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Structural Polarities in Mechanosensitive Sensilla and Their Influence on Stimulus Transmission (Arthropoda)*

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Summary. 1. The fine structural architecture of arthropod sensory hairs which had been identified as mechanoreceptive both electrophysiologically and by the presence of a tubular body were examined in serial sections.

2. In addition to the tubular body they are characterized by cuticular elements: a joint membrane, a socket septum and usually by suspension fibers too.

3. In all cases studied at least one of these elements forms the basis for a structural bilateral symmetry along whose plane of symmetry the direction line of the maximum receptor sensitivity lies.

4. The tubular body lies between the hair shaft and the socket septum or an equivalent structure. The hair shaft provides leverage to displace the tubular body and the socket septum (or its equivalent) limits the extent of the tubular body's lateral displacement.

5. The same elements and structural relationships were found in the insertion systems of other arthropod sensory hairs too which were identified by their tubular body but for which no electrophysiological evidence is available.

A. Introduction

The first electrophysiological investigations of the hairlike mechanosensitive sensilla of the cockroach (Pumphrey, 1936), the locust (Haskell, 1959) and of flies (Wolbarsht and Dethier, 1958; Wallis, 1962) revealed a directional sensitivity. Thurm (1963), who investigated bristles of the bee, conjectured that the directional sensitivity might give information on the stimulus mechanism.

Subsequently correlations were found repeatedly between the ultrastructure of such sensilla and their directional sensitivity (Nicklaus, 1965; Hoffmann, 1965; Camhi, 1969; Spencer, 1974). Hoffmann (1965) wrote: "... Eigenschaften wie Richtcharakteristik

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und die Fähigkeit, ein räumliches Reizmuster abzubilden, sind in der Regel schon aus dem strukturellen Gefüge des Sinnesorgans zu erkennen". Further on he proposed that structural polarities are always to be understood in relation to directional sensitivity of the receptors. Our findings have confirmed that structural polarities of the sense cell as well as structural polarities of the cuticular insertion apparatus are responsible for characteristic directional sensitivity.

As early as in 1962 Larsen had taken into consideration that a structural component in the socket apparatus (membrane) of the taste hairs in the fly could be involved in the process of stimulus transmission. Unfortunately the corresponding structures were often neglected in descriptions of other tactile sensilla. It is characteristic of these structures to form a linkage between the hair socket and the distal part of the dendrite (tubular body = place of the primary process, Thurm 1964). For this reason it seemed to be logical to examine their significance in the transmission of mechanical stimuli.

B. Material and Methods

Sensilla chaetica were investigated: a) on the heads of *Locusta migratoria* (L.) (Saltatoria), *Calliphora vicina* Rob.-Desv. (Diptera) and *Polyxenus lagurus* (L.) (Diplopoda), b) on the antennae of *Hemilepistus reaumuri* (Audouin et Savigny) (Isopoda), c) on the ovipositor of *Calliphora vicina* Rob.-Desv. (Diptera), d) on the tarsi of *Phormia terraenovae* Rob.-Desv. (Diptera) and e) on the episternal cone of *Apis mellifera* L. (Hymenoptera). The bees were collected near Heidelberg; the diplopods were collected in the greenhouse of the Regensburg University; all other animals were descended from laboratory cultures of the Fachbereich Biologie, University of Regensburg.

Fixation and dehydration was undertaken according to Gaffal and Hansen (1972) and Altner and Thies (1973). The preparations were embedded either in Durcupan ACM (Fluka, Buchs, Switzerland) or in ERL (Serva, Heidelberg) as described by Spurr (1969). Serial sections were made with a diamond, either on a LKB-Ultratome III or a Reichert Mikrotom OmU$_3$. The sections were double-stained (uranyl acetate, lead citrate). Observations were made in part with a Siemens Elmiskop IA; otherwise with a Siemens Elmiskop 101.

Electrophysiology. Only females of *Calliphora vicina*, not older than 1 week, were investigated by electrophysiology. The hair shafts were deflected by hooks at the tips of electrolytically sharpened tungsten wire (diameter: ca. 20 μm) mounted on the membrane of a loud-speaker. Definite deflection angles and velocities resulted from ramp-like voltage changes in the loud-speaker. Details of the method will be published elsewhere (Theiß, in prep.). The nerve impulses were recorded by standard methods with tungsten electrodes from the axon of the receptor. The average impulse frequencies from the phasic and the tonic portions of the response were evaluated. Nerve impulse from the hairs on the ovipositor were recorded with a capillary electrode, placed over the hair shaft whose tip was amputated (Wolbarsht and Dethier, 1958).

C. Results and Discussion

I. SENSILLA CHAETICA ON THE HEAD OF *LOCUSTA MIGRATORIA*

The distribution, range of sizes, preferred direction of the hair shaft curvature and structure of these hairs as resolved by light microscopy were thoroughly described by Smola (1970a). Corresponding hairs of *Schistocerca* (Guthrie, 1966) are similarly constructed: Tripartition of the socket structures into joint membrane (JM, Figs. 1 and 2; Manschette, Smola, 1970a), suspension fibers (SF; hair socket diaphragms, Guthrie, 1966; Gelenkmembran, Smola, 1970a) and socket septum (SS; drawn, but not designated by Guthrie in Fig. 1 and by Smola in Fig. 4) is distinctly seen.

In contrast to the observations of Guthrie (1966), Camhi (1969) and Smola (1970a) these sensilla are innervated as a rule by two bipolar sensory cells (in some cases as in typical contact chemoreceptors even five sensory cells were counted). Only sensilla with

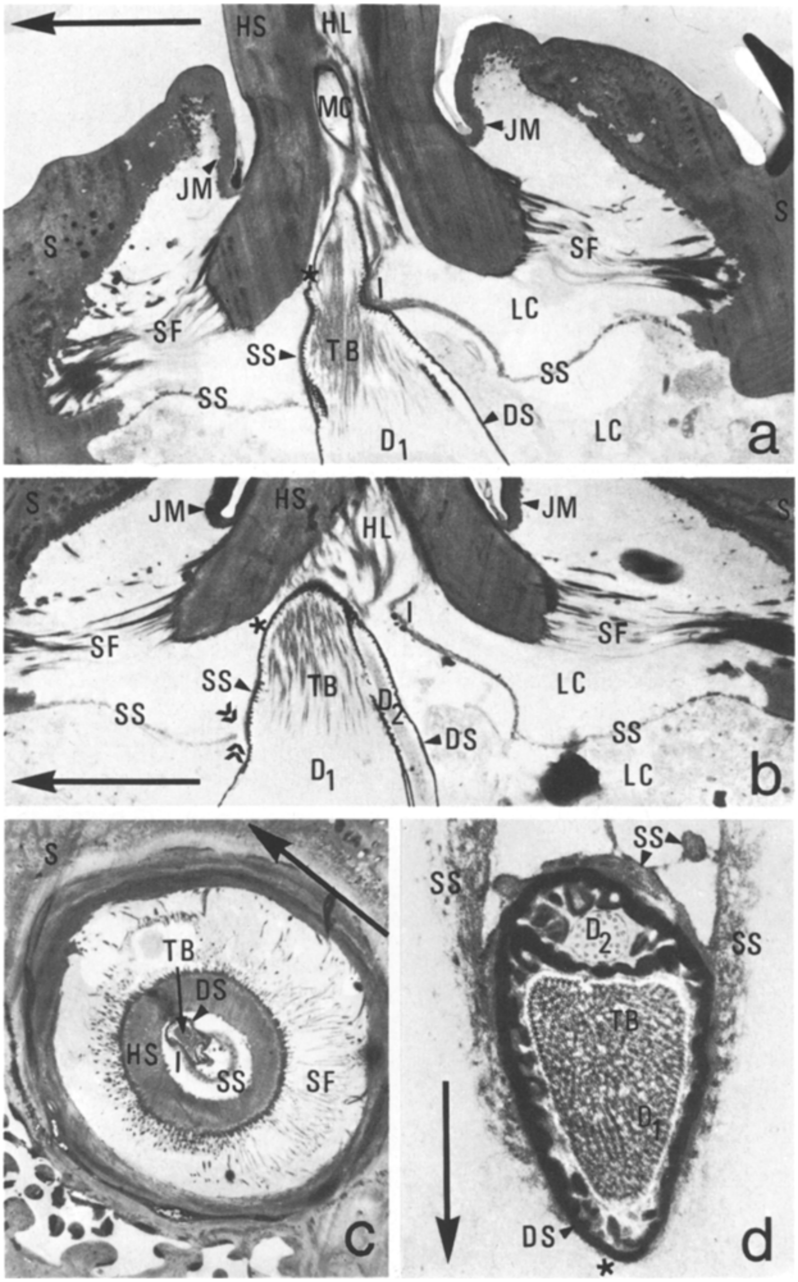

Fig. 1a–d. Tactile sensilla on the head of *Locusta migratoria*. The direction of maximal sensitivity is indicated by arrows. (a) Longitudinal section (slightly rotated out of the plane of symmetry) through articulating apparatus; X 5000. (b) Slightly oblique longitudinal section through socket apparatus. The hole in the socket septum is indicated by double arrow; X 5400. (c) Cross section through socket at level of hair shaft base; X 3000. (d) Cross section of triangular tubular body; X 25500

two sensory cells were investigated in detail. The two dendrites (D_1, D_2, Figs. 1 and 2) surrounded by the dendritic sheath (DS) enter the lumen of the hair shaft (HS), the base of which is widened. They adhere to the convex side of the shaft base and are not attached at the center, as the interpretation of transmitted light micrographs led Haskell (1959) to suggest. They are in contact with the outside through the dendritic moulting channel (MC). Only the thicker dendrite (D_1) contains a tubular body (TB) which is nearly triangular in cross section.

The hair lumen (HL) is filled at the base more or less densely by cuticular material (= cytoplasmatic reticulum, Guthrie 1966). This material is continuous with the roughly hat-shaped socket septum (SS) which surrounds the dendrites at the level of the tubular body. The expanded brim of this hat-like structure extends up to the exocuticle of the socket (S). The socket septum shows a marked bilateral symmetry, the symmetry plane being coincident with the curvature plane of the hair shaft. The bilateral symmetry is evident at several points: 1. The crown of the socket septum bulges out more towards the side opposite the moulting channel (Figs. 1 and 2). 2. The socket septum is grooved (I, Figs. 1 and 2) on both sides along the upper two-thirds of the tubular body. As a result its wall and the dendritic sheath are in close contact with one another. 3. The socket septum completely surrounds the dendritic sheath only at the base of the tubular body. More distally a slit (*, Figs. 1 and 2) opens at the side of the moulting channel. 4. The outer lymph cavity (LC) is divided by the socket septum into an upper and a lower compartment. Both compartments are in communication with one another via an opening about 200–250 nm in diameter (indicated by double arrow, Figs. 1 and 2).

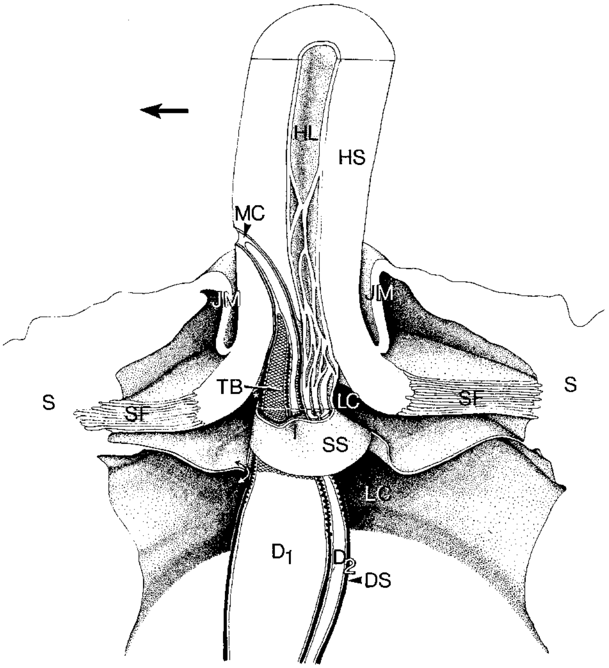

Fig. 2. Diagrammatic reconstruction of sensillum on the head of *Locusta* bisected except for inner region of socket septum. The direction of maximal sensitivity is indicated by arrow; X ca. 1300

1. *Function of the Socket Septum*

In the tactile sensory hairs of the cotton stainer (Gaffal and Hansen, 1972) deflections of the hair shaft in preferred directions seem to be suitable to produce lateral displacement of the tubular body by the action of a special lever-like projection (= hebelartiger Fortsatz). A counter force against the tubular body is exerted by a structure (Widerlager) in *Dysdercus* comparable to the socket septum of *Locusta.* Thus compression (= adequate stimulus, Thurm, 1964; Barth 1972, 1973) is exerted on the tubular body by pinching it against the socket septum. Although the socket septum has only a thin wall and therefore seems to be rather unstable, its hat-shaped construction and its attachment at the socket cuticle provide sufficient stability to offer the needed resistance to the lateral displacement of the tubular body. Apparently both the compressive stability on one side and the tensile stability on the other side of this cuticular structure are utilized so that the part of the socket septum, in close contact with the tubular body is relatively less displaced than the base of the hair. The indentations of the socket septum could cause its stiffening in a similar fashion to that seen in corrugated sheet.

2. *Correlations between Physiological and Morphological Characteristics*

a) Stimulus Transmission

Fig. 3 presents a possible mechanism of stimulus transmission in the sensilla of *Locusta.* The cleft between the hair shaft and the joint membrane is so small that the hair shaft, when deflected about 3° in the direction of maximal sensitivity, strikes against the socket's bulge (Fig. 3a). If deflections are greater than 3° the fulcrum is at the touch point (Fig. 3b), as was postulated by Smola (1970a) from light microscope oberservations. Based on experiments with simple models and considering that the weakest point of the articulating apparatus is the lower edge of the joint membrane, it seems plausible to place the fulcrum within the circle of Fig. 3a. The length of the lever arm which presses against the tubular body will differ depending upon the placement of the fulcrum, and the displacement of the tubular body per degree of deflection of the hair shaft will also differ accordingly. This can further be equated with differences in lateral pressure. The static characteristic curve of these sensilla is divided into three regions (Smola, 1970b). Compared with the initial region (deflection: 0–3°) the slope in the linear region (deflection: 3–12,6°) is considerably steeper. The magnitude of the receptor potential shows no further increase in the saturation region. The range of the deflections up to the touch point corresponds well with the initial region, an agreement between anatomical and physiological characteristics which points (at least up to the beginning of the saturation region) to a causal relation between the length of the lever arms and the slopes of the static characteristic curve.

b) Directional Characteristic

Electrophysiological investigation has shown both in *Locusta* and *Schistocerca* that these sense hairs respond most sensitively to deflections contrary to their direction of curvature. Deflections in the direction of their curvature were without effect (Haskell, 1959; Sviderskii, 1967, cit. with Camhi, 1969; Camhi, 1969; Smola, 1970b). The following anatomical characteristics may explain this result: 1. Because of the off-center position of the dendritic tip the hair shaft wall is able to displace the tubular body much

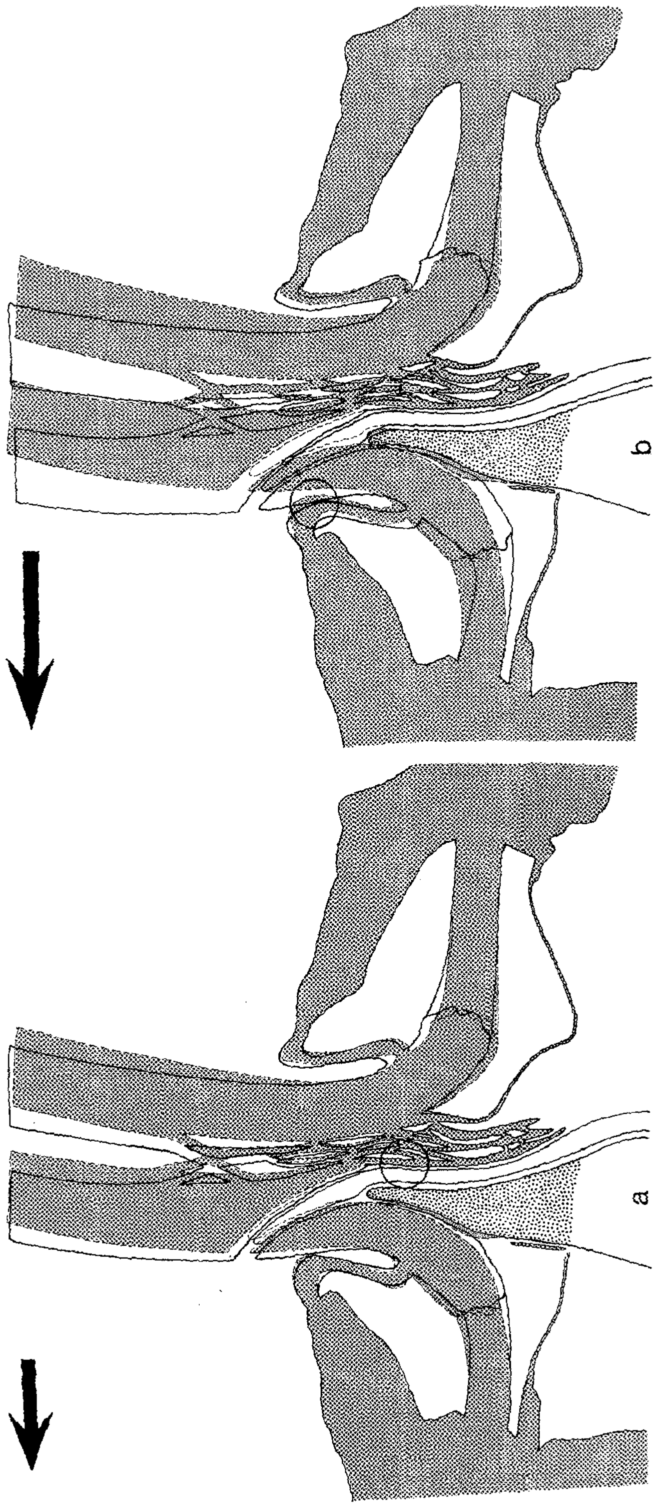

Fig. 3a and b. Schematic conception of stimulus transmission in the sensilla of *Locusta*. The resting positions of sensory hairs are represented by dotted areas and the dashed lines. Solid lines indicate displacements of the hair shaft, the socket structures, the dendritic ends and the fulcrums (circles when the hair is deflected in the most sensitive direction (arrow). (a) 3°; (b) more than 3°

more readily when the hair shaft is deflected to the sensitive side than when deflected in the opposite direction. 2. The tubular body, triangular in cross section, offers its broadest sides and accordingly the greatest surface for action to the points of contact between the socket septum and the dendritic sheath (especially the lateral grooves). Possibly as a result of this fact, these sensilla still respond maximally even to deflections which deviate considerably from the main direction (half-magnitude angle of the directional characteristic diagramm = 162°; Smola, 1970b). 3. Due to the longitudinal slit in the socket septum, the tip of the tubular body is able to give way when deflections of the hair shaft are sufficient to exert pressure from opposite side (compare with point 1).

3. Comparison with Similarly Constructed Sensilla

The funnel-shaped hair base is circular in cross section instead of elliptical as in *Gryllus* (Gnatzy and Schmidt, 1971) and *Periplaneta* (Nicklaus, 1967; Gnatzy, 1973). Furthermore we observed no special differentiations in the ultrastructure of the articulating apparatus which might restrict freedom of movement as those in *Periplaneta* (Nicklaus, 1965) for example. These findings agree with light microscope investigations and with measurements of the elastic forces which appear when the hairs are deflected in different directions (Richtungsabhängigkeit der Auslenkempfindlichkeit; Smola, 1970a). In contrast in the corresponding sensory hairs of *Schistocerca* (Camhi, 1969) asymmetrical socket structures, which he does not describe in detail, are presumed to restrict the hair shaft's freedom of movement to a single preferential direction. In *Locusta* we have an example which (without having to take into consideration structural polarities within the articulating apparatus) allows us to attribute the directional characteristic to the bilateral symmetry of the dendritic ending and the socket septum alone.

The tactile sensory hairs of *Locusta, Gryllus* (Gnatzy and Schmidt, 1971), *Periplaneta* (Gnatzy, 1973) and *Dysdercus* (Gaffal and Hansen, 1972) display moulting channels which are typical in hemimetabolous insects. These moulting channels open in every case at the convex side of the hair. In *Locusta* and *Periplaneta* the direction of maximal sensitivity (Smola, 1970b; Nicklaus, 1965) coincides with the moulting channel's orifice. The tactile hairs of *Gryllus* and *Dysdercus* were not investigated electrophysiologically. Interpreting their socket structures in the same light as above, we propose: 1. In *Gryllus* the direction of maximum response should agree with the direction indicated by the moulting channel. 2. In *Dysdercus* the direction of maximum response should be the opposite, that is away from the moulting channel. In *Dysdercus* the dendritic tip is attached at the opposite side of the hair base from what it is in *Locusta*, but the counteracting socket septum lies in both instances on the same side (see Fig. 4). Thurm (1963) has postulated that the eccentric attachment of the dendritic tip can be considered as the fundamental cause of the directional sensitivity. In *Dysdercus*, however, the position of the pressure transmitting apparatus (hebelartiger Fortsatz and Widerlager) seems to determine the position of the directional sensitivity. In this case the off-center position of the tubular body would be better interpreted as an adaptation to embryological development (for the significance of the moulting channels see: Schmidt and Gnatzy, 1971; Gnatzy and Schmidt, 1972; Altner and Thies, 1972; Ernst, 1972). If the stimulus-effecting direction coincides with the direction of the moulting channel, the solid part of the hair wall itself is the pressure transmitting structure, as in *Locusta* (Fig. 4) and the filiform hairs of the cricket

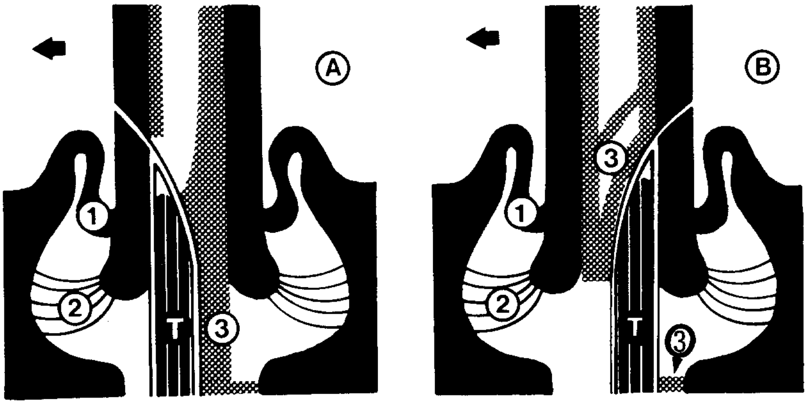

Fig. 4 A and B. Simplified models of mechanosensitive sensilla. (A) Moulting channel points in direction of maximum sensitivity (*Locusta*). (B) Moulting channel points away from direction of maximum sensitivity (*Dysdercus*). See arrows. Joint membrane (*1*); suspension fibers (*2*); socket septum (*3*); tubular body (*T*)

(Gnatzy and Schmidt, 1971) and of the cockroach (Gnatzy, 1973). If the two directions oppose each other, the additional development of a pressure transmitting structure as in *Dysdercus* (hebelartiger Fortsatz) should be necessary (Fig. 4).

The socket septum and its slit are nearly the same in *Locusta* and *Periplaneta* (Scheide, Nicklaus, 1967; Glocke aus fibrillärem Material, Gnatzy, 1973). In *Periplaneta*, however, a communication between the lymph cavity and the space above the socket septum is described as being absent. In *Locusta* at least this open communication makes speculations on a possible stimulus transmission by hydrostatic pressure (Guthrie, 1966) more or less baseless.

II. TACTILE BRISTLES ON THE EPISTERNAL CONE OF *APIS MELLIFERA*

Work done by Thurm (1963, 1964, 1965) on the tactile bristles of the bee has made crucial contributions in explaining the properties of mechanosensitive insect sensilla. Familiarity with these publications is necessary for complete understanding of the anatomy of the bristles, because only supplementary structural findings are presented here.

The upper half of the tubular body (TB, Fig. 5) is not cylindrical but elliptical in cross section. The short axis of this ellipse forms an angle of 10–30° with the sensory hair's plane of symmetry (PS). Angular displacements to the right as well as to the left side were observed from above. The ratio of left to right displacements could not be determined because only a fraction of all the episternal sensilla were investigated in detail.

The dense substance between the microtubules is not distributed uniformly across the whole tubular body, but is restricted to a cylindrical zone similar in shape to the tubular body (Fig. 5a). The outer dimensions of this flattened cylinder and its wall thickness vary considerably; but in none of the cases investigated did the outer dimensions reach the full values of the tubular body. The tip of the dendritic sheath (DS) which surrounds the tubular body enters the lumen of the hair shaft eccentrically. This lumen (HL) is filled completely by strands of cuticular material. The dendritic

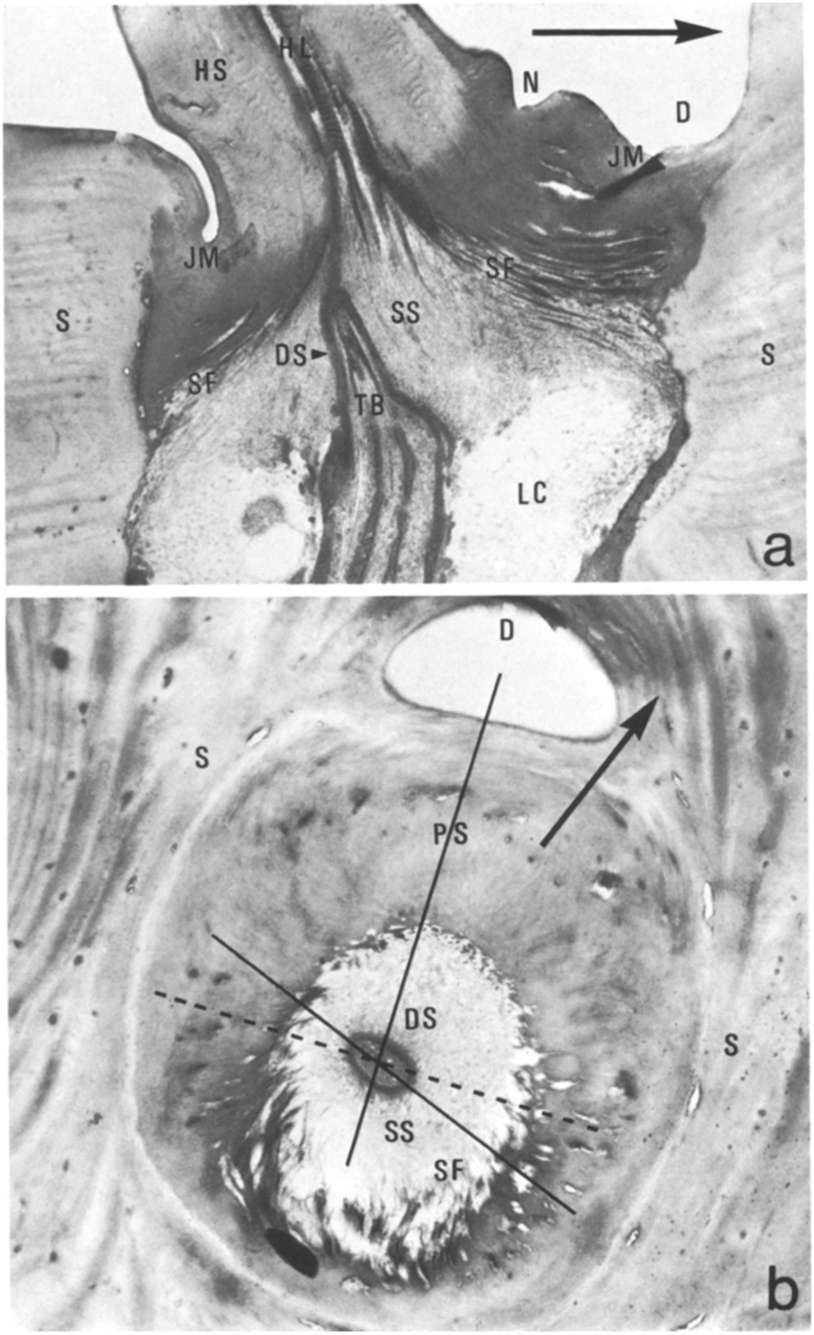

Fig. 5a and b. Episternal bristles of the bee. The direction of maximum sensitivity is indicated by arrows. (a) Longitudinal section through socket (in the plane of symmetry); X 12000. (b) Oblique cross section through socket. The axis of symmetry (*PS*) is given by line passing from center of tubular body to center of depression in joint membrane. The dashed line drawn through the center of tubular body to center of depression in joint membrane. The dashed line drawn through the center of the tubular body is perpendicular to this axis and forms acute angle with long axis of tubular body (solid line). Direction of maximum sensitivity (arrow) perpendicular to long axis; X 11300 sheath touching the wall of the hair shaft terminates at the level of the integumental surface.

The socket structures are contiguous. Accordingly there is a gradual transition between the joint membrane (JM) and the suspension fibers (SF, both together = joint membrane, Thurm, 1964). The transition from the suspension fibers to the socket septum (= cap, Thurm, 1964) is delineated more clearly. The tip of the socket septum is joined to the contents of the hair lumen. There is a depression (D) within one quadrant of the joint membrane. The hair shaft is notched horizontally in this region at the level at which the joint membrane is connected to it (N, depth of the notch: 0,5 μm).

1. Correlations between Anatomy and Directional Characteristic

From our investigation the tubular body is flattened. Its long axis forms an obtuse angle with the axis of symmetry. The direction of maximal sensitivity manifests a corresponding rotation from the sensory hair's plane of symmetry (Thurm, 1963). Therefore this deviation from the plane of symmetry would seem to be related to the slant of the tubular body. When Thurm interpreted his findings, he took the tubular body to be radially symmetrical. Therefore he looked elsewhere for the anatomical asymmetry which would provide a basis for the functional asymmetry and felt he found it in the joint membrane. For its length is not the same on all sides. Much later he and others (1975) discussed the flattening of tubular bodies with regard to their absolute change in volume. In the bee the broad side of the tubular body presents 2–3 times more working surface to forces acting on it than the small side. Therefore forces perpendicular to the broad side should be most effective. Electron micrographs of these sensilla sectioned perpendicular to their plane of symmetry also show different lengths for the joint membrane and for the suspension fibers too. The ability of these articulating structures to be strongly contrasted by uranyl acetate and lead citrate may correspond to their ability to be stained by methylen blue (Thurm, 1963). For this reason it is still uncertain which of the two deviations from the sensillum's symmetry exerts the decisive or exclusive influence on the functional characteristics. A greater influence from the slant of the tubular body is indicated by our finding that the plane perpendicular to the long axis of the tubular body forms an obtuse angle with the plane symmetry usually to the right side but sometimes to the left side. Deviations in some directional characteristic diagramms, considered to be due to technical difficulties by Thurm (1963), could be explained by tubular bodies turned to the left side.

2. Architecture and Function in Comparison to Other Sensilla

The tactile bristles of the bee show a mechanism of stimulus transmission which is different from a simple lever effect (Thurm, 1963, 1964, 1965). By reason of its position and structure, the cap can be compared with the socket septum of other mechanoreceptive sensory hairs. In the special case of the bee we have to take into consideration that both the pressure caused by indentation of the joint membrane and the counter-pressure caused by the socket wall are transmitted to the tubular body by the socket septum (= cap).

The lever-like projection of the material inside the hair lumen of antennal tactile hairs in *Dysdercus* is connected to the socket septum (= Widerlager, Gaffal and Hansen, 1972) by means of a fibrous thread (Gaffal, unpublished). Accordingly two sections of the same structural part (= socket septum) provide pressure and counter-pressure. But in *Dysdercus* unlike the bee these two sections are situated in different planes. On the other hand, in the sensory hairs of *Locusta* (*cf.* part I), *Gryllus* (Gnatzy and Schmidt, 1971) and *Periplaneta* (Gnatzy, 1973) pressure and counter-pressure are transmitted apparently by two different structures (base of the hair shaft itself and socket septum).

III. TACTILE BRISTLES ON THE HEAD OF *CALLIPHORA VICINA*

1. External Construction

The two large (900–1000 μm) bristles investigated are situated inside the triangle formed by the ocelli (Ocellarborsten, Zumpt, 1956). They are bent ventrally and laterally. On the concave side the socket has a very distinct ridge (R, Figs. 6a and 7; height 15–20 μm). On the convex side of the hair the margin of the socket is much lower (ca. 5 μm). In the region of the socket, the hair shaft (HS) has a smaller diameter (22 μm) than above the high socket ridge (28 μm). As it rises out of the socket, the diameter of the hair shaft increases more on its concave side (Fig. 7). In resting position the inclination of the hair shaft to the surface of the cuticle is about 45°. An angle of 8–12° is made with the high socket wall (Fig. 6a).

2. Internal Construction

The hair shaft articulates on the joint membrane (JM) and on the adjoining densely packed suspension fibers (SF). The socket septum (SS) is made of spongy and fibrous material (wall thickness: 0,3 μm) and is cone-shaped. The socket septum is perforated laterally by a hole (diameter: 3–5 μm) just below its apex and then continues into the hair lumen (M in HL). In the region of this hole the dendritic sheath (DS), which contains the dendrite of one sensory cell, is attached to the socket septum at the convex side of the hair. The tubular body (TB) is situated at this level inside the dendrite. The dendritic sheath and the socket septum enter the hair shaft on its convex side behind a finger-like projection (P) of the shaft. Here the dendritic sheath abruptly tapers to an end.

3. Electrophysiology

Responses, elicited by deflections of the ocellar bristles characterize the receptor as being typically phasic (Theiß, in prep.). Nerve impulses only appear during motion and only when the bristle is deflected in the direction indicated by its curvature and within 90° to either side. The dependence of the averaged impulse frequency on stimulus direction is evident from Fig. 9. The direction of maximal sensitivity coincides with the direction of the bristle curvature. When the deflections of the bristle deviate from the main direction the sensitivity gradually declines. It is about half its maximum value at + or –75 °. The threshold angle which elicit at least a single impulse is ca. 1°.

IV. TACTILE HAIRS ON THE OVIPOSITOR OF *CALLIPHORA VICINA*

The distribution of these sensilla on the tip of the ovipositor of *Calliphora* is very similar to that of *Phormia* (Wallis, 1962). In *Phormia* these hairs are situated on the ventro-lateral surface of the anal leaflets and are named T_1 and T_2 (giants). These

Fig. 6a and b. Tactile sensilla of *Calliphora.* Arrows indicate direction of maximum sensitivity. (a) Oblique longitudinal section through sensillum on the head. X 2100. Inset: Transition from the hair shaft (*HS*) to the suspension fibers (*SF*); X 9600. (b) Longitudinal section through sensillum on ovipositor; X 8000

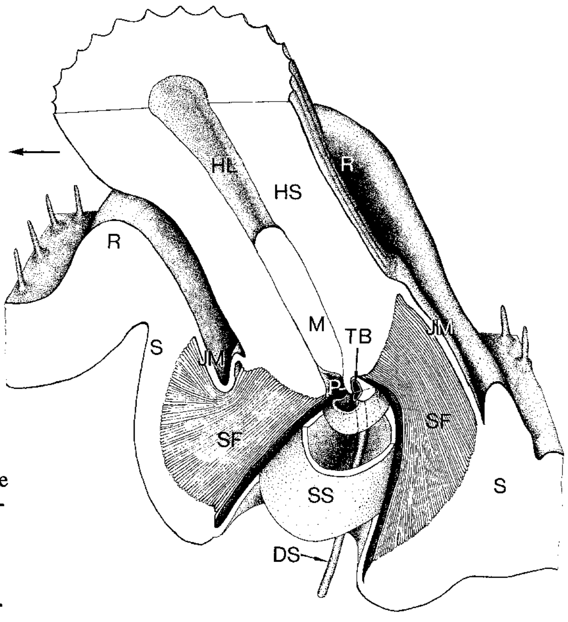

Fig. 7
Diagrammatic reconstruction of bristle on the head of *Calliphora* bisected except for the socket septum. Arrow indicates direction of maximum sensitivity. The cone-shaped socket septum with three cut out sections; X ca. 500

sharp tipped hairs (length: 270 μm; diameter at the base: 5–6 μm) point outwards and distally. They are curved slightly in the same direction.

The margin of the extremely flattened hair socket (S, Fig. 6b) is barely raised above the surrounding cuticle. The base of the hair shaft (HS) has a step-like projection (TP) on the side pointing towards the head. Because of this projecting ridge the slit between the inner surface of the socket and the hair wall is much narrower on this side. It is also only half as deep on this side. The hair shaft is articulated over a joint membrane (JM, ca. 1 μm thick) and an about equally thick layer of suspension fibers (SF) of which the parallel texture can hardly be seen. About 0,5 μm below the suspension fibers the socket septum (SS, thickness at the periphery: ca 0,15–0,2 μm) is spread rather flat. It consists of spongy and fibrous material and is penetrated centrally by a hole (diameter: ca. 1 μm). The dendritic sheath (DS) which contains the tubular body (TB), passes through this hole eccentrically and is attached eccentrically to the base of the hair *i.e.*, to the concave side of the hair shaft. The processes of cuticular material (M) inside the hair lumen (HL) end in this region at the dendritic sheath and at the socket septum.

1. Electrophysiology

It is evident from our investigation that the impulse frequency of the T_1 and T_2 hairs of *Calliphora* in response to deflections is similar to that of the corresponding hairs in *Phormia* (Wallis, 1962). The response to fast ramp-like stimuli is phasic-tonic. Nerve impulses are elicited by deflections in every direction, but in each of eight different sensilla it could be shown that the phasic as well as the tonic part of the response is 15–20 % smaller when the hairs are deflected in the direction of curvature than when they are deflected opposite or perpendicularly to it.

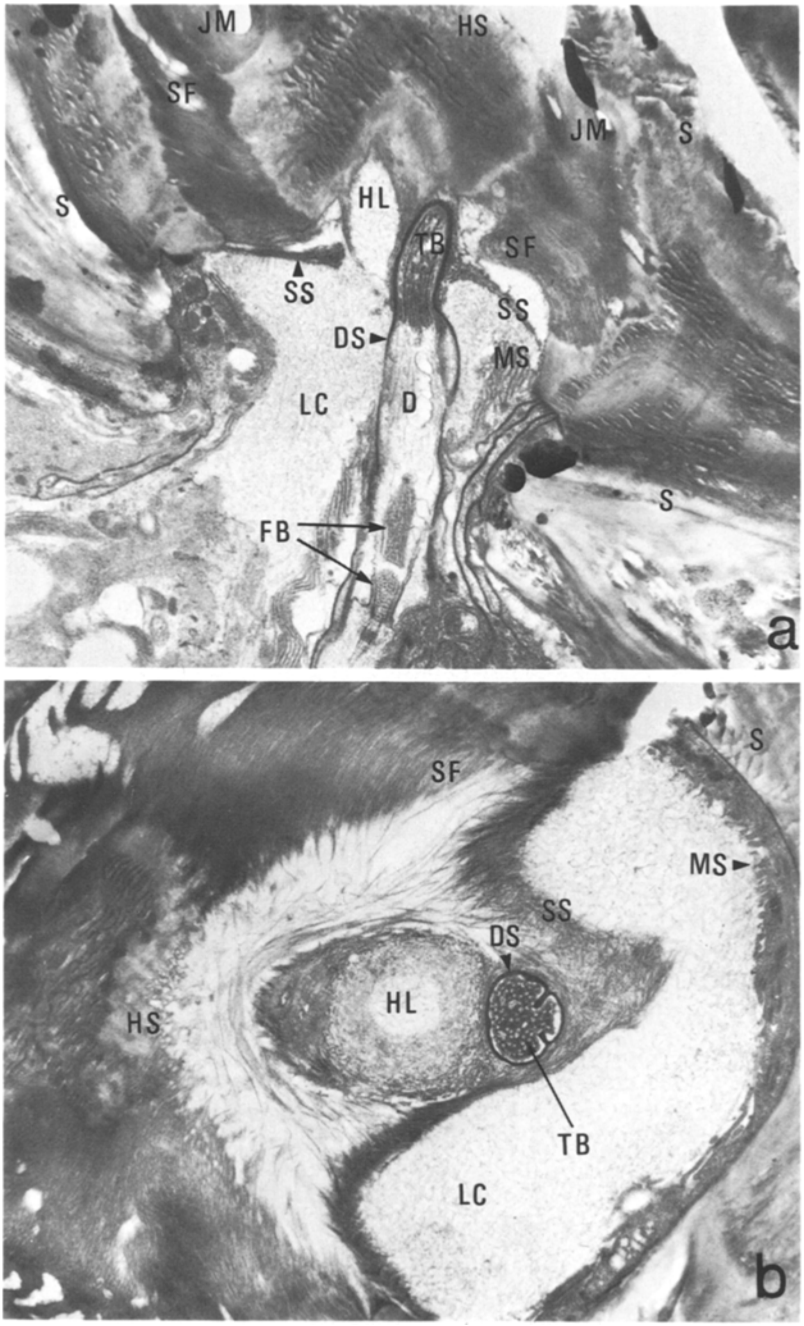

Fig. 8a and b. Tarsal sensilla of *Phormia.* (a) Longitudinal section through socket. Membrane septa (*MS*) of enveloping cells extend into lymph cavity (*LC*); X 10500. (b) Oblique cross section through socket; X 10000

V. TARSALE TACTILE HAIRS OF *PHORMIA TERRAENOVAE*

These tactile hairs (length: 80–120 μm; basal diameter: 4–5 μm) are on the bottom side of the first tarsomeres on the front pair of legs. They are constructed very similarly to the hairs on the ovipositor of *Calliphora*. Therefore only the differences will be mentioned. Unlike the tactile hairs on the ovipositor the hair shaft is not curved to the side of the eccentric attachment of the tubular body (TB, Fig. 8), but to the opposite side.

Compared to the layer of densely packed suspension fibers (SF, thickness: 2–2,5 μm) the joint membrane (JM, thickness: ca. 0,5 μm) is essentially thinner than in the tactile hairs on the ovipositor. The suspension fibers form a ridged collar half way around the tubular body (Fig. 8).

Attached eccentrically to the base of the hair shaft (HS) the dendrite (D) shows fibrillar bodies (FB) and filaments, which pass through the tubular body in longitudinal direction. This is typical in flies (Smith, 1969; Uga and Kuwabara, 1967; Thurm, 1970; Hansen and Heumann, 1971; Chu-Wang and Axtell, 1972a, b) but unlike other ciliary structures in sensory cells of insects (*cf.* Gaffal and Bassemir, 1974).

1. Comparative Aspects

Assuming the leverage of the hair shaft and the counteraction of the socket septum, the direction of maximal sensitivity can be explained by the anatomy of the socket structures in both tactile bristles of *Calliphora*. When the bristles are deflected to the insensitive (ocellar bristles) or less sensitive (hairs on the ovipositor) side, the required counterpressure cannot be at all or cannot be fully generated because of the hole in the socket septum. This explanation supports the presumption of Wallis (1962) that the differential sensitivity of the corresponding tactile organs on the ovipositor of *Phormia* is reflected in the structures of the socket.

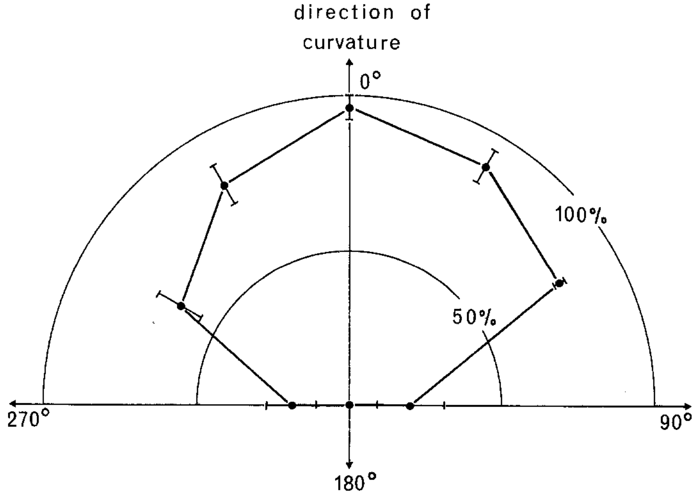

Fig. 9. Directional characteristic diagramm of ocellar bristles of *Calliphora*. The impulse frequencies during the motion phase of ramp stimuli (deflection angle = 10°; deflection velocity = 60°/sec) were averaged. Their values depend on stimulus direction. The results of tests on three different animals (5 measurements for each direction in all 3 animals) were averaged and plotted with standard error of each mean

A comparison of the two bristles of *Calliphora* distinctly shows that neither the direction of the hair shaft's inclination nor its direction of curvature[1] have an immediate influence on its directional sensitivity. Further comparison of these tactile hairs with those of *Phormia* suggest that the tarsal hairs of *Phormia* should respond maximally to deflections towards the tip of the tarsus.

Direct observations (Theiß, in prep.) showed that fixing and dehydrating agents did not move the hair out of its resting position (instrument error = 1°). Barring other sources of error, the angles between the hair shaft and the socket wall as observed in electron microscope preparations should thus coincide with the conditions in the living animals. In the bristles on the head of *Calliphora* these angles range between 8 and 12°. If deflections of the hair shaft exceed these values, the hair shaft fulcrum is at the point where it strikes against the socket's edge. If deflections are smaller than 8–12°, the fulcrum may well lie nearer to the base of the shaft. From the knowledge of the theshold value (the angle of the hair shaft's deflection which causes at least one spike = approx. 1°) and of the maximal length of the lever arm (ca. 35 μm), one may estimate that the structures which counteract the lateral displacement of the dendrite must be within 0,7 μm or less of the finger-like projection of the hair shaft. Only the dendritic sheath and the socket septum come into question. It is improbable that only the dendritic sheath serves as the counteracting structure because one would then expect reactions to deflections in every direction with hemimetabolous insects whose dendritic sheaths are fixed inside the moulting channel. In the ocellar bristles of *Calliphora* the dome shape of the socket septum which surely weakens the counteraction, seems to be a concession to the size of the sensilla. This disadvantage in comparison with a plain socket septum could be compensated for by a longer (in comparison to the other sensilla of flies) lever arm. In the tarsal hairs of *Phormia* the socket septum is possibly reinforced by the ridged collar.

VI. ANTENNAL SENSORY HAIRS OF THE DESERT WOODLOUSE *HEMILEPISTUS REAUMURI*

The distribution of these sensory hairs on the distal antennal segment, their variations in dimensions and the arrangement of different layers inside the cuticular apparatus was described recently by Seelinger (1972). Here we will only deal with structures which seem to participate in the transmission of mechanical stimuli.

The socket (S, Figs. 10 and 11) is formed like a bristle. A channel runs at a slightly oblique angle up the middle of the socket and opens in a U-shaped slit on the side facing away from the antenna. The real hair shaft (HS), which is perforated at the tip by a pore, runs up this channel.

The dendrites (D_{1-4}) of the four sensory cells by which these 'double hairs' are usually innervated enter the lumen of the hair (HL) on the same side as the slit. The dendrite closest to the slit side gradually tapers off at the level of the hair shaft's base and terminates there. This dendrite contains a tubular body (TB) at its tip. The other dendrites nearly reach the hair shaft pore. The dendritic sheath (DS) shrouds the

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[1] In *Schistocerca* (Camhi, 1969), however, the directional sensitivity of the hair may be affected in an air stream by its curvature. On the other hand in *Locusta* (Smola, 1970a) the deviations in responding to wind direction are related rather to different air-current conditions in the immediate environment of the hair.

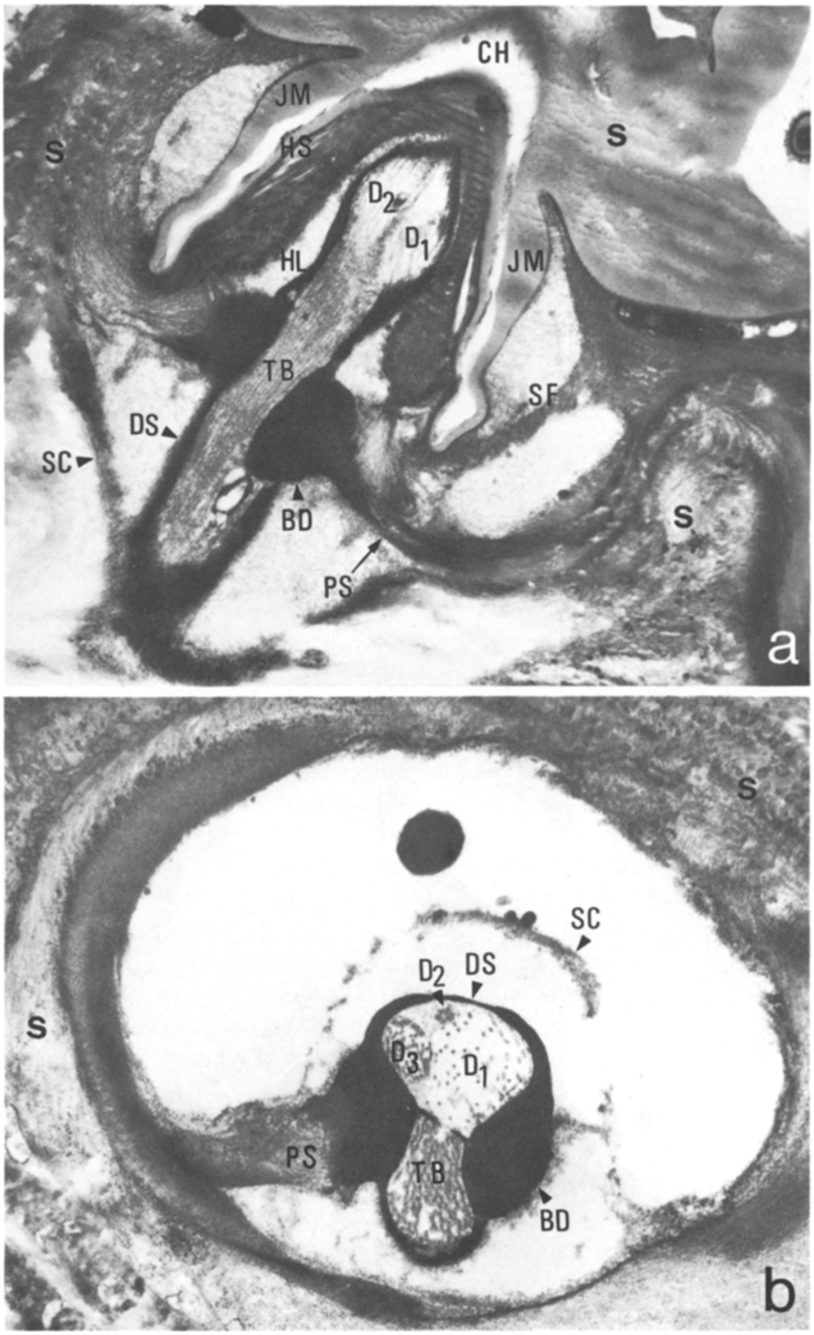

Fig. 10a and b. Antennal sensillum of *Hemilepistus*. (a) Longitudinal section through socket (perpendicular to plane of symmetry); X 14500. (b) Slightly oblique cross section through socket at the level of the socket projections (*PS*); X 18700

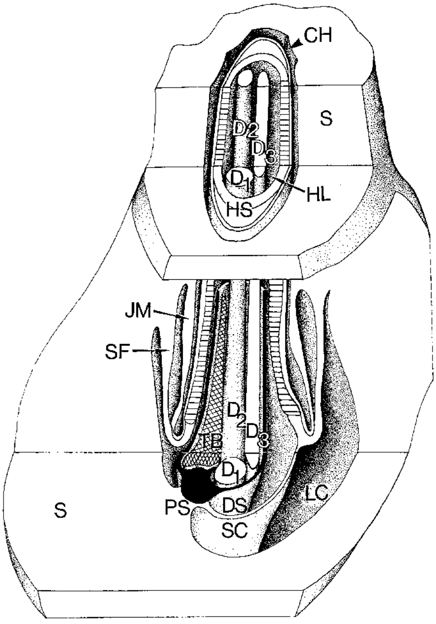

Fig. 11
Diagrammatic reconstruction of socket region in antennal sensilla of *Hemilepistus*; X ca. 700

dendrites up to the point where the tubular body ends. The wall of the dendritic sheath bulges out at both sides of the tubular body (BD, diameter of the bulge: 0,6–0,8 μm; length of the bulge: 1–1,5 μm). The cuticular socket projects inwardly (PS) from two sides at this level and at right angles to the sensory hair's plane of symmetry. These projections connect with the bulges of the dendritic sheath.

The hair shaft, which is circular at the base, is inserted into the socket by a solid joint membrane (JM) and by another (0,15–0,2 μm thick) layer of fibrous cuticular elements (SF, suspension fibers?). The proximal prolongation of this fibrous layer is only half as thick and varies in length. It is like an open bracelet (SC) which closes in on the bulges with its ends. Further out the hair shaft flattens in cross section into an ellipse whose long axis is perpendicular to the plane of symmetry of the sensillum. Towards its tip the shaft becomes circular again.

VII. TACTILE HAIRS ON THE HEAD OF *POLYXENUS LAGURUS*

The hairs investigated (length: 100–150 μm) are flattened, leaf-like and grossly indented at the border. The external construction has been described by Masson (1971) too. Their surface is corrugated by a system of ridges and grooves about 0,5 μm wide and which run mainly in longitudinal direction. The base of the hair shaft (HS, Figs. 12a and 13) is conical. Its circular cross section becomes flattened (bilaterally symmetrical) as it emerges from the socket (S). At this level the hair shaft is bent to form an angle of about 20° with the broad side (Fig. 12a).

The cuticle forms a sleeve around the lower end of the hair shaft with a very tight fit at its base. The other end of the sleeve (CC) flares out to form a bridge with the cylindrical socket. The socket bulges outward at the surface. The bulge (R) is broader

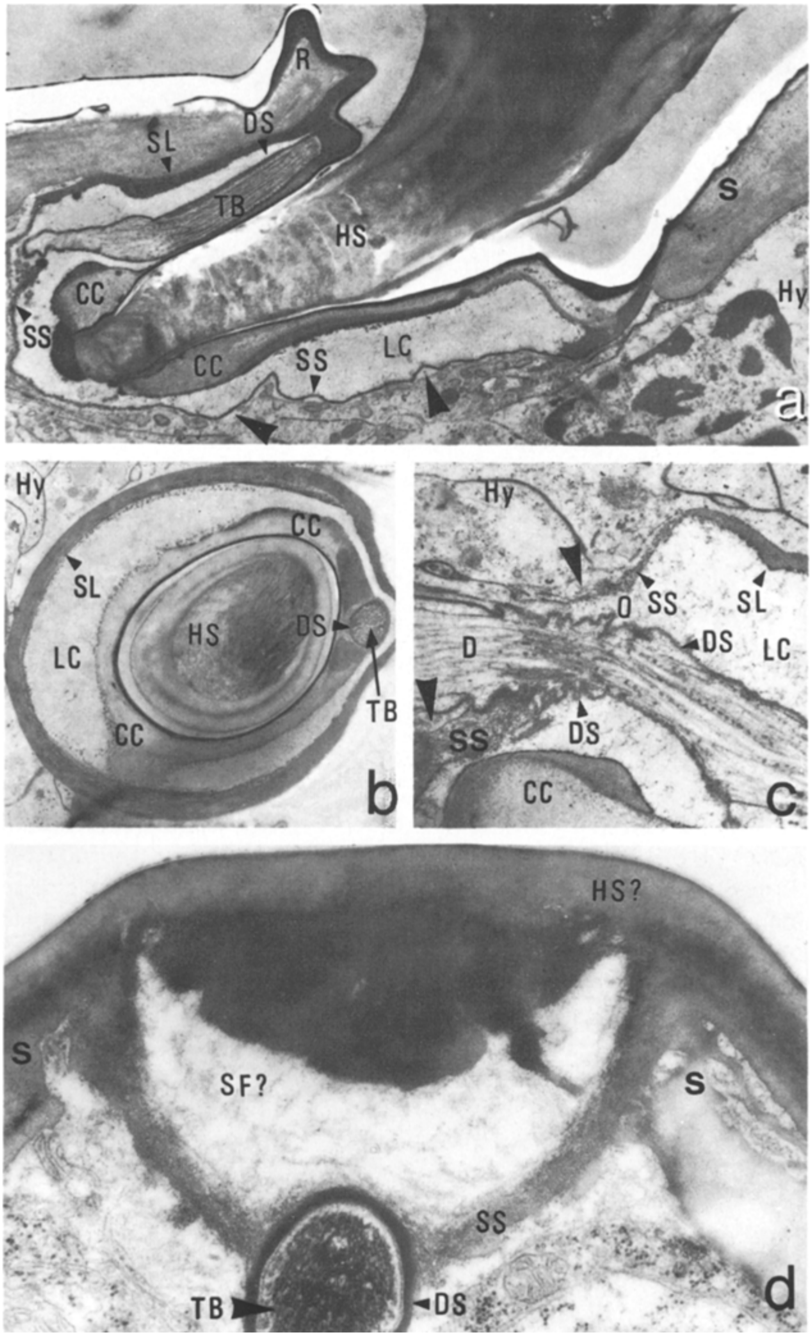

Fig. 12a–d. Sensilla on the head of *Polyxenus*. (a) Longitudinal section through articulating apparatus; X 3600. (b) Cross section through socket at level of tubular body; X 2600. (c) Longitudinal section through dendrite at the level of passage through socket septum; X 12000. (d) Oblique longitudinal section through antennal hair-less sensillum of Cimex; X 24000

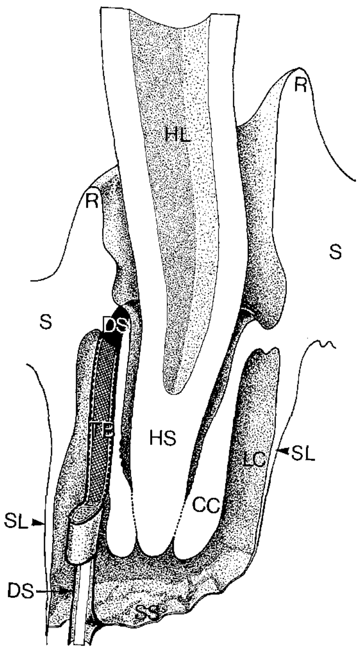

Fig. 13
Diagrammatic reconstruction of bisected sensillum on the head of *Polyxenus*; X ca. 900

(3–5 μm) and higher (3,5 μm) at the concave side of the hair shaft than at the convex side (height: 1 μm; breadth at the base: 2 μm).

About 2 μm below the articulating sleeve a wrinkled septum (ca. 0,1 μm thick) of spongy fibrous material (SS) runs across the bottom of the socket and is attached to the base of the innermost cuticular layer (SL) of the socket. This layer stains heavily (outer endocuticle, Seifert 1967). The septum separates the liquor cavity (LC) from the narrow extracellular space (arrow, Fig. 12a and c) overlying the sheath cells and hypodermal cells (Hy). These two spaces communicate directly only by a small opening (O) near the dendritic sheath passage.

The dendrite (D) of the single sensory cell innervating these sensilla is divided into two ciliary structures (9x2+2). At its tip each cilium contains a tubular body (TB, elliptical diameter: 1 μm x 0,7 μm; length: 8 μm). Both cilia pass through the socket septum surrounded by their dendritic sheath (DS). The sheath has multiple folds here and is in close contact with the septum (Fig. 12c).

The tubular bodies fit in a groove in the articulating sleeve (CC) at the side towards which the hair shaft is bent. This groove extends from about 3 μm above the proximal end of the sleeve up to the point where it flanges out towards the socket. There the sheath is inserted into the flange.

1. Comparative Aspects of the Socket Structures

The manner in which hair-like sensilla are articulated is in principle the same in all Arthropods. The joint membrane is formed by the outer cuticular layers. The suspension fibers, if present (they are absent in some trichobothria), are formed by pro-

Table 1. List of terms used by the investigating authors to describe the socket structures (joint membrane, suspension fibers, socket septum) in mechanosensitive sensilla with hair shafts. The sign (—) was used when indicated structures were neither described by the investigating authors nor recognizable from figures

Generic name	Type of sensillum	Joint membrane	Suspension fibers	Socket septum	Authors
Onychiurus (Collembola)	chaet.	not named but to be seen in Fig. 13a	not named but to be seen in Fig. 13a	not named but to be seen in Fig. 13a	Karuhize (1971)
Dilta (Archaeognatha)	chaet,	Gelenkhaut	—	not named but to be seen in Fig. 2a	Schmidt (1973)
Nemurella *Leuctra* *Nemoura* (Plecoptera)	chaet. chaet.	Gelenkhaut Gelenkmembran	kutikulare Stränge — —	not named but to be seen in Fig. 5b not named but to be seen in Fig. 4	Gnatzy and Rupprecht (1972), Rupprecht and Gnatzy (1974)
Gryllus (Saltatoria)	chaet.	Gelenkhaut	—	elektronendichtes inhomogenes Material	Gnatzy and Schmidt (1971)
Periplaneta (Blattaria)	chaet.	Gelenkhaut	—	fibrilläres Material	Gnatzy (1973)
Dysdercus (Heteroptera)	chaet.	Gelenkmembran	Aufhängefasern	Widerlager	Gaffal and Hansen (1972)
Nepa (Heteroptera)	chaet.	Gelenkhaut	not named but to be seen in Fig. 1b	not named but to be seen in Fig. 1b	Bonke (1975)
Protophormia (Diptera)	chaet.	articulating membrane	loose fibrous elements or fibrous cap structure	not named but to be seen in Fig. 10	Lewis (1970)
Phormia (Diptera)	chaet.	dünne elektronendichte Schicht	elastisches Sockelmaterial	Sockelseptum	Hansen and Heumann (1971)
Apis (Hymenoptera)	chaet.	joint membrane		cap	Thurm (1964)
Araneus (Araneae)	chaet.	not named but to be seen in Figs. 11 (1973a) and 16 (1973b)	fibrous connecting membrane	fibrous strands or intercalated cuticular fibers	Foelix (1970), Foelix and Chu-Wang (1973 a,b)
Tegenaria (Araneae)	Trichobothrium	Membran	Fibrillen	innere Auskleidung des Lymphraumes	Christian (1971, 1973)
Amblyomma (Acari)	A-type	exocuticle	articulating membrane	not named but to be seen in Fig. 10	Foelix and Chu-Wang (1972)

Table 2. List of terms used to describe structures in mechanosensitive sensilla without hair shafts. These structures probably correspond to the socket structures in mechanosensitive sensilla with hair shafts (*cf.* Table 1). In cases where the structures which correspond to the suspension fibers and to the socket septum cannot be distinguished, the term is set in a block covering both columns

Generic name	Type of sensillum	Reduced hair shaft and joint membrane	Suspension fibers	Socket septum	Authors
Machilis lepisma (Thysanura)	camp.	kutikulare Kuppel	not named but to be seen in Fig. 83	kutikularer Dom	Schmidt (1972)
Cloeon baetis (Ephemeroptera)	camp.	not named but to be seen in Figs. 77–79	not named but to be seen in Figs. 77–79	kutikularer Dom	Schmidt (1972)
Gryllus (Saltatoria)	camp.	kutikulare Kuppel	spongiöses Chitin	kutikularer Dom	Schmidt and Gnatzy (1971), Gnatzy and Schmidt (1971)
Blaberus (Blattaria)	camp.	layer 1 of the cap L_1 = outer layer of cap cuticle	layer 2 of the cap not named but to be seen in Figs. 5 and 9	L_2 = inner layer of cap cuticle	Moran *et al.* (1971), Moran and Rowley (1975)
Chrysopa (Neuroptera)	camp.	elektronendichter Kutikulaüberzug	spongiöses Chitin	kutikularer Dom	Schmidt (1969)
Calliphora (Diptera)	camp.	hinged cuticular bar narrow osmiophilic layer (dome)	spongy inner cuticular cap		Smith (1969)
Drosophila (Diptera)	camp.	cuticle C_2 (cap membrane) cuticle C_1	fibrous cuticle (C_3?)	cuticle C_3	Chevalier (1969)
Apis (Hymenoptera)	camp.	cap membrane	cap		Thurm (1964)
Cupiennius (Araneae)	Spaltsinnesorgan	äußere Membran	Kutikulastege	innere Membran	Barth (1971)

longed fibrous elements of deeper lying cuticular layers (exocuticle in insects). Possibly the ability of these structures to be stained by methylene blue (Thurm, 1963; Smola, 1970a) can be explained by their proteinoid nature.

In every case examined structures comparable to the socket septa are found in mechanosensitive sensilla chaetica, whether in insects, arachnids, diplopods and crustaceans (*cf.* Table 1). Further in all cases where the physiology of these sensilla is also known, it can be clearly correlated with these structures. Moreover even in those cases where the physiology has not yet been investigated and even though these examples vary in detail, there remains such uniformity in structure that it seems permissible to argue from the structural uniformity to uniformity in the mechanism of stimulus transmission in hair-like sensilla. The hair shaft acts as a lever and a second stationary structure exerts counterpressure. This conclusion, however, will probably have to retain its hypothetical character until experiments can be devised to determine the physiological properties of these substructures.

If we consider sensilla chaetica and sensilla campaniformia to be homologous – which is the opinion of Lees (1942), Thurm (1964) and Schmidt (1969, 1973) – then the socket structures of these organs should be comparable to one another. It seems plausible that in hairless sensilla campaniformia the joint membrane and the suspension fibers, which otherwise would carry the hair shaft, are largely functionless. Therefore they should either be modified or more of less reduced. Strong indications for the validity of this assumption can be seen from comparison of the socket structures in sensilla chaetica (Table 1) and sensilla campaniformia (Table 2). An especially clear example is presented by an antennal hair-less sensillum of *Cimex* (Fig. 12d, courtesy of Dr. R.A. Steinbrecht).

In the sensilla campaniformia of *Phormia* (Thurm *et al.*, 1975) the stimulus transmitting function is ascribed to a structure which corresponds to the socket septa. But it is impossible to draw a general conclusion regarding the function of such structures in the transmission of pressure and counterpressure, respectively. In an 'analogous' organ of *Cupiennius* (Barth, 1971, 1972a, b) participation of the inner membrane (= socket septum) in stimulus transmission is ruled out.

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