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THE ANATOMY AND HISTOLOGY OF THE DIGESTIVE SYSTEM OF *HOLOTHURIA SCABRA* JOGER *

M. MARY BAI

Sri Avinashilingam Home Science College, Coimbatore-11

ABSTRACT

Holothuria scabra a common species occurring along the east coast of India, was collected from Pamban and around Krusadi Islands and studied for anatomy and histology of its digestive system. The results obtained from this study will help in understanding the regeneration of organs and will also provide information on the comparative and functional anatomy of the digestive system in holothurians.

INTRODUCTION

OUR KNOWLEDGE of anatomy, structure, histology and the function of various organs of echinoderms has been summarised by Hyman (1955), Choe (1962) and Anderson (1966). Although *Holothuria scabra* is a common species occurring in large numbers along the east coast of India, no detailed anatomical and histological studies of its digestive tract, haemal-vessels and respiratory tree have been attempted so far. Hence, in the present study a comprehensive investigation of the morphology and histology of the above-mentioned systems have been undertaken as a necessary foundation to the experimental studies on the regeneration of the organs and also to provide further information on the comparative, functional anatomy and histology of these systems in holothurians.

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MATERIAL AND METHODS

The holothurians were collected from an area of 20 sq/km near Pamban (09° 16′ N, 79° 13′ E) around Krusadi Islands, 156.4 km away from Madurai, and maintained at room temperature (28- 30°C) in cement concrete tanks (120-150 l) with circulating water system.

For anatomical studies, the animals were slightly anasthetised with 8% Magnesium chloride in tap water for thirty minutes and thoroughly rinsed in sea water to prevent movement or evisceration. A posterio-anterior incision was made along the dorsal curvature of the body wall to expose the internal organs.

For histological studies the tissues were fixed in Bouin's Fluid, 10% Formalin, susa's fluid, (all made with sea water) Zenker—formal and Helly's fluid. Sections of 5μ thickness were cut and stained with Heidenhein's iron hematoxylin, Malloryis triple stain (MTS), Heidenhein's azan (HA) and Masson's trichrome stain (MT).

OBSERVATION

A. Alimentary Canal

*Morphology**

The general morphology of the alimentary canal is shown in Fig. 1. The mouth leads into an oesophagus which occupies the centre of aquapharyngeal bulb. It is attached to the calcareous ring by a number of radiating

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The nomenclature used by Hyman (1955) is followed in this study.

bands of connective tissue. The yellowish bulbous stomach is visible as an enlarged region of limited length (about 15 cms). The thin-walled region (1 to 2 cm long), pinkish red in colour is known as 'constriction'. The intestine is looped within the coelom and is two to three times longer than the body. The intestine is divisible into two regions, a small intestine and a large intestine. The small intestine consists of a descending and an ascending region. The descending small intestine first runs towards the posterior end along the mid dorsal region, and then bends and connects with the ascending small intestine which runs anteriorly along the left side of the body, reaching the level of aquapharyngeal bulb. It then turns and descends again forming the large intestine. The large intestine runs along the mid ventral region directly backward to the anus.

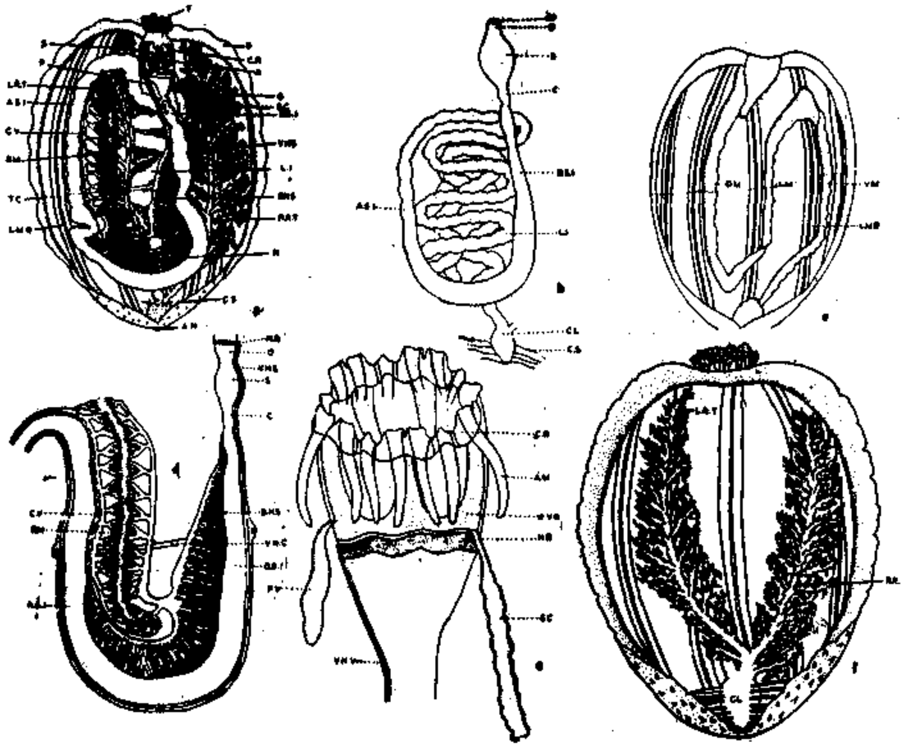

Fig. 1. Diagrammatic representation of the viscera of *Holothuria scabra* showing the position of various systems: a. viscera, b. gut, c. course of mesentry, d. vessels of the haemal system, e. aquapharyngeal bull and f. respiratory tree.

A—Aquapharyngeal bulb, AN—Anus, A.S.I—Ascending small intestine, B—Body wall, C—Constriction, C.L—Cloaca, C.R—Calcareous ring, C.S—Cloacal suspensors, C.V—Collecting Vessel, D.H.S—Dorsal Haemal sinus, D.S.I—Descending small intestine, G.—Gonad, L.I—Large intestine, L.M.B—Longitudinal muscle band, L.R.T—Left respiratory tree, N—Network of haemal vessel, P—Polian vesicle, R.M—Rete mirabile, R.R.T—Right respiratory tree, S—Stomach, S.C—Stone canal, T—Tentacle, T.C—Transverse connecting vessel, V.H.S—Ventral haemal sinus. (The arrow marks indicate the region of rupture during evisceration).

The terminal part of the large intestine, the cloaca, is an expanded region and is attached to the surrounding body wall through radiating strands, the cloacal suspensors. The respiratory tree opens into the cloaca.

The digestive tract is supported by a mesentery, which is divisible into three portions namely, a dorsal mesentery which attaches the anterior part of the digestive tract (oesophagus, stomach and 'constriction'), the descending small intestine to the middorsal inter radius and the gonoduct; a lateral mesentery which supports the ascending small intestine connecting it with the body wall to the left side of the dorsal inter-radius; and a ventral mesentery, springing from the ventral body wall which supports and attaches the large intestine to the ventral inter-radius (Fig. 1 c).

Histology

The gut wall consists of mainly four distinct layers, namely, an outer peritoneal epithelium (PE, Pl. I A) lined with cilia; the muscle layer composed of circular and longitudinal fibres (CM and LM, Pl. I A); the connective tissue (CT, Pl. I A) which is continuous with that of the haemal system and the mesentary; and a lining epithelium (LE, Pl. I A) which contributes principally to the thickness of the wall of the gut (Pl. I A).

Oesophagus

The peritoneal epithelium (PE, Pl. I B) consists of densely packed, ciliated basophilic (as revealed by Masson's trichrome stain) cells of 24 to 28 μ thickness with an acidophilic ovoid granular nucleus towards one end (as observed from Mallory triple stain method). The outer circular muscle (CM, Pl. I B) fibres (26 μ) are closely packed forming a continuous layer. The inner longitudinal muscle (LM, Pl. I B; 10 μ) is diffused and embeded in the periphery of the connective tissue. The connective tissue (96 μ) which occupies a major portion of the oesophageal wall, is divisible into an outer dense region packed with few amoebocytes, large lacunae, and an inner fluid region packed with numerous amoebocytes and secretory products (A and S, Pl. I C). The lining epithelium consists of compactly arranged mucosal cells, with their elongated nuclei lying at varying levels (LE, Pl. I C). The cells of the lining epithelium in the oesophagus are closely arranged to form a villus like structure (Pl. I A) supported by lamellar extensions, projecting inwards from the basal connective tissue layer. A few lumps of secretory granules and amoebocytes are present at the basal portion of the epithelial cells. The periphery of the lining epithelium is lined by a thin 'cuticle' (C, Pl. I D) as revealed by Mallory's triple stain.

Stomach

The peritoneal epithelium (PE, Pl. I E; 20 μ thick) consists of columnar, closely packed ciliated cells with centrally placed nuclei. The circular muscle (CM, Pl. I E; 16 μ) thick is present throughout the stomach. The longitudinal muscle (LM, Pl. I E; 5-8 μ) is interspersed with the circular muscle in some portions. The connective tissue (CT, Pl. I E; 218 μ) of the stomach wall consists of a thick outer zone adhering to the muscle layer with numerous amoebocytes and morula cells and an inner zone of fluid nature with fewer amoebocytes. The inner zone of the connective tissue invades the base of the villi of the lining epithelium and break up into fine channels as in *Thyone briareus* (Farmanfarmian, 1969 a). In the inner zone of the connective tissue secretory materials are present (S, Pl. I E). The lining epithelium (42 μ) of the stomach is thrown into simple villi and such villi are few in the anterior and numerous in the posterior part. Numerous gland cells and lacunae are interspersed among the typical epithelial cells (Pl. I F).

Constriction

In the 'constriction' the peritoneal epithelium (PE, Pl. I G; 1-56 μ) consists of groups of

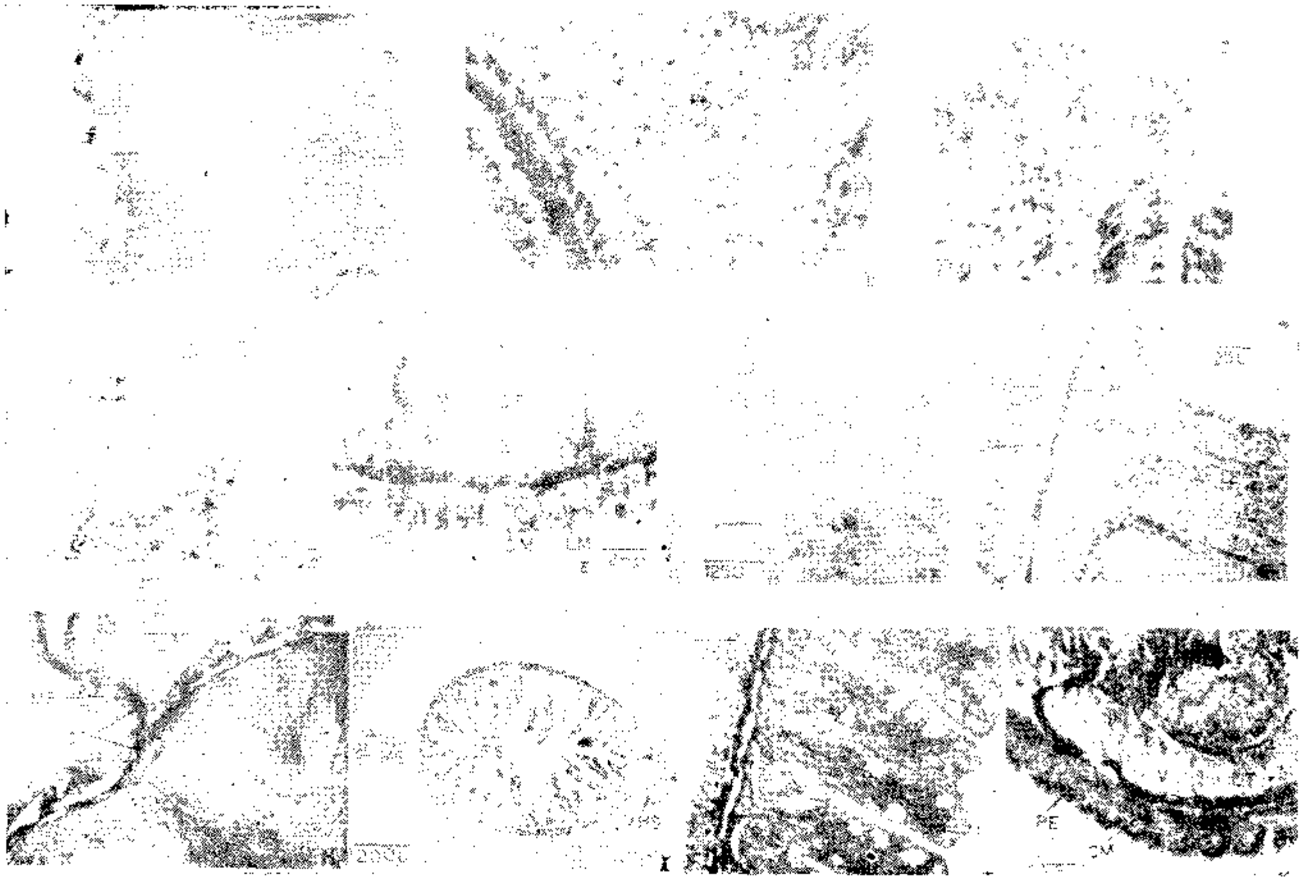

PLATE I. A—D. T.S. of oesophagus. E, F. T.S. of stomach and G-K. T.S. of the 'constriction'.

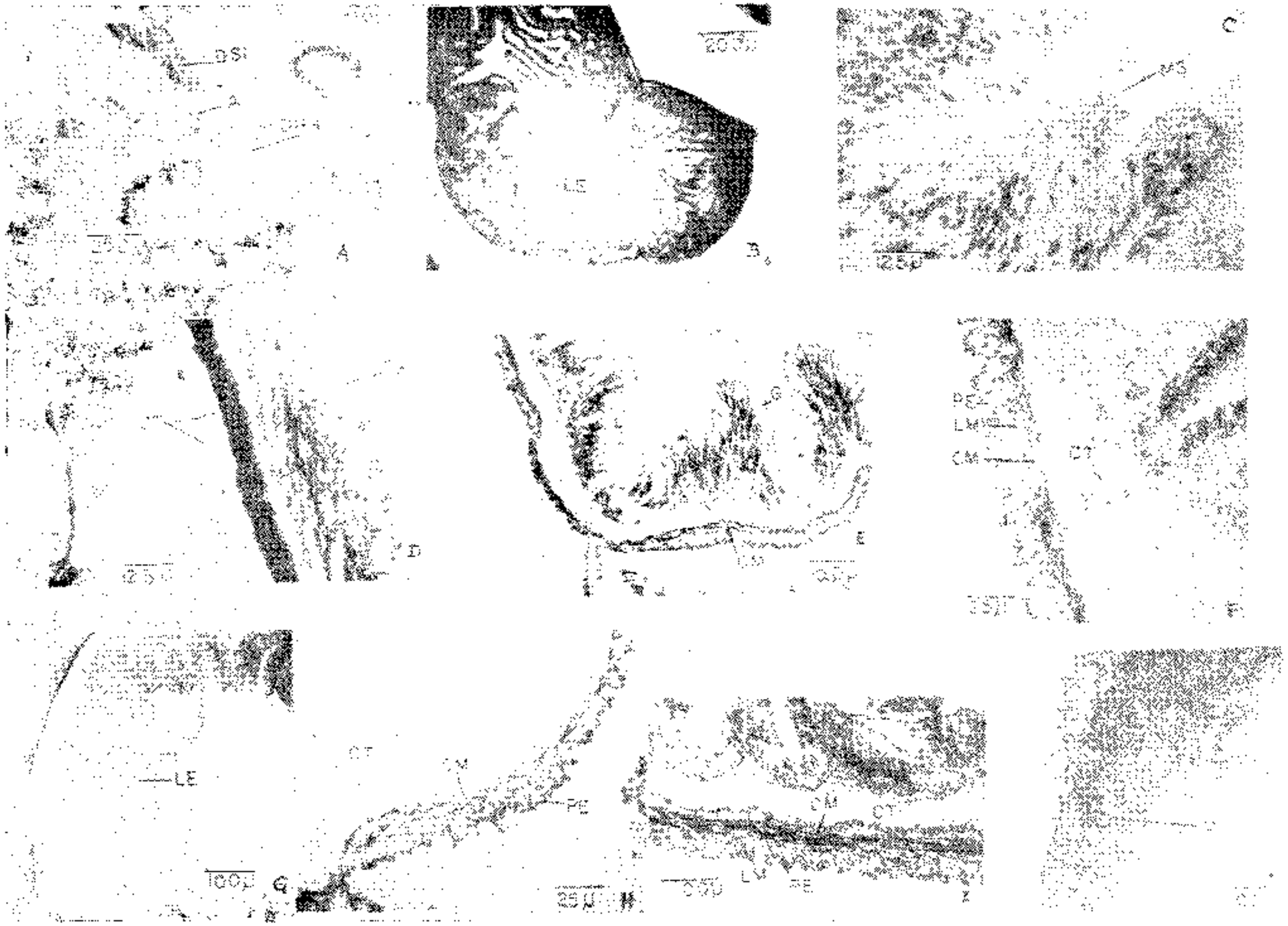

Plate II. A-C. T.S. of the descending small intestine. D, E. T.S. of the anterior part of the ascending small intestine. F, G. T.S. of the large intestine. H, I. T.S. of the cloaca and J. T.S. of the mesentery.

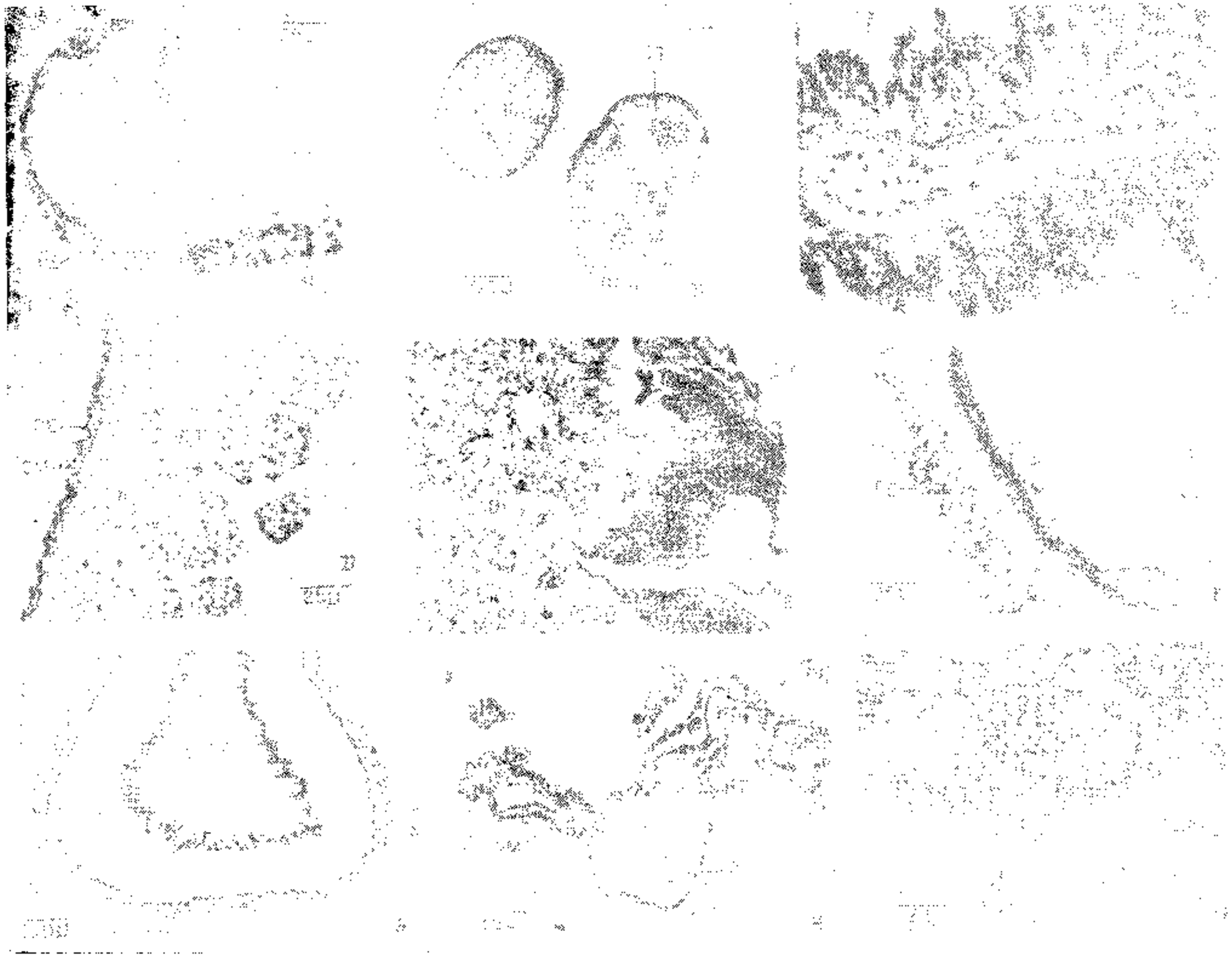

PLATE III. A. B. T.S. of the dorsal haemal sinus. C. T.S. of the 'rete mirabile'. D. L.S. of the haemal ring encircling the oesophagus. E. T.S. of the body wall at the place of the radial water canal. F. T.S. of the stem of the respiratory tree. G. T.S. of the respiratory tree. H. T.S. of the terminal branch of the respiratory tree and I. T.S. of the branches of the respiratory tree closely packed columnar cells, the nuclei of which lie towards the surface (Pl. I F). The muscle layer of this part of the alimentary canal differs from other regions in that the circular muscle (CM, Pl. I G) is compact; comparatively thinner (4 μ) and continuous, whereas the longitudinal muscle (LM, Pl. I G) is diffuse at the base of the peritoneal epithelium. A point to be noted is that the longitudinal muscle fibres are found to be present outside the circular muscle. The reverse is the case in the oesophagus and stomach. The posterior part of the constriction from where the rupture takes place during evisceration is completely devoid of longitudinal muscle fibres (Pl. I H).

The connective tissue (CT, Pl. I A; 64 μ) is thin and vacuolar and throughout its distribution sends long branching fibres into the lining epithelium. Prominent but sparsely distributed amoebocytes are seen to enter into the villi of the lining epithelium. The fluid of the connective tissue is in continuation with that of the ventral haemal sinus and mesentery (Pl. I H, I). The lining epithelium of the construction which is composed of elongated cells is very thick (356 μ). The villi of this region is more elongated leading to the reduction in the area of lumen (*Fig.* 1 a). Sections of the villi of the 'constriction' stained with Heidenhein's iron hemotoxylin show a faintly stained area (Fig 1 a.) This area represents the distal portions of the epithelial cells as found in *cucumaria elongata* (Fish, 1967 a). The deeply staining nuclei of the lining epithelium are seen at the base and mucous globules are found to stream outwards the free border. Both empty vacuoles and those filled with secretory products are found scattered throughout the epithelial cells (Pl. I J).

Descending small intestine

The peritoneal epithelium (PE, Pl. I K; 1-32μ) of the descending small intestine resembles that of the 'constriction'. Ovoid granular amoebocytes are observed at the base of the epithelial cells and the muscle layer. The circular muscle fibres (CM, Pl. I K; 16 to 24 μ) are compactly packed, but the longitudinal muscle is completely absent in this region of the intestine. The outer zone of the connective tissue (CT, Pl. I K) forms a strong supporting layer to circular muscle fibres, while the inner zone, which is fluid in nature, has several vacuoles (C, Pl. I K). A fewer number of amoebocytes are lodged in the connective tissue while they are found in abundance in the villi. The connective tissue of the intestine is continuous with both the dorsal and ventral haemal sinuses (DHS, Pl. II A) and numerous amoebocytes are seen passing into the intestine from the dorsal haemal sinus. The lining epithelium (LE, Pl. II B) gets branched profusely, as a result of which the lumen is completely obliterated by the numerous villi of the epithelium. The cells here are packed with secretory globules. Mucous secretion (MS, Pl. II C) is seen at the tip and in between the villi.

Ascending small intestine

The peritoneal epithelium (PE, Pl. II D) of the ascending small intestine (24 μ) also resembles that of the 'constriction'. The circular muscle fibres (CM, Pl. II D) are distinct and uninterrupted, while longitudinal muscle is completely missing. The connective tissue (CT, Pl. II D) appears to be thicker and amoebocytes are concentrated in the outer zone. Vacuoles and secretory material are completely absent. Mucous secretory glands are prominently distributed in the ciliated epithelium of the anterior part of the ascending small intestine (Pl. II E) while they are completely absent in the posterior region. The lining epithelium of the small intestine, which is devoid of cuticle, is packed with numerous amoebocytes.

Large intestine

The peritoneal epithelium is thin (7 μ) and grouped into bundles presenting a wavy appearance of the free surface. Nuclei are found towards the outer margins of the cells (Pl. II F).

The musculature of the large intestine is different from the small intestine, in that the longitudinal muscle fibres are present outside the circular fibres (LM, CM, Pl. II F). The longitudinal muscle fibres increase in number towards the posterior region. As in the small intestine, the outer zone of the connective tissue is thicker than the inner zone but with lesser number of amoebocytes. The villi are shorter and more in number (LE, Pl. II G). The secretory granules and mucous glands are, however, absent.

Cloaca

The peritoneal epithelium of cloaca which is thick (40 μ) resembles that of the other regions. The longitudinal muscle is absent (Pl. II H) at the anterior region of the cloaca from where rupture takes place during evisceration. In other regions a compactly packed dense circular muscle (24 μ) and a feeble longitudinal muscle layer (8 μ) are present (CM, LM, Pl. II J). Fewer number of amoebocytes but greater number of morula cells are seen in the connective tissue. In the villi only fewer number of amoebocytes are present.

Mesentery

The mesentery consists of thick connective tissue (36 μ) covered by a distinct circular muscle layer (4 μ) and a peritoneal epithelium (CT, CM, PE, Pl. II J).

The epithelium of the mesentery is continuous with the peritoneal epithelium of alimentary canal which forms the outermost layer and is connected with the inner lining of the body wall. The longitudinal muscle is absent in the mesentery. Morula cells are seen in the connective tissue (M, Pl. II J).

B. Haemal System

Morphology

In this group of holothurians (Aspidochirota), the haemal system is reported to be well developed (Hyman, 1955). A diagrammatic representation of this is shown in Fig. 1 d.

The haemal system consists of a haemal ring encircling the oesophagus directly behind and closely attached to the water vascular ring Fig. 1 c and two main sinuses, a dorsal and a ventral vessel running along the small intestine. From the haemal ring five radial sinuses, ascend along the aquapharyngeal bulb accompanying the radial water canals. They run along the body wall and lie between the hyponeural sinus and radial water canals of the body wall.

The ventral sinus extends along the entire length of the stomach, 'constriction' and small intestine, finally merging with the posterior most part of the ascending small intestine. In the oesophageal region the ventral sinus is very thin and opens into the haemal ring. The ventral sinus is in close association with the gut wall and during its course along the descending and ascending small intestine, it is connected transversely by a simple horizontal vessel (Fig. 1 d).

The dorsal sinus runs along the whole length of the small intestine on the side where it is attached to the dorsal mesentery. It is connected to the intestinal wall by numerous branches. It gives off many long branches to the loop of the intestine. Thereafter, the dorsal sinus is connected to the ascending small intestine through tufts of lacunae forming the 'rete mirabile' (Fig. 1 d).

Between these network of lacunae and the wall of ascending small intestine there is a collecting vessel connecting the lacunae tufts and ascending small intestine. This vessel is continuous with the main dorsal sinus and is connected with the anterior and posterior end as shown in Fig. 1 c. The lacunae tufts ends of the 'rete mirabile' are closely connected with the terminal ends of the left branch of the respiratory tree. The dorsal sinus does not open anteriorly into the haemal ring and so both the stomach and 'constriction' are devoid of it. At the anterior part of the small intestine the dorsal sinus ceases to exist as a separate channel and serial sections at this point show that it merges with the connective tissue of the intestine.

Histology

The histological examination of the dorsal and ventral haemal sinuses shows an outer peritoneal epithelium, a middle circular muscle layer and an inner connective tissue (PE, CM, CT, Pl. III A). The peritoneal epithelium (28 μ) is composed of columnar cells with centrally placed nuclei. The circular muscle layer is distinct, thick (14 μ) and uninterrupted (PE, Pl. III A). However longitudinal muscle fibres are absent. The connective tissue is thick (86 μ) with scattered amoebocytes. A distinct lumen is present in the dorsal, ventral and ventral-transverse connecting vessels which in some portion contain fewer Amoebocytes.

The histology of vessels of the dorsal sinus that are connected with the looped region of the small intestine differs from the histology of the dorsal sinus. The connective tissue is very thick and is seen occupying most of the area of the vessels with numerous lacunae spaces either empty or filled with granular amoebocytes with intensely staining nuclei (CT, LS, A, Pl. III B). Lymphocyte like cells, the haemocytes, emerge from the connective tissue into the lumen of the vessel (H, CT, Pl. III B).

The 'rete mirabile' is composed of a thick peritoneal epithelium, (57 μ) thin circular muscle layer and a thin connective tissue (PE, CM, CT, Pl. III C). The peritoneal epithelium is composed of columnar cells which are elongated. It is grouped into distinct bundles which give a wavy appearance to the epithelium. It is presumed that such an arrangement may help to increase the surface exposed to the coelom. The lumen is empty or with fewer amoebocytes.

The structure of the haemal ring encircling the oesophagus consists of an outer thin peritoneal epithelium, a thin circular muscle layer and a thick connective tissue (PE, CM, CT, Pl. III D) which is folded into villi like projections, seen close to the peritoneal epithelium of the oesophagus. Numerous amoebocytes are seen in the connective tissue. Sections of the body wall at the place of radial water canal show a distinct haemal lacunae filled with amoebocytes in between the dermis and the circular muscle layer (HL, A, D, CM, Pl. III E).

C. Respiratory Tree

Morphology

The respiratory tree originates from the anterior part of the cloaca near the region where the large intestine opens into it and is attached to the body wall by irregular strands of connective tissue. It is further divided into a right and a left arborescent tubes which project anteriorly into the coelom extending upto the aquapharyngeal bulb (Fig. 1 f). The two arms give rise to finer branches of tubules which fill the entire coelomic cavity, surrounding the internal organs. The tubules are colourless, transparent and terminate into small thin walled vesicles. The left branch is intermingled with the 'rete mirabile' of the ascending small intestine (Fig. 1 a, f). Apart from these two main branches, there are two to three short branched tubes originating from the base of the common stem of the respiratory tree.

Histology

The respiratory tree are said to be formed as evaginations of the cloacal portion of the gut (Hyman, 1955) and hence the histological picture resembles basically that of the gut with certain simplifications. Its stem and branches consist mainly of four layers; a peritoneal epithelium, a muscle layer made up of only circular muscle fibres, a layer of connective tissue and a lining epithelium (PE, CM, CT LE, Pl. III E). The peritoneal epithelium (56 μ thick) consists of columnar epithelial cells, the nuclei of which are located towards the free margin (Pl. III F). The muscle layer is composed of continuous thick circular muscle fibres (14 μ) closely resembling the fibres seen in the region of the cloaca. Inner to these is the layer of broad connective tissue (210 μ) consisting of two distinct zones; an outer thicker and an inner fibrous, vacuolar, thin and fluid like zone (CT, Pl. III F). Numerous amoebocytes are seen in the connective tissue. The innerlining epithelium (56 μ) consists of closely packed columnar cells with their nuclei at different positions (LE, Pl. III G). This layer is thrown into finger-like projections into the lumen. Large number of amoebocytes are seen in the lining epithelium. The lumen of the respiratory tree contains a fluid in which amoebocytes occur (F, A, Pl. III G).

The terminal branches consist of a single or double layer of epithelial cells (PE, P. III G). The left branch of the respiratory tree which is connected with the 'rete mirabile' are found to intermingle with the branches of the haemal vessel. Eventhough they appear to have connections with haemal system externally, the histological studies have shown that the finer branches lie only side by side without being connected (RM, RT, Pl. III H). In some of the terminal branches which lie closer to the haemal vessel the lumen is filled with amoebocytes in fluid phase. Deeply staining coelomocytes are accumulated near the finer branches of the respiratory tree (RTB, Pl. III J).

DISCUSSION

The histological investigations of digestive system of *H. scabra* presents some interesting features. In the oesophagus and stomach, the muscle layer consists of an inner longitudinal and an outer circular layer as mentioned by Hyman (1955) in other species. In 'constriction' on the other hand, this arrangement is reversed in *H. scabra*, in that longitudinal muscle is found outside the circular muscle. Further, in the place of rupture during evisceration, only the circular muscle is present. In the intestine also some changes in the arrangement of the muscle fibres have been noticed. The point to be noted is the absence of longitudinal muscle layer both in the 'constriction' and in the cloacal regions from where rupture takes place. Such an absence of longitudinal muscle fibres at the place of rupture has not been recorded in the gut wall of the holothurians so far. Hyman (1955) is of the opinion that, the place of reversal of muscle fibres constitutes a week region at which the digestive tract contracts during evisceration. In *H. scabra*, not only a reversal of muscle fibres has been noticed in 'constriction' and cloaca, but also the complete absence of longitudinal fibres at the place of rupture. It is therefore presumed, that in this species also, such an arrangement of muscle fibres aids in the evisceration.

In all the regions, such as oesophagus, stomach, 'constriction' and the intestine, the connective tissue which makes up for the bulk consists of an outer dense and an inner fluid zone. Vacuoles and secretory materials are present in the connective tissue.

The changes in the structure of the lining epithelium and the presence of the mucous, secretory glands, goblet cells, secretory granules and vacuoles in the lining epithelium of different regions of the alimentary canal suggests a degree of regional and functional specialisation. This recalls the studies of Anderson (1953, 1954, 1959), who, after observing such a change in different parts of the pyloric caeca and the stomach of the starfish *Asterias forbesi*, *Patiria miniata* and *Henricia* sp. found such regional specialisation. Hamann (1883) and Gerould (1896) have described the gland cells including mucous glands in the stomach and intestine of *Leptosynapta*, *caudina* sp. and *Holothuria* sp. respectively. Fish (1967a) however, has stated that such mucous glands are present only in the oesophagus and 'constriction' whereas they are absent in the stomach, intestine and cloaca. In *H. scabra* on the other hand, mucous and secretory glands are interspersed among the lining epithelial cells of all the regions, except the posterior part of the ascending small intestine and large intestine.

A thin cuticle covering the different regions of the alimentary canal has been reported in *caudina arenata* (Gerould, 1896) and *Cucumaria elongata* (Fish, 1967 a). Hyman (1955) has mentioned that, in holothurians, in general a thin cuticle lining is present not only in the pharyngeal and stomach regions, but extends into the intestine throughout its length. The ultrastructure of *Stichopus japonicus*, however, has failed to show the cuticle lining in the intestine (Kawaguti, 1964). In *H. scabra* where a pharynx is absent ; the oesophagus is lined with a thin cuticle. This may have a functional significance, in that, it may prevent the rupture of the lining epithelium by hard, fritty materials, like mud mixed with sand which is normally taken in while feeding.

The presence of circular muscle layer in the mesentery is reported for the first time, the only two previous studies on the histology of mesentary (Gerould, 1896; Dawbin, 1949 a) have failed to mention this.

This origin of coelomocytes in holothurians has been a subject of controversy. Cuenot (1897) put forward the view that these may originate from haemal ring and vessels. This has been confirmed by Hatanaka (1939), Prossor and Judson (1952) and Hetzel (1965). The present investigation lends support to this hypothesis and has also shown that it is localised in the mesenchymal tissues of the vessels of dorsal sinus.

The function of haemal system and the amoebocytes in the transport of nutrients have been intensively studied, different views have been expressed regarding their role. The emergence of amoebocytes in and out of the gut and haemal sinuses, the presence of five distinct haemal sinuses, lying between the dermis and circular muscle of the body wall suggest their role in this. This observation is in confirmity with the reports of the investigation of Enriques (1902), Oomen (1926) and Schreiber (1930, 1932 a, b). Recently, studies using radioactive sugars (Krishnan and Krishnaswamy, 1970 a; Krishnan, 1970 b) have lent further support to this. Ferguson (1964), Farmanfarmian and Phillips (1962), Farmanfarmian (1963, 1969 b) on the other hand, have concluded that the haemal sinuses do not have a significant role to play. Ferguson (1970), however has concluded from his autoradiographic studies on the sea stars, that haemal sinuses do play a significant role in the nutrient transport as found in the present study. In H. *Scabra*, the haemal vessels pulsate at 8-10 beats per minute at room temperature, i.e., 28°C as found in *Caudina chilensis* (Kawamoto, 1927) and in the echinoid *Strongylocentrotus purpuratus* (Boolotian and campbell, 1964) and in *Stichopus californicus* (Prosser and Judson, 1952). It may be suggested that the amoebocytes produced in the connective tissue of the branches of the dorsal haemal sinus, are carried through them to the gut, from where they carry away the products of digestion to different tissues of the body confirming the view of Kawamoto (1927).

The differences seen in the histology of the haemal vessels may be correlated to the specific function. The presense of groups of amoebocytes in the connective tissue and their emergence into the lumen of the branch vessels of the dorsal haemal sinus suggest that their function is concerned with the production of amoebocytes. The presence of elongated peritoneal epithelium, thin circular muscle layer and connective tissue in the 'rete mirabile' and the entrance of the coelomocytes from the coelomic fluid into it, indicate their role in absorption.

A review of literature on the histology of respiratory trees show that the absence of longitudinal fibres in the respiratory tree has not been reported so far. The absence of longitudinal fibres may be attributed to the fact that they are mere evaginations from the cloacal region adjacent to the opening of the large intestine into the cloaca which lacks longitudinal fibres. The histology of the respiratory tree reveals their possible role in the physiology of respiration of *H. scabra*. The idea that the respiratory tree helps in respiration has been shown by experimental studies by Bertolini (1933 b) as referred in Hyman (1955). The presence of fluid material in the lumen, the close association of the 'rete mirabile' and the respiratory branches especially the fluid material with amoebocytes in the finer branches, all point to their possible role in respiration.

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