

ELECTRON MICROSCOPIC STUDIES OF ANTENNAL SENSILLA
IN THE AMBROSIA BEETLE TRYPODENDRON LINEATUM (OLIVIER)
(SCOLYTIDAE)

by

HENRY A. MOECK

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Department of Zoology

The University of British Columbia
Vancouver 8, Canada

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ABSTRACT

The antennae of the ambrosia beetle Trypodendron lineatum (Olivier) were examined with the light and electron microscopes to determine the types, distribution, and structure of sense organs found thereon.

At least six types of sense organs were found, with an additional seventh cuticular structure, the hypodermal gland pore, which is thought to be non-sensory. The sensilla are sensilla chaetica, three types of sensillum trichoideum, sensilla basiconica, and sensilla campaniformia. Distribution maps of the various sensillum types and the gland pores are presented, for one each of female and male left antenna.

Sensilla chaetica, evenly distributed over all parts of the antennae, as well as the rest of the body, consist of a long thick-walled hair 20 to 140 micra long which articulates in a socket composed of a hair root, socket lining, and spongy cylinder. A single bipolar neuron terminates in a scolopale attached at one side of the hair base.

Sensilla trichoidea, Type I, situated at the base of the scape and the base of the first funicular segment, are short thin hairs articulating in a socket. Their fine structure and innervation are not known.

Sensilla trichoidea, Type II, found on the distal periphery of the club only, consist of sharply pointed smooth hairs 18 to 25 micra long, the hair wall being thin and perforated. The hair is solidly joined to the body cuticle. The sensillum has two bipolar neurons, the dendrites of which extend, with slight branching, to the distal limits of the hair lumen. No dendritic endings could be demonstrated at the hair perforations.

Sensilla trichoidea, Type III, are evenly distributed over the distal half of the anterior club surface. The hair is 26 to 36 micra long, blunt-tipped, and curved in reverse, with the result that the hairs protrude at right angles to the club surface and beyond all other vestiture. The hair

articulates in a socket, and has a double lumen. The dendrites of four to seven bipolar neurons extend through the eccentric small lumen to the hair tip, where, presumably, they are open to the air.

Sensilla basiconica cover both club surfaces. At least two types exist, one group being short pegs 6 to 8 micra long, and another group being longer pegs or hairs 14 to 18 micra long. The long sensilla basiconica have a thin perforated hair wall, the openings being slit-shaped (700Å by 100 to 200Å). The two nerve cells of this sensillum send two distal processes into the hair where subsequent repeated branching occurs. The relationship of the dendrite branches to the hair perforations is not clear.

Sensilla campaniformia are found in small numbers on all parts of the antennae, as well as other parts of the body. They consist of a short thin canal leading from the outside to a sub-surface dome 3 micra in diameter, in the centre of which lies the nerve ending similar in appearance to the scolopale and nerve of the sensillum chaeticum.

Also, a cross section of the antennal nerve in the proximal portion of the scape revealed about 2100 axons. A count of the sensilla, corrected for the number of sense cells present per sensillum, gave expected axon numbers of 1845 and 1921 for female and male antennae, respectively, with Johnston's organ not accounted for. Since more axons than expected are present, axon fusion is considered unlikely.

This study may serve as the basis for further electrophysiological work to determine the functions of the various sense organs.

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SYMBOLS AND ABBREVIATIONS

△	sensilla chaetica		
⌘	sensilla trichoidea, Type I		
•	sensilla trichoidea, Type II		
×	sensilla trichoidea, Type III		
◦	sensilla basiconica		
◻	sensilla campaniformia		
.	hypodermal gland pores		
AX	axon	H L	hair lumen
B	body cuticle	H P	hair perforation
BM	basement membrane	H R	hair root
C	centriole	H W	hair wall
C E	cytoplasmic extensions	I S	inner segment of dendrite
C L	central lumen	L L	large lumen
C R	ciliary rootlet	MI	mitochondrion
C S	ciliary segment of dendrite	MT	microtubule
CU S	cuticular sheath	MV	microvilli
D	dendrite	NL	nucleolus
D B	dendrite branch	NU	nucleus
DO	dome	O S	outer segment of dendrite
DS	desmosome	P	pore canal
E B	elliptical body	S	scolopale
E C	epidermal cell	S C	sponge-like cavity
EP	epicuticle	S L	socket lining
E R	endoplasmic reticulum	SM L	small lumen
EX	exocuticle	S N	sensory neuron
EX CA	external canal	T B	tubular body
G	Golgi body	TO C	tormogen cell
G C	glial cell	TO V	tormogen vacuole
GL C	gland cell	TR C	trichogen cell
GL C V	gland cell vacuole	TR V	trichogen vacuole
H	hair	U M	unit membrane
HE	hemocoele		

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INTRODUCTION

The sensilla of insects have been objects of interest and study by entomologists for a long time. Knowledge of the sensory equipment of insects is of interest to the insect anatomist, and to the behaviourist who wishes to investigate the sites and kinds of specific behavioural responses. The ambrosia beetle Trypodendron lineatum¹ (Olivier) has been a specific object of behaviour studies in recent years (see references). These studies have been of a gross nature on the entire organism, conducted in the absence of detailed knowledge of the physical nature of the sensory equipment involved.

Heretofore our knowledge of insect sensilla has been based mainly on studies utilizing conventional histological methods and optical microscopes. Due to the relatively low resolving power of the light microscope, and the extremely small dimensions of sensilla and their components, a precise understanding of their structure was uncertain, giving rise to much speculation, discussion, and debate among entomologists. The application of the electron microscope, with its superior resolving power, to biological specimens in the past decade has settled many arguments regarding sense organ structure and possible function, provided more precise definition of problems which could be investigated with other methods, particularly electrophysiological, and either confirmed or refuted findings based on light microscopy.

It is known from various kinds of evidence that the antennae of insects, as well as other arthropods, are the site of various types of sensilla (for a recent review on insect antennae, see Schneider, 1964). Accordingly,

¹Synonyms: Xyloterus lineatus (Erichson) in Europe; and T. bivittatum (Kirby), T. cavifrons (Mannerheim), T. vittiger (Eichhoff), T. borealis (Swaine).

attention in the present study was directed toward antennal sense organs, particularly those of the club region (Fig.1), because the work of Borden and Wood (1966) on Ips confusus, another scolytid beetle, based on conventional microscopic techniques, ablation-behavior and covering-behaviour studies, as well as some preliminary electrophysiological work (Borden, 1966, 1967) indicated that this region in Scolytidae is the site of a number of different sensilla mediating several behavioural responses, particularly to specific odorous chemicals. In T. lineatum it has been established that adults of both sexes are attracted to a suitable host tree by primary attractants produced in the wood, and that beetles deprived of their antennae fail to respond to attractive wood odours (Graham and Werner, 1956). The purpose of the present study is to furnish a description of the types, distribution, and structure of sense organs situated on the antennae of T. lineatum, as a basis for further work on this and related species.

MATERIALS AND METHODS

1. The Insect

The two-striped ambrosia beetle Trypodendron lineatum (Olivier) is a species of the family Scolytidae. The adults are of a dark brown to black coloration, with alternating dark and light longitudinal stripes on the elytra. Adult length varies between 3 and 3.5 millimeters. They are bisexual, and therefore it may be presumed that while all individuals possess certain sensory equipment characteristic of the species, they may also possess other sensory equipment peculiar to one sex which searches for mates. It was necessary therefore to identify the sex of each individual studied. Since the sexes are conspicuously dimorphic, the task of distinguishing them is easy. The female pronotum appears rounded anteriorly as seen from above, and the front of the head is rounded, whereas in the male the pronotum appears straight anteriorly, and the front of the head is deeply excavated (hence the synonym T. cavifrons).

The antennae (Figs.1,2), which were chosen as the specific region for this study, are composed of three regions, namely an elongated basal segment, the scape (0.31 to 0.34 mm long by 0.10 mm at widest point), a series of four very short segments, the funicle (0.13 to 0.15 mm total length by 0.07 mm at widest point) and a terminal, flattened club of oval form (0.28 to 0.31 mm long by 0.18 to 0.20 mm at widest point). Additionally, the sex of the specimen can be identified from the shape of the antennal club under the light microscope, the male's having a narrower and more elongate proximal portion than the female's, which appears more oval in form (compare Figures 1 and 2).

The base of the scape articulates with the head, and the base of the

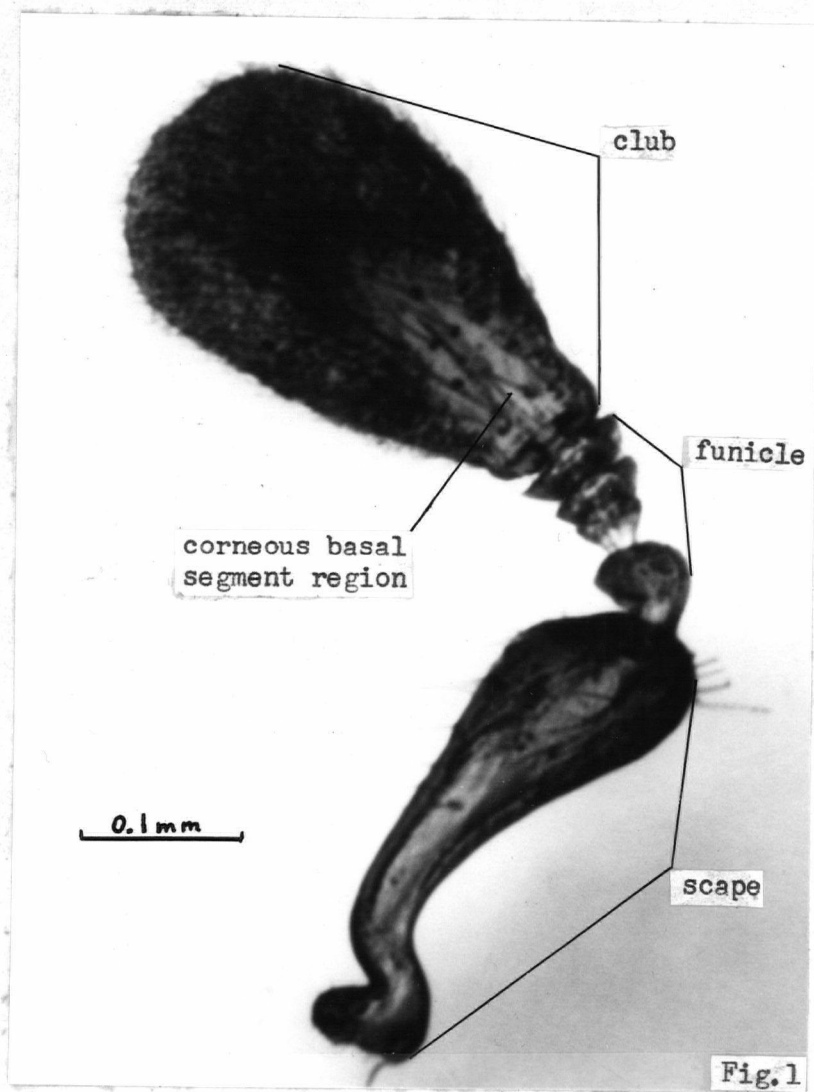


Figure 1. Photomicrograph of *Trypodendron lineatum* male left antenna, anterior surface. Compare club shape to that of female (Fig.2). Distilled water mount.



Figure 2. Photomicrograph of Trypodendron lineatum female left antennae, (at left, posterior surface, at right, anterior surface). Note greater density of sensilla on anterior club surface. Distilled water mount.

first funicular segment articulates, by membrane only, with the distal portion of the scape; both joints are provided with muscles.

2. Methods

Adult beetles were removed from galleries in logs and stored in the refrigerator at 4 degrees C until used. Whole mounts of antennae were made from dead dry beetles, as well as from fresh.

Light microscopy

Whole mounts of unstained antennae were made in distilled water (Refractive index 1.33), Permount (R.I. 1.53), and Hyrax (R.I. 1.63), between cover slips to permit observation of both surfaces. Sections were made from Epon-embedded material, prepared as below, and stained with methylene blue (1% in 1% aqueous borax solution) (Richardson et al, 1960). Maps and other drawings were made with the aid of an eyepiece grid.

Electron microscopy

(a) Antennae from live beetles were fixed for two hours in phosphate-buffered 5% glutaraldehyde (Sabatini et al, 1963), washed in buffer, post-fixed in 1% OsO_4 , washed, dehydrated in the ethanol series, followed by propylene oxide, and embedded in Epon 812 (Luft, 1961; Kay, 1965). Sections were cut on glass knives on the Sorvall Porter-Blum MT-1 ultramicrotome, mounted on carbon-collodion and carbon coated copper grids (Molenaar and Schotanus, 1962), stained with lead citrate, and examined in the Hitachi HS-7S and HU-11A Electron Microscopes, at accelerating voltages of 50 KV for the former, and 50 and 75 KV for the latter.

(b) Antennae were fixed for two hours in phosphate-buffered 1% OsO_4 , washed in buffer, dehydrated with 15%, then 40% ethanol, stained for one hour in 1% phosphotungstic acid (PTA) in 70% ethanol, washed in 0.01% NaOH in 95% ethanol (modified from Kay, 1965), dehydrated to completion in absolute ethanol, stained for two hours in saturated lead acetate in alcohol:

acetone as 1:1, washed in alcohol-acetone (Kushida, 1966), followed by propylene oxide, and embedded in Epon. Sections were cut and mounted as before, and examined without further staining.

(c) For correlating light microscope observations with the electron microscope, thick sections (5 to 10 μ) were cut on the ultramicrotome from blocks prepared by method (a), and examined with the light microscope; areas containing known sense organ(s) were then cut out with a micro-scalpel, and the section pieces embedded, with the desired orientation, in the thermoplastic chlorinated polyphenol resin Aroclor 4465², with the aid of an electrically heated minutennadel. Thin sections were then cut, stained, and examined with the electron microscope as before.

²Organic Chemicals Division, Monsanto Chemical Company, St. Louis, Mo.

RESULTS

With the light microscope one can distinguish six main types of cuticular sense organs on the antennae of both sexes of T. lineatum. Using the terminology of Snodgrass (1926), they are, respectively, sensilla chaetica (Fig.15), three types of sensillum trichoideum, sensilla basiconica (Fig.15), and sensilla campaniformia (Fig.85). The main distinguishing features of the trichoid sensilla are as follows: the Type I sensilla are short (1μ to 8μ) hairs situated at the base of the scape and the base of the first funicular segment; no other sensilla are present in these regions (Figs.34,35). The other two types are only on the club, the Type II sensilla being 18μ to 25μ long, thinwalled, and sharply pointed, whereas the Type III sensilla are 26μ to 36μ long, thicker-walled, and blunt-tipped (Figs.40,41).

A seventh recognizable cuticular structure, the hypodermal gland pore (McIndoo, 1926), distributed over most parts of the body, including the antennae, is believed to be non-sensory, and will not be referred to further (Figs.3 to 11,14,87).

The following descriptions are based on evidence obtained with both the light and electron microscopes.

1. Sensilla Chaetica

The sensilla chaetica are distributed over most of the body as well as the antennae (Figs.16-19), and consist of a long stiff hair set in a socket, with formative cells, and a sensory bipolar neuron which terminates at the base of the hair (Fig.20).

The hair may be from 18μ to 140μ long, the majority of hairs being about 40μ long. The longest ones are on the mid-distal portion of the scape in such a position that when the club and funicle are bent back along the scape they come in contact with these long hairs (Fig.13). Each hair is gently curved, with many small pointed projections, and tapers to a very fine point

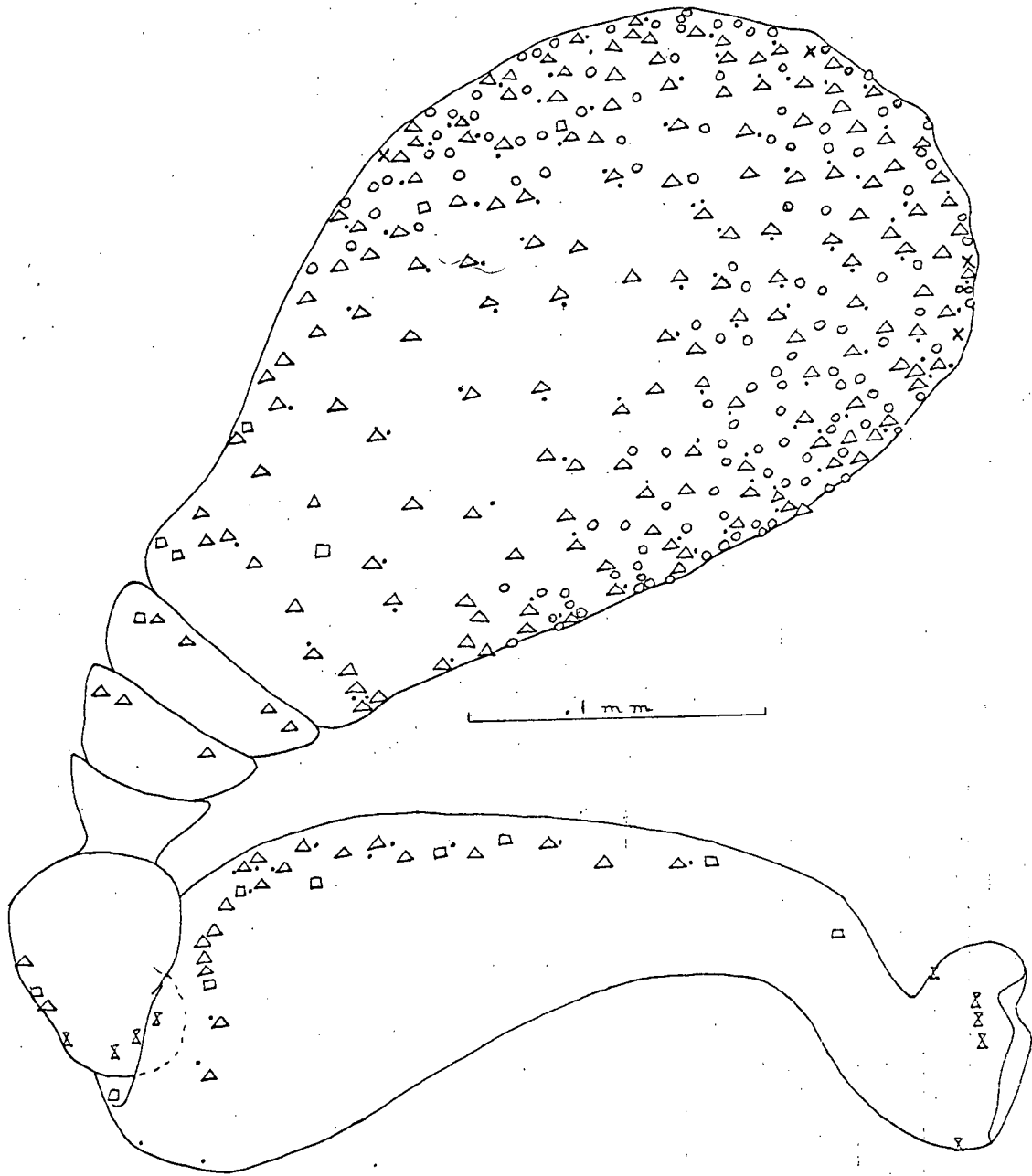


Figure 3. Distribution map of all sensilla and hypodermal gland pores on male left antenna, posterior surface.

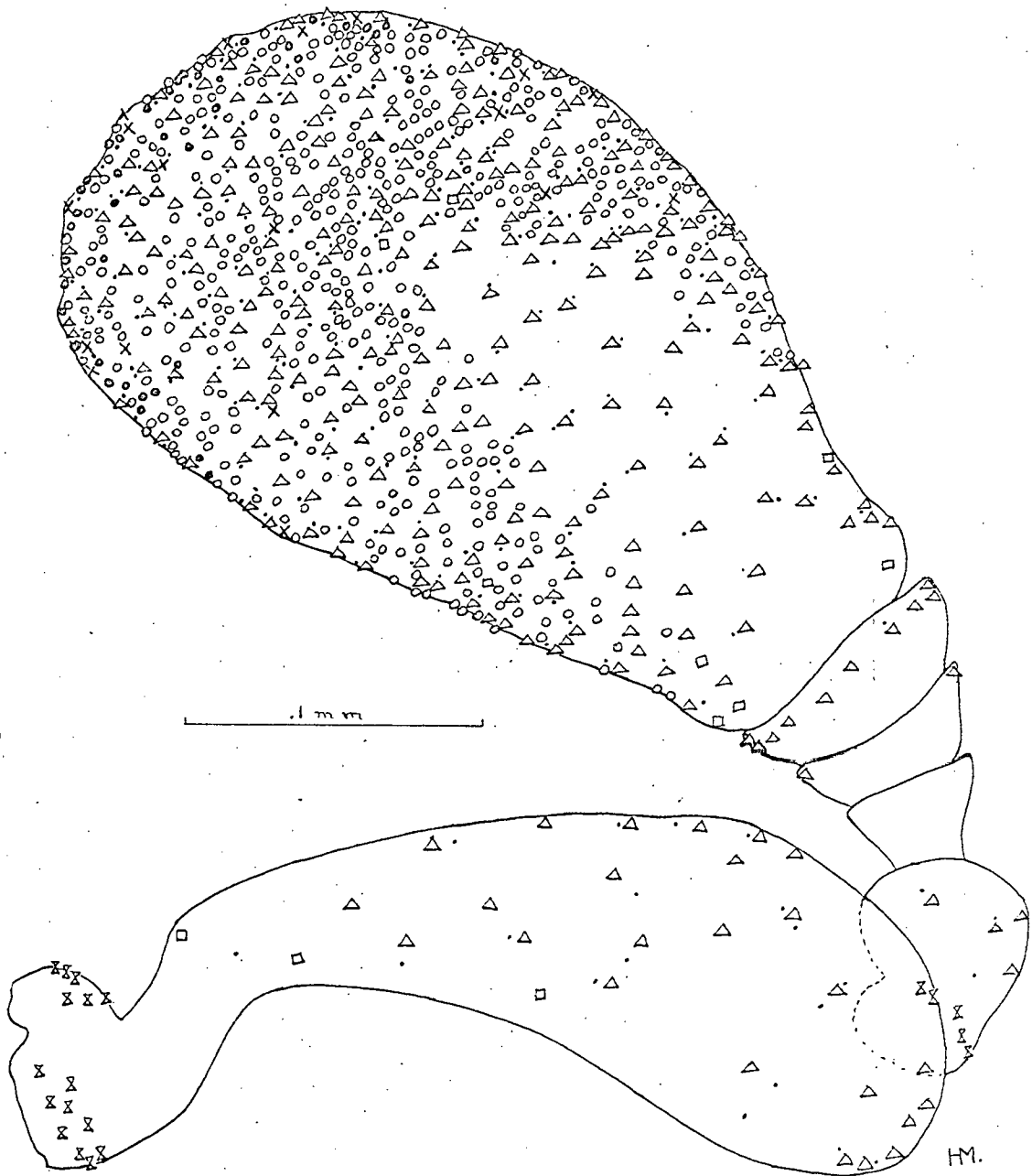


Figure 4. Distribution map of all sensilla and hypodermal gland pores on male left antenna, anterior surface.

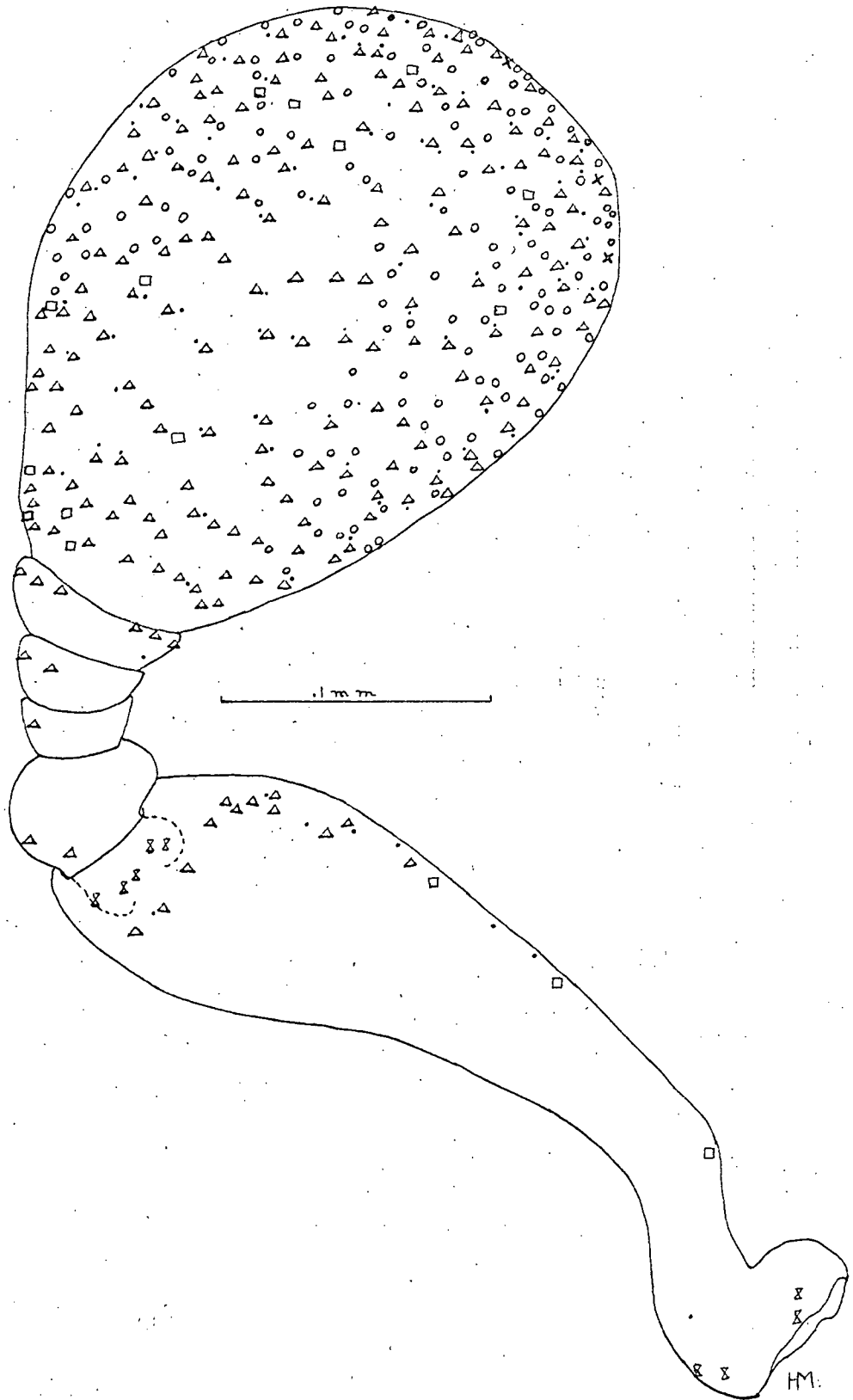


Figure 5. Distribution map of all sensilla and hypodermal gland pores on female left antenna, posterior surface.

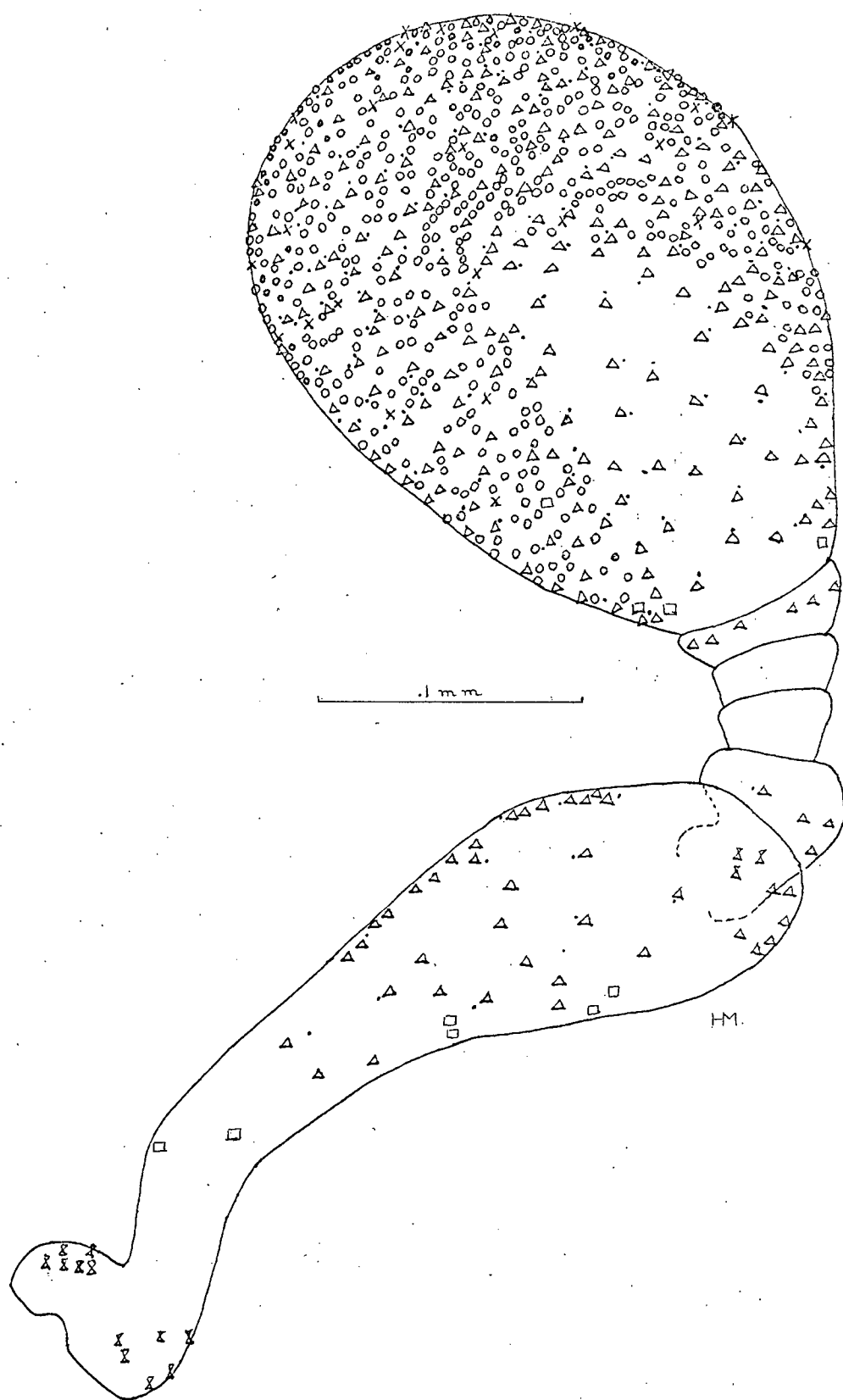


Figure 6. Distribution map of all sensilla and hypodermal gland pores on female left antenna, anterior surface.

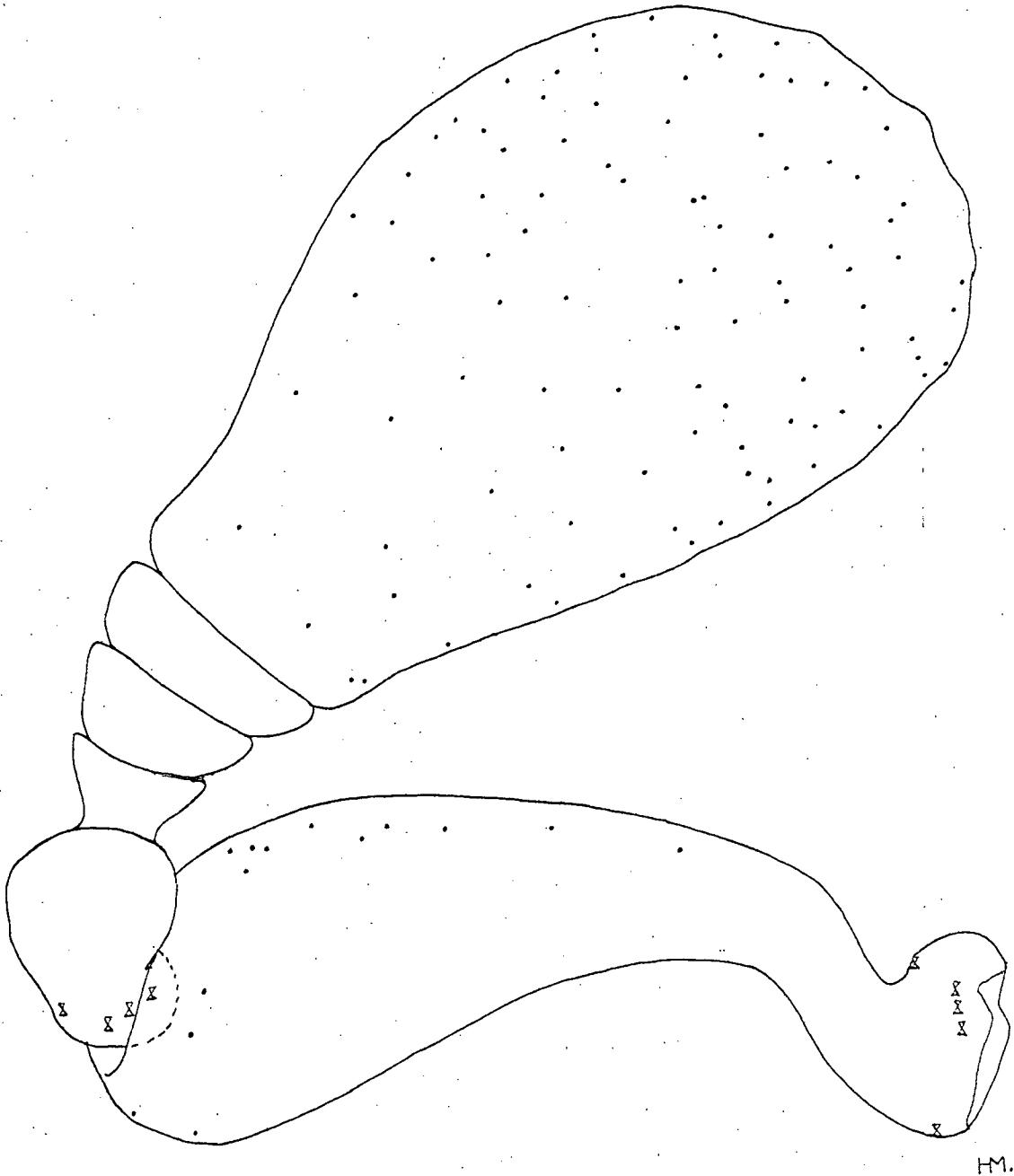


Figure 7. Distribution map of hypodermal gland pores and sensilla trichodea, Type I, on male left antenna, posterior surface.

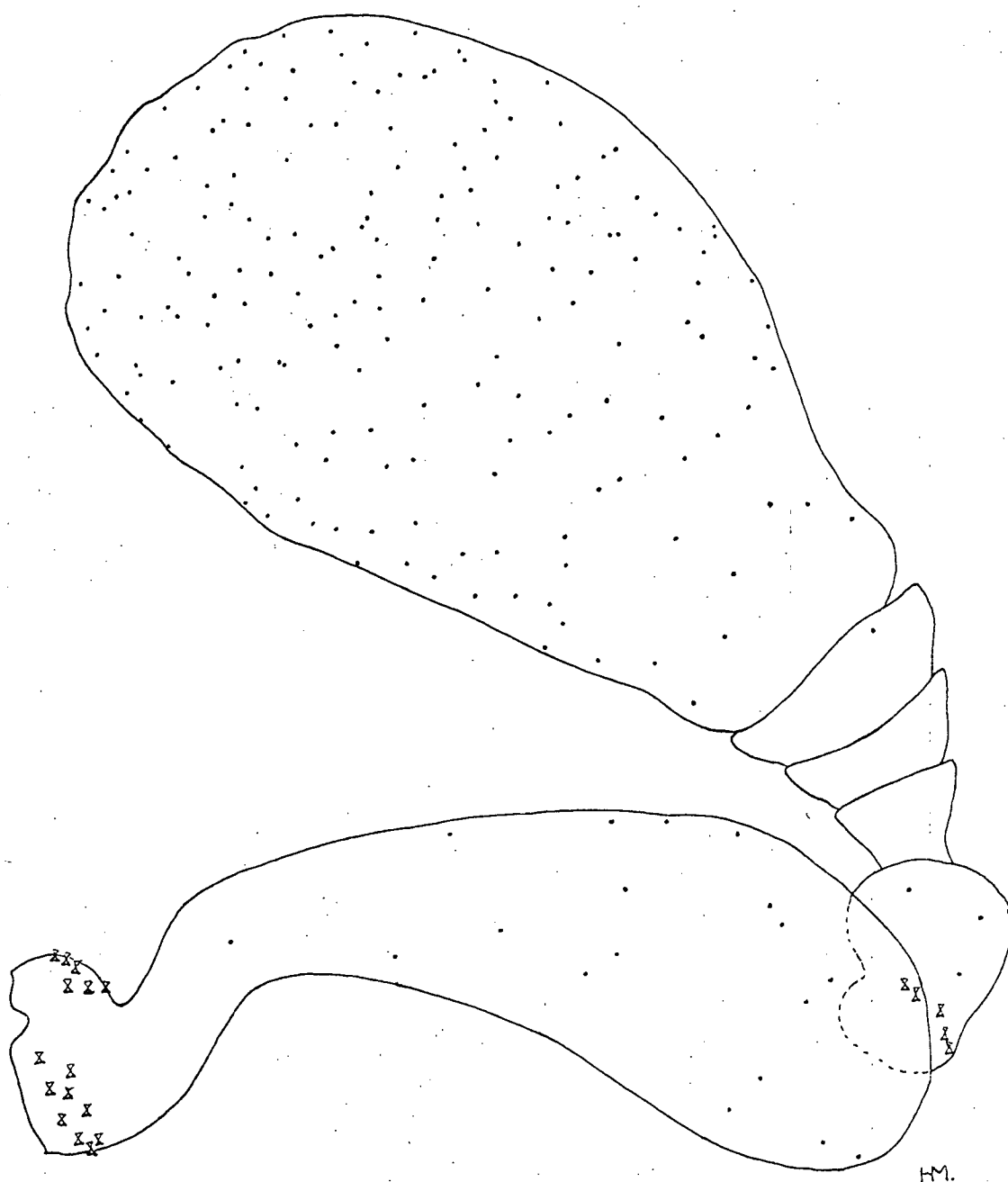


Figure 8. Distribution map of hypodermal gland pores and sensilla trichoida, Type I, on male left antenna, anterior surface.

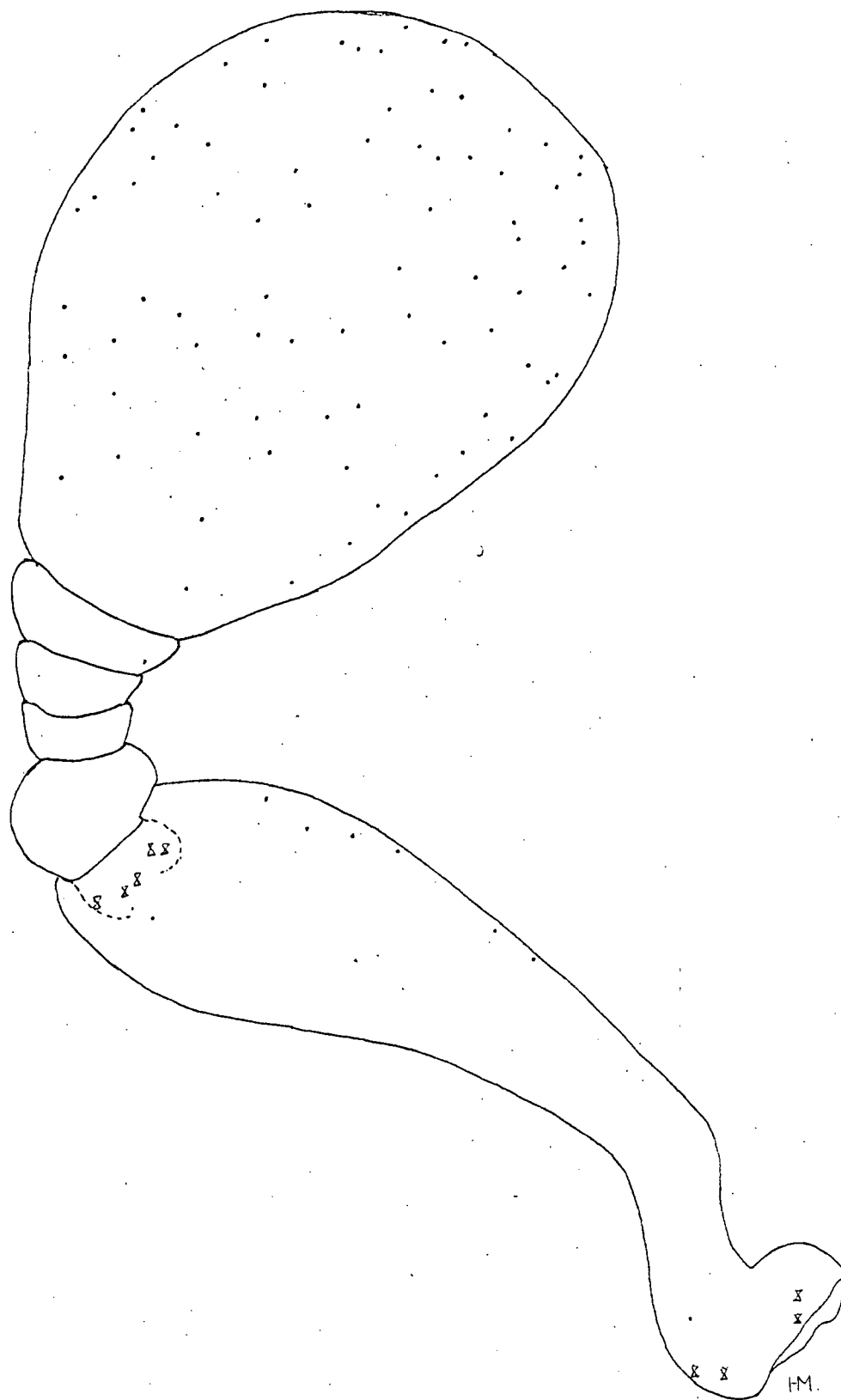


Figure 9. Distribution map of hypodermal gland pores and sensilla trichodea, Type I, on female left antenna, posterior surface.

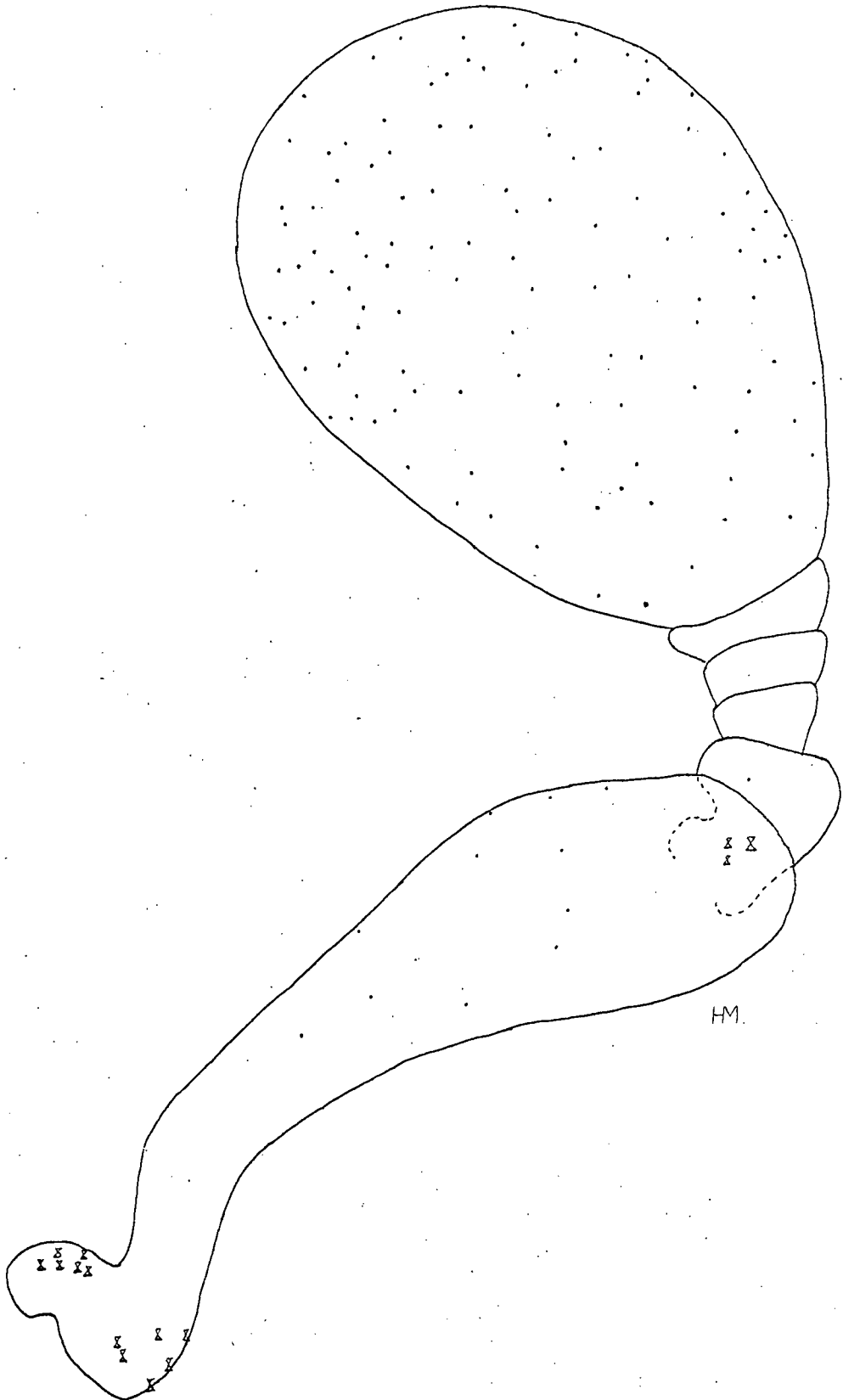


Figure 10. Distribution map of hypodermal gland pores and sensilla trichodea, Type I, on female left antenna, anterior surface.

Figure 11. Photomicrograph of hypodermal gland pore. 'Permout' mount.

Figure 12. Photomicrograph of sensilla chaetica. Note sharp long points, pointed projections along hairs. Distilled water mount. 12

Figure 13. Photomicrograph of same antenna as in Fig. 12, showing long sensilla chaetica on scape (arrow) which may act as proprioceptors for club position in relation to scape.

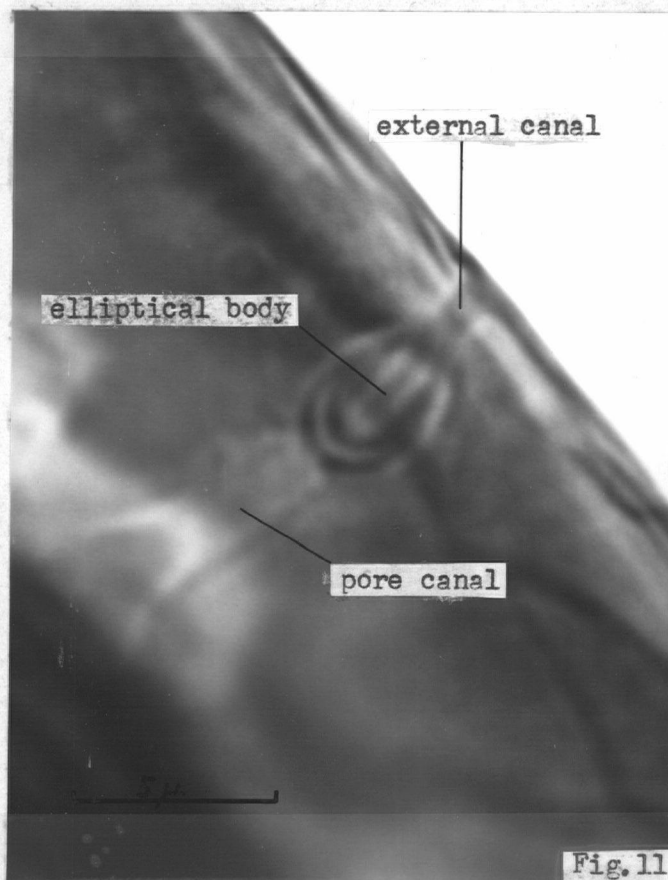


Figure 14. Electron micrograph of hypodermal gland pore cell.

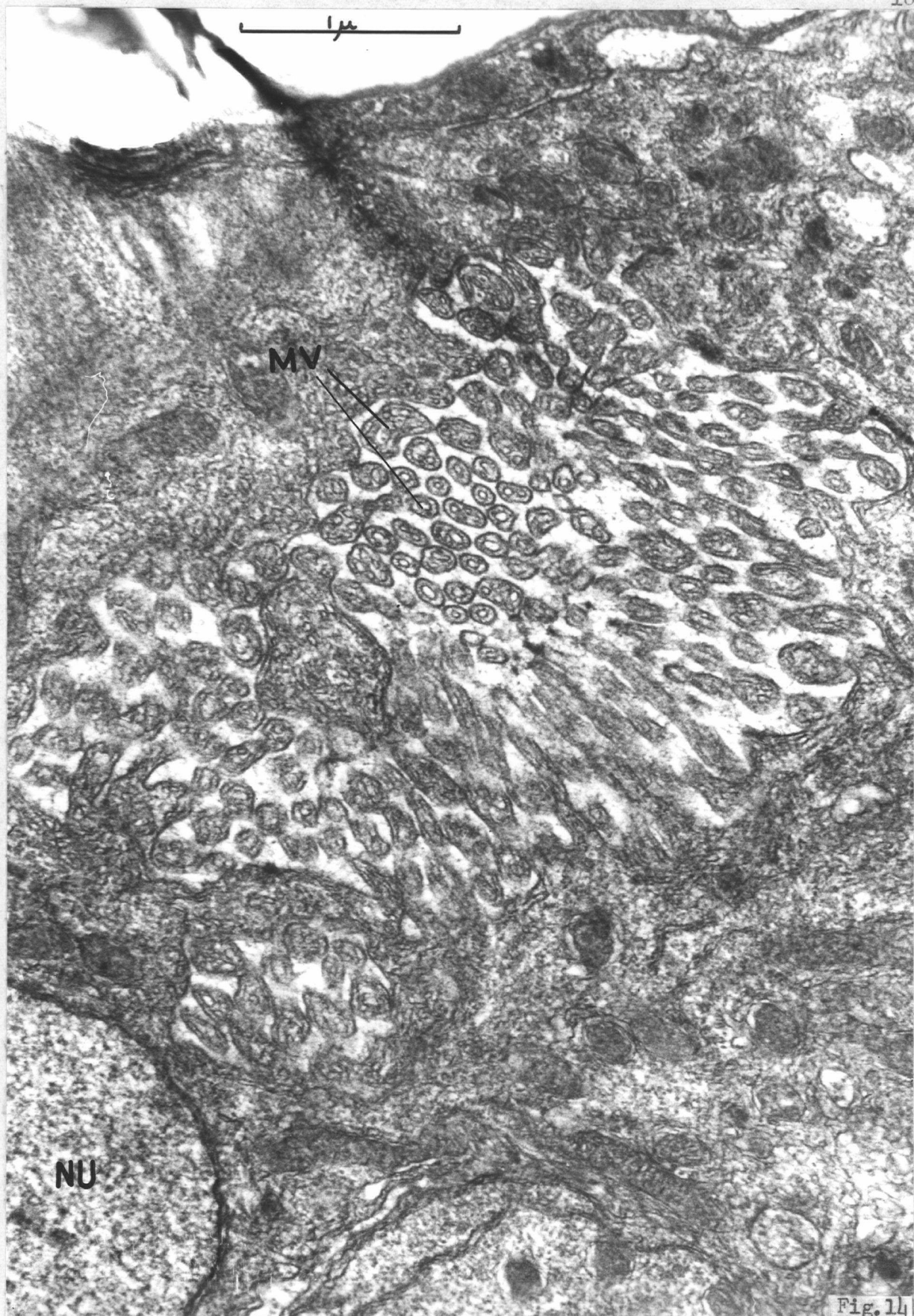
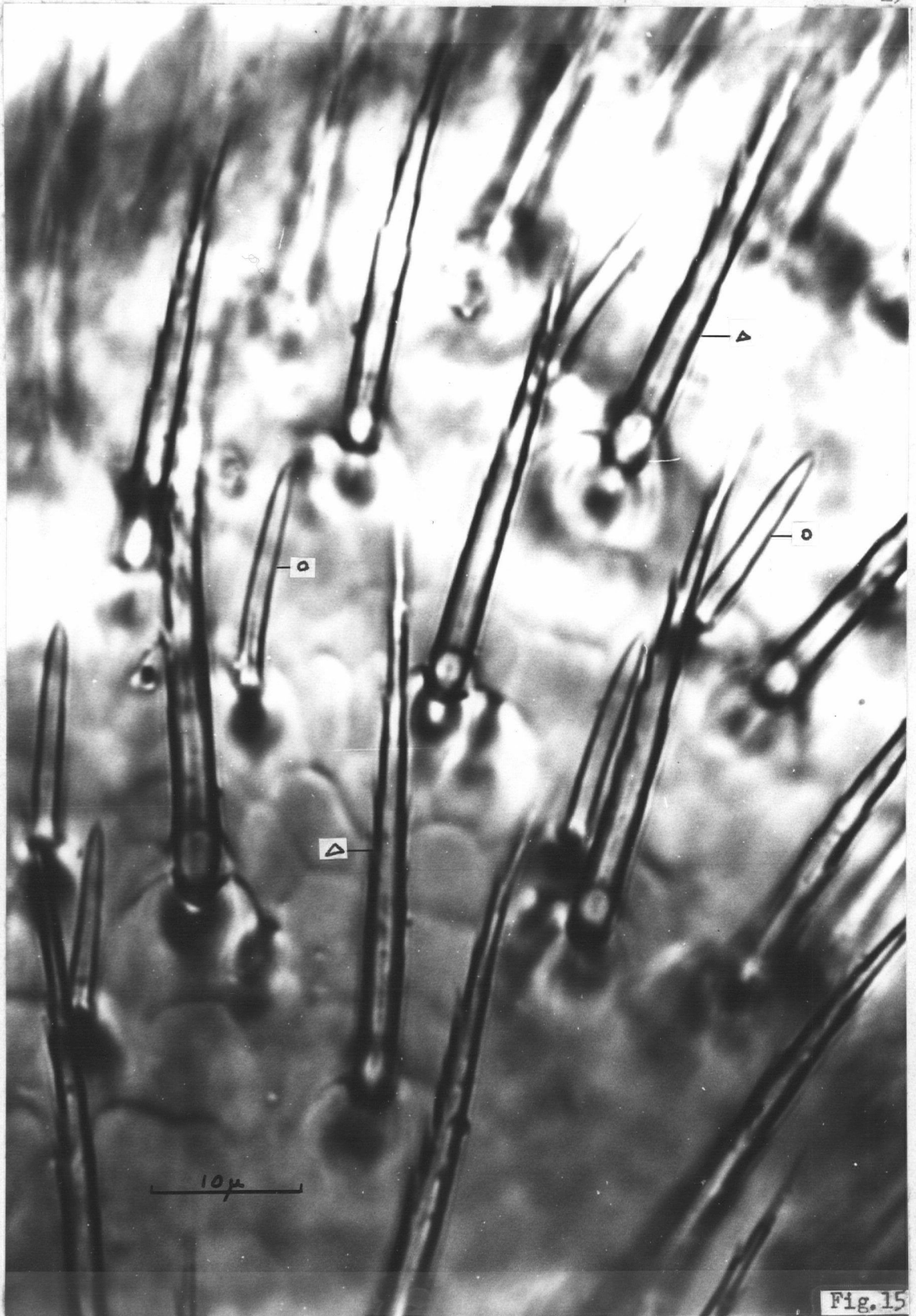


Fig. 14

Figure 15. Photomicrograph of antenna at left in Fig.2, showing sensilla chaetica and long sensilla basiconica. Note thick hair wall, small central lumen in sensilla chaetica, and thin wall of sensilla basiconica.

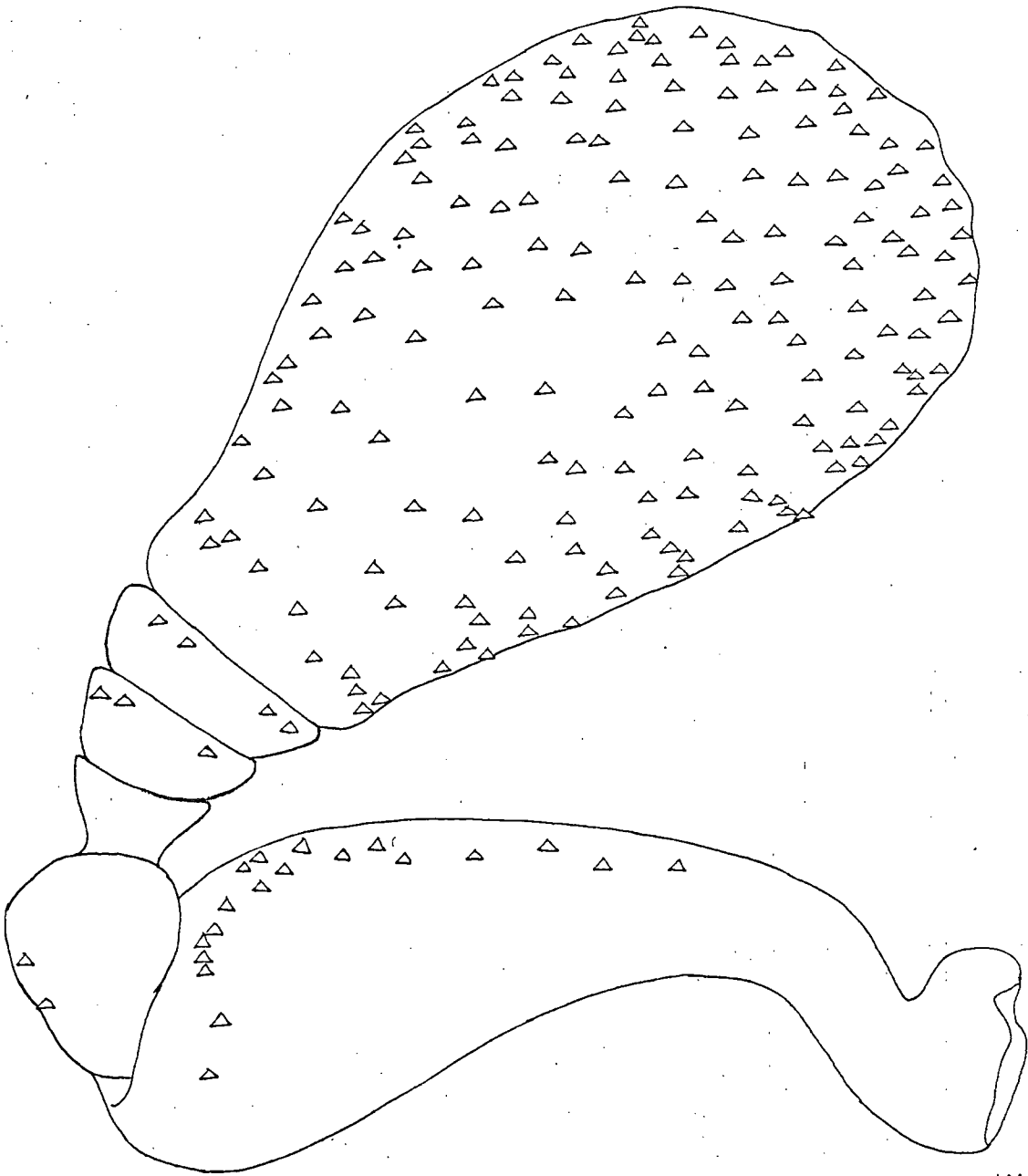


(Fig.12). The hair appears circular and solid in cross section, save for a small empty central lumen (Fig.23).

The hair base and socket are of a complex structure, with the following features (Fig.22): the proximal portion of the hair is attached to the body cuticle by a conical ring of longitudinally ribbed cuticle (hair root) which stains like articulating membrane, as for example that between the scape and first funicular segment. In a hair of $1\ \mu$ diameter near the base the cone has a diameter of $1.8\ \mu$ at point of hair attachment, $2.5\ \mu$ at widest point of body-cuticle attachment, and a wall thickness of $0.4\ \mu$ to $0.5\ \mu$. Total height of the cone is about $1.8\ \mu$. The socket lining is cylindrical proximally, flaring outwards distally. It is composed of a similarly staining, though more homogeneous cuticular material, and has a wall thickness of $0.15\ \mu$. It partly bends inwards at the point of hair attachment just distal to the hair root, thus forming a slightly wider groove around the hair base. The socket lining and the distal half of the hair root are surrounded by a sponge-like cavity which seems to be filled with air, and does not communicate with the external and internal environments (during specimen preparation nothing penetrates into this cavity)(Fig.26). The maximum diameter of about $2\ \mu$ of the cavity occurs where the socket lining and distal portion of the hair root join. There is a ring-like constriction of the body cuticle just proximal to the base of the hair root. In a hair of the above dimensions the base of the socket lies approximately $4.5\ \mu$ below the external cuticular surface.

The length of the pore canal leading from the base of the hair towards the interior depends upon the cuticle thickness at that point. Indeed, if the cuticle is very thin, it shows a thickening interiorly in the immediate vicinity of the sensillum. In the sensillum described above the cuticle is $5.5\ \mu$ thick at the sensillum and only $3.5\ \mu$ thick $6\ \mu$ away.

The cellular component of the sensillum consists of the following: a



H.M.

Figure 16. Distribution map of sensilla chaetica on male left antenna, posterior surface.

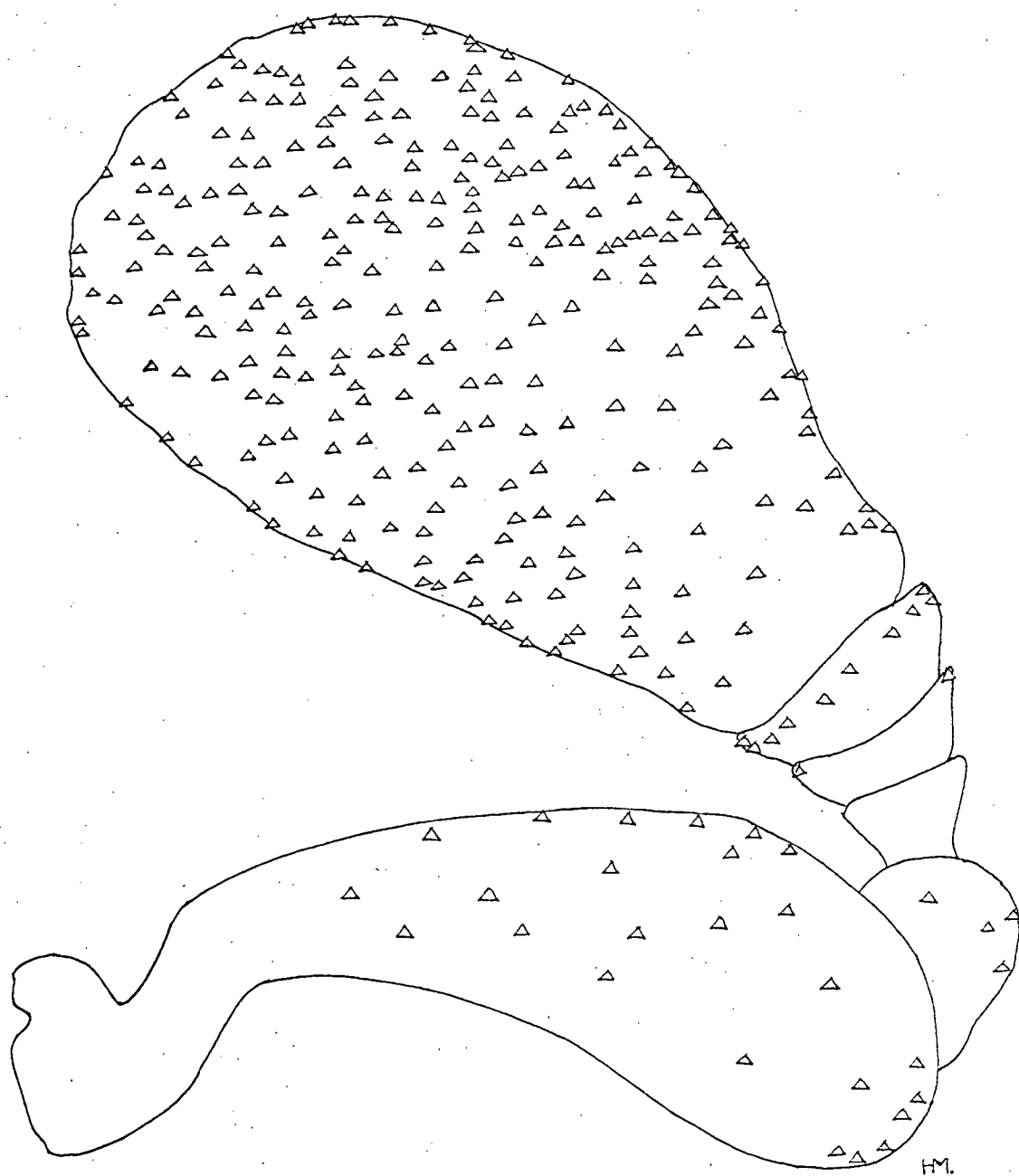


Figure 17. Distribution map of sensilla chaetica on male left antenna, anterior surface

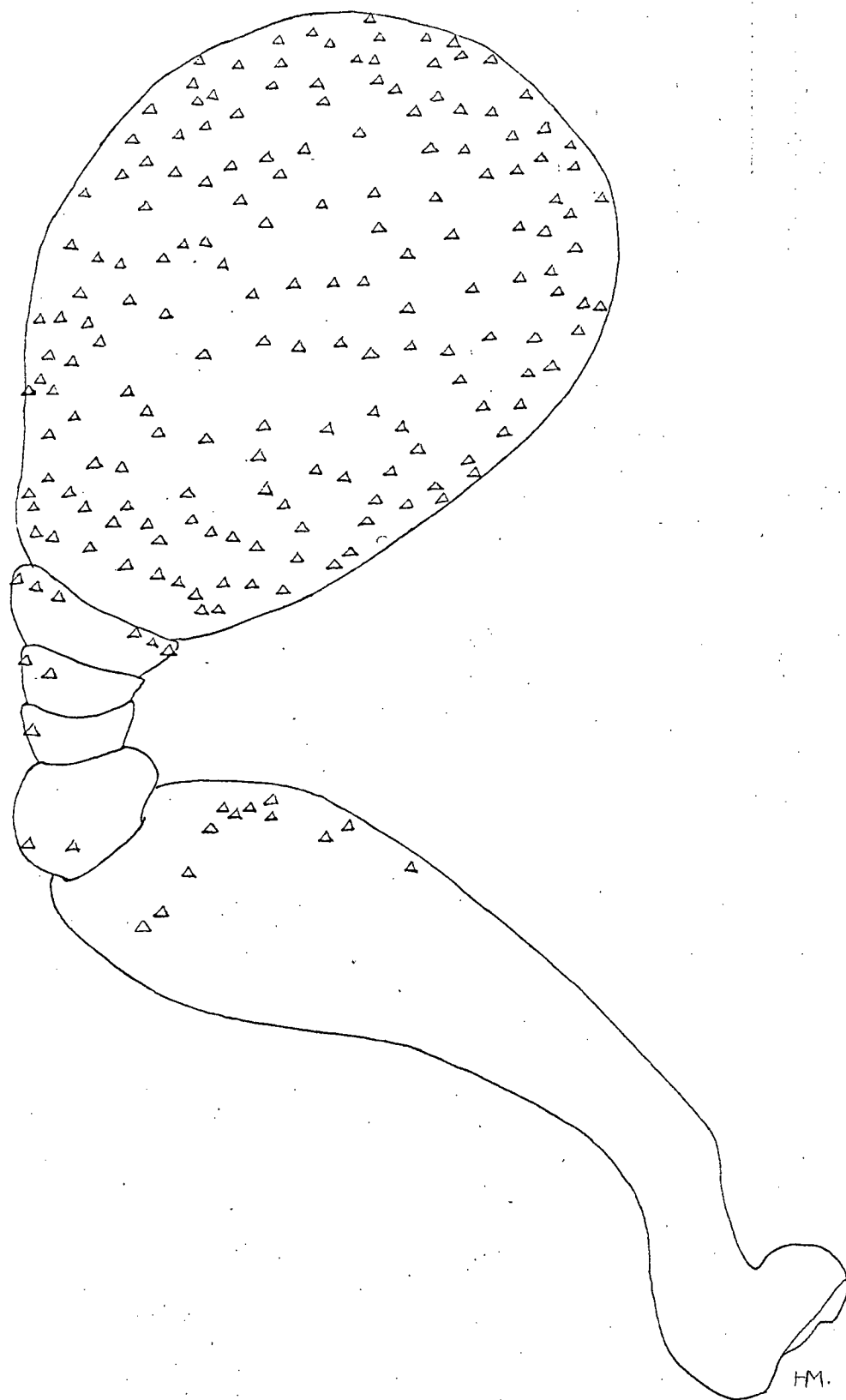


Figure 18. Distribution map of sensilla chaetica on female left antenna, posterior surface.

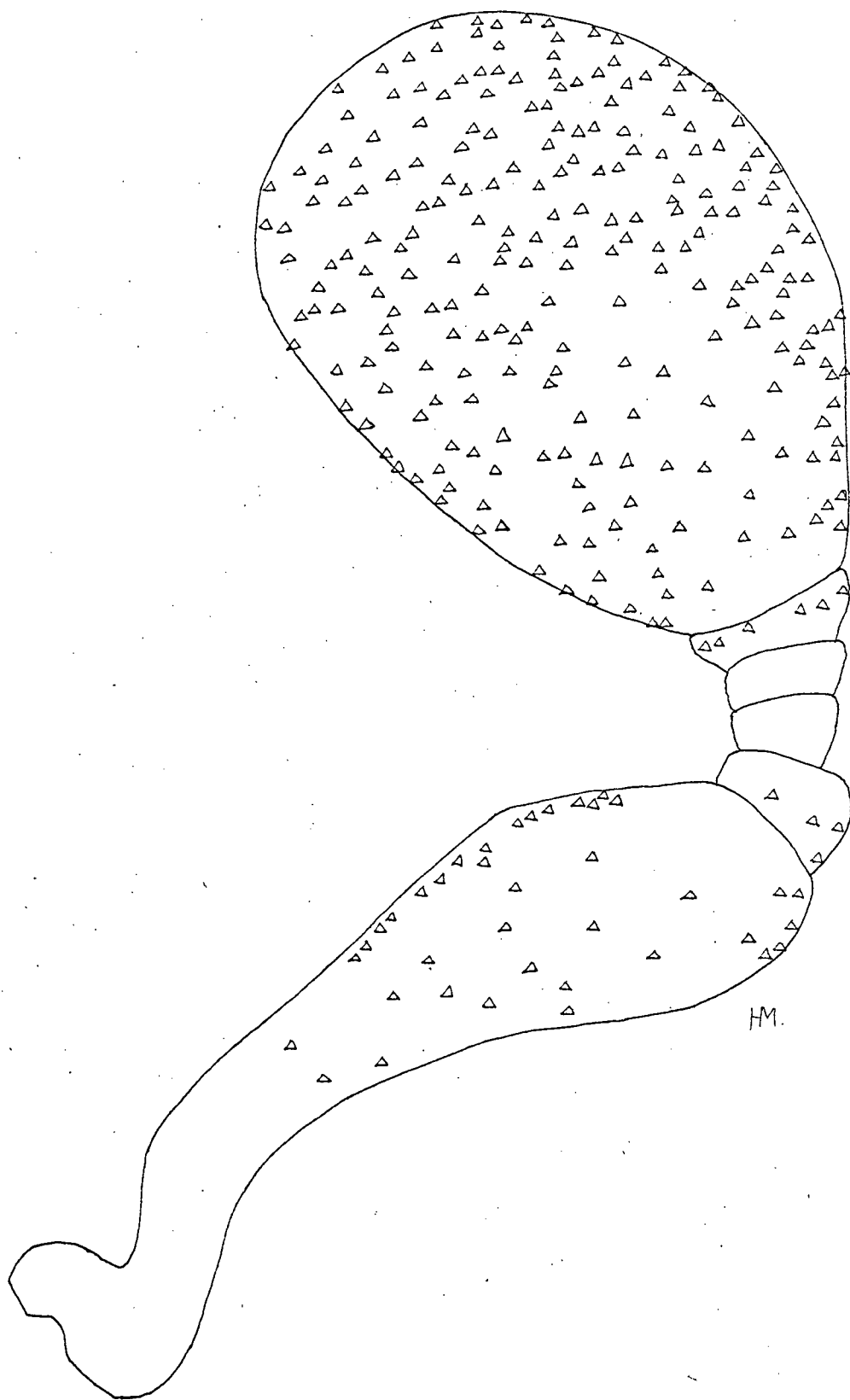


Figure 19. Distribution map of sensilla chaetica on female left antenna, anterior surface.

Figure 20. Schematic diagram of sensillum chaeticum, to scale.

Figure 21. Schematic diagram of sensillum chaeticum, ciliary region, with cross sections at levels indicated.

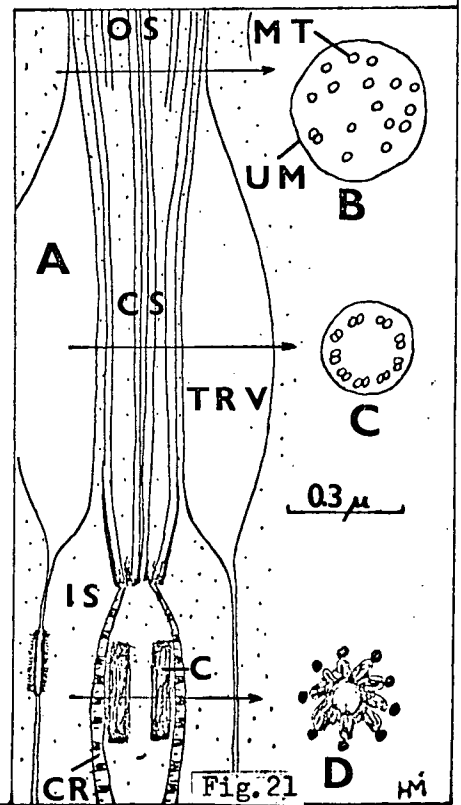
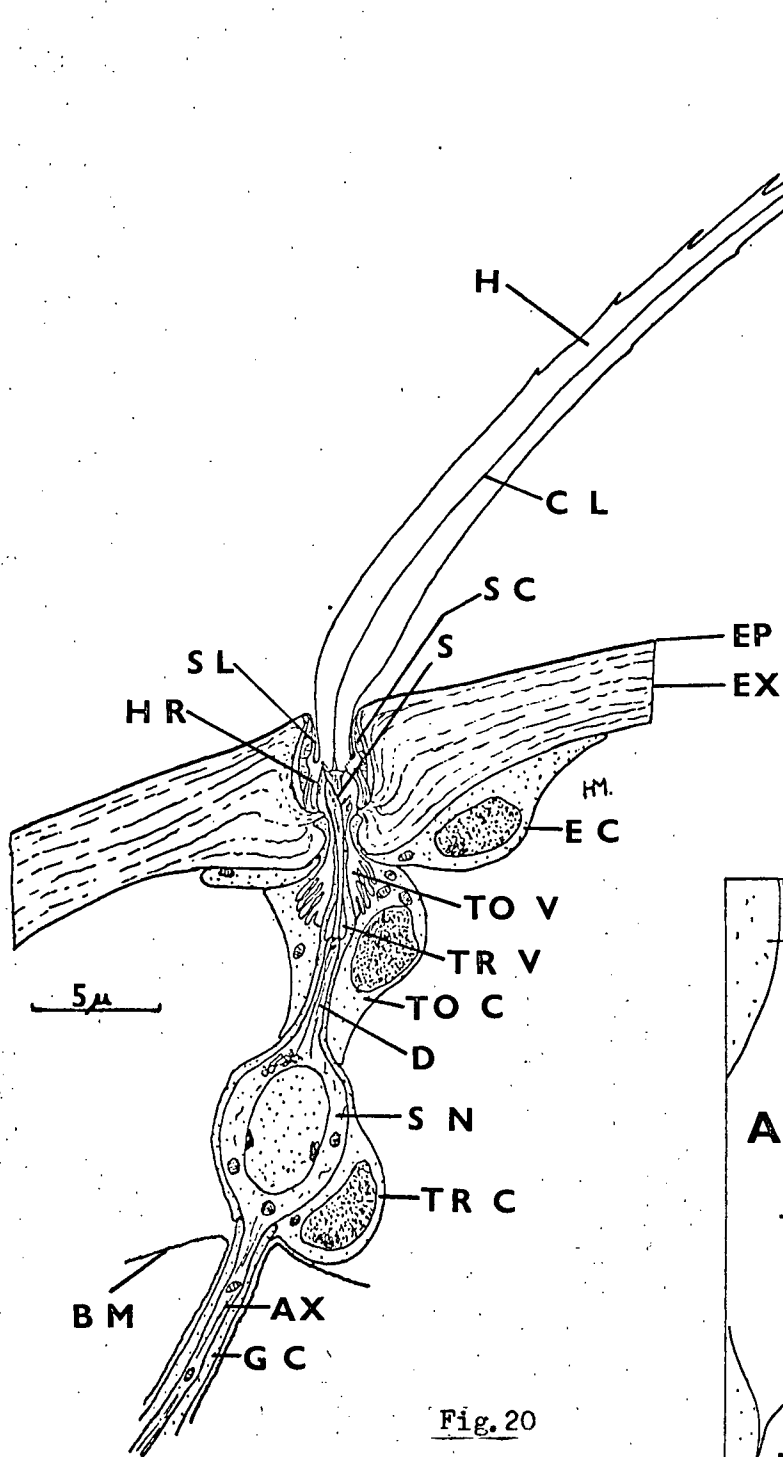
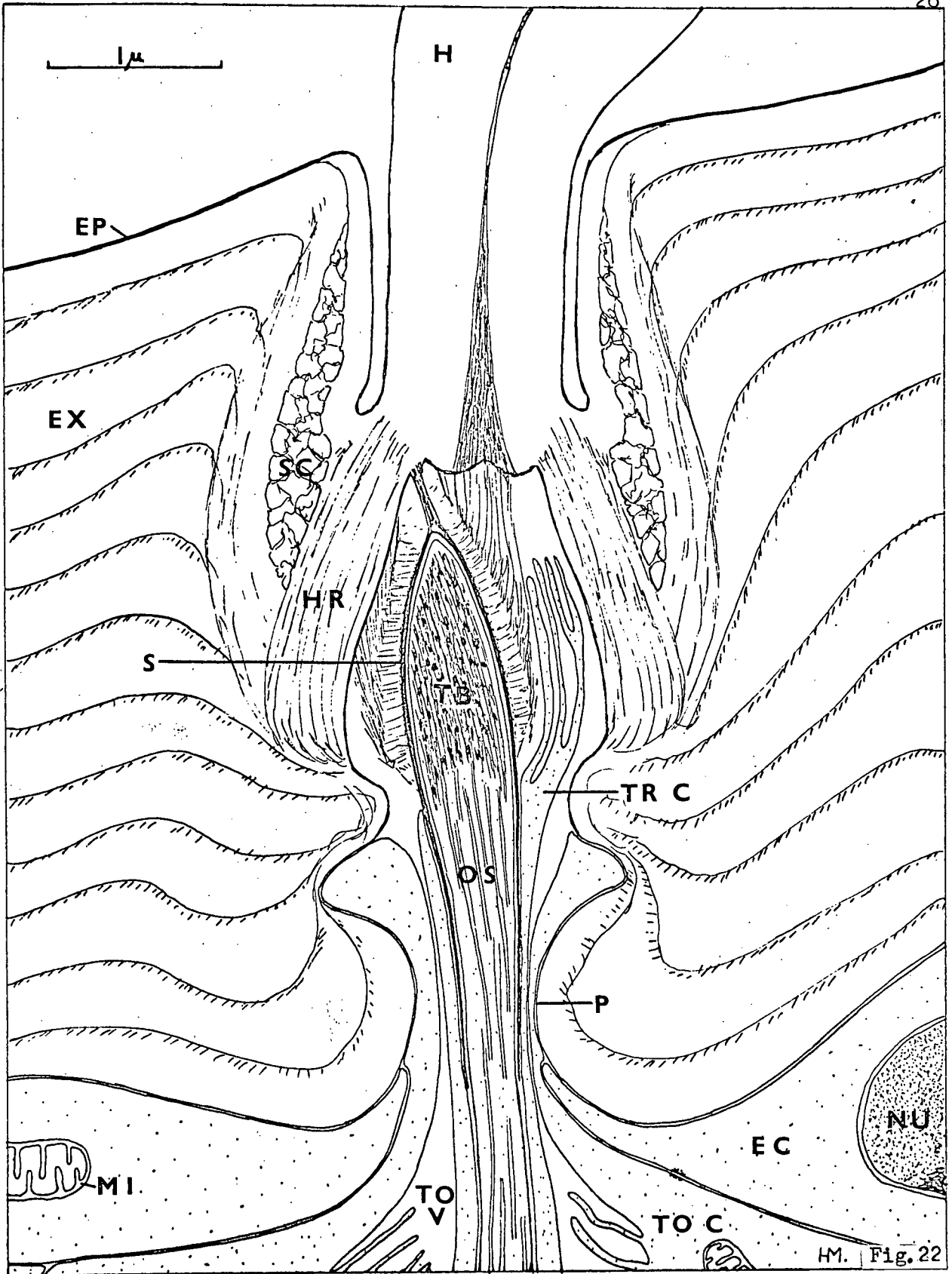


Figure 22. Schematic diagram of sensillum chaeticum, socket region.



tormogen or socket-secreting cell (also called a cap cell), a trichogen or hair-secreting cell (enveloping cell), a single bipolar neuron, and its associated glial cell (Figs.20,30).

The tormogen cell has an elongate shape, forming a sheath around the trichogen cell and the dendrite, and extending as a thin lining of the sensillum canal to the constricting cuticular ring at the base of the socket. Fine cytoplasmic villiform processes extend into an extracellular vacuole (tormogen vacuole) which surrounds the distal portions of the trichogen cell and nerve process, and extends from the base of the hair to about 1.5μ to 2μ proximal to the inner surface of the cuticle. Endoplasmic reticulum, smooth or rough, appears to be largely absent, whereas wellformed mitochondria of an ovoid shape (0.6μ by 0.9μ) are abundant. A few microtubules are present in the homogeneous cytoplasm. The cell nucleus, with its darkly staining central nucleolus, is variously situated, apparently depending on space considerations within the club, but is often found just proximal to the above-mentioned vacuole. Maximum cell dimensions are about 5μ by 10μ .

The trichogen cell is even more elongate, extending from the proximal portion of the nerve cell body to the base of the hair, a distance of 20μ or more. It forms a thin (0.3μ) sheath around the neuron except around a small portion of the ciliary process, where a small flask-shaped extracellular vacuole (trichogen vacuole) is found. This is a constant feature in this sensillum, but of unknown significance. The distal portion of the trichogen cell in the tormogen vacuole just beneath the hair base is extended into concentric incomplete lamellae which are about 600\AA thick (Fig.27). Desmosomes joining the cell membrane to overlapping parts of itself or to neural membrane are present. Endoplasmic reticulum is sparse, and mitochondria are small and few. Microtubules again are present and longitudinally oriented.

The bipolar neuron is attached at its distal end to the base of the hair by means of a darkly staining cuticular sheath or scolopale which terminates distally in a short (0.3μ to 0.4μ) strand of cuticle continuous with the cuticle at the point of juncture of hair base and hair root (Figs. 24, 25). The point of attachment is constant, being in the plane of curvature of the hair, and on the outside curve. The scolopale is bullet-shaped, pointed distally, about 0.6μ in diameter, 3μ long, and with a maximum wall thickness of 400\AA , which decreases proximally and disappears. The scolopale is surrounded by a 0.13μ thick lightly staining area which in turn is surrounded by cuticular strands extending to the hair base (Fig. 27). Fine radially arranged strands connect the outer strand layer with the scolopale.

Within the scolopale the nerve ending is separated from it by a clear extracellular layer 75\AA thick. The unit membrane is separated from structures internal to it by another clear layer about 200\AA thick (Fig. 27). The distal 1μ portion of the nerve process contains a darkly staining mass (tubular body) which at higher magnification has a mottled appearance, and shows uniform curved striation both in longitudinal and in cross section, reminiscent of protein crystals (Figs. 24, 28). The periodicity of 130\AA to 150\AA is unrelated to microtubule diameter (200\AA to 250\AA). Microtubules are abundant, and all are longitudinally oriented in the more proximal portion of the outer segment (Figs. 21, 32), gradually decreasing in number proximally until in the region of the trichogen vacuole the dendrite has the appearance of a cilium in cross section, that is, nine double peripheral strands (lacking, however, the two central single ones) bounded by the cell membrane. This ciliary segment is about 1.5μ long, and 0.21μ to 0.26μ in diameter, with the base situated about 6μ to 10μ from the tip of the scolopale, depending on canal length. A ciliary rootlet apparatus is found at the tip of the inner segment of the dendrite, and consists of a dense cup-shaped region of

Figure 23. Electron micrograph of sensillum chaeticum, cross section just distal to hair base. Hair socket was broken open during specimen preparation. Note small empty hair lumen, thick hair wall staining like surrounding body exocuticle, and darkly staining socket lining. OsO_4 fixation, PTA and lead acetate block stain.

Figure 24. Electron micrograph of sensillum chaeticum longitudinal section in socket region. Note tubular body, attachment of scolopale to hair base. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 25. Electron micrograph of sensillum chaeticum, longitudinal section through tubular body. Osmium fixation, PTA and lead acetate block stain.

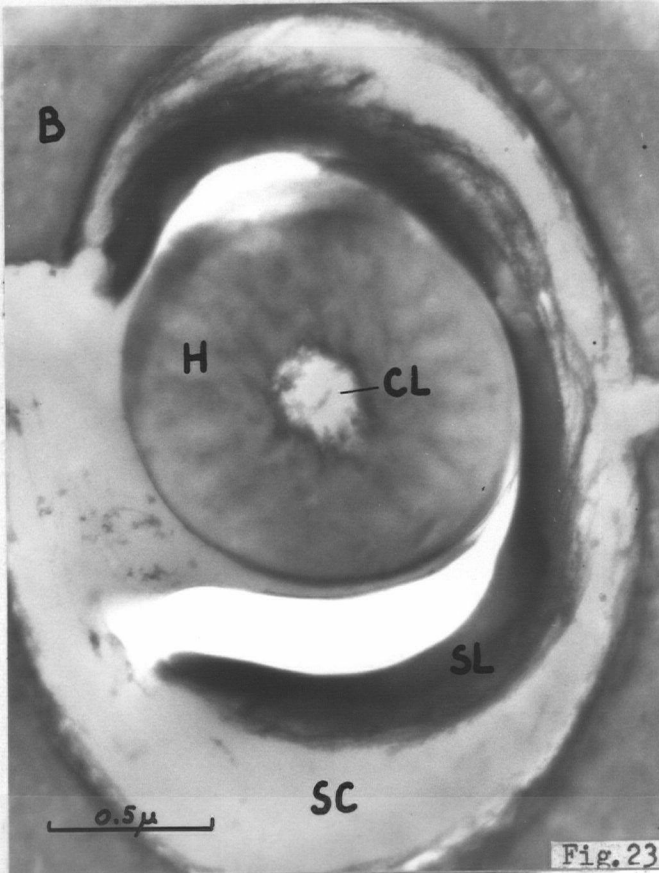


Fig. 23

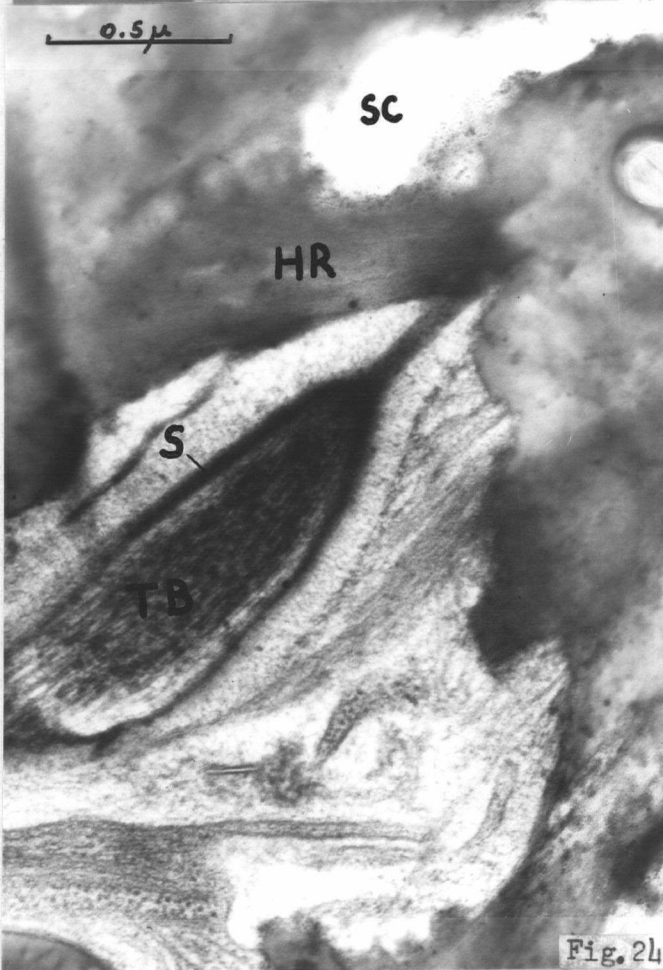


Fig. 24

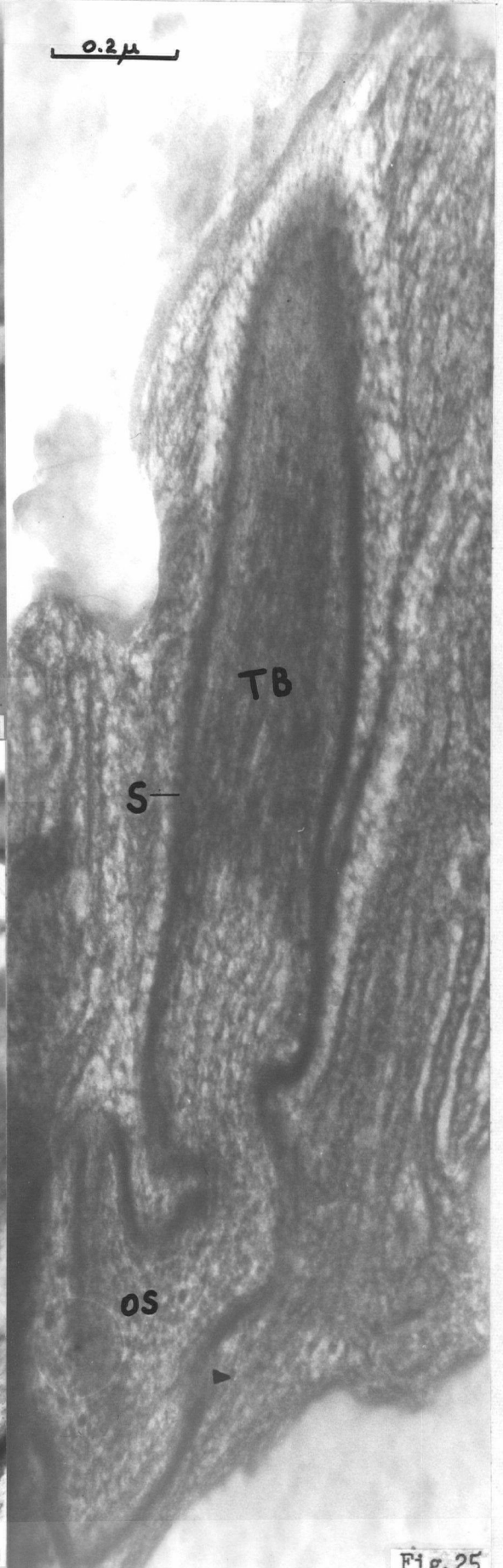


Fig. 25

Figure 26. Electron micrograph of sensillum chaeticum, cross section through tubular body. Osmium fixation, PTA and lead acetate block stain.

Figure 27. Electron micrograph of sensillum chaeticum, cross section through tubular body. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 28. Electron micrograph of sensillum chaeticum, cross section of tubular body. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 29. Electron micrograph of sensillum chaeticum, cross section of tubular body. Osmium fixation, PTA and lead acetate block stain.



Fig. 26

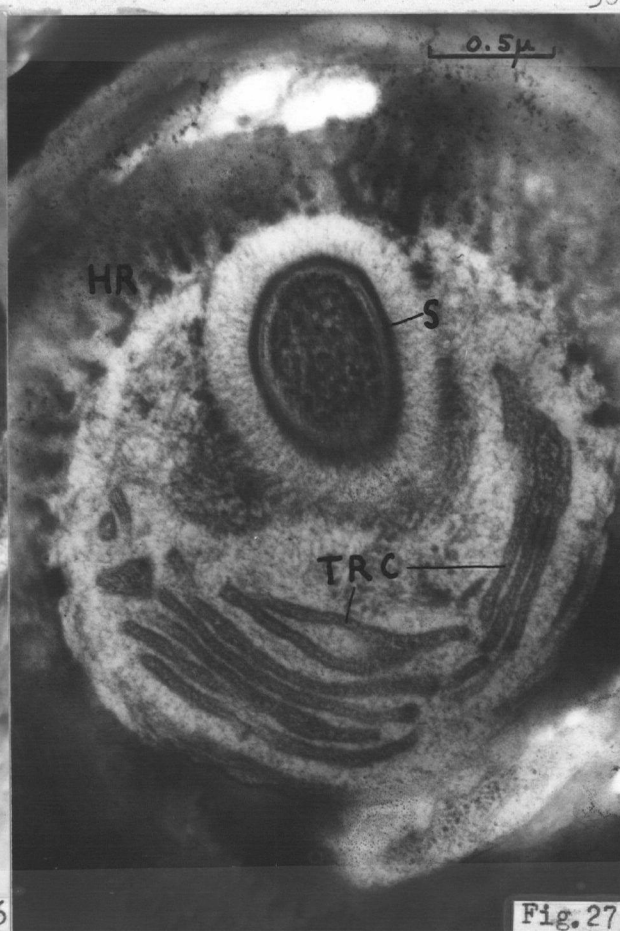


Fig. 27



Fig. 28

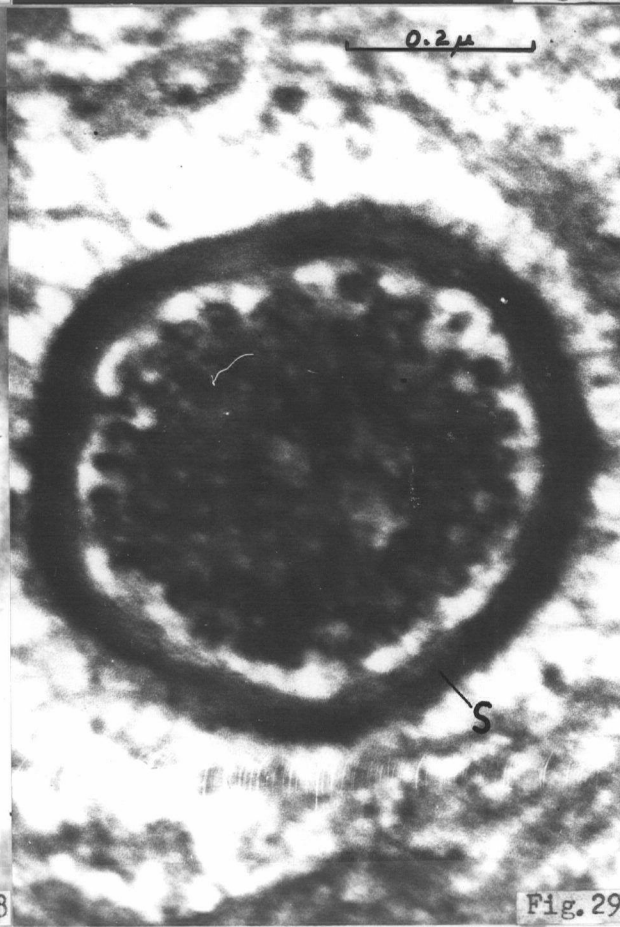


Fig. 29

0.15 μ diameter from the proximal base of which emerge nine solid fibres which pass on the outside of the centriole and continue proximally as the ciliary rootlets which appear collagen-like, being banded at 730 \AA intervals (Fig.30). The centriole, situated 0.15 μ below the basal cup, is a hollow cylinder 0.25 μ long and 0.16 μ in diameter (Fig.31). The inner segment, which is 0.5 μ in diameter, contains some smooth endoplasmic reticulum, microtubules, and occasionally mitochondria.

The nerve cell body is elongate, about 5 μ in diameter, with a comparatively large oval nucleus (Fig.33). Endoplasmic reticulum is sparse, but the Golgi complex is very prominent. Mitochondria and microtubules are relatively abundant. An interesting structure is found in most neurons near the axonal process: it is spherical, 0.8 μ to 1 μ in diameter, and consists of a dome-shaped homogeneous mass from the surface of which emerge concentric lamellae 50 \AA thick, separated by 70 \AA . The solid mass appears crystalline (Fig.33).

The axon, which proceeds without synapse to the brain, is about 0.6 μ to 0.8 μ in diameter, becoming thinner proximally, and contains mitochondria and microtubules along its entire length. The axon surface is coated with a dense extracellular layer which apparently is produced by the glial cells (Fig.89).

The neurones characteristically show a lighter staining than the formative cells, making their identification somewhat easier.

2. Sensilla Trichoidea, Type I

These sensilla, which are situated at the base of the scape and the base of the first funicular segment (Figs.7-11), are short (4 μ to 8 μ) thin hairs articulating in a socket (Figs.34,35). Little else is known of their structure, since no sections of these sensilla were studied in the electron microscope.

Figure 30. Electron micrograph of sensillum chaeticum, longitudinal section of cellular components. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 31. Electron micrograph of sensillum chaeticum, cross section through inner segment of dendrite at the level of the centriole. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 32. Electron micrograph of sensillum chaeticum, cross section of outer segment of dendrite. Note abundant microtubules. Glutaraldehyde-osmium fixation, uranyl acetate and lead citrate section stain.

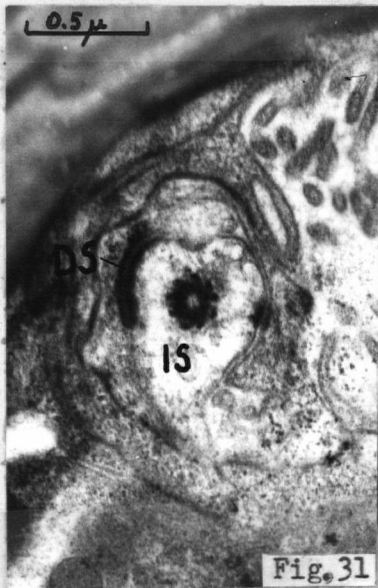


Fig. 31

outer segment

scolopale

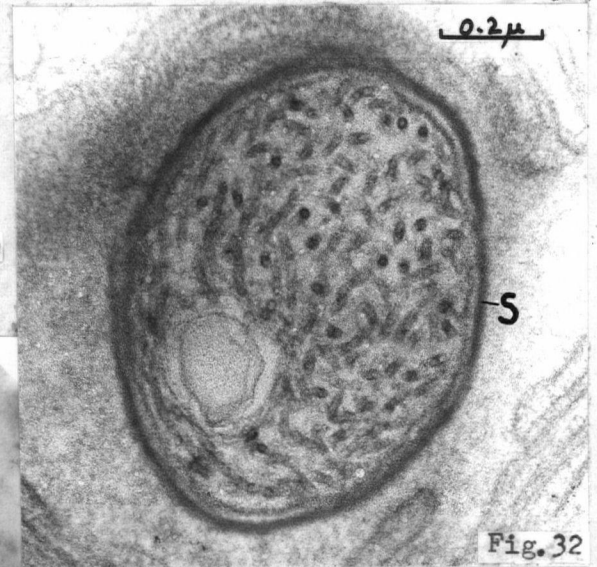
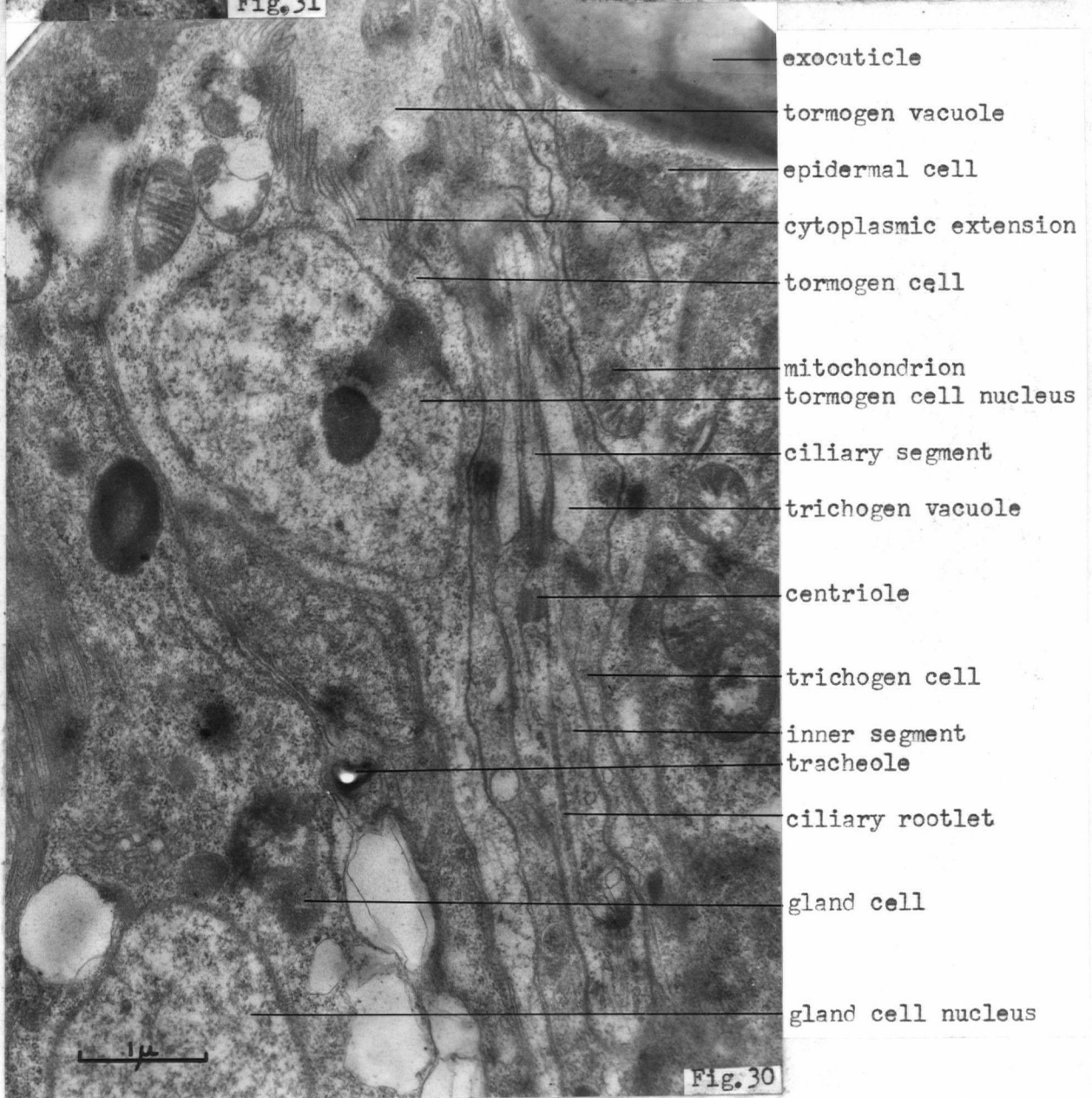


Fig. 32



exocuticle

tormogen vacuole

epidermal cell

cytoplasmic extension

tormogen cell

mitochondrion

tormogen cell nucleus

ciliary segment

trichogen vacuole

centriole

trichogen cell

inner segment

tracheole

ciliary rootlet

gland cell

gland cell nucleus

Fig. 30

Figure 33. Electron micrograph of typical sensory neuron cell body and axon. Glutaraldehyde-osmium fixation, lead citrate section stain.

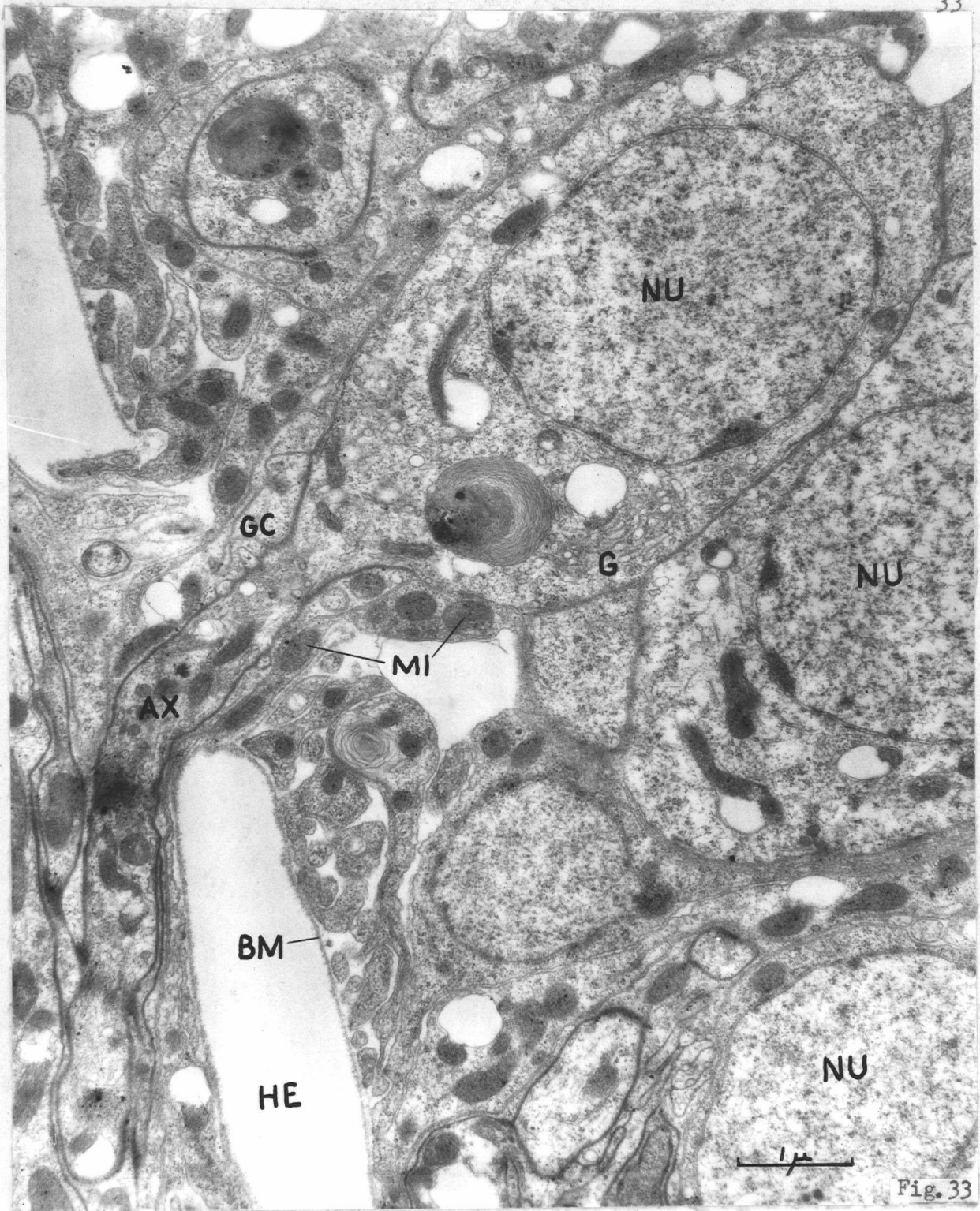
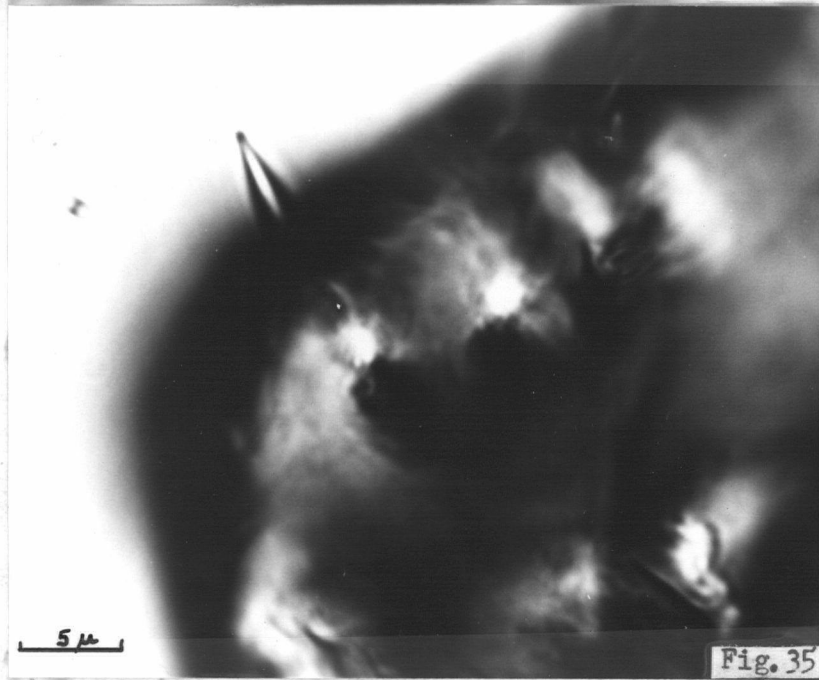
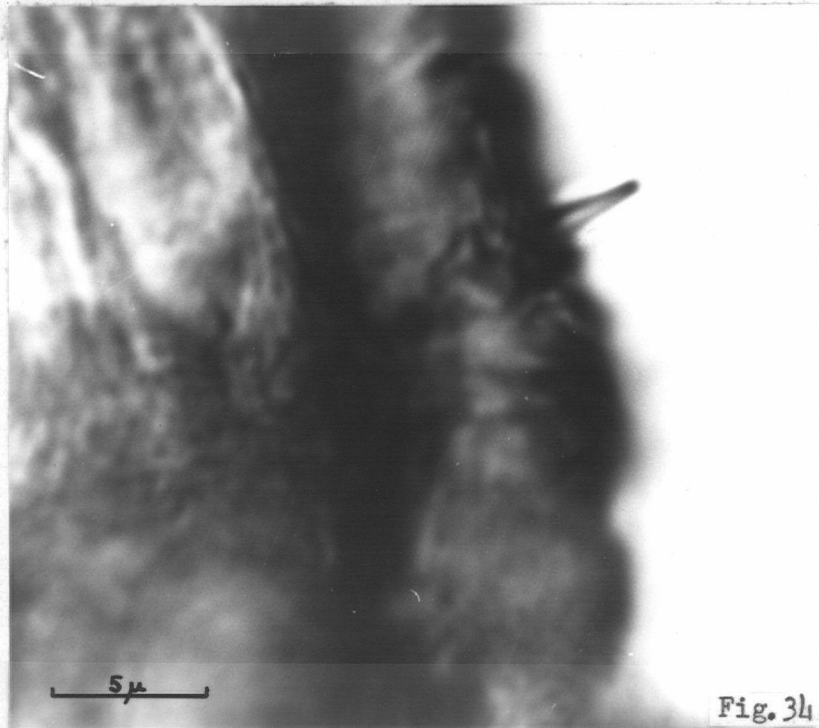


Figure 34. Photomicrograph of sensillum trichoideum, Type I, on first funicular segment. Distilled water mount.

Figure 35. Photomicrograph of sensillum trichoideum, Type I, on proximal bulb of scape. Distilled water mount.

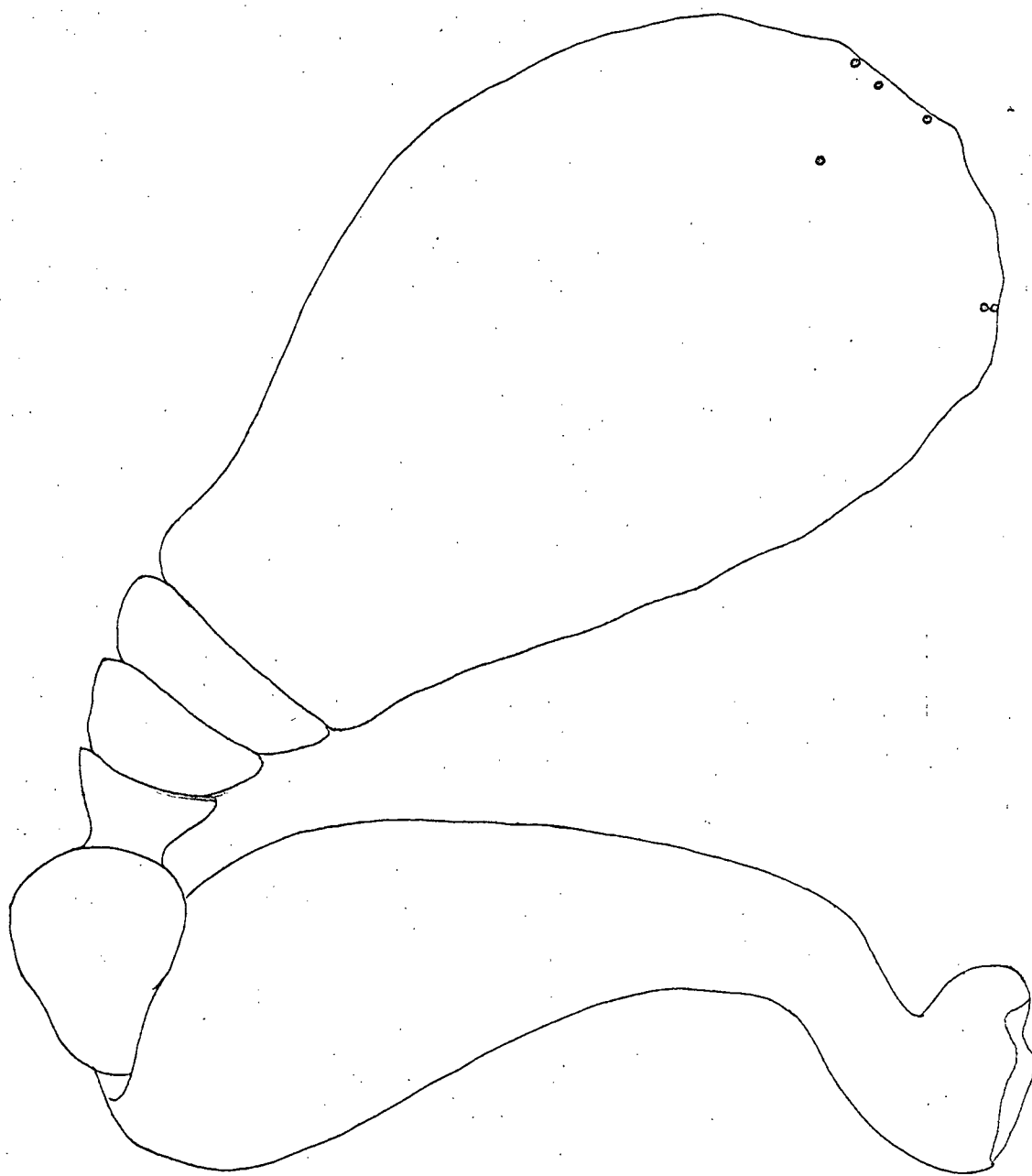


3. Sensilla Trichoidea, Type II

These sensilla trichoidea are found on the distal periphery of the club only, and are about four dozen in number, with most of these being on the anterior club surface (Figs.36-39). The hair is 18μ to 25μ long, smooth, sharply pointed distally, and hollow, with a wall thickness of 0.2μ proximally, tapering to 0.1μ distally. The hair diameter near the base is about 1.5μ . The gentle curvature of the hair is in a direction opposite to that of the sensilla chaetica, but is not as pronounced as that of the Type III sensilla trichoidea described below (Figs.40,41). The hair wall is perforated, the holes appearing flask-shaped, with a narrow (200\AA) diameter opening to the exterior (Fig.43). No hair socket per se exists, the hair base being joined directly to a softer cuticular ring which tapers to a sharp line proximally, and is solidly joined by its outer surface to the surrounding body cuticle. Only slight bending of the hair is thus possible. On this basis this sensillum could be called a long sensillum basiconicum. The pore canal is straight and wide, and is lined by the tormogen cell. A large tormogen vacuole is present (Fig.44).

The sensillum has two bipolar neurons, the dendritic processes of which are enclosed loosely in a cuticular sheath which extends a short way into the hair lumen (Fig.42). One dendritic process is larger in diameter (0.25μ) than the other (0.17μ). The processes, which contain only microtubules, extend, with slight branching, to the distal limits of the hair lumen. No dendritic endings were demonstrated at the hair perforations.

The appearance and limits of the remainder of the tormogen cell, as well as of the trichogen cell and the nerve cell bodies are not known, since only one sensillum of this type was successfully sectioned to slightly past the base of the hair. However, no significant differences in structure are expected from that described for sensilla chaetica.



HM.

Figure 36. Distribution map of sensilla trichoidea, Type II, on male left antenna, posterior surface.

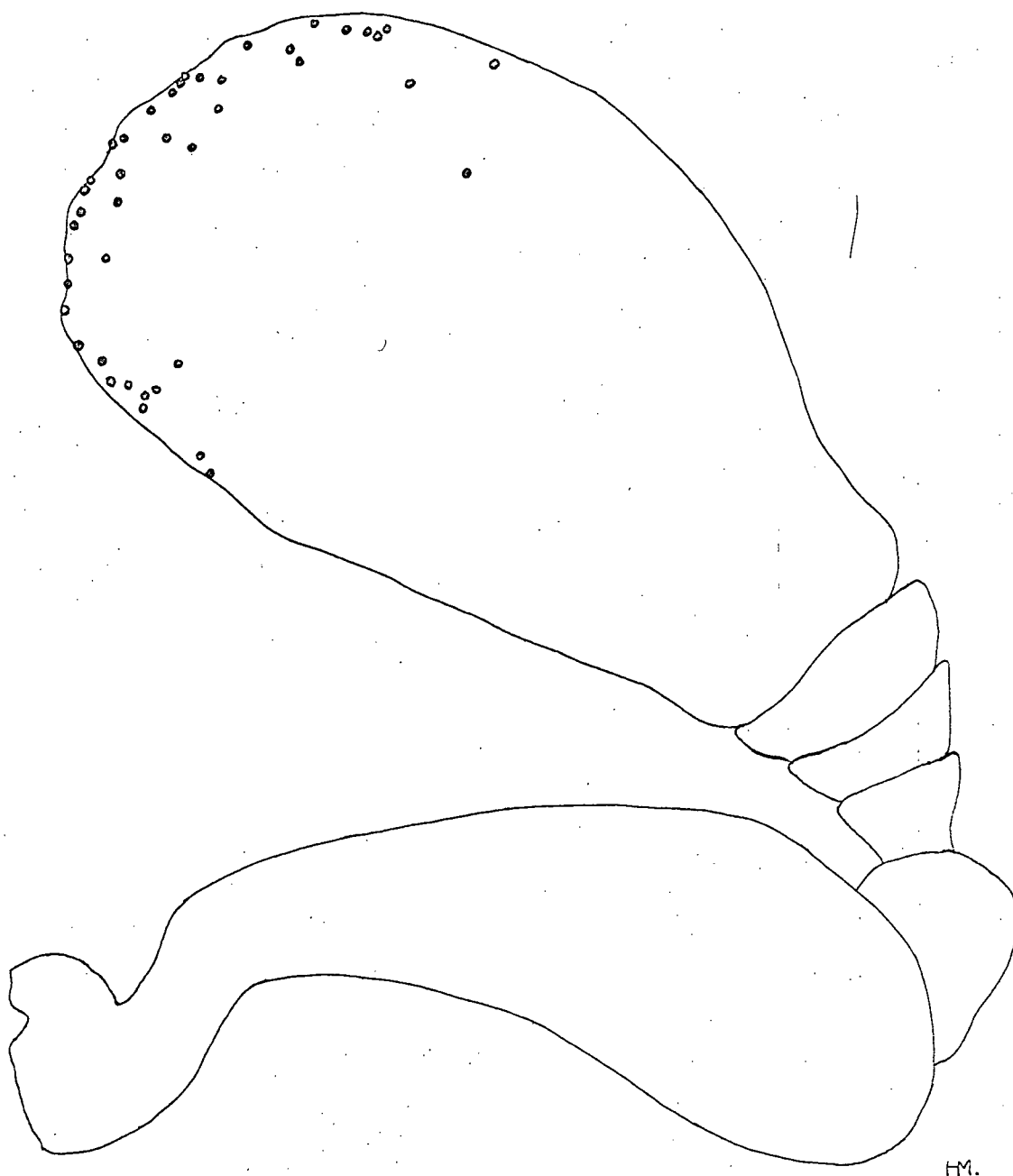


Figure 37. Distribution map of sensilla trichoidea, Type II, on male left antenna, anterior surface.

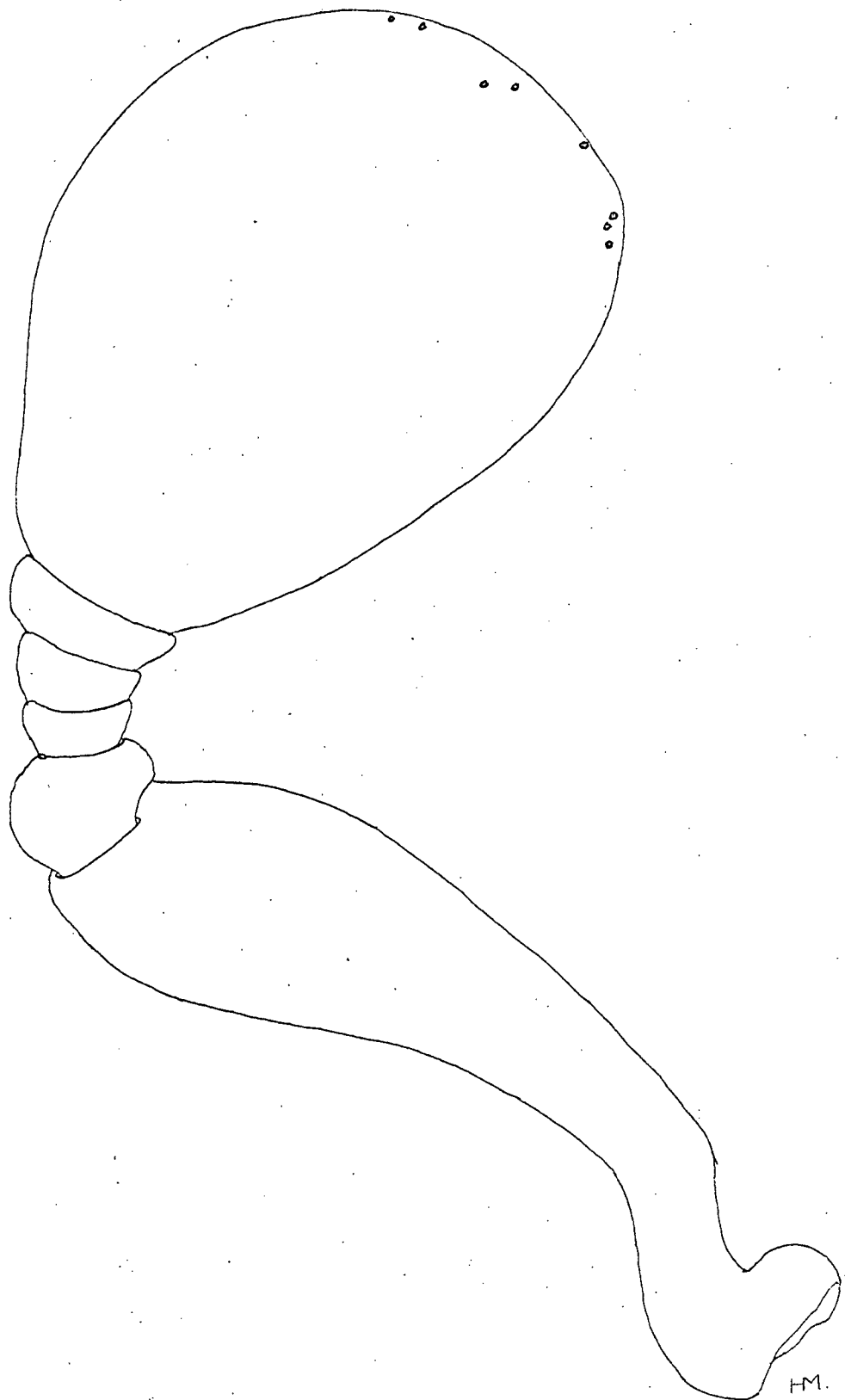


Figure 38. Distribution map of sensilla trichoidea, Type II, on female left antenna, posterior surface.

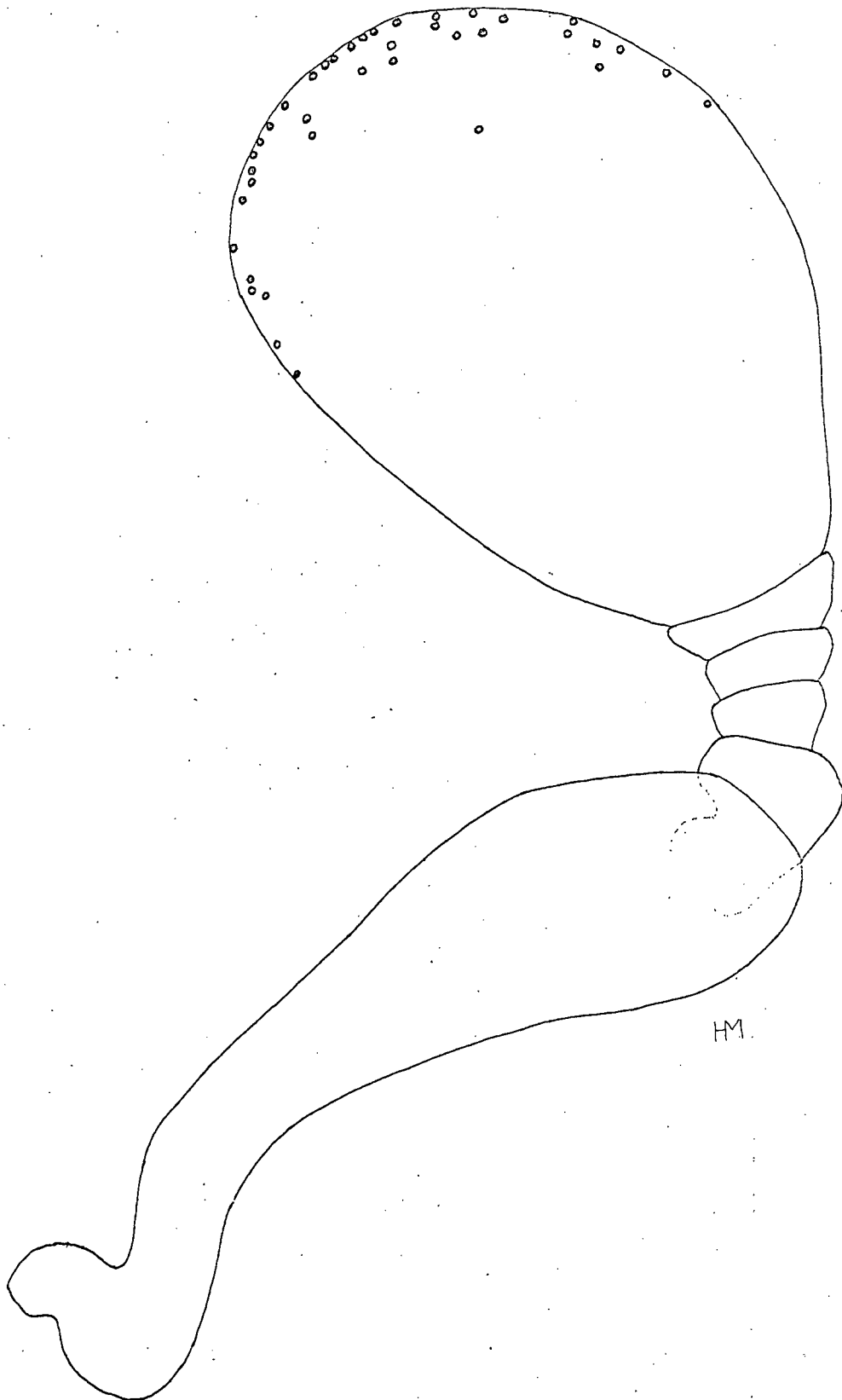


Figure 39. Distribution map of sensilla trichoidea, Type II, on female left antenna, anterior surface.

- Figure 40. Photomicrograph of distal edge of club, showing Types II and III sensilla trichoidea. Compare length, shape, and tips. Distilled water mount.
- Figure 41. Photomicrograph of distal edge of club, showing tips of Types II and III sensilla trichoidea. Distilled water mount.
- Figure 42. Electron micrograph of sensillum trichoideum, Type II, cross section near hair base. Note two dendrites, cuticular sheath. Glutaraldehyde-osmium fixation, lead citrate section stain.
- Figure 43. Electron micrograph of same hair as in Fig. 42, cross section near tip. Note dendrite branches, perforated hair wall.

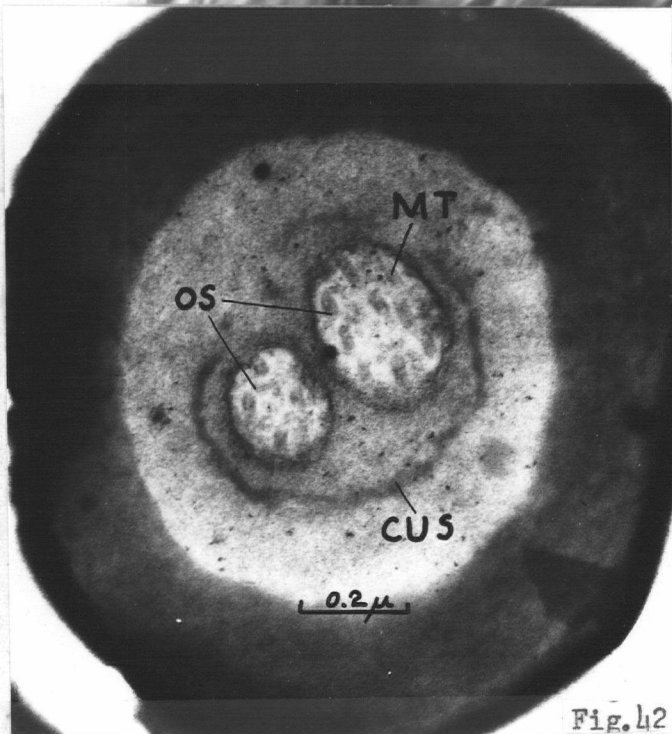
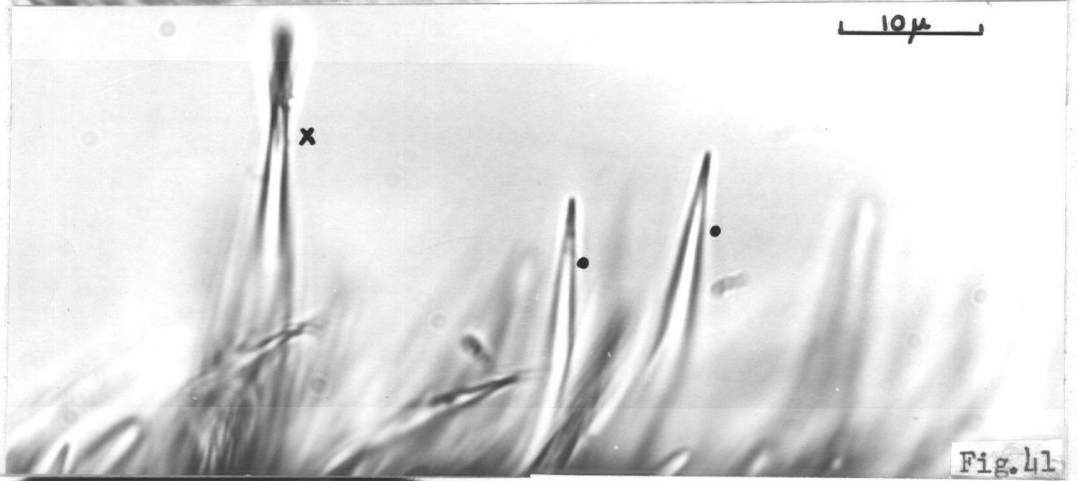
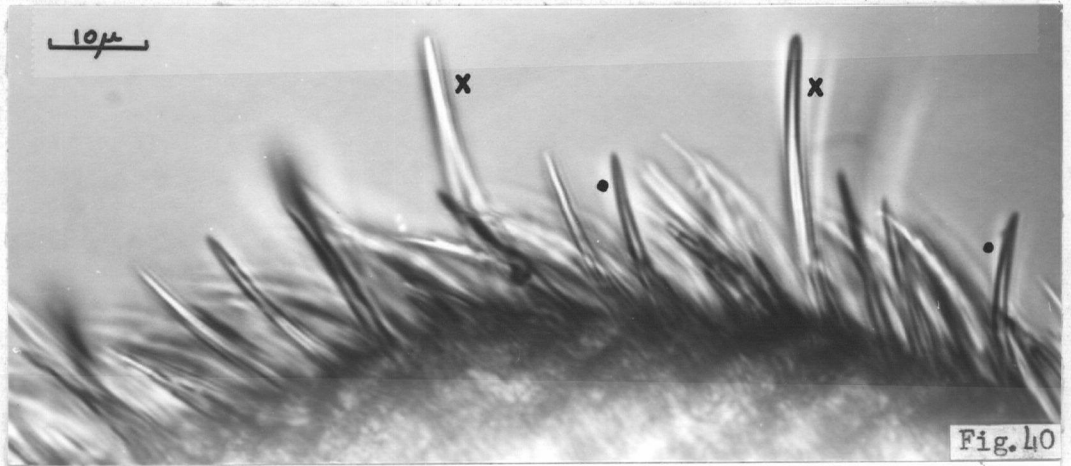
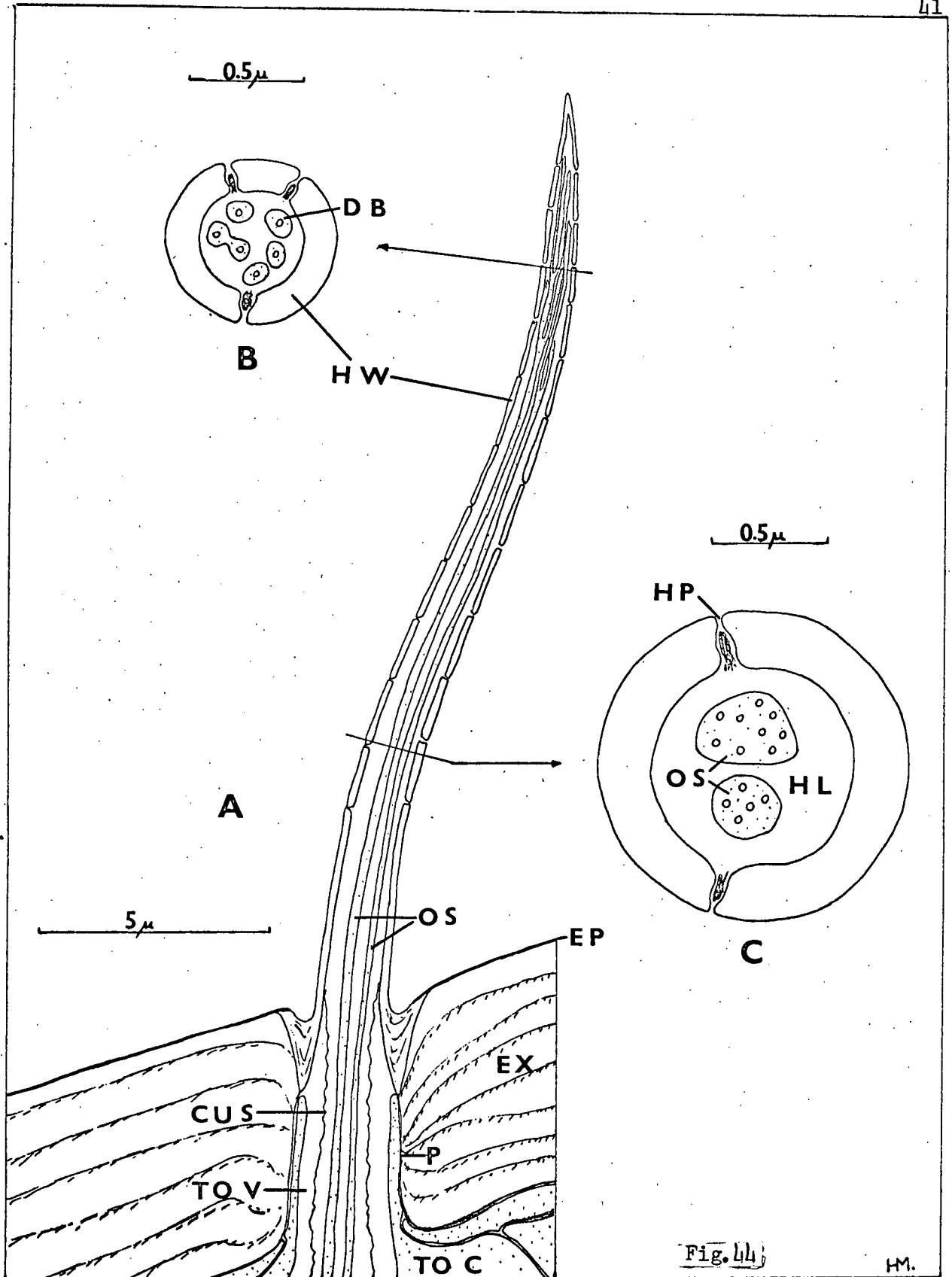


Figure 44. Schematic diagram of sensillum trichoideum, Type II, with cross sections at levels indicated.

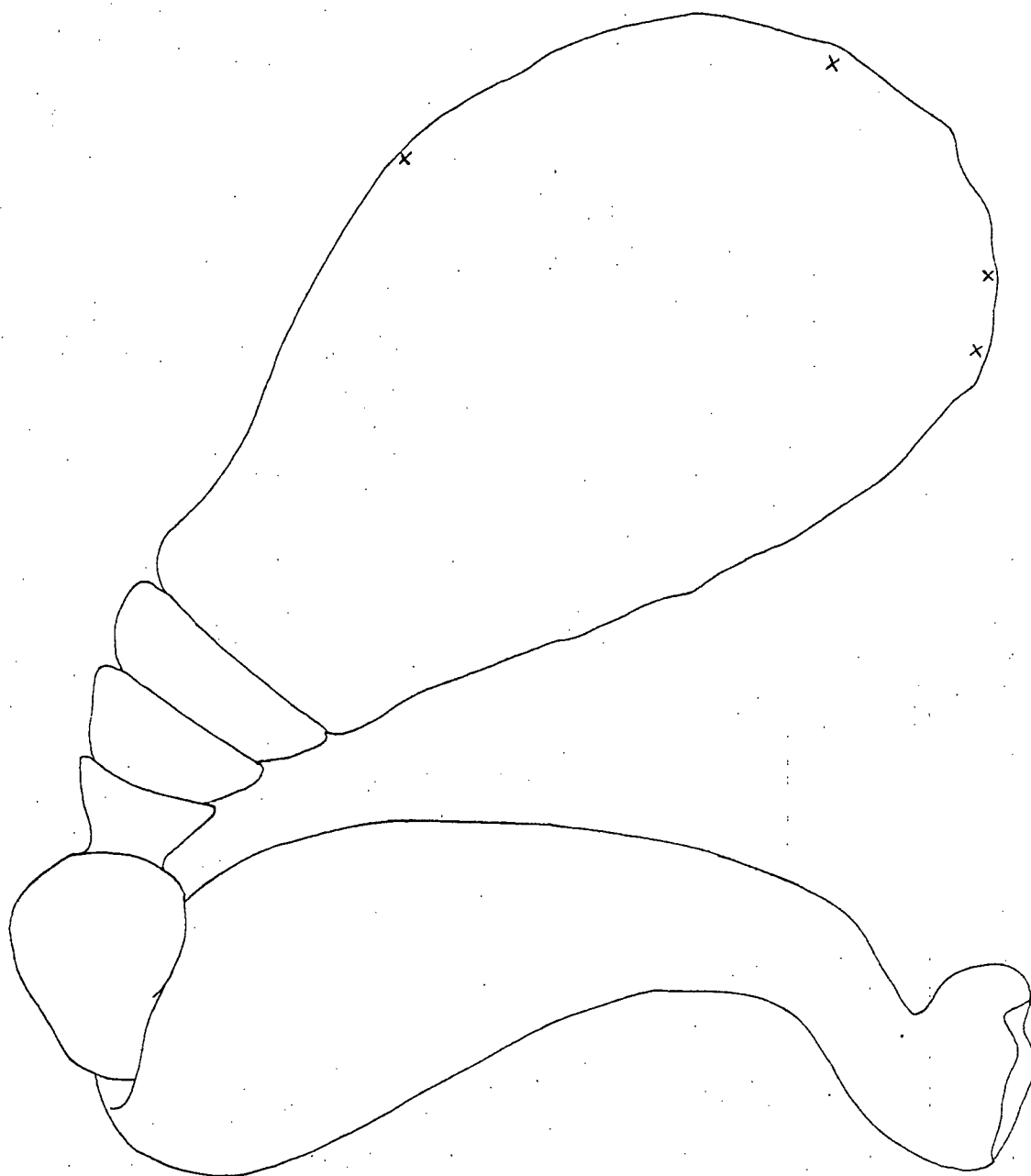


4. Sensilla Trichoidea, Type III

Type III sensilla trichoidea are evenly distributed over the distal half of the anterior club surface, very few of the approximately 20 to 30 sensilla occurring on the posterior surface, and these being only on the periphery (Figs. 45-48). The distinctive feature of these hairs, which are 26μ to 36μ long, is their curvature, which is quite pronounced in a direction opposite that of the sensilla chaetica, with the result that the hairs, distal halves at least, protrude at right angles to the club surface, and beyond all other vestiture. Thus the tips of these sensilla would be the first to come in contact with any substrate the beetle encountered with its antennae (Fig. 40). These also are the only blunt sensilla, all others of the hair type being sharply pointed (Fig. 49). The hair exhibits longitudinal fluting which in cross section appears as a wavy hair surface, this being more pronounced distally (Fig. 50). An eccentric lumen with a diameter one-third that of the hair contains the nerve cell distal processes. A lighter staining central region in the proximal half of the hair contains an extracellular homogeneous material of unknown nature. The impression is thus one of a double lumen, a small one apposed to one side of the hair wall and extending into a large one which thus has a crescentic form in cross section. The hair wall is relatively thick (Fig. 52).

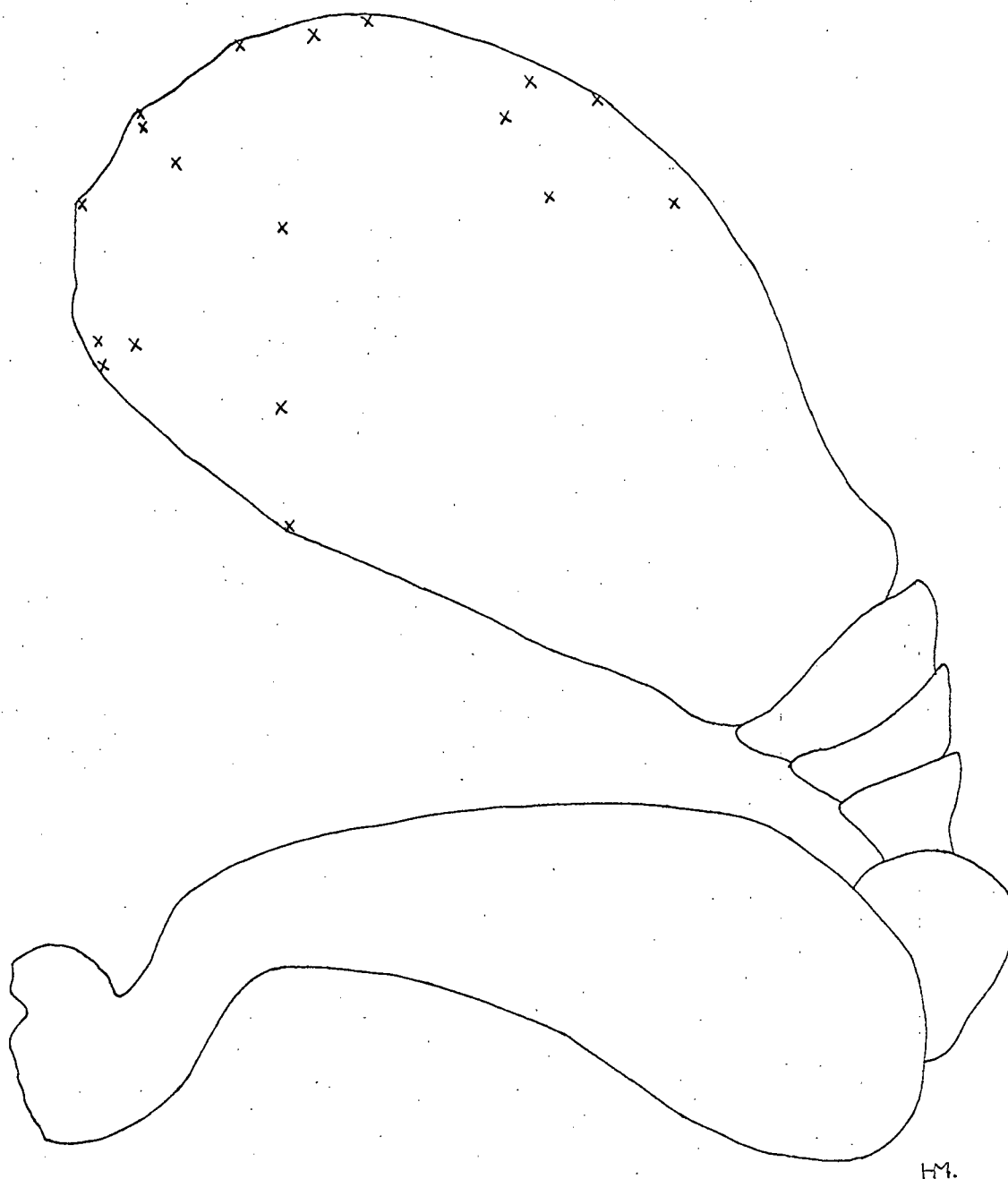
The hair base and socket are very similar in structure to those of the sensilla chaetica, differing only in a slightly greater total socket diameter (3μ), the presence of a hair lumen, and a less pronounced sponge-like cavity. The pore canal also is shorter and wider. The hair is thus probably more rigid in its socket (Fig. 58).

The large tormogen vacuole is almost totally filled with lamellate cytoplasmic extensions of the tormogen cell (Fig. 54). The proximal limits of the tormogen cell, as well as of the trichogen cell, are however poorly known,



HM.

Figure 45. Distribution map of sensilla trichoidea, Type III, on male left antenna, posterior surface.



HM.

Figure 46. Distribution map of sensilla trichoidea, Type III, on male left antenna, anterior surface.

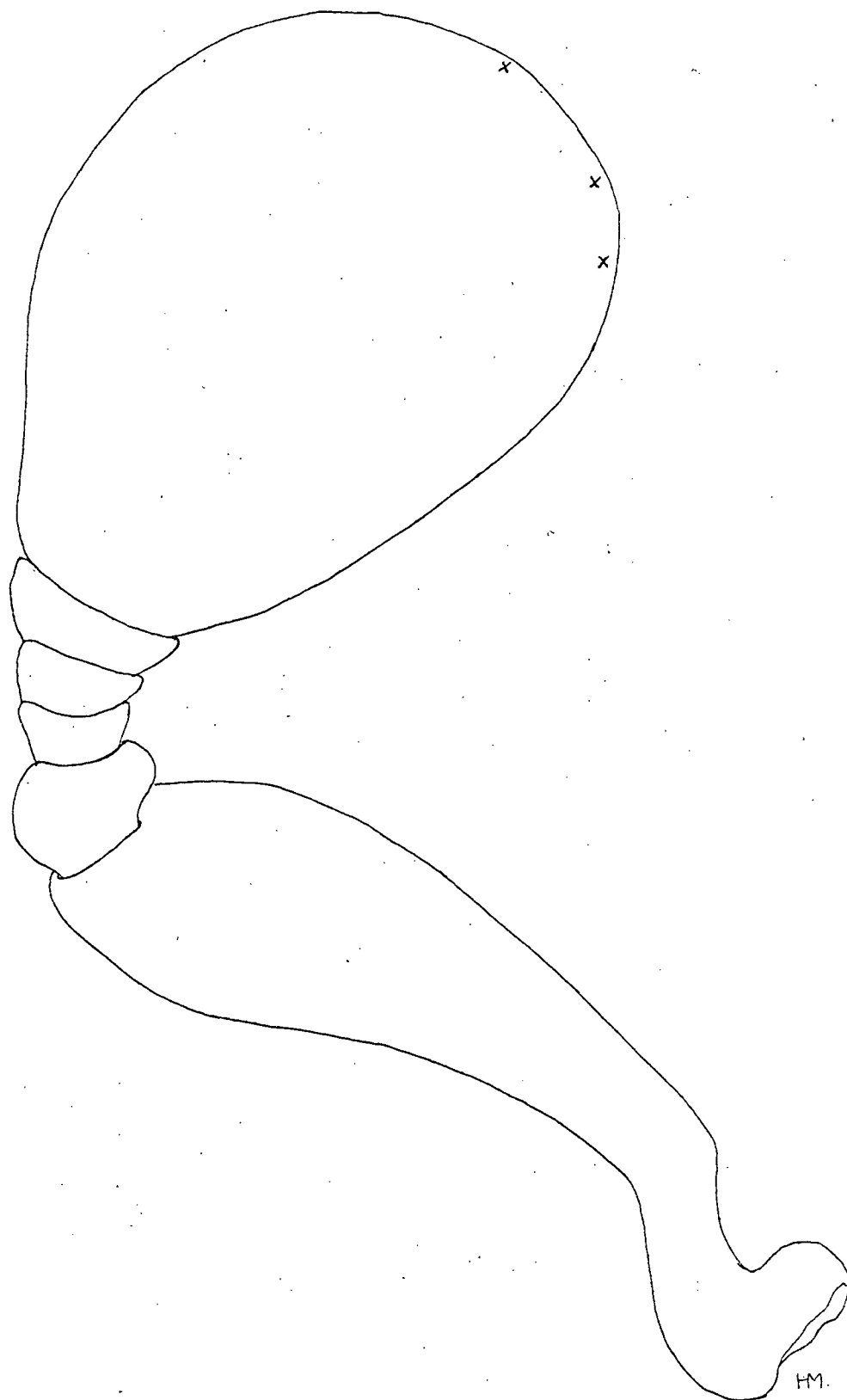


Figure 47. Distribution map of sensilla trichoidea, Type III, on female left antenna, posterior surface.

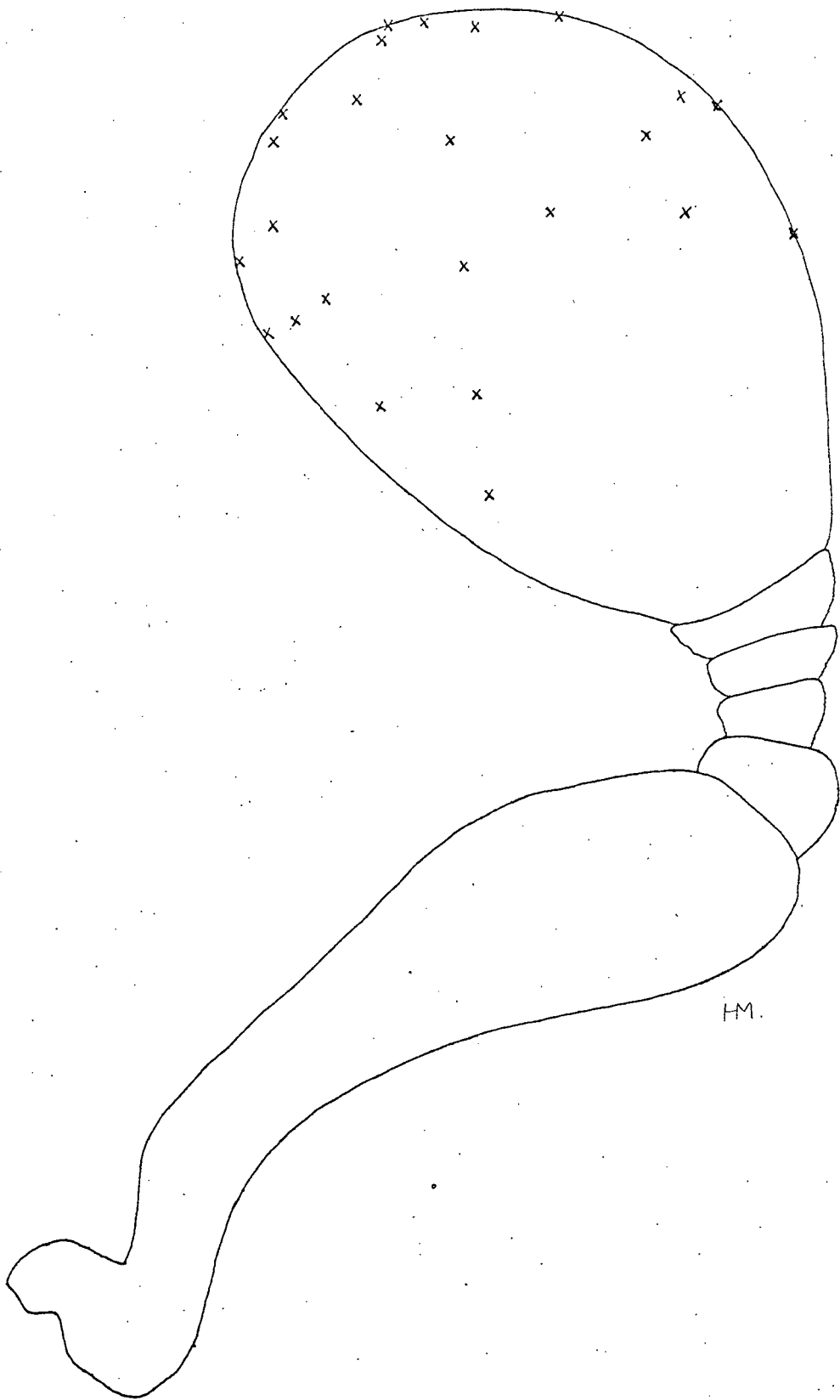


Figure 48. Distribution map of sensilla trichoidea, Type III, on female left antenna, anterior surface.

- Figure 49. Photomicrograph of sensillum trichoideum, Type III. Note blunt hair tip. Distilled water mount.
- Figure 50. Electron micrograph of sensillum trichoideum, Type III, cross section near tip, showing four dendrites, fluted hair wall. Glutaraldehyde-osmium fixation, lead citrate section stain.
- Figure 51. Electron micrograph of sensillum trichoideum, Type III, oblique section showing two lumina, six dendrites. Glutaraldehyde-osmium fixation, lead citrate section stain.
- Figure 52. Electron micrograph of sensillum trichoideum, Type III, cross section showing two lumina, seven dendrites. Glutaraldehyde-osmium fixation, lead citrate section stain.

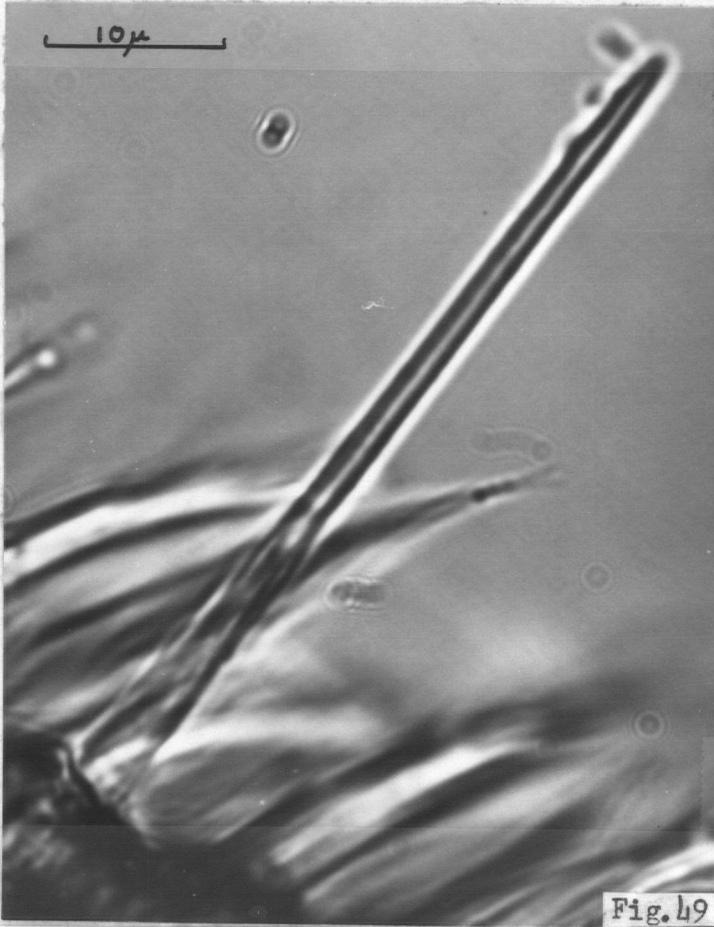


Fig. 49

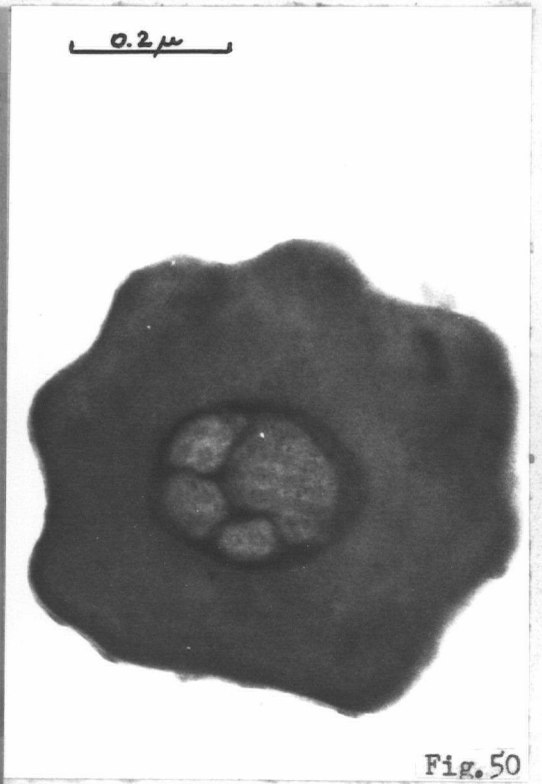


Fig. 50



Fig. 51

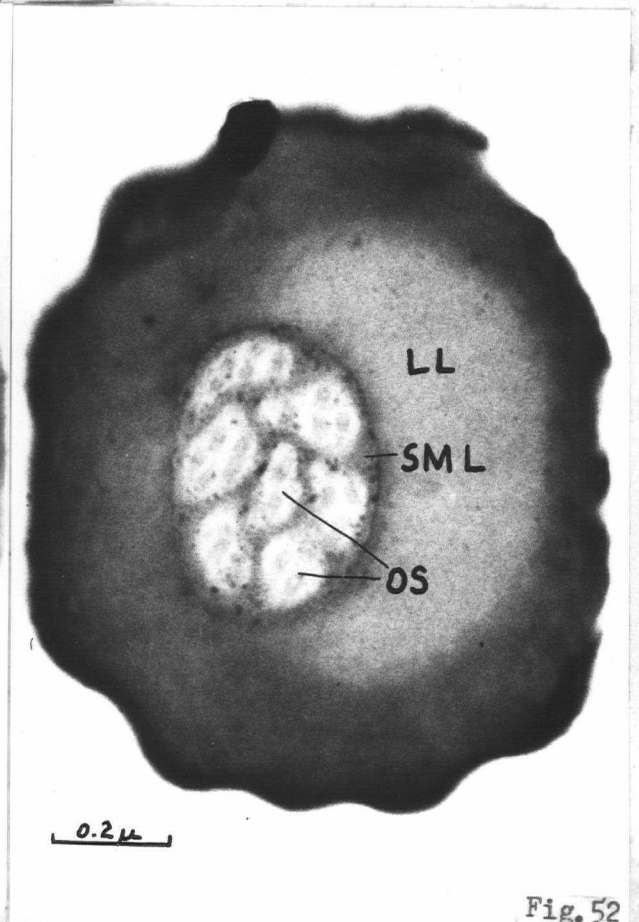


Fig. 52

Figure 53. Electron micrograph of sensillum trichoideum, Type III, cross section through pore canal showing cuticular sheath containing six dendrites. Osmium fixation, PTA and lead acetate block stain.

Figure 54. Electron micrograph of sensillum trichoideum, Type III, cross section just proximal to pore canal, showing five, possibly six dendrites. Glutaraldehyde-osmium fixation, lead citrate and uranyl acetate section stain.

Figure 55. Electron micrograph of sensillum trichoideum, Type III, cross section just distal to ciliary regions of dendrites, showing five dendrites. Osmium fixation, PTA and lead acetate block stain.

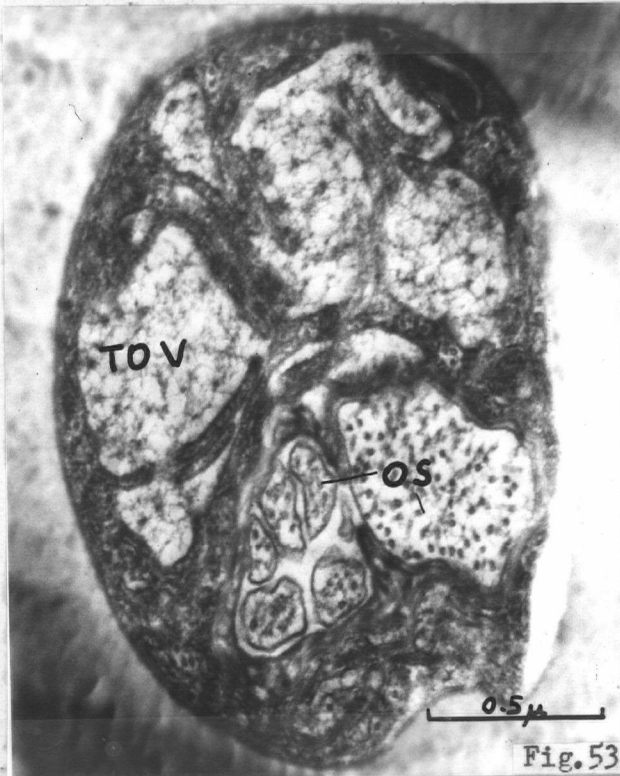


Fig. 53

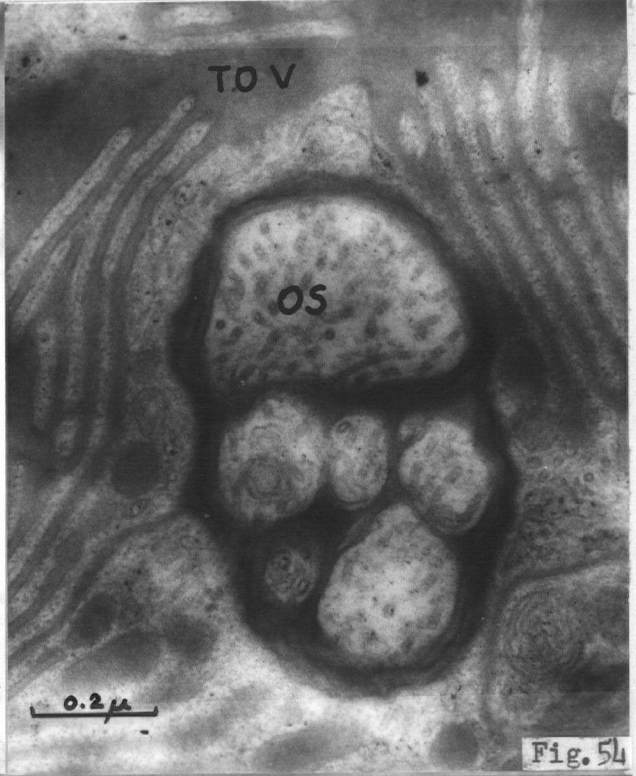


Fig. 54

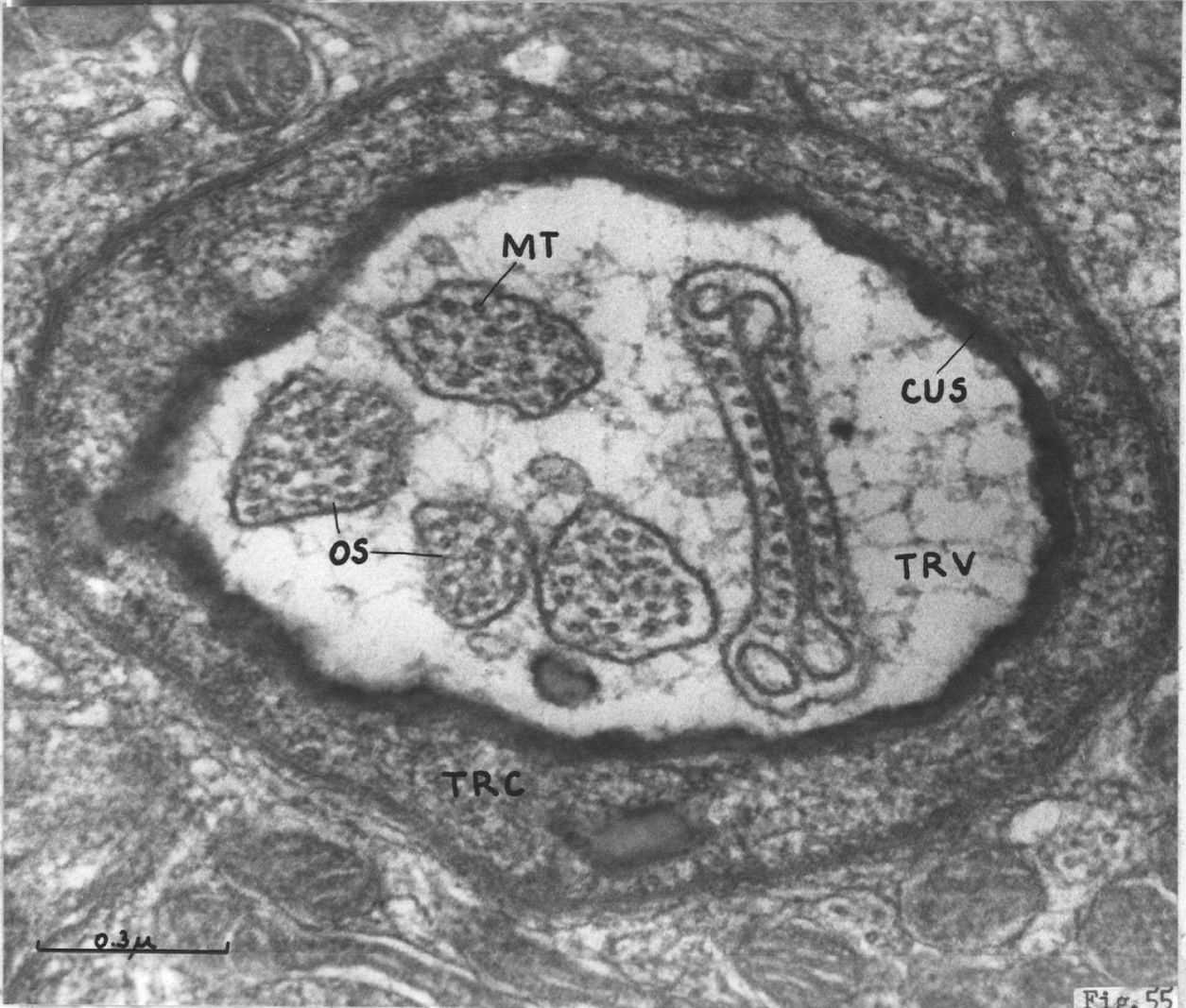


Fig. 55

Figure 56. Electron micrograph of sensillum trichoideum, Type III, longitudinal section showing inner segment, ciliary rootlet apparatus, and portion of ciliary segment of one dendrite. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 57. Electron micrograph of sensillum trichoideum, Type III, slightly oblique section through outer segments of dendrites, showing microtubules. Glutaraldehyde-osmium fixation, lead citrate section stain.

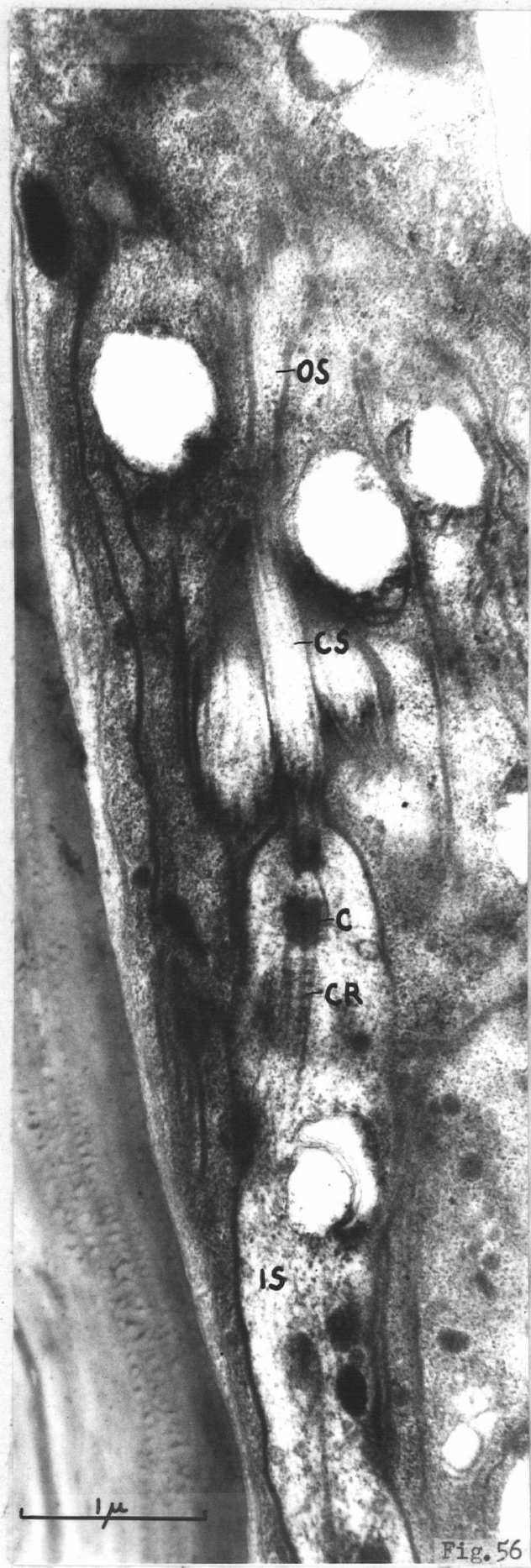


Fig. 56

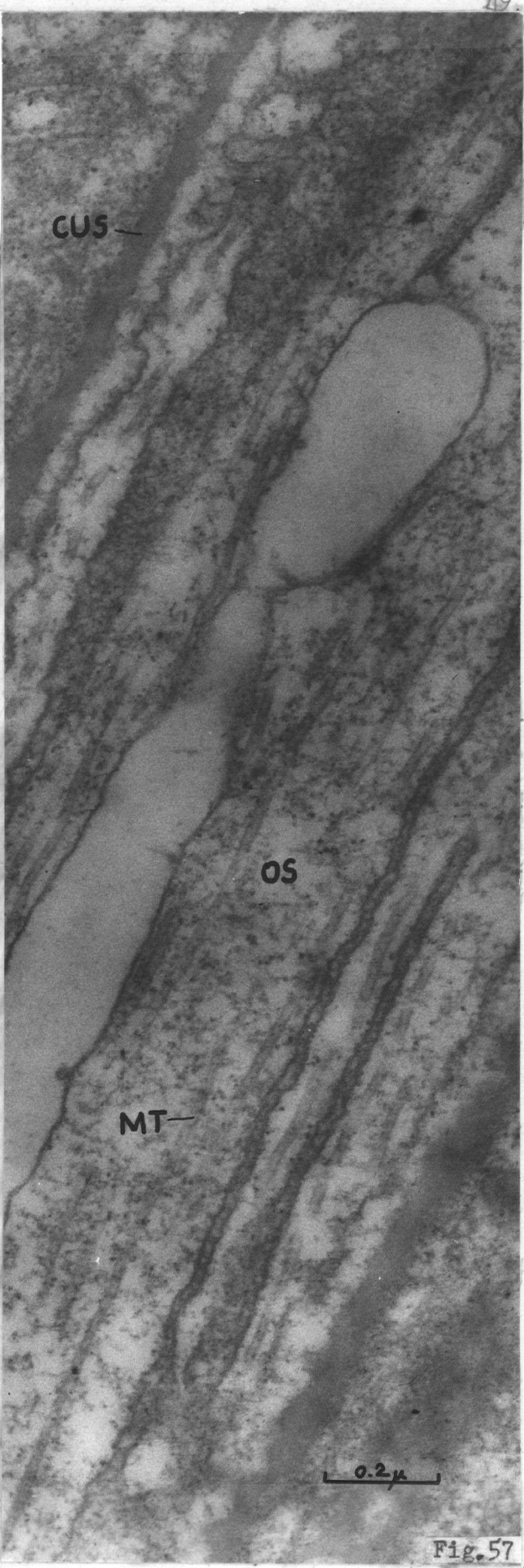
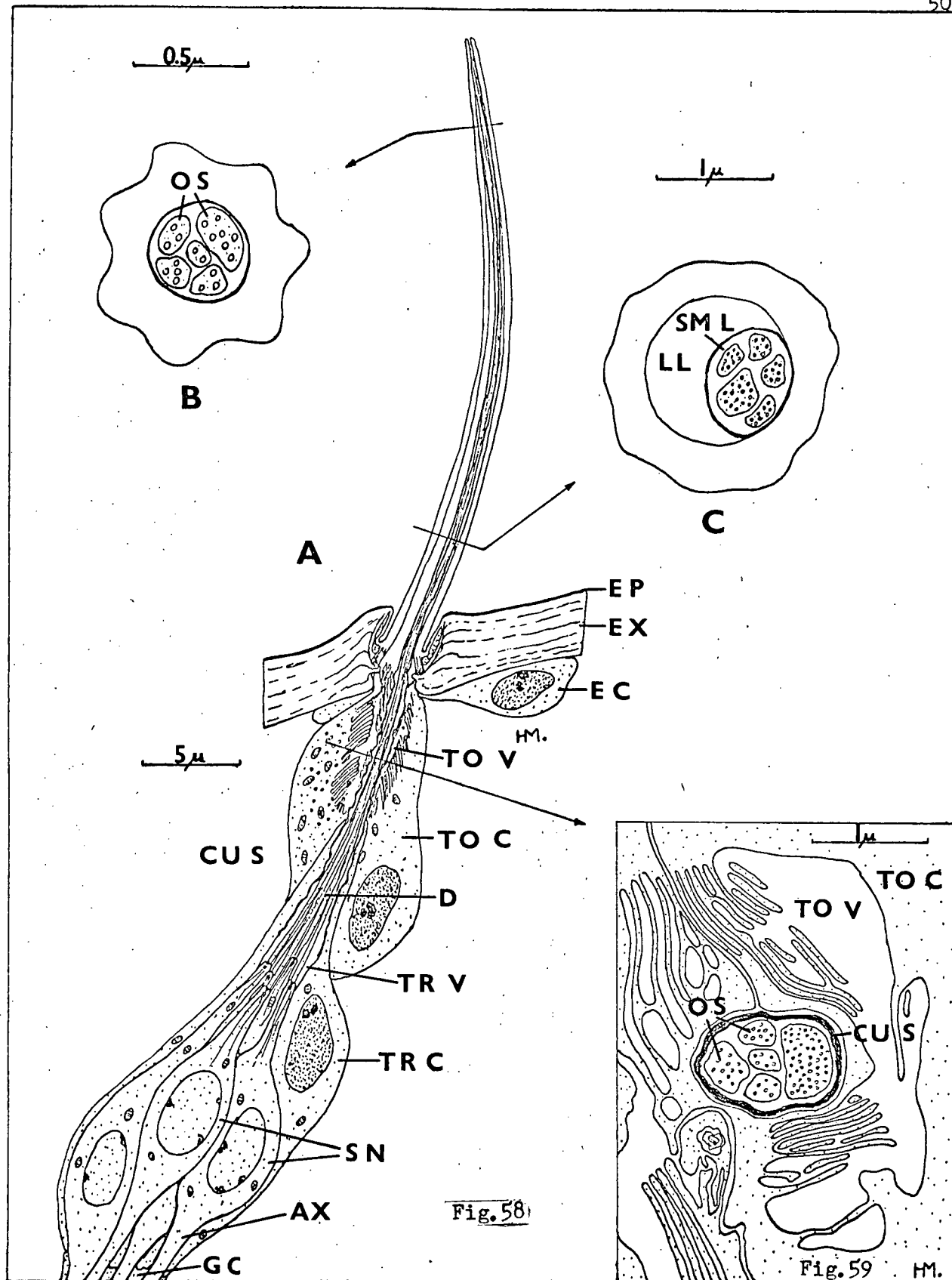


Fig. 57

Figure 58. Schematic diagram of sensillum trichoideum, Type III, with cross sections of hair at levels indicated.

Figure 59. Schematic diagram of sensillum trichoideum, Type III, cross section at level indicated in Fig. 58.

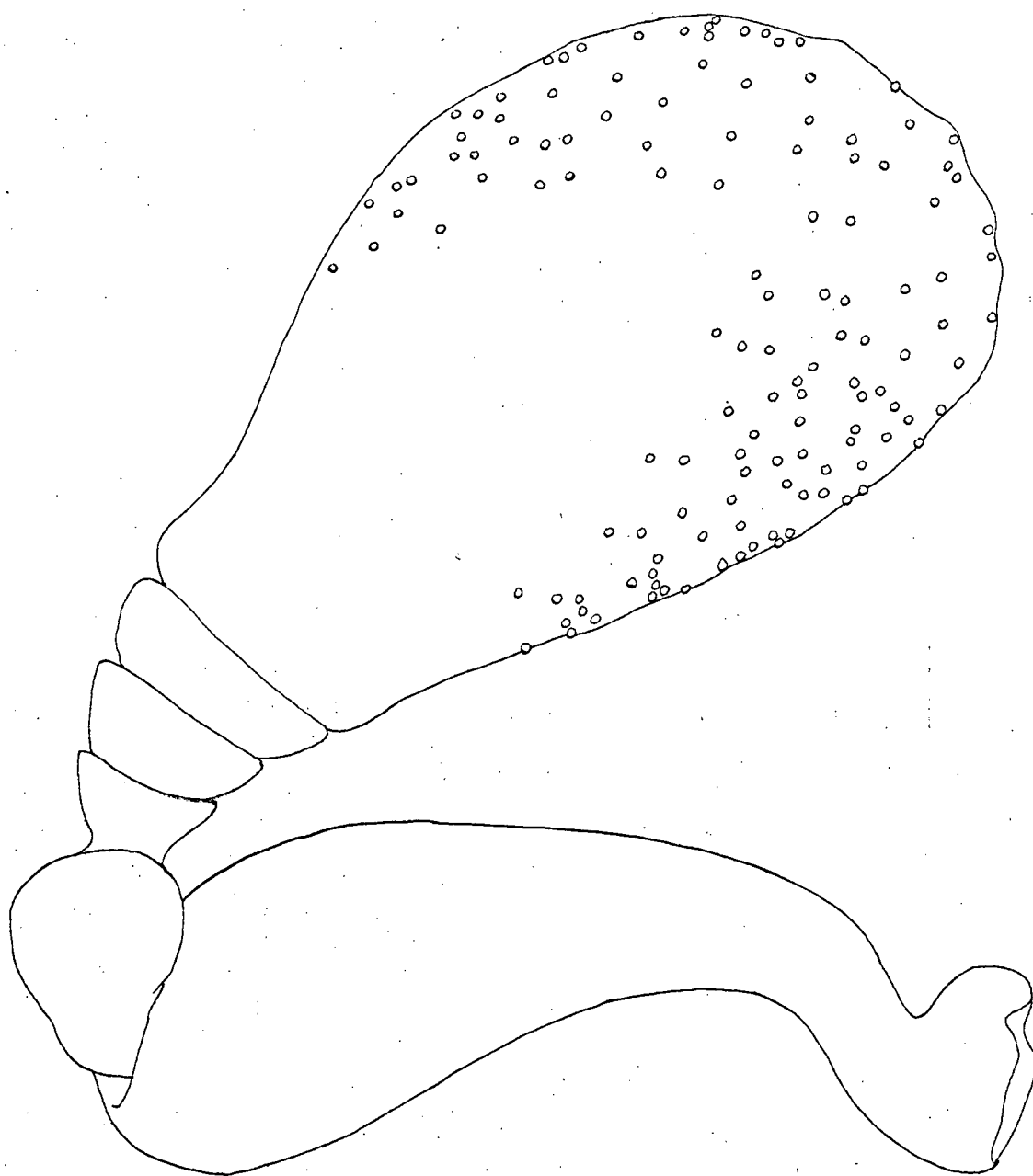


owing to the difficulty of obtaining longitudinal sections of the rather long (30μ or more) cellular component of the sensillum.

The nervous component consists of four to seven bipolar neurons (Figs. 50-52), which send their distal processes, containing only microtubules, through the eccentric lumen of the hair to the tip, where, presumably, they are open to the air; no sections of the hair tip were obtained. A cuticular sheath encloses the nerve processes from the distal parts of the inner segments of the dendrites to the hair tip, forming the wall of the small lumen (Figs. 54, 55, 57). No pores along the hair wall are evident. The distal ends of the inner segments show exactly the same ciliary rootlet apparatus as that described in the sensillum chaeticum (Fig. 56). The appearances of the inner segments, nerve cell bodies, and axons are also the same. The nerve cell bodies form a cluster which can be readily recognized in the sections. No nerve ending terminating at the base of the hair was found.

5. Sensilla Basiconica

Sensilla basiconica occur only on the club, covering both surfaces except the corneous basal segment region (Figs. 60-63). The density of sensilla on the anterior surface is approximately three times that on the posterior surface, the total number being about 550. The length of the sensilla varies continuously between 6μ and 18μ . However, it is probable that at least two types of sensillum basiconicum exist. One group occurs in small numbers on the anterior club surface, the sensilla being short (6μ to 8μ), almost straight, continuously tapering to a sharp point, and having a wider pore canal (Fig. 65,s). Those of the other group covering both club surfaces are long (14μ to 18μ), cylindrical for most of their length and sharply tapering to a point, bent sharply near the base so that the sensillum lies parallel to the club surface, and have a narrower pore canal (Figs. 64, 65, 1). Hair diameter is 1.4μ to 1.6μ . The sensilla of intermediate length appear to be less fully



HM.

Figure 60. Distribution map of sensilla basiconica on male left antenna, posterior surface.

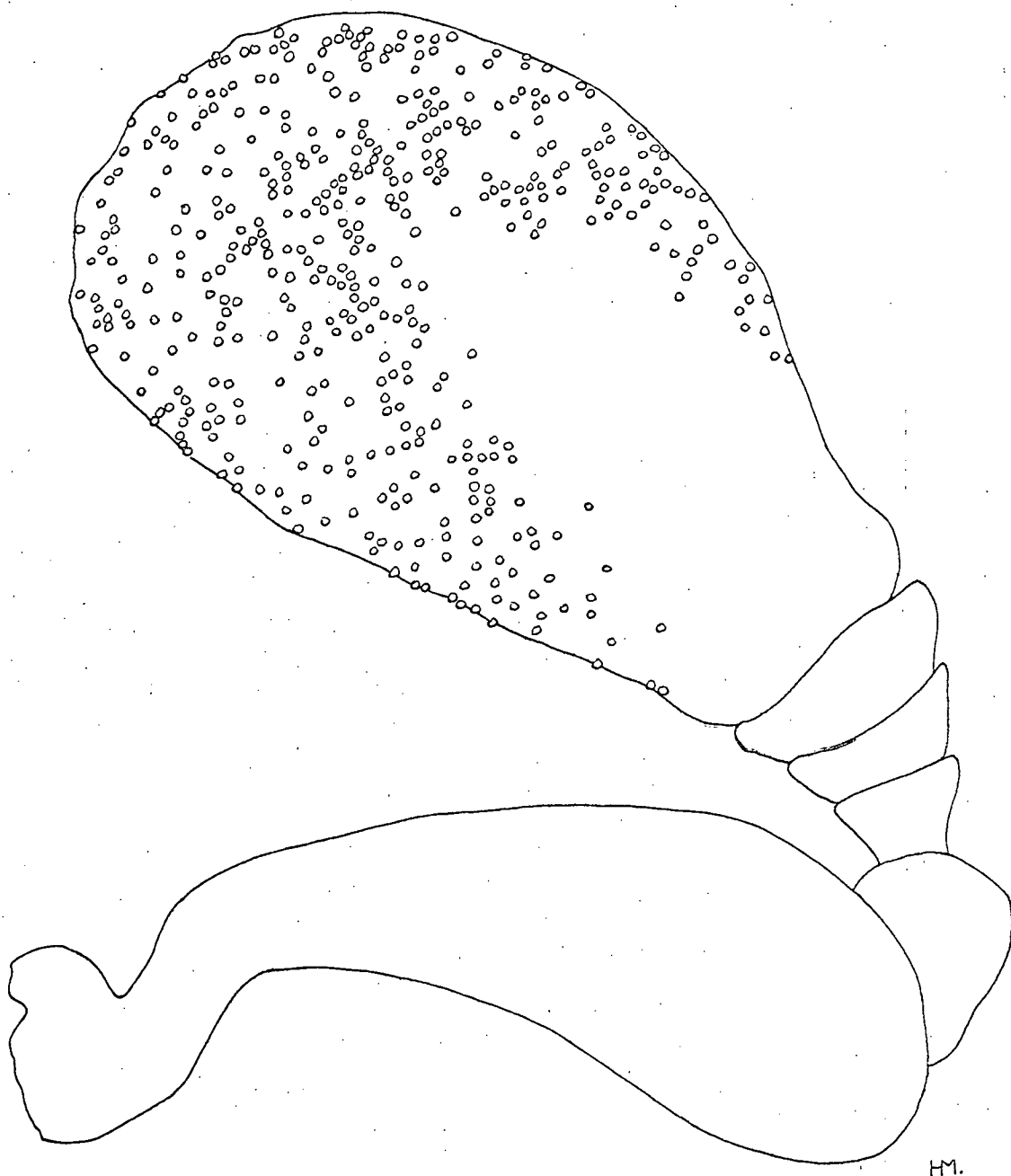


Figure 61. Distribution map of sensilla basiconica on male left antenna, anterior surface.

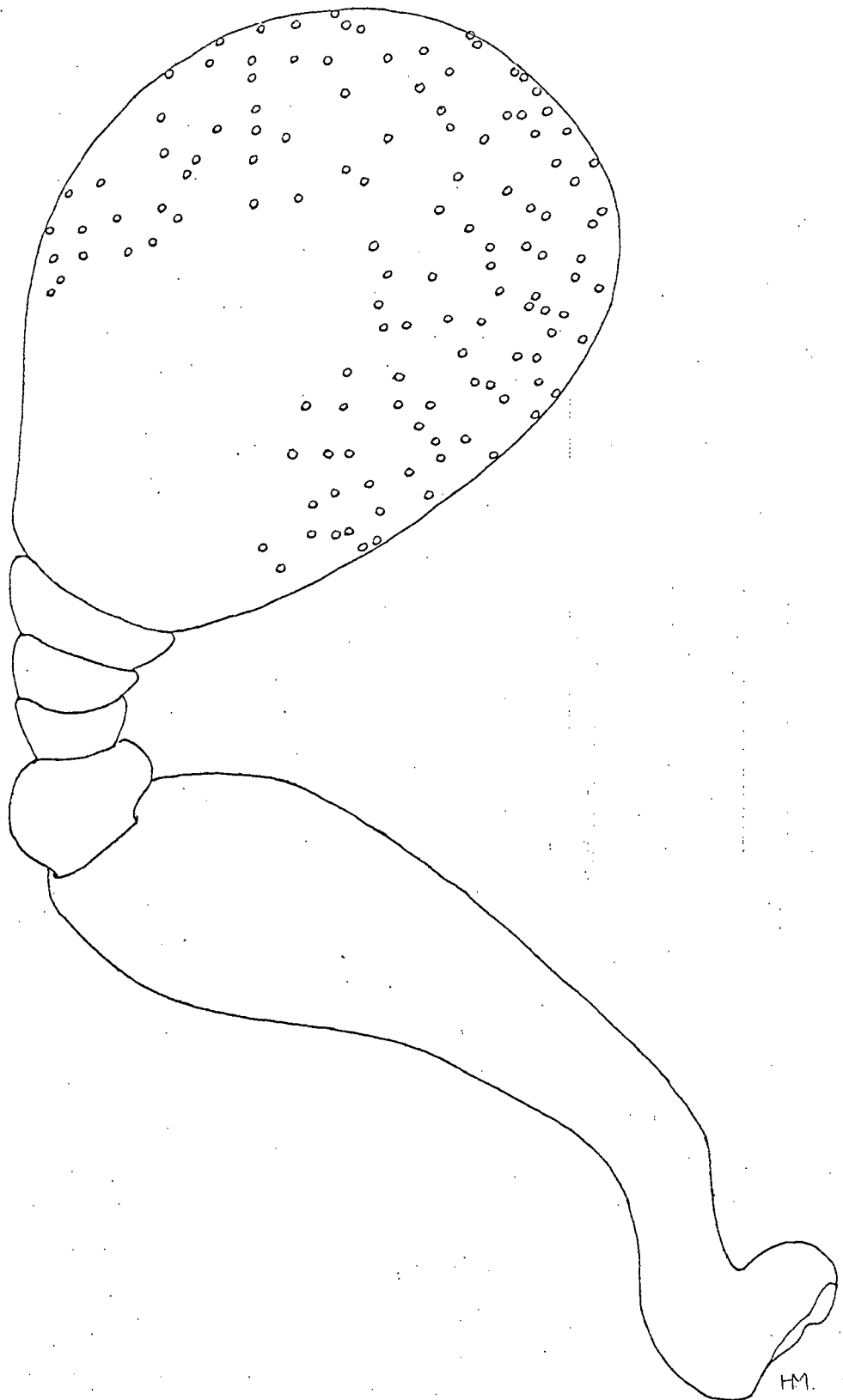


Figure 62. Distribution map of sensilla basiconica on female left antenna, posterior surface.

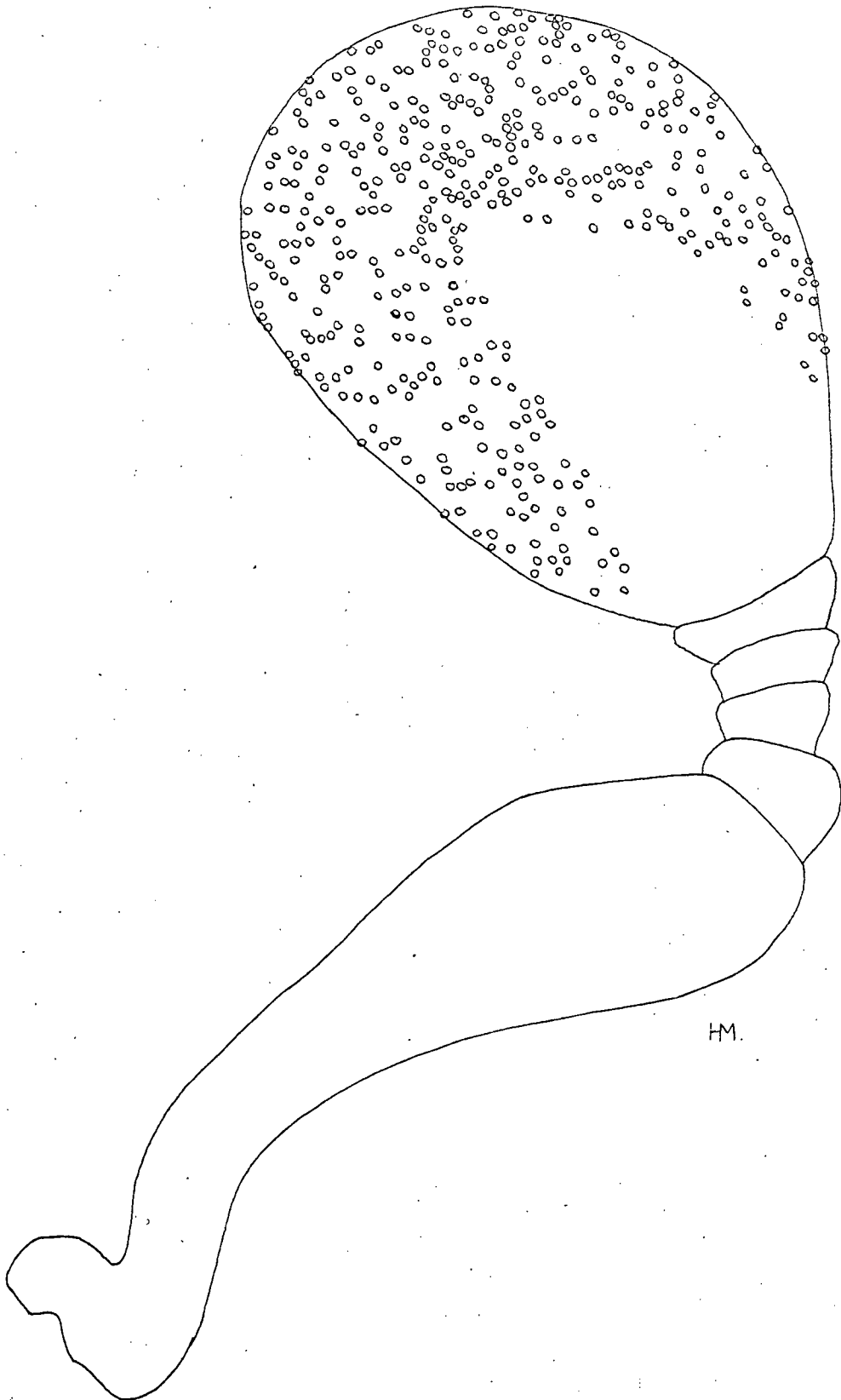


Figure 63. Distribution map of sensilla basiconica on female left antenna, anterior surface.

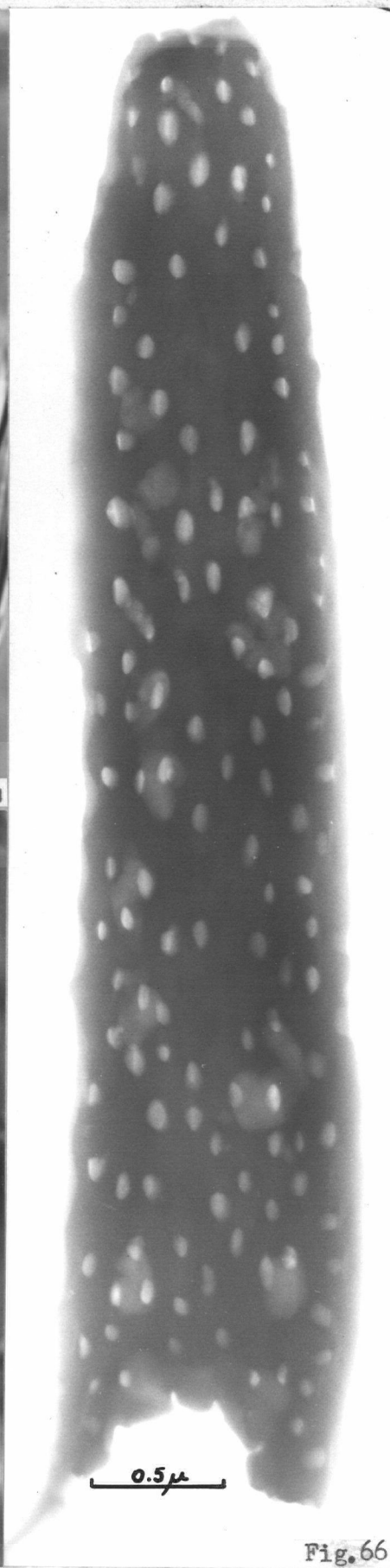
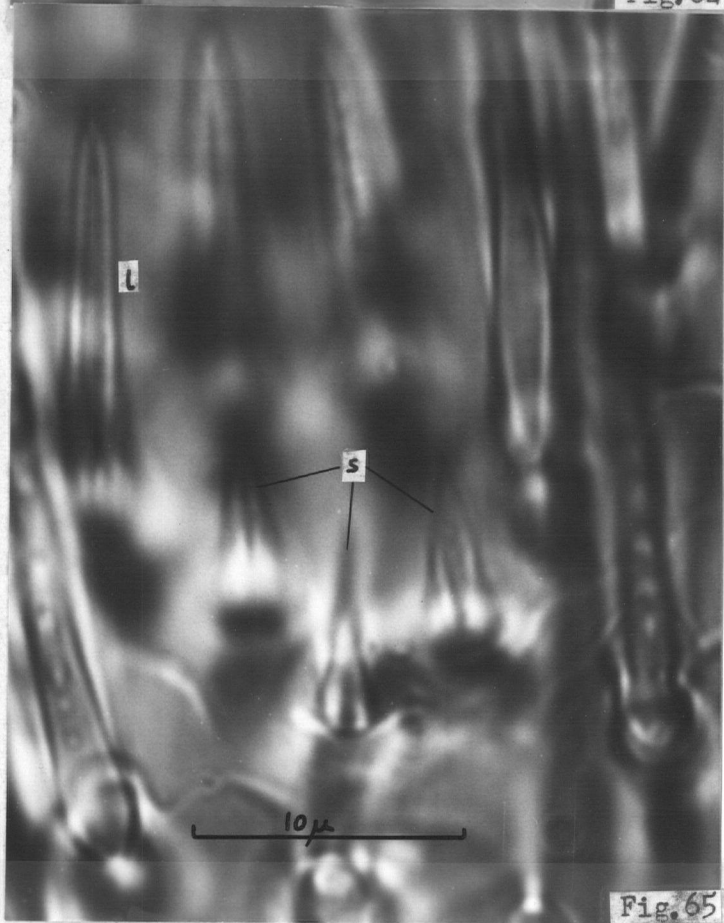
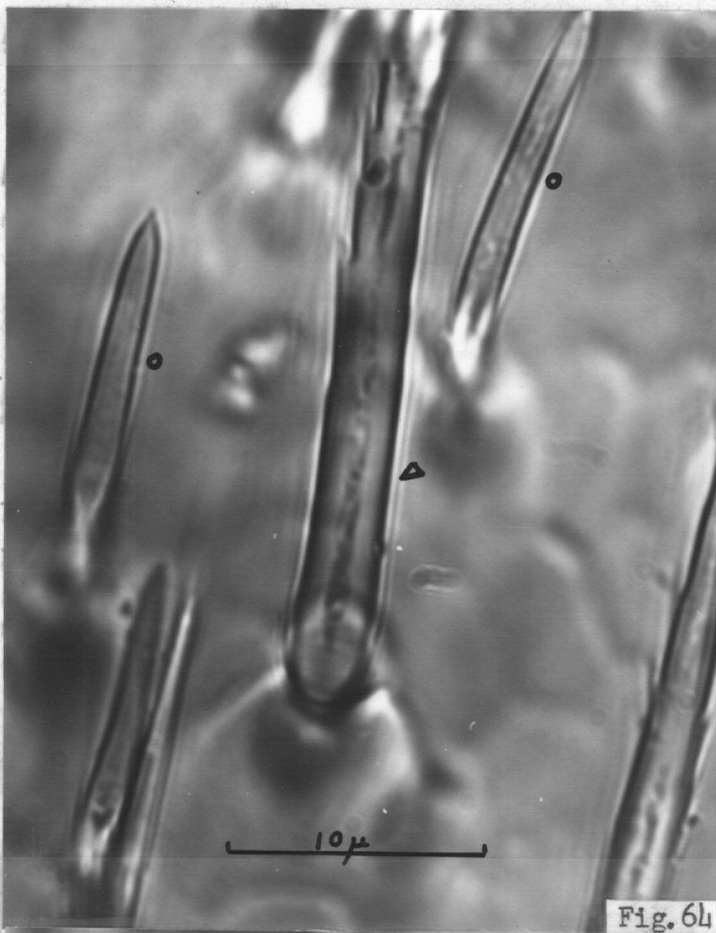
developed long sensilla basiconica, although a third similar but smaller type is not excluded. Since these differences were not noted until most of the fine structure work had been done, the following description probably holds for the long basiconic sensilla, which, since they are most numerous, would be most frequently sectioned.

The typical sensillum basiconicum is about 16μ long, curved, with a non-articulated base. These sensilla are shielded from contact with a substrate by the sensilla chaetica, and the Types II and III sensilla trichoidea. Since they come to a very sharp point, an opening at the tip is presumed absent. The hair wall is very thin, tapering from 0.22μ near the base to 0.10μ near the tip. From about 3μ from the base the hair wall shows many perforations, about 50 to 60 per square micron of surface area (Fig.66). The holes are flask-shaped, being wide internally (500\AA), and opening to the exterior by a narrow longitudinally oriented slit which is about 700\AA long and 100\AA to 200\AA wide. The base is not articulated, the hair wall being joined directly to the body cuticle as in the Type II sensilla trichoidea. The pore canal is simple, cylindrical, about 3μ long and 1.7μ in diameter (Fig.79).

The tormogen cell again is typically disposed, forming the pore canal lining, and ensheathing proximally the trichogen cell. The tormogen vacuole is characteristically very large, extending from the base of the hair to 4μ or more proximal to the inner cuticular surface, and with a maximum diameter approaching 4μ . The vacuole is loosely filled with tormogen cell cytoplasmic extensions which are villiform to somewhat lamellate, and which centrally terminate 1μ to 2μ proximal to the pore canal (Fig.71). The cytoplasm is dense, with sparse endoplasmic reticulum, and a moderate number of mitochondria. The nucleus is usually situated proximal to the vacuole.

The trichogen cell shows a characteristic specialization: a large

- Figure 64. Photomicrograph of long sensilla basiconica and sensilla chaetica. Note the hint of perforations in the hair wall of the sensilla basiconica. Distilled water mount.
- Figure 65. Photomicrograph of short (s) and long (l) sensilla basiconica. Compare length and peg shape. 'Permunt' mount.
- Figure 66. Electron micrograph of sensillum basiconicum, surface view of sectioned unstained unfixed dried hair. Note slit-shaped openings.



- Figure 67. Electron micrograph of sensillum basiconicum, oblique section of hair showing dendrite branches, hair perforations. Glutaraldehyde-osmium fixation, lead citrate section stain.
- Figure 68. Electron micrograph of sensillum basiconicum, cross section of hair showing numerous hair wall perforations and dendrite branches in the hair lumen. Note dendrite branch ending in a perforation (arrow).
- Figure 69. Electron micrograph of sensillum basiconicum, oblique section of hair showing fine filaments extending part-way into the hair perforations. (arrow). Osmium fixation, PTA and lead acetate block stain.
- Figure 70. Electron micrograph of sensillum basiconicum, cross section of portion of hair wall, showing three dark bodies with fine finger-like projections in wall perforations. Glutaraldehyde-osmium fixation, lead citrate section stain.

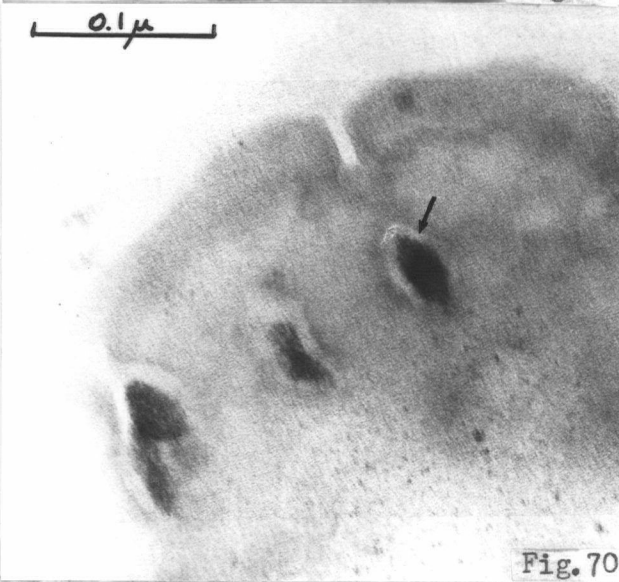
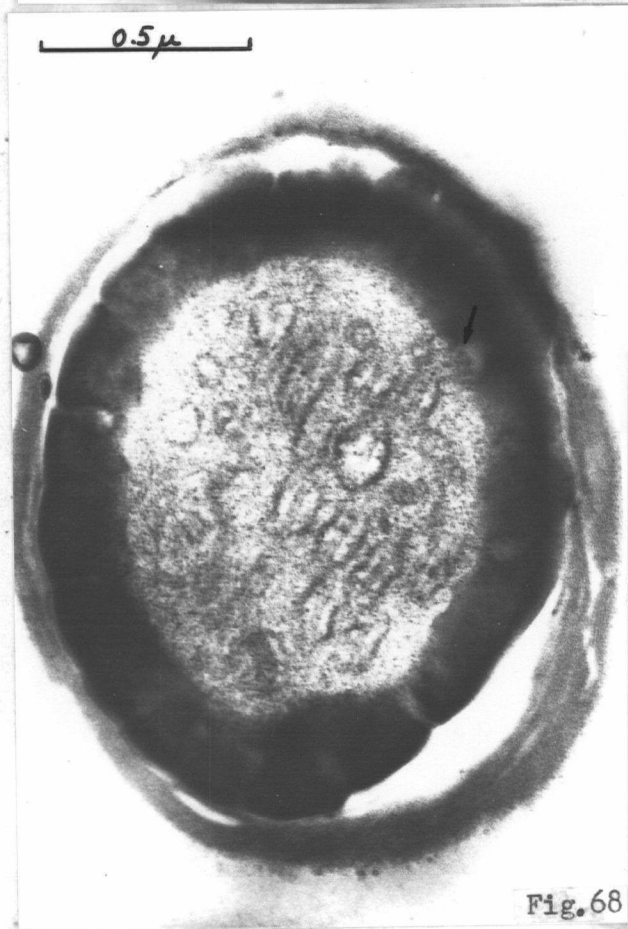


Figure 71. Electron micrograph of sensilla basiconica, oblique section through cellular components. Osmium fixation, PTA and lead acetate block stain.

Figure 72. Electron micrograph of sensillum basiconicum, cross section in region of pore canal. Note two dendrites. Osmium fixation, PTA and lead acetate block stain.

Figure 73. Electron micrograph of sensillum basiconicum, longitudinal section. Glutaraldehyde-osmium fixation, lead citrate section stain.

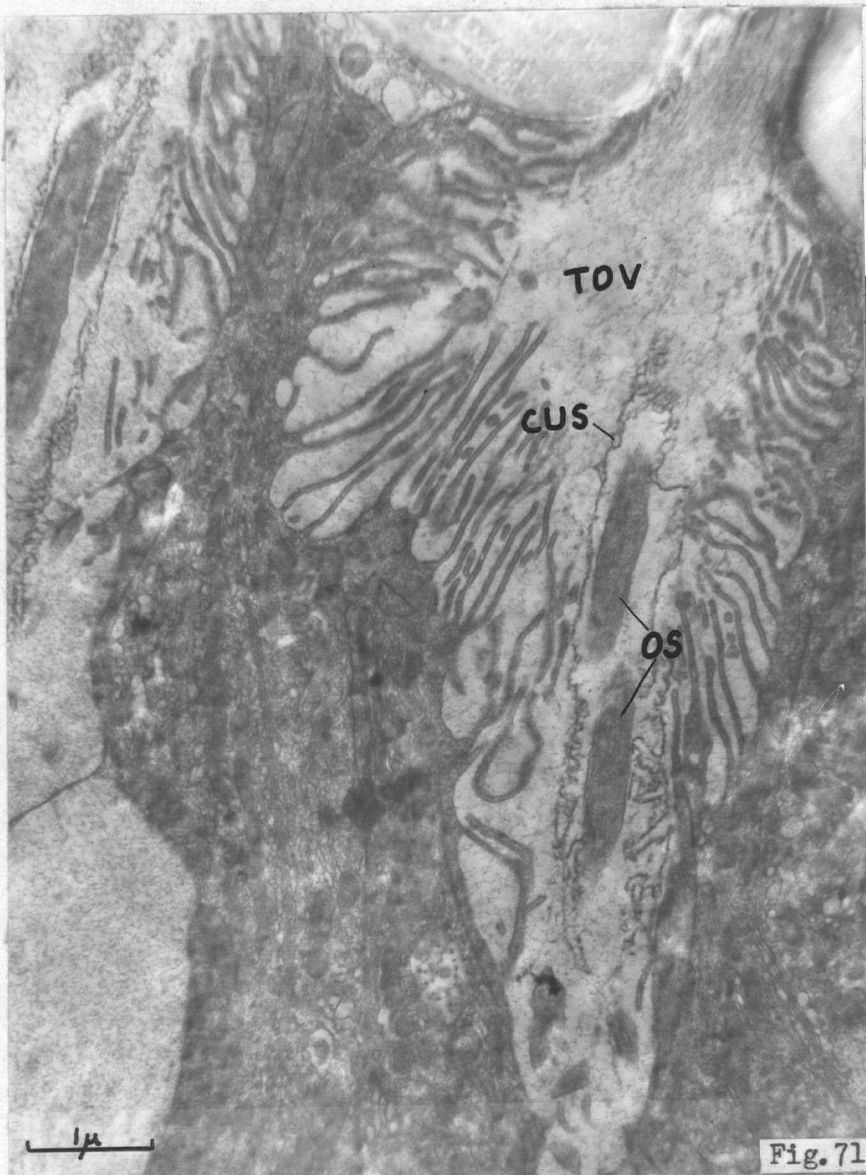


Fig. 71

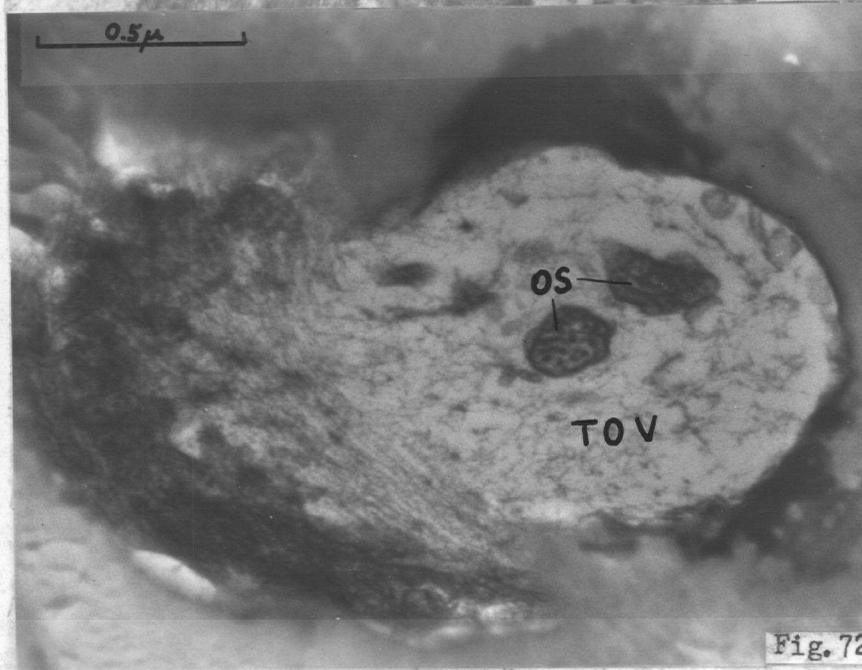


Fig. 72



Fig. 73

trichogen vacuole, approximately 5μ long and 4.5μ in diameter, extends from 3μ proximal to the tips of the two inner segments of the dendrites of this sensillum to the tormogen vacuole, from which it is separated by a cuticular sheath which encloses the dendritic outer segments (Figs.76,77). In this region the dendrites are completely but loosely surrounded by 5 to 7 cytoplasmic anastomosing lamellae which originate at the proximal end of the trichogen vacuole, with occasional connections to the lateral cytoplasmic walls, giving this region a myelin-like appearance in cross section. The lamellae contain microtubules, and mitochondria which cause local swellings. Desmosomes join the inner lamellar membranes to the dendrite cell membranes. (Fig.80). Proximally the trichogen cell encloses the remaining parts of the inner segments and the nerve cell bodies. The nucleus is near the proximal part of the nerve cell bodies, 25μ to 30μ from the base of the hair.

The cuticular sheath mentioned earlier is thin-walled (300\AA to 400\AA), 0.5μ to 0.8μ in diameter, an irregularly wavy line in longitudinal section, and extends from the distal portion of the trichogen vacuole to a short distance into the hair lumen where it flares outwards to join the hair wall (Figs.71,73).

The two nerve cells of this sensillum, similar in appearance to those of the other sensilla, send two distal processes (which again are cilium-like proximally, with the ciliary rootlet apparatus, Figs.74-77) unbranched into the hair, where subsequent repeated branching occurs. Curiously, each of the 15 to 20 branches contains at least one microtubule. Each hair perforation contains a darkly staining body which fills the small cavity, but bears no apparent connection to the nerve branches in the hair lumen (Fig. 70). Only one hair section photographed shows a nerve branch terminating within a perforation, with several small finger-like projections about 130\AA thick (Fig.68). The dark bodies also have on their distal border finger-like

Figure 74. Electron micrograph of sensillum basiconicum, cross section of outer segments of dendrites, showing single and paired tubules. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 75. Electron micrograph of sensillum basiconicum, cross section of ciliary region of one of two dendrites, showing 9 peripheral tubule pairs, absence of central pair. Glutaraldehyde-osmium fixation, lead citrate section stain.

Figure 76. Electron micrograph of sensillum basiconicum, cross section through inner segments of dendrites at level of centrioles. Glutaraldehyde-osmium fixation, lead citrate section stain.

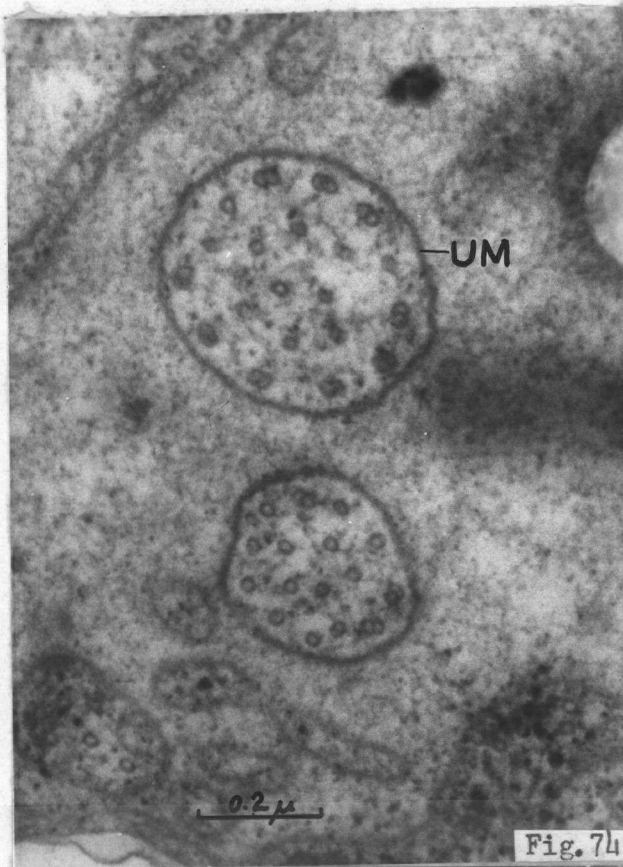


Fig. 74

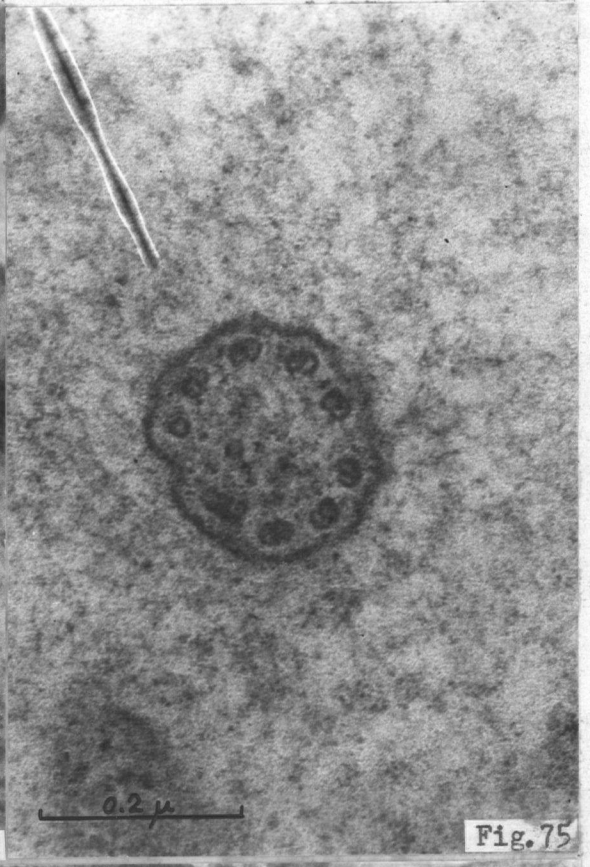


Fig. 75

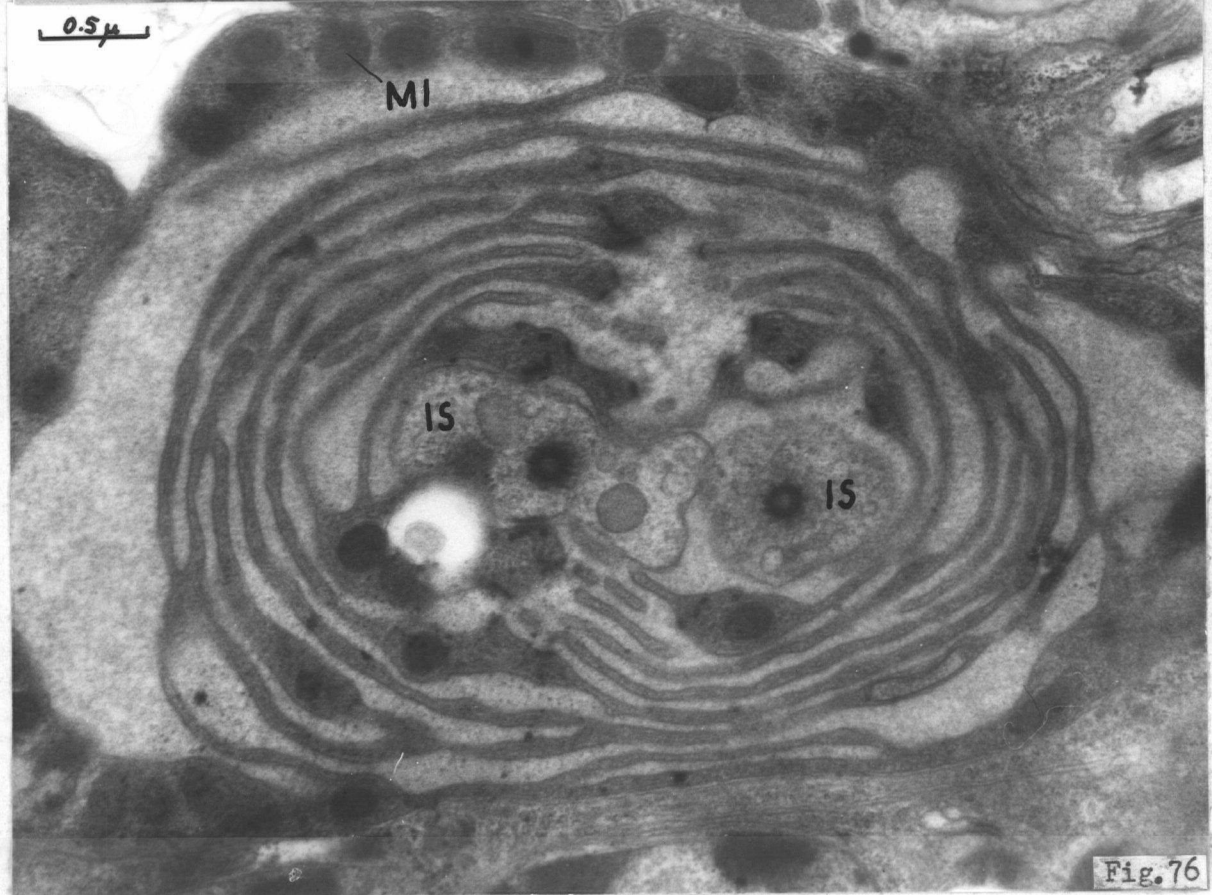


Fig. 76

Figure 77. Electron micrograph of sensillum basiconicum, cross section through inner segments of dendrites proximal to centrioles. Note ciliary rootlets, desmosomes. Glutaraldehyde-osmium fixation, lead citrate section stain.

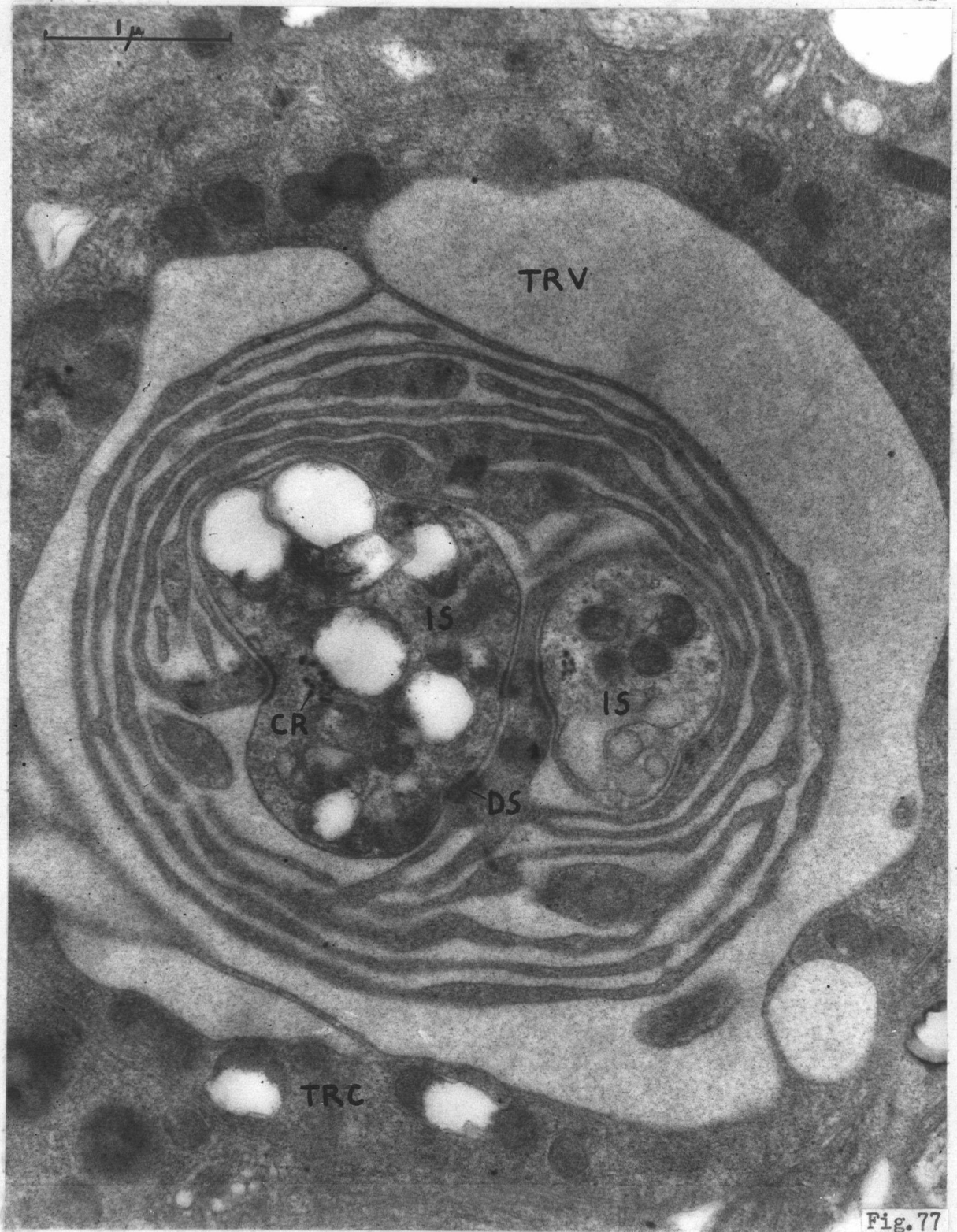


Figure 78. Electron micrograph of nerve cell body. Osmium fixation, PTA and lead acetate block stain.



Figure 79. Schematic diagram of sensillum basiconicum, with cross section of hair at level indicated.

Figure 80. Schematic diagram of sensillum basiconicum, cross section at level indicated in Fig. 79.

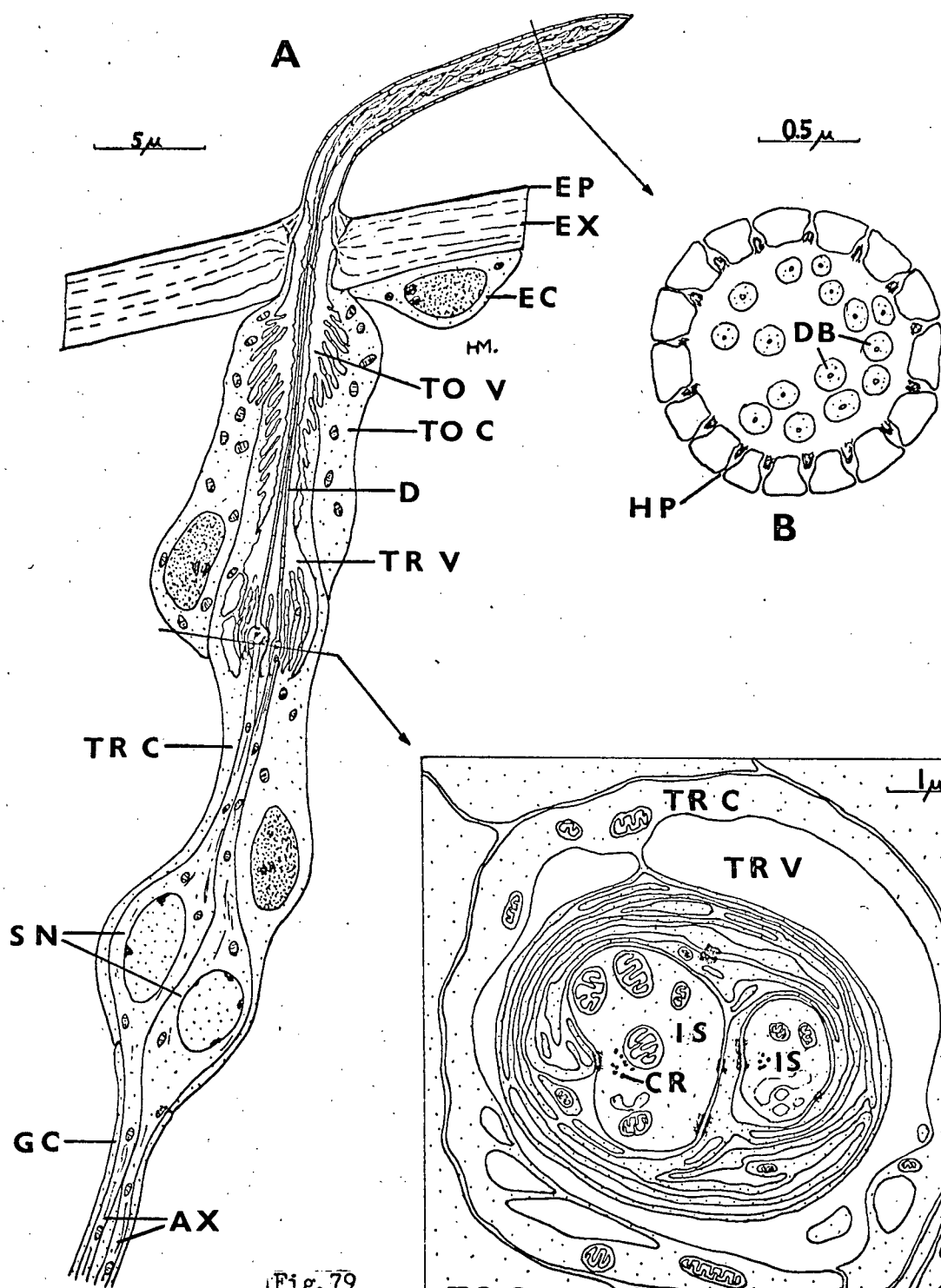


Fig. 79

Fig. 80. HM.

projections, these, however, being only 15\AA to 20\AA in diameter (Fig.70).

This point is still unsettled, and could bear further critical examination.

6. Sensilla Campaniformia

The sensilla campaniformia occur in small numbers on all parts of the antenna, as well as other parts of the body (Figs.81-84). They consist of a short thin canal leading from the outside to a subsurface solid dome-shaped structure 3μ in diameter, into the centre of which extends the nerve ending similar in appearance to the scolopale and nerve of the sensillum chaeticum (Figs.86,88). The pore canal flares outwards distally, giving the entire structure the appearance of an icecream cone. Little else is known of the structure of these sensilla due to their infrequent appearance in sections.

7. Axon Fusion

Mention can be made at this time of the attempt to determine whether fusion of sensory axons occurs in the antennae, as has been reported in other insects (Wigglesworth,1959; Dethier, Larsen, and Adams,1963). A cross section of the antennal nerve in the proximal portion of the scape of a female revealed approximately 2100 axons (Fig.89). The sensillum count and expected nerve fibres in the illustrated antennae is given in Tables I and II. The total expected axons thus are 1845 and 1921 for female and male respectively, with Johnston's organ not accounted for. Fusion of axons is thus considered unlikely, since more axons than expected are present in the antennal nerve.

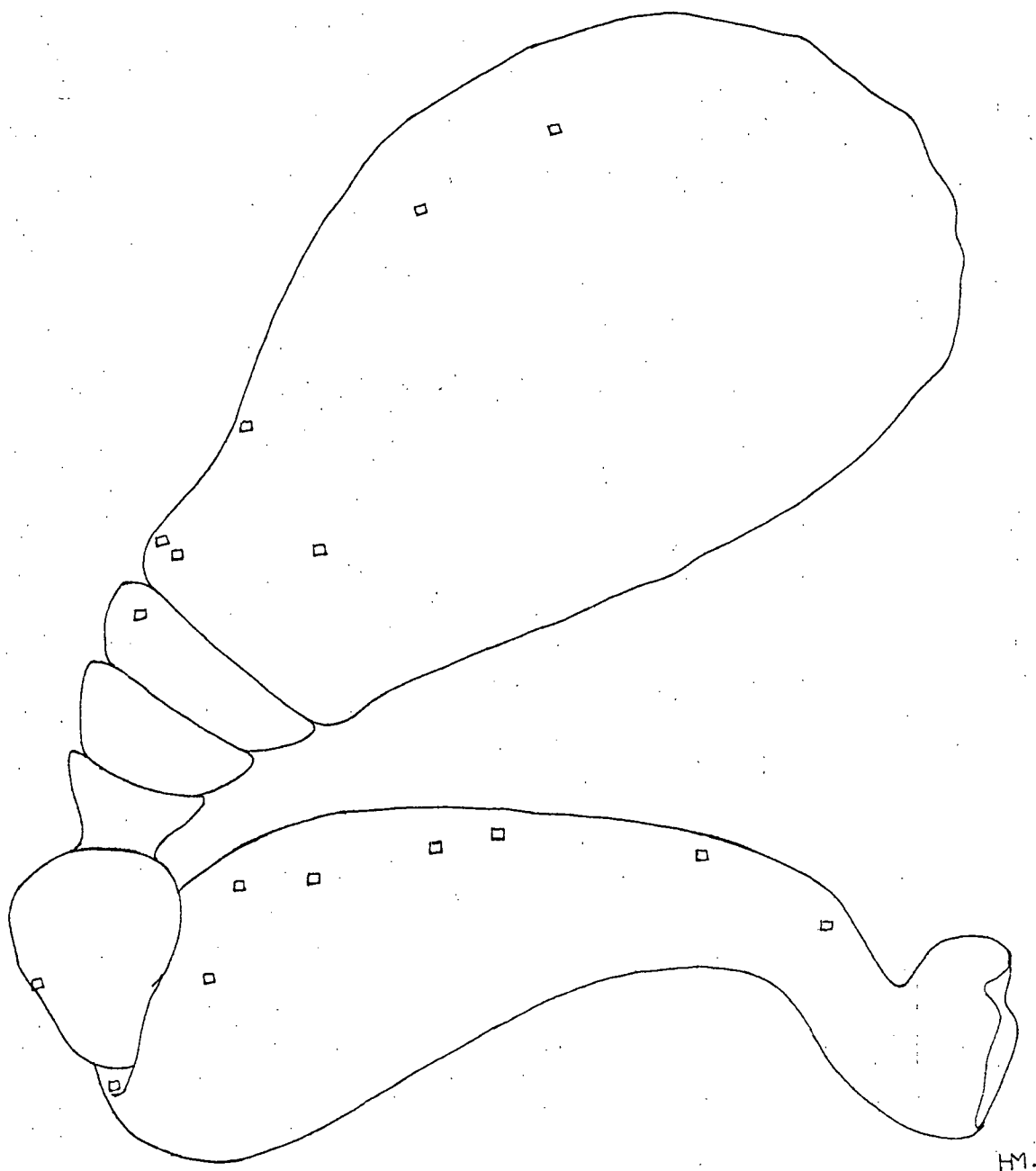
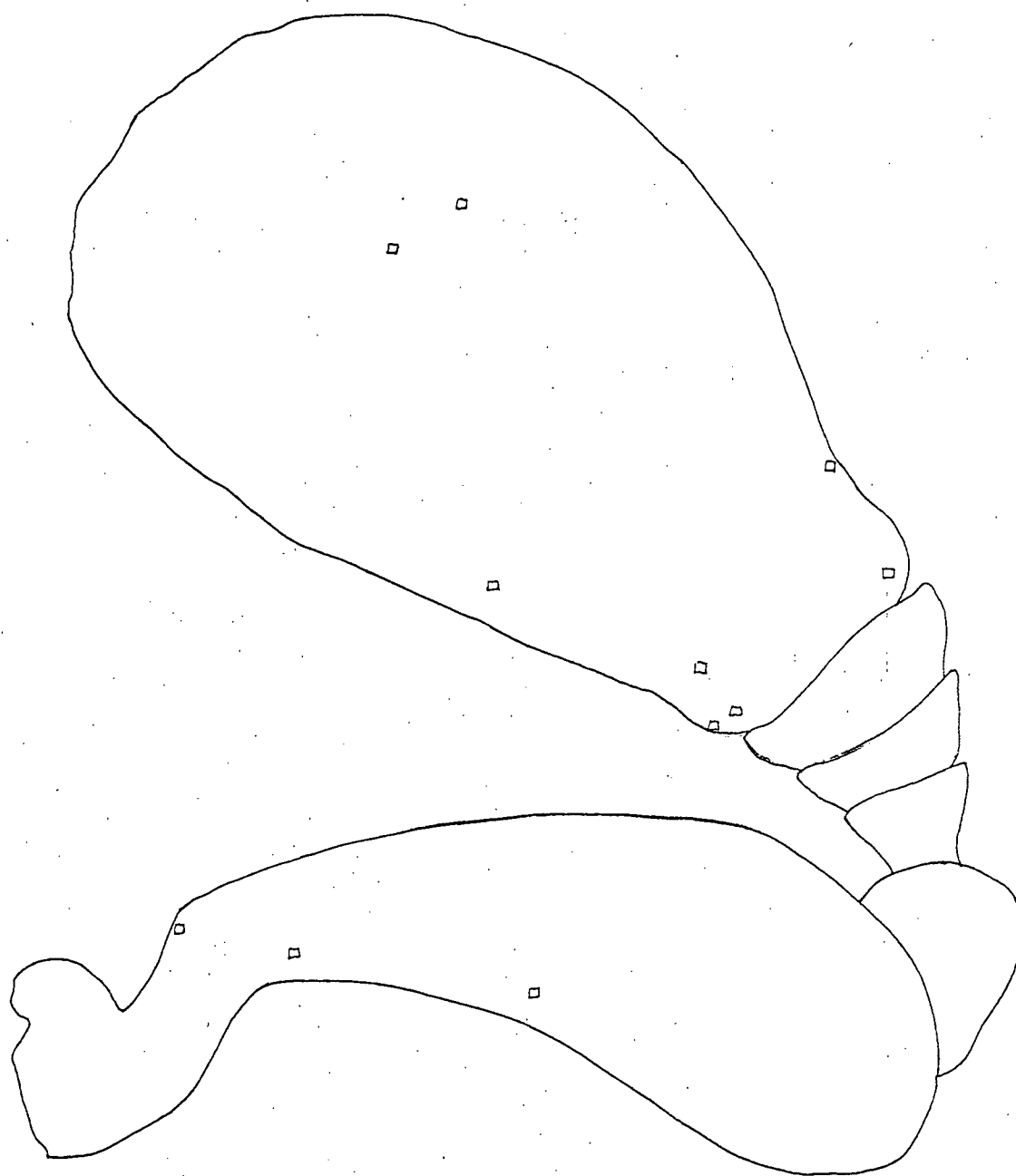


Figure 81. Distribution map of sensilla campaniformia on male left antenna, posterior surface.



H.M.

Figure 82. Distribution map of sensilla campaniformia on male left antenna, anterior surface.

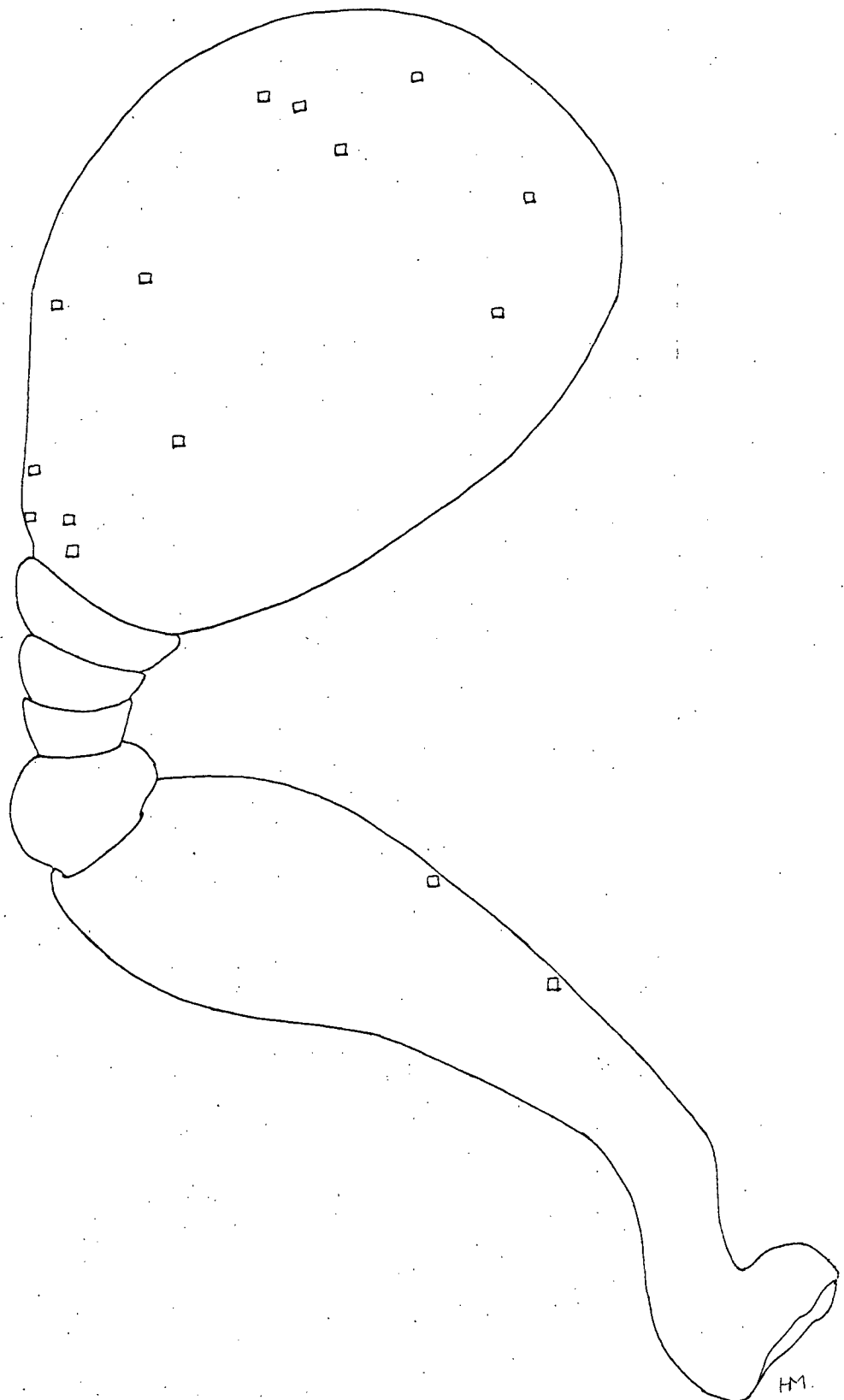


Figure 83. Distribution map of sensilla campaniformia on female left antenna, posterior surface.

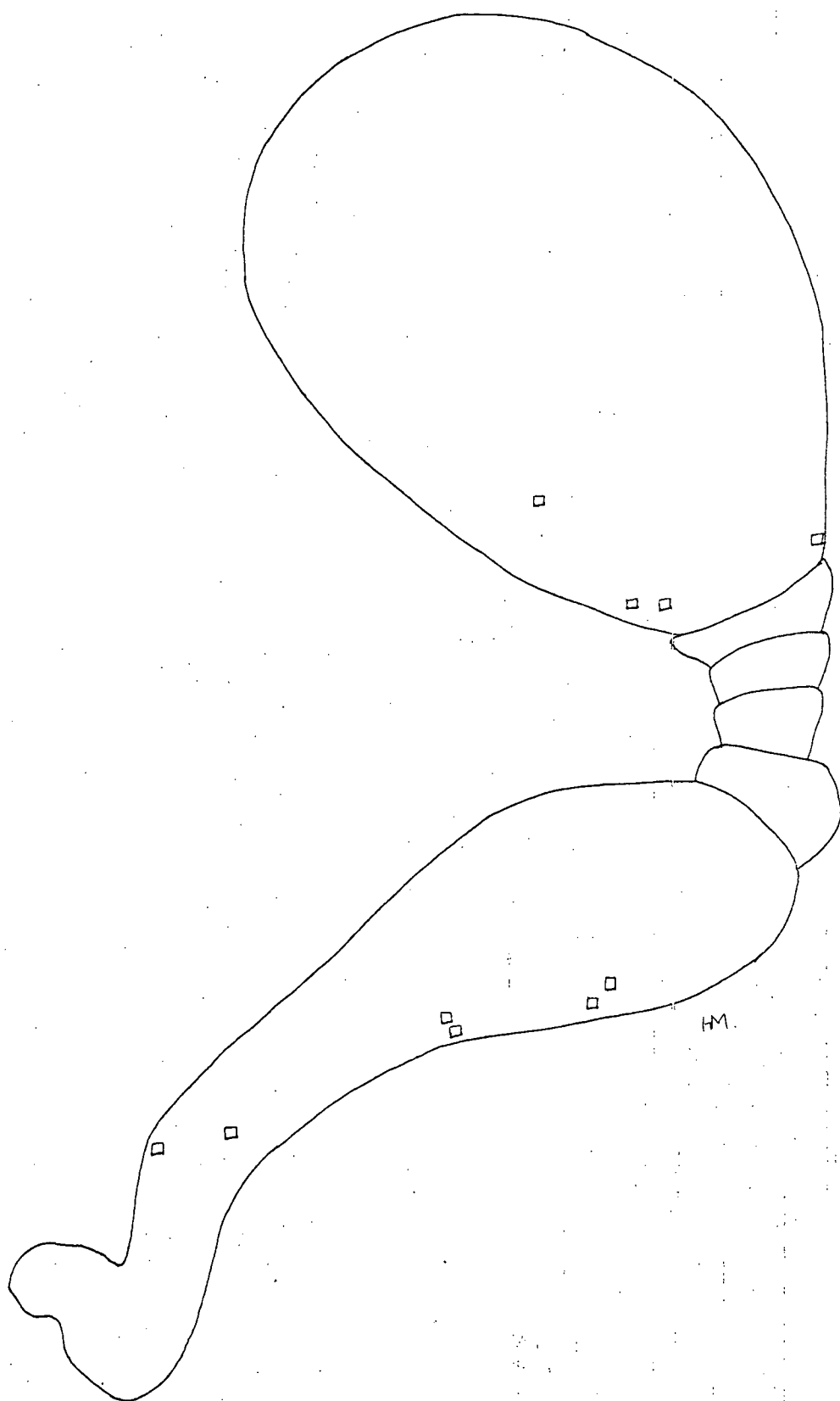


Figure 84. Distribution map of sensilla campaniformia on female left antenna, anterior surface.

Figure 85. Photomicrograph of sensillum campaniforme. Distilled water mount.

Figure 86. Electron micrograph of sensillum campaniforme, oblique section through tubular body and dome. Glutaraldehyde-osmium fixation, lead citrate section stain.

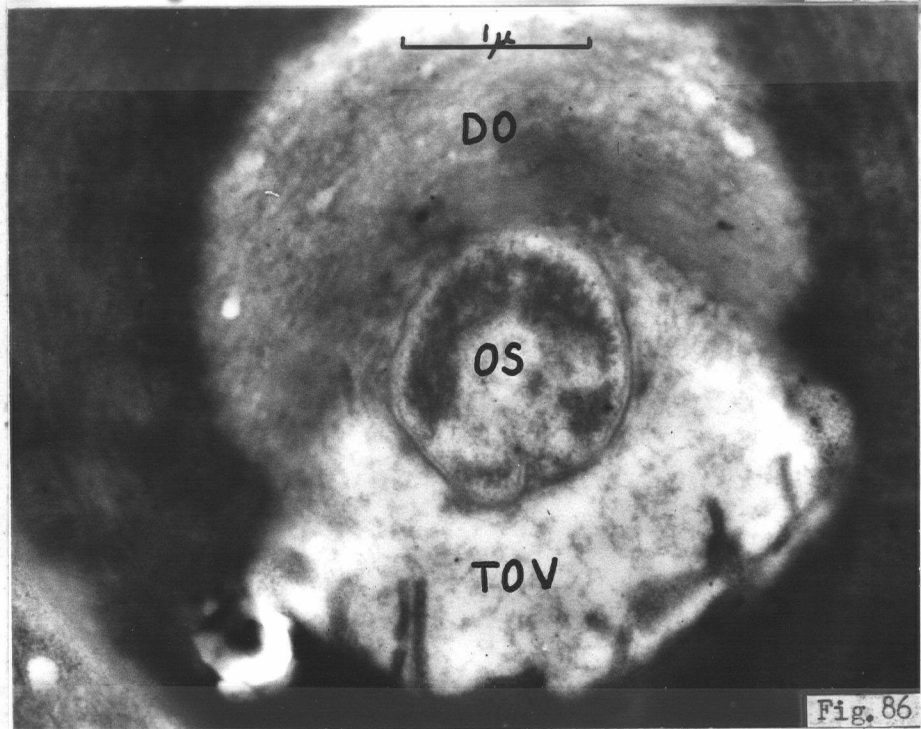
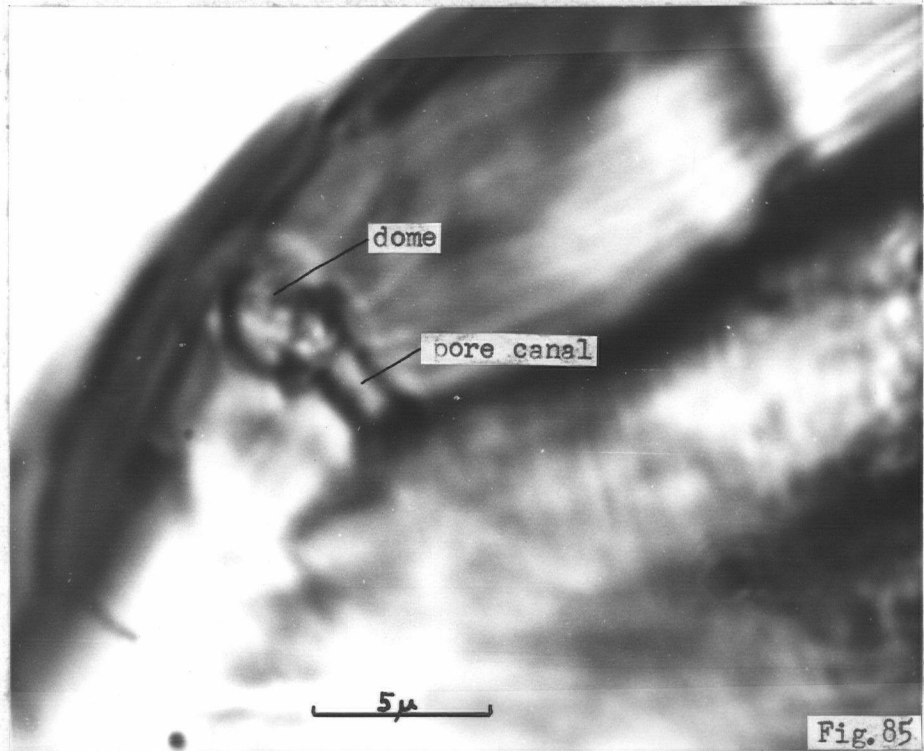


Figure 87. Schematic diagram of hypodermal gland pore.

Figure 88. Schematic diagram of sensillum campaniforme.

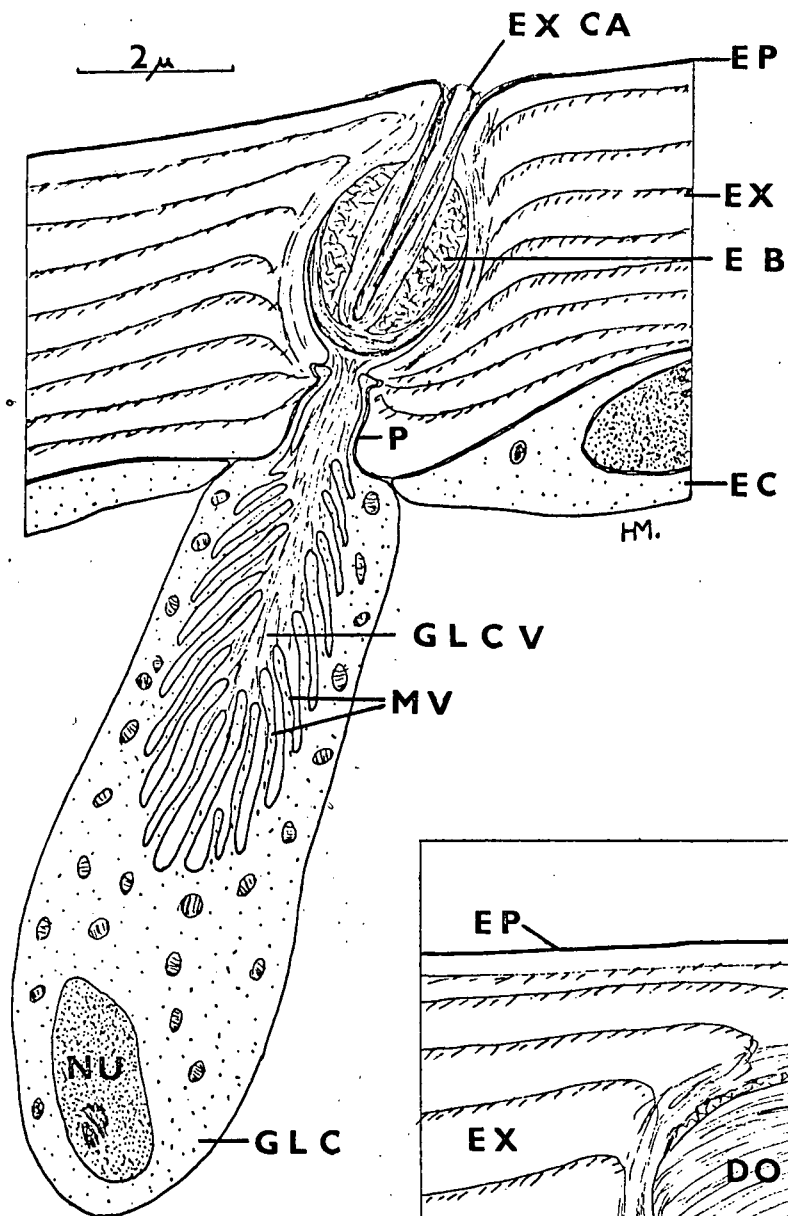


Fig. 87

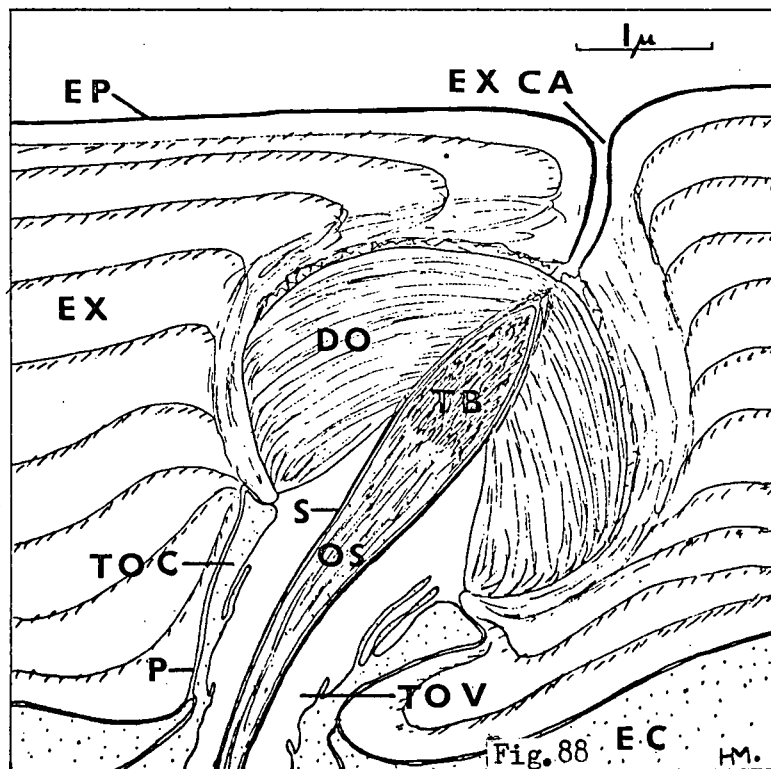


Fig. 88




Figure 89. Electron micrograph of antennal nerve, cross section at proximal portion of scape. Glutaraldehyde-osmium fixation, lead citrate and uranyl acetate section stain.

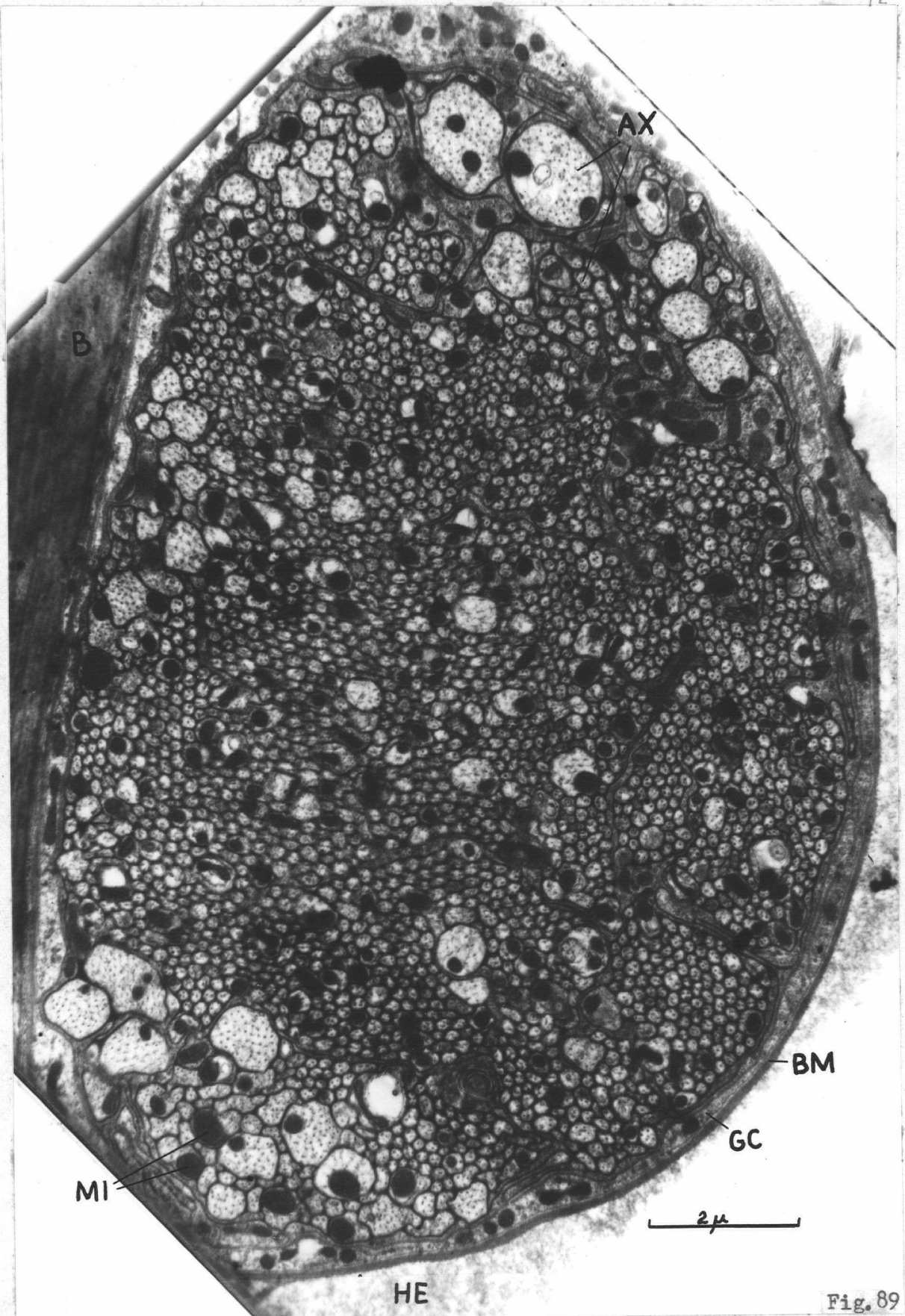


Fig. 89

Table I. Sensillum count on T. lineatum female antenna (Figs.5,6)

Type of sensillum	Number of sensilla			Nerve cells per sensillum	Total nerve fibres
	Posterior surface	Anterior surface	Total		
Sensillum chaeticum	192	280	472	1	472
Sensillum trichoideum Type I	9	15	24	1?	24
Sensillum trichoideum Type II	8	39	47	2	94
Sensillum trichoideum Type III	3	24	27	6	162
Sensillum basiconicum	126	408	534	2	1068
Sensillum campaniforme	15	10	25	1	25
Totals	353	776	1129		1845

Table II. Sensillum count on T. lineatum male antenna (Figs.3,4)

Type of sensillum	Number of sensilla			Nerve cells per sensillum	Total nerve fibres
	Posterior surface	Anterior surface	Total		
Sensillum chaeticum	195	314	509	1	509
Sensillum trichoideum Type I	9	20	29	1?	29
Sensillum trichoideum Type II	6	42	48	2	96
Sensillum trichoideum Type III	4	18	22	6	132
Sensillum basiconicum	130	434	564	2	1128
Sensillum campaniforme	16	11	27	1	27
Totals	360	839	1199		1921

DISCUSSION

1. General

Much of the existing confusion regarding insect sense organ function stems from the fact that sense organs, of necessity, were originally classified according to gross morphological characteristics (Snodgrass, 1935). Since most of the critical specialized structures of the nerve endings are smaller than the resolving power of the light microscope, few conclusions could be drawn regarding the possible functions of sense organs. Behavioural studies, coupled with ablation experiments could, at best, give information only on the bodily location of sense organs, but due to the abundance and density of various types of sensilla on, for example, the antennae, little could be said regarding the sense organ(s) actually mediating a given behavioural pattern. Matters are further complicated by the presence of up to sixty sense cells in one sensillum (Slifer, 1961), each possibly responding to different stimuli, or in a different manner to the same stimuli. Only under very favorable conditions could a function be ascribed to a given sense organ. This, however, did not mean that the ascribed function was the only one the sense organ possessed, if more than one sense cell was present. For example, each of up to five sense cells of the labellar hairs of blowflies has a different function (Hodgson, 1965). Furthermore, electrophysiological work has revealed qualitative as well as quantitative differences in response to the same stimuli by the sense cells of morphologically indistinguishable sensilla (Stürckow, 1963; Schneider, Lacher, and Kaissling, 1964). Thus great care must be taken when attempting to make generalizations about the function of a given type of sensillum, even when fine-structural and electrophysiological evidence is available.

The present study on insect sensilla has revealed several interesting features. Firstly, all bipolar neurons so far studied are virtually indis-

tinguishable from each other proximal to and including the ciliary portion of the dendrite. The main differences lie in the terminal specialization of the outer segments, i.e. the manner in which the sense cell is exposed to the environment, which is either directly through holes in the cuticle, or by means of a cuticular transducer mechanism. Secondly, sense cells which respond to similar environmental modalities show a similar fine-structural organization of the outer segments. This does not necessarily apply to the Type II multidendritic neurons. Comparison of the present results with those of other workers using the electron microscope indicates that the above features may be common to most cuticular sense organs found in other insect orders (Adams and Holbert, 1963; Adams, Holbert, and Forgash, 1965; Anonymous, 1964; Boeckh, Kaissling, and Schneider, 1965; Dethier, 1963; Dethier, Larsen, and Adams, 1963; Dethier and Wolbarsht, 1956; Gray, 1960; Hodgson, 1965; Kuwabara, 1963; Larsen, 1962, 1963; Larsen and Dethier, 1963; Noble-Nesbitt, 1963a, 1963b; Osborne, 1963, 1964; Osborne and Finlayson, 1965; Peters, 1960; Prestage, Slifer, and Stephens, 1963; Schneider, 1964; Schneider, Lacher, and Kaissling, 1964; Slifer, 1961, 1963; Slifer, Prestage, and Beams, 1957, 1959; Slifer and Sekhon, 1961, 1962, 1963, 1964a, 1964b, 1964c; Slifer, Sekhon, and Lees, 1964; Thurm, 1964, 1965; Uga and Kuwabara, 1965).

2. Sensilla Chaetica

The abundant and widely distributed sensilla chaetica are probably all innervated by a single neuron each. For that reason multiple function of a given sensillum can be excluded. Also, chemical function, as well as responses to temperature, osmolarity, and CO₂ can be readily excluded, since the hair is thick-walled with an empty small lumen, and the sense cell terminates at the base of the hair, being additionally encased by the scolopale, thus effectively shielding the neuron from stimulation by those modalities. On the other hand, the structure of the socket and hair, with the attached

scolopale, provides an excellent opportunity for stimulating the cell by a bending of the hair. Whether this is accomplished by contact with a substrate, by air-borne sound, by air currents, or by differential cuticular absorption of water as a result of humidity changes can at present not be resolved, but the first seems the most likely possibility. The thickness of the hair, relative shortness, curvature, and apparent stiffness make air-borne sound and air currents unlikely stimuli; hairs which are known to respond to sound or air currents are usually very long, thin, protruding almost at right angles to the cuticle surface, and set in a wide membrane, all features apparently making deflection of the hair easier (Dethier, 1963; Schwartzkopff, 1964). Since the hair itself seems to be constructed entirely of non-staining impermeable exocuticle, and since no differential substructure was noted, water absorption as a means of humidity detection is considered unlikely. If an effect does occur in the socket only, the hair itself would be superfluous, and one would have to explain its presence as well as structure; the single sense cell precludes a double function. The remaining choice of function, touch reception, is a logical one when one considers the presence of the sensilla on all exposed body parts, their greater density on critical parts like the antennae, front of the head, pronotum, legs, posterior region, and their orientation and fine structure. The distal nerve process of known mechanoreceptors, the hair plate sensilla and campaniform sensilla of bees examined by Thurm (1963, 1964a, 1964b, 1965), contains a special terminal structure in the form of a bundle of tubules designated the 'tubular body', consisting of 50 to 100 tubules lying parallel to one another in an electron dense material. The total diameter of each tubule is approximately 150Å. Physiological and morphological results indicate that compression at the site of this body probably acts as the stimulus at the cellular level (Thurm, 1964a). A similar structure is found in the terminal nerve process

of the sensilla chaetica examined here, although the tubular nature has not been so clearly demonstrated. The 130Å to 150Å periodicity described, however, agrees closely with the above measurement. (See Fig.29.) The hair plate sensilla were found by Thurm (1965) to possess directional sensitivity, this being directly related to the point of attachment of the scolopale to the hair base. A similar relationship appears to hold in the sensilla chaetica; by comparison, a force acting on the hair from upper left to lower right in Fig.20 would be most readily perceived. This would be of maximal advantage to the animal, since this is the most likely direction a natural stimulus would have. Electrophysiological verification is of course essential. Sensillum position may further indicate function: The long sensilla chaetica on the scape may act as proprioceptors, informing the beetle of the position of the club when the antenna is withdrawn against the head.

3. Sensilla Trichoidea, Type I

Since nothing is known of the fine structure of the Type I sensilla trichoidea, nothing can be said about the possible function on this basis. However, their very localized distribution, as well as their gross resemblance to hair plate sensilla of other insects, suggest proprioception as a likely function. In some whole mounts of antennae the hairs on portions of the first funicular segment are visibly bent against the cuticle of the scape. Similarly, different hairs on the proximal bulb of the scape would be bent against the surrounding head capsule, depending on antennal position. Further work to determine fine structure of these sensilla is required.

4. Sensilla Trichoidea, Type II

The most interesting feature of these sensilla is the perforated hair wall. Although the relationship between the nerve branches and the pores could not be clearly demonstrated, comparisons can still be drawn between these sensilla and the long trichoid sensilla of Bombyx and Antheraea

males (Boeckh, Kaissling, and Schneider, 1965), and the basiconic sensilla of several insect orders, including Coleoptera (Slifer, 1961, 1963; Slifer et al, 1957, 1959; Slifer and Sekhon, 1961, 1962, 1963, 1964a, 1964b, 1964c): the nerve branches each contain at least one microtubule, and the number of cuticular pores far exceeds the number of nerve branches in the hair. Since Slifer and Sekhon (1964a, 1964c) have clearly demonstrated filaments passing from the sides of the nerve branches to the pores, a similar relationship is assumed to hold here; Fig. 69 indicates that this is probably the case, at least in the sensilla basiconica.

The long trichoid sensilla on the antennae of male Bombyx mori and Antheraea pernyi were examined electrophysiologically (Boeckh, Kaissling, and Schneider, 1965; Schneider, Lacher, and Kaissling, 1964) and were found to respond to the respective female-produced sex attractant. No reaction was found to mechanical, thermal, CO₂, or humidity stimuli. The other one or two cells of the sensilla trichoidea usually present did not respond to the sexual attractant but gave a phasic impulse increase or decrease to the general odour. Curiously, the females, which do not respond to their own sex attractant, lack the long sensilla trichoidea. In the present case it is thus assumed that the Type II sensilla trichoidea are olfactory receptors, not excluding possible responses to temperature, humidity, and CO₂. Mechanoreception is considered unlikely: the hair base is not articulated, and no neuron terminates at the base.

5. Sensilla Trichoidea, Type III

The Type III sensilla trichoidea hold a considerable number of features in common with the contact chemoreceptor trichoid sensilla of many other insects. These are the reverse curvature of the hair, the longitudinal hair fluting, the blunt tip, the double lumen, the eccentric small lumen apposed to one side containing the distal processes of several neurons, and the arti-

culated hair base. It is thus very tempting to consider these sensilla as contact chemoreceptors. The position of these sensilla on the distal half of the anterior club surface, as well as their exposed nature, facilitating contact with a substrate, further strengthen this view. Sections of the hair tip are still required to determine the relationship of nerve endings to the external environment; at this time the presence of terminal pores is assumed. Since a systematic study of the fine structure of each hair on a given club was not undertaken, the relationship between hair position and nerve cell number, and the absence or presence of a nerve cell terminating at the hair base were not determined. This would have to be done if any attempts are made at electrophysiological recording of responses. Furthermore, it must be kept in mind that morphological identity, with respect to nerve cell number and disposition, does not necessarily mean physiological identity, since different combinations of cells responding to various stimuli may be present in hairs of similar appearance. Each hair must thus be examined separately, both for morphology and function. Speculation on the function of individual cells is pointless since this insect has a highly specialized diet (ambrosia fungus), the chemical composition of which is unknown. Contact chemoreceptor cells responding to water, carbohydrates, and salts were found in Diptera (Dethier, 1963); this information may be used as an initial guide. Additionally, some contact chemoreceptor sensilla were found to respond to mechanical stimulation - bending of the hair, this being related to the presence of a nerve termination at the hair base (Dethier 1963).

6. Sensilla Basiconica

In common with the Type II sensilla trichoidea, the sensilla basiconica have a perforated hair wall, two neurons each, and branching of the outer segments, differing only in the greater amount of nerve branching and the greater number of hair perforations. Since their fine structures are so si-

milar, the sensilla basiconica are also assumed to be olfactory organs, again not excluding possible reception of water vapor, CO₂, and temperature. Due to their stoutness, lack of articulation, and protected nature, they are also considered unlikely as mechanoreceptors. The exact nature of the receptor membrane, and the relationship of pores to dendrite branches remain to be elucidated. Since no study exists in which given sensilla basiconica were examined both electron microscopically and electrophysiologically, no reasonable comparisons can be made using only fine structure as the basis. Furthermore, at least two general types of sensillum basiconicum presumed responsive to odours exist: one type with perforated hair walls as described above, and another type in which the cuticular sheath containing the dendrites passes up the hair lumen to the tip of the hair, where the dendrite tips are exposed to the air (Slifer, Prestage, and Beams, 1957, 1959). Due to the large differences in receptive surface area presented to the environment, these two types undoubtedly differ greatly in the types of chemicals to which they can respond, as well as to their concentration. Perforated hairs and pegs were found by other workers on the antennae of bees (Slifer and Sekhon, 1961), moths (Boeckh, Kaissling, and Schneider, 1965), mosquitoes (Slifer and Sekhon, 1962), bugs (Slifer and Sekhon, 1963), flies (Slifer and Sekhon, 1964b), grasshoppers (Slifer and Sekhon, 1964c), and beetles (Slifer and Sekhon, 1964a). The second type of sensillum basiconicum has not yet been found on the antennae of T. lineatum; their presence is however not excluded.

7. Sensilla Campaniformia

The mechanoreceptive function of campaniform sensilla has been well established for some time (Pringle, 1938a, 1938b), contrary to McIndoo's belief that they functioned as olfactory receptors (McIndoo, 1914). More specifically, the sensilla respond to stresses in the cuticle resulting from mechanical deformation (Dethier, 1963). Since no significant differences in structure

were found in the sensilla of this insect, compared to those of others, a similar function is assumed. The fine structure of the nerve ending appears almost identical to that of the bee campaniform sensillum examined with the electron microscope by Thurm (1964). He concludes that compression at the site of the tubular body is the adequate stimulus at the cellular level.

8. Axon Fusion

The probable absence of sensory cell axon fusion is an important finding since it means that the function of each sense cell can be individually recorded in the brain, without summation effects. Since Steinbrecht (unpublished, cited in Boeckh, Kaissling, and Schneider, 1965), using the electron microscope, also found no evidence of axon fusion in Bombyx antennae, and since many of the nerve fibres are of a size below the resolution limit of the light microscope, the situation should be reinvestigated with the electron microscope in Rhodnius and Phormia antennae, in which extensive axon fusion supposedly exists (Wigglesworth, 1959; Dethier, Larsen, and Adams, 1963).

SUMMARY AND CONCLUSIONS

The antennae of the ambrosia beetle Trypodendron lineatum (Olivier) were examined with the light and electron microscopes to determine the types, distribution, and structure of cuticular sense organs found thereon. Whole mounts of antennae were used to determine types and distribution of sensilla. Sections of Epon-embedded specimens were either stained with methylene blue and examined with the light microscope, or stained with heavy metal salts and examined with the electron microscope. A brief investigation was made of the presence or absence of sensory axon fusion in the antennae.

The conclusions are as follows:

1. Six main types of sense organs are present on the antennae, with an additional seventh cuticular structure, the hypodermal gland pore, which is thought to be non-sensory.

2. The sensilla are sensilla chaetica, sensilla trichoidea Types I, II, and III, sensilla basiconica, and sensilla campaniformia.

3. Distribution maps of all sensilla and the hypodermal gland pores on one each of left male and female antenna are presented.

4. Sensilla chaetica, of wide distribution, possess one bipolar neuron terminating in a scolopale at the base of the thick-walled articulated hair.

5. Type I sensilla trichoidea are short hairs at the base of the scape and the base of the first funicular segment. Their fine structure and innervation are not known.

6. Type II sensilla trichoidea are sharp-pointed hairs of intermediate length, with thin, perforated hair walls and two neurons with slightly branched dendrites as the main features. Distribution is restricted to the distal periphery of the club.

7. Type III sensilla trichoidea, on the distal half of the anterior club surface, are blunt-tipped, reversely-curved hairs possessing a double

lumen and four to seven bipolar neurons, the unbranched dendrites of which extend to the hair tip. The presence of hair tip perforations is assumed.

8. *Sensilla basiconica*, on both club surfaces, are relatively short thin-walled perforated hairs or pegs, possessing two neurons each, with much-branched dendrites. The relationship of dendrite branches to hair perforations is not clear.

9. *Sensilla campaniformia*, of wide distribution, consist of a sub-surface dome in the centre of which lies the nerve ending of one neuron similar in appearance to that of the *sensilla chaetica*.

10. The number of antennal nerve axons exceeds the expected number of axons obtained by a sensillum count corrected for the number of nerve cells present per sensillum type, with Johnston's organ unaccounted for, indicating the probable absence of sensory axon fusion in the antennae.

11. The possible functions of the six sensillum types are discussed.

12. The implications of past research into insect sense organ function, and the value of studies such as the present one, are discussed.

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