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SENSORY STRUCTURES ON THE ANTENNIFORM LEGS OF WHIP SPIDER *PHRYNICHUS PHIPSONI* (ARACHNIDA, AMBLYPYGI) FROM THE INDIAN STATE OF GOA: SCANNING ELECTRON MICROSCOPIC ELUCIDATION

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Sensory Structures on the Antenniform Legs of Whip Spider *Phrynichus phipsoni* (Arachnida, Amblypygi) from the Indian State of Goa: Scanning Electron Microscopic Elucidation. Borkar, M. R., D'Sa, V. Q., Sail, P. & Lizanne, M. — Amblypygi have a tropical and sub-tropical distribution and their first of the four pairs of legs, is modified as feelers. Their activity period and dark habitats render visual cues ineffective and they rely on non-visual sensory perception. There is agreement among researchers that the whip spiders invest in olfactory and tactile senses imparted by sensory structures concentrated on the tarsal segment of the first pair of long, well-articulated non-ambulatory legs that are constantly moved in all directions to sample the environment for detecting location of prey, as also for navigating. This is the first attempt to elucidate the sensory structures present on the antenniform legs of the whip spider, *Phrynichus phipsoni* (Pocock, 1894), collected from the state of Goa, India; using scanning electron microscope, and paves way for further research on sensory biology of this cryptic arachnid order. The examined specimen generally conforms to the diversity and morphology of sensory assemblage on the antenniform legs reported in other amblypygi species. Sensory structures elucidated include terminal trident tarsal claws, tarsal organ, bristles, porous sensilla, club sensilla, rod sensilla, slit sensilla, trichobothria, plate organ, pit organ and foliate leaf like hairs.

Key words: sensory structures, antenniform legs, whip spider, electron microscope.

Introduction

Whip spiders belong to Amblypygi, an order of cryptic arachnids distributed in tropics and subtropics occupying diverse microhabitats such as tree hollows, cave crevices and leaf litter; seeking refuge from harsh environment and potential predators. (Weygoldt, 2000).

Generally nocturnal, these flat-bodied predators are distinguished by their robust raptorial pedipalps and long whip like antenniform first pair of walking legs that have lost the ambulatory function. While their complex habitat and nocturnal habit offers little visual cue for navigation, homing, mate recognition and prey finding; the sensory assemblage on the tarsal segment of their whip like first pair of modified legs is replete with sensilla and structures that aid in chemo-sensory, mechano-sensory and hygro-sensory perception (Foelix, 1975; Beck et al., 1977; Santer & Hebets, 2011).

As of 2020, there are five extant families, 17 genera and over 210 species of Amblypygi that have been described globally (American Arachnology Society, 2023). India has eight Amblypygi species, of which five belong to family Charinidae and three belong to family Phrynichidae. Of these, four species belong to the genus *Sarax* and one species to genus *Charinus* under family Charinidae; whereas family Phrynichidae has a single genus *Phrynichus* with three species.

Since the current investigation involves whip spider genus *Phrynichus*, it is only pertinent to understand the current distribution of its species globally and in India. Thus far 17 valid species of *Phrynichus* (Karsch, 1879) have been reported across Asia, Arabian Peninsula and Africa, Seychelles Islands, Mauritius Island, Madagascar; higher species diversity being reported from the countries along African east coast like Somalia, Kenya and Tanzania (Miranda et al., 2018; Weygoldt, 1998). Yemen has the highest number of species reported in the Arabian Peninsula.

India has three phrynichid species namely *Phrynichus phipsoni* (Pocock, 1894), *P. nigrimanus* (C. L. Koch, 1847) and *P. andhraensis* (Bastawade, Rao, Maqsood Javed and Krishna, 2005).Thus far only a single species *P. phipsoni* has been reported from the Indian state of Goa (Borkar et al., 2006). The relatively low count of Amblypygi species in India despite its large spatial extent only reflects insufficient exploratory surveys, a view corroborated by Weygoldt (1998, 1999).

Of the many interesting research questions in amblypygid biology, their behavior concerning habitat selection, navigation and prey-finding is intriguing; but apart from some gross ethological observations, not much species-specific information is available on structural correlates of their sensory ability. While Gebhardt (1983) has contributed to our understanding of physiology of rudimentary vision in Amblypygi, sensory deprivation by ablating tarsal portion of antenniform legs have clearly implicated the whips in chemo-mechanical perception critical to navigation as well prey detection (Hebets, 2014 a, b).

In all probability, navigation, homing and prey finding behavior of amblypygi is aided by neural integration of multimodal sensory cues, a view also corroborated by Weigmann et al. (2016). However, investigations on neuroanatomy and sensory integration pathways of amblypygids are lacking.

Unlike true spiders, the first pair of legs in whip spiders is covered with thousands of mechanosensory, olfactory, and gustatory sensilla; conveying critical sensations through unique sensory pathways (Sinakevitch et al., 2021). Charting these sensory structures on the antenniform legs is a prerequisite to understanding neuroethology of amblypygi, and the present study elucidates these sensory structures in *Phrynichus phipsoni* from the state of Goa, using scanning electron microscopy. This is the first ever attempt at charting sensory assemblage of the whip of any Indian species of amblypygi.

Material and Methods

Individuals of *Phrynichus phipsoni* (Pocock, 1894) were collected from the Dharbandora taluka of the Indian state of Goa (15°23'6.34" N, 74° 7'8.53" E), and brought to the Biodiversity Research Cell of Carmel College for Women, Nuvem Goa. The collection was individually housed in ventilated plastic containers, measuring 10 cm × 15 cm, with dry leaf litter bedding and a wooden climb. The terrarium interiors were mist sprayed to maintain requisite hygro-thermal profile. The set-up was subject to natural photoperiod. Individuals were given a weekly feed of freshly collected live grasshoppers.

Procurement of sample for SEM

Adult live specimen was restrained and placed in the refrigerator at 2 °C for approximately thirty seconds to be mildly anesthetized. Surgical ablation of antenniform legs was performed when the specimen was significantly less responsive to touch. The cold anesthetized specimen was positioned on dissection board for ablation of the antenniform leg at the patella-tibia and tibia-tarsus joints. The surgically manipulated specimen was given adequate hydration and observed for recovery. The ablated tibia and tarsal segments were further cut into relatively shorter pieces, leaving the distal tip of the tarsal segment intact. All regions of the antenniform tibia and tarsus were processed following standard protocol, before being examined under scanning electron microscope (Models JEOL 5800LV and JSM-6360LV).

Results

In situ observations on morphology, morphometry, and movement of antenniform legs of *Phrynichus phipsoni* (Pocock, 1894)

Observations in field and captivity reveal that the whip spider activity in general is clearly guided by a diurnal rhythm. During the day, the individuals retreat to dark microhabitats and lay still without any movement, while the ambulatory appendages as well as the antenniform first pair is folded and held close to the body. The pedipalps are folded and held parallel to the ground with femur-patella-tibia (f-t) joint of each pedipalp projecting laterally. The horizontal distance between the two f-t joints measure the maximum width of any part of the body in resting position. The folding pattern of the antenniform legs in resting individual is archetypical (see fig. 1) across the order that gives it the name 'whip spiders'. Antenniform legs of *Phrynichus phipsoni* in this investigation were the longest of the prosomal appendages; each individual whip of the investigated specimen measured a total length of 17 cm. These non-ambulatory appendages were motile and rotated in different planes being constantly moved in front, back and sides as the individual resumed activity in its dark habitat. This extraordinary manoeuvrability is imparted by joints between femur-patella-tibia, tibia-tarsus and the inter-tarsal joints. The number of articles on the tibio-tarsal segments is species-specific and in the investigated specimen of *P. phipsoni* the count was found to be 31 tibial and 68 tarsal articles.

The entire sequence of prey detection, approach and capture occurred in a ritualized behavioural sequence that can be broadly divided into 1. Steering antenniform legs in the direction of prey without movement of body. 2. Orientation of the body in the direction of the prey and slow cautious inching towards the prey 3. Forward lunge and capture of prey with raptorial pedipalps.

During captive feeding it was observed that after introducing a live prey in the enclosure, the antenniform legs were raised and slowly moved in all directions and also over the substrate. The animal then oriented itself in the direction where the prey had settled

Fig. 1. Resting captive specimen of whip spider *Phrynichus phipsoni* (Pocock, 1894).
Note the whip like configuration, position, and length of the antenniform first pair of non-ambulatory leg. The various segments have been marked for reference: 1 — vertically raised femur; 2 — femur-patella-tibia joint; 3 — tibia; 4 — tibio-tarsal articulation; 5 — tarsus; 6 — distal tarsal tip.

and slowly crept towards it. If the prey moved in the meantime to another spot, the whip spider would reorient only after completing the first trail and repeating the movement of antenniform legs for fresh detection. Every time, there was a lag of a few minutes between the movement of the prey and the predator. The movement all along was slow with simultaneous manoeuvring of the whips. It seemed necessary that the whips touch the prey or the substrate where the prey had settled, after which the whip spider approached it within striking distance and then rushed forward to clasp the prey with its raptorial pedipalps, simultaneously retracting the antenniform legs away from the prey.

Sensory structures on the antenniform legs of *P. phipsoni* (Pocock, 1894) with special emphasis on tarsal portion

As stated in the previous section, the observations on *P. phipsoni* activity clearly indicate the significant role of antenniform legs in sensory perception of the environment. Further, that most of the activity happens in dark, the eyes may only be appreciative of sensing changes in light intensity but not image formation (Weygoldt, 2000).

Micro-morphological character of the antenniform legs of *P. phipsoni* revealed an assortment of sensory structures particularly located in the apical tarsal segments. Particu-

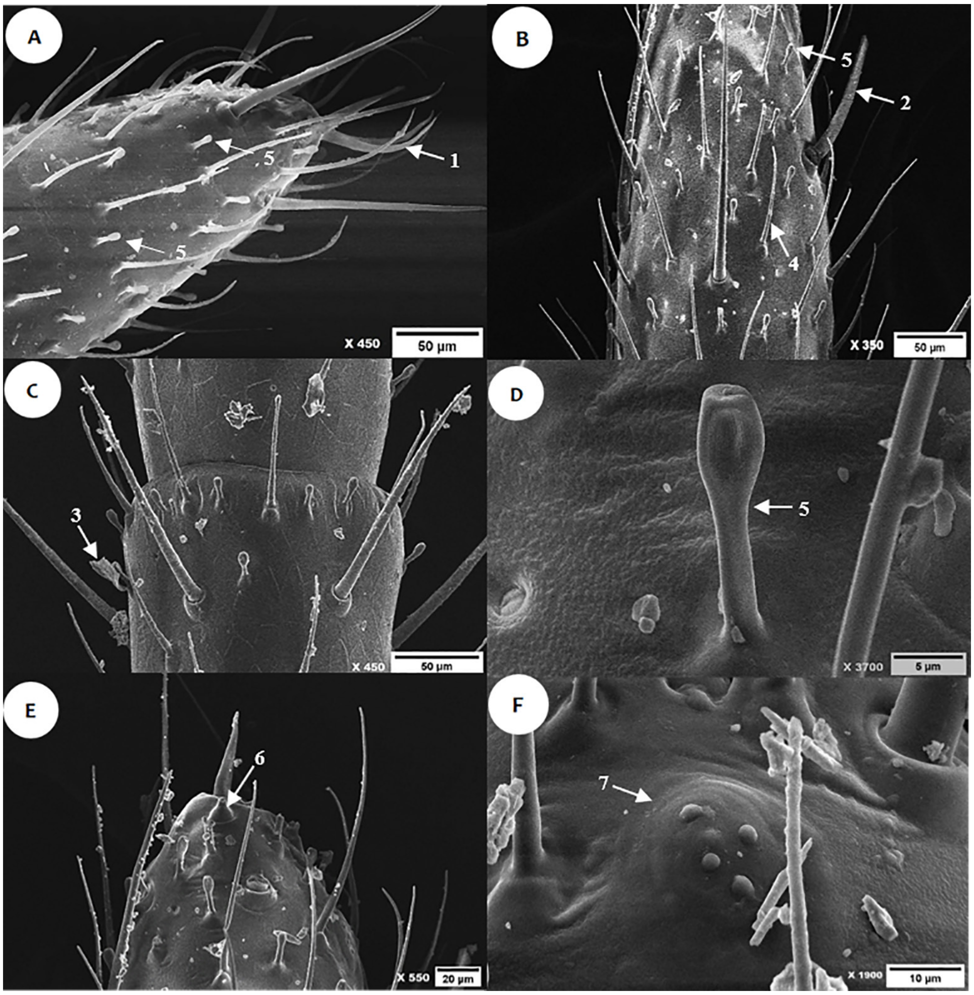

Fig. 2. Sensory assembly on the whip (Antenniform leg) of *Phrynichus phipsoni* from Goa, India: 1 — terminal tarsal claw; 2 — bristles; 3 — leaf like sensilla; 4 — pore sensilla; 5 — club sensilla; 6 — tarsal organ; 7 — pit organ.

larly, the whip tarsus was seen to be covered with a whorl of several longitudinal rows of bristles right up to the terminal tip, interspersed between which were shorter hair and club like structures, besides other sensory micro-sculpture.

The following distinctive structures were observed.

1. Terminal tarsal claws (fig. 2, A). This presented as a stunted apical protrusion of 3 claw like projections with a common base; middle being straight and shorter, and the two-lateral showing a curvature. Their maximum length from base to tip varied in the range of 70–75µm. The terminal location appeared strategic in sensory perception.
2. Bristles (fig. 2, B). These were among the most conspicuous, longest, thickest and abundant of the tibio-tarsal projections comprising of a proximal socket arising from which is a moveable serrated shaft. The bristles arise from the cuticle with which it is articulated in a girdled socket. Their distribution was not close set, and within each tarsal annulus the longer bristles were distally placed, their length varying in the range of 74–88 µm.
3. Leaf-like sensilla (fig. 2, C). These were relatively sparse and irregularly spaced within the bristle rows. Much smaller (ranging between 30–35 µm length) than a regular bristle sensilla, in construct they were similar to bristles in having an articulated base lodged in the cuticle, but differed with respect to the foliate shape of their shaft which is flattened like a blade whose tip tapered into an angular point. The flattened, blade like shaft was seen to be stiffly articulated into the cuticular socket.
4. Pore sensilla (fig. 2, B). These were found between rows of bristles at the distal podomeres of the antenniform tarsus and differed from the bristles in two respects i. e. their size is smaller, and variable length from 55 to 78 µm and filiform shape. Unlike the bristles, the pore sensilla were not socketed in the cuticle.
5. Club sensilla (fig. 2, A, B, D). Unmistakable by their characteristic appearance that gives them the name, these socketed sensilla have a short shaft that terminates into a swollen tip. Their lengths ranged between 15 to 23 µm. They were frequently encountered on the distal podomeres of the tarsus.
6. Tarsal organ (fig. 2, E). A discrete knob like structure with apical region showing presence of papillae, this structure was positioned beneath the terminal tarsal claw.
7. Pit organ (fig. 2, F). In the examined specimen, this sensory structure resembled a small eye shaped pit (30 µm long and 12 µm wide) with thickened cuticular ridges and was located on the S1 tarsal annulus. A few protuberances could be seen inside the pit, presumably with the raised pore openings.
8. Rod sensilla. These were closely set clusters of long (70–100 µm) and short sensilla (21–25 µm) that sat in a narrow longitudinal groove measuring 340 x 88 µm (L x W) on the dorsal surface of the apical tarsal segment in the examined specimen (fig. 3, G). Additionally small clusters of a few short rod sensilla were also seen on the dorsal edge of the lower tarsal podomeres (fig. 3, H).
9. Plate organ (fig. 3, I, J). This structure occurred as a distinct oval depression measuring about 80 µm long on the proximal end of the S8 tarsal article of the antenniform leg. Lying centrally in the depression along its floor was seen a single elongate projection.
10. Slit sensilla (fig. 3, K). A single slit with raised borders, measuring 57 µm was present parallel to the length of the antenniform leg on the lower tarsal podomere. Its location close to the inter-annular junction. Also, the annulus bearing this slit sensillum did not show any other sensory structures except for a few bristles.
11. Trichobothria (fig. 3, L). These filiform fine hair sensilla measuring about 280–320 µm were among the longest sensory structures and occurred on the tibial segments

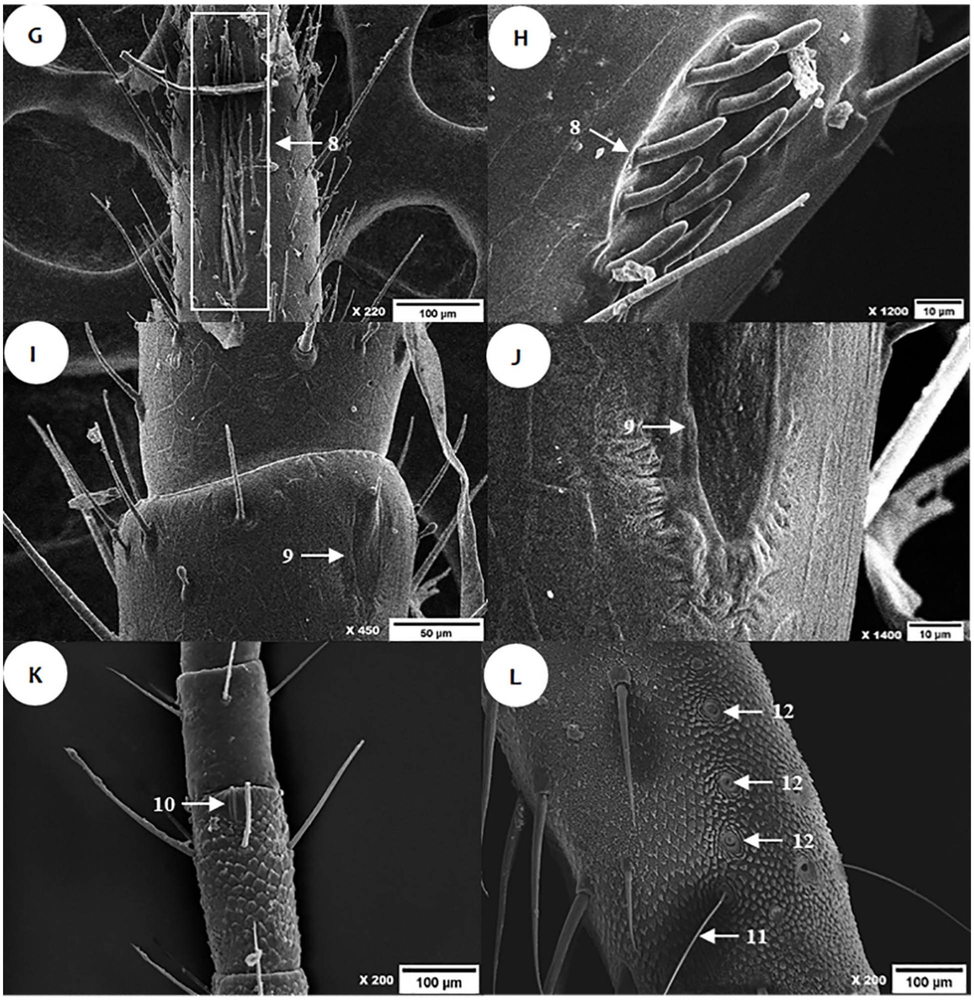

Fig. 3. Sensory assembly on the whip (Antenniform leg) of *Phrynichus phipsoni* from Goa, India: 8 — rod sensilla within groove, 9 — plate organ, 10 — slit sensilla, 11 — trichobothria, 12 — sockets of trichobothria

of the antenniform legs; but conspicuously absent on the tarsal segment. They abounded on the ambulatory appendages, but the one on the antenniform legs were seen to be shorter. The base of the shaft was lodged in a deep cup shaped socket surrounded by a rosette of cuticular scales that were arranged in concentric whorls and differed from the archetypical triangular scales on the general surface. Inter-trichobothrial distance in a row varied from 75 to 100 µm.

Discussion

Much of the work on this enigmatic arachnid order of Amblypygi is hitherto focused on their species diversity, and a few classical works have addressed their behavior *in situ* and captivity. Of the most intriguing among the many behavioural attributes of this cryptic arachnid; is their ability to assess the habitat, navigate and detect conspecifics and prey, in spite of being visually compromised (Beck & Gorke, 1974; Peretti, 2002; Hebets et al., 2014 a; Bingman et al, 2017; Wiegmann et al., 2019). Recent field experiments implicate sensory inputs from the antenniform legs in amblypygid navigation, and confirm that visual cues alone are insufficient for navigation and homing of whip spiders (Wiegmann et al., 2016). The quintessential whip like non-ambulatory first pair of antenniform legs is the functional analogue of 'blind man's stick' in whip spiders across the species diversity. Yet, a few species of amblypygi have been investigated for the sensory investments of these antenniform appendages.

In the present investigation, prey detection behaviour in captivity has been observed with special reference to use and orientation of antenniform legs in *Phrynichus phipsoni*, to ascertain importance of these appendages in prey detection and capture. From the recorded observations of several trials following introduction of prey in the captive arena, it is clear that the whip spider that initially has its whips folded, raises and opens them wide. It remains stationary though the movement of whips gets progressively rotatory and intense, both in air as also touching the substratum as if to sample olfactory cues. The ritualized sequence of antenniform leg activity documented in *P. phipsoni* is similar to that documented in other species of amblypygi (Santer & Hebets, 2009; Seiter et al., 2019). The flexibility of the tarsal portion of the whip despite absence of musculature is attributed to changes in hemolymph pressure there within (Foelix et al., 1975).

The morphology and morphometry of the antenniform leg is valuable information in species typing, for instance the respective tibial and tarsal article numbers of 31 and 68 in the investigated specimen tallies with the count prescribed for the *Phrynichus phipsoni* species (Weygoldt, 2000)**.** The impressive extension and rotator ability of the whips does not require of the individual to move the whole body.

The eyes of amblypygi may sense light intensity flux but unlikely to form image (Weygoldt, 2000; Lehmann et al., 2018), as such they rely on non-visual perception of the environmental variables including substratum characteristic, mates and prey by investing in chemo-mechanoreceptors and olfactory sensilla concentrated on the distal articles of the antenniform legs, that continually 'palpate' the surroundings. The role of olfactory cues in navigation (Bingman et al., 2017) and the significance of visual inputs for shelter recognition have been recently recognized (Flanigan et al., 2021).

Sensory structures on the antenniform leg of *Phrynichus phipsoni* (Pocock, 1894) have been studied using scanning electron microscopy. In all, 11 discrete sensory structures were elucidated, measured and described. Their basic structure corroborates well with previous reports in other species. Thus, the variety is constant across the species but positions and fine morphology is variable and species-specific.

Sinakevitch et al. (2021) have thrown light on the neural circuitry of these sensory structures on the antenniform legs of whip spiders, though not many amblypygi species have been investigated from this perspective. The dorso-ventrally compact body and laterigrade legs of whip spider allows it to creep into crevices and fissures, as also seek shelter under tree bark (Weygoldt, 2000). Their nocturnal foraging habits and site fidelity has been well documented (Weygoldt, 2000; Hebets et al., 2014 a, Bingman et al., 2017).

All the sensory structures listed for amblypygids by Weygoldt (2000) have been identified and described in our present study. However, in absence of transmission electron microscopy (TEM) studies, their neural investments could not be ascertained, as such the functions assigned are based on established structural corroborations. Barring the trichobothria which were located on the tibia of the antenniform legs, rest of the sensilla were present on the distal tarsal podomeres. The terminal tarsal podomere particularly has as many as 7 sensory structures, such concentration being strategic as arthropods generally have the tips of their legs bearing structures for interaction with substratum (Wolff et al., 2013).

The distally located tarsal claw is a strategic contact chemoreceptor (Foelix et al., 1975; Foelix & Hebets, 2001) and is reasoned to be a vestigial apotele of the tarsus. Similar triad of claws have been reported from the pre-tarsus of spiders (Wolff et al., 2013). Bristles abound all over the cuticle of the terminal segments of the antenniform legs, particularly the tarsal article; and are arranged in several rows forming a whorl around the antenniform leg when seen in axial view. Their arrangement and morphology in *P. phipsoni* matched with the description given by Weygoldt (2000). The micro-morphology is commensurate with previous descriptions in other species (Beck et al., 1977; Igelmund, 1987). The leaf-like sensilla or the 'foliate bristles' were sparse and distinguished by their flat blade-like shaft (Igelmund, 1987). Such a design is somewhat nonconforming for a typical air flow sensors that the bristles are, and their strategic location at the tibia-tarsal joint has led to the speculation that these structures could be aiding in generation of action potential for kinaesthetic responses from the lyriform organ (Igelmund, 1987). The pore sensilla could be easily differentiated from the bristles from the differences in length and lack of cuticular sockets. There is evidence that these could be olfactory in function and operate similar to the ones on antennae of insects (Hebets & Chapman, 2000). The quintessential club sensilla are the smallest of the sensory projections distributed on the tarsal annuli, and have been implicated in dual sensory perception. Likelihood of their sensitivity to humidity was suggested by Altner & Loftus (1985) and later their olfactory role was proposed by Weygoldt (2000). The rod sensilla have a close-set arrangement unlike any other and are either located in a groove or on the proximal edge of lower tarsal segments. Similar arrangement has been reported from *P. marginemaculatus* (Spence & Hebets, 2006). This is one structure whose exact function has not been clear, but in the classical SEM-TEM correlative investigation of antenniform legs of *Admetus pumilio* (Foelix et al., 1975) the innervations did not commensurate with olfactory purpose. There have been no fresh attempts to address this gap, and the question is yet unanswered.

In our investigation of sensory structures on antenniform legs, we have come across a tarsal organ whose construct matches with that described in *Charinus asturius* (Segovia et al., 2020). Its functional significance in amblypygi remains unknown, though the fine morphology is suggestive of its receptivity to humidity, temperature and odours (Anton & Tichy, 1994; Talarico et al., 2005; Gainett et al., 2017). The pit and the plate organs on the whips of *P. phipsoni* are in structural conformity with those reported in a few other species. While the pit organ is implicated in hygro-thermal sensitivity as well as chemoreception (Ehn & Tichy, 1994), the strategic occurrence of the plate organ near the inter-segmental joint hints at its proprioceptive ability (Seyfarth, 1985; Barth, 2002). By virtue of its location at the inter-annular junction, the conspicuous slit organ is also assumed to be sensitive to bending of the tarsal segment and thereby could be a potential proprioceptor (Igelmund & Wendler, 1991). This further finds support in the observation that the slit sensilla respond to minute strains in the cuticular exoskeleton (Barth, 2012; Blickhan et al., 2021). Mechanical significance of different slit sensilla arrays in arachnids has been researched by Hößl et al. (2007).

The long filiform trichobothria are the longest elucidated sensory structures in this exercise, their fragile construct indicating a likely role in perception of air turbulence. Whip spider trichobothria by their ability to detect air movements may affect, critical behaviour such as locating a mobile prey, and triggering startle response following a sudden change in micro air currents around it (Beck & Gorke, 1974; Igelmund & Wendler, 1991). The antenniform leg of the *P. phipsoni* clearly is a sensory appendage of immense value with as many as 11 different sensory structures concentrated on it. Recently, Moore (2019) has upheld the view that integration of inputs from such multisensorial structures helps in refining behavioural responses as compared to a single sensory structure.

The diversity of these structures matches with that reported from other investigated amblypygi species as inferred from literature, however it would be interesting to delve into their neural investments using TEM approach to verify species specific neural nuances if any.

Conclusion

From observations on feeding trials in captivity and the SEM elucidation of the sensory structures on the antenniform leg of *Phrynichus phipsoni,* it is clear that this species like other amblypygi has an assortment of sensilla on its non-ambulatory whips, and further that the whips are indispensable for prey detection, as well as navigatory orientation. This is the first attempt to elucidate the micromorphology of sensory whip in any Indian species of Amblypygi.

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