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ANATOMY AND HISTOLOGY OF EMBOLYNTHA
BATESI MACLACHLAN, 1877 (EMBIIDINA).¹

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(With 68 figures)

The order *Embioptera* (fig. 1) is formed by a small group of tropical insects. These gregarious insects construct silken tunnels in which they live. The silk glands are situated in the first articles of the tarsus in the first legs (fig. 12). **Melander** (1903), **Rimsky-Korsakow** (1914) and **Barth** (1954) studied the secretion, origin, mechanism and the spread out of the secretion.

The literature on the *Embioptera* mostly refers to the systematics aspect, like works of **Davis** (1936), **Friedrichs** (1906 to 1935), **Navas** (1900 to 1934) and **Ross** (1940 and continuing) and many other authors. However, there are little informations available about the internal anatomy of the *Embioptera*.

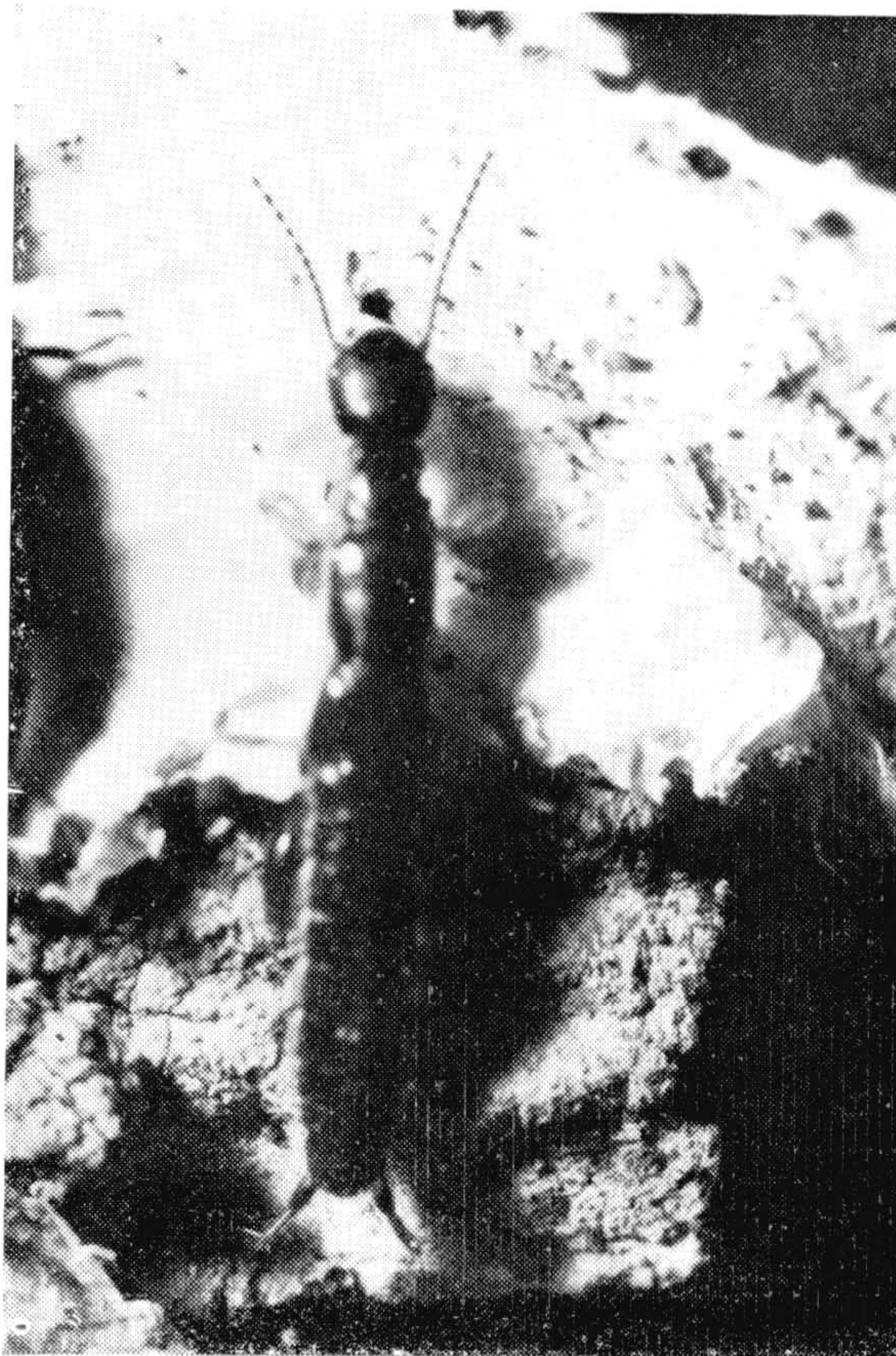
The classic Monographies by **Krauss** (1911), **Enderlein** (1912), **Hagen** (1855) and **Verhoeff** (1904) formed up to now the basis of the anatomy and biology studies of this order. **Lacombe** (literature cited) wrote some papers about the internal organisation of *Embolynta batesi*, and **Stefani** (1953 to 1962) published a lot of papers on the cytology, embryology and reproduction of the different families of this order.

The *Embioptera* group has primitive characteristics, but frequently shows these characteristics in progressive evolution. **Lacombe** studying the nervous system found a typical example for this hypothesis, beginning with condensation of the abdominal ganglion system. The simplicity of the anatomy of all the apparatus without important modification, that are common in other orders of the insects, demons-

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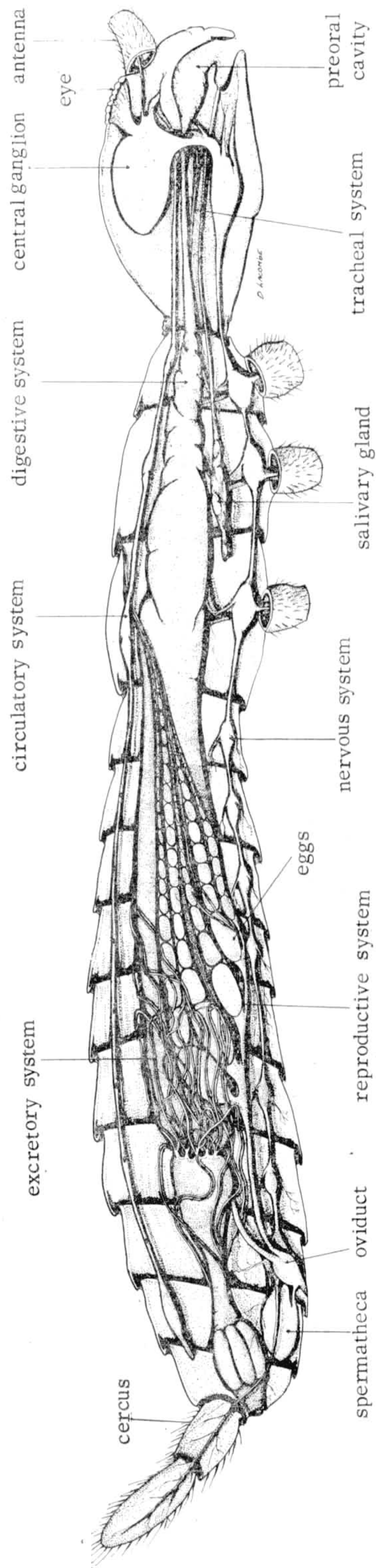
trated the primitiveness of the order (fig. 2). By the simplicity of the anatomy of the digestive, circulatory, respiratory, nervous and reproductive systems, the *Embiopoda* form an ideal group for studying the anatomy and histology of insects.



1 — Photo of female and male of *E. batesi*.

MATERIAL AND METHODS

The adult male and female of *Embolynta batesi* were collected on Governador Island, Rio de Janeiro, Brazil. The animals were fixed in Bouin, Carnoy, Susa and in formalin containing 10% of calcium phosphate. After fixation, the specimens were dehydrated and infiltrated with paraffin. The paraffin embedded tissue cut in serials at 7 microns. The section was stained with Delafied's hematoxylin and



2 — Disposition of internal systems of *E. batesi*.

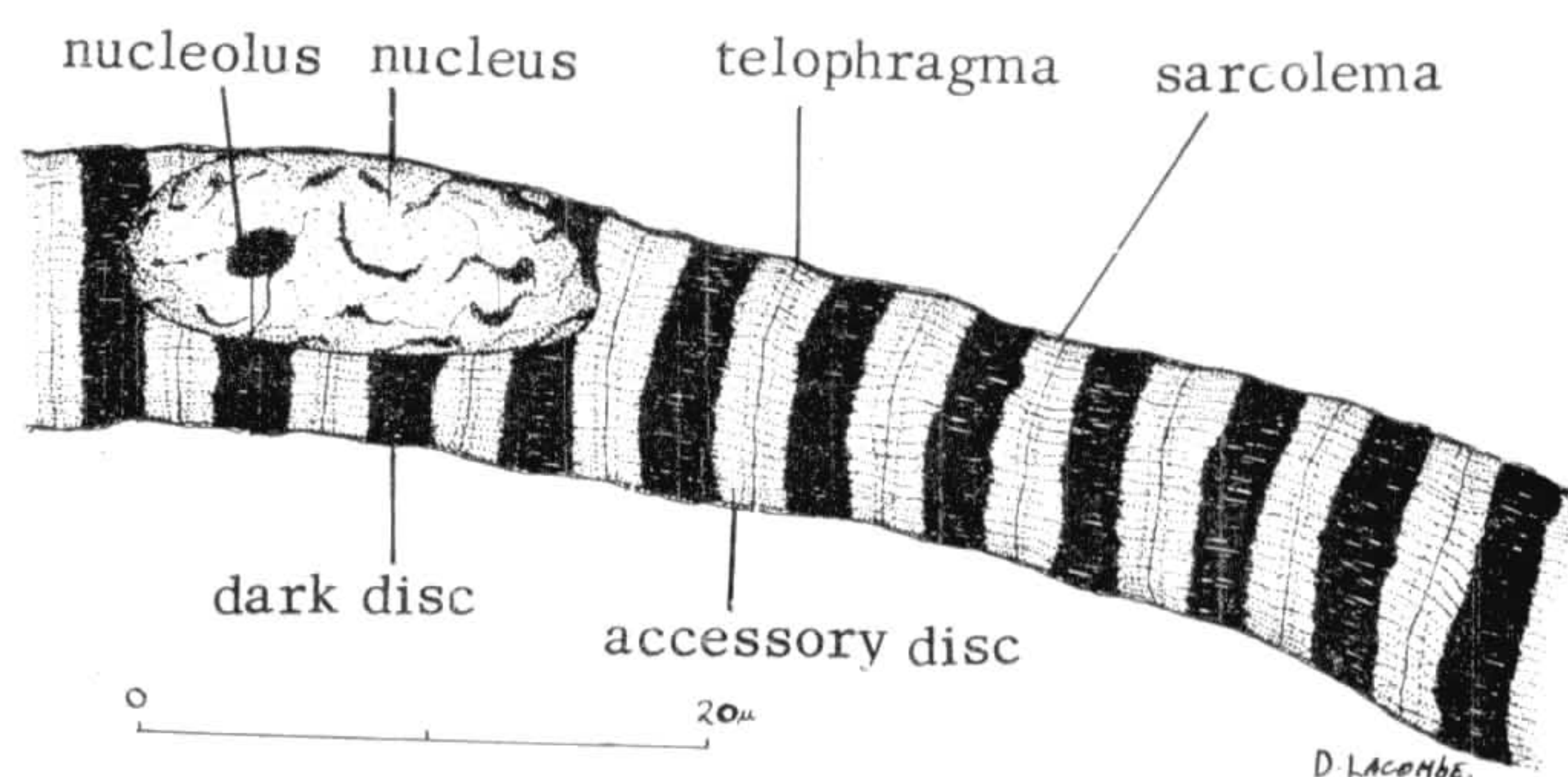
Orange G.G., Ehrlich's hematoxylin and Cromotrop 2R, Alcian blue at pH 2.3, Nuclear fast red with Naphtol green and Congo red.

For the anatomical study of the different systems the proceeding was as follows: The *Embioptera* were fixed on a paraffin dish and opened at the dorsal, lateral or ventral sides. The systems in study were dissected, separated from the body and transferred in Petri dish with formalin-calcium fixative. After this, it was dehydrated and stained with GG Orange and clarified by the methods of Spalteholtz and mounted in Balsam.

MUSCULAR SYSTEM

The insects muscular system has been studied by many authors, however literatur is scarce on the order of *Embioptera*. We may cite the publication of **Verhoeff** (1904), **Maki** (1938) and **Lacombe** (1961).

Like other insect orders, the muscular system is composed of striated fibres and attached by tonofibrillae or tendons to the exoskeleton or to different visceral systems. The muscle fibres (fig. 3) are composed of many myofibrills. Each myofibrill is formed of dark discs (anisotropic) and light discs (isotropic) that gives the characteristic cross-striation to the muscles. These regions are also, called "incomata", and are separated one from the other by the telophragma or *Krauss* discs, which appear clearly in *Embioptera*. The muscle fibers are embedded in a nucleated matrix, the sarcoplasm, which forms a peripheral sheath or sarcolemma.

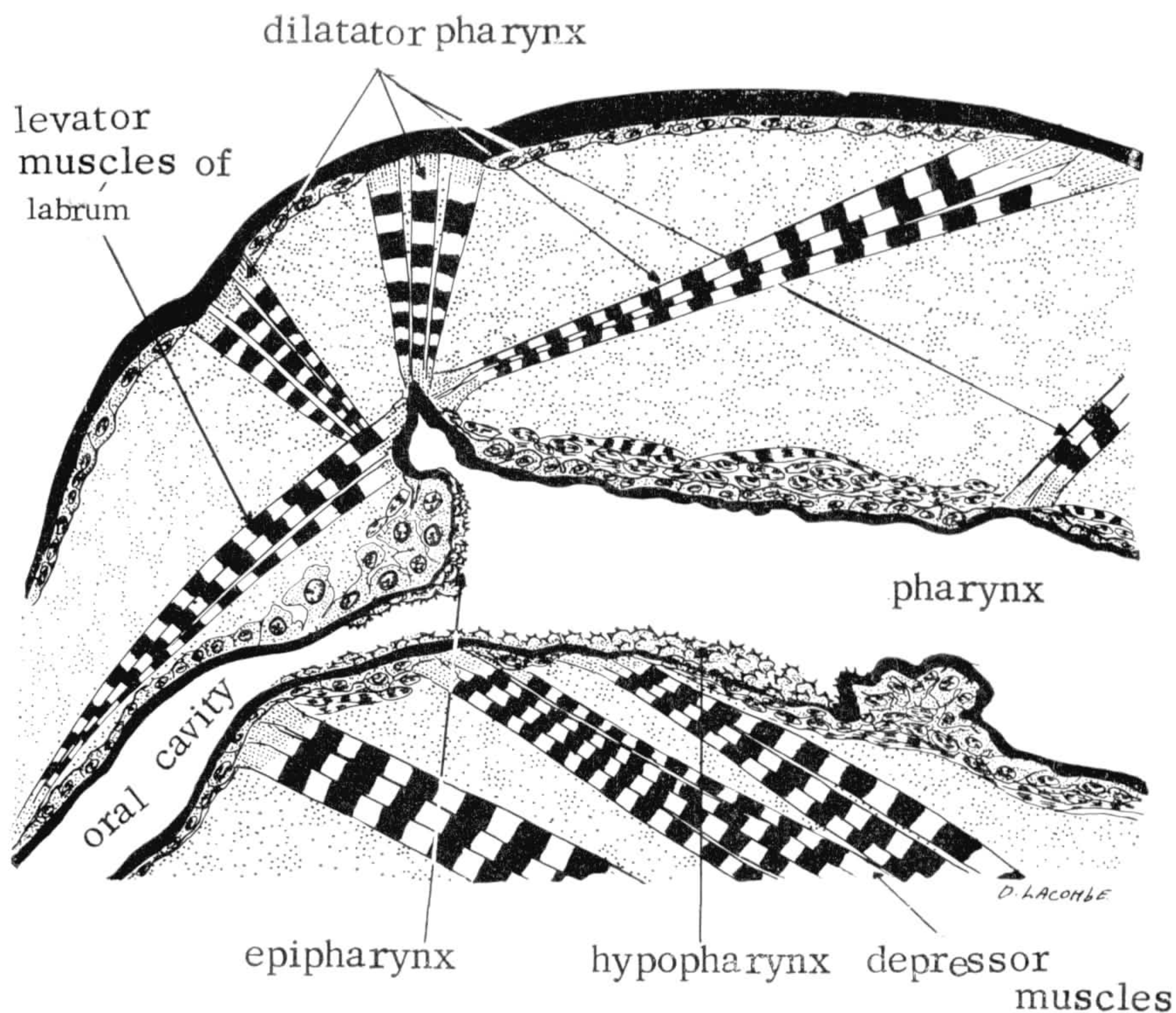


3 — Morphology of the muscle fibers.

MUSCLES OF THE CRANIAL CAPSULE: The head of the *Embioptera* shows large sexual dimorphism (**Lacombe**, 1968), but the position of the muscles are the same in both sexes.

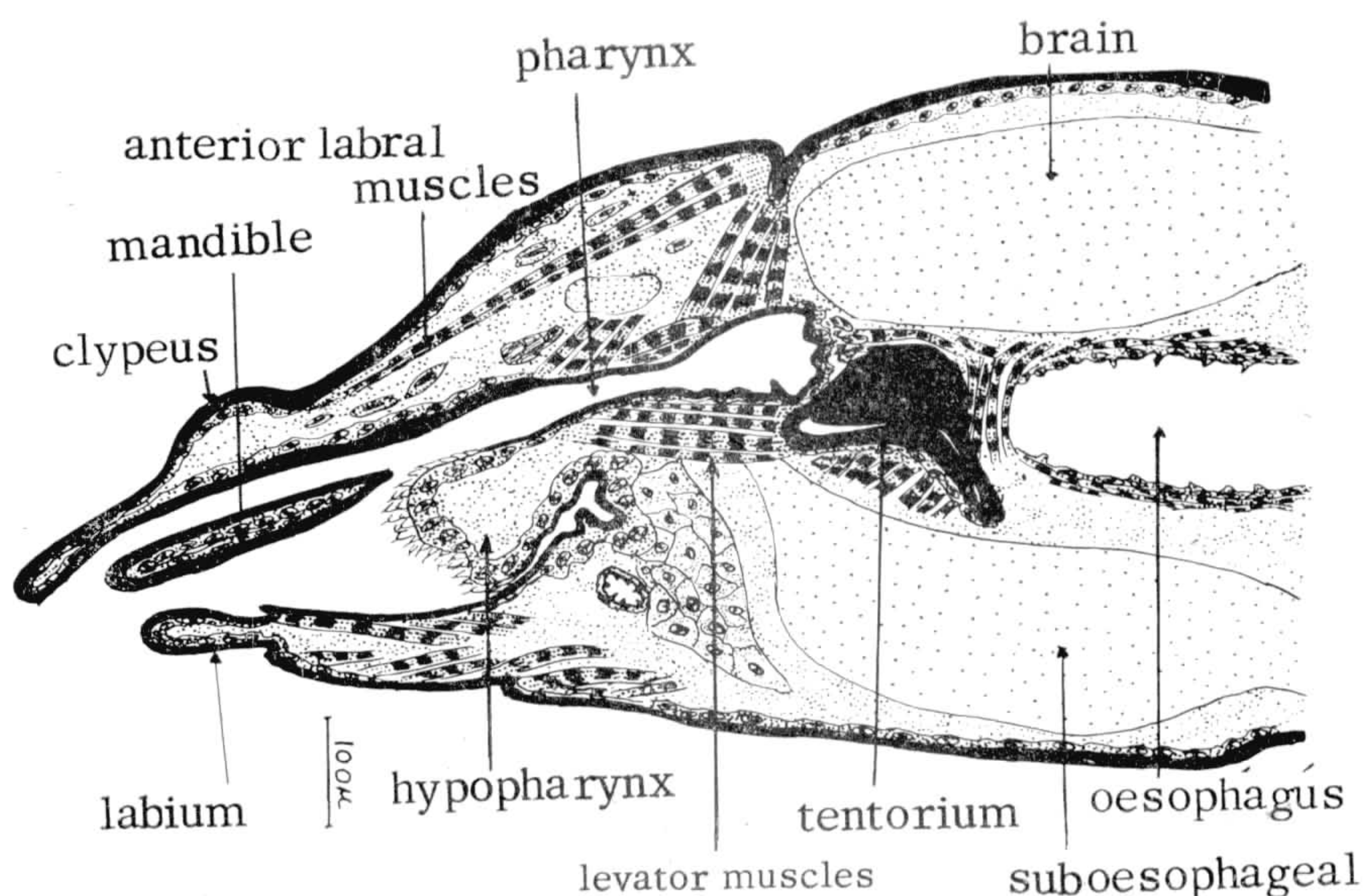
MUSCLES OF THE CERVICAL REGION (FIGS. 4, 5 and 6) : A pair of muscles extends in the cervical region from the latero-cervical sclerites to the post-occipital region of the head. Another pair extends from these sclerites to the dorsal neck sclerites. These muscles control the twisting motions of the head. Muscles motivating dorso-ventral movement of the head extend from the margins of the occipital foramen to the anterior phragma of the mesothorax. These muscles are long, large, and extend parallel to the longitudinal axis of the body.

The dilatator muscles of the pharynx (fig. 4) extend in the head from the pharynx to the cephalic wall. The strong muscles which begin at the enlargement of the dorsal cuticular wall, locks the reentrance situated soon after the epipharynx. The clypeus-pharynx and frons-pharynx muscles during its contraction also take part in the expansion of the oral cavity and the pharynx. They are called the clypeus-pharyngeal and go from the bottom of the oral cavity to the tentorium, and on to the pharynx there are longitudinal, transverse and circular muscles which have been histologically studied by Lacombe (1958).



4 — Dilatator muscles of the pharynx.

The hypopharynx of *Embioptera* (fig. 5) is well developed, with many fine setae in squaliforme formation. Many short muscles are found extending from the hypopharynx to the different regions of the tentorium. However, we describe here, only the levator and depressor muscles of the hypopharynx. The levator muscle originates on the posterior dorsal cuticular wall of the hypopharynx and extends to the corpotentorium. The depressor muscle starts in the ventral wall and ends in the corpotentorium (fig. 4).



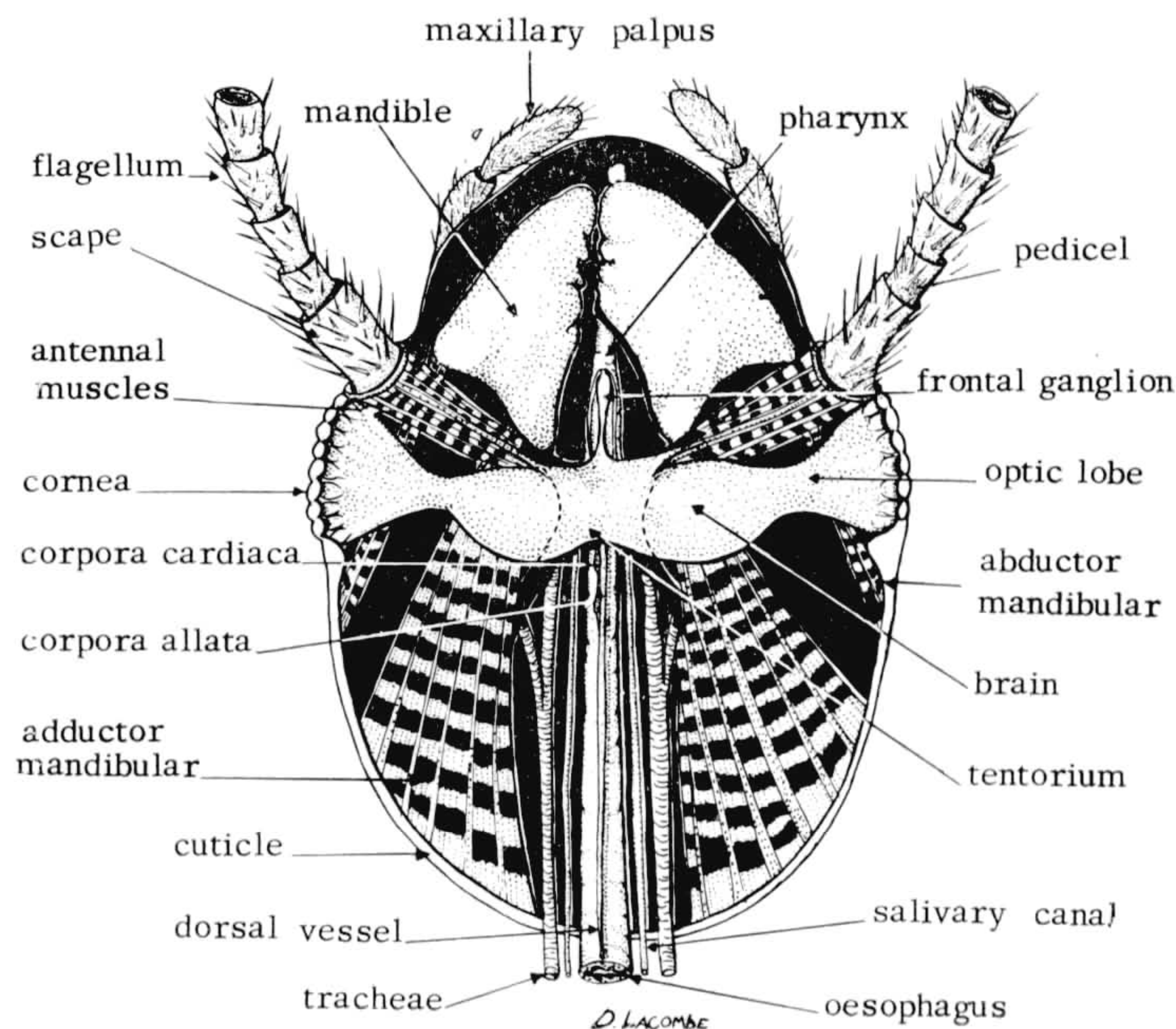
5 — Hypopharynx muscles.

The internal skeleton or tentorium of the head serves as the attachment of various cephalic muscles as well as a support for the cephalic nervous system (fig. 6). The tentorium of the *Embioptera* is represented by two pairs of cuticular invaginations; the anterior branch and the posterior branch, which unite to form a central body. The central body has a quadrangular pattern and represents a primitive type. Marginally these branches are more heavily sclerotized less than centrally and therefore give the false impression that they are double and not simple.

The levator and depressor muscles of the antennae insert on the anterior arms of the tentorium. The mandibular adductor muscle

passes sideways from the corpotentorium, and above to its two posterior arms. They are attached to the posterior wall of the cranial capsule.

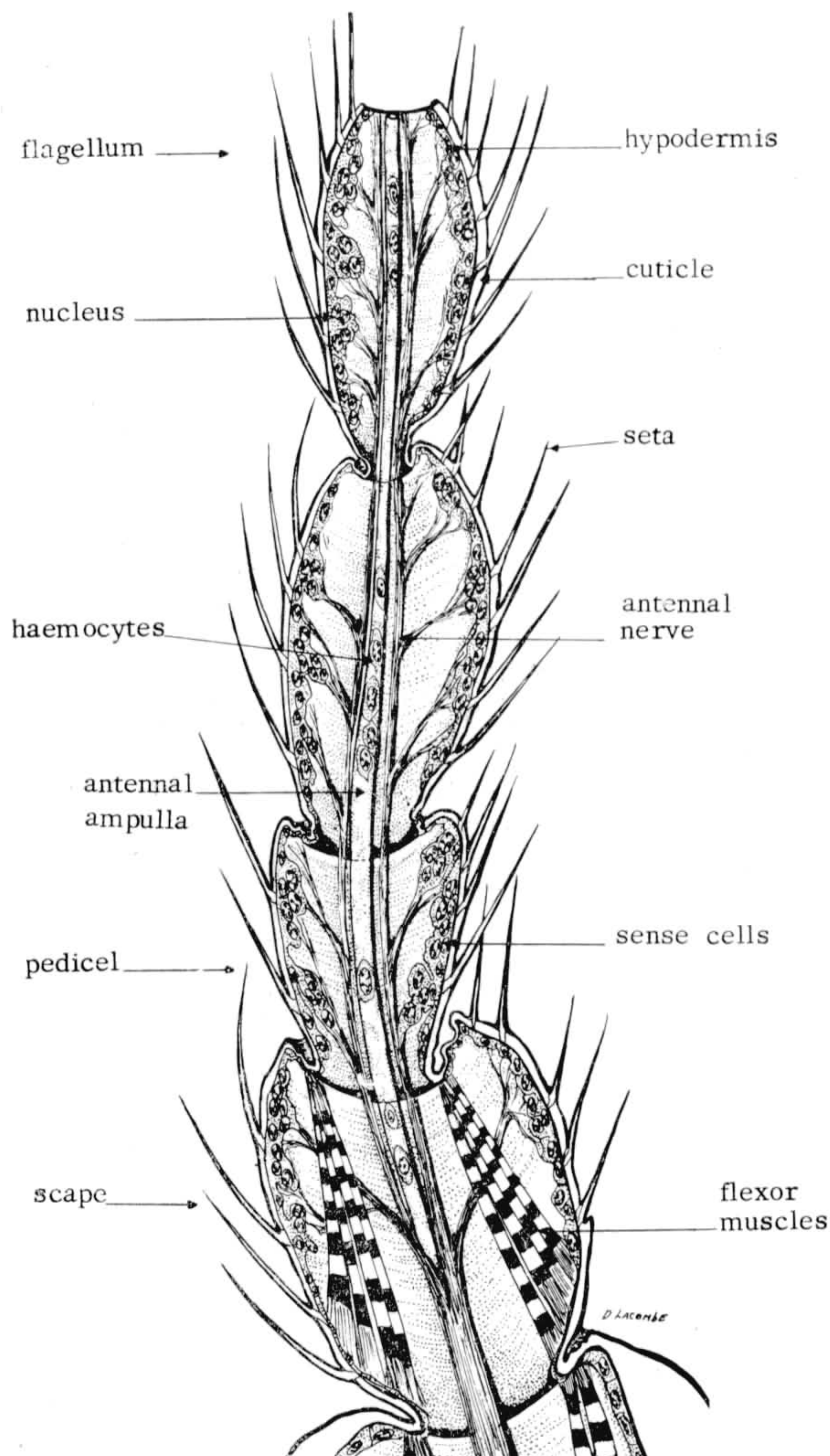
In drawing 6, we can observe the dorsal disposition of the brain, which is supported on its ventral side by the corpotentorium and, also the position of the other systems like digestive, circulatory and respiratory, which pass beneath the tentorium in the medial zone of cranial capsule.



6 — Internal anatomy of the head.

MUSCLES OF THE ANTENNAE (Fig. 7): The antenna of the *Embioptera* is very simple. The pattern, number and size of the segments, are important for the sexual dimorphism characters. But in both sexes the antenna possesses special sensitive organs with many sensillae. The antenna corresponds to the annulated type of **Imms** (1939), in which the intrinsic muscles occur only in the scape segment. The others lack muscles, but have two antennal nerves and prolongations of the circulatory ampulla which contains haemolymph. All segments possess numerous sensitive hypodermal cells which account for the great sensitivity of the antenna. The scape muscles comprise two groups attached distally at the contact with the flagellum and basally

in the inner wall of the scape. Their positions, in angles, are responsible for the movement of the pedicel and the flagellum. Two depressor muscles and the levator muscles are attached at the antennal base extending to the dorsal arm of the tentorium (see fig. 6).

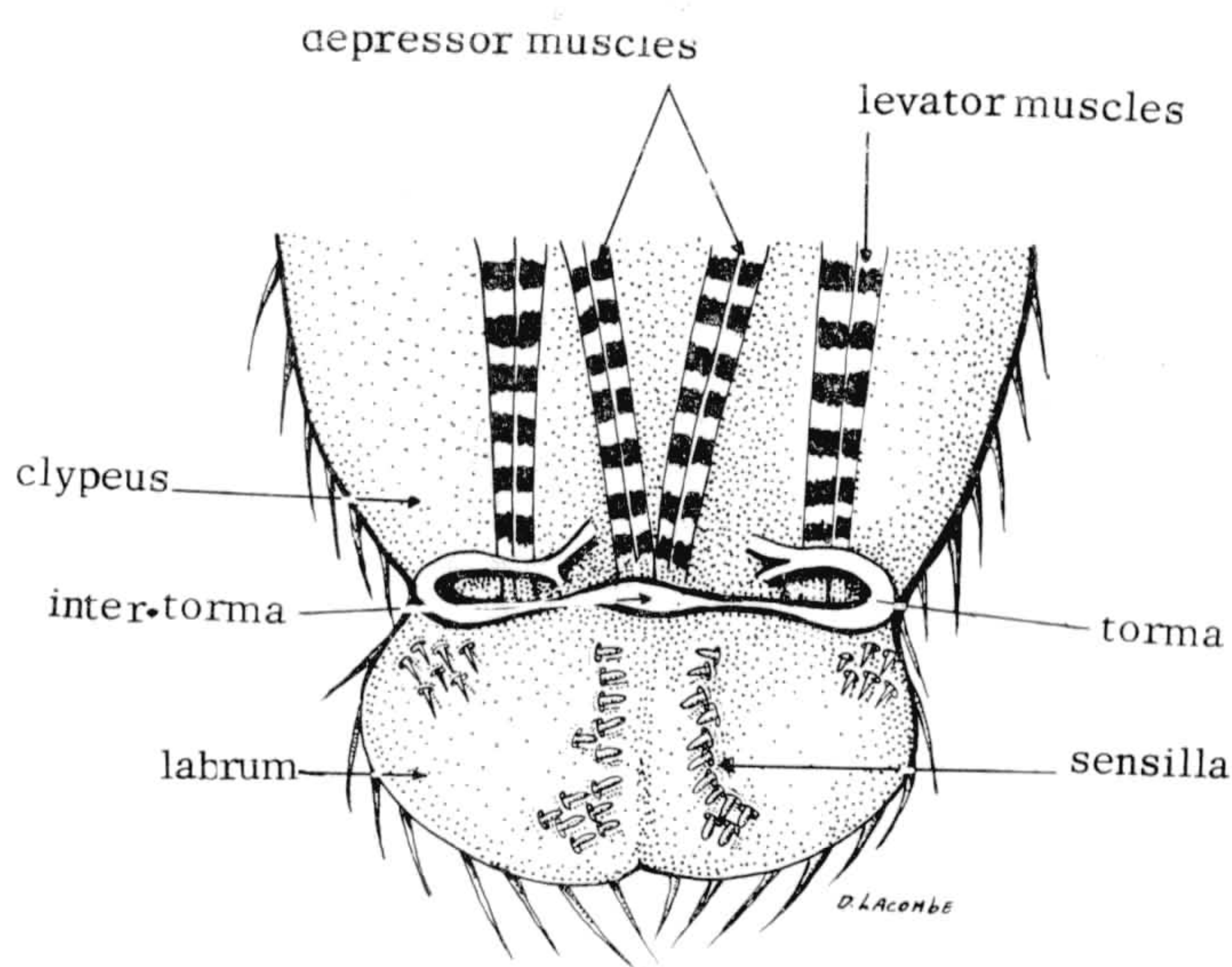


7 — Internal anatomy of the antennae.

MUSCLES OF MOUTHPARTS: *Clypeus-labrum* (fig. 8). In both sexes, the clypeus and the labrum are recovered by little setae of the same form that is found on the cervical capsule. They are more frequent in males than in females. The ventral surface of the labrum is usually

provided with two different types of gustatory sensillae. One group is located in the anterior lateral parts and another groups is organized in two median lines (fig. 8).

The levator and depressor muscles of the labrum are found in the epypharyngeal zone. The depressor muscles start from the intertorma to the dorsal cuticle of the epypharynx, and the levator muscles goes from the torma to the enervated process of the epypharynx (see fig. 4).

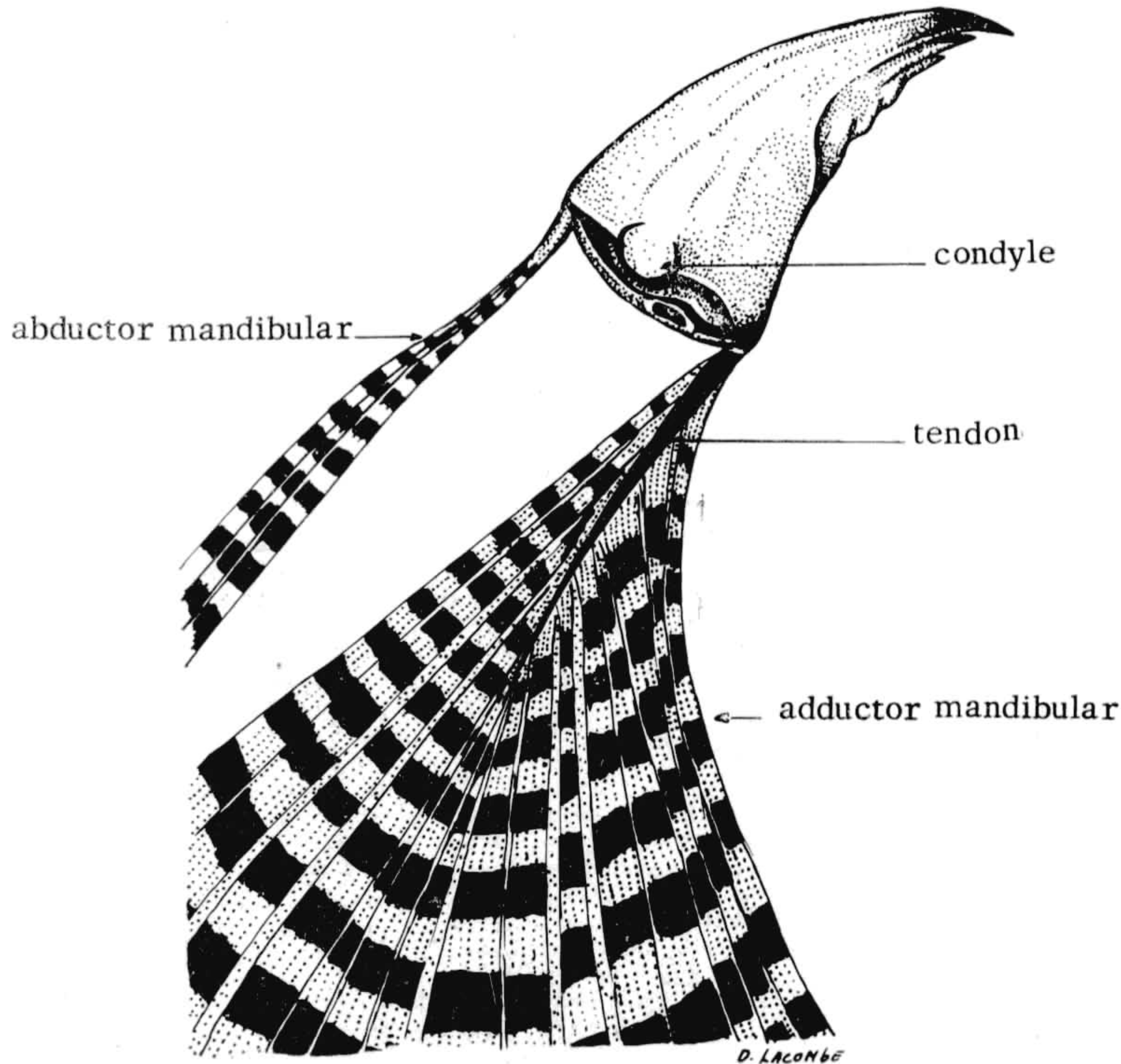


8 — Clypeo-labrum muscles.

MANDIBULARS (fig. 9): The mandibles of the *Embioptera* exhibit sexual dimorphism. In the male it is more slender than in the female (Lacombe, 1958). However, in both sexes the muscular system of the mandible is strongly developed and fills in a large part of the cranial cavity.

The adductor muscle, is the largest (fig. 9), because of the strength required for chewing food and in the case of the adult males, for gripping the females head. The muscle fibers are attached on a lamellate tendon forming an angle, between anterior and posterior tentorial arms, extending to their points of attachment latero-dorsally, within the cranial capsule (fig. 6). The abductor muscle

fibers are attached to a small tendon at the cranial wall behind the ocular region. When these muscles contract the mandible opens and permits the entrance of food.

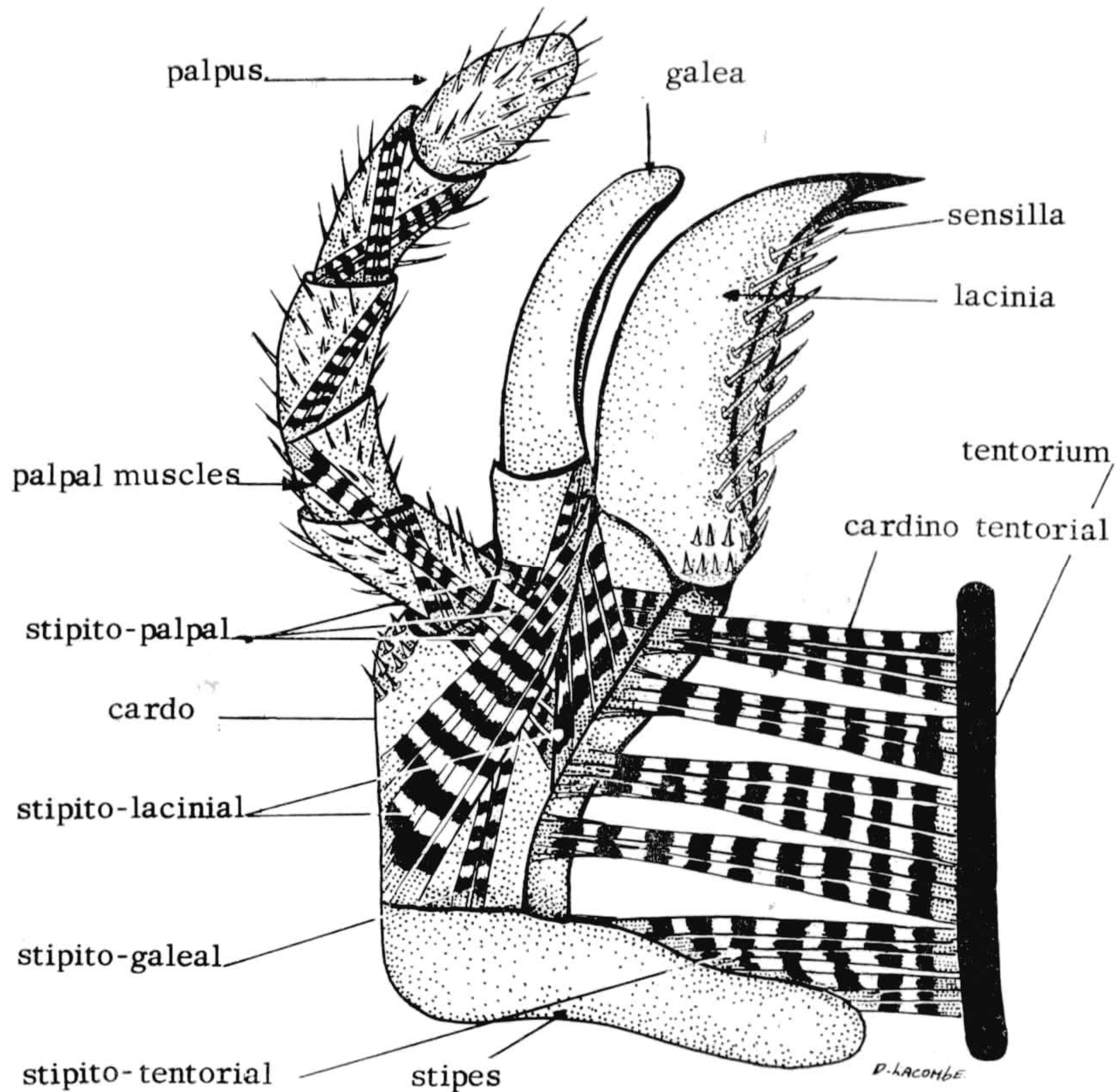


9 — Mandibles muscles.

MAXILLAE (Fig. 10): The maxillae are generally more robust in the female than in the male, and have a row of sensillae on the inner margin of the lacinia. These bucal parts are from the primitive types with all parts very clearly differentiated in both sexes.

The muscles of the various portions of the maxillae extend in all directions (fig. 10). The muscles from the stipes are: (a) the lacinial musculature which comprise two long, strong groups, extending from the tendon on the base of the lacinia to the lateral wall of the stipes and are called stipito-lacinial; (b) the galeal muscles which are called stipital flexors of the galea, extend from the inner base of the galea to the base of the stipes; (c) the maxillary palpi muscles comprise three groups, called stipito-palpal and are responsible for the movement of the palpi.

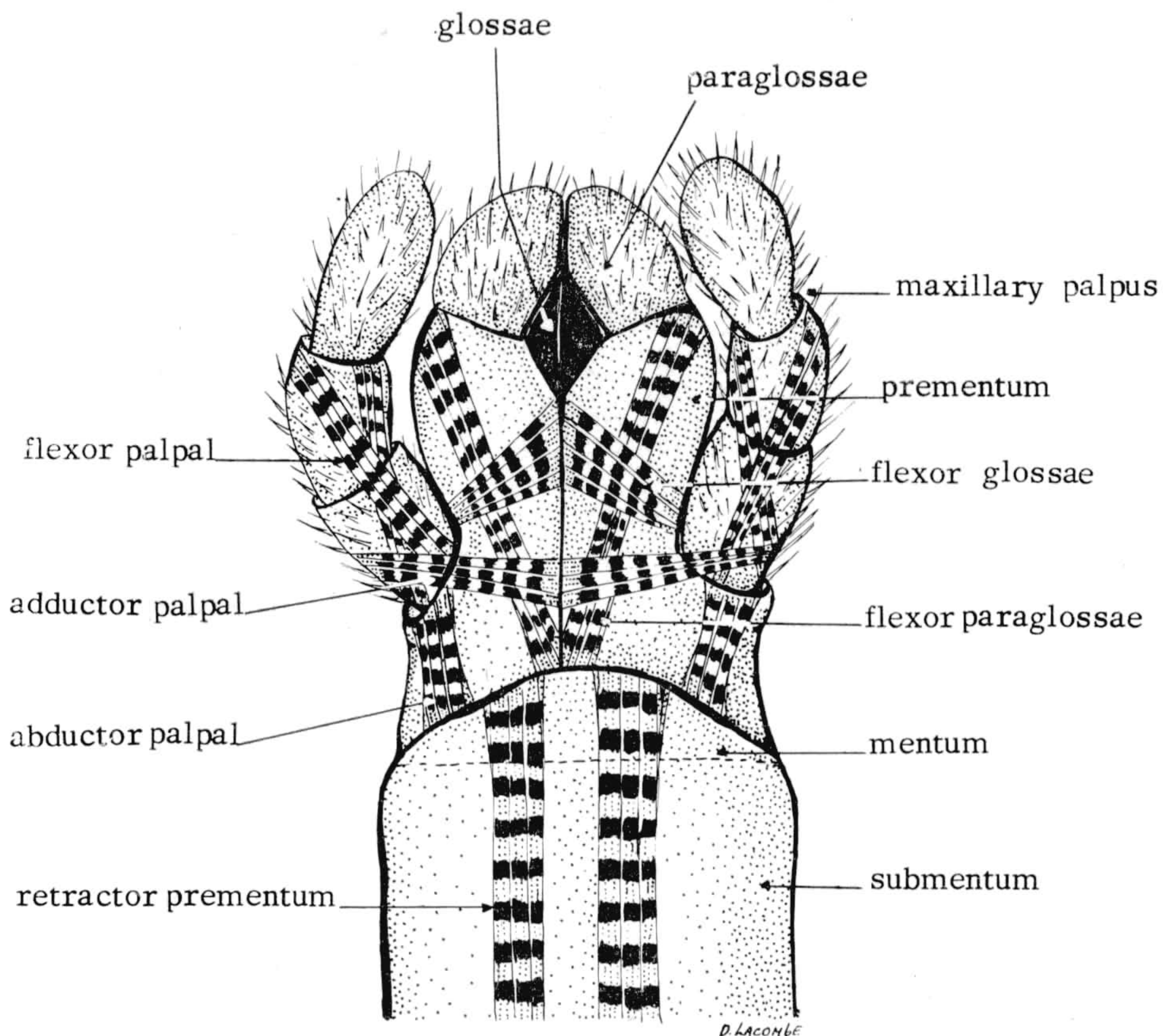
The segments of the maxillary palpi have an interesting muscle distribution. The basal segment has a muscle extending from its outer-basal rim to the inner-basal rim of the second segment. The second segment has a muscle extending crosswise from its outer-apical rim to the dorso-basal rim of the basal segment. In the third segment the muscle extends from its outer-basal rim to the inner-basal rim of the fourth inner and outer extremities of the segment. The fifth or distal segment lacks muscles.



10 — Maxilar muscles.

The fixing maxillae muscles (stipital-tentorial) of the buccal cavity, extend from the stipes to the corpotentorium and from the cardo to the corpotentorium (cardino-tentorial).

LABIUM (Fig. 11): The great part of the labial muscles are found in the prementum. The adductor muscles of the paraglossae extend from the outer-lateral base of the paraglossae to the medio-basal region of the prementum showing a V figure. The abductors of the glossae extend from the latero-basal region of the prementum to the anterior-median line in the neighbourhood of the glossae. Also in the prementum are found the adductor muscles of the labial palpi, which extend from the outer basal wall of the first palpal segment to the baso-medial line of the prementum, and the adductor muscles of the palpi which extend from the basal rim of the first palpal segment to the lateral base of the prementum. The labial palpi are composed of three segments. The basal segment has two crossing muscles which extend to outer and inner apical rims of the second segment. The apical or third segment lacks muscles.



11 — Labium muscles.

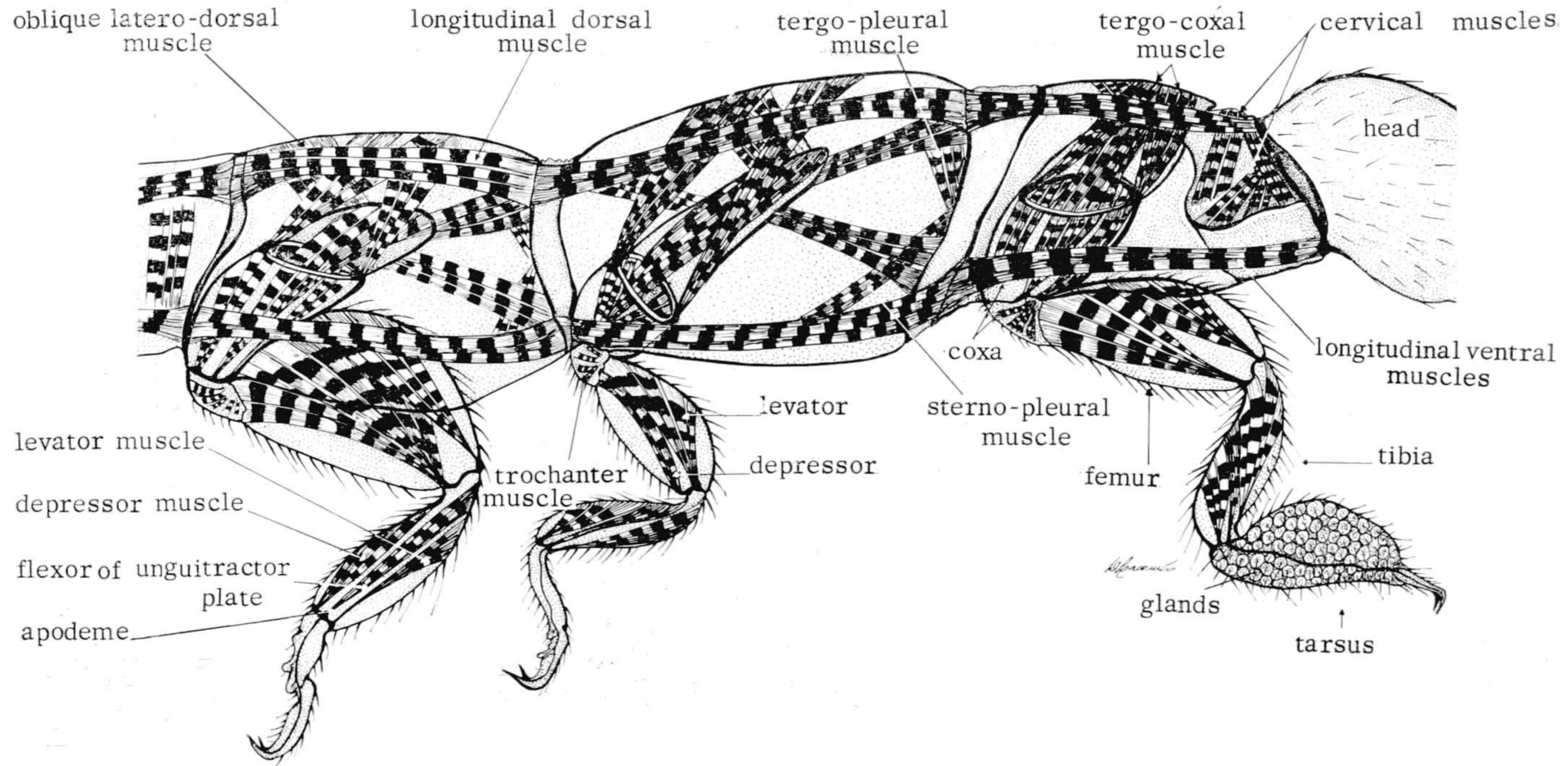
The principal muscles of the thorax are: (a) dorso-longitudinals and ventro-longitudinals which extend from one to another segment; (b) dorso-bentral muscles and; (c) intersegmental muscles.

The longitudinal dorsal and ventral muscles (fig. 12) that extend from the two apodemae of the post-occipital suture going to the phragma, between the prothorax and mesothorax, belong to the muscles of the cranial capsule. These cause the dorso-ventral movements of the insects head. There are little muscles in different positions in the cervical zone, which are studied above in the chapter under cervical muscles. The tergosternal muscles are the principal levators of the wings in the males; the females have no wings. We find the intersegmental muscles, tergo-pleural and sterno-pleural in the mesothorax and metathorax of the insect. Between the tergo-pleural muscles we find also the axillary muscles responsible for the downward movement of the wings.

Another group of muscles, tergo-coxal muscles, are responsible for leg movements. Such muscles are attached to the basicoxae and extend to the tergites. Others extend from the coxatrochanter articulation to the basicoxa and still others extend from the trochanter base to the pleural apophyses. These are responsible for the femur movement. Within the trochanter there are small muscles confined to the segment.

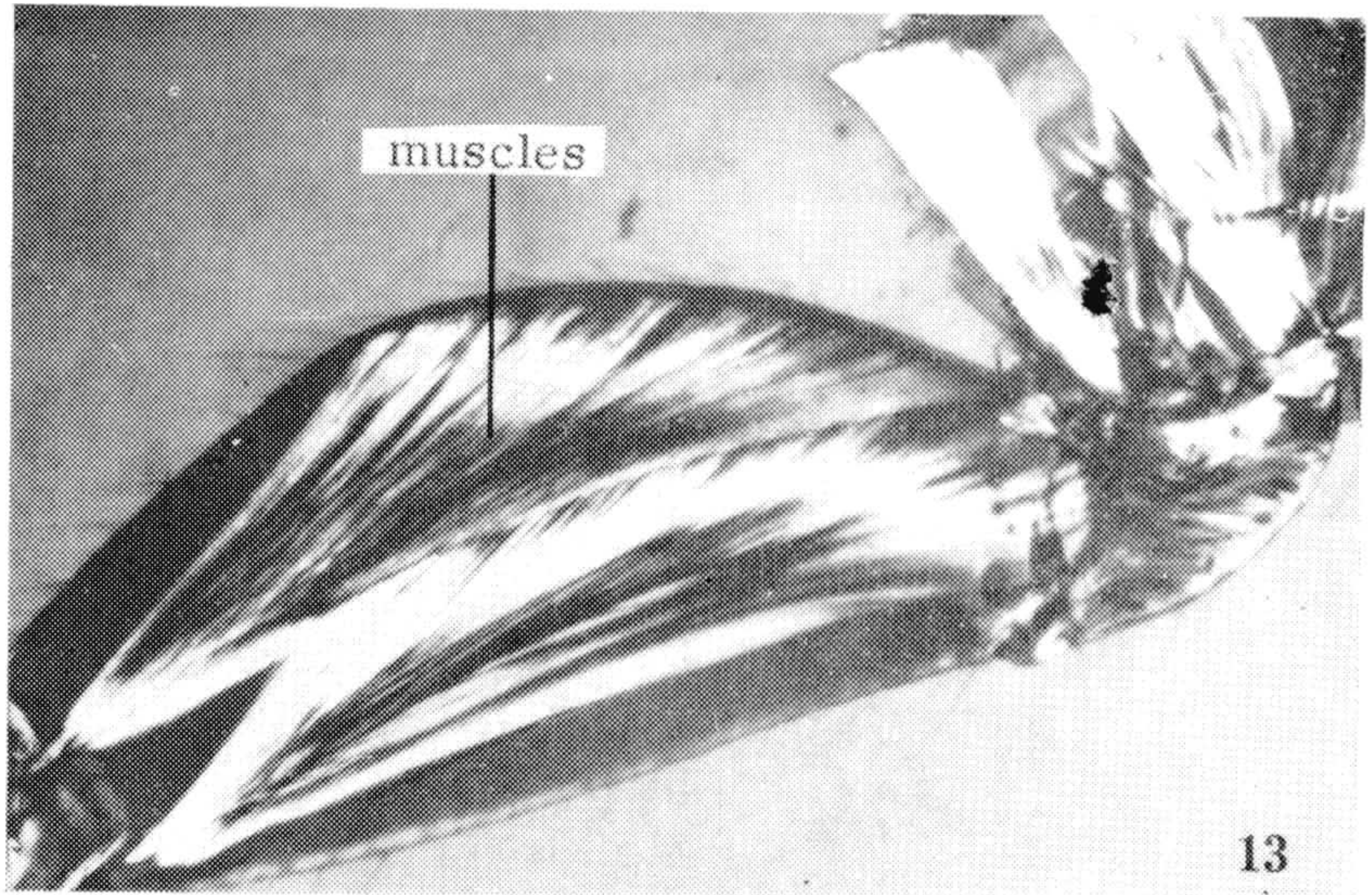
The levator and the depressor muscles of the tibia are located within the femora (fig. 12 and fig. 13), those of the hind femur are the strongest, of the three pairs, due to their frequent important use in motivating backward locomotion of the insect. Similar muscles in the mid-leg are very small due to their lack of important function. These femur-muscles are attached to the basal rim of the tibiae and extend to the dorso-lateral walls of the femora. Within the tibiae (fig. 12 and fig. 14) are found the levator and depressor muscles of the tarsi and its long tendon which extends through the tarsus to the unguitractor plate (fig. 12 and fig. 15). The fore legs are almost as strong as the hind, due to their frequent movements which assist the spinning function of the fore tarsi (**Barth, 1954**).

In the linkage is the attachment of muscles extending from the acrotergites as well as from the poststerna. There are, also, muscles extending from various pleural sclerites to the scuta.

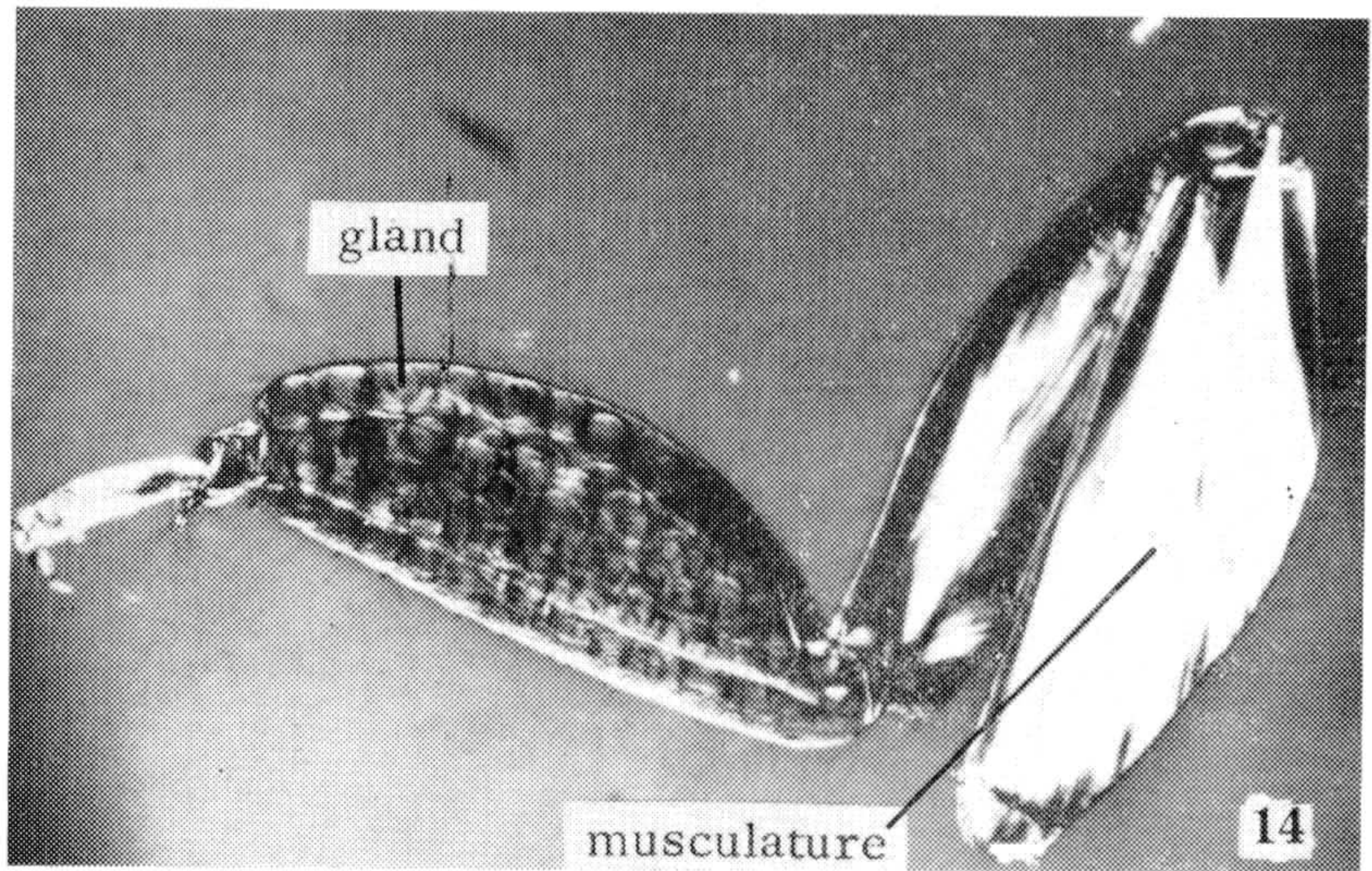


12 — Schematic drawing showing some muscles of the thorax.

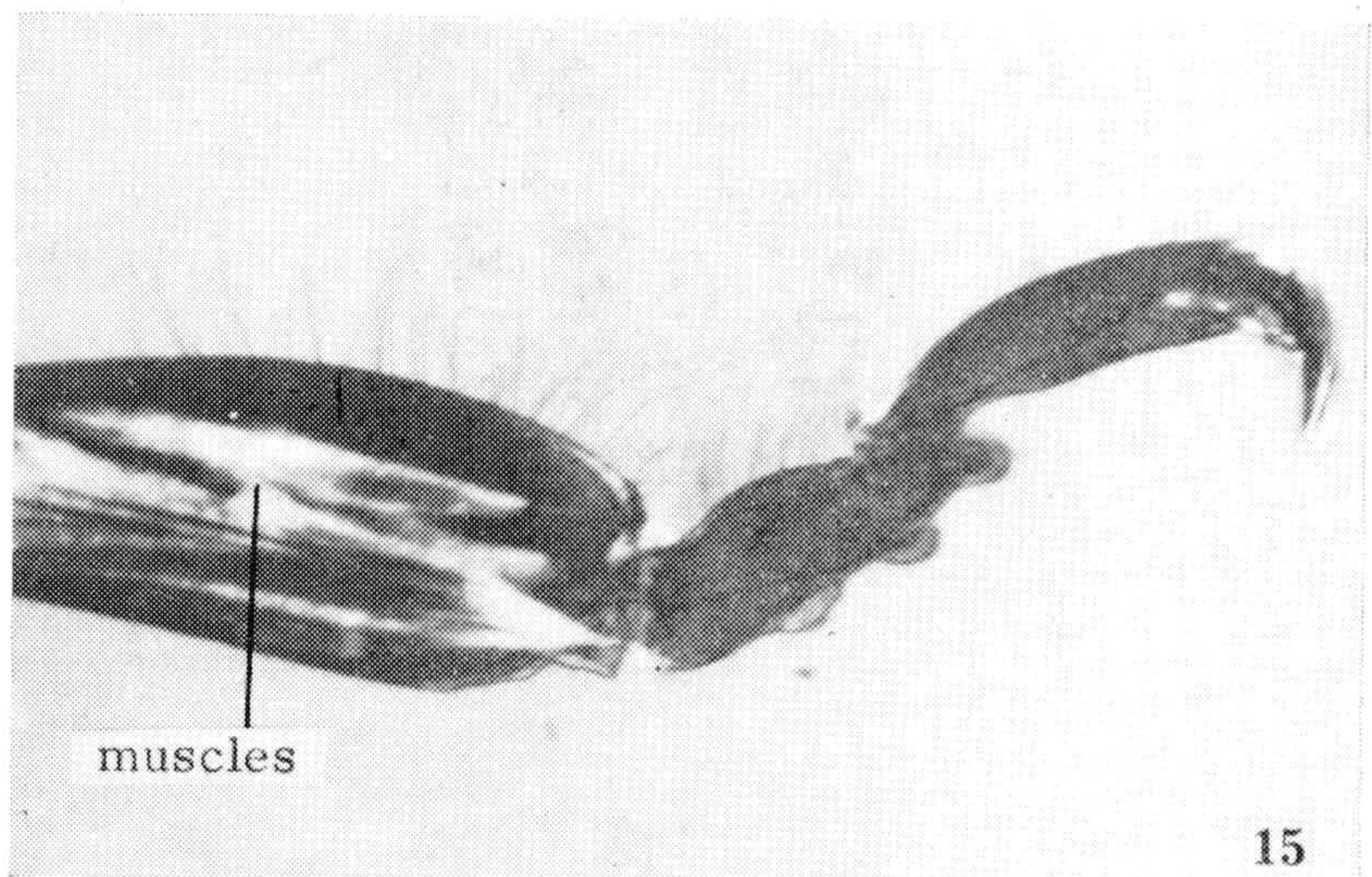
13 - Levator and depressor muscles of the tibia.



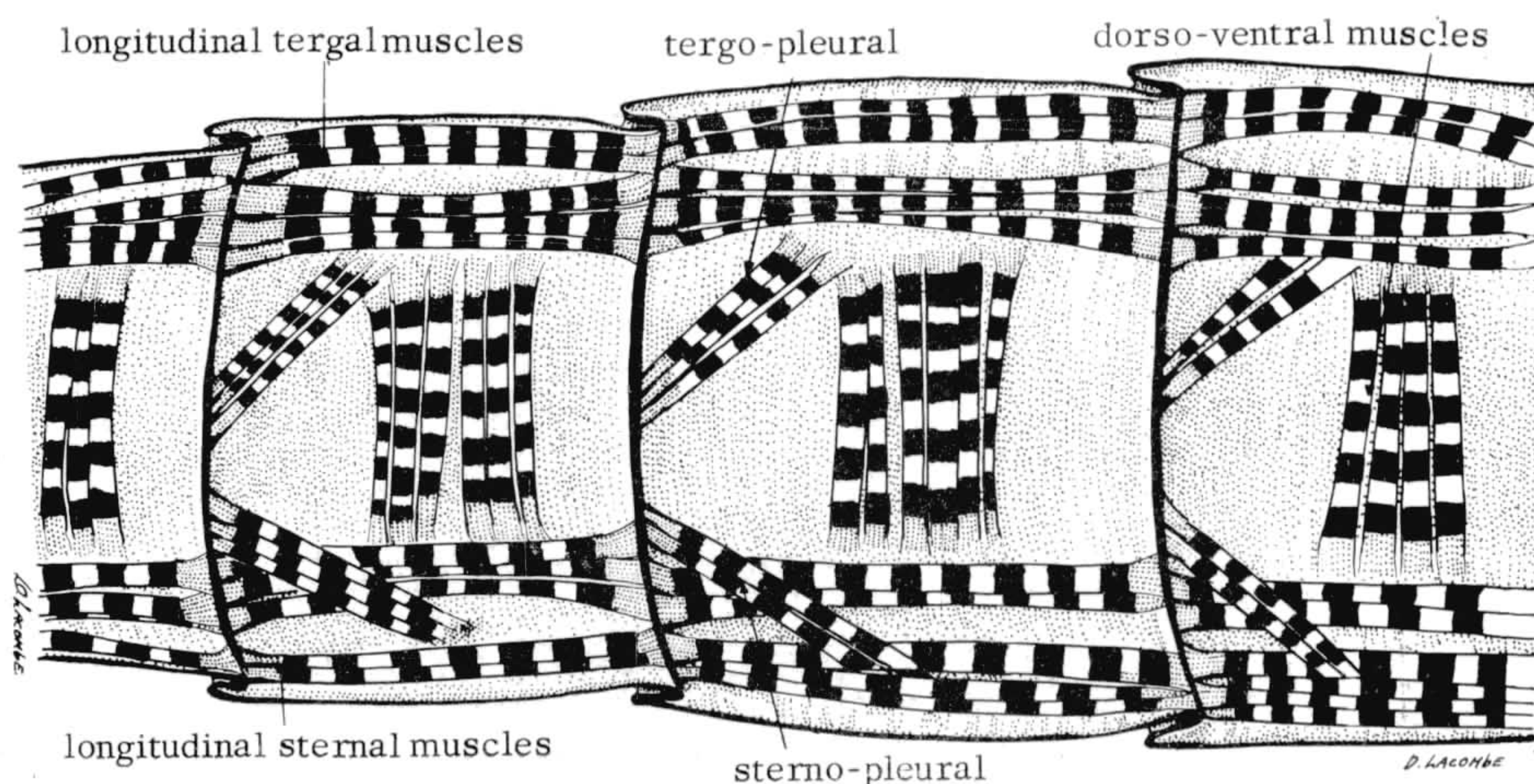
14 - Muscles for the movement of the tarsi.



15 - Depressor muscles of the unguitractor plate.



ABDOMINAL MUSCLES (Fig. 16): The principal abdominal muscles are: (a) dorsal longitudinal and ventral longitudinal muscles functioning as retractors of the abdomen, and originate from the antecosta of each segment; (b) tergo-pleural muscles which extend from the pleurites to the tergites; (c) sternopleural muscles from the pleurites to the sternites, and (d) dorso and ventral muscles which are found in each segment (fig. 17).



16 — Schematic drawing showing some muscles of the abdomen.

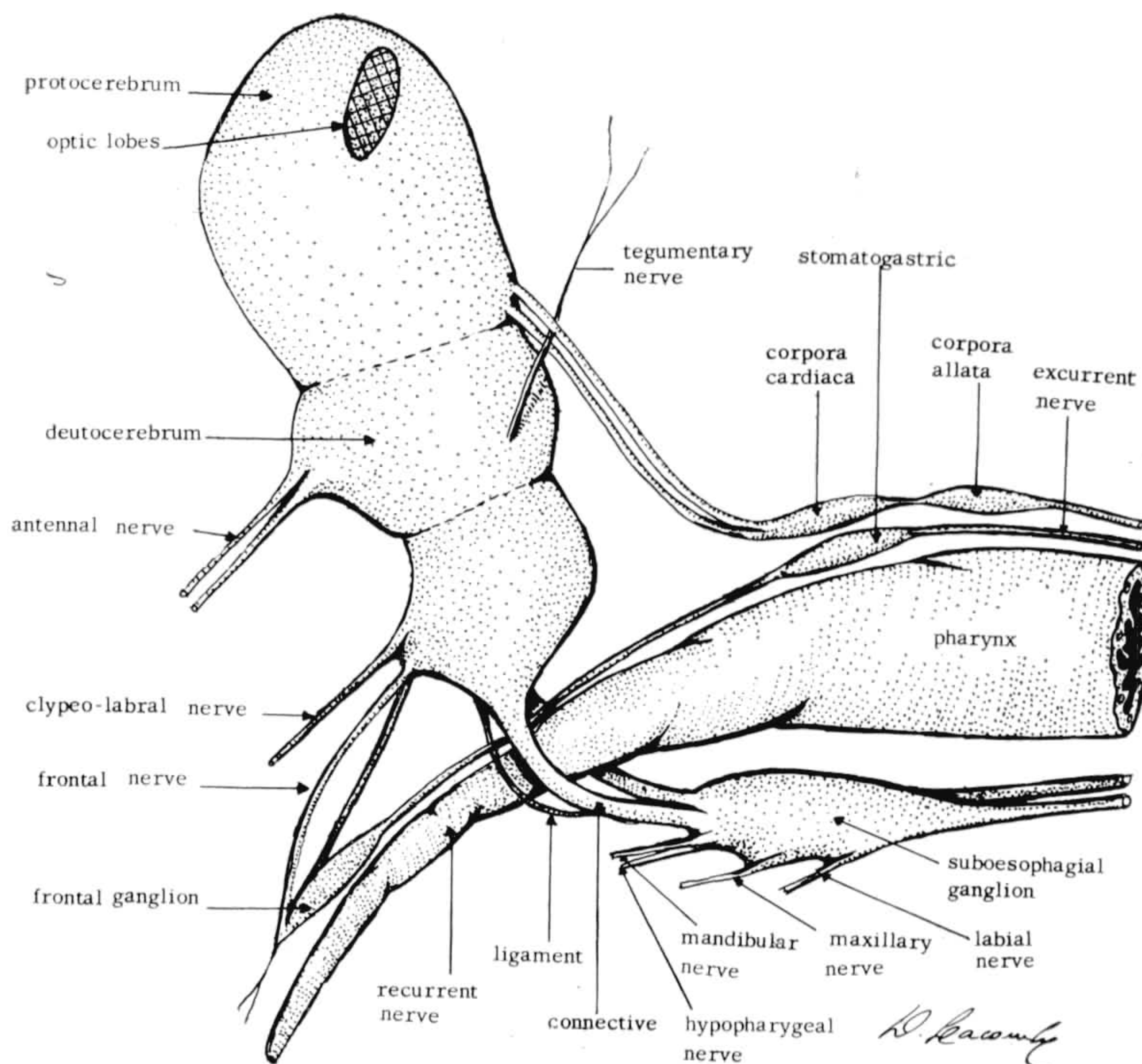
The last abdominal segment has special muscles which are associated with the genitalia and cerci. These muscles must be carefully studied to increase for a proper understanding of the structure and function of the terminalia which are of vital importance in systematic studies.

THE NERVOUS SYSTEM

The nervous system is of a primitive type (fig. 2). It was briefly treated by **Melander** (1903) in his studies of *Embiatexana*. Later, **Hilton** (1936-37) discussed the distribution of ganglia in a work which also included *Isoptera*, *Anoplura*, and *Corrodentia*. **Hanstroem** (1940) published a fine general work on the structure and histology of sixteen orders of insects, including the *Embioptera*. Recently, **Lacombe** (1963) studied the nervous system of *Embolynta batesi*.

The supraoesophageal ganglion, or brain, is located in the anterior-dorsal region of the head capsule just above the oesophagus. The suboesophageal ganglion is situated in the ventral region of the head, beneath the oesophagus. The ventral nerve cord consists of ten pairs of fused ganglia linked by a double nerve cord.

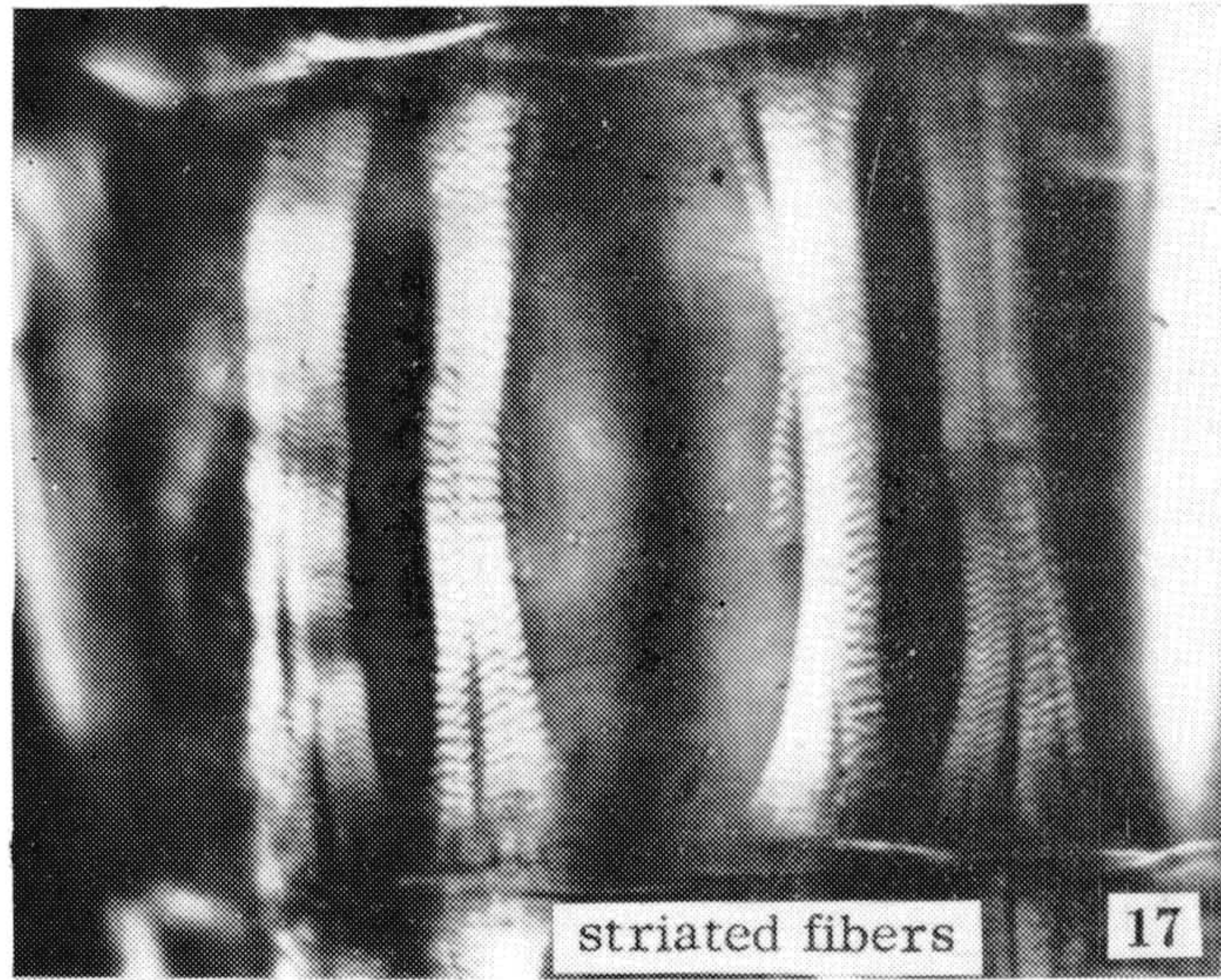
The brain is divided in three distinct regions (fig. 18): the protocerebrum, the deutocerebrum, and the tritocerebrum. The protocerebrum, the largest portion of the brain, results from the a fusion of the pair of ganglia of the optic segment. The protocerebrum interspecifically varies in size and shape. Laterally it forms the optic lobes, but enervation for ocelli is absent due to the universal lack of ocelli in the order.



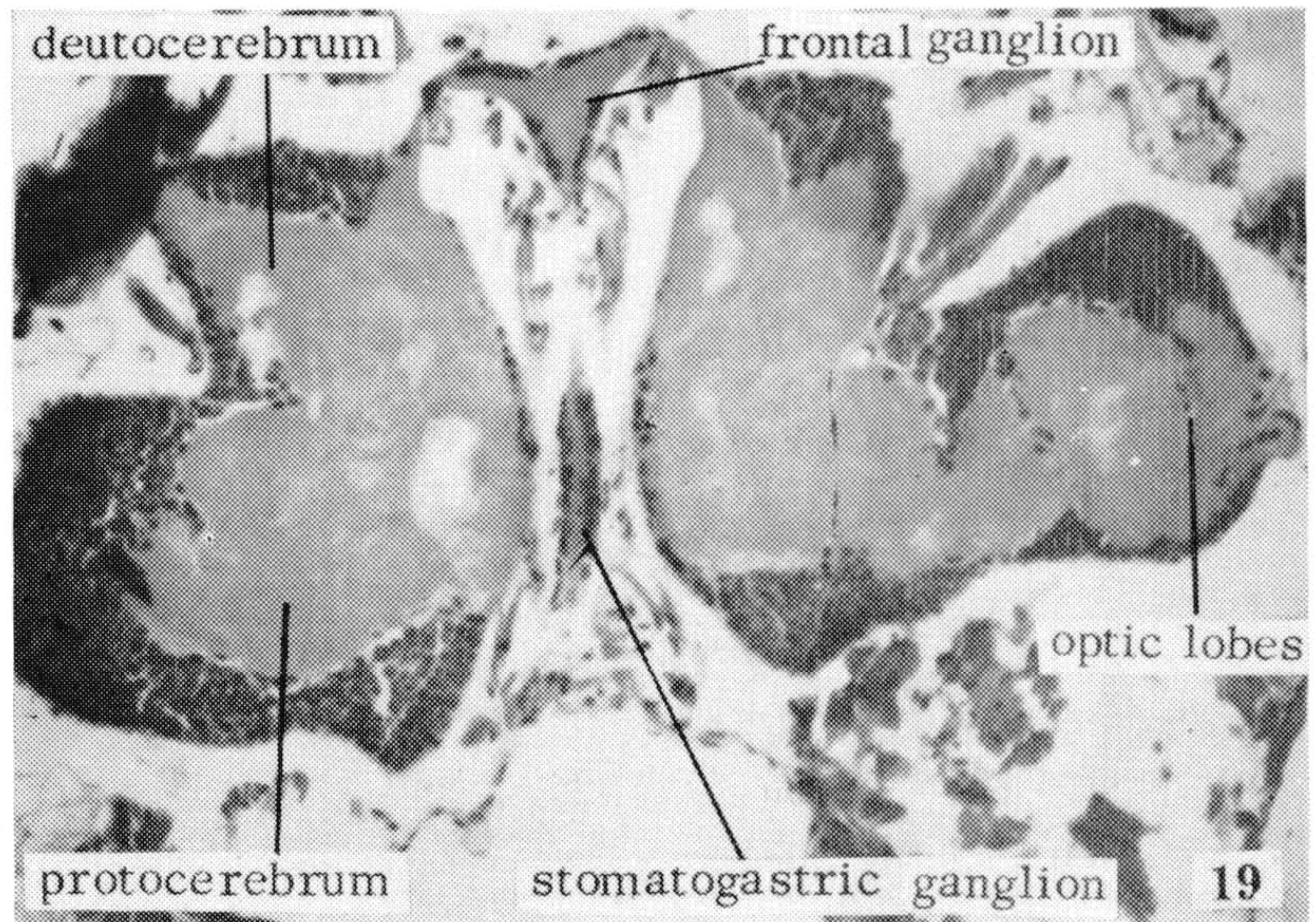
18 — Schematic drawing of the nervous system.

The deutocerebrum (fig. 18 and fig. 19) results from fusion of the ganglia of the antennal segment. Each antennal nerve is long and simple and inserts the antennal scape medially. The nerve divides

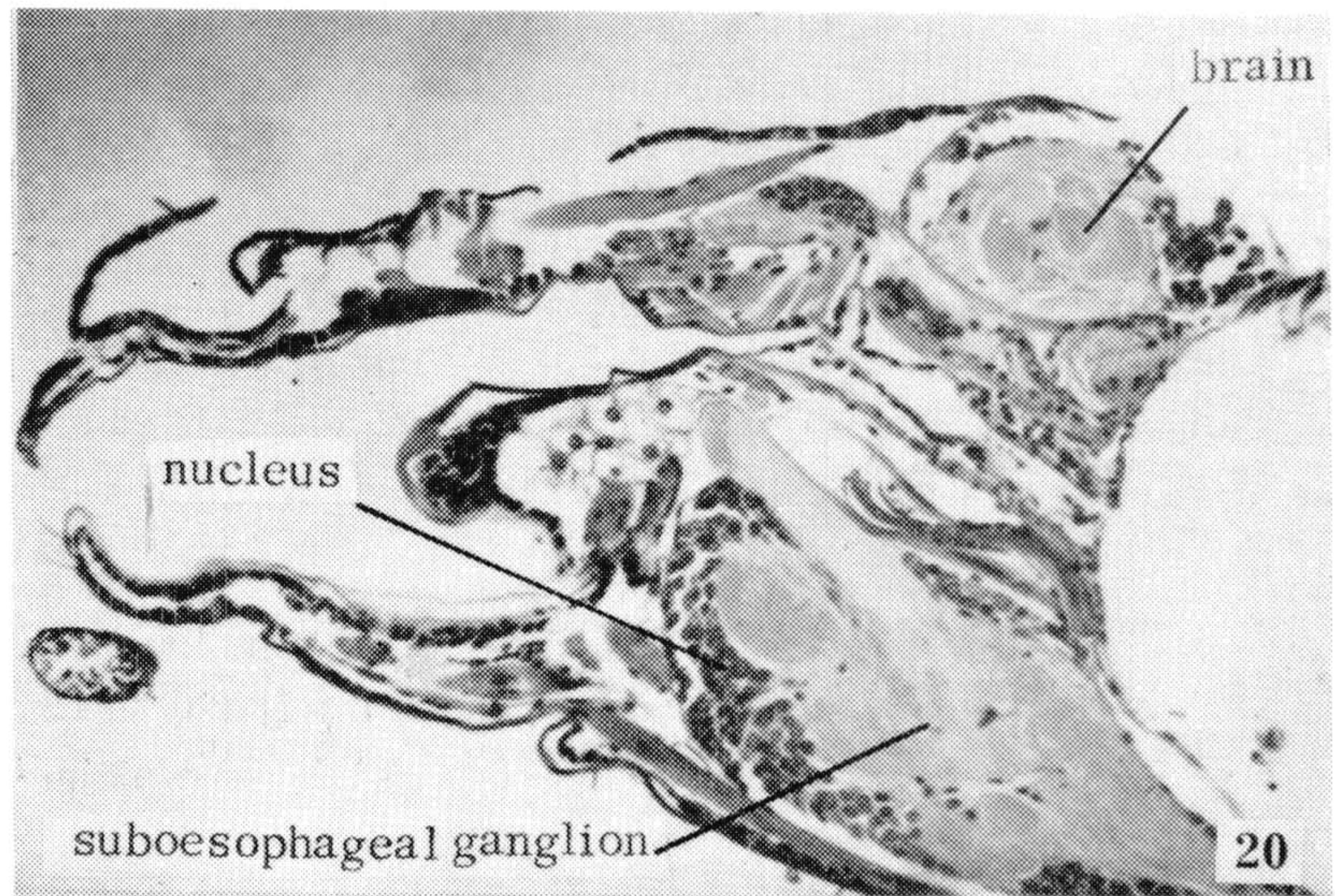
17 - The dorso-ventral muscles of the abdomen segment.



19 - Longitudinal histological cut of the brain of the E. batesi.



20 - Histological section from the head showing the central nervous.



into two long branches extending up into the distal antennal segment. Each antennal nerve has motor fibers. The sensory fibers enervate the antenna's many sensillae and chordotonal organs (see fig. 28). The motor nerves of the antennae enervate the head's antennal muscles as well as those due within the scape.

Between these nerves is found a slender blood vessel which extends distally from an ampulla in the base of the antenna. Blood from the apex of the dorsal blood vessel enters an opening in the ampulla and circulates distal in this antennal blood vessel. After passing through a distal opening in the antennal vessel, the blood returns to the head.

The tegumentary (fig. 18) nerve, which arises on the posterior surface of the tritocerebrum, is at first short and simple and then it branches beneath the dorsal cranial wall. Nerves which enervate the clypeo-labral region, the epipharynx, and the labrum arise from the anterior portion of the tritocerebrum, as well as the connectives to the frontal ganglion. Posteriorly of the tritocerebrum are the circumoesophageal and suboesophageal connectives.

The suboesophageal ganglion (fig. 20) has a ventral position beneath the pharynx and behind the tentorium. It is the motor nerve center for the mouth parts as a result of a fusion of the ganglia of the mandibular, maxillary, and labial segment. The ganglion also enervates the hypopharynx, salivary glands and, of course, has posterior connectives to the first thoracic ganglion.

The mandibular nerves are long, fine, and simple (fig. 18). Near the base of each mandible they divide into a large and a small branch. The smaller branch goes to sensory cells of the mandibular hypodermis and the large branch goes to the neurones within the mandibles.

The maxillary nerves (fig. 18) are located beneath the mandibular nerves and go to the maxillae. In a position beneath the maxillary muscle, which extend from the tentorium to the maxillae, the nerve divides into two branches. One branch goes to the hypopharynx and the other to a group of sensitive cells within the maxillae where it ramifies and enervates the hypodermic sensorial cells of the maxillae.

The labial nerve arises on the posterior region of the suboesophageal ganglion and is directed toward the labium where it divides and enervates various portions of the labium.

The ventral nerve cord in *Embioptera* has three thoracic and eight abdominal ganglia which represent fused pairs. The organization is primitive with all ganglia, linked by pairs of separate connectives (fig. 21). The size and form of the ganglia varies according to sex. In males the prothoracic ganglion is oval; that of females is polygonal. The females mesothoracic ganglion is larger than that of males and in both sexes the metathoracic ganglion is the largest of the three.

The prothoracic and mesothoracic ganglion have the same nerve distribution; each enervates the muscles of the segment, as well as its legs. The metathoracic ganglion is of particular interest in the *Embioptera*, because the first abdominal ganglion is combined with the fused metathoracic ganglia. In most insects such a combination is so complete that the abdominal ganglion is impossible to distinguish, but in *Embioptera* it is easily decomposed during dissection and staining *in situ* (fig. 22). It is a concentration from obsolescence of the connectives between the metathoracic and abdominal ganglia.

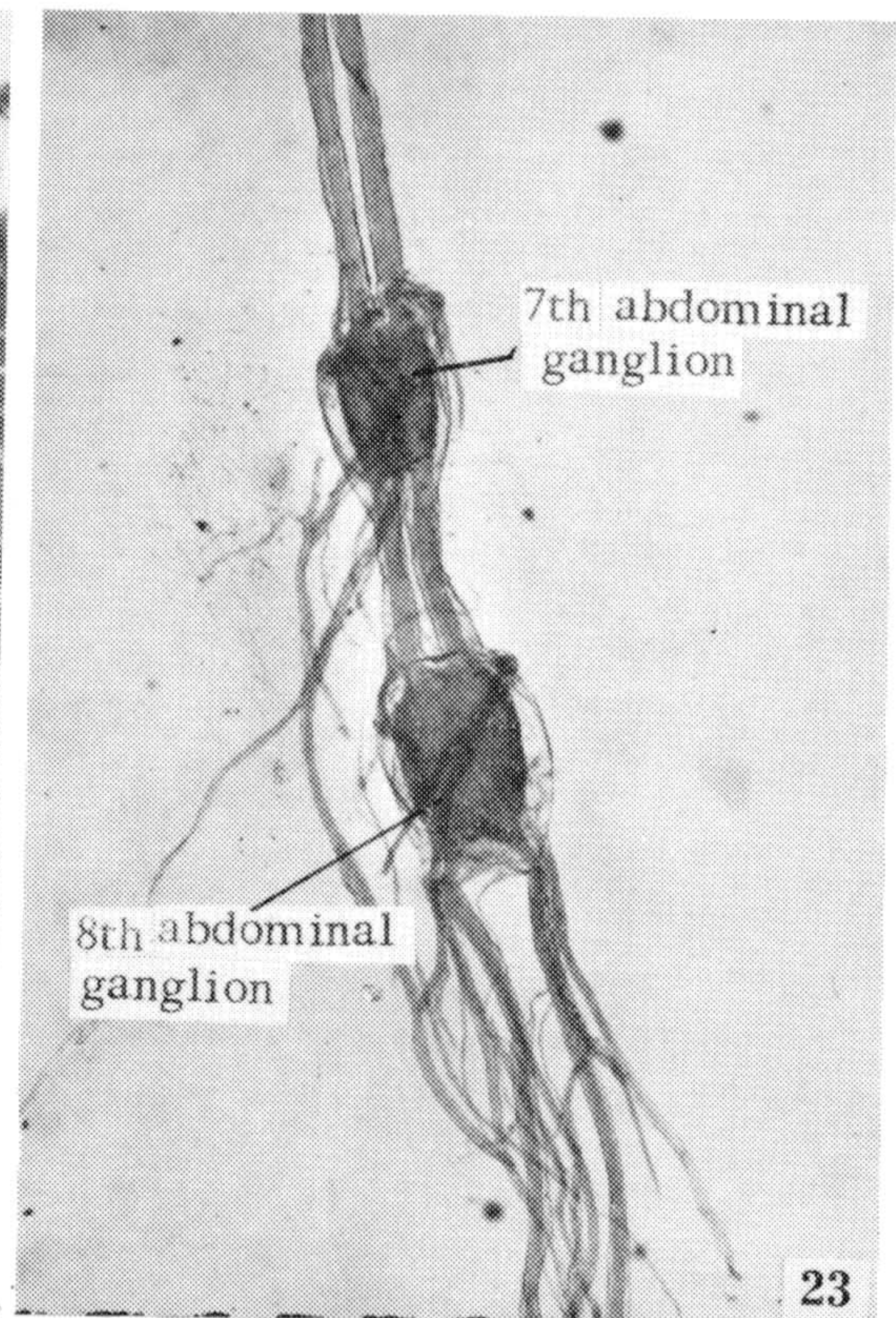
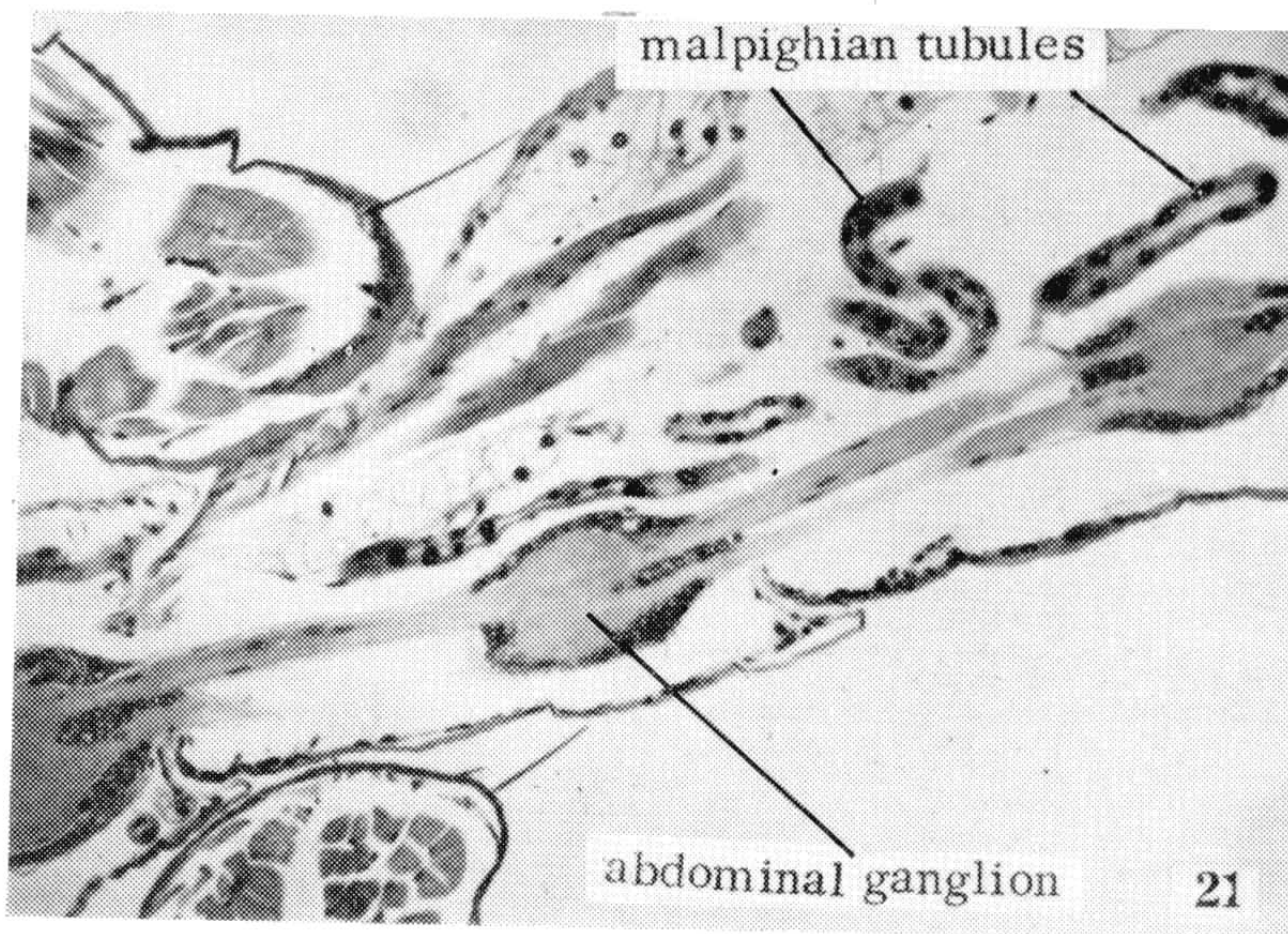
Because the first abdominal ganglion is combined with that of the metathorax, the ganglia of the second, third, fourth, and fifth abdominal segments are displaced to a forward position and thus their corresponding segments do not occur. The fifth abdominal segment lacks a ganglion and this is characteristic of all *Embioptera*.

The last abdominal ganglion, representing a fusion of the eighth, ninth and tenth pair, is located in the eighth segment (fig. 23).

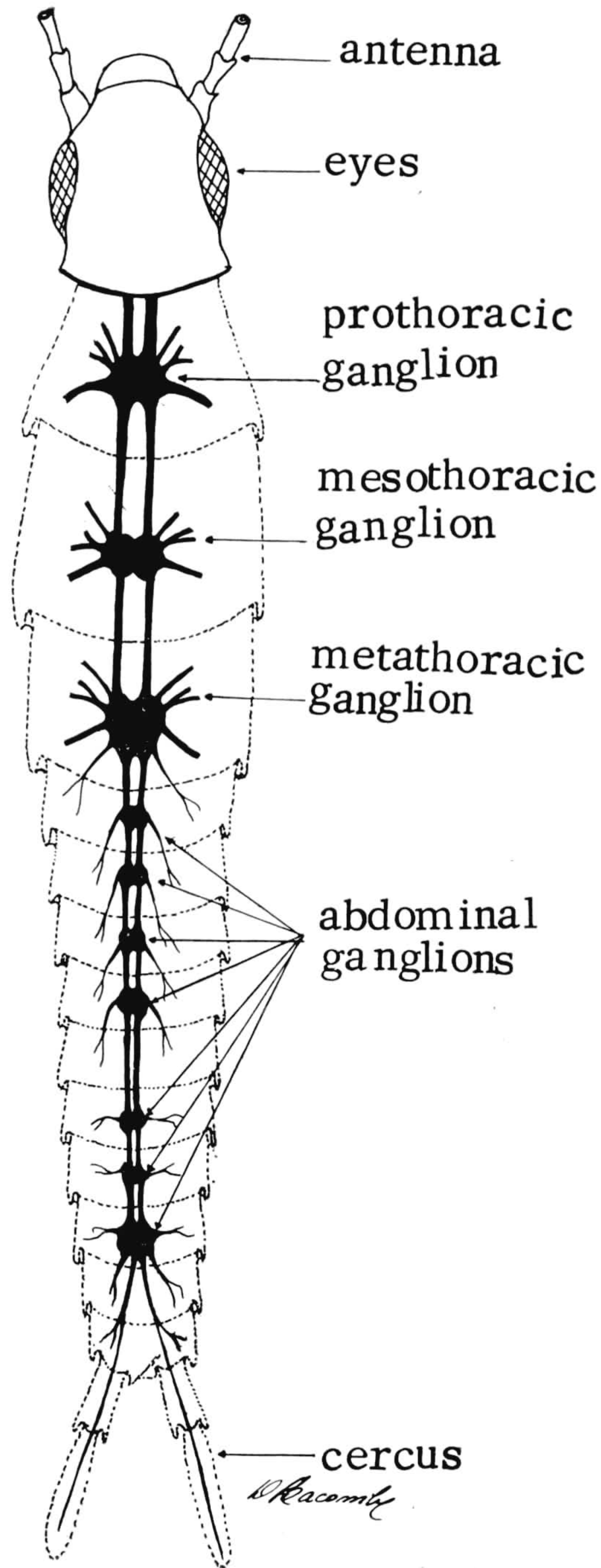
The dislocation of the ventral cord is responsible for the different sizes of connectives between them (fig. 24). The connectives between the first abdominal ganglion (actually the second) and the metathoracic ganglion, and between the sixth and seventh are very short in comparison to the other abdominal connectives. Those between the fifth and sixth are very long and pass through the fifth abdominal segment which lacks a ganglion.

All abdominal ganglia radiate fine nerves to the fatbody, muscles, cuticle, etc. The last composite ganglion enervates the last three abdominal segments and the sensitive, two-segmented cerci.

The stomatogastric or visceral system (see fig. 19). This system comprises the frontal ganglion with bilateral connectives and the recurrent nerve to the visceral ganglion.



- 21 — Longitudinal histological section through the ventral nervous system.
 22 — Histological view from the metathoracic and first abdominal ganglia.
 23 — The last abdominal ganglion.



24 — Schematic drawing of the nervous system.

The frontal ganglion in *Embioptera* is exceptionally large. It connects with the tritocerebrum via a pair of frontal nerves. From its caudal surface arises a recurrent nerve which extends along the median line of the oesophagus, passing just beneath the brain and the anterior end of the dorsal vessel to reach the hypocerebral ganglion.

Nesbitt (1941) in his study of the nervous systems of *Orthoptera*, *Dermaptera*, and *Isoptera* observed that in the more highly evolved insects the stomatogastric nerve is paired while in more generalized insects, such as *Dermaptera*, *Embioptera* and *Isoptera* the nerve is simple and referred to as the median excurrent nerve.

The hypocerebral ganglion is located behind the brain and beneath the aorta. The posterior recurrent nerve enervates the dorsal wall of the stomodeum.

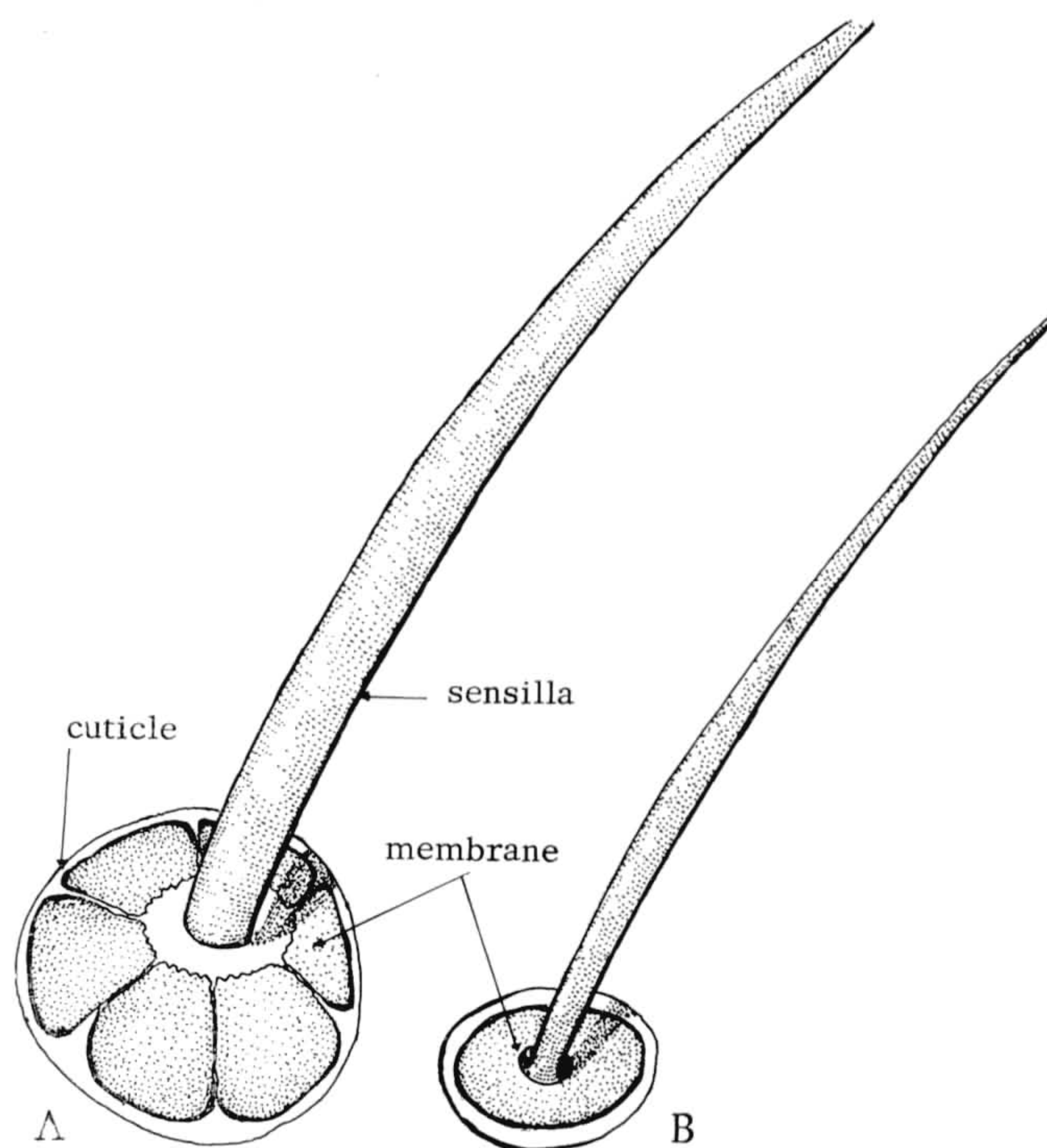
THE PERIPHERAL NERVOUS SYSTEM. This system extends from the suboesophageal ganglion to the caudal extremity of the insect. The diversity of the system in insects was studied by **Zawarzin** (1924). It enervates the tracheal system, rectal region of the digestive system, dorsal vessel, salivary glands, oesophagus and genital organs. The sympathetic system consists of median and transverse nerves associated with each ganglion of the ventral nerve cord. The transverse nerves serve the spiracles and have small ganglia along their courses.

THE SENSE ORGANS: Sensory hairs occur all over the body surface of the *Embioptera* and include for exemple trichodeal and tactile taste setae and bell shape sensillae, and chordotonal organs. All consist of a sense cell connected to a sensory nerve. The tactile hairs consist of fine or coarse long setae associated with sensitive cells situated in the hypodermis.

In both sexes of the *Embioptera* the cerci have many sensory setae and trichodeal sensillae (Fig. 25, a-b). The latter have interesting structure; their bases are elevated and divided into six or eight sections separated by sclerotized reinforcements which respond to the movement of the setae.

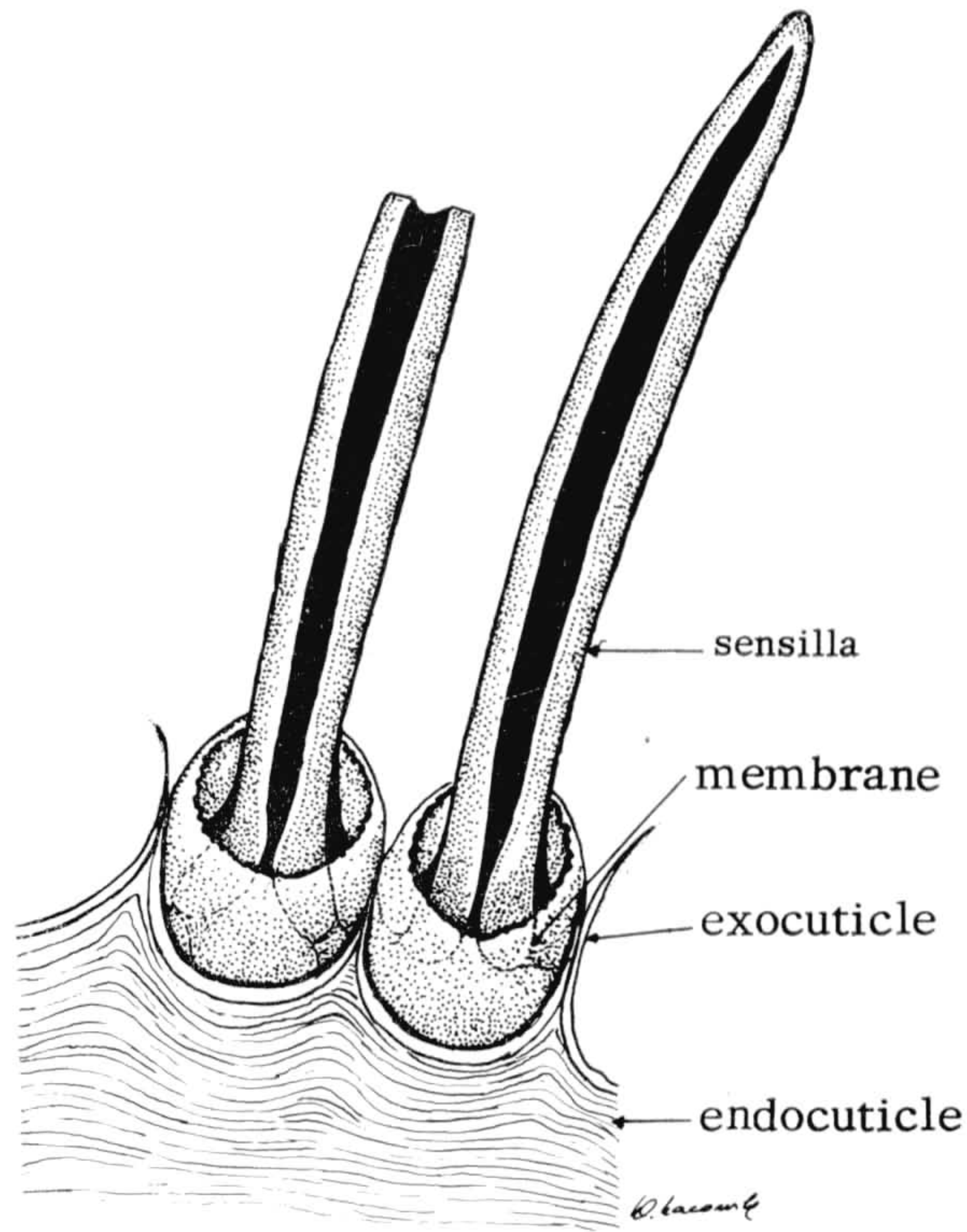
In simple sensory setae the socket membrane is not elevated and not divided by sclerotized lines of reinforcement. It is a simple circle delimited by exocuticle (fig. 25, b).

The sensillae of the lacinia belonging to the maxilla (fig. 26) are of various types and include sensory setae and taste sensillae. The latter have conical base and are never formed so long as fine setae. They are readily distinguished from all other sensillae. Another type of taste sensilla is found on the inner surface of the labrum (fig. 27). These occur in two longitudinal lines in the median region of this surface. The structure of these is shown in a schematic drawing of a histological section of one of these setae (fig. 27). A sensory nerve extends the full length of these sensillae and passes through the hypodermis to reach the sensory cells which lie beneath it.

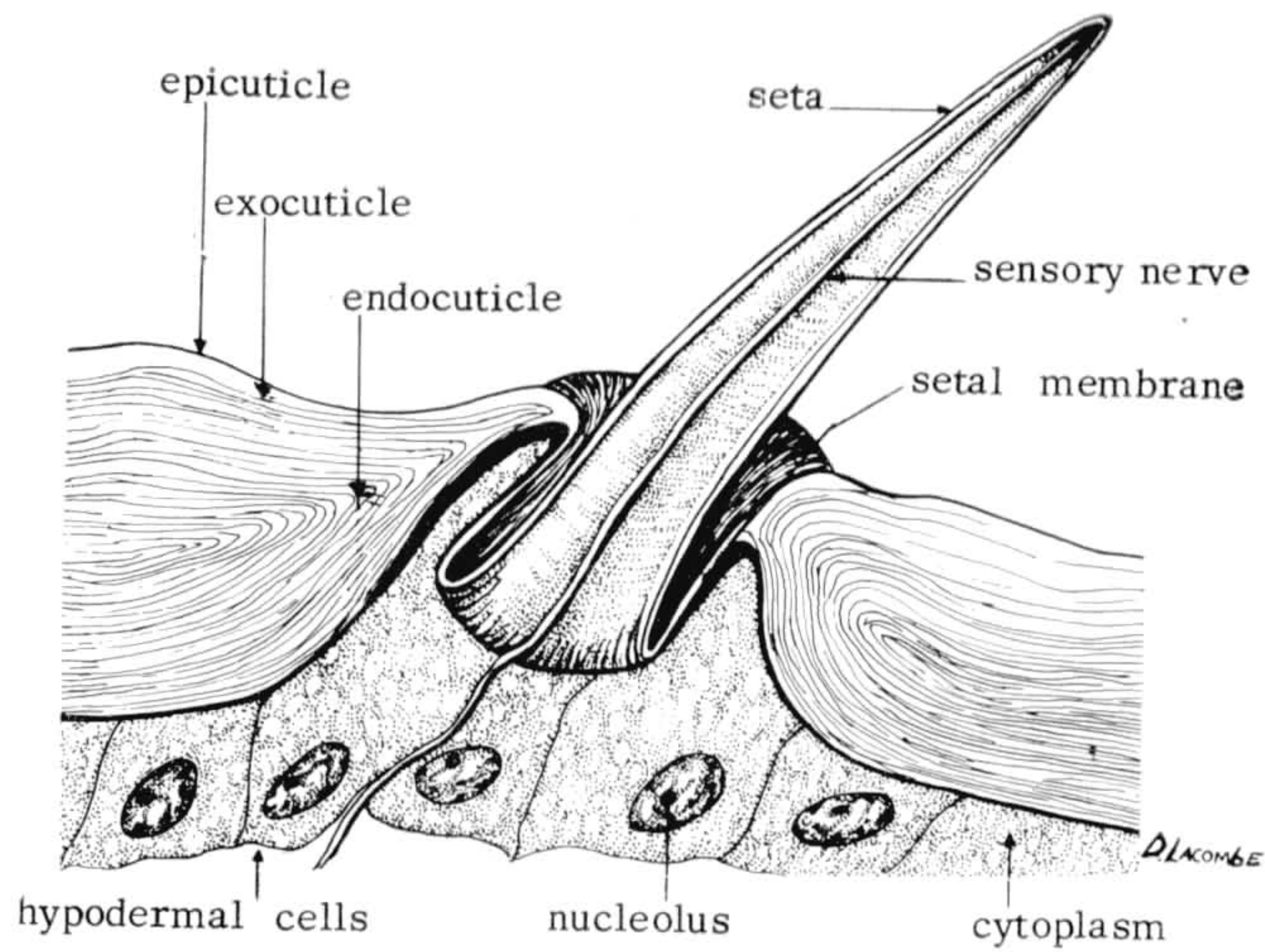


25 — The trichodeal sensillae types.

CHORDOTONAL SENSILLAE. These sensillae are readily recognized in the first (scape) and second antennal segment (fig. 28). They consist of a group of eight or more sense cells, each with two points of attachment in the cuticle.

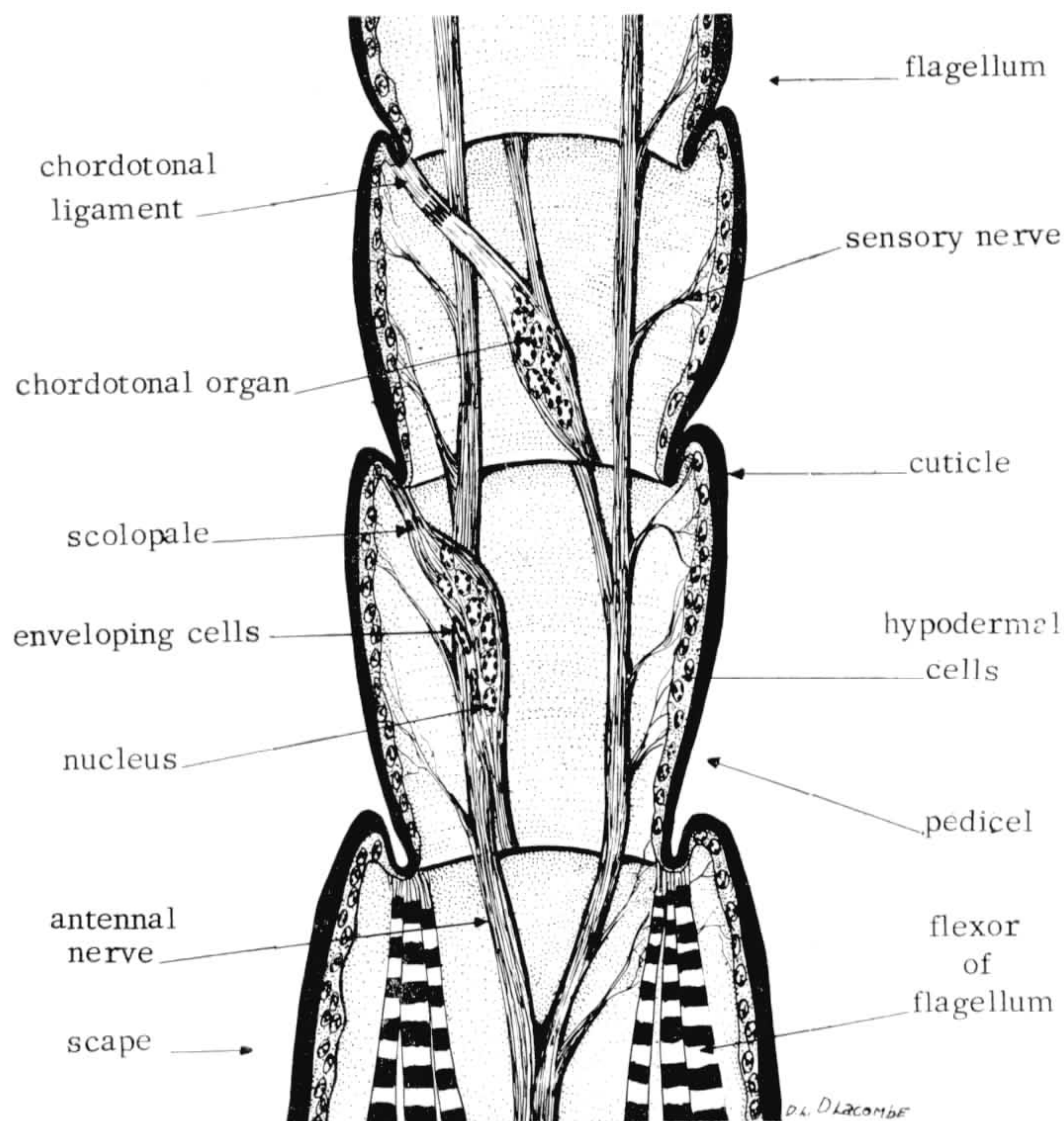


26 — The maxillary sensilla.



27 — Histological cut from the base of the labrum setae.

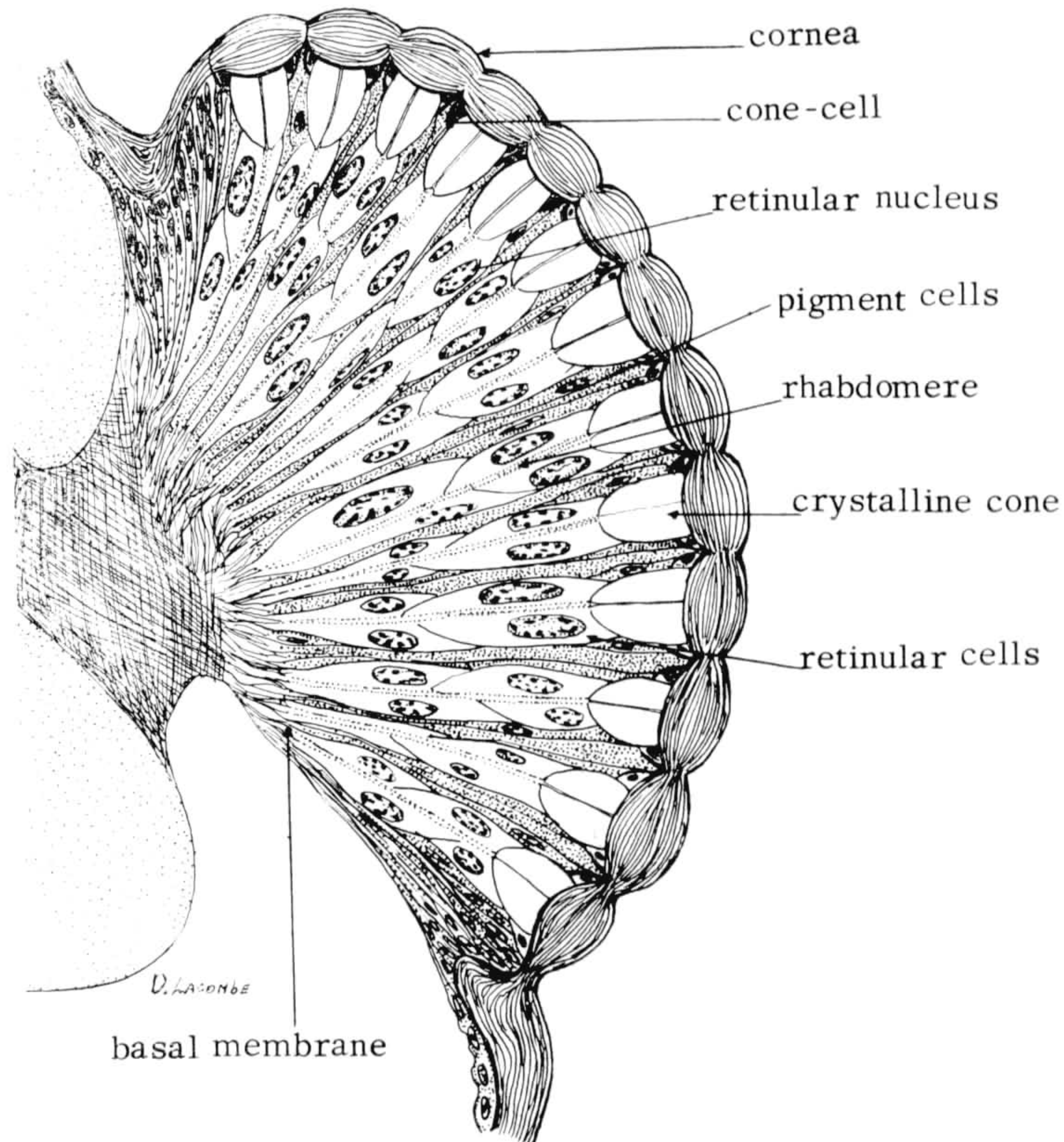
The sense cells are connected to the cuticle by chordotonal ligaments of the cap cells. The scolopale is well defined at the apex of each sense cell. All groups of sense cells communicate with the antennal nerves. Around these groups are enveloping cells with small, chromatin-rich nuclei and a denser cytoplasm than that of other sense cells. These chordotonal organs are stimulated by change in tension during passive movements of the antennal segments.



28 — Microanatomy of the antennae showing the chordotonal organs.

COMPOUND EYES (Fig. 29): These are the only organs of sight, ocelli being absent in all the *Embioptera*. The compound eyes of the two sexes are generally very distinct in size and form. These of females and nymphs being smaller and flatter, those of males are generally larger and more inflated. Eyes of nocturnally-active males are often exceptionally large with prominent facets.

The eyes of the *Embioptera* are of a cone type (fig. 29) and composed of many ommatidia. Each ommatidium consists of a transparent, bi-convex cornea which is formed by a group of four cells.

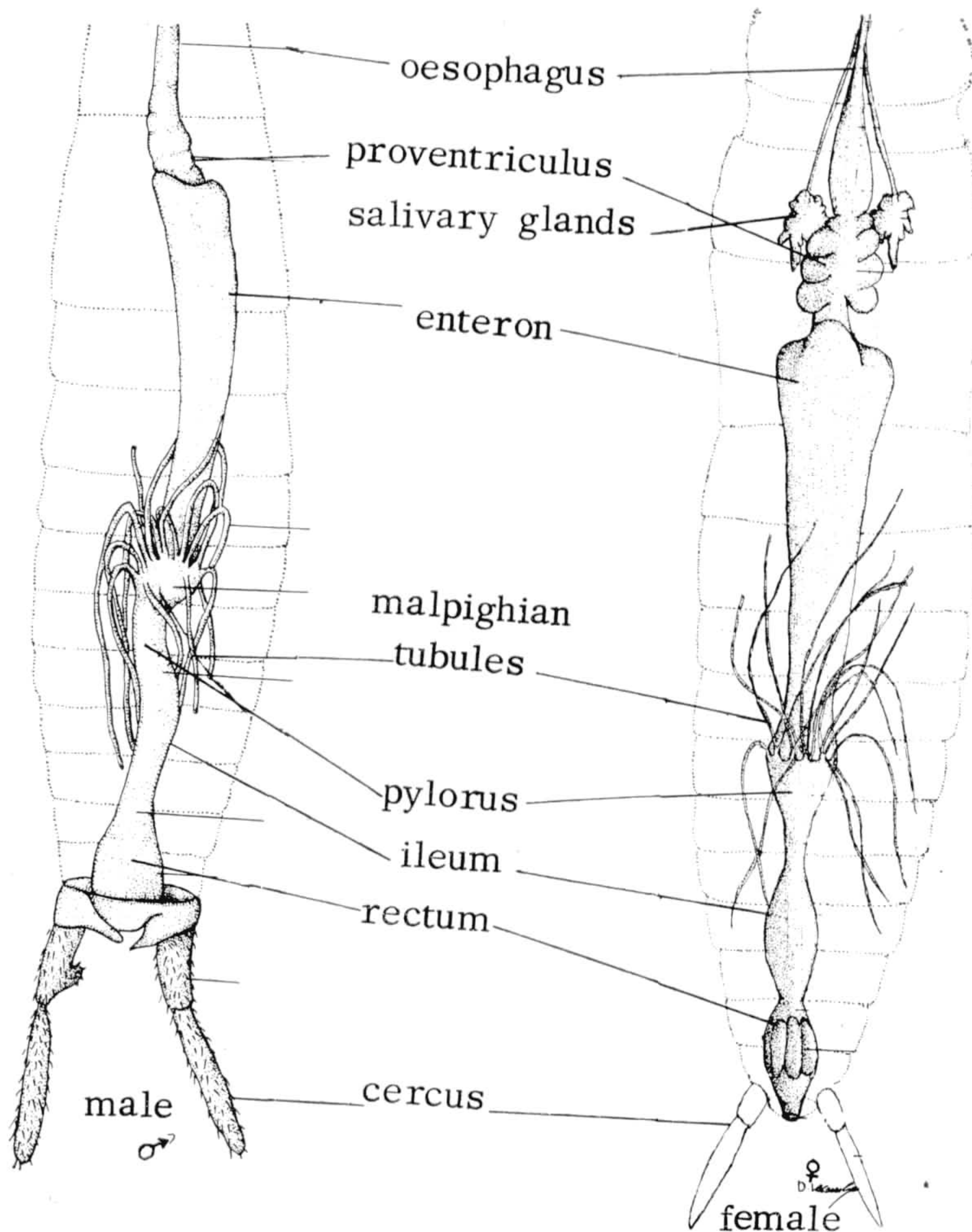


29 — Microstructure of the eye.

The nuclei of the cone-cells are located distolaterally to the crystalline cone and they are very small and contain concentrated chromatin. The cells of the chrystaline cone are elongated and transparent. The receptive parts of the eyes, are composed of eight visual cells. The receptive part of each cell is differentiated into a striated band, the rhabdomere, which compose the rhabdom. The retinular cells have a narrowed base and penetrate the basement membrane, and become fibers of the optic nerve. Elongated pigment cells, commonly found around the retinula, serve to isolate optically each ommatidium from its neighbour. The cytoplasm of the retinular cells is homogeneous and the nuclei is large with the chromatin finely granulated throughout the nuclear plasma.

THE DIGESTIVE SYSTEM

The digestive tract of the *Embioplera* is an almost straight tube. Of all the internal systems, except of course the reproductive, the digestive system has the greatest sexual dimorphism (fig. 30) in the adults. In both sexes, however, the tract includes the same primary regions.



30 — Comparative morphology of the digestive tract of ♀ and ♂

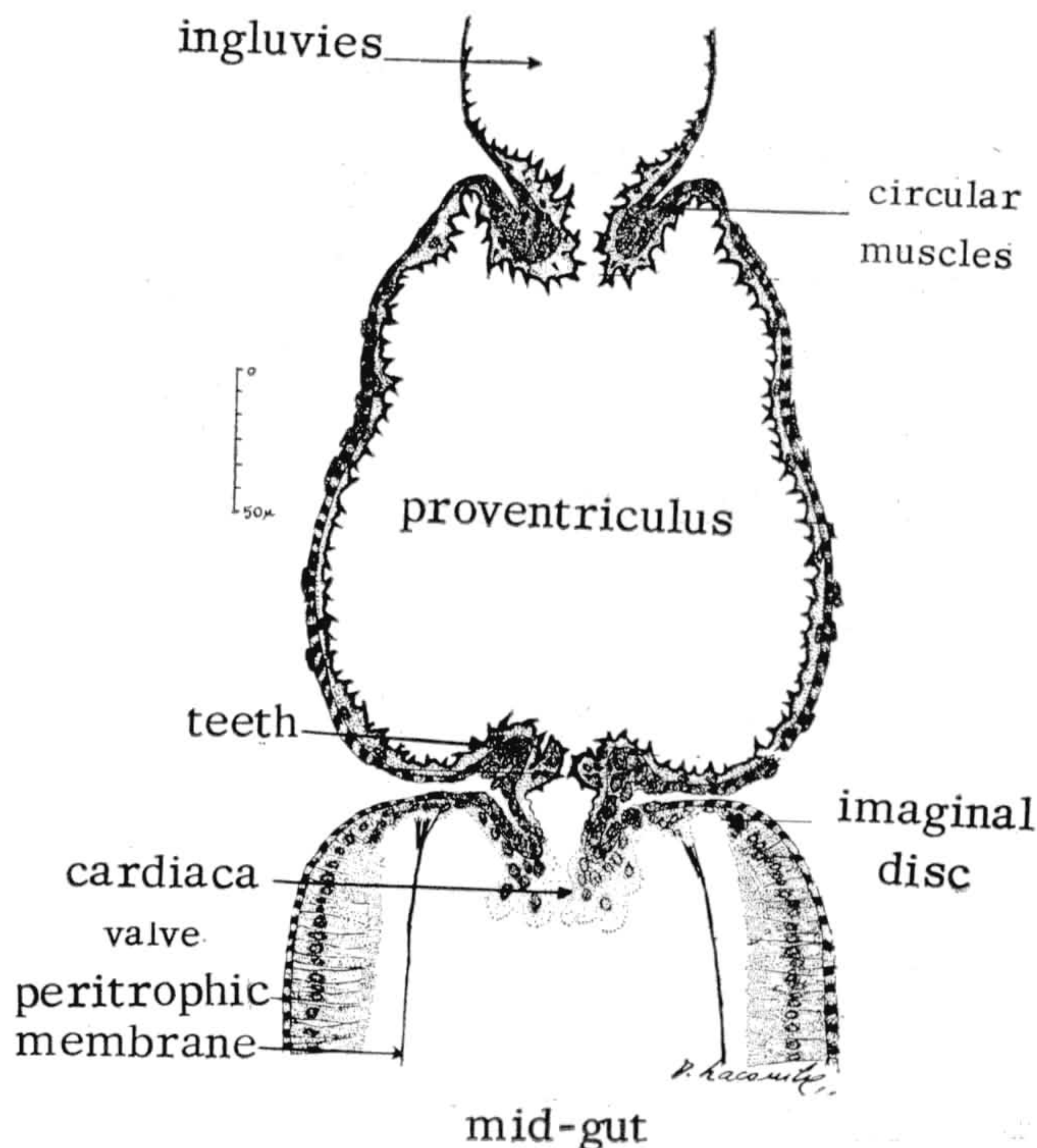
STOMODEUM: The first region, or fore-gut, originates as an anterior ectodermal invagination. The buccal cavity is followed by the pharynx which in female embiids is larger than that of males. In both sexes the pharynx has elaborated musculature attached to

the cranial wall. The pharyngeal wall consists of a syncytial epithelium with a visible basement membrane. The wall of the lumen has many folds which are more numerous in females than in males.

The dorsal wall has a prominence, the epipharynx, covered with many taste sensillae and spines on its cuticular wall (fig. 5). Below this is the hypopharynx which has a similar surface structure. These are specialized surfaces for the ingestion of food.

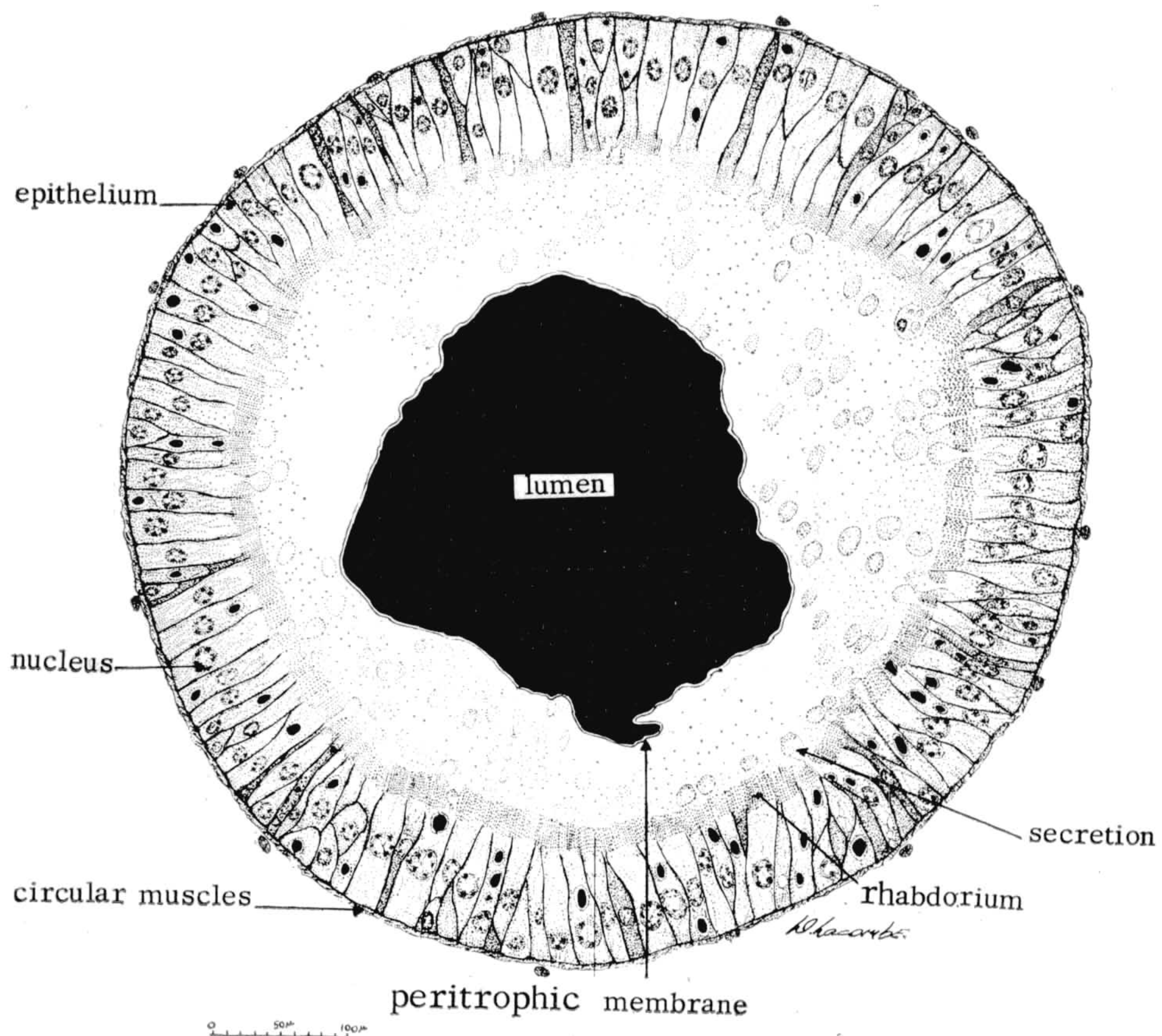
The position of the dilator muscles of the pharynx delimits this intestinal region. This is followed by the oesophagus which is a simple tube, lacking folds, but with many spines throughout the cuticular wall. The oesophagus is limited posteriorly by the crop, or ingluvina, which is well defined in the female but obsolete in males. The crop is only a simple dilatation of the oesophagus and may be a temporary food reservoir. In the *Embioptera* saliva reacts over the food and digestion apparently begins in the crop.

Between the crop and proventriculum there are circular muscles and the crop walls are prominently invaginated to form a sphincter (fig. 31). The proventriculus is more strongly developed in females



31 — Schematic drawing of the proventriculus.

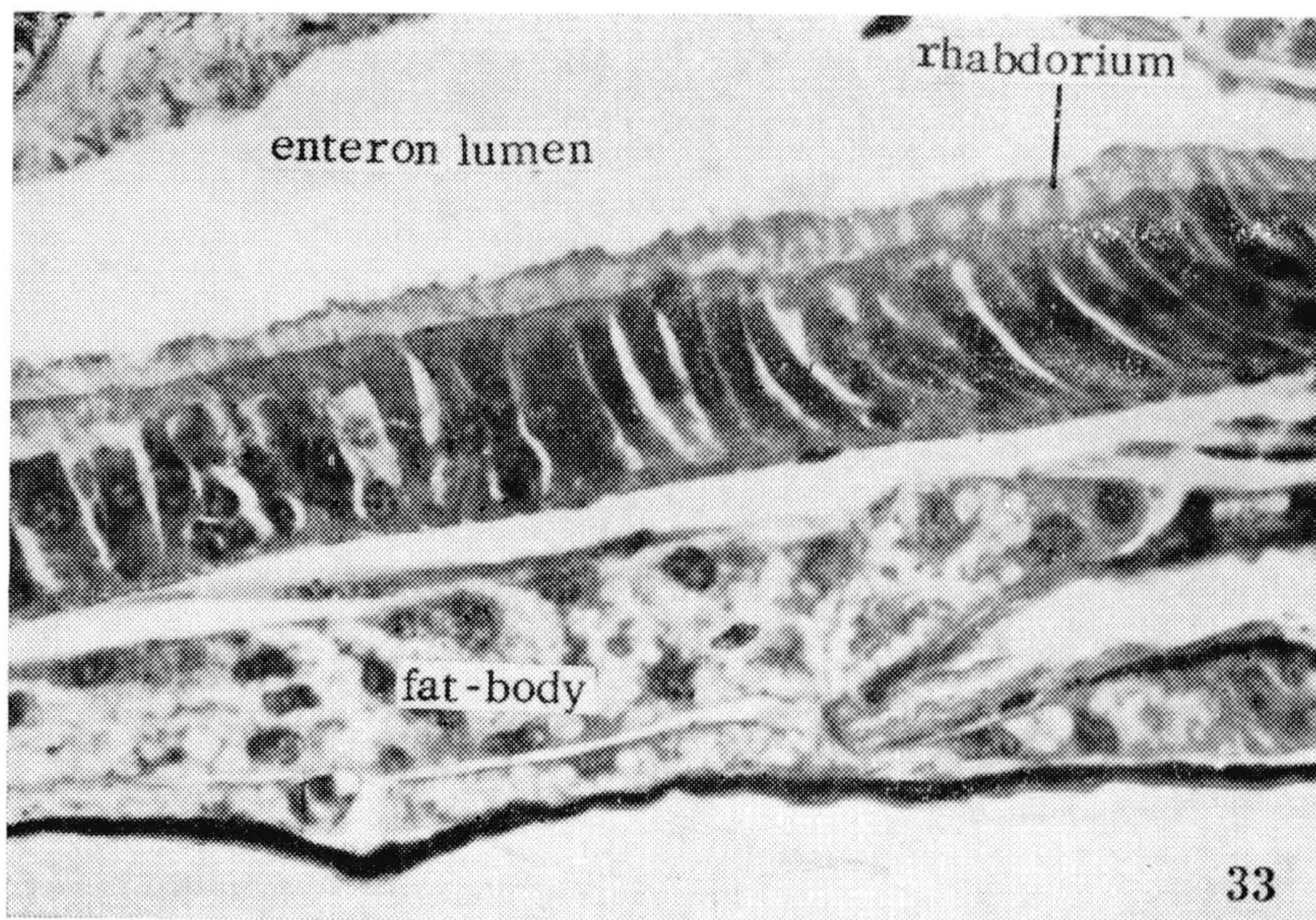
than in males. In females the wall has sclerotic spines throughout and two or more teeth in the posterior extremity which help to occlude the premature passage of food from the fore-gut to the mid-gut. A layer of strong circular muscles runs continuously around the proventriculus. There are also longitudinal fibers. In males (**Lacombe, 1960**), the epithelium of the proventriculus is not strong because it has a fine cuticle without folds, spines, or teeth. The proventriculus functions chiefly in the trituration of food before its passage into the mid-gut through the oesophageal valve. This is composed of a ring fold, which is covered on each side by stomadeal intima (fig. 31).



32 — Histological transversal section by the medium region of the enteron.

In the *Embioptera* the peritrophic membrane is of **Wigglesworth's** Type II (1939), consisting of a single, uniform layer secreted by a group of cells at the anterior end of the mid-gut. The function of the oesophageal valve is to prevent the return of food into the proventriculus during peristaltic movement of the mid-gut.

ENTERON OR MID-GUT: The mid-gut is lined with columnar cells bordered internally by a striated border (fig. 32). The size of these cells vary according to their developmental stage and role in secretion or absorption which correlates with their age. The enteron has a very distinct appearance in the two sexes. In females the cells are very elongated and their cytoplasm and nuclei vary greatly according to their stage and function in the digestive process. **Barth** and **Lacombe** (1955) described these cells in *Embolynta batesi*. When in the resting stage, the cells are very elongated and narrow with dense cytoplasm and undifferentiated granulation. The nuclei are oval with nucleolus and poor chromatin in the cellular periphery. The striated border is long (fig. 33). During progressive changes of cells when

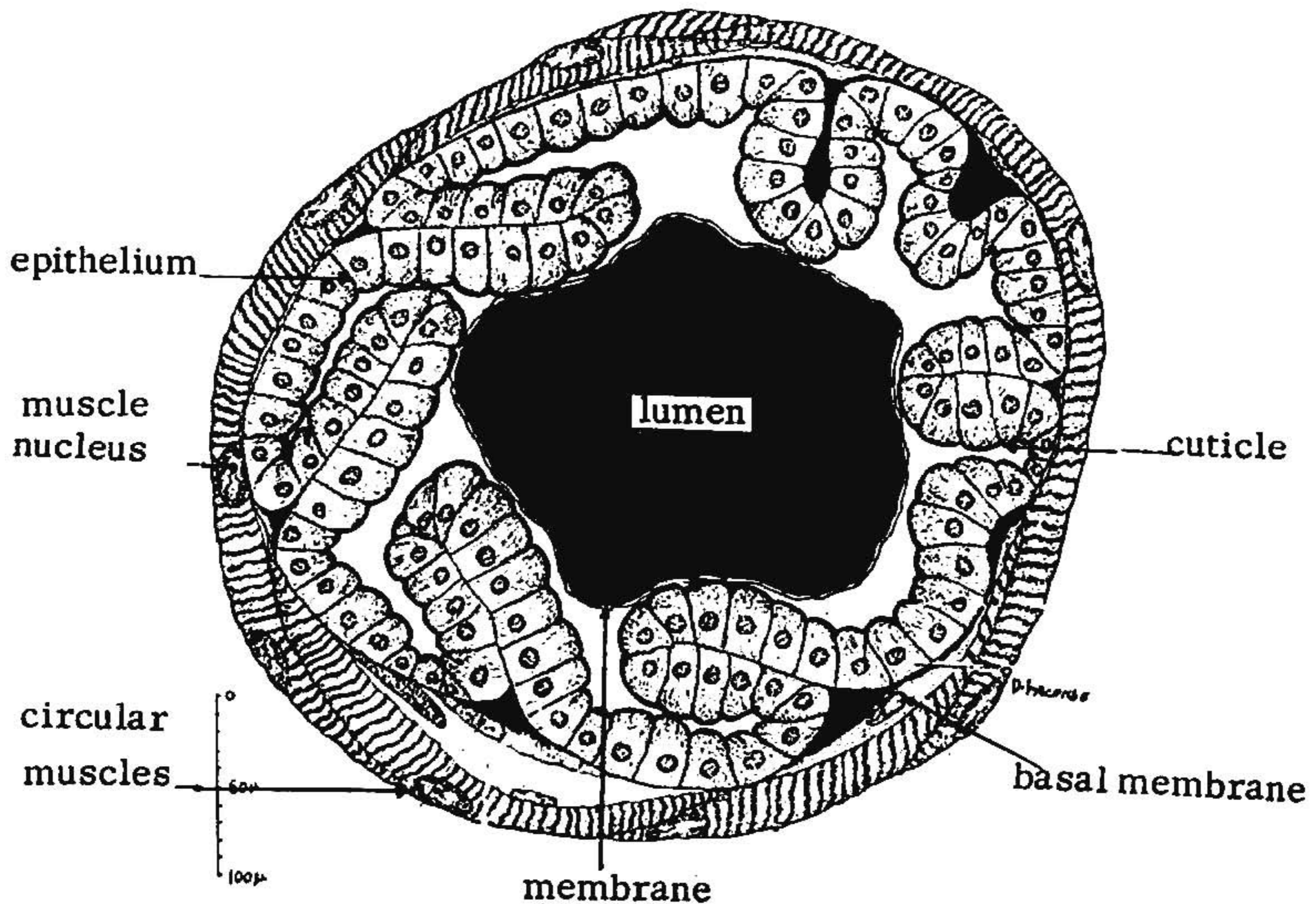


33 — Histological cut of the layer of the enteron, showing the striated border of the longer cells.

secretion begins, the cells grow in size, the cytoplasm is no longer dense and ergastoplasm is visible at their base. After this the rhabdiorial region of the cells rupture and discharge the secretory material into the lumen of the enteron. The cell wall then closes and the striated border rejuvenates.

Among the active epithelial cells, there are regenerating cells which usually form definite groups, or "nidi". New cells which replace the exhausted digestive cells develop in these regenerative centers.

By the use of osmic acid, it is possible to demonstrate the frequent presence of food particles within the mid-gut cells of females. In males of *Embolyntba batesi*, the mid-gut cells near the cardiac valve are narrow with dense cytoplasm and small nuclei. But in all other portions of the enteron the cells are very small and flat. The intestinal cells of males resemble those of females only in the proctodeum-near portion of the enteron.

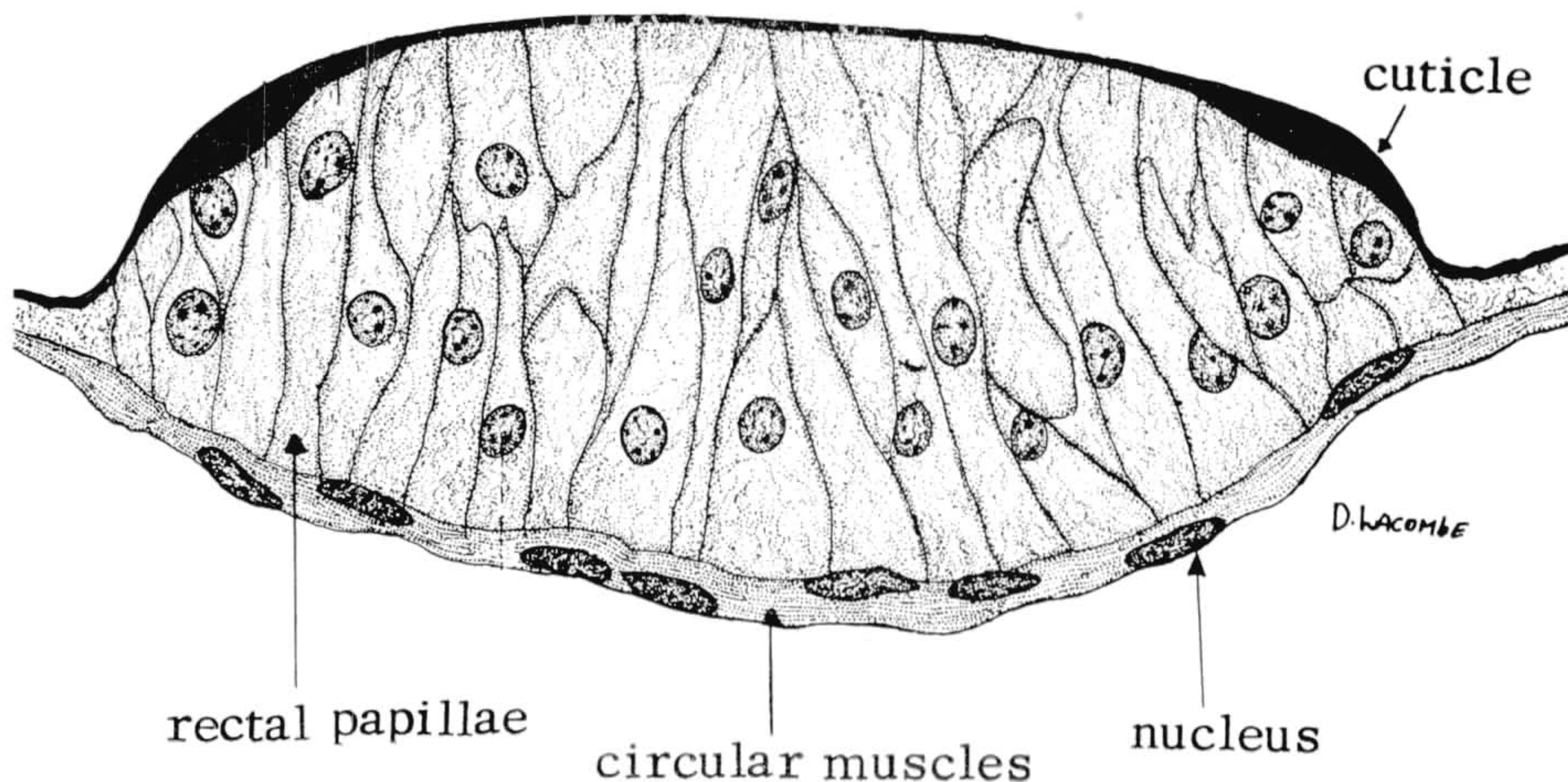


34 — Histological cut from the ileum showing the many folds in its lumen.

PROCTODEUM, OR HIND-GUT: The hind gut is the posterior and like the anterior part also an ectodermal portion of the digestive tract. The anterior portion, or pylorus, is marked by the bases of the Malpighian tubules (fig. 30). The cuticle is thin and thus not similar to that of the oesophagus.

The juncture of the proctodeum and enteron is generally constricted and its aperture regulated by a pyloric valve. The cells of the wall of the pylorus are flat and covered by a fine cuticle. The second portion of the hind-gut, the ileum (fig. 34), has many longitudinal folds in its lumen. Its circular muscles are distinct and its cells are cubiform with centrally-located nuclei.

The rectal portion of the hind gut has six prominent rectal papillae (fig. 35), the same number as in the *Orthoptera* and *Neuroptera*. These papillae are characterized by the increased size of their epithelial cells. These cells form elongate-oval bodies bulging on their lumen side. The papillae are of a simple type consisting of a single layer of cells. The apical section of the cells are covered by a cuticle which is more heavily sclerotized and strong on both sides of each papilla. The microfibrillae of the annular muscles of the region are attached to the rectal papillae.



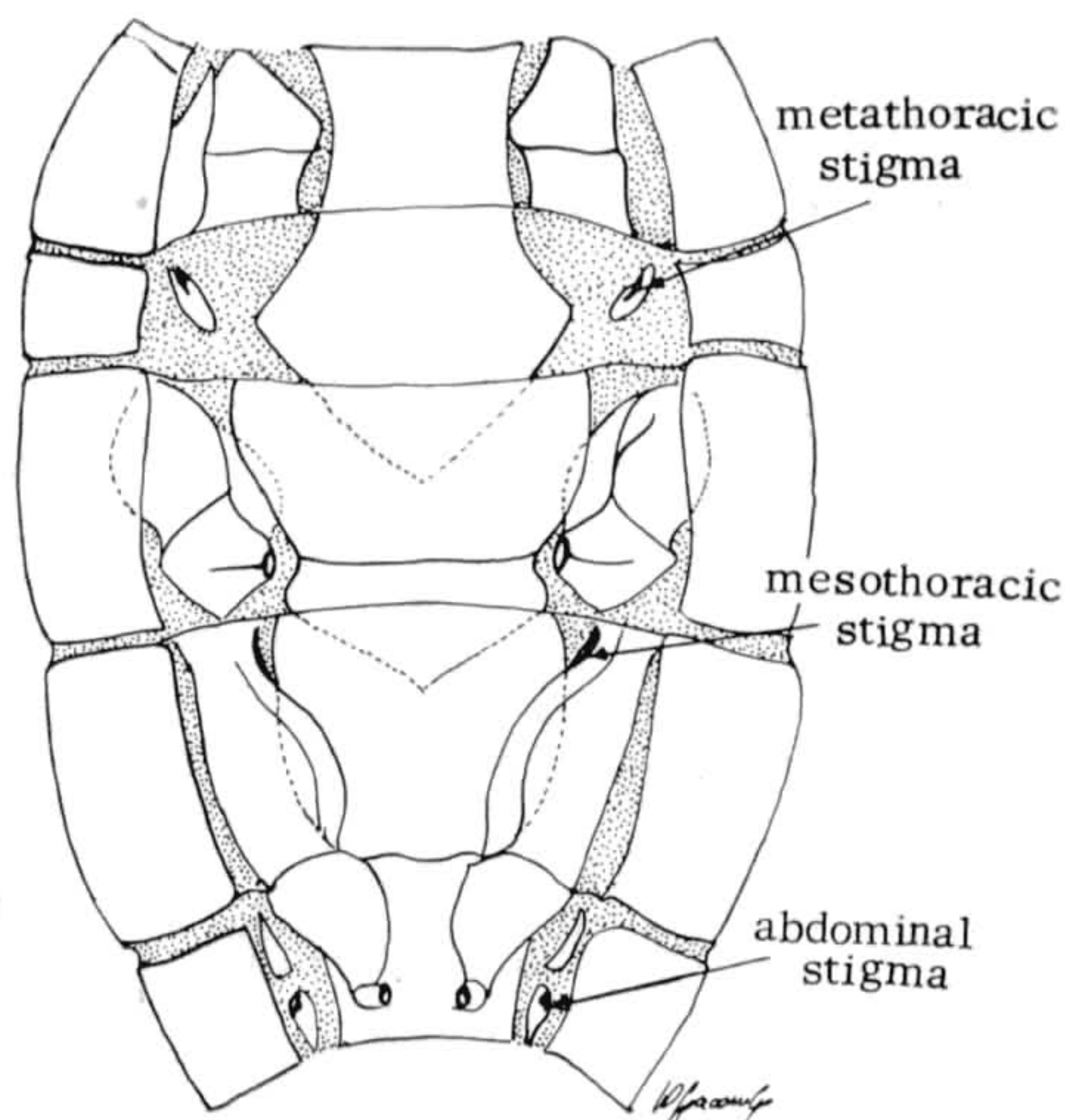
35 — Rectal papillae.

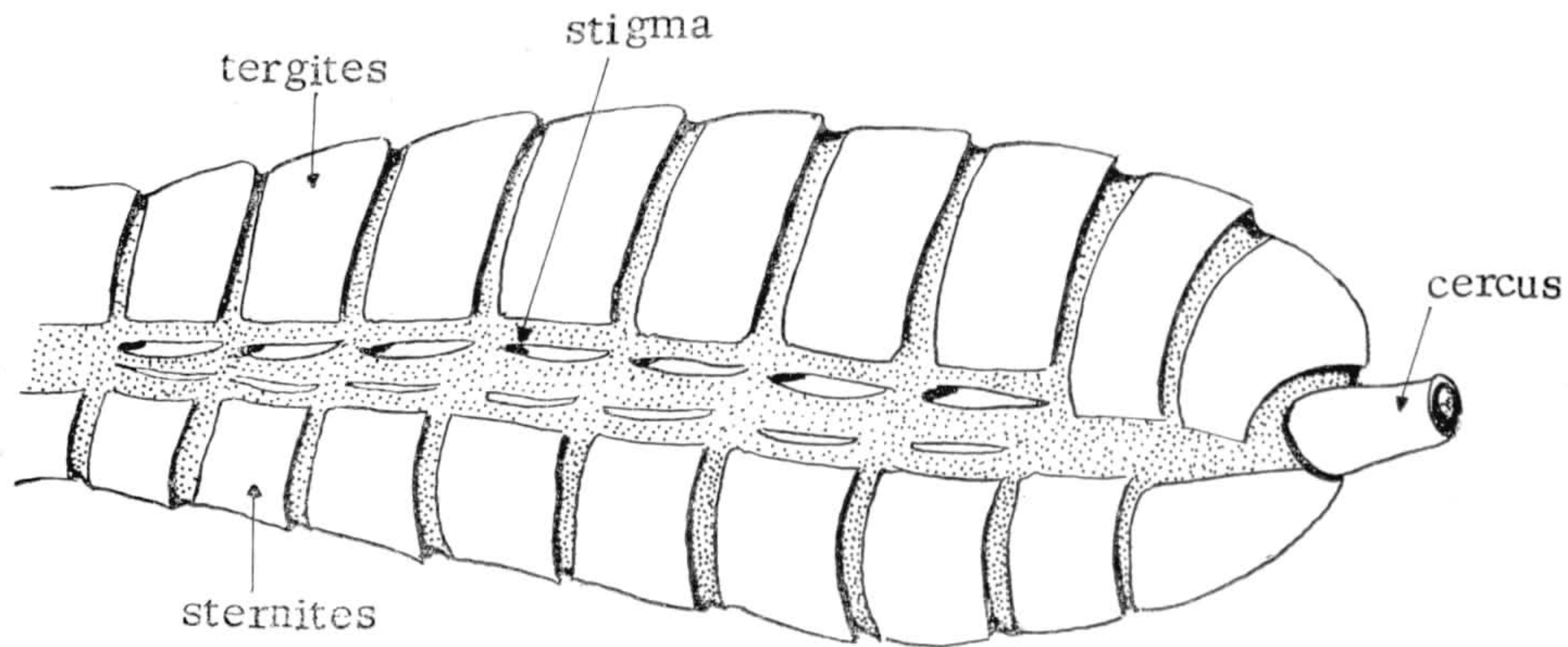
The rectal papillae function is the reabsorption of water from fecal material compacted in the rectum. It serves to maintain the insects water supply (**Wigglesworth**, 1939).

THE RESPIRATORY SYSTEM

Respiration in the *Embioptera* is by means of a complete system of principal and secondary tracheae, and not a segmented system. However, the system is not as complex as that of the *Hymenoptera*, or as simple as in the *Apterygota*, in view of the complex mechanism of the spiracles. **Grassi** (1889) and **Mukerji** (1927) referred to the spiracles of *Embia*, and **Lacombe** (1958) studied the anatomy of the respiratory system of *Embolynta batesi*.

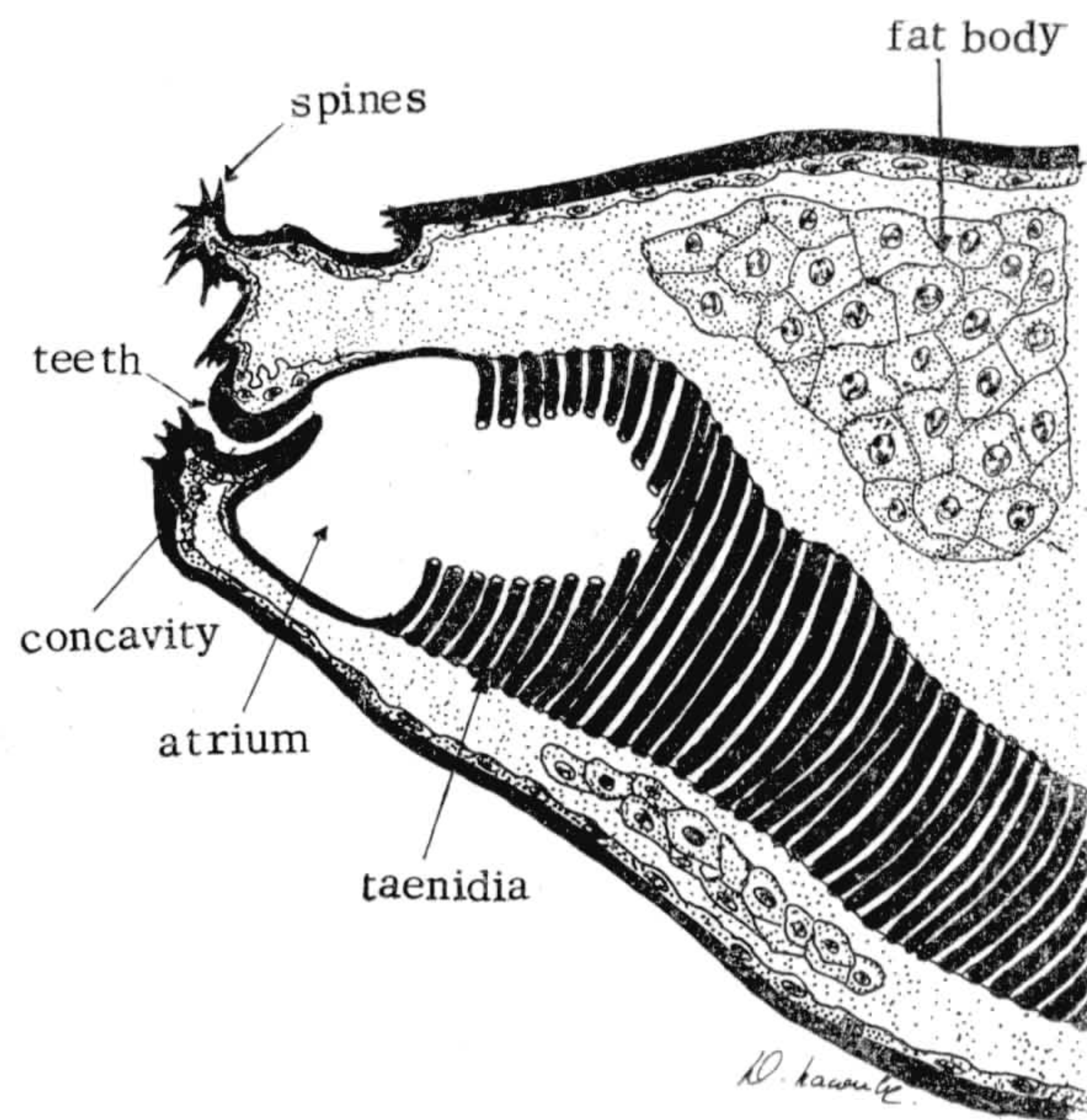
The respiratory system includes ten pairs of spiracles (two thoracic and eight abdominal). All spiracles occur along lateral lines — those of the thorax in a pleural position, those, of the abdomen in the laterotergites (figs. 36 and 37).





37 — Schematic drawing of the position of the abdominal stigmatae.

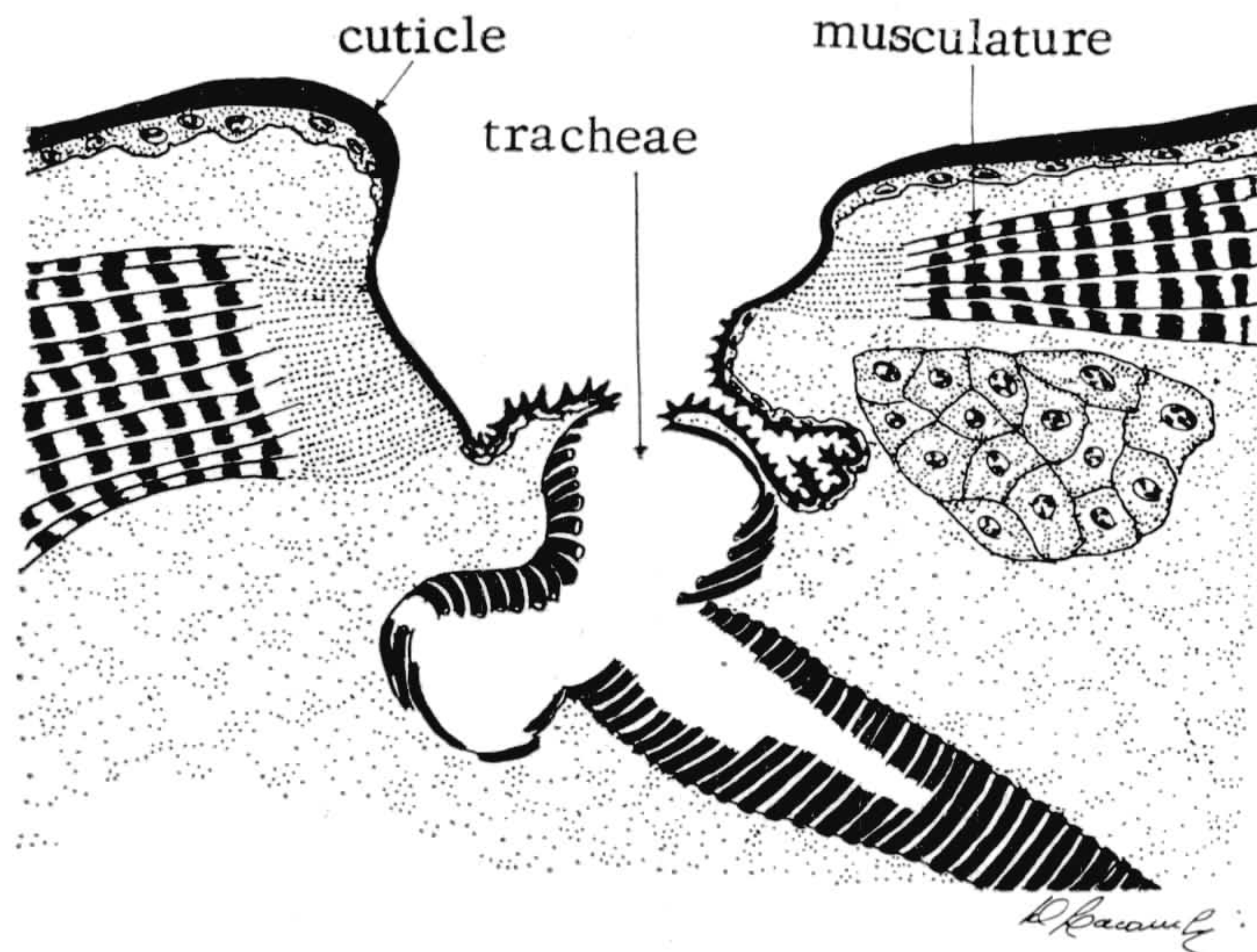
SPIRACULAR STRUCTURE: The mesothoracic spiracles are displaced to the front of this segment, behind the first pairs of legs. These spiracles are very easily to be located because of their position on 3 spiracular lobes and their large size — larger than all other spiracles. In the median portion of this spiracle (fig. 38) there is one long opening bordered by many spines, variable in position, which protect the entrance of the atrium.



38 — Anatomical view of the mesothoracic spiracles, showing the various parts.

The cuticle in the anterior region of the atrium (fig. 38) is thicker and has one strong tooth, which inserts in an opposing concavity when the spiracles are tightly closed. The aperture of this spiracle is never complete — only a medial portion can be opened. This opening occurs when muscles in the ventral region of the spiracle are contracted and cause the lowering of the concavity opposite to the sclerotic tooth. The thoracic muscles also assist in the inspiration of air. The spiracle is closed by cuticular elasticity during relaxation of the thoracic muscles which are thus indirectly responsible for the movement of air into the trachea. The mesothoracic spiracles function only for the inspiration of air.

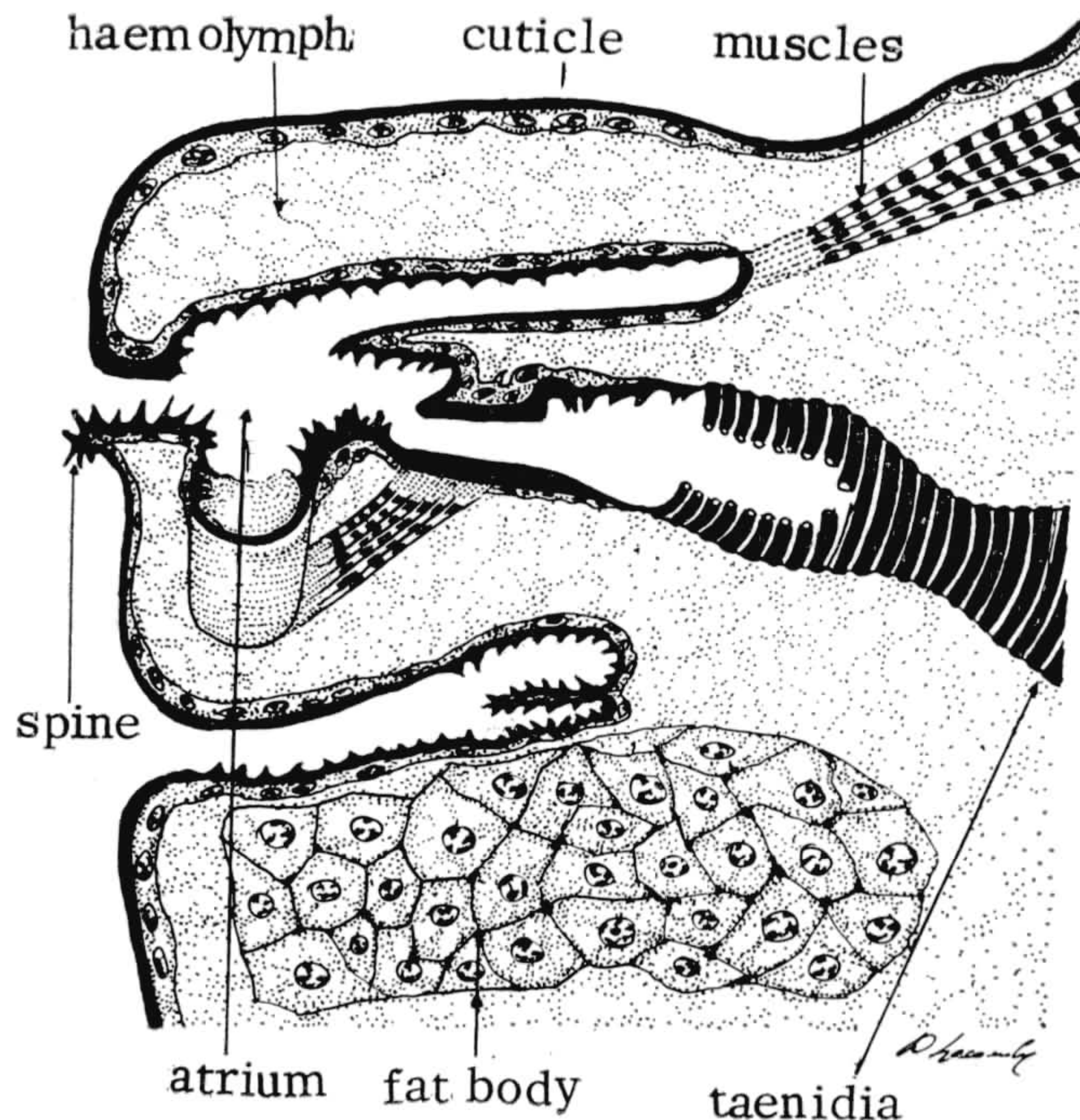
The metathoracic spiracle (fig. 39) is located in the pleural region above the third pair of legs and is sometimes covered by these legs during locomotion. Its form is elliptical and has neither spines nor a combination of a tooth and concavity. The cuticle is very fine with many folds around its opening. These spiracles function only in the expiration of air. The spiracles open as tergo-sternal muscles contract and flatten the folds surrounding their openings. When these muscles relax the spiracles are closed.



39 — View of the metathoracic spiracle.

The abdomen has eight pairs of spiracles, each located in the anterior part of the laterotergites (see fig. 37). The first pair is dislocated into a metathoracic position behind the third pair of legs.

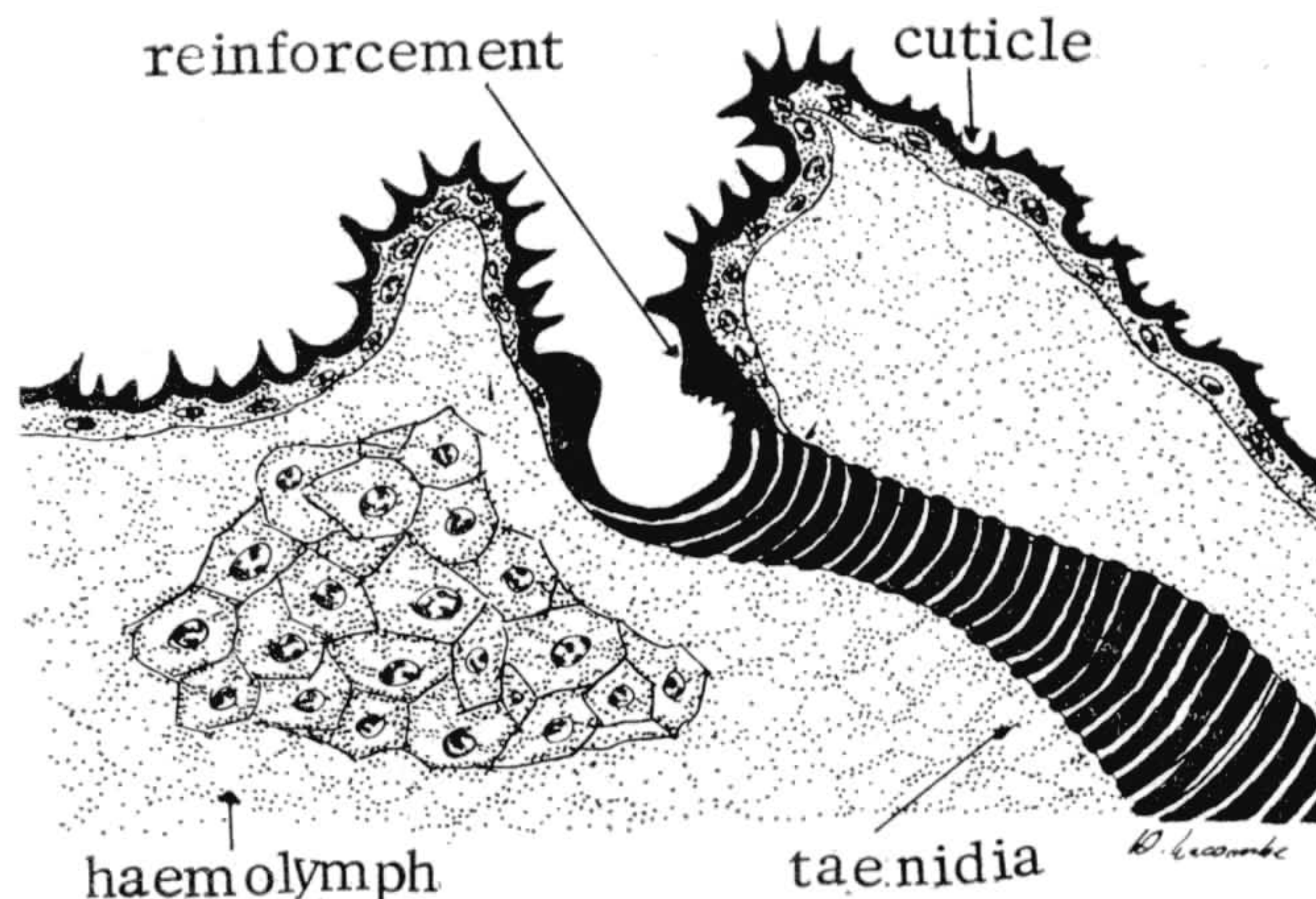
Verhoeff (1904) reported only seven abdominal spiracles and three thoracic spiracles, because he erroneously regarded the spiracles of the first abdominal segment as belonging to the metathorax. All abdominal spiracles have a similar funnel-like shape and many long and marginal spines. All abdominal spiracles have the same air inspiration function.



40 — Histological section of the first abdominal spiracle, showing its structure.

The first pair of abdominal spiracles have a distinct microstructure (fig. 40). In the region where the tracheae join the spiracles the cuticle is more sclerotic and serves to close the spiracles during expiration of air though the metathoracic spiracles. The atrium has many spines located on the same level as the closing structure. Muscles associated with such closure have an oblique position and an attachment in the atrium wall and in the cuticle of the laterotergite. By the contraction of these muscles the spiracles are opened. The muscles of the tergites help the spiracle muscles in increasing the volume of the abdomen and thus the air inspiration.

The other seven pairs of abdominal spiracles have a structure similar to that of the first pair, but with more spines in the atrium (fig. 41). In this series each atrium represents an accentuated lateral invagination, like a spine-lined pouch. The spiracular muscles are attached to the cuticle of the atrium. When the abdomen is dilated by distension of the dorso-ventral muscles, and those of the spiracular opening, inspiration occurs. The closure of the spiracle is passive.



41 — Anatomical view of the second abdominal spiracles.

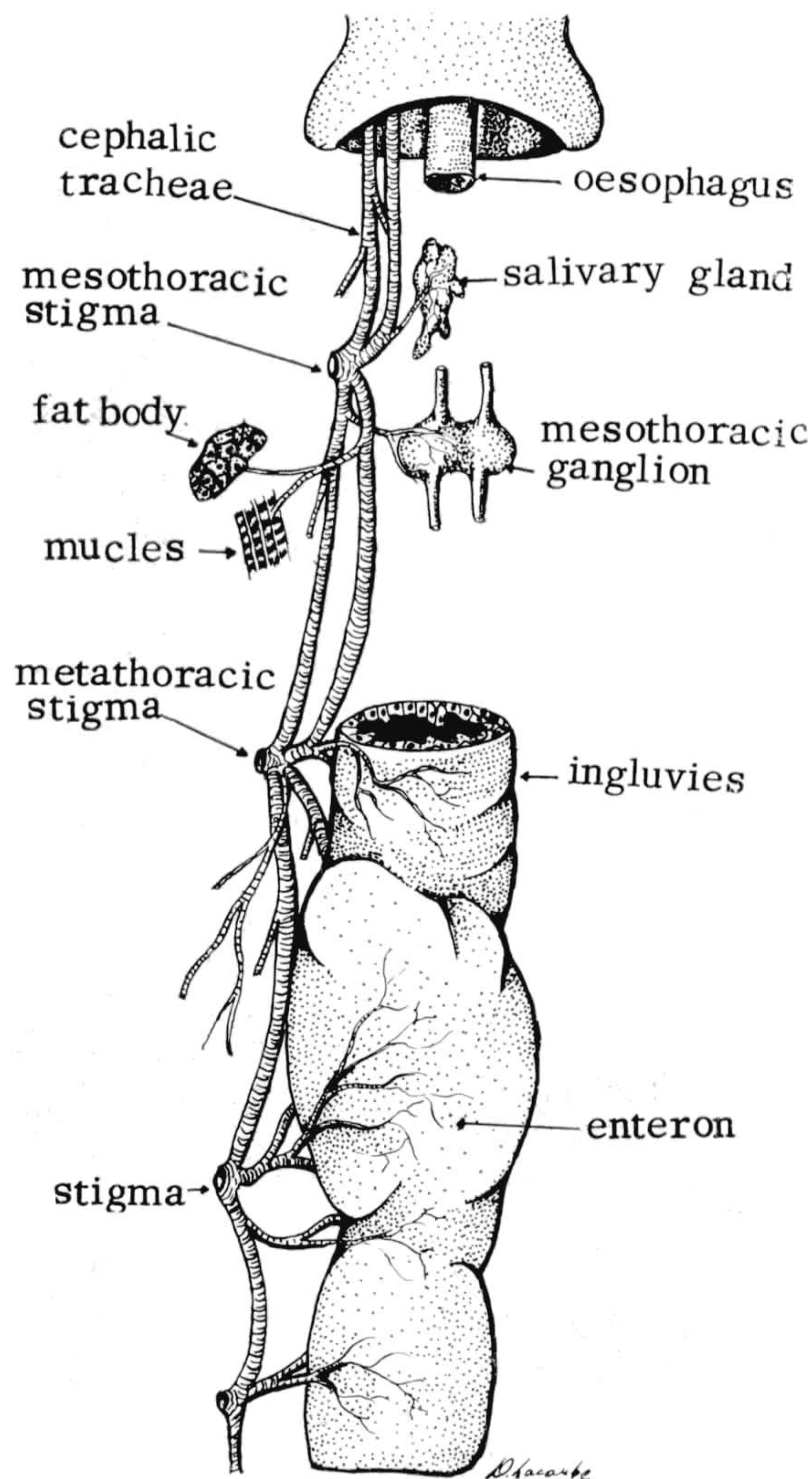
TRACHEAL SYSTEM (fig. 42): The tracheal system in the *Embioptera* is of the holopneustic type and similar to the most of all other insects. Each trachea consists of a layer of epidermal cells and a cuticle. Folds in the interior cuticle form spiral filaments, or taenidia. *Embioptera* have no air sacs.

The mesothoracic spiracles have two pairs of major tracheae directed toward the head (fig. 42). These are the largest tracheae in the body. During the course of the ventral trachea the prothoracic legs and the prothoracic ganglion are provided. Within the head this ventral trachea sends branches to the macilae and labium, etc. The dorsal trachea sends branches to prothoracic muscles, fat-body, ingluvia, oesophagus, antennae, eyes, mandibles, etc. The tracheal branch serving the salivary glands originates near the mesothoracic spiracles between the dorsal head trachea and the ventral head trachea.

From the mesothoracic spiracles also rise two caudally-directed major tracheae. These tracheae (fig. 42) provide tracheation to the mesothoracic legs and ganglion, fat-body, muscles, and the anterior

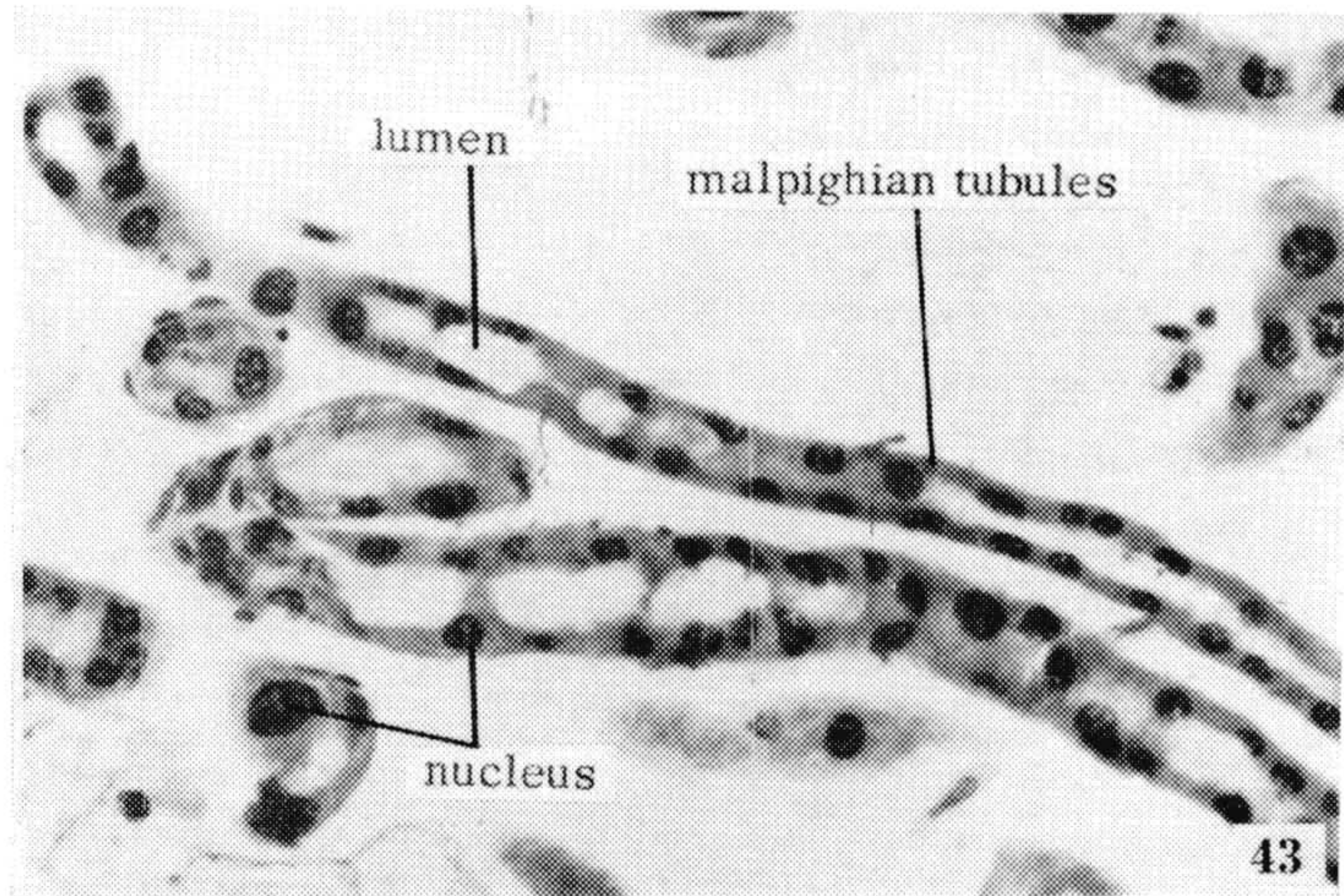
portion of the proventriculus. Both of these major, longitudinal tracheae connect with the metathoracic spiracle. In turn two longitudinal tracheae connect with the first abdominal spiracles. During the course the latter branches are directed to the metathoracic legs and ganglion, muscles, and the posterior portion of the proventriculus.

The first abdominal spiracles receive the two longitudinal tracheae from the metathoracic spiracles and each sends a principal trachea to the second abdominal spiracle. These immediately give

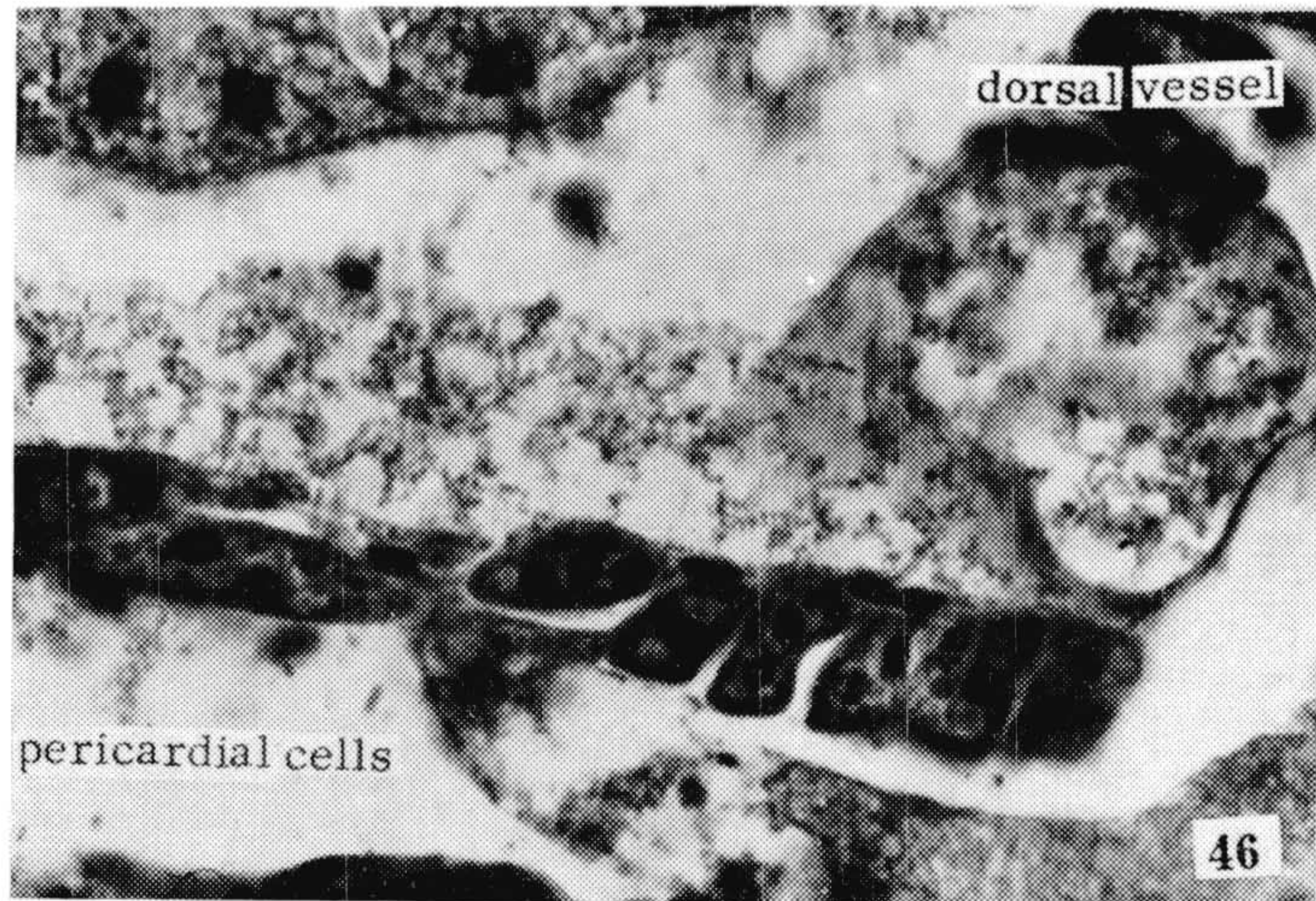


42 — Schematic drawing showing the disposition of the tracheae system related to other system.

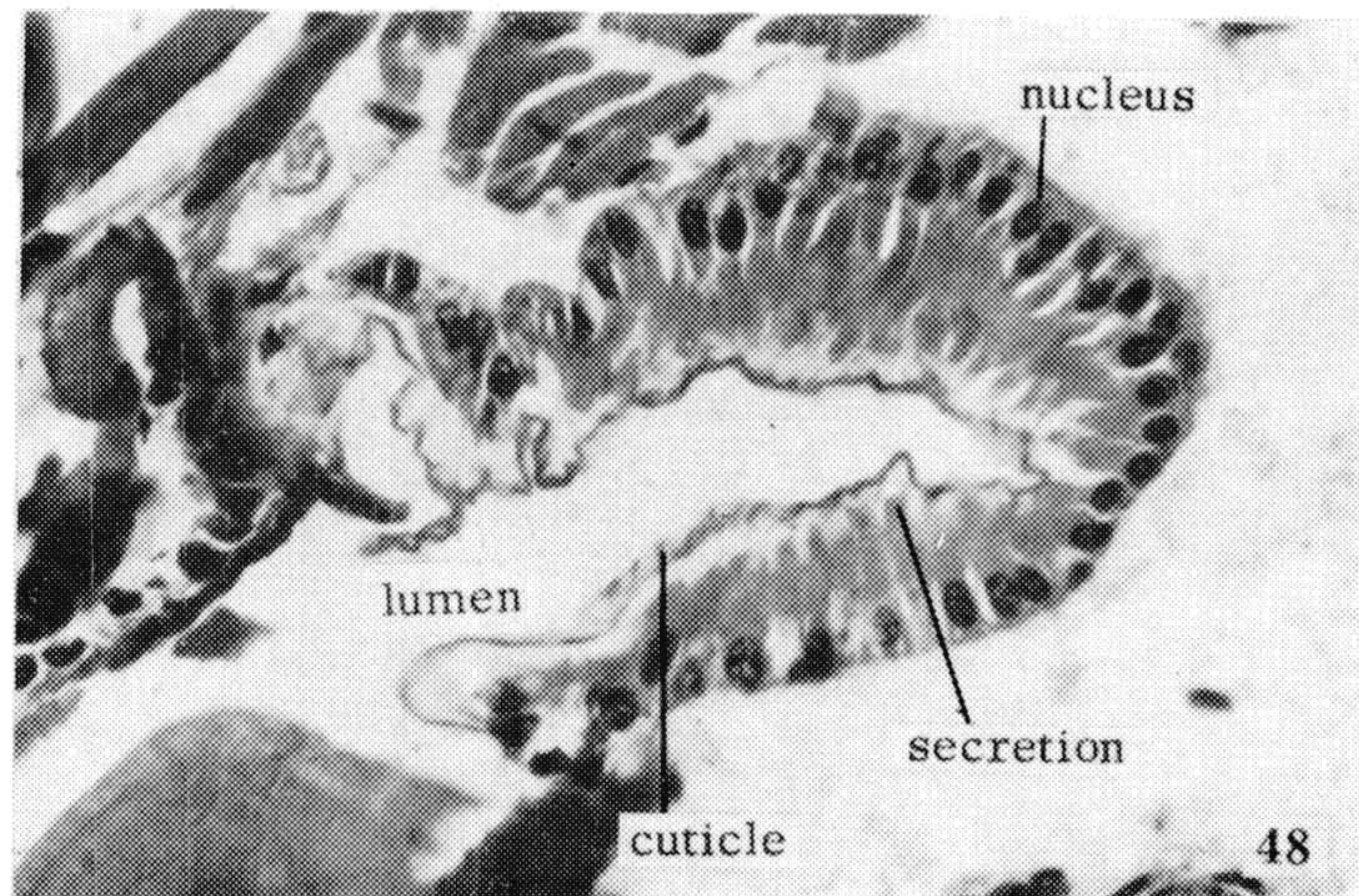
43 - Histological longitudinal section of the Malpighian tubes.



46 - Histological cut from the pericardial cells.



48 - Histological section through the mandibular gland.



rise to a dorsal and a ventral branch which tracheate the anterior region of the enteron and form the transversal ventral commissures connecting the lateral branches of each abdominal segment. Before joining the second abdominal spiracles there are new branches to the visceral system. All remaining abdominal tracheation repeats this pattern.

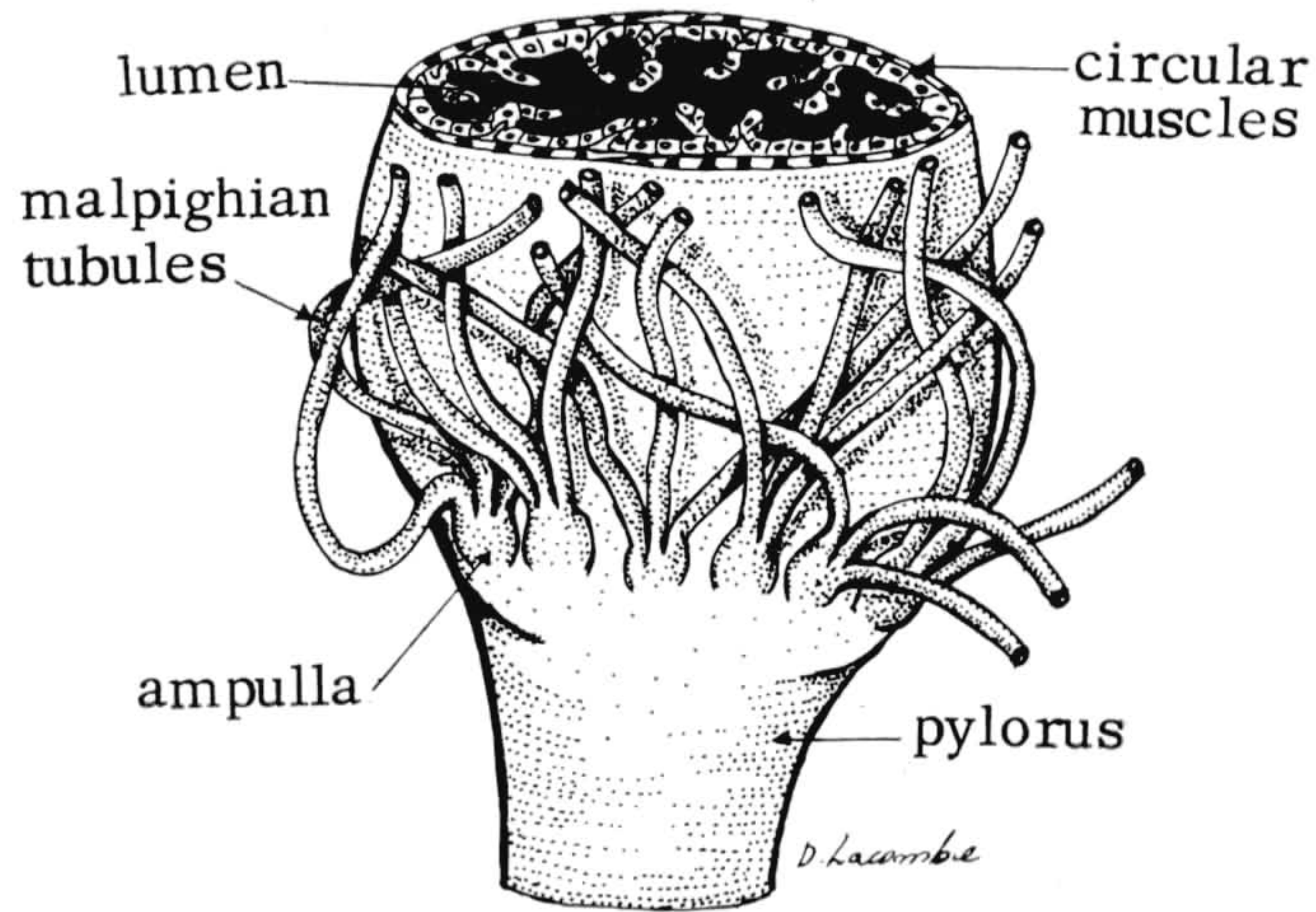
Lacombe (1958) concluded that there are two directions of movements of air in the tracheal system of *Embolynta batesi* which correlate with the structure of the various pairs of spiracles. In the first, the air enters the mesothoracic spiracle and passes forward into the head and is expelled via the metathoracic spiracle. In the second system, air enters all abdominal spiracles and passes forward into the metathorax and is expelled by the metathoracic spiracles.

THE EXCRETORY ORGANS AND FAT-BODY

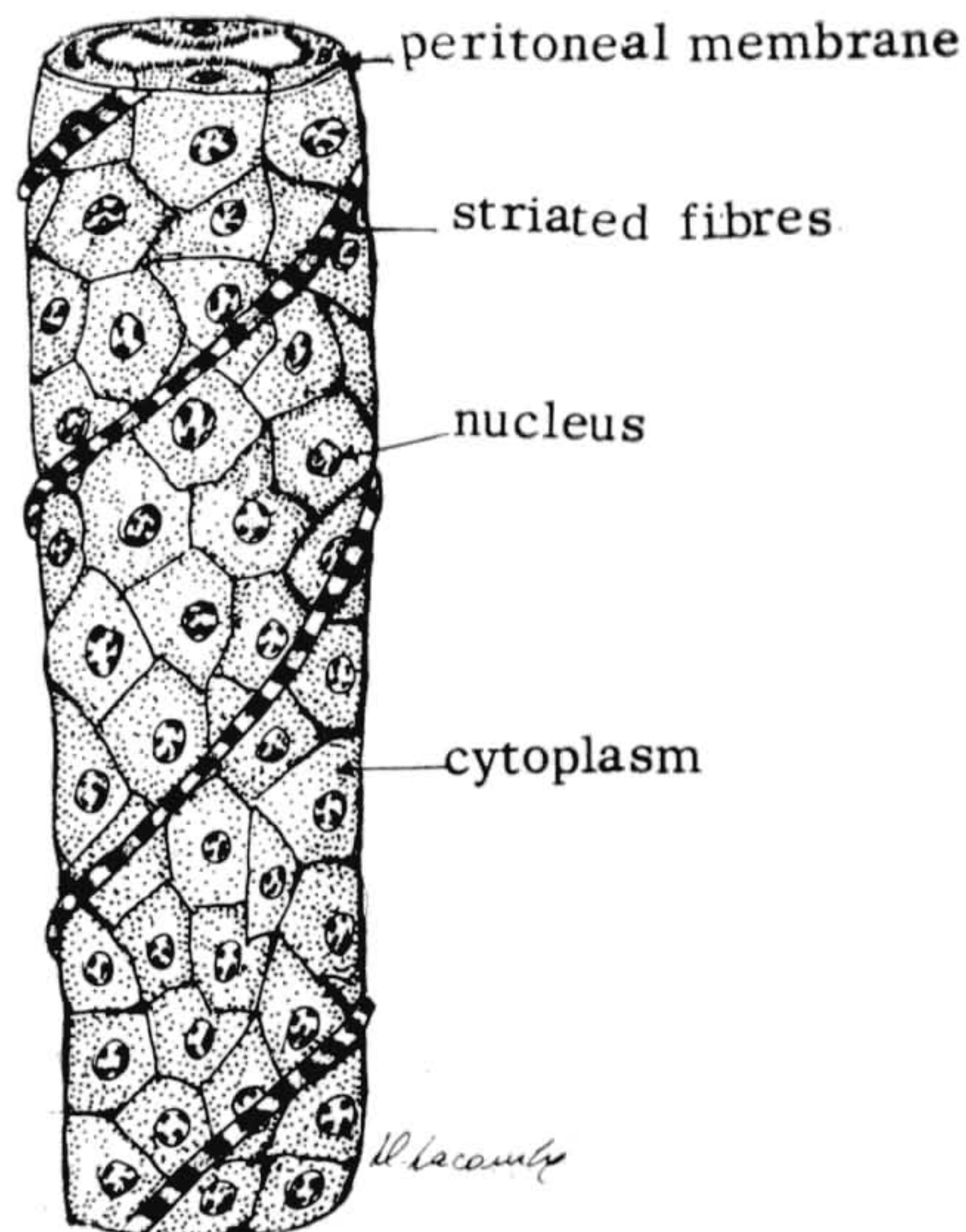
The excretory organs include the Malpighian tubules, the fat-body, masses of pericardial cells, and groups of similar cells in other parts of the body, including cells of the haemolymph.

MALPIGHIAN TUBULES: These are specific excretory organs in insects, and their general structure, histology, and physiology have been discussed by many authors. **Marchal** (1890-96) treated the excretory system of all animals. **Veneziani** (1940). **Lison** (1937), and **Palm** (1946, 50, 52) reported on the elimination of different stains by the Malpighian tubes in insects. **Wigglesworth** (1931), using *Rhodnius prolixus*, showed that walls of the tubules change in structure from section to section.

In the *Embioptera* tubules are very long, narrow, epithelial tubes, (fig. 30 and fig. 43). They are found in groups of three or four tubules, per base or ampulla, forming sets of seven or nine, depending on the genus. **Lacombe** (1965) found a total of twenty-one tubules in groups of three in seven ampullae in *Embolynta batesi* and these exhibited interesting alternating, regular arrangements at their bases (fig. 44). On each ampulla base two tubules project together while the third branches. On the next base the third tubule angles in an opposing direction. As in all insects, the tubules arise at the juncture of the enteron and proctodeum. Their extremities extend entirely free in the body cavity but linked to each other by tracheae.



44 — Anatomical disposition of the Malpighian tubules



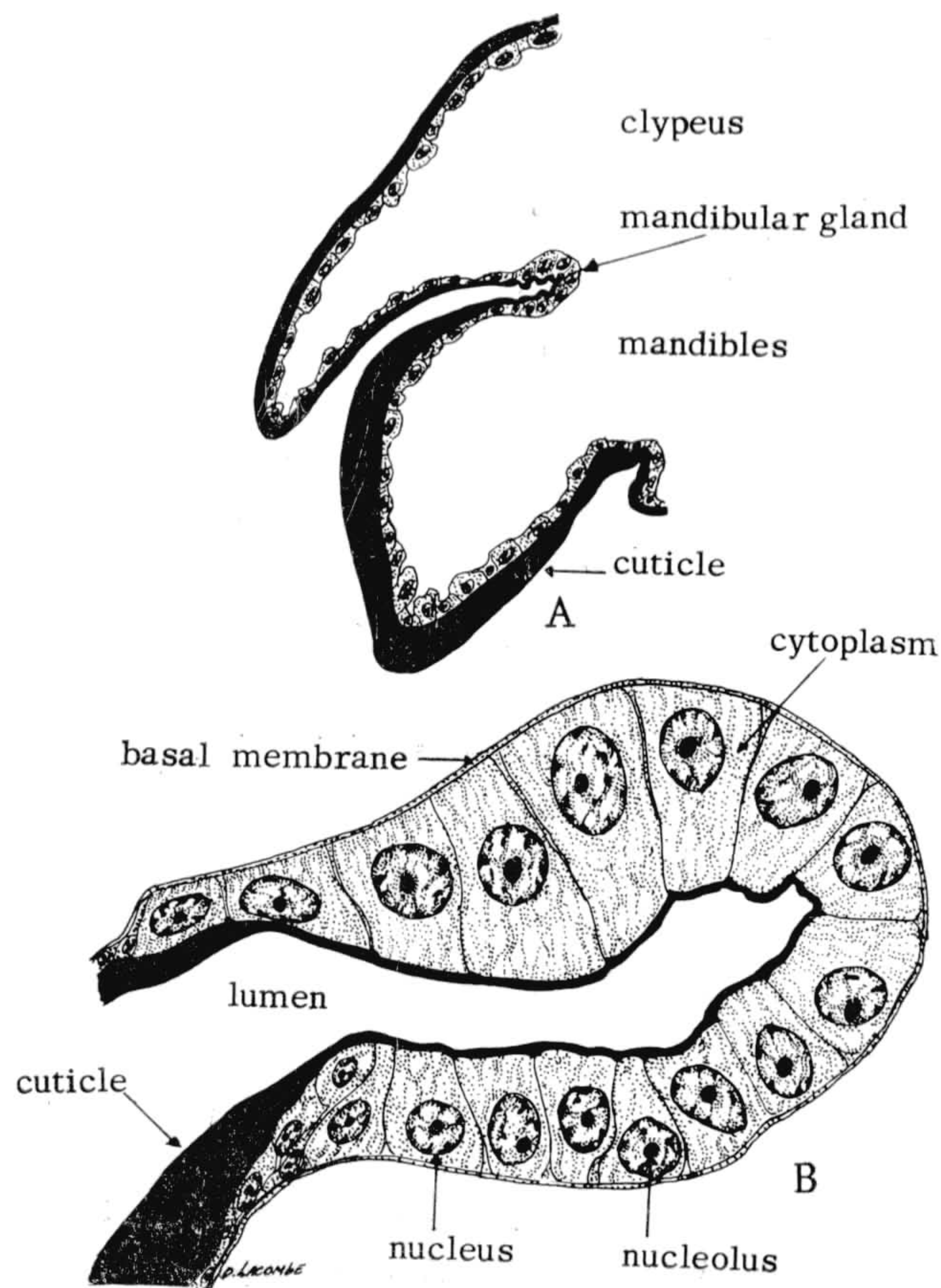
45 — Schematic drawing of the Malpighian tubules showing the striated fibers around the tubules.

Histological sections of the distal epithelial cells have striated borders (rhabdoria). The largest cells in a more advanced stage have the shortest rhabdoria and a greater excretory function. These cells are about 26 μ . height before excretion and 14 μ . after excretion. Their

cytoplasm is not very dense and sometimes shows mitochondria accumulations at the bases of the rhabdioria. The nucleus of such cells is large (fig. 43) and has two or more nucleoli. The chromatin is dense and dispersed through the nucleoplasm.

As in other insects (Leger and Duboscq (1899); Bordas (1916); Trappman (1923); Wigglesworth (1931), and Palm (1946) the *Embioptera* has two long muscular layers beneath the peritoneal covering of each tubule. These consist of a single layer of striated fibers forming wide spirals around the full length of the tubules (fig. 45).

Lacombe (1965) observed numerous spherical urate particles of different sizes in the lumens of the tubules of males and females of *Embolynta batesi*. These particles are also visible in the cytoplasm of the epithelial cells in histological sections, stained with nuclear fast red and naphthol green.



47 — Localization and histological view of the mandibular gland.

FAT-BODY: The fat-bodies are composed of irregular masses of polyhedral cells which contain many vacuolated inclusions of various kinds. In the female of the *Embioptera* it is possible to distinguish a parietal layer of fat-bodies beneath the body wall and an inner or visceral layer which surrounds and lies between the various organs. In males the visceral layer is denser around the digestive tract and in both sexes the fat-body even extends into the second segment of the cercus.

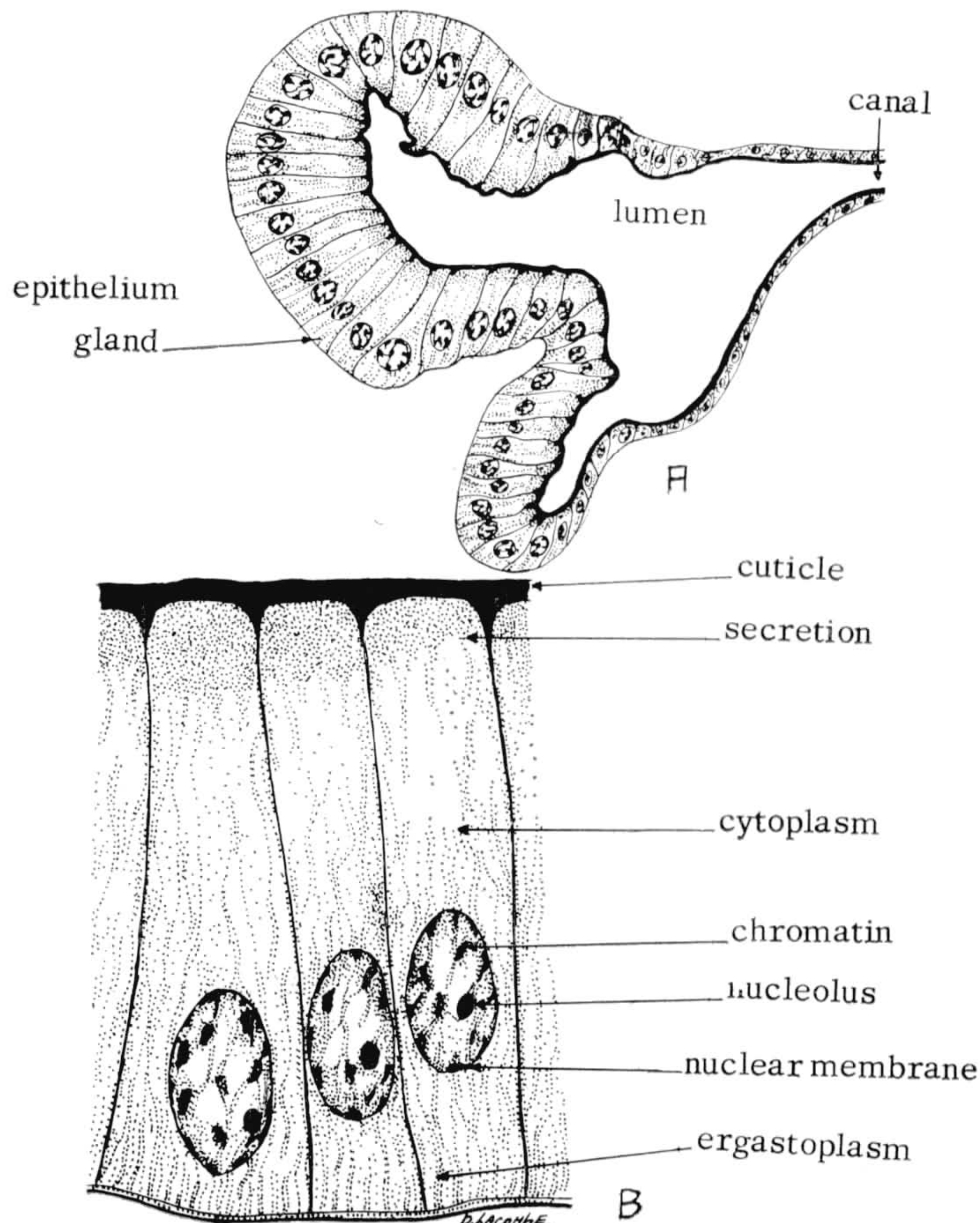
NEPHROCYTES OR PERICARDIAL CELLS: These cells principally occur in the pericardial sinus where they form masses on each side of the heart (fig. 46). **Hollande** (1921) studied the physiology of these cells in insects and pointed out their important role in excretion. In the *Embioptera* they occur around the entire dorsal vessel and its alary muscles and enter the head near the apical opening of the heart. The cells are large, numerous, almost filled by the nucleus, and contain many vacuoles and crystals. **Lacombe** (1965) observed that they absorb trypan blue and ammonia carmine.

GLANDS OF APPENDAGES

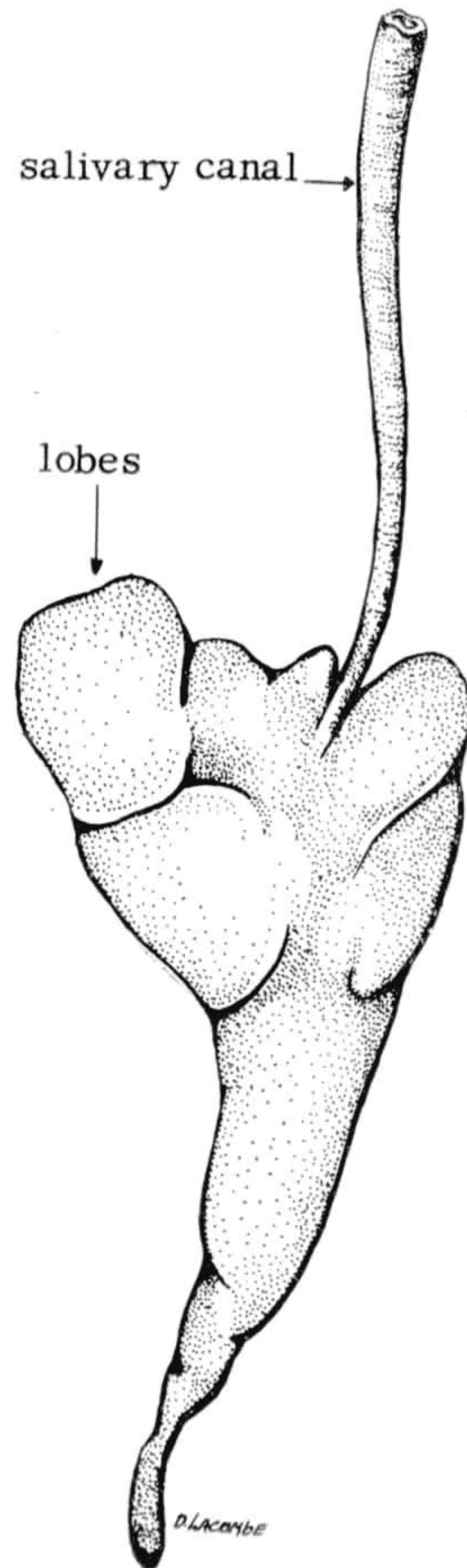
All glands of the head are entirely of ectodermal origin being derived from invaginations of hypodermal epithelium. In the *Embioptera* there are paired mandibular, maxillary and labial glands.

MANDIBULAR GLANDS (fig. 47): These are found in the dorsal articulation membrane of the mandibles beneath the labrum and clypeus (fig. 47-a). In the *Embioptera* the glands are represented by a simple increase in hypodermal cells at the base of the mandibles. The secretion of these cells probably aid the digestion of food. Histological sections show that the gland cells (fig. 47-b and fig. 48) have large nuclei which are rich in chromatin near the nuclear membrane. The nucleoli is centrally located in all gland cell nuclei. The cytoplasm is granulated, dense, and homogeneous with fine ergastoplasm at the base of each cell. The secretions which are diffused throughout the cytoplasm, originate in the basal end of the cells and exude through a fine membrane into the gland lumen when the cells are active. Such secretions are of apocrinal type.

MAXILLARY GLANDS (fig. 49): These are larger than the mandibular glands but have a similar origin and appearance. They are located in the membrane between the maxillae and labium and consist of invaginations extending deep into the head cavity. (fig. 49-a). Each gland cell is tubular in shape. Their cytoplasm is fine with accentuated ergastoplasm in the base (fig. 49-b). In each cell the secretions which accumulate at the anterior end beneath the cuticle of the lumen form a differentiated zone. Chromatin is distributed throughout the nuclear membrane. During secretory activity the nucleus shifts from a basal position to a medial position in each cell. As in the mandibular glands, the secretions pass through the cell walls into the gland lumen and probably assist digestion of food.



49 — Microanatomy of the maxillary gland.



50 — Morphology of the salivary gland.

LABIAL OR SALIVARY GLANDS (fig. 50): These are the largest glands in the head. They are invaginated in the ectodermal epithelium between the maxillae and labium. Their size and shape are highly variable in insects. Those of the *Embioptera* are simple in form, having long excretory ducts and extend into the meso and meta-thorax. In the enlarged gland body, where the active cells are located, there are many lobes which progressively secrete into the reservoir portion of the gland. These gland bodies are located on either side of the proventriculus. The glandular epithelium in the *Embioptera*

is aciniform and the cells are of different sizes (fig. 51). The salivary ducts are located along the side of the oesophagus and open at the ventral base of the hypopharynx. The secretory function connected with food ingestion has been observed by means of injections with indigocarmin and trypan blue stains into the gland body (Lacombe, 1965).

THE CIRCULATORY SYSTEM

The body of insects is divided longitudinally into three sinuses by dorsal and ventral diaphragms: (a) the pericardial sinus that extends across the abdominal cavity above the alimentary tract and encloses the dorsal vessel and surrounding blood space; (b) the visceral sinus which contains the principal internal organs and (c) the perineural sinus which encloses the ventral nerve cord. Both diaphragms are perforated. To this date little has been published on the heart of *Embioptera* except for a brief reference to that of a species of *Oligotoma* in a comparative study of the dorsal vessel of orthopteroid insects by Nutting (1951). The present treatment is a condensation of a larger work by the writer which will shortly be published.

In the *Embioptera* the dorsal vessel extends from the ninth abdominal segment and terminates in the head behind or beneath the brain in front of the connective ganglion. As in all insects the dorsal vessel of the *Embioptera* is differentiated into an anterior part, the aorta, and a posterior part, the heart.

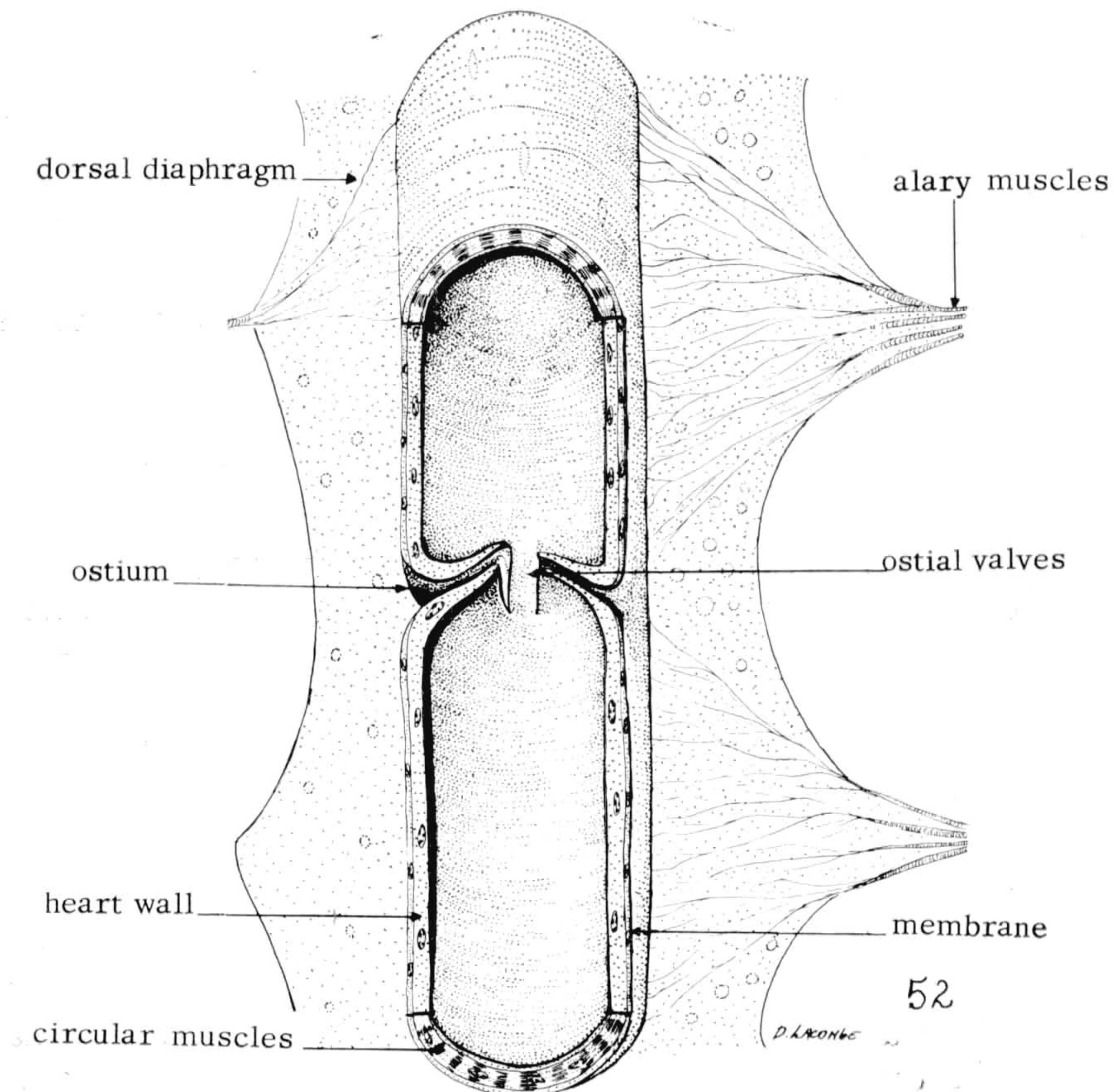
The wall of the dorsal vessel (fig. 52) is composed of a single layer of syncytial cells; the circules, striated fibrillae, and a homogeneous membrane derived from the sarcolema. The aorta and the heart have the same cellular structure and both are contractile. In *Embolynta batesi* the aorta is short, extending only to mid-prothorax. It is a very simple tube without diverticulae. The circular fibrillae are easily seen throughout the full length of the aorta, including its funnel-like opening in the head, by means of a polarized xenon light.

The heart is usually marked by the presence of chambers. These are formed by an invagination of ostial valves. In the *Embioptera* the heart chambers are primitive and begin in the mesothorax. Each has a pair of lateral ostia similar to those observed in *Ephemerida* nymphs by Grassi (1887) and by Popovici-Bazosanu (1905). Eight heart cham-

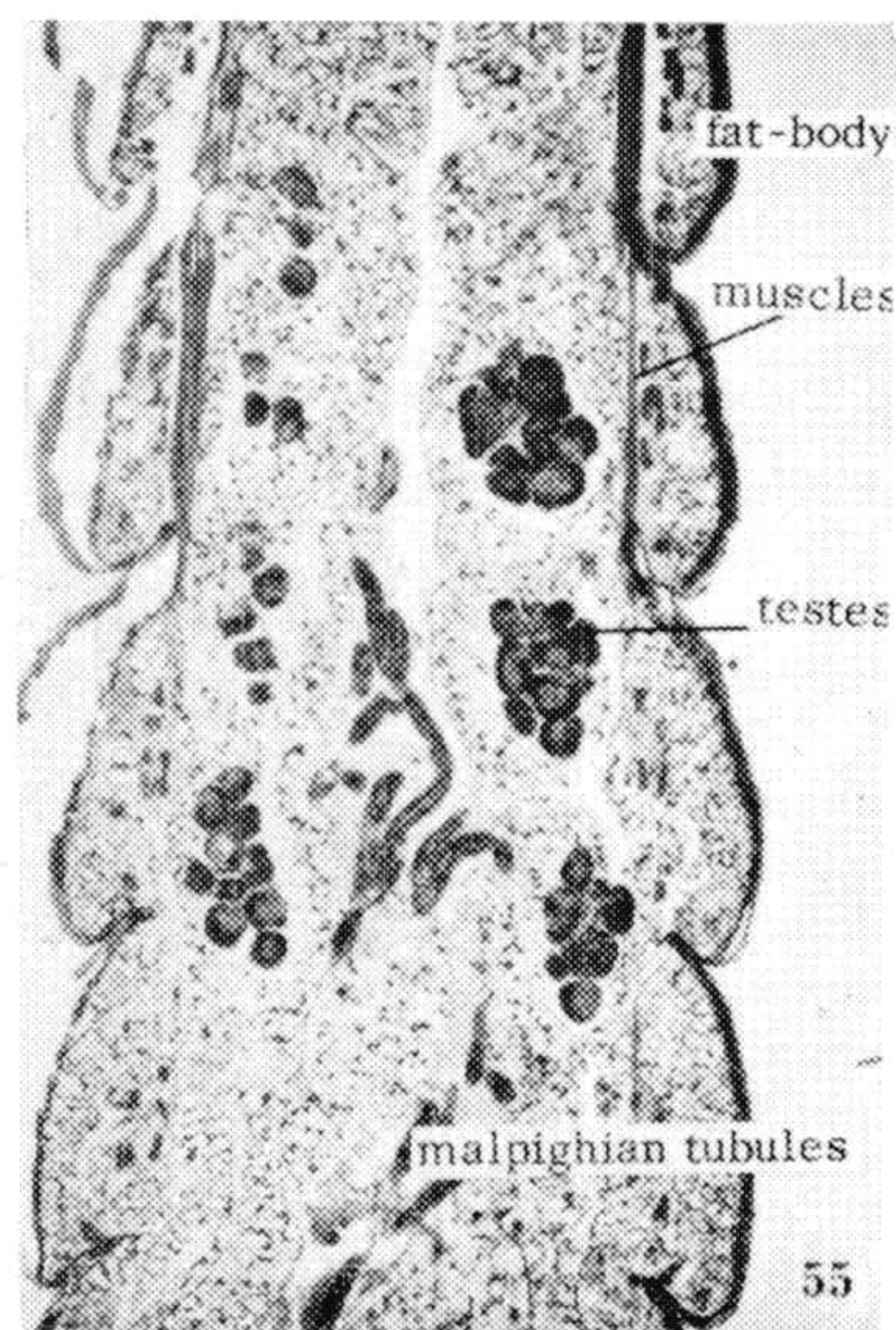
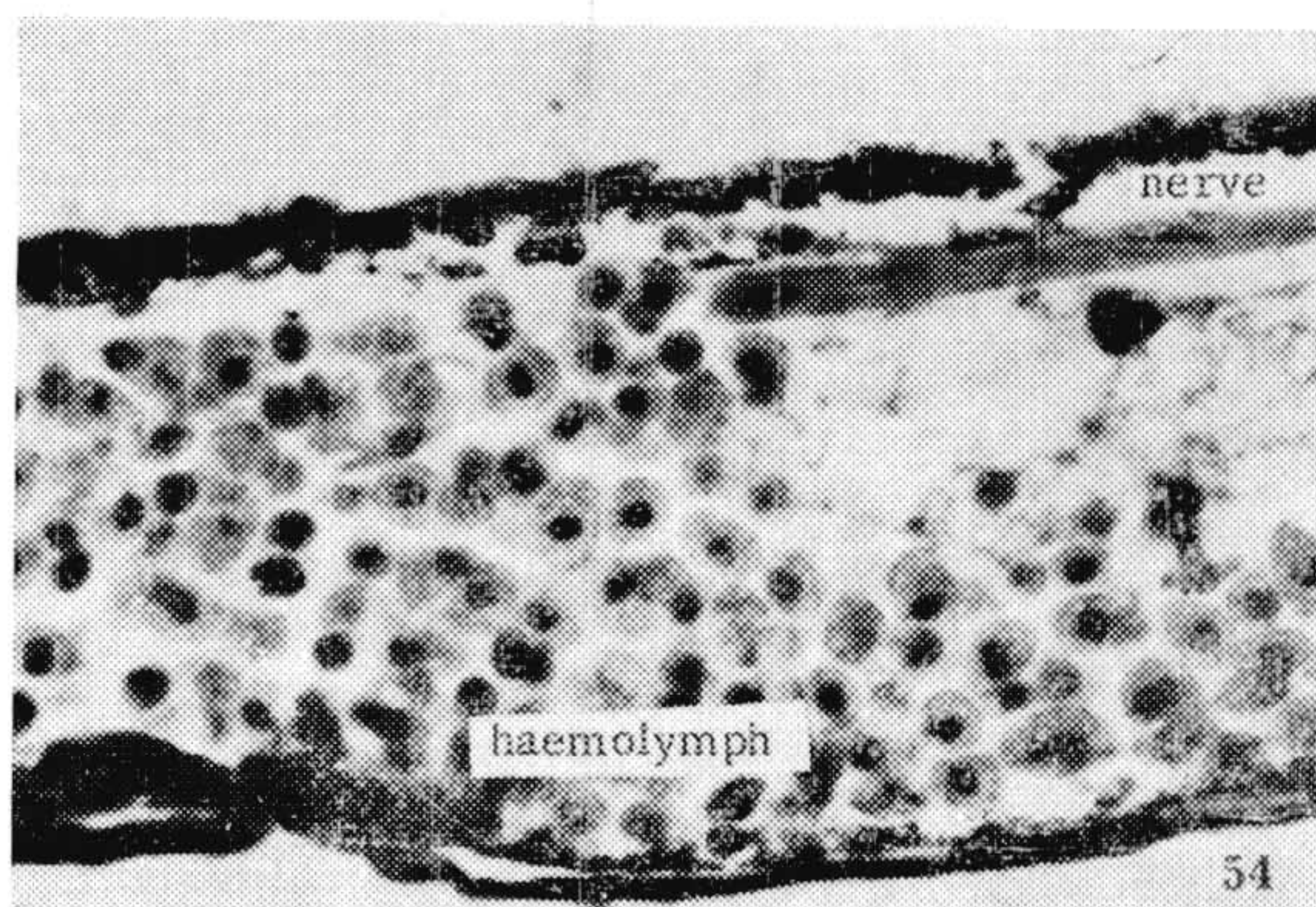
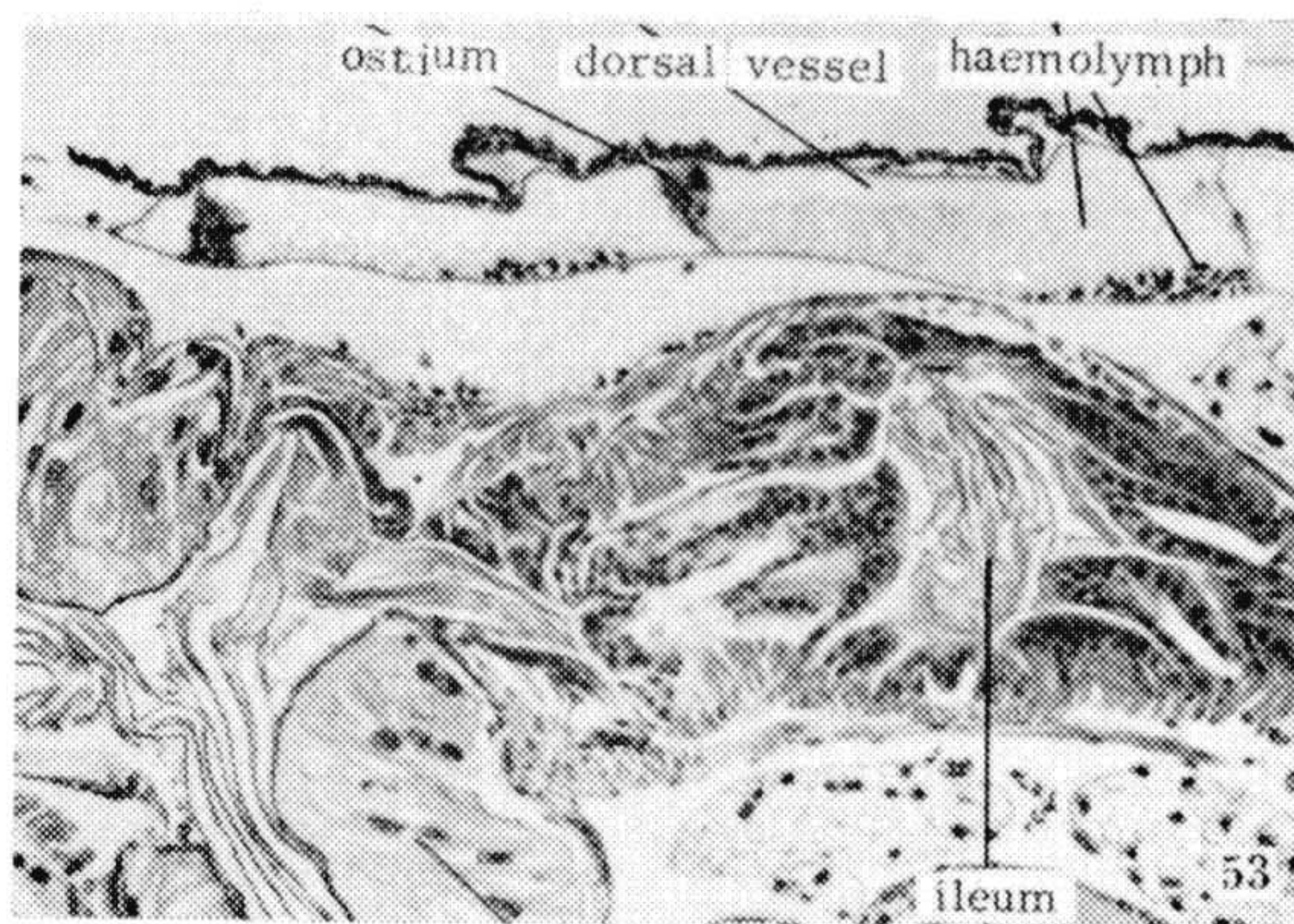
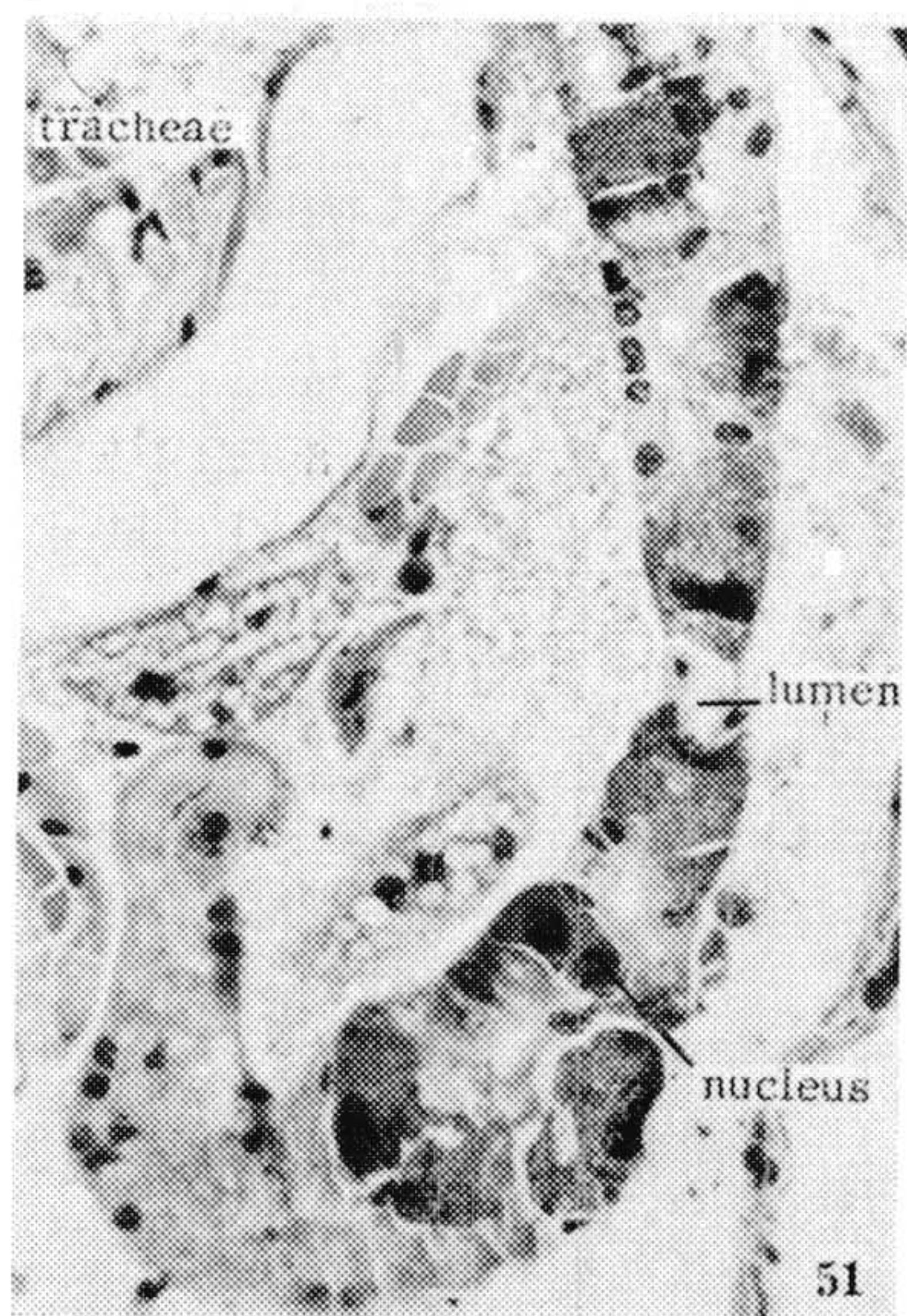
bers are found in the abdominal region and the last section is extended as a narrowed tube, into the ninth segment at this point the vessel has a simple closure (fig. 53).

In *Embolynta batesi* the author reported the presence of a small ampulla extending into a long vessel running the full length of the antenna. Each ampulla communicates with a blood space in front of the brain (fig. 6). This antennal blood vessel is parallel to antennal nerves.

The interior of each leg is divided into two sections by one fine membrane. Blood flows down from the perineural sinus down in one section of each leg and back up in the other. After this the blood flows into the visceral sinus whence it passes into the pericardial sinus. In the male *Embioptera*, blood circulation in wings, has not yet been studied. No pulsatile organs have been found in the wings.



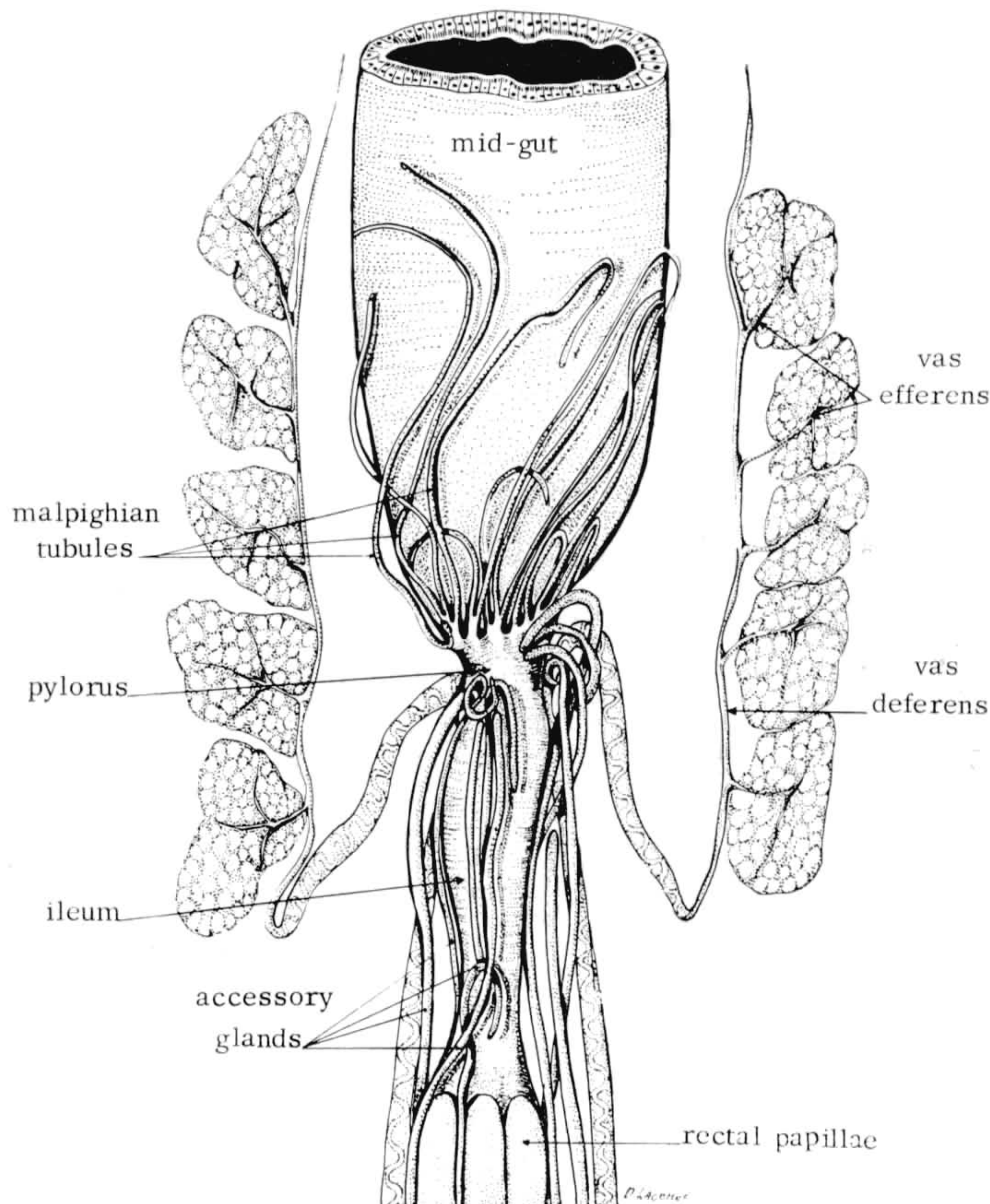
52 — Microanatomy of the circulatory system.



- 51 — Histological section through the salivary glands, showing the secretion in formation.
- 53 — Histological longitudinal section through the dorsal vessels, showing the ostium in the last segment of the cerci.
- 54 — Histological section through the first segment of the cerci showing different forms of lymphocits.
- 55 — Histological section through abdominal region.

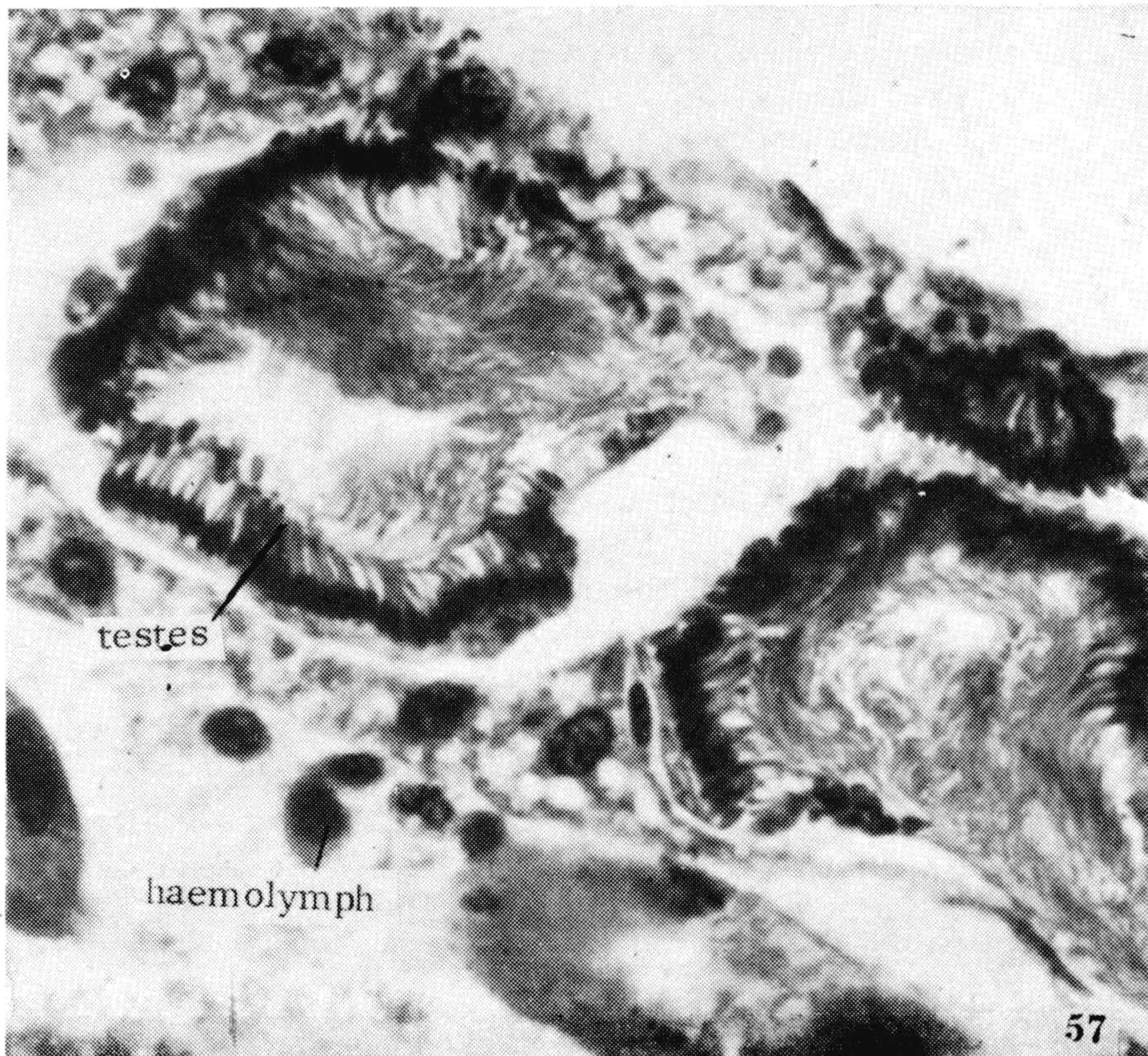
The dorsal vessel is suspended from the terga by means of radiating filaments and is connected with the dorsal diaphragm by fine branching of the alary muscles.

The heart mechanism of the *Embioptra* is the same as that of all insects. Blood enters the heart from the pericardial sinus by means of the ostia as the heart dilates while the ventricular valves are closed. During systole these valves are open and the blood flows forward in the heart chamber. At this moment the ostia are closed. In the head the blood flows into the body cavity and ampullary organs. Contraction of the alary muscles cause enlargement of the heart and its internal pressure becomes less than the external pressure. As a result blood flows into the chambers. In the *Embioptra* there are ten pairs of alary muscles formed by flattened bundles of muscle fibers arising on each side of the dorsal vessel (fig. 52).



56 — Schematic drawing showing the position of the reproductive organs of the males.

LYMPHOCYTES (fig. 54) : The lymphocytes develop in the embryo from undifferentiated endodermic cells, and in *Embolyntba batesi* **Lacombe** observed that mature haemocytes develop from mesodermal tissue beneath the hypoderm of the two segments of the cerci. The nuclei of these mesodermal cells divide two or three times and the cells migrate to the lumens of the cerci. In these lymphocytes, cytoplasm is denser around the nuclei. Within both segments of the cercus the nuclei and cytoplasm are modified and develop into the various types of blood cells as classified by **Wigglesworth** (1939).



57 — Histological section through the tests showing the disposition of the spermatozoa.

THE REPRODUCTIVE SYSTEM

Generally *Embioptera* reproduce bisexually, however, parthenogenesis occurs throughout the order and in some species males are entirely unknown. Sporadically gynandromorphs, intersexes, neoteny, and anomalous individuals are found.

REPRODUCTIVE ORGANS OF MALES: The paired testes comprise five pairs of globular follicles with segmented organization (fig. 56). Each follicle is connected to the vas deferens by means of a slender vas efferens. The testes extend on either side of the second to the sixth abdominal segment (fig. 57). Their position in the abdomen is maintained by associated fat-bodies and tracheae. Each follicle has a layer of epithelium around the basal membrane and contains successive zones of sex cells in different stages of development which are observable during late nymphal instar. Adult males show only the last phase of spermatogenesis. Only spermatids and spermatozoa can be found (fig. 55). This condition undoubtedly is correlated with the short life-expectancy of males in the *Embioptera*, whose sole function is the reproductive. But, in immature *Embioptera* the four different zones of development of the testes are easily seen. These are: (a) the germarium with primordial cells, or spermatogonia; (b) the spermatocyte zone where the spermatogonia increase in size. The spermatogonia are covered by a mantle or cyst of somatic cells and are called spermatocytes; (c) the zone of maturation — where the spermatocytes become pre-spermatids of the first and second order. During the first order, reduction division of the chromosomes takes place; (d) the zone of transformation where the spermatids, while still enclosed in their cysts, transform into spermatozoa.

After this, the spermatozoa pass into the vasa deferentia through the vasa efferentia. The vasa deferentia are simple fine tubes frequently enveloped by the testes as these organs increase in size. Along their course the vasa deferentia become enlarged and form seminal vesicles in which the mature spermatozoa are stored after they leave the testes. These seminal vesicles are tightly coiled to provide a maximum reservoir for sperm storage.

Posteriorly the vasa deferentia unite to form the single ejaculatory duct. The wall of this duct is surrounded by strong circular and longitudinal muscle fibers and its terminus is enclosed in an invagination of the body wall which forms an aedeagus. The accessory glands open at the anterior or basal end of the ejaculatory duct (fig. 58).

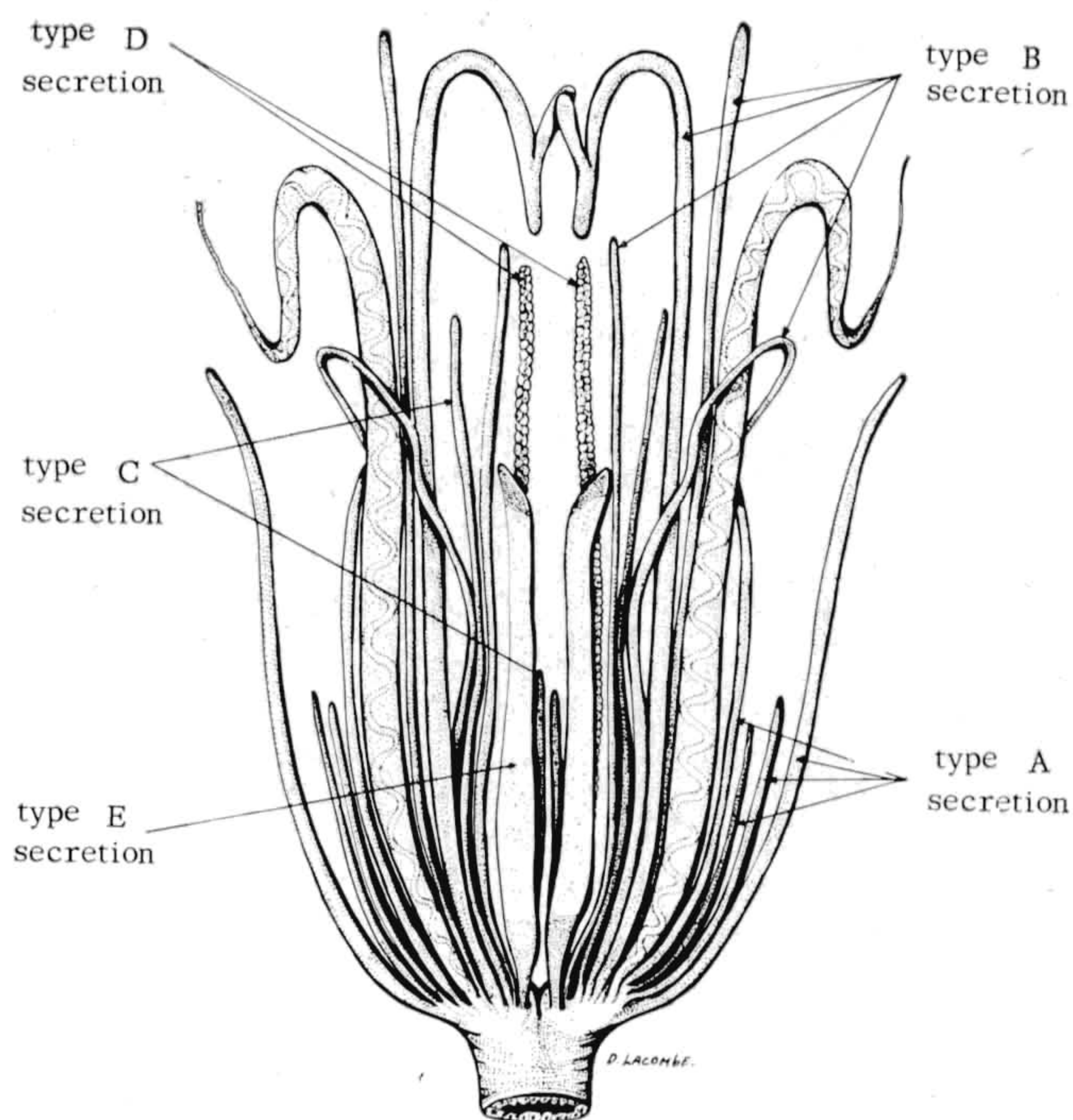


58 — The accessory glands of the reproductive organs.

Accessory glands in the *Embioptera* exhibit great variation in number, form, cellular structure, size and kind of secretion. They promise to provide useful characters for systematic interpretation. However, all have the different tubular glands (fig. 59) parallel to one another and a position around the hind-gut. In *Clothoda nobilis* the writer found twelve pairs of glands. Each type has a different color which probably indicates the production of a distinct secretion. Four pairs of small

tubular glands, which are orange in colour due to their secretion, are here called Type A. Four pairs of long tubular glands, which extend to the pyloric region and are red in color, are called Type B. Two pairs of fine tubular glands, which are transparent-white, are called Type C. One pair with a peculiar, granular, surface texture, which produces an oily secretion, is called Type D. The largest pair of glands, located medio-ventrally and opaque-white with yellowish extremities, are called Type E.

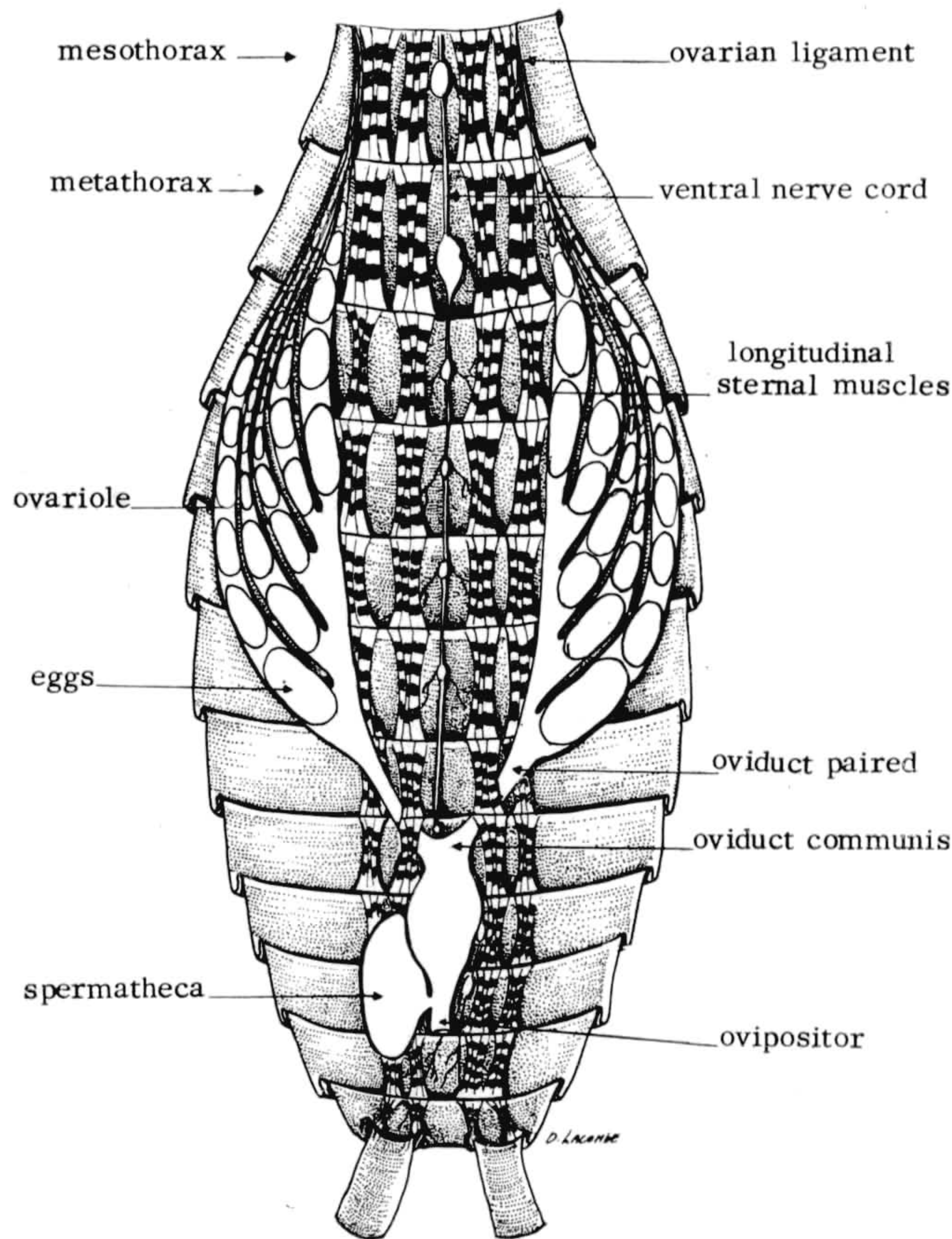
Perhaps during copulation the secretions of these glands mix with the spermatozoa and apparently are essential for the formation of the spermatophore. Histological sections clearly reveal the different secretions, but their chemical analysis must be determined by histoenzymological technique.



59 — Semi-schematic drawing of the different accessory glands with genital ducts.

REPRODUCTIVE ORGANS OF FEMALES: The ovaries of the *Embioptera* are composed of five long ovarioles which are of the primitive panoistic type (fig. 60). The anterior or apical extremity of each ovariole is attached by its terminal filament to the body cuticle near the mesothoracic phragma. The posterior part of the ovary is

fixed in the ventral region of the abdomen by the intersegmental muscles of the fifth and sixth sternites which pass over the paired oviducts. The network of the tracheae around and among the ovarioles help to hold them together.



60 — Female reproductive organs and related with longitudinal sternal muscles.

Within the elongated ovarioles (Pl. VI, 61) the developing eggs are aligned one after the other in a simple chain (Pl. VI, 62) with the oldest oocyte located near the common, or paired, oviduct. The ovarioles have a delicate peritoneal membrane with elongated nuclei rich in chromatin (fig. 63). Between the eggs, the tunica propria membrane separates then from the peritoneal membrane and converges inward as clearly shown in figures 64 and 65. The peritoneal membrane originates in the terminal filament at the apex of each ovariole and terminates where the ovariole joins the paired oviduct.

The tunica propria is a delicate, transparent membrane which forms the basal membrane of the follicular epithelium. This anista membrane is poor in cytoplasm and has few nuclei.

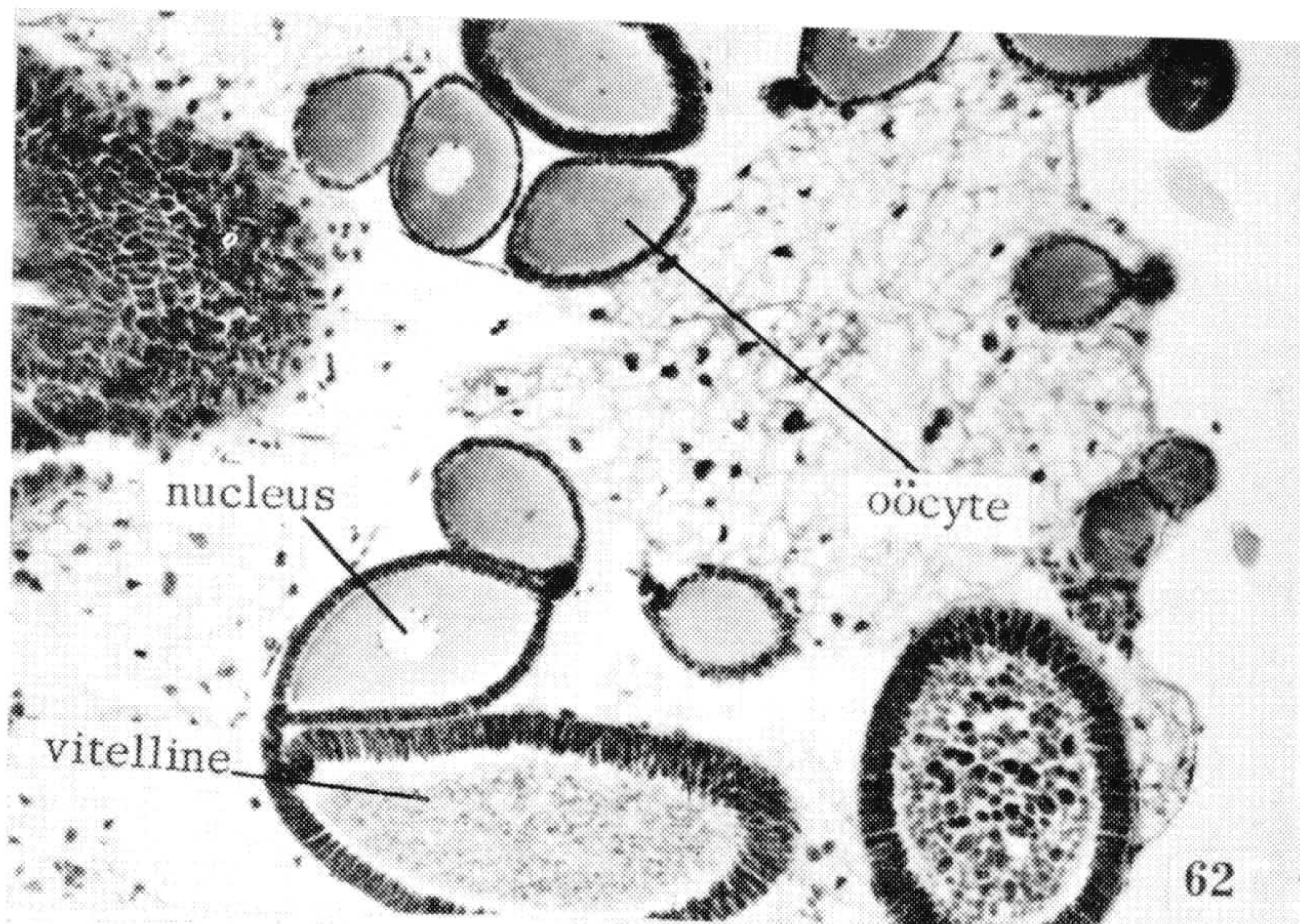
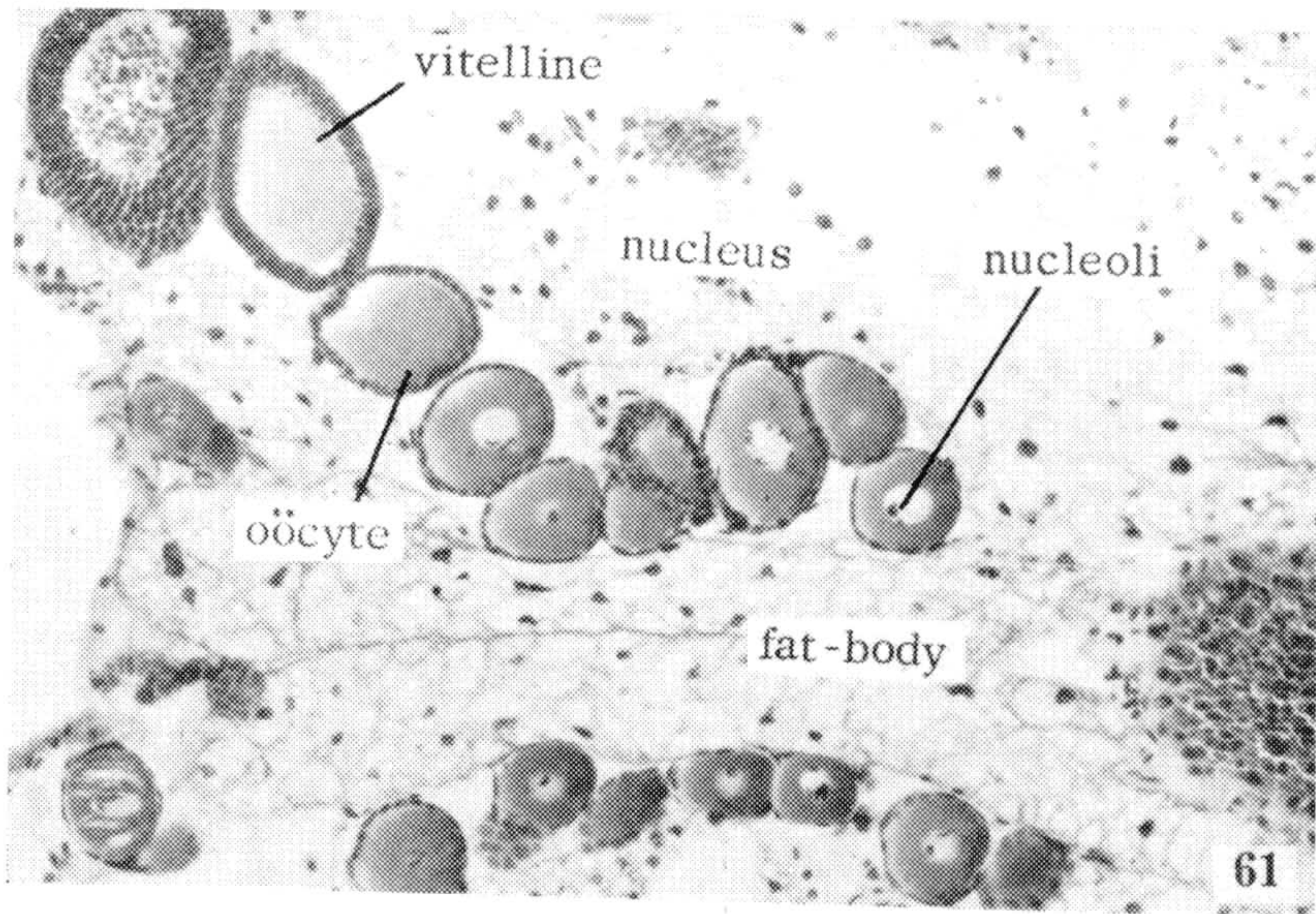
The follicular epithelium, which is composed of somatic cells, is responsible for the protection and nutrition of the eggs.

In the *Embioptera* an ovariole consists of three regions (fig. 63): (a) The terminal filament; (b) the germarium region (longest in immature forms, small in adults); and (c) the vitellarium region.

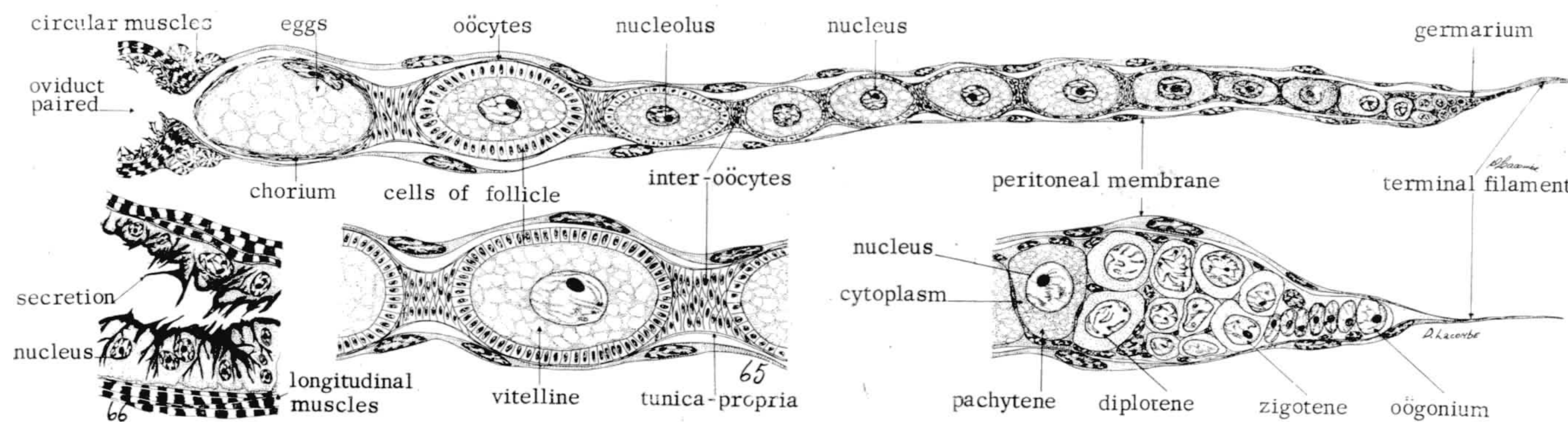
The germarium region (fig. 64) is the most important part of the ovarioles. It contains the germ cells which shortly develop into oogonia and the follicle cells which have an epithelial arrangement around the oocytes. In the *Embioptera* there are seven primordial oogonia which have large nuclei with clear nucleoli and chromatin in various positions. These nuclei are located in a single line near the terminal filament. Chromosomes in the zygotene phase are very clear and in the diplotene phase the longitudinal division of the chromosomes is clearly visible. In this phase the cytoplasm is hyaline but during the pachytene phase it is dense and homogenous. After this multiplication is completed the oogonia begin to grow and to form oocytes. In this region the follicle cells are flat and have small nuclei. After mitotic division these cells enclose the oocytes (fig. 64).

The vitellarian region contains the developing oocytes and follicular cells of increasing height (fig. 65). The latter cells have little cytoplasm and are at times bi-nucleate and grow inward to surround each oocyte. The oocytes pass into their vegetative phase when vitellogenesis takes place and their volume increases (fig. 65). The follicle cells, which at first are cubical and then become columnar (fig. 63) finally are flattened. When vitellogenesis is completed the follicle cells secrete the chorion. Also, the cells of the inter oocytes region undergo mitotic, transverse division and thereby form a well defined separation between the oocytes. When a mature egg is laid the remaining inter-oocyte cells serve to protect the next egg until it is ready to be laid.

In the regions where the ovariole stalk meets the paired oviducts, *Embolynta Batesi* exhibits longitudinal and stronger circular muscles which create a sphincter action as the oocytes pass along (fig. 63). The energy for the movement of the oocytes in the follicles toward the oviducts is due to the growth of the younger oocytes. Finally, the eggs pass from the vitellarium into the ovariole stalk where they lost their follicle cells, which here degenerate and gradually disappear.



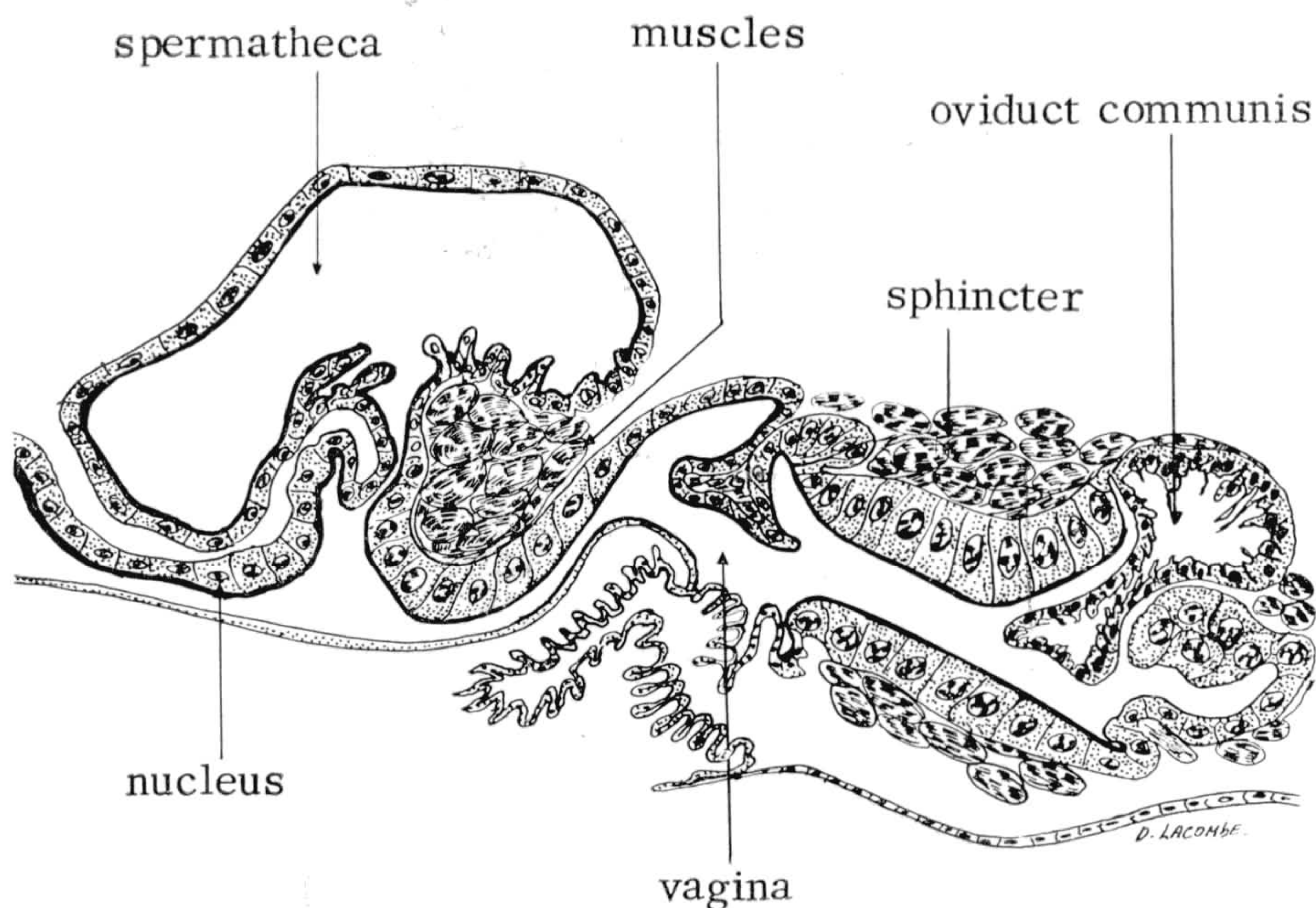
61 — and 62 — Histological section through the ovariole.



- 63 — Anatomical view of the ovariole.
 64 — Germarium region view.
 65 — Vitellarium region view.
 66 — Vagina epithelial wall.

The two oviducts combine to form a single oviduct, with walls having many folds. The wall cells have hyaline, filamentous cytoplasm with large nuclei which are poor in chromatin and have small nucleoli. Secretions from these cells pass through the cell's membrane into the lumen of the oviduct and surround the egg-shell. Externally the oviduct's epithelial cellular wall is covered by a sheath of muscles which increase in number toward the vagina (fig. 66).

In *Embolynta batesi* the epithelium of the common oviduct receives a secretion from the accessory glands which promotes adhesion of the eggs to the substrate.

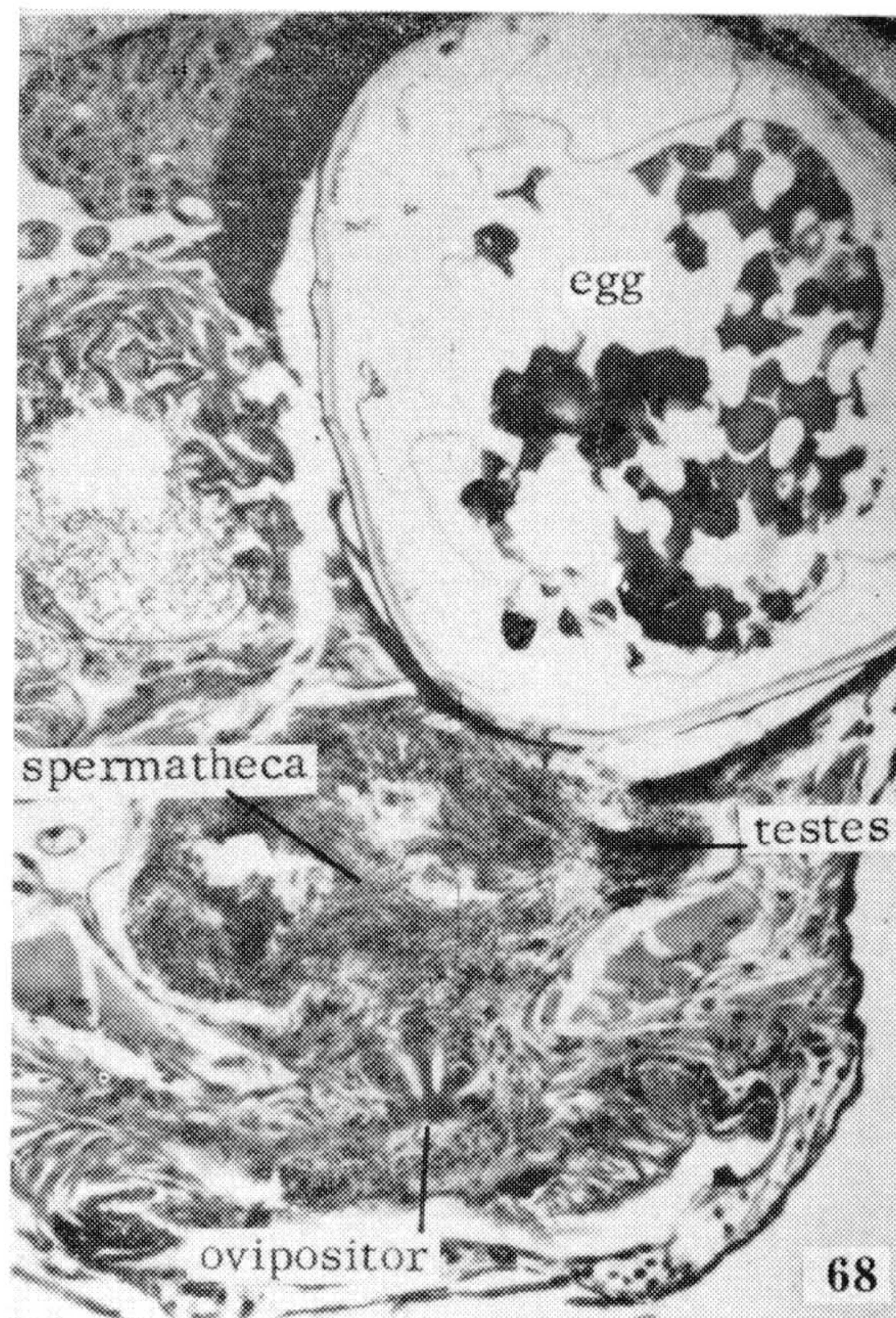


67 — Spermatozoa and vagina in the ninth abdominal segment.

The vagina, a derivative of the genital chamber, opens between the eight and ninth sternite. It has communication with the spermatheca located in the ninth abdominal segment (fig. 67). The seminal receptacle is sack-like and brown in color when it contains spermatozoa (fig. 68). The spermatheca walls are composed of flat cells covered by a fine cuticle. Near its opening into the vagina the cells are modified to form the spermathecal gland.

Muscle fibers located around the spermatheca, and concentrated near the aperture, function like a pump to assist fertilization of the eggs, and probably also serve to transfer spermatozoa from the

spermatophore to the spermatheca. When eggs pass down the oviduct the spermatozoa leave the seminal receptacle, and fertilize the formers. They are then deposited in the silk galleries in a manner characteristic of the particular species.



68 — Histological cut from the receptacle seminal.

SUMMARY

The *Embioptera* are rather generalized insects whose internal anatomy is simple and not subject to great modifications. For this reason these insects form an ideal group for elementary anatomical and histological studies (fig. 2).

The digestive tract is a long, simple tube without convolutions or diverticulae from the buccal cavity to the rectum. The buccal structures are of the chewing type. The oesophagus and ingluvia are differentiated only by slight dilation of their walls. In nymphs and females the proventriculus is very distinct due to folds which flatten as the structure becomes packed with food. The enteron is the largest in such forms and in both sexes limited caudally by the Malpighian tubules. The proctodeum has six large rectal papillae.

The nervous system is complete with only the fifth abdominal segment lacking a ganglion. It terminates caudally in the eighth abdominal segment. The ganglion in the metathorax includes the ganglion of the first abdominal segment. The brain exhibits very clear structure in histological sections.

The tracheal system includes two pairs of thoracic spiracles and eight abdominal pairs. Only the metathoracic spiracle has an air expiration function; all others serve for inspiration. Various structures in the spiracles protect the atrium.

The circulatory system includes a long, simple dorsal vessel which extends forward from the ninth abdominal segment into the cranium. It opens anteriorly near the circumoesophageal connectives. The dorsal vessel has a pair of ostia and valves corresponding to each abdominal and thoracic segment. It lacks the diverticulae or folds commonly found in more highly evolved insects.

The excretory system is represented by Malpighian tubules, pericardial cells, and fat-body. The number and disposition of Malpighian tubules is variable within the order. The pericardial cells are localized around the entire dorsal vessel up to the opening of the aorta in the head.

The fat-bodies form compact layers in the dorsal and ventral regions of the body. In males they are more developed in the abdominal region.

The mandibles, maxillae, and salivary glands are of a simple type with very few cytological modifications. Only the salivary glands which extend into the mesothoracic region show appreciable specialization.

The reproductive system is bi-sexual and shows considerable sexual dimorphism. Males have five pair of testes with a metameric disposition, two distinct ducts, two epididymis, and the ejaculatory organs. The accessory glands vary in number and size and open in the anterior portion of the ejaculatory duct.

The female reproductive organs are of the panoistic type. The system includes five pairs of ovarioles, two long paired oviducts a small, unpaired oviduct and the spermatheca which opens in the vagina. Reproduction usually involves a union of male and female gametes, and eggs are usually laid in clusters attached to a substrate.

RESUMO

ANATOMIA E HISTOLOGIA DE *EMBOLYNTHA BATESI* MACLACHLAN, 1877 (EMBIIDINA)

Os *Embioptera* constituem uma ordem de insetos de anatomia interna muito simples e com poucas modificações. Por esta razão formam um grupo ideal para estudos anatômicos e histológicos dos insetos (fig. 2).

O tubo digestivo é longo e simples, sem divertículo e dobras. A estrutura bucal é do tipo mastigador. O esôfago e a inglúvia diferenciam-se pela forte dilatação, epitélio e formação muscular. Em ninfas de ambos os sexos e em fêmeas, o proventrículo é repleto de dobras. O enterom é muito longo, sendo limitado, posteriormente, pelos tubos de Malpighi. O proctodeo apresenta 6 largas papilas retais.

O sistema nervoso é completo. O 5.º segmento não apresenta gânglios. O par de gânglios do metatórax inclui também um par de gânglios abdominais do 1.º segmento abdominal. O sistema traqueal possui dois pares de espiráculos torácicos e oito pares abdominais. Somente o espiráculo do metatórax tem função de expiração; os demais servem para inspiração. Várias estruturas quitinosas protegem o átrio dos espiráculos.

O sistema circulatório é constituído por um longo tubo dorsal, que se estende do 9.º segmento até a região do crânio, onde se abre próximo ao conectivo do anel esofágial. Os pares de óstia com as válvulas, correspondem aos segmentos torácicos e abdominais. O sistema excretor é representado pelos tubos de Malpighi, células pericardiais e corpo gorduroso. O número e disposição dos tubos de Malpighi é variável nesta ordem. As células pericardiais estão situadas do lado do vaso dorsal. O corpo gorduroso forma compacta camada dorsal e ventral, e nos machos é ainda mais desenvolvido na zona abdominal.

As glândulas mandibulares, maxilares e salivares são do tipo simples, com poucas modificações citológicas.

Os sexos são separados. Os machos têm cinco pares de testículos, dois ductos distintos e o órgão ejaculatório. As glândulas acessórias variam em número e tamanho e se abrem na porção final do ducto ejaculatório.

O aparelho reprodutor feminino corresponde ao tipo panoístico: Inclui cinco pares de ovaríolos, dois longos pares de ovidutos e a espermateca que se abre na vagina.

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REFERENCES

- BARTH, R., 1954, Untersuchungen an den Tarsaldrüsen von *Embolynta batesi* MacLachlan, 1877 (*Embioidea*). *Zool. Jahrbücher*, (Anatomie) Jena, 74: 172-188, 22 figs.
- BARTH, R. and LACOMBE, D., 1955, Estudos anatômicos e histológicos do ducto intestinal de *Embolynta batesi* MacLachlan 1877 (*Embioidea*). *Mem. Inst. Oswaldo Cruz*, 53 (1): 67-86, 34 figs.
- BORDAS, L., 1916, Nouvelles observations sur le structure histologique et les fonctions physiologiques des tubes de Malpighi des Lepidoptères. *Insecta*, Rennes, 6: 9-11, 1 fig.

- DAVIS, C., 1936, Studies in Australian Embioptera. Part I: Systematics. *Proc. Linneu Soc. New South Wales*, 61: 229-258, 50 figs., Pl. XIII.
- DAVIS, C., 1944, Revision of the Embioptera of Western Australia. *Journ. R. Soc. West. Australia*, 28 (1941-42): 139-147, 1 Pl.
- ENDERLEIN, G., 1912, Embiiden. *Coll. Zool. Selys Longchamps*, 3: 1-78. figs. A-G, Pls. 1-4.
- FRIEDRICHS, K., 1906, Zur Biologie der Embiiden. Neue Untersuchungen und Übersicht der bekannten, arten mit Beiträgen über die Systematik und postembryonale Entwicklung mediterraner. *Arten. Mitt. Zool. Mus. Berlin* 3: 215-238, 19 figs.
- FRIEDRICHS, K., 1935, Check list of the Embiidae (Embioptera) of Oceanic. *B. P. Bishop Mus. Occ. Papers*, 11: 3-4.
- GRASSI, B., 1887, Nuove ricerche sulli Termiti. Nota preliminare. *Bull. Ent. Ital.* XIX: 75-80.
- GRASSI, G. B., 1889, Intorno al genere Embia. *Bull. mes. Accad. Gioenia Sci. Nat. Catania*, 9: 6-8.
- HAGEN, H. A., 1885, Monograph of the Embiidina. *Canad. Ent.* 17: 145-155, 171-178, 190-199, 206-229.
- HANSTROEM, B., 1940, Inkretorische Organe, Sinnesorgane und Nervensystem des Kopfes einiger niederer Insektenordnungen. *K. svensk. Vetensy. Akad. Handl., Stockholm* (3) 18 (8): 266 pags., 239 figs.
- HILTON, W. A., 1936, The nervous system and sense organs. LVIII. *Insects, General. J. Ent. and Zool.*, 28 (2): 29-38. 151-155 figs.
- HILTON, W. A., 1937, The nervous system and sense organs LXV. *Insects, Isoptera. J. Ent. and Zool.*, 29 (4): 88-99, 14 figs.
- HOLLANDE, C., 1921, La cellule péricardiale des Insectes (cytologie, histochimie, rôle physiologique). *Arch. Anat. Microsc. Paris*, 18: 85-307, 4 Pls., 31 figs.
- IMMS, A. D., 1939, *A General Textbook of Entomology*. Metuen & Co. Ltd. 885 pags., 609 figs.
- KRAUSS, H. A., 1911, Monographie der Embien. *Zoologica* (Stuttgart), 23: 1-78, figs. A-G, Pls. I-V.
- LACOMBE, D., 1958, Contribuição ao estudo dos Embiídeos. III parte: Aparelho respiratório de *Embolynta batesi*. *Studia Entom.* I (1-2): 177-195. 17 flgs.
- LACOMBE, D., 1958, Polimorfismo sexual da região cefálica de *Embolynta batesi*. *Mem. Inst. Oswaldo Cruz*, 56 (2): 655-684, 25 figs.
- LACOMBE, D., 1960, Diferenças anatômicas e histológicas no aparelho digestivo de *Embolynta batesi*. *Bol. Museu Nacional, n. s. Zoologia*, n.º 219, 16 pags., 16 figs.
- LACOMBE, D., 1961, Contribuição ao estudo dos Embiidae. Musculatura da região cefálica do *Embolynta batesi*. *Bol. do Museu Nacional, Zoologia*. N.º 245, 20 págs., 13 figs.

- LACOMBE, D., 1963, Sistema nervoso de *Embolynta batesi*. *An. Acad. Ciências*, 35 (3): 393-411, 2 Pls., 18 figs.
- LACOMBE, D., 1965, Anatomia, histologia e excreção de corantes pelos tubos de Malpighi de *Embolynta batesi*. *An. Acad. Brasil. Ciências*, 37 (3-4): 503-517, 5 Pls., 5 figs.
- LEGER, L. and DUBOSCQ, O., 1899, Sur les tubes de Malpighi des Grillons. *C. R. Soc. Biol.*, 1 (11 série) 527-529.
- LISON, L., 1937, Etudes histophysiologiques sur le tube de Malpighi des Insectes. *Arch. Biol.*, 68 (2): 321-360.
- MARCHAL, P., 1890, L'acide urique et la fonction rénale chez les Invertébrés. *Mem. Soc. Zool. Fr.*, 3: 31-87.
- MARCHAL, P., 1896, Remarque sur la fonction et l'origine des tubes de Malpighi. *Bull. Soc. Entom. France*, 257-258.
- MAKI, T., 1938, Studies on the thoracic musculature of insects. *Mem. Fac. Sci. Agric. Taihoku imp. Univ.*, 24: 343 pgs., 17 Pls.
- MELANDER, A. L., 1903, Notes on the structure and development of *Embia texana*. *Biol. Bull.*, 4: 99-118, 6 figs.
- MUKERJI, S., 1927, On the morphology and bionomics of *Embia minor* sp. n. with special reference to its spinning organ. *Rec. Ind. Mus. Calcutta*, 29: 253-282, 10 figs., 1 Pl.
- NAVAS, L., 1900, Notas entomológicas. V. Neuropteros del Moncayo y Zaragoza. *Acta. Soc. Espaniola de Hist. Nat. Mayo*, 6-11 pags.
- NAVAS, L., 1934, Insecta Orientalia XIII. *Mem. Pont. Accad. Sci. Nuovi Lincei*, 1 (3): 217-228, 97-105 figs.
- NESBITT, H. J., 1941, A comparative morphological study of the nervous system of the Orthoptera and related order. *Amer. Ent. Soc. Amer.*, 34: 51-81, 7 Pls., 10 figs.
- NUTTING, W. L., 1951, A comparative anatomical study of the heart and accessory structures of the Orthopteroid insectes. *J. Morph., Philadelphia*, 89 501-597, 21 Pls.
- PALM, N. B., 1946, Studies of the peristaltic of Malpighian tubes in insects. *Lund. Univers. Ars.* 2B.D 42 (n.º 11): 1-39, 17 figs.
- PALM, N. B., 1950, The use of the vital staining method in insects, histology research. *Proc. VIII Inter. Cong. Ent. Stockol.*, 282-288, 9 figs.
- PALM, N. B., 1952, Storage and excretion of vital dyes in insects. *Ark. Zool.* 3 (18): 195-272, 76 figs.
- POPOVIC-BAZNOSANU, A., 1906, Sur l'existence des vaisseaux sangrins caudaux chez les Ephémérines adults. *C. R. Soc. Biol.*, 60: 1049-1050.
- RIMSKY-KORSAKOW, M., 1914, H. Sauter's Formosa Ausbeute: Embioidea. *Ent. Mitt.*, 3: 117-119, 3 figs.

- ROSS, E., 1940, A revision of the Embioptera of North America. *Ann. ent. Amer., Columbus*, 33: 629-676, 50 figs.
- STEFANI, R., 1953, Un particolare modo di accoppiamento negli Insetti Embiotteri. *R. Accad. Naz. Lincei*, 14 (8): 544-549, 1 fig.
- STEFANI, R., 1962, La comparsa della multazione tetrasomica nel biotipo anfigonico diploide *Haploembia solieri*. *Atti. Accad. Naz. Lincei*, 32 (8): 116-120, 1 fig.
- TRAPPMAN, W., 1923, Die Malpighischen Gefäße von *Apis mellifera*. *Arb. Biol., Reichsanst. Land.u. Forstw. Berlin*, 11, 565: 622 pags., 31 figs.
- VENEZIANI, A., 1904, Valore morfologico e fisiologico dei tubi Malpighi. *Redia*, 2: 177-230, tabs. XVIII-XX, 43 figs.
- VERHOEFF, K. W., 1904, Zur vergleichenden Morphologie und Systmatik der Embiiden. Zugleich 3^{tr}. Beitrag zur Kenntnis des Thorax der Insecten. *Nova Acta. Acad. Caes., Leop. Carol., Halle*, 82: 145-205, Pls. 4-7.
- WIGGLESWORTH, V. B., 1931, The physiology of excretion in a blood sucking insect, *Rhodnius prolixus*. Anatomy and histology of the excretory system. *J. Exp. Biol.* 8: 428-442, 5 figs.
- WIGGLESWORTH, V. B., 1939, *The principles of Insect physiology*. Methuen & Co. Ltd., London, 434 pags., 316 figs.
- ZAWARZIN, A., 1924, Structure of nervous ganglion in the nymph of *Aeschna*, Odonata. *Z. Wiss. Zool.*, 122: 97-115, 5 figs.