

THE SUBGENUS *PERSICARGAS* (IXODOIDEA: ARGASIDAE: ARGAS). 16. FINE STRUCTURE OF HALLER'S ORGAN AND ASSOCIATED TARSAL SETAE OF ADULT *A. (P.) ARBOREUS* KAISER, HOOGSTRAAL, AND KOHLS*

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ABSTRACT: Haller's organ setae and certain dorsal sensilla on tarsus I of the adult *Argas* (*Persicargas*) *arboreus* Kaiser, Hoogstraal, and Kohls (family Argasidae) were studied by scanning and transmission electron microscopy and compared with those of *Amblyomma americanum* (L.) (family Ixodidae). The 2 distal setae (d_1 , d_2) of the tarsus stand separately in ixodids but are grouped with the 7 anterior pit sensilla (A_1 to A_7) of the argasid Haller's organ. The lateral, posterior, medial, and proximal setae occupy approximately the same relative positions on tarsus I in both families. The *Argas* Haller's organ capsule contains only 4 sensilla; these are exposed to the environment by numerous perforations in the capsule roof. Most sensilla are multi-innervated and possess various pore systems. Large plugged pores (1,100 to 2,000 Å), always associated with branching dendrites, occur in A_1 , A_2 , and in the thin-walled capsule sensilla. Small pores (100 to 400 Å) either irregularly penetrate the wall (d_1 , d_2 , A_4 , A_6 , A_7 , and posterior setae) or form a spoke-wheel arrangement of convoluted canals (A_3 , A_5). Medial setae have slit pores with narrow canals extending toward the lumen. All tarsal sensilla have at least 1 luminal dendrite communicating with the environment through a pore and probably functioning as a chemoreceptor. The presence of 2 additional basal mechanoreceptors in d_1 and A_1 suggest both chemo- and mechanoreception in these sensilla. The *Argas* pattern of $9 + 0$ microtubules of the dendritic ciliary region is common among arthropod sensilla, but the *Amblyomma* pattern of $11 + 0$ is exceptional.

Recent investigations by scanning and transmission electron microscopy on tarsal sensilla and Haller's organ of *Amblyomma americanum* (L.) (family Ixodidae) (Foelix and Axtell, 1971, 1972) revealed numerous fine structural details common among arthropods (Larsen, 1962; Thurm, 1964; Richter, 1964; Moeck, 1968; Coons, 1970; Slifer, 1970; Foelix, 1970). Most sensilla are multi-innervated. They com-

municate with the environment through complex pore systems and are considered to be chemo- and/or hygroreceptors. Several sensilla also possessing two mechanoreceptors at the base are capable of responding to mechanical and chemical stimuli. Similar tarsal sensory receptors occur in the macrochelid mite, *Macrocheles muscaedomesticae* Scopoli (Coons, 1970), and the ixodid tick, *Haemaphysalis inermis* Birula (Axtell et al., in press).

In the present study, *Argas* (*Persicargas*) *arboreus* Kaiser, Hoogstraal, and Kohls was selected as a representative of the family Argasidae to compare the fine structure of tarsus I sensory receptors in ticks of the families Argasidae and Ixodidae.

The terms bristles, setae, hairs, and sensilla have been used by various authors to define the same structures in arthropods. We consider seta and bristle to be synonymous, purely morphological terms for a cuticular surface extension. The term sensillum denotes an innervated seta (or even another sensory organ) and implies a receptive function. The term hair should be restricted to mammals and avoided in arthropod chaetotaxy. In the present study, we use setae in descriptions based on scanning electron microscopy and sensilla

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only in transmission electron microscopy where innervation is demonstrated.

MATERIALS AND METHODS

Argas (Persicargas) arboreus were from a NAMRU-3 Medical Zoology laboratory 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.

For scanning electron microscopy (SEM), alcohol-preserved larvae, first-instar nymphs, and adults were coated with carbon-gold and examined in a JEOL-JSM2 stereoscan electron microscope.

For transmission electron microscopy (TEM), the adult tarsus I was fixed in cold cacodylate-buffered, 5% glutaraldehyde (Sabatini et al., 1963), postfixed in 1% OsO₄ (Palade, 1952), dehydrated in ethanol series, and embedded in Epon 812 over propylene oxide. Thin sections were cut in consecutive series with a diamond knife on a Reichert OmU2 ultramicrotome and picked up with Formvar-coated slot grids. Double-stained sections (uranyl acetate and lead citrate, 15 min each) were examined in a Siemens Elmiskop 1A at an accelerating voltage of 80 kv.

OBSERVATIONS

Scanning electron microscopy

The *Argas* Haller's organ and associated tarsal setae were examined chiefly in the adult stage; those of larvae and first-instar nymphs were examined comparatively. Notable differences between setal numbers and position were observed in immature and adult stages.

Haller's organ

As in other ticks, the Haller's organ, situated in a dorsal hump near the apex of tarsus I, consists of an anterior pit and a posterior capsule containing several setae involved in various receptive functions (Lees, 1948; Zolotarev and Sinitsyna, 1965). There are no fine structure differences in the Haller's organs of male and female *Argas*.

The circular anterior pit contains nine setae (Figs. 1-3), two of which (d_1 , d_2) are larger than the others and are interpreted as corresponding to the distal setae of ixodid ticks (Foelix and Axtell, 1971, 1972; Axtell et al., in press). This interpretation is supported by: (1) the absence of setae distal to the anterior pit group in the adult, (2) the distal separation of d_1 from the other setae in the first nymphal and larval stages, (3) the arrangement of the

other seven setae in a manner essentially like that of the seven setae in the anterior pit of *Amblyomma americanum* (L.), and (4) in the larval stage a loss of two of the seven anterior pit setae (as occurs in *A. amblyomma*) and the retention of d_1 and d_2 . The remaining seven setae are comparable to the anterior pit setae in *Amblyomma americanum* and are numbered similarly (A_1 to A_7).

The largest seta (d_1) measures ca. 150 μ long and 6.5 μ in basal diameter, is mesad, distally directed, serrated on one side, possesses a distinct socket, and lacks detectable pores in the wall surface. The smaller d_2 is laterad, stout, cone-shaped (ca. 12 μ long and 5 μ in basal diameter) and has no apparent surface pores.

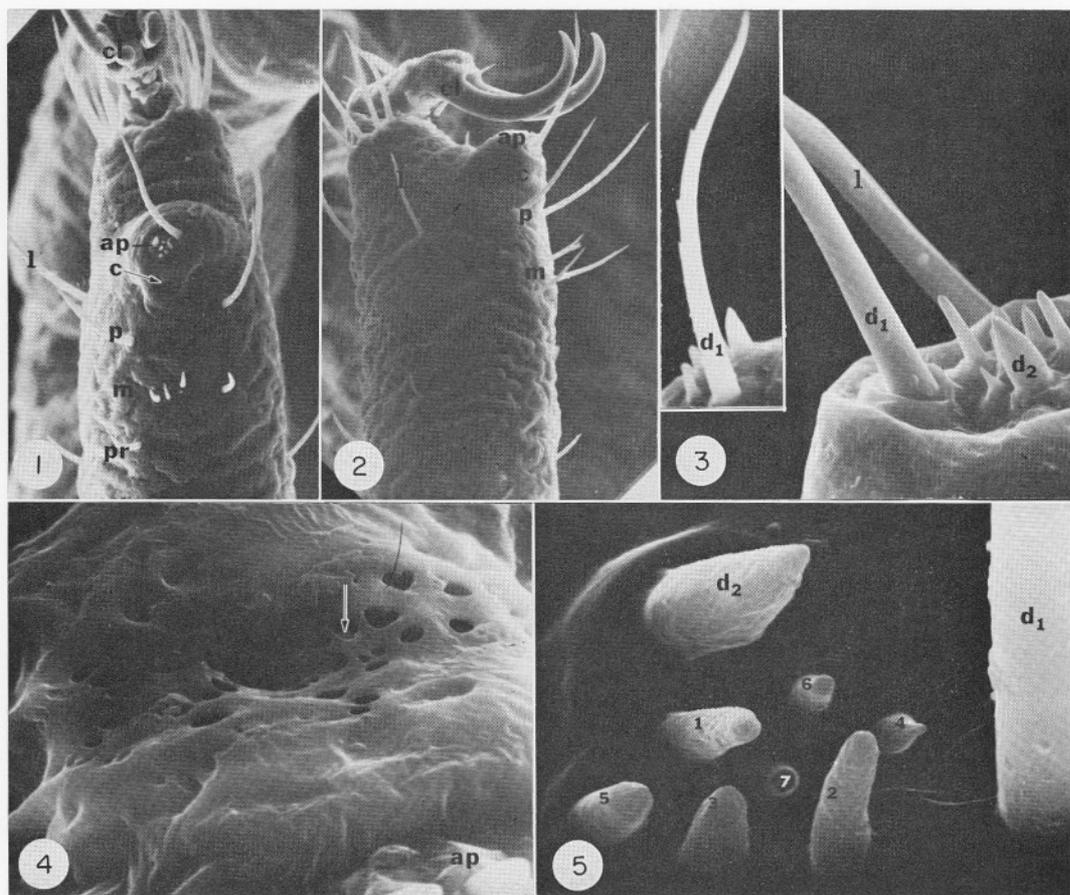
A_1 and A_2 , immediately posterior of d_1 and d_2 , are apically blunt, relatively longer than the other five setae (each ca. 11 μ long and 3 μ basal diameter), and possess numerous obvious surface pores (Fig. 5). A_3 , A_4 , and A_5 are subequal in dimensions (8.5 μ long, 3.5 μ basal diameter), pointed apically, and lack detectable surface pores. The shortest setae, A_6 and A_7 (3.5 μ long, 2.5 μ basal diameter), lie in the center of the pit, possess no surface pores, and are pointed apically.

In the larva and first nymphal instar, d_1 is distally separated from the anterior pit group. In addition to d_2 , the anterior pit contains only five setae in the larva but seven in the first nymph. Further investigation is needed to determine which setae are absent in the larva.

The posterior capsule (Figs. 1, 2) lacks the aperture characteristic of some ixodid ticks (Foelix and Axtell, 1972; Axtell et al., in press; Roshdy, unpublished). However, the capsule roof contains numerous, irregularly distributed perforations 0.5 to 2.5 μ in diameter. High magnification shows a larger central aperture, 6.0 by 3.5 μ , with a cuticular perforated margin extending into the cavity (Fig. 4).

Tarsal setae associated with Haller's organ

Dorsal setae of the adult tarsus I selected for comparison with those of ixodid ticks were named posterior, medial, and proximal according to their position relative to Haller's organ (Foelix and Axtell, 1971; Axtell et al., in press).



FIGURES 1-5. Scanning electron micrographs of Haller's organ and associated tarsal setae in female *Argas (Persicargas) arboreus*. 1. Dorsal view. ap, anterior pit; c, capsule; l, lateral seta; m, medial setae; p, posterior seta; pr, proximal seta. Note other setae around claws (cl). $\times 130$. 2. Lateral view showing the same setae. $\times 130$. 3. Closeup of anterior pit setae. d_1 and d_2 , distal setae; l, lateral tarsal seta. $\times 1,000$. Inset: d_1 serrated on one side. $\times 500$. 4. Capsule roof showing perforations and larger central aperture. Arrow, blunt tip of an inner sensillum seen through the roof perforations; ap, distal part of the anterior pit. $\times 1,900$. 5. Top view of the seven anterior pit seta (1 to 7) and the two distal setae (d_1 , d_2). Note distinct surface pores in setae 1 and 2. $\times 3,400$.

These correspond to the paramedian capsular (pc), posterior hair tuft (HT), and dorsal posteromedian (PM) setae of Dumbleton and Hoogstraal (1960) for certain *Argas* and *Ornithodoros* species.

The two posterior setae (Figs. 1, 2) measure 135 to 140 μ long and ca. 6 μ basal diameter, possess distinct sockets, are pointed apically, and lack detectable surface pores.

The medial and proximal setae, pointed apically and measuring, respectively, 90 and 40 μ long and 6 and 5 μ basal diameter, vary in number and relative position in the adult.

Most adults have two medials and two proximals distinctly separated from each other but some have three medial setae close to or nearly in line with the proximals (Figs. 1, 2). In the first nymphal instar, medial setae consistently number two.

Transmission electron microscopy

Most setae were studied in consecutive cross sections from the apex to the base. Special attention was directed to Haller's organ setae. Some tarsal setae (posterior and medial) were compared with those in *Amblyomma*

americanum (family Ixodidae). All setae were found to be innervated, and are therefore referred to as sensilla.

Distal sensilla

The d_1 and d_2 differ in size but their fine surface structure is similar. The walls of both possess fine canals extending from the lumen to the exterior surface. The straight, basal two-thirds of the canal, ca. 400 Å wide, is apparently filled with "sensillum liquor" (Ernst, 1969). This basal part forms a short, bulbous expansion before continuing as a narrow (300 Å) convoluted, electron-lucent tube opening to the exterior.

The d_1 lumen contains three dendrites, each surrounded by a thin, electron-dense dendritic sheath, the scolopale (Figs. 6, 7). Most of the lumen is occupied by an extension of an enveloping cell, possibly a trichogen cell from the hypodermal layer. The peripheral zone of the lumen is filled by sensillum liquor. In addition, d_1 is also equipped with two basal mechanoreceptive dendrites possessing tubular bodies (Thurm, 1964) in the dendritic terminals (Fig. 8). Notably, these two tubular

bodies differ structurally. One type has an array of rather regularly spaced microtubules interconnected by an electron-dense substance; the outermost layer of the microtubules underlying the dendritic membrane follows a sharply defined line. In the second type, microtubules linked as a chain meander through the dendritic terminal. These two forms may represent different tubular body types or physiological phases of a single structure.

The d_2 sensillum has only one dendrite inside the lumen and lacks mechanoreceptive elements.

Anterior pit sensilla (A_1 to A_7)

The seven thick-walled sensilla of the anterior pit (Fig. 9) can be divided into four structurally similar groups.

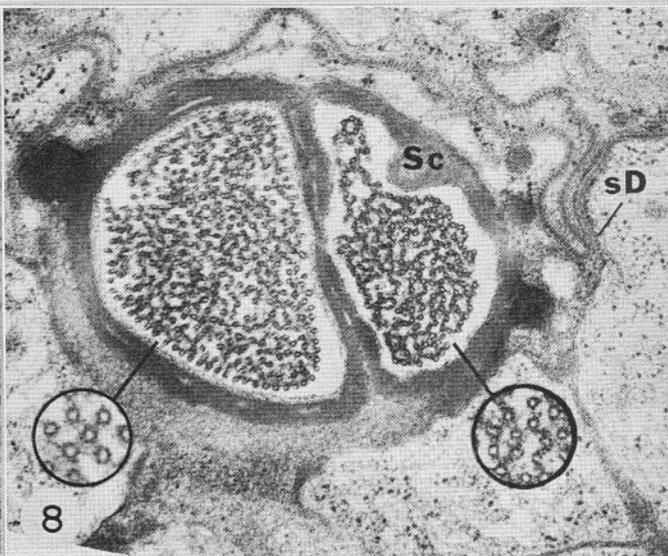
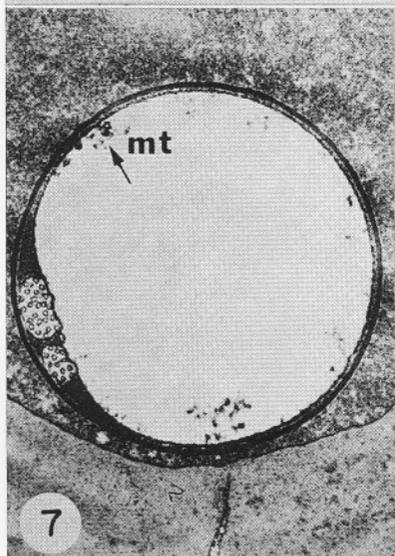
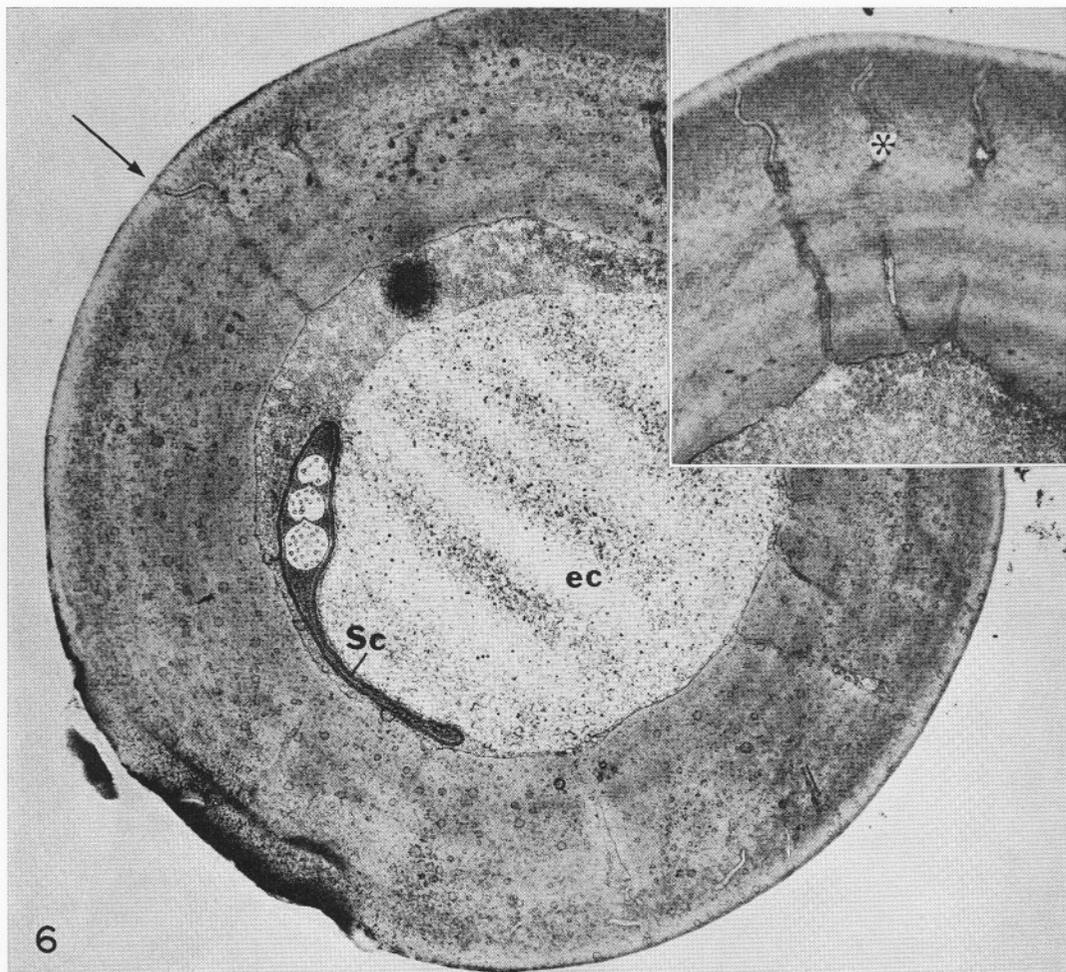
A_1 and A_2 possess numerous large pores ca. 1,400 Å diameter in the cuticle wall, which is 0.4 μ thick. The pores are centrally plugged by a cuticular body suspended by fine strands (Fig. 10). Each sensillum is innervated by five dendrites which ramify into more than 20 branches after leaving the scolopale at the sensillum base.

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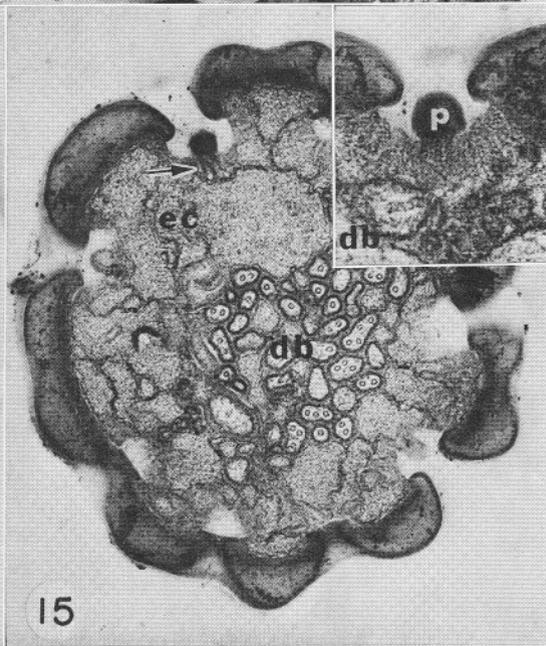
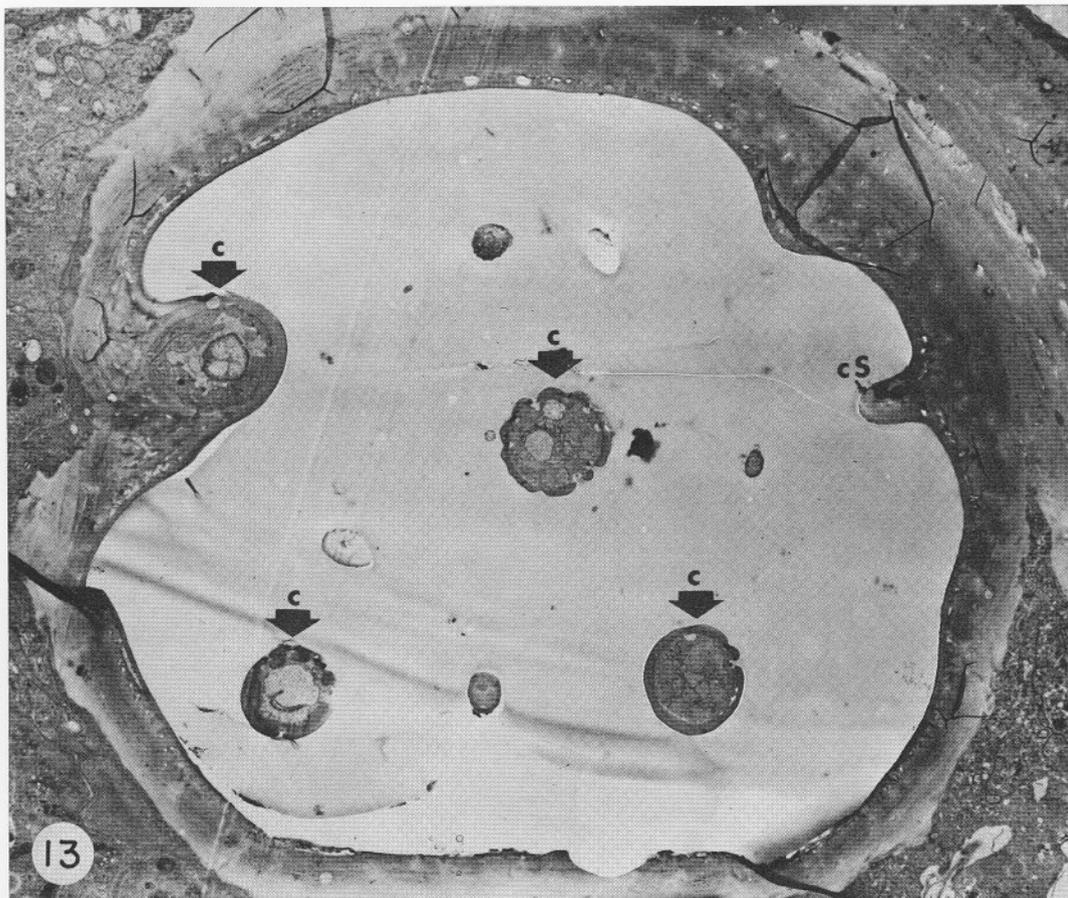
FIGURES 6-8. Transmission electron micrographs of d_1 seta in female *Argas (Persicargas) arboreus*. **6.** Cross section showing three basal dendrites surrounded by a thin scolopale (Sc) inside the lumen. Arrow, surface pores; ec, portion of an enveloping cell in the lumen. $\times 20,000$. Inset: Three canals traversing the cuticular wall of the seta. Asterisk, bulbous expansion between the two portions of the canal. $\times 33,000$. **7.** Same but at a distal level, showing one of the three dendrites enormously inflated, stretching the scolopale into a wide circle; this stretching may be artificial. mt, microtubules at the dendrite periphery. $\times 29,000$. **8.** Two basal mechanoreceptive dendrites enclosed by a thick scolopale (Sc). Note two structurally different tubular bodies (insets: left $\times 90,000$, right $\times 70,000$). sD, septate desmosomes interconnecting basal enveloping cells. $\times 33,000$.

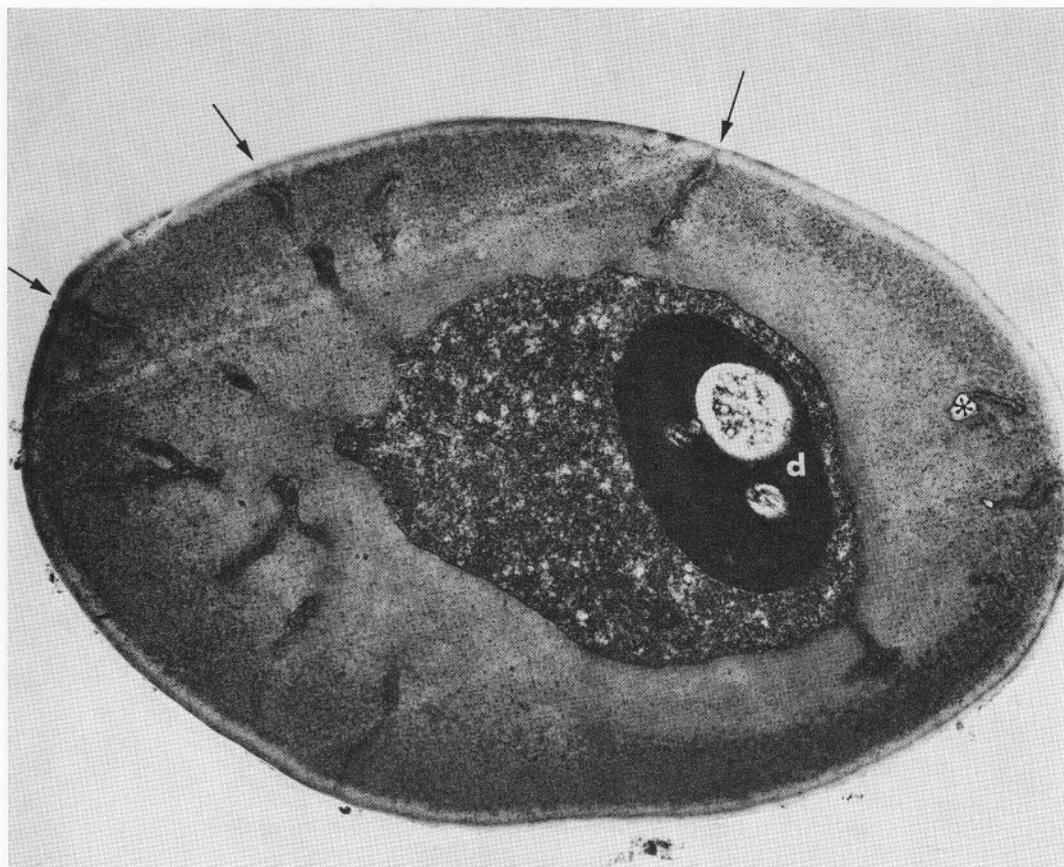
FIGURES 9-12. Transmission electron micrographs of anterior pit sensilla in female *Argas (Persicargas) arboreus*. **9.** Cross sections of A_1 to A_7 and d_2 . Note five dendrites in A_1 and A_2 , and one or two in other sensilla. $\times 7,200$. Inset: Cross section of the ciliary region of a dendrite showing nine peripheral double microtubules and a large central vesicle. $\times 55,000$. **10.** Portion of a cross section of A_1 wall showing large pore with a cuticular plug (p). db, dendrite branches in the lumen. $\times 57,000$. **11.** Cross section of A_1 showing few narrow canals (arrows) in the wall and one dendrite in the lumen. $\times 20,000$. **12.** Cross section of A_2 showing the spoke-wheel configuration of the wall. Arrows, narrow canals connecting the lumen with the surface grooves. $\times 20,000$.

FIGURES 13-15. Transmission electron micrographs of Haller's organ capsule in female *Argas (Persicargas) arboreus*. **13.** Cross section of the capsule showing four thin-walled sensilla (c) in the cavity. cS, nonsensory cuticular projections. $\times 4,000$. **14.** Cross section of a sensillum at a basal level showing nonporous thick wall and five luminal dendrites (1 to 5). $\times 19,500$. **15.** Same but at a more distal level, showing thin plug-pored wall, and numerous membrane-electron-dense, dendritic branches (db), surrounded by processes of the enveloping cell (ec) in the lumen. Arrow, radial striations in the pore plugs. $\times 28,000$. Inset: A pore plug (p) showing filamentous extensions in direct connection with a dendritic branch (db). $\times 50,000$.

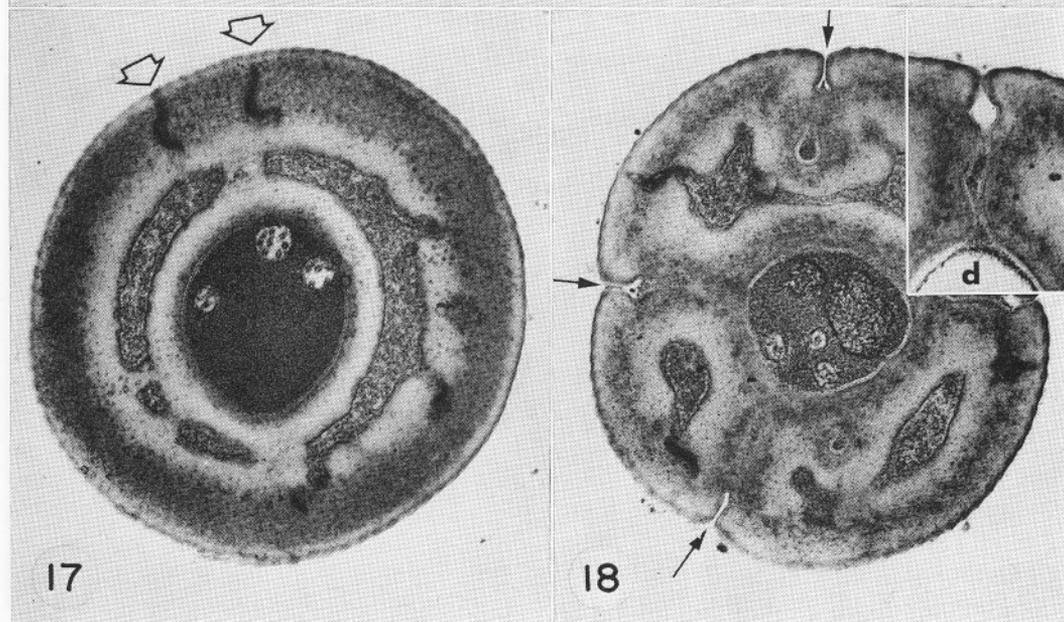








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A_3 bears ca. 10 longitudinal grooves along the shaft. In cross section, the shaft exhibits a spoke-wheel pattern (Fig. 12). From two or three central dendrites, fine canals (400 Å) pass through the spokes to the surface grooves. The structure of A_3 and A_5 is probably alike but too few sections of A_5 were obtained for precise study.

A_4 is innervated by one scolopale-enclosed dendrite which ascends the lumen centrally. A few irregular canals traverse the cuticle wall (Fig. 11). A_4 is the only anterior pit sensillum with two basal mechanoreceptive dendrites. The structure of the tubular bodies in the two dendritic terminals is the same as that of the d_2 sensillum.

A_6 and A_7 surfaces are slightly scalloped. Very fine canals (ca. 100 Å in diameter) penetrate the cuticle from the surface indentations and communicate with the lumen. Both sensilla are innervated by two dendrites, but in A_6 the second dendrite does not ascend into the lumen of the cuticular shaft.

The ciliary region, which separates the dendrites of each sensillum into an inner and an outer segment, shows the common arrangement of nine peripheral double microtubules lacking center elements ("9 + 0," Fig. 9, inset).

Haller's organ capsule

The capsule, immediately proximal to the anterior pit, is ca. 30 μ in diameter. The capsule wall bears numerous cuticular projections pointing toward the center of the cavity. Four thin-walled sensilla (0.2 to 0.3 μ) emerge from the proximal wall (Fig. 13). The sensillar lumen is filled by 30 to 40 branches of four or five dendrites (Figs. 14, 15) and also by large extensions of an enveloping (tricho-

gen?) cell. Each sensillum wall is perforated by large plug pores, 1,100 to 2,000 Å in diameter. The material suspending the central plug is radially striated (Fig. 15, inset). Occasional filamentous extensions similar to pore tubules in insect olfactory sensilla (Ernst, 1969) may be in direct contact with dendritic branches (Fig. 15).

Tarsal sensilla

Posterior and medial setae were briefly examined. The two setae posterior of the Haller's organ capsule are typical thick-walled sensilla with several dendrites inside the lumen. An extensive canal system penetrates the cuticle wall (Fig. 16) and connects to the outside. Structurally these canals correspond to those described for the d_1 sensillum, except that they may branch within the cuticle wall.

The medial sensilla are characterized by narrow slit pores (100 Å or less) and adjoining convoluted canals leading to the dendrites in the central lumen (Fig. 18). The outer lumen (Fig. 17), which appears as a result of a thickened scolopale, also sends extensions toward the surface. These are filled by an electron-dense substance clearly differing from the sensillum liquor. The direct connection of the dendrites to the outside is established by the slit pores and their adjoining canals.

DISCUSSION AND CONCLUSIONS

Study by SEM of tarsus I setae of adult *Argas (Persicargas) arboreus* (family Argasidae) revealed morphological features very similar to those of *Amblyomma americanum* and *Haemaphysalis inermis* Birula (family Ixodidae) (Foelix and Axtell, 1971; Axtell et al., in press). Most setae of these species occupy the same location relative to Haller's organ. However, the distal setae (d_1 , d_2),

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FIGURES 16–18. Transmission electron micrographs of tarsus I posterior and medial sensilla in female *Argas (Persicargas) arboreus*. **16.** Cross section of a posterior sensilla showing two dendrites (d) embedded in a highly electron-dense medium and enclosed by a thin scolopale. Arrows, numerous surface pores of fine canals in the wall. The fine structure of the canals is similar to that in Figure 5. $\times 27,000$. **17.** Cross section of a medial sensillum at a basal level, showing three dendrites enclosed by a thick scolopale contacting the wall to create a double lumen in places. Arrows, electron-dense canals connecting the outer lumen to the surface. $\times 30,000$. **18.** Same but at a distal level showing four slit pores (arrows) connected to the inner lumen or dendrites by fine convoluted canals. $\times 38,000$. Inset: Connection of the dendrite (d) with the slit pore. $\times 48,000$.

which stand separately in each ixodid developmental stage, join the anterior pit setae in the *Argas* adult and d_1 arises distad of the anterior pit in the larva and first-instar nymph.

The location of the long d_1 seta relative to the anterior pit of Haller's organ varies considerably in different argasid species examined by the light microscope. The d_1 lies anterior of the pit in larval *Ornithodoros* (*Allectorobius*) *capensis* Neumann, *O. (Reticulinasus) batuensis* Hirst, and *O. (R.) faini* Hoogstraal. It is apparently inserted on the pit in *O. (R.) solomonis* Dumbleton, but absent in larval *A. (P.) persicus* (Oken) and *A. (Carios) vespertilionis* (Latreille) (Dumbleton, 1958, 1959; Hoogstraal, 1960). However, the unequal d_1 and d_2 stand separately anterior of the pit in the adult *O. (R.) batuensis* and *O. (R.) salahi* Hoogstraal (Dumbleton, loc. cit.).

Medial setae (= posterior hair tuft) also vary in numbers in ixodid and argasid species examined by the light microscope and by SEM. In ixodids they number four in the adult and nymph and two in the larva (Foelix and Axtell, 1971; Axtell et al., in press; Roshdy, unpublished), but in *A. arboreus* they number two or three in the adult, two in the first nymphal instar, and one in the larva. Medial setae number three in larval *O. batuensis*, *O. salahi*, *O. faini*, and *O. capensis*, two in *O. solomonis* and *A. vespertilionis*, and none in *A. persicus* (Dumbleton, 1959; Hoogstraal, 1960). Moreover, Dumbleton illustrated four medial setae in adult *O. capensis*, *O. batuensis*, and *O. salahi*.

The *A. arboreus* pattern of anterior pit setae numbering five in the larva and seven in the first-instar nymph and adult also occurs in the argasid species discussed above and in several ixodid species (Arthur, 1953, 1956; Foelix and Axtell, 1972; Axtell et al., in press; Roshdy, unpublished).

Most sensilla seen by transmission electron microscopy in both *A. arboreus* and *Amblyomma americanum* are multi-innervated and possess various pore systems in the wall. Sensilla with large, plugged pores are practically identical in both species but have not been reported for any other arthropod.

The *A. arboreus* d_1 and d_2 sensilla have chemoreceptive dendrites similar to those in

Amblyomma americanum. However, d_1 in *arboreus* and d_2 in *americanum* possess two additional mechanoreceptors, suggesting both chemo, and mechanoreception.

Notably, *Argas arboreus* has many sensilla (d_2 , A_4 , A_6 , A_7 , and posterior), in addition to d_1 , with small pores and fine canals in the walls. Corresponding sensilla of *Amblyomma* previously thought to have only a single apical pore (Foelix and Axtell, 1971) have now been restudied and observed to have pore systems similar to those described here for *Argas*.

The typical double innervation of A_1 sensillum (4 + 5 dendrites) in *Amblyomma* is not found in *Argas* which has only five dendrites. Moreover, in *Argas A_4* has two mechanoreceptors but in *Amblyomma* it has none.

The dendritic ciliary region of all sensilla examined follows the common 9 + 0 formula in *Argas* and 11 + 0 formula in *Amblyomma americanum* (Foelix and Axtell, 1971, 1972). In this respect, *Amblyomma americanum* may represent an exception to a general rule since all other studied arthropod sensilla exhibit a 9 + 0 ciliary region.

The Haller's organ capsule is much smaller and less conspicuous in argasids than in ixodids and its morphology may be characteristic of genera, subgenera, or species (Bonnet, 1907; Schulze, 1941; Arthur, 1962). The interesting perforated roof of the *A. (P.) arboreus* capsule has not been observed in *A. (P.) persicus* and *A. (Carios) vespertilionis* examined by the light microscope (Dumbleton, 1959). Reticulation of the roof of Haller's organ capsule has been observed by light microscopy in the seven species of the bat-infesting subgenus *Reticulinasus* Schulze of *Ornithodoros* (Hoogstraal, 1953, 1960; Dumbleton, 1959). However, in *Ornithodoros erraticus* (Lucas) the deep, oval, thick-walled capsule lacks a roof but several setae project over the open cavity (El-Ziady, 1958). These various forms of argasid capsule provide diagnostic features and a greater variety of species should be studied by SEM for comparison with the present findings in *Argas* and ixodid ticks.

The capsule sensilla number four in *Argas* but seven in *Amblyomma*. Four similar sensilla were illustrated in larval *A. (P.) arboreus*, *A. (P.) reflexus*, and *A. (A.) hermanni* (Kaiser

et al., 1964). *A. (Carios) australiensis* Kohls and Hoogstraal (Hoogstraal and Kohls, 1965), and *O. (Alectorobius) capensis* (Dumbleton, 1958).

The families Argasidae and Ixodidae differ distinctly in many morphological characteristics, biological habits, and behavior toward hosts. Behavior particularly might be reflected in organization of specialized sensory receptors. However, our observations on *Argas arboreus* (Argasidae) and *Amblyomma americanum* (Ixodidae) show considerable similarity in basic setal morphology and in ultrastructure of tarsal sensilla. Species of other genera should be investigated to determine organization patterns and various adaptations of tarsal sensilla throughout the Ixodoidea.

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