# SECTION D

## NUTRITION

## 1. INTRODUCTION

The morphological studies of Graham (1934 a & b) and Yonge (1949a) have shown that the genus <u>Donax</u> belongs to the well defined group of Eulamellibranchiata, the Tellinacea, which is characterised mainly by the possession of two mobile separate siphons, a cruciform muscle with associated sense organ, and a large muscular foot. Furthermore, Yonge has demonstrated in his classical work on the Tellinacea that the structural features which define the group are all associated with the habit of feeding on bottom deposits and have enabled the different families to exploit as nutriment the organic detritus occurring on all types of bottom materials. These bottom materials range, as described by Yonge, "from finely graded mud to muddy gravel and from fine sand (fine or silty) to coarse shell gravel".

The position of the genus <u>Donax</u> within the Tellinacea was further considered by Yonge (1949a) who noted that it had evolved within the superfamily with features suitable for life within relatively firm substrata concurrent with a tendency for a change away from the deposit-feeding habit towards that of a suspension feeder.

"In the Donacidae . . . only the loose surface deposits with suspended material are taken in although much more freely and in far greater quantity than in the true suspension feeders".

Elsewhere in the same paper, Yonge was more explicit:

"The general impression (is) that *Donax ~~denticulatus~~* vittatus is specialised for life in firm sand where organic debris is largely absent, so that it must feed primarily on suspended matter".

In another publication (Yonge 1949b) went still further in stating:

"Descended from deposit feeders, it (*Donax vittatus*) has become a suspension feeder".

Observations by Coe (1955) on *D. gouldi* (Dall) supported these views.

"Whenever the clams are covered by water, they feed on particles of organic matter in suspension".

Yonge's conclusions on the feeding habits of the Donacidae were based solely on a study of *D. vittatus* which included observations of live animals and morphological investigations on the siphons, cruciform muscle and associated sense organ, foot and pedal gape, ctenidia and palps, and the alimentary canal. Throughout his study Yonge was impressed by the reduction or loss of many of the deposit-feeding features in the clam, but he was unable to report the presence of any organs specialised for suspension-feeding. Furthermore, there was little knowledge at the time of the habits and morphology of any other species of *Donax*, and what conclusions he made had therefore to be based largely on evidence from the one species. This was unfortunate since the species he studied and treated as a representative member of the genus *D. vittatus* is in fact atypical of the genus in many features. (These are brought out in the course of this account). Nevertheless despite the insufficiency of material and positive evidence in Yonge's work, the conclusions he arrived at in regard to the feeding habit of the genus were generally correct and can now be supported and further expanded on the basis of the evidence obtained from a study of D. denticulatus and D. striatus.

Because the functional morphology of Donax is so closely associated with its mode of nutrition, it follows that any change or evolution in the one will be accompanied by a similar occurrence in the other. What may bring these about and why it is that Donax should revert to a suspension-feeding habit are questions that need to be answered if an understanding of the evolutionary processes is to be obtained. In investigating nutrition in D. denticulatus and D. striatus these questions have been borne in mind and the account which follows on this aspect of the clams is intended to provide some answers to them.

## II. FEEDING

### 1. The intake of food

Normally in the saturated region of the wash zone D. denticulatus and D. striatus live buried in the sand with their siphons extruded and lying flush with the surface of the sand (Figure 14A). The inhalant siphon is held vertically upwards while the exhalant, which is extruded further from the shell than the inhalant, is kept at an angle pointing away from it. When washed out of the sand the siphons assume characteristic positions at different phases of the wash (Figure 14B & C) but when the clams bury in again as soon as the backwash recedes, they quickly revert to their original positions. With every wave sequence, whether the clams are buried or not, they are covered by at least a thin film of water and, except when they are actually in the process of burrowing, have their siphons extruded and drawing in water. Any food material in suspension is therefore taken in passively.

In two families of the Tellinacea, the Tellinidae and Semelidae, the siphons are very long and the inhalant siphon gropes over the surface, actively drawing in bottom deposits (Yonge 1949a). In the Donacidae the siphons are shorter and wider and there is no such groping over the substratum. Yonge, however, found that in D. vittatus they were extruded beyond the surface of the sand and, although they did not explore the bottom, were occasionally observed to quiver slightly. Purchon (1963) reported that in the fresh water Donacid, Egeria radiata (Lamarck) the orifice of the inhalant siphon was held well away from the surface of the sand. The conditions in D. vittatus and E. radiata seem to be less adapted for suspension-feeding than in D. denticulatus and D. striatus in which the siphons are flush with the surface and show no movement whatever in taking in water. Comparison between these conditions and those in a deposit feeder, Tellina, and a suspension feeder, Mya, are shown in Figure 39.

The feeding rate of adult clams of D. denticulatus was measured experimentally as the volume of water cleared per unit time from suspended particles of colloidal carbon (Aquadag) - The experimental procedure is outlined in Appendix XIII and the results are given in Table 25.

TABLE 25:- The feeding rate of adult clams of D. denticulatus in five different concentrations of Aquadag in sea water.

| Carbon concentration | Feeding rate |
|---|---|
| 1.65mg/litre | |
| 3.18 | 257 cc./hr |
| 4.61 | 328 |
| 5.93 | 181 |
| 7.17 | 163 |
| 8.32 | 100 |

The concentrations of carbon used were in the range of those occurring naturally in the sea water at the Donax beds so that there would be as little discrepancy as possible

Figure 39

The appearance of the siphons above the substratum in A, <u>Tellina</u>; B, <u>D. vittatus</u>; C, <u>D. denticulatus</u> and <u>D. striatus</u>; and D, <u>Mya</u>. A, B, & D after Yonge (1949a).

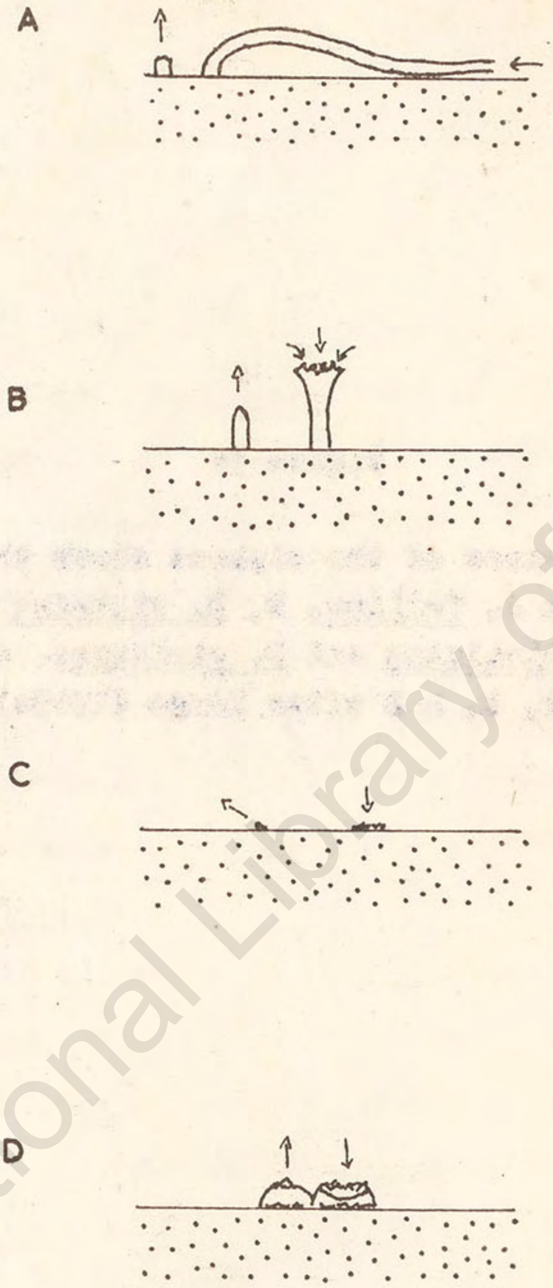

Figure 39

in the rate of filtration in the laboratory with that in the field. The results show that the adult clams are capable of filtering more than 300 cc of water per hour and that generally, the amount of water filtered by the clams is reduced when there is an increase in the amount of suspended material in the water.

## 2. Siphons

The functional features of the siphons in the Tellinacea have been summarised by Yonge (1949a) as follows:

> "In the Tellinacea, maximum mobility is achieved, and there are no straining tentacles as in the siphonate suspension feeders with a resultant capacity for indiscriminate intake of bottom deposits".

This summary was based on observations of several species of the Tellinacea including *D. vittatus* and was later supported for the Donacidae by Purchon's (1963) description of *Egeria radiata*:

> "As in *Donax* the six conical papillae of the inhalant orifice bend very slightly outwards, and do not serve to strain the inhalant water stream".

Preliminary observations on *D. denticulatus* and *D. striatus* showed that the siphons were different from those in *D. vittatus* and *E. radiata* and represented much more nearly the conditions which exist in the siphonate suspension-feeders such as *Mya*. This account is therefore a description of the form and function of the siphons in the two species.

As previously described, the siphons of *D. denticulatus* and *D. striatus* are held flush with the surface of the sand when the animal is buried and there is no movement of any sort to exploit the substratum for bottom deposits. Water is drawn in passively through the inhalant siphon, the orifice of which is lined by forty-eight sensitive tentacles comprising six primaries, six secondaries, twelve tertiaries, and twenty-four quaternaries (Figure 40A). Unlike D. vittatus and E. radiata in which the lips of the aperture are curled back exposing the opening, the tentacles in D. denticulatus and D. striatus bend over the opening of the inhalant siphon to form an intricate straining device (Figure 40B & C) so that particles above a certain size are prevented from passing through.

In order to determine the effectiveness of the tentacles, the diameters of the largest sand grains found in the mantle cavity of two groups of actively feeding clams in which the tentacles had been (a) left intact, and (b) removed were measured and it was found that in those with tentacles, the average maximum size of the grains was 246 µ while in those without, the average maximum size was 456 µ. That is, when the tentacles were removed, the size of the particles which passed through the siphons was almost twice as much as when they were left intact, and in one instance, particles as large as 700 µ were admitted into the mantle cavity.

The exhalant siphon bears only six conical papillae which are held upright and which therefore have no straining function.

Yonge (1949a) found that associated with the need for indiscriminate intake of food into the mantle cavity was the fact that the siphons of the Tellinacea in general were very

Figure 40

A: The arrangement of the tentacles around the inhalant aperture of the inhalant siphon of D. denticulatus and D. striatus.

B: A whole mount of a primary tentacle of the inhalant siphon of D. denticulatus. Note numerous papillae.

C: The inhalant aperture of the inhalant siphon of D. denticulatus. Note numerous straining tentacles.

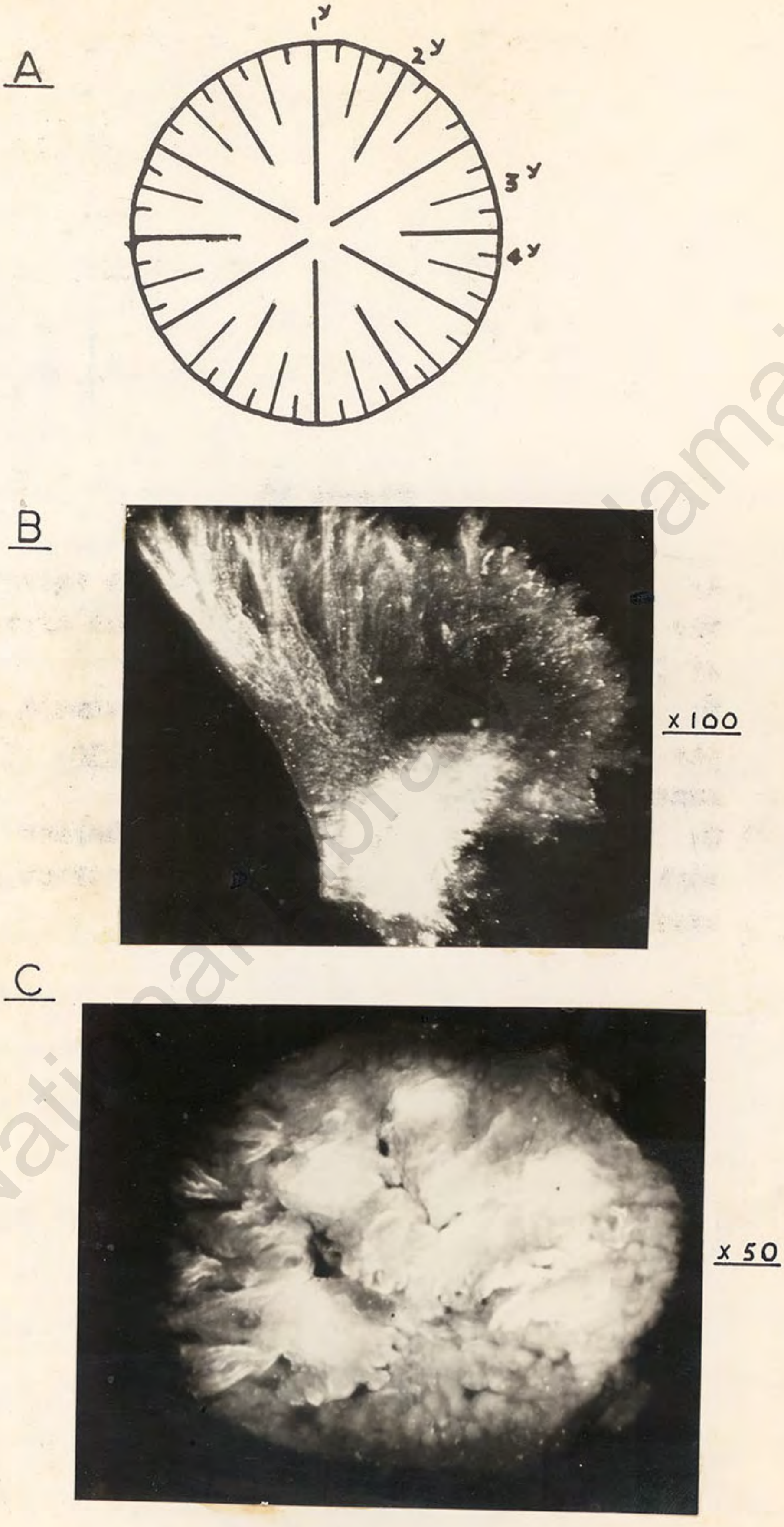

Figure 40

insensitive, and noted in particular that in D. vittatus:

> "The tentacles have no sieving action and the siphon shows little sensitivity".

Purchon (1963) reported a similar condition in E. radiata:

> "Also as in Donax, the siphons are comparatively insensitive to mechanical disturbances".

In D. denticulatus and D. striatus, it has been found that the inhalant siphon is quite sensitive, and necessarily so because of its straining function. When the siphon is extruded to the surface, the tentacles bend over to touch one another so that there is very little free space between them. Particles suspended in the water which are too large to pass through are strained off on the outer surfaces of the tentacles and are got rid of by the siphon constricting its aperture and partly retracting. As the particles fall off, the siphon extends itself again and reopens its aperture so as to resume feeding. Occasionally something very large or a heavy accumulation of sand may rest on the tentacles, in which case the clearing is more violent and consists of a rapid partial retraction of the siphon with a vigorous straightening up and bending outwards of the tentacles so that the rejected material is literally thrown off. If this occurs too often both siphons may retract completely so that feeding is temporarily suspended, and in extreme cases, even the foot may be withdrawn for a short time.

Rawitz (1892), Graham (1934b), Yonge (1949a), and Chapman and Newell (1956) have studied in detail the morphology and physiology of the siphons of several members of the

Tellinacea and have found that they all possess the same basic features though differing in detail. Yonge described and figured the appearance in transverse section of the siphons of D. vittatus to which those of D. denticulatus and D. striatus agree[1] (Figure 41A), but did not investigate the functional morphology of the tentacles presumably on account of their apparent lack of function. Because, however, they do have an important sieving function in D. denticulatus and D. striatus and show a high degree of sensitivity, they have been examined in this study in some detail as is now described.

Transverse sections were cut 10 to 15 μ thick from the base of the inhalant siphon to the tip of the tentacles from which permanent preparations were made with Eosin-Haematoxylin and Mallory stains.

For the greater part of the length of the siphons the structure is the same and comprises an outer epithelium with a thin cuticle, four circular layers of collagen fibres, three layers of longitudinal muscle, several strands of radial muscle, haemocoeles, and an inner epithelium (Figure 41A). Six conspicuous nerves are seen in transverse section. At the base of the tentacles, the inner collagen layer and haemocoeles enlarge while the longitudinal nerves bend inwards and innervate the primary tentacles which are comprised mostly of loose connective tissue and blood spaces (Figure 41C). Further upwards (Figure 41D) the longitudinal muscles

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[1] Except that the layers which Yonge described as circular muscle are really collagen layers (Chapman and Newell, 1956).

Figure 41

A - F: Transverse sections at different levels through a part of the wall and a primary tentacle of the inhalant siphon of <u>D. denticulatus</u>.

OE - outer epithelium
$C_4$, $C_3$, $C_2$, $C_1$ - layers of collagen
$LM_3$, $LM_2$, $LM_1$ - layers of longitudinal muscle
H - haemocoel
R - radial muscle
N - nerve
IE - inner epithelium
CT - loose connective tissue
T - tentacle
CM - circular muscle
TRM - tentacular radial muscle

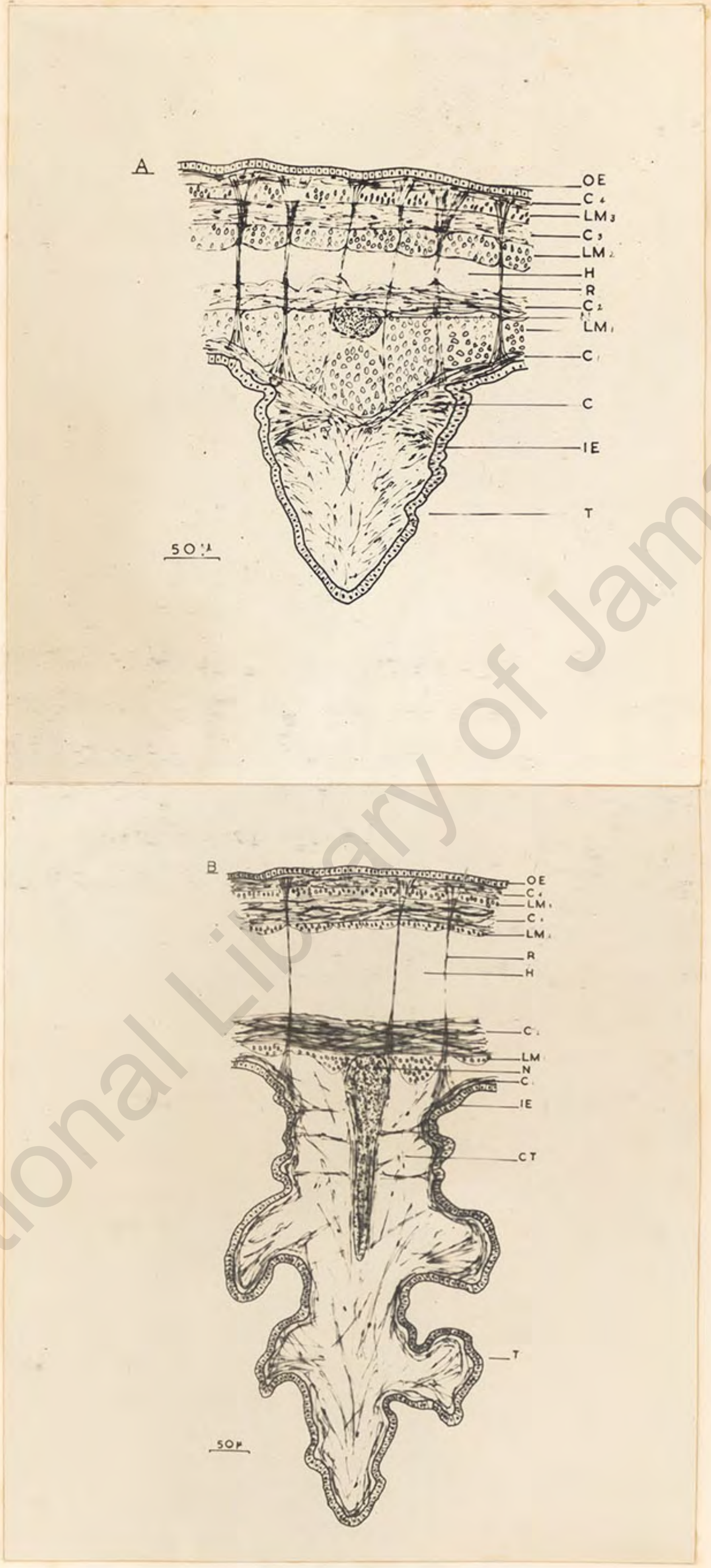
A
OE
C4
LM3
C3
LM2
H
R
C2
LM1
C1
C
IE
T
50µ
B
OE
C4
LM3
C3
LM2
R
H
C2
LM1
N
C1
IE
CT
T
50µ

Figure 41

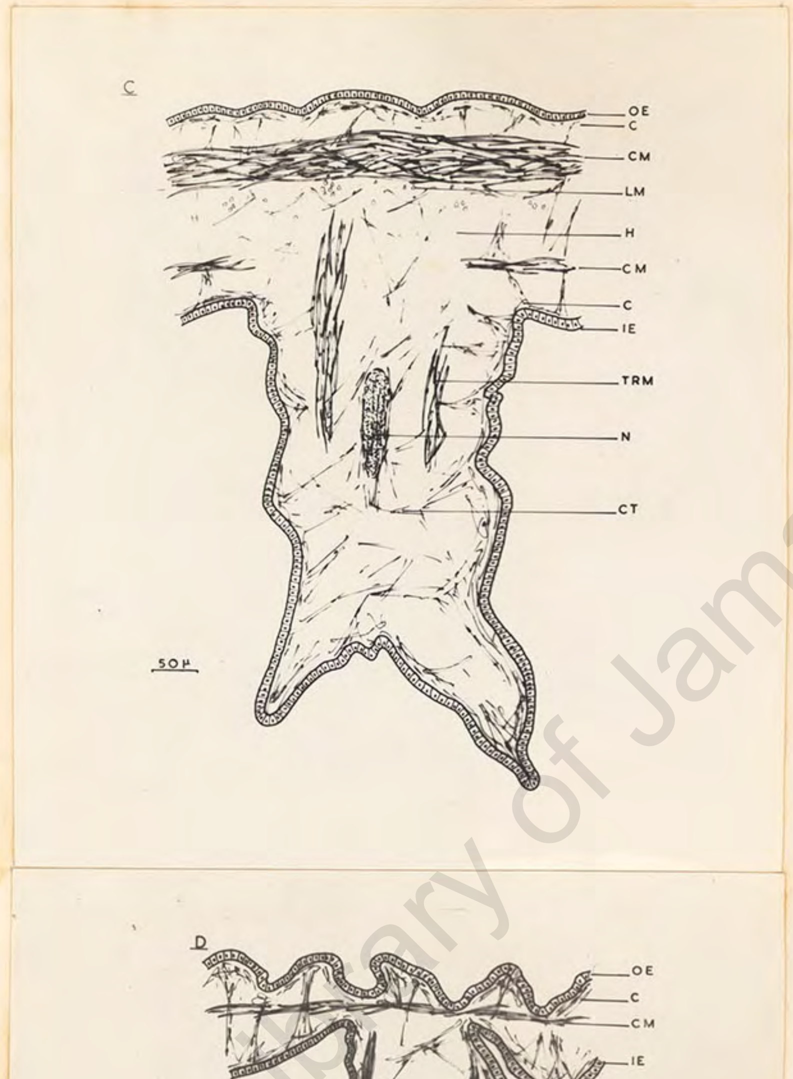

Figure 41

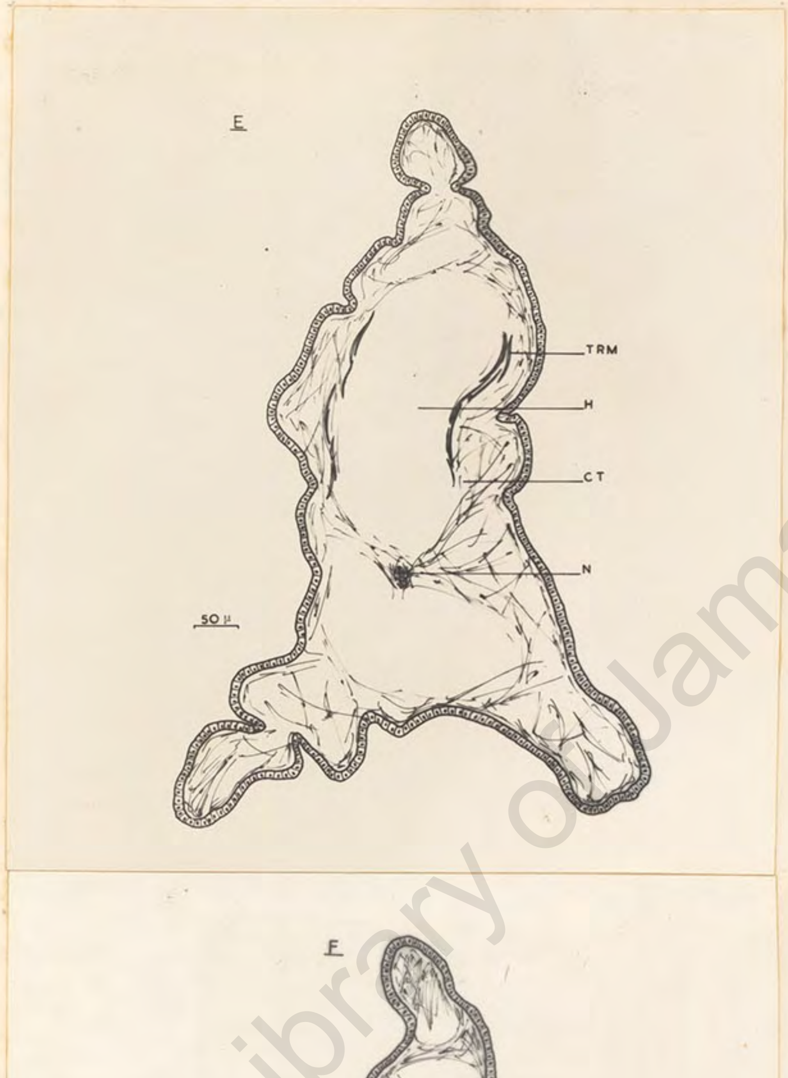

Figure 41

disappear altogether, the circular collagen layers are replaced by circular muscles, the radial muscles become enlarged and extend into the tentacles, and the blood spaces enlarge still further until they are almost completely continuous with one another. The main nerves gradually become smaller and disappear, while the connective tissue and radial muscles are reduced considerably so that the upper parts of the tentacles consist almost entirely of a haemocoel bounded by epithelium (Figure 41E and F).

In longitudinal section (Figure 42), the above features are clearly shown and give a good idea of the way in which structure and function may be related. First, the innervation of the primary tentacles is seen to be along almost their entire length and is further indication of the degree of sensitivity of the tentacles. The muscle bands which cause lengthening and shortening of the siphons are, as has been shown by Chapman and Newell (1956), the radials and longitudinals respectively. At the base of the tentacles, the thick layers of circular muscles perform an important function as constrictors and serve to reduce or close the aperture of the siphon when large particles are caught on the tentacles. These circular muscle layers have not been previously described for any other member of the Tellinacea, and this is not surprising since the constriction of the inhalant siphon has not been reported in any others. On the inside walls at the base of the tentacles and to a lesser extent along their lengths, thick beds of collagen

Figure 42

Longitudinal section of a part of the wall and a primary tentacle of the inhalant siphon of <u>D. denticulatus</u>. Lettering as in Figure 41.

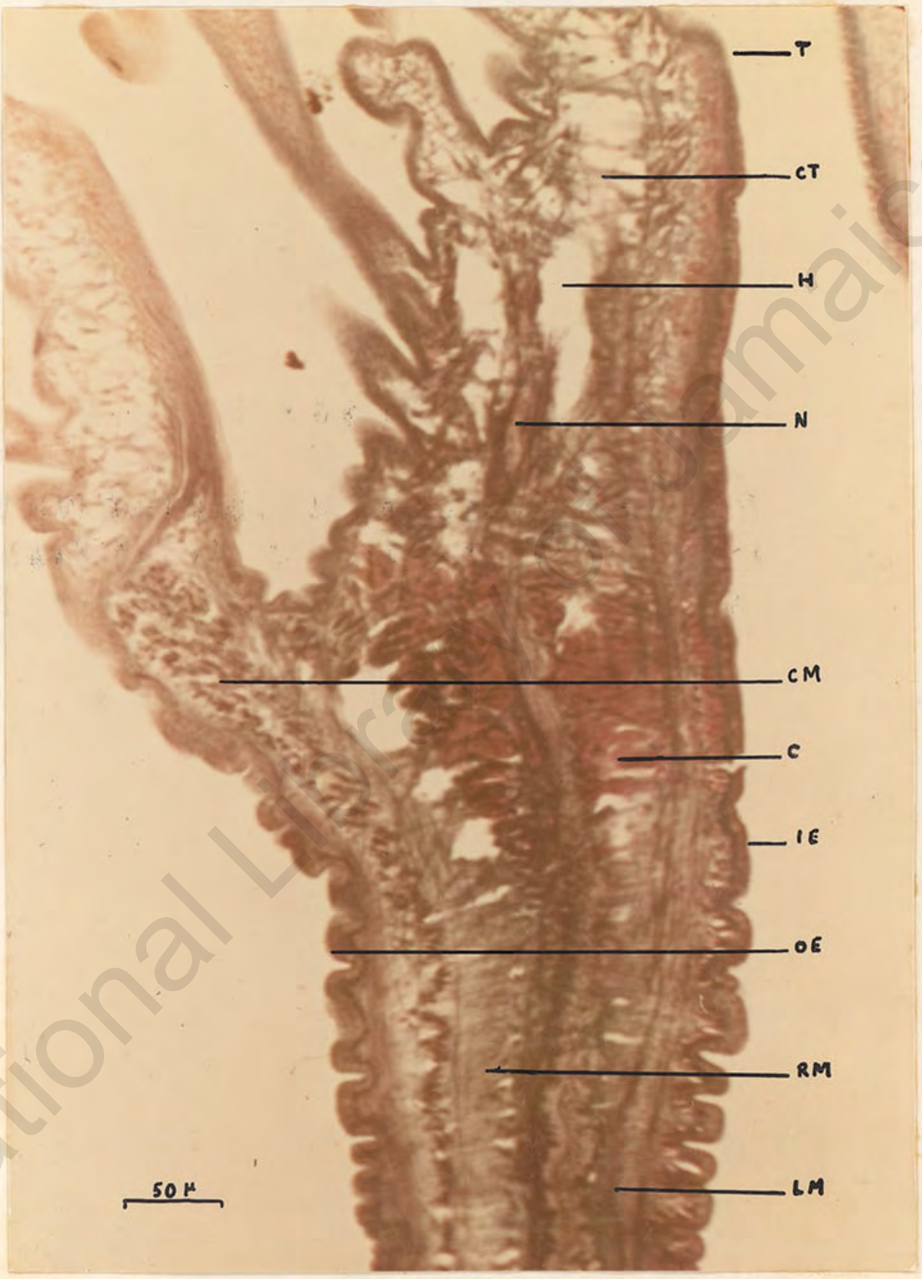

Figure 42

apparently serve as skeletal supports to prevent the tentacles from collapsing when blood is withdrawn on retraction of the siphons. Straightening up and bending backwards of the tentacles such as occasionally occur in rejection of particles is almost certainly the function of the tentacular radial muscles. Longitudinal contraction in the siphon only takes place as far up as the base of the tentacles since the longitudinal muscles do not extend into them.

The nervous supply of the tentacles has been given special attention in view of their importance as sensitive sieving structures. Sections both transverse and longitudinal were cut and stained with Schiff's reagent following Owen's (1959) modification of Liang's (1947) method (Appendix XIV). In transverse section (Figure 43A), the main nerves are seen to be joined together by nerve fibres with several branches supplying the tentacles. There is little innervation of the siphonal walls and there are no apparent sense organs in the outer or inner epithelia. (This agrees with observations of Rawitz (1892) and Yonge (1949a). In the primary tentacles, however, and to a lesser extent in the others the nerve fibres end in conspicuous nerve cells in the sub-epithelial connective tissue (Figure 43B), but as far as can be ascertained, these cells are not concerned with the reception of simple tactile stimuli since they do not send out sensory processes to the outer surfaces. They probably serve, however, as mechano-receptor units which respond to stimulation of the tentacles, and therefore do not need to be disposed on their outer surfaces (Gray, 1960; Alexandrowicz, 1960). In this

Figure 43

A: Transverse section through a part of the wall and primary, secondary, tertiary, and quaternary tentacles of the inhalant siphon of D. denticulatus. The nerve supply to each tentacle is shown.

B: Transverse section near the distal end of a primary tentacle of the inhalant siphon of D. denticulatus showing the nerve supply.

C: Longitudinal section through a primary tentacle of the inhalant siphon of D. denticulatus showing the nerve supply.

N - nerve
T - tentacle
H - haemocoel
CT - connective tissue
NC - nerve cell
TP - tentacular papilla

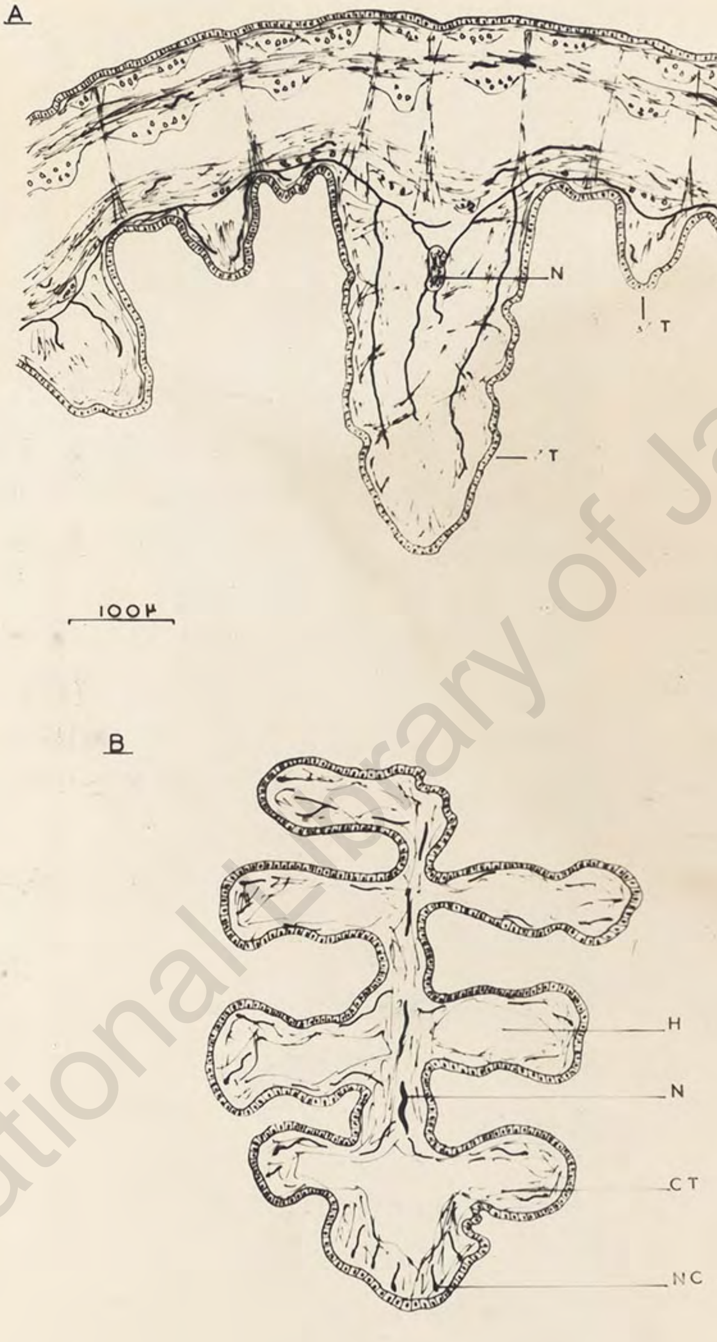

Figure 43

Figure 43

way they may perform essentially the same function as tactile receptors and may even be more sensitive to stimuli generated by large heavy particles. In longitudinal section (Figure 43C), the innervation of the tentacular papillae is seen and from which it can be perceived how pressure on the tentacles such as is caused by an accumulation of sand grains may be appreciated by the sub-epithelial nerve cell.

The nervous supply of the exhalant siphon is of the general pattern described by Rawitz (1892) and shows no special features. Epithelial sense organs are absent and there are no sub-epithelial nerve cells in the conical papillae. As a result, this siphon is less sensitive than the inhalant siphon.

From the above descriptions, it may be concluded that although the inhalant siphon in D. denticulatus and D. striatus is of the same basic structure as that in other members of the Tellinacea, it shows certain features (tentacles, sensory cells, musculature) which are associated with a suspension-feeding habit and which therefore make it significantly different in form and function. Hence its role in the feeding process is the passive intake of water with selective sorting of suspended particles, and not as in other genera of the Tellinacea, the active exploration of the sub-stratum with indiscriminate intake of bottom deposits.

### 3. Circulation of material in the mantle cavity

Figure 44 illustrates the organs in the mantle cavity of D. denticulatus after removal of the left shell

## Figure 44

D. denticulatus: The organs of the mantle cavity seen on removal of the left valve and most of the left mantle. The foot and siphons are retracted.

AD - anterior adductor muscle
AR - anterior retractor muscle
LP - left labial palp
EP - elevator pedis muscle
ID - inner demibranch
OD - outer demibranch
V - ventricle
HG - hind gut
PR - posterior retractor muscle
PA - posterior adductor muscle
ES - exhalant siphon
IS - inhalant siphon
SR - siphonal retractor muscle
VM - visceral mass
M - mantle
F - foot

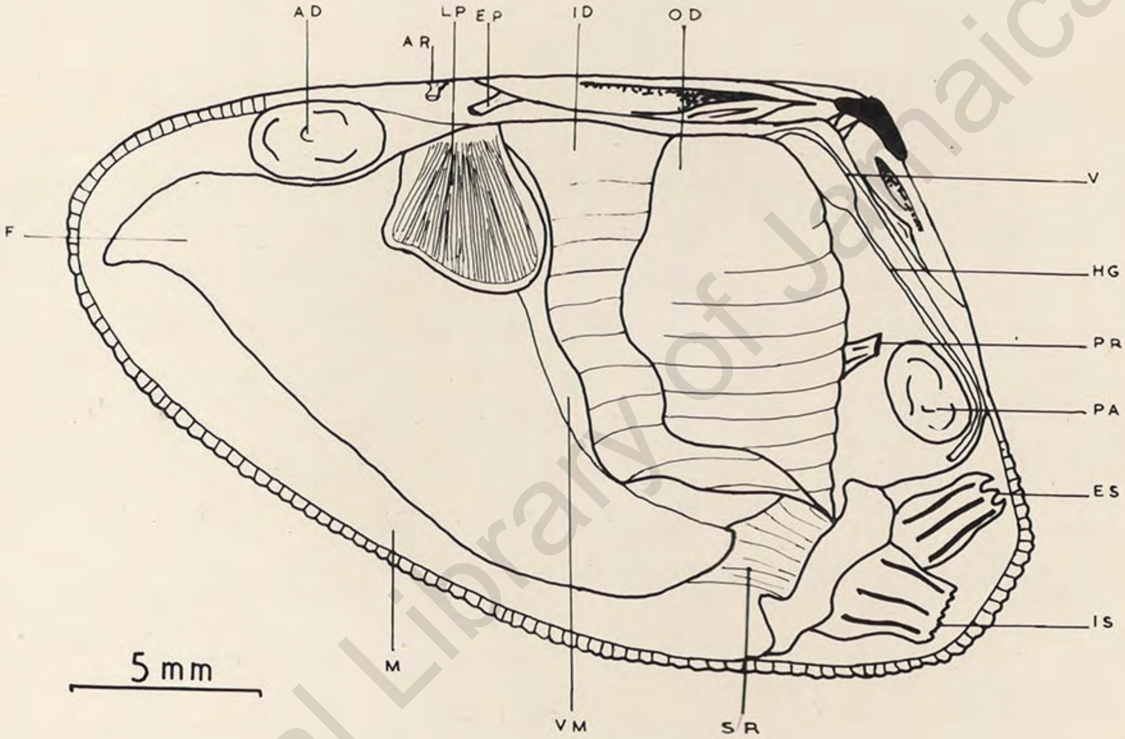

Figure 44

and most of the left mantle lobe. The siphons and foot are retracted.

When food-laden water is drawn into the mantle cavity through the inhalant siphon, the finer particles are caught up in the water currents on the ctenidia while the larger particles fall on the ventral margins of the mantle. Atkins (1937) and Yonge (1949a) have described the form of the ctenidia and labial palps in D. vittatus and the general course of currents upon them, and although those in D. denticulatus are basically the same, there are important differences, the significance of which are here considered.

Each ctenidium consists of two demibranchs of which the inner is deeper than the outer (Figure 45). Both are heterorhabdic and therefore plicate, eight or nine plicae being on the outer demibranch and eleven or twelve on the inner. On both faces of the inner demibranch are currents which are directed towards the marginal groove in which food material is transported oralward, while on the outer demibranch the main currents are towards the margin on the outer face and towards the ctedenial axis on the inner face. In the ctedenial axis is a second oralward current which carries material upwards and forwards towards the labial palps. Extending forwards between the bases of the inner and outer labial palps is a triangular area of the inner demibranch which is non-plicate. On the opposed faces of the labial palps are strong currents which are directed obliquely away from the oral groove and which therefore serve as rejection currents. The predominant and possibly the only acceptance

Figure 45

The main currents on the ctenidia and labial palps of <u>D. denticulatus</u>.

ILP - inner labial palp
OLP - outer labial palp
OG - oral groove
TA - non-plicate part of inner demibranch
ID - inner demibranch
OD - outer demibranch
CA - ctenidial axis

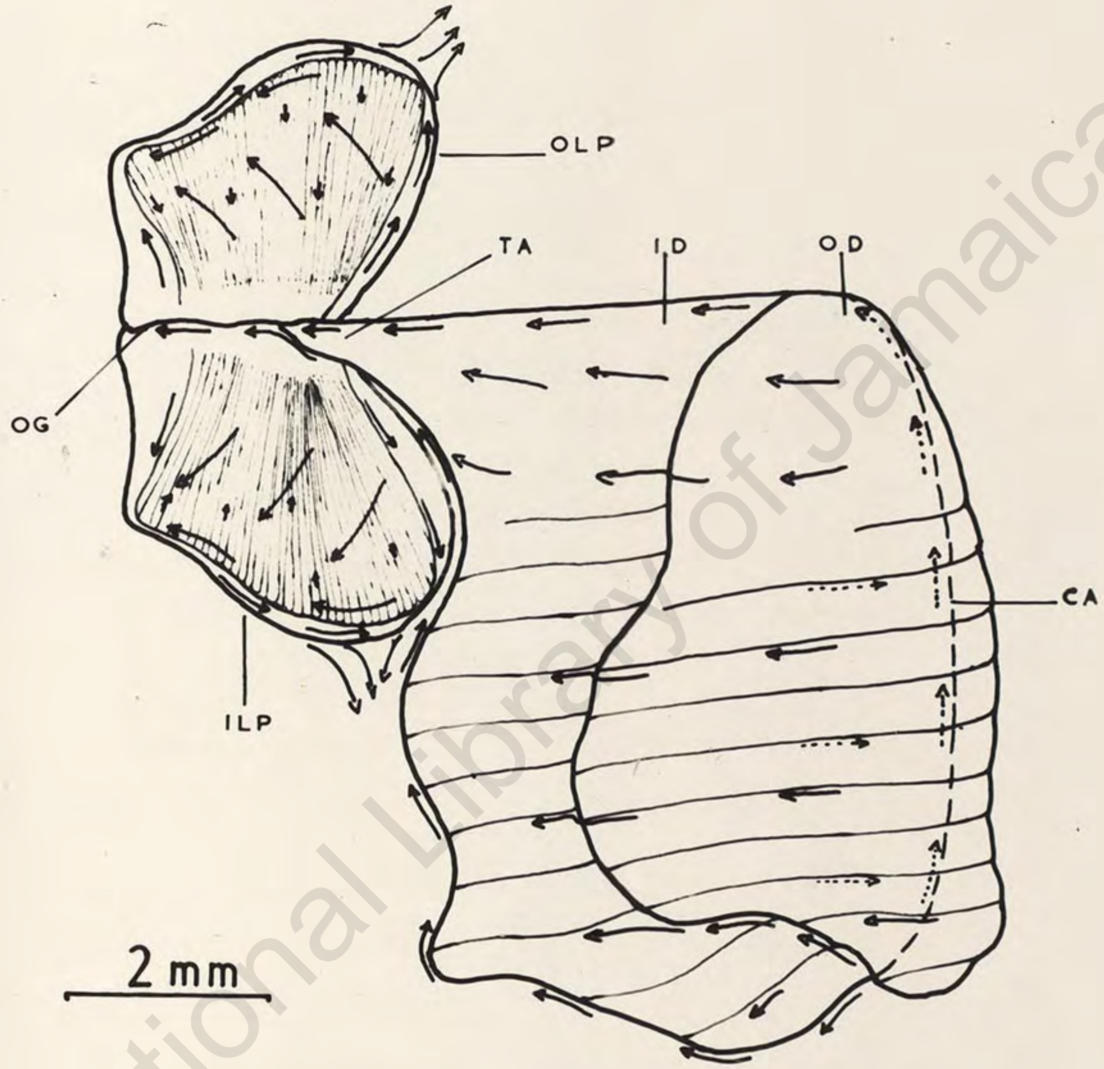

Figure 45

tract is in the oral groove, although very weak oralward currents may sometimes be detected between the folds.

The ctenedia and palps in D. striatus are similar to those in D. denticulatus except that there are only three or four plicae on the inner demibranch and none on the outer.

The arrangement in D. denticulatus and D. striatus differ from that in D. vittatus in the following respects. In the first two the demibranchs are wholly or partly heterorhabdic while in D. vittatus they are completely homorhabdic. The significance of this is not clear and cannot be related either to habitat or nature of food since even in D. denticulatus and D. striatus in which habitat and food are similar the filaments are different.

Yonge (1949a) has figured the main currents on the labial palps of D. vittatus and has shown them to be directed transversely across the folds of the palps towards the oral groove. (The folds are arranged parallel to the oral groove). In D. denticulatus and D. striatus, however, the main currents are directed away from the oral groove and diagonally across the folds which are arranged at right angles to the oral groove. Hence, unlike the currents in D. vittatus, these are rejection currents and determine that the labial palps in D. denticulatus and D. striatus perform the function of a guarding and not a guiding organ.

Attention has been drawn by Yonge (1949a) to the inverse relationship between the size of the palps and that of the ctenidia in the Tellinacea and he has concluded that;

"In general the palps tend to be large when the gills are small . . ."

With regards to the palps in D. vittatus, Yonge reported:

"The palps are very small and the gills relatively large . . ." In both shape and size, however, the labial palps of D. denticulatus and D. striatus differ from those in D. vittatus and appear to be significant in respect of differences in habitat. Those in D. vittatus are triangular and are approximately one-fifth the total area of the gills (Estimated from Yonge's drawing) while in D. denticulatus and D. striatus they are laminar and nearly one-third the area of the gills. According to Yonge, there is a tendency for the palps to be larger in those species in which much very fine material is taken into the mantle cavity, and since D. denticulatus and D. striatus filter water which is usually more turbid than that taken in by D. vittatus, this occurrence of the larger palps in these two species would seem to fit into the general pattern. Purchon (1963) arrived at the same conclusion regarding Egeria radiata:

"This river water presumably contains rather more suspended silt than the sea water filtered by Donax (meaning D. vittatus) and in Egeria the labial palps are comparatively large and efficient sorting organs".

The general impression gained on comparison of the gills and palps of D. denticulatus and D. striatus with those of D. vittatus is that these organs in the first two species are better adapted than those in D. vittatus for life on sandy beaches where, because of constant wave action, there is always much finely particulate material suspended in the water.

Particulate material that is rejected by the ctenidia and labial palps is removed from the vicinity of these organs by ciliary cleansing currents on the visceral mass and mantle lobes. The currents on the visceral mass are directed antero-ventrally except in the region of the labial palps where they are directed postero-ventrally (Figure 46B). These latter are the strongest currents presumably on account of the great amount of material that is rejected by the palps.

The ciliary cleansing currents on the inner surface of the mantle are shown in Figure 46A. They are directed postero-ventrally over a wide area although there are important antero-ventralward currents adjacent to the region of the ctenidia. The strongest currents are, as on the visceral mass, in the vicinity of the labial palps where anterior and posterior currents converge. From here rejection currents follow a definite tract ventralwards around and below the siphonal retractor muscles and backwards towards the base of the inhalant siphon where pseudofaeces accumulate. Yonge (1949a) found that in D. vittatus the pseudofaeces actually accumulate within the base of the siphon, but this has not been observed in D. denticulatus and D. striatus.

### 4. Removal of material from the mantle cavity

A. Disposal of pseudofaeces: As the rejected material is carried along by the rejection currents on the mantle, it becomes entangled in a copious secretion of mucus so that

Figure 46

D. denticulatus: The ciliary cleansing currents on the mantle (A), and visceral mass (B).

ES - exhalant siphon
IS - inhalant siphon
PF - pseudofaeces
SR - siphonal retractor muscle
RT - rejection tract
VM - visceral mass
F - foot

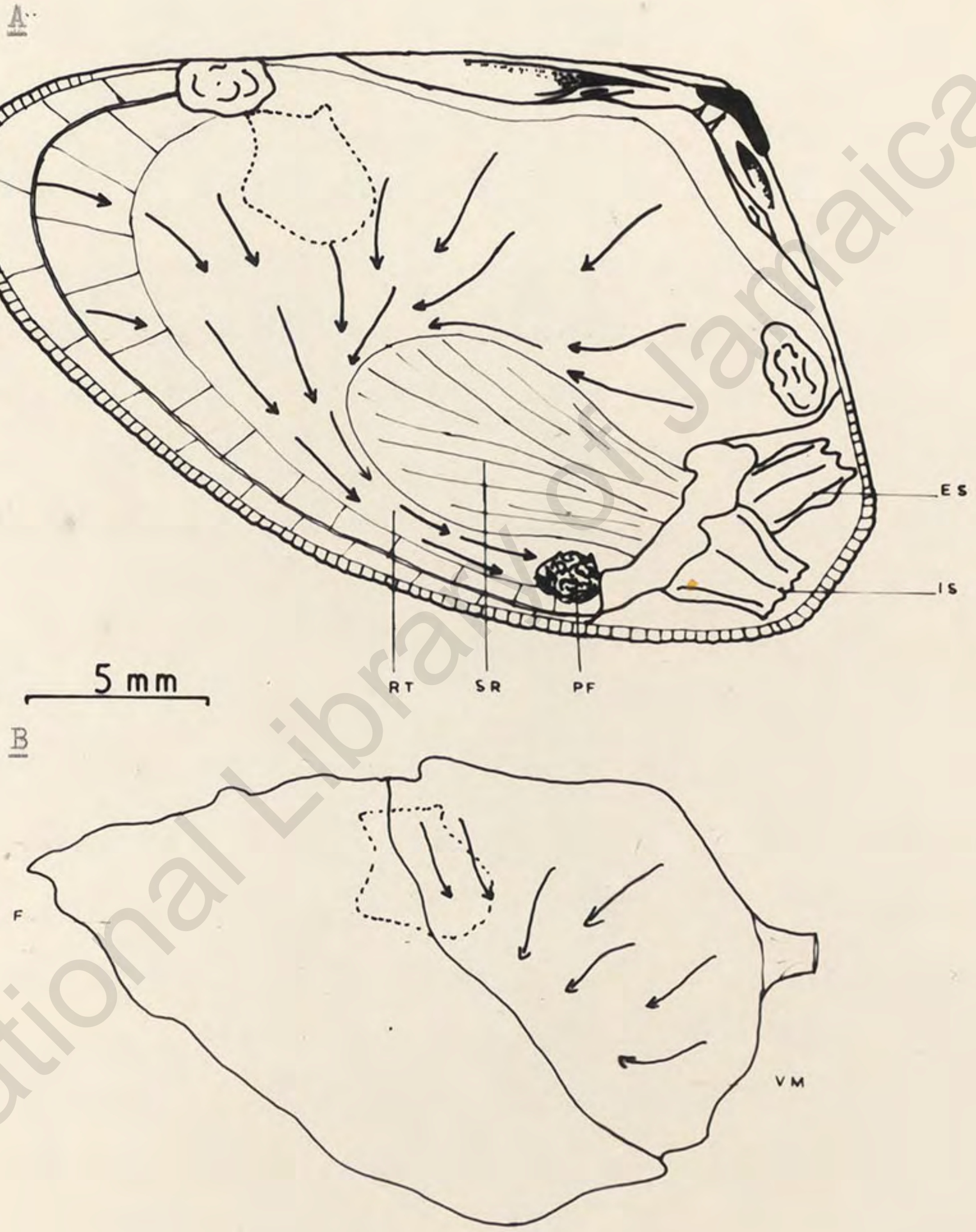

Figure 46

the pseudofaeces formed appear as a compact rounded mass at the base of the inhalant siphon. When a sufficient quantity has accumulated, it is rapidly ejected through the inhalant siphon in a strong current of water by a sudden contraction of the animal and closure of the exhalant siphon. This action may be so powerful as to eject the pseudofaeces as much as five centimetres away from the animal.

The rate of disposal of pseudofaeces depends on the amount of unwanted material that is taken into the mantle cavity. Generally, however, it is approximately once every half a minute when the animals are feeding actively on the beach. In experiments in which the tentacles of the inhalant siphon were removed, it was noticeable that the rate of disposal of pseudofaeces increased considerably because of the greater amount of sand grains admitted into the mantle cavity.

B. Defaecation: The anus opens just below the posterior adductor muscle near the internal aperture of the exhalant siphon. Defaecation is through this siphon and occurs inconspicuously while the animal is feeding. The faeces emerge as long threads of mucus-entangled waste and not as pellets as in some other members of the Tellinacea (Yonge 1949a). In one instance, a clam of length 18 mm. was observed to eject a faeces thread of more than 30 mm.

The disposal of faeces in mucus threads is apparently to prevent them from being stirred up into suspension in the sea water, and may therefore be regarded as an adaptation for life on the turbulent sandy beach.

## III. THE ALIMENTARY CANAL

The course of the alimentary canal in D. denticulatus and D. striatus is shown in Figure 47. In D. denticulatus the oesophagus is short and straight and passes backwards to enter the stomach on its anterior face. The stomach consists of two parts, namely a proximal globular region into which the oesophagus enters, and a distal style sac which extends ventrally through the visceral mass and into the base of the foot. Surrounding the globular region of the stomach is a mass of pale green digestive diverticula (Not shown in figure) which open into it by way of several ducts. The midgut arises from the right anterior wall of the globular region of the stomach and passes ventralwards through one and a half loose spirals to the bottom of the visceral mass. Here it loops upwards and ascends behind the style sac to the dorsal region of the visceral mass. The hindgut passes from the visceral mass through the pericardium and ventricle, back along the posterior margin of the mantle and around the posterior adductor muscle to terminate at the anus.

In D. striatus the course of the alimentary canal is more or less similar to that in D. denticulatus except in the way in which the midgut is coiled. Both, however, differ from D. vittatus, the only other species in which the alimentary canal has been studied (Graham, 1934b) especially in the form of

Figure 47

The course of the alimentary canal in
A, <u>D. denticulatus</u>, and B, <u>D. striatus</u>.

M - mouth
O - oesophagus
PRS - proximal region of stomach
SS - style sac (distal region of stomach)
MG - mid gut
V - ventricle
HG - hind gut
A - anus

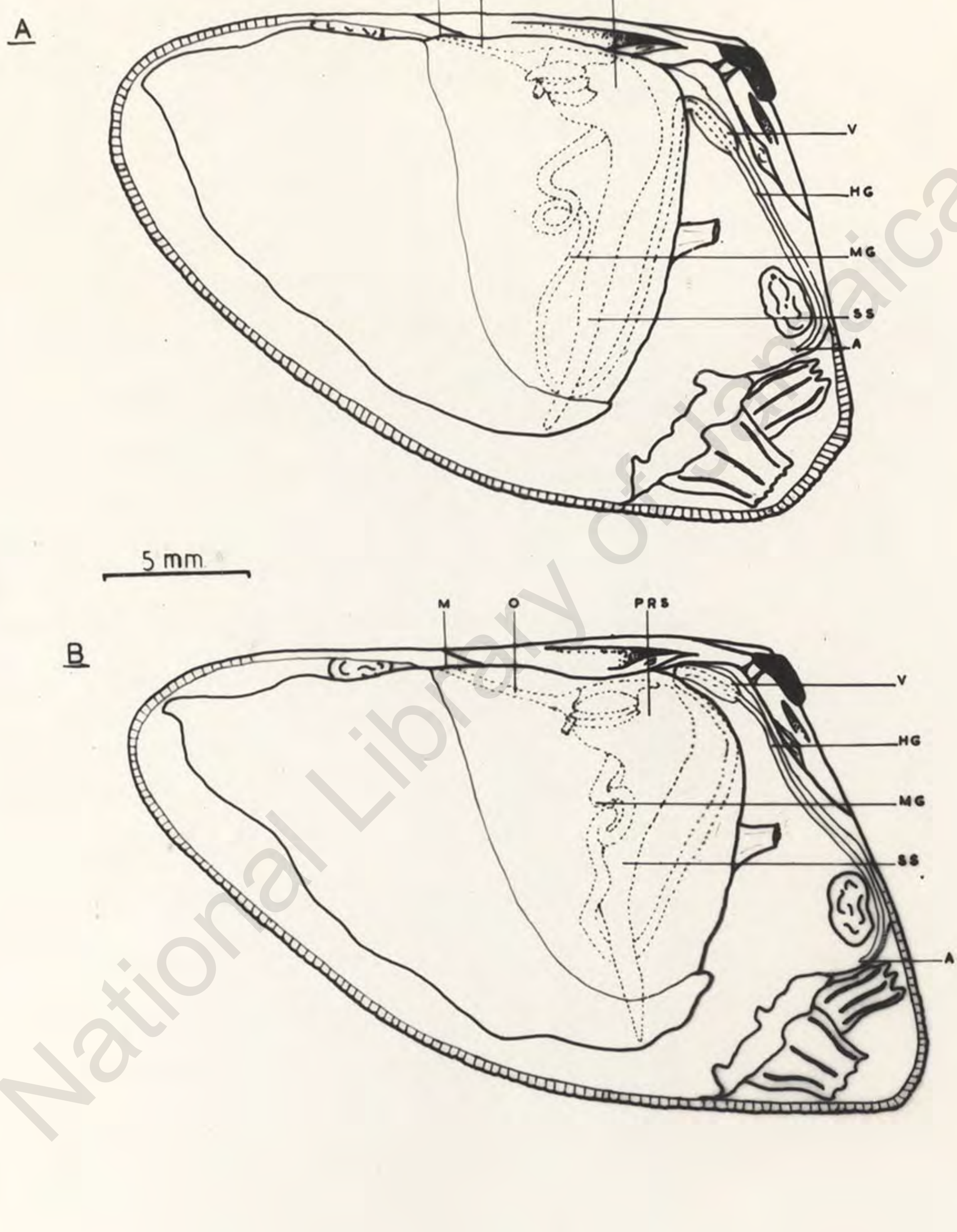

Figure 47

the stomach.

Yonge (1949a) briefly considered the structure of the stomach of D. vittatus in his account of the deposit-feeding characteristics of the Tellinacea, and Purchon (1960) figured and described the stomach of D. faba (Gmelin) in a review of the stomach types found in the Eulamellibranchiata. Since, however, the structure and functioning of this organ is important in indicating the evolution of the feeding habit in the genus and previously has not been fully investigated, opportunity was taken in this study to make a detailed examination of it in D. denticulatus and D. striatus.

Throughout the examination both live and fixed specimens were dissected in various stages of feeding. Fixation was done in 4% Formalin in sea water. In dissecting fresh specimens it was found that the wall of the stomach tended to be very soft and prone to damage on removal of the surrounding tissues, and on dissecting the entire stomach free, it became twisted and distorted. In fixed specimens, however, the tissues of the stomach were more resistant and it was possible to remove surrounding tissues and dissect the stomach free without much damage. As a result, the greater part of the dissections were done on fixed specimens although all structures and some of the living processes were eventually observed in fresh specimens.

The stomach as mentioned previously consists of a proximal globular region (PRS) and a distal style sac (SS) (Figure 47). The latter in an animal of shell length 20 mm. is about 8 mm. long and 1 mm. wide at its upper end. Within

Figure 48

*D. denticulatus*: Proximal stomach from A, left, and B, right sides.

O - oesophagus
DH - dorsal hood
LP - left pouch
PC - postero-dorsal caecum
SS - style sac
MG - mid gut
LD - left duct of diverticulum
PSA - posterior sorting area
RD - right duct of diverticulum

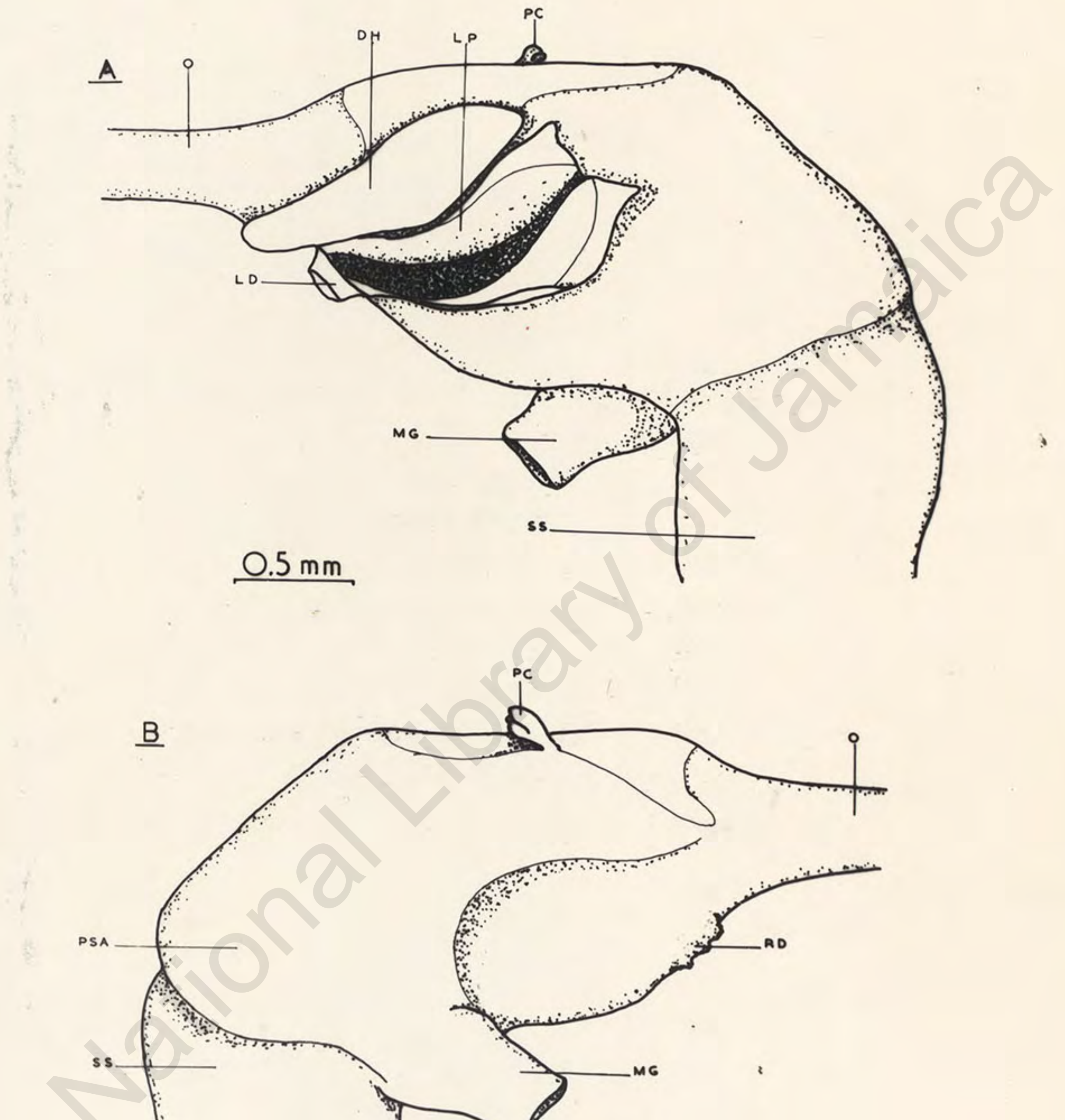

Figure 48

Figure 49

__D. denticulatus__: Anterior view of proximal region of stomach.

PC - postero-dorsal caecum
O - oesophagus
DH - dorsal hood
LP - left pouch
LC - left caecum
LD - left duct of diverticulum
SS - style sac
MG - mid gut
PSA - posterior sorting area
RD - right duct of diverticulum

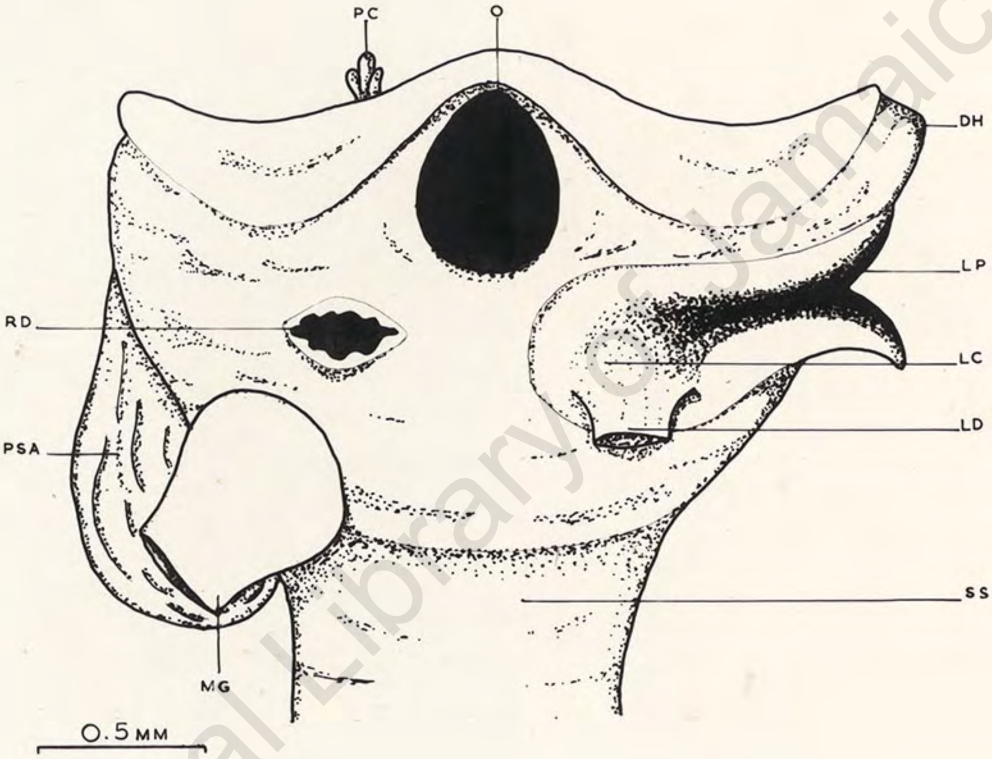

Figure 49

Figure 50

D. denticulatus: Stomach opened from right side showing A, curved crystalline style in proximal region of stomach, and B, partial encirclement of crystalline style by gastric shield.

CS - crystalline style
T - tongue of style
GS - gastric shield
GST - tooth of gastric shield

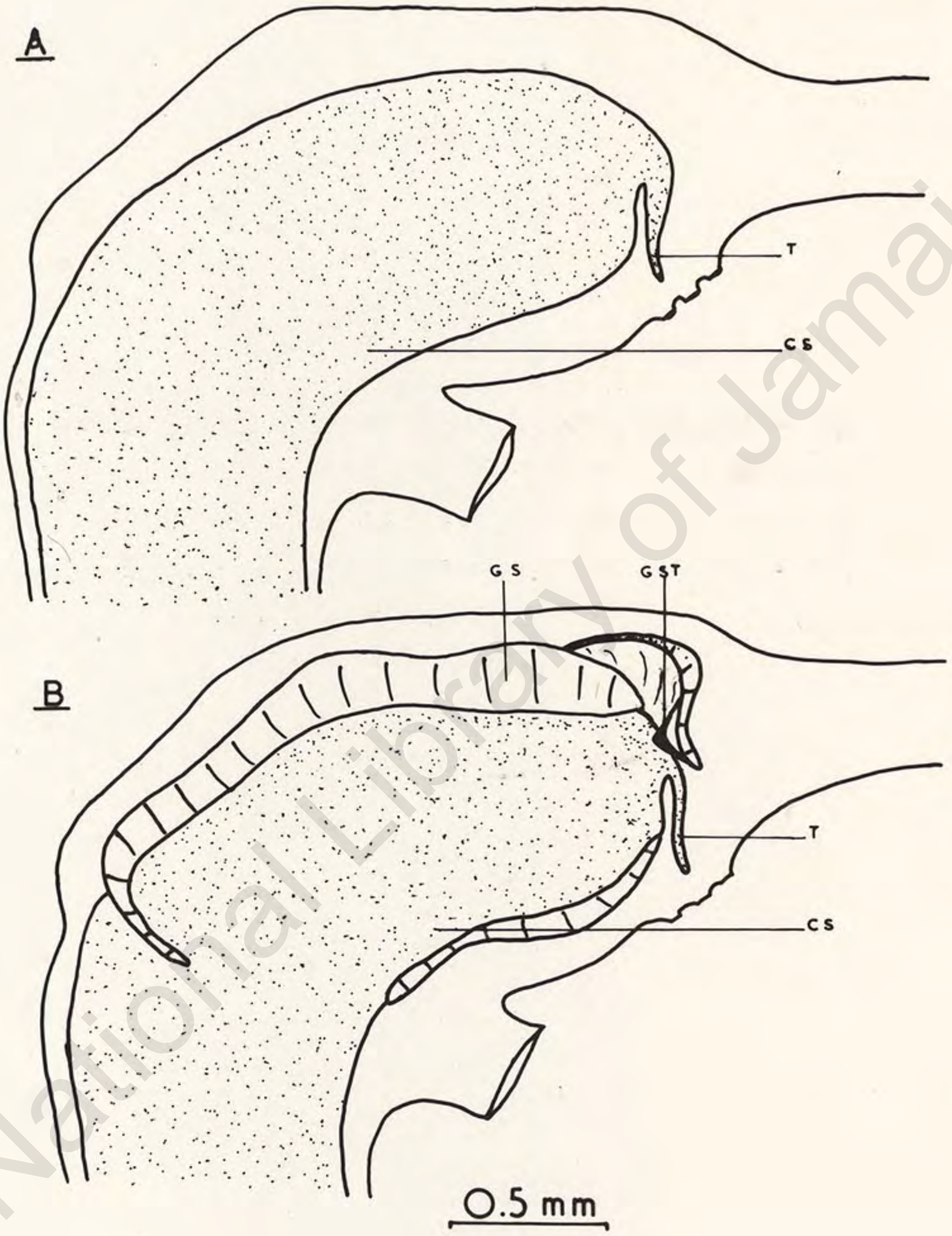

Figure 50

Figure 51

*D. denticulatus*: Gastric shield drawn A, anteroventrally after removal from stomach, and B, anteriorly in situ.

GST - tooth of gastric shield
DWG - groove of dorsal wing
DW - dorsal wing
VW - ventral wing
VWG - groove of ventral wing
GSF - gastric shield fold
DH - dorsal hood
LP - left pouch
T - tongue of crystalline style
CS - crystalline style

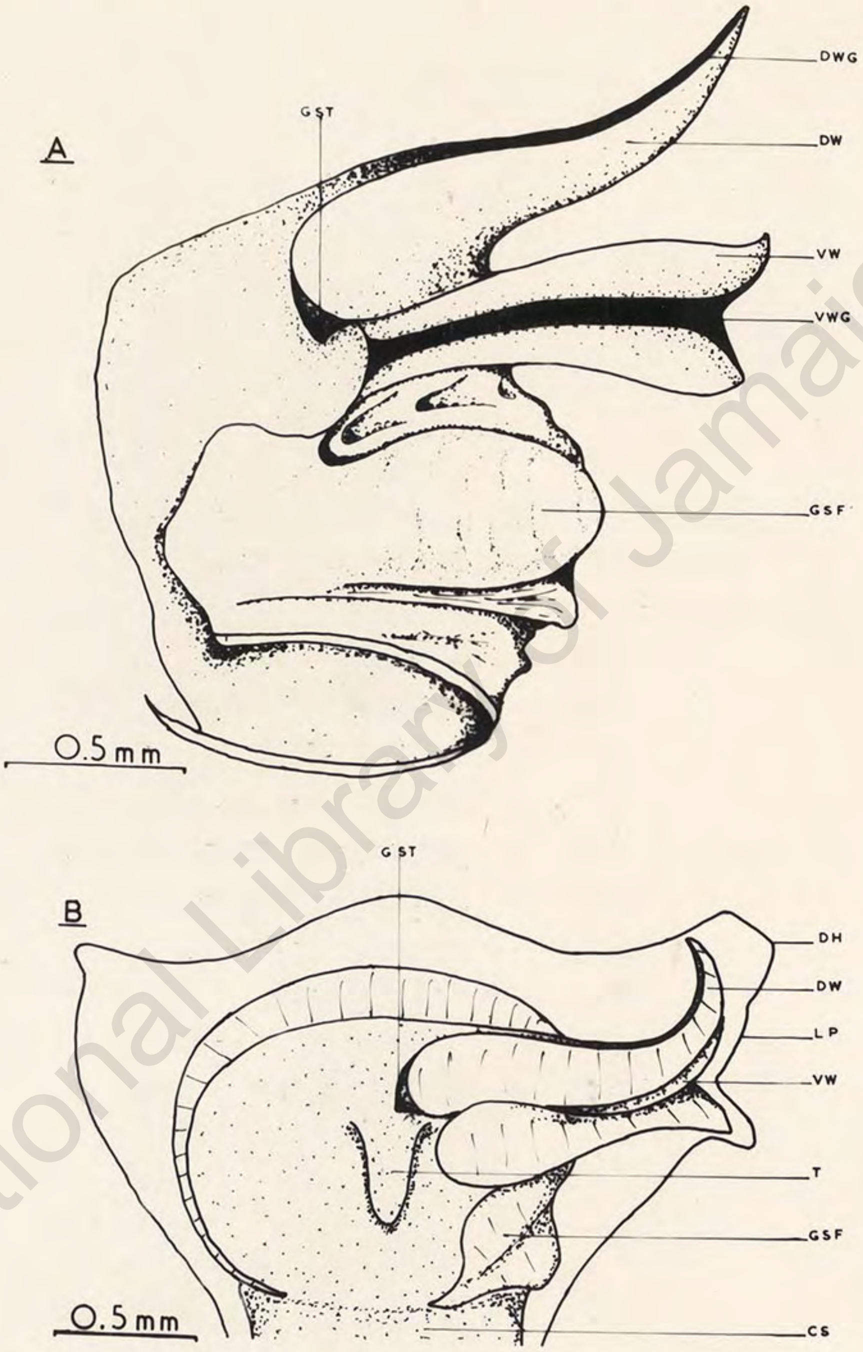

Figure 51

Figure 52

*D. denticulatus*: Interior wall of stomach drawn after opening by a mid-dorsal incision and removing the gastric shield.

LP - left pouch
DH - dorsal hood
LC - left caecum
LD - left duct of diverticulum
O - oesophagus
R - ridge
TY - typhlosole
RD - right duct of diverticulum
IG - intestinal groove
MG - midgut
PSA - posterior sorting area
SS - style sac

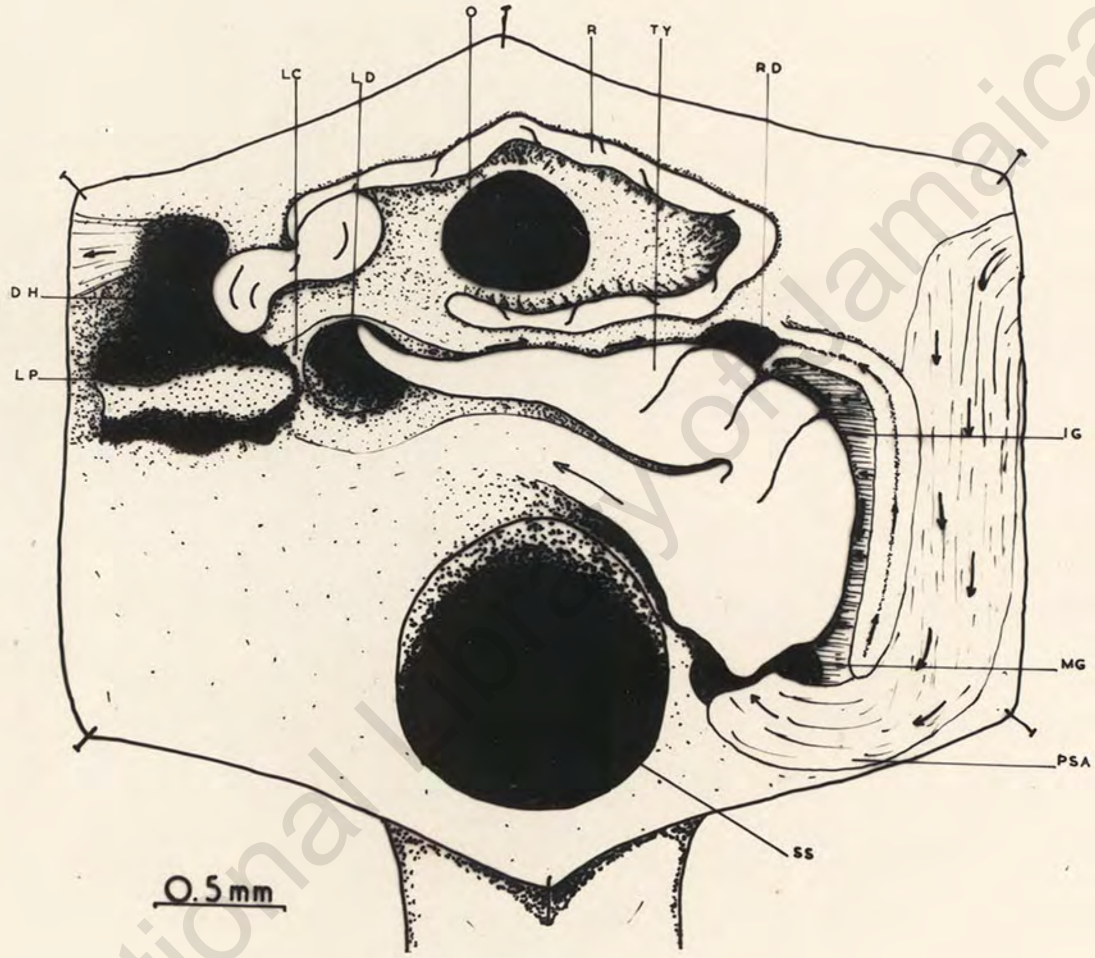

Figure 52

it is contained the crystalline style (CS) which is straight for most of its length but is curved through an angle of nearly ninety degrees within the proximal stomach (Figure 50A & B). This curved condition is unusual among the Tellinacea[1] although Yonge (1949a) described it as a characteristic feature of the suspension-feeding Eulamellibranchiata. Near its anterior end in the proximal stomach, the crystalline style constricts to form a flexible tongue (T), the presence of which is also unusual in the Tellinacea.

Within the proximal stomach the crystalline style is largely surrounded by the cuticular gastric shield (GS). As shown in Figures 50 and 51, this shield entirely covers the left side of the head of the style and also extends for some distance around the postero-lateral wall on the right side. Arising from its anterior surface are two prominent wing-like extensions which curve around sharply to the left wall of the stomach (Figure 51A & B). The upper or dorsal wing (DW) has a deep but narrow groove (DWG) and bears at its proximal end a very conspicuous tooth (GST) which impinges on the head of the crystalline style at the base of the flexible tongue (T). The lower or ventral wing (VW) differs from the dorsal wing in that it has a much wider and shallower groove (VWG), and does not bear a tooth. Below the ventral wing is a deep fold which originates on the left dorsal side of the shield and which runs forwards and

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[1] The only other member of the Tellinacea in which the crystalline style is known to be curved within the proximal stomach is the fresh water Donacid, <u>Egeria radiata</u> (Lamarck) (Purchon, 1963).

downwards and then to the right to open out in the mid ventral region of the shield. This is the gastric shield fold (GSF).

The oesophagus (O) enters the stomach anteriorly near the dorsal surface and immediately above the tooth of the gastric shield (Figures 48 & 49). Partly surrounding the opening of the oesophagus is a marked ridge (R) which apparently prevents food entering the stomach from passing down its antero-ventral wall. On the left dorsal wall of the stomach is the dorsal hood (DH) into which the dorsal wing of the gastric shield fits. Below the dorsal hood is the capacious left pouch (LP) into which fits the ventral wing of the gastric shield. The left pouch extends forwards into a shallow left caecum (LC) on the left anterior wall of the stomach. On the right side of the stomach in the postero-ventral region is a second capacious pouch designated by Graham (1949) the posterior sorting area (PSA).

Arising from the right postero-dorsal wall of the stomach is a small lobular appendix, the postero-dorsal caecum (PC) (Figures 48 & 49). In D. denticulatus this consists of three or four small lobes about 0.3 mm. long, while in D. striatus it is a little larger. In D. denticulatus in both the full and empty stomachs examined, this caecum was the same in size and shape and contained no particles. In D. striatus the caecum contained a few sand grains. Yonge (1949a) points out that in the members of the Tellinacea he examined, the postero-dorsal caecum was very elastic and varied greatly in size depending on the amount of food in the stomach. In his note on the postero-dorsal caecum of

D. vittatus, however, he mentioned that in all the specimens he examined it was very small although he added that the animals had previously been starved. Purchon (1960) described the postero-dorsal caecum of D. faba as being long, cylindrical, and thin walled.

The digestive diverticula form a dense mass of pale green tubules around the stomach and open into it on the right and left anterior walls midway between the oesophagus and midgut (Figure 49). On the right side the diverticula open into the stomach by two or three ducts which join very near to the wall of the stomach to form a single large orifice (RD), while on the left side the diverticulum opens into the stomach in the region of the left caecum by a single large duct (LD).

Originating in the left caecum is a well developed typhlosole (TY) which arches over the intestinal groove (IG) which accompanies it throughout its course (Figure 52). On leaving the left caecum, this typhlosole passes transversely across the anterior wall of the stomach before curving sharply and passing down towards and into the midgut.

Food passing from the oesophagus into the stomach becomes entangled in mucus strings on the flexible tongue of the style. As the style rotates the mucus strings are drawn into the lumen of the stomach and come to lie between the style and shield, this mechanism thus acting as an efficient device for regulating a steady stream of food into the stomach. With the rotation of the style, food taken in under the gastric shield is subject to mixing and stirring. Yonge

(1949a) has stated that in so doing coarse particles are brought under the grinding influence of the style and shield especially in the region of the teeth, but this does not occur in D. denticulatus and D. striatus as evidence below shows. What happens instead is that with the clockwise rotation of the style, particles are carried towards the dorsal wing of the shield and into the narrow groove up towards the dorsal hood. Because of the size of the groove only the smaller particles can enter and the coarser particles are thus forced to continue in their clockwise direction into the gastric shield fold from which they pass out ventrally. It is possible that from here some of them may once more be drawn between the style and shield although it seems more likely that the majority pass directly by way of the intestinal groove out of the stomach into the midgut. In this process it would appear that the gastric shield performs a crude sorting function which has not previously been attributed to it.

Yonge (1949a) in his consideration of the role of the gastric shield in the Tellinacea has attributed its development to the need for a fairly rigid surface on which the style can grind. He points out that in the suspension feeders such as Mya in which there is no need for a triturating stomach, the shield is not greatly developed. To substantiate his view of the triturating function of the Tellinacea stomach, Yonge measured the diameters of the largest sand grains found in the stomach and midgut of Tellina tenuis (daCosta) and found that these measurements were in the ratio of 4:1. From this he concluded that the sand grains must have been ground down within the stomach and specifically between the style and shield. When similar measurements were made in this study of the sand grains in the stomach and midgut of D. denticulatus and D. striatus, however, it was found that they were in the ratio of 1:1. The largest roughly rounded particles in the stomach of an animal of shell length 20 mm. had diameters of no more than 160 µ.

From this it is clear that the stomach in D. denticulatus and D. striatus does not perform a triturating function and we must therefore seek another explanation for the presence of such an elaborate and extensive gastric shield. The probable explanation is that with the evolution of the deposit-feeding habit in the Tellinacea the gastric shield did develop as a grinding surface, but then with a subsequent change to a suspension-feeding habit and the loss of the need for a triturating stomach, the shield lost this function and assumed the new role of a sorting device although at the same time retaining its essential features.

When an animal is feeding actively food particles which are conveyed to the dorsal hood are passed into the left pouch until ready for use. They are then carried forwards by ciliary action into the left caecum where sorting takes place and then into the digestive diverticula by way of the ducts. Rejected particles and waste matter from the diverticula are swept along in the intestinal groove towards the midgut and out of the stomach (Figure 52). In so doing they are prevented from mixing with the general contents of the stomach by the well developed typhlosole.

When the stomach is very full and the left pouch apparently cannot contain any more particles, food material is stored in the pouch at the posterior sorting area. Sorting takes place on the ridges and grooves of the wall and rejected material passes directly into the midgut. The accepted material is carried upwards and forwards in a deep ciliated groove towards and into the orifice of the ducts of the right diverticula.

The significance of certain features of the stomach must now be considered. Firstly, it has been pointed out that the curvature of the crystalline style within the proximal stomach is unusual in the Tellinacea. Because it is curved in D. denticulatus and D. striatus the great efficiency with which the style rotates in other Tellinacea is lost and the condition becomes much like that which exists in the typical suspension feeders. Furthermore because of the resulting curvature of the proximal stomach, that which corresponds to the posterior wall in other Tellinacea now becomes the dorsal wall, a condition which is also similar to that found in the typical suspension feeders (Figure 53).

The role of the gastric shield has already been discussed and evidence put forward to show that with the loss of the deposit-feeding habit in Donax, it has lost its triturating function.

The food pouches in Donax are larger than in other members of the Tellinacea and are more suitable for dealing with smaller particles. The postero-dorsal caecum is also

Figure 53

Semi-diagrammatical drawings of stomachs, viewed from right side of A, *Mya arenaria* (as type of suspension-feeding eulamellibranch) ; B, *Donax denticulatus*; C, *Tellina tenuis* (as type of deposit-feeding eulamellibranch). A and C after Yonge (1949a).

CS - crystalline style
GST - tooth of gastric shield
DH - dorsal hood
PC - postero-dorsal caecum

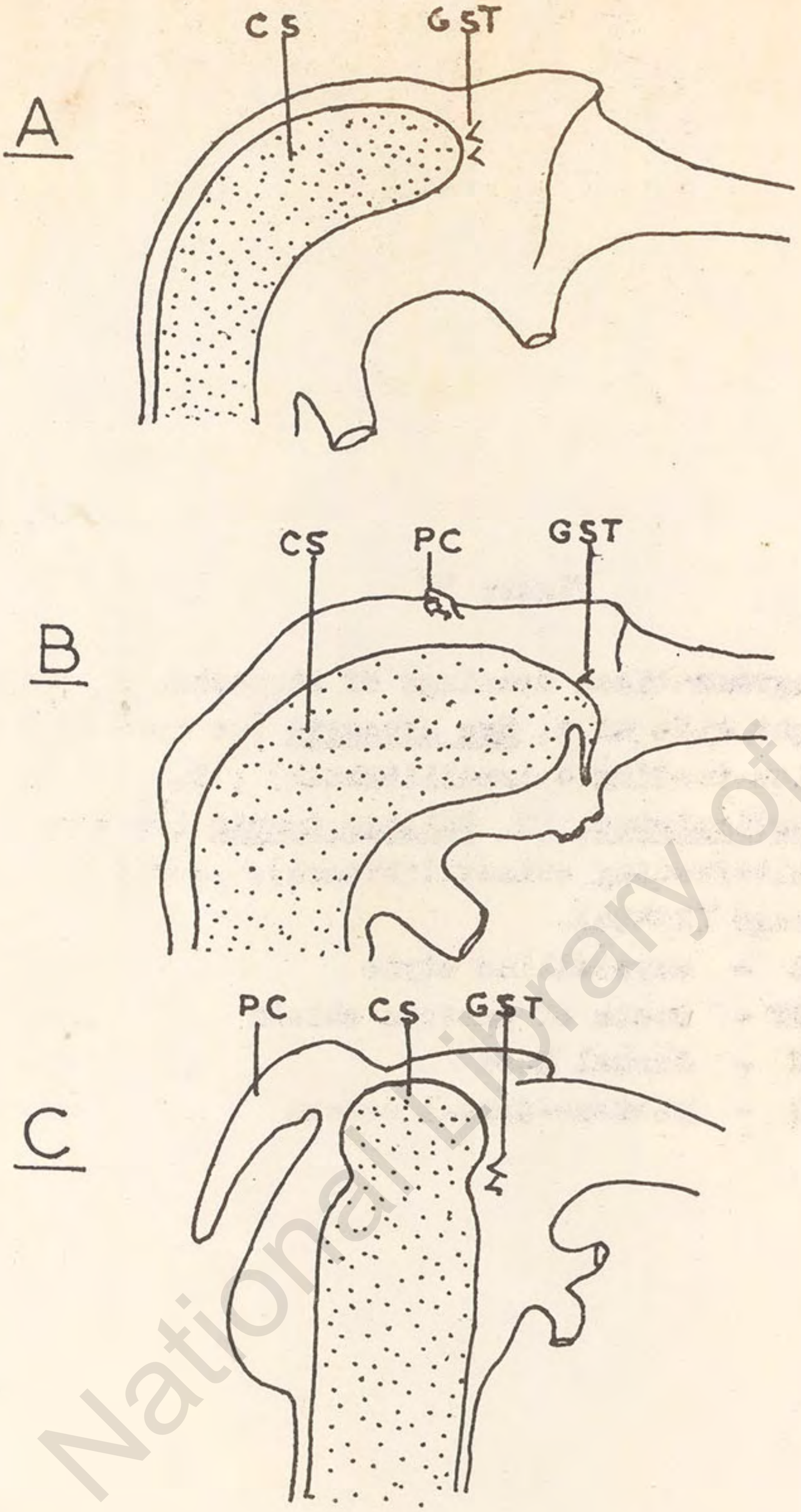

Figure 53

smaller and less elastic and in D. denticulatus never contains any sand grains. It therefore seems to have lost its function as a safety valve preventing blockage of the proximal region of the stomach by too great an influx of large particles.

Because of all the above considerations it must be concluded that although the stomach of D. denticulatus and D. striatus possesses the basic structures of the stomach of the deposit-feeding Tellinacea, it is similar in many respects to those in the typical suspension feeders and appears to be better adapted for a suspension-feeding habit.

## IV. FOOD MATERIALS

Coe (1955) reported that the diet of D. gouldi included:

> " . . . small diatoms, dinoflagellates, bacteria, minute ova of invertebrates, spermatozoa, and a large proportion of detritus derived from the disintegration of animal and plant cells".

In order to determine the diet of D. denticulatus and D. striatus and the relative importance of each fraction of it, stomach and hindgut contents were examined microscopically as smears and counts made of the occurrence of each identifiable fraction. Initially, the contents of four monthly samples (January, April, July, October) of clams of D. denticulatus were examined to determine the occurrence of possible detectable seasonal differences, but when it was found that there were none, further samples were then examined at random. Table 26 shows the results of counts made of the material seen in sixty such smears of stomach and hindgut contents.

The stomach contents were found to be comprised of the following:

(1) Detritus: Most of the material in the stomach is made up of accumulations of dead or decaying organic matter adhered together as irregular particles of

TABLE 26:- The occurrence of materials in the stomach and hindgut of <u>D. denticulatus</u> as counted in sixty smears.

| Material | Stomach | Hindgut |
|---|---|---|
| Detritus | 391 | - |
| Phytoplankton | 173 | 5 |
| Dinoflagellates | 11 | 0 |
| Invertebrate eggs | 7 | 0 |
| Spines and spicules | 120 | 46 |
| Sand grains | 45 | 121 |

detritus. These vary greatly in size but are nevertheless with the exception of sand grains larger than all other particles. Detritus is almost certainly the major fraction of the food material of <u>D. denticulatus</u> and <u>D. striatus</u>.

(2) Phytoplankton: This is the second most abundant material in the stomach and is comprised mostly of diatoms. Examination of hindgut contents showed that only the largest and hardiest diatoms pass through the stomach without being digested.

(3) Dinoflagellates: In sixty smears only eleven dinoflagellates were seen and appear therefore to be of little significance as food.

(4) Invertebrate eggs: Only a few eggs were seen in the stomach and only in clams collected between October and January. This is at the time when the clams themselves spawn actively and may mean that they simply ingest some of their own eggs. The importance of these eggs as a food fraction is difficult to assess.

(5) Spines and spicules: Calcareous and siliceous spines and spicules are common in the stomach and hindgut but are of no apparent food value.

(6) Sand grains: Despite the efficiency of the gills and palps, some sand grains enter the stomach but they pass through to the gut without being changed in any way.

The rate of passage of material through the alimentary canal is very rapid. When adults were placed in carmine-suspension water and allowed to feed actively, they were observed to pass faeces with carmine particles after only thirty minutes.

## V. SUMMARY

In summary it may be said that *D. denticulatus* and *D. striatus*, although possessing the basic morphological features of the deposit-feeding Tellinacea, are better adapted for feeding on suspended material than on bottom deposits.

The intake of food takes place passively through the inhalant siphon and there is selective rejection of large particles by the sensitive tentacles of the inhalant aperture. The rate of water intake may exceed 300 cc. per hour, but this is reduced with an increase in the amount of suspended material in the water.

The inhalant siphon is specialised in respect of the structure and nervous supply of the tentacles. In the distal region of the siphon are layers of circular muscle which constrict the aperture, and in the tentacles are radial muscles which bend the tentacles outwards when they contract. Innervating the primary tentacles are the six main nerves of the siphon and in the sub-epithelial connective tissue of the tentacles are possible mechanoreceptor nerve cells which respond to stimulation of the tentacles.

The organs of the mantle cavity are adapted for dealing with much finely particulate material. The labial palps in particular are increased in size and efficiency and serve as important rejection organs.

The alimentary canal is unusual among the Tellinacea because of the structure of the stomach. The crystalline style is curved within the proximal stomach and constricts at its anterior end into a flexible tongue. The gastric shield is extensive but does not have the crystalline style working against it to perform a triturating function. There are two large food pouches in the proximal stomach which are well adapted for dealing with small particles, and the postero-dorsal caecum which evolved within the Tellinacea for dealing with large particles is reduced in size and function.

The major part of the diet of the clams is comprised of organic detritus and phytoplankton, but other organic materials in suspension may also be taken in and digested.