CILIARY CURRENTS AND ASSOCIATED ORGANS OF *MARTESIA FRAGILIS,* A WOOD BORING PHOLAD OF MADRAS[1]

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INTRODUCTION

THe ciliary feeding currents and their associated organs of bivalve molluscs have been extensively studied both morphologically and experimentally (Ridewood, 1903; Wallengren, 1905 ; Kellogg, 1915 ; Yonge, 1923, 1926b, 1928 ; Atkins, 1936, 1937, 1937a, 1937b, 1938, 1938a; Purchon, 1941, 1955). Among the wood boring lamellibranchs, such a study has been carried out on Teredines like *Teredo navalis* (Sigerfoos, 1908) and *Bankia indica* (Nair, 1957). The gills in these forms are highly reduced and do not possess any ciliary mechanisms for sorting waterborne food items. Purchon (1941) has demonstrated a similar condition in the pholad *Xylophaga dorsalis* while he found five species of rock-boring pholads *(Barnea parva, Pholadidea loscombiana, B. Candida, Pholas dactylus, Zirphaea crispatd)* possessing well developed ctenidia and ciliary currents capable of sorting food material. Purchon infers that the well developed ctenidia with food sorting mechanisms are associated with their plankton feeding habit. The only other pholad known to be wood boring is *Martesia* sp. of which two are known to occur in Madras waters; *M. striata* and *M. fragilis* and these wood boring pholads appear to feed exclusively on plankton. It was felt that a detailed study of the ciliary sorting currents and the anatomical features of the mantle, the siphons and the ctenidia of *M. fragilis* will be of interest by itself and for comparison with other rock-boring pholads.

MATERIAL AND METHODS

About 1500 living specimens of *M. fragilis* were obtained both from test planks submerged in the sea and from small wooden pieces and drift logs washed ashore on the Madras beach. The course of ciliary currents were studied in live specimens with the help of mercuric chloride and carmine particles suspended in the water. Sections of the entire body were cut using Bouin's fluid, Altmann's fluid and Zenker's fluid as fixatives.

The mantle and the siphonal process

The mantle on either side of the body is fused with each other subterminally so that ventrally there appear to be three lobes, the free edges of the mantle on either side and the fused middle part. The mantle cavity so formed is bounded dorsally by the visceral mass and contains the gills and the foot. In the young forms of *M. fragilis* as in the young *of Barnea parva, P. losombiana* and *Pholas dactylus* the incomplete fusion of the mantle lobes leave the pedal aperture, while in the adults, this

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aperture is closed resulting in the separation of the foot. However in the adults of *B. parva* and *P. dactylus* the pedal aperture remains as such, enabling the foot to be protruded throughout their life. The free edge of each mantle shows three thickenings on the inner surface.

Histology

In a transverse section passing through the ventral edge (Fig. 1) the epidermal cells of the outer (OM) and inner lobes (IM) are found to be columnar with darkly staining nuclei. The cells of the inner lobes are ciliated interspersed with mucus cells staining with acid fuchsin. Beneath the epithelium is the connective tissue (CT) staining with aniline blue, penetrated by muscle fibres (MF). The epithelium of the middle lobe (MM) consists of flat irregular cells with distinct nuclei and considered to be secretary in function, while the inner surface has an epithelium composed of cells which are longer than those of the inner lobe and these are nonciliated. The mantle lobe on either side of the body shows three layers ; an outer columnar epithelium with oval nuclei arranged towards the basal half, an inner epithelium of ciliated cells facing the mantle cavity with mucous glands (MUG) interspersed between the ciliated cells (Fig. 9). These cilia are of uniform length measuring 13 /t and are distributed all over the inner surface of the mantle. In *Xylophaga dorsalis* the major portion of the mantle is unciliated and in *Teredo norvegica* the cilia are found in scattered groups. The middle layer is of loose connective tissue, which is filled with numerous lobed spaces and traversed by muscle bundles staining dark red in acid fuchsin.

Siphons

The siphonal process is a slender backward prolongation of the fused mantle and its cavity. Of the three thickenings on the inside of the mantle the inner, middle and inner-margins of the outer lobe become included in the siphonal process. Therefore the siphonal process of *M. fragilis* belongs to Type C (Yonge, 1948) like those of the rock-boring pholads and *Xylophaga dorsalis* (Purchon 1941, 1955). The siphonal process (Fig. 2) is long, delicate pale brown in colour, the outer surface of which is smooth. The walls are contractile and the process can be withdrawn within the valves which are slightly bulged for their retraction. Inside, the siphonal process is subdivided distally into a dorsal exhalent and ventral inhalent siphon (IS & ES) which are both encircled by a mantle sheath which forms a delicate rim close to the siphonal apertures as in *P. loscombiana.* The rim bears about 54 tentacle-like processes of which 34 are longer. In addition there are two very long tentacles situated on the wall of the siphonal process proximal to the rim. The entire rim and the inner surface of all the tentacles are dotted with brownish and whitish pigment spots, which are considered to be the openings of pigmented glands (Johnstone, 1899). Both the inhalent and exhalent tubes are united upto the siphonal rim and beyond it they are free.

The inhalent aperture is borne on a long slender funnel which is guarded by a variable number (usually six) of tentacles projecting across the aperture. There are also some very small tentacles which curve slightly inward to cover the inhalent aperture. In *Xylophaga* the circular aperture of the inhalent siphon is fringed with about 6 delicate tentacles.

The inhalent siphon extends far beyond the exhalent siphon and is 3 mm. to **14.5** mm. long measuring from the rim in specimens of length ranging from 3 to 10 mm. The exhalent siphon is not so retractile but can be closed in such a way as to form a cone at its tip. The outside and inside of this funnel is of a brownish hue

with scattered whitish spots on the outer surface. During excretion the exhalent aperture is closed and opened at intervals of 20 to 40 seconds.

Histology

In a section across the wall of each siphon (Fig. 3) we find the outer wall is reinforced by the common sheath and is of the same structure as the outer mantle epithelium. On the innerside the epithelium is of cubical ciliated cells. Between the two epithelia the connective tissue is traversed by four groups of muscle fibres two being longitudinal (LM_X & LM_2) and two circular (CM_X & CM_2) arranged alternately. These muscle fibres are responsible for the greater contractility of this siphonal extension of the mantle. The gross as well as minute structure of the mantle and siphonal process of *M. fragilis* are very closely similar to those of other pholads {*B. parva, P. Loscombiana, B. Candida, Z. crispata, P. dactylus* and *X. dorsalis,* Purchon, 1941 & 1955), Teredines *(T. norvegica,* Lazier, 1924; *B. indica,* Nair, 1957) and *Cardium* (Johnstone, 1899).

The Ctenidia

The ctenidia (Fig. 4) of *M. fragilis* consist of two pairs of creamy white demibranchs one on each side of the visceral mass, extending from the labial palp anteriorly to the middle of the siphons beyond the hinder border of the valves (Fig. 5). The ctenidium measures 7 mm. in a specimen of 8.5 mm. long and nearly two-thirds of the ctenidium lies behind the visceral mass. The two demibranchs of a side are approximately equal in depth posteriorly but anteriorly the inner demibranch is deeper and extends upto the base of the labial palps. In this respect *M. fragilis* resembles the rock-boring pholads and differs from *Xylophaga* in which the ctenidium is greatly reduced having only the direct lamella of the outer demibranch. The axes of the two ctenidia meet in front of the inhalent siphon.

Each branchial filament is V-shaped so that owing to the serial arrangement of the filaments on the axis there is a groove formed along the margin of the gill. The gill especially on the inner demibranch is so shaped that the filaments become shorter at the anterior end of the axes and the marginal groove opens at the front end of the gill between the two palps close to the mouth. In *M. fragilis,* unlike what obtains in P. *loscombiana* and *B. Candida,* the outer demibranch also has the marginal groove which opens like that of the inner demibranch but farther away from the mouth. However, in *Xylophaga* all the demibranchs are devoid of marginal grooves. The inter lamellar septa which occur at intervals of 10 to 13 filaments are thick junctions extending vertically from the margin upto the axis and contain the vertical blood vessels which are connected by horizontal vessels running in the subfilamentar tissue where the different filaments are fused along the axis. The suprabranchial chamber formed by the mantle above the axis and filaments of each gill are long cylindrical median canals running dorsal to the visceral mass. Anteriorly where the gills are more slender and confluent with the labial palps, these chambers become very slender canals in the substance of the mantle.

Transverse sections passing through the epithelium of each branchial filament (Fig. 6) reveal the presence of the ciliated, non-ciliated and the secretory cells. Three cells with short cilia measuring 3 /* are located in the frontal area of the filament. There are two laterofrontal cells bearing long cilia. The cilia of the adjacent branchial filaments interdigitate. These laterofrontal cells are tall measuring 8 *H* containing nuclei which stain dark red with acid fuchsin. The non-ciliated cell layer separates the laterofrontal cells and the lateral cells and is made up of three cubical ciliated cells containing large oval nuclei. The wall of the epithelium

posterior to the lateral cells consists of a single layer of non-ciliated cells containing small nuclei. Internally the filament is filled with loose connective tissue. In sections blood vessels are seen to pass through the filament. The secretory cells (SEC) occur between the epithelium. They are typical mucous cells.
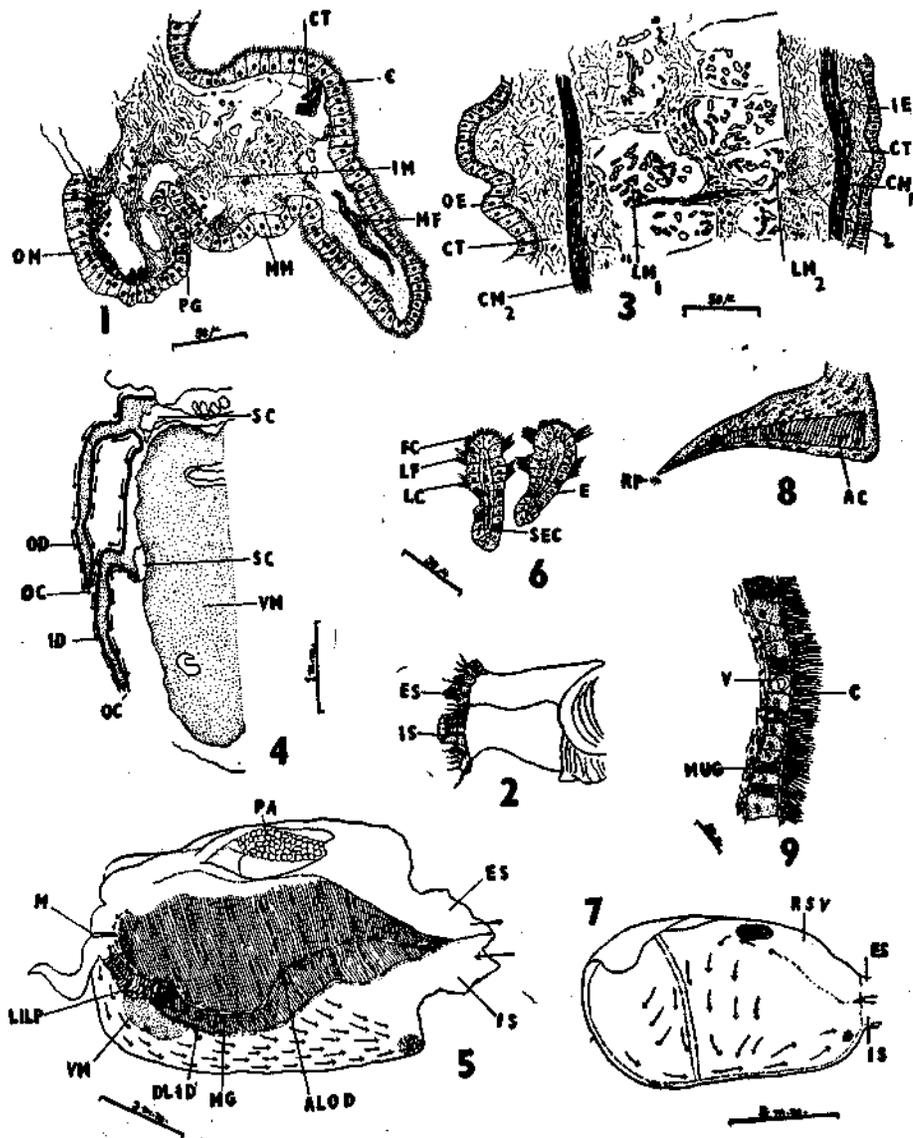
The Ciliary currents

Currents over the mantle surface.—The course of water currents in the mantle cavity have been shown diagrammatically in Fig. 7. The water which enters the inhalent siphon bears particles of suspended matter. Water and very fine particles pass from the mantle cavity into the gills whereas large and heavy particles which cannot enter the branchial meshes are sent out through the inhalent aperture by which they enter as 'pseudofaeces'. Thus the cilia occurring on the inner side of the mantle *(vide* supra) are responsible for a strong current or ciliary movement which take the large particles to the mantle margin. Powerful rejection tracts arise near the antero-ventral end and runs backwards close to the mantle margin carrying with it particles entangled in mucus backwards to the base of the inhalent siphon. The cilia responsible for this movement being on the lower margin do not interfere with the circulation of water along the upper and middle region of the mantle cavity. The heavier particles which sink down to ventral mantle edge by gravity therefore do not travel with the rest of the water current. The water currents are set up by the beat of the cilia on the rest of the mantle surface principally in the upper part of the mantle chamber from the inhalent siphon extending up to the anterior end. As the water flows along the upper margin of the chamber the particles are conveyed downwards over the surface of the gills by the vertical rows of cilia on them. In *Xylophaga* the major part of the mantle is unciliated and particles are efficiently removed under normal conditions by ctenidia (Purchon, 1941) and in *T. norvegica* (Lazier, 1924) the scattered groups of cilia on the mantle beat towards the ciliated mantle tracts and assist in keeping the surface of the mantle clean. In both of these forms the cilia of inner surface of the mantle which are restricted to the mantle tracts serve to limit the quantity of food particles which are passed from the ctenidia to the mouth.

Branchial currents.—The course of water currents over the gills have been shown diagrammatically in Fig. 5. Since the gills are filamentary the water in the mantle cavity can gain entry into the inter lamellar space through the space between the successive filaments. This is facilitated directly by the laterofrontal cilia which move anteroposteriorly and directly by the lateral cilia moving the water within the lamella upwards into the suprabranchial chamber and thus taking the water in. The frontal cilia beat towards the margin of the gill so that the water which has not entered the upper levels of the gill filaments are made to enter through the middle and ventral areas of the gill surface. The water which continues to enter the suprabranchial chamber is forced through the exhalent siphon by the beat of the cilia in the suprabranchial chamber. In short the entire circulation through the gills is designed to draw water in the mantle cavity through the inhalent siphon.

As already mentioned before the very large and heavy particles of matter nutritive or otherwise which may enter the inhalent siphon fall by gravity to the ventral region of the pallial cavity and are pushed backwards through the inhalent siphon by which they enter. The medium size and finer particles which are moved along the incurrent water reach the gills.

The medium sized and fine particles which fall on the surface of the gills are pushed from either sides of the filament towards the frontal surfaces by the for-

wardly beating long cilia belonging to the laterofrontal band. They come under the action of the downwardly beating frontal cilia and are swept down towards the marginal groove (Fig. 4) from where they travel forwards through the forward beat of the strong cilia of the marginal groove until they reach the lateral oral groove between the two labial palps. Larger particles were dropped over the surface of the mantle cavity. The very fine particles which enter the gill through filaments are carried out of the body. On all lamellae of the ctenidia currents move ventrallv to the margins, where material is received into the grooves. *M. fragilis* is identical with *B. parva, P. dactylus* and *Z. crispata* in this respect. Hence *M fraeilis* falls into the ctenidial category C_2 of Atkins (1937a). However in *B. Candida mdP loscombiana,* marginal groove is present at the free edge of the inner but not of the outer demibranch. So they fall under the type C_r of Atkins (1937a).

Currents over the labial palps.—Labial palps were removed and pinned on to a board. Ciliary currents over the palps were observed and are indicated diagrammatically in Fig. 8.

The labial palps of *M. fragilis* are small possessing few large transverse ridees When carmine particles are applied to the palps it is noticed that some particle's are swept downwards in the groove between the folds of the palp. There the cilia beat ventralwards and particles pass out of the groove and reach the anteroventral end of the palps. From here they pass backwards to the tip of the palps and then fall on the floor of the mantle from where they are taken outside the mantle chamber by the currents of the mantle. These currents which remove the rejected material from the mantle are called the ' rejection currents' (Purchon, 1955) The finer particles are seen to be carried from fold to fold rapidly. These reach the anterior end of the palps and later lead towards the mouth. These currents are called the 'acceptance currents ' (AC) (Purchon, 1955). In *M. fragilis* the medium sized aid heavy particles fall into grooves between folds and are swept by rejection currents out of the groove centrally and later to the ventral margin of the palps Thev are taken by the rejection currents on the mantle and swept towards the baseof the siphon (Fig. 8). These together with heavy particles which are dropped down from the gills are expelled from the mantle cavity by the combined actiohof the cilia on the tracts and by the muscular action of the mantle, through the inhalent siphon as pseudofaeces The finer particles are carried by the acceptance currents from fold to fold towards the mouth. Similar acceptance and rejection currents have been described in plankton feeding *Barnea parva* and *Zirphaea crispata* (Purchon 1955} *In Teredo megotara* selection is displayed only by rejection mechanism of the'mantle and not by the labial palps. Sorting does not take place on the palps and all he maenal is passed to the mouth. This is probably due to its capacity to feed exclusively on wood fragments. However, in *X. dorsalis* (Purchon 1941} the labial palps retain to a certain degree the power of quantitative selection. Over the greater extent of the surface of the labial palps the cilia beat outwards removing the particles from the labial palps. Only small quantities of food particles ire taken to the mouth but larger quantities are removed by the outwardly beating cilia This lends further support to the view held by Purchon (1941) that though *Xylophaga* derives nutriment from wood through which it bores, yet under certain circumstances it is independent of wood as a source of food.

Fig 7   ^zi^^^&^riZL^zf^6   surface Rsv: Rht she

Fig. 8.   S h TM ^ ^   over the right inner palp. AC: Acceptance

Fig. 9. ^ ^ g ^ J ^ i g j g f r i h . inner mantle epithelium, v: Vac,,o,e,

Fig. 1. Shows the transverse-section through the mantle edge. CT: Connective tissue, C : Cilia, IM : Inner mantle lobe, MF : Muscle fibres, MM : Middle mantle lobe, PG : Pericardial groove, OM : Outer mantle lobe.

Fig. 2. Diagram showing the inhalent and exhalent siphons. ES : Exhalent siphon, IS : Inhalent siphon.

Fig. 3. Shows the transverse-section through a part of the inhalent siphon. OE; Outer epithelium, CT : Connective tissue, XM2 : Circular layer of muscles, LM1 : Circular layer of muscles, CT : Connective tissue, IE : Inner epithelium.

Fig. 4. Shows the transverse-section through the visceral mass, and ctenidia showing the course of the ciliary currents over the gills. OD : Outer demibranch, OC : Oralward current. ID : Inner demibranch, OC : Oralward current, VM : Visceral mass, SC : Suprabranchial chamber.

Fig. 5. Shows the course of ciliary currents over the gills. M : Mouth, LILP : Left inner labial palp, VM : Visceral mass, DLID : Descending lamella of inner demibranch, MG: Marginal groove, ALOD : Ascending lamella of outer demibranch, IS : Inhalent siphon, ES : Exhalent siphon.

Fig. 6. Shows the transverse-section through two adjacent branchial filaments. FC: Frontal cilia, LF: Laterofrontal cilia, LC : Lateral cells, SEC; Secretory cells, E: Epithelium.

REMARKS

In any assessment of the efficiency of filtering mechanisms of different borer it is essential to grade the sizes of particles and to locate the sites at which particles are rejected and to assume that the particles which are retained are digested in the gut.

Only very line (20 /*) particles are seen all over the gills en route to the mouth. Since very few are rejected it is permissible to conclude that these small particles are injested and thus retained.   Particles of medium and larger size are found rejected early in the course of the current unlike what is obtained in *Xylophaga* and Teredines. The sites of rejection in *Martesia* appears to be at the powerful rejection tracts over the mantle, at the marginal groove and at the rejection currents over the labial palps. The study of the ciliation and the structure of the gill and the mantle *{vide* supra) supports these observations regarding the retention of these particles.

In all these features and in the structure of the gills, mantle and the labial palps *M. fragilis* shows close resemblances to rock-boring pholads like *Pholadidea loscombiana, Barnea parva* and *Zirphaea crispata* which possess well developed plankton feeding mechanisms.   It however differs from *Xylophaga* and Teredines in which the ctenidium and labial palps are highly reduced and which therefore lack a sorting mechanism.   However, these forms are capable of controlling the amount of planktonic food carried to the mouth by virtue of their possessing ciliated rejection tracts over the mantle.

SUMMARY

A detailed account of the structure of mantle, siphons and the ctenidia are given.   These show a close resemblance to those of other rock-boring pholads.   The ciliary mechanisms of the mantle and ctenidia which aid in its feeding on planktonic organisms are seen to be well developed and efficient.   The labial palps play an important part in the grading of various sizes of food particles and reject all except the finest particles.   Comparisons with *Xylophaga* and Teredines are made.

' ACKNOWLEDGEMENTS

REFERENCES

ATKINS, D.   1936.   On the ciliary mechanisms and inter-relationships of lamellibranchs.   Part I   New observations on sorting mechanisms.   *Quart. J. Micr. Sci.,19 :* 181-215.

————.   1937.   Part II.   Sorting devices on the gills.   *Ibid.,* 79 : 339-373.

————.   1937, a.   Part III.   Types of lamellibranch gills and their food currents.   *Ibid.,* 79 : 375-421.

————.   1937, b.   Part IV.   Cuticular fusion with special reference to the fourth aperture in certain lamellibranchs. *Ibid.,* 79: 423-445.

_————.   1938.   Part VI.   Pattern of lateral ciliated cells of the gill filaments of the lamellibranchia, *Ibid.,* 80 : 331-344,

ATKINS, D. 1938, a. Part VII. Laterofrontal cilia of the gill filaments and their phylogenetic value. *Ibid.,* 80 : 345-436.

EGQER, E. 1887. *Jouametia cumingii. Arab. Inst. Wurzb.* 8: 129-199.

JOHNSTONE, J. 1899. ' *Cardium' L.M.B.C. Memoir, No.* 2. Liverpool University Press.

J^RGENSEN, C. B. 1955. Quantitative aspects of filter-feeding in invertebrates. *Biol. Rev.* 30: 391.

KELLOGG, J. L. 1915. Ciliary mechanism of lamellibranchs with descriptions of anatomy. /. *Morph.,* **26**: 625-76.

LAZIER, E. L. 1924. Morphology of digestive tract of *Teredo navalis. Univ. Calif. Publ. Zool.,* **22**:455-469.

NAIR, BALAKRISHNAN, N. 1957. Structure and physiology of the timber borer *Bankia indica* with special reference to boring habit. /. *Mad. Univ.,* B 27 : 335-372.

PURCHON, R. D. 1941. On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). /. *Mar. biol. Ass. U.K.,* **25**: 1-39.

————. 1955. The structure and function of the British pholadidae (Rock-boring lamelli-branchia). *Proc. zool. Soc. Lond.,* **124** : 859-911.

————. 1956. Notes on the biology of *M. striata Vmn6. Ibid.,* **126:** 245-258.

RIDEWOOD, W. G. 1903. On the structure of the gills of the lamellibranchia. *Phil. Trans, roy. Soc. Lond.* **195:** 147-284.

SiGERFOos, C. P. 1908. Natural history, organisation and late development of the Teredinidae or ship-worm. *Bull. U.S. Bur. Fish.* 27 : 191.

WALLENGREN, H. 1905. Zur biologie der Muscheln. I. Die wasserstromungen; II. Die Nahrungsaufnahme. *Lund. Univ. Aarskr.,* Ser. II. i. Nos. 2 & 3.

YONGE, C. M. 1923. The mechanism of feeding, digestion and assimilation in the lamellibranch, *Mya. J. exp. Biol.,* 1: 15-63.

————. 1926, b. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis. J. Mar. biol. Ass., U.K.,* **14** : 295-368.

————. 1928. Feeding mechanism in invertebrates. *Biol. Rev.* 3 : 21-76.

————. 1948. Formation of siphons by Lamellibranchs. *Nature, Lond.,* **161**: 18-199.