STRUCTURE OF DORSAL SETAE IN THE TWO-SPOTTED SPIDER-MITE *TETRANYCHUS URTICAE* KOCH, 1836

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ABSTRACT

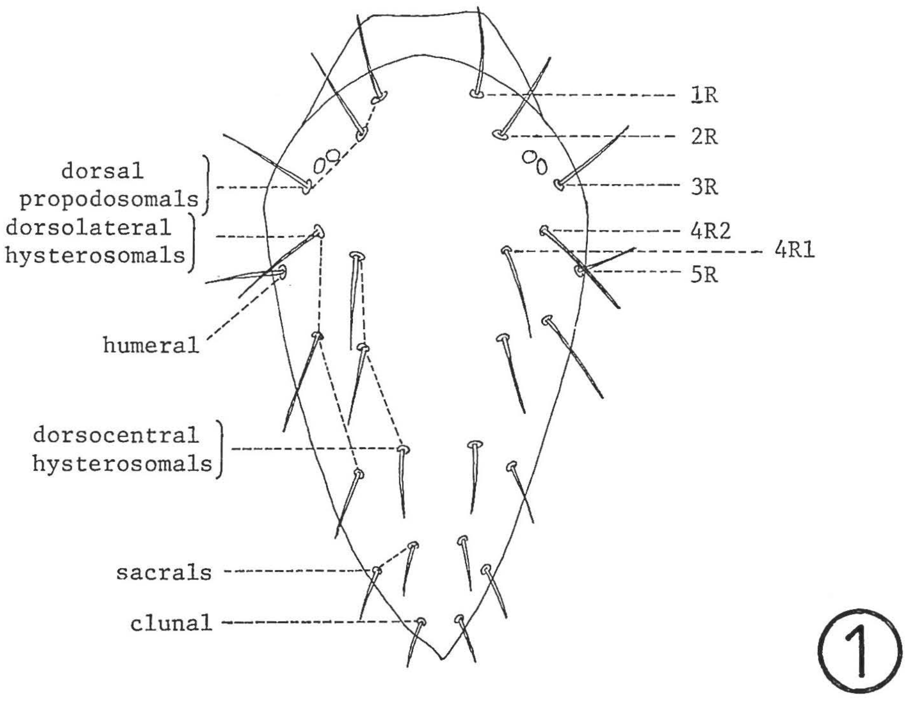
The dorsal propodosomal setae of *Tetranychus urticae* are of two types : pure mechanoreceptors, and dual chemo/mechanoreceptors. The mechanoreceptors are each innervated by two sensory cells, the dual receptors by three or four sensory cells. A seta of the second propodosomal row has two tormogen cells, one trichogen cell, and one sheath cell, located beneath the base of the hair. Its two sensory cell bodies are located in the excretory duct apparatus of the dorsal silk gland. These setae might aid the mite in controlling the spinning of webs, and may also be involved in regulating the mite's vision. The setal cilia of this species have an 8 + 0 pattern of microtubules.

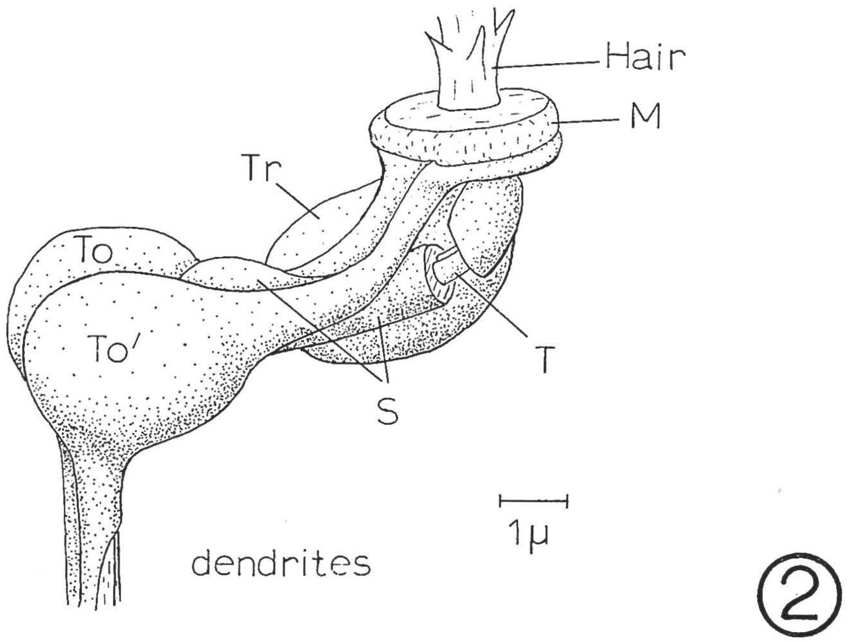
RÉSUMÉ

Les soies dorsales du propodosoma de *Tetranychus urticae* sont de deux types : mécanorécepteurs et chemo-mecanorécepteurs. Chaque mécanorécepteur est innervé par deux cellules sensorielles, chaque chemo-mecanorécepteur par trois ou quatre cellules sensorielles. Un poil de la deuxième rangée du propodosoma a deux cellules tormogènes, une cellule trichogène et une cellule enveloppe située au-dessous de la base du poil. Ses deux corps cellulaires sensoriels sont situés dans le système du conduit excréteur de la glande séricigène dorsale. Ses soies pourraient aider l'animal à controler le filage de la soie et peuvent peut-être jouer un rôle dans la régulation de la vision de l'animal. Le cil de la soie de cette espèce à une formule de microtubules égale à 8 + 0.

INTRODUCTION.

Only a few investigations into the structure of acarine sensilla have been reported. The papers of CLAPARÈDE (1869), HENKING (1882), SCHAUB (1888), and JONES (1950) discuss the " pseudostigmatic organs " — dorsal sensilla found on certain mites. NEWELL & VERCAMMEN-GRANDJEAN (1964) have described setae on the legs of *Pteridopus auditor*, which they believe mediate a sense of hearing. FOELIX & AXTELL (1971), FOELIX (1972), and FOELIX & CHU-WANG (1972) have reported a dual chemo- and mechano-receptive role for certain sensilla on the tarsi and palps of the tick *Amblyomma americanum* (L.). These sensilla are innervated by two mechanoreceptive dendrites and several chemo-receptive dendrites. The Haller's organ of *A. americanum* has also been investigated (FOELIX & AXTELL, 1972), and found to contain fourteen sensilla





FIGS. 1-2 : 1) Dorsum of an adult male *Tetranychus urticae*. At the left : the setal nomenclature of Pritchard & Baker (1955). At the right : the nomenclature used in the present study ; 2) Seta 2L : the accessory cells and the base of the hair, seen medially.

Abbreviations : M) articulating membrane ; S) sheath cell (inner enveloping cell) ; T) tubular body ; To, To′) tormogen cells (outer enveloping cells) ; Tr) trichogen cell.

of several types — all of them purely chemo-receptive. These authors report a gland lying beneath the Haller's organ, and a nerve fiber and a neurosecretory fiber penetrating the gland. McEnroe (1969), on the basis of light microscopy, has described a sensory neuron innervating a tactile setal hair on the dorsum of *Tetranychus urticae* Koch. Bostanian & Morrison (1973) have studied the setae of the legs of *T. urticae* by electron microscopy and have found three types of receptors : mechano-receptors, chemo-receptors, and receptors which function in both modes. The hair of the latter type of receptor is characterized by its numerous spicules, each of which has an apical pore. These authors state that the dorsal setae, which are also spiculated, have pores, but it is not clear whether these setae are otherwise similar to the spiculated tarsal setae.

Terminology.

Figure 1 depicts the dorsum of an adult male specimen of *T. urticae*. Its setae are identified on the left according to the terminology given by Pritchard & Baker (1955), and on the right by a quite different terminology that will be used here for reasons of simplicity. The general setal name will be of the form rS, where r is the row number, and S is the side of the mite, i.e., either L (left) or R (right).

Materials and methods.

Colonies of *Tetranychus urticae* Koch were grown in the laboratory on pinto bean plants under a 250-watt floodlight. These conditions kept the mites in their summer form.

Selected specimens were fixed in glutaraldehyde, post-fixed in osmium tetroxide, embedded in Epon-Araldite plastic, and serial thin sections were made. The sections were stained with lead citrate and examined with an electron microscope. All techniques were standard ones, and details are given elsewhere (Mills, 1973 a).

The setae of three adult male specimens were used in this study. Sections cut above and below the base of the hairs of setae 1R, 2R, 1L, 2L, 4L and 5L were examined in one specimen, setae 2L and 3L were studied in another, and the ciliary region of a palpal seta was examined in the third. The most extensive series of sections used were those of seta 2L — the same seta that was described in McEnroe's 1969 paper (W. D. McEnroe, personal communication).

Results.

Generalities.

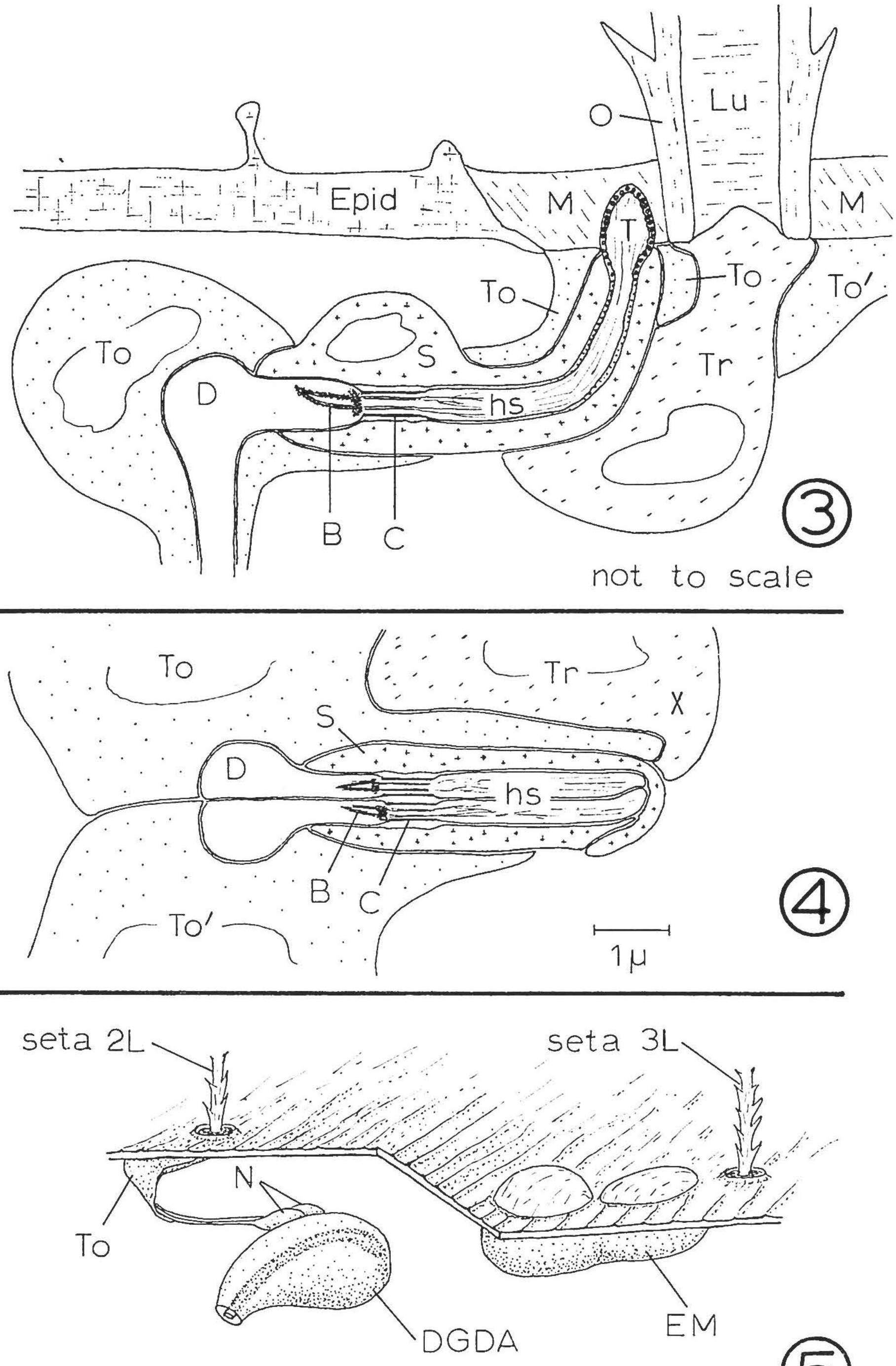
The setae of rows 1, 2, and 3 are each innervated by two sensory cells.

Too few photographs of setal rows 4 and 5 were obtained to afford a full reconstruction, but it appears that row 4 setae are innervated by four sensory cells, while those of row 5 are probably innervated by two.

A series of 19 sections from seta 2L yielded a reconstruction of most of the structure below the base of the hair. The remainder of this report refers to this seta, unless otherwise indicated.

Sensory cells.

Embedded in the articulating membrane which holds the hair there is an ovoidal chamber with two compartments : a so-called " tubular body " (Figs. 3 & 8). The chamber consists of a



FIGS. 3-5 : 3) Seta 2L : schematic view in vertical section ; 4) Seta 2L : schematic view in horizontal section ; 5) A region of the dorsal propodosomal integument.

Abbreviations : B) basal body ; C) cilium ; D) dendritic elbow ; DGDA) dorsal gland's duct apparatus ; EM) eye-manifold ; Epid) cuticular epidermis ; hs) horizontal segment of tubular body ; Lu) lumen of hair ; M) articulating membrane ; N) sensory cell bodies ; O) exo-cuticle of hair ; S) sheath cell (inner enveloping cell) ; T) tubular body ; To, To′) tormogen cells (outer enveloping cells) ; Tr) trichogen cell ; X) position of overlying hair.

thin electron-dense outer wall, on the inner surface of which is a single layer of 85 mμ granules. The interior space of the chamber is occupied by the distal ends of the two sensory dendrites of the seta. The membranes of these two dendrites, which lie close to the granules, define the two compartments of the chamber. In each of the compartments are several dozen microtubules. The two dendritic membranes meet along the vertical mid-plane of the chamber, forming there a double membrane. No granules are present between these membranes.

Proximally, the chamber becomes narrower, the granules smaller, and the membranes lie further from the granules. It descends at first almost vertically (Fig. 6), then turns to the horizontal, running anteriorly (Fig. 4). In the horizontal segment many of the microtubules fuse together, so that there are fewer of them visible in a cross section. The points of fusion are Y-shaped structures like those reported by SLIFER & SEKHON (1969) in insect sensilla.

About 2.5 μ from the vertical segment, the compartments of the tubular body terminate in a pair of cilia 0.25 μ in diameter (Fig. 3). The extra-cellular space around the cilia is filled with a homogeneous grey-staining substance (Fig. 9), and is continuous with the space containing the granules of the tubular body. This circa-ciliary space is bounded by an enveloping cell (the " sheath cell ") which is wrapped around the horizontal segment and most of the vertical segment of the tubular body.

The setal cilia of *T. urticae* have an 8 + 0 pattern of doublet microtubules (Figs. 7 & 9). Five different cilia in setae of rows 1 and 2, and two cilia of an unidentified palpal seta, all showed this pattern. Consistent ciliary 8-patterns, though quite rare in Nature, are not unheard-of (LEMBI & WALNE, 1971). Another acarine species, the tick *Amblyomma americanum* (L.), has been shown to possess an 11 + 0 pattern (FOELIX & AXTELL, 1971 & 1972) and thus, with *T. urticae*, belongs to a very small group of animal species that are known to deviate from the usual 9-pattern.

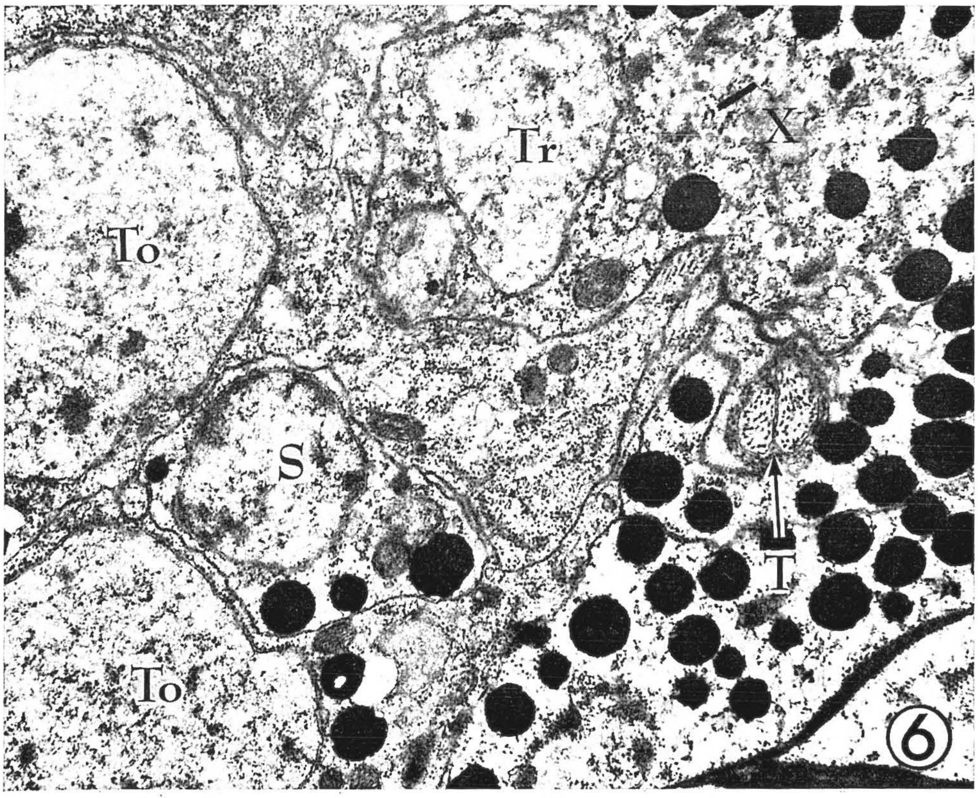
The cytoplasmic segments of the dendrites begin just proximal to the cilia ; here the circa-ciliary space narrows to become an ordinary inter-cellular space. The eight doublet microtubules pass out of each cilium and form a basal body by approaching each other to make a bundle (Fig. 7). It was not determined whether the basal body consists of eight triplet microtubules, as one would expect by analogy with the situation in other species. No rootlets were seen in the dendrites, but these could have been present in a set of missing sections. A number of vesicles occur near the basal bodies.

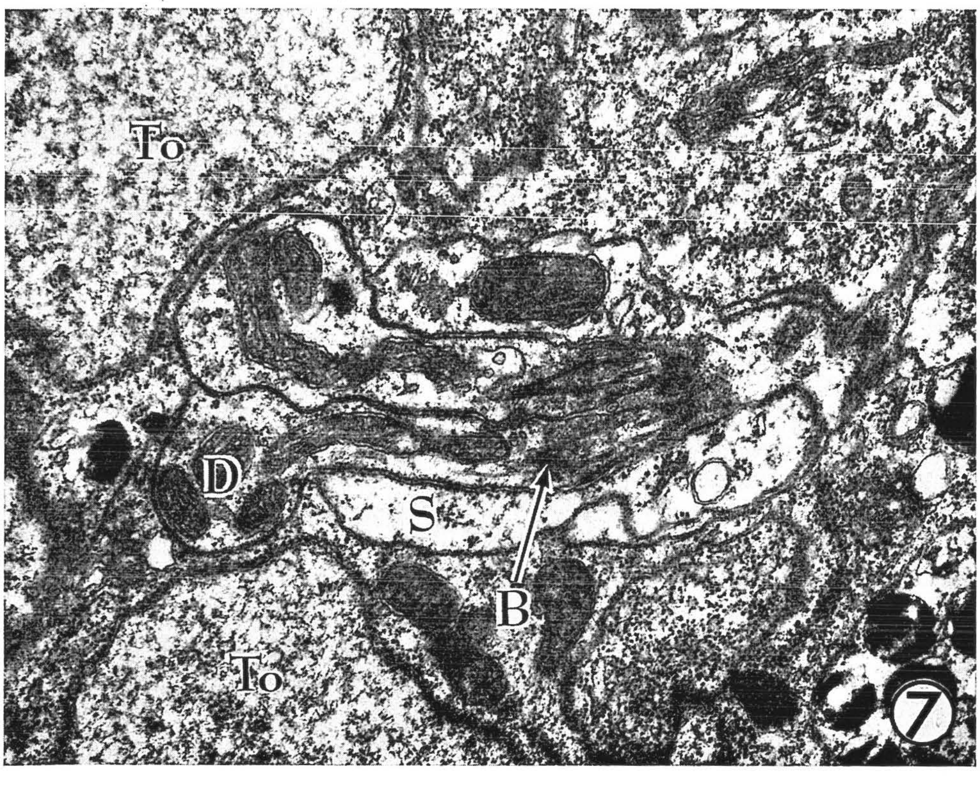
The dendrites continue to run horizontally and anteriorly for about 1.5 μ. They then widen and make a sharp turn downward, still closely apposed (Fig. 7). Proximal to these dendritic elbows, the dendrites narrow and continue downward, running along the posterior surface of the muscle DV2 (notation of BLAUVELT, 1945) for a short distance. They thenr un posteriorly for some 9 μ to meet their sensory cell bodies, which are located on the medial side of the excretory duct apparatus of the left dorsal silk gland, and seem to belong to that apparatus (Figs. 5 & 11). The morphology of the silk glands has been discussed alsewhere (MILLS, 1973 a & 1973 b). No attempt was made to follow the axons which these neurons presumably send to the brain.

Accessory cells.

Four cells, in addition to the two sensory cells, are associated with seta 2L (Figs. 2, 3, 4 & 6).

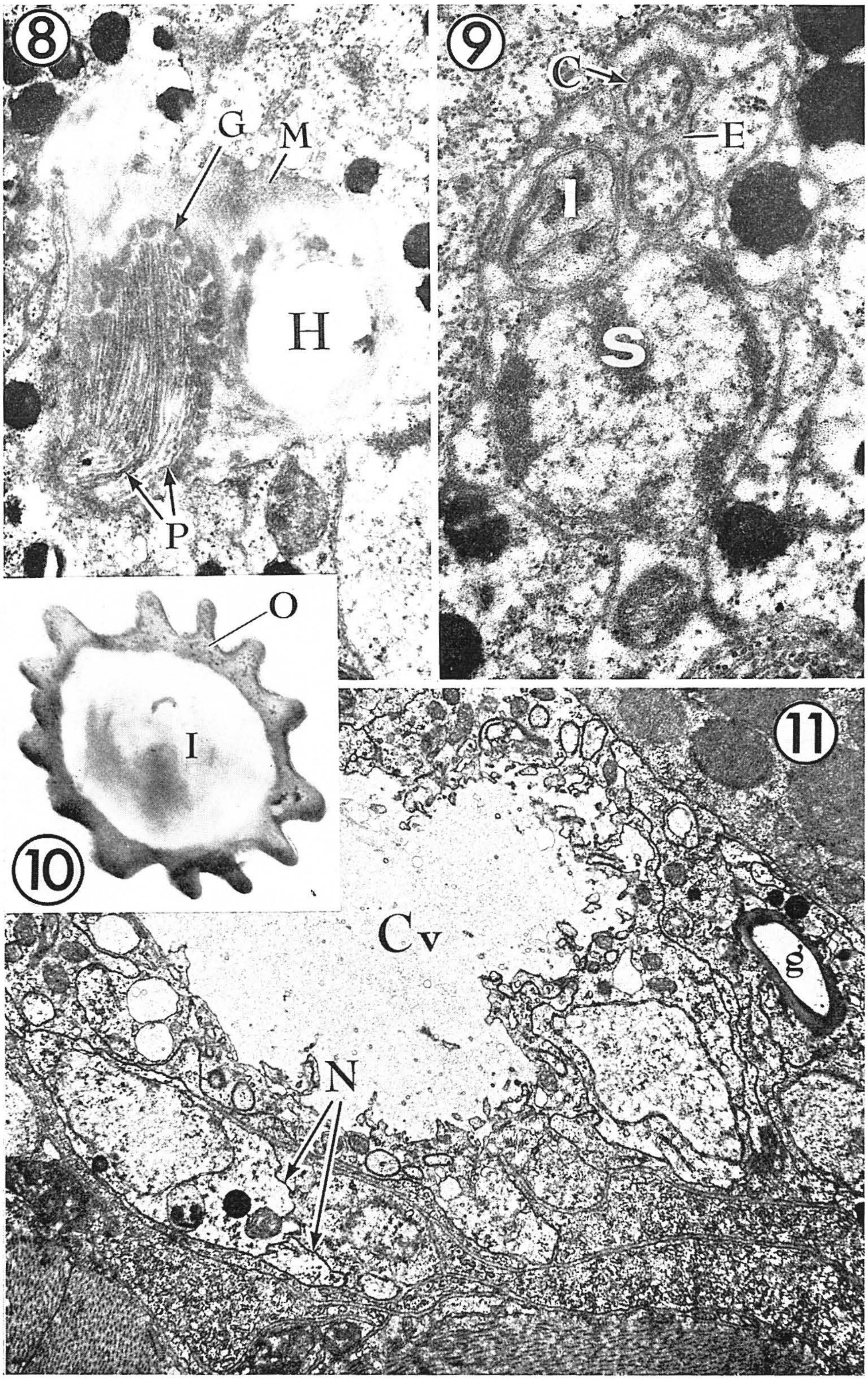
One of these is an inner enveloping cell, a small cell that ensheaths the sensory cells from the dendritic elbow to the point where the tubular body enters the articulating membrane (Figs. 3, 4 & 9). This cell will be referred to here as the " sheath cell " since it provides the sheath for all of the primary transducers of the sensillum.





FIGS. 6-7 : 6) Seta 2L : horizontal section, just below the articulating membrane. × 20600 ;
7) Seta 2L : horizontal section at the level of the cilia (i.e., ventral to figure 6). × 32000.

Abbreviations : B) basal body ; D) dendritic elbow ; S) sheath cell (inner enveloping cell) ; T) tubular body; To) tormogen cell (outer enveloping cell) ; Tr) trichogen cell ; X) position of overlying hair.



FIGS. 8-11 : 8) Seta 1L : horizontal section at the level of the articulating membrane, showing tubular body. × 29800 ; 9) Seta 2R : oblique section, almost perpendicular to the cilia. Note the inclusion (I), which is found in most or all hypodermal, neural, and tracheal cells of *T. urticae*. × 42000 ; 10) Seta 2R : cross section of the hair, not far above the level of the integument. The inhomogeneity of the lumen (I) is greatly exaggerated here by a deliberate overexposure of this part of the print. × 27000 ; 11) Seta 2L : cell bodies of the sensory cells, lying in the duct apparatus of the dorsal silk gland. × 13200.

Abbreviations : C) cilium ; Cv) central cavity of duct apparatus ; E) extra-cellular space ; g) duct of dorsal silk gland ; G) granule in tubular body ; H) hair -socket(hair is missing) ; I) (see legend of figure) ; M) articulating membrane ; N) sensory cell bodies ; O) exo-cuticle of seta ; P) cell wall of one dendrite ; S) sheath cell (inner enveloping cell).

A second and third cell are of one type and appear to be the producers of the articulating membrane of the hair (Figs. 2 & 4). Only one badly shattered section was available at the base of the hair, so this part of the reconstruction draws upon inferences from other setae. These cells will be tentatively identified as tormogen cells. Their nuclei lie on either side of the neurons' dendritic elbows ; proximal to this point these cells replace the sheath cell as the provider of a sheath for the dendrites. The tormogenic sheath follows the dendrites for many microns proximally, but does not completely surround the dendrites throughout this whole distance.

The remaining cell of seta 2L lies almost directly beneath the hair (Fig. 3) and appears to be the cell that gives rise to the hair itself. This cell would therefore be a trichogen cell.

Discussion.

The dorsal setae of the rows 1 and 2 are mechano-receptors and not chemo-receptors. That this is true of seta 2R is demonstrated by figure 10, which shows a cross section of the hair just above the level of its socket. The lumen of the hair is a nearly homogeneous electron-lucid material, entirely lacking in pores, channels, or dendritic processes. The dendrites of this seta terminate as a " tubular body " inside the articulating membrane at the hair-base and do not enter the setal lumen. The same situation occurs in the setae of row 1. The condition in setae of row 3 is similar, in that there are two dendrites which form a tubular body in the articulating membrane ; however there is a process of some kind — conceivably dendritic, though no corresponding dendrite was seen below the hair — which enters the setal lumen and runs at least a short distance up the shaft. This setal row is therefore mechano-receptive, and an additional chemo-receptive role cannot yet be ruled out. Seta 4L1 very likely has a dual role. As was stated above, it appears to be innervated by more than two dendrites. Two of these form a tubular body at the hair-base, and the setal lumen contains a process that probably represents the remaining one(s). The shaft of seta 4L2 was not seen, and so it is not known if chemo-receptive dendritic processes are located there. The setae of row 5 must be purely mechano-receptive because the setal lumen is homogeneous like those of rows 1 and 2.

That seta 2L's sensory cell bodies are located in the duct apparatus of the dorsal silk gland is a curious fact which suggests that these setal hairs may be part of the mite's web-spinning system. The sensory cells make close contact with cells of the duct apparatus ; only on their anterior-ventral surfaces are they separated from the other cells of the apparatus by a membrane thicker than an ordinary cell membrane (Fig. 11). Whether or not the sensory cells for setae of row 1 are similarly associated with the anterior silk glands was not determined by the present study. It has been reported (Mills, 1973 b) that the duct apparatuses of the dorsal and anterior silk glands of *T. urticae* contain a substance which might act as a plug for these glands' ducts. The plugs could be made to expand or contract — thereby covering or uncovering the ends of the ducts — upon the reception of an appropriate signal from the dorsal setae of rows 1 and 2. As W. D. McEnroe has pointed out (personal communication), these dorsal setae may function as transducers which measure the internal hydrostatic pressure of the propodosoma, their degree of erection being the relevant variable. If this is the case, then it is easy to see how this part of the mite's spinning system might operate. The flexing of certain muscles causes the hydrostatic pressure to increase, which in turn causes the dorsal setae to become more erect. The setal movement signals the duct apparatuses, which bring about a contraction of the plugging substance. With the ends of the ducts now open, the raised hydrostatic pressure forces the glandular product out of the glands into the ducts. To stop the spinning process, the mite simply relaxes the muscles which control internal hydrostatic pressure. This causes the setal hairs to fall. Signals from the setae trigger the expansion of the plugging substance, and the ends of the ducts become sealed. The plugging of these ducts may serve to protect the mite from an unwanted extrusion of glandular material into the ducts due to small or rapid fluctuations in hydrostatic pressure.

Another area in which the dorsal propodosomal setae may play a role is in the regulation of this mite's visual behavior. It is known from the work of McEnroe and Dronka (1969 & 1971) and of HUSSEY and PARR (1963), that the experimental photobehavior of female *T. urticae* depends upon the mite's physiological state. There are three such states, and one of the variables which determine these states is the mite's degree of dehydration. McEnroe has therefore suggested (personal communication) that the dorsal propodosomal setae, by acting as transducers for internal hydrostatic pressure, may be one of the determinants of a mite's physiological state, and therefore of the mite's visual mode.

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