Some Observations on Living Animals of
Dentalium entalis L.

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Scaphopods are benthic marine molluscs, which are adapted to burrow in wet, shelly sand of medium to coarse grade.

The food, method of feeding and gut contents are described; the significance of burrowing movements and water currents generated in the mantle cavity are discussed in relation to feeding processes.

Living animals have been examined in the past by various workers interested in the kind of food, method of feeding, gut contents, burrowing cycle and water currents produced through the mantle cavity.

The particular concern of this account is with feeding, so that attention has been directed to the kind of food eaten, and how it is obtained. This necessitates some consideration of the burrowing habit and associated ciliary currents.

Observations and Discussion

Examination of gut contents

The animals studied were obtained from Skate Island at a depth of approximately 30-40 metres. The nature of the food taken was determined by examination of the gut contents.

D. entalis is specialized to feed on hard microbenthos such as foraminiferans (Clark 1849) a view supported by Morton (1959). Dinamani (1963) who studied *D. conspicuum* proposed that they may be ciliary deposit feeders and that the chief article of food of members of this species could be diatoms, algal cells and detritus.

Morton (1959) stated that *D. entalis* is chiefly a selective feeder on foraminifera. Examination of gut contents here confirms the intake of foraminifera. Living animals

were opened and their gut contents were examined within 3-6 hr after being dredged from their natural habitat. The contents of each region of the gut were examined under the microscope. In general only sand grains and forams were recognizable. The contents of the proboscis were examined after rinsing them out into a small petri dish. They showed living foraminiferans mixed with their empty shells and sand. Further back, especially in the stomach and intestine, examination of sections revealed only shell fragments among the sand grains.

When the entire gut of animals kept in capitivity for a month or more was macerated, the contents showed only sand containing fragments of foraminiferan shells mixed with drops of reddish brown pigment and isolated cells apparently animal in origin which could have been amoebocytes.

Foraminiferans from the proboscis of recently captured individuals were photographed. An attempt was made to identify them tentatively by reference to Murray's Atlas of British Recent Foraminiferids (1971). Plate 1 shows what appears to be *Elphidium,* Plate 2 may be *Quinqueloculina* and Plate 3 *Discorbis.* The first two genera corresponding with those observed by Morton (1959) in the same situation in both living and preserved specimens of *D. entalis.* Although foraminiferans constitute the only recognisable food, it must be borne in mind that animals may also be deriving nutriment from micro-organisms or organic matter associated with sand grains.
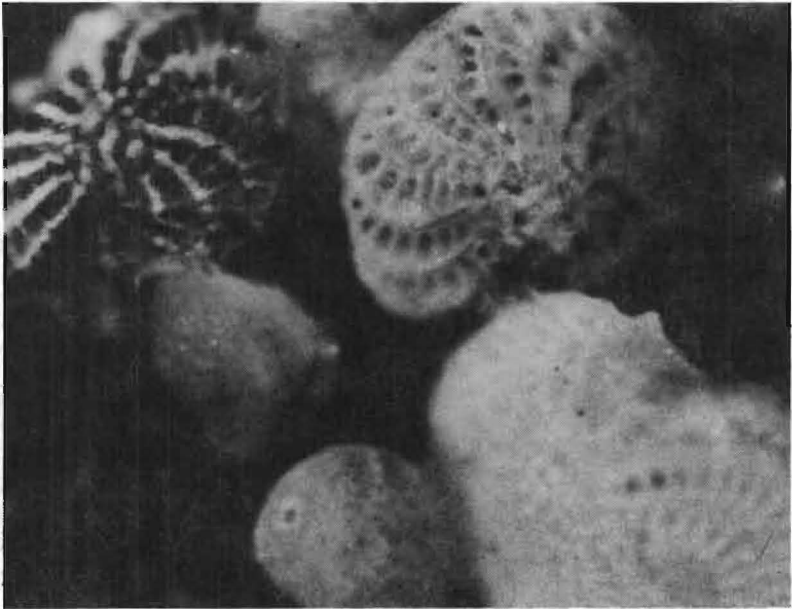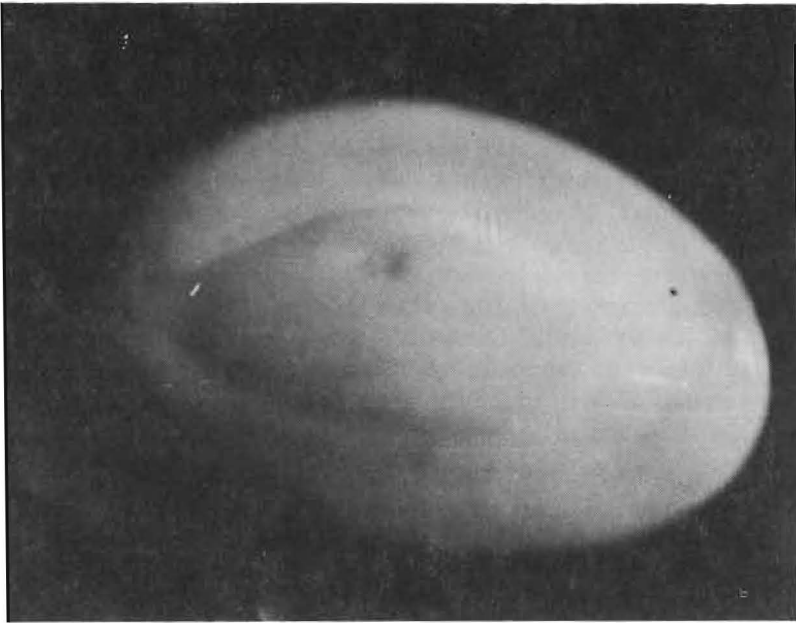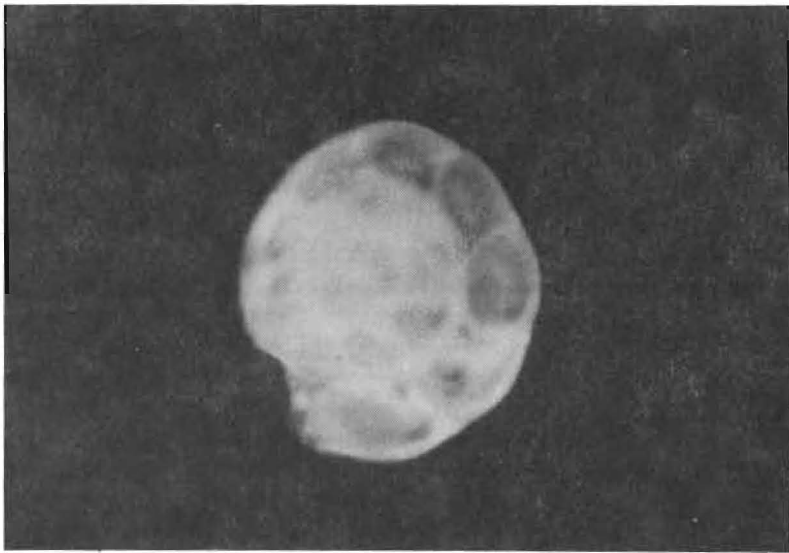

Plate 1

Plate 2

Plate 3

Plates 1, 2 & 3: Some of the contents of the proboscis (see P.130) The organisms appear to be *Elphidium,*
Plate 1, *Quinqueloculina,* **Plate 2, and** *Discorbis,* **Plate 3.**
Scales = 250 μ m, 195 μ m, and 190 μ m respectively.

Methods of gathering food

Feeding has been described in several species of *D. entalium* by various workers. Unhappily the accounts do not always agree even when applied to the same species. Accordingly it was re-examined here.

Essentially there are two methods of feeding by the captacula. Yonge (1937) working with *Dentalis* whilst acknowledging the part played by captacula, described the part played by the ciliary currents which also serve respiration (see later). On the other hand Morton (1959) working with the same species stated that the captacula formed the sole method of food gathering due to their expanded sticky lips, to which particles of substratum adhered. The particles were then transferred to the mouth by contraction of the captacula. Dinamani (1963) working with *D. conspicuum* described the transfer to the mouth of diatoms, algal cells and detritus along the captacula by means of cilia. All the above conducted their observations on animals which were not burrowing.

More recently, Gainey (1972) described food gathering in *D.psedohexagonum* and *D.eboreum* whilst the animals were buried. He showed that feeding involved the captacula in addition to the foot.

Gainey's observations were made on animals confined in special chambers and in view of his assertions concerning the importance of the foot, it was decided to make observations on *D.entalis* to see whether in this species also the foot was important. To do this chambers similar to these used by Gainey were employed, the animal being allowed to burrow in a thin layer of wet sand sandwiched between two glass plates. The sand was taken from the site at which the animals were dredged, it was irrigated by the sea water circulating through the laboratory but chilled by passage through sea water ice. The animals were observed by a low power stereoscopic microscope.

Activities of the foot

Scaphopodes are characteristically adapted to burrow in soft substrata leaving a small part of the posterior end of the shell exposed. Such a disposition is normally adapted by *D.entalis,* though this is not so in the case of *D.eboreum* as observed by Gainey (1972). The activities of the foot are therefore primarily concerned with burrowing.The size, highly muscular character and expanded epipodial lobes of the foot are related to this function as are the reduced head, short conical proboscis and tubular shell. The burrowing activities of the foot have received much attention, but are largely outside the scope of this account. They have been studied in detail by Morton (1959), Dinamani (1964), Trueman (1967) and Gainey (1972), but because of their possible significance in feeding some observations were made in order to verify the main tenets of their description.

Burrowing is achieved by the rhythmical extension and contraction of the tip (t.f., Fig.1) and epipodial lobes (e.l., Fig. 1). The following phases can be distinguished:
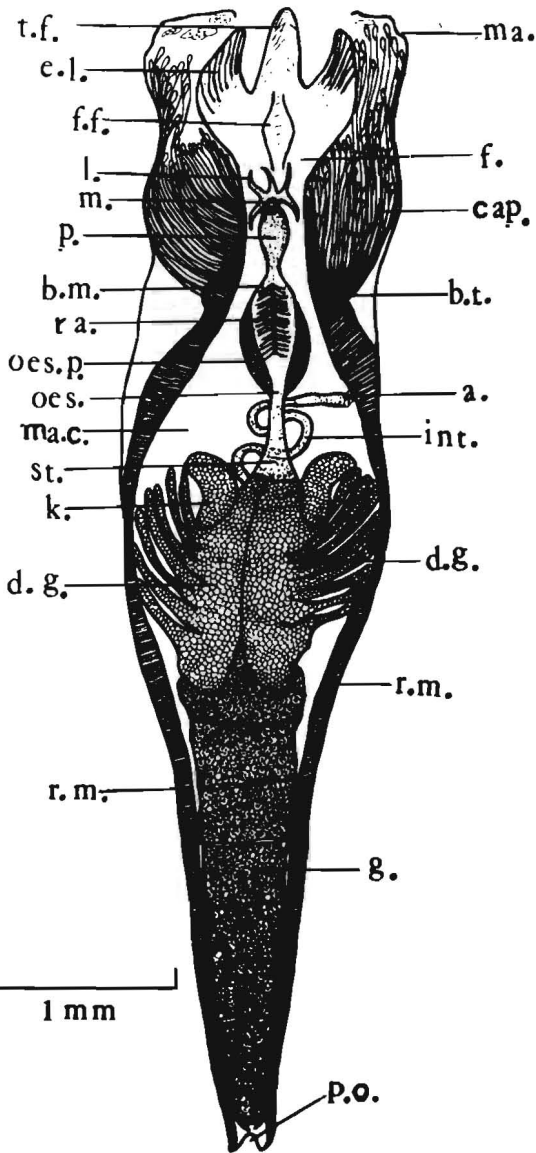
Fig. 1. The alimentary canal of *Dentalium entalis in situ,* seen from above.
a., anus; h.ma., buccal mass; b.t., a horse-like ride; cap., captacula; d.g., digestive gland; e.l., epipodial lobe; f., foot; F.F., foot furrow; g., gonad; int., intestine; k., kidney; 1., lip; m., mouth; ma., mantle; ma.c., mantle cavity; oes., oesophagus; oes.p., oesophageal pouch; p.o., posterior opening; pr.,proboscis; r.m., retracor muscles; ra., radula; st., stomach; t.F., tip of the foot.
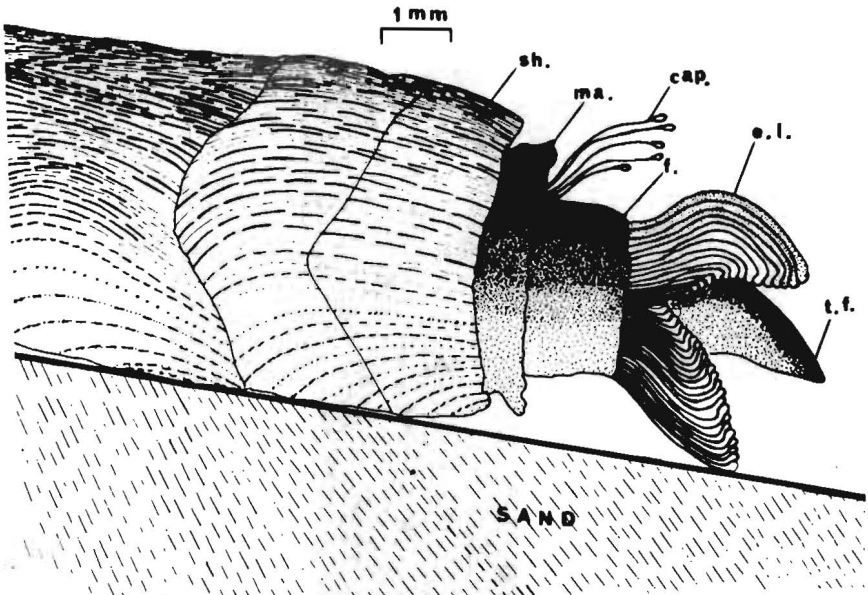
Fig. 2. Diagram illustrating the first stage in the burrowing process.
e.l., epipodial lobe; F., foot; ma., mantle; sh., shell; t.f., tip of the foot.
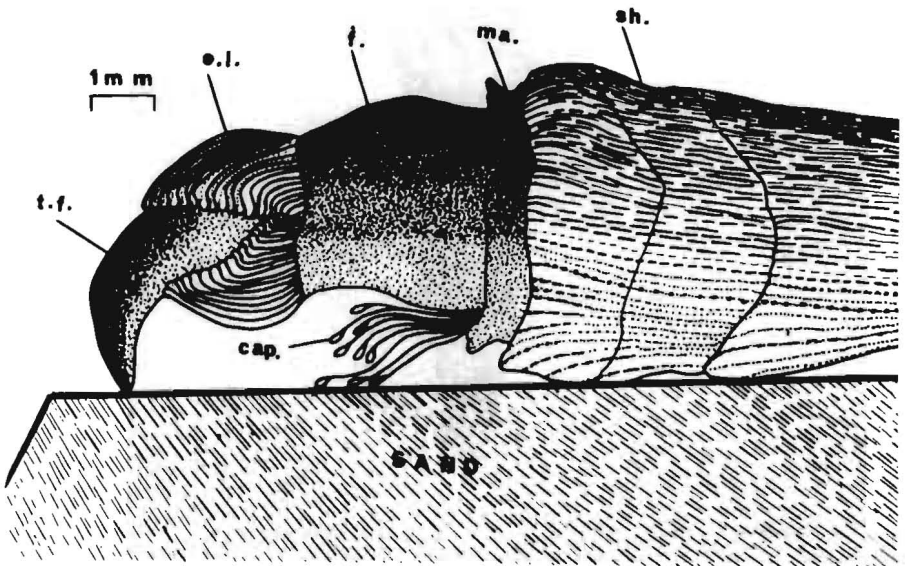

Fig. 3. Diagram showing the beginning of the rhythmic probing of the substratum by the tip of the foot.
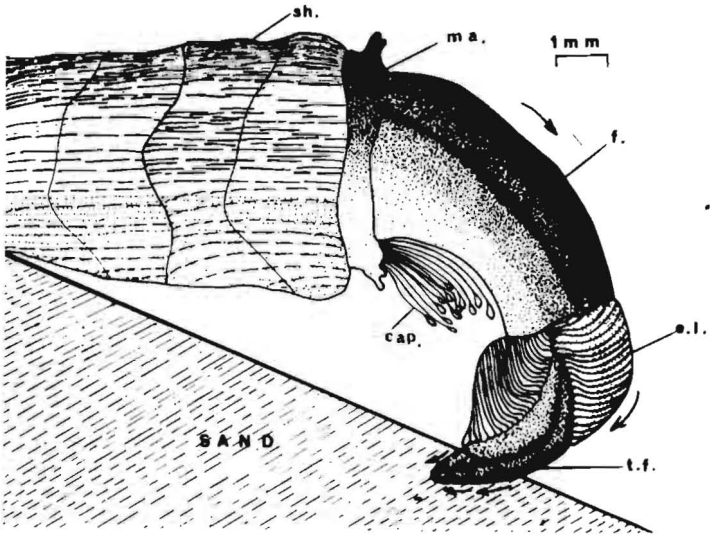(For interpretation of lettering, see above).

Fig. 4. Diagram illustrating the disposition of the foot in the second stage of the burrowing probess. e.l., epipodial lobe; F., foot; ma., mantle; sh., shell; t.f., tip of the foot.
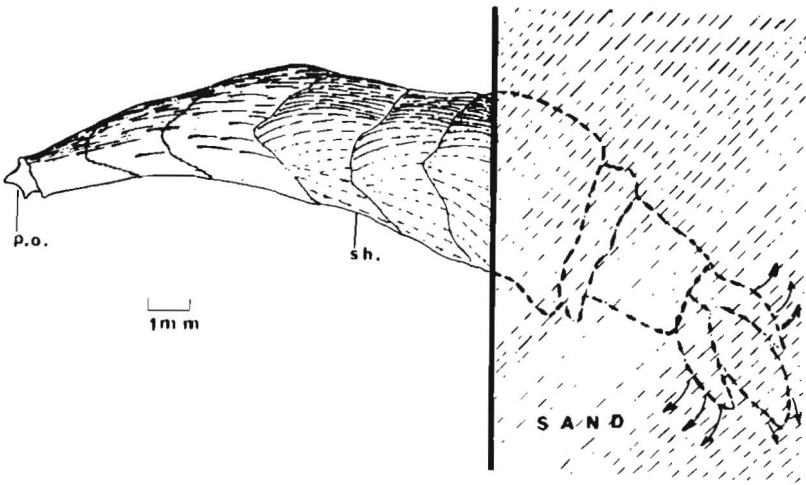

Fig. 5. A stage in burrowing subsequent to that shown in Fig.4
p.o.. posterior opening; sh., shell.

1.   Slow extension of the whole foot from the mantle cavity in the attitude shown in Fig. 1 followed by rhythmic probing of the substratum with the tip which is turned towards it as shown in Fig. 2. To assist penetration, the epipodial lobes are folded to clasp the tip. This is followed by rapid retraction of the whole foot. Such movements are repeated several times.

2.   The tip of the foot is thrust into the substratum (Fig. 3) already loosened by the foregoing movements and the animal's body is then rotated so as to bring the side of the shell facing downwards into a position facing upwards, followed by a partial return to the original position.

3.   After several such twists the epipodial lobes are moved outwards assisting the formation of terminal anchor, upon which, by contration of the longitudinal musculature of the foot, the mouth of the shell is drawn into the substratum.

4.   Repetition of these movements draws the animal progressively into the substratum with the shell more or less upright (Fig. 4).

5.   The epipodial lobes are again folded to clasp the tip of the foot which is then withdrawn, anchorage now being effected by the shell (Fig. 5).

It is clear that such activities could also be important in feeding as indicated by Gainey (1972) who stated the rhythmical probes of the foot pass detritus back along its surface. Most of these particles fall off however, some of them are passed to the foot furrow where they are ingested by the proboscis.

My own observations support this view.

The Captacula

The structure of these highly mobile, tentacle-like organs, including their histology has already been described recently by Morton (1959) and Gainey (1972). When fully extended they are seen to be of varying lengths. The salient features of their structure are shown in Fig. 7. From the standpoint of this account we should note their muscular structure, about ten longitudinal muscles (l.m., Fig. 7 A & C) being prominent and well developed. The middle zone of each organ is extended into external papillae, supported by circularly disposed connective tissue fibres (c.c.t., Fig.7 A). The disposition of these elements suggests their importance in relation to extensibility. We should also note the nerve supply (ne., Fig. 7 A & C) involving a ganolion (ga., Fig. 7 A & B) and central nerve (ne., Fig. 7 A & C) suggesting a sensory function. Of particular interest is the large number of unicellular glands concentrated at the smaller tip. The reaction of these cells to P.A.S. and Alcian Blue indicates their production of mucosubstances.

Another important feature is the ciliated groove, termed by Morton, Dinamani and Gainey the 'alveolus' (al., Fig.7 A).

Previous accounts differ in their description of the ciliation. Fol (1889) described the presence of 'une bandelette virbatile longitudinale' running along the flattened side of the filament. Morton found no trace of cilia in fixed captacula except around the free end where he noted particularly long cilia in the alveolus. Dinamani (1963), from a study of living material, reported the presence of cilia covering the entire captaculum. Gainey reported a similar disposition of cilia.

My own observations indicate that this dispa⁻.ty may be consequence of fixation. Living captacula were found to be completely covered by cilia whereas after fixation while the tip retains its ciliation, the cilia disappear from varying proportions of the remainder.

Gathering food by captacula

The gathering of food by captacula has already been described by Morton (1959), Dinamani (1963) and Gainey (1972). Morton describes these organs as extending in all directions to pick up particles from the substratum by their club-like ends which are sticky due to the mucus. The adhering particles are then transferred to the mouth by contraction of the filament. Dinamani described the collection of diatoms, algal cells and detritus by means of the investing cilia which transfers particles to the 'alveolus', the ciliary currents in which transfer the particles to the mouth. Gainey observed collection of particles by both methods. No mention is made of the sorting or selection of particles.

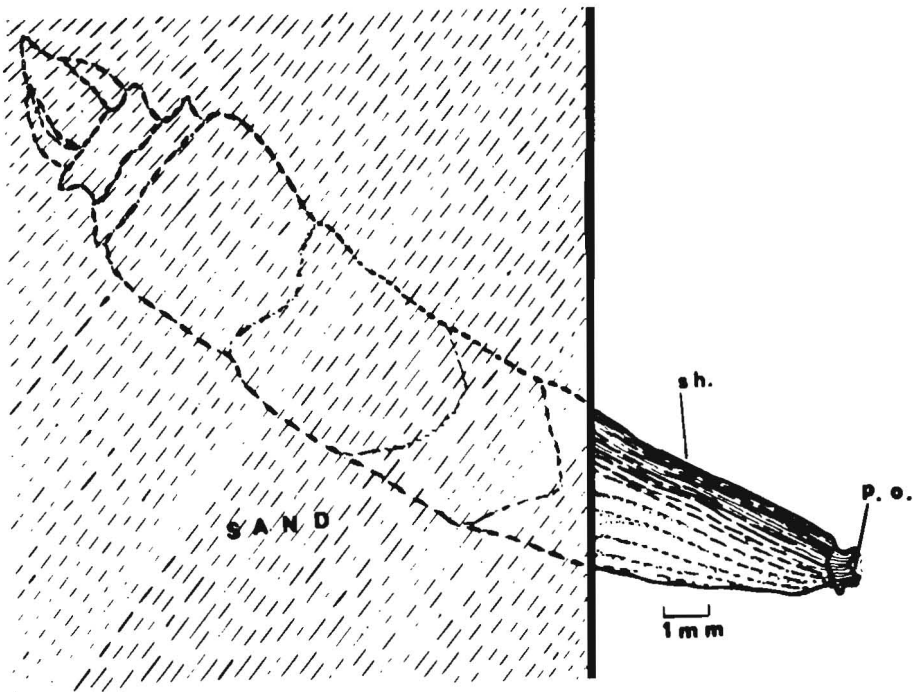My own observations were conducted on animals confined between glass plates

Fig. 6 Diagram showing the final stage of the burrowing process.
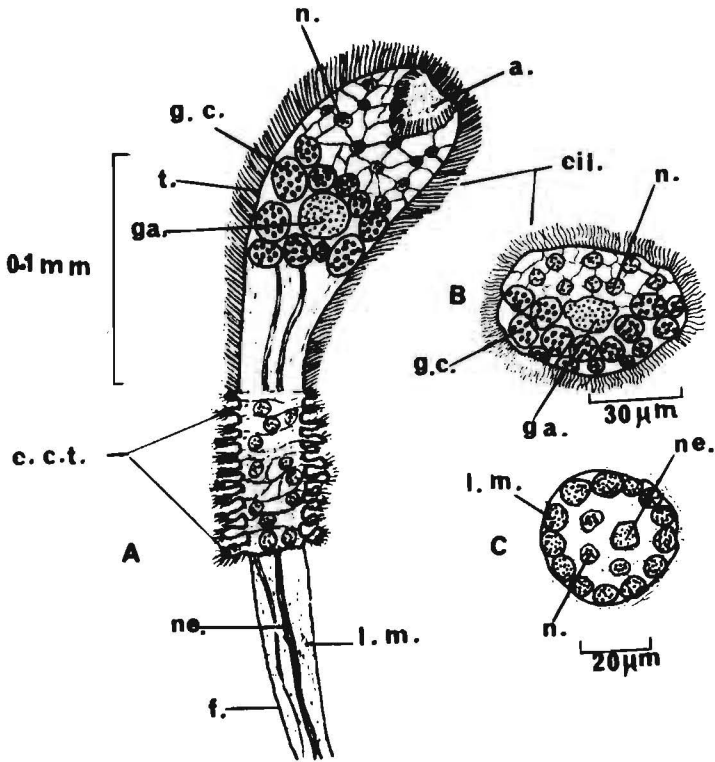p.o., posterior opening;   sh., shell.

Fig. 7.

A, longitudinal section of a captaculum.
B, cross section of a captaculum at its tip.
C, transverse section of a filament. Fixed in Flemming without acetic acid and stained in safranin and light green.

al., 'alveolus';   c.c.t., circular connective tissue;   cil., cilia;   Fi., filament;   g.c. gland cell;   g.a., ganglion;   l.m.longitudinal muscle fibres;   n., nucleus;   ne., nerve;   t., tip of a captaculum.

and to facilitate observation the anterior part of the shell and mantle were removed. Feeding was observed by a stereoscopic microscope.

As asserted by Gainey, both methods were seen to involve the foot, which in executing the burrowing movements already described, excavated a small cavity (termed by Dinamani and Gainey the 'feeding cavity'). The former suggested that it served as a filtering chamber, the latter as an exposed surface for the searching activities of the captacula. Whilst this may be true in certain situations, I have not found it so in *D. entalis,* for although the cavity is always produced, the captacula do not necessarily use it and extend in all directions in the substratum. From this point on, two processes may occur.

In the first, as described by Morton and Gainey, the club-like ends of the captacula are pushed into the substratum so that particles of varying size adhere to the club-like ends, which are sticky with mucus. Such behaviour is shown by the longest captacula which are then withdrawn into the mantle cavity where they encounter the shorter captacula. The load of adherent particles is then transferred to successively shorter captacula and finally reaches the proboscis. There was no indication of particles being selected, the opening of the proboscis dilating to receive the larger particles.

In the second method, the smallest particles were seen to be taken up by the ciliary covering at the free ends of the longer captacula and transferred to the 'alveolus', the cilia lining which convey them along the groove to the foot furrow (f.f., Fig. 1) in front of the proboscis. During this process the 'alveolus' was seen to open and close from time to time. The five mobile lips (l., Fig. 1) guarding the opening of the proboscis, by their movements assist the transfer of the particles into the canal within the proboscis. This method is essentially the same as that described by Dinamani and Gainey.

The process was seen to be the same when intact animals were used, except that the lips of the proboscis could not be seen due to the rim of the shell. Thus the part played in this activity by the lips could not be discerned. The precise nature of the particles taken in has already been reported.

Currents in the mantle cavity

The mantle cavity is seen to be extensively irrigated by water currents which are assumed to be primarily involved in external respiration and in voiding excreta. In addition Yonge (1937) has already signalled their possible importance in feeding. For this reason I have examined them more closely both in animals isolated in petri dishes and in those partially burried in their normal substratum.

The currents are essentially oscillating, moving regularly and gently in and out of the mantle cavity by the posterior opening of the shell. From time to time this regular rhythm ceases, water being taken in for a longer period followed by a correspondingly longer expulsion phase. At intervals of 10-15 minutes the rhythm is punctuated by a violent expulsion of fluid from the mantle cavity.

Yonge (1937) maintained that the currents were due in part to ciliary action and

in part to activities of the foot.

The nature of the currents suggests this, but to verify the suggestion, it was decided to examine the mantle cavity of living individuals. For this purpose part of the shell was cut away in animals recently dredged, and contained in petri dishes with chilled sea water (6-8°C). It was then possible to see the contribution of the podial contractions to the currents; which were visualized by means of finely powdered carmine pipetted on to the terminal opening of the shell.

It became clear that the gentle flow in and out corresponded in periodicity with the slow movements of the epipodial lobes of the foot which alternately clasp and unclasp the terminal lobe of the foot producing currents in the manner of fans or paddles, as shown in Fig. 8 & 9.

Yonge attributed this current to the action of cilia and foot; he does not mention the particular significance of the epipodial lobes.

The spasmodic vigorous current from the posterior shell opening is seen to be due to sudden withdrawal of the foot and its epipodial lobes into the mantle cavity, expelling contained water.

The ciliary currents through the mantle cavity were studied by using live animals recently removed from their shells and examined as before but with the ventral wall of the mantle cavity opened up.

The movement of carmine particles due to the action of the ciliary currents is illustrated in Fig. 10. The pattern of currents is simple and corresponds exactly with description.given by Yonge (1937), currents passing from the posterior opening of the mantle cavity and along both dorsal and ventral aspects to the foot. However, the carmine particles swept to the base or to either side of the foot by these currents were not observed to reach the captacula as suggested by Yonge. To seek confirmation of this, animals kept in suspensions of carmine were well washed to remove adhering carmine particles from their bodies, quickly dissected, and their gut contents examined for the presence of carmine. No traces were found.

Effect of temperature on the currents in the mantle cavity

A few experiments were conducted to reveal the effect of temperature on the currents just described. Observations were made on animals partly buried in muddy sand in their normal positions. The sea water containing them was warmed or chilled and the currents entering and leaving the mantle cavity were visualized by using suspensions of carmine and examined by a stereoscopic microscope.

At temperatures between 0 and 3°C, animals were withdrawn completely into their shells and there were no signs of currents. At 4-5°C the regular oscillating currents appeared, but they were much weaker than those reported at 6-8°C. Their rhythm was also much slower in that there was a long period between in take and expulsion, the interval between two successive expulsions was 3-4 minutes. There was no sign of spasmodic vigorous expulsions of water.

Between 6 and 10°C the foot slowly extended and began burrowing cycle. At the same time the animals showed greater activity so that the regular, gentle oscillating

rhythm, the interval between two successive expuslions was 0.5-1.5 minutes. The spasmodic vigorous expulsion of water was seen to begin and was repeated at intervals of 10-15 min.

Between 15 and 20°C, the foot remained partially retracted. The interval between two successive expulsions in the gentle oscillating rhythm was the same as at 4-5°C. Spasmodic vigorous expulsions occurred at intervals of 20-25 min.

When animals were exposed to temperatures between 24 and 25°C, no currents were visible.

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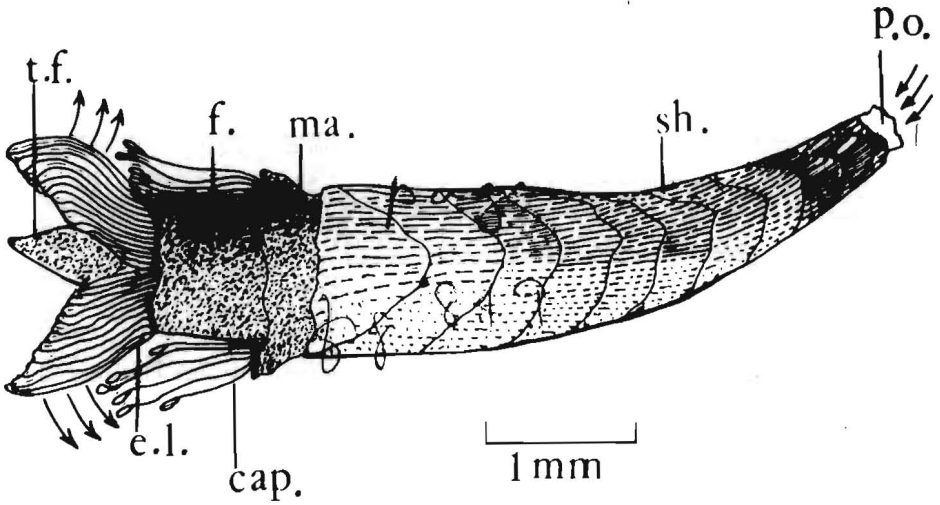
Fig. 8 Diagram showing the action of the epipodial lobes of the foot during the steady intake of water. The anterior part of the shell has been removed. Arrows at the tip of the shell indicate the movement of the water into the mantle cavity. Arrows alongside the epipodial lobes indicate the direction of movement of the lobes.

cap., captacula; e.l., epipodial lobe; F., foot; ma., mantle; p.o., posterior opening; sh., shell; t.F., tip of the foot.
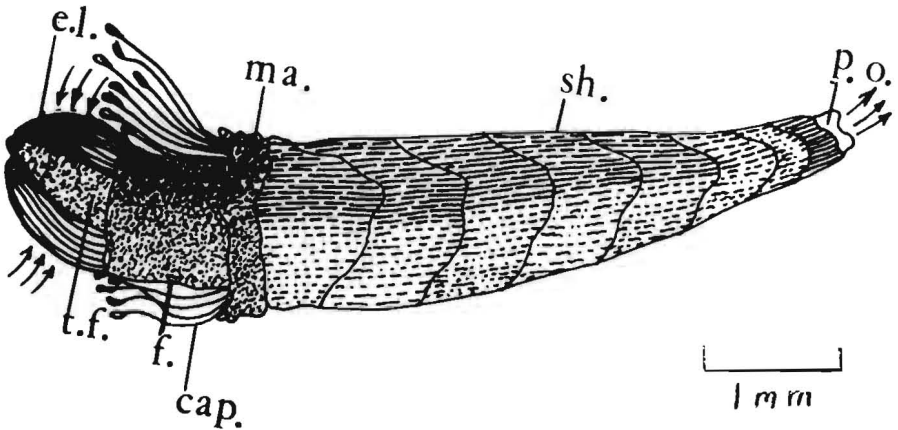

Fig. 9. Diagram showing the action of the epipodial lobes of the foot during the expulsion phase. The anterior part of the shell has been removed. Arrows at the tip of the shell indicate the movement of the water from the mantle cavity. Arrows alongside the epipodial lobes as in Fig. 8.
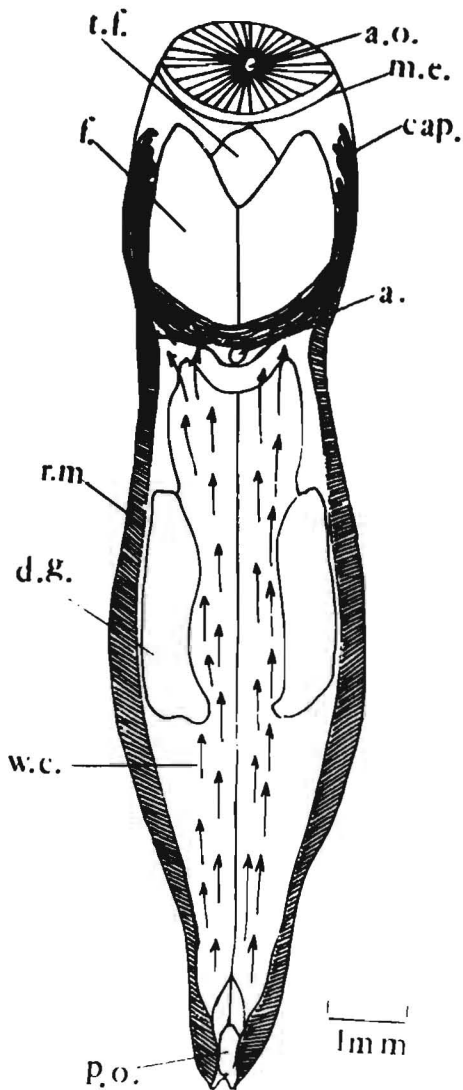
(For interpretation of lettering, see above).

Fig. 10 Diagram illustrating the water currents produced by cilia in the mantle cavity as seen from the ventral side (from Yonge, 1937).

a., anus;   a.o., anterior opening;   cap., captacula;   d.g., digestive gland;   F., foot;   m.e., mantle edge;   p.o., posterior opening;   r.m., retractor muscles;   t.F., tip of the foot;   w.ci., weak ciliary currents.

بعض الملاحظات على الحيوانات التابعة لنـوع « الانتالـم انتالس »

نورى طاهر الطيب

قسم علم الحيوان ، كلية العلوم ، جامعة الرياض ، الرياض ، المملكة العربية السعودية

زورقية القدم هى قواقع بحرية مكيفة على المعيشة بين أحجار رطبة مكونة من رمال خشنة ومتوسطة النعومة .

الأكل وطريقة التغذية ومحتويات الأمعاء شملها الوصف وأهمية التحركات داخل الأحجار وتيارات الماء التى تتكون على سطح أجسام هذه الحيوانات قد نوقشت علاقاتها بالنسبة إلى عمليات التغذية .