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DIGESTIVE SYSTEM AND PHYSIOLOGY OF DIGESTION IN A STYLE-BEARING MESOGASTROPOD SNAIL *CERITHIDEA CINGULATA* (GMELIN)

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ABSTRACT

An elaborate description of the digestive system of a style-bearing mesogastropod snail *Cerithidea cingulata* (Gmelin), along with its digestive glands is given in this paper. The histology and histochemistry of foregut, midgut, hindgut, digestive and hypobranchial glands have also been dealt in detail. The physiology of the digestive system of this snail has shown that the foregut secretes no enzyme, while the midgut is the site of high enzyme activity. The pH of the gut is neutral in the oral cavity, acidic in oesophagus, stomach, style sac, digestive gland and intestine, but again alkaline in the rectum.

The studies on food and feeding habits of this snail have indicated that *C. cingulata* is a selective bottom feeder and feeds on detritus with a preference of soft fine sandy muddy substratum. Analysis of gut content showed the presence of sand grains, unicellular diatoms and minute scraps of algal filaments. Gut microflora include gelatinolytic, caesinolytic, amylolytic, cellulolytic and lipolytic bacteria. The microbes aid in digestion by splitting complex food materials into simple products to be acted upon by the native enzymes and of help in extra- and intracellular digestion.

INTRODUCTION

POTAMIDID snails are mesogastropods which are unique in resembling bivalves in having crystalline style, a proteinaceous structure that produces digestive enzymes. The digestive systems of some potamidid snails are known from the works of Seshaiya (1932) on *Cerithidea cingulata*, Bright (1958) on *Cerithidea californica* and Driscoll (1971) on *C. californica* and *Batillaria zonalis*. Qualitative and quantitative works on the digestive system and enzymes include those of Alexander and Rae (1974), Alexander *et al.* (1979), Cutler and Yellowlees (1979) and Yellowlees (1980). In this account, a comprehensive description of functional morphology of digestive system, histology and histochemistry, quantitative and qualitative analyses of enzymes, gut microflora and their role in the digestion in the potamidid snail *C. cingulata* is given.

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MATERIAL AND METHODS

Specimens collected from the Vellar Estuary (Tamil Nadu) during 1984-85 were

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utilised for the present study. For histological and histochemical studies, required organs were removed and preserved in Zenker's and Helly's fluids. Double embedding in celloidin and paraffin was used, following Peterfi's method (Pantin, 1962). 5 μ sections were cut uniformly and stained for histological and histochemical studies as outlined by Drury *et al.* (1967) and Pearse (1977). For qualitative analyses of the enzymes, extracts from the foregut (comprising the buccal complex and oesophagus including the salivary glands), the midgut (comprising stomach and style sac), the hindgut (comprising the intestine and the rectum) and the digestive glands were prepared. The pH of the gut was determined with BDH indicator paper (Ward, 1966).

Suitable substrates were used for determination of the presence of various enzymes. Quantative estimation of amylase activity was carried out using Somogyi-Nelsons' photometric method (Nelson, 1944). Proteolytic activity was quantitatively estimated by Soransen's Formal titration method (Hawk *et al.,* 1954). Quantitative estimation of lipolytic enzyme activity was done using the method of Tietz *et al.* (1959). In all the above estimates, boiled extracts were used as control and all the experiments were repeated five times.

For the analysis of gut microflora, suspected colonies of Total Viable bacterial Count (TVC), proteolytic, caesinolytic, amylolytic, lipolytic and cellulolytic bacteria were enumerated following the methodology of Harrigen and McCance (1972). All results were computed for CFU/g.

Results

Morphology

Foregut : The mouth is a crescentic slit leading into the buccal cavity. A pair of horny jaws are located dorsally. Behind the jaws, the dorsal lining is folded longitudinally and a pair of dorsal folds so formed are ciliated. The dorsal folds extend beyond the limit of the buccal cavity forming the beginning of the

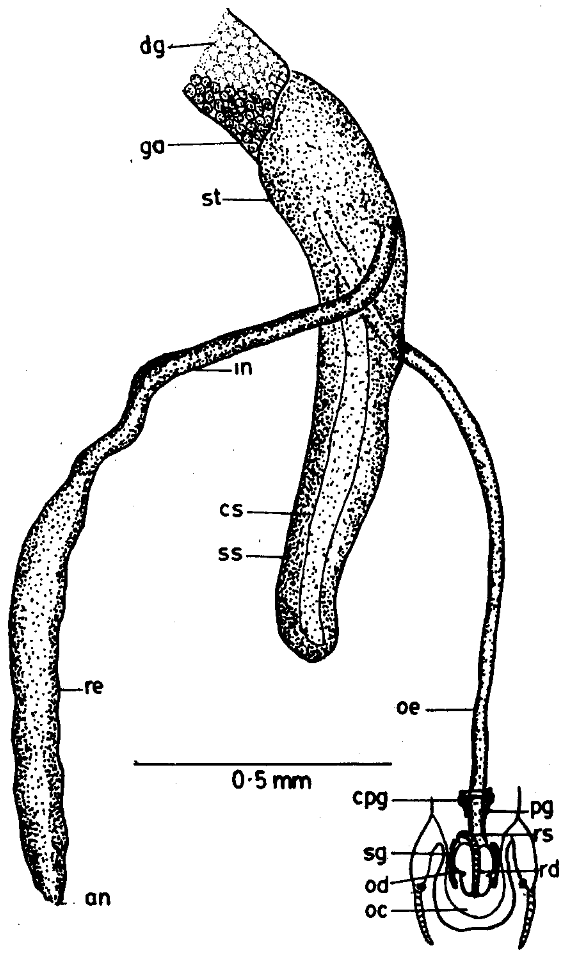

Fig. 1. Digestive system of *C. cingulata* (For abbreviations, please see Pl. I)

dorsal food groove. The entire buccal mass is surrounded by a thick layer of interacting smooth muscles, which allow movement in all directions including partial extrusion of radula through the mouth opening (Fig. 1).

The radula (Fig. 2 a), located in the oral cavity just above a pair of odontophores (Fig. 2 b) is typically taenioglossate with one median, one pair of lateral and two pairs of marginals (2-1-1-1-2). The radular sac opens ventrally into the posterior end of the buccal cavity. The radula extends anteriorly from the radular sac and is held against the floor of the buccal cavity by the radular membrane.

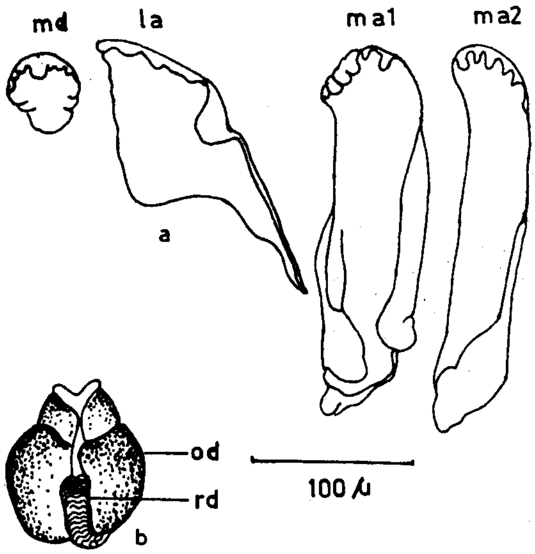

Fig. 2. a. Radular teeth of *C. cingulata* and b. Odontophore of *C. cingulata* (For abbreviations, please see Pl. I)

The radular ribbon measures 1.6 to 1.8 mm in a specimen of 28 to 30 mm in shell length, the ratio being about 0.06. The median tooth of the radula is triangular and bears a prominent middle cusp and three smaller lateral cusps on each side. The lateral tooth is larger than the median and bears six denticulations, the outer being the largest. Two marginals, inner and outer are similar in size and shape and bear six denticulations of uniform size. The number of rows of teeth varied from 65 to 71 in snails of same shell length.

Dorsal to the radula and lateral to the dorsal ciliated grooves, a pair of salivary glands (more specifically buccal glands) open into the buccal cavity. The salivary glands are wormlike and tubular.

Oesophagus is tubular and commences behind the radular sac and extends to the stomach. The dorsal food groove is formed by two lateral folds, which are extensions of the lateral folds in the buccal cavity. Posterior to the nerve ring, the lateral folds of buccal cavity twist to the left and the grooves become centrally oriented due to torsion. The lateral folds disappear just behind the nerve ring and in the rest of the region many longitudinal folds are present. These folds increase in number towards the end of the oesophagus near the stomach.

Midgut : The midgut region consists of two portions *viz.* the stomach proper and the style sac without any external demarcation to separate them

Within the stomach of *C. cingulata,* the oesophagus opens midventrally and the intestine opens topographically anteriorly (Fig. 3). The digestive gland opens by a pair of ducts adjacent to the oesophageal opening posteriorly and to the right of the latter. There is a large, midventral ridge which originates to the right of the opening of the duct of the digestive gland and extends posteriorly, ending near the stomach. There are two smaller ridges, anterior portion of one of which runs between the openings of oesophagus and intestine. This ridge prevents the food material entering from oesophagus not to be carried by ciliary currents directly to the intestine. The second small ridge extends from a point between the oesophageal opening of the duct of digestive glands, posteriorly around the base of the large ridge and anteriorly towards the gastric shield, ending about the middle of the large ridge. The gastric shield, which is only a cuticular thickening, is triangular in outline; its anterior end is slightly curved and exhibits a shallow trough into which crystalline style is rotated. The dorsal wall of the stomach is thrown into many ciliated folds, which act as sorting areas for food particles.

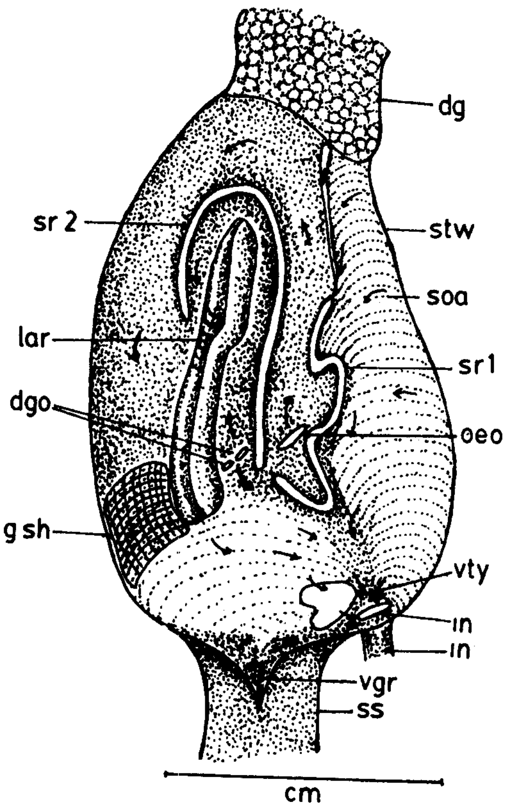

Fig. 3. Stomach of *C. cingulata* opened by a dorsal longitudinal cut-arrows indicate direction of ciliary currents (For abbreviations, please see Pl. I).

The style sac is double the stomach size and measures about 15 mm in a specimen of 25 mm in length. The opening of the style sac lies close to the opening of the intestine, latter lying to the left of the former. The ventral typhlosole is seen in the form of a muscular bulge, behind the opening of the style sac and that of intestine. There is a prominent longitudinal ventral groove in the style sac.

The crystalline style normally extends along the whole of the style sac and measures about 13 mm in a specimen of 25 mm length, the ratio being 0.52. The style is transparent, firm but flexible, cylindrical, rod-like and does not dissolve in seawater or formalin or in fixatives like Zenker, Helly or in alcohol. The style has blunt posterior end and a tapering anterior end. The blunt end rotates against the surface of the gastric shield.

Digestive gland : The digestive gland is a coiled diverticulum, dark brown in colour, occupying the last few whorls. In mature snails, the digestive gland is interspersed with gonad. The gland is composed of numerous smaller minute tubules, closely coiled together and covered by a layer of connective tissue. As already indicated, the digestive gland communicates with the stomach by two openings, located in the midventral region.

Hindgut : The intestine of *C. cingulata* originates from topographically anterior side of the stomach between the style sac and stomach proper, opposite the oesophageal opening. It passes along the side of the style sac anteriorly before making S-shaped coil over the stomach. It confluences with a broad tubular rectum at the posterior end of the mantle cavity. There are number of projections of the wall into the lumen of the intestine as well as in that of rectum. The rectum is attached to the mantle roof and opens exteriorly through the anus, located a little behind the mantle edge.

Histology and histochemistry

Foregut : The lips surround the mouth and lead to the oral cavity. They are lined by tall columnar epithelial cells devoid of cilia. At the anterior end of the mouth, these cells are lined by cuticle and form the horny jaws (Pl. I A). These epithelial cells are continuous with the epithelium of the snout, but the latter are taller and narrower than the former.

The dorsal food channel consists of mucous and supporting cells. The mucous cells are of two kinds, namely, acid and neutral mucopolysaccharides secreting cells, alternating with each other (Pl. I B). The radular sac has a glandular epithelial layer with prominent nuclei. The paired buccal cartilages, which resemble vertebrate cartilage histologically, are symmetrically placed and appear J-shaped. The supporting cells which do not show any cilia, are tall, narrow, columnar and have elongated nuclei. Mucous cells are barrel shaped and some of them pyriform with a basal nucleus and prominent vacuole containing mucus. The ventral food channel also showed a similar organisation, but more mucous cells are seen here. In the posterior part of the buccal region, the dorsal and ventral food channels are almost equal in size, being separated by two lateral ridges resulting in S-shaped food channel.

The tubules of the salivary glands are lined by a single layer of cells, with connective tissue and muscle fibres surrounding them (Pl. I C). There are about six to eight barrel shaped mucocytes alternating with wedge shaped supporting cells. Mucus secreted by these cells are neutral mucopolysaccharides.

The oesophagus (Pl. I D) has a mucous lining with short wedge shaped columnar cells, which are ciliated and have prominent oval nuclei. Barrel shaped mucocytes (Pl. I E) are also seen in the epithelial lining. There are eleven folds anteriorly of which 8 major and 3 minor ones. Posteriorly, these folds become uniform and number about 14 (Pl. I F). Excepting for these changes in the number of folds, histologically there is not much of difference in the organisation of the oesophagus.

Midgut : The lumen of the stomach is divided into numerous chambers by ridges and grooves (Pl. I G). The epithelium as a whole composed of a single row of tall and narrow cells. The mucous cells are absent in the posterior region of the stomach, which contains ciliated cells, secretory cells and absorptive cells.

The ciliated cells are long and narrow, but their lengths depend on the height of the ridges in the sorting area (Pl. I I). Their cilia show metachronal rhythm and their nuclei are spiral, central, subcentral or basal due to crowding by ciliated cells. Very fine, granular mitochondria are abundant in the apical region of these cells (Pl. II A).

The secretory cells are uniformly tall and narrow with subcentrally located nuclei, which have prominent nucleoli (Pl. II B). Small to large spherical secretory granules are located in the apical part of these cells (Pl. II C, D, E). Each such zymogen granule appears to be distinctly enveloped by a membrane which appears dark blue in Heidenhein's haemotoxylin. Further, these cells are covered by a cuticular layer. The secretory cells are apocrine, releasing the enzyme into the lumen of the stomach.

The absorbtive cells are grouped as ridges. In PAS preparations, a distinct darkly staining striated (brush) border can be seen (Pl. II F). The cells are long and narrow with basally located nuclei. The fine particles of food are seen to enter through the striated border and to traverse parallel to the axis of the cells towards their bases. The particles of food are uniformly small sized and are probably phagocytised. Thus these cells seem to be concerned with food absorption.

In the posterior region of the stomach phagocytosis by amoebocytes is discernible (Pl. II G), but not much pronounced due to the enormous area of absorption available in the stomach region. The absorptive cells appear in a sizeable number in the gastric epithelium (Pl. II H).

The anterior part of the stomach has numerous ridges and grooves, which vary in different regions. The lining is composed of tall, narrow, ciliated cells whose lengths depend on the extent to which the ridges project into the lumen. The nuclei are spherical, subspherical, elliptical or elongated depending on the length of the cells. No secretory cells are discernible in the epithelium. Very fine particles of food are absorbed by epithelial cells continuously. Amoebocytes can be seen entering through the wall, enclosing particles of food in the lumen, and freely to move back into the connective tissue and in the visceral haemocoel.

The style sac consists of mucosal lining of epithelium surrounded by loose connective tissue (Pl. III A). The epithelial cells are of two types. In the anterior tapering end of the style sac, the epithelium consists of short, broad columnar cells with cilia extending into the lumen of the sac. The cilia are as long as the cells and are closely set (Pl. III B). The nuclei are spherical and basal in position. The cells of the central and right wall of the style sac are exceptionally tall and narrow (Pl. III C) and glandular in nature. These cells are nearly thrice in length compared to the ciliated cells. Their elongated nuclei are central or subcentral in location. The cytoplasm of the cells, which secretes the style is basiphilic and very short cilia can be seen in some of the cells. Nearer to the stomach region, the number of such secretory cells are less. The ciliated cells cover more area of the epithelial lining of the style sac.

The ventral groove is an evagination of the style sac and its walls are composed of ciliated epithelial cells with spherical nuclei, with connective tissue on the outside (Pl. III D). The long central groove assumes the form of a duct in the posterior region and ultimately communicates with the stomach.

Digestive gland : Tubules of the digestive gland consists of two kinds of cells which are invested by connective tissue (Pl. III E, F). The interspaces between tubules are the visceral haemocoel, where blood corpuscles and amoebocytes are located.

Among the two types of cells, the first one includes large triangular secretory cells in the corners with their bases facing the haemocoel. The second type, which occurs in large numbers, appear long cylindrical and are digestive in function.

The secretory cell is characterised by large basal nucleus with prominent nucleoli. These cells show yellowish or yellowish brown excretory granules in the cytoplasm. In most of these cells are also seen spherical dark spherules which are the excretory spherules. In addition, large sized spherical secretory globules are also met with in the cytoplasm of these cells. The secretions are positive to PAS and to acrolein Schiff reaction and to Heidenhein's Iron haemotoxylin, and possibly of glycoprotein nature. The secretory droplets, apocrine in nature, are released into the lumen of the digestive tubules.

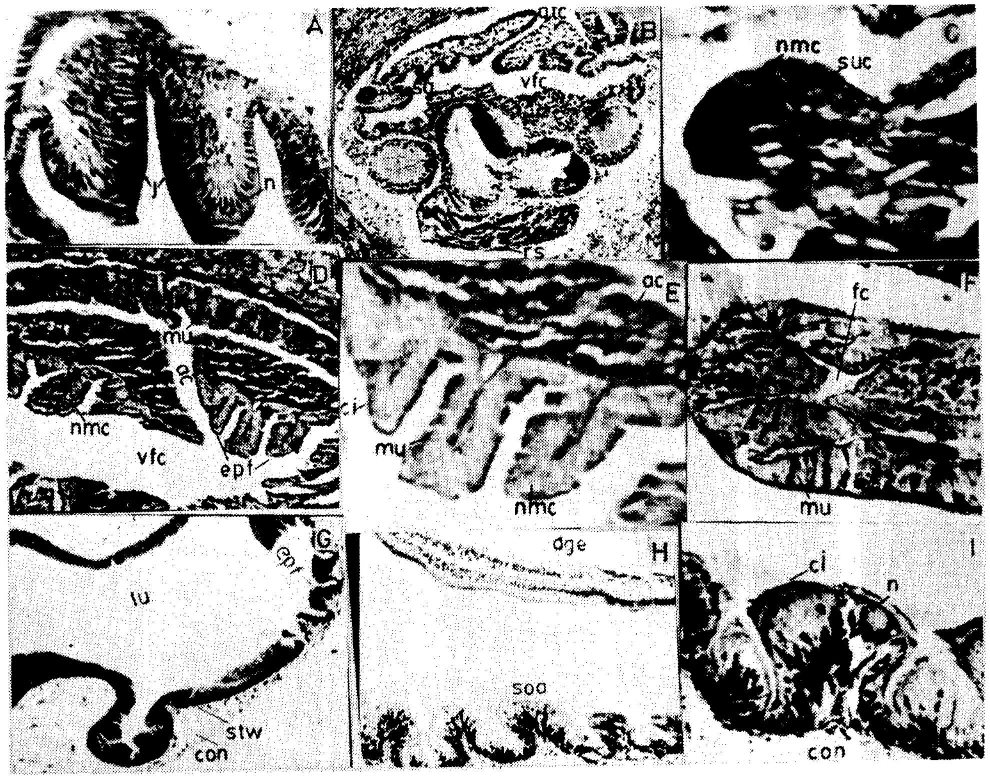

PLATE I A. Section through anterior part of oral cavity (x 300); B. Section through anterior oesophagus (x 150); C. Salivary gland - mucus secreting cells with secretions (x 750); D. Wall of oesophagus - darkly stained acid and neutral mucopolysacharides secreting cells with secretions (x 300); E. An enlarged view of a portion of above - mucus secretions are being poured into the food channel (x 750); F. Section through oesophagus - folds in the wall and mucus secreting cells with secretions (x 300); G. T.S. through stomach - sorting area with epithelial foldings (x 75); H. T.S. through stomach - sorting area and digestive epithelium (x 150) and I. A closer view of folds in the sorting area - cilia in metachronal rhythem (x 300). (Abbreviations - ac : mucocytes producing acid mucopolysacharides; an : anus; ci : cilia; con : connective tissue; cpg : cerebro-pleural ganglion; cs : ciliated cells; cst : crystalline style; cu : cuticular layer; dge : digestive epithelium; dgc : digestive cells; dfc : dorsal food channel; dg : digestive gland; epf : epithelial fold; exs : excretory spherules; fc : food channel; fo : folds in the stomach wall; fop : food particles; glc : glandular cells; go : gonad; gsh : gastric shield; in : intestine; ino : intestine opening; j : jaw; la : lateral tooth; lar : lateral ridge; lu : lumen; ma_1 and ma_2 : marginal teeth; md : median tooth; me : mantle edge; may : major typhlosole; mu : mucus; muc : mucus cells; n : nucleus; nmc : mucus cells producing neutral mucopolysaccharides; oc : oral cavity; od : odontophore; oe : oesophagus; oeo : oesophageal opening; ovf : ovarian follicles; pg : pedal ganglion; phg : amoebocytes; rd : radula; re : rectum; rs : radular sac; sc : secretory cells; seg : secretory granules; sg : salivary gland; soa : sorting area; sr_1 and sr_2 : smaller ridges; ss : style sac; st : stomach; stb : striated border; stw : stomach wall; suc : supporting cells; ty : typhlosole; vfc : ventral food channel; vgr : ventral groove; vty : ventral typhlosole).

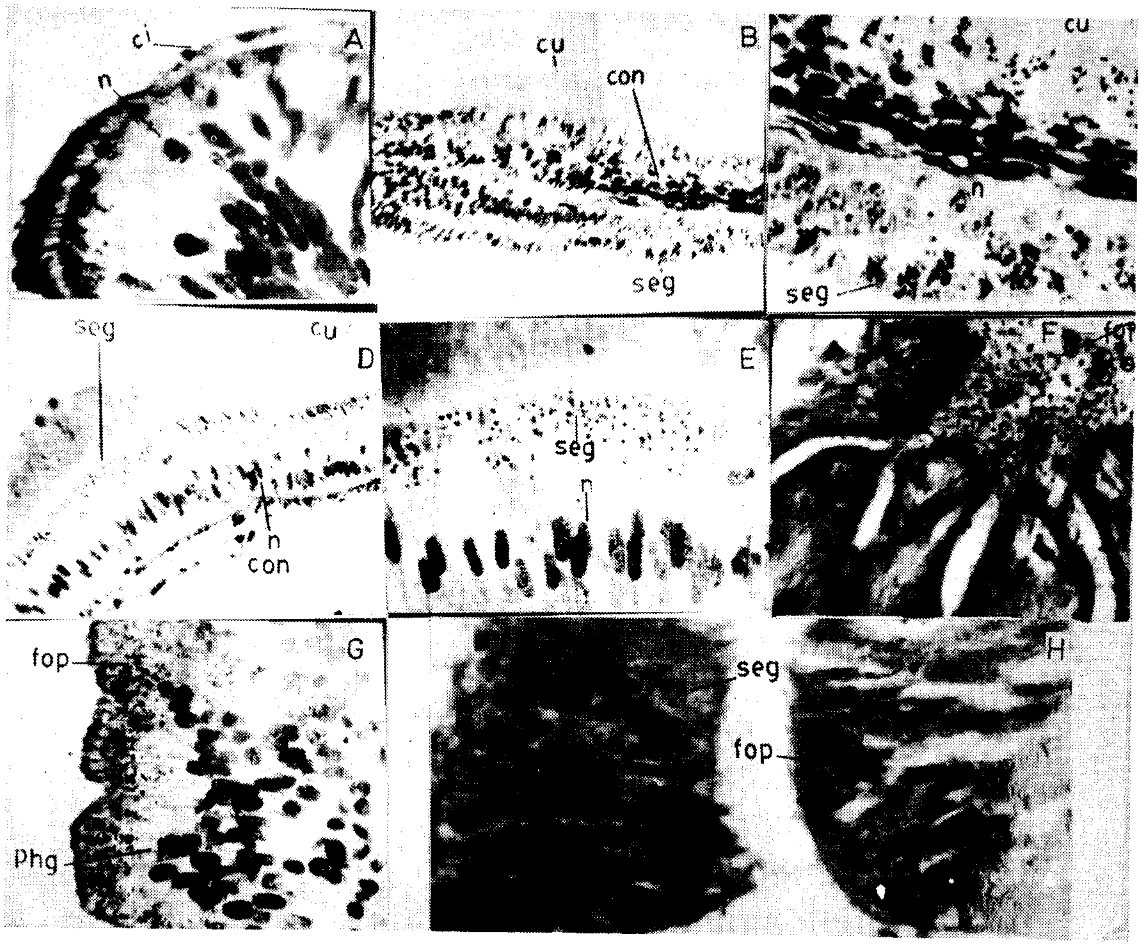

PLATE II A. An enlarged view of folds with ciliated cells (x 750); B. Secretory cells in the stomach wall-cuticular layer over epithelium protecting the walls of high enzymatic activity (x 300); C. Secretory granules in closer view (x 750); D. Secretory cells in the stomach with zymogen granules at top and large nuclei at base (x 300); E. An enlarged view of the above-basal large nuclei and fine secretory granules visible (x 750); F. Absorptive cells of stomach wall - brush border (striated border) over the cells visible (x 750); G. Absorption of fine food particles by stomach wall-phagocytic activity with empty and food laden amoebocyte seen (x 750) and H. Absorption and secretions in the stomach - proteinacious secretions and food particles visible (x 750). (For abbreviations, please see Pl. I)

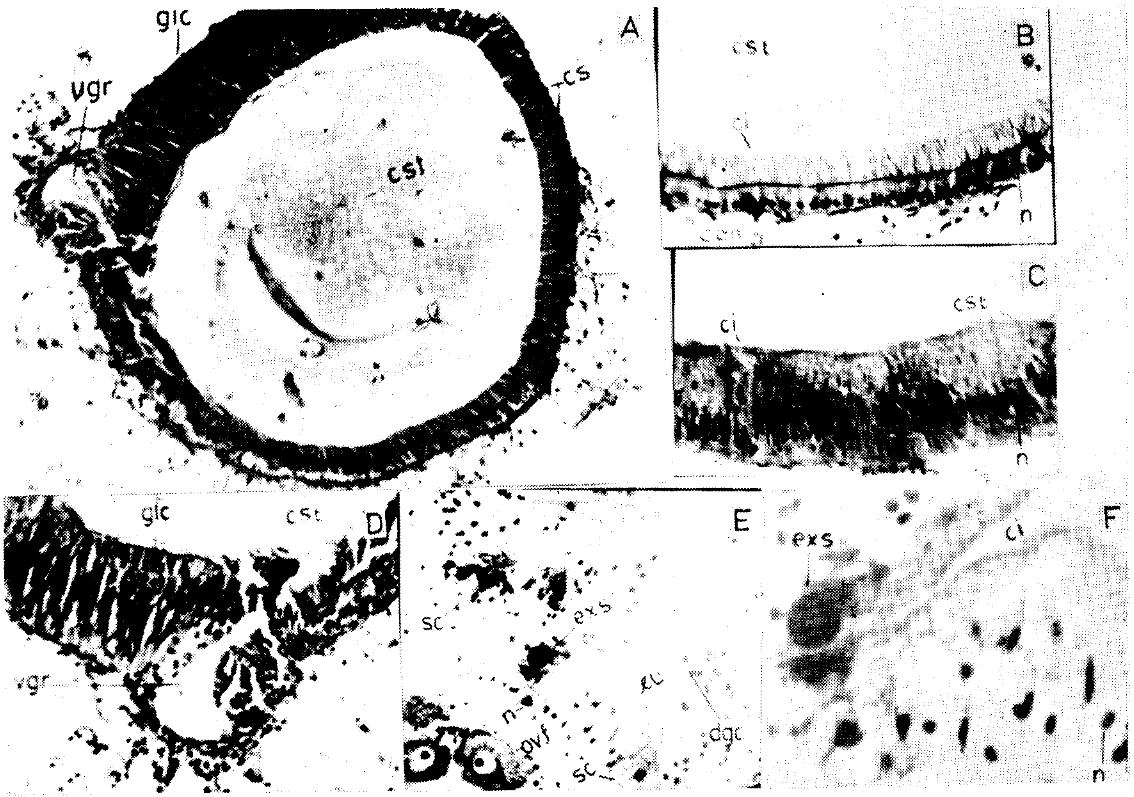

PLATE III A. Crystalline style in style sac (x 300); B. Glandular cells of style sac (x 300); C. Glandular cells of style sac (x 300); D. Ventral groove and its connection with style sac (x 300); E. Tubules of digestive gland (x 300) and F. A closer view of the above (x 750). (For abbreviations, please see Pl. I)

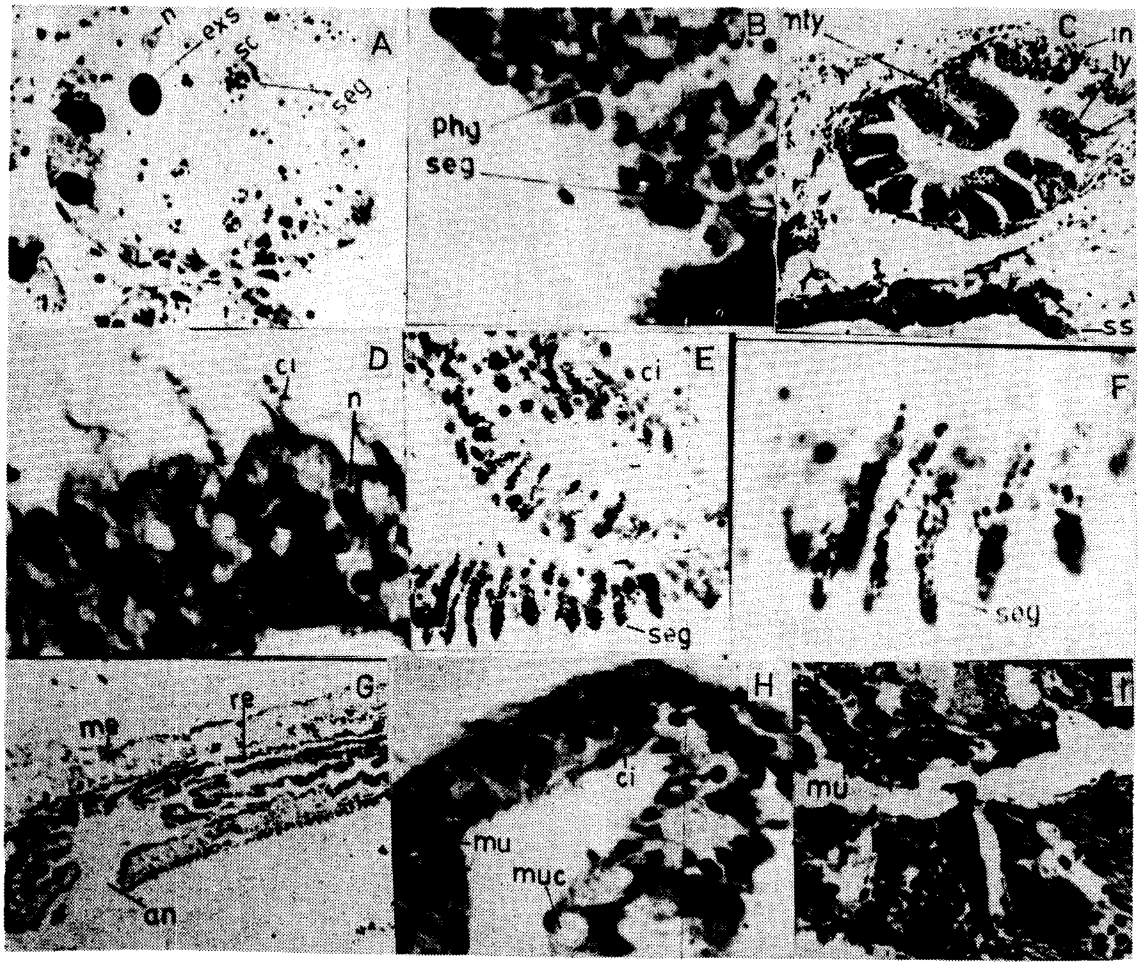

PLATE IV A. Tubules of digestive gland - excretory spherules being dropped into lumen (x 750); B. An enlarged view of tubule of digestive gland-secretory granules and phagocytes seen (x 750); C. T.S. throguh intestine (x 150); D. Ciliated cells in the intestinal wall (x 750); E. A closer view of intestinal wall with secretions (x 300); F. Secretory cells in the intestinal wall - zymogen granule visible (x 750); G. Rectum with anus (x 75); H. Ciliated cells and secretory cells in the rectal wall (x 750) and I. An enlarged view of hypobranchial gland showing mucus secretions (x 750). (For abbrevations, please see Pl. I)

The secretory cells thus seem to perform a dual role of secretion and excretion. The excretory spherules are released into the lumen (Pl. IV A) from where they pass into the stomach and to the hindgut, to be compacted with faeces.

The digestive cells of the tubules are long and cylindrical. Their nuclei are relatively small. The cytoplasm shows large number of vacuoles and other inclusions. Yellowish green pigments, in the form of irregular masses in the cytoplasm do not stain with any cytoplasmic stains. The digestive cells are not of uniform height and as a result, the lumen appears irregular in outline. The apical regions of these cells are dome shaped. The digestive gland shows phagocytic activity; amoebocytes are found in the haemocoel, in the tubules and also in their walls (Pl. IV B).

Hindgut : The lumen of the intestine (Pl. IV C) is lined by two kinds of cells, the supporting ciliated cells (Pl. IV D) and the secretory cells (Pl. IV E). The secretory cells are pyriform with basal spherical or subspherical nuclei and prominent nucleoli; the spherical secretory granules are large or small and fill the cytoplasm in large numbers in the apical region before being discharged. These cells show long filamentous mitochondria, particularly in the apical region. The secretory droplets can be well seen being released into the lumen. The secretory granules are positive to acrolein Schiff and PAS reactions and are intensely stained by Heidenhain's Iron haemotoxylin indicating their glycoprotein nature. Secretions are apocrine (Pl. IV F, G) as observed in the stomach.

The supporting cells are long with elongated subcentral nuclei. The long cilia show metachronal rhythm. The outer wall of the intestine consists of connective tissue and muscle fibres.

There is pronounced phagocytic activity in the intestine by amoebocytes. These cells can be seen in various stages of infiltration from the haemocoel through the wall of the intestine. The amoebocytes are also seen to engulf the food particles after which they again move through intestinal wall. They then deposit the food particles in the connective tissue sorrounding the digestive tract. It is to be noted that phagocytosis augments the assimilation efficiency of the digestive tract although it is a primitive method of digestion. Perhaps due to abundant availability of nutritive material in food, active phagocytosis has been resorted to, besides intracellular digestion in the digestive tract of *C. cingulata*.

Rectal wall consists of an outer membranous layer, a middle connective tissue layer and an inner mucosal layer (Pl. IV H). There are seven to eight folds in the mucosal lining. The mucous layer consists of broad, large elliptical or oval epithelial cells. The nuclei are large and elliptical or oval. The cells bear uniformly short cilia. There are a number of barrel shaped cells which produce both acid and neutral mucopolysaccharides.

Hypobranchial gland : This gland even though is not a part of the digestive tract, helps in consolidation of faeces and of food particles and prevents fouling of the ctenidium. Therefore, it is considered here along with the digestive system, but not as a part of it.

The hypobranchial gland is a closely attached ridge between the ctenidium as its left side and the hindgut on the right side. In the anterior part of the mantle cavity, it is broad, occupying almost half of the mantle roof on the right side of the mantle. It is divided into two halves by rectum, one half lying between the rectum and ctenidium and the other between the rectum and genital ridges. Further backwards, the intestine runs between the mantle wall and hypobranchial gland.

The hypobranchial gland has mucous secreting cells and tall ciliated cells lying in between (Pl. IV I). In addition there are pyriform cells filled with fine granules which appear to

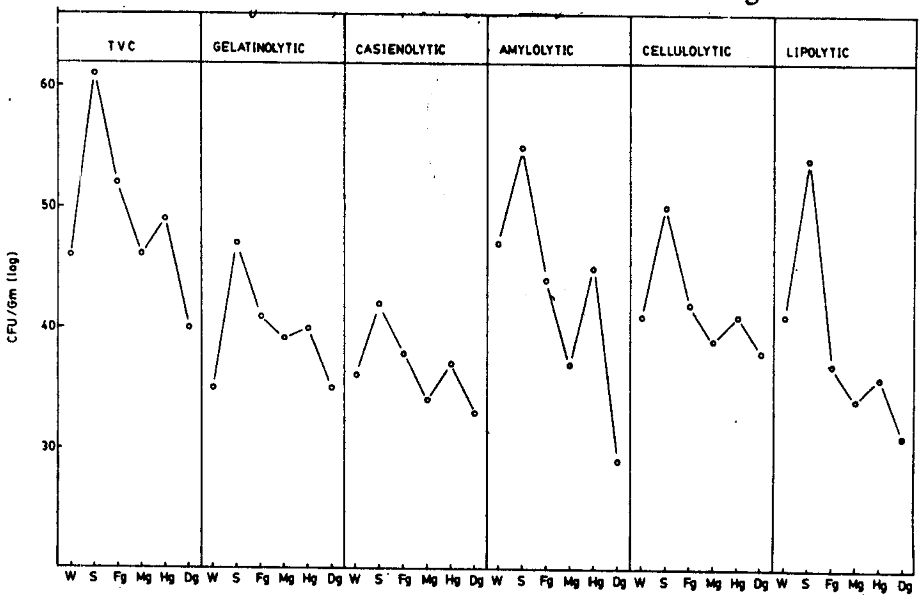

Fig. 4. Colony forming units/gm (log) of different types of bacteria in water, sediment and gut of *C. cingulata* (Dg : digestive gland; Fg: foregut; Hg : hindgut; Mg : midgut; S : sediment; TVC: total viable count; W : water).

TABLE 1. *Secretory activity in the alimentary tract of C. cingulata (Reactions in stains)*

Region	H.H.	PAS/Alcian Blue	Acrolein Schiff	Aldehyde Fuchsine	Remarks
Buccal cavity	Negative	Positive for both	Negative	Negative	Acid and neutral mucopolysacharides
Salivary gland	-do-	Positive to PAS	-do-	-do-	Neutral muco polysachaides
Oesophagus	-do-	Positive to both	-do-	-do-	Acid and neutral mucopolysacharides
Anterior region of the stomach	Positive	Positive to PAS	Positive	Negative	Enzymes of glycoprotein nature
Posterior region of the stomach	-do-	-do-	-do-	-do-	-do-
Style sac	-do-	-do-	-do-	-do-	-do-
Digestive gland	-do-	-do-	-do-	-do-	-do-
Intestine	-do-	-do-	-do-	-do-	-do-
Rectum	Negative	Positive to both	Negative	-do-	Acid and neutral mucopolysachrides
Hypobranchial gland	-do-	-do-	-do-	-do-	-do-

H. H = Heidenhein's Haemotoxyline

be proteinaceous. The mucous cells are of two kinds, secreting neutral or acid mucus. The ciliated cells have fairly long cilia. The connective tissue binds the hypobranchial gland to mantle wall and to the wall of the hindgut.

During feeding, the snail extends its protrusible snout and with the help of the radula, rasps the substratum and ingests fine particles. The snail makes short feeding excursions during low tide near the water edge.

TABLE 2. *Enzyme activity in different regions of the digestive tract of* C. cingulata
+ = Weak ++ = moderate +++ = prominent

Substrate	Enzyme	Foregut	Midgut	Digestive gland	Hindgut
Carbohydrases					
Starch	Amylase	—	+++	+	+
Lactose	Lactase	—	+++	+	+
Maltose	Maltase	—	+	+	+
Sucrose	Invertase	—	+	+	—
Glycogen	Glycogenase	—	+	+	—
Dextrose	Dextrase	—	+	+	—
Filter paper	Cellulase	—	—	—	—
Cotton wool	Cellulase	—	—	—	—
Saw dust	Cellulase	—	—	—	—
Agar agar	Cellulase	—	—	—	—
Protease					
Gelatin	Protease	—	—	+	—
Gelatin of photofilm	Protease	—	—	+	—
Lipase					
Boiled milk	Lipase	—	—	+	—
Olive oil	Lipase	—	—	+	—

The secretory activities found in the digestive tract of *C. cingulata* are summarised in Table 1.

Food and feeding habits

C. cingulata subsists mainly on detritus present in the substratum where the snail lives. It prefers soft fine sandy muddy substratum and can be considered as selective bottom-feeder. Stomach contents recorded were fine detrital matter, sand grains, unicellular diatoms such as *Navicula, Nitzschia, Coscinodiscus, Fragilaria* and *Pleurosigma* and also minute scraps of algal filaments. In the laboratory, *C. cingulata* was observed to rasp on algae present in addition to rasping-off the fine substratum.

Such movements leave characteristic curved or zig-zag trails in the soft substratum.

The snail survives starvation upto 30 days without any mortality. The material in the gut seems to last for 5 or 6 days, after which time there was no production of faecal matters. During active feeding, faecal matters, mixed with a lot of mucus are excreted and these contain undigested plant material and sand grains.

pH in the gut

The buccal cavity is neutral (7.0) and the rectum is slightly alkaline (7.2). The oesophagus (6.8), digestive gland (6.1), stomach (6.2), style sac (5.9) and intestine (6.7) are acidic and the style is the most acidic.

Digestive enzymes

Qualitative analysis : The results of the tests carried out to record the nature and activity of enzymes present in the digestive tract of *C. cingulata* are given in Table 2.

Of the ten substrates of carbohydrases, complex polysaccharides such as filter paper, cotton wool, saw dust and agar agar, were not acted upon by extracts from any of the four regions indicating the absence of cellulase in any part of the digestive tract. Glycogen, dextrose and sucrose are digested in the digestive gland and the midgut, while starch, lactose and maltose appear to be hydrolysed in all parts of the tract excluding the foregut.

Proteolytic and lipolytic activities of digestive tract of *C. cingulata* were confined to the digestive gland region only and both the enzymes were also found to be weak in their activities.

Quantitative analysis : The activities of amylases, proteases and Lipases in four different regions of the digestive tract are given in Table 3. Amylase activity is high in the midgut followed by the digestive gland and the hindgut, while proteolytic and lipolytic activities could be recorded only in the digestive gland.

TABLE 3. *Amylase, protease and lipase activities in the digestive tract of* C. cingulata

Amylase activity (μ g glucose/mg tissue/hr)	
Foregut	—
Midgut	8.5
Digestive gland	18.5
Hindgut	14.7
Protease activity (0.2 N NaOH consumed)	
Foregut	—
Midgut	—
Digestive gland	0.3 ml
Hindgut	—
.*Lipase activity* (0.2 NaOH consumed)	
Foregut	—
Midgut	—
Digestive gland	0.1 ml
Hindgut	—

Gut microflora

Distribution of different groups of microflora in the gut of *C. cingulata* and in the water and sediment samples are given in Fig. 4. The TVC was higher in the digestive tract than in water but less than in sediment. Amylolytic bacteria were more dominant in the gut as a whole, followed by gelatinolytic bacteria and cellulotic bacteria in that order. Caesinolytic and lipolytic populations were quite low. In general, microbes were found to be more in the sediment than in the water or in the gut. Among various regions of the digestive system, the digestive gland harboured the least number of bacteria followed by the midgut.

DISCUSSION

The organisation of the buccal region of *C. cingulata* is similar to that of *C. californica* and *Batillaria zonalis* (Bright, 1958; Driscoll, 1971). The extensible snout with strong musculature helps in swallowing the food particles. The taenioglossate radula of *C. cingulata* suits the benthic microphagous feeding habit. Kohn (1983) considers this type of teeth with less complex musculature is the most successful of all gastropod radular types. Fretter and Graham (1962) correlated the ratio of radular length with the size of the snail and type of substratum in which the snail lives. Driscoll (1971) found the radular ratio of 0.11 for *B. zonalis* and 0.09 for *C. californica*. According to him, the former lives on much coarser substratum than the latter. For *C. cingulata*, the ratio obtained (0.06) indicates that the snail can thrive only on finer sediments.

Reasons for reduction of salivary glands in the style-bearing gastropods could be major involvement of the cyrstalline style in the secretory activity, making redundant secretory functions of the salivary glands. Therefore, these glands appear to serve only the function of mucus secretions for binding the food material, but not for the digestion. The crystalline style is generally associated with microphagous herbivorous food habit. The presence of crystalline style can also be taken as an indication of absence of free proteolytic enzymes in the stomach region since such a condition can pose problems to the very existence of the style itself. The style ensures an enzyme supply continuously sufficient to fully digest the available food material, which is advantageous for a slow, continuously feeding snail.

The presence of cellulase in the digestive system of prosobranch snails has always been a subject for conflicting opinions. Morton and Stone (1958) reviewed in detail the occurrence of cellulases among molluscs and concluded that in many molluscs they are present. Felback *et al.* (1983) however, indicated that animal genomes appear to lack information-coding for complete set of enzymes required for degradation of complex cellulose and cellulolytic function is performed by enzymes provided by symbionts, notably by gut microflora. Therefore, it appears that the bacteria in the gut of C. cingulata have an active role to play in the digestion of food and their numbers in various regions of the gut are inversely related to enzyme activity in that region. Wherever enzyme activity was absent, the bacteria become complementary in function and helped in digestion, thus playing a significant role in the digestive process of the snail.

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