STRUCTURE AND FUNCTION OF THE FASCICULAR STYLETS, AND THE LABRAL AND CIBARIAL SENSE ORGANS OF MALE AND FEMALE *AEDES AEGYPTI* (L.) (DIPTERA, CULICIDAE)

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Since male mosquitoes feed exclusively on plant juices and most females on both blood and plant juices, sexual differences exist between the fascicles and the associated sense organs. Mandibles are present only in the female, and these form the floor of the food canal at the distal end of the fascicle. The salivary duct within the hypopharynx is open dorsally, and it is probably through this opening that the saliva comes to bind and lubricate the stylets. Other reports on "binding structures" for the stylets are shown to be based on incorrect observations. Apical and subapical labral sense organs are present in females, but not in males. They are thick-walled chemoreceptors, each containing five chemoreceptive dendrites which probably function in blood detection. Labral ridge receptors are described for the first time in both sexes of mosquito. These receptors probably provide information to the mosquito about the position of the tip of its labrum during feeding. The labral campaniform sensilla are probably flow-monitors, initiating the regular pumping of the cibarial and pharyngeal pumps. In the cibarial pump, the male has the same types of sense organs as the female, but a different number of trichoid sensilla. Trichoid sensilla probably monitor the food flow into the pump. Papilla-like sensilla in the cibarium are probably chemoreceptors capable of distinguishing between blood, sugar, and unacceptable compounds. The inability of newly-emerged mosquitoes to feed is probably due to the fact that their stylets are not fully sclerotized.

Comme les moustiques mâles se nourrisent exclusivement de jus de plante et que la plupart des femelles se nourrissent de sang et de jus de plante, il y a des differences sexuelles entre les fascicules et les organes des sens associés. Les mandibles se rencontrent que chez les femelles. Ces mandibules forment le plancher du canal nourrissier dans la région distale du fascicule. Dans l'hypopharynx le conduit salivaire est ouvert dorsalement. C'est probablement par cette ouverture que la salive unit et lubrifie les stylets. Les données publiées par d'autres sur ces "structures d'union" sont basées sur des observations incorrectes. Les organes sensoriels apicaux et sous-apicaux du labre existent seulement chez les femelles. Ces organes sont des récepteurs chimiques à mur épais. Chacun de ces récepteurs est composé de cinq dendrites pour réception chimique. Ces dendrites probablement détectent le sang. Les récepteurs sillonnés du labre sont décrits pour la première fois chez les deux sexes des moustiques. Ces récepteurs probablement informent le moustique de la position de l'extrémité du labre lors du repas. Les sensilla campaniformia *du labre probablement détectent le flux sanguin et initie le pompage regulier des pompes ciberiales et phryngiales. Dans la pompe ciberiale, les organes sensoriels sont sembables chez les deux sexes, mais le nombre de* sensilla trichodea *diffère entre les sexes. Les* sensilla trichodea *probablement détectent le flux sanguin dans la pompe. Les* sensilla *en forme de papille qui se trouvent dans le cibarium sont probablement des récepteurs chimiques capable de distinguer entre le sang, le sucre et d'autre composés chimiques inacceptables. Les moustiques récemment émergés sont incapables de se nourrir, car probablement leurs stylets ne sont pas entièrement solidifier.*

INTRODUCTION

The mouthparts of female mosquitoes consist of an elongate labium enclosing a fascicle of six slender stylets: two mandibular, two maxillary, one labral and one hypopharyngeal. During feeding, only the fascicle is inserted into the host tissue. The structure and function of these mouthparts have been widely studied in female mosquitoes (Annett, Dutton and Elliott, 1901; Nuttall and Shipley, 1901, 1903; Kulagin, 1905; Vogel, 1921; Robinson, 1939; Schiemenz, 1957; Snodgrass, 1959; and Walbauer, 1962, among others), but less so in males (Marshall and Staley, 1935; Vizzi, 1953).

The sense organs of the stylets and of the walls of the cibarial pump are poorly known. The distal part of the hypopharynx in female *Aedes aegypti* has been examined by transmission electron microscopy (TEM) (Nehman, 1968) and the fascicular stylets of three species of mosquito by scanning electron microscopy (SEM) (Hudson, 1970). Both SEM and electro-physiological techniques have been used to elucidate the role of the labral apical sense organs of *A. aegypti* (Pearson, 1970). Unfortunately, conclusions arising from behavioural studies of labral sense organ function (Gordon and Lumsden, 1939; Hosoi, 1954, 1959; Griffiths and Gordon, 1952; Owen, 1963; Salama, 1966) are contradictory. In addition, the fine structure of the labral sense organs remains undescribed.

In this paper, I compare the fine structure of the fascicular stylets, the sense organs on the stylets, and the cibarial sense organs in both sexes of *A. aegypti.* Their function is then discussed in relation to reports by other workers.

MATERIALS AND METHODS

An *A. aegypti* culture was started with eggs kindly donated by Dr. A. S. West (Department of Biology, Queen's University, Kingston, Ontario). The colony was maintained in the insectary at 27° and 65% R.H. For light microscopy, heads from adults of known age were preserved in alcoholic Bouin for 48 hours or more, double-embedded in 2% celloidin and paraplast, sectioned at 6 μ, stained with Gomori's trichrome (Humason, 1967), and mounted in DPX. Sections and whole mounts of fascicular stylets mounted in DPX were examined by conventional and phase microscopy.

For SEM, Slifer and Sekhon's (1970) method was used. Heads of young adults (one to three days old) were fixed in 5% Formalin. The labium was removed from the head using a fine needle. Heads with fascicles attached were dehydrated through a graded series of alcohols, with the stylets being dissected out in absolute alcohol. The stylets were cleared in xylene and air-dried on a glass slide. Each stylet was then mounted individually on a specimen stub with a drop of Silver Dag (Ted Pella Company) with the tip of the stylet pointing upwards. The specimens were then coated evenly with 150 Å of carbon and gold, and viewed with a Cambridge Stereoscan S 4.

For TEM, mosquitoes of known age were anesthetized with chloroform. The tip of the proboscis containing the fascicle was severed from the remainder with a fine scalpel. The fixation procedure of Hooper *et.al.* (1972) in 3% glutaraldehyde and 1% Osmium tetroxide was used. Specimens were embedded in Araldite (Luft, 1961) and in Spurr's (1969) low viscosity epoxy medium. Sections were cut on a Reichert Om-U2 Ultramicrotome using glass and diamond knives. Single-hole grids with hole diameters of 0.5 and 1.0 mm supported with carbon coated Formvar film were used. Sections were stained with uranyl acetate and lead citrate (Reynold, 1963), and examined in a Philips EM 300 electron microscope. Thick sections (about 0.5 μ) were cut periodically to check the orientation of the specimen by light microscopy. These were stained with Azure II-Methylene blue (Richardson *et.al.*, 1960).

RESULTS AND DISCUSSION

The fascicle is situated in the labial gutter and projects out from between the labellar lobes at the tip of the proboscis. The arrangement of the fascicular stylets in a female is shown in Figure 1. The labrum (lr) is the most dorsally situated stylet of the fascicle. The two mandibles (md) are situated one above the other, at least at the distal part of the fascicle, and form the floor of the food canal. The hypopharynx (hp), containing the salivary duct, is situated ventral to the mandibles. The two maxillae (mx) extend longitudinally on either side of the mid-rib of the hypopharynx. The ligula (lg) forms the floor of the fascicle and extends in between the two labellar lobes (lb).

In male mosquitoes, the labrum (lr) forms the food canal (F) (Figs. 10, 11), and the mandibles are absent (Fig. 24). The hypopharynx (hp) is fused with the labium (L) proximally (Figs. 11, 12) and with the ligula (lg) distally (Figs. 10, 24, 25). The two maxillae (mx) are situated dorso-lateral to the food canal (F) (Fig. 12).

Labrum (lr) (Figs. 1-6, 10-21, 27, 29).

The labrum in both sexes of *A. aegypti* is double-walled, with the inner (epipharyngeal) wall (ep) lining the food canal (F) (Figs. 2-4, 12). At the distal end, the dorsal and epipharyngeal walls are fused to form a solid pointed structure (Figs. 15, 19, 21). Proximally, the two walls have been reported to be connected to each other by membranous cuticle (Christophers, 1960; Walbauer, 1962; Hudson, 1970), but according to my material (20 sectioned females), such membranous attachment occurs only for a short distance at the anterior end (Figs. 21D, 27). The membranous lateral wall (lw) is always broken near the labral nerve canal (lrc), even in teneral forms (Figs. 4-6). Since other parts in the sections do not show any tearing or pulling due to sectioning, such breakage here is unlikely to be an artifact. In TEM sections, the membranous lateral wall is found to be curled up on the labral nerve canal, but it is not connected to it. In male mosquitoes, the membranous lateral wall is connected to the labral nerve canal (Fig. 12).

Bhatia and Wattal (1957) reported that there are "septal-rings" occurring at various intervals on the inner surface of the labrum in both sexes of *Aedes, Anopheles,* and *Culex* mosquitoes. They suggested that these rings serve to keep the hypopharynx, mandibles and maxillae firmly applied against the lips of the ventral opening of the labrum, and rejected Robinson's (1939) suggestion that it is the fascicular fluid that holds the stylets together. Snodgrass (1959) mentioned that he could not see these "septal-rings" in these genera of mosquito. Walbauer (1962) was also unable to find these "septal-rings" in female *Psorophora ciliata.* I have found them in some preparations made using the technique recommended by Bhatia and Wattal, and also in some permanent mounts. However, these "septal-rings" occur only in those preparations in which the labra were not straight in the mounting medium. SEM study of the labrum leaves no doubt that these "septal-rings" are artifacts (Fig. 17). They are probably "wrinkles" in the membranous lateral wall of the labrum. This would explain the variable number of "septal-rings" Bhatia and Wattal (1957) reported for specimens of the same species.

Structural details of the labrum differ in the two sexes. In the male, the tip is forked, and a longitudinal groove (lgg) 2.2 μ in width runs along the mid-dorsal line of the dorsal wall throughout its length (Fig. 19). Proximally, this groove widens, and forms the whole dorsal wall (Fig. 12, dw). In females, quadrangular cuticular thickenings are found on the dorsal wall (Fig. 18).

Proximally, the dorsal wall of the labrum is continuous with the clypeus. The epipharyngeal wall extends into the cibarial pump where it becomes the dorsal hard palate which bears cibarial sense organs (Fig. 29). The articulation of the labrum to the head capsule and the labral

musculature has been fully described by Schiemenz (1957) and Walbauer (1962). A spine (S) occurs at the base of the male labrum (Fig. 13), but not of the female labrum. The significance of this spine is unknown.

In teneral specimens less than 10 hours old, the labrum is not as fully sclerotized as it is in mosquitoes two to three days old. Epidermal cells occur between the two walls of the labrum (Figs. 4-6), indicating that labral cuticle continues to be deposited after emergence.

In both sexes, the tip of the fascicle is slightly rotated along its longitudinal axis (Figs. 4, 10). MacGregor (1931) reported that the labrum can rotate on its own axis, while Schiemenz (1957) described the clypeo-labral muscle as being the rotator of the labrum. Walbauer (1962) doubted Schiemenz's statement, but did not give any alternative explanation. Nehman (1968) also reported that the fascicle is rotated "approximately 30° from the central axis of the proboscis". This whole subject requires further study.

Labral Sense Organs (Figs. 15, 16, 20). — With SEM, three pairs of sensilla can be seen at the distal end of the female labrum (Figs. 15, 16), and one pair in the male (Fig. 20). These sensilla have been mentioned by many workers, but most of their descriptions include only one or two pairs, and there are discrepencies in papers that quote the descriptions of earlier workers. Von Gernet and Buerger (1966) reviewed this subject comprehensively, and only papers not mentioned by them, and those published since will be referred to below.

Nuttall and Shipley (1903) illustrated two pairs of apical labral sense organs in female *Anopheles maculipennis* (Plate 7, Fig. 7). Unfortunately, they described these sensilla as chitinous teeth which increase the boring power of the labrum. Patton and Evans (1929) included three groups of sensilla in their diagram (Fig. 52B) of the labrum of female *Anopheles maculipennis,* but only mentioned that "the distal end of the labrum-epipharynx is armed with minute sensory structures". Martini (1931) alluded to "sensory pegs" on the *Anopheles bifurcatus* labrum, but did not give any further details. His illustration (Fig. 86) is a cross-section through four apical labral sense organs. Schiemenz (1957) noted the presence of three pairs of "sensory bristles" at the tip of the labrum in *Theobaldia annulata,* called them tactile sense organs, and suggested that they might be involved in blood detection. He also indicated that the labrum is the only innervated stylet. Hudson (1970) described two pairs of peg-like organs on the labrum of female mosquitoes, missing the third pair. One of the subapical sensilla can be seen in her Fig. V(1). Pearson (1970) called the "apical labral pegs" in female *A. aegypti* basiconic sensilla, although he could not find any pores on the pegs. He explained that this may be due either to clogging of the pores during vacuum coating prior to viewing, or because of the relatively low resolving power of the SEM (180 $\overset{\circ}{A}$). Froelich (1971) confirmed von Gernet and Buerger's (1966) observation of three groups of sense organs on the labrum of female *Culex pipiens fatigans* with her light microscope study.

The terms used by various authors for the labral sense organs are listed in Table I. Von Gernet and Buerger (1966) called the two groups of sensilla at the distal end of the labrum "apical setiform organs", and the proximal pair "subapical sensilla". In this paper, I use the terms apical (as), subapical (ss) and campaniform (cs) sensilla for the three pairs of labral sense organs (Figs. 15, 16, 20).

(a) Apical Sensilla (as) (Figs. 15, 21A, 22, 23).

These occur only in females. They are socketed, are located at the tip of the labrum along the labral ridge (Fig. 15), are 5.5-7.6 μ long and 2.0-3.0 μ wide, and each has a longitudinal groove along its outer surface. Pearson (1970) gave their measurement as 3 μ long by 1 μ maximum diameter. This is undoubtedly incorrect, as the measurement I have is taken from SEM pictures of 15 specimens. An opening 0.17 μ in diameter is found near the tip of each sensillum (Fig. 21A). This opening is difficult to see with the SEM, and staining with crystal violet (Slifer, 1960) also failed to reveal its location. The opening was found in serial TEM sections.

Table I. Terminology used by various authors for the labral sense organs.

Author(s)	Species studied	Apical Sensilla	Subapical Sensilla	Campaniform Sensilla
von Gernet & Buerger (1966)	*A. aegypti* + 21 other species	Apical setiform organs	Apical setiform organs	Subapical sensilla
Nuttall and Shipley (1903)	*Anopheles maculipennis*	Labral teeth	Labral teeth	
Vogel (1921)	*Culex pipiens, Anopheles maculipennis, A. bifurcatus*	Chitinous spines	Chitinous spines	
Patton and Evans (1929)	*Anopheles maculipennis*	Sensory structure	Sensory structure	Sensory structure
Martini (1931)	*Anopheles bifurcatus*	Sensory pegs	Sensory pegs	
Robinson (1939)	*Anopheles maculipennis*			Peg-like sense organs
Schiemenz (1957)	*Theobaldia annulata*	Tactile sense organ	Tactile sense organ	Tactile sense organ
Christophers (1960)	*A. aegypti*			Gustatory papillae
Clements (1963)				Sensory pegs
Hudson (1970)	*Aedes stimulans Aedes atropalpus Wyeomyia smithii*	Distal peg-like organs	Second pair of peg-like organs	
Pearson (1970)	*A. aegypti*	Apical labral pegs	Apical labral pegs	

Five dendrites enclosed in a dendritic sheath occur inside each sensillum. As the dendritic sheath is fused to one side of the wall of the sensillum, the shaft of the sensillum appears double-chambered in cross-sections (Fig. 22). The dendrite-free chamber contains the remnants of the trichogen cell that formed the sensillum (Larsen, 1962). In Figure 22, six dendrites can be seen inside the sensillum, but these are associated with only five ciliary regions (Fig. 23). One of the dendrites has probably branched after entering the base of the socket. Foelix and Chu-

Wang (1973) have made similar observations in the tarsal organ of a web spider *Araneus dia-dematus*. According to Hansen and Henmann (1971), splitting dendrites occur also in the contact chemoreceptors of the blowfly *Phormia terraenovae*. All five dendrites enter the shaft of the sensillum, but only the largest one (Fig. 22, arrow) and three smaller ones extend to near the apical opening. The lumen containing the remnant of the trichogen cell does not open to the outside. Sensilla having two openings exist in the shorter labellar hairs of *Lucilia serricata* (Lewis, 1970).

The ciliary region of the dendrites has a 9 + 0 microtubular configuration (Fig. 23). Triplets are found at the region of the basal body (Fig. 23, inset). Proximally these dendrites are surrounded by trichogen and tormogen cells.

Structurally these apical sensilla can be classified as thick-walled chemoreceptors (Slifer, 1970).

(b) Subapical Sensilla (ss) (Figs. 15, 22).

The subapical sensilla are present only in females. They are located a short distance behind the apical sensilla, along the lateral side of the labrum (Fig. 15). They are 7.0-9.2 μ long and 1.1-1.5 μ wide (compared to Pearson's 2.5 μ by less than 1.0 μ in maximal diameter). An opening 0.16-0.18 μ wide occurs on a little protruberance 1.5-2.0 μ from the tip of the sensillum (Fig. 15, arrow). Five dendrites enclosed in a dendritic sheath (Fig. 22, inset) extend proximally into the labral nerve canal to join the axons from other labral sense organs. Inside the labral nerve canal, one of the dendrites is larger than the others, and is partially isolated by an indentation of the dendritic sheath. There is no mechanoreceptor attached to the base of the sensillum at the socket area. Structurally these sensilla are similar to apical sensilla, and also can be classified as thick-walled chemoreceptors.

(c) Labral Ridge Receptors (lbr) (Figs. 15, 22, 26).

Inside each labral ridge (Fig. 15, lrr), are two dendrites in both sexes of mosquitoes (Figs. 22, 26). These end blindly before the tip of the labral ridge. In females, the ciliary region is situated proximal to the socket of the subapical sensilla.

Structurally, these sense organs resemble the "pore canal organs" described by Zacharuk (1962) in the mandibles of certain elaterid larvae. This type of sensillum has also been described from the mandibles of *Pieris brassicae* larvae (Ma, 1972); from the incisor and molar regions of *Locusta migratoria* nymphal mandibles (Le Berre and Louneaux, 1969); and from the mandibles of the coleopteran *Speophyes lucidulus* (Corbière, 1971). These pore canal organs were previously thought to be chemoreceptive, but Ma (1972) concluded from his electrophysiological experiments that they are tactile.

(d) Campaniform Sensilla (cs) (Figs. 16, 20, 27, 28).

In both sexes, a pair of campaniform sensilla are situated at the proximal end of the labral food canal openings (Figs. 16, 20). The base of each sensillum measures 1.5-2.5 μ in diameter, and supports a conical peg in its centre that is 1.0-1.5 μ long in the male and 1.5-1.8 μ long in the female. The tip of the peg is of thickened cuticle, and it is here that the tubular body (tb) (Thurm, 1964) attaches to the cap-membrane (cm) (Fig. 28). Microtubules of the tubular body are closely packed within a dense dendritic sheath. Electron dense particles occur between the microtubules (Fig. 28). These particles resemble the filaments described by Smith (1969) in the haltere campaniform sensilla of the blowfly *Calliphora erythrocephala*. Proximally, the tubular body enters the labral nerve canal through an opening (Fig. 27). The ciliary region occurs inside the labral nerve canal and has a 9 + 0 microtubule formula. Electron dense granules about 800 Å in diameter are found along the inner surface of the dendritic sheath at the level of the ciliary region. In an oblique longitudinal section of the tubular body made distal to the ciliary region, the dendritic sheath is indented at two regions.

Von Gernet and Buerger (1966) noted that, in surface view, these sense organs look like

campaniform sensilla. However, since they noticed a peg at the center of the sensillum in some of the mosquitoes they studied, they called them "basicone-like organs". I have studied the labra of most of the species listed in their paper and 20 other species using SEM. A peg is always found associated with the sensillum. There is no doubt that these sense organs are campaniform sensilla.

Campaniform sensilla are generally found on those parts of insect cuticle where stresses are believed to develop (Pringle, 1938). The ultrastructure of these organs has been studied on the head of the honeybee *Apis mellifera* (Thurm, 1964); on the halteres of the blowfly *Calliphora erythrocephala* (Smith, 1969) and fruitfly *Drosophila melanogaster* (Chevalier, 1969); on the legs of the cockroach *Blaberus discoidalis* (Moran, *et.al.*, 1971); and on the ovipositor of the facefly *Musca autumnalis* (Hooper, *et.al.*, 1972), among others. In all of these insects, the cap-membrane is dome-shaped, and has a relatively thick cuticle. The conical-shaped membrane of the mosquito labral campaniform sensilla is unusual but resembles the type C campaniform sensilla described by Zacharuk (1962; Plate 1, Fig. L) on the head of some elaterid larvae. Zacharuk (*in litt.*) now has TEM and SEM micrographs of these, and the resemblance is obvious in these as well.

Function of the Labral Sense Organs. — The labral nerve in mosquitoes is a branch of the fronto-labral nerve, which originates in the frontal ganglion (von Gernet and Buerger, 1966).

Most of the information on the role of the labral sense organs during feeding has resulted from behavioural studies. Whether these sense organs are involved in food detection is still unsettled, as the results of these studies differ.

(a) Apical and Subapical Sensilla.

Bishop and Gilchrist (1946) studied the behaviour of *A. aegypti* feeding through membranes. They reported that the female mosquito "gorges freely on glucose or honey from drops and yet seldom imbibe the former and never the latter fluid through a membrane". They also noted that the proportion of mosquitoes ingesting whole blood through a membrane is higher than the proportion ingesting it from drops. When mosquitoes were offered alternating layers of glucose and blood separated by membranes, close to 50% of the mosquitoes that gorged had blood in their stomachs, with no trace of glucose either in the stomach or in the diverticula. Only one of 156 mosquitoes tested gorged on glucose. They therefore suggested that the factor or factors which attract a mosquito to feed upon glucose or honey drops do not operate through a membrane. The labellar hairs have since been found to be sensitive to sugar (Hosoi, 1954; Owen, 1963; Salama, 1966), and to NaCl and water (Owen *et.al.*, 1974). As the labellar lobes do not enter the host tissue during piercing and sucking, Bishop and Gilchrist's suggestion is probably true. Their results also suggest that the labral sense organs might be capable of detecting blood, as they are the only sense organs present on the stylets that enter the host tissue.

Hosoi (1954) found in his behavioural and amputation experiments on feeding in *Culex pipiens pallens*, that the labrum is sensitive to blood. He also suggested that receptors might be present along the complete surface of the labrum, since mosquitoes with the apical 3/4 to 4/5 of the proboscis amputated, were still capable of imbibing blood, especially when the proboscis stump was artificially pushed into blood-containing cotton. However, his later investigations led him to agree with Day (1954) in thinking that some of the cibarial sensilla are sensitive to sugar and blood, "whereas the labrum is no longer considered as bearing any specific chemoreceptors" (Hosoi, 1959). In his 1959 study, he also found that adenosine-5'-phosphate is the main factor in blood cells which promotes gorging in mosquitoes. Galun *et.al.* (1963) confirmed Hosoi's observation, and reported that ingestion of blood by female *A. aegypti* is stimulated by adenosine tetraphosphate, ATP, ADP, and AMP listed in order of decreasing effectiveness. They also ascribed blood detecting ability to the cibarial sense organs.

Owen (1963) concluded from his behavioural studies that in *Culiseta inornata* and *Aedes dorsalis*, the fascicle bears no contact chemoreceptors. He reported that the cibarial sense organs detect blood and mediate the contraction of the cibarial and pharyngeal pumps. Salama (1966) determined from behavioural studies, that in *A. aegypti*, the labral sense organs are sensitive to blood. Pearson (1970), using electrophysiological techniques, could not get any response from the labral sense organs when these were tested with different chemicals including ATP. He gave two explanations for his results: (1) that they are vestigial receptors that once functioned as detectors of food but are no longer capable of performing this function, and (2) that they are chemoreceptors whose response to chemicals has not been tested adequately. He considered the latter possibility unlikely, as Hosoi and Owen's experiments and his own electrophysiological studies "should have indicated a receptor function if it existed". Additional electrophysiological studies may elucidate the function of these sensilla.

The apical and subapical sensilla I have described here are structurally similar to thick-walled chemoreceptors. I have since studied the labra of 40 species of mosquito representing 14 genera (Lee, in preparation). Sexual dimorphism in the sensilla occur consistently in all these mosquitoes, except for two species of *Toxorhynchites* (*brevipalpis* and *rutilus*), in that apical and subapical sensilla occur only in females, and campaniform sensilla in both sexes. *Toxorhynchites* adults do not feed on blood but on plant juices, and apical and subapical sensilla are absent in both sexes. Campaniform sensilla have been found only in *T. splendens* (von Gernet and Buerger, 1966). Thus, it appears that there is a direct relationship between blood feeding behaviour and the presence of apical and subapical sensilla.

(b) Labral Ridge Receptors.

This is the first time that these sense organs have been described. The fact that they are present in both sexes, and also that the apical and subapical sensilla do not have any mechano-receptive dendrites associated with them, suggest that these sense organs might have a proprioceptive function, supplying information about the position of the tip of the labrum during feeding, or bending during insertion.

(c) Campaniform Sensilla.

These sensilla may monitor the bending of the labrum during feeding, a function suggested by von Gernet and Buerger (1966). When a mosquito feeds on the host, the labrum bends at right angles to the plane of insertion after entering the host tissue, and the bend usually occurs dorso-ventrally in the distal fifth of its length (Gordon and Lumsden, 1939; Griffiths and Gordon, 1952). When the tip of the labrum bends dorsally, this bending will probably stretch the cap-membrane of the campaniform sensilla, thus pushing the tubular body downwards. According to Thurm (1964), the compression of the tubular body is most stimulatory in insect mechanoreceptors. But as the labral campaniform sensilla are found also in male mosquitoes, which do not normally feed on blood but on plant juices, the bending of the labrum is not likely to occur when the males are "drinking" (no studies of this have been done). This suggests that the theory of "bend-detector" is unlikely. The other possibility is that these sensilla may function as flow-detector in both sexes.

Mosquitoes often display "discontinuous suction" when they are feeding on water and sugary solutions (MacGregor, 1931). Whether such intermittent suction occurs when the mosquito is probing in the host tissue for blood is not known. Nevertheless, if such interrupted suction is a common event when the mosquito is searching for food with the fascicle, then, as soon as the food source is found, the rushing of liquid food over the campaniform sensilla will probably deform the tubular body through the cap-membrane. Rice *et.al.* (1973) suggested a "bend-stretch transduction mechanism" for insect mechanoreceptors. They proposed that in a mechanoreceptive hair where the tubular body is attached to the base of the hair, movements of the hair will bend the tip of the tubular body, so that the receptor membrane is stretched

against the neurotubular body, thereby providing stimulus. They also mentioned that such a mechanism is applicable to campaniform sensilla, hair-plate sensilla, tactile setae and stretch receptors. In feeding mosquitoes, the flow of food over the campaniform sensilla is bound to bend the tubular body posteriorly. Therefore, bend-stretch theory of Rice *et.al.* might explain the functioning of the labral campaniform sensilla. As soon as the liquid reaches the cibarium, the sensilla in the cibarium can "sample" the food entering it, thereby initiating the pumping of the cibarial and pharyngeal pumps if the food is acceptable. The rushing of food over the labral campaniform sensilla will then reinforce the regular pumping action of the two pumps.

Cibarium

At the proximal end of the labrum is a muscular pump referred to as the pharynx by many workers. Snodgrass (1959) noted that this structure is homologous to the cibarium of the cockroach, and I here follow his interpretation.

The mosquito cibarium is a dorso-ventrally flattened, tubular structure lying under the clypeus. At its anterior end, the cibarium is attached to the ventral wall of the labrum dorsally, and to the upper surface of the hypopharynx ventrally. Posteriorly, the cibarium is connected to the pharyngeal pump. Muscles originating on the clypeal wall are inserted into the dorsal wall of the cibarium, forming a pump that assists in sucking liquid food. For a detailed description of the cibarium and its musculature, see Christophers (1960).

Cibarial Sense Organs (Figs. 8, 9, 29). — Vogel (1921) noted several sensory bristles in the dorsal wall of the cibarium in *Culex pipiens, Anopheles maculipennis* and *A. bifurcatus.* He suggested that these bristles might be taste organs. The possible use of cibarial sense organs in taxonomic studies has been discussed by Sinton and Covell (1927), Barraud and Covell (1928), and Chwatt (1945). Patton and Evans (1929) figured the dorsal cibarial sense organs of female *Anopheles costalis,* but included only three pairs of sense organs in their diagram. They also mentioned the presence of "specialized hairs" in the postero-ventral wall of the cibarium; structures which Annett, Dutton and Elliot (1901) called "rods and cones". MacGregor (1931) suggested that the sense organs in the cibarium can determine the nature of the food coming into the cibarium, but he did not give any evidence supporting his idea.

Day's (1954) description of the cibarial sense organs in female *A. aegypti* included only the dorsal group. Christophers (1960) mentioned both groups of sense organs, but only his Fig. 64(4) shows the normal position of the sense organs. Owen (1963) described the sensilla in the dorsal wall of the cibarium in female *Aedes dorsalis* and *Culiseta inornata* as hairs and spines. Apparently he did not recognize the campaniform sensilla reported earlier by Day (1954). He called the sense organs present in the postero-ventral wall of the cibarium sensilla basiconica.

Von Gernet and Buerger (1966) concluded from their study of both sexes of 22 species of mosquito, that only differences in pattern are found in individuals of different species and genera. The sense organs in male and female mosquitoes "vary slightly in location, but no more than between specimens of the same sex and species".

I have studied whole mount preparations of the cibaria of 34 male and 32 female *A. aegypti,* and found definite differences existing in the number of sense organs occurring in the two sexes. In the following description, the terminology used resembles that of Day (1954), except that the term "trichoid sensilla" is used instead of "hair-like sensilla". The general arrangement of the sense organs is illustrated in Figure 29.

(a) Palatal Papillae.

Two pairs are present, normally arranged in a quadrangle. They are situated on the anterior dorsal hard palate of the cibarium. These papillae are heavily sclerotized, and each is inserted into a circular membranous socket which is also heavily sclerotized along the rim. The diameter of the socket averages 3.0 μ and the length of the papillae 6.0-9.0 μ.

The arrangement and number of these papillae is identical in both sexes.

(b) Campaniform Sensilla.

One campaniform sensillum is situated on either side of the dorsal hard palate in both sexes. The diameter of each averages 3.0 μ. Under the light microscope, the shape of the cap-membrane is seen to be similar to the labral campaniform sensilla.

(c) Dorsal Papillae (Figs. 8, 14).

One dorsal papilla is situated on either side of the dorsal hard palate behind the campaniform sensillum in both sexes. They are morphologically similar to the palatal papillae.

(d) Trichoid Sensilla

These are the "hair-like sensilla" of Day (1954) and von Gernet and Buerger (1966). They also are located in the anterior dorsal wall of the cibarium and are situated lateral to the campaniform sensilla. In each, a thin seta 7.0-9.0 μ long projects from the middle of a socket, the latter having a diameter of 3.0 μ. The number of sensilla varies between specimens of the same sex, but a difference in number does exist between the two sexes (Table II). A Chi-Square test for correlation between sex and sensilla number shows these two traits to be dependent on each other. ($\chi^2_{2D.F.}$ = 13.78; P < 0.005).

Table II. Distribution of trichoid sensilla in the cibarium of A. $aegypti$. "Left-Right" refers to the location of the sensilla on either side of the dorsal hard palate. The number in parentheses is the number of specimens showing that particular type of configuration.

	Left-Right 2 - 2		Left-Right 2-3 or 3-2		Left-Right 3 - 3		Left-Right 3 on one side or both		Total No. of Specimens Studied
	%	No.	%	No.	%	No.	%	No.	
Male	64.70	(22)	23.52	(8)	11.76	(4)		0	34
Female	28.12	(9)	18.75	(6)	34.37	(11)	18.75	(6)	32

(e) Ventral Papillae (Fig. 9).

The ventral papillae (vp) are arranged in two groups in the postero-ventral wall of the cibarium just cephalad of the opening of the cibarium into the pharyngeal pump (Fig. 9). Each group has two papilla-like sensilla. These papillae also are socketed, the latter having an average diameter of 3.0 μ. The number and location of these papillae are the same in the two sexes.

Function of the Cibarial Sense Organs. − The sensilla in the dorsal wall of the cibarium are innervated by nerves from the frontal ganglion (Day, 1954; Christophers, 1960; and von Gernet and Buerger, 1966). Those on the postero-ventral wall are probably innervated by a small branch of the fronto-labral nerve (von Gernet and Buerger, 1966).

Very little is known about the function of the cibarial sense organs in mosquitoes. Day (1954) suggested that one of the four types of sensilla he described is capable of detecting the presence of blood plasma, and that the dorsal papillae may be capable of detecting the flow of erythrocytes. Later workers mostly attributed the detection of blood to the cibarial sense organs.

Recently, Rice (1973) using SEM, reported the presence of 30-40 trichoid sensilla and four campaniform sensilla in the anterior wall of the cibarium in the blowfly *Calliphora erythrocephala*. He suggested that the trichoid sensilla are likely to be fluid flow monitors, registering the direction and rate of flow of materials going through the pump, while the campaniform

sensilla may detect the viscosity of the materials in the pump. He supported his latter view with his observation that campaniform sensilla are absent from the cibarial pump of tsetse flies, where the diet is exclusively vertebrate blood, a fluid having uniform viscosity. In the mosquito, the trichoid sensilla are probably flow receptors; whether the campaniform sensilla are capable of detecting viscosity is still unknown.

Ventral papillae also occur in the cibaria of other flies, and appear to be present in flies of all dipteran suborders (Rice, 1973). These sensilla are referred to as basiconic sensilla by Owen (1963) in *Aedes dorsalis* and *Culiseta inornata* mosquitoes, and by Rice (1973) in the blowfly *Calliphora erythrocephala*. Rice noted that only one circular opening less than 0.5 μ in diameter occurs in the center of the sensillum, and suggested that these sensilla are probably innervated by a single chemoreceptive neurone. In aphids, Wensler and Filshie (1969) reported paired groups of five dendrites each, passing to the ventral wall of the food canal. Ultrastructural study of these sense organs in mosquitoes is now underway.

Mandibles (md) (Figs. 1-6, 27, 32, 34).

Mandibles are absent in male mosquitoes. In females, they are situated immediately below the labrum (Figs. 1-3). These stylets are very fragile, are leaf-like, and are thickened at the base and at the tip (Figs. 6, 27). No teeth are present in female *A. aegypti* (Fig. 32). Mandibular teeth are reported to occur only in anopheline mosquitoes (Robinson, 1939). Using SEM, I have observed such teeth 0.7 μ long occurring along the lateral edge of the mandible in female *Anopheles farauti* No. 2 of Bryan and Coluzzi (1971). The mandibles have no sense organs.

Mosquito mandibles were long believed to have only retractor muscles (Robinson, 1939; Schiemenz, 1957; Snodgrass, 1959; Walbauer, 1962), with protraction being caused by the elasticity of the "suspensory mechanism" when the retractor muscles were relaxed. However, Wenk (1961) found two protractor and one retractor muscle in four genera of mosquitoes.

The mandibles appear to be capable of considerable independent movement. MacGregor (1931) noted the dislodgement of particles occluding the tip of the proboscis by the mandibles and maxillae, but did not elaborate on the mechanism of such action. Robinson (1939) suggested that the mandibles cover the opening of the labrum when the latter is not in use, and protect the labrum during penetration. When the mosquito is sucking, he suggested that the mandibles are "apparently withdrawn by means of the retractor muscles". Later workers (Snodgrass, 1959; Christophers, 1960; Walbauer, 1962; and Hudson, 1970) agree with him about this function of the mandibles.

As the labrum is open ventrally, previous workers often described the hypopharynx as forming the floor of the food canal. Both Vogel (1921) and Robinson (1939) have already pointed out that the hypopharynx is not a part of the food canal. Vogel suggested that the sides of the labrum close together ventrally at the distal end. Proximally, the hypopharynx forms the floor of the food canal. He also mentioned that the ventral sides of the labrum either interlock along the mid-line (in *Culex*), or lie on top of one another (in *Anopheles*). During blood sucking, these overlapping layers become pressed against each other, and form the ventral closure. In *A. aegypti*, the lateral sides of the labrum are neither interdigitated nor overlapped as described by Vogel (Figs. 5, 34). The overlapping mandibles (md) below form the floor of the food canal at the distal end of the fascicle. At the base of the fascicle, the two mandibles become separated, and the hypopharynx takes over this role (Figs. 3, 6).

Vogel (1921) noted that the mandibles overlap, but did not recognize that they formed the floor of the food canal. Later workers pictured the mandibles as lying side by side below the labrum (e.g. Snodgrass, 1959; Christophers, 1960; Walbauer, 1962). The overlapping arrangement of the mandibles can be seen in the TEM pictures of Nehman (1968) of female *A. aegypti*, in those of Larsen and Owen (1971) of female *Culiseta inornata,* and also in a diagram by

T. Binder on page 661 in "The Insects of Australia" (1970), which was drawn from an electron micrograph of *A. aegypti* prepared by B. K. Filshie. In all accounts, the significance of such an arrangement was ignored. With the discovery that the salivary duct in the hypopharynx is not a closed canal but a furrow (see below), it is clear that the mandibles, besides forming the floor of the food canal, also serve to separate the salivary duct from the food canal (Fig. 34), forming a two-channel system: one to suck up liquid food and the other to inject saliva.

When serial sections are cut from the anterior end of the proboscis to the posterior, the left mandible is always seen above the right (Figs. 1, 2, 27). Such knowledge is useful for recognizing the orientation of sections.

In teneral specimens less than 10 hours old, the mandibles are not fully sclerotized, and have only a thin layer of cuticle surrounding them. In older adults, the mandibles are solidly sclerotized at their distal ends (Fig. 27).

Hypopharynx (hp) (Figs. 10-13, 24, 25, 30, 31, 34).

The hypopharynx, like the labrum, is an unpaired stylet, except that it lacks sense organs. In females, it is a delicate, flat stylet with the salivary duct (sd) running along its midline and forming a midrib (Fig. 30). Interdigitating, finger-like projections are found at its tip (Fig. 31). The salivary duct was considered by many workers to be a closed tube extending throughout the length of the hypopharynx but opening to the outside at the tip.

In female *A. aegypti*, the salivary duct is open along its dorsal wall, but is closed by the interdigitating edges of the hypopharynx (Fig. 34), as reported by Nehman (1968). The interdigitation consists of a "ridge and mortise" system: one margin being a longitudinal sulcus, and the other margin projecting into the sulcus. The sulcus always appears on the left side when serial cross-sections are cut starting at the anterior end of the proboscis. Whether this interdigitation extends the whole length of the hypopharynx is uncertain, although at least the anterior 2/3 are involved. The limited resolving power of the light microscope makes it difficult to decide with any certainty. Some earlier workers have already recognized that the salivary duct in the mosquito is not a tube. Annett, Dutton and Elliott (1901) called the hypopharynx in *Anopheles costalis* "salivary gutter", Nuttall and Shipley (1903) reported the presence of overlapping edges about midway along the length of the salivary duct of *Anopheles maculipennis*, and Kulagin (1905) has pointed out that, in *Anopheles bifurcatus* and *Culex pipiens*, the salivary duct is a furrow.

Robinson (1939) described an "oily fascicular fluid" which, he supposed, held the stylets together by surface tension. He believed the source of this fluid to be the cuticular glands in the theca, but admitted that "sources such as salivary glands must not be overlooked". Both Walbauer (1962) and Hudson (1970) suggested that the fascicular fluid could be saliva, but they did not explain how the saliva could get in between the stylets. Knowing that the hypopharynx is open dorsally at least at its distal end, it can be postulated that the saliva escapes from the salivary duct to lubricate and to hold the stylets together by surface tension.

Nehman (1968) described "winglike" extension of the hypopharynx that articulated with the lacinia in some of her sections, and she suggested that small areas of articulation occur discontinuously along the lengths of both structures. Such articulation would hold the stylets together during piercing and withdrawal of the fascicle, making Robinson's (1939) "oily fascicular fluid" unnecessary.

I have also found such "winglike" structures in my TEM sections. They not only exist between the hypopharynx and laciniae, but also between the labrum and mandibles. These "structures" are irregular, and exhibit an electron density comparable to that of the cuticle of the stylets. The "articulation" described by Nehman is non-existent (Figs. 30, 34-40). Her "winglike structures" are probably remnants of the fascicular fluid (saliva).

Hudson (1970) described finger-like projections at the tip of the hypopharynx in the female mosquitoes she studied. She observed that they "bear a closer resemblance to sense organs than to teeth". I have found that these projections are cuticular and have no nervous connection. Christophers (1960) discussed MacGregor's (1931) artificial feeding studies, and went on to say that two small sensory pits situated at the tip of hypopharynx have an olfactory or gustatory function. He probably meant the labral sense organs he described earlier in the book, since the hypopharynx has no sense organs.

Larsen and Owen (1971) reported that, in *Culiseta inornata*, the ligula swells by 76.65% when touched with a test solution (1 M sucrose or water). It is possible that this swelling will press the tip of the hypopharynx against the mandibles, causing the interdigitation to tighten and to close the apical opening of the salivary duct. This might help to conserve saliva when the mosquito is drinking.

In male *A. aegypti*, the hypopharynx (hp) is fused at the tip with the ligula (lg) (Figs. 10, 24), and throughout its length with the labium (L) (Figs. 11-13), as reported by many workers in other mosquitoes (Nuttall and Shipley, 1901; Thompson, 1905; Marshall and Staley, 1935; Vizzi, 1953). The dorsal wall of the salivary duct (sd) of the male shows the same type of interdigitation as that in the female (Fig. 25).

In *Anopheles quadrimaculatus*, Vizzi (1953) reported that the hypopharynx is apparently free at the tip, and has short cuticular hairs at its distal end. This is certainly not true. The ligula must have come out with the hypopharynx during his dissection, so that the hairs he described are actually ligular hairs. In male *Culex*, the salivary duct appears to be free in the labial gutter (Snodgrass, 1959).

Maxillae (mx) (Figs. 1-7, 12, 33-40).

The two maxillary stylets of mosquitoes have long been considered to be the galeae, but most recent authors have called them laciniae (Snodgrass, 1959; Matsuda, 1965; Nehman, 1968; Hudson, 1970), except for Owen *et.al.* (1974) who have labeled them as mandibles in their paper on female *Culiseta inornata.*

In female mosquitoes, the laciniae (mx) are situated on either side of and below the midrib of the hypopharynx (hp) (Figs. 1-7, 34). Each lacinia is thickened at its inner margin and is membranous laterally. At its distal end, its outer margin is thickened and bears a row of proximally-directed teeth (lt) (Fig. 35). Christophers (1960) considered there always to be 12 of these, but I have found their number to vary between 10 and 12 (Figs. 35, 36, 39). A row of five to eight small, distally-pointed teeth (mt) occur also on the mesial side of the stylet (Fig. 36). These exist also in female *Psorophora ciliata* (Walbauer, 1962) and *Aedes atropalpus* (Hudson, 1970).

Posterior to the lateral teeth and in line with them, are repeating rows of tiny projections (vt) present throughout the length of the stylet (Figs. 36, 37). Hudson (1970) called these projections vestigial teeth. They are deep-rooted in the membranous part of each lacinia (Fig. 38). Eight to 12 longitudinal ridges (lgr) course along the dorsal surface of the membranous lateral edge (Fig. 40). These can also be seen in cross-sections of the fascicle (Figs. 2, 3, 5).

In female adults less than 10 hours old, epidermal cells are still present within the distal part of each stylet, and the cuticle is not fully sclerotized. In older adults, cells occur only in the proximal part of the stylet. Thus the maxillary stylets continue to develop after adult emergence.

In male mosquitoes, the laciniae are rod-like and are only about one third the length of the proboscis (Fig. 33). They are located dorso-laterally in relation to the labrum (Fig. 12), rather than ventro-laterally as in females. Distally, each stylet is a thin, membranous sheet. Proximally, the stylet is thickened, is triangular in cross-section, and contains cells (Fig. 12). According to

Vizzi (1953), the laciniae in male *Anopheles quadrimaculatus* are located ventro-lateral to the labrum. Teeth, annulations, and ridges are not found on male stylets.

No sense organs occur on the laciniae of either sex.

Function of the Laciniae. — The musculature and the mechanism of piercing by the laciniae were described in detail by Robinson (1939). Observations made by later workers all support Robinson's description. Walbauer (1962) suggested that the mesial teeth probably cut the tissue during protraction, thus easing the forward progress of the stylet. Hudson (1970) suggested that the mesial teeth may act as a brace during fascicle removal. However, these teeth are too fragile to be of any use in cutting or bracing. The mesial teeth are frequently absent in blood feeding species. They are found in most species of *Aedes, Culiseta, Armigeres, Coquillettidia, Psorophora, Orthopodomyia,* and *Eretmapodites,* but are absent in species of *Uranotaenia, Anopheles, Culex* and *Trichoprosopon* (unpublished data). It is likely that mesial teeth play no active role during piercing.

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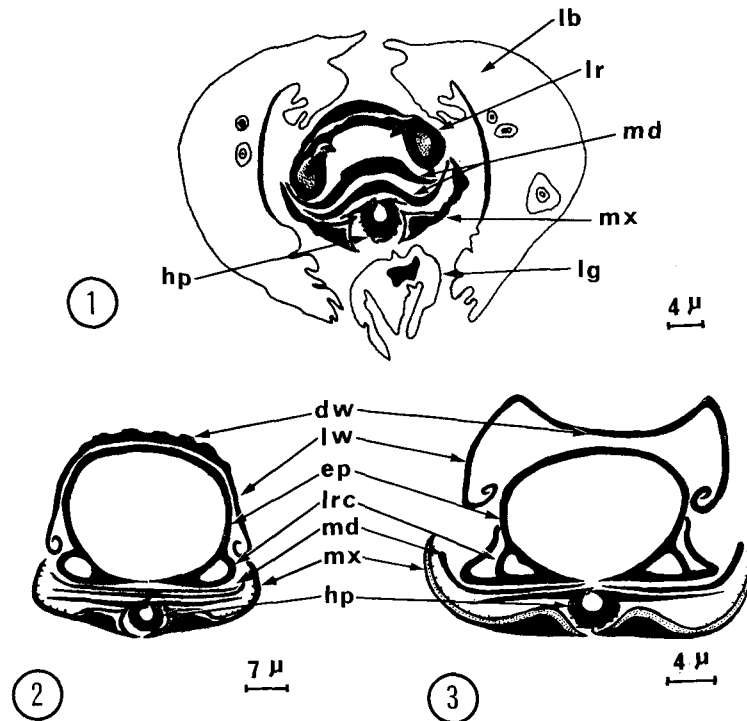
Fig. 1. Transverse section through tip of female proboscis, showing arrangement of fascicular stylets and labellar lobes (lb). hp, hypopharynx; lg, ligula; lr, lábrum; md, mandibles; mx, lacinia. Fig. 2. Same posterior to Fig. 1, showing separation of lateral (lw) from epipharyngeal wall (ep) of labrum. Note that the two mandibles (md) are overlapped. dw, dorsal wall; lrc, labral nerve canal. Fig. 3. Same as Fig. 2, but near head capsule. Note position of mandibles (md).
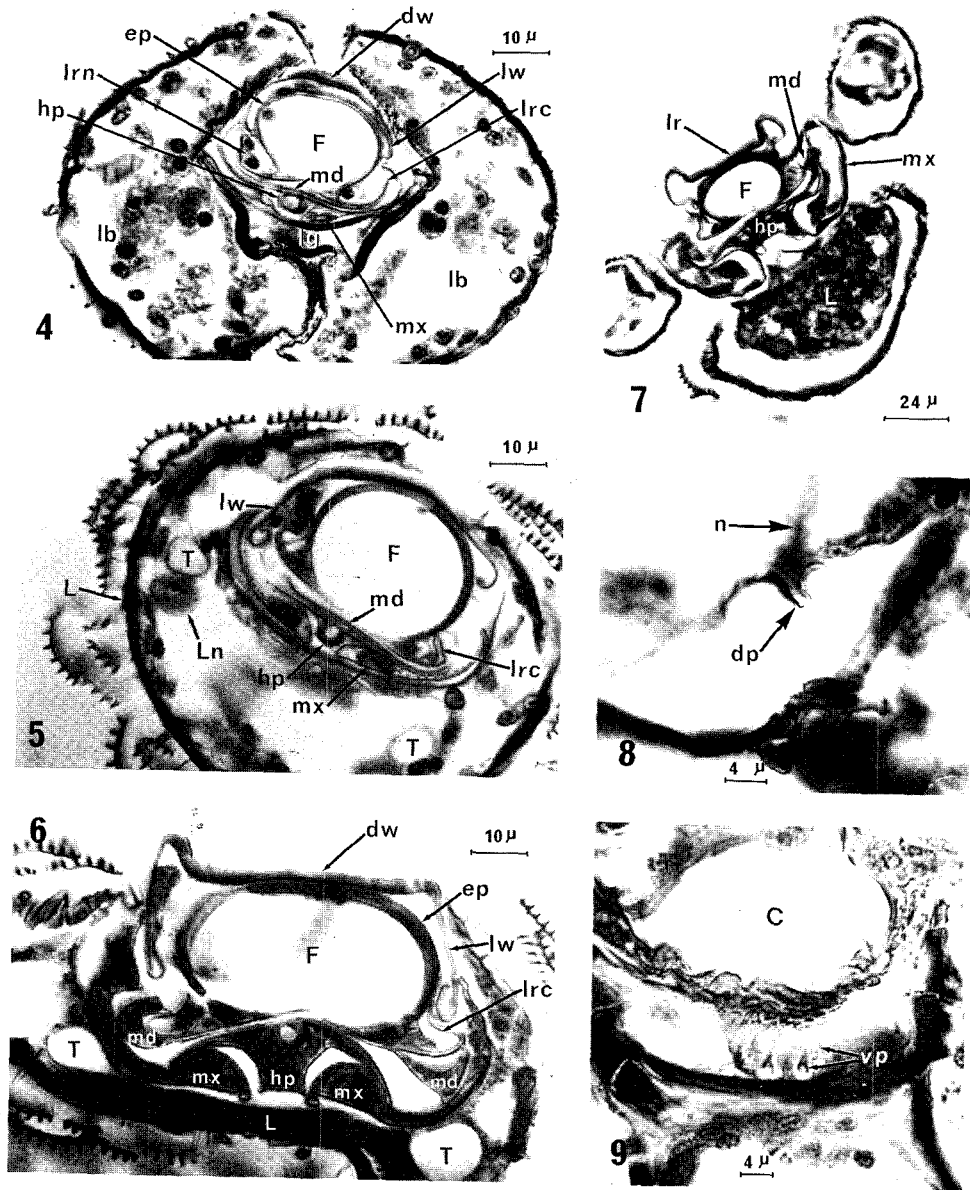
Figs. 4-9. Transverse sections of proboscis of teneral female. Fig. 4. Through proboscis tip, showing partially closed nerve canal (lrc) containing the labral nerve (lrn). Cells occur between dorsal (dw) and epipharyngeal (ep) walls of labrum. F, food canal; lg, ligula; lb, labella. Fig. 5. Through overlapping mandibles (md) forming floor of food canal (F). Note longitudinal ridges on the membranous part of lacinia (mx). hp, hypopharynx; L, labium; Ln, labial nerve; T, tracheal tube. Fig. 6. Through proboscis near base, showing the two separated mandibles (md). Here, the hypopharynx (hp) forms the floor of the food canal (F). Cells occur within all stylets. dw, dorsal wall; ep, epipharyngeal wall; lw, lateral wall. Fig. 7. Through base of proboscis, showing cell-packed labium (L). Fig. 8. Through cibarial pump, showing dorsal papilla (dp). n, nerve. Fig. 9. Same, showing four ventral papillae (vp) arranged in two groups at posterior end of cibarium (C).
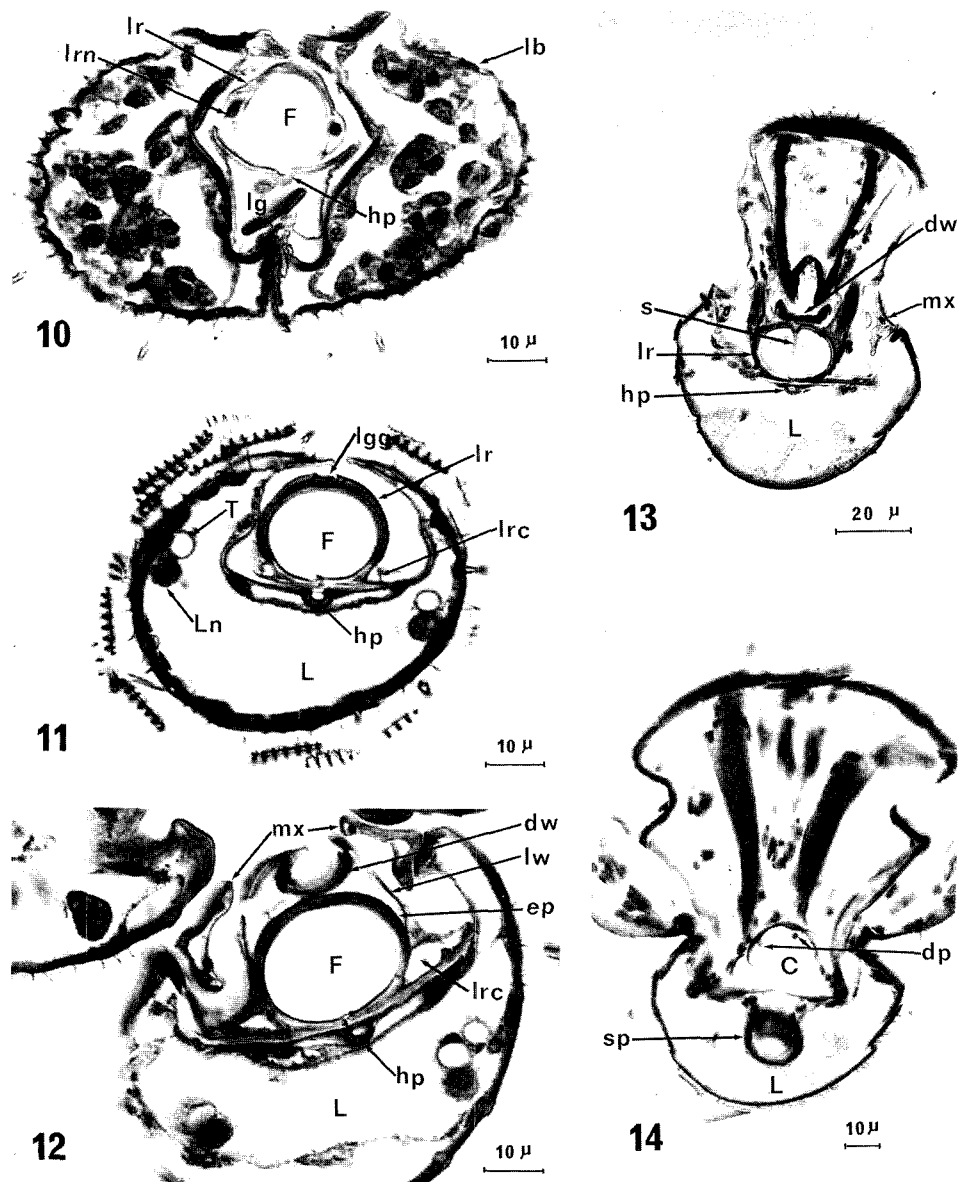
Figs. 10-14. Transverse sections of male proboscis. Fig. 10. Through tip of proboscis, showing labrum (lr) and labellar lobes (lb). The hypopharynx (hp) is fused with the ligula (lg), and forms the floor of the food canal (F). lrn, labral nerve. Fig. 11. Through proboscis proximal to labellar lobes, showing the hypopharynx (hp) fused to the labium (L). Paired tracheal tubes (T) and labial nerve (Ln) run longitudinally within either side of the labium. The longitudinal groove (lgg) of the labrum is still narrow. The lateral edges of the labrum meet ventrally at the midline, forming the ventral closure of the food canal (F). lrc, labral nerve canal. Fig. 12. Through proboscis near base, showing how the entire dorsal wall (dw) here forms the widened longitudinal groove. The lateral wall (lw) is attached to the labral nerve canal (lrc), and the two laciniae (mx) are situated dorso-lateral to the food canal (F). ep, epipharyngeal wall. Fig. 13. Through base of labrum (lr), showing spine (S). Fig. 14. Through anterior end of cibarium (C), showing two dorsal papillae (dp). The salivary pump (sp) is situated ventral to the cibarium within the labium (L).
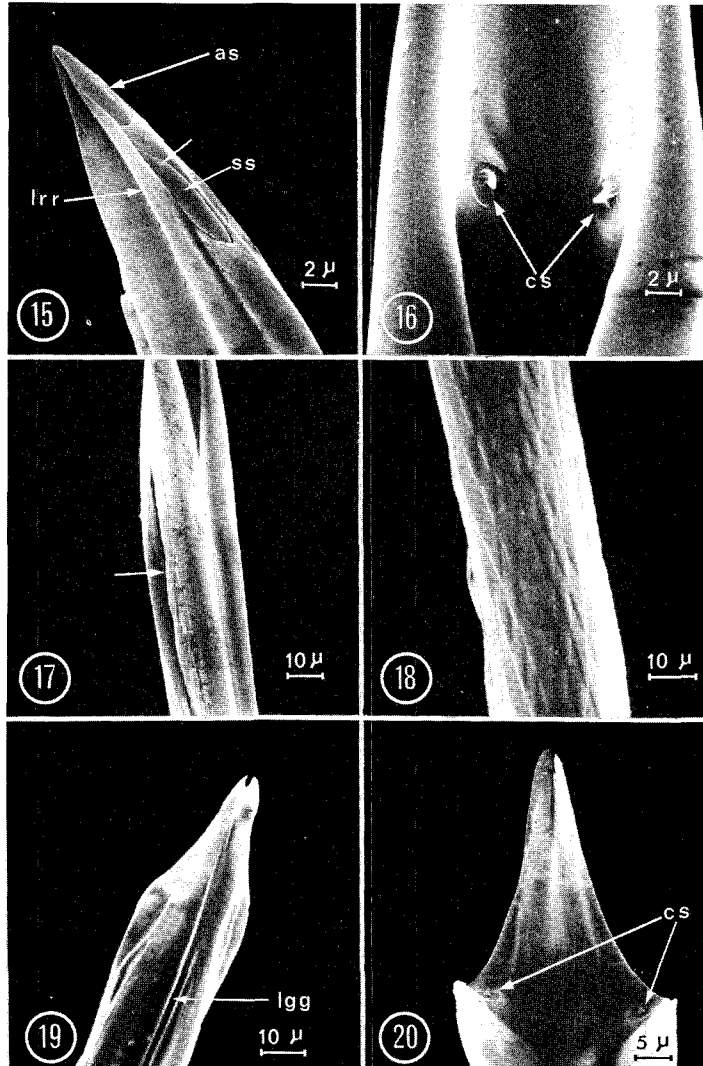
Figs. 15-20. Scanning electron micrographs of labra. Fig. 15. Tip of female labrum, showing apical sensillum (as) with longitud-
inal groove, subapical sensillum (ss) with opening on a protruberance (arrow), and the labral ridge (lrr). Fig. 16. Campaniform
sensilla (cs) on inner surface of female labrum. Fig. 17. Ventro-lateral aspect of female labrum, showing lack of membrane
(arrow) joining the two walls. Fig. 18. Dorsal aspect of female labrum, showing quadrangular thickenings. Fig. 19. Dorsal
aspect of male labrum, showing longitudinal groove (lgg). Fig. 20. Ventral aspect of tip of male labrum, showing campaniform
sensilla (cs).
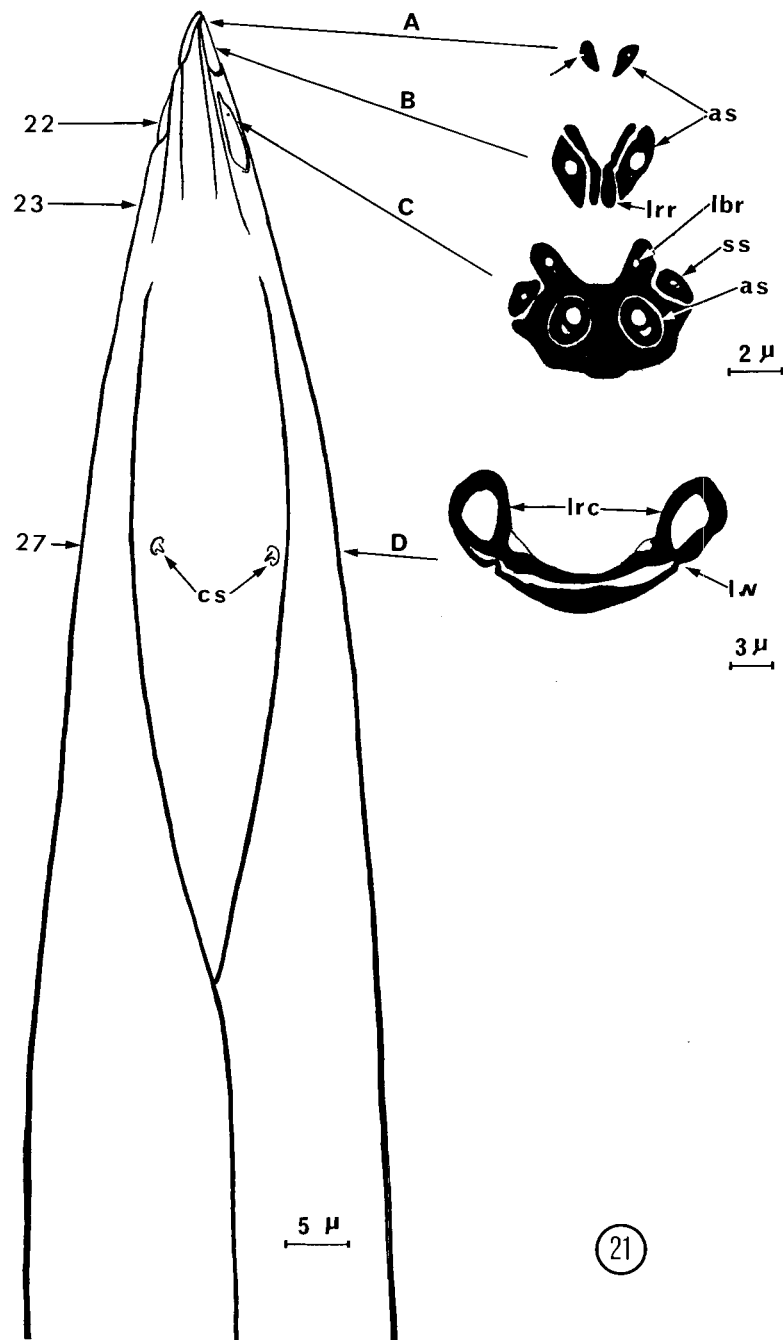
Fig. 21. Diagram of ventral aspect of female labrum. A-D are transverse sections of labrum taken at points indicated by arrows. Numbers on the left are figure numbers of sections taken at points indicated by arrows. A, through apical sensilla showing opening in one (arrow); B, through apical sensilla (as) with the labral ridges (lrr) in between; C, through apical (as), and subapical (ss) sensilla and labral ridge receptor (lbr); D, through labrum near campaniform sensilla (cs), showing the labral nerve canal (lrc), with the membranous lateral wall (lw) of the labrum connected to it.
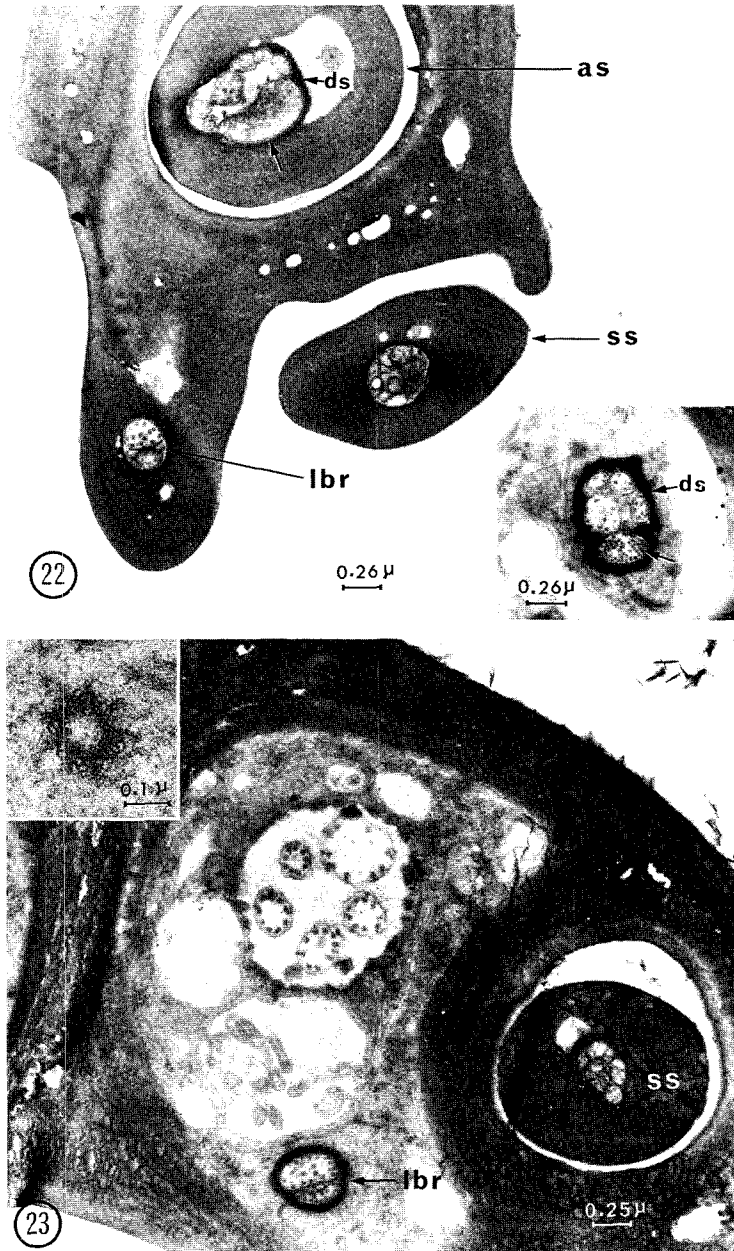
Fig. 22. Transverse section through tip of female labrum at point indicated by arrow in Fig. 21. Six dendrites (two of these are probably branches of one) enclosed within a dendritic sheath (ds) are within the apical sensillum (as). The dendritic sheaths of the subapical sensillum (ss) and labral ridge receptor (lbr) are fused to the cuticle at this level. Inset: dendrites from subapical sensillum enclosed within a dendritic sheath (ds) inside labral nerve canal. Note that the dendritic sheath is indented, partially isolating one dendrite from the rest (arrow). Fig. 23. Transverse section through female labrum at point indicated by arrow in Fig. 21. Note the five ciliary regions of the dendrites of the apical sensillum. Two dendrites from the labral ridge receptors (lbr), and five from the subapical sensilla (ss), are enclosed by dendritic sheaths at this level. Inset: Transverse section through one of basal bodies of apical sensillum, showing microtubular triplets.
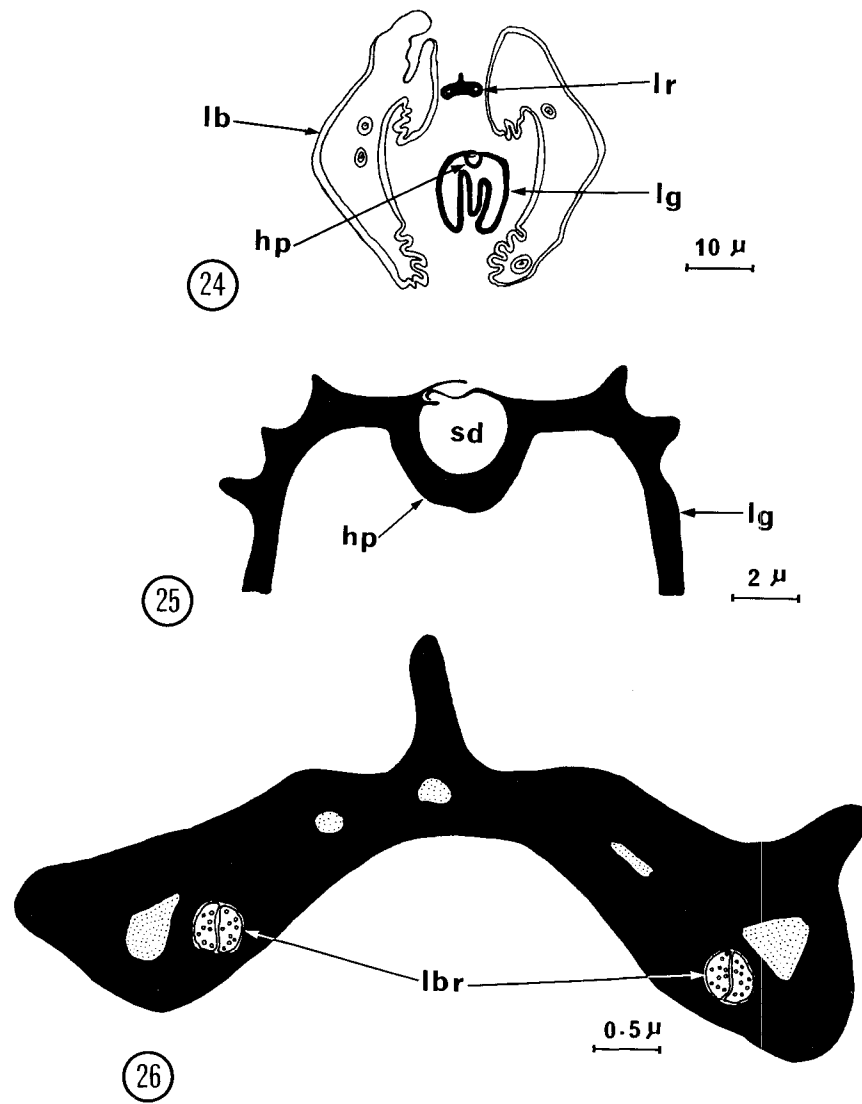
Fig. 24. Transverse section through tip of male proboscis, showing hypopharynx (hp) fused to ligula (lg). lr, labrum; lb, labella. Fig. 25. Same at higher magnification, showing hypopharynx (hp) and interdigitated dorsal wall of salivary duct (sd). Fig. 26. Through tip of male labrum, showing labral ridge receptors (lbr), each containing two dendrites.
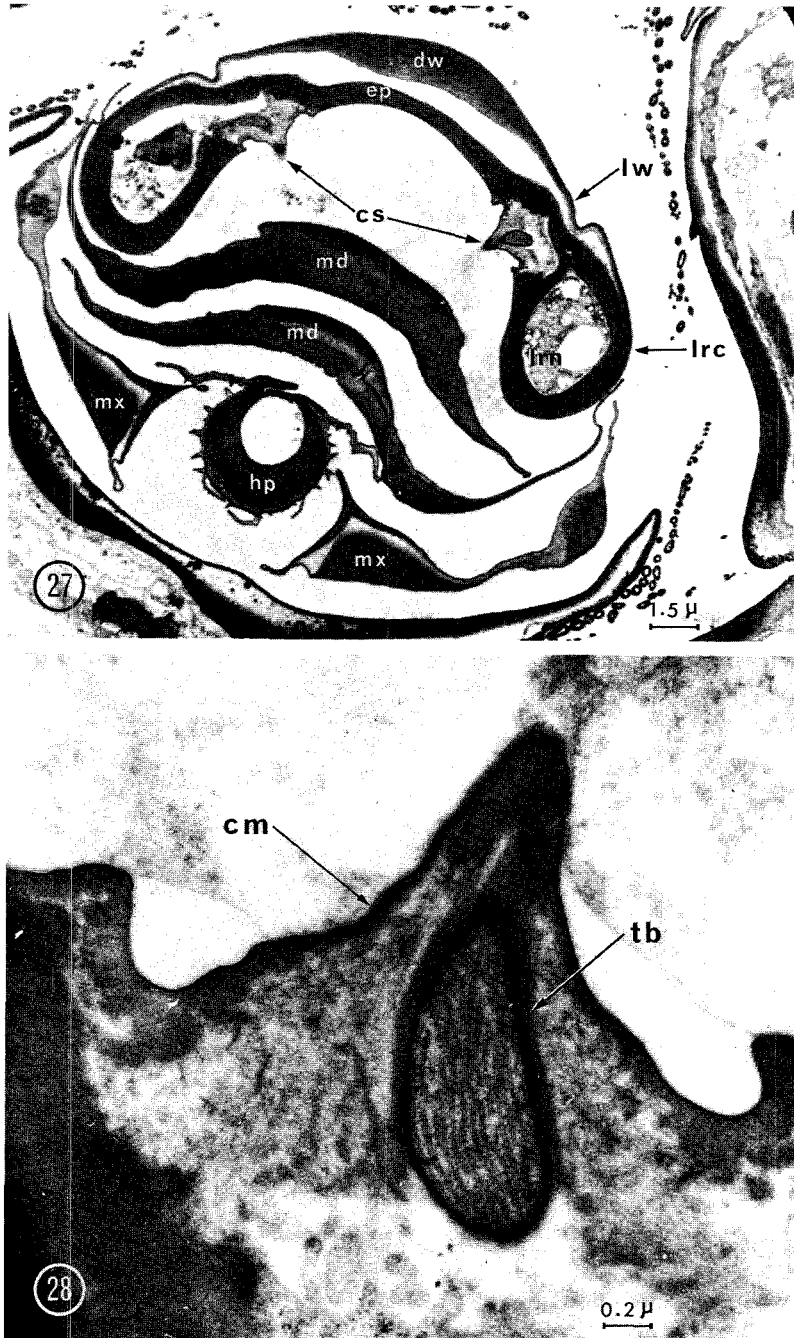
Fig. 27. Transverse section through tip of female fascicle, showing arrangement of fascicular stylets. The tubular body of
the left campaniform sensillum (cs) is seen entering the labral nerve canal. Note the membranous lateral wall (lw) of the labrum
is connected to the labral nerve canal (lrc). dw, dorsal wall; ep, epipharyngeal wall; hp, hypopharynx; lrn, labral nerve; md,
mandible; mx, lacinia. Fig. 28. Longitudinal section through female labral campaniform sensillum. cm, cap-membrane; tb,
tubular body.
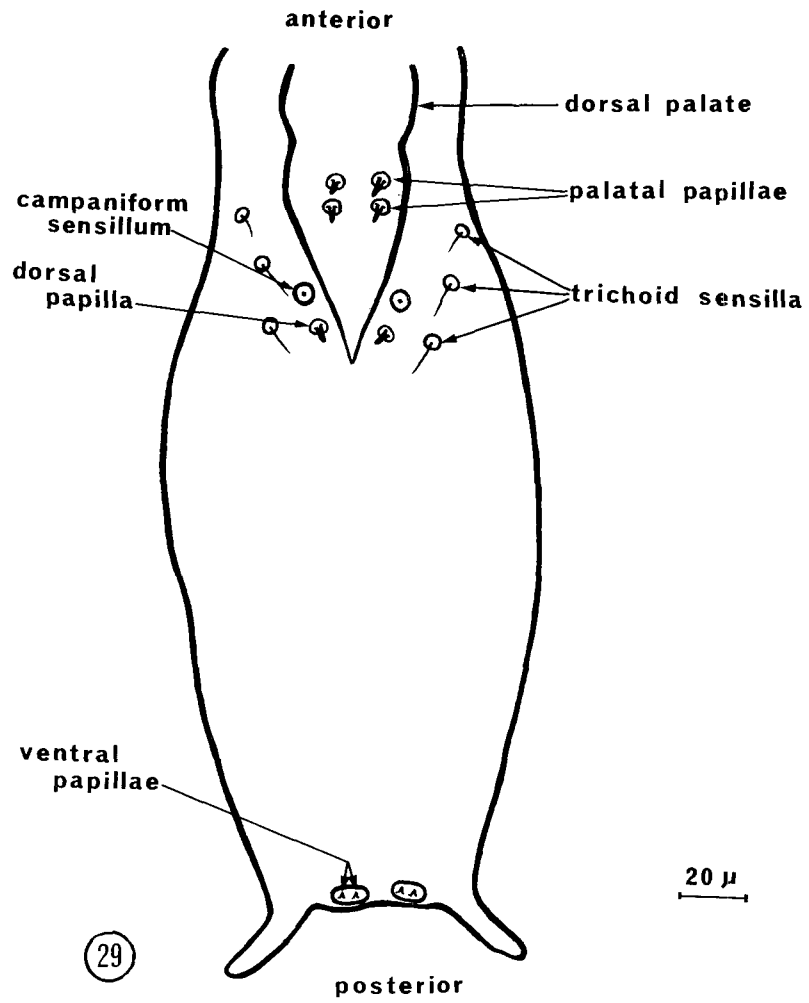
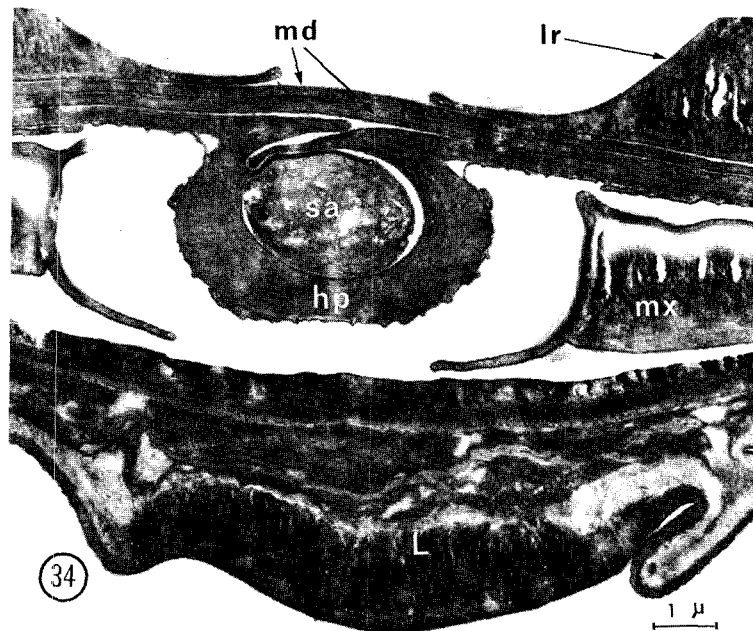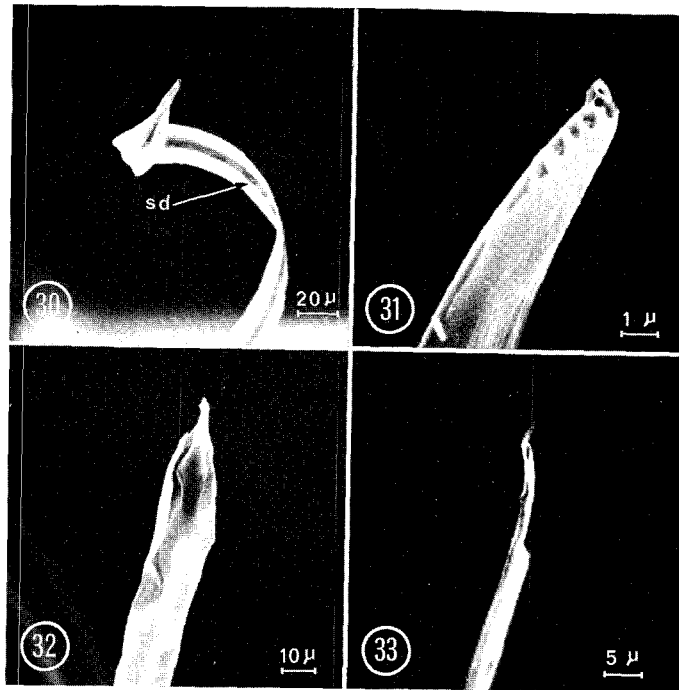Fig. 29. Diagram of dorsal aspect of cibarium, showing arrangement of cibarial sense organs of female.

Fig. 30. Scanning electron micrographs of female hypopharynx, showing salivary duct (sd) running along midline. Fig. 31. Same of tip of female hypopharynx showing interdigitated, finger-like projections. Fig. 32. Same of female mandible. Fig. 33 Same of male lacinia. Fig. 34. Transverse section through distal end of female fascicle, showing the two overlapping mandibles (md) forming the floor of the food canal. Note the electron density of the saliva (sa) in comparison to that of the cuticle of the stylets. hp, hypopharynx; mx, lacinia; lr, labrum; l, labium.
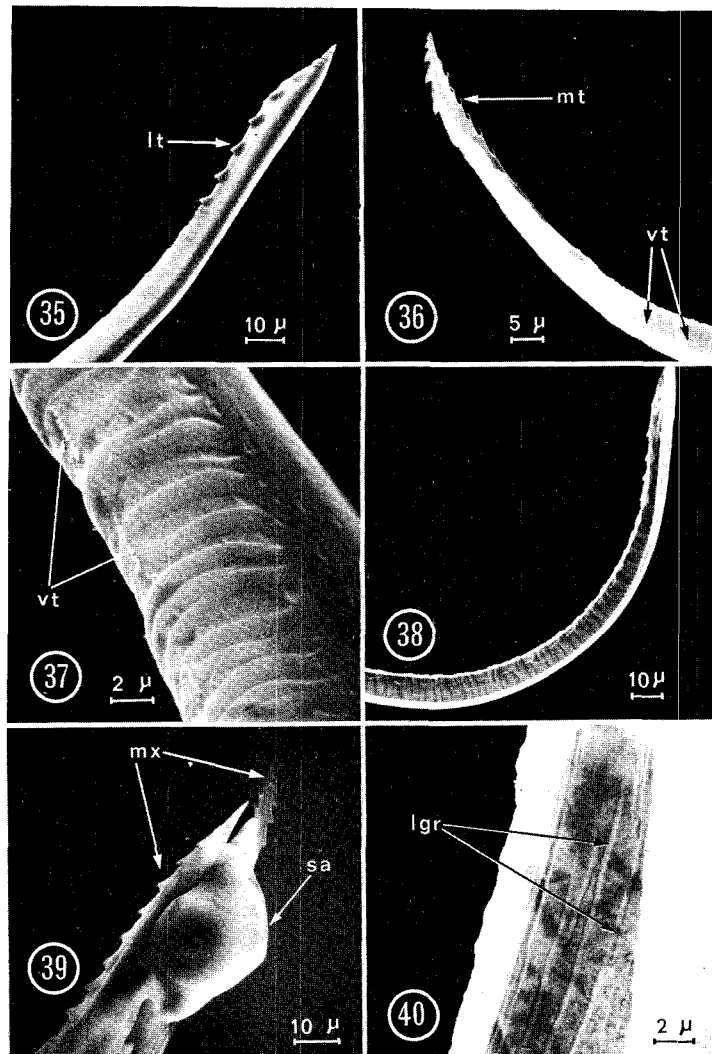
Fig. 35. Scanning electron micrograph of lateral aspect of female lacinia, showing 10 lateral teeth (lt). Fig. 36. Same of ventro-lateral aspect of female lacinia, showing eight mesial teeth (mt). vt, vestigial teeth. Fig. 37. Same at higher magnification, showing vestigial teeth (vt). Note annulations of membranous part, and cuticular depressions of thickened part, of the lacinia. Fig. 38. Dorsal aspect of female lacinia, showing bases of vestigial teeth. Fig. 39. Drop of saliva (sa) in between the tips of the two laciniae (mx). Fig. 40. Dorsal aspect of female lacinia, showing longitudinal ridges (lgr).