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COMPARATIVE FINE STRUCTURE OF THE CLAW SENSILLA OF A SOFT TICK, *ARGAS (PERSICARGAS) ARBOREUS* KAISER, HOOGSTRAAL, AND KOHLS, AND A HARD TICK, *AMBLYOMMA AMERICANUM* (L.)

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ABSTRACT: The claw setae (at the distal end of the tarsus) of the first leg of the adult soft tick, *Argas (Persicargas) arboreus* Kaiser, Hoogstraal, and Kohls, and the adult hard tick, *Amblyomma americanum* (L.), were studied by scanning and transmission electron microscopy. Six pairs of setae in the soft tick and 3 pairs in the hard tick are symmetrically located at the lateral and the medial side of the claw. Three different types of sensilla are described. Type 1 sensillum, a blunt-tipped thick-walled seta, is innervated by 2 sets of dendrites: one set of 2 mechanoreceptive dendrites ending in the socket and another set of 4 to 5 chemoreceptive dendrites ascending into the shaft. Seven canal openings (140 Å) at the tip allow communication between the dendrites and the environment. Type 2 sensillum, a sharp-pointed thick-walled seta, also has 2 mechanoreceptive dendrites and 0 to 4 chemoreceptive dendrites in the shaft receiving chemical stimuli through a single subterminal slit opening (140 Å). Type 3 sensillum, a sharp-pointed seta, having only 2 dendrites at the base, is a typical mechanoreceptive sensillum. In the type 1 and 2 sensilla, 2 sets of dendrites are separately encircled by their own internal enveloping cell but share a common external enveloping cell. An extra middle enveloping cell only surrounds the internal enveloping cell of the chemoreceptive dendrites. This is apparently a unique feature of tick sensilla.

The first pair of legs of ticks are frequently waved in the air and serve a major role in the sensory perception of the animal. Recent investigations by scanning and transmission electron microscopy have revealed the fine structural details of the tarsal sensilla and Haller's organ of *Amblyomma americanum* (L.) (family Ixodidae, "hard ticks") and *Argas (Persicargas) arboreus* Kaiser, Hoogstraal, and Kohls (family Argasidae, "soft ticks") (Foelix and Axtell, 1971, 1972; Roshdy, Foelix, and Axtell, 1972; Axtell et al., in press). Similar sensilla types have been described on the palps (Foelix and Chu-Wang, 1972). From the morphology and permeability studies (Foelix, 1972) chemo- and mechanoreceptive functions can be ascribed to particular sensilla.

Additional setae arise from the tip of the tarsus and project distally in proximity to the claws. These "claw setae" were not included in previous investigations but due to their locations should also have a significant role in sensory perception. In *Ixodes persulcatus* P. Sch. and *Hyalomma asiaticum* P. Sch. and E. Schl., these setae were shown experimentally to be involved in the detection of repellents and were individually classified as chemo- or mechanoreceptors on the basis of shape and a gross electrophysiological response (Zolotarev and Elizarov, 1963, 1964; Zolotarev and Sinitsyna, 1965). No fine structure investigations using electron microscopy were conducted on those species, however.

We investigated the fine structure of the claw setae of *Argas arboreus* and *Amblyomma americanum* by means of scanning and transmission electron microscopy. Since these setae are innervated, it is appropriate to refer to them as sensilla. These results will contribute to a more complete basis for future behavioral and electrophysiological studies on the sensory perception of these representative species of ticks.

MATERIALS AND METHODS

Argas (Persicargas) arboreus were from a NAMRU-3 Medical Zoology colony originally collected from rookeries of *Bubulcus i. ibis* in the type locality of this tick species, near Cairo, and subsequently maintained on domestic pigeon hosts. The *Amblyomma americanum* were field-collected with a cloth drag in the vicinity of Jacksonville and Came Lejeune, North Carolina.

For scanning electron microscopy the ticks were

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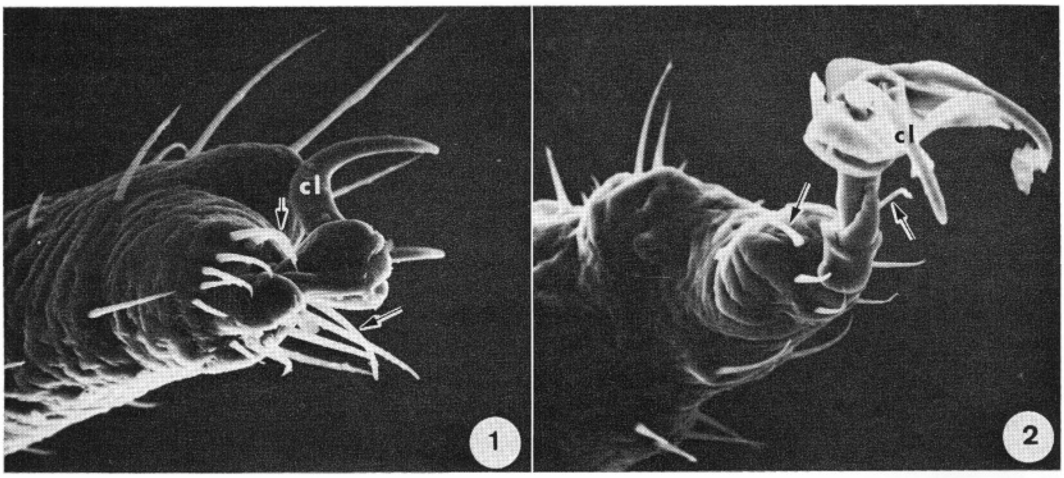


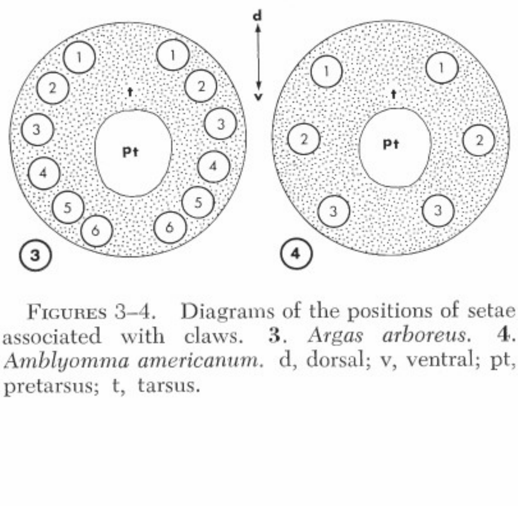
FIGURES 1–2. Scanning electron micrographs of the tarsus tip of the first leg. **1**. *Argas arboreus*, adult, medial-ventral view. × 210. **2**. *Amblyomma americanum*, adult, medial-frontal view. × 220. Arrows, first pair of claw setae; cl, claws.

killed in hot water, coated with gold-palladium in a vacuum evaporator, and examined in a JEOL JSM-2 stereoscan electron microscope.

For transmission electron microscopy, tarsi of the first legs were fixed in 5% glutaraldehyde buffered with sodium cacodylate (Sabatini et al., 1963), postfixed in 1% OsO_4 buffered with veronal acetate (Palade, 1952), and embedded in hard Epon 812 over propylene oxide after dehydration with ethanol. Thin sections were cut with a diamond knife on a Reichert Om U2 ultramicrotome, picked up with Formvar-coated slot grids, double-stained with uranyl acetate and lead citrate, and examined in a Siemens Elmiskop IA.

OBSERVATIONS

Several setae arise at the distal end of the first tarsus and encircle the base of the pretarsus. Since these are closer to the claw than



FIGURES 3–4. Diagrams of the positions of setae associated with claws. **3**. *Argas arboreus*. **4**. *Amblyomma americanum*. d, dorsal; v, ventral; pt, pretarsus; t, tarsus.

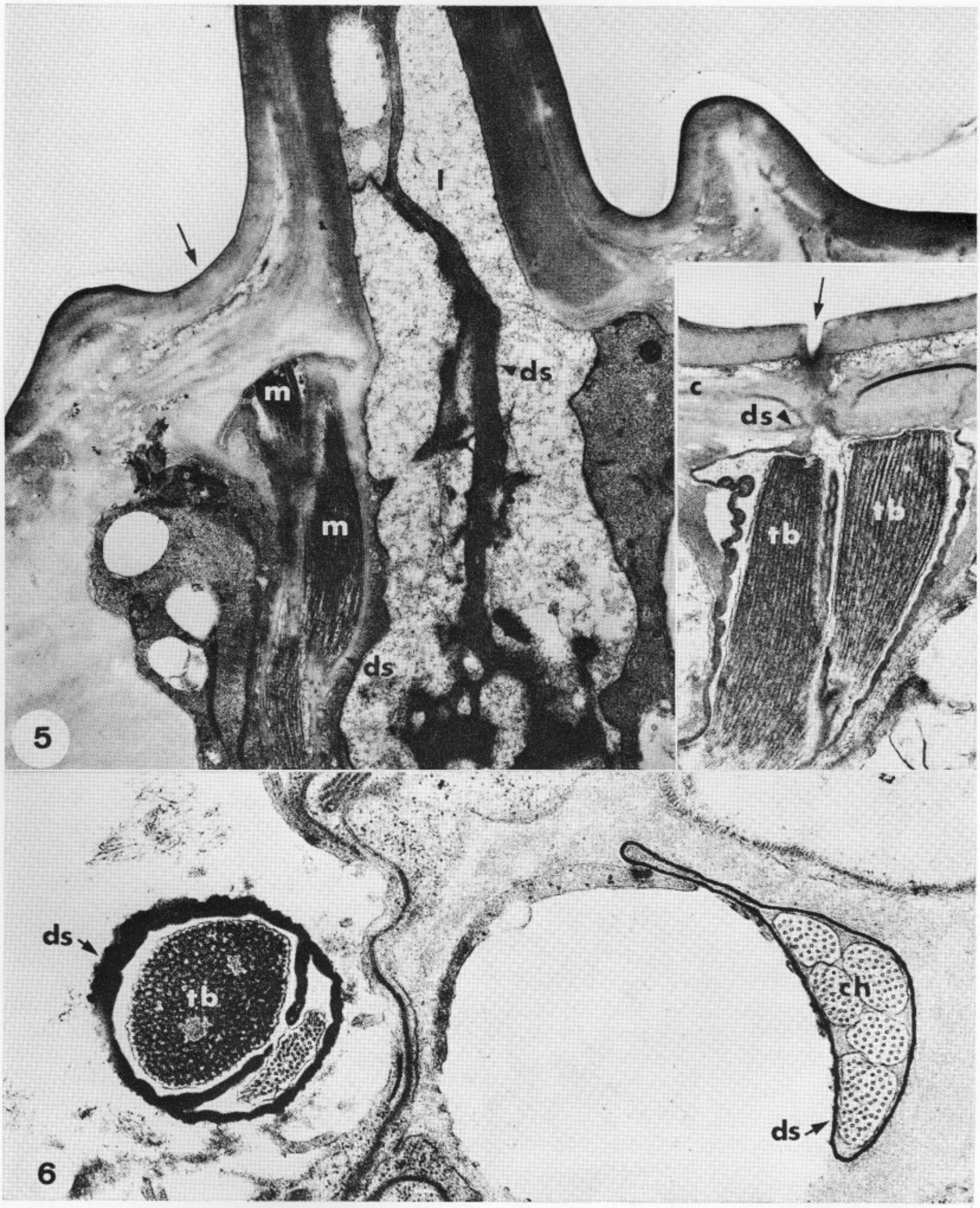
any others, they are loosely called "claw setae" to distinguish them from other tarsal setae. In the adult soft tick, *Argas arboreus* (Figs. 1, 3), usually six pairs of setae are arranged symmetrically on the lateral and the medial sides of the claws. However, the number varies from four to seven in different specimens. In the adult hard tick, *Amblyomma americanum* (Figs. 2, 4), there are consistently three pairs of setae.

The Soft Tick, *Argas arboreus*

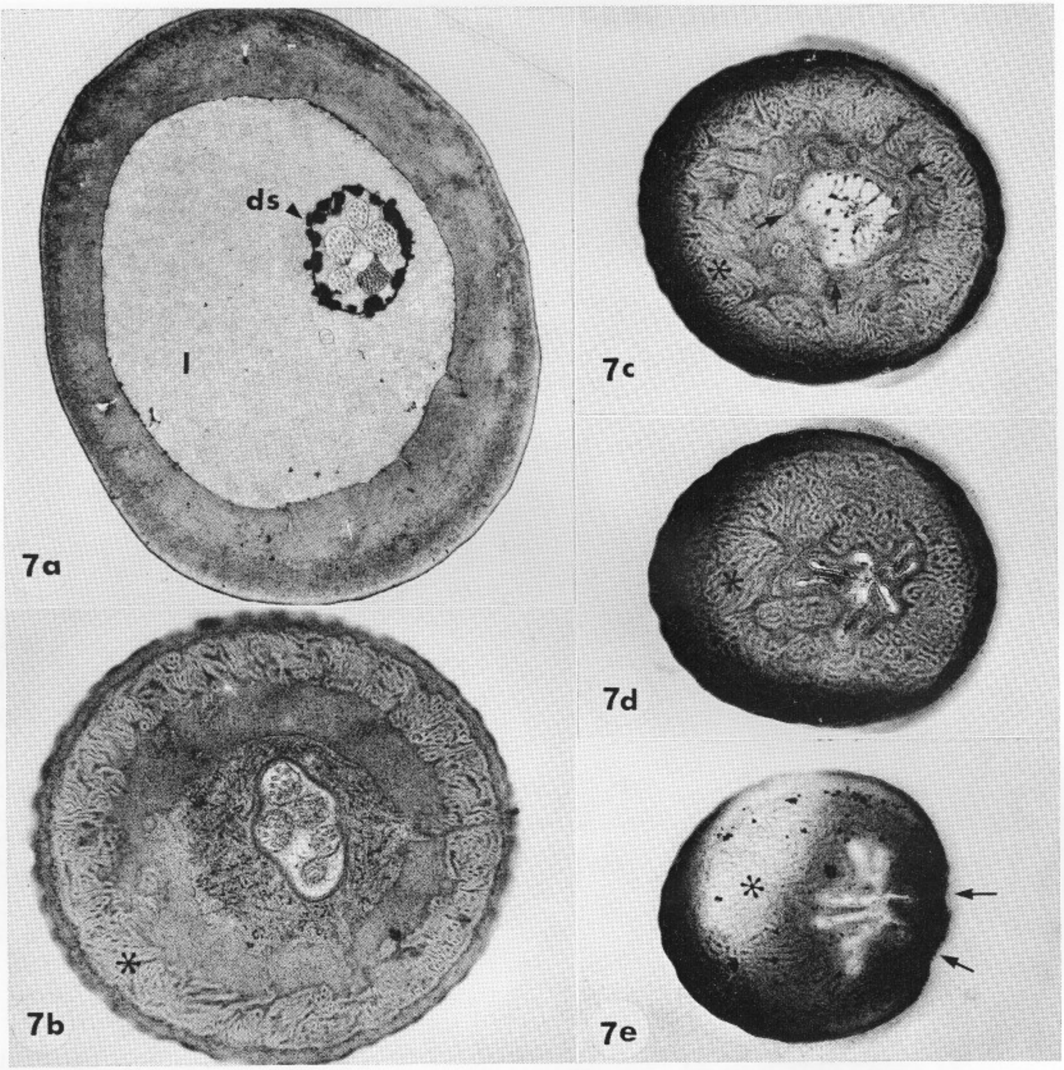
The claw setae can be grouped into three types according to their fine structural differences.

Type 1 sensillum: The first pair of claw setae (Fig. 3) are type 1. They are slightly curved, blunt-tipped, 80 μ in length and ca. 6 μ in diameter at the base. Transmission electron microscopy studies revealed that each sensillum is innervated by two sets of dendrites: two mechanoreceptive dendrites ending at the setal base and five chemoreceptive dendrites in the shaft lumen.

The two dendrites (Figs. 5, 6) terminating at the socket each possess a "tubular body" (Thurm, 1964) at the distal end and therefore are probably mechanoreceptors. Each tubular body is composed of abundant parallel microtubules, a few microfilaments and some electron-dense substances among them. The two dendrites are enclosed and partially separated by a continuous electron-dense dendritic



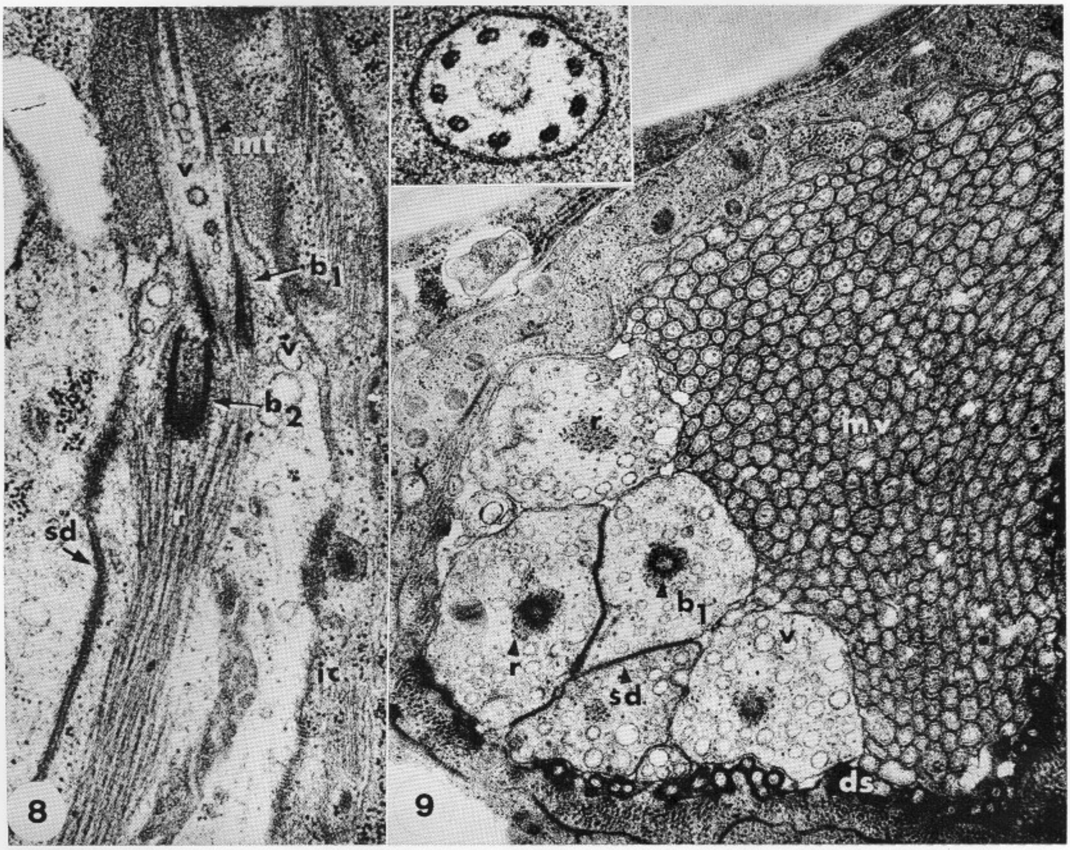
FIGURES 5–6. Transmission electron micrographs of type 1 sensillum in *A. arboreus*. **5**. Oblique-sagittal section showing 2 mechanoreceptive dendrites (m) attached to the base and fluid-filled lumen (l) in the shaft which contains 5 chemoreceptive dendrites (not shown here). Arrow, the location of the ecdysial canal; ds, dendritic sheath. × 9,000. Insert: Higher magnification of the same mechanoreceptive dendrites with tubular bodies (tb) inside showing the connection of dendritic sheath (ds) to the cuticle (c). Arrow, oblique view of the ecdysial canal. × 12,000. **6**. Cross section through the setal base showing 2 mechanoreceptive dendrites, one of them with the tubular body (tb), and 5 chemoreceptive dendrites (ch). ds, dendritic sheath. × 30,000.



FIGURES 7a–e. Consecutive cross sections of the shaft of type 1 sensillum from base to tip. **a.** Close to the base. Note 5 dendrites encased by an electron-dense dendritic sheath (ds) in a fluid-filled lumen (l). × 11,000. **b.** Farther distally the cuticular wall has a network of channels (*). × 29,000. **c.** Near the tip the dendrites disappear. Note the continuity between the dendritic sheath and cuticular wall (arrows). × 34,000. **d.** Relatively close to the tip 7 narrow canals appear. × 40,000. **e.** At the tip, 2 of the 7 canals are shown connecting to the exterior (arrows). × 51,000.

sheath. At the distal end, the dendritic sheath fuses directly to the ecdysial canal (Fig. 5, insert) as has been found in other arthropods (Gnatzy and Schmidt, 1971; Schmidt and Gnatzy, 1971; Chu-Wang and Axtell, 1972a, b).

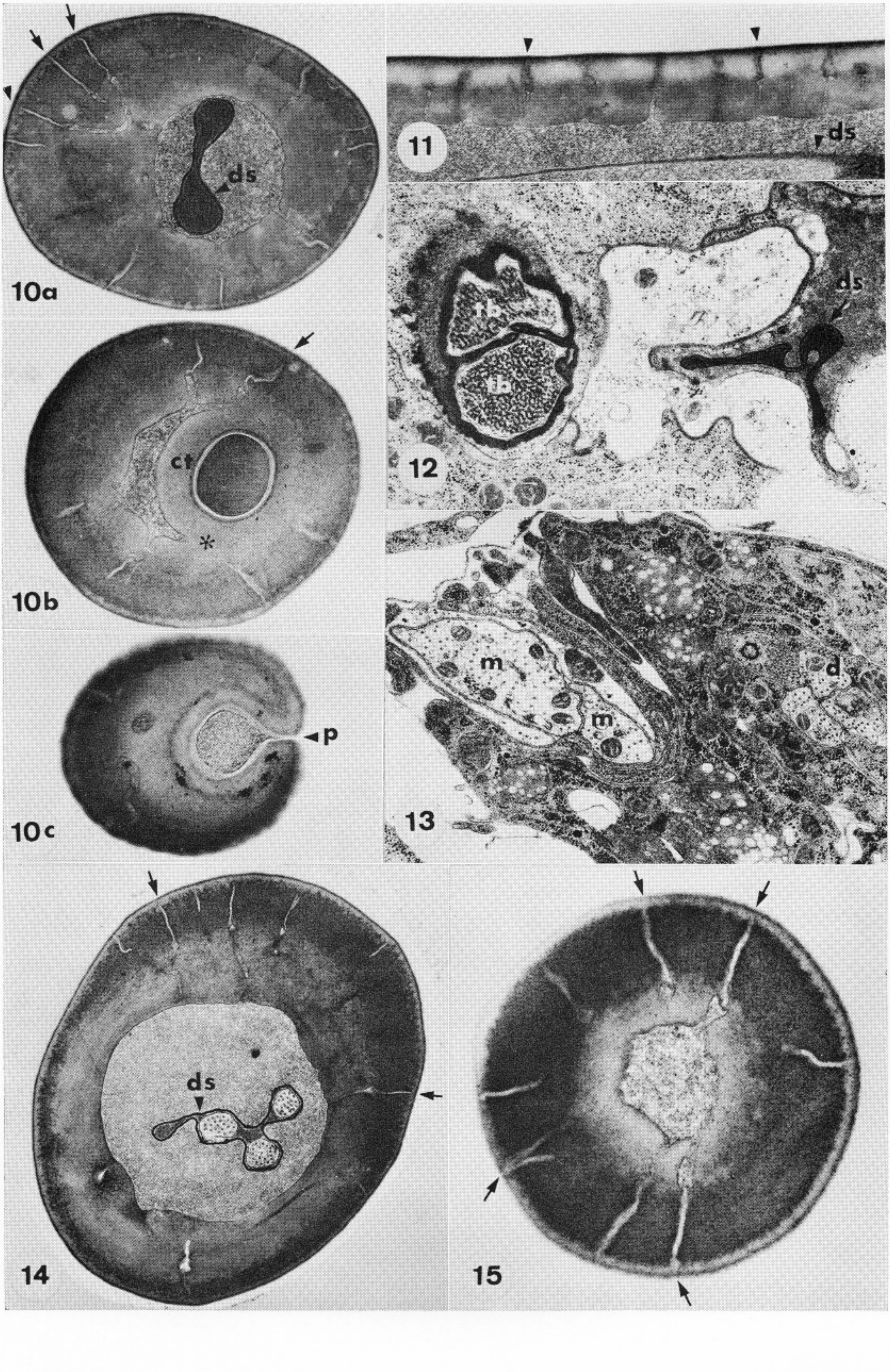
The other five dendrites (Fig. 6) ascending distally without branching inside the setal lumen are likely chemoreceptive dendrites (see Discussion). The dendrites (Fig. 7a) are encircled by a highly electron-dense dendritic sheath immersed in an electron-lucent fluid in the lumen. The smooth setal wall is composed of a solid, uniform cuticle. But close to the tip the surface becomes scalloped and the inner wall has a compact, intricate network of cuticular channels while the fluid inside the lumen becomes granular in appearance (Fig. 7b). Further distally, the dendritic sheath gradually merges with the wall and completely fuses with the wall near the tip (Fig. 7c). Typically



FIGURES 8–9. Transmission electron micrographs through dendritic ciliary region in type 1 sensillum. **8**. Longitudinal section. Note many vesicles (v) not only in the inner dendritic segment but also in the outer segment. b_1, distal basal body; b_2, proximal basal body; ic, internal enveloping cells; mt, microtubule; r, rootlets; sd, septate desmosome. $\times$ 30,000. **9**. Cross section of 5 dendrites in the inner segment. ds, dendritic sheath; mv, microvilli of the middle enveloping cells. $\times$ 27,000. Insert: Cross section of the ciliary region showing 9 doublet-microtubules in the periphery and a vesicle in the center. $\times$ 65,000.

seven narrow canals (140 Å in width) radiating from the apex of the seta establish a means of communication between the dendrites and the outside environment (Figs. 7d, e). Dendrites terminate about 0.4 μ below the openings (calculated from several serial cross-sections at the tip region).

As in other arthropod sensilla (Slifer, 1970), each dendrite is divided typically by a constricted region into the distal outer dendritic segment and the proximal inner dendritic segment (Figs. 8, 9). Only nine doublet-microtubules ("9 + 0") ascending from the distal basal body are present in the peripheral constricted region (Fig. 9, insert). The outer dendritic segment contains only microtubules whereas the inner dendritic segment has basal bodies, rootlets, vesicles, rosettelike glycogen, mitochondria, and a few microtubules. Two basal bodies occurring just proximal to the constricted region are arranged one behind another but not always in the same axis as the usual case found in arthropod sensilla. Actually, the distal basal body is parallel to the long axis of the outer dendritic segment and the proximal basal body to the long axis of the inner segment. In some cases the two basal bodies were observed at right angles to one another similar to the configuration of centrioles. A prominent feature found only in the chemoreceptive dendrites is that abundant vesicles are not only present in the inner seg-


10a
ds
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ment but also in the outer segment near the ciliary region. In this case, one or two vesicles are frequently found in the center of the ciliary region. The dendritic sheath encasing the distal dendritic segments terminates near the ciliary region. Long septate desmosomes are frequently found linking the surfaces of adjoining inner dendritic segments.

Each set of dendrites is encircled by an internal enveloping cell. An additional middle enveloping cell surrounds the internal enveloping cell of the chemoreceptive dendrites. These enveloping cells are in turn surrounded by a single external enveloping cell. Beneath the epidermis, many microvilli of the middle enveloping cell are adjacent to the chemoreceptive dendrites in the extracellular space (Fig. 9).

Type 2: Four pairs (2nd to 5th) of slightly curved, sharp-tipped setae are type 2 sensilla (Figs. 1, 3). The second pair are 120 μ long, the third and fourth 100 μ long, and the fifth about 55 μ long. There is considerable variation in the number and ultrastructure of these sensilla among different specimens. The number of setae on either the lateral or the medial side varies from 3 to 5; in most cases 4 are present on each side. Each sensillum is consistently innervated by 2 mechanoreceptive dendrites ending at the base as described in the type 1 sensillum; the number of chemoreceptive dendrites entering the lumen varies from 0 to 3 (Figs. 10a, 14). The fine structure of the dendrites below the setal base is similar to that of the type 1 sensilla.

A highly electron-dense fluid, with or without dendrites, is enclosed by a dendritic sheath which is immersed in a less dense fluid in the shaft lumen. Distally, the thin dendritic sheath attaches to one side of the wall and converts to a thick cuticular tube; the circular lumen of the shaft is reduced considerably and becomes crescent-shaped (Fig. 10b). The electron-dense fluid is exposed to the outside (Fig. 10c) through a single subterminal slit opening (140 Å wide and 0.5 μ long based on five serial cross sections passing through the opening). When dendrites are present, they are bathed in the electron-dense fluid, do not branch, and terminate just below the slit opening.

In addition to a subterminal slit opening, the thick wall (0.7 to 0.9 μ) is penetrated by rather sparsely distributed fine canals through the length of the shaft (Figs. 10, 11, 14). The canals are circular in cross section, ca. 450 Å wide in the inner half and 250 Å wide in the outer half of the shaft wall. The inner part of the canal sometimes branches and is filled with fluid while the outer part is electron-transparent. The canal appears to narrow to a fine exterior opening (ca. 100 Å diameter). These fine canals are also present in type 1 (but less numerous) and type 3 sensilla.

Some type 2 sensilla lack chemoreceptive dendrites in the shaft but still possess the dendritic sheath and a subterminal slit opening. These striking features have not been previously reported. The dendritic sheath and dense fluid are still present beneath the base of the shaft (Fig. 12). More proximally they are replaced by three dendrites (Fig. 13) which contain the cellular organelles of a typical inner dendritic segment (e.g., microtubules, mitochondria, rosettelike glycogen, etc.).

Type 3: The most ventral (6th) pair of

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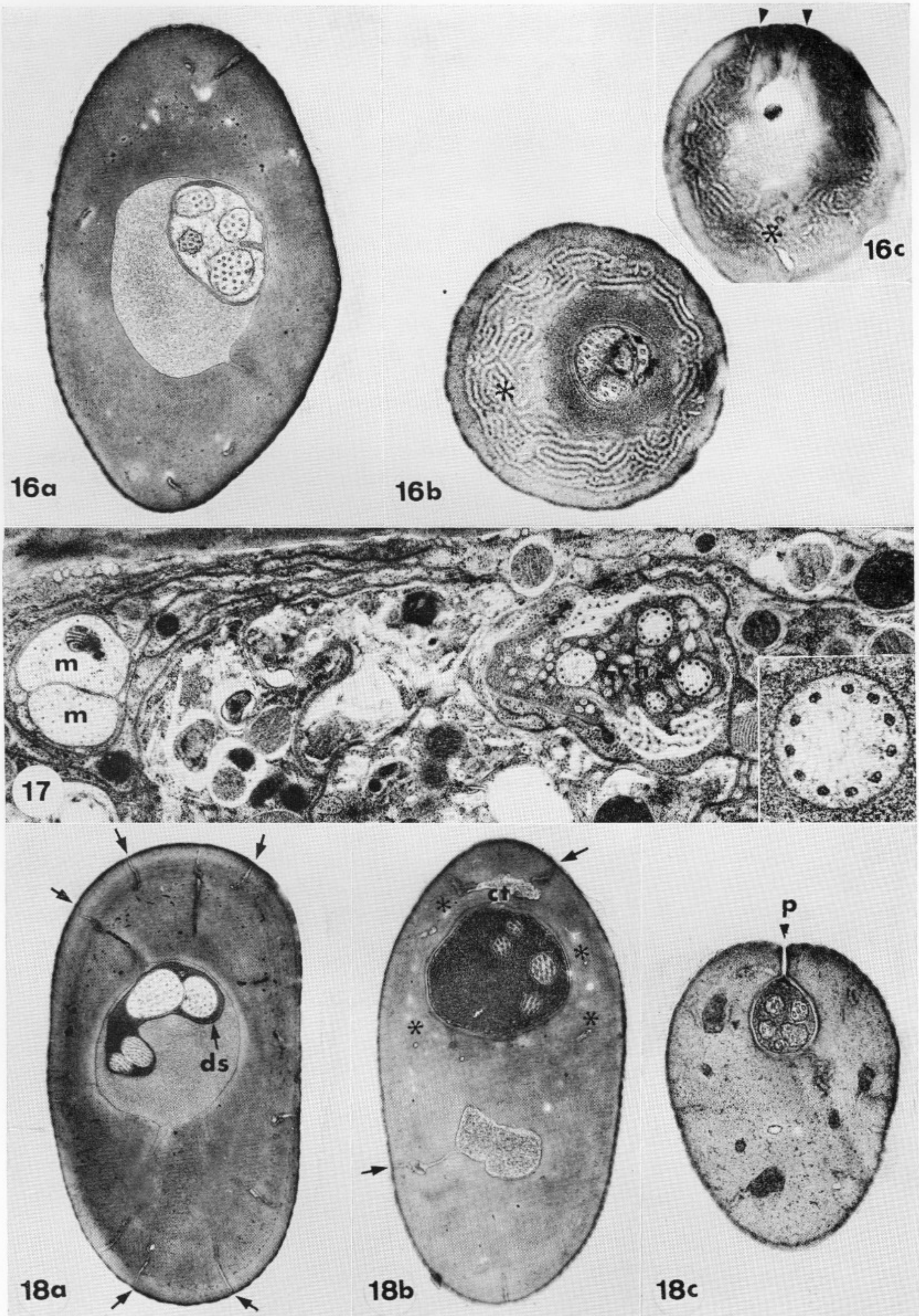
FIGURES 10–15. Transmission electron micrographs of type 2 and type 3 sensilla. **10a–c**. Consecutive cross sections of the shaft of a type 2 sensillum from base to tip. Note that no dendritic process occurs inside the dendritic sheath (ds). Arrows, fine canals traversing the setal wall. a. Close to the base. × 20,000. b. Distally, the thin dendritic sheath converts into cuticular tube (ct) and fuses with setal wall (*). × 22,000. c. Close to the tip, a narrow slit pore (p) occurs subterminally and the electron-opaque fluid inside the lumen protrudes to the outside. × 47,000. **11**. Portions of the longitudinal section of the same wall showing fine canals (arrows). × 15,000. **12**. Cross section of the same sensillum beneath the base showing 2 mechanoreceptive dendrites with tubular bodies (tb) and a highly electron-dense fluid without dendrites surrounded by dendritic sheath (ds). × 15,000. **13**. Cross section farther proximally. Note that the highly dense fluid is replaced by 3 dendrites (d). m, mechanoreceptive dendrites. × 15,000. **14**. Cross section of the shaft of another type 2 sensillum showing 3 dendrites inside the dense fluid encircled by dendritic sheath (ds). × 13,000. **15**. Cross section of the shaft of a type 3 sensillum showing fine canals (arrows) in the wall. Note absence of dendrites and dendritic sheath. × 35,000.


16a
16b
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m
m
18a
ds
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short, sharp-tipped setae (52 μ long) are type 3 sensilla. They are solely mechanoreceptors having two dendrites with tubular bodies at the base (as described in type 1 sensilla) and no neural processes in the shaft lumen (Fig. 15). Their morphology resembles that of tactile sensilla of insects (Thurm, 1964).

The hard tick, *Amblyomma americanum* (L.)

The tarsal claw sensilla in the hard tick (Figs. 2, 4) are fewer than those in the soft tick—three pairs in the adult hard tick vs. six pairs in the soft tick. These three pairs of claw sensilla have basically the same fine structures as the three types described for *Argas arboreus.*

The first pair of setae are similar to the first pair (i.e., type 1 sensillum) in the soft tick except there are four chemoreceptive dendrites instead of five invading the lumen (Fig. 16). The second pair of setae resemble the type 2 sensillum in the soft tick. Two mechanoreceptive dendrites are inserted at the base but consistently four chemoreceptive dendrites innervate the lumen (Figs. 17, 18) and sometimes branch as they approach the tip (Fig. 18c). The third pair of setae are typical mechanoreceptors, i.e., similar to the type 3 sensillum in the soft tick. Fine canals in the wall, like those described for the soft tick, were also found in all the setae of the hard tick.

All the setae in cross section are elliptical-shaped compared to the circular-shaped in the soft tick. The fine structural details in the neural components and enveloping cells are also quite similar to the soft tick except that 11 doublet-microtubules ("11 + 0") (Fig. 17, insert) instead of "9 + 0" occur in the ciliary region and a few vesicles occur only in the inner dendritic segment.

The nymphal stage of the hard tick possesses only two pairs of tarsal claw sensilla; these are circular in cross section. The first pair is essentially the same as the first pair in the adult stage, but the fluid occurring inside the dendritic sheath is electron-dense in contrast to the electron-lucent fluid in the adult sensilla. The second pair of setae are typical mechanoreceptors like the third pair of setae in the adult stage. Therefore, the second pair of setae in the adult are added to the nymphal complement.

DISCUSSION

The type 1 and type 2 claw sensilla closely resemble the type B and type A sensilla, respectively, in the tick palpal organ (Foelix and Chu-Wang, 1972). They have a thick wall, multiple innervation, and a single opening at tip which are the typical features for contact chemoreceptors in arthropods (Dethier, 1963; Slifer, 1970). In addition, two dendrites with tubular bodies attach to the setal base, a typical feature of mechanoreceptors (Thurm, 1964). Apparently, these sensilla play a role in both contact chemoreception and mechanoreception. The structural differences in these two types of sensilla probably reflect some differences in their response to various stimuli.

The claw sensilla in the hard tick exhibited no variation between individuals whereas in the soft tick considerable variation occurred. The variation was in the number of type 2 sensilla. The first and last pair of setae were always type 1 and type 3, respectively, and no variation in the number of dendrites was found. The type 2 sensillum varied in the degree of innervation of the shaft. Even those without dendrites in the shaft had a dendritic sheath in the lumen and an opening near the tip. Whether this represents a new type sen-

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FIGURES 16–18. Transmission electron micrographs of the sensilla in the adult hard tick, *Amblyomma americanum.* **16a–c**. Consecutive cross sections of a type 1 sensillum. a. Near the base. Note 4 dendrites in the lumen. × 19,000. b. Farther distally showing network of channels in the wall (*). × 40,500. c. Near the tip showing narrow pores communicating to the exterior (arrows). × 36,500. **17**. Transverse section of the neural components of the type 2 sensillum showing 2 mechanoreceptive dendrites (m) in the inner dendritic segment and 4 chemoreceptive dendrites (ch) in the ciliary region. × 40,300. Insert: Higher magnification of "11 + 0" doublet-microtubules in the ciliary region. × 48,500. **18a–c**. Serial sections of type 2 sensillum from base to tip. a. Near the base showing 4 dendrites in the lumen and fine canals in the wall (arrows). ds, dendritic sheath. × 12,000. b. More distally showing the fusing points (*) of the cuticular tube (ct) with the wall. × 18,000. c. Near the tip showing the subterminal slit opening (p). Note the 5 dendrites in the lumen resulting from branching. × 33,000.

sillum or is a case of degeneration of the dendrites is not known.

The presence of both a terminal opening and fine canals in the shaft wall of the type 1 and 2 sensilla should be noted. The terminal opening provides an apparent route between the exterior and the interior fluid which leads to the dendrites (Figs. 7e, 10c, 16c, 18c). From the micrographs it appears that the fluid can flow through the opening. Use of the silver protein penetration method (Ernst, 1969) to detect routes of access from the exterior resulted in erratic, inconsistent deposits of silver granules and no defensible evidence that the fine cuticular canals are a means of stimuli access to the dendrites. It should be noted that the dendrites are surrounded by a dendritic (cuticular) sheath which might be a barrier to outside stimuli. In view of these findings, we conclude that the fine cuticular canals are not involved in stimuli reception. This was postulated for certain sensilla of *Argas arboreus* and extrapolated to reinterpret the findings of *Amblyomma americanum* (Roshdy et al., 1972; footnote, Foelix and Axtell, 1972). It is more likely, as originally stated (Foelix and Axtell, 1971, 1972) that the d_2, A_4, A_6, A_7, and posterior sensilla of *A. americanum* have an opening near the tip (although this has not been demonstrated) even though there are fine canals in the cuticular wall. Likewise, the d_1, d_2, A_4, A_6, A_7, and posterior sensilla of *Argas arboreus* probably have an opening at or near the tip.

All the claw setae possess two mechanoreceptive dendrites at the socket base. An interesting feature of these sensilla is the termination of the mechanoreceptive dendrites only on the dorsal side of the setal base. This morphological characteristic correlates well with the behavior. When a tick walks and/or quests for the host, the claw setae bend toward the dorsal side where the mechanoreceptive dendrites are located. The distortion of the tubular body at the distal end of the mechanoreceptive dendrites could cause a response to the mechanical stimulation.

The dendrites of the soft tick exhibit "9 + 0" doublet-microtubules in the ciliary region as found in other arthropods and other tarsal sensilla of the soft tick (Roshdy, Foelix, and Axtell, 1972), while the hard tick always has an "11 + 0" configuration as described in the other tarsal sensilla of the hard tick (Foelix and Axtell, 1971, 1972).

An interesting feature of the tick sensilla is the arrangement of the enveloping cells. The chemo- and mechanoreceptive dendrites have separate internal enveloping cells but share a common external enveloping cell. The mechanoreceptive dendrites lack a middle enveloping cell (see fig. 3 in Foelix and Chu-Wang, 1972). In insect sensilla the two types of dendrites share a common set of three enveloping cells (internal, middle, and external) as shown by Gnatzy and Schmidt (1972). According to their findings, the internal enveloping cell lays down the dendritic sheath, the middle enveloping cell forms the shaft, and the external enveloping cell builds the socket base; during the molting process the dendrites and dendritic sheath extend through the terminal pore of the newly formed shaft and there is no separate ecdysial canal for the mechanoreceptive dendrites as found in a solely mechanoreceptor (Schmidt and Gnatzy, 1971). It is reasonable to assume that in the tick the internal enveloping cells form the separate dendritic sheaths, the middle enveloping cell of the chemoreceptive dendrites forms the shaft, and the common external enveloping cell forms the socket. In the socket base there is a separate ecdysial canal for the mechanoreceptive dendrites. During molting the chemoreceptive dendrites and their dendritic sheath presumably extend through the apical opening of the newly formed shaft and the mechanoreceptive dendrites and their sheath extend through the ecdysial canal at the socket.

Our findings on the ultrastructure of the claw sensilla correlate well with the behavior of the ticks. In feeding and walking the tip of the first tarsus is periodically touched to the substrate. The mainly contact chemoreceptive claw sensilla would be especially significant in detection of the nature of the substrate. Likewise the contact chemoreceptors of the palps are brought into contact with the substrate during feeding and mating.

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