THE FEEDING MECHANISM OF BALANOGLOSSUS GIGAS *

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(9 Figs.)

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INTRODUCTION

Hitherto studies on the feeding mechanism and processes of alimentation in the Enteropneusta have been limited to those of Barrington (1941) and Knight-Jones (1953) on comparatively small species. The rediscovery in some quantity on certain shores in Brazil of *Balanoglossus gigas* Fr. Müller (Sawaya, 1951), the largest known species of Enteropneusta and probably one of the most robust, made a more detailed study possible.

Observations were made in the field and in the laboratory on the feeding mechanism and food transport through the gut.

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* Work carried out at the Marine Biological Laboratory of São Sebastião — Dept. of General & Animal Physiology — Univ. São Paulo, whilst visiting Brazil under the very kind auspices of the British Council and the National Research Council of Brazil.

Stock animals maintained in aquaria in the laboratory with and without their native substrate lived for many weeks. They varied in length from 75 cm. to almost 1.5 m., when fully relaxed with isotonic magnesium chloride solution.

The paths of the ciliary currents were plotted with the aid of Aquadag suspensions of graphite, talc, titanium oxide and copper phthalocyanide, having a particle size range of 1 to 50μ. Starch grains, miscellaneous diatoms, organic debris, carmine and various grades of sand and fine gravel up to 3 mm. in size were also used.

Dissections of the various regions of the animal lived for several days in clean running sea water and so enabled the observations to be repeated several times. Excised preparations were thoroughly irrigated in running sea water to remove excess mucus before being used.

HABITAT

Balanoglossus gigas occurs at several points along the Brazilian coast, but tends to favour comparatively sheltered shores with substrates of fine sand with underlying layers of fine to coarse gravel, a habitat common to many of the Enteropneusta (Burdon-Jones, 1950, 1956). A granulometric analysis of the various layers of sand and gravel from the surface down to a depth of 0.5 m. on a well populated shore, is given in Appendix p. 279.

The animals occupied tubular burrows which followed a sinuous course from the cast on the surface down to depths of almost 0.5 m. passing through several layers of sand and gravel. The burrows were circular or ovoid in cross section and from 1.5 to 2.0 cm. in diameter. They varied in length from 2 to 3 m. and were probably longer. A complete burrow was never exposed. They were lined with a thin layer of mucus, but could not be isolated from the surrounding substrate. Although numerous burrows were exposed an entrance hole was never found. Many surface holes that might have belonged to the burrow were seen within a radius of 2 to 3 m. from a cast, but when the burrow was exposed no contact could be established with any of them, and the search was usually abandoned when the animal was finally overtaken. These burrows tended to be confined to the layers of sand lying between the strata of gravel, but made brief and shallow excursions into the gravel or passed directly through it into the sand below. There was no evidence that secondary burrows were formed, but their existence cannot be excluded, since it was never certain that the burrows examined were entire. The thin mucus lining of the burrows suggested that they were temporary structures. The failure to locate an entrance hole lends some support to this idea.

Specimens were collected immediately after the tide had receded and were located by the enormous casts they produced during the ebb. The frequency and volume of the casts produced indicated a considerable amount of activity either just prior to or during the ebb of the tide. To date it has not been possible to make observations on cast formation during the flood. It is reasonable to suppose that some specimens did not cast during the ebb, yet counts of up to 100 and more were not uncommon for a section of the shore extending 20 m. from mid-tide level down to low water springs and about 250 m. in length, on one well populated shore. Within this area the specimens were irregularly distributed, and were rarely less than 1 m. apart. There was no apparent tendency for them to aggregate at any one particular level of the shore, or to be localised in any way. Their offshore distribution is unknown.

During the ebb the water table was at, or very close to, the surface of the sand wherever the casts were seen. The population thinned out rapidly above the mid-tide level, and in the more heavily drained areas below this level.

The associated fauna consisted of a large population of the lamellibranch *Anomalocardia brasiliana* (Gmelin, 1792), some burrowing decapod crustacea, a variety of small errant polychaetes, and numbers of the very large polychaete *Eunice* sp. The latter was the next largest animal in the biocoenose and tended to occupy a higher level of distribution on the shore, but overlapping with that of the *Balanoglossus*. It also penetrated to greater depths in the substratum.

When handled *Balanoglossus* produced enormous quantities of thick mucus which adhered tenaciously to the hands and emitted a powerful smell of iodoform. This strong odour greatly facilitated the identification and tracking of the burrows in the field. It, and the mucus, must serve as a effective deterent to any predator. When handled in a darkened room the animals luminesced strongly. The entire body produced a greenish light and this appeared to be associated in some way with the secretion of mucus, because the latter glowed for a very short period as it streamed off the body when the animal was swirled around in an aquarium.

CASTS AND CASTING

The casts resembled those of *Arenicola marina* (L.) in form, but were very much larger and consisting of continuous faecal cords of diameter 1.0 to 1.5 cm. and length ca. 0.5 to 1.0 m. Coiled upon themselves these cords formed a mass that measured 6 to 10 cm. in height and 10 to 15 cm. at the base, and weighed about 200-250 gm. when freshly cast. All the casts examined had evidently been made after the tide had receded.

The process of casting was similar to that described for *Saccoglossus*. The anus appeared very slowly at the exit of the burrow and equally slowly began to extrude the faecal cord. As the cord lengthened the posterior end of the animal was protruded further and further until it came to lie several cms. above the substratum, and except for the terminal centimeter or two it remained completely enveloped by the irregular coils of the cast. There was no circular movement of the extruded portion as noted for *Saccoglossus ruber* (Knight-Jones, 1953), so the cast did not assume the regular spiral form characteristic of many of the Harrimanidae. Instead it fell in loose irregular coils around the protruding tail region. The process of protrusion of the tail and the extrusion of the faecal cord took place simultaneously. The tail was not always withdrawn after the extrusion of the cord had ceased, but frequently remained visible within the coils of the cast until the next period of intestinal activity forced still more of the cord out through the anus. Shallow annulations on the cord resulted from the contractions of the anal orifice and the irregular rate of extrusion of the cord. The cords contained very little mucus, were loosely compacted, and readily dispersed by the incoming tide. There was no evidence, as in *Arenicola* which occupies a permanent burrow, of several casts being produced one on top of another forming a shallow cone of sand upon which subsequent casts are extruded. Specimens kept in aquaria with a substrate of sand a few cms. deep made short burrows and extruded short very loose casts on the surface. The absence of an adequate depth of substratum prevented them from making deep burrows and producing large casts. In the field the terminal portion of the burrow immediately below the cast rose vertically through 20 to 30 cm. of sand to the surface, so that the posterior end of the animal would also be so orientated when casting. In the aquarium the terminal portion presented a very oblique angle to the surface so the cast tended to remain uncoiled.

Specimens kept for several days in aquaria devoid of a sandy substratum extruded two long thin yellow mucus cords which twisted upon each other as the animal moved around. These cords were rarely more than 0.5 to 1.0 mm. in diameter and were produced by the lateral furrows of the intestine (see p. 276). Similar but single cords have been observed in *Saccoglossus*. In *B. gigas* they are composed of the indigestible or partly digested fine particulate matter carried into the pharynx by the respiratory and ciliary feeding currents, embedded in mucus along with the secretions of the dorsal sacs.

The alimentary canal of newly caught specimens was often empty except for some fine sand in the hind gut and thin cords of mucus and sand within the anterior regions of the gut. Others were found in which the gut was gorged with sand throughout. In aquaria the burrowing activities of these animals were spasmodic so that the gut was sometimes distended with sand and at other times almost empty and flaccid.

Specimens placed on a substrate composed of alternate layers of sand and coarse gravel in an aquarium and irrigated by water flowing in at the bottom, rapidly burrowed down as far as one of the underlying layers of gravel. Graphite suspensions introduced into the substrata showed that in this position the respiratory stream entering the mouth was drawn primarily from the layer of gravel immediately adjacent to the proboscis. Subsequently the graphite appeared in the cords extruded from the intestine. Dissections showed that it had been extracted by the sieving action of the pharynx. Moreover this action of the pharynx could be demonstrated whenever an animal had reversed its position and was drawing its respiratory water through the entrance to the burrow.

CILIARY FEEDING MECHANISM

1) *Proboscis* (figs. 1, 2 & 3)

The epidermis of the proboscis was uniformly ciliated and liberally supplied with mucus gland cells. The exudate from these seemed to be more copious when the animal was burrowing or feeding by engulfing the substrate. It formed an enveloping sheath around the proboscis and was propelled posteriorly at an even velocity towards the base of the proboscis. The base of the proboscis was surrounded by the crenated anterior margin of the collarette, a funnel-like extension of the collar to which it is attached by a short stalk mid-dorsally.

The currents created by the cilia of the proboscis drive the mucus and any adhering sand and debris towards the margin of the collarette. At this point some selection takes place and whilst most of the mucus sheath appears to pass back over the collar, some of the finer material within the inner layers of the sheath are drawn into the vestibule of the collarette (see fig. 1). The cilia on the base of the proboscis all beat towards the stalk and the preoral ciliary organ which almost surrounds its point of insertion into the proboscis. The cilia on the base help to propel the sand and mucus aggregating within the vestibule radially towards the mouth.

During the process of ciliary feeding whether within a few cms. of the mouth of the burrow or deeper down in the vicinity of a layer of gravel, the proboscis moved gently to and fro around the walls of the burrow collecting any fragments of debris and sand as they were drawn into the burrow with the currents set up by the pharyngeal apparatus. At other times, when the animal was fully relaxed and quiescent, the proboscis became deeply fluted and almost immobile. Particulate matter entering the mouth on these occasions was sieved off by the branchial apparatus in the manner described on p. 259. When stimulated, or about to resume its activities the proboscis was inflated and resumed its normal elongated egg shape.

2) *Preoral Ciliary Organ* (Figs. 1 & 2)

This organ is present in many enteropneusts and in *B. gigas* it is a deep U-shaped depression in the base of the proboscis, the limbs of which almost meet in the mid-dorsal line above the stalk. This depression is surrounded by a raised epidermal ridge covered with strong densely packed cilia, which beat continuously inwards towards the depression. Within the depression the cilia beat ventrally from the ends of the limbs towards the bend of the U. The cilia on the ridges beat more rapidly than those on the surrounding epidermis.

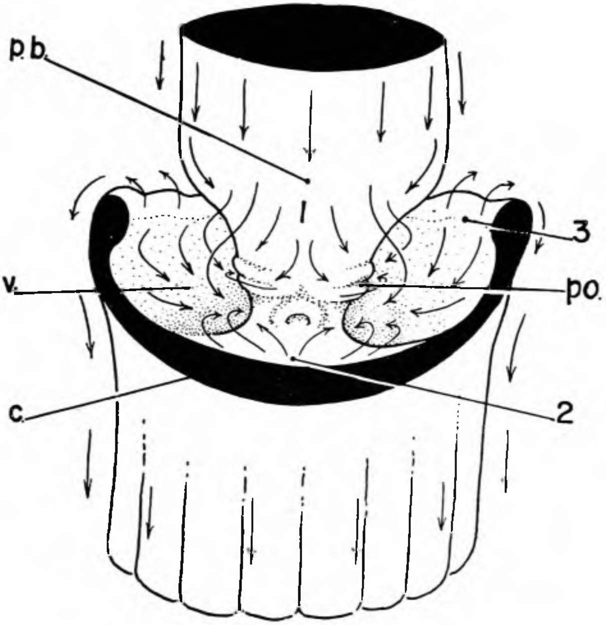

Fig. 1. Dorsal view of the proboscis and the collarette with a portion of the latter cut away to show the paths of the currents within the vestibule, indicated by arrows.

(1) mid-dorsal cleavage of currents over the base and stalk of the proboscis
(2) mid-dorsal cleavage of currents set up by the ciliated epithelial lining of the vestibule
(3) sub-marginal cleavage of currents around the rim of the collarette.
Lettering: — c. cut edge of collarette; p.b. proboscis; p.o. preoral ciliary organ; v. vestibule.

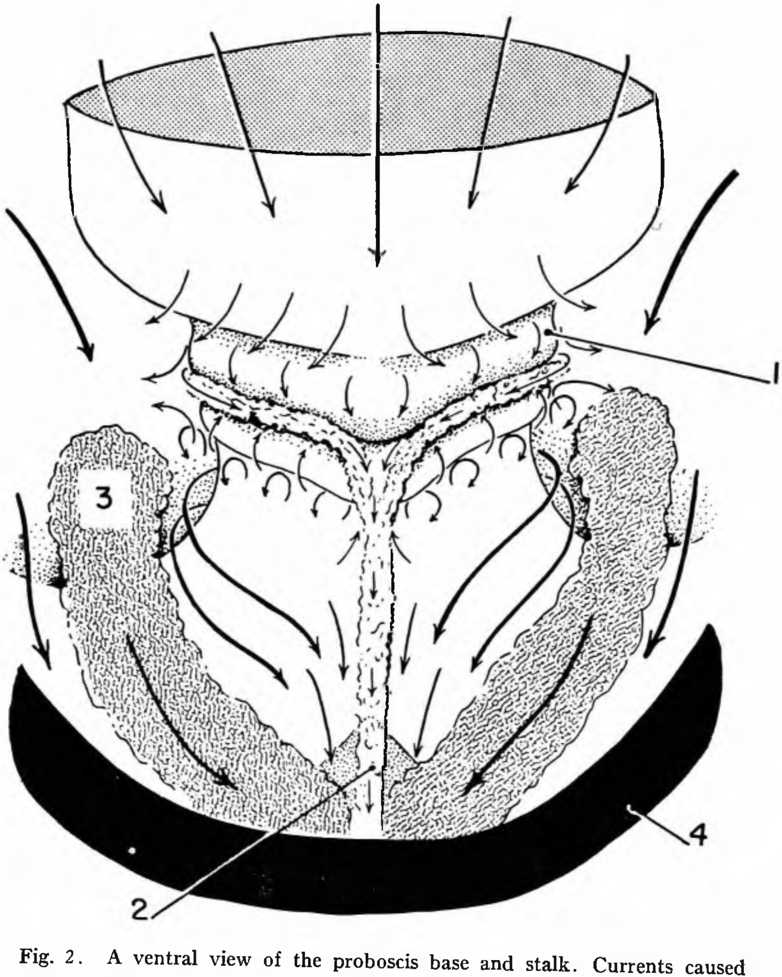

Fig. 2. A ventral view of the proboscis base and stalk. Currents caused by the cilia of these regions are indicated by arrows.

(1) anterior ridge of the preoral ciliary organ.

(2) fine particles and mucus formed into a cord in the depression of the preoral organ and passing ventrally under the proboscis towards the mouth

(3) food stream from the proboscis and margin of the collarette, shown entering from the dorso-lateral regions only. Food enters the vestibule from all parts of the margin.

(4) margin of collarette cut away to display the vestibule.

The cilia of the epidermis within a few mm. from the organ all beat towards it and help to create small eddies and vortices in its neighbourhood from which the cilia on the ridges draw off fine particles and thrust them into the depression. Here they are compacted into mucus cords which pass out of the organ ventrally and are swept into the mouth either by the respiratory current when the animal is filter feeding or with the main stream of sand etc. when the animal is engulfing and burrowing. By this simple process of drawing off minute quantities of the fine particles from the main respiratory and feeding streams the preoral organ seems to fulfil the function of a chemoreceptive organ. These observations tend to confirm those of Knight-Jones (1953) and the author's on *Saccoglossus* and *Protoglossus* (Burdon-Jones, 1956). Coarse particles entering the mouth were never caught up by the preoral organ during the process of ciliary feeding, but must inevitably brush past it when the animal is burrowing. Direct observations of the action of the organ on these occasions were difficult because of the masking effect of the sand being engulfed, but clearly only a very small percentage of the material being swallowed can come in contact with the organ. The comparatively feeble orally directed currents contributed very little to the powerful streams set up by the cilia of the vestibule of the collarette, the buccal cavity and the pharyngeal apparatus. The mucus cords produced by it were no more than by-products of its more likely function of testing the streams of sand, food and water entering the mouth.

3) *Collarette* (figs. 1, 3, 4 & 5)

The funnel-like vestibule of the collarette can embrace the greater part of the proboscis when the latter is fully retracted. It is a highly sensitive, versatile organ, which plays a very prominent role in the feeding and burrowing activities of the animal. The interior face of the vestibule is lined with densely packed cilia which are primarily responsible for propelling some of the material collected by the proboscis and anterior margin of the collarette into the mouth. The cilia lining the dorsal half of the vestibule beat latero-ventrally from the mid-dorsal line and so divide into two streams any material entering this region from the base and more anterior regions of the proboscis. The cilia on the lateral and ventral walls of the vestibule beat towards the mouth. The cilia on the outer face of the collarette all beat posteriorly and their action helps to clear the excess mucus, sand and food material as it collects in and wells out of the vestibule.

When ciliary feeding is in progress the collar is dilated so that it almost fills the burrow. The margin of the collarette is slightly everted so that the ciliary surfaces of the vestibule are presented to the incoming stream of water and thus assist in propelling it into the pharynx. The mouth is held wide open and the proboscis contributes in the manner described above (see p. 260).

The smooth and sometimes crenate anterior margin of the collarette is capable of considerable flexure and is used to exclude and in some degree select material approaching the vestibule.

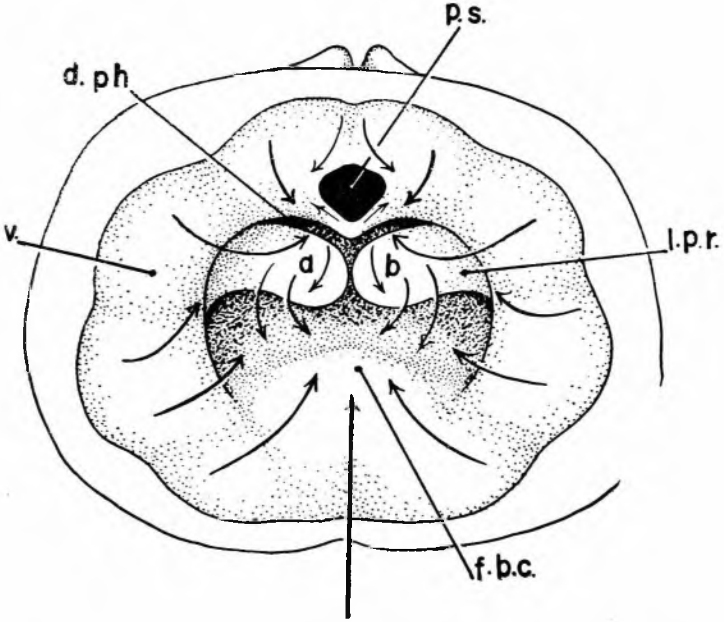

Fig. 3. Anterior of the vestibule, mouth and buccal cavity, with the proboscis cut away to show the ciliary currents, indicated by arrows, converging on the mouth and the rejection currents on the anterior ends of the parabranchial ridges.

Lettering: — d.ph. dorsal pharynx; f.b.c. floor of buccal cavity; l.p.r. swollen anterior end of the left parabranchial ridge; p.s. cut end of proboscis stalk; v. vestibule.

APPENDIX 1

The table given below is a granulometric analysis of 50 gm. samples different substrates commonly traversed by the burrows of *Balanogloss gigas,* and of the gut contents and casts. The samples ranged from the surfa down to a depth of almost 0.5 m. Column 1 is a surface scraping and 2 w taken from within the next 10 cm depth. Columns 3 to 7 were taken from eac succeeding distinct layer of sand and gravel. Columns 8 & 9 are of gut conten and cast respectively.

	Quantity of each size range expressed as a percentage.					
Sample no.	> 1.98 mm	1.98 — 1.65mm	1.65 — 1.17mm	1.17 — 0.88mm	0.88 — 0.42mm	0.42 — 0.3 mm
1	0.28	0.06	0.06	0.04	0.10	0.06
2	3.44	1.04	2.32	2.06	2.10	1.60
3	18.72	6.48	12.08	11.70	13.10	4.12
4	10.90	2.10	3.30	4.36	5.78	1.60
5	16.72	5.00	12.72	15.02	20.98	6.00
6	17.28	3.24	5.32	4.26	3.80	0.88
7	11.08	1.34	2.54	2.36	2.64	0.90
8	3.74	1.14	2.68	2.62	3.40	1.28
9	1.32	0.72	1.68	1.80	3.36	1.34

0.3 — 0.2mm	0.2 — 0.15mm	0.15 — 0.1 mm	0.1 — 0.07mm	0.07 — 0.05mm	0.05 — 0.04mm	< 0.04 mm
0.14	0.36	4.66	79.80	12.42	0.62	1.34
0.54	0.60	2.94	64.92	14.76	1.20	1.48
3.36	1.56	2.40	21.22	3.96	0.20	1.10
1.68	1.74	7.72	53.26	6.60	0.30	2.64
3.32	1.30	2.44	13.82	1.30	0.08	1.24
0.86	1.02	4.94	46.12	6.66	0.82	4.80
0.98	1.26	6.58	57.68	8.66	0.70	3.36
1.38	1.40	6.92	62.04	9.04	0.80	3.56
1.60	1.80	7.02	68.58	8.00	0.62	2.00

This it appears to do primarily according to the size of the object. It is much more selective when the animal is ciliary feeding than when it is engulfing. On the latter occasions the observer gets the impression that the animal is prepared to swallow anything that it can possibly squeeze into the mouth. The boundary between the inner and outer ciliated faces of the collarette was set just within the anterior margin, so that unless this margin was slightly everted the greater part of the material thrown back in the mucus sheath from the proboscis passed on over the collar. Retraction of the proboscis also produced the same result, and tended to stem the flow of material into the vestibule. Thus the intake of food is automatically minimised whenever the proboscis is adversely stimulated. By flexure, eversion and inversion and presentation of the inner or outer ciliated surfaces to the oncoming stream of sand from the proboscis the collarette exercised some degree of selection of the material to be ingested. Any larger particles of sand or debris which evaded this process of selection and entered the vestibule but could not be swallowed, were dealt with in a different way. Ciliary feeding ceased, the mouth closed, the proboscis and the walls of the collarette contracted and the unwanted object and everything else within the vestibule was squeezed out. Local inversion of the margin of the collarette facilitated the expulsion of the vestibular contents and was deepest in and around the objects to be evicted.

Pieces of shell and gravel up to 4 mm. in size have been found within the intestine of large specimens, but only in very small quantities and were probably swallowed when the animal was burrowing rapidly.

4) *Mouth and Buccal Cavity* (figs. 3, 4 & 5)

The mouth lies in the ventral half of the vestibule, immediately below the insertion of the proboscis stalk. The latter is keeled ventrally and triangular in cross section. The cilia on the sides of the keel beat towards the preoral organ and in consequence against the main currents entering the mouth. The food stream from the dorsal surface of the proboscis passes down on either side of the stalk into the mouth. The latter can be closed by muscular contraction and elevation of the floor of the buccal cavity, thus sealing off the entrance to the ventral pharynx. Closure of the entrance to the dorsal pharynx is effected by the elevation and convergence of the anterior ends (a & b, fig. 3) of the parabranchial ridges.

The buccal cavity is short, about 4 to 5mm. long, circular in cross section and lined throughout with a strongly ciliated epithelium. The greater part of the dorsal half of the cavity is occupied by the protruding ends of the parabranchial ridges. Ventrally the cavity leads straight into the non-branchial region of the pharynx. The roof of the cavity is ridged median dorsally and the cilia on this ridge and on the roof beat latero-ventrally and obliquely down the right and left walls towards the pharynx. Everything solid that enters the mouth is thus driven ventrally onto the floor of the cavity where the cilia beat posteriorly towards the ventral pharynx. The oblique ventrally directed beat of the cilia on the walls of the buccal cavity helps to maintain the cleavage of the food stream produced by the proboscis stalk and the cilia on the dorso-lateral walls of the vestibule. Entry of these cords into the dorsal pharynx was prevented by the swollen anterior ends of the parabranchial ridges (see fig. 3), which moved upwards and inwards whenever any large quantities of sand entered the buccal cavity. As they moved upwards they converged mid-dorsally on the ridge running along the roof of the cavity. In this way the entrance to the dorsal pharynx was sealed off except for a narrow transverse slit which excluded all but the finest particles of sand, but permitted the passage of the respiratory current. The cilia on the anterior ends of the parabranchial ridges (see figs. 4 & 5) all beat antero-ventrally, so that any sand grains which, because of their size or angle of presentation at the entrance to the dorsal pharynx became lodged there were rejected and propelled downwards to join the main stream entering the ventral pharynx. The cilia on the walls of the buccal cavity all beat in a direction which assisted this process of rejection and cleansing at the entrance to the dorsal pharynx.

Under normal feeding conditions coarse material never enters the dorsal pharynx, but fine sand, silt and small organisms in suspension are not excluded and pass directly into the pharynx with the respiratory current. If when the animal is filter feeding, as described

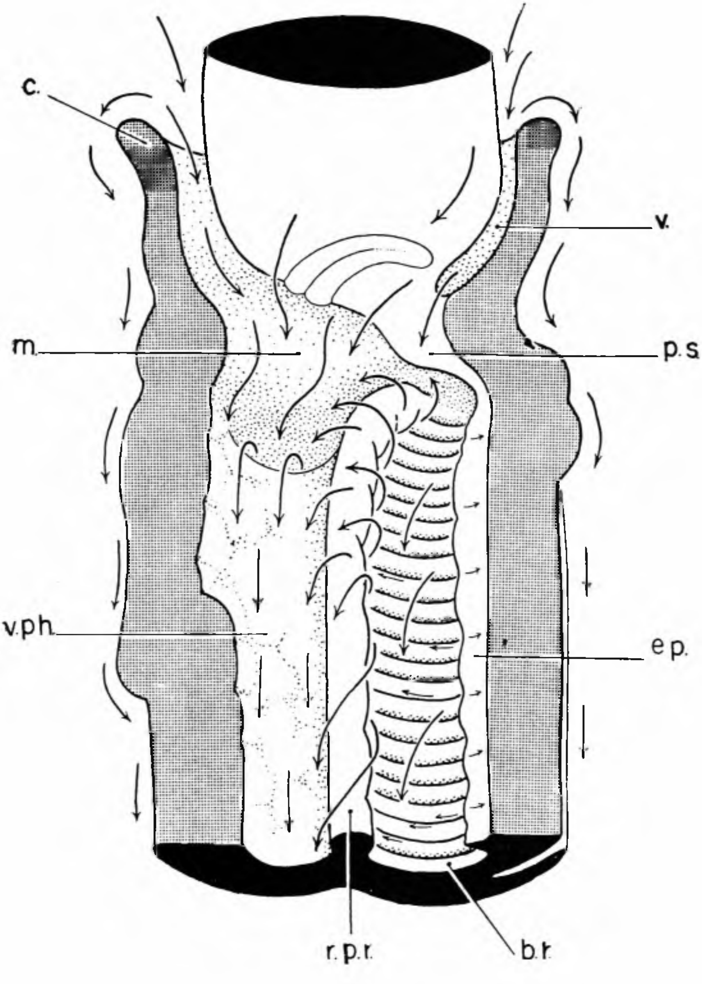

Fig. 4. An almost median vertical section through the anterior end of the pharynx and collar to show the arrangement of the organs within the vestibule and buccal cavity when feeding, and the rejection and cleansing currents set up by the parabranchial ridges.

Lettering: b.r. branchial ridges in dorsal pharynx; c. collarette; ep. epibranchial ridge; m. mouth; p.s. proboscis stalk; r.p.r. right parabranchial ridge; v. vestibule; v.ph. ventral pharynx.

on p. 270, any stray sand grains settle on the ventral side of the vestibule they are borne directly into the ventral pharynx, but any that settle in the dorsal region of the vestibule are carried down one

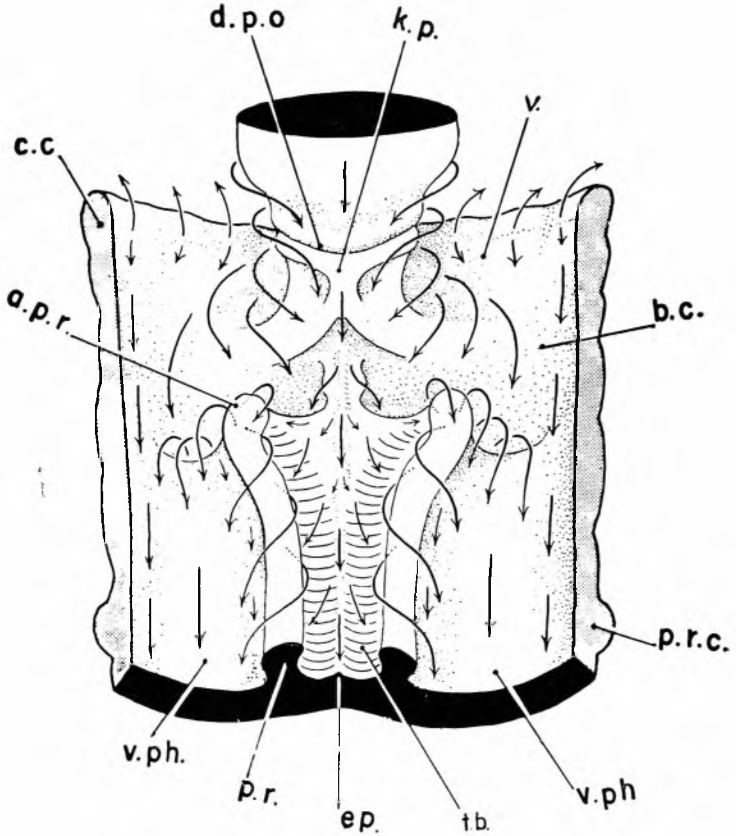

Fig. 5. A dissection from the mid-ventral line showing the ciliary currents, indicated by arrows, within the vestibule, buccal cavity and the anterior region of the pharynx.

Lettering: — a.p.r. swollen anterior end and parabranchial ridge showing rejection currents; b.c. buccal cavity; c.c. cut edge of collarette collar and collar; d.p.o. depression of preoral organ; ep. epibranchial ridge; k.p. keel of proboscis stalk; p. r. right parabranchial ridge; p.r.c. posterior rim of collar; t.b. tongue-bars separating branchial-clefts in dorsal pharynx; v. vestibule.

on the other side of the stalk and along the dorso-lateral walls of the buccal cavity towards the parabranchial ridges which deflect them into the ventral pharynx.

5) *Pharynx* (figs. 4, 5, 6 & 7)

In *B. gigas* the pharynx is separated into dorsal and ventral regions by two prominent parabranchial ridges which protrude from its lateral walls. The dorsal portion contains the branchial apparatus, which comprises about 300 to 350 pairs of branchial clefts extending vertically downwards from the base of a prominent median dorsal epibranchial ridge and terminating just short of the parabranchial

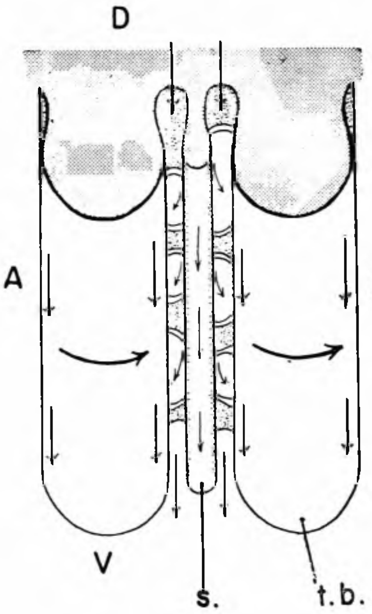

Fig. 6. A small portion of the dorsal pharynx, showing diagrammatically the septum with synapticulae on either side lying deep within the cleft bounded by the prominent tongue-bars, and the ciliary currents as indicated by the arrows.
Lettering: A, anterior; D, dorsal; P, posterior; t.b, tongue-bar; s, septum; V, ventral.

ridges. These ridges are highly glandular and densely ciliated structures. Their elevation and protrusion is under muscular control and determined by the amount of food material in the ventral pharynx over which they form a roof. They extend to the posterior limit of the branchial clefts after which they curve sharply upwards and converge on the mid-dorsal line where they terminate abruptly. When closely adpressed they serve to seal off the posterior end of the pharyngeal apparatus and so help to prevent any fouling of this region by regurgitated food. (see p. 271).

The branchial apparatus is made up of a series of clefts separated from one another by the strongly ciliated and glandular ridges of the tongue-bars and the thinner more deeply set septa. The tongue-bars are considerably thicker and more prominent than the septa and envelop them so completely that they cannot be seen from within the lumen of the pharynx. The synapticulae and apertures leading into the branchial chambers, and thence through the branchial apertures to the exterior, lie on either side of the septa deep within the clefts bounded by the tongue-bars. The frontal cilia on the pharyngeal surfaces of the tongue bars beat posteriorly. The cilia on the parabranchial ridges beat obliquely postero-ventrally from the dorsal into the ventral pharynx. Excision of these ridges showed that their cilia were responsible for the oblique element in the movement of the mucus film over the branchial clefts, because in their absence this film moved directly posteriorly. The cilia lining the lateral walls of the clefts beat ventrally towards the parabranchial ridges. (see fig. 6).

Thin graphite suspensions released at the margin of the collarette were swiftly drawn into the dorsal pharynx and onto the branchial ridges. They were then transported postero-ventrally and accumulated in shallow grooves at the base of the parabranchial ridges. The finer particles in the suspension were drawn into the clefts, sieved off by the mesh of synapticulae and transported slowly ventralwards and ultimately disgorged into the grooves alongside the ridges. Within these grooves the graphite and mucus from the clefts and ridges was gently rolled into a loose cord and transported slowly posteriorly until ultimately caught up by the powerful beat of the cilia on the parabranchial ridges and whisked over into the ventral pharynx. This sieving mechanism was very efficient and prevented particles 1 to 2µ from passing out through the branchial pores. In this way the branchial apparatus was able to cleance itself within seconds of any fine suspended matter entering the dorsal pharynx and to make a small contribution to the main mass of food passing ventrally. Even coarse sand injected into the dorsal pharynx was dealt with speedily and rarely traversed more than 2 cm. of the pharynx before being swept over the ridges into the ventral regions.

TRANSPORTATION THROUGH THE GUT

1) *Oesophagus* (figs. 7 & 8)

This region is often three to four times as long as the branchial, presenting a wide lumen and a low obliquely grooved epithelium on its lateral walls. It is bounded dorsally by the genital pleurae throughout its length and the coloration of the genital sacs may be seen through its thin dorsal walls. There is no apparent differentiation into regions except for a shallow tranverse grooving on the lateral and ventral walls. The roof is comparatively smooth or only slightly grooved transversely. There are no oesophageal pores.

At the junction of the oesophagus and the pharynx there are two shallow dorso-lateral pockets, the cavities of which are posteriorly directed. Their function is not certain, but they may serve as safety valves to prevent regurgitation of food into the dorsal pharynx in the event of back pressure being exerted upon the food cord in the oesophagus, when the animal retracts quickly or even during the normal rhythmic contractions of the body as the animal burrows. The inflation of these pockets by such a back pressure would also tend to force the parabranchial ridges closer together and so help to seal off the dorsal pharynx as mentioned above.

The epithelium on the walls of the oesophagus is transversely grooved and the fine cilia within these grooves beat dorsally whilst the more powerful ones on the intervening ridges beat posteriorly. Median dorsal and ventral grooves are also present and in them the cilia also beat posteriorly. The transport of the food cord through this region is assisted by peristaltic movements of the walls. Posteriorly, in the transitional region, the grooving of the walls becomes progressive-

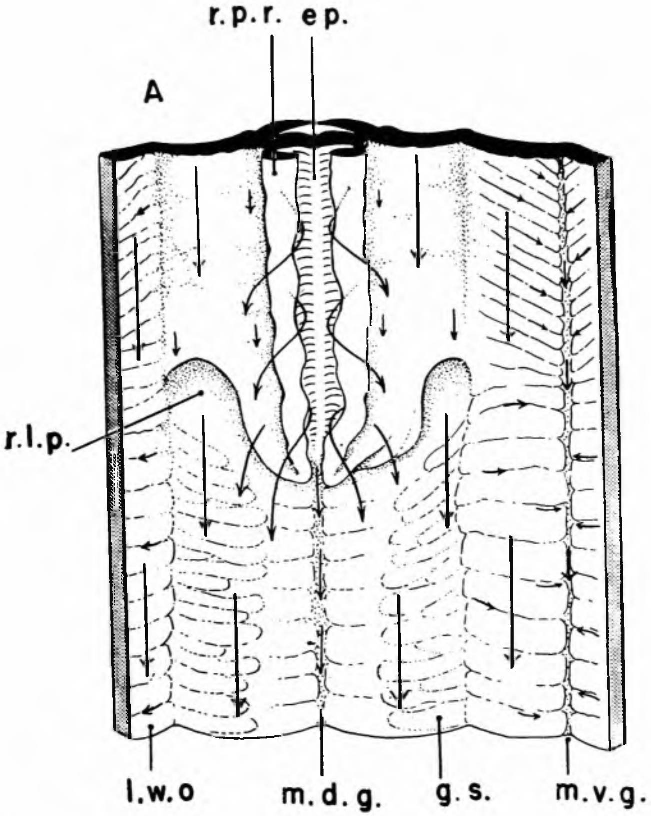

Fig. 7. A view of the posterior branchial region dissected from the ventral side, showing the termination of the parabranchial ridges mid-dorsally and the lateral pockets. The ciliary currents are indicated by arrows.

Lettering: A, anterior; ep, epibranchial ridge; g.s. genital sacs showing through the thin roof of the oesophagus; l.w.o, lateral wall of oesophagus; m.d.g, median dorsal groove; m.v.g, median ventral groove; r.l.p, right lateral pocket; r.p.r, right parabranchial ridge.

ly more oblique and subtends an angle of 45° or more to the mid-ventral line.

2) *Transitional Region* (fig. 8)

Within this region the posterior end of the oesophagus overlaps with the non-sacculated anterior end of the intestine. At this level there are two more shallow depressions in the dorso-lateral walls of the gut, at the point where the genital pleurae terminate externally. The cilia within the grooves bordering on these depressions all beat towards them, whilst those on the neighbouring ridges are very much stronger and beat obliquely towards the mid-dorsal line (see fig. 8). Thus in the transitional region the gut contents are subjected to the action of two major currents converging mid-dorsally, and a number of minor ones converging on the depressions. Such an arrangement will tend to loosen and disperse the food before it passes into the intestine.

3) *Intestine* (figs. 8, 9)

The walls of the intestine are grooved throughout. Anteriorly the grooves on the lateral walls are inclined towards the mid-dorsal line and merge with those of the oesophagus. Dorsally the transition from the deep transverse ridging of the intestine to the smooth epithelium of the oesophagus is more abrupt (see fig. 8).

Posterior to the short transitional region, the roof of the intestine becomes deeply sacculated for about 25% of the overall length of the gut. This is the 'hepatic' region and is divisible by colour into three distinct regions and for convenience these have been designated 1, 2 and 3.

In region 1 the first few sacs are elongated and ovoid in shape and irregularly arranged dorsally. The succeeding 20 or more pairs are flattened antero-posteriorly and auriculate, serially arranged on either side of the mid-dorsal line and a deep brown in colour. In region 2 the sacs are similar in form and arrangement and have a pale olive green to fawn colour. The first 10 pairs of sacs often have a lighter colour than the succeeding 50 or more pairs. Posteriorly

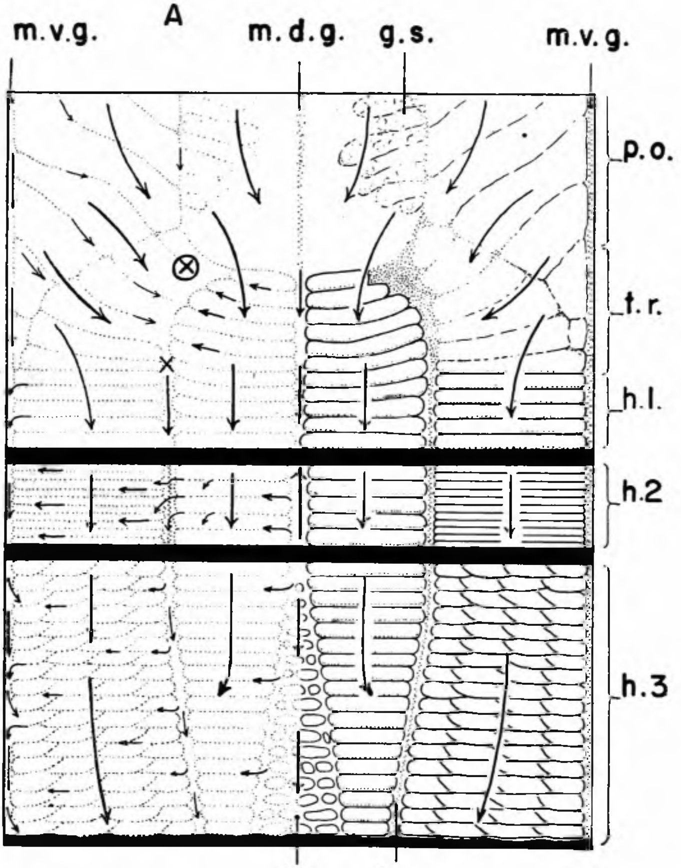

Fig. 8. A semidiagrammatic view of the posterior oesophagus, transitional region and the sacculated anterior end of the intestine as seen in ventral dissection. Stippling has been used to outline the structures on the left of the diagram so that the arrows indicating the directions of the ciliary currents can be inserted. Lettering: A, anterior; d.t, dorsal tract of glandular lobules; g.s, genital sacs showing through the dorsal wall of the oesophagus; h.1, h.2, h.3, first, second and third sacculated regions of the intestine; l.f, lateral furrow; m.d.g, median dorsal groove; m.v.g, median ventral groove; p.o, posterior limit of oesophagus; t.r, transitional region; X, right dorso-lateral depression.

these sacs lose their serial arrangement and laminar form and become bunched ovoid sacs. This form and arrangement persists for the first few centimeters of region 3, but their colour becomes dominantly pink shaded with brown. Posteriorly these ovoid sacs become progressively more widely spaced and once again arranged in a single series on either side of the mid-dorsal line. Their size and shape diminishes from elongated ovoid sacs anteriorly to small globular elevations posteriorly. The total number of sacs in each region is roughly in the proportion of 1 : 2 : 10. Thus in region 3 the number of pairs of sacs may exceed 200.

The pigmentation of these regions is distinguishable internally, the epithelial linings of the cavities of the sacs of 1 and 3 being brown and pink respectively, whilst those of region 2 are a pale yellow or fawn. There is also a ring of deep green pigmentation about 2 mm. wide around the lumen at the junction of regions 1 and 2.

The cavities of the sacs of regions 1 and 2 open into the intestine through slit-like orifices which lie in between the transverse ridges on the roof. These prominent ciliated ridges are opposable and control the opening and closing of the orifices. In region 3 they are replaced by small circular pores at the base of conical depressions. The cilia on the lips of the sacs of region 1 beat towards the mid--dorsal line, whilst those in the transverse grooves on the ventral walls beat ventrally. This mid-lateral divergence of the currents traversing the grooves may further assist in the dispersal of intestinal secretions at this level and in the mixing of the contents of the lumen. At the junction of regions 1 and 2 this divergence ceases and the currents in the transverse grooves all travel ventrally, whilst the median dorsal convergence of the currents which persists throughout region 1 is replaced by a divergence.

In region 1 the median dorsal groove is a shallow depression in which the cilia create a posteriorly directed current. In region 2 the groove is much deeper and tends to form a channel partially cut off from the lumen of the intestine by the overlapping dorsal extremities of the lips of the sacs. Within this channel the ciliary currents are anteriorly directed. Any fine particulate matter introduced at its posterior end is rapidly transported forwards and wells out at the junction of regions 1 and 2. There is also some degree of lateral dispersion over the lips of the sacs. (see fig. 8). In the absence of a more detailed knowledge of the secretions of the dorsal sacs and other glandular regions in this part of the intestine the nature of the fluids which pass through this channel must *pro tem* remain obscure. In region 3 the channel opens out gradually and the ridging on the roof breaks down and becomes irregularly lobular.

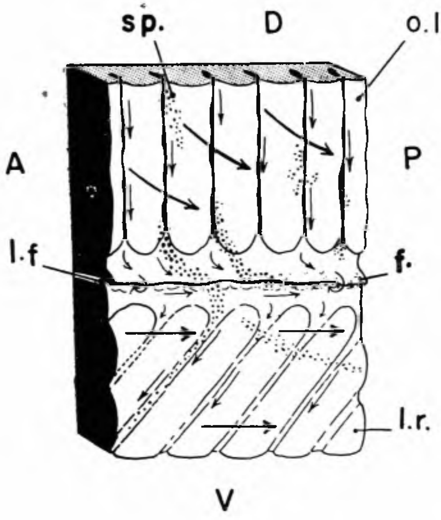

Fig. 9. A portion of the right lateral wall of the intestine (region 2), showing the lateral furrow, and the currents (as indicated by arrows) which disperse the yellow spherules exuding from the dorsal sacs. (Diagrammatic)
Lettering: A, anterior; D, dorsal; f, flange overlapping lateral furrow; l.f, lateral furrow; l.r, oblique ridges on lateral walls of intestine; o.l, opposable lips of dorsal sacs; P, posterior; sp, yellow spherules; V, ventral.

The sacs of regions 1 and 2 move constantly in a rhythmic fashion to and fro as waves of contraction and dilation pass over them in an anteroposterior direction, whilst internally the transverse ridges on the roof roll laterally over one another exposing alternately the linings of the anterior and posterior walls of the sacs. In region 2 this activity of the ridges appears to assist in the extrusion of fine streams of yellowish cream spherules which seep slowly out of the sacs onto the walls of the intestine, and ventrally towards the lateral furrow (see fig. 9).

These furrows are a prominent feature of the intestine at this level, and consist of two dorso-laterally placed depressions which extend longitudinally from the orifices of the first pair of dorsal sacs (see X fig. 8) throughout the intestine to within a few centimeters of the anus. The ridging on the roof of the intestine ceases abruptly just above the furrows, which are acute depressions in the intestinal walls with an overlapping flange dorsally. Both the furrow and the flange are strongly ciliated and the cilia on the outer face of the flange beat ventrally towards the margin, whilst those on the inner face beat obliquely inwards and posteriorly. The cilia deep within the furrow beat posteriorly.

Posterior to region 3 the ventral groove and the lateral furrows retain their identity to within a short distance of the anus, but the overlapping flange loses its prominence towards the latter end of region 3. The glandular lobules on the roof and immediately lateral to the furrows become more widely spaced until finally those within the furrows disappear whilst those outside them become elongated in an antero-posterior direction before disappearing. (see fig. 8). The grooves on the ventral walls of the intestine become more and more widely spaced posteriorly, so that near the anus they are several millimeters apart, whilst in region 1 they are less than 0.5 mm apart. Latero-dorsally the ridges and the grooves are shallow and set obliquely against the direction of flow of the faecal cord, but the cilia within the grooves on the walls all beat ventrally and those on the shallow ridges beat very strongly analwards. The passage of the faecal cord along this part of the intestine is primarily effected by ciliary activity assisted in some degree by a weak peristalsis of the walls. The anus is terminal and closed by a sphincter.

CONCLUSIONS

Balanoglossus gigas obtains its food in three ways:

a) by engulfing large quantities of the substratum collected and selected by the proboscis and the collarette, and digesting the debris and organisms taken in with it as well as the bacterial film on the sand grains,

b) by ciliary feeding with the proboscis and collarette on the detritus and suspended matter washed into the burrow by the tide, or draining into it from a gravel substrate, or drawn into it by the respiratory current, and

c) by sieving the respiratory current, which although it is automatic and always accompanies a) and b) can also provide a steady trickle of nutrient material into the ventral oesophagus when both are inoperative.

The interstitial fauna engulfed or seived out of the sand and gravel layers may also be a potential source of food, although little is known of its composition in these substrates.

The granulometric analysis given in Appendix 1 indicates a certain degree of selectivity in favour of sand within the range 0,05 to 0.1 mm. Over 80% of the gut contents and the casts was within this range. Since fine sand of this size was also dominant in the surface layers (columns 1 and 2) it seems probable that these animals had been feeding at or near the surface. Alternatively selective feeding may have taken place at or within one of the gravel layers, because these also contain 40 to 60% of sand within this range (columns 4 and 6).

Whereas the greater proportion of the contents of the gut are derived from method a) the most nourishing component will probably be collected by method b) supplemented by c).

SUMMARY

Balanoglossus gigas lives in substrates composed of layers of sand and gravel. The collection of food material in this very large enteropneust is effected by a combination of engulfing and ciliary feeding. On the shores examined, it tended to feed selectively on fine particulate matter, the collection of which involved the cilia of the proboscis, collarette, vestibule, buccal cavity and the pharynx. Fouling of the branchial apparatus was prevented by a ciliary cleansing mechanism which automatically supplemented the general supply of food in the ventral pharynx.

The ciliary tracts and currents throughout the intestine and their role in the propulsion of the food cord, the mixing of the gut contents and dispersal of intestinal secretions are described.

RESUMO

Balanoglossus gigas vive em substrato de camadas de areia fina e grossa (cascalho). A coleta de material alimentar por êste enorme enteropneusto efetua-se por meio de uma combinação de tomada de alimento por engolimento e de movimento ciliar. Nas praias examinadas, êste animal procura alimentar-se seletivamente com material finamente reduzido, participando na coleta do mesmo os cilios da proboscis, do colar, do vestíbulo, da cavidade bucal e do farínge. Obstrução do aparelho branquial é prevenida por um mecanismo de limpeza por meio dos cilios que, automàticamente, suprem a tomada de alimento pelo farínge ventral.

Descrevem-se os tratos ciliares e as correntes através do intestino e sua função na propulsão do cilindro de alimento, a mistura do conteúdo intestinal e a dispersão das secreções intestinais.

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