AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

THE BIOLOGY AND FUNCTIONAL MORPHOLOGY OF THE CORAL-SAND BIVALVE **FIMBRIA FIMBRIATA** (Linnaeus 1758).

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SUMMARY

Fimbria fimbriata Linnaeus 1758 is an infaunal inhabitant of coral sands in the Indo-Pacific. The structure and mineralogy of the shell (Taylor, Kennedy and Hall, 1973) confirms its taxonomic position as a member of the Lucinacea. Nicol (1950) erected (giving no reasons) a new family, taking its name (the Fimbriidae) from the genus. This study supports the view of Allen and Turner (1970) and Boss (1970) that *Fimbria* is closely related to the Lucinidae Fleming 1828 though a study of fossil fimbriids will have to be undertaken before the extreme view of Allen and Turner (1970) that *Fimbria* is a lucinid, can be validated. The Lucinidae and *F. fimbriata* possess the following features in common.

1. An enlarged anterior half of the shell with an antero-dorsal inhalant stream.
2. A single (inner) demibranch with type G ciliation (Atkins, 1937b).
3. Reduced labial palps.
4. "Mantle palps".
5. A stomach closely similar in structure.
6. A unique method of withdrawing the posterior exhalant siphon.

The specialisations adapting *Fimbria* for a deposit feeding mode of life have also been elucidated and include:
1. Reduced ctenidia and labial palps.
2. The modification of the foot to form a food collecting organelle.
3. The development of "mantle palps".
4. Complex, efficient and complementary rejectory tracts on the visceral mass and inner mantle surface.
5. The copious production of mucus from all organs involved in the processing of potential food material.
6. Few sorting areas in the stomach.
7. Strong rejectory tracts in the stomach.
8. A small number of large apertures leading from the stomach to the digestive diverticula.
9. A short intestine.
10. An extensive pedal gape bordered by many sensory papillae.

The mode of life of *F. fimbriata* is described; the morphological features it possesses must be seen from two viewpoints. Primitive features give some support to the contention of McAlester (1966) that the Lucinacea are a phylogenetically old and quite distinct separate line of evolution in the Bivalvia. This study supports the view of Boss (1970), however, that the Lucinacea possess many typical heterodont characters and, though primitive, must be considered a significant component of the mainstream of eulamellibranch evolution.

Alternatively the specialisations of *F. fimbriata* suit it to life in nutrient deficient sediments and waters and are generally uniquely different to the solutions offered by other bivalves to similar modes of life.

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INTRODUCTION

Fimbria fimbriata (Linnaeus 1758), like many members of the Lucinacea (Allen, 1958) is an inhabitant of coral sands in the tropics. It has been little studied though both Valenciennes (1845a, b) and Thiele (1935) commented on various aspects of its anatomy. Later descriptions of the species are incomplete (Allen and Turner, 1970; Boss, 1970) because living material was unavailable. These examinations of preserved material left unanswered a wide range of questions with respect to the mode of life and the functional significance of the organs of the mantle cavity and alimentary canal. More importantly the relationships of *Fimbria* within the Lucinacea would benefit from a closer inspection of the living animal especially since Allen and Turner (1970) assert that it is a member of the Lucinidae and further question its present placement in, and the validity of, the Fimbriidae (Nicol, 1950).

This paper reports upon a study of living *Fimbria fimbriata*.

SYSTEMATICS

Fimbria fimbriata (Linnaeus 1758) is a member of the Fimbriidae Nicol 1950 one of six families of the Lucinacea Fleming 1828 recognised by Chavan (1969). In the Fimbriidae Chavan (1969) further recognises 9 genera of which only *Fimbria** Megerle von Mühlfeld 1811 (=*Corbis* Cuvier 1817) is extant. Synonyms of *F. fimbriata* (Linnaeus 1758) include *F. fimbricatum* Roeding 1798, *F. magna* Megerle von Mühlfeld 1811, *F. perforata* Schumacher 1817 (Cernohorsky, 1972). According to Nicol (1950) there are only two living species, both distributed in the Indo-Pacific.

A recent study of *Fimbria fimbriata* by Allen and Turner (1970) has suggested that this genus is more closely allied with the Lucinidae Fleming 1828 and contend that in the original description of the genus no reasons were given for the erection of the Fimbriidae by Nicol (1950). Boss (1969, 1970) accepted the view of Nicol, however, and wrote "Most probably a basic lucinoid stock gave rise to the distinct fimbriids which paralleled the lucinids. . . . " Not until further study has been undertaken of the fossil fimbriids,

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* The nudibranchiate genus *Fimbria* Bohadsch 1761 (Taylor and Sohl, 1962) has been rejected by the I.C.Z.N. thereby invalidating the family name based on this genus.

however, will it be possible to decide on the validity of the Fimbriidae, but this study re-examines *F. fimbriata* and specifically compares it with members of the Lucinidae.

More importantly, McAlester (1965, 1966) has asserted that "This lineage (Lucinacea, Leptonacea and *Babinka)* should probably be treated as a separate bivalve taxon of the highest rank" that are "probably unrelated to most other "heterodont" forms". This view, refuted by Boss (1969), also bears further re-examination and in this context a detailed examination of *F. fimbriata* might well prove valuable.

BIOLOGY

The Lucinacea occur in a variety of substrates ranging from coarse sand to fine mud. They are particularly prevalent, however, in coral sands where the associated fauna is sparse. *Fimbria fimbriata* occurs in a similar habitat at a range of depths and was common in the coral sands of Lizard Island. The species is widely distributed in the Indo-Pacific and ranges from Hawaii to Tonga and from Indonesia to Australia. The distribution has been recorded by Nicol (1950) and subsequently by Cernohorsky (1972).

The animal lies, as suspected by Boss (1970), with the dorsal region of the swollen anterior portion of the shell upwards, just underneath the surface of the sand; the position
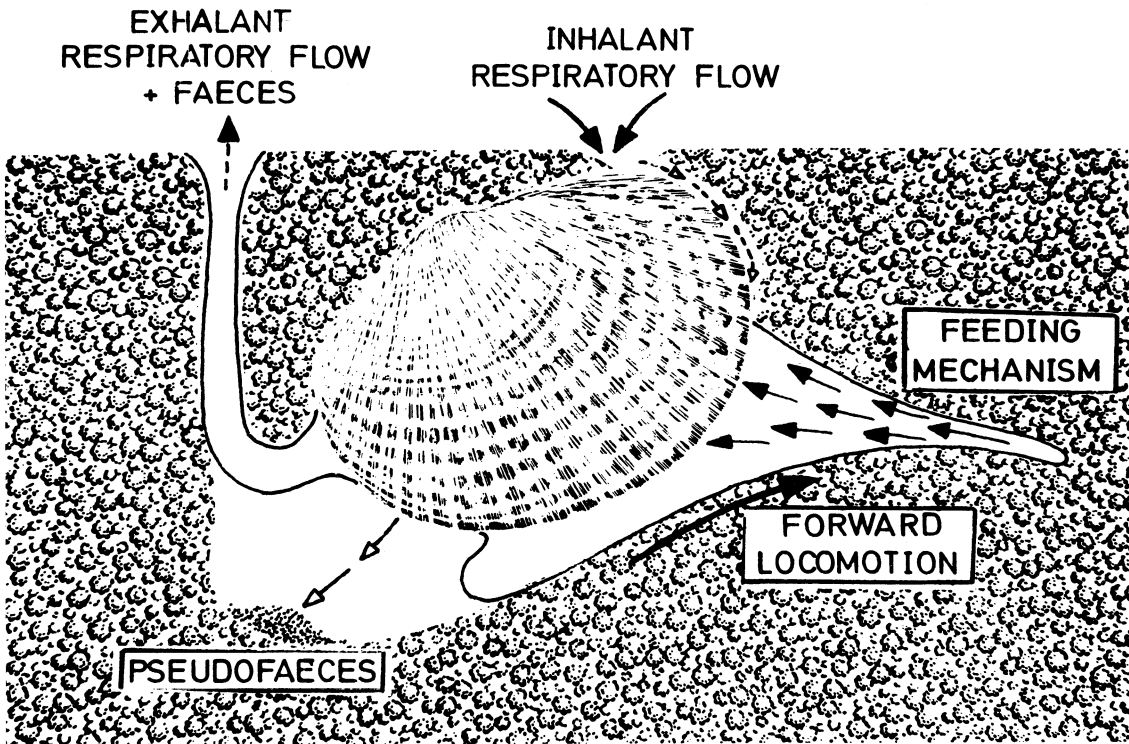

Fig. 1. *Fimbria fimbriata.* A diagrammatic representation of the living animal in its natural environment.

of the anterior inhalant aperture being marked by a shallow depression (Fig. 1). The posterior exhalant siphon was never observed extended; it possibly being quickly retracted when the animal was disturbed and also only periodically extended as the animal moved forward. *Fimbria* is, as suggested by Allen and Turner (1970), a slow mover; locomotion being the function of the foot, particularly the heel. The tip of the foot was seen to extend; the shell being pulled up after it presumably by contraction of the longitudinal muscles of the foot. The movement forward was also accompanied by a rapid adduction of the shell valves. Locomotion should best be compared with the description of this action in the leptonid *Mysella cuneata* by Gage (1968). The foot is also the food collecting organelle and does not, as it does in many lucinids (Allen, 1958; Allen and Turner, 1970), play any part in the construction of the anterior inhalant tube. There is no information on the rate of growth, population dynamics or reproduction in *Fimbria;* such subjects would be of considerable interest especially since, as will be explained later, *Fimbria* possibly incubates its larvae in the suprabranchial chamber. An un-named leptonid occurs around the inhalant aperture, typically attached to the periostracum.

THE SHELL AND LIGAMENT

The aragonitic shell of *Fimbria fimbriata* comprises (Taylor, Kennedy and Hall, 1973), as in all other lucinaceans, a complex crossed lamellar inner layer, a crossed lamellar middle layer, a composite prismatic outer layer and a thin prismatic pallial myostraca.
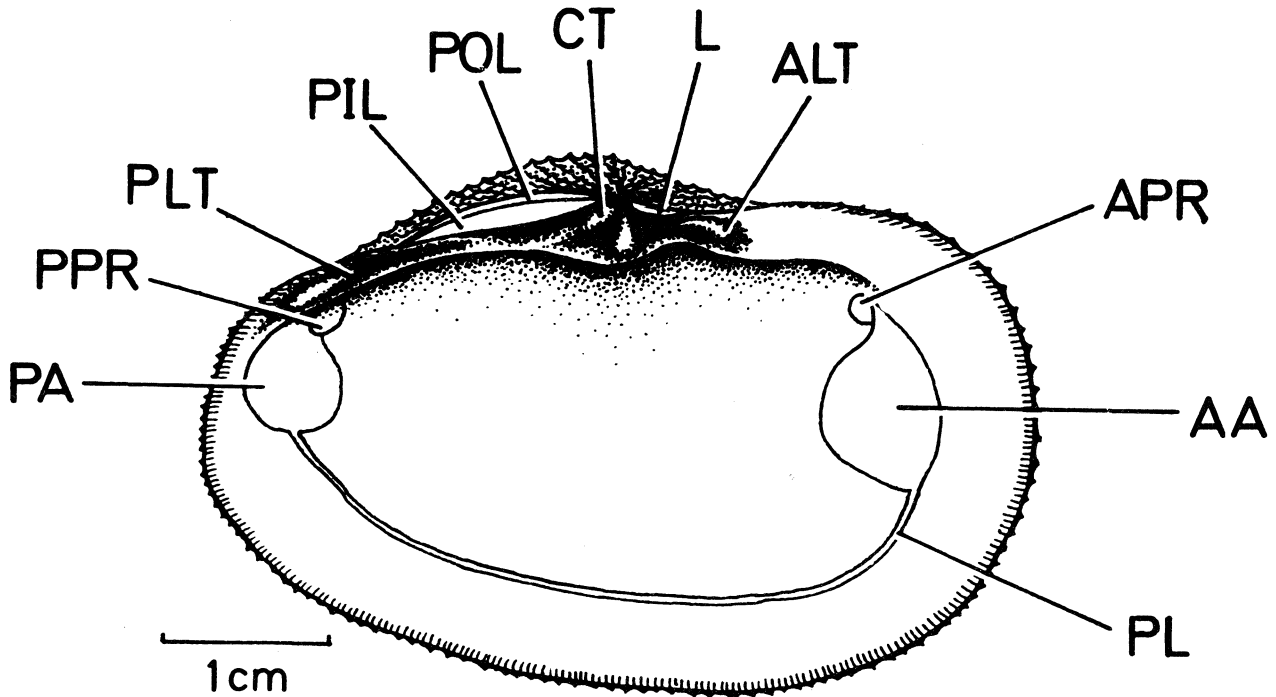

Fig. 2. *Fimbria fimbriata*. An internal view of the left shell valve. (For abbreviations see page 419.)

The shell of *F. fimbriata* is thick, equivalve, but distinctly inequilateral (Fig. 2). The anterior half of the shell is more swollen than the posterior which is unusual especially since the ligament is opisthodetic. The umbones point anteriorly and there is a well defined heart-shaped lunule (Fig. 4A). Externally the shell is white changing hue to a delicate pink antero- and posterodorsally. The shell sculpture is reticulate, there being well defined concentric cords forming projections dorsally and feeble radial striae. The concentric cords form overlapping plates anteriorly and posteriorly.

Internally the hinge plate (Fig. 3) possesses in each valve two cardinal teeth (CT) and two lateral teeth — anterior (ALT) and posterior (PLT). The anterior lateral tooth is located under the lunule (L) while the posterior lateral tooth is located at the posterior extremity of the hinge plate. The margins of the shell valves meet at all points and prominent denticles on both valves interlock making the shell extremely difficult to open. The internal margin of the shell is coloured pink, the remainder of the shell being white except underneath the hinge plate which is yellow. *F. fimbriata* is approximately isomyarian though the anterior adductor muscle scar (Fig. 2, AA) is slightly larger than the posterior (PA). The adductor muscles are flanked internally by small, dorsally located anterior (APR) and posterior pedal retractor muscle scars (PPR). The pallial line (PL) is entire and there is no pallial sinus — a feature which would indicate in other bivalves that there are no, or only short, siphons. However, as will be seen later the Lucinidae and *F. fimbriata* have evolved an unusual method of withdrawing their exhalant siphon (Allen, 1958). Boss (1970) notes that the pallial line is contiguous with the scar of the anterior (but not the posterior) adductor muscle — a feature, as will be discussed later, associated with the position of the anterior inhalant stream.
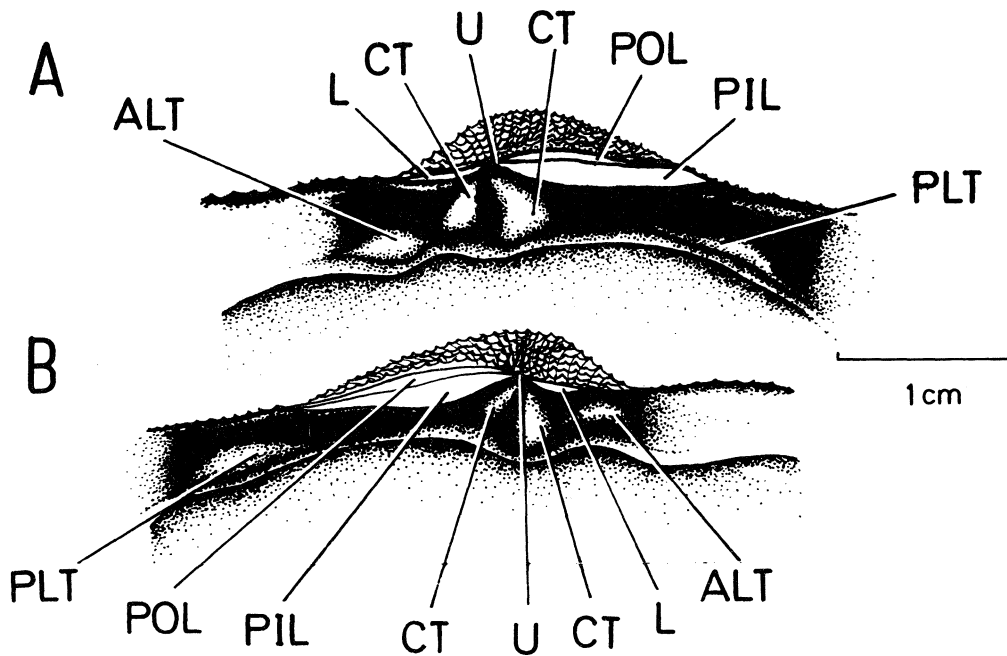

Fig. 3. *Fimbria fimbriata*. The hinge plate of (A), the right and (B), the left shell valves. (For abbreviations see page 419.)

The opisthodetic ligament of *F. fimbriata* (Fig. 3) has been described in detail by Allen and Turner (1970) who recognised that the ligament was covered, as is the lunule, by a layer of fused periostracum. Internal to this, posterior outer (POL) and inner ligament layers (IL) can be recognised, though Allen and Turner recognised a further fourth or "fusion layer" located between the periostracum and the posterior outer ligament layer. The structure of the mantle region that secretes the ligament has also been described in detail by Allen and Turner (1970).

The Mantle

The mantle comprises three folds as in all bivalves. Mantle fusions occur between the exhalant and inhalant siphons and between the inhalant siphon and the pedal gape. Dorsally the mantle forms the ligament, a process that has been explained for the Lucinacea (Allen, 1960) and for *Fimbria fimbriata* (Allen and Turner, 1970). Elsewhere mantle fusions are of the inner folds only and thus of type A (Yonge, 1957). Each mantle lobe possesses a double row of papillae — a feature noted by Thiele (1935), Allen and Turner (1970) and Boss (1970); those comprising the inner row are longer and are pointed inwards, those on the outer row are directed outwards. A similar double row of papillae also occur in the lucinid *Codakia orbicularis* (Allen and Turner, 1970).
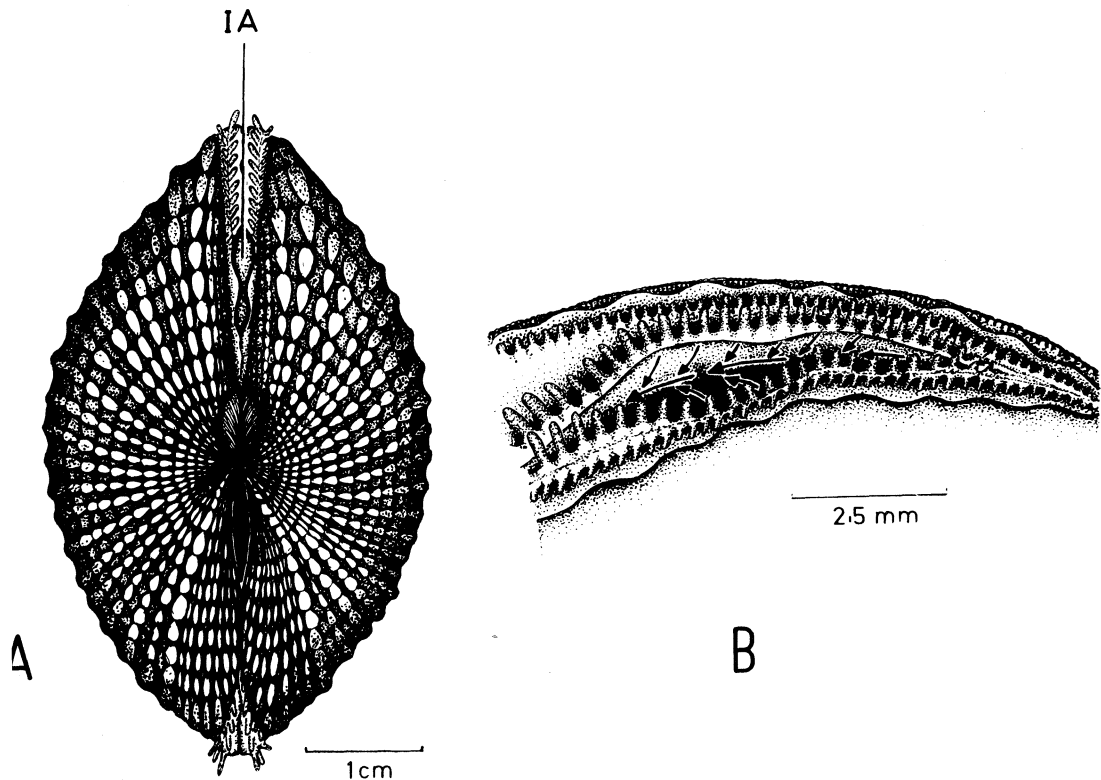
Fig. 4. *Fimbria fimbriata*. (A) A dorsal view of the shell with the inhalant aperture open. (B) A dorso-lateral view of the inhalant aperture. (For abbreviations see page 419.)
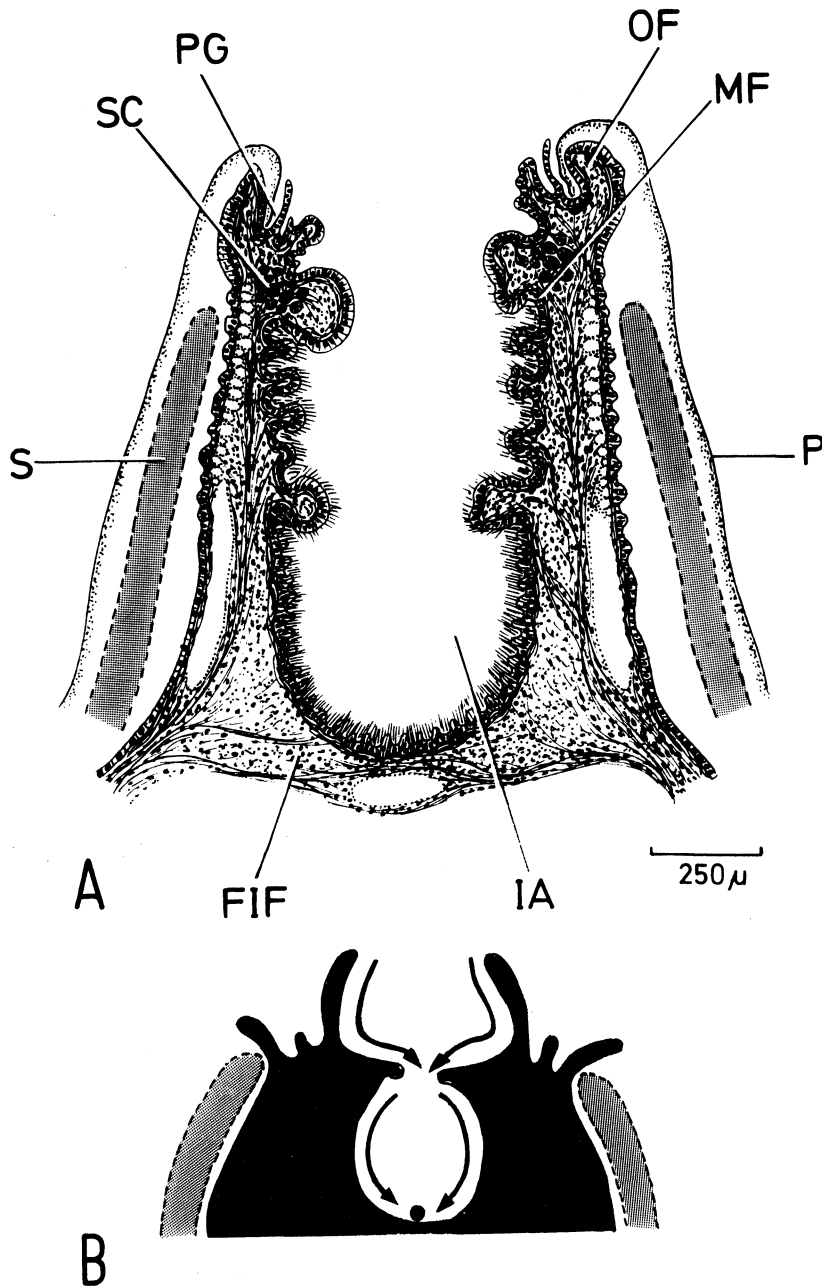
Fig. 5. *Fimbria fimbriata*. (A) A transverse section through the inhalant aperture. (B) A diagrammatic representation of a tranverse section through the inhalant aperture showing the ciliary currents. (Closed circle = oral acceptance tract). (For abbreviations see page 419.)

The inhalant stream (Figs. 4 and 5) is located antero-dorsally. When specimens of *F. fimbriata* were positioned in a tank of sand through which fresh sea water flowed, a shallow depression was seen to be created by ciliary action on the outer surface of the middle fold of the antero-dorsal region of the mantle. The selective apposition of the middle folds of
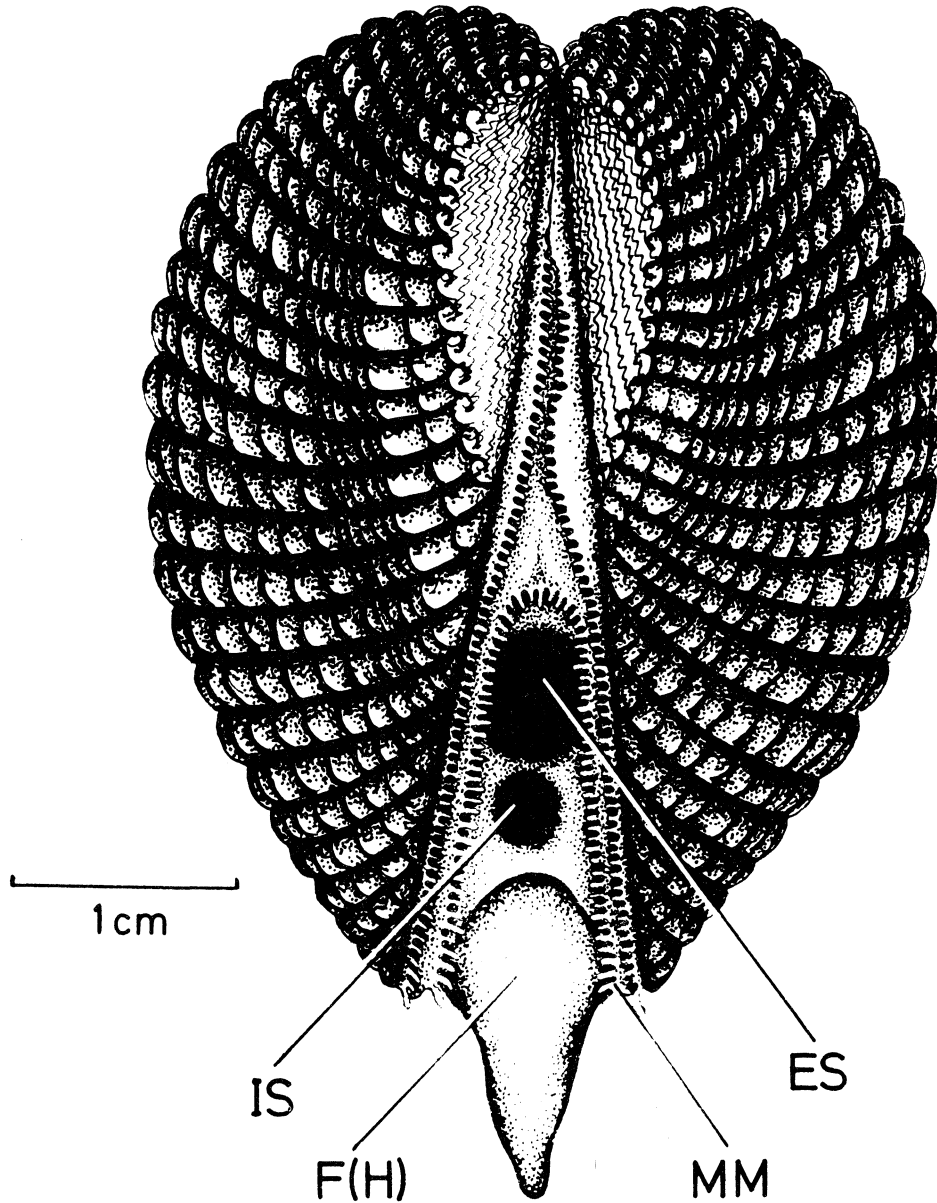
IS

F(H)

ES

MM

Fig. 6. *Fimbria fimbriata.* A posterior view of the shell showing the inhalant and exhalant siphons. (For abbreviations see page 419.)

both lobes creates a false inhalant "aperture" (IA) (false, since the inner folds are fused underneath) (Fig. 5). Boss (1970) was misled by this "false" aperture into believing that the mantle lobes were not fused. The aperture leads down to a groove formed by the outer surface of the fused inner mantle folds (FIF) and roofed over by the inner surface of the middle mantle fold (MF). Particles of carmine added to the groove were quickly transported antero-ventrally around the outside of the anterior adductor muscle and entered the mantle cavity ventral to the anterior adductor muscle via the pedal gape (Fig. 9). This explains the contiguous nature of the pallial line and anterior adductor muscle noted by Boss (1970) and the hypertrophy of the anterior half of the shell. The middle mantle fold can occlude the inhalant aperture without disturbing the sandy depression around it and the papillae surrounding the groove form a sensory defensive mesh. The foot of *F. fimbriata* unlike the foot of other members of the Lucinacea (Allen, 1958) plays no part, as will be discussed later, in the construction or maintenance of the inhalant aperture in the sand.

The short, rounded inhalant siphon (Fig. 6, IS) is located posteroventrally and is smaller than that of the exhalant siphon. Neither is crowned (as is typically the case in the Bivalvia) with tentacles. From this aperture pseudofaeces were occasionally expelled (Fig. 9, PS); this being undertaken by the rapid contraction of the shell valves.

The exhalant siphon (ES) is long and flared distally. The exhalant siphon alone is retractable within the supra-branchial chamber (Fig. 12C); by invagination. A similar mechanism of siphonal retraction is seen in members of the Lucinidae (Allen, 1958) and in *Myadora ovata* (Pelseneer, 1911) where in the latter case the inhalant siphon invaginates into the infrabranchial chamber. The exhalant stream is directed from the exhalant siphon in *Fimbria*.

The pedal gape is extensive and from between the separate mantle lobes is extended the long, subtrigonal foot.

The structure of the ventral margin of the mantle of *F. fimbriata* has been described by Allen and Turner (1970). This description (Fig. 7A) adds to the earlier account. The periostracum (P) secreted from within the periostracal groove, possibly from apical cells as in *Astarte* (Saleuddin, 1974), comprises a single layer 6 thick. In many other heterodonts the periostracum is two layered e.g. *Dreissena polymorpha, Galeomma polita* and *Geloina erosa* (Morton, 1969, 1973, 1976b), whereas in the Mytilacea it comprises three layers (Beedham, 1958; Morton, 1973a). As noted by Allen and Turner (1970), the mantle margin possesses two types of secretory cell (SC). In the inner mantle fold (Fig. 7B, IF) the secretory cells are epidermal and some 25 tall whereas in the middle mantle fold (Fig. 7C, MF) the secretory cells are sub-epidermal with channels passing between ciliated epithelial cells of reduced height (10-12). The mantle possesses an extensive musculature (PM) and a concomitant large pallial line (PL) is seen on the shell. The mantle is thick with bands of muscles cross-connecting the two epithelia. A pallial blood vessel has been described by Allen and Turner (1970) and Boss (1970).

The ciliary currents of the mantle

The ciliary currents of the mantle are complex (Fig. 8). An anterior, oralward, current marks the line of attachment of the descending lamella of the inner demibranch to the mantle (FO) i.e. the ctenidial axis. Ventrally each mantle lobe possesses a posteriorly directed current that leads to the base of the inhalant siphon (IS). This current travels within a well defined ciliary groove in each mantle lobe and is supplied with material from the inwardly directed currents of the mantle edge. The general surface of each mantle lobe can be divided into two halves, anterior and posterior. In the anterior half, ciliary currents
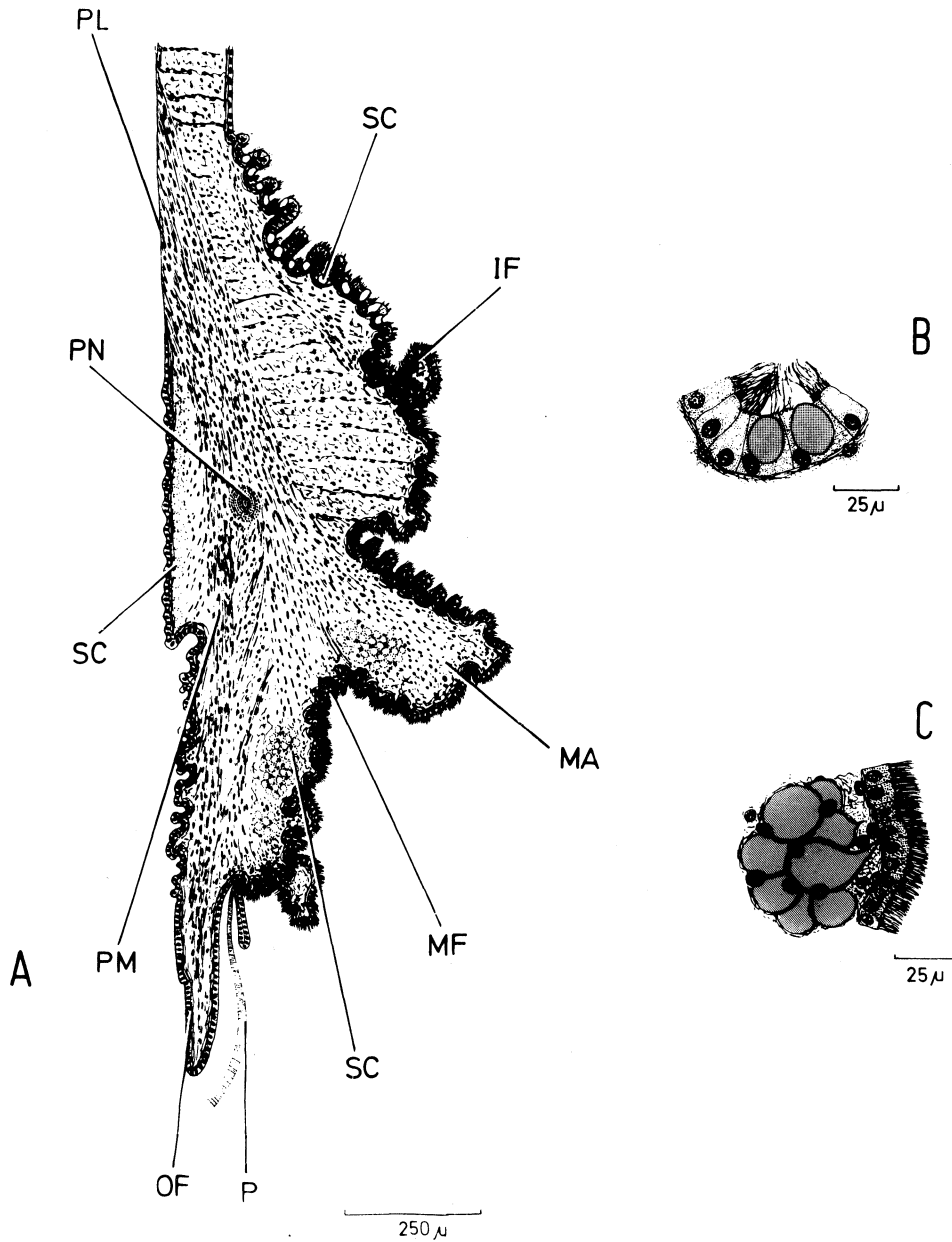
Fig. 7. *Fimbria fimbriata*. (A) A transverse section of the mantle margin in the region of the pedal gape. The secretory cells of (B) the inner mantle fold and (C) the middle mantle fold are also represented. (For abbreviations see page 419.)
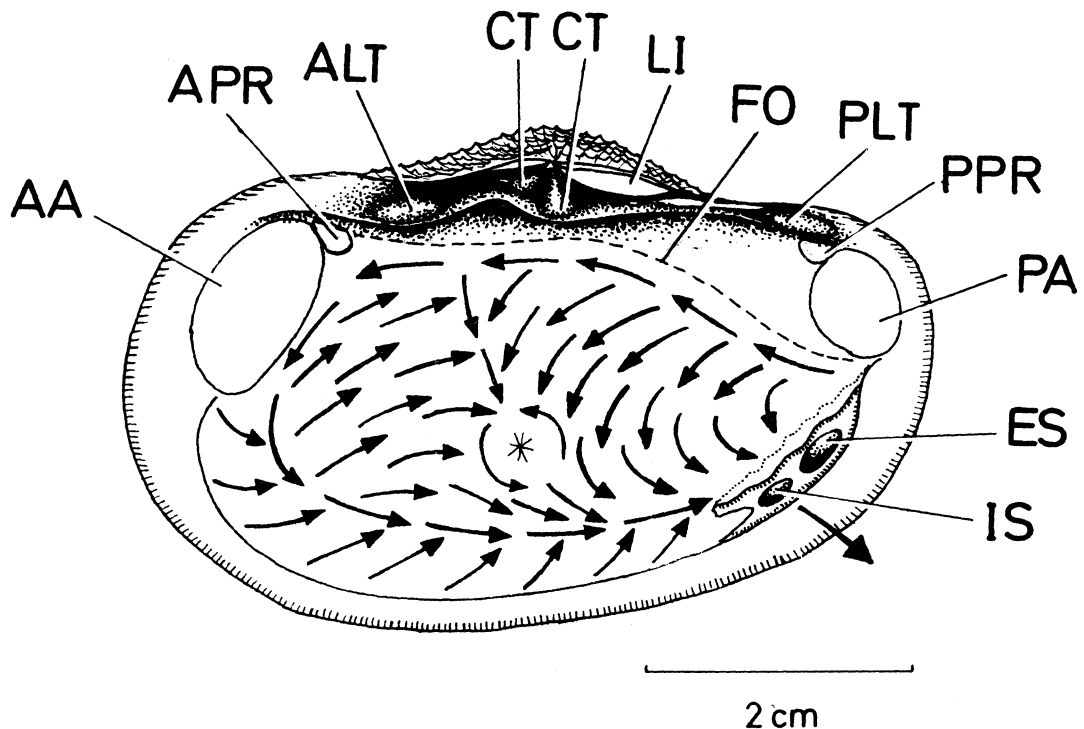
Fig. 8. *Fimbria fimbriata*. The ciliary currents of the right mantle lobe. (* = area of ciliary confluence). (For abbreviations see page 419.)

are directed posteriorly; in the posterior half, anteriorly. They meet in the mid line and create a ventrally directed ciliary tract that connects up the dorsal anterior tract and the ventral posterior tract. At the confluence of the latter ciliary tracts the conflicting ciliary currents set material in a circular anti-clockwise rotation on the right side and in a clockwise direction on the left side. The region of confluence on each mantle lobe has a partner on the visceral mass. These currents are more complex than those of the various lucinaceans described by Allen (1958).

The ctenidia

The ctenidia are homorhabdic, non plicate and eulamellibranchiate. Each comprises one demibranch — the inner, though Purchon (1939) considered it the outer. The ascending lamella is attached to the visceral mass anteriorly by ciliary fusion (Fig. 10A) as for example in various anomiids (Atkins, 1937a; Morton, 1976a). The interlocking cilia are some 8 long. Posteriorly the dorsal edges of the left and right ascending lamellae fuse behind the visceral mass by tissue fusion (Fig. 12C). For comparison the tissue fusion of the ctenidial axis is also figured (Fig. 10B).

The ciliary currents of both lamellae (Fig. 12B) beat ventrally towards a ventral marginal food groove which transports material orally. The ciliary currents are thus of type G (Atkins, 1937b) and similar currents are possessed by the Lucinidae, Montacutidae and Teredinidae. Material passing into the ventral marginal food groove is passed directly

between the palps and so to the mouth. In view of their smallness it is likely that particles arriving at the palps on the crests of the groove are similarly not selected against and also enter the mouth.

Oralward currents in the ctenidial axis and in the junction of the ascending lamella of the inner demibranch with the visceral mass are created by the mantle and the visceral mass respectively and not by the ctenidia.

Each ctenidial filament (Fig. 11A) typically comprises four apical cells possessing frontal cilia (FC) 8 long; these cilia create the ventral flow of particles. The apical cells are flanked on each side by one, but occasionally two cells with large nuclei, 10 in diameter. These cells possess the stiff, interlocking eulaterofrontal cilia (EFC) (12 long) which flick particles onto the frontal cilia. Laterally a pair of cells possess the lateral cilia (LC) which create the inhalant stream. These cilia are 12 long. The arrangement of the filament cilia is the same as in many other lucinids e.g. *Divaricella* and ungulinids e.g. *Diplodonta,* but differs from thyasirids which also possess prolaterofrontal cilia (Allen, 1958). The filament is very long and is lined by large cells (GC) containing brown granular material. Similar cells are seen in the Lucinacea and Allen (1958) considered them excretory. Cords of these granular cells (Fig. 11B, GC) also line the inner, but not the outer, surface of the capacious supra-branchial chamber (SBC).

The labial palps

The labial palps (Fig. 13, ILP; OLP) are minute and comprise two triangular flaps of tissue delicately marked with three or four shallow ridges. They form extensions to the
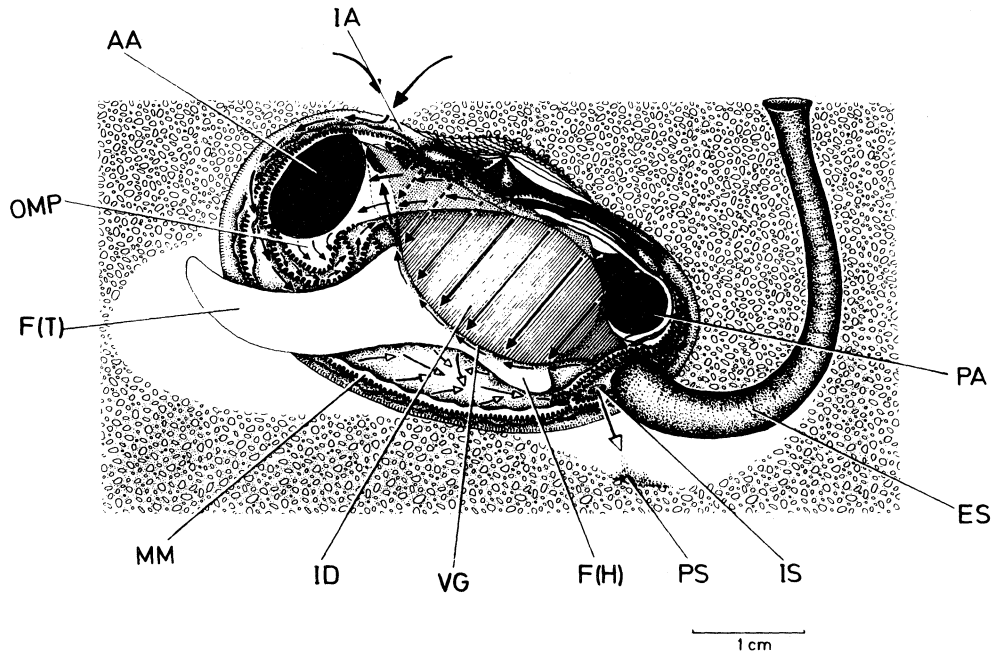

1 cm

Fig. 9. *Fimbria fimbriata.* The ciliary currents of the mantle cavity after removal of the left shell valve and mantle lobe. The animal is lying in its natural position in the sand. (Closed arrows, acceptance tracts; open arrows, rejectory tracts). (For abbreviations see page 419.)
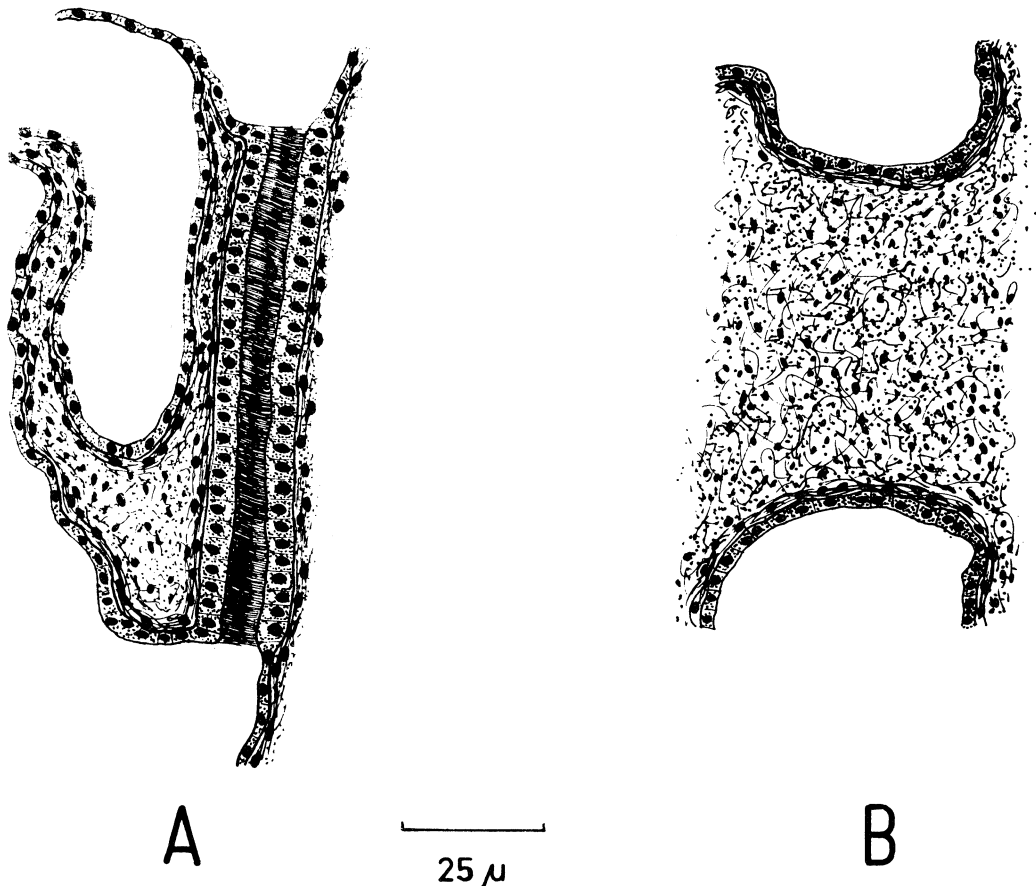
A

└─────────┘

25 μ

B

Fig. 10. *Fimbria fimbriata*. (A), the mode of attachment of the ascending lamella of the inner demibranch to the visceral mass. (B), the ctenidial axis. (For abbreviations see page 419.)

fleshy inner and outer lips (LP) of the mouth (MO). The lips possess rejectory currents which pass material laterally to the palps. The ctenidia pass between the palps, this being junction category 3 (Stasek, 1963) and typical of a condition seen in many bivalves including all the Lucinacea.

The "mantle palps"

The "mantle palps" (Fig. 14; IMP; OMP) are flaps of the inner surface of the mantle hanging in the anterior mantle cavity close to the mouth and anterior adductor muscle (AA). Allen and Turner (1970) and Boss (1970) following Pelseneer (1911) named them "mantle gills" ascribing a respiratory function to them since they are endowed with a good, secondary blood supply directly from the heart. Allen and Turner (1970), however, acknowledged that these structures might have a sensory and directional function. In section (Fig. 12A) the mantle palps are triangular in shape with an outer lateral surface (OMP), an inner surface (IMP) and an inner lateral surface. They are well ciliated and the

A

EFC   FC   N

LA

GC   25 µ

MM

B   GC

ME   SBC
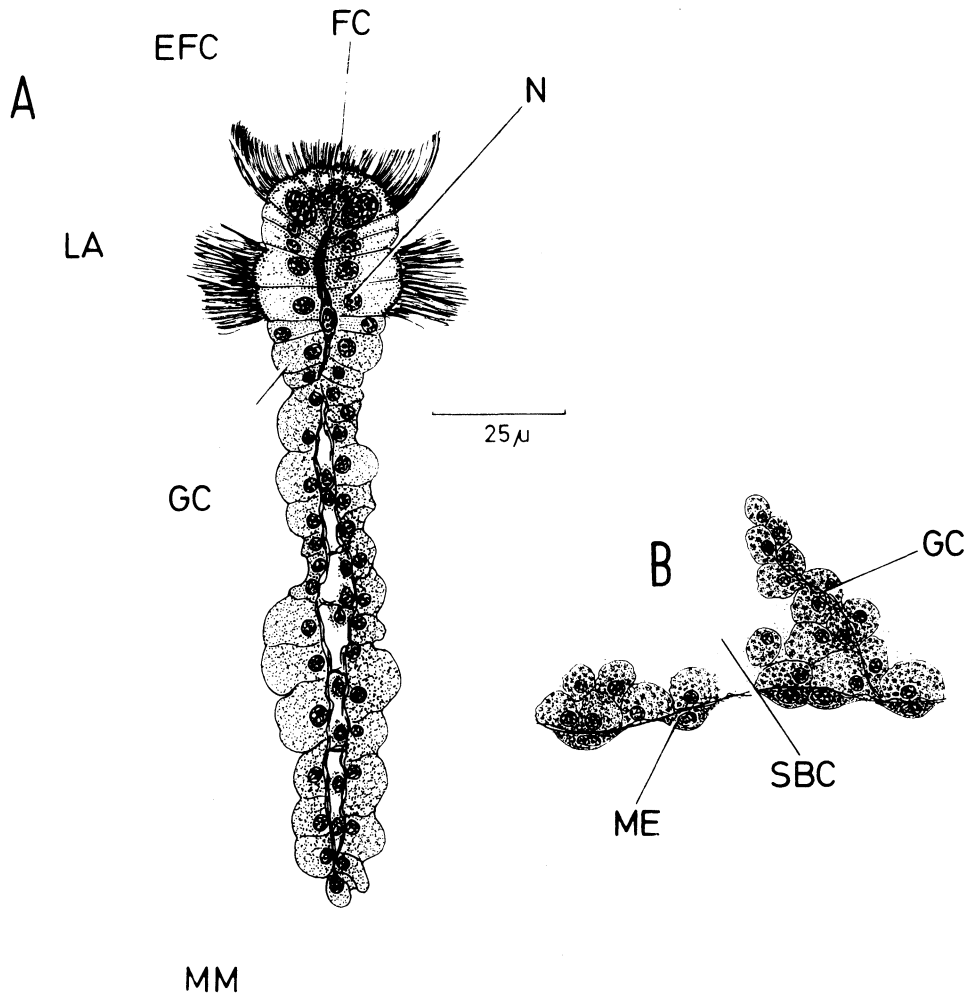
Fig. 11. *Fimbria fimbriata*. (A), The structure of a single ctenidial filament as seen in transverse section. (B), The granular cells which line the supra-branchial chamber. (For abbreviations see page 419.)

ciliary currents on their lateral outer surface (Fig. 14; OMP) are directed inwards. The inner margins of the mantle palps are fringed and on their inner surface (IMP) the ciliary currents are directed outwards and upwards from a dorsally directed central tract which takes material close to the mouth. The ciliary tracts on the inner lateral surface (Fig. 12A) pass material inwards and upwards towards the mouth. The inner and outer lateral surfaces of the mantle palps possibly trap or collect material arriving in the mantle cavity with the anterior inhalant stream (Fig. 16). The inner surface of the mantle palps, it is here suggested, serve to remove material from the foot which can, as will be discussed later, be considered the major food collecting organell. The inner surface of the mantle palps possibly wrap

around the foot as it is withdrawn into the mantle cavity removing particulate material from it by entrapping such material in the copious amounts of mucus produced by the epithelium of the inner surface of the mantle palp. Sections of the mantle palp show that the outer and inner lateral palp surfaces (Fig. 15B) comprise a squamous, non-secretory epithelium. The inner surface, however, comprises a mucous producing columnar epithelium (MC), 22 tall, that is also ciliated. Interspersed between these cells are other large globular secretory cells (SC).

The mantle palp arises as a fold (Fig. 12A and B; Fig. 14) from the junction of the ctenidial axis and mantle in the anterior half of the mantle cavity. The ciliary currents on the flap, prior to its enlargement to form the triangular-shaped mantle palp, pass material from the outer surface to the inner. The ciliary currents on the inner surface beat dorsally and contribute to an orally directed tract in the axis of the mantle palp and ctenidium (Fig. 12B).

The ciliary currents of the visceral mass

The ciliary currents of the visceral mass (Fig. 17) complement those of the mantle and the ctenidia. Postero-dorsally a weak anteriorly directed current gives way, where the fold of the mantle palp begins, to a strong anterior oralward current or acceptance tract located in the junction of mantle palp and visceral mass. In the dorsal half of the visceral mass the
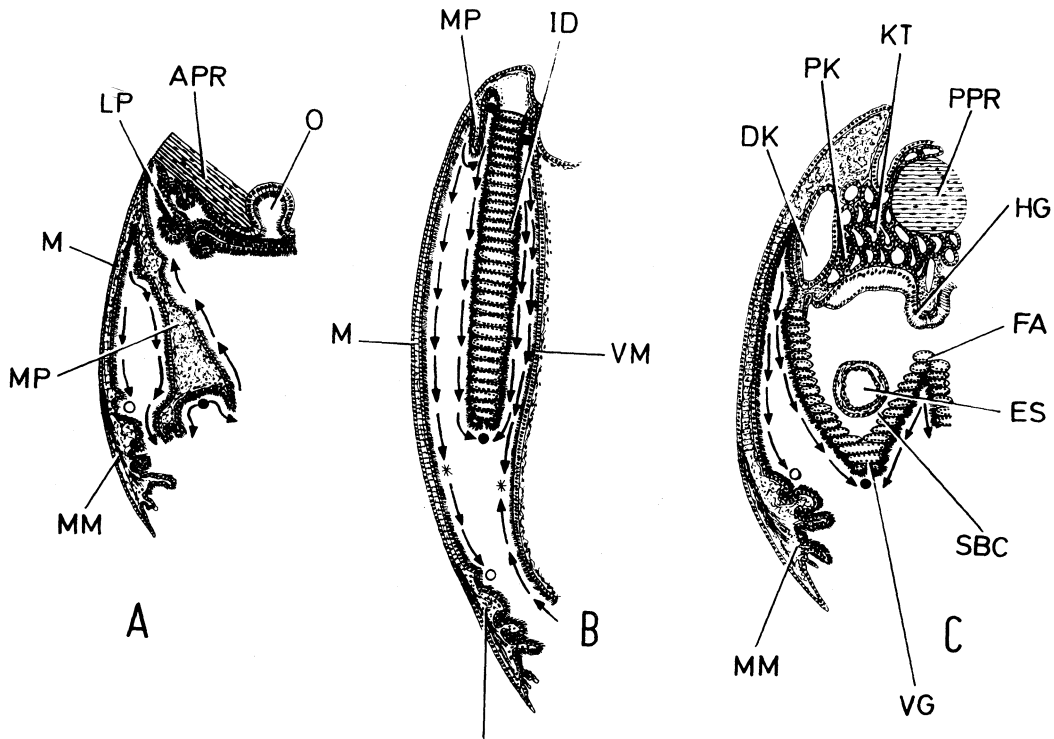

Fig. 12. *Fimbria fimbriata*. Semi-diagrammatic representations of transverse sections through the left side of the body. (A), anterior; (B), mid line; (C), posteriorly. (Closed circles = acceptance tracts; open circles = rejection tracts; * = areas of ciliary confluence). (For abbreviations see page 419.)
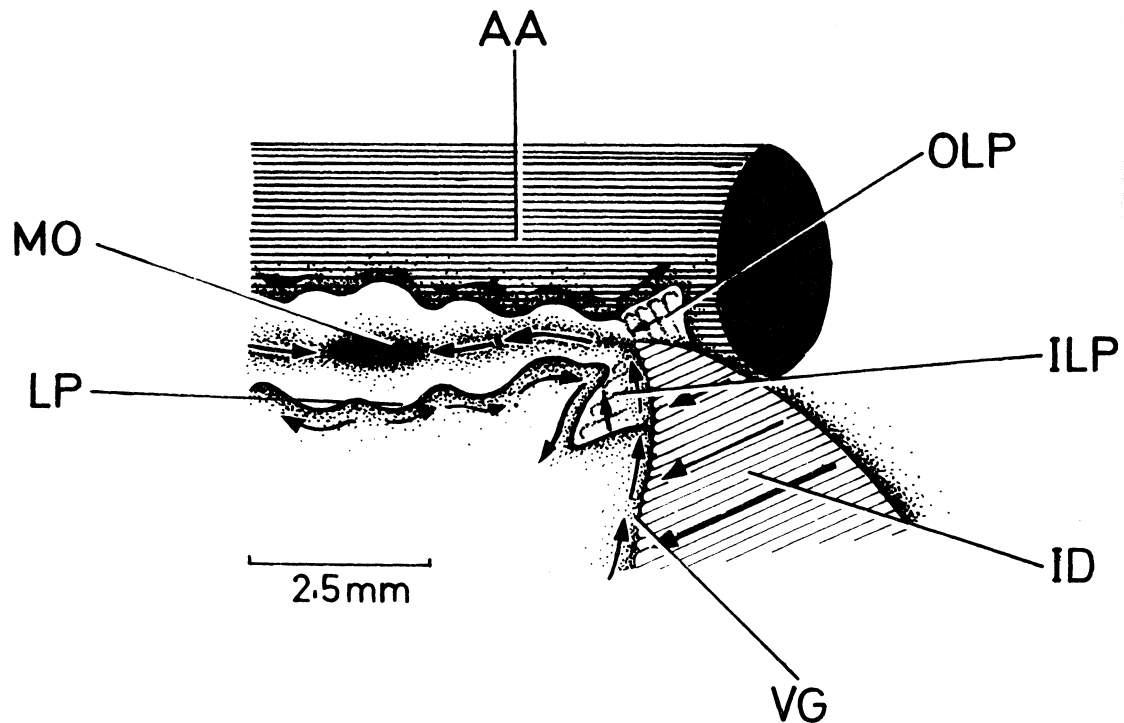
Fig. 13. *Fimbria fimbriata*. The mouth, lips and labial palps of the left side. (For abbreviations see page 419.)

currents are directed ventrally and contribute to longitudinal rejectory tracts that pass particles posteriorly from the anterior half and anteriorly from the posterior half of the visceral mass. These longitudinal tracts are also contributed to by the dorsally directed ciliary currents of the foot (F(T)). The confluence of these currents in the centre of the visceral mass results in material being circulated in a clockwise direction on the right side and in an anti-clockwise direction on the left side. The position of this area of confluence on the visceral mass approximates the position of the similar, but opposing directional ciliary confluence on the mantle. Thus, particles arriving in this region are wound into two mucous-bound streams that are removed by the major ventral rejectory tracts of the mantle to be expelled as pseudofaeces from the inhalant siphon (IS).

The foot

In the Lucinacea the tip of the foot is modified to form a long narrow tubular structure that is used to create and maintain the anterior inhalant tube. The posterior heel of the foot is locomotory. Allen and Tuner (1970) envisaged that the foot of *Fimbria fimbriata* similarly built the inhalant tube, but this is not so and the copious amounts of mucus produced by the foot are not used to bind together the sand grains of the tube, but are for the collection of sediment for food. The anterior tip of the foot (Fig. 17, F(T)) possesses strong ciliary currents that carry particles upwards towards the currents of the ctenidia and visceral

mass. The secretory areas of the foot are more dense towards the tip and comprise two types of subepithelial secretory cells. More granular eosinophilic secretory cells (Fig. 18 SC(E)) lie just under the foot epithelium, which, as noted by Allen and Turner (1970), is internally ringed by a thin layer of circular muscle. Internal to and overlapping with the eosinophilic cells are large numbers of basiphilic cells. Internal to these can be found bundles of longitudinal muscle fibres (LM) and radiating out from the centre of the foot, which possesses a central blood space, are numerous radial muscle bands (RM). The epithelium of the foot, comprising columnar cells 14 tall, is densely covered by cilia 5 long. Further evidence that the tip of the foot serves as a food collecting organelle and not a tube building structure, comes from a single specimen of *F. fimbriata* 76 mm long which had no
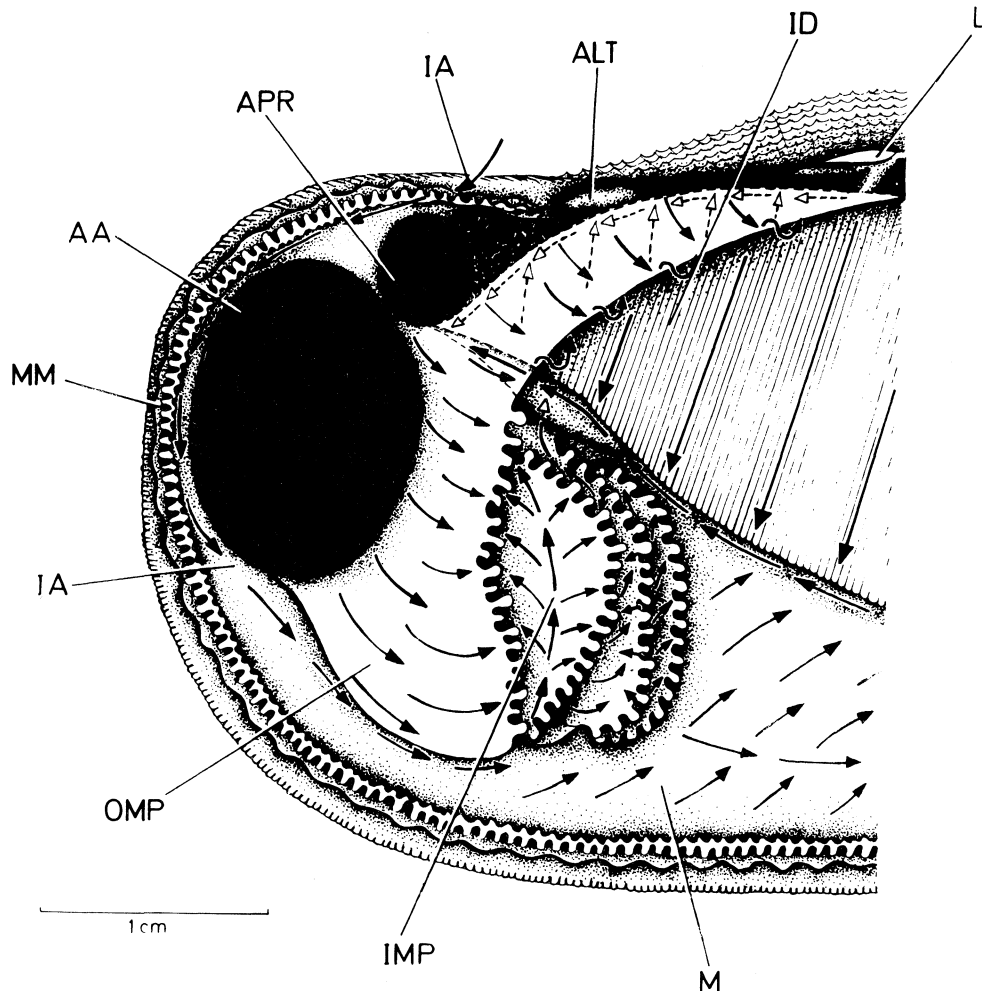
Fig. 14. *Fimbria fimbriata*. The ciliary currents of the anterior region of the mantle cavity, viewed from the left side after removal of the left shell valve and mantle lobe. (Closed arrows = ciliary tracts; open arrows = ciliary currents on the inner surface of the posterior region of the mantle palp). (For abbreviations see page 419.)
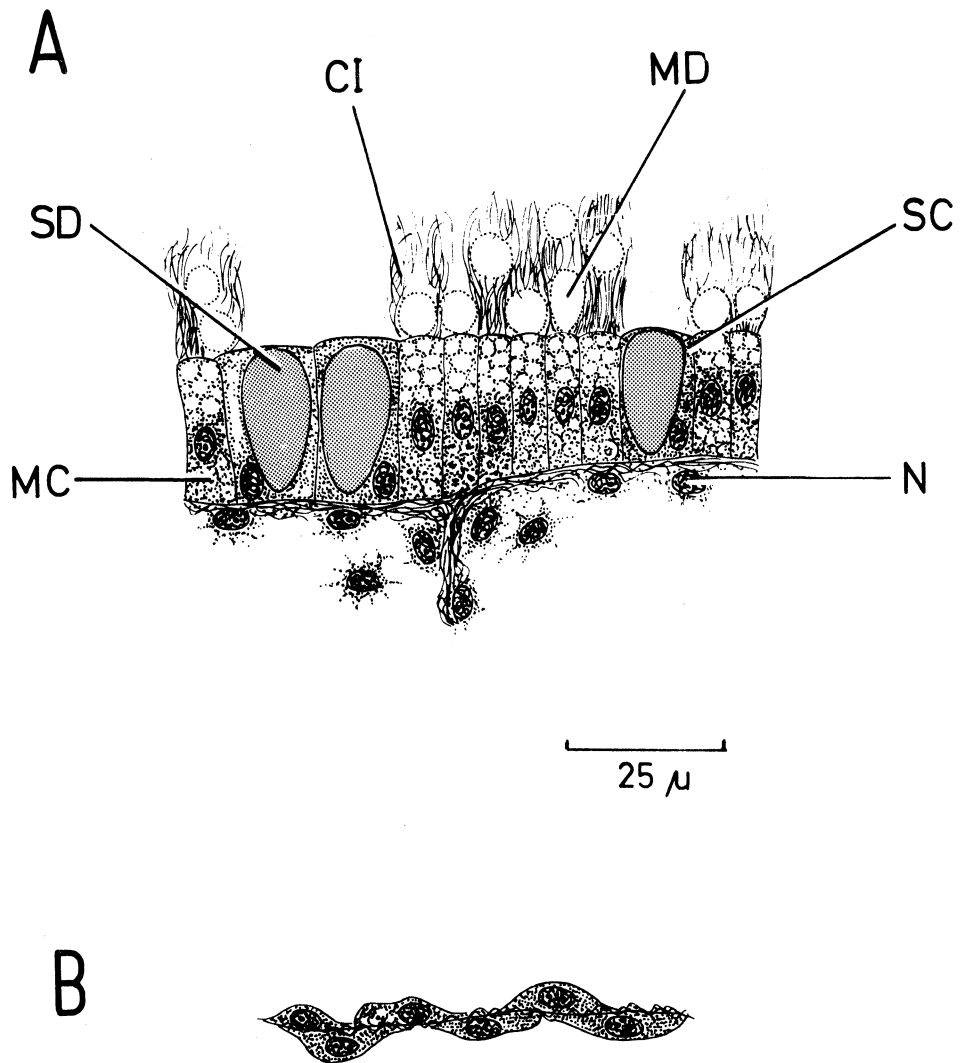
Fig. 15. *Fimbria fimbriata*. The structure of (A) the secretory epithelium of the inner surface of the mantle palp and (B), the outer surface. (For abbreviations see page 419.)

tip to the foot but which could still create the typical anterior inhalant depression in the sand. The small size of the heel (F(H)) of the foot indicates, as suggested by Allen and Turner (1970), that *F. fimbriata* is not a fast burrower. This is true.

The hypobranchial gland

The posterior surface of the visceral mass and the surface of the supra-branchial chamber is covered by an epithelium that has virtually all the characteristics of a hypobranchial gland (Fig. 19, HG) hitherto reported only from the Protobranchia e.g. *Nucula delphinodonta* (Drew, 1901) and prosobranch gastropods (Fretter and Graham, 1962).

2·5 mm
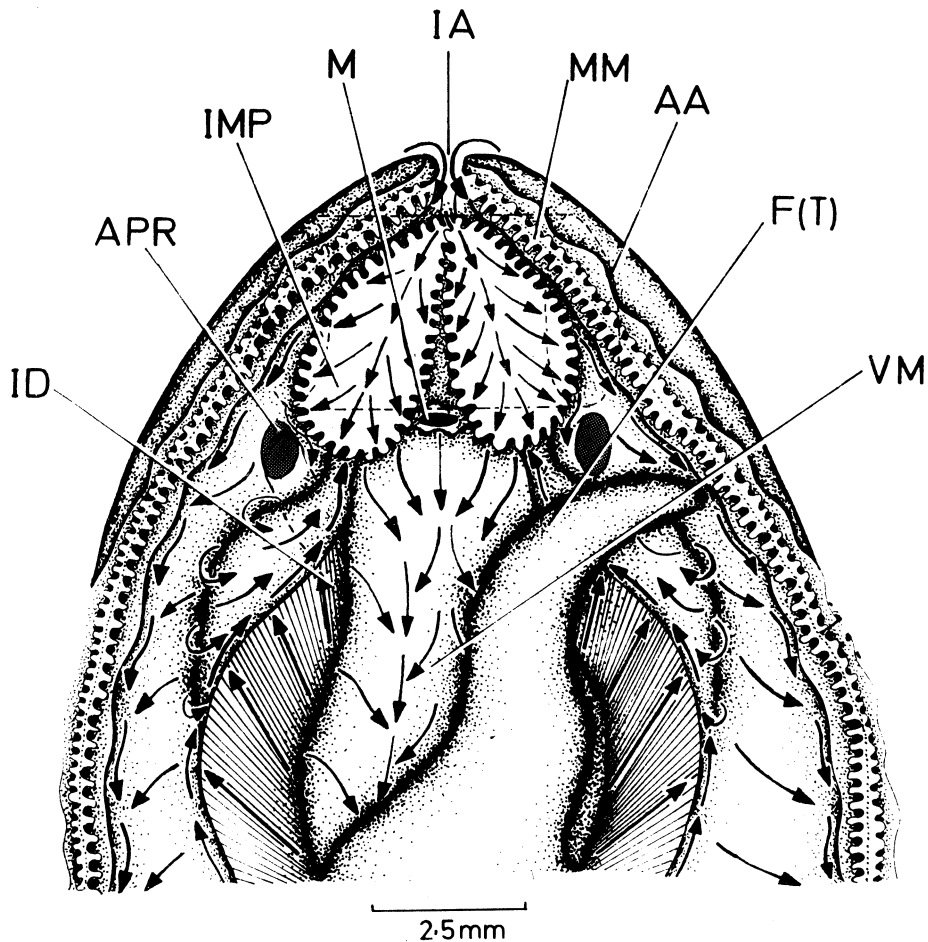
Fig. 16. *Fimbria fimbriata*. A ventral view of the organs of the mantle cavity, showing their ciliary currents. The animal has been removed from the shell. (For abbreviations see page 419.)
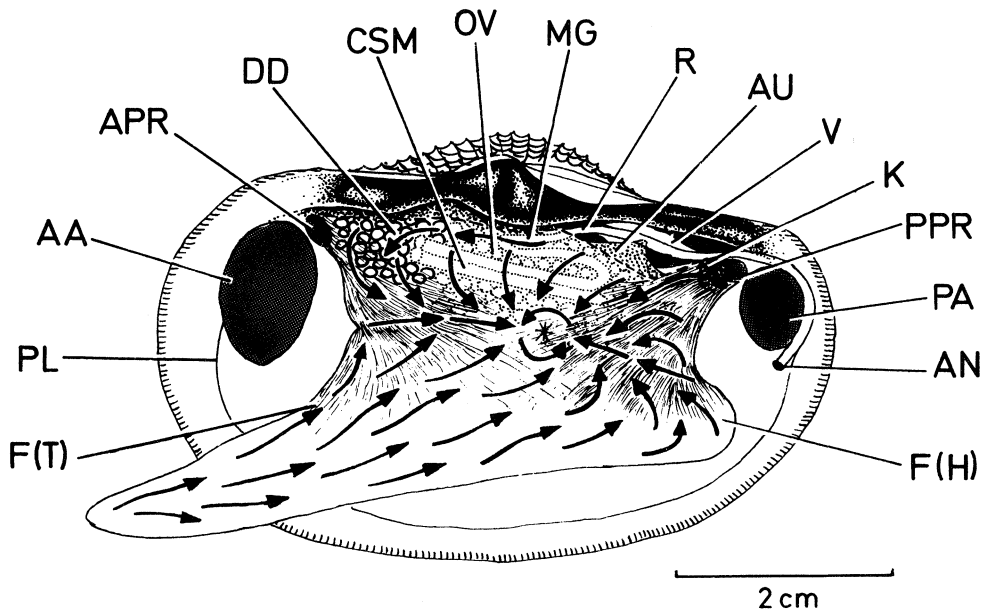
Fig. 17. *Fimbria fimbriata*. The ciliary currents and structure of the foot and visceral mass viewed from the side after removal of the left shell valve, mantle lobe and ctenidium. (* = area of ciliary confluence). (For abbreviations see page 419.)
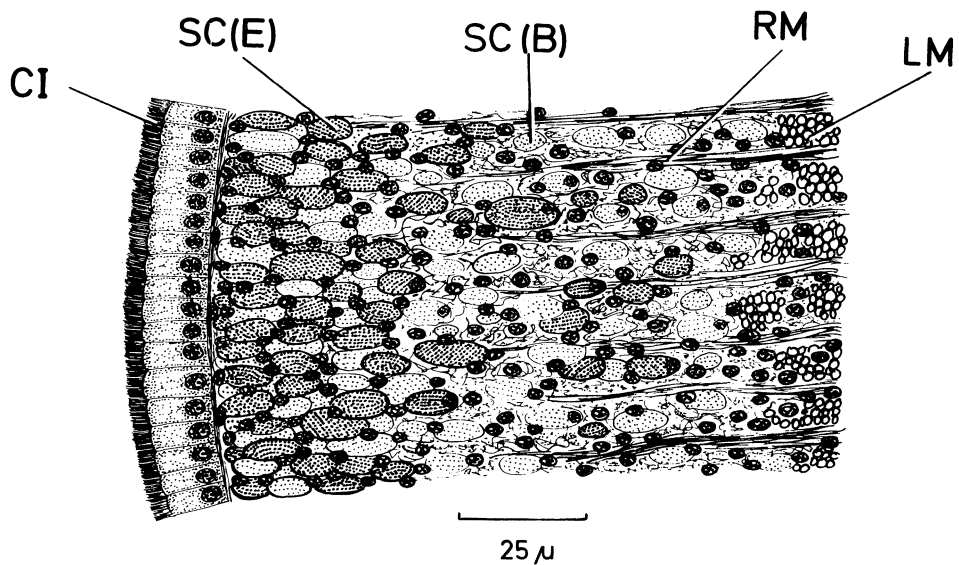
Fig. 18. *Fimbria fimbriata*. A semi-diagrammatic representation of a transverse section through a portion of the tip of the foot. (For abbreviations see page 419.)
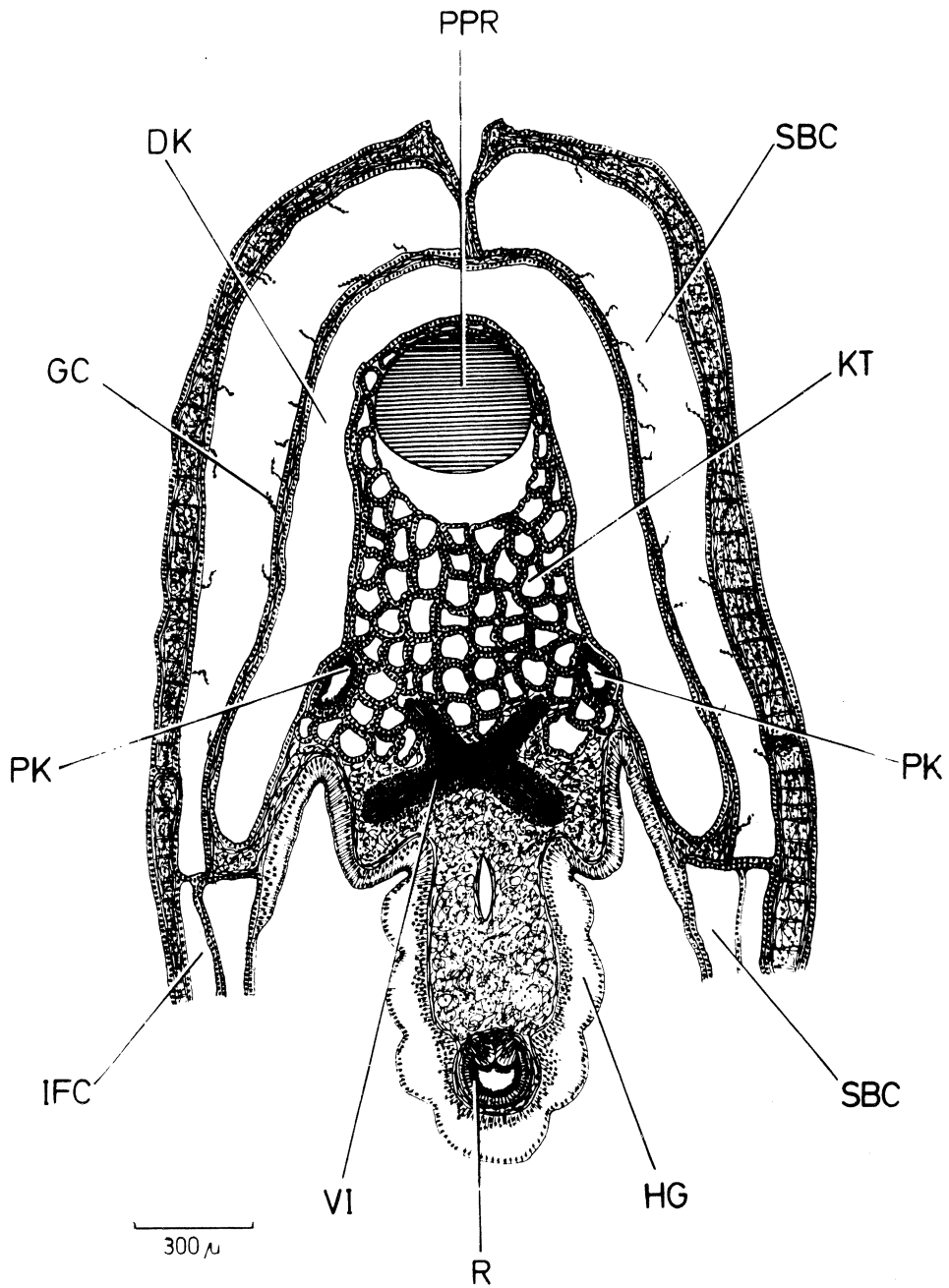
Fig 19. *Fimbria fimbriata*. A semi-diagrammatic representation of a transverse section through the posterodorsal region of the body. (For abbreviations see page 419.)

The detailed structure of the hypobranchial gland of *Nucula, Solemya, Fimbria* and *Corbicula* has recently been described by Morton (1977) but it is pertinent to briefly describe it here. The gland comprises two cell types, a tall columnar epithelium of mucous secreting cells 100-120 tall interspersed at the apices by small inversely flask-shaped cells of unknown but possibly regenerative function. These cells are not ciliated as they are in *Solemya* and *Nucula*. The possible function of such an extensive gland in *F. fimbriata* will be discussed later.

THE DIGESTIVE SYSTEM

The oesophagus

The oesophagus is very long (not short as suggested by Boss (1970)) and (Fig. 21A) passes upwards from the mouth which in turn lies under the anterior pedal retractor muscle. In transverse section the oesophagus which is some 160 in diameter, comprises a ciliated epithelium that is thrown into 11 pleats; four dorsally, seven ventrally. The cells range in height from 25-60 and the cilia are 10 long. The oesophagus enters the stomach anteriorly (Fig. 20, 0).
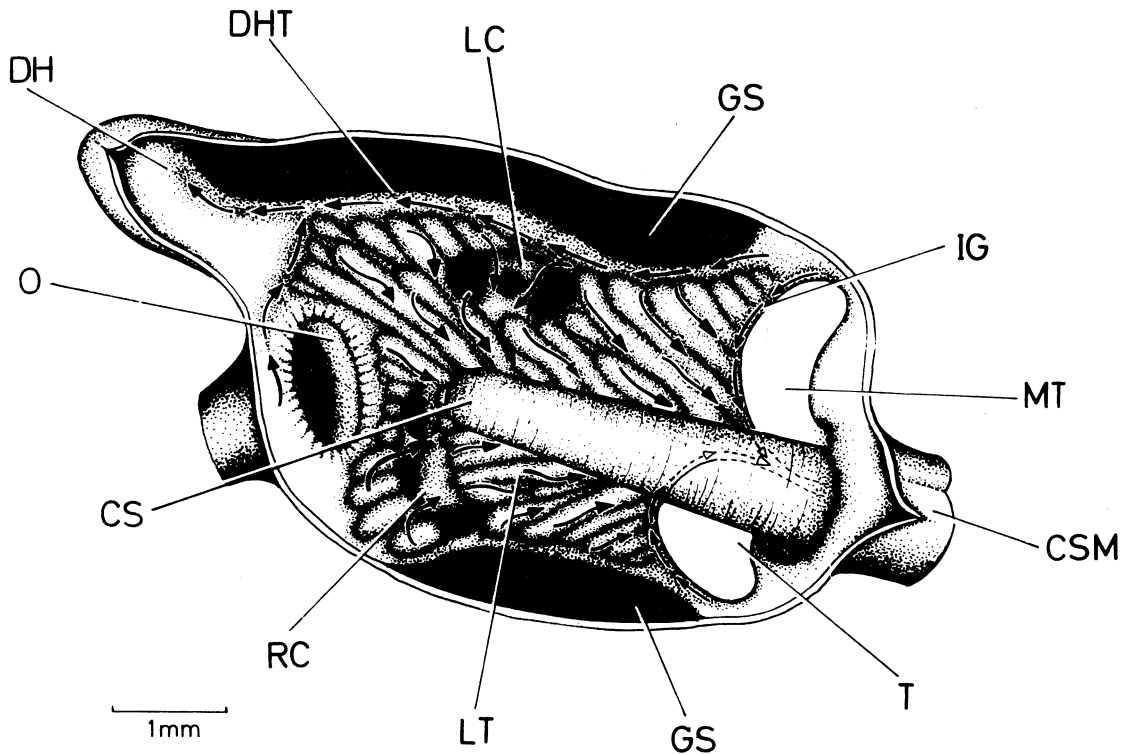
Fig. 20. *Fimbria fimbriata*. The structure and ciliary currents of the internal surface of the stomach after being opened via a dorsolateral incision in the left wall. (For abbreviations see page 419.)

The stomach

The structure of the stomach of *Fimbria fimbriata* has been reconstructed from sections by Allen and Turner (1970) but this study is of the living animal. The elongate, thin walled stomach (Fig. 20) is of type IV (Purchon, 1958) and is very simple. There are two typhlosoles, the minor (MT) and the major (T). Both arise from the conjoined style sac and mid gut (CSM) and flare out onto the floor of the stomach, where they terminate. The crystalline style (CS) is small and rotates against an extensive gastric shield (GS) that lines the left side of the roof of the stomach and the dorsal hood (DH). No spur of the gastric shield is sent into the apertures leading to the digestive diverticula though there is, as noted by Allen and Turner (1970), a tooth anterior to the lower side. There is a ciliated tract — the dorsal hood tract (DHT) — recirculating material to the dorsal hood and gastric shield and is located just below the gastric shield on the left side of the stomach.

The floor of the stomach comprises a series of longitudinal folds or pleats (LT) that extend towards the intestinal grooves (IG) of both minor and major typhlosoles. Down longitudinal furrows that are located between the pleats is carried particulate material that is, presumably, too large to be taken into the openings to the ducts of the digestive diverticula. The openings to the digestive diverticula are, however, large.

According to Allen and Turner (1970) the digestive diverticula open into the stomach via "three ducts close together on the right hand side, one large duct on the left and a second large duct ventral and posterior to the latter on the floor of the stomach." Certainly three ducts open into the stomach on the right side close together and constitute the right caecum (RC). On the left side, the two separate ducts referred to by Allen and Turner (1970) are no more than the two components of the left caecum (LC). Thus the structure of the stomach is very simple, though not as simple as those lucinids e.g. *Thyasira flexuosa* and *Lucinoma borealis* described by Purchon (1958). Significantly the stomach of *F. fimbriata* is more similar to that of the lucinids *Lucinoma* (Purchon, 1958), *Lucina* and *Loripes* (Allen, 1958) than it is to other members of the Lucinacea.

The style sac

The style sac and mid gut are conjoined and pass from the posterior edge of the stomach into the visceral mass posteriorly (Fig. 17, CSM). They do not penetrate the foot deeply as in many other bivalves e.g. *Geloina erosa* (Morton, 1976b). The structure of the separated mid gut will be described later.

In transverse section (Fig. 21D) the style sac, which is some 280 in diameter, is seen to comprise a number of epithelial zones earlier recognised for a number of other bivalves by Kato and Kubomura (1954) and by Morton (1969, 1973b,c, 1976a,b). The A cell layer comprises a columnar epithelium of cells 25 tall and possessing cilia (Cl) 10 long. The nucleus of these cells is located basally. The A cell layer constitutes some 50% of the epithelium of the style sac and is thought to facilitate the rotation of the style (CS). The A cell layer is separated from the mid gut, which is lined by a short (10) sparsely ciliated epithelium, by the two typhlosoles — major (T) and minor (MT(B_1)). In *F. fimbriata* the cells of the minor typhlosole (MT(B_1)) are modified and possess a granular cytoplasm. They are some 100-120 long and possess an elongate nucleus 10 long located in the centre of the cell. They are sparsely ciliated by cilia 10 long and from the distal surfaces of these cells could be seen secretory droplets in the process of being budded off and which had formed a layer of unsolidified style material (US) around the solid crystalline style. Similarly Goreau, Goreau and Yonge (1966) and Bernard (1973) have shown that the typhlosoles of
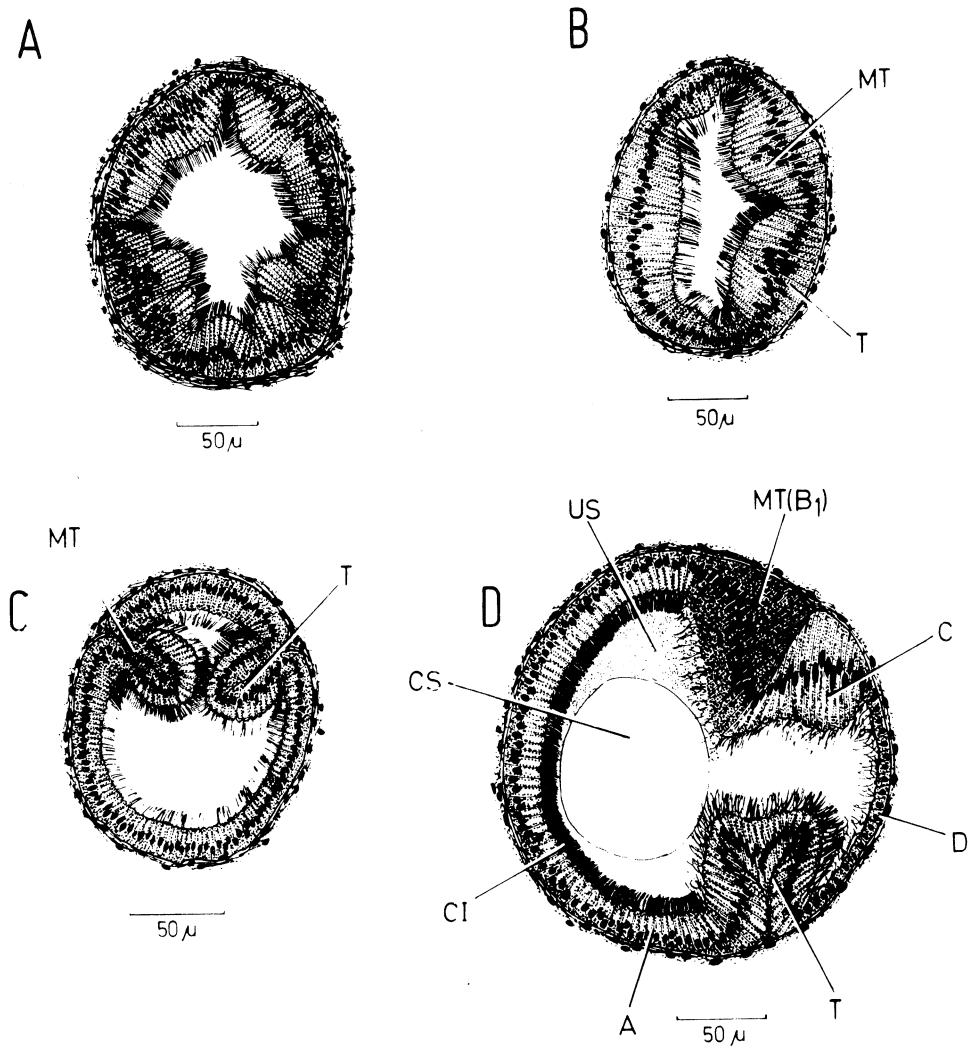
Fig. 21. *Fimbria fimbriata*. Transverse sections though (A), the oesophagus; (B), the mid gut; (C), the rectum and (D), the conjoined style sac and mid gut. (For abbreviations see page 419.)

Tridacna and *Crassostrea* are secretory. Opposite the minor typhlosole is the major typhlosole (termed the B cell layer in other bivalves) which in the case of *F. fimbriata* appears little modified and comprises cells approximately 80 tall with a central nucleus and long cilia distally. Abutting the B_1 cell layer (the minor typhlosole) can be seen a group of cells which appear to be a modified region of the minor typhlosole. They too are tall (100) and possess an elongate nucleus. The cilia they possess are long and sparse, though the ciliary rootlets are easily discernible within the cells. These cells are reminiscent of the C cell layer of other bivalves e.g. *Dreissena polymorpha* (Morton, 1969) though they do not

possess the short stiff cilia of these bivalves. The D cell layer (the mid gut) unites the two typhlosoles. In other bivalves this region of the style sac and mid gut secretes the matrix of the style, e.g. *D. polymorpha* and *Galeomma takii* (Morton, 1969, 1973b).

The mid gut and rectum

After separating from the style sac posteriorly, the mid gut (Fig. 17, MG) then loops back above itself to pass anteriorly. It undertakes another turn to penetrate the ventricle (V) of the heart as the rectum (R). The rectum passes over the posterior adductor muscle (PA) and terminates on the posteroventral face of this muscle as the anus (AN).

In transverse section (Fig. 21B) the mid gut is some 130 in diameter and possesses both minor (MT) and major typhlosoles (T), the cells being some 40-45 tall and possessing cilia 12 long. The opposite side of the mid gut comprises an epithelium 50 tall which also possesses long cilia.

The rectum, some 125 in diameter, (Fig. 17C) also possesses the two typhlosoles which are reduced to small prominent flaps composed of cells 18-20 tall possessing long cilia. The remainder of the rectum comprises an epithelium of approximately similar height, similarly ciliated.

THE PERICARDIUM AND THE KIDNEY

The pericardium lies under the ligament. The heart (Fig. 17) comprises a single ventricle (V) and two auricles (A) — the latter being somewhat pigmented. The ventricle is penetrated by the rectum (R).

The black kidney (K) lies behind the pericardium and lines the anterior faces of the posterior pedal retractor muscles (PPR). From the posteroventral surfaces of the pericardium arise two renopericardial apertures which open into the small ciliated proximal ducts of the kidney (Fig. 19, PK). These ducts posteriorly communicate with the much larger and non-ciliated distal limb of the kidney (DK) which opens into the supra-branchial chamber via a slit-like renal aperture ventrally. The distal limbs of the kidney communicate one with the other above the posterior pedal retractor muscles (PPR). The walls of the distal limbs of the kidney comprise a system of meandering tubules similar in structure to those of *Laternula truncata* and *Cleidothaerus maorianus* (Morton, 1973c, 1974). The cells of the kidney are some 12-15 tall and contain few yellowish concretions.

DISCUSSION

Scientific interest in *Fimbria fimbriata* centres around its systematic status; Nicol (1950) creating a new family for it — the Fimbriidae. Allen and Turner (1970) argued, however, that the species is a member of the Lucinidae and this latter assertion gains considerable support from the results of this study. Boss (1969, 1970), however, did not question the creation of a new family by Nicol (1950), but acknowledged that the Fimbriidae and Lucinidae were very close phylogenetically.

The general similarity of the shell of *Fimbria* to that of the Lucinacea, is enhanced by the researches of Taylor, Kennedy and Hall (1973) who have shown, on the basis of shell structure and mineralogy, that the shell of *Fimbria* is essentially similar to the shell of members of the Lucinidae. *Fimbria*, as in other lucinids (Allen, 1958) possesses but one demibranch that Purchon (1939) considered to be the outer but which Allen (1958) showed

to be the inner. The ciliary currents of the single demibranch are of type G (Atkins, 1937b). In the Ungulinidae and Thyasiridae both demibranchs are present — Boss (1969) unwisely suggesting that "the Diplodontidae and Thyasiridae have secondarily evolved an external demibranch." The detailed structure of the ctenidial filament of *Fimbria* is also similar to that of the lucinid *Divaricella quadrisulcata* whereas the filaments of *Thyasira flexuosa* possess prolatero frontal cilia (Allen, 1958).

The labial palps of *Fimbria* are reduced to mere enlargements of the lips of the oral groove as in various lucinids whereas the palps of members of the Ungulinidae and Thyasiridae are larger and possess typical ciliated folds (Allen, 1958). Most significantly *Fimbria* like *Codakia orbicularis* and *Lucina pennsylvanica* (Lucinidae) (Allen, 1958; Allen and Turner, 1970), possesses what Allen (1958) and Boss (1970) termed (following the term "pallial gills" erected for three species of *Lucina* by Pelseneer (1911)) "mantle gills"; ascribing to them a respiratory function, because they are well supplied with blood. In *Fimbria,* however, they possess a different function. They wipe (by the production of a, presumably sticky, secretion from the epithelium of their inner surface) sand grains and detritus particles from the foot. The foot, which also possesses abundant secretory cells is the major food collecting organelle of the mantle cavity; the water above the sand being typically nutrient deficient. The mantle palps by means of the complex currents on their inner surface pass the collected material dorsally towards the mouth. In the clean, well aerated coral sands it is difficult to see why *Fimbria* should need extra respiratory surfaces. Similarly both *C. orbicularis* and *L. pennsylvanica* (Allen, 1958) live in clean coral sands and it is here suggested that in these species too the prime function of these structures is to replace the vestigial labial palps that were presumably lost early on in the adaptive radiation of the Lucinidae. A primitive trend in the Lucinacea towards reduction of the labial palps has favoured, presumably as a greater adaptive radiation in life styles subsequently ensued, the evolution of structures with an essentially similar function but different origin, i.e. the inner mantle surface. A more detailed study of the ciliary currents of the "mantle palps" (as they should possibly be more correctly termed) in the various lucinds studied by Pelseneer (1911) and Allen (1958) might more clearly reveal their true function. The stomach of *F. fimbriata* is more closely similar to that of the lucinids *Lucina pennsylvanica* and *Loripes lucinalis* (Allen, 1958) and is exceptionally simple as in those lucinids described by Purchon (1958). Extensive areas of the floor of the stomach of *F. fimbriata* remove particulate matter towards the intestinal grooves of the typhlosoles for eventual defaecation via the mid gut. This is undoubtedly a reflection of the large amounts of sediment ingested; the stomach of the anomiid *Enigmonia aenigmatica* (Morton, 1976a) is, because the animal feeds in turbid mangrove waters, convergently similar to that of *Fimbria.*

The peculiar mode of withdrawal of the exhalant siphon — so like that of the Lucinidae — is a final factor which clearly allies *Fimbria* with this family. This method of siphonal retraction appears to be unique to the Lucinidae and is a means to house and protect long siphons within the mantle cavity other than the method possessed by more conventional bivalves where the siphons are withdrawn (but not invaginated) into the infra-branchial chamber by siphonal retractor muscles. Hence the deep pallial sinus of deep burrowers e.g. the Tellinacea (Yonge, 1949).

There can be little doubt therefore that *F. fimbriata* is closely related to the Lucinidae and future research must now be directed towards deciding whether subsequently described (fossil) members of the Fimbriidae (Chavan, 1969) similarly closely recall the condition in the Lucinidae and whether there is any justification for the erection of the Fimbriidae by Nicol (1950).

McAlester (1966) has suggested that the Ordovician fossil *Babinka* is an evolutionary transition between the bivalve superfamily Lucinacea and some monoplacophoran-like ancestral bivalve. McAlester further suggests, a thesis subsequently supported by Boss (1970), that the Lucinidae are more primitive than other lucinaceans and if this is so then the primitive probing foot of *F. fimbriata* as opposed to the tube-building foot of other lucinids might indicate that *Fimbria* is one of the more primitive members of this ancient group. Moreover, the mode of life of *F. fimbriata,* lying with the antero-dorsal inhalant aperture close to the sand surface closely recalls that position postulated for *Babinka* (McAlester, 1965; Fig. 6).

Allen (1958) suggested that the Thyasiridae and Ungulinidae were more primitive because modern representatives of these families possess both ctenidial demibranchs and large labial palps. This would indicate a trend towards a reduction in the sorting of particulate material and an increase in the acceptance of large particles and thus a change from a filter feeding to a detritus feeding mode of life. The fossil record is irrefutable, however, (McAlester, 1965, 1966; Chavan, 1969; Boss, 1970), and as noted by Boss(1970) "the geological record itself provides a better clue to phylogeny than do inferences based on supposed anatomical features of fossil lineages".

It would thus seem that *Fimbria* is the sole surviving genus of an ancient lineage that is closely allied to the Lucinidae. It has retained a number of primitive features which give a greater insight into the mode of life of the early bivalve *Babinka*. The taxonomic status of the Fimbriidae must await a close examination of the fossil members of this group and their comparison with fossil lucinids.

The unique features of the Lucinacea certainly set them apart from all other bivalves and McAlester (1966) concludes that they should be treated as a separate bivalve taxon of "the highest rank" that are probably unrelated to most other "heterodont" forms with which they are commonly associated (Newell, 1965, 1969). More extensive comparative researches are therefore needed upon the functional morphology of the Heterodonta Neumayr 1884 to determine the validity of this assertion. Boss (1970), however, disagrees with this view and summarises his arguments thus: "I have shown that the Lucinacea, old and persevering, are distinctly and obviously heterodont". There can be no doubt that the Lucinacea are phylogenetically old and though possessing unusual, possibly primitive, features, the major features of their morphology, as detailed by Boss (1970) and further in this study, do ally them with the Heterodonta and with the mainstream of eulamellibranch evolution.

The Lucinacea are, however, closely allied to the Leptonacea Gray 1847 which comprise a large group of typically small, often symbiotic (a term used here in the widest possible sense) bivalves which have simple mantle fusions, an anterior inhalant aperture, a posterior exhalant siphon, a wide pedal gape and a foot similar to that of *Fimbria,* and used only in locomotion and attachment but not in feeding. Many leptonaceans similarly also only possess a single, inner demibranch.

There can be little doubt that *Fimbria* possesses many primitive features. Not the least of these is the presence of a hypobranchial gland with a structure similar to that of the hypobranchial gland of *Nucula* and *Solemya* (Morton, 1977). In *Fimbria* the hypobranchial gland lines the roof of the suprabranchial chamber, behind the visceral mass and under the rectum — a position similar to that seen in the primitive protobranchs. The structure of the hypobranchial gland of *Fimbria* strongly suggests a secretory function which in the primitive "protobranch" bivalves was thought to coalesce particles leaving via the exhalant stream. Since in this "lamellibranch" particles are filtered out on the ctenidia, few reach the suprabranchial chamber. The gland possibly possesses a function similar to that seen in

the prosobranch *Gibbula* (Gersch, 1936) and the protobranch *Nucula delphinodonta* (Drew, 1901) where a secretion is produced to nourish externally protected eggs. In the lamellibranch *Corbicula fluminea* (Morton, 1977) the gland nourishes larvae developing within the inner demibranch. Given the close relationship existing between the Lucinidae (and *Fimbria*) and the Leptonacea — a superfamily which characteristically incubate eggs within a ctenidial marsupium — is it possible that *F. fimbriata* also incubates its eggs within the supra-branchial chamber and nourishes them with a secretion from the hypobranchial gland? Possibly the hypobranchial gland in the Bivalvia is a structure producing a secretion that was primitively concerned with the cleansing of the mantle cavity but which has, with the evolution of the lamellibranch ctenidium, come to be used to nourish incubated young. Significantly the supra-branchial chamber of *Fimbria* is capacious and lined by peculiar granular cells that possibly possess an excretory function in the Thyasiridae (Allen, 1958).

Despite primitive features *Fimbria* must also be examined with regard to the specialisations that adapt it for life in nutrient deficient tropical coral sands. *F. fimbriata* is infaunal utilising an anterior inhalant stream to maintain a supply of oxygen-rich water for respiration. In the same water stream may be carried food particles that are filtered on the ctenidia and carried orally. The major food source is, however, the sand grains and detritus collected by the sticky probing tip of the foot. Such material is transported to the mantle cavity by cilia and removed from the foot by special "mantle palps" that transport it towards the mouth. Complex and highly efficient rejectory tracts on the mantle and visceral mass remove sediment towards the posterior inhalant siphon where it is expelled, mucus bound, into the sand as pseudofaeces. *Fimbria* probably progresses forwards as it feeds and the posterior exhalant siphon is possibly periodically retracted and re-extended as it moves, albeit slowly. The alimentary canal, particularly the stomach, is similarly modified to receive large amounts of ingested food material; there being few sorting areas and extensive rejection tracts. In addition there are few apertures (but with large openings) leading to the digestive diverticula. Finally the stomach does not possess an appendix for the temporary storage of unwanted particulate material (Reid, 1965) as in the other major phylogenetic group — the Tellinacea — that has colonised coarse sands and are detritus feeders (Yonge, 1949).

The function morphology of *F. fimbriata* must thus be viewed from a number of perspectives. It has many specialised features adapting it to a life in clean coral sands, but the major interest lies in the primitive features that tell us more of the life style of an old bivalve lineage.

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ABBREVIATIONS USED IN THE FIGURES

A	A cell layer of the style sac
AA	Anterior adductor muscle or scar
ALT	Anterior lateral hinge tooth
AN	Anus
APR	Anterior pedal retractor muscle or scar
AU	Auricle
C	C cell layer of the style sac
CS	Crystalline style
CSM	Conjoined style sac and mid gut
CT	Cardinal tooth
D	D cell layer of the style sac
DD	Digestive diverticula
DH	Dorsal hood
DHT	Dorsal hood tract
DK	Distal limb of the kidney
EFC	Eulaterofrontal cilia
ES	Exhalant siphon
F(H)	Foot (heel)
F(T)	Foot (tip)
FA	Point of fusion of ascending lamellae of inner demibranchs
FC	Frontal cilia
FIF	Fused inner mantle folds
FO	Ctenidial axis
GC	Granular cell
GS	Gastric shield
HG	Hypobranchial gland
IA	Inhalant aperture
ID	Inner demibranch
IF	Inner mantle fold
IFC	Infrabranchial chamber
IG	Intestinal groove
IL	Inner ligament layer
ILP	Inner labial palp
IMP	Inner surface of "mantle palp"
IS	Inhalant siphon
K	Kidney
KT	Kidney tubules
L	Lunule
LA	Lateral cilia
LC	Left caecum
LI	Ligament
LM	Longitudinal muscles
LP	Lips of the mouth
LT	Longitudinal tracts
M	Mantle
MA	Mantle papilla
MC	Mucous cell
MD	Mucous droplet
ME	Mantle epithelium
MF	Middle mantle fold

MG	Mid gut
MM	Mantle margin
MO	Mouth
MP	"Mantle palp"
MT; MT(B1)	Minor typhlosole
N	Nucleus
O	Oesophagus
OF	Outer mantle fold
OLP	Outer labial palp
OMP	Outer surface of "mantle palp"
OV	Ovary
P	Periostracum
PA	Posterior adductor muscle or scar
PG	Periostracal groove
PK	Proximal limb of the kidney
PL	Pallial line
PLT	Posterior lateral hinge tooth
PM	Pallial musculature
PN	Pallial nerve
POL	Posterior outer ligament layer
PPR	Posterior pedal retractor muscle or scar
R	Rectum
RC	Right caecum
RM	Radial muscles
S	Shell
SBC	Suprabranchial chamber
SC	Secretory cell
SC(B)	Secretory cell (basiphilic)
SC(E)	Secretory cell (eosinophilic)
SD	Secretory droplet
T	Major typhlosole
U	Umbo
US	Unsolidified style material
V	Ventricle
VG	Ventral marginal food groove
VI	Visceral ganglion
VM	Visceral mass

THE LIZARD ISLAND MALACOLOGICAL WORKSHOP

A Molluscan Workshop, with nine malacologists participating, was held on Lizard Island, Queensland during 1 to 12 of December, 1975.

The aim of the Workshop was to get together a small number of malacologists at the Lizard Island Research Station on the Great Barrier Reef. Each scientist undertook one or two projects, the results of which are to be published in a collected series of papers. This issue of the 'Records' contains the first of these papers.

The scientists in attendance were:

Dr J. B. Burch (then of The Australian Museum, now at the University of Michigan);

Mr R. Burn (Research Associate of the Australian Museum and Associate of the National Museum of Victoria);

Dr B. Morton (University of Hong Kong);

Dr W. F. Ponder (The Australian Museum);

Dr C. F. E. Roper (Museum of Natural History, Washington, D.C.);

Mrs S. M. Slack-Smith (Western Australian Museum);

Dr J. B. Smith (National Museum of Victoria);

Dr B. R. Wilson (Western Australian Museum);

Sir C. M. Yonge (University of Edinburgh);

The projects included a survey of the non-marine Mollusca (Burch and Smith), studies on opisthobranchs (Burn), bivalve functional morphology (Wilson, Slack-Smith, Morton and Yonge), cephalopods (Roper) and gastropod reproductive morphology (Ponder).

Lizard Island (Figure 1) is a continental island in the northern end of Australia's Great Barrier Reef (lat. 14°40'S, long. 145°28' E). It is predominantly composed of granite, is about 2 square miles in area and at its highest point is about 360 m. It lies 30 km off the coast and is 17 km from the outer barrier reefs.

The Research Station on Lizard Island is operated by the Australian Museum. The participants of the Workshop acknowledge the support given them by the then Director, Mr S. Domm.

Mr P. H. Colman, Mr I. Loch, Ms B. Duckworth, Mr E. K. Yoo and Mrs M. Burch are also gratefully acknowledged for their able assistance with running and organizing the workshop.

One paper resulting from the workshop has been published elsewhere:

Morton, B., 1978. The diurnal rhythm and the processes of feeding and digestion in *Tridacna crocea* (Bivalvia:Tridacnidae). *J. Zool., Lond.*, 185: 371-387.

<div align="right">W. F. PONDER</div>

N

Mermaid Cove
(Kapok Cove)

North Point

North East Face

Granite Bluff
(Granite Head)

Turtle Beach
(Aboriginal Beach)

Huxley's Hump

50

150

50

50

100

150

Crystal Beach

Mrs Watson's Beach

Watsons Bay

200

250

300

Captain Cook Mountain

Cooks Lookout

350

Chinaman's Head

PRINCE CHARLES ISLAND
(Osprey Island)

Anchor Bay

Rocky Point

First Beach

Pebbly Beach

Third Beach

South Bay Point
(West Point)

Corner Beach

Ferriers Creek

Chinaman's Ridge

Pandanus
Swamp

LIZARD ISLAND

Air Strip

50

200

Pidgin Point
(East Face)

Coconut Beach

Casuarina
Beach

Research
Point

Freshwater Beach

Mangrove Beach
(Windy Beach)

Trawler Beach
(Fishermans Beach)

Lizard Head
(South Point)

Blue Lagoon

BIRD ISLAND

PALFREY ISLAND

Lighthouse

100

50

SOUTH ISLAND

100

50

SCALE 1:10,000

200 100 0   200   400   600

Coral Reef ......
Creeks -----
Metric Contours,
10 m. intervals