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THE ALIMENTARY SYSTEM OF THE LITTORAL MYSID *GASTROSACCUS SIMULANS* (VAN BENEDEN)

C. N. NATH AND N. K. PILLAI

Department of Zoology, Govt. P. G. College, Mandsaur, Madhya Predesh and Marine Biology Laboratory, Trivandrum-7, Kerala, India

ABSTRACT

The very well developed gastric armature of the littoral mysid, *Gastrosaccus simulans* (Van Beneden) shows that filter feeding has lost much of its importance in the animal and that it feeds mainly on large food masses. The hepatopancreas is very elaborately branched and very complex in structure. Paired glandular ridges are present in all the tubules of the hepatopancreas. The food consists of a wide variety of animal and vegetable matter. The animal is cannibalistic, feeding on disabled companions.

INTRODUCTION

APART from the work of Gelderd (1909) who studied the alimentary system of six European mysids, nothing is known of the alimentary system of mysids. Recently we undertook a detailed study of the alimentary canal of a subterranean mysid, *Spelaeomysis longipes* (Nath and Pillai, in press). For the sake of comparison, *Gastrosaccus simulans* (Van Beneden) was studied in detail. The present paper embodies the result of this study.

Gastrosaccus simulans is the most common Indian species of the genus occuring along both the east and west coasts. This mysid appears in swarms along the coast during the monsoon season. At such times, they are washed ashore by the incoming tide. When the tides recede they get exposed, but quickly burrow into the wet sand. During these periods, large quantities of this mysid can be collected by holding a piece of cloth against the retreating tides. Nothing definite is known about this curious habit, but other species of *Gastrosaccus* are also known to swarm like this (Fishelson and Loya, 1968). This has apparently some relation with the breeding of the animals, since berried females are found to predominate during such times.

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ALIMENTARY CANAL

Buccal cavity and oral appendages: The mouth is situated ventrally, bounded by the oral appendages, which include the labrum, the mandibles and the labium. The labrum is produced anteriorly into three spines, a long median spine flanked by two small spines . The labium has well developed, closely-set paragnaths, whose distal border and ventral surfaces are hirsute. The left mandible has a tridentate incisor process and an extremenly well developed molar process. The molar process has a serrated edge and bears numerous minute denticular prominences. The lacinia mobilis is trilobed. The spine row is absent. The right mandible has a quadridentate incisor process and its molar process is as well developed as that of the left. The lacinia mobilis is represented by a stout serrated structure. The spine row is absent here also.

Oesophagus: The mouth leads into the oesophagus which runs obliquely forwards and upwards to open into the stomach. The wall of the oesophagus is raised into four ridges. Continuous with the labrum and running upto the stomach is the labral ridge (Fig. 2a; lr). Opposite this, but originating from the middle of the oesophagus and running upto the stomach is the labral ridge (Fig. 2a; lbr). Lying on either side are the lateral ridges (Fig. 2a; lr). These ridges also originate a short distance up the oesophagus. The presence of these four ridges restricts the lumen of the oesophagus, which appears nearly X-shaped in transverse section (Fig. 2a). The labral ridge is the most prominent of the four ridges while the lateral ridges are the least prominent. The oesophageal wall is lined by a thin cuticle bearing numerous minute hairs directed towards the stomach.

Stomach: The oesophagus opens into a very spacious stomach which is clearly demarcated into an anterior, globular cardiac region and a posterior smaller pyloric region. The latter is about one fourth the size of the former. The gastric armature is highly developed.

The entrance of the oesophagus into the gastric stomach is guarded by a pair of lateral valvular folds. They bear numerous minute hairs which seem to form some sort of a sieve. These folds may be termed the oesophageal valves (Fig. 1 a; ov).

The ventral wall of the cardiac stomach is medially raised into a ridge, the median ventral cardiac ridge (Fig. 2b; mvcr). This ridge carries minute hairs directed backwards. On either side of this ridge, there is, on the ventrolateral wall of the cardiac stomach, a prominent ridge carrying stout backwardly directed bristles running the entire length of the cardiac stomach. This may be called the ventrolateral cardiac ridge (Fig. la; vlcr). The posterior extrimity of this ridge lies opposite the dorsomedian cardiac prominence as will be seen below.

The midlateral walls of the cardiac stomach are produced into two prominent ridges, which bear on their anterior face very well developed teeth-like structures and on their inner face long curved setae directed towards their fellows of the opposite side. They may be called the lateral cardiac ridges (Fig. 1 a; lcr).

Starting from the middle of the cardiac stomach and stopping short of its posterior extremity is a semicircular ridge bordered by long setae. This ridge lies dorsal to the lateral cardiac ridge and may be called the dorsolateral cardiac ridge (Fig. 1 a; dlcr). Posteriorly, behind the regions where this ridge ends, are a pair of teeth-like projections, one on either side, called the cardiac teeth (Figs. 1 a, b; lct). They are very prominent and trifid at their tips. On the posterior borders, each carries a short plumose seta (Figs. 1 a, b; s).

Lying between the lateral cardiac ridges and the median ventral cardiac ridge is a groove, the lateral cardiac groove (Fig. 2 b; lcg), which is in continuity with the lateral pyloric groove as discussed later.

Just at the junction with the pyloric stomach, the dorsal wall of the cardiac stomach is produced into the structure known as the dorsomedian cardiac prominence (Figs. 1 a, b; dmcp). It is directed downwards and backwards. On its anterior surface, the prominence bears two pairs of stout barbed setae, each pair with an external simple seta directed anteriorly. The lateral borders of the prominence bears a row of twelve to fifteen stout setae on either side. The anterior ones are directed lateralwards and the rest backwards.

The dorsal wall of the cardiac stomach on either side of the dorsomedian cardiac prominence is produced into a conical elevation surmounted by a tooth almost similar to the cardiac teeth (Fig. 1 b). These teeth and setae of the dorsomedian prominence seem to help in crushing large food particles, which the animal generally consumes. The posterior extrimity of the dorsomedian prominence marks the posterior limit of the cardiac stomach.

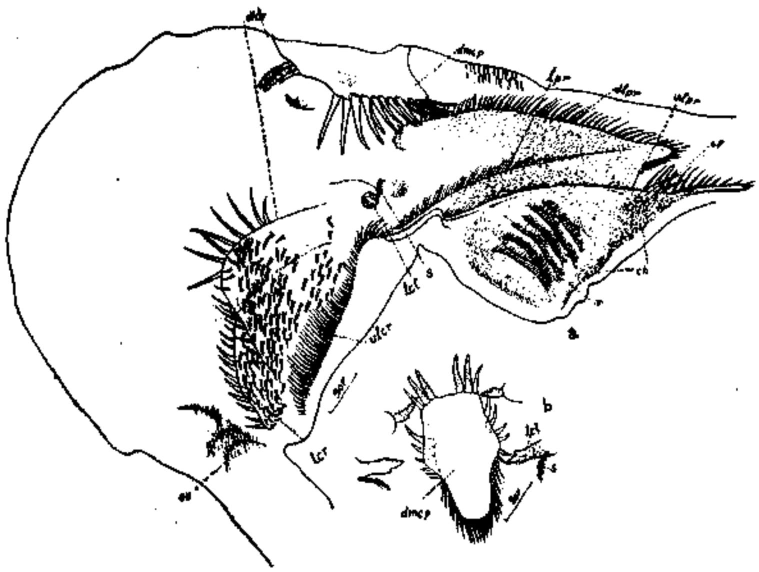

Fig. 1 *Gastrosaccus simulans* (Van Beneden) a. The gastric armature and b. The dorsomedian cardiac prominence of the gastric armature.

The pyloric stomach is a laterally compressed more or less quadrangular chamber (Fig. 2d), whose median ventral wall is raised into a prominent ridge called the median ventral pyloric ridge. The presence of this ridge considerably reduces the space inside the pyloric stomach.

Running anteroposteriorly in the pyloric stomach is a pair of dorsolateral pyloric ridges (Figs. 1a, 2 d; dlpr), which arise from just behind the cardiac teeth. The summit of this ridge is provided with a row of setae which increase in length backwards. Projecting into the pyloric stomach between the tip of the median ventral ridge and the dorsolateral ridge is a pair of lateral pyloric ridges (Figs. 1 a , 2 d; lpr). These ridges divide the cavity of the pyloric stomach into a spacious dorsal chamber and a less spacious ventral chamber (Fig. 2 d). The lateral ridges are bordered by short setae which decrease in length towards the extrimities (Fig. 1 a; lpr).

Since the median ventral pyloric ridge is very high, it converts the ventral pyloric chamber into an inverted V shape or more correctly a U. The dorsal chamber is further divided into a very narrow upper chamber and a more spacious lower chamber by the dorsolateral pyloric ridges. The presence of the lateral and the dorsolateral pyloric ridges thus makes the pyloric stomach three-chambered (Fig. 2d).

The median ventral pyloric ridge is a continuation of the median ventral cardiac ridge. This ridge is tall and bears on its lateral sides three (rarely four) subsidiary ridges running dorsoventrally in an oblique manner. These subsidiary ridges are fringed with closely set long setae (Fig. 1a, 2d). Between the subsidiary ridges, the surface of the median ventral ridge is channeled. The function of these channels is not clearly known. The summit of the median ventral ridge is convex in outline and is supplied with fine setules (Figs. 1a, 2d), except at the hind end where these are fairly stout. Posteriorly, the median ventral ridge extends backwards as a long narrow structure (Fig. la). On either side of the base of this prolongation is a stout spine and long setae on its border (Fig. 1 a). The posterolateral and the dorsolateral sides of the median ventral ridge have a clothing of minute cuticular hairs (Fig. 1 a; ch).

The lateral walls of the ventral pyloric chamber are thrown into five or six closely-set pairs of low ridges placed at an angle with those of the median ventral ridge. The ridges (Figs. 1a, 2d; r) are surmounted by stiff hairs and the intervening spaces form shallow grooves as on the median ventral pyloric ridges.

At the hind end, the dorsolateral pyloric ridges bend sharply and continue downwards for a short distance as the ventrolateral pyloric ridges (Fig. 1a; vlpr). The setae at the junction of these two ridges are much longer than those elsewhere, and progressively decrease in length along the ventrolateral ridges. Lateral walls of the pyloric stomach, especially the region immediately below the dorsolateral pyloric ridges are sparsely hirsute. The hairs are directed backwards to drive the food in the posterior direction. The dorsal wall of the cardiac and pyloric regions of the stomach is devoid of hairs except for the region lying immediately behind the dorsomedian cardiac prominence.

The entire stomach is lined by cuticle which varies in thickness in different regions. The cuticle on the dorsal wall is very thin while that of the cardiac teeth, stout setae and bristles is much thicker (Fig. 2 c).

Lying beneath the cuticle is the epithelium (Figs. 2 c, d; ep) which is throughout of a syncitial nature and has a large number of nuclei without corresponding cellular demarcation. Each nucleus has one nucleolus. Outer to the epithelium is the circular muscles layer which is very prominent (Fig. 2d; cm). The longitudinal muscles are absent. The entire stomach has a coat of connective tissue (Figs. 2 c, d; ct) with scattered oval nuclei.

Midgut: The midgut runs from the third thoracic segment to the hind end of the fifth abdominal segment. It is thus a long tube and has almost the same diameter throughout, when empty.

The midgut gives off at its junction with the foregut, seven pairs of diverticula known as the hepatopancreatic caeca. Ventrolaterally there is a pair of very short caeca which are directed anteriorly and which resemble the midgut closely in structure. They are simple outgrowths of the midgut. Similarly, a very short dorsomedian outgrowth having the same histological structure as the midgut itself is present. These two midgut diverticula may be absorptive in function as the midgut itself.

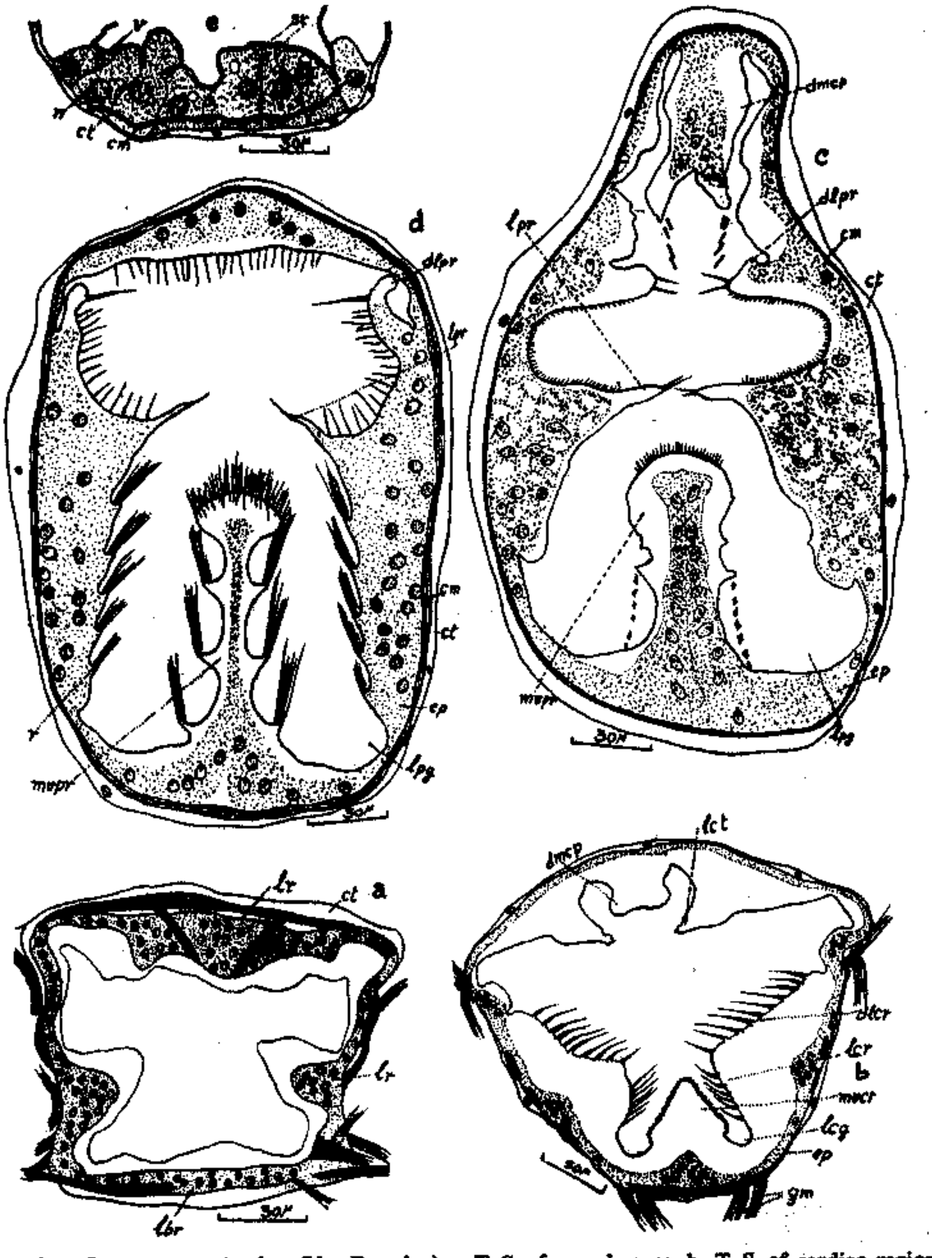

Fig. 2. *Gastrosaccus simulans* (Van Beneden) a. T. S. of oesophagus; b. T. S. of cardiac region at its junction with the pyloric region; c. T. S. of pyloric region close to cardiac stomach; d. T. S. of pyloric stomach; and e. T. S. of liver.

The midgut has an outer connective tissue coat continuous with the tissue present elsewhere (Fig. 3 e; ct). The muscle layers beneath this are formed of an outer thick layer of circular muscles (Fig. 3 e; cm) and an inner layer of longitudinal muscles (Fig. 3 g; lm). Inner to this is the relatively thin basement membrane. The midgut epithelium (Fig. 3 e; ep) is formed of clearly defined cells which are almost as tall as broad. Their cytoplasm appears granular and their nuclei (Fig. 3 e; n) are well developed, rounded and central in position; each has one nucleolus. The inner border of the midgut epithelial cells shows what has been described as 'striated border' (Fig. 3 e; st) in other Crustacea. These cells seem to be absorptive in function.

Hepatopancreas: From where the foregut and the midgut meet, originate three pairs of outgrowths called the hepatopancreatic caeca; a dorsal pair, a lateral pair and a ventral pair. From the base of each of the dorsal caeca arises a forwardly directed diverticulum. Each of the ventral caecum undergoes division successively three times, these secondary divisions affecting only the dorsal branch (Fig. 3 c). This in other words is typical monopodial branching. This branching of the two ventral caeca displaces the lateral and dorsal caeca upwards so that at this region the midgut gets surrounded by a total of twelve caecal branches, arranged in three groups; a ventral group, a middle group and a dorsal group (Fig. 3 d). Of these, the dorsal group is formed of the displaced dorsal and lateral caeca and the other two groups by the branches of the ventral caeca. Thus, altogether there are seven pairs of hepatopancreatic caeca in *G. simulans* of which one pair is short and forwardly directed, while the others are long and backwardly directed. These occupy the greater part of the thorax of the animal and run below and above the intestine parallel to each other. The branches of the ventral caeca are of varying lengths, some of them reach even upto the middle of the second abdominal segment.

The caeca have a thin outer covering of connective tissue which is drawn out posteriorly into filaments attaching the caeca to the other structures inside the body. Lying inner to the connective tissue is the circular muscle composed of striated fibres. These muscles are arranged in distinct successsive rings, the adjacent ones separated by a muscle-free interval. These aid in the regular slow contractile movements of the caecal tubes.

The epithelium of the caeca is as usual formed of two types of cells. The secretory cells are broad and considerably distended due the presence of large vacuoles (Fig. 2e , 3 a; v). They project into the lumen of the caeca. Their contents (Fig. 3 a; sm) stain blue with aniline blue of Heidenhain's Azan. Numerous such cells with their contents expelled by the burating of the cell wall can be observed in all the caeca in transverse sections (Fig. 3 a; ec). The free ends of these secretory cells with intact vacuoles show a 'plateau' (Fig. 3 a; pl) of some thickness with vertical striations. Similar structures were observed by Gelderd (1909) in the mysids studied by him. He found them to be of a chitinous nature. This, however, could not be confirmed during the present study. The cytoplasm of smaller secretory cells with small vacuoles show clear vertical striations (Fig. 2 e; st) throughout their lengths.

In certain regions of the caeca, some of the cells are considerably differentiated and larger than the others. These form very singular ridges, such ridges were first observed by Gelderd (1909) in the mysids he studied. He expressed the opinion that this formation is characteristic of 'schizopods'. The ridges consist of a mass of elongated cells (Fig. 3 b; gc) which project prominently into the lumen of the caeca.

In longitudinal sections these ridges are seen to be of different heights at different regions and run along the caeca for some distance. The cells comprising the ridges develop in them a large vacuole (Fig. 3 b; v) which nearly fills the cell leaving only the cell membrane which itself is not very clear. Towards the tip and the base of the cells a small quantity of cytoplasm is evident. The basal nuclei (Fig. 3 b; n)

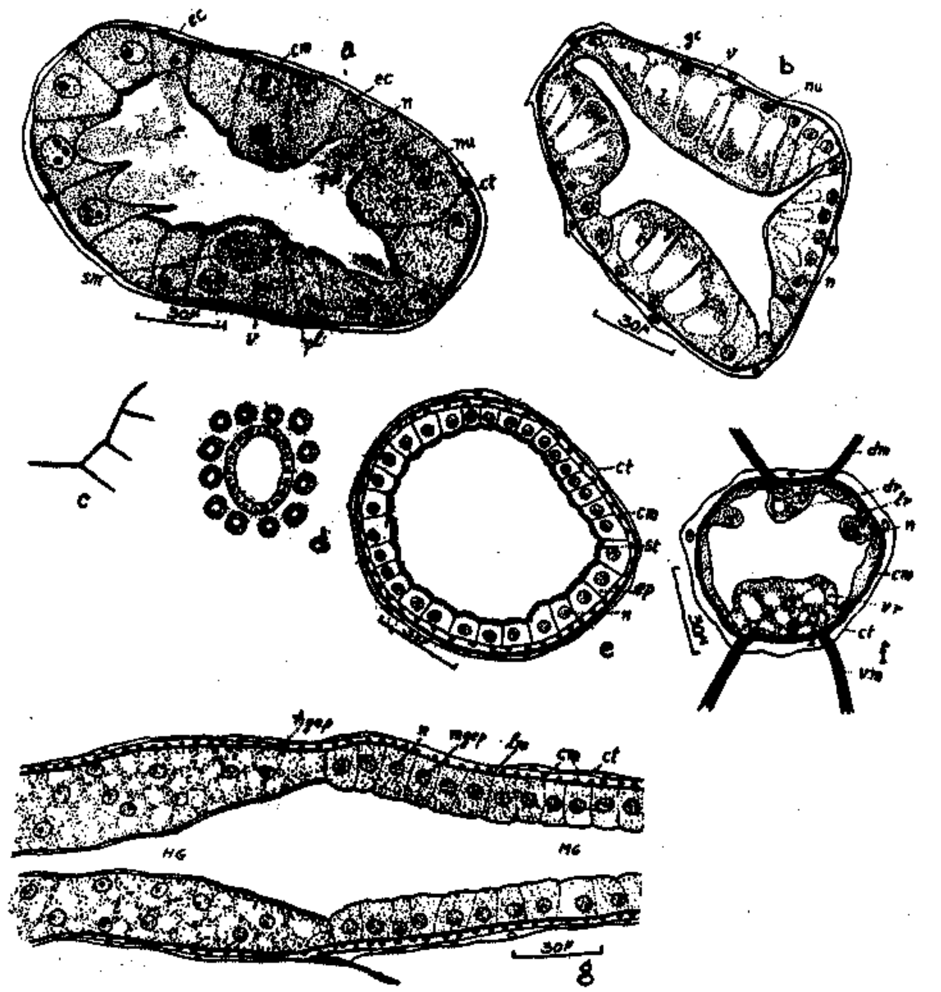

Fig. 3. *Gastrosaccus simulans* (Van Beneden) a. T. S. of liver at the region of the gland cells; b. T. S. of liver at the level of the glandular ridges; c. Diagrammatic representation of branching of liver; d. Arrangement of liver tubules; e. T. S. of midgut; f. T. S. of hindgut; and g. L. S. of junction of midgut and hindgut.

are prominent, each with one or two nucleoli. The vacuolisation increases progressively distalwards. Gelderd calls these ridges "glandular ridges". In the dorsal and lateral caeca these glandular ridges originate the beginning of the third thoracic segment and end at the hind end of the same segment. The ridges of all the other caeca originate at the level where those of the lateral and dorsal caeca end. They are well developed in all the caeca upto the level of the sixth thoracic segment, but further on get replaced by ordinary gland cells. Unlike as in the mysids studies by Gelderd, in *G. simulans* the glandular ridges are present in all the caecal tubules at some place or the other. In each of the tubes there are two pairs of ridges, but they do not stand out as prominently as in *Macromysis* or *Siriella. G. simulans* resembles *Mesopodopsis slabberi* in possessing two pairs of glandular ridges.

The second type of cells found in the hepatopancreas is absorptive. These cells are characterised by their cytoplasm supplied with numerous small vacuoles. The nuclei are central and the cells themselves columnar. Gelderd has not described absorptive cells in the hepatopancreas of the mysids he studied.

Dorsal diverticulam: As mentioned earlier, there is a very short, anteriorly directed diverticulum at the junction of the foregut and the midgut. This dorsomedian structure called the dorsal diverticulum closely resembles the midgut histologically and seems to be its outgrowth. Similar diverticula have been reported in other mysids (Gelderd, 1909). Recently, Nath and Pillai (in press) described a long diverticulum in the subterranean mysid, *Spelaeomysis longipes* where it is as long as the stomach itself. In all these cases the structure has been considered to be absorptive.

Hindgut: The hindgut is confined to the sixth abdominal segment and is slightly wider than the midgut. Its epithelium (Fig. 3 g; hgep) is formed of a mass of cytoplasm without definite cellular limits, "very closely resembling the fatty tissue of the insects in appearance" (Gelderd, 1909). The change in nature of the epithelium from the midgut to the hindgut is sudden. This epithelium has a thin lining of cuticle and is raised into ridges (Fig. 3f). Of these ridges, two are lateral and very poorly developed, one is dorsal and the other ventral. The dorsal and the ventral ridges are well developed though do not meet each other as do the lateral ridges of *Spelaeomysis* (Nath and Pillai; loc. cit.) The wall of the hindgut has very well developed circular muscles (Fig. 3 f; cm). In addition, numerous striated muscles run from the ventral side of the wall of the hindgut to the outer integument. Regular peristaltic and antiperistaltic movements have been observed in the hindgut of live individuals and these help to draw water in out of the hindgut.

FOOD AND FEEDING

Gastrosaccus simulans has been found to eat two types of food. Normally the food is composed of suspended particles in the water. These are collected by an elaborate filtering apparatus. The animal is also capable of feeding on larger food masses when available.

Filter feeding: In the aquarium, *G. simulans* was very often seen to resort to this type of feeding. In all essentials, the method of feeding is exactly as in *Hemimysis lamornae* described by Cannon and Manton (1927). The feeding current is produced by the working of the maxillary exite, which actsas a suction pump drawing water forwards, through the narrow ventral food groove, from the still water at the median ventral part of the body.

Examination of their stomach contents showed that diatoms and dinoflagellates formed the main items followed by algal filaments. Specific identification of food objects was not attempted.

At no time was the animal noticed to stand vertically on its head stirring up suspended food, as has been noticed by Cannon and Manton (1927) in *H. lamornae*.

In the absence of fresh supplies of food, the gut gets empty in one to two hours. The food remains in the stomach for a long time, nearly one and a quarter hours. In the midgut the food is retained for 30 to 45 minutes. It is in the hindgut that the food stays least, and it passes through this part on a few minutes. Defaecation is a quick process and the faecal cylinder is ejected out as one piece, 2 to 3 mm in length.

Large food masses: These mysids attack and devour disabled or dying companions. Among the other food consumed by the mysid in captivity are *Sagitta*, pieces of flesh of other animals such as crab, mussel etc. Copepods also appear to be included in the menu, as evidenced by the presence of their skeleton in the stomach. Our colleague Mathew Abraham (personal communication) has observed *G. simulans* catching and eating small amphipods and small copepods in the laboratory in fresh plankton collections. Whether *G. simulans* can do the same in nature is not certain.

During feeding the food is held below the mouth parts and manipulated by the multiarticulate carpopropodites. The mandibular incisors and the maxillular endites cut into the food and tear off pieces from it. The molars grind the food before sending it into the mouth.

DISCUSSION

The detailed study of the gastrid armature suggests that *G. simulans* is not mainly a filter feeder as is generally believed. While well developed spines, bristles, teeth and stiff setae abound in the cardiac stomach, cuticular hairs are almost totally absent. Thus, it would appear that *G. simulans* feeds largely and mainly on large objects and filter feeding, even if resorted to, in nature, is only rare. The stomach contents, however, indicate an omnivorous diet.

The fact that the food is retained in the stomach for a comparatively long period indicates that not only digestion but a large part of absorption also takes place in this region, through the activity of the hepatopancreas. It is laso significant that the food is retained in the midgut only for a very short period since most of the food has already been absorbed by the hepatopancreas.

The digestive gland of *G. simulans* is very well developed with as many as fourteen branches. The secretory cells are large and the conspicuous glandular ridges secrete digestive ferments. Under laboratory conditions the animal feeds continuously and the intestine is always filled with food.

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LEGEND TO LETTERING

cm- circular muscle
ch-cuticular hairs.
ct-connective tissue
dlcr-dorsolateral cardiac ridge
dlpr-dorsolateral pyloric ridge
dmcp-dorsomedian cardiac prominence
dr- dorsal ridge
ec- secretion emptied cell
ep- epithelium
gc - gland cell
gm-gastric muscle
HG- hindgut
hgep- hindgut epithelium
lar-labral ridge
lbr - labial ridge
lcr - lateral cardiac ridge
lcg- lateral cardiac groove
lct - lateral cardiac tooth
lm- longitudinal muscle
lpr - lateral pyloric ridge
lpg-lateral pyloric groove
lr- lateral ridge
MG- midgut
mgep- midgut epithelium
mvcr-median ventral cardiac ridge
mvpr-median ventral pyloric ridge
n - nucleus
nu - nucleolus
ov- oesophageal valve
pl - 'plateau' of liver cells
r - ridge
s-seta near lct
sm - secretary matter
sp - spine
st - striations
v - vacuole
vlcr - ventrolaterai cardiac ridge
vlpr- ventrolateral pyloric ridge
vm- ventral muscle
vr - ventral ridge