The Morphology of *Fimbria fimbriata* (Linné) (Bivalvia : Lucinidae)[1]

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ABSTRACT: The morphology of the shell and soft parts of *Fimbria fimbriata* is described and compared with that of other members of the Lucinacea. Particular attention is given to the ligament and hinge of the shell, and to the tissues and organs involved in food collection, sorting and digestion.

IN EARLIER STUDIES on the Lucinacea (Allen, 1958), specimens of the genus *Fimbria* (= *Corbis*) were unobtainable. Since then, through the kindness of Mme. A. Lapelerie, Magenta, Noumea, a few preserved specimens have been obtained. Therefore, the object of this study is to describe the morphology of this genus and make comparisons with other members of the Lucinidae (Allen, 1958).

The generic name *Fimbria* Megerle 1811 takes precedence over *Corbis* Cuvier 1817, although in past literature the latter is more commonly used. *Fimbria fimbriata* (Linné) occurs in coral sand in shallow water of tropical reefs in the south and central Pacific and northeastern Australia (Allan, 1950; Nicol, 1950). The very beautiful, large white shell was known to Victorian conchologists who described and pictured it. However, most accounts appear to have been taken from Reeve (1841). Information on the soft parts is scant, and recent descriptions are transcripts from those of Cuvier (1817) and Reeve (1841). Thus Woodward (1881) records: "Mantle open below, doubly fringed, siphonal opening single, gills single on each side, thick quadrangular, plaited, united behind." The only other studies since then are those of Lamy (1921) and Nicol (1950). Nicol gives details of its taxonomy, geographical distribution, and shell characters. At the same time, without giving any reasons, he erects a new family, the Fimbriidae.

OBSERVATIONS

Shell Characters

The shell of *Fimbria* is typical of the Lucinacea, being rounded with the umbones pointing anteriorly. The shell is white, becoming somewhat pink at either end where the radial ridges are flattened and form overlapping plates. The shell is heavy and thick (approximately 6 mm in thickness in a specimen 78 mm total length) and is extremely large for the rather small body of the animal it contains (Fig. 1). The sculpturing of the shell is reticulate; the concentric ridges are very pronounced but do not always extend continuously round the whole valve. The radial ridges are most pronounced at either end, and in addition there are short radial indentations between the concentric lines.

Anterior to the umbo there is a well-defined lunule which is brown in color, and posteriorly, less well defined, is a long oval escutcheon. Both are covered with thickened periostracum. There is no posterior radial indentation that corresponds in position with the gill axis, such as is found in other species of the Lucinacea (Allen, 1958).

The hinge plate bears two cardinal teeth below the umbo; in addition there are two lateral teeth which are widely separate from the car-

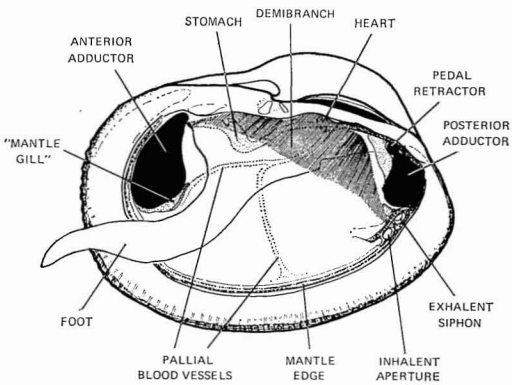

FIG. 1. *Fimbria fimbriata* (7 cm total length). Semidiagrammatic view of the arrangement of organs seen when the left valve is removed.

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dinals (Fig. 2). The anterior lateral tooth is situated below the lunule, and the posterior lateral tooth is close to the posterior limit of the hinge plate and posterior to the adductor scar.

Internally the valves are delicately colored pink and yellow—pink along the deeply crenellate ventral edge and yellow internal to the pallial line. The elongate anterior and more rounded posterior adductor muscle scars are large and white. Above the anterior adductor scar and merging with it can be seen the much smaller anterior retractor muscle scar. The posterior retractor muscle scar is discrete from the posterior adductor muscle scar, and it lies dorsal to it and underneath the posterior lateral tooth. Joining the two adductor muscle scars there is a white line marking the insertion of the pallial muscle, and internal to this and diagonally across the shell is a paler line that corresponds to the position of the large pallial blood vessel which runs across the mantle.

The ligament is internal and opisthodetic (Fig. 2). It corresponds to the condition in most other lucinids and in the genus *Codakia* in particular (Allen, 1960). In these earlier studies the ligament was shown to be composed of four layers—inner and outer layers, fusion layer, and periostracum. Yonge and Campbell (1968) have now suggested, from their work on *Dreissena,* that the fusion layer reported for many groups of bivalves may be an additional layer of fused periostracum, which is the result of the union of the inner surfaces of the outer mantle folds, and that union of the outer surface of the outer mantle fold, which would result in the production of a fusion layer, has not occurred. Certainly four layers can be distinguished in the Lucinacea, and *Fimbria* is no exception. These are the inner and outer layers, the periostracum, and a layer which lies between the periostracum and the posterior layer and which would formerly have been regarded as the fusion layer. This fourth layer is particularly thick in *Fimbria* and secondarily extends the ligament posteriorly.

Transverse sections of the mantle tissue underlying the ligament and traversing the posterior part of the mantle isthmus and the fused mantle edges posterior to the isthmus show that in the region of the fourth layer there is a pair of grooves separated by a slender ridge of tissue in the sagittal plane (Fig. 3*A*). This ridge extends to the posterior limit of the outer layer of the ligament. Below the outer layer, the secretory epithelium has a single sagittal groove. Examined by light microscopy, the epithelial cells secreting the outer layer and the fourth layer are

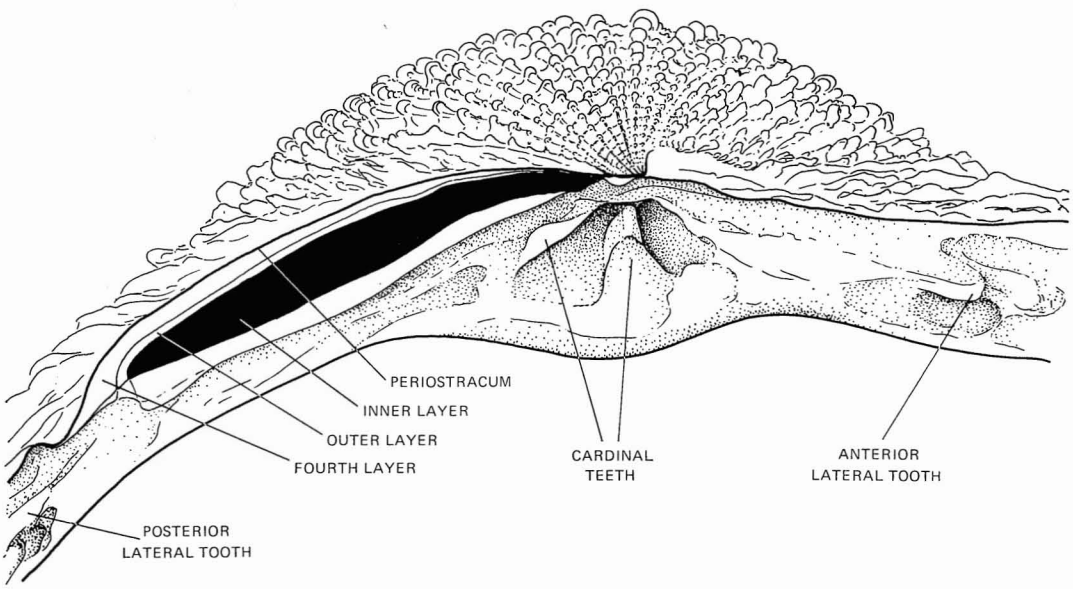

FIG. 2. *Fimbria fimbriata.* Lateral view of ligament and hinge region of the left valve.

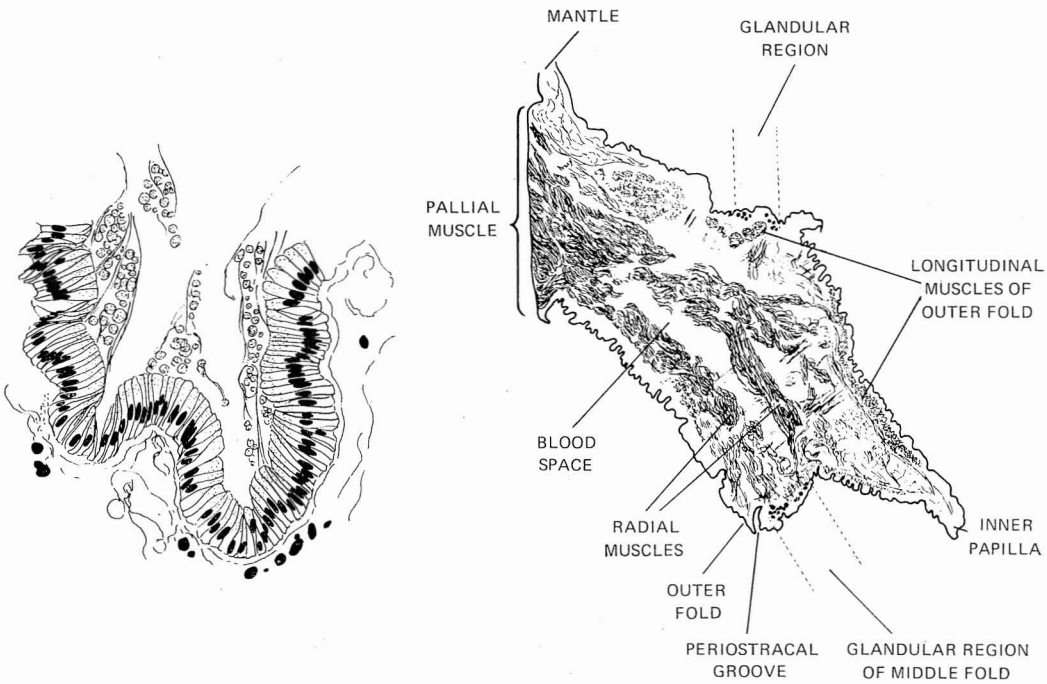

FIG. 3. *Fimbria fimbriata. A* (*left*), Transverse section through the mantle below the fourth layer of the ligament and immediately posterior to the primary ligament. For further details see text. *B* (*right*), Transverse section through the mantle edge on the ventral side.

indistinguishable from one another. They are tall narrow columnar cells with elongate central nuclei and with a granular cytoplasm.

Above this epithelium are numerous spherules containing granules. The sections indicate that these are cut off from the tips of the epithelial cells. In addition, in the region of the fourth layer, strands of a clear material can be seen between the spherules and originating from between the epithelial cells (Fig. 3*A*). Below the outer layer only spherules are present. Both types of material must be in the process of being added to the fourth layer of the ligament. This is unlike the typical sheet of periostracum produced, say, at the ventral edge of the mantle or that above the fourth layer. The strands and spherules are produced not only in the depths of the grooves, but extensively by the general epithelium of the region (Fig. 3*A*). It may be that the material forming strands is homologous with periostracum. Nevertheless, together with the spherules it does form a distinct and characteristic layer which has the function of extending the ligament, and we suggest that the term "fusion layer" be retained for this additional layer in *Fimbria* and in the Lucinacea generally. It should be noted that there is no extension of the pallial line from the posterior adductor below this fourth layer. This further supports the contention that this is fusion layer (Owen, 1958).

The free mantle edge is broad and comprises three folds. The outer fold is responsible for secreting the outer layer of the shell, while the periostracum is secreted by the cells at the head of the well-defined groove between the outer fold and middle sensory fold. The middle fold has a fringe of fine papillae along the entire length of its outer edge. To the inside of these papillae there is a second row of larger papillae or short tentacles which are best developed in the region of the exhalent and inhalent apertures. Two such rows are found in many lucinids (Allen, 1958). The inner muscular lobe is extremely well developed, although in the preserved specimens it has contracted greatly.

The histological details of the mantle edge are similar to those of other members of the family (Fig. 3*B*). The main rejection tract along the mantle edge is probably at the outer edge of the shelf formed by the inner boundary of the inner mantle fold. Beneath the epithelium of the shelf are numerous mucus-secreting cells which stain heavily with Aluminium Methylene Blue. These cells probably facilitate the conveyance of rejected material to the posterior part of the mantle cavity. Other mucus-secreting cells are found below the epithelium of the lower part of the inner fold and also of the middle fold. Internal to the inner fold there is no additional fold forming a roof to the main rejection tract, such as is found in *Phacoides borealis* and *Codakia orbicularis* (Allen, 1958).

The pallial musculature in *Fimbria* is very well developed and muscles extend well into all three folds (Fig. 3*B*). Longitudinal fibers running the length of the mantle edge extend in a broad band at the outer edge of the well-developed inner fold. At right angles and below the longitudinal muscles, radial muscles extend from the pallial line to the three folds. Those to the outer and middle fold run ventral to a large central blood space. In addition, transverse fibers from the outer epithelium and outer lobe cross blood spaces and packing tissue between the radial muscles to a position below the longitudinal fibers of the inner fold (Fig. 3*B*).

The extensive development of muscular tissue and the high degree of contraction of the preserved specimens suggest that this animal is capable of maintaining long periods of closure.

A pair of elongate, wedge-shaped structures, which are extensions of the inner mantle, lie adjacent to the right and left posteroventral margins of the anterior adductor muscle (Fig. 1). Each consists of a ridge of tissue with a groove running the length of the free edge, the lips of the groove being somewhat convoluted. Each ridge extends from the base of the adductor along the line of a pallial blood vessel for about 10–15 mm. They are probably homologous to similar structures described for *Codakia orbicularis* and *Lucina pennsylvanica* (Allen, 1958). *Fimbria* lacks the complex knot of tissue seen in *Codakia orbicularis,* nor does it develop a series of additional ridges, such as are present in these two species and which give rise to the term "mantle gill."

In transverse sections the central area of the ridge in *Fimbria* appears as a network of spaces outlined by thin cellular walls (Fig. 4*A*). The diameter of the spaces is in the order of 0.2 mm and they extend along the length of the ridge. The epithelial cells are ciliated, and below, parallel to their relatively thick basement membrane, there is a thin layer of muscle fibers. In addition, a few transverse muscle fibers run across the ridge through the inner spongy tissue. In the region of the groove and below the muscle layer there is a number of gland cells with granular contents, from which ducts lead to the outside between the epithelial cells. In this respect *Fimbria* differs from other lucinids, in which few gland cells have been recorded in the mantle gills (Pelseneer, 1911; Allen, 1958).

The function of the ridges in *Fimbria* may be respiratory; they lie adjacent to the inhalent current, and the blood spaces are extensive and in close connection with the pallial blood vessel. However, their position at the base of the anterior adductor muscle suggests that they may also act in the manner of guides and help in directing the inhalent current, together with its contained food particles, around the ventral limit of the adductor muscle toward the mouth. It is difficult to assign a function to the central groove of the ridges.

A pallial blood vessel extends from the ventral limit of the anterior adductor muscle across the mantle to join the axial vessel from the gills at a point where it enters the auricle. It is a large vessel, and from transverse sections it is clear that its lumen has a definite epithelial lining (Fig. 4*B*). Undoubtedly it acts as the main collecting vessel for the mantle haemocoele. In addition, there is a smaller vessel originating midventrally which connects with the main pallial vessel. Small numbers of muscle fibers are present along the outside of the wall of the main vessel, and it is possible that their contraction assists the passage of blood from the mantle to the auricles.

Apart from the region of the ligament, mantle fusion is minimal. As in other species of the Lucinidae, the whole outer face of the anterior adductor muscle is exposed and, pos-

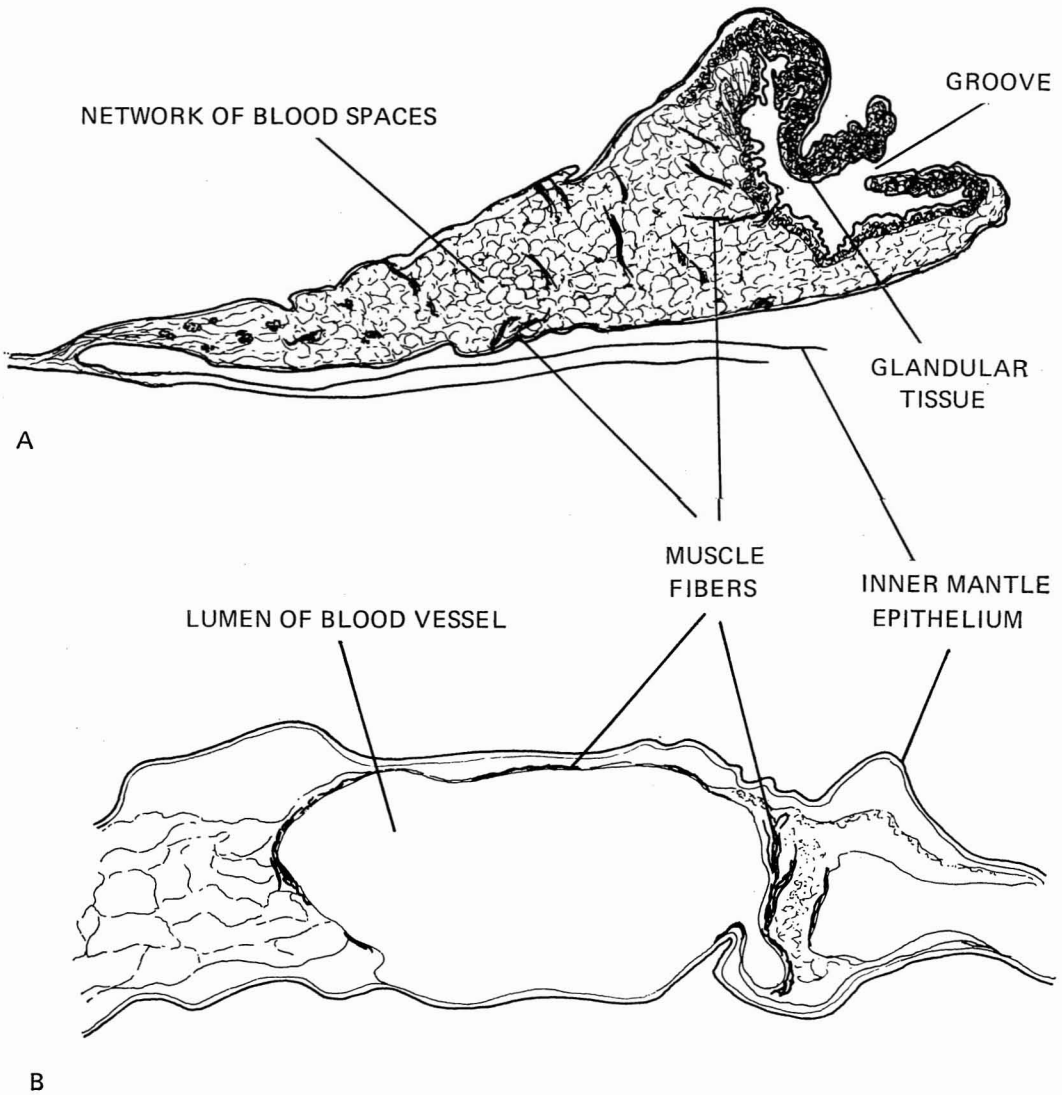

FIG. 4. *Fimbria fimbriata. A,* Transverse section through the "mantle gill." *B,* Transverse section through the pallial blood vessel.

teriorly, fusion between the inhalent aperture and the pedal aperture is slight, involving the innermost pallial muscles (Fig. 1). A double row of sensory papillae form a border to the apertures. This arrangement is similar to that in another large lucinid, *Codakia orbicularis*. In other species, papillae are either absent or border only the inhalent aperture where they are confined to the inner fringe of the sensory lobe (Allen, 1958). In *Fimbria* there are approximately 12 papillae on each side of the inhalent aperture and 40 on each side of the exhalent aperture.

The Lucinidae typically possess an exhalent siphon and no inhalent siphon. The exhalent siphon is developed from the inner muscular lobe of the mantle edge only, and is of a type unique in the Lamellibranchia (Allen, 1958). *Fimbria* is no exception, and the exhalent siphon when retracted lies inside out with the supra-

branchial cavity at the base of the posterior retractor muscle (Fig. 1).

Gills

As in other species of the Lucinidae, the gills of *Fimbria* consist of the inner demibranchs only. The demibranchs are large and, posteriorly, extend below the visceral mass (Fig. 1). In other species of the Lucinidae, the demibranchs are homorhabdic and nonplicate; they are also thick in cross section owing to extension of the abfrontal region of the filament (Allen, 1958). In *Fimbria* the gills are homorhabdic but plicate, although this condition is not immediately noticeable because the plicae are not thrown into folds. Sections show that the principal filaments occur at approximately 8 to 10 filament intervals. This arrangement recalls the condition in another lucinacean family, the Diplodontidae (Ridewood, 1903; Allen, 1958). The abfrontal surface of the filaments is not extended in *Fimbria,* so that the demibranch is not in any way thickened.

Palps

The palps, as in other lucinids, are much reduced and merely form slight enlargements of the outer limit of the lips. The latter are elongate ridges extending on either side of the mouth as far as the anterior limit of the ventral ciliated groove of the demibranchs (Fig. 5).

Alimentary Canal

The course of the alimentary canal in *Fimbria* is simple and differs little from that reported in other *Lucinacea* (Allen, 1968). In the preserved animals studied, the tissues surrounding the stomach were found to be very fragile and dissection was difficult. Therefore, a reconstruction of the anterior part of the gut as far as the style sac was made from serial sections (Fig. 6).

The oesophagus is unusually long, and its inner lining is longitudinally ridged. The stomach is also elongate, with a small dorsal hood anterior and to the left side. The style sac and midgut are combined and leave the stomach posteroventrally, and the hind gut continues as a simple loop passing through the ventricle of the heart and terminating ventral to the posterior adductor muscle (Fig. 1).

The form of the stomach is intermediate between that of *Loripes lucinalis* and *Codakia orbicularis* (Allen, 1958). The gastric shield lies to the left side. It has an anterior flange extending into the entrance of the dorsal hood, and there is no second lateral flange such as would fit into a left pouch. There is the usual well-defined tooth anterior and to the lower side of the gastric shield (Fig. 6). The apertures from the stomach to the digestive diverticula comprise 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

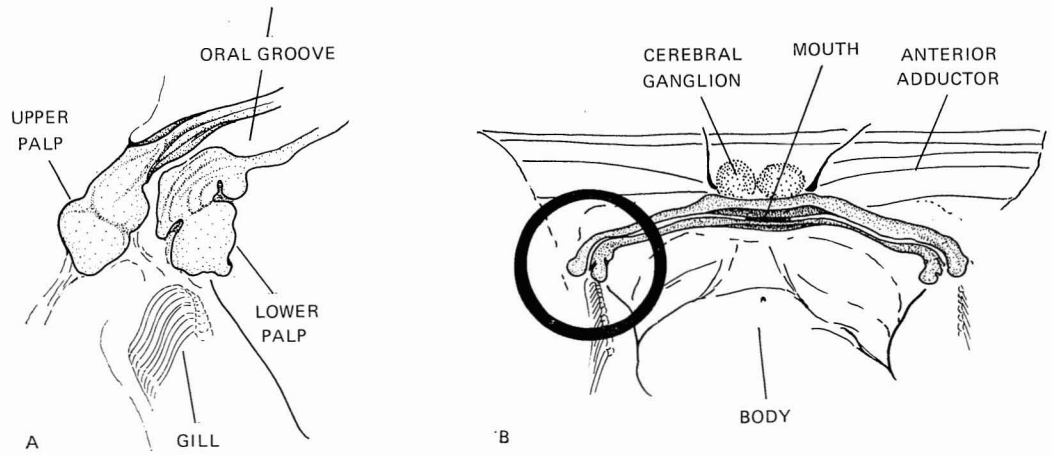

FIG. 5. *Fimbria fimbriata. A,* Enlarged drawing of the encircled region in *B,* to show more detail of the palps of the right side. *B,* Semidiagrammatic drawing of the region of the mouth.

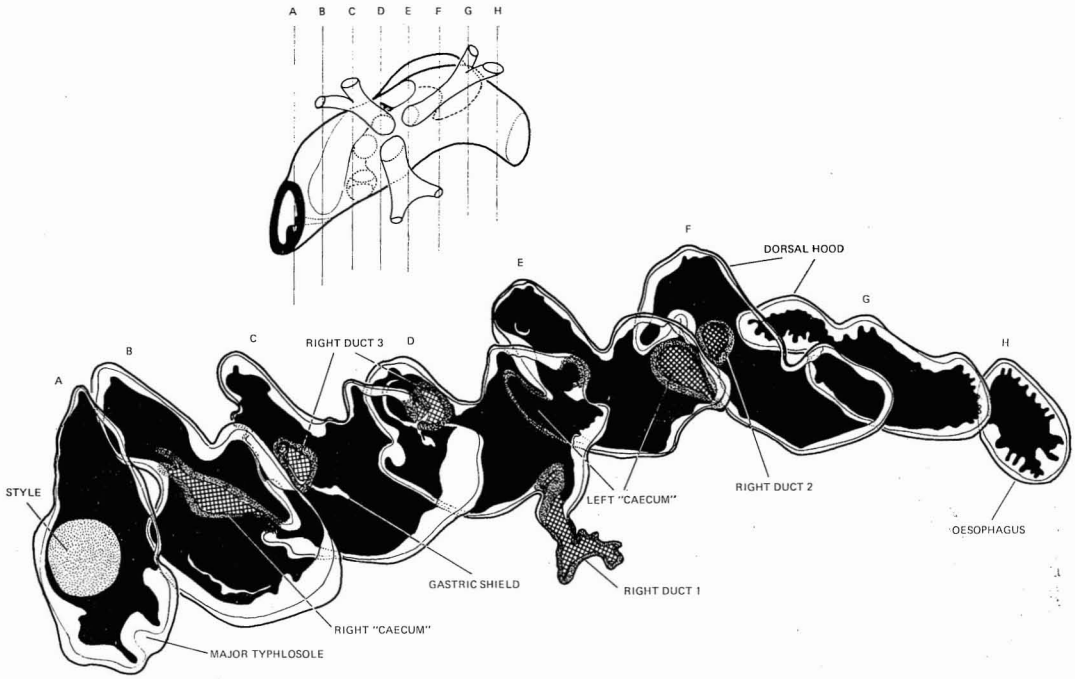

FIG. 6. *Fimbria fimbriata.* Transverse sections of the stomach arranged in an overlapping sequence. The sections are 10μ in thickness and each is 0.6 mm from the next. A diagrammatic reconstruction of the stomach, which is drawn from 450 or more serial sections, indicates the position of each of the eight selected sections *A–H*.

latter on the floor of the stomach. Of the ducts on the right side, two lead to diverticula on the right side and one to the ventral side of the stomach. The large left duct, which is probably homologous with the left caecum, serves the anterior diverticula of the left side and the duct leading from the floor of the stomach, which doubtfully may be homologous with the right caecum, serves the remaining diverticula of the left side. Like other lucinids, the stomach is unusually simple in its form, and sections show little evidence of sorting areas. Similarly, the digestive diverticula, although extensive and with a finely branched duct system, show no exceptional features to those already described (Allen, 1958).

The Foot

In the Lucinacea generally the anterior part of the foot is responsible for building the anterior inhalent tube, while the posterior part or heel performs the locomotory function. The foot of *Fimbria* is divided into anterior and posterior parts (Fig. 1), but the posterior part is less well developed than in many other species (Allen, 1958) which may indicate that the species remains in the same position for much of its life.

The anterior part of the foot is elongate with a pointed tip that is heavily and uniformly ciliated. Below the epithelium layer of the tip of the foot there is a thin layer of circular muscle and, internal to this, a great mass of muscle fibers running in all directions within loose connective tissue. The central blood space which is crossed by a few muscle fibers has no definite boundary. The most striking feature of the tip of the foot is the very large number of mucus-secreting gland cells which presumably provide the material that binds together the walls of an anterior inhalent tube (Allen, 1958). These cells are similar in appearance to those seen in the mantle edge and "mantle gill."

DISCUSSION AND CONCLUSIONS

From this study it appears that *Fimbria* is in most respects a typical member of the Lucinidae, and there seems to be little reason to erect a new family, the Fimbriidae. The gill is unusual as compared with other lucinids in that it is plicate and not noticeably thickened abfrontally.

The following features should be noted. The palps are mere vestiges in comparison with eulamellibranchs other than the Lucinidae. There is no evidence of selection of food particles according to size, and sorting of filtered material must be minimal. The presence of a simple "mantle gill" with an associated pallial blood vessel might indicate auxiliary respiratory function, although sensory and directional functions are also possible. The stomach shows typical lucinid modifications and probably accepts all particles whatever their size. The foot is supplied with numerous mucus gland cells at the tip that presumably are used to build an anterior inhalent tube. All of these features are to be found in members of the Lucinidae.

Fimbria shows great development of muscle in the mantle edge, with the pallial muscles some distance in from the edge of the shell. This indicates that it may be capable of remaining closed for long periods of time with the mantle folds retracted. The small size of the heel of the foot suggests a fairly stationary existence. The persistence of a double row of papillae on the mantle edge around both the inhalent and the exhalent siphon has been observed in one other of the *Lucinidae* species—*Codakia orbicularis*. Both *Fimbria* and *Codakia orbicularis* are large, and this feature may be little more than a reflection of their size. The inhalent aperture is not extended as a siphon, and it is doubtful if it is used other than for the disposal of pseudofaeces. *Fimbria* is found in warm tropical waters which may well account for the great size and thickness of the shell.

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