

The tarsal sensory system  
of *Amblyomma variegatum* Fabricius  
(Ixodidae, Metastriata)

I. Wall pore and terminal pore sensilla

by

Ernst HESS \* and Michèle VLIMANT \* <sup>1</sup>

With 22 figures

ABSTRACT

Seven different types of wall pore and terminal pore sensilla of larvae, nymphs, male and female of *A. variegatum* are described. Wall pore single-walled (wp-sw) sensilla A and B have numerous plugged pores with pore tubules. Types A and B differ mainly in the thickness and the structure of the shaft wall. Wall pore double-walled (wp-dw) sensilla A and B have continuous longitudinal grooves. Vase-shaped radial canals lead from the central cavity to the grooves. Types A and B differ in the structure of the base and in the mode of innervation. Wp-dw/C sensilla have interrupted grooves and fine, somewhat twisted radial canals. Terminal pore (tp) sensilla have a terminal pore opening which is slit-like in type A and starfish-shaped in type B. Type A has two lumina while type B possesses a single lumen and a striking electron-dense intermediate layer in the tip. Wall pore and terminal pore sensilla are supposed to be mono- or multimodal chemosensory hairs.

INTRODUCTION

In spite of the information available from an increasing number of papers, knowledge of the structure and specific function of tick sensory organs is still fragmentary

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\* Institut de Zoologie de l'Université, Chantemerle 22, 2000 Neuchâtel, Switzerland.

Most of the published studies are purely morphological, and ultrastructural works are often incomplete. Physiological studies based on structurally analyzed sensilla are still inadequate.

In this paper data on the ultrastructure of wall pore single-walled (wp-sw) sensilla, wall pore double-walled (wp-dw) sensilla, and terminal pore (tp) sensilla, occurring on adults (A), nymphs (N), and larvae (L) of *Amblyomma variegatum* are presented.

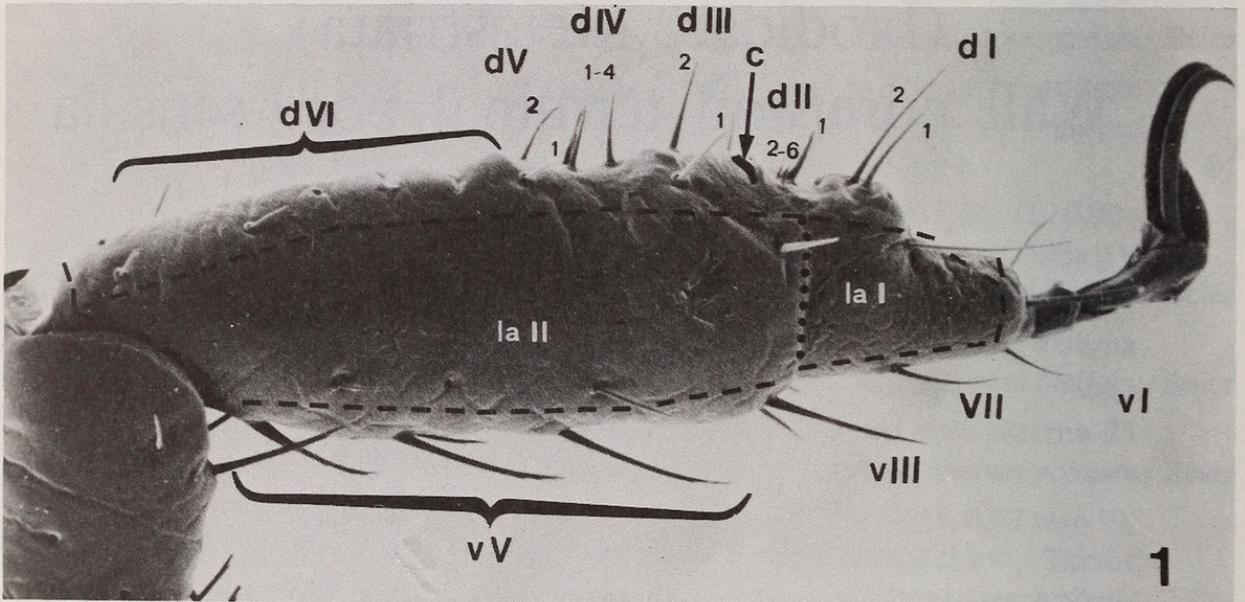


FIG. 1.

Nymphal tarsus with dorsal (d I - d VI, c: capsule of Haller's organ), ventral (v I - v V), and lateral anterior (la I, II) groups of sensilla. Group v IV is lacking in larvae and nymphs. In the groups d I to d V the mode of individual numbering of the hairs by ciphers is indicated. Dashed lines designate the limits between the dorsal, lateral anterior, and ventral faces. The dotted line indicates the pseudosegmental groove which is the limit between the groups la I and la II. Further information in the text. (224 ×).

Such hairs are presumed mono- or multimodal chemosensory hairs (Altner and Prillinger, 1980). Further papers in preparation will deal with no pore sensilla and the distribution of the sensory hairs on the tarsus I.

The nomenclature of tarsal tick sensilla is a matter of conjecture. Both, numbering and naming are used and both have disadvantages: For example "the four group" of *Amblyomma* species has only two sensilla in larvae, and "the distal group" is often missing in Argasids, where it is probably integrated in the "anterior pit". In this paper the conventional names introduced by previous authors will be given but the designations used in our laboratory will also be indicated. This designation uses letters (d for dorsal, v for ventral, lp for lateral posterior, la for lateral anterior) for the four faces of the tarsus, a roman figure to designate a group of sensilla (numbering from distal to proximal) and a cipher to designate the position of a distinct sensillum within the group (numbering from anterior to posterior and from distal to proximal) (fig. 1).

## MATERIAL AND METHODS

Larvae, nymphs, male, and female from the *A. variegatum* colony of our institute were used for this study. These ticks were reared on bovines generously placed at our disposal by Ciba-Geigy Ltd (Domaine des Barges, Vouvry, Switzerland). For scanning electron microscopy (SEM), ticks were killed, and fixed in 80% ethanol for several days, cleaned in a solution of 20% detergent in 80% ethanol by ultra-sound and then rinsed and dehydrated in acetone, and critical point dried in CO<sub>2</sub> in a Balzers CPD device. The mounted specimens were coated with carbon in an Edwards evaporator prior to be gold sputtered in a Balzers sputtering apparatus. The animals were observed in a PHILIPS 500 PSEM. Other specimens were fixed as for TEM.

For transmission electron microscopy (TEM) the tarsi were cut into small pieces in the fixing solution. Usually 3 different fixations were applied in parallel: glutaraldehyde (SABATINI *et al.* 1963) for at least 1 week, a modified Karnowsky's fixation (800 mosm) (KARNOWSKY 1965), both followed by OsO<sub>4</sub> post-fixation (PALADE 1952), and Dalton's fixation (DALTON 1955). The ultrathin sections were observed in a PHILIPS 201 EM.

## RESULTS

### Observations concerning all types of sensilla

There is no structural difference between male and female tarsal sensilla. Slight differences in length are observed between smaller and larger individuals. The surface of all sensilla is longitudinally striated (periodicity 50-60 nm) in freshly hatched animals. In older ones, the striation becomes weaker or disappears.

The cuticle of ticks is traversed by pore canals as in other arthropods. Their distal part as well as the outermost layers of the cuticle are electron-dense. These canals occur also in sensory hairs where they have their origin in the outer receptor lymph cavity. In the porous part of wp-sw sensilla they are extremely scarce. We will not mention these canals again in the description of the different types of sensilla except for a particular reason.

The sensory cells of tick sensilla have the typical structure of arthropod sensory cells with a thick inner and a thin branched or non-branched outer dendritic segment. Their ciliary region is however of special interest. In *A. variegatum*, it shows always a "(12 × 2) + 0" pattern of microtubules (fig. 21).

The pair of mechanoreceptors associated with the base of tick sensilla chaetica are typical tubular bodies (THURM 1964). Their fine structure has been described in detail by CHU-WANG & AXTELL (1973), FOELIX & AXTELL (1972), FOELIX & CHU-WANG (1972) and ROSHDY *et al.* (1972) for ticks. They will not be treated further in this paper.

### Wp-sw/A sensilla

Wp-sw/A sensilla are sensilla basiconica. Two of them are found on each tarsus I. The distal one (sensillum d I 1) (fig. 1) is 50-60 μm long and has a base diameter of 10 μm (N: 50-60/5 μm; L: 40-50/4 μm). The second one which is situated in the anterior

pit of Haller's organ (sensillum d II 1) (fig. 1) is 45-50  $\mu\text{m}$  long and 10  $\mu\text{m}$  large at the base (N: 25-35/5-6  $\mu\text{m}$ ; L: 12-14/2  $\mu\text{m}$ ).

The wall of these sensilla is pierced by a large number of evenly distributed plugged pores (pore diameter about 0,1  $\mu\text{m}$ ) (fig. 2). The minimum distance (centre to centre) between the pores is about 0,3  $\mu\text{m}$  in all instars. In adults, the shaft of wp-sw/A sensilla is relatively thick-walled (0,6-1  $\mu\text{m}$ ) but much thinner in nymphs and larvae (N: 0,3-0,7  $\mu\text{m}$ ; L: 0,2-0,3  $\mu\text{m}$ ) (figs. 3, 4).

The pore system is studied best in cross sections (figs. 3-6). In nymphs and adults, radial canals (diameter 0,2  $\mu\text{m}$ ) lead from the central cavity to the surface. In larvae which have a thinner setal wall (0,2-0,3  $\mu\text{m}$ ) the radial canals are missing or very short

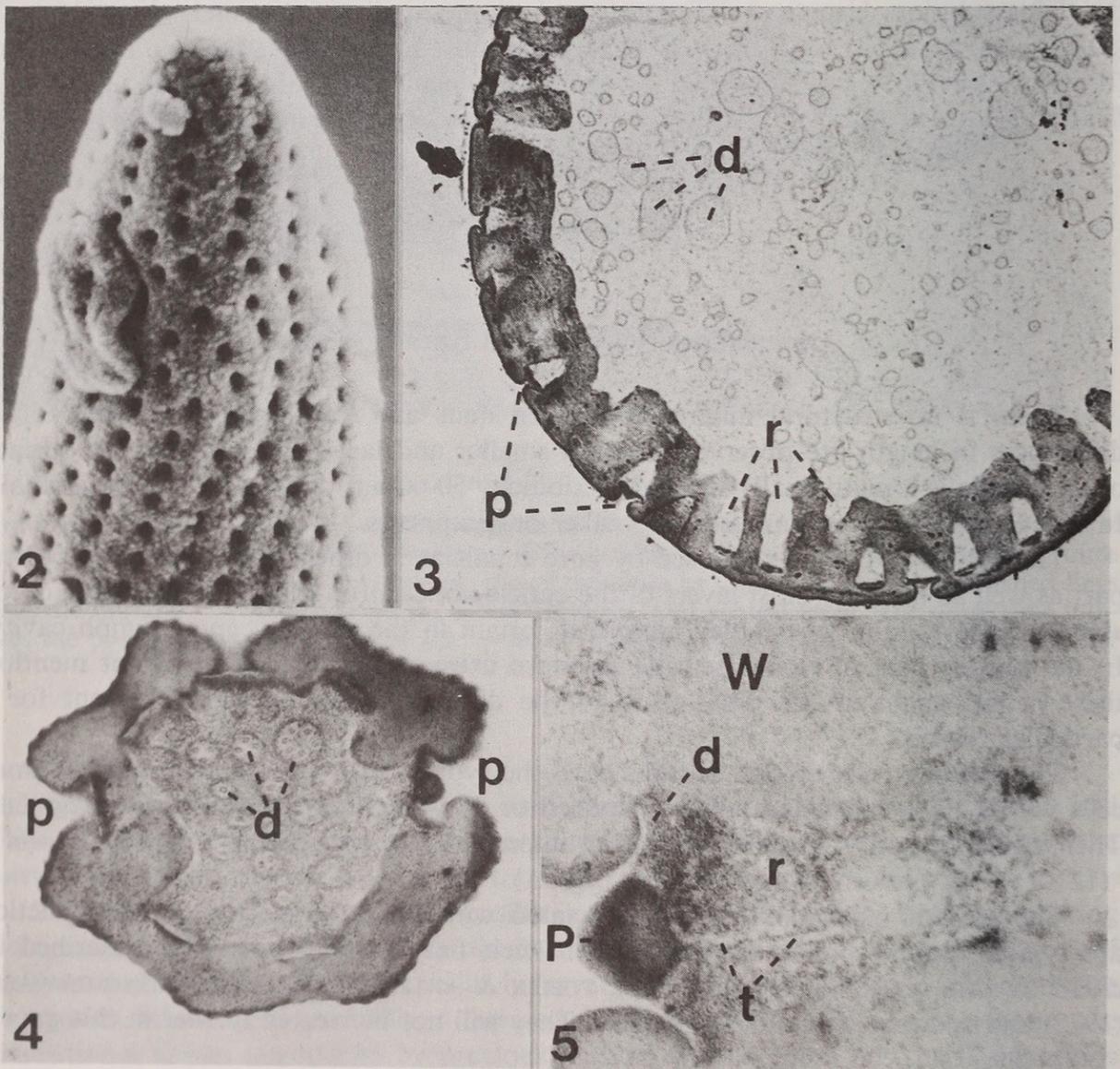


FIG. 2-5.

Fig. 2. Tip of a wp-sw/A sensillum of an adult with numerous pores. (18.000 $\times$ ). — Fig. 3. Cross section of an adult wp-sw/A sensillum. p: plugged pores; r: radial canals; d: dendritic branches. (9840 $\times$ ). — Fig. 4. Cross section of a larval wp-sw/A sensillum without radial canals. p: plugged pore; d: dendritic branches. (41.350 $\times$ ). — Fig. 5. Detail of a plugged pore. P: plug; d: diaphragm; t: pore tubules; r: radial canal filled with liquor; W: setal wall. (130.000 $\times$ ).

(fig. 4). Each of the radial canals narrows 0,15-0,16  $\mu\text{m}$  below the setal surface and opens, through a pore of about 0,1  $\mu\text{m}$  diameter, to the exterior. A 30-40 nm thick diaphragm separates the radial canal from the pore. It bears a lens-shaped cuticular plug (0,12-0,14  $\times$  0,08  $\mu\text{m}$ ) at the external face. Pore tubules or pore strands of 9-10 nm diameter

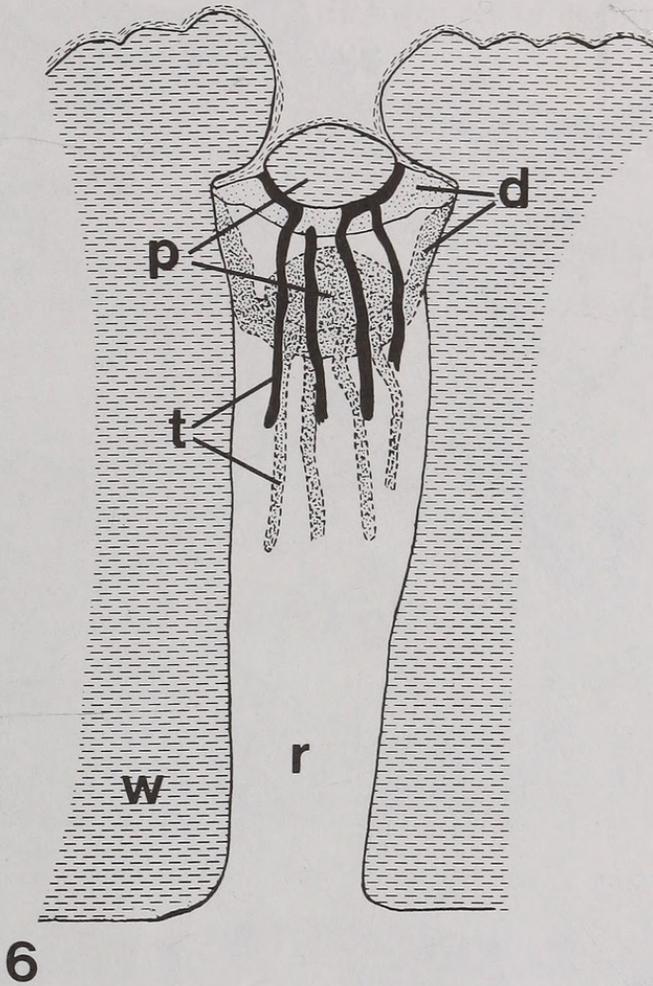


FIG. 6.

Wp-sw/A sensillum. Semi schematic representation of the pore system in its two extreme positions.

p: plug; d: diaphragm; pt: pore-tubules; r: radial canal; w: setal wall. (approx. 100.000  $\times$ ).

cross the diaphragm. They have their origin at the periphery of the plug and extend into the radial canal (fig. 5). The diaphragm-plug system is more or less retracted into the radial canal (fig. 6). The maximum distance which has been measured between the two extreme positions of the plugs is of about 0,08  $\mu\text{m}$ .

The distal wp-sw/A sensillum (d I 1) of all instars and the larval wp-sw/A sensillum of the anterior pit of Haller's organ (d II 1) are innervated by 5 neurons each. The wp-sw/A sensillum of the anterior pit of Haller's organ (d II 1) of nymphs and adults is however innervated by 3 distinct groups of sensory cells. Two of them have 5 neurons and the third, 4 (fig. 7). Each of the neurons projects a branching dendrite into the receptor lymph cavity of the hair shaft. In adults, the outer dendritic segments are about 0,7  $\mu\text{m}$  thick at the base (N: 0,4  $\mu\text{m}$ ; L: 0,3  $\mu\text{m}$ ). Distally, they have at least

10 branches each. The smallest ramifications have diameters of 70-90 nm and contain a single microtubule. The dendrites float in the receptor lymph cavity. Accidentally, one of them has been seen to extend into a radial canal, ending just behind the plug

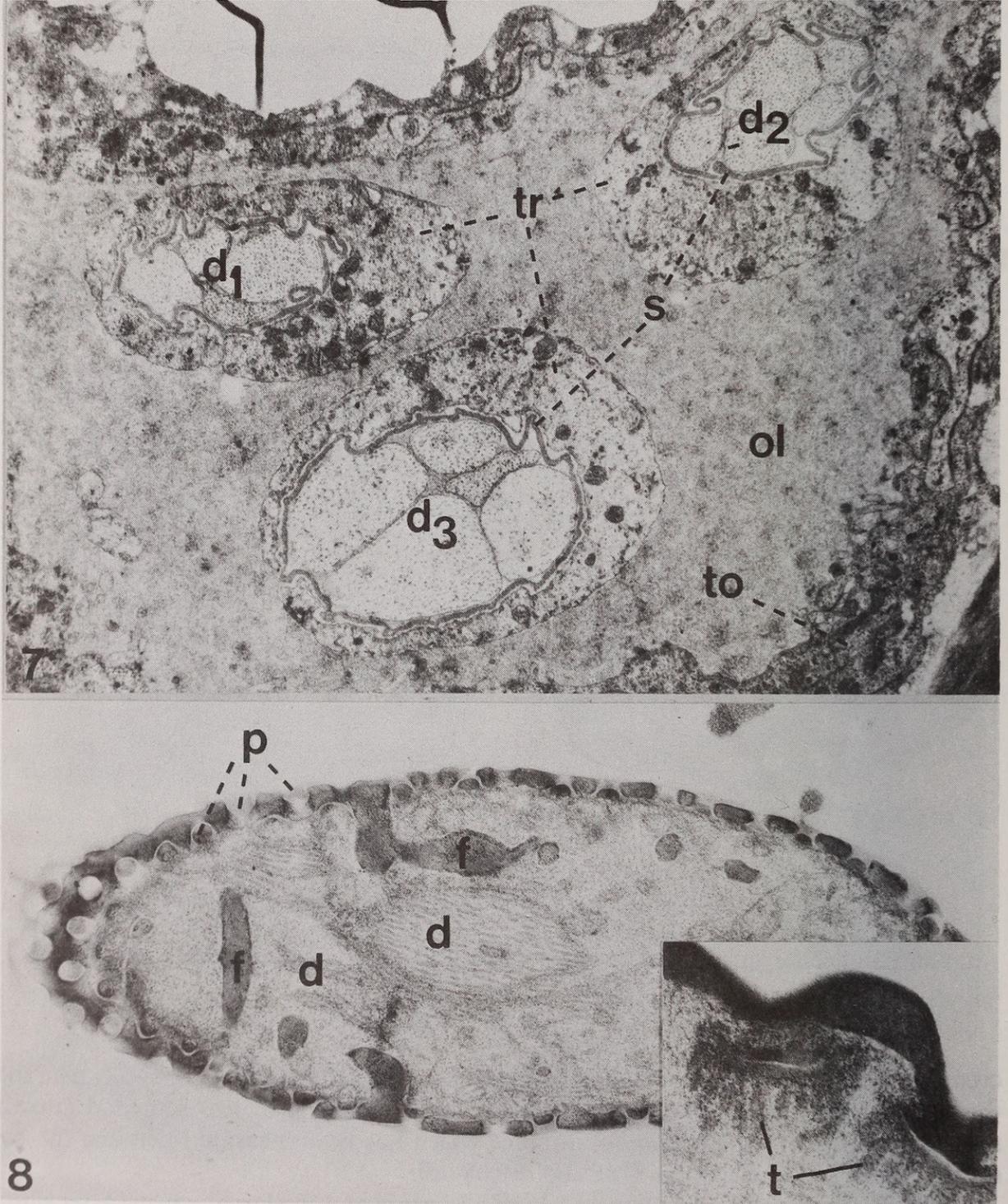


FIG. 7-8.

Fig. 7. Wp-sw/A sensillum d II 1 (anterior pit of Haller's organ) possessing 3 groups of neurons.  $d_1$ ,  $d_2$ ,  $d_3$ : dendrites; s: sheaths; tr: trichogen cells; ol: common outer receptor lymph cavity; to: tormogen cells. (9750 $\times$ ). — Fig. 8. Wp-sw/B sensillum. p: plugged pores; f: cuticular framework; d: dendrites. (17.950 $\times$ ).

Inset: Parasagittal sections of two pores. t: pore tubules. (55.740 $\times$ ).

diaphragm. The dendrites are surrounded by a cuticular sheath which has its origin in the sheath cell and frays out at the base of the hair shaft.

In wp-sw/A sensilla with a single set of neurons (d I 1 all instars and larval d II 1), the sensory cells are surrounded concentrically by a thecogen cell, and two enveloping cells supposed to be the trichogen and tormogen cells. This group of cells is enclosed by the hypoderm. In sensilla with 3 groups of neurons (nymphal and adult d II 1), each group possesses a thecogen cell and a trichogen cell of its own, the tormogen cells form a common outer receptor lymph cavity (fig. 7).

#### Wp-sw/B sensilla

Sensory hairs of this type are restricted to the capsule of Haller's organ which consists of 2 compartments partially separated by a transverse cuticular wall. The roof of the capsule is perforated by a transverse slit. The orifices of cuticular glands are

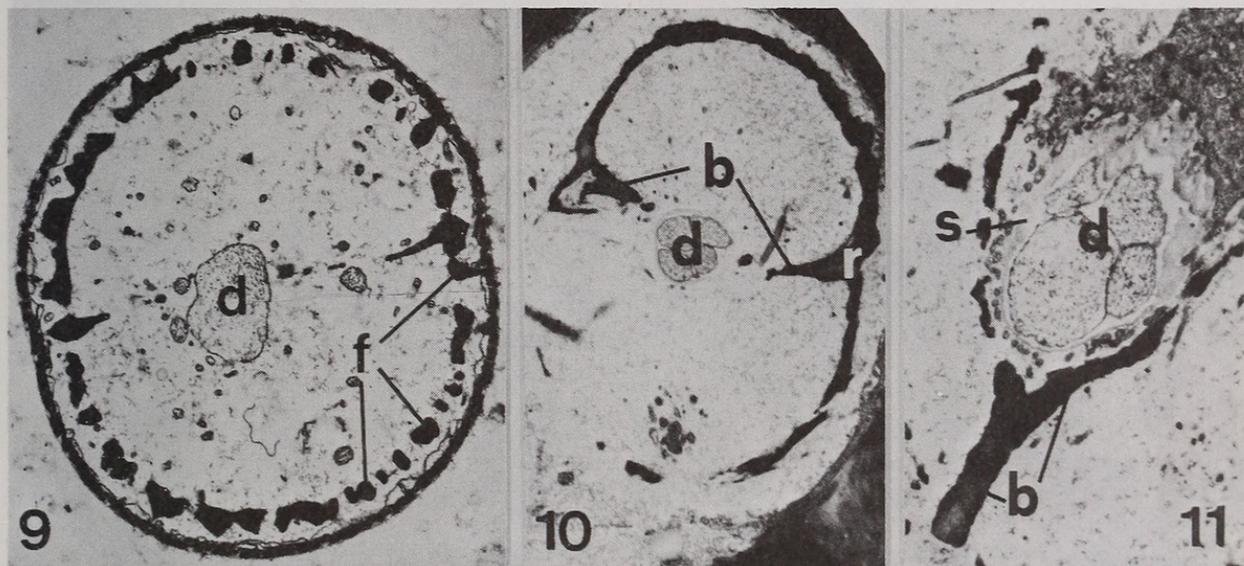


FIG. 9-11.

Fig. 9. Wp-sw/B sensillum sectioned near the base. f: longitudinal rods of the cuticular framework. d: dendrites. (5570 $\times$ ). — Fig. 10. Wp-sw/B sensillum. Section proximal to that in figure 9. r: basal ring of the cuticular framework; b: centrally directed bars of the central framework; d: dendrites. (4350 $\times$ ). — Fig. 11. Wp-sw/B sensillum. Section proximal to that in figure 10. b: centrally directed bar of the cuticular framework surrounding the dendrites. s: dendritic sheath. (6800 $\times$ ).

concentrated in the smaller distal chamber, while the proximal part is equipped with 7 wp-sw/B setae (N: 7; L: 4) and some pleomorphic cuticular projections. The sensilla (basiconica or trichodea) project from the floor and from the proximal and lateral walls of their compartment towards the slit opening. Occasionally, they are bifid. At the base they are 6  $\mu\text{m}$  thick (N: 3  $\mu\text{m}$ ; L: 2  $\mu\text{m}$ ). The shaft wall is very thin (0,08-0,14  $\mu\text{m}$ , in all instars) and pierced by numerous pores, spaced by 0,25  $\mu\text{m}$  (fig. 8). It is supported by a cuticular framework which consists of a basal ring from which irregularly shaped rods project distally. The latter attach at several points to the setal

wall (figs. 8-10). Two bars project centrally from opposite places of the basal ring towards the bundle of dendrites, partially surrounding them (fig. 11). In nymphs and larvae, the framework and the basal ring are less developed than in adults.

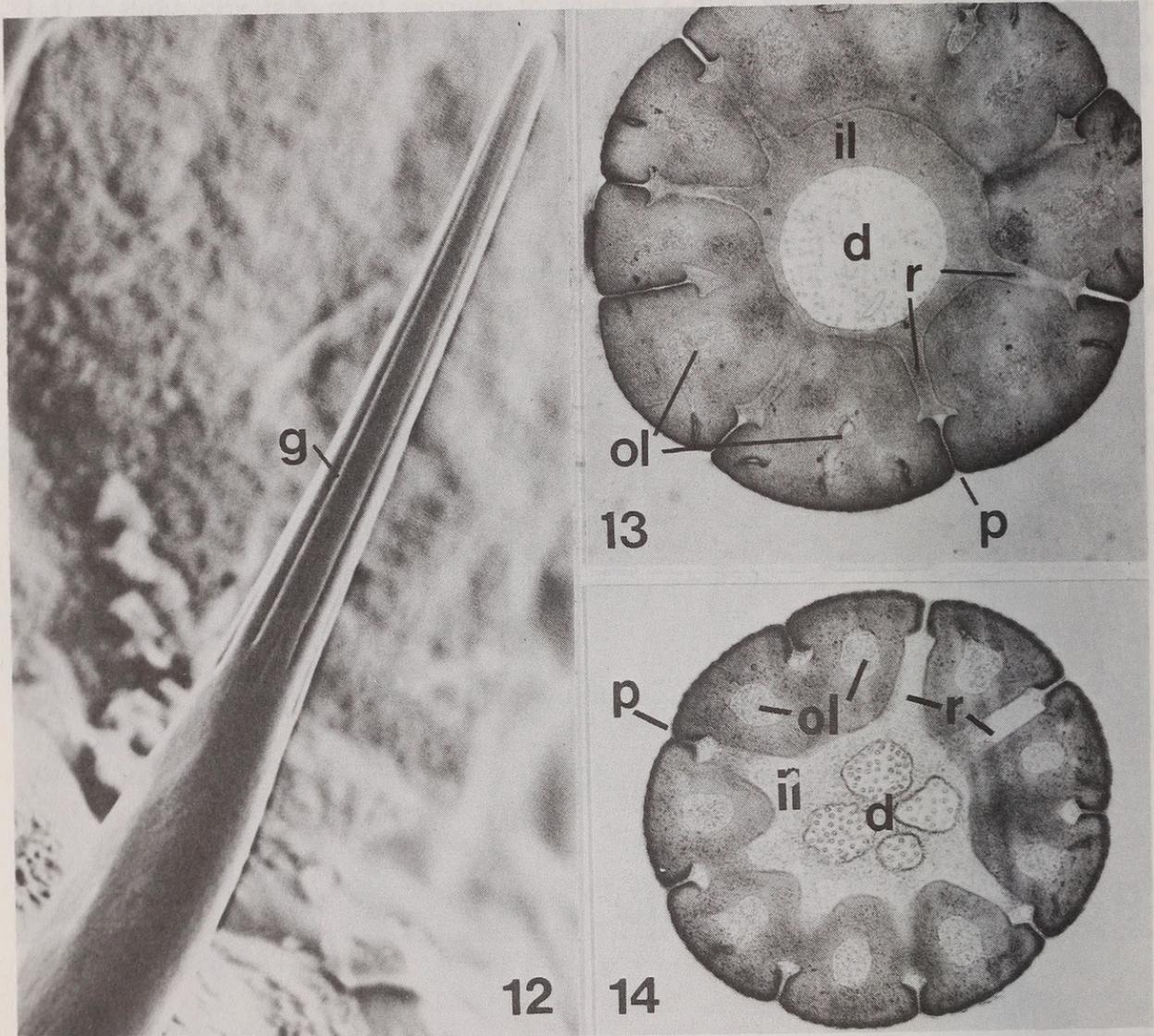


FIG. 12-14.

Fig. 12. Wp-dw/A and B sensilla have both continuous longitudinal grooves (g). (2100 $\times$ ). — Fig. 13. Wp-dw/A sensillum. p: pores opening into the grooves; r: radial canals; il: inner receptor lymph cavity; ol: outer receptor lymph cavity; d: dendrite. (22.860 $\times$ ). — Fig. 14. Wp-dw/B sensillum. Legend as for figure 13. (10.150 $\times$ ).

As wp-sw/B sensilla are thin-walled, there are no radial canals leading to the pores. The pores resemble minute funnels with the wide opening at the inside of the sensillum, the plug bearing diaphragms attached to the edges. Compared to wp-sw/A sensilla, the pores of wp-sw/B sensilla are wider (0,1-0,16  $\mu\text{m}$  in all instars) while the plugs have the same dimensions in both types (0,12-0,14  $\times$  0,08  $\mu\text{m}$ ). The pore tubules which cross the diaphragm in the same manner as in wp-sw/A sensilla are particularly well preserved in larvae fixed with Karnovsky's solution (800 mosm) (fig. 8 inset). They are 0,11-

0,14  $\mu\text{m}$  long and 26 nm thick. They seem to have a trilaminated wall and a slightly electron-dense centre. Contact between pore tubules and dendrites was not observed.

Wp-sw/B sensilla are innervated by 3-5 neurons with branching dendrites. The degree of branching varies from one sensillum to the other. Microvilli are frequently observed in the receptor lymph cavity. They may even reach the tip of the sensillum. The microvilli are almost lacking in some bristles in which case the shaft wall is covered

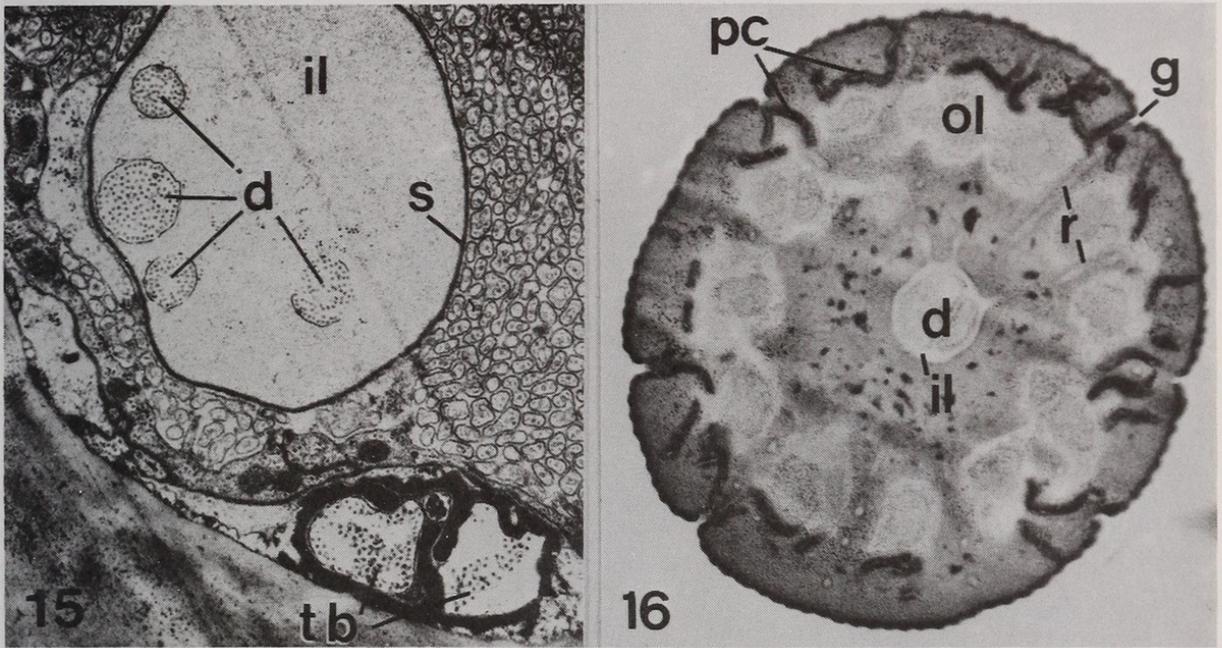


FIG. 15-16.

Fig. 15. Wp-dw/B sensillum sectioned at the base. d: outer dendritic segments projecting into the shaft. il: inner receptor lymph cavity; s: sheath; tb: tubular bodies. (14.500 $\times$ ). — Fig. 16. Wp-dw/C sensillum. r: fine radial canals opening into the surface grooves (g); il: inner receptor lymph cavity; d: dendrites; pc: pore canals converging to the surface grooves. (33.770 $\times$ ).

by a cytoplasmic layer. The latter as well as the microvilli originate, probably, from the trichogen cell. The proximal part of the dendrite bundle is surrounded by a sheath which ends at the base of the shaft where it may be fixed to the centrally directed rods of the central cuticular ring.

#### Wp-dw/A sensilla

Wp-dw/A sensilla are sensilla trichodea. They are 40-50  $\mu\text{m}$  long (N: 35-40  $\mu\text{m}$ ; L: 20-25  $\mu\text{m}$ ), and have a base diameter of 4,5  $\mu\text{m}$  (N: 3,5  $\mu\text{m}$ ; L: 3  $\mu\text{m}$ ). They are only found in the group d IV, "the four group". These sensilla have 9-12 longitudinal grooves on the upper 2/3-4/5 of the shaft (N: 7-8; L: 6-7) (fig. 12).

The basal ungrooved part is slightly thicker than the distal one. The shaft is single-walled at its base but becomes double-walled in the grooved part (wall thickness at mid-length, A: 0,7-1  $\mu\text{m}$ ; N: 0,5  $\mu\text{m}$ ; L: 0,4  $\mu\text{m}$ ). Cross sections of the shaft have a spoke wheel appearance. Vase-shaped radial canals placed one above another are situated in the spokes. They lead from the central cavity (inner receptor lymph cavity) to the

grooves. Each radial canal has a long proximal part with a diameter of  $0,08-0,1 \mu\text{m}$  (all instars), widens distally into a pore chamber ( $0,15-0,2 \mu\text{m}$  in all instars), and opens finally into the groove by a  $10-20 \text{ nm}$  narrow pore (fig. 13). The spaces between the spokes are extensions of the outer receptor lymph cavity and have no transverse communi-

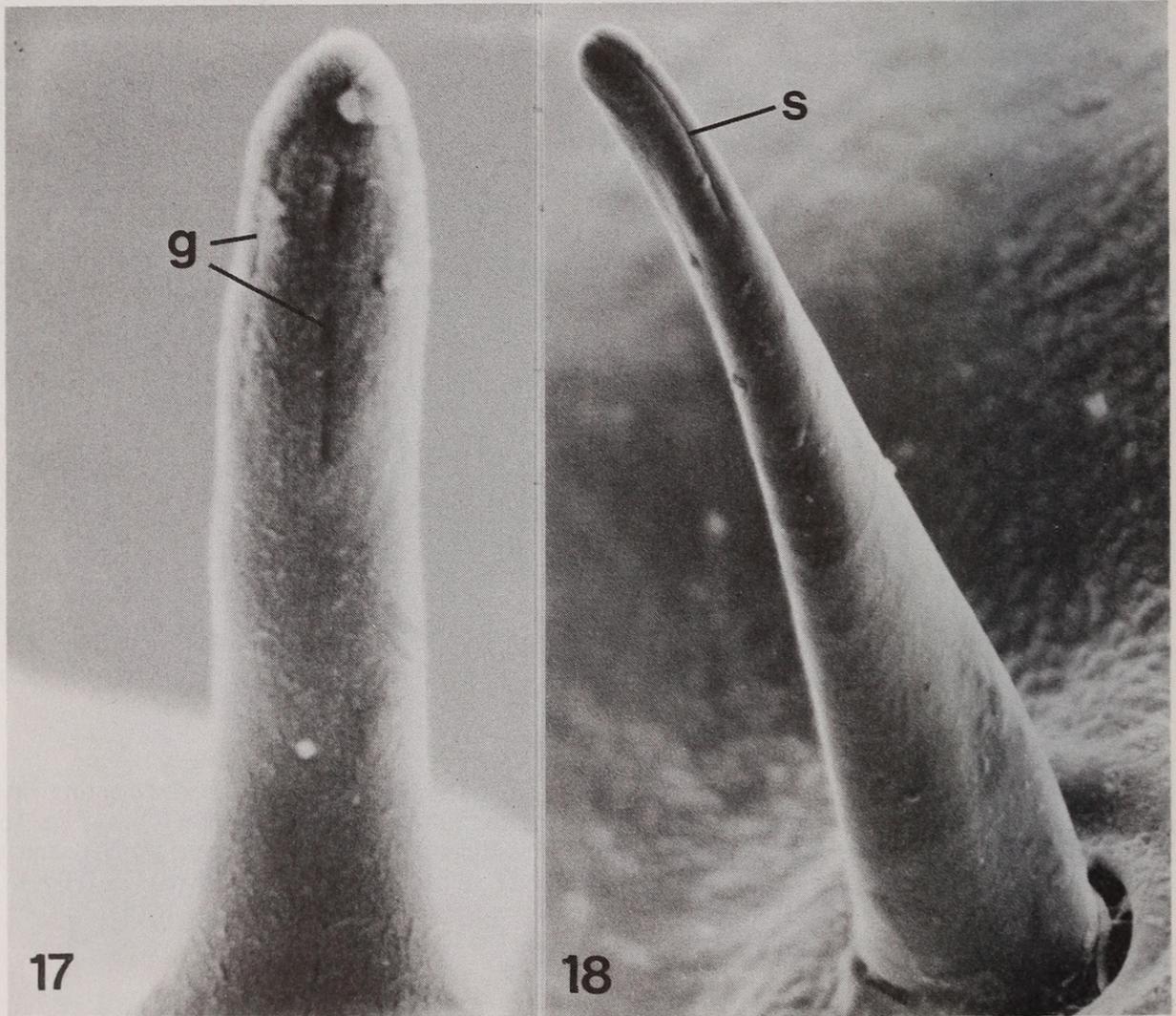


FIG. 17-18.

Fig. 17. Wp-dw/C sensillum with interrupted longitudinal grooves (g). ( $16.130\times$ ).  
 Fig. 18. Tp/A sensillum with terminal slit opening (s) and distorted shaft. ( $4570\times$ ).

cations. In the single-walled basal part, the sheath separates completely the inner receptor lymph cavity from the outer. The lymph of the inner cavity seems to be electron-denser than the liquid of the outer. Wp-dw/A sensilla possess only one or two sensory cells (fig. 13). In group d IV ("the four group") of adults and nymphs there are always 2 sensilla with 2, and 2 sensilla with 1 neuron. Larvae have only 2 wp-dw/A sensilla innervated by 2 neurons each. The unbranched outer dendritic segments of the sensory cells reach the tip. They are thick, measuring up to  $0,8 \mu\text{m}$  (N:  $0,3 \mu\text{m}$ ; L:  $0,2 \mu\text{m}$ ) in diameter.

**Wp-dw/B sensilla**

These are sensilla chaetica and they are slightly longer and larger than wp-dw/A sensory hairs (A: 60-70/7  $\mu\text{m}$ ; N: 40-50/4  $\mu\text{m}$ ; L: 30-40/3  $\mu\text{m}$ ). They appear in various groups of sensilla of the dorsal, ventral and lateral faces (d III, v I, v III, 1a II, 1p II). Except for the socketed base the morphology and structure of the wd-dw/B shaft is identical to the wp-dw/A type (fig. 14). The innervation differs however radically from the former type.

Wp-dw/B sensilla have a double innervation. Two neurons forming a tubular body each are attached to the membranous base of the hair (fig. 15). Another group of 4-7

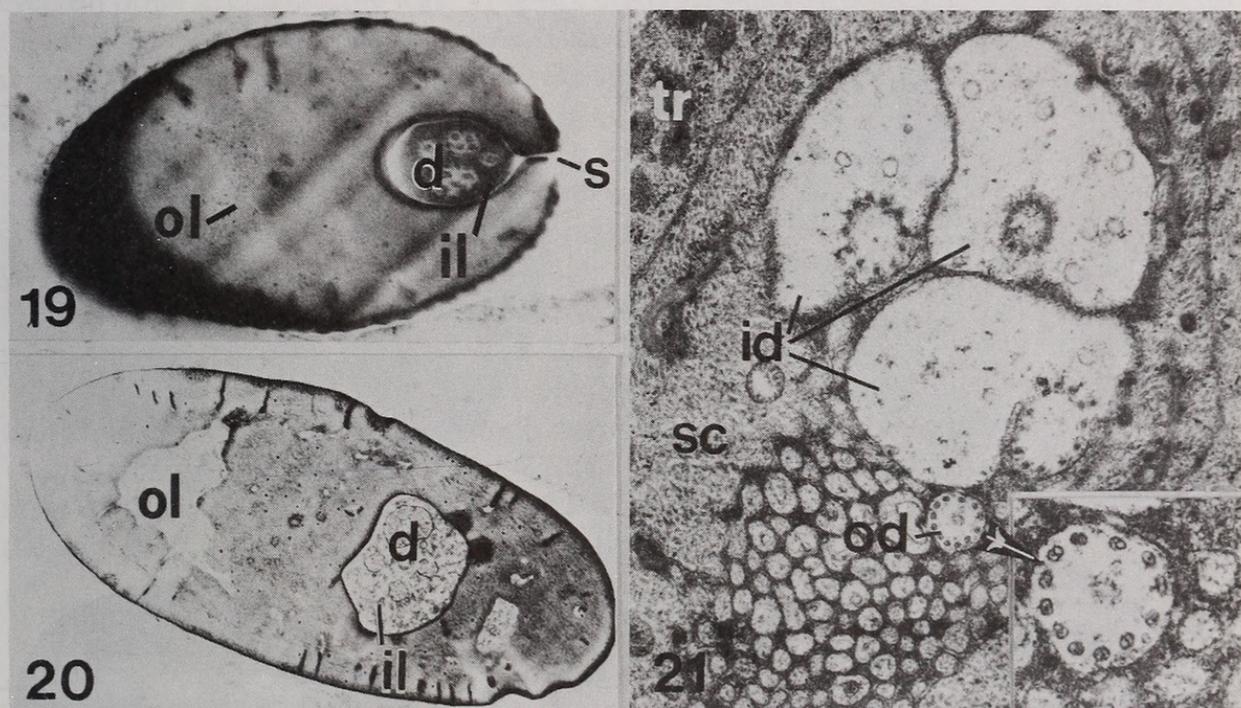


FIG. 19-21.

Fig. 19. Tp/A sensillum sectioned at the tip. s: slit opening; d: dendrites; il: inner receptor lymph cavity; ol: outer receptor lymph cavity. (44.950  $\times$ ). — Fig. 20. Tp/A sensillum. Section proximal to that in figure 19. Legend as in figure 19. (7900  $\times$ ). — Fig. 21. Tp/A sensillum. Section through dendritic ciliary region showing four sensory cells. id: inner dendritic segments; od: outer dendritic segment; sc: sheath cell; tr: trichogen cell. (18.400  $\times$ ). Inset: Base of the outer dendritic segment with “(12  $\times$  2) + 0” arrangement of microtubules. (46.300  $\times$ ).

neurons projects dendrites into the shaft (fig. 14). Their outer unbranched dendritic segments (diameter, A: 0,15-0,35  $\mu\text{m}$ ; N: 0,15  $\mu\text{m}$ ; L: 0,1  $\mu\text{m}$ ) end at different levels. The liquor of the inner receptor lymph cavity is less electron-dense than in wp-dw/A sensilla.

**Wp-dw/C sensilla**

Wp-dw/C sensilla are confined to the anterior pit of Haller's organ (sensilla d II 5 and 6). They are small sensilla basiconica with about 12 interrupted longitudinal grooves (N: 8; L: 6) on the distal 2/3-3/4 of the shaft (fig. 17). They are 15  $\mu\text{m}$  long (N: 7-9  $\mu\text{m}$ ;

L: 7  $\mu\text{m}$ ) and have a base diameter of 4  $\mu\text{m}$  (N: 2-3  $\mu\text{m}$ ; L: 1,5-2  $\mu\text{m}$ ). Like wp-dw/A and B sensilla, they are single-walled at the base and double-walled in the distal part (fig. 16). The inner receptor lymph cavity is a cuticular tube which terminates underneath the tip. Fine somewhat twisted radial canals (diameter 30 nm in all instars) enclosed in cuticular spokes lead from the central cavity to the grooves. The spokes in wp-dw/C sensilla are not continuous as in wp-dw/A and B hairs but are interrupted by transverse

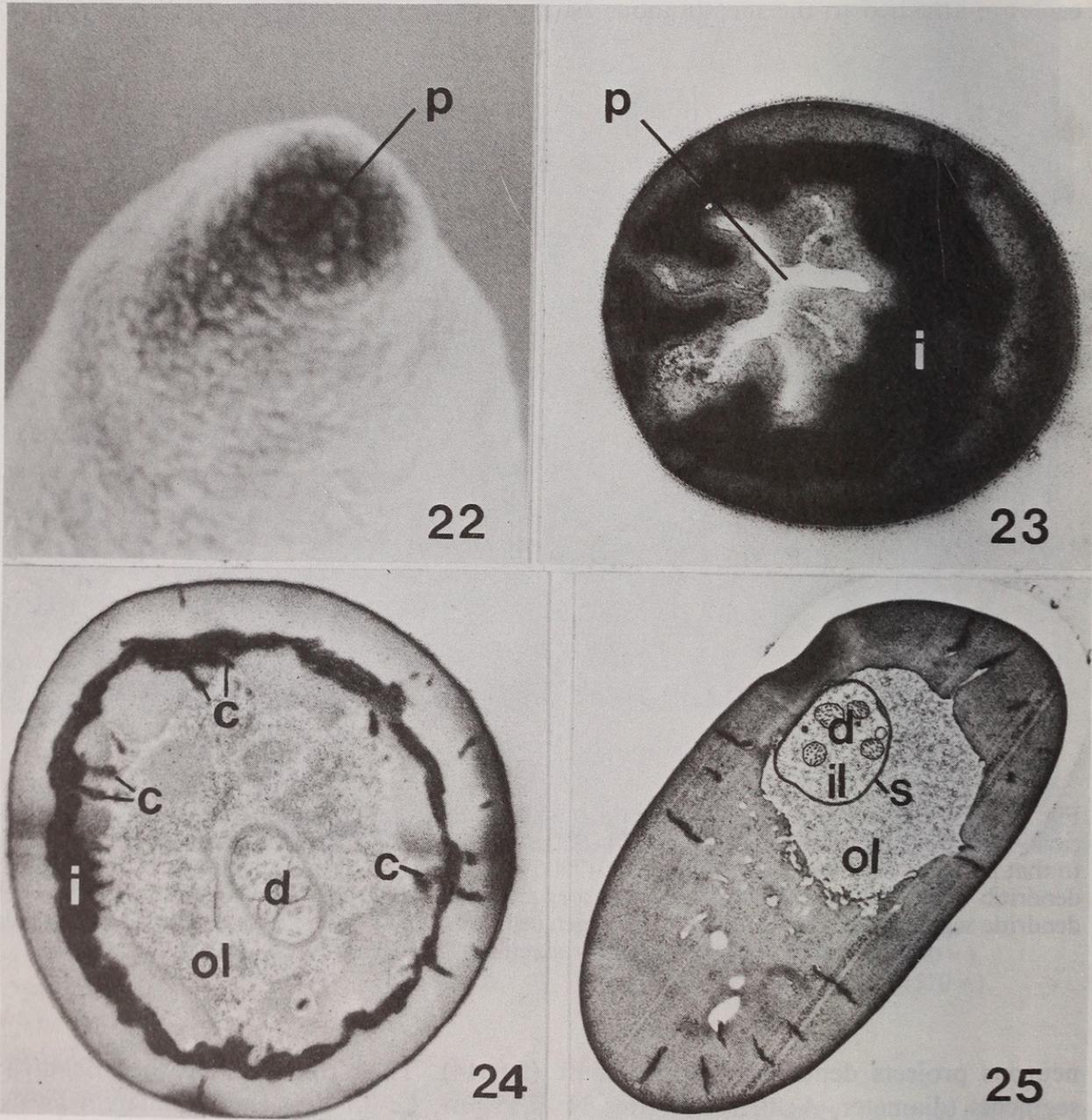


FIG. 22-25.

Fig. 22. Tip of a tp/B sensillum. p: terminal starfish-shaped pore. (37.210 $\times$ ). — Fig. 23. Tp/B sensillum sectioned at the tip. p: starfish-shaped pore; i: intermediate layer. (50.340 $\times$ ). — Fig. 24. Tp/B sensillum. Section proximal to that in figure 23. il: intermediate layer of lamellated structure; ol: outer receptor lymph cavity and the intermediate layer; s: sheath; d: dendrites. (26.030 $\times$ ). — Fig. 25. Tp/B sensillum at mid-length of the shaft. ol: outer receptor lymph cavity; il: inner receptor lymph cavity; s: sheath; d: dendrites. (9700 $\times$ ).

canals which connect the longitudinally running lumina of the outer receptor lymph cavity. The latter join in the tip to form a small terminal sinus. The interruptions of the spokes are externally visible as interruptions of the grooves. The pore canals originating from the outer receptor lymph cavity tend to converge to the grooves which is not the case in wp-dw/A and B sensilla.

Wp-dw/C sensilla are innervated by 3 (rarely 1 or 2) neurons with unbranched dendrites extending into the shaft.

### Tp/A sensilla

Tp/A sensilla are sensilla chaetica with a terminal slit opening (fig. 18). The slit is always oriented proximally. These sensilla are found on all faces of the tarsus I and even on other articles of the legs. They are 60 to 90  $\mu\text{m}$  long (N: 30-65  $\mu\text{m}$ ; L: 20-50  $\mu\text{m}$ ), the shortest being those of the lateral faces. In the ventral group v V of adults, tp/A sensilla are inserted perpendicularly to the leg surface while the other sensilla are directed distally. Their cross sections are elliptic (diameters near the base, A:  $6 \times 9 \mu\text{m}$ ; L:  $2,5 \times 4 \mu\text{m}$ ; L:  $3 \times 3 \mu\text{m}$ ). The shaft is distorted by about 60 to 90° from the base to the tip. Thus these sensory hairs are easily recognizable by SEM (fig. 18). Tp/A sensilla are thick walled (minimum diameter near base, A: 1,3  $\mu\text{m}$ ; N and L: 0,5  $\mu\text{m}$ ). At the base, the inner and outer receptor lymph cavities are completely separated by the cuticular sheath which is attached to the shaft. Distally, the two cavities run in separate canals (figs. 19, 20). The inner receptor lymph cavity which contains the dendrites opens to the outside through a slit which is situated subterminally or extends over the tip (fig. 19). The outer receptor lymph cavity does not open to the exterior.

Tp/A sensilla are innervated by 2 sets of neurons. Two sensory cells form a tubular body each at the base. Another set of 3-6 neurons projects unbranched dendrites into the hair shaft, most of them reaching the tip (figs. 19-21).

### Tp/B sensilla

Sensory hairs of this type are blunt-tipped sensilla chaetica with a starfish shaped terminal pore (figs. 22, 23). Two of them occur in the group v I (claw sensilla) of all instars. They are 100  $\mu\text{m}$  long (N: 60  $\mu\text{m}$ ; L: 40  $\mu\text{m}$ ). Their cross section is elliptic (A:  $6 \times 3 \mu\text{m}$ ; N:  $4 \times 3 \mu\text{m}$ ; L:  $3 \times 2 \mu\text{m}$ ) at the base. The shaft is not distorted but slightly bent medially towards the long axis of the tarsus. These sensilla have a single central lumen the surface of which is smooth in the lower part but scalloped in the tip (figs. 24, 25). The wall of the shaft is at least 0,4  $\mu\text{m}$  thick (N: 0,3  $\mu\text{m}$ ; /: 0,2  $\mu\text{m}$ ). The dendritic sheath which separates the inner from the outer receptor lymph cavities seems to consist of several layers, at least in the tip. It forms a wide tube at the base of the hair and narrows distally. In the tip where it fuses with the shaft wall it encloses tightly the 4 unbranched dendrites (fig. 24). The outer receptor lymph cavity contains cell fragments, probably remains of the trichogen cell. In the upper part of the shaft, it communicates by numerous canaliculi with a large sinus filled with an extremely electron-dense substance which often is of lamellated structure (intermediate layer) (figs. 23, 24). The pore canals originating from this sinus are also entirely electron-dense.

Tp/B sensilla are innervated by 2 sets of neurons. One group of 4 sensory cells has dendrites which ascend into the tip of the shaft without branching. Two sensory cells having a tubular body each terminate at the socket.

## DISCUSSION

Sensilla with plugged pores have been described first by FOELIX & AXTELL (1971) from *Amblyomma americanum*. Since then, this type of sensory hair has been found to be common in ixodid and argasid ticks (FOELIX & AXTELL 1972; LEONOWITCH 1977, 1978, 1979, 1980; HESS & VLIMANT 1980; ROSHDY *et al.* 1972; THONNEY 1980). In mites of the genus *Dermanyssus* and *Mesonyssus* (DAVIS & CAMIN 1976; MORITSCH *et al.* 1974) 3 porous sensilla which appear to belong to the wp-sw/A type have been identified on the distal sensory field of tarsus I which is considered to be homologous to the Haller's organ of ticks. Thus sensilla with plugged pores are typical for Acari.

Two distinct types of sensilla with plugged pores are distinguished in *Amblyomma variegatum*: wp-sw/A and wp-sw/B sensory hairs. Both lack a specialized socket region with mechanoreceptive function. If sockets appear in SEM they are due to inadequate drying of the specimens. Wp-sw/A sensilla are relatively thick-walled in adults and nymphs but thin-walled in larvae. Thus the thickness of the wall and the length of the radial canals do not seem to be modality specific structures. The pore system (pore, diaphragm, plug, pore tubules) on the other hand does not vary in dimension or structure from one instar to the other. Wp-sw/B sensilla which are restricted to the capsule of Haller's organ are thin-walled and possess a complicated cuticular framework the exact function of which remains enigmatic.

Further differences between wp-sw/A and wp-sw/B sensilla concern the pore system. In wp-sw/A sensilla, the pores have equal or smaller diameters than the plugs while the pores of wp-sw/B sensilla are slightly larger than the corresponding plugs. Another difference concerns the chemical structure of the pore tubules. These stimulus conducting structures which have first been described in olfactory sensilla of *Necrophorus* (ERNST 1969) occur also in ticks, contrary to the note of FOELIX (1972). In wp-sw/A sensilla they are more difficult to preserve than in wp-sw/B sensory hairs where they are numerous and easily demonstrated by adequate fixation (modified Karnowsky's). Thus one can admit chemical differences between the two types of pore tubules which should have modality specific consequences.

As to wp-sw/A sensilla, there is evidence that they are olfactory chemoreceptors. In electrophysiological experiments they respond to short-chain carboxylic acids, the corresponding aldehydes, 2,6-dichlorophenol and extracts of *A. variegatum* assembly pheromone (HESS and VLIMANT 1980 and in preparation). Recently, HAGGART & DAVIS (1981) also presented electrophysiological evidence for the olfactive activity of these sensilla.

FOELIX (1972) has demonstrated that the diaphragm which bears the cuticular plug is impermeable to Protargol®. The more or less retracted positions of the plugs could be a fixation artefact, but we cannot exclude the possibility that the plug-diaphragm system is mobile, capable of moving there and back on the long axis of the radial canal. The function of such a system would however remain enigmatic.

The mode of innervation of the wp-sw/A sensillum of the anterior pit of Haller's organ (sensillum d II 1) of *A. variegatum* is worth mentioning. In larvae there is one set of neurons but nymphs and adults have 3 distinct groups of 5, 5 and 4 neurons respectively. Thus the number of neurons increases during the development of the animal. The situation is identical in *Hyalomma asiaticum* (LEONOWITCH 1978). In *Amblyomma americanum* the corresponding larval sensillum has also 5 neurons but nymphs and adults possess two wp-sw/A sensilla in the anterior pit of Haller's organ

(FOELIX & AXTELL 1972). The one is innervated by 2 distinct groups of 5 and 4 neurons respectively and the other has a single set of 5 neurons. This could imply that wp-sw/A sensilla innervated by 2 or 3 distinct groups of neurons have evolved by the fusion of sensilla with a single set of neurons. Prostriata (genus *Ixodes*) have 1 sensillum of this type innervated by 6 neurons in the anterior pit (LEONOWITCH 1977; Thonney, personal communication).

Sensilla with longitudinal grooves belong to the wp-dw type. They are characterized by wall pores which open into the bottom of the grooves, and they lack pore tubules. On tarsi I of *A. variegatum*, wp-dw/A, B, and C sensilla have to be distinguished. Wp-dw/A and B sensilla have an identical structure of the shaft. They differ however by the structure of the base, their innervation and their location. Previous authors did not distinguish between grooved sensilla trichodea (wp-dw/A) and chaetica (wp-dw/B). They must however be considered as two different types. Their function is still unknown apart from the mechanosensibility of the wp-dw/B sensilla tubular bodies.

Wp-dw/C sensilla occur only in the anterior pit of Haller's organ. Their function is unknown. They resemble the grooved sensilla described by ALTNER *et al.* (1977) on the antennae of *Periplaneta americana* responding to odors and temperature decrease as well as the grooved pegs (c) of *Cimex lectularius* whose function are unknown (LEVINSON *et al.* 1974).

Two types of tp sensilla have been distinguished. The typical morphological features of tp/A sensilla are the terminal or subterminal slit opening and the distorted shaft. For the rest, tp/A sensilla are not restricted to the tarsi I but are also found on most articles of all the legs. They are common for the legs of ticks (CHU-WANG & AXTELL 1973; FOELIX & AXTELL 1971). Similar or identical sensilla have been reported from the palpal organ of *Hyalomma asiaticum* and *Amblyomma americanum* (BALASHOV *et al.* 1976; FOELIX & AXTELL 1972). Following the electro-physiological recordings presented by BALASHOV *et al.* (1976), they contain units reacting to NaCl and water. Tp/A sensilla are very similar to blunt tipped mechano-gustatory sensilla chaetica on the antennal flagellum of the second nymphal stage of the Pyrrhocorid *Dysdercus intermedius* (GAFFAL 1979).

In conclusion one might admit that tick tp/A sensilla could be mechano-gustatory sensilla. It can however not be excluded that they also contain thermosensitive units. The sensillum "Md7" of *Rhipicephalus appendiculatus* which contains a unit reacting to temperature drop (WALADDE *et al.* 1981) is probably situated in a tp/A sensillum. Unfortunately the structural description of the hair given by these authors does not permit to identify unequivocally the mentioned sensillum.

A pair of tp/B sensilla is found on each tarsus I of *A. variegatum* in the group v I (claw sensilla) of all instars. In *Amblyomma americanum* and *Argas arboreus* they are found at the same place (CHU-WANG & AXTELL 1973). Sensory hairs which are possibly identical to tp/B sensilla are situated in the palpal organ of *Hyalomma asiaticum* (BALASHOV *et al.* 1976) and *Amblyomma americanum* (FOELIX & CHU-WANG 1972). The presence of tubular bodies indicates mechanical sensibility but the functions of the remaining 4 units are unknown in spite of the electrophysiological research of BALASHOV *et al.* (1976).

The fact that tp/B sensilla are only found on the most distal parts of the legs and palps could indicate that they are involved in gustatory exploration. This hypothesis is supported by the fact that tp sensilla of insects mostly contain chemosensory units and by the observation that sensilla chaetica with an almost identical structure occur on the tip of the labia of *Dysdercus intermedius* (GAFFAL 1979). BRESCH (1973) demonstrated the gustatory function (sugar receptors) of these sensilla.

An interesting feature of tick sensory cells is the great difference in organization of the basal ciliary region. LEONOWITCH (1977, 1979) found a number of " $(9 \times 2) + 0$ " microtubules in *Ixodes persulcatus* and *Argas tridentatus*. This number has also been detected in *Ixodes ricinus* (THONNEY, personal communication). This is the most common type in invertebrates. WALADDE & RICE (1977) observed a " $(10 \times 2) + 0$ " configuration in *Boophilus microplus*. *Amblyomma americanum* and *Hyalomma asiaticum* sensory cells have a " $(11 \times 2) + 0$ " pattern of microtubules in the ciliary region (FOELIX & AXTELL 1972; LEONOWITCH 1978) while it is " $(12 \times 2) + 0$ " in *Amblyomma variegatum*. This uncommon variation of the number of the ciliary microtubules in ixodid ticks would be worth examining in detail.

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