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RAINER FOELIX & EILEEN HEBETS

Sensory biology of whip spiders (Arachnida, Amblypygi)

Abstract
Whip spiders belong to a small arachnid order (Amblypygi) that is not well known. Their most conspicuous feature are the elongated, extremely thin front legs ("whips", or antenniform legs). These are no longer used for walking but are modified extremities carrying various sense organs – very much like the antennae of insects. Whereas hundreds of olfactory hairs are concentrated near the tip of each antenniform leg, large bristles (contact chemoreceptors) are evenly distributed over the entire antenniform leg. The sensory hairs of each antenniform leg contribute about 30,000 small sensory axons which proceed toward the central nervous system (CNS). The sensory fibers originating from the mechanoreceptive bristles make chemical synapses with a few giant interneurons in the periphery. The giant axons (10-20 µm in diameter) of these large interneurons transmit nerve impulses with a high velocity (6 m/s) to the CNS. The purpose of this fast pathway still needs to be determined. Originally it was thought that the fast giant axons would trigger quick escape reactions, but this was not confirmed in physiological experiments. However, other possible behaviors that may be aided by the giant interneurons are prey capture, fighting, and orientation.
What makes whip spiders unique is that both synapses and giant neurons are located far out in the peripheral nervous system. In all other arthropods – except for some arachnids – synapses and giant fiber systems are always found inside the CNS, never in the periphery.

Kurzfassung
Geißelspinnen gehören zu einer kleinen, wenig bekannten Ordnung der Spinnentiere, den Amblypygi. Ihr auffallendstes Merkmal sind die stark verlängerten, extrem dünnen Vorderbeine ("Geißeln"). Diese werden nicht mehr zum Laufen benutzt, sondern dienen – ähnlich wie die Antennen der Insekten – als Träger verschiedener Sinnesorgane. Während die Geißelspitze Hunderte von Geruchshaaren aufweist, ist die übrige Geißel ziemlich gleichmässig mit Borstenhaaren (Kontaktchemorezeptoren) bestückt. In jeder Geißel ziehen ca 30.000 kleine sensorische Nervenfasern zum Zentralnervensystem (ZNS). Dabei werden die mechanorezeptiven Nervenfasern über chemische Synapsen auf einige periphere Riesen-Interneurone aufgeschaltet; deren Riesenaxone (10-20 µm ø) leiten Nervenimpulse mit großer Geschwindigkeit (6 m/s) zum ZNS. Wofür dieses Schnellleitsystem im Verhalten der Tiere eingesetzt wird, ist noch nicht geklärt – die ursprüngliche Vorstellung im Sinne einer raschen Fluchtreaktion ließ sich physiologisch nicht bestätigen. Andere Einsatzmöglichkeiten (Beutefang, Kommentkämpfe, Orientierung) werden diskutiert.
Sowohl Synapsen als auch Riesenneurone liegen bei anderen Arthropoden stets innerhalb des ZNS; nur bei einigen Spinnentieren sind Synapsen im peripheren Nervensystem gefunden worden – ein peripheres Riesenfasersystem dürfte auf Geißelspinnen beschränkt sein.

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Key words
Arachnida, Amblypygi, sensory biology, behavior

1. Introduction

Whip spiders – even most zoologists have not heard of these animals, and even fewer have ever seen one in nature. They are "exotic" indeed: although whip spiders are true arachnids (Order Amblypygi) and closely related to web spiders (Araneae), they differ in several aspects. Unlike "true" spiders they do not possess silk glands or poison glands. Most unusual is the fact that whip spiders walk only on six legs, not on eight as most other arachnids do. This is because their first pair of legs are very thin (< 0.5 mm) and long (up to 30 cm!) and are held out above the ground. These elongated antenniform legs greatly resemble insect antennae and correspondingly are equipped with thousands of sensory organs that perceive a variety of mechanical and chemical stimuli from their environment (BECK 1968, BECK et al. 1977, HÖFER & BECK 1995). The six walking legs also possess sensory hairs (mechanoreceptors for touch and vibrations), but the antenniform first legs provide the main sensory input. Whip spiders deprived of those important first extremities can no longer locate or catch any prey, nor can they orient themselves in their environment (BECK & GÖRKE 1974; GÖRKE 1973).
What is the typical habitat of whip spiders? Almost all species live in warm tropical regions, usually in rain forests (Plate 1b) or caves (WEYGOLDT 2000). Due to their strictly nocturnal habits, most people have never seen a whip spider. They hide in crevices, behind bark, in holes in the ground and even under rocks during the day and venture out only at sunset (BECK & PABST 1969, HEBETS, in prep.). In tropical forests whip spiders spend much of the night sitting on the vertical surfaces of large tree trunks, waiting for prey. Their long antenniform legs probe the (dark!) environment by slowly moving and circling around in front of them. If a prey item, usually a small arthropod, is detected, the whip spider approaches directly yet slowly. The

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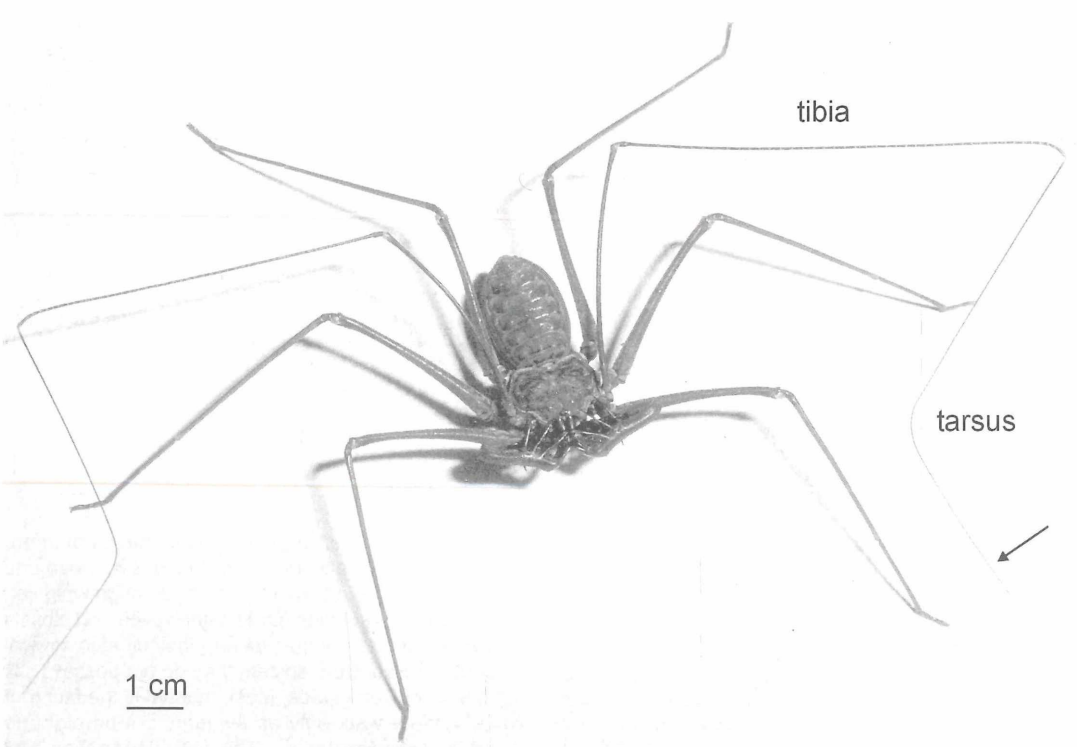

Figure 1. Whip spiders typically cling to the vertical surface of tree trunks with their heads down. Their first legs are no longer used for walking but are specialized sensory organs, comparable to the antennae in insects. Note the extremely elongated tibia and tarsus, each about 10 cm long; these bear thousands of sensory hairs, particularly on the tarsal tip (arrow).

heavily spined pedipalps are opened wide and once within close range, the animal quickly lunges forward and stabs the prey. If whip spiders are disturbed in any way, either by touch or by a slight puff of wind, they rapidly withdraw into the closest retreat. They are not aggressive at all towards humans but seem to avoid all contact.

2. Sensory equipment of the antenniform legs

It is clear simply from watching their behavior that whip spiders must possess excellent sensory organs and that most of them lie on their antenniform legs (fig. 1). Their distal segments are the longest with the tarsus alone measuring about 10 cm and the tibia between 5 and 6 cm. Both leg segments are subdivided into many subsegments (also called "annuli" or "articles") of 1-2 mm in length. The number of these annuli varies between species; for instance, *Heterophrynus longicornis* has about 100 tarsal and more than 40 tibial annuli, in the cavernicolous *Stygophrynus longispina* there are less, i.e. 45 in the tarsus and 25 in the tibia (Weygoldt 1994).

The antenniform legs are highly motile: not only do they bend at the segmental joints but they can also flex within the tarsus, thus giving the impression of a thin rubber hose. How this tarsal movement is achieved is not quite clear, since muscles are lacking in the distal part of the legs. There are, however, two slender cuticular tendons which traverse the entire tarsus up to the reduced claws at the tarsal tip. These tendons are in contact with the hypodermis at various points and probably act like internal reins. At any rate, in *Heterophrynus* one can easily observe a strong bending (> 90°) of the tarsus between annuli 30 and 40 while they probe their environment (fig. 1; Igelmund & Wendler 1991a).

Looking at the antenniform legs with the naked eye, one can only detect relatively large bristles (about 500 mm long and 10-15 µm thick) which are arranged in five longitudinal rows along the entire tarsus. Under the microscope, however, hundreds of small hair sensilla become visible, especially on the 20 distal tarsal annuli (figs 2, 3). Since the wall of these sensory hairs is perforated, they most likely act as chemosensory receptors (olfactory, taste, humidity).

Actually, a large variety of sensory organs is present on the antenniform legs (Beck et al. 1974, 1977;

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FOELIX et al. 1975; IGELMUND 1987): 1. Bristles, 2. Trichobothria, 3. Slit sensilla, 4. Pore hairs, 5. Club hairs, 6. Rod hairs, 7 Pit organ, 8. Plate organ, 9. Proprioreceptors, 10. Tarsal claws.

2.1 Bristles

Bristles are the longest and most numerous hair sensilla on the tarsus and tibia. In *Heterophrynus* species their length ranges from 200 – 1000 µm and their number varies between 1200 and 1700 on the tarsus of adult animals (BECK et al. 1977; IGELMUND 1987). The hair shaft is relatively thick and has grooves and small spines on its surface. The hair lumen encloses 9-12 dendrites that run up to a terminal pore; two further dendrites end at the hair base and exhibit tubular bodies that are typical of mechanoreceptive neurons. Actually, the bristles are the only sensilla with a distinct socket and a movable hair shaft. Touching the bristles elicits action potentials, as was shown by electrophysiological recordings (IGELMUND & WENDLER 1991a). Thus, the bristles can be interpreted as typical contact chemoreceptors, responding to both mechanical and chemical stimuli.

A variation of the regular bristles are the "leaf-like hairs", which have a flattened shaft. This may cause more resistance to air currents and since they sit rather firmly in their sockets, they may transmit mechanical load to slit sensilla in the cuticle (IGELMUND 1987)

2.2 Trichobothria

There are only a few trichobothria on the antenniform legs (tibia), but many on the walking legs (tibia, metatarsus). Trichobothria, or filiform hairs, have a long, slender shaft suspended in a deep, cup-shaped socket; the slightest air currents make them quiver and therefore they are considered as long range tactile organs (BARTH 2000, BARTH & HÖLLER 1999). The trichobothria on the walking legs seem to be very important for prey detection – even at distances of 50-60 cm (BECK & GÖRKE 1974). Strong stimulation of these long trichobothria (2 mm!) can also trigger escape responses; this is in contrast to the short trichobothria (200-300 µm) located on the tibia of the antenniform legs, which do not elicit escape reactions (IGELMUND & WENDLER 1991a).

2.3 Slit sensilla

Slit sensilla are very inconspicuous slits in the leg cuticle, usually 10 µm long and 3 µm wide. Each slit is covered by a thin cuticular membrane to which two dendrites of sensory cells are attached; as in other arachnids these sensilla measure strain in the cuticle. There are 1-3 slit sensilla on each tarsal annulus, always lying parallel to the longitudinal axis of the leg. One exceptionally large slit sensillum (80 mm) lies on annulus 22 (in *Heterophrynus elaphus*); it responds to bending between annuli 21/22 and thus acts as a proprioreceptor (IGELMUND & WENDLER 1991a). If several single slits lie close together they are called "lyriform organs" Although very common in web spiders (Araneae), they are rare in whip spiders (HANSEN 1893, BARTH & STAGL 1976). One lyriform organ composed of 7 slits lies at the border of the tibia and tarsus in the antenniform legs (IGELMUND 1987); it is somewhat reminiscent of the metatarsal lyriform organ in spiders, which is a well-known vibration receptor (BARTH 1985).

2.4 Pore hairs

Pore hairs are small (120 µm long, 3-4 µm in diameter) sensilla with rather thin, perforated walls. They are restricted to the distal 20 annuli and are most densely clustered at the tarsal tip (fig. 3). Fine structural studies showed two types of hairs, one with many pores and many dendrites (40), the other one with fewer pores and fewer dendrites (20-30) (FOELIX et al. 1975). Both types closely resemble olfactory hairs on insect antennae and there is good pysiological evidence that they react to different odors (HEBETS & CHAPMAN 2000). Between 400 and 500 of these pore hairs were counted on the distal tarsus of one antenniform leg *(Heterophrynus longicornis*; BECK et al. 1977).

2.5 Club hairs

Club hairs are the smallest sensilla, measuring only 30 µm in length and 3-4 µm in diameter. The bulbous tip (6-8 µm diameter) exhibits a central pore, at which 4-6 dendrites are exposed to the environment (fig. 3). Like the pore hairs they are non-socketed and they occur only on the distal 20 annuli; their total number is close to 400. The function of those club sensilla is not known but most likely they represent some kind of chemoreceptors.

2.6 Rod hairs

Rod hairs always occur in one cluster on each annulus of the distal tarsus (fig. 2). Again, two types can be distinguished, one with very thin walls (0.1 µm) and a terminal pore in a 20 µm long hair shaft, the other one with numerous pores in a thicker wall (0.4 µm) of a longer shaft (40 µm). The total number of rod sensilla was 65 in *Heterophrynus longicornis* (BECK et al. 1977) but only 35 in *H. elaphus* (IGELMUND 1987). No specific function could be assigned to the rod hairs so far.

2.7 Pit organ

On the tarsal tip (annulus 1) lies a small pit with 5-6 raised pore openings inside. At each pore 2-5 dendrites are exposed to the outside. This structure resembles closely the so-called "tarsal organ" in spiders and similarly may function as a hygroreceptor (EHN & TICHY 1994).

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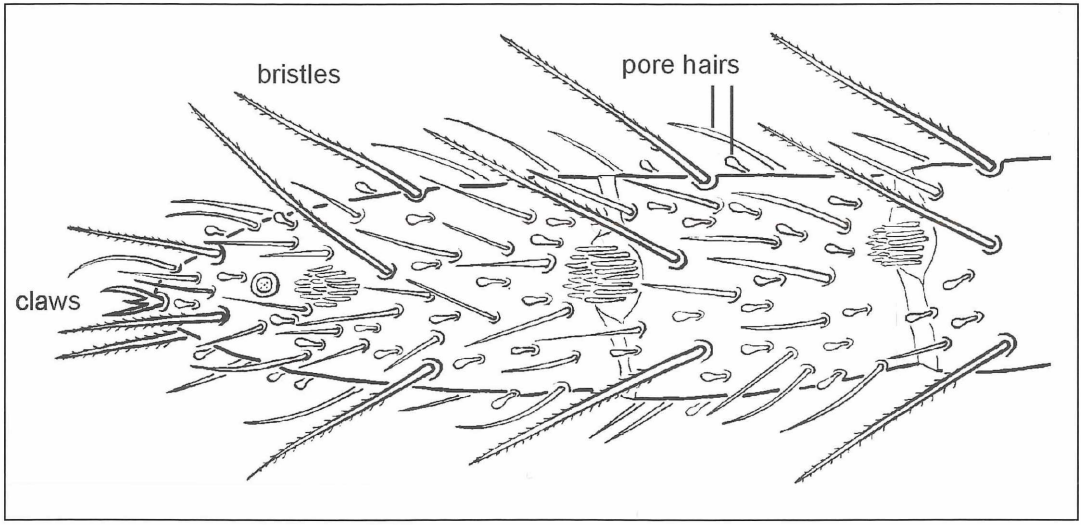

Figure 2. In *Heterophrynus longicornis* the tarsus of the antenniform legs is subdivided into one hundred small segments (annuli); they are studded with large bristles (contact chemoreceptors) and near the the tip with hundreds of pore hairs (olfactory receptors). The distalmost part of the tarsus ends in three tiny claws; after GÖDEKE & KAISER 1975.

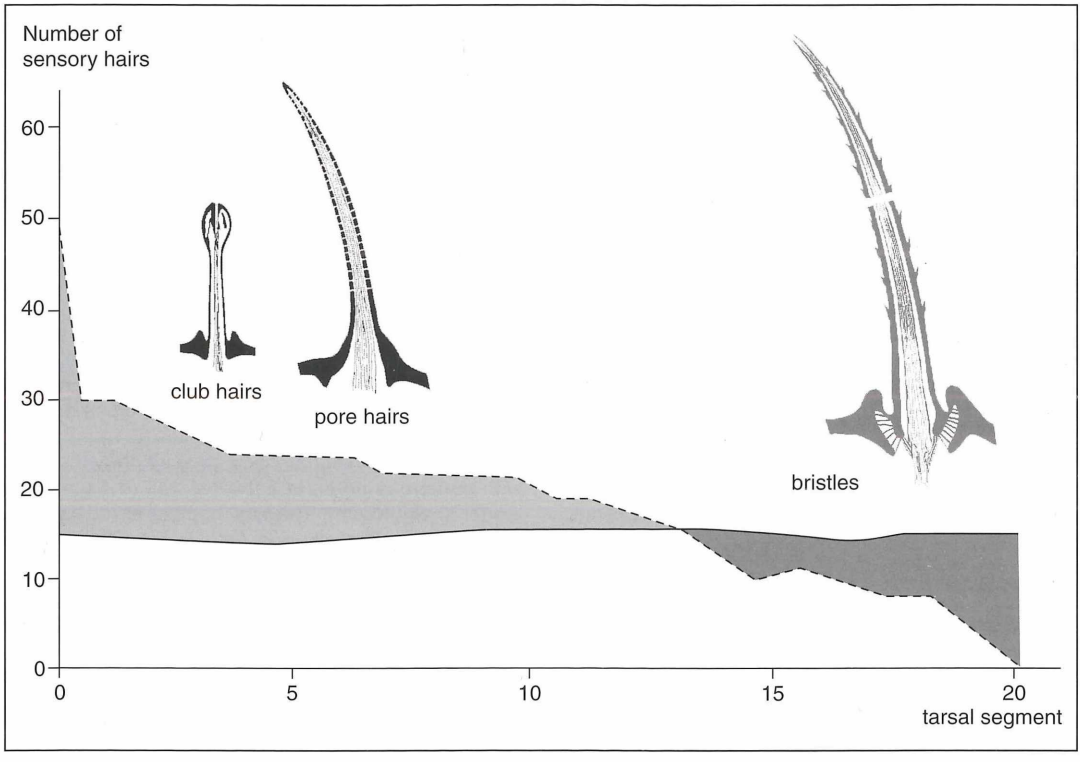

Figure 3. The number of pore hairs is highest near the tip of the tarsus and decreases proximally; no olfactory hairs are present between tarsal segments 20 and 100. In contrast, the concentration of the mechanosensitive bristles remains the same throughout the entire tarsus; after data from GÖDEKE & KAISER 1975.

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2.8 Plate organ

On annulus 12 or 13 lies a oval shaped depression, about 70 µm long and 25 µm wide. From its distal surface arises a cuticular cone with a terminal pore; it is innervated by 12 dendrites. Nothing is known about the function of this organ.

2.9 Proprioreceptors

Two large sensory cells lie in annulus 22 and their dendrites extend distally into the hypodermis (IGELMUND 1987). Both the morphology and the physiology point to a function as joint receptor (FOELIX & CHOMS 1979; IGELMUND & WENDLER 1991a). Groups of bipolar neurons were observed near the tibio-tarsal joint, lying freely in the hemolymph; they were also interpreted as proprioreceptors (FOELIX, unpublished).

2.10 Tarsal claws

Three reduced claws sit at the very tip of the tarsus of the antenniform legs (fig. 2). Each claw has a subteminal opening and is innervated by several dendrites; the middle claw actually has three bundles of 3-5 dendrites each (FOELIX et al. 1975). The fine structure indicates some sort of contact chemoreception.

3. Internal organization of the tarsus in antenniform legs

An unusual feature of arachnid sensilla is the relatively high number of neurons associated with each sensory hair (FOELIX 1985). Whereas a typical insect contact chemorector has 4-6 neurons per sensillum, arachnid taste hairs have more than 20. The pore hairs in whip spiders exhibit even more neurons, namely up to 40 per sensillum. Such a high number of sensory cells necessarily leads to thousands of afferent fibers within the sensory nerves. Before we deal with the actual numbers of sensory axons, we want to have brief look at the internal organization of an antenniform leg.

A cross section of the tarsus shows the following features under the microscope: Beneath the cuticle lies a single epidermal layer (hypodermis) that harbors most of the sensory neurons. The small axons of the sensory cells form small nerve bundles which soon join one of the two tarsal nerves (fig. 4). These two conspicuous nerves lie in the central hemolymph space of the tarsus. Additionally, there are two long tendons, one lying dorsally in the hemolymph space, the other being enclosed by the large leg artery ventrally. As in true spiders (Araneae) these tendons traverse the entire tarsus, but their muscular part lies within the tibia. In spiders these two muscles serve to raise or lower the tarsal claws, but since the claws are very reduced in the antenniform legs of whip spiders, this

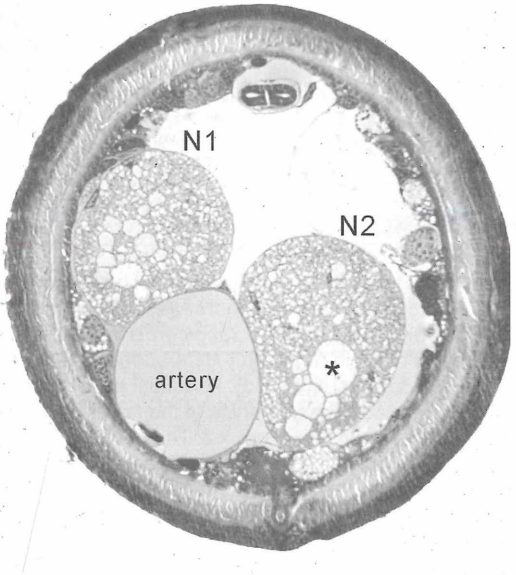

Figure 4. A cross section through the tarsus of an antenniform leg shows two conspicuous sensory nerves (N1, N2). The nerves contain mostly very small afferent fibers but also a few giant axons (*), 500x.

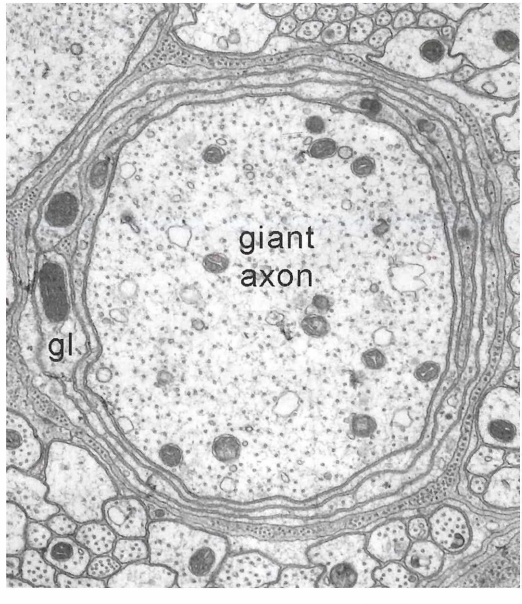

Figure 5. A single giant axon as seen in the electron microscope. Note the extensive glial wrapping (gl) and the surrounding small sensory axons, 5,000x.

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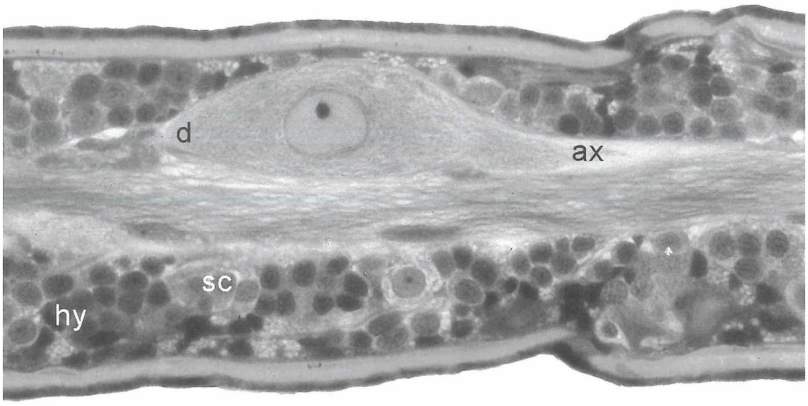

Figure 6. Several large interneurons lie within the antenniform legs and receive sensory input from hundreds of bristles. Compare the size of the giant neuron to that of sensory cells (sc) and hypodermal cells (hy). ax, axon and d, dendrite of giant neuron, 300x.

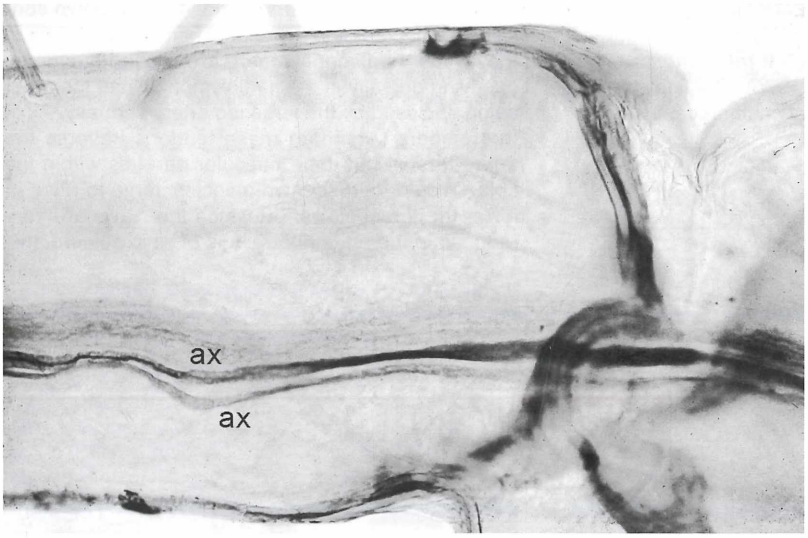

Figure 7. The giant neurons give rise to large axons of 10-20 µm diameter that proceed toward the central nervous system. In this photograph two giant axons (ax) entering the tarso-tibial joint stand out because they have been marked with cobalt sulfide, 350x.

function is no longer present. Instead, these tendons may be responsible for flexing the long tarsus (see above).

Since there are no muscles within the tarsus, the two tarsal nerves must be purely sensory; this is an important precondition when counting the number of axons in the tarsal nerves and relating them to the number of tarsal sensory organs (see below).

How do these thousands of sensory organs send their information to the central nervous system? Most of the sensory axons are of very small calibre (0.1 – 0.2 µm in diameter) which allows for several thousands of nerve fibers to fit into the narrow lumen of the antenniform legs. After compiling a quantitative list of all the sensilla present on a tarsus of an antenniform leg and knowing from electron microscopy how many sensory cells were associated with each sensillum type, the total number of sensory fibers was calculated as 24,400 for *Heterophrynus longicornis* (Beck et al. 1977) and close to 30,000 for *Heterophrynus elaphus* (Igelmund & Wendler 1991a). An actual axon count of cross-sectioned sensory nerves at the tibio-tarsal joint yielded 23,050 axons (Foelix & Troyer 1980). This close correspondence between the theoretical and the actual axon count allowed the following conclusions: 1) that all the nerve fibers within the two tarsal nerves are afferents, and 2) that all the primary sensory axons proceed to the central nervous system (CNS). At least theoretically there was the possibility that the high number of afferent fibers in the periphery could be reduced, for instance by converging the input from many sensory fibers onto a few interneurons. How-

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ever, such interneurons are generally restricted to the CNS in arthropods. It turned out that whip spiders are quite exceptional in this respect, i.e. they do have large interneurons in their peripheral nerves.

4. The giant fiber system

Although more than 99 % of all sensory axons are very small, a few large fibers are present in each sensory nerve, measuring between 5 and 20 µm in diameter (figs 5, 7). The obvious question was: Where are the corresponding cell bodies of these giant fibers located – do they lie within the CNS in the prosoma (as one would expect), or do they perhaps lie in the periphery, somewhere within the antenniform legs? After much serial sectioning it became clear that these giant neurons lie indeed in the periphery, i.e. mostly far out in the tarsus – sometimes as far as 26 cm away from the CNS (IGELMUND & WENDLER 1991b).

It is also remarkable that these giant neurons (fig. 6) are located in specific annuli of the tarsus, i.e. in subsegments 1, 5, 6, 13, 21, 25 and 101 in *Heterophrynus longicornis* (FOELIX & TROYER 1980); this knowledge enabled one to relocate specific giant somata for more detailed studies. Compared to hypodermal or sensory cells the giant neurons have very large somata (up to 160 µm long and 50 µm wide). Most conspicuous is the large pale nucleus (25 µm in diameter) with a distinct nucleolus. Aside from a large variety of the usual cell organelles, the cytoplasm contains also some unusual "twisted filaments", which may represent a new class of intermediate-sized filaments (FOELIX & HAUSER 1979).

The giant neurons are bipolar or multipolar nerve cells, distally with a relatively short, branching dendrite and proximally with a long giant axon. The next obvious question was: what is the function of these giant neurons? The first hints came from the observation of synapses within the antenniform leg nerves (FOELIX 1975). The presence of synapses in peripheral nerves was rather surprising, since synaptic contacts in arthropod nervous systems are generally restricted to ganglia, i.e. to the CNS. A closer look revealed that these synapses were almost exclusively restricted to the dendritic branches of the giant neuron and only few were seen on the soma or on the giant axon (figs 8, 9).

The fine structure of these peripheral synapses closely resembles synapses of other arthropods (FABIAN-FINE et al. 1999, 2000; FAHRENBACH 1979; FOELIX 1985; TOLBERT & HILDEBRAND 1981). Basically, there are many synaptic vesicles clustered around a presynaptic density ("bar"). In whip spider synapses, however, several presynaptic bars lie parallel to each other, resulting in rather large synaptic contacts. The synaptic vesicles are usually large (62 nm diameter) and round, but flattened synaptic vesicles were also observed. Whether the shape of the synaptic vesicles is correlated with excitatory or inhibitory synapses, as is often claimed, needs to be determined. In peripheral synapses of spiders at least four different vesicle populations have been demonstrated; larger synaptic vesicles apparently contain L-glutamate as a neurotransmitter, whereas smaller synaptic vesicles seem to be filled with g-aminobutyric acid (GABA) (FABIAN-FINE et al. 2000). Unfortunately, similar immunocytochemical labeling studies have not been done on whip spider synapses.

What kind of connections do these peripheral synapses represent? Most likely the presynaptic input onto the giant neuron stems from sensory hairs. Whether this input is provided by mechanoreceptive or chemoreceptive sensilla (or both?) cannot be decided from electron micrographs. It was argued however, that mechanoreceptors would be the most likely candidates, since synaptic contacts on giant fibers were also observed on proximal tarsal levels, where bristles are the only sensory hairs present (BECK et al. 1977). This hypothesis was fully confirmed, when IGELMUND & WENDLER (1991a, b) stimulated single tarsal bristles mechanically and thereby elicited action potentials in the giant fibers. Furthermore, they demonstrated convincingly that most of the synaptic input (90%) actually occurred along the giant axons. Although the density of synapses is very high on the short dendrite of the giant neuron, the absolute number of synapses is higher on the long giant axon. This means that the first "wiring diagram" of the whip spider's giant interneuron (FOELIX & TROYER 1980) needs to be modified by adding many more synaptic contact points, mainly to the giant axon and to a lesser extent to the soma (fig. 10). One interesting feature remains unchanged, however: the sensory axons apparently do not terminate on the giant neurons after making synaptic contacts, but continue as individual nerve fibers into the CNS. This means that despite a convergence of numerous afferent nerve fibers onto a few giant neurons there is no reduction in the actual number of axons within the sensory nerves of the antenniform legs.

The electrophysiological recordings yielded further interesting results: 1) each giant neuron covers a certain receptive field, and 2) the receptive fields of neighboring giant neurons overlap (IGELMUND & WENDLER 1991b). For instance, in *Heterophrynus elaphus* giant neuron 1 receives mechanoreceptive input from all 750 bristles on annuli 1-40, while giant neuron 2 covers the 1500 bristles on annuli 10-74. There is thus an overlap between annuli 10 to 40. Consequently, bristles standing between segments 10 and 40 trigger action potentials in both giant axons.

For giant neuron 1 maximal mechanosensitivity was observed distally (at the tarsal tip) and less on the proximal side, for giant neuron 2 the mechanosensitiv-

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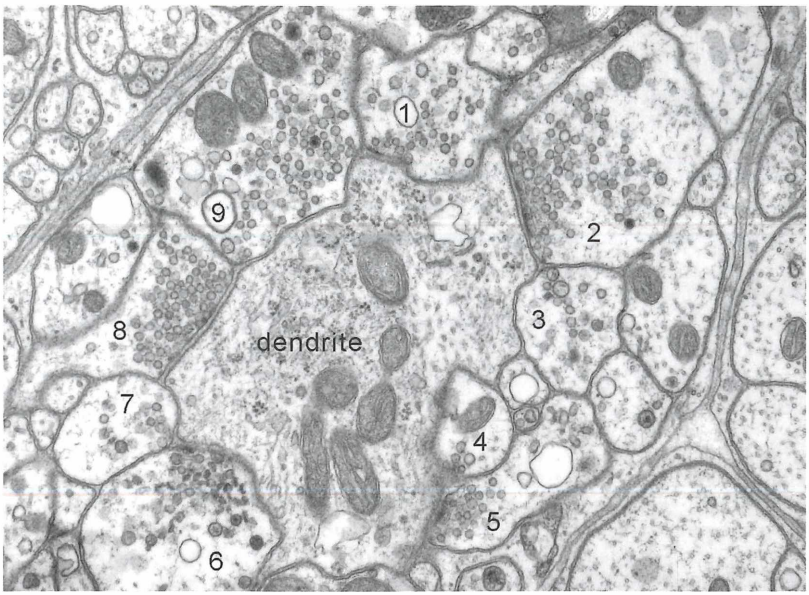

Figure 8. The dendrite of the giant neuron shown here is densely covered with synapses (1-9) originating from the mechanoreceptive bristles. Note that most synapses contain spherical vesicles, whereas some contain flattened ones (Nr. 6), 30,000x.

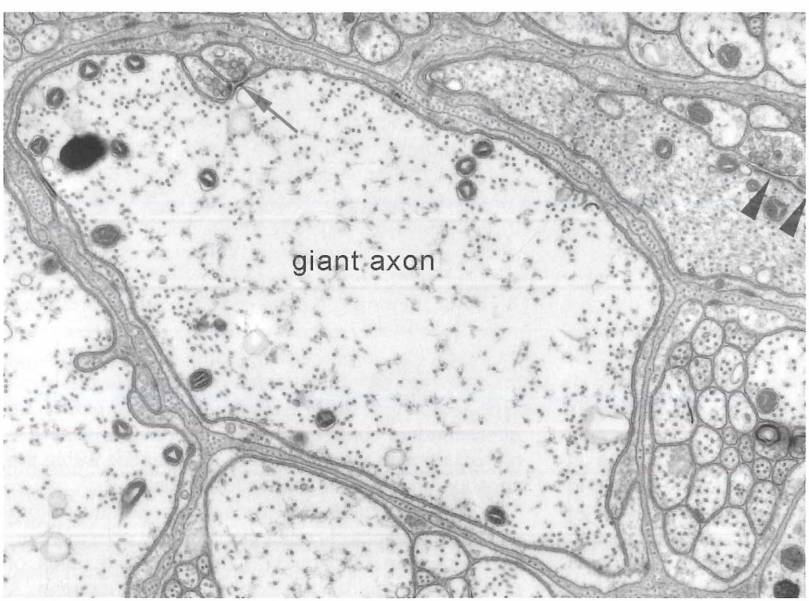

Figure 9. Giant axon in a sensory nerve of the tibia. Small synaptic terminals are seen at the upper left (arrow) and also on a smaller fiber at the upper right (arrow heads), 22,000x.

ity was opposite, i.e. more pronounced proximally. Other giant interneurons that were investigated were also mechanoreceptive (e.g. responding to bending of the tarsus), but some may react to chemicals.

Physiologically, the diameter of nerve fibers is directly correlated with the velocity of conduction, i.e. small axons are rather "slow", whereas impulse transmission in large axons is "fast". Since most of the sensory fibers in the antenniform legs of whip spiders are very small (0.1 - 0.2 µm in diameter), one would expect fast impulse conduction only in the giant fibers. Using electrophysiological methods, conduction velocities of 5-6 m/s were measured in the tarsal giant fibers of *Heterophrynus elaphus* (figs 11, 12; IGELMUND & WENDLER 1991a). These values are quite comparable to those found in giant fiber systems of other invertebrates (e.g. insects, crustaceans or earthworms) or even to those in myelinated nerve fibers of verte-

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Plate 1. a) The tropical rain forest is the main habitat of whip spiders. The best way to get there is by boat, as seen here on a side branch of the Rio Negro near Manaus; b) Large trees are a prerequisite for the occurrence of whip spiders. At night whip spiders sit on the lower trunks, about 1-2 m above ground, and during the day they hide in small crevices between the roots.

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brates. FOELIX & TROYER (1980) measured the reaction time of the antenniform legs of whip spiders after mechanical and chemical stimulation of the tarsal tip. In high speed film analyses they observed leg withdrawal responses 120 ms after mechanical (touch) and 160 ms after chemical stimulation (chloroform vapor). They calculated that the corresponding nerve conduction speed had to be around 1 m/s, a value that presumably could only be accounted for by transmission of the impulses in the giant fibers. The conclusions rendered were that the giant fibers would act as a fast pathway from the periphery to the distant CNS (fig. 12), and that mechanical stimuli in particular would be transmitted rapidly to elicit a motor reaction (withdrawal of the antenniform leg).

Although this model seemed quite attractive, it was not corroborated by electrophysiological studies; no motor reactions were observed in response to giant fiber activity (IGELMUND & WENDLER 1991b). Thus, avoidance reflexes are apparently independent of the giant fibers, being perhaps transmitted by smaller nerve fibers. If so, then the question remains, what are the giant fibers actually good for? In insects it is certain that giant fibers are directly involved in escape responses, but in insects the entire system is fundamentally different (motor fibers within the CNS of insects, sensory fibers in peripheral nerves of whip spiders). A rapid escape response can indeed be triggered in whip spiders, but only by stimulating the walking legs and not the antenniform legs (IGELMUND & WENDLER 1991b).

What other functions could the giant fiber system serve in whip spiders? It is tempting to think of prey capture (see below). Yet although the attacks of these animals are often very precipitous, it is baffling that there is usually a distinct delay between the last contact with the prey and the execution of the actual grasping response. Still, there may be times, such as seizing a moth straight from the air, when the giant fibers do come into play. Another possibility would be during mating and fighting (WEYGOLDT 1977, 1997/98). Courtship involves much mutual touching with the antenniform legs and so does fighting between males. In both cases there is a rapid exchange of signals during which a fast conducting system via giant fibers would be of advantage. Nevertheless, at this stage we have to concede that the specific purpose of the giant fibers of whip spiders has still to be elucidated.

What makes whip spiders special is that their giant fiber system lies outside the CNS, i.e. in the peripheral nervous system. This is in contrast to giant fibers in all other invertebrates. In cockroaches, for instance, cercal sensory hairs activate giant interneurons in the last abdominal ganglion, which in turn transmits the excitation to leg motoneurons in the thoracic ganglia (WESTIN et al. 1977, RITZMANN & CAMHI 1978). Thus all these giant fibers are efferent and perform motor functions, whereas the whip spider's giant fibers are afferent and transmit sensory input. Furthermore, the system is highly sensitive: even stimulation of a single bristle produces impulses in the giant fiber (IGELMUND & WENDLER 1991b). In comparison, a considerable summation from multiple receptors is necessary for the excitation of giant fibers in cockroaches, crickets or crayfish (CALLEC et al. 1971, PALKA & OLBERG 1977, ZUCKER 1972).

5. Sensory processing

The importance of sensory input in whip spiders is apparent in several of their behaviors. Prey capture, courtship, orientation and territoriality depend on highly processed sensory information. A first nervous

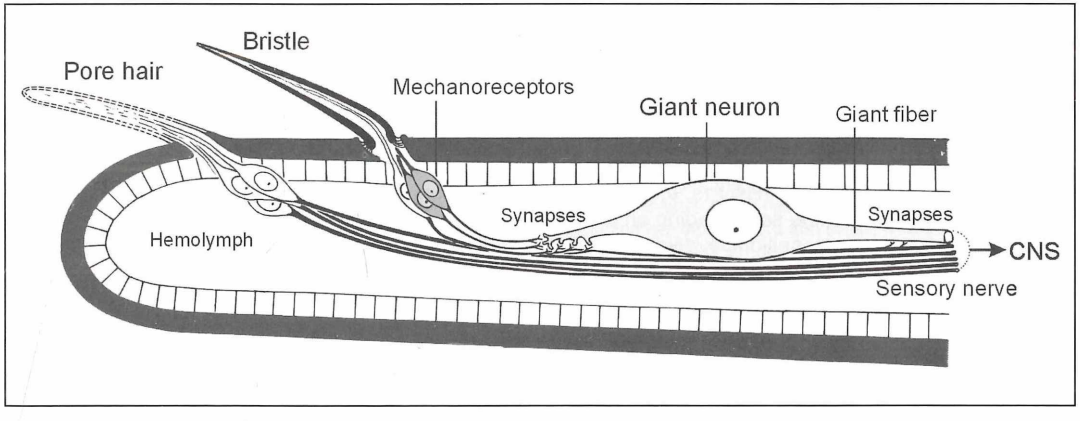

Figure 10. "Wiring diagram" of a peripheral giant interneuron in the antenniform legs of whip spiders. The mechanoreceptive sensory cells lying near the bristle base make synapses with the dendrite and the axon of the giant neuron. The giant fibers have a high conduction velocity and probably provide a fast pathway to the central nervous system (CNS). Modified after FOELIX & TROYER 1980.

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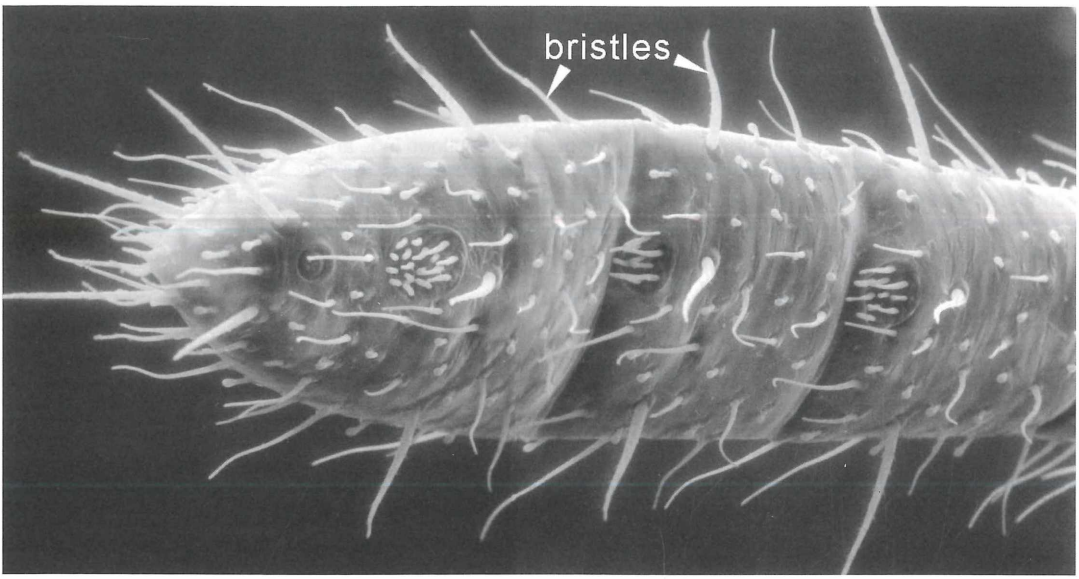

Figure 11. The large bristles on the antenniform legs are the only socketed hairs and they are the only external mechanoreceptors present. Movement of these bristles elicits action potentials in the giant fibers of the tarsal nerves. This SEM picture shows the three distalmost tarsal segments. 150x. Photo: GÖDEKE & KAISER.

integration may happen already in the periphery, as is indicated by the wide spread occurrence of peripheral synapses. Further processing takes place in extensively developed areas of the CNS, the "corpora pedunculata"; so far only preliminary studies have been done on these structures (GÖDEKE & KAISER 1975).

Courtship and mating have been described extensively for many species of whip spiders (WEYGOLDT 2000) and therefore will not be covered here.

5.1 Prey capture

Whip spiders can be seen exiting their diurnal retreats (crevices, holes at the bases of a trees, etc.) just as the sun begins to go down. They remain at the entrance of their retreat until darkness falls, at which point they venture out either onto the horizontal ground above their hole or onto the vertical surface of their tree (BECK & GÖRKE 1974; HEBETS, unpubl.). In the field, whip spiders can be seen feeding on crickets, katydids, cockroaches, opilionids, spiders, millipedes, and moths. In the laboratory they have been known to feed on conspecifics, but to our knowledge this does not happen under natural conditions. In the field they mainly sit and wait for prey, slowly exploring their immediate environment with their long antenniform legs. When they sense a potential prey, these legs become extremely active. If the tips of the legs come in contact with the prey, they are immediately withdrawn and the whip spider slowly approaches the prey. Once within reach, the animal suddenly opens its spined pedipalps, lunges forward and stabs the victim, pulling it in with both pedipalps. The rather small chelicerae are pushed into the prey which is then slowly mascerated. Since whip spiders possess no venom glands, a prey item may often remain alive during much of the initial feeding period and sometimes will even escape while the whip spider attempts to reorient it.

Whip spiders are such quick predators that they can even capture moths out of the air. The vibrating wings of moths can be registered over a distance of 60 cm! The trichobothria on the walking legs most likely act as the vibration receptors. If the trichobothria are removed on all legs, a fluttering insect is only perceived if it is less than 20 cm away. At such close range the prey can be captured successfully, provided that at least one antenniform leg is still intact. If both antenniform legs are lacking, prey capture is severely handicapped or impossible, even though the wing beat is sensed by the trichobothria on the walking legs (WEYGOLDT 1972, BECK & GÖRKE 1974).

5.2 Movement patterns and orientation

When whip spiders leave their crevices at dusk, they tend to move very slowly and cautiously and will retreat back in at the slightest perturbation. They typically remain near their retreat entrance until the sun has set completely. Initially, whip spiders remain stationary, exploring their environment with their antenni-

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Figure 12. Recording simultaneously from two different sites (E1, E2, 30 mm apart) along the tarsus yielded a shift of 5 ms between matching nerve impulses (arrow). This corresponds to a conduction speed of 6 m/s. Courtesy of Dr. P. IGELMUND.

form legs until they decide to move. Once in motion, whip spiders move with purpose; they move rather quickly and in spurts of up to 30 cm at a time. Although they are known to wander great distances (>30 m), many species are quite loyal to their retreats (BECK & GÖRKE 1974).

When removed from their retreat but placed back onto the opposite side of the same tree, individuals easily find their way back to their retreat. When displaced from the tree altogether, they not only navigate back to their original tree, but even to their original crevice. This is certainly true for close ranges (up to 7 m), where the animals find back during the same night. If displaced for more than 10 m, it may take several days until the home tree has been located again. As one might expect, the antenniform legs play an important role in this navigation. Whip spiders in which both antenniform legs had been amputated, were no longer capable to find their way back (BECK & GÖRKE 1974).

Females are more likely than males to remain in the same crevice over a long period of time (HEBETS, unpubl.). The retreats are generally occupied by just one individual at a time, the only exceptions being cases where both a mature male and a mature female inhabit the same retreat for up to 2 weeks, suggesting some type of mate guarding behavior. Both males and females are capable of roaming tens of meters and preliminary results indicate that individuals have home ranges that encompass several different trees (HEBETS, unpubl.). Over three consecutive nights of observation, eleven different individuals were seen exiting and re-entering the same retreat. Individual movement patterns mapped onto the trees indicate that individuals are not using the same paths to exit or re-enter their retreats. Thus, simple trail following behavior cannot explain the movement patterns of whip spiders, suggesting that they have more complex navigational capabilities.

In summary, anyone who is lucky enough to study live whip spiders, either in tropical rain forests at night or under controlled conditions in the laboratory, cannot help being impressed by these exceptional creatures.

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