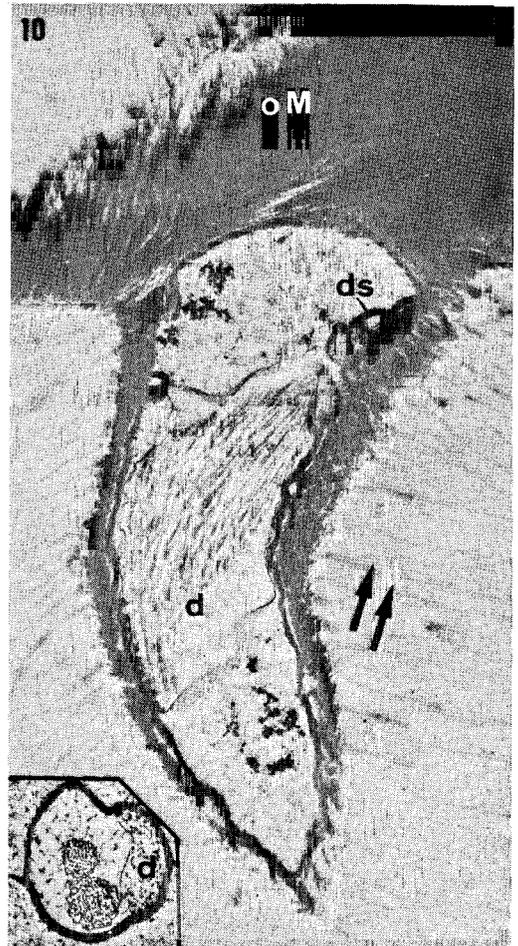
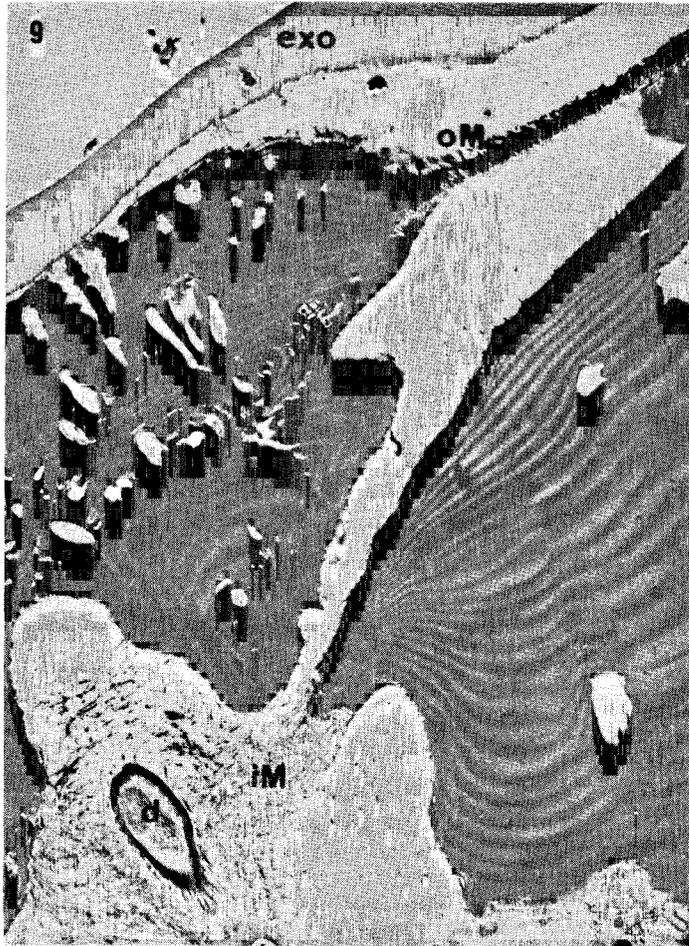
Each pore is supplied by 6-9 neurons, the dendrites of which end at or near the opening (Figs. 22, 28). These dendrites exhibit the usual division into an inner and an outer segment (Fig. 24) with a typical ciliary region at the connecting site. The inner segments lie at the periphery of a well-developed sheath cell (Fig. 25). This cell has numerous centrally

located microvilli and also many dense cytoplasmic inclusions which are probably secreted and accumulated inside the dendritic sheath. The same dense secretion is seen concentrated into a ball at the pore opening (Fig. 23). The dendrites are surrounded by further (outer) sheath cells, all of which seem to be glandular. A receptor lymph cavity is almost absent in the tarsal organ; instead, the entire cone-shaped space underneath each pore is taken up by extensions of the glandular cells (Fig. 28).

Tarsal nerves

Cross-sections of the tarsus show three distinct nerves, two of them traversing the haemolymph space laterally, the third one dorsally. Since the scorpion tarsus lacks muscles, all nerve fibres must be axons arising from the sensory cells. This was checked on a third leg by counting all axons at the tarsus/basitarsus joint and comparing this number (905) with the theoretically expected number of axons. The latter is the effective sum of the various receptors multiplied by their respective sensory cells: the 68 mechanoreceptive hairs should contribute $68 \times 7 = 476$ axons, the 18 chemoreceptive hairs $18 \times 22 =$

Figs. 9-12: Fine structure of slit sensilla. **9** Oblique section of the slit. Note the exocuticular cover (exo), the coarse outer membrane (oM) and the more delicate inner membrane (iM), which is penetrated by the dendrites (d). $\times 5,000$. **10** Attachment of the dendritic sheath (ds) to the outer membrane (oM). The space between outer membrane and surrounding cuticle is bridged by fine, parallel fibres (arrows). d = distal dendrite. $\times 18,500$. *Inset*: Cross-section of the dendritic sheath with three dendritic outer segments inside. The distal dendrite (d) is in close contact with the sheath and has only a few microtubules at this level. $\times 12,000$. **11** Longitudinal section through the slit showing the entrance of the distal dendrite (d) into the outer membrane (oM). The dendritic sheath is indented (arrows) at the bend. exo = exocuticle, tb = tubular body. $\times 23,000$. *Inset*: Cross-section of the dendritic terminal. $\times 16,000$. **12** *Top*: Cross-section of the two proximal dendrites at the beginning of the outer segment. The ciliary structures are clearly visible, but contain 10 and 11 doublets instead of the usual 9. *Bottom*: Modified ciliary region of the distal dendrite, showing 24 peripheral and 4 central doublets. $\times 42,000$.



396 axons, the 9 slit sensilla $9 \times 2 = 18$ axons and the tarsal organ about 17 axons. The expected number of all sensory axons would thus be 907, which is very close to the 905 fibres actually counted.

The cytological organisation of the leg nerves in scorpions is very similar to that described for spider nerves (Foelix, Müller-Vorholt & Jung, 1980). Each nerve is compartmentalised by glial cell extensions which surround a group of closely packed axons. The axon diameter varies from $0.5 \mu\text{m}$ to $6.5 \mu\text{m}$; this is much larger than in spider tarsal nerves, where most fibres measure less than $0.4 \mu\text{m}$ and never more than $2 \mu\text{m}$. As in spiders, however, many of the sensory axons exhibit synaptic contacts with neighbouring fibres (axo-axonal synapses) (Figs. 26, 27). This is particularly true for the small hypodermal nerve bundles and to a large extent also for the tarsal nerves themselves. The basitarsus contains only two nerves which also comprise some large motor fibres. No synaptic contacts were observed within the basitarsal nerves.

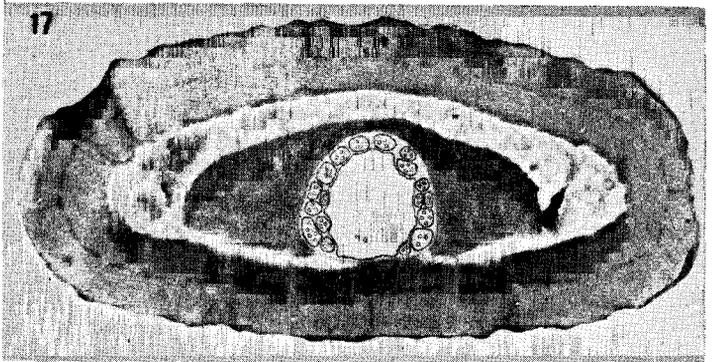
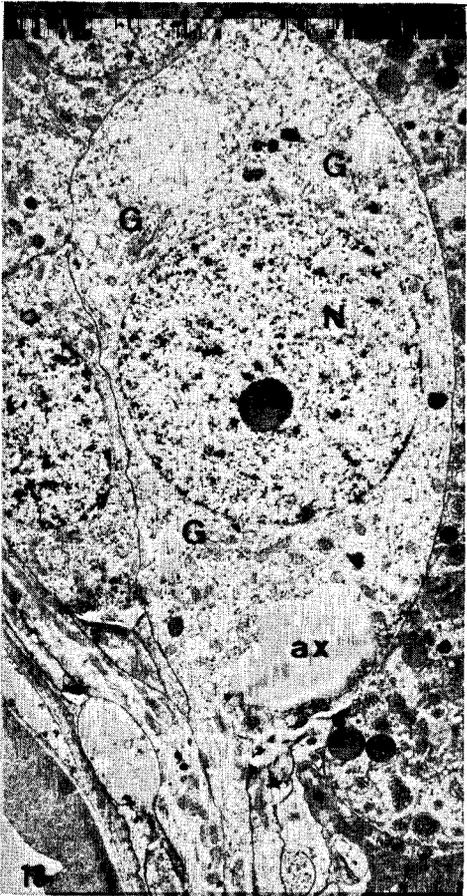
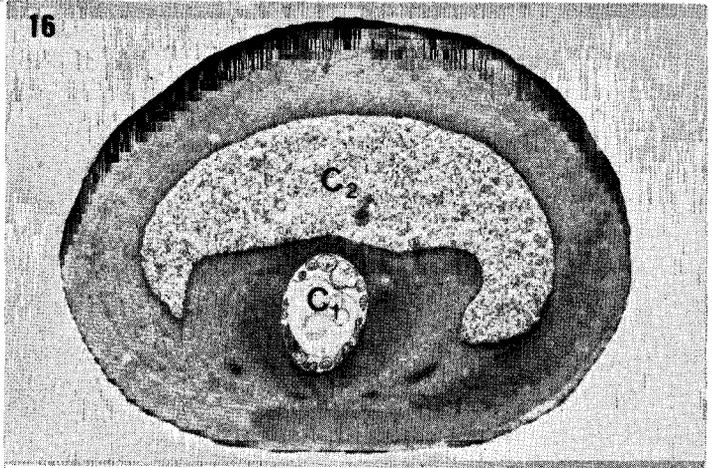
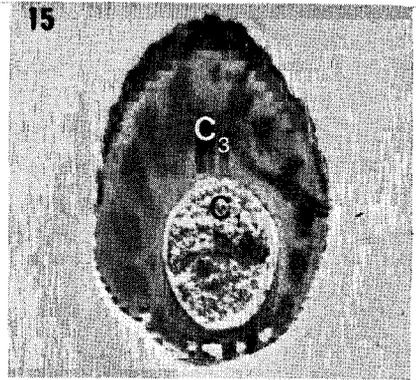
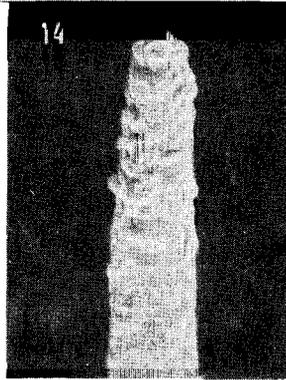
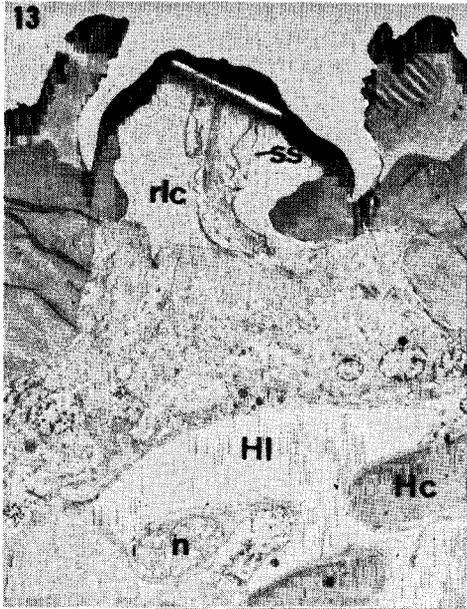
Discussion

The conclusion drawn from physiological studies that mechanoreceptors in scorpions are multiply innervated, has been fully confirmed by our morphological investigation. Sanjeeva-Reddy (1971) deflected single hair sensilla in the scorpion *Heterometrus fulvipes* (C. L. Koch) and recorded nerve impulses from 4-5 different units; in this work an anatomical study on sensilla of the same species is cited (Venkateswara Rao, 1963) also showing 4-5 sensory cells per hair. Brownell & Farley (1979a) studied the tarsal hairs in the desert scorpion *Paruroctonus mesaensis* Stahnke and found them sensitive to substrate vibrations. They also mention some electron-microscopical observations, in which 'seven dendritic processes could be distinguished in favorable sections'. Since we consistently found seven neurons associated with each mechanoreceptive hair sensillum, it may well be that a seven-fold innervation is the rule for scorpions. The more general question of what advantage is gained by such a multiple innervation still remains. Sanjeeva-Reddy (1971) concluded that each scorpion hair can encode several parameters of a mechanical stimulus, namely the beginning, duration and velocity of movement of

a hair, the duration of the static phase, and the position of the hair. Compared with insect mechanoreceptive hairs, which are always singly innervated, this would seem to be a highly advanced state. From an evolutionary point of view, however, it can be argued that multiply innervated mechanoreceptors are 'primitive' or plesiomorphic (since scorpions are phylogenetically older than insects), whereas the single innervation of mechanoreceptors in insects represents a 'derived' or apomorphic character. This argument would also apply to chemoreceptors, for scorpions and spiders possess more than 20 sensory cells per chemoreceptive hair, while insect taste hairs have usually only 4-6.

In general, there is a close resemblance between the sensory organs of scorpions and spiders. The mechanoreceptive hairs of all spiders investigated have always three neurons per sensillum but are otherwise very similar to the scorpion hair sensilla (except for the multicellular gland). A comparison of the slit sensilla also reveals only minor differences which concern mostly the cuticular components of the sensillum. A consistent difference in the neuronal

Figs. 13-20: Fine structure of chemoreceptive hairs. **13** Longitudinal section of the hair base. rlc = receptor lymph cavity, ss = socket septum, Hl = haemolymph, Hc = blood cells with haemocyanin crystal, n = small sensory nerve. $\times 1,700$. **14** Scanning electron micrograph of the hair tip. The pore opening is covered by dried-up receptor lymph. $\times 2,800$. **15-17** Consecutive cross-sections of the hair shaft ($\times 20,000$); **15** Just below the tip only the C_1 and C_3 lumina are present; **16** The upper half of the hair shaft appears elliptical with all dendrites in the circular lumen (C_1), surrounded by a crescent-shaped lumen (C_2); **17** Closer to the base the hair shaft flares laterally. The C_1 -lumen is filled by 19 dendrites; the C_3 -lumen is barely visible as an interrupted dark line in the hair wall. **18** One of the 22 bipolar sensory cells lying proximad of the hair base. Note the round pale nucleus (N) with a distinct nucleolus, many Golgi apparatus (G) and a large crystalline inclusion at the axon hillock (ax). $\times 10,000$. **19** Cross-section of slender chemoreceptive dendrites (d) near hair base. ds = dendritic sheath, ss = socket septum. $\times 40,000$. **20** As Fig. 19, but two larger mechanoreceptive dendrites with many microtubules are pictured. $\times 23,000$.



organisation is the termination of the dendrite: in scorpions it ends horizontally within the outer membrane, whereas in spiders it is attached vertically to the slit membrane (Barth, 1971). However, such variations of a basically similar design are to be expected between different orders of arachnids (Barth & Stagl, 1976). The slit sensilla also have corresponding functions in scorpions and spiders. It has been clear for many years that the metatarsal

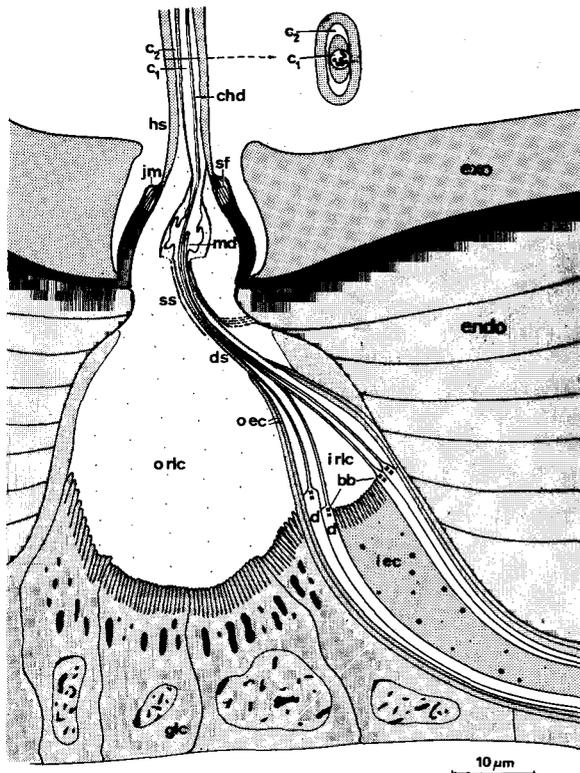


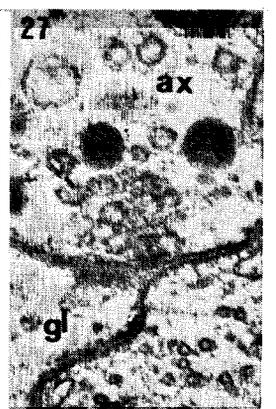
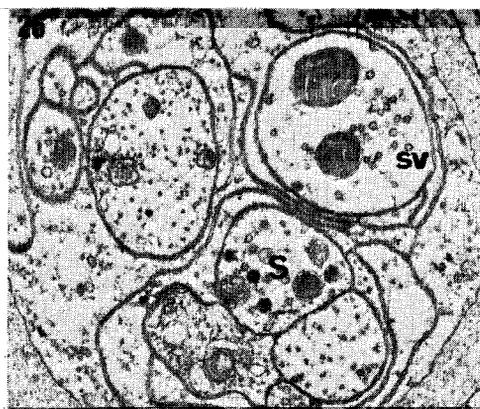
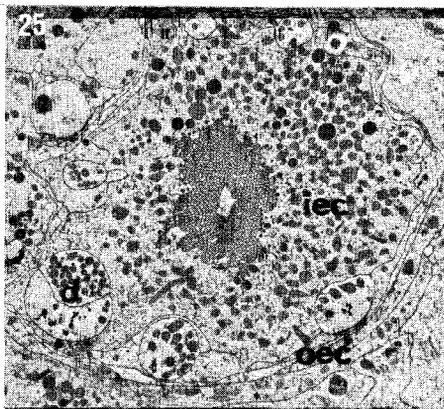
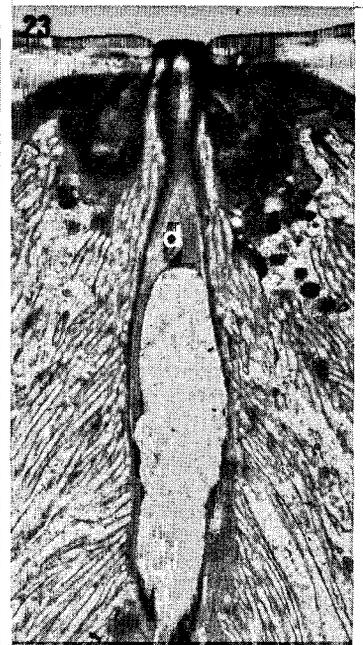
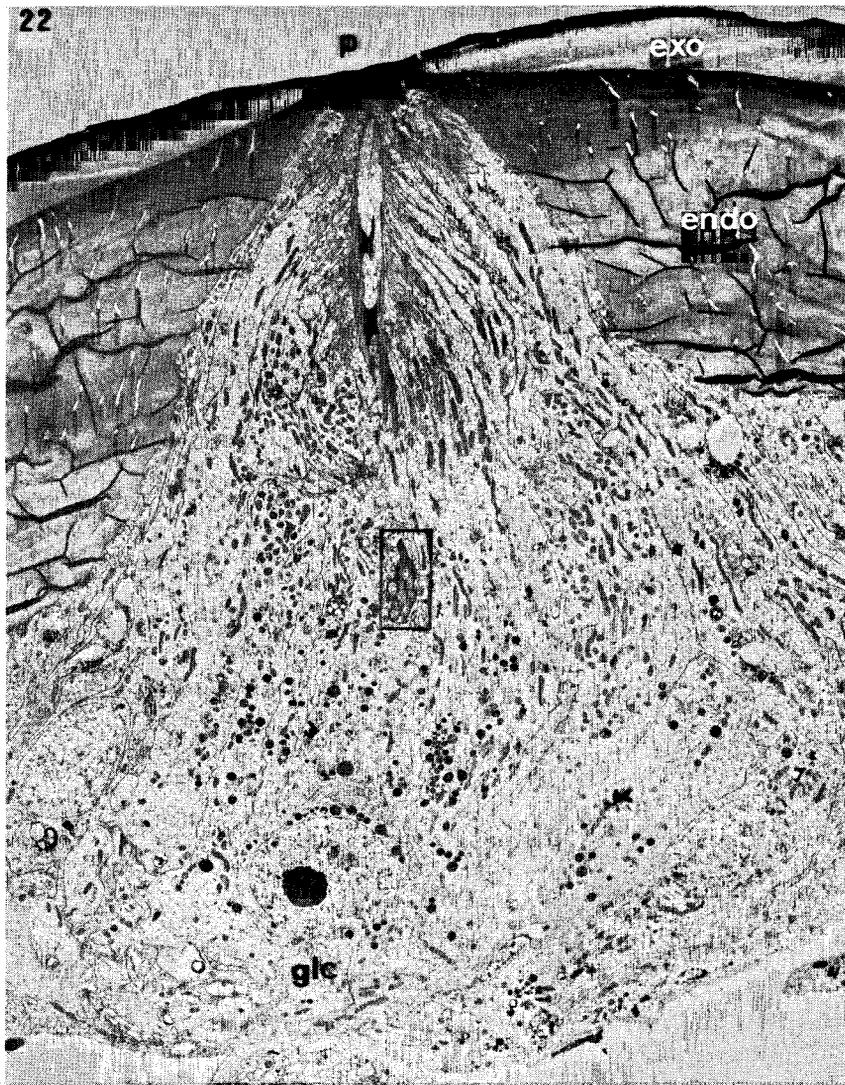
Fig. 21: Diagram of the innervation of a chemoreceptive hair. The mechanoreceptive dendrites (md) end in the hair base while the chemoreceptive dendrites (chd) enter the C_1 -lumen of the hair shaft (hs). The socket septum (ss) is attached to the socket base via fibres. The large outer receptor lymph cavity (orlc) extends into the C_2 -lumen, the inner receptor lymph cavity (irlc) into the C_1 -lumen. sf = suspension fibres of the joint membrane (jm); ds = dendritic sheath, oec = outer enveloping cells, iec = inner enveloping cell, d = inner dendritic segment with basal bodies (bb), glc = gland cell; exo, endo = exo- and endocuticle. The inset figure (top) shows a cross-section of the hair shaft.

lyriform organ of spiders is a vibration receptor (Walcott & van der Kloot, 1959; Liesenfeld, 1961); the homologous basitarsal compound slit sensillum is also excited by substrate vibrations and is used to determine the direction of a vibration source, e.g. a moving insect (Brownell & Farley, 1979a, b).

The chemoreceptive hairs on the legs of scorpions are almost identical to the taste hairs in spiders except that four mechanoreceptive dendrites terminate at the hair base in scorpions compared with two dendrites in the spider sensillum (Foelix & Chu-Wang, 1973b; Harris & Mill, 1973). Despite this multiple mechanoreceptive innervation, we could not elicit a behavioural response when deflecting a single chemoreceptive hair. In contrast, the bending of a single mechanoreceptive hair leads to a withdrawal of the respective leg. The same response was seen when a single chemoreceptive hair was brought into contact with a piece of paper soaked in salt solution. Thus it seems that each receptor type needs its appropriate stimulus to trigger a behavioural reaction.

The discovery of a tarsal organ in scorpions is not really surprising, since spiders (Araneae) and whip spiders (Amblypygi) have a very similar organ in about the same location (Blumenthal, 1935; Foelix, Chu-Wang & Beck, 1975). For spiders it has been shown electrophysiologically that the tarsal organ is an olfactory receptor (Dumpert, 1978). On the basis of behavioural observations, a hygroreceptive function has also been attributed to spider tarsal organs (Blumenthal, 1935). There is similar evidence for the presence of hygroreceptors on the tarsi of scorpions (Abushama, 1964).

Figs. 22-27: Fine structure of the tarsal organ. 22 Longitudinal section of one pore region (P). Several dendrites can be recognised in oblique (top) and in cross-section (rectangle). exo, endo = exo- and endocuticle, glc = gland cell. x 3,100. 23 Pore opening with dendrite (d) exposed to the outside. x 17,000. 24 Cross-section of outer dendritic segments (cf. Fig. 22). x 11,000. 25 Inner enveloping cell (iec) in cross-section with dendritic inner segments (d) at the periphery. oec = outer enveloping cells. x 3,500. 26 Sensory axons from the tarsal organ in cross-section. Note synaptic vesicles (sv) and synaptic contact (S). x 20,000. 27 Higher magnification of synapse shown in Fig. 26. ax = axon, gl = glial cell. x 65,000.



Finally, the peripheral nervous system of scorpions also closely resembles that of spiders and whip spiders (Foelix, Müller-Vorholt & Jung, 1980; Foelix & Troyer, 1980). There are numerous synaptic contacts between peripheral nerve fibres, especially in the hypodermal nerve bundles. Although many sensory axons in the legs of scorpions were found to have rather large diameters ($> 5 \mu\text{m}$), a giant fibre system, such as is present in whip spiders and whip scorpions, was not observed.

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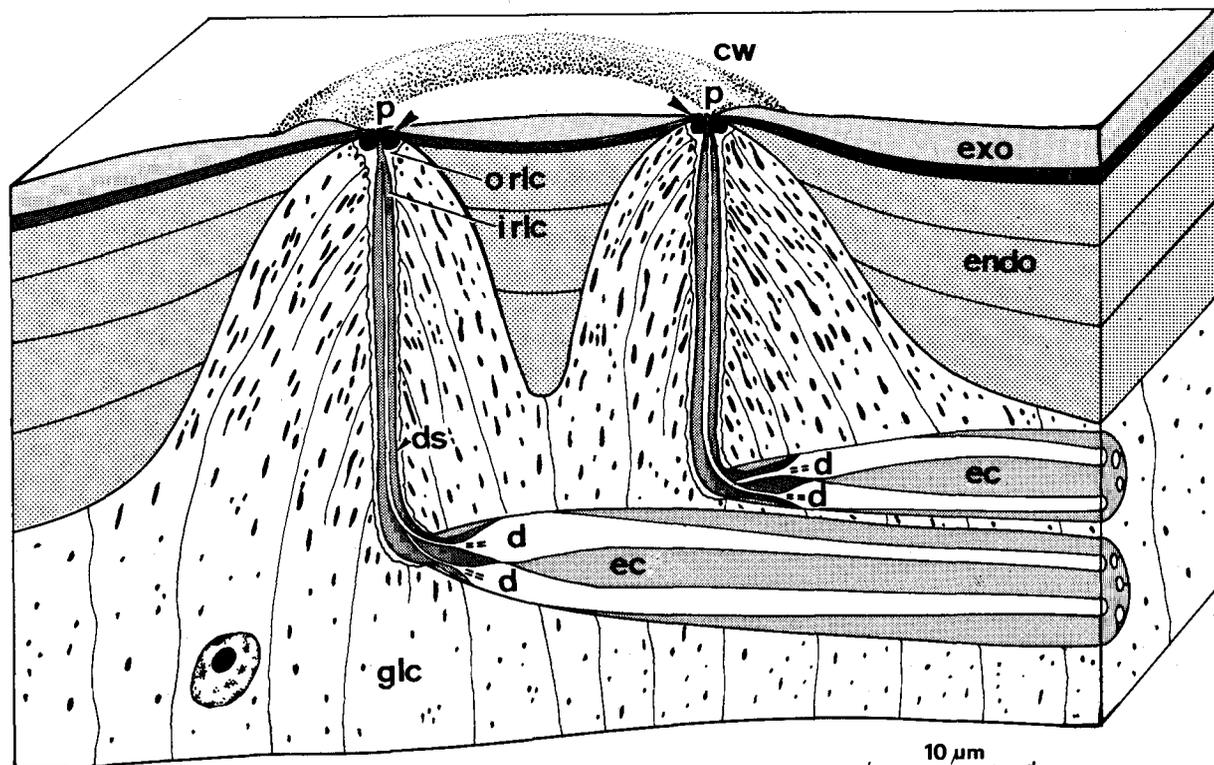


Fig. 28: Diagram of the tarsal organ. Two pore openings (p) lie on the inside of a slight cuticular wall (cw) and several dendrites (d) are exposed there to the outside. exo, endo = exo- and endocuticle; orlc, irlc = outer and inner receptor lymph cavity; ds = dendritic sheath, ec = enveloping cells, glc = gland cell.

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