Slit Sense Organs on the Scorpion Leg (*Androctonus australis* L., *Buthidae*)

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**ABSTRACT** As in other arthropods the exoskeleton of arachnids is subjected to loads generated by external stimuli and behavioral activities. Far from being mere by-products of various activities such loads act as signals for mechnoreceptors capable of detecting minute displacements caused by them in the cuticle. In arachnids the slit sense organs serve in this capacity.

Spiders have the most elaborate system of slit sense organs. Our previous studies clearly pointed to a functional significance of their specific location and orientation, as well as degree and type of aggregation (isolated, grouped, compound or lyriform) on respective body parts.

The present study extends our work to the slit sense organs of scorpions. It gives a detailed account of the topography of the organs on the walking legs. In general slits are less orderly arranged on the legs of scorpions than on those of spiders. In the scorpion they never aggregate to form lyriform organs. Instead there are groups at comparable locations forming much more irregular, but still specific patterns. Isolated slits are more numerous on the scorpion leg, but are also less regularly distributed there. A common feature of the majority of slits on both the spider and the scorpion leg is their position on the lateral surfaces and their orientation roughly parallel to the long axis of the leg.

In recent years the knowledge of both the structure and function of the slit sense organs in spiders has been extended considerably. A combination of electrophysiological and fine structural studies including model experiments has revealed that slit sense organs are a kind of strain gauge responding to the minute displacements in the cuticle caused by compressional load roughly perpendicular to the long axis of the slit (Barth, '71; '72a,b; '73). One of the main inferences from these experiments was that deformation of the dendritic end by monoaxial compression forces leads to mechanoelectrical transduction (Barth, '72b). In addition compound or lyriform organs on the femur and tibia of the walking leg were shown to be involved in kinesthetic orientation behavior (Barth and Seyfarth, '71; Seyfarth and Barth, '72).

All these studies, including older ones on the vibration sensitivity of the metatarsal lyriform organ (Walcott and van der Koot, '59; Liesenfeld, '61) and an investigation of a tarsal slit sense organ's response to airborne sound (Barth, '67) refer only to spiders. It has been known for about 85 years, however, that other arachnid orders are also equipped with slit sense organs (Gaubert, 1890, 1892; Hansen, 1893, 1894; Hansen and Sörensen, '04). Subsequent to these initial, rather crude investigations only Edgar ('63) reported on campaniform and slit sensilla in the phalangid leg and Pringle ('55) investigated slit sense organs in a scorpion and an amphiopygid. Pringle was the first to demonstrate the mechanoreceptive function of the slit sense organs which had previously been suggested in a very general way by Vogel ('23). Due to the lack of proper experiments other authors had considered the slits to be chemoreceptors (McIndoo, '11; Kaston, '35).

**MATERIALS AND METHODS**

Females of the North African scorpion *Androctonus australis* L. (*Buthidae*) were used and sexed according to Vachon ('52).

A total of 27 legs were prepared for light microscopy. They were bisected with a razor blade along their long axis, then softened in 10% KOH for about 15 hours, washed alternately with distilled water and 70% alcohol, and finally embedded as whole...
mounts in ZEISS W 15 embedding medium which does not require total dehydration.

Parts of a leg were dehydrated with acetone for scanning electron microscopy. Thus prepared they could be examined in the microscope without previous metal coating for roughly 30 minutes without serious charging.

The exact position of the organs as well as their length and orientation were checked under a light microscope usually with phase contrast and with the help of a calibrated ocular grid. Figures 7, 8, 10–16 represent typical views of a single leg. The variation found among different legs of the same and of different animals, respectively, is shown separately in figure 17. Although there are numerous sensory and non-sensory specializations in the cuticle, it is possible to distinguish the slit sense organs clearly (figs. 1–6). The segments of the scorpion leg were named according to Vachon (52) using the abbreviations: Co, coxa; Tr, trochanter; PFe, prefemur; Fe, femur; Ti, tibia; BTa, basitarsus; Ta, tarsus. Those surfaces of the leg that face the head when the leg of the scorpion is in its natural walking position are called anterior. Surfaces looking towards the back or ground are referred to as dorsal and ventral, respectively.

RESULTS

Single organs and groups

In spiders slit sense organs occur in two main configurations, namely as isolated single slit sense organs and as compound or lyriform ones.1 Lyriform organs are composed of several (from 2 to about 30) slits lying closely side by side (fig. 3). As noted earlier there are intermediate cases between these two extremes (Barth and Libera, '70). These are slits clearly arranged in groups (grouped single organs) but forming much more irregular patterns than are found in lyriform organs. Scorpions lack lyriform organs on the leg and only isolated and grouped slits are found (figs. 1–6). Such groups of organs are easily recognized under the microscope, since they occur at well-defined places and show a specific pattern of slit arrangement.

The following definitions were found useful in distinguishing between isolated and grouped organs. 1. An isolated organ has a shortest distance of 100 μm or more from the most closely neighbouring slit. To simplify the search for organs we have concentrated on isolated slits measuring 30 μm or more and applied the definition to these. Scorpion legs have a profusion of isolated slits smaller than 30 μm. We have taken the slits of the femur as representative (fig. 9). 2. A group of single slits comprises at least one slit measuring 30 μm or more plus a minimum of one additional slit less than 100 μm away. If belonging to a group slits shorter than 30 μm (see under 1.) were fully incorporated into the study. Groups consisting only of slits shorter than 30 μm were not observed, though this was not studied specifically. The length of the 385 slits measured varied from 9.5 to 152 μm. From 2 to 16 slits comprise a group.

Basic pattern

Slit sense organs occur on all segments of the walking leg including the claws, the posttarsus, and those parts of the first leg’s coxa which participate in forming the scorpion’s preoral cavity.

Most of the grouped as well as large isolated slits (length 30 μm or more) occur on the lateral surfaces of the leg. Exceptional is one group located dorsally on the tibia (post. 6) and another one (post. 1) ventrally on the trochanter (figs. 7,8). Whereas small isolated slits (length less than 30 μm) — also found on the lateral surfaces — are distributed all along the leg segment (fig. 9) large single slits as well as groups concentrate on the more distal and proximal parts of them. Most of them thus occur close to a joint. Particularly prominent are those at the distal ends, i.e., the majority of them (7 large isolated slits, 8 groups; s. figs. 10–16). This does not mean, however, that such organs always lie right at the borderline between the hard leg cuticle and the soft articular membrane nor that they always are in the closest possible proximity to the articular condyles. Three out of four groups on the proximal part of a leg segment lie on the trochanter, the fourth one on the femur.

In general the topography of the groups is characterized by asymmetry when comparing the anterior aspect of the leg with the posterior one. The same is true for the

1 This term was introduced by Gauert in 1890, who also noted that scorpions lack lyriform organs.
joints. Usually the slits are oriented roughly parallel (angle of deviation ≤ 45°) to the long leg axis, by be isolated or grouped. Deviations of more than 45° are seen only in group 5 on the anterior surface of the basitarsus (figs. 7, 8, 12).

Variability

As in spiders (Barth and Libera, '70), the topography of the small isolated slits varies more than that of the large ones and the groups. The latter two types are found at their specific sites regularly; slits can be identified individually and compared in different preparations. When comparing the first leg with others, however, slight differences are seen. The first leg, to give an example, has a small group of four slits on the anterior surface of the coxa and two other groups (comprising three and four slits, respectively) as well as a large isolated slit on the posterior surface of the trochanter which are all lacking on the fourth leg. By contrast a large isolated slit located anteriorly on the coxa and a group of two slits on the posterior surface of the trochanter are missing on the first leg.

Figure 17 shows in some detail the variability of the five groups with the largest number of slits. The first and fourth right and left legs of one individual are compared with the left first and fourth legs of another one. The specificity and constancy of the five basic patterns are evident. Slight deviations are found in the number of slits, their length, and orientation. The length of homologous slits on different legs of the same individual varied by up to 17% and the number of slits within homologous groups by a maximum of two. We found slight differences between right and left legs of the same individual. They are not systematic, however, as would be expected for reasons of symmetry between the left and right side of the scorpion. Even in two different individuals the number of slits making up homologous groups varied only by up to three and in a seemingly inconsistent way.

DISCUSSION

Comparative morphology

The topography of slit sense organs is well known both for web building (McIndoo, '11; Vogel, '23; Barth and Grill, '70) and hunting spiders (Barth and Libera, '70). Comparing the results of these studies with those of the present one, both common and differing features of the spider and scorpion leg emerge.

In general isolated, grouped, and lyriform slit sense organs are to be distinguished. The most striking difference is the complete absence of lyriform organs from the scorpion leg. Whereas the lyriform organs of spiders are a characteristic feature of the extremes and are particularly numerous and well developed on the walking legs (15 on each of them comprising a total of 184 slits in Cupiennius: Barth and Libera, '70), there is not even one on the scorpion leg. Instead the scorpion leg is equipped with groups of slits lacking the neat parallel arrangement. All these groups, however, are found close to the joints as is also typical for lyriform organs. In the scorpion leg there is no strict confinement of the groups to the distal part of a leg segment which is the case with lyriform organs of spiders (the organs of the patella are exceptional in this respect). Instead four out of twelve groups are located close to the proximal ends of the femur (1) and trochanter (3), respectively.

The legs of phalangids (Edgar, '63) and amblypygids (Barth, unpublished) occupy a position between those of spiders and scorpions: they have only one lyriform organ distally on the trochanter.

In the scorpion isolated slits clearly outnumber those of spiders. In spiders the femur is the leg segment richest in isolated slits. For example, Cupiennius, a lycosid spider, has about 20 of them on its anterior surface (Barth and Libera, '70), whereas we found about 70 in the scorpion. Another difference is that the isolated slits of spiders are generally arranged in lines on the laterodorsal and (or) lateroventral aspects of the leg, whereas in the scorpion they are found apparently irregularly distributed on the leg's lateral surfaces (fig. 9).

Both the lack of lyriform organs and the much more irregular arrangement of the isolated slits may indicate a more primitive situation in scorpions.

Functional aspects

A lateral position on the leg is typical for all slit sense organs (isolated, grouped, and lyriform) in spiders, scorpions, and ambly-
pygids (Barth, unpublished). The slits of the leg are generally oriented roughly parallel (angle of deviation \( \aleph 45^\circ \)) to the long axis (for exceptions see figs. 7, 8). Both findings are of functional significance. Previous experiments (Barth, '72a,b; '73) have shown that the sensitivity of a slit sense organ has pronounced directional properties. According to electrophysiological recordings from individual slits they respond to compressional deformation resulting from stresses roughly perpendicular to their axis. This finding disagrees with Pringle's ('55) proposal that dilatation of the slit represents the adequate stimulus. A tension optical study of a model spider leg (Barth, in preparation) has shown that stresses running roughly perpendicular to the long axis of the leg have indeed to be expected on the lateral surfaces of the leg under normal loading conditions. We assume that the same or a similar reasoning applies to the scorpion leg.

In spiders the metatarsal lyriform organ is unusual for its orientation perpendicular to the leg axis and its dorsal position. Walcott and van der Kloot ('59) and Liesenfeld ('61) have demonstrated its vibration sensitivity. Recently the functional significance of its above mentioned topographical peculiarities have been analysed (Barth, '72b). The scorpion also has a group exceptional for its dorsal location on the distal part of the tibia (fig. 8, group 6). Its muscular supply, however, suggests that the tibia of the scorpion is not homologous to a spider's metatarsus. In addition the slits of the organ mentioned above are oriented parallel to the long axis of the leg so that even a functional analogy alone is unlikely. A better candidate is group 5 on the basitarus (fig. 7). It resembles the spider metatarsal organ in its close vicinity to a cuticular process (lying right behind it) at the joint. Also about half of its slits are oriented roughly perpendicular to the leg axis. In addition arachnologists often consider the basitarus homologous to the spider's metatarsus.

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LITERATURE CITED


Barth, F. G., and R. Grill 1970 Versuche zur Bedeutung der Spaltinnenseorgan für das Lokomotionsverhalten der Spinnen. Staatsexamensarbeit (unpubl.).


--- In Cupiennius (Barth, '71) the metatarsal lyriform organ does not differ from other lyriform organs with respect to the attachment site of its dendrites as was postulated by Salpeter and Walcott (‘60) for Achaearanea. Furthermore the fine structure of an isolated slit is basically the same as that of a lyriform organ’s slit (Barth, ’71).
PLATE 1
EXPLANATION OF FIGURES

1 Scanning electron micrograph of grouped slit sense organs on the tibia (Ti) of the scorpion leg (group 6, fig. 8). BTa, basitarsus.

2 Scanning electron micrograph of grouped slit sense organs on the femur (Fe) of the scorpion leg (group 4, fig. 8).

3 Scanning electron micrograph of a lyriform slit sense organ typical for the spider leg, but not found on the scorpion leg. Note the parallel and close arrangement of the slits. C. salei Keys., posterior surface of tibia (Ti).
PLATE 2

EXPLANATION OF FIGURES

4 Whole mount cuticle preparation in transmitted light showing a group of slits (arrows) on the ventral side of the scorpion trochanter (group 1, fig. 8). A slight dilatation of the slit marks the area of the dendrite (De) attachment to the covering membrane of the slit. Note the cuticular walls surrounding the slit. Ep, epicuticular ribs forming a honeycomb pattern.

5 Slit sense organ of the scorpion leg as seen in a whole mount preparation of the cuticle in transmitted light and with the epicuticle in focus. The slit is out of focus here since it is covered by a layer of epicuticle (Ep, note honeycomb pattern) about 4 μm thick.

6 The same slit as in figure 5 but in focus. Note the invisibility of the epicuticular ribs. Po, pore canals which are particularly numerous around the outer margin of the cuticular wall (Wa) surrounding the slit. De, site of dendrite attachment.
PLATE 3

EXPLANATION OF FIGURES

7 Anterior view of the fourth right walking leg of the scorpion. The topography of isolated slits longer than 30 μm (−) and of groups (■) is shown. Details of the groups drawn to scale are given as insets. The dendrite attachment sites are indicated by circular dilatations of the slits. The arrows run parallel to the axis of the respective leg segment and point towards its distal end. The coxa (Co) is seen from anteriodorsal since it is twisted relative to the trochanter (Tr). The symbols for the slit sense organs (−, ■) are not drawn to scale. PF, prefemur; Fe, femur; T1, tibia; BTa, basitarsus; Ta, tarsus.

8 The same leg as in figure 7. For explanation see legend figure 7. The coxa (Co) is viewed from ventro-lateral in this case.
PLATE 4

EXPLANATION OF FIGURES

9 Anterior view of femur of fourth right walking leg showing the abundance of isolated slits (–) shorter than 30 μm. Note the irregular distribution of the organs all over the lateral surface of the femur. ■, group close to proximal end of femur; see also inset.

10 Posterior view of the tibia/femur joint region with a group of slits close to the distal end of the femur (Fe).

11 Anterior and posterior view of the tarsus (Ta). As in figures 12–16, which are all taken from the same preparation as figure 11 and figures 7 and 8, all groups as well as isolated slits longer than 30 μm are shown to scale and precisely in the position found on the leg. Note the orientation of the slits in the group; it is exceptional in being roughly perpendicular to the leg axis.

12 Anterior and posterior view of the basitarsus/tarsus joint region. Compare figure 11 for further explanation.
PLATE 5
EXPLANATION OF FIGURES

13 Dorsal and posterior view of the basitarsus/tibia joint region. Compare legend of figure 11.

14 Anterior and posterior view of femur/prefemur region. Compare legend of figure 11. Note the position of the group proximal on the femur.
EXPLANATION OF FIGURES

15 Anterior and posterior view of the prefemur/trochanter joint region. Compare legend of figure 11.

16 Anterior and posterior view of the trochanter/coxa joint region. Compare legend of figure 11. The coxa is seen from ventral due to its twisted position relative to the trochanter. Note the position of the groups on the proximal part of the trochanter.
Variability of patterns in the five groups with the largest numbers of slits. R1, L1 etc., first walking leg of the right and left side, respectively. Ant. 5, post. 6 etc., number of organs as given in figures 7 and 8. A and B mark two different animals.
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The diagram illustrates the slit sense organs on scorpion legs, with different rows and columns labeled with specific positions and orientations. The labels R4, R1, L4, and L1 denote different segments or sides of the scorpion legs, and the numbers (9, 6, 15, 11, 10, 8) likely indicate scale or measurement references. The diagram compares different parts of the scorpion legs, potentially showing variations or patterns in the slit sense organs.