THE HISTOLOGY OF THE ALIMENTARY CANAL AND ASSOCIATED STRUCTURES OF METOPOLOPHIUM DIRHODUM (HOMOPTERA: APHIDIDAE)

BY

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CONTENTS

ABSTRACT

Key words: Metopolophium dirhodum; Aphididae; Alimentary tract; salivary gland.

The gross morphology and histology of the alimentary canal and the associated structures are described. The long tubular alimentary tract is divisible into different regions. The filter chamber and Malpighian tubules are absent. The peritrophic membrane is also absent. The rectum, or hindgut is extremely thin, expanded and transparent. The salivary gland complex consists of two sets of glands; the principal and accessory glands. The common salivary duct opens at the base of the maxillary stylets.

INTRODUCTION

The existing literature contains very few detailed accounts of the morphology and histology of the alimentary canal of Aphidoidea. Weber (1928) can be regarded as the pioneer in this field with his classic work on the black bean aphid, Aphis fabae. With the realization that aphids were vectors of plant viruses interest increased in the morphology and histology of aphids as a means of attempting to explain how transmittion of viruses takes place.

The rose grain aphid, Metopolophium dirhodum Wlk., is one of six aphids species that are pests in the South Western Cape. It first attracted attention in South Africa in the early 1970's as a cerial pest of some economic importance. M. dirhodum is capable of transmitting Barley Yellow Dwarf virus (Vickerman and Wratten, 1979). It is also apparently heteroecious between Rosaceae and Poaceae (Theobald, 1927; Hille Ris Lambers, 1974). The most noticable symptom of the virus is the discolouration of infected leaves. Infected barley leaves turn bright yellow in colour, oat leaves red-purple and wheat leaves bronze-red (Bruehl, 1961; Plumb, 1974); the virus also causes stunting. Although the degree of yield loss is usually related to the severity of visible symptoms, this is not always the case. Yield loss is usually greater when early infection takes place. According to Anneke and Moran (1982), this species seems to prefer irrigated to dry-land wheat and occurs thoughout the year, although mainly in winter.

The adult is moderate to large - sized, pale green with few hairs and a brighter, or darker green spinal stripe along the body which is rather elongate. It has a distinct median prominence on the head. Antennae are half as long as the body with joints darkened at the apices. The apterae and alatae females produce live young.

The present study was undertaken to supply information on the morphology and histology of the alimentary canal and associated structures. Such studies are necessary for further investigations with regards to aphid feeding and virus transmittion. The terminology used throughout this paper is the same as used by Forbes (1964) to retain uniformity.

MATERIALS AND METHODS

Material was obtained from a colony of M. dirhodum which was maintained in the laboratory on Triticum aestivum (wheat, c.v. sst 44). Only adult apterous aphids were used throughout this study.

Before placing the specimens in the fixatives, up to 4 legs were removed to ensure complete penetration of the fixative. Two fixatives were used, viz. Bouin's fluid and Duboscq-Brasil (alcoholic Bouin). (Pantin, 1960).

Alcoholic Bouin's proved to be the more successful of the two as the period needed for fixation was short (24 hrs.) and alcoholic Bouin's did not cause the tissues to harden while Bouin's fluid tended to crystalize in the tissues after long periods and resulted in problematic sectioning and staining. A double imbedding method was followed (Grey, 1952). The material was infiltrated for approximately 12 hrs. in paraffin wax ("Histowax" M.P. 58°C). This wax provided good impregnation and clear blocks which resulted in high quality serial sections being cut.

Transverse, saggital and frontal serial sections were cut at 5 µm, 8 µm and 10 µm and were stained with either Mallory's triple stain, Mann's Methyl Blue-Eosin of Mayers Haemalum prepared as described by Pantin (1960).

The times needed to stain the sections differed considerably from those suggested by Pantin (1960) and adjustments had to be implemented. The times used were invariably much shorter and the reason for this is possibly the small size of the specimen as well as the thickness of the section.

Transverse sections of 8μm proved to be the most suitable for recontruction of the alimentary canal. Drawings were made with the aid of a projection apparatus, and the method used for reconstruction was the same as that of Pusey (1936).

Drawings through choosen sections of the alimentary canal of the aphid were made with the aid of a camera lucida extention on the microscope. Finer detail was made free hand, so the drawings must be regarded as diagramatic although care was taken to reproduce detail as accurately as possible.

GROSS MORPHOLOGY (Fig. 2, 3, 4 & 5)

The alimentary canal begins anteriorly with the food canal which is formed by the interlocked maxillary stylets. From the stylets it passes into the sucking pump which then passes vertically through the head to the dorsally situated tentorial bar (Fig. 2: TB). The eyes mark the proximity of the tentorial bar as well as the beginning of the oesophagus (foregut).

The oesophagus which lies dorsally to the oesopharyngeal ganglion, extends posteriorly from the tentorial bar, through both the pro- and mesothorax, descending between the salivary glands and finally ascending to enter the stomach by means of an oesophageal valve which extends into the lumen of the stomach.

The first thoracic spiracle on the mesothorax marks the proximity of the start of the midgut. The midgut is divided into two distinguishable regions viz., the stomach (Figs.3,4 & 5: ST) and the intestine (Figs. 3, 4 5: I). The stomach is situated approximately between the first thoracic and the fourth abdominal spiracle, but the size may vary considerably depending on whether it is shrunken or distended due to the amount of plant sap ingested. The anterior part of the stomach is centrally situated and then runs posteriorly to lie close to or parallel to the dorsal body wall.

The intestine leaves the stomach ventrally in the proximity of the fourth abdominal spiracle and runs anterio-ventrally for a

length equivalent to approximately half the length of the stomach before reversing direction in the proximity of the first, second and third abdominal spiracle. The intestine then runs posteriorly alongside the hindgut for a length approximately equivalent to that of the stomach. The intestine then tergiversates in the proximity of the sixth abdominal segment to retrace its path anteriorly alongside and ventrally to the hindgut and descending intestine for a length slightly greater than that of the stomach. The intestine again reverses direction and immediately reverses direction once again forming a kink which transverses the stomach ventrally in the region of the second thoracic segment. The intestine now first descends and then ascends ventrally across the stomach in an arc to a point between the first and second thoracic spiracles where it reverses direction and gradually leads into the hindgut. The total length of the intestine is approxamitely 5 times the lenght of the stomach while the hindgut is approximately twice the length of the stomach.

The posterior end of the hindgut, the rectum, ends at the anus which opens to the exterior below the cauda. The position of the alimentary tract varies according to how many embryo's the aphid is carrying.

In M. dirhodum, as in all other aphids studied so far, Malpighian tubules are lacking. A filter chamber is also lacking.

HISTOLOGY

SUCKING PUMP (Figs.1 & 2)

The funtion of the sucking pump is to act as a pumping organ to bring the liquid food through the food canal and to force it into the foregut.

The pump chamber in M. dirhodum is cresentric in shape with a thick posterior wall and a thinner, flexable anterior wall which extends posteriorly into the lumen of the sucking pump as shown in Fig. (1).

The large dilator muscles extend from the interior of the clypeus to the medial cuticular tendon which arises from the anterior wall of the sucking pump.

FOREGUT (OESOPHAGUS). (Figs. 6 & 12)

The oesophagus is a long thin tube extending posteriorly from the tentorial bar, between the salivary glands to end in the oesophageal valve. The diameter of the oesophagus increases slightly towards the midgut (12 µm - 18 µm).

The oesophagus consists of a single layer of squamous epithelium with indistinct borders which secrete the chitinous intima (Fig. 12). The oesophagus is surrounded by a tunica propria.

The inner walls of the epithelial cells extend into the lumen of the oesophagus, but the number of extended cells varies depending on the position in the oesophagus. Posterior to the tentorial bar and upto approximately midway along the oesophagus their are a maximum of three extentions into the lumen. These extentions gradually increase in number to a maximum of five near the posterior end of the oesophagus. This gives the lumen a star shaped appearance. A short distance anterior to the oesophageal valve the epithelial cells lose all protrusions, thus enlarging, and giving a tubular appearance to the lumen.

Sections through the epithelial cells that are stained with Mann's Methyl Blue-Eosin are blue in colour. The nuclei are elongate in transverse section and are stained light red. The nucleoli are stained orange-red and are spherical in shape.

OESOPHAGEAL VALVE (Figs. 6, 6a & 12)

The oesophageal valve is a short protrusion of the foregut into the midgut and marks the transittion of foregut to midgut. Both the inner and outer cell layers of the oesophageal valve are continuations of the epithelial cells of the oesophagus. The inner layer consists of squamous cells while the outer layer consists of columnar cells.

The columnar cells contain small round nuclei which stain red with Methyl Blue-Eosin. The intima of the foregut continues througout the lumen of the oesophageal valve and terminates

at the base of the outer layer of cells. The average length of the valve is approximately 90 m.

MIDGUT (Figs. 6, 6a, 6b, 6c, 8 & 9)

The midgut is the largest part of the alimentary canal and consists of both the stomach and the intestine.

The epithelium of the entire midgut consists of a single layer of cells. These cells rest upon a tunica propria which is a connective sheath enveloping the gut. The tunica propria stains blue with Mallory's tripple stain.

The epithelial cells of the stomach can be differentiated into three distinct regions. The anterior region consists of densely packed cuboidal to columnar cells which are smaller in size in relation to the rest of the cells of the stomach (12 - 20 µm). They have striated borders at the lumen surfaces as do all the cells of the stomach and intestine. This striation is indicated by a blue colour when stained with Mallory's tripple stain and Mann's Methyl Blue-Eosin. The cells contain round to oval nuclei which in turn contain round nucleoli. (Fig. 6a).

The second region of the stomach is marked by an increase in the size as well as the shape of the cells (Fig. 6b). These cells are usually pyramidal in shape and their striated borders protrude into the lumen. The cells contain large nuclei which are basally to centrally situated. These cells, which constitute

the largest section of the epithelium, are granular in appearance and are the active cells of the stomach (Weber, 1928).

In various sections through the middle region of the stomach it was noted that some of the cells had undergone constrictions at their apices. Complete constriction eventually takes place releasing the apical part of the cell into the lumen of the stomach, indicating holocrine secretion. These cells average between 25 - 40μm in height. The third or posterior region of the epithelium consists of cuboidal cells which are smaller than those of the central region (15 - 25μm). Their striated borders do not protrude far into the lumen. These cells have been described as "resting cells" by Weber (1928).

The transittion from stomach to intestine is gradual with a decreasing number of epithelial cells. A typical transverse section will reveal the most anterior section of the intestine as being large in diameter, consisting of seven to eight epithelial cells, and having a large lumen (Fig. 8).

Posterior to the zone of transittion, the diameter as well as the number of epithelial cells decreases. A typical transverse section will reveal upto only five epithelial cells (Fig. 9). The lumen is also reduced in size due to the fact that the apices of these triangular cells protrude into the lumen. The diameter of the intestine may vary in size at different times depending on whether the circular muscles in that region are relaxed or contracted. The free surface of the epithelium is striated and stains dark blue with Mallory's tripple stain.

The cytoplasm surrounding the ovoid nuclei is granular, vacuolated, and stains lighter than that of the borders of the cells which is more densely granular. The cytoplasm stains light purple while the nuclei and nucleoli stain red-orange with Mallory's tripple stain. The intestine is surrounded by a tunica propria.

HINDGUT (Figs. 7 & 13)

The transittion from the intestine to the hidgut is gradual and no pyloric valve can be seen. The anterior section of the hindgut consist of columnar cells which eventually flatten completely towards the posterior region of the hindgut (Fig. 7). These posterior cells have indistinct intercellular membranes. Oval nuclei surrounded by cytoplasm protrude into the lumen of the hindgut. The inner margins of the cells have a folded appearance. An intima is once again visible and the whole hindgut is surrounded by tunica propria.

The hindgut narrows at its posterior end to form the rectum (Fig. 13). The anterior section of the rectum consists of cuboidal to columnar cells with round to oval nuclei. The posterior end of the rectum which eventually ends with the anal opening is an invagination of the epidermis. The intima can be seen as a continuation of the cuticula. Near the anal opening muscles are attached to the rectum and presumably are involved in the control of honeydew released from the anus.

ASSOCIATED STRUCTURES

SALIVARY GLANDS (Fig. 10 & 11)

The salivary glands in M. dirhodum are found in the prothoracic region, dorsal to, and along suboesophageal ganglion. They are situated on either side of the oesophagus. The salivary gland complex consists of two pairs of glands; the principal and accessory glands. The bilobed principal glands (PSG) can be divided into an anterior membranous region and a posterior glandular region. The pear shaped accessory glands (ASG) lie anterior to the principal glands. The principal and accessory glands are connected to each other by means of ducts; the salivary ducts (Fig. 10: SC). The ducts from both pairs of salivary glands join medially to form a single common salivary duct (Figs. 2 & 11: CSD) which passes ventrad vertically between the suboesophageal and thoracic ganglions. The duct then runs ventrally and parallel to the suboesophageal ganglion in an anterior direction for a short distance before turning ventrally and running vertically to enter the salivary pump (Fig. 2).

PRINCIPAL GLANDS

The large principal glands (Fig. 10: PSG) consists of two distinct regions; the anterior region which is membranous and the posterior region which consists of large closely packed granular cells.

The anterior region (Deckzellen; Fig. 10: DZ) consists of cuboidal to columnar cells which are not as closely packed as the cells of the posterior region (Hauptzellen; Fig. 10; HZ). The cells contains round nuclei and the cells do not stain as intensely as those in the posterior region. The hauptzellen are large cells with distinct borders. They are granular in appearance and stain intensely. The nuclei and nucleoli are round.

ACCESSORY GLANDS (Fig. 10: ASG)

Each principal gland is connected to a pear shaped accessory gland which is situated anteriorly close to it. Ducts running posteriorly from the accessory glands join the ducts from the principal plands at the hilus which is situated close to the principal gland.

The accessory glands consist of 2 - 3 cuboidal cells with large round nuclei and nucleoli. The cells are granular in appearance and stain light purple with Mallory's tripple stain.

SALIVARY DUCT (Fig. 11)

The entire salivary duct consists of columnar cells surrounding a chitinously lined lumen. The salivary duct is enveloped by a thin membrane which stains blue with Mallory's tripple stain. The epithelial cells have indistinct boundaries and have a somewhat spongy appearance containing numerous vacuoles

of various sizes. The inner boudaries of the cells have a striated appearance.

DISCUSSION

In general, the morphology of the alimentary canal of Metopolophium dirhodum (Walker) shows many similarities with that of other aphid species (Pelton 1938; Smith, 1939; Saxena and Chada, 1971; Ponsen, 1972, 1982, 1983) consisting of sucking pump, foregut, midgut and hindgut but lacking a filter chamber, Malpighian tubules and a pyloric valve.

According to Forbes (1963) filter chambers have been described from several of the more "primitive" aphids, including Longistigma caryae (Knowlton 1925), several species of Lachnus (Leonhardt 1940), Subsaltusaphis ornata (Ponsen 1979) and Eulachnus brevi-pilosus (Ponsen 1980) where the organ serves to filtrate the excess of liquid food directly from the anterior region of the midgut to the hindgut. Filter chambers are lacking in most "higher" aphids studied so far, including: Aphis fabae (Weber, 1928); Marcosiphum solanifolii (Smith, 1939); Schizaphis graminum (Saxena and Chada, 1971) and species of the Chiato-phoridae (Ponsen, 1983).

Snodgrass (1935) describes the pump chamber of Homoptera as representing the preoral cibarium of the generalized orthopteroid insect. The posterior part was formed from the proximal part of the hypopharynx, whereas the anterior wall was derived from the epipharynx. He further suggested that this pump should be called the sucking pump on the basis of its function, and not the pharynx or pharyngeal pump.

The dilator muscles of M. dirhodum are similar to those described by Weber 1928), in Aphis Fabae Scopoli, where the muscles are inserted along the midline of the distal end of the anterior wall of the pump chamber. These muscles are attached by a long cuticular tendon. Forbes (1964), described how the pump functioned as follows: When the dilators contract the invaginate anterior wall is pulled forward increasing the size of the lumen, creating pressure in the chamber. This draws plant sap into the chamber. When the dilators relax, the wall springs back expelling the sap into the foregut. The concept that the uptake of sap depends mostly on turgor pressure in the plant was disproved by Mittler and Dadd (1962) with their success in getting M. persicae to ingest sugary fluids through a membrane.

As with all aphids studied so far, the oesophagus of M. dirhodum runs over the tentorial bar and between the salivary glands. Most aphids that have been studied revealed a relatively short oesophagus consisting of a single layer of epithelial cells. In contrast to this Subsaltusaphis ornata possesses a very long foregut of which the length is about three times that of Myzus persicae (Ponsen, 1979).

As with all aphids lacking a filter chamber, an oesophageal or cardiac valve is present in M. dirhodum. Snodgrass (1935) believed that the outer epithelial layer of the oesophageal valve is an extension of the oesophageal epithelial layer. Weber (1928) described the oesophageal valve as being enclosed in the stomach epithelium which folds back around the valve. Observations on

M. dirhodum in this respect agree with those of Weber with the inner layer op epithelial cells being flattened while the outer layer of epithelial cells are more columnar resembling those of the stomach but being much smaller. The role of the valve is to prevent regurgitation of ingested food from the stomach to the foregut (Smith 1931).

The intimal lining of M. dirhodum continues to the outer epithelial layer and hangs freely, as reported by Forbes (1964) in M. persicae and does not stop at the end of the valve as reported by Saxena and Chada (1971) in Schizaphis graminum. Weber (1928) described the membrane surrounding the valve in A. fabae as being continuous with the intima of the foregut. According to Weber, the sac is filled by secretion from cells of the outer layer of the valve. He thought that this secretion might diffuse through the sac wall to be involved in digestion, but that more probably it functioned to give the sac greater turgidity, thus increasing the valve's efficiency.

Three distinguishable cell types are found in the stomach epithelium of M. dirhodum. Forbes (1964) also distinguished three types of cell in the stomach epithelium of M. persicae: replacement cells lying adjacent to the oesophageal valve, active digestive cells representing most of the epithelial cells in the process of holosecretion, and resting digestive cells occuring in the posterior region of the stomach. Saxena and Chada (1971) reported the presence of only two cell types, namely, large columnar cells and small basal or regenerative cells.

Weber (1928) working with Aphis fabae, showed that the epithelial cells of the stomach secrete by constriction of the apical parts (i.e. holocrine secretion). According to Ponsen (1972) this was observed for Macrosiphum sunbornii (Miller, 1932), Lachnus piceae (Leonhardt, 1940), Lachnus roboris (Michel, 1942), M. persicae (Schmidt, 1959), Crytomyzus ribis, Metopleuron fuscoviride, Pentatrichopus tetrarhodus (Machauer, 1959), and Megoura viciae (Ehrhardt, 1963). Constrictions were also noted with the epithelial cells of M. dirhodum.

Their is no intimal lining in the stomach and intestine of M. dirhodum, although Knowlton (1925) reported the presence of a peritrophic membrane covering the inner surface of the digestive epithelium in Longistigma caryae. Pelton (1938) studying Prociphilus tesselata, suggested that the columnar shaped cells in the stomach around the oesophageal valve may be the remains of the cells that secrete the peritrophic membrane. In M. dirhodum, the epithelial cells around the oesophageal valve are continuous of the epithelial layer. Forbes (1964), likewise, did not observe a peritrophic membrane or the presence of a circle of specialized peritrophic cells around the oesophageal valve in M. persicae. Saxena and Chada (1971), in their study on the greenbug, S. graminum were also unable to observe a peritrophic membrane.

The striated border which is found throughout the midgut of M. dirhodum is almost universal for the lumen surfaces of insect midgut epithelia. Forbes (1964) described the border as consisting of microvilli, but their function is problematic as they have been found on cells which have no known absorptive function.

Histologically there is no sharp line of demarcation between the stomach and the intestine. The pyloric valve, marking the posterior end of the midgut in many other insects, and the Malpighian tubules, are not present in M. dirhodum. The absence of the pyloric valve in other aphids has been reported by Knowlton (1925) in L. caryae, Smith (1939) in M. solanifolii, and Forbes (1964) in M. persicae. However, Pelton (1938) stated that the pyloric valve in P. tessellatus consisted of a constriction and differentiation of cells where large irregular cells of the mid-intestine end abruptly, and irregular columnar cells of the hind-intestine arise.

The rectum or hindgut of M. dirhodum is similar to that of all other aphids studied so far, being an extremely thin transparent structure that opens to the exterior by the anus.

The general anatomy of the salivary glands in the Hemiptera was discussed by Baptist in 1941. He stated that "the size and shape of the glands are highly variable in different insects, but within an order (Hemiptera) a certain degree of uniformity becomes apparent". The salivary gland complex in M. dirhodum is very similar to that observed in the greenbug, S. graminum by Saxena and Chada (1971), consisting of principle and accessory glands. It has been found by means of histochemical studies done by Miles (1959), on Aphis craccivora, that two types of saliva are secreted by the principle glands, a watery saliva and a viscid secretion which forms the stylet sheath. The exact function of the accessory glands or type of secretion they produce is unknown.

SUMMARY

The alimentary canal can be divided into three distinct regions namely, the foregut, midgut and hindgut. The foregut consists of a thin tube made up of a single layer of flattened epithelium surrounding the chitinous intima. The oesophageal valve marks the transition of foregut to midgut and is responsible for the prevention of backflow of liquid fluid from the stomach into the oesophagus. The epithelial cells of the stomach are divided into three distinguishable regions; the anterior replacement cells, the active digestive cells and the posteriorly situated resting digestive cells. The start of the intestine is marked by a decreased number of epithelial cells. No pyloric valve is present. The rectum is extremely thin, membranous and transparent and opens to the exterior by means of the anus. No Malpighian tubules were present and a filter chamber was also lacking.

The salivary gland complex consists of two pairs of glands; the principal and accessory glands. The principal glands are divisible into an anterior membranous part and a posterior glandular portion. The accessory glands are located close to the principal glands. The duct from the accessory gland unites with the duct from the principal gland to form the salivary duct. The salivary ducts from either side join to form a single common salivary duct which opens at the base of the maxillary stylets.

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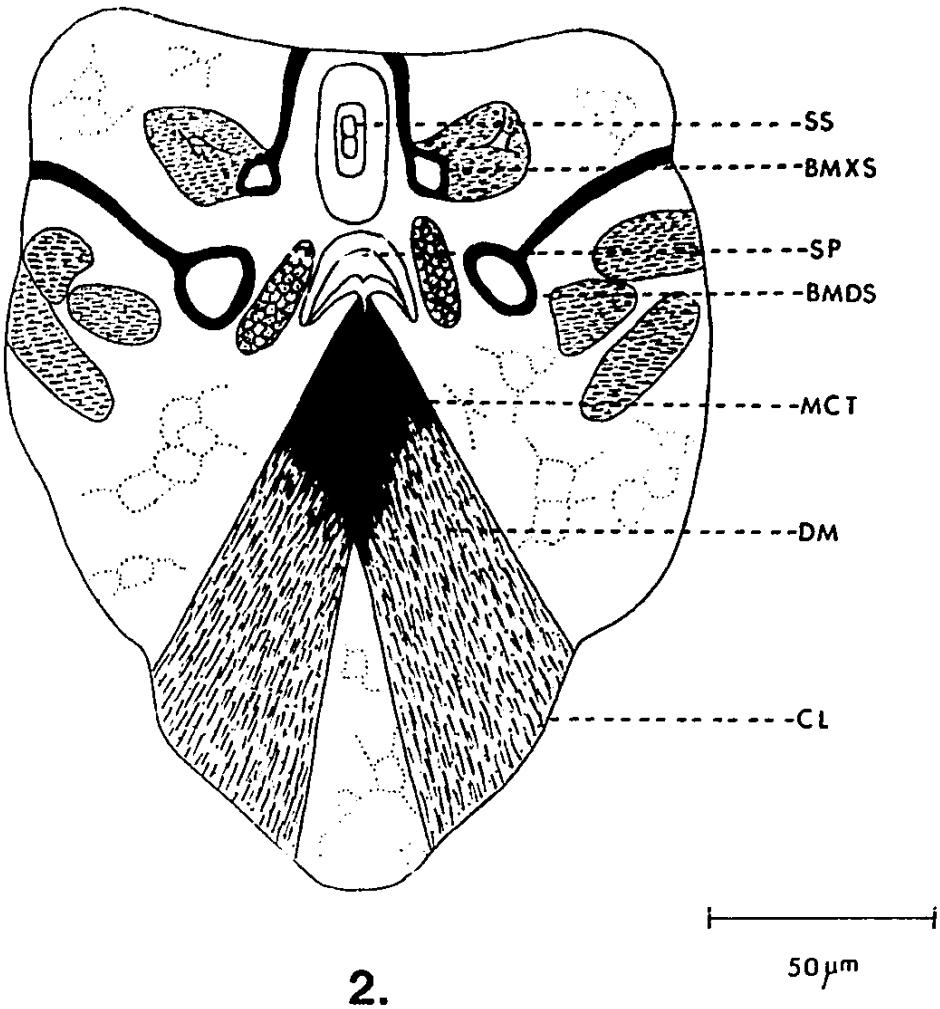
ABBREVIATIONS USED IN FIGURES

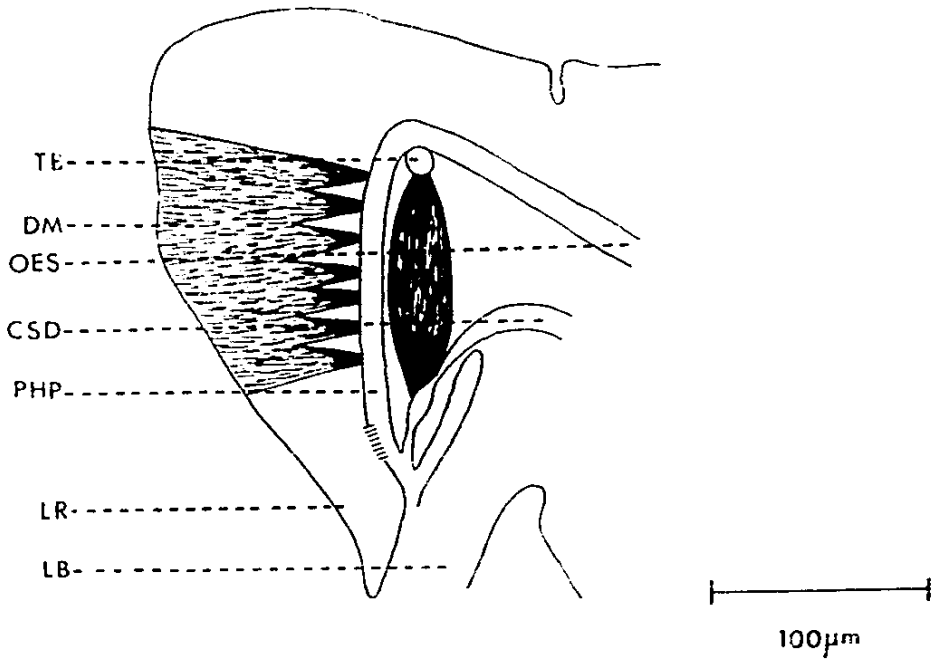
AD	Anal opening.
ASG	Associated salivary gland.
BMDS	Base of mandibular stylet.
BMXS	Base of maxillary stylet.
CL	Clypeus.
CO	Cauda.
CSD	Common salivary duct.
CU	Cuticule.
DM	Dilator muscle.
DZ	Deckzellen.
EPC	Epidermal cells.
FG	Foregut.
HG	Hindgut.
HZ	Hauptzellen.
I	Intestine.
IN	Intima.
LB	Labium.
LR	Labrum.
MA	Retractor muscle fibres of anal opening.
MCT	Medial cuticular tendon.
N	Nucleus.
NU	Nucleolus.
OES	Oesophagus
OV	Oesophageal valve.
PHP	Pharyngeal pump.
PSG	Principal salivary gland.
SB	Striated border.

SC	Salivary canal.
SP	Salivary pump.
SPR	Spiracle.
SS	Salivary syringe.
ST	Stomach.
TB	Tentorial bar.
TP	Tunica propria.

1.



2.



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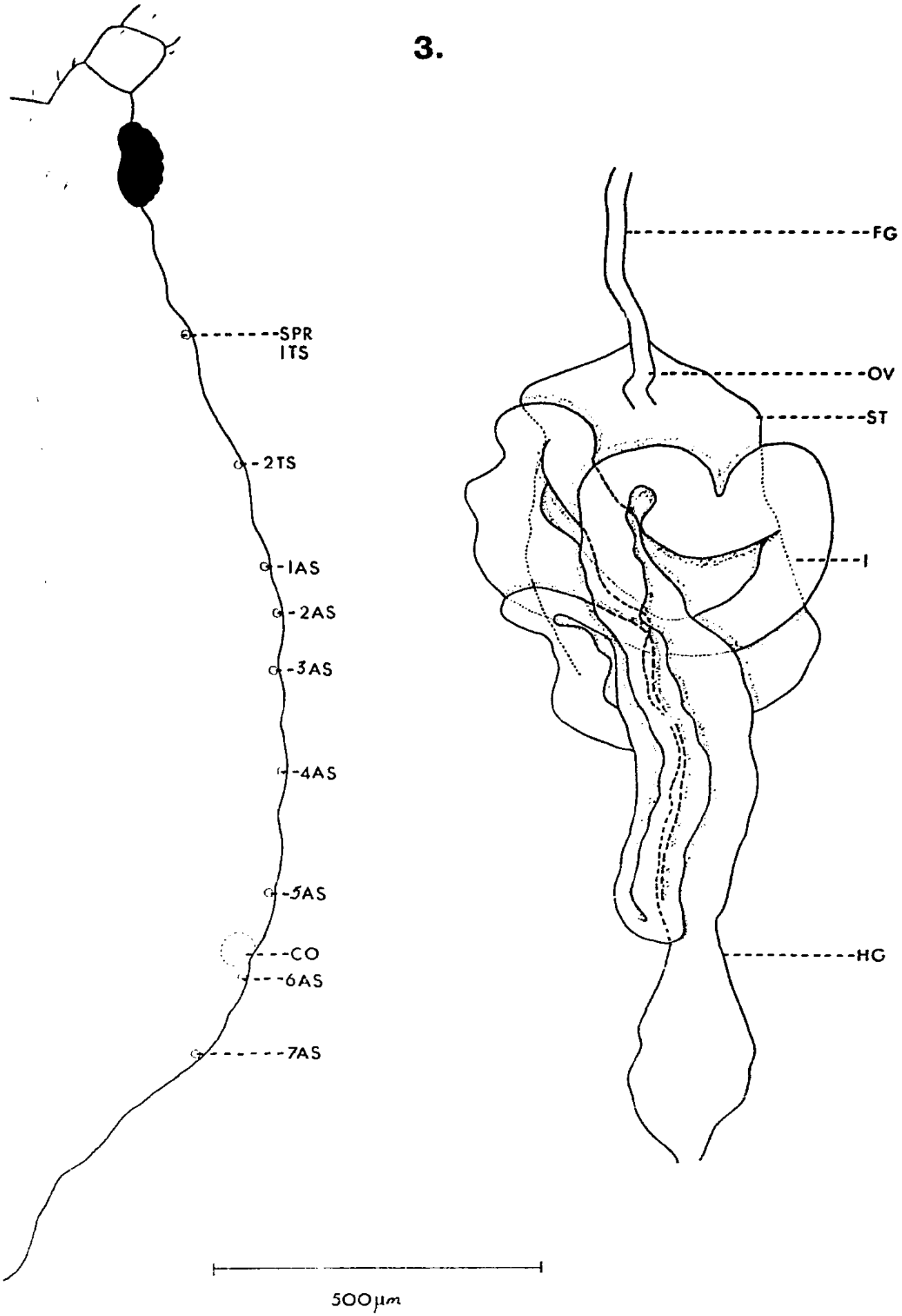

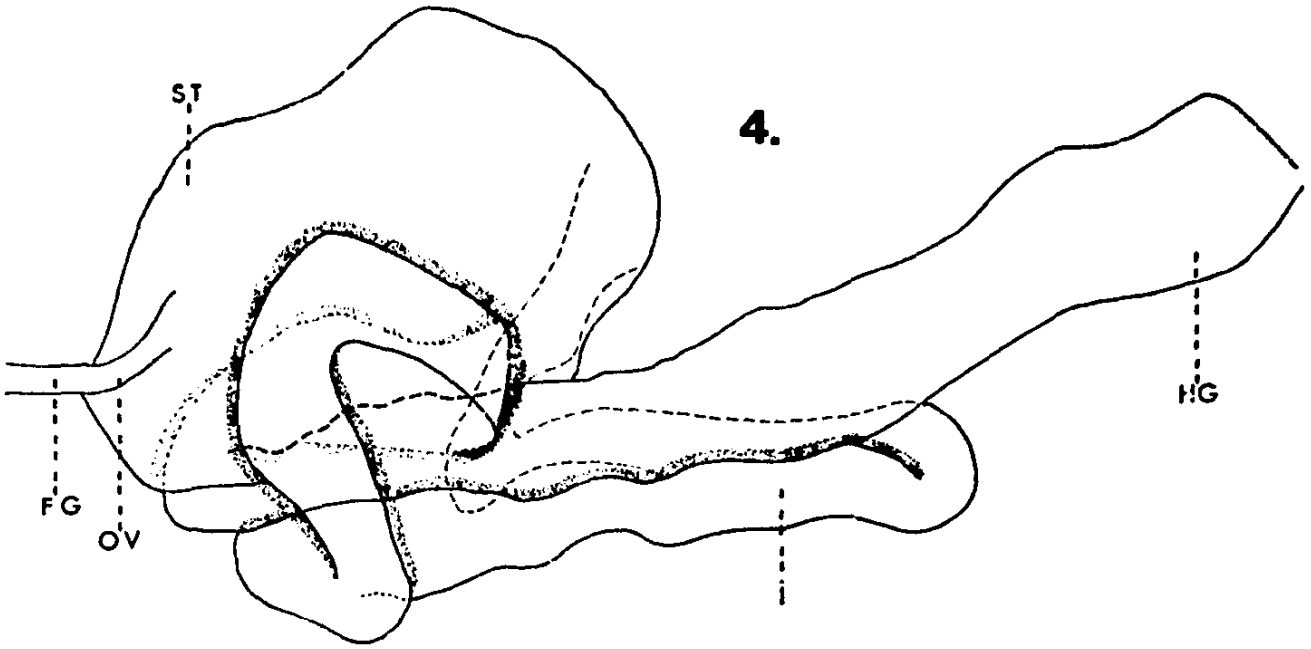

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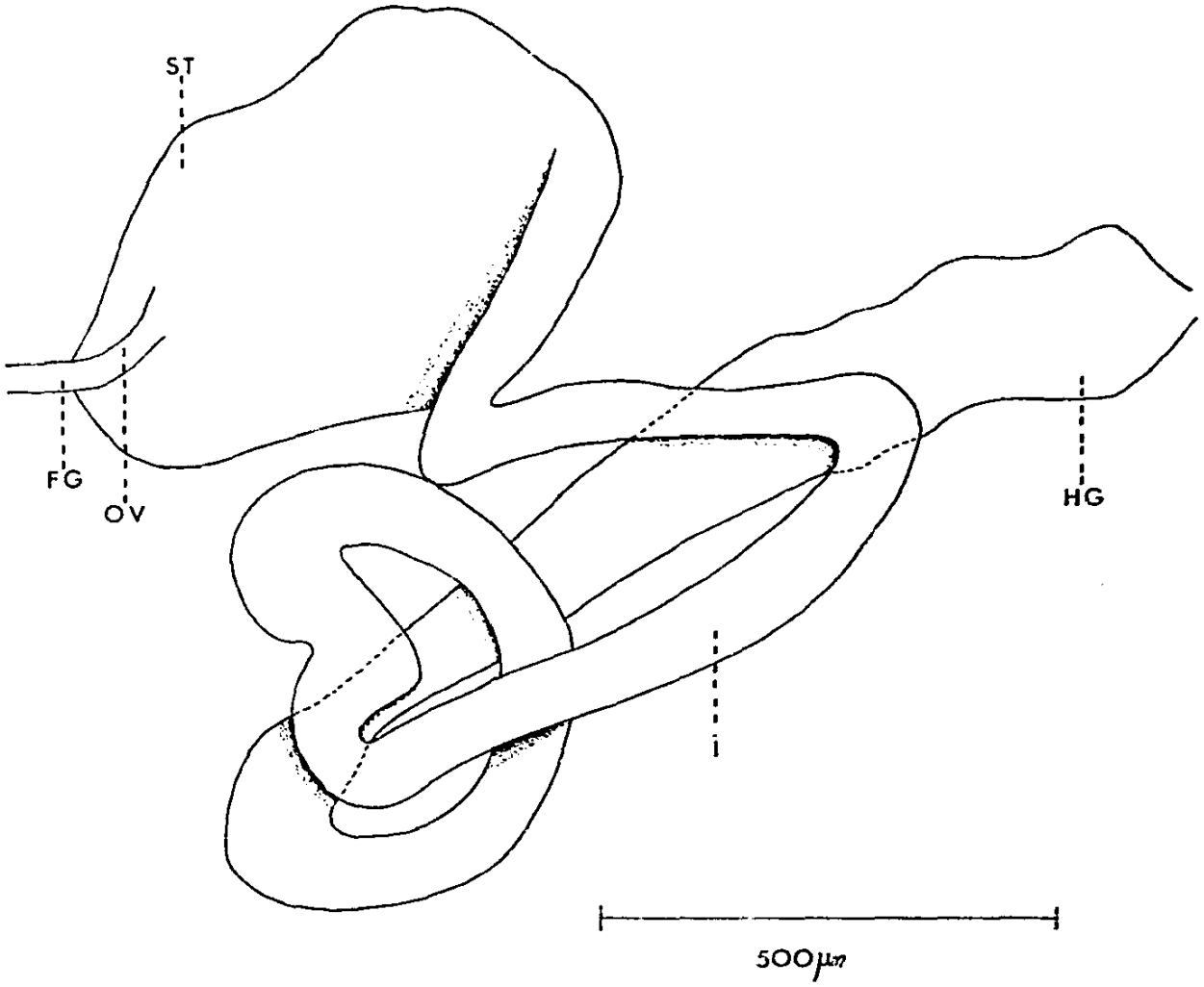

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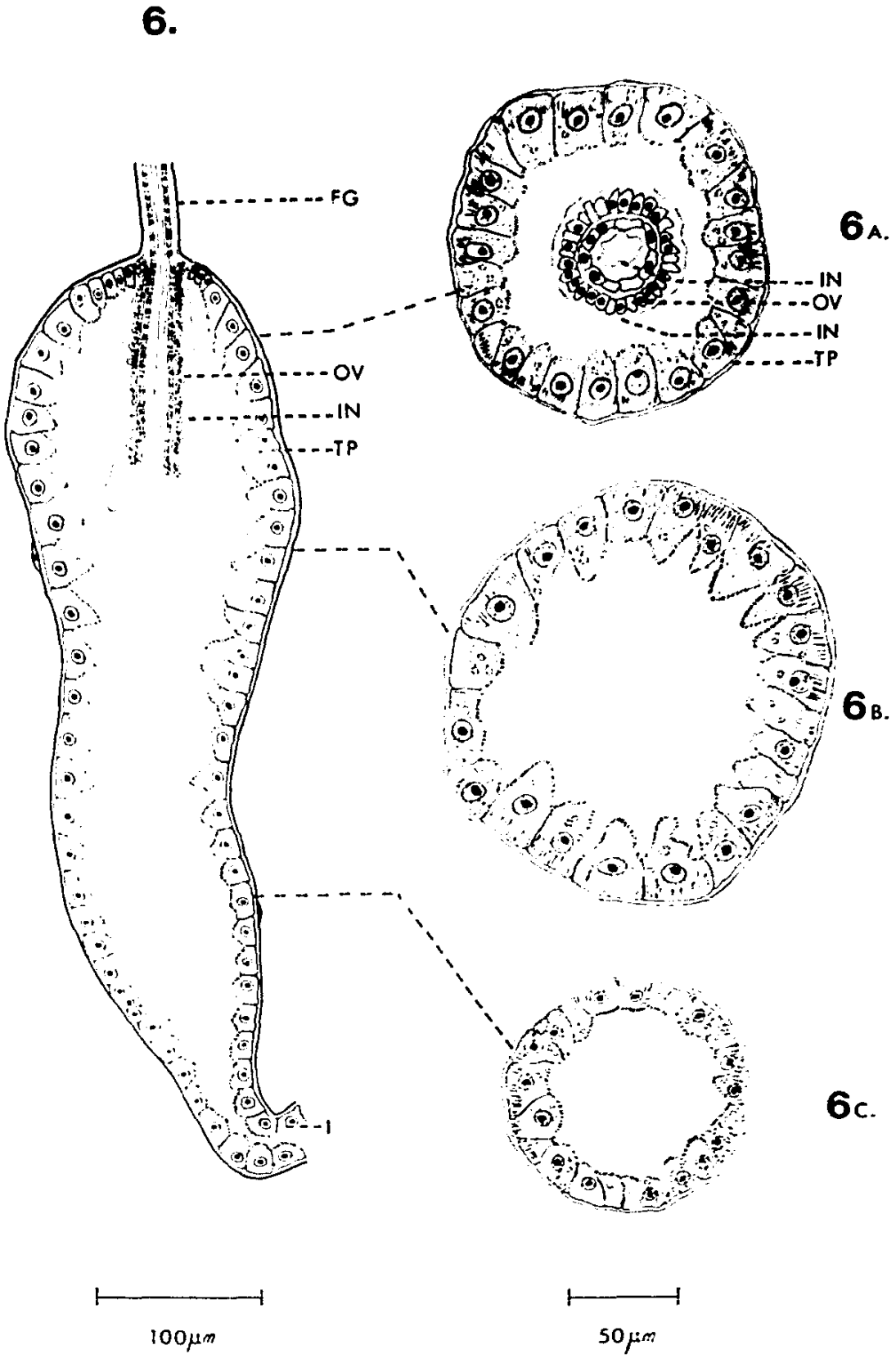

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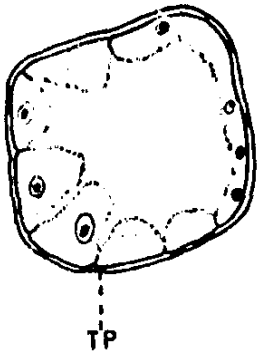

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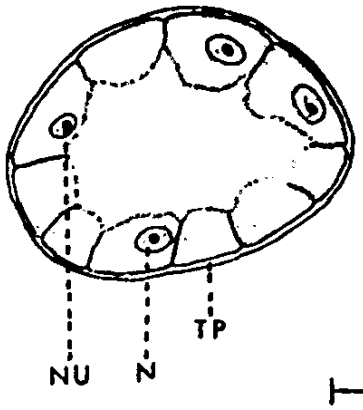

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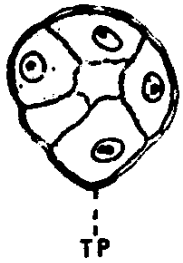
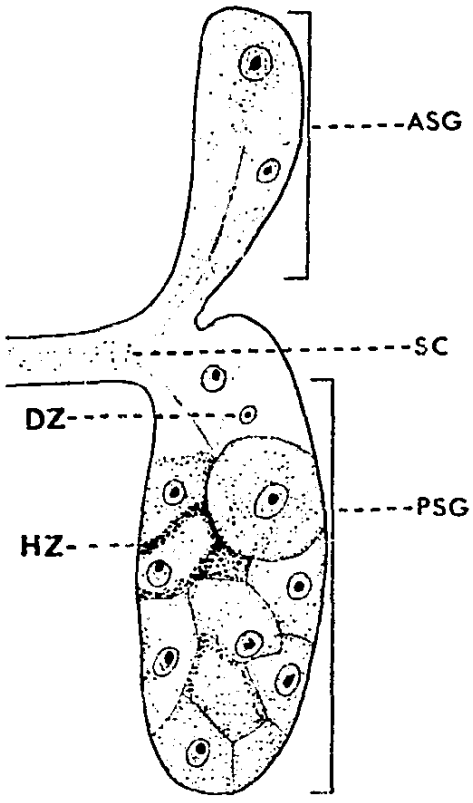
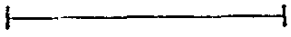


20μm

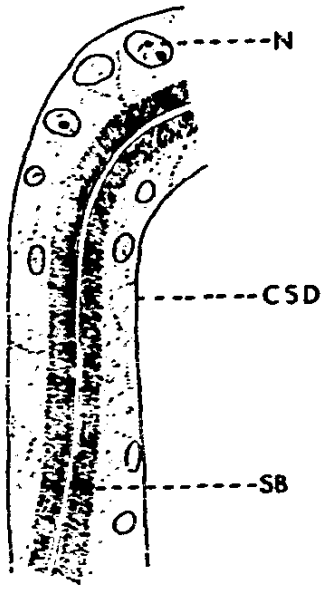
10.





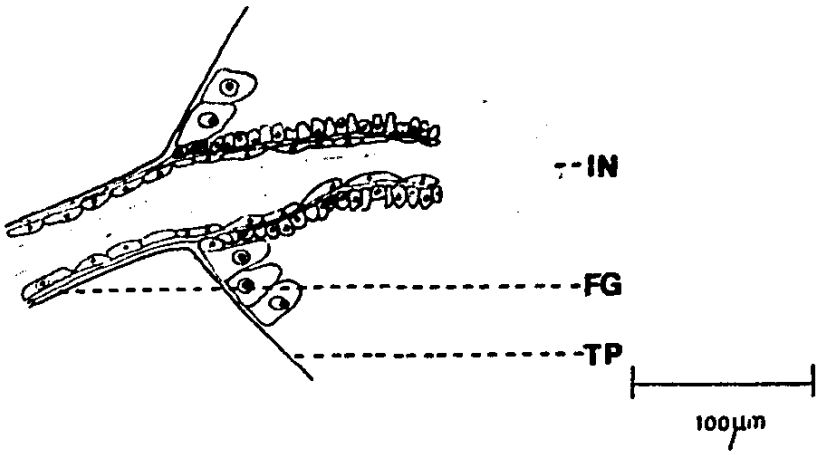
50μm

11.



10μm

12.



13.