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FURTHER NOTES ON THE ANATOMY OF *MARTESIA FRAGILIS*

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Introduction

The pholads, majority of which bore into rock, have received only very little attention compared to the wood-boring teredines. But some species of pholads especially those belonging to the genus *Martesia*, are essentially wood-borers, and are of considerable economic importance. It is not known whether they resemble the Teredines in their adaptations for wood-boring, physiology of digestion associated with it and the mechanism of boring. Brief accounts of these aspects of study are available thanks to the works of Poli (1791), Fischer (1858-60), Egger (1887), Dubois (1892), Kellogg (1915) and Purchon (1955, 1956). *Martesia*, while possessing the wood-boring habit in common with *Xylophaga* and Teredines, differs from them in having adaptations to live on planktonic food, like the rockboring pholads. It was felt therefore of interest to study in detail the anatomical features of *Martesia* which may throw light on their adaptation to the wood-boring habit and also on their ability, if any, to digest cellulose. Such a study will be helpful for comparisons with *Xylophaga* and other rock-boring pholads as well as for further studies on the physiology and development of these wood-borers. The common pholadid wood-borer *Martesia fragilis* Verrill and Bush (1890) has been used in this study.

Material and Methods

Martesia collected from small floating wooden pieces and drift logs washed ashore on Madras beach were used in the present study.

In addition to Bouin-Duboscq's, Altmann's and Zenker's fluids were also employed as fixatives. Serial sections of 5 to 10 microns thickness were stained in Delafield's Haematoxylin, Iron Haematoxylin counter stained with Eosin, Mallory's Triple and Mason's Trichrome. Mayer's mucicarmine was used for detection of Mucin.

The General Organisation of the Body

M. fragilis has a slender pear-shaped and soft body (Pl. I, Figs. 1 & 2). The shell covers the entire visceral mass, and functions as the main organ for burrowing. The siphons extend to a great length, and are capable of complete withdrawal within the valves. The shell valves of the young (Pl. I. Fig. 3) animals when in contact gape widely in front for the projection of the foot while those of the adults close the pedal gape completely resulting in the retraction of the foot.

Fig. 1 shows the general arrangement of the organs in *M. fragilis* as seen from the left side when the left shell valve and the mantle are removed. The visceral mass occupies approximately three-fourths of the body while the ctenidium extends from the labial palps anteriorly to the middle of the siphons, beyond the hinder border of the shell valves. Most of the organs lie anterior to the posterior adductor muscle. In the young forms (Fig. 6a) the foot occupies the anteriormost portion in relation to its use as an organ holding the shell in position while boring. The pericardial cavity with its contained heart occupies a position above the intestines. Associated with it the position of the various parts of the organs of circulation has been arranged. The posterior aorta continues posteriorly from the ventricle, while the anterior aorta proceeds forwards. The kidney comes to lie ventral to the posterior adductor extending anteriorly over the dorsal side of the visceral mass. The gonads are creamy white conspicuous body occupying the antero-ventral and posterior portions of the visceral mass. The renal and reproductive openings have been shifted behind as also the visceral ganglion. The stomach lies in the middle of the visceral mass and is surrounded anteriorly by the digestive diverticula. The style-sac and the intestine open separately but close together into the stomach. The intestine coils twice in the anterior part of the visceral mass, passes backwards along the right side of the style-sac and emerges into the hind-gut which passes through the substance of the ventricles. The mouth and the anus retain their usual position, the former between the anterior adductor muscle and the visceral mass and the latter on the dorsal side of the posterior adductor muscle. The mantle cavity extends behind as a long cylindrical canal accommodating the ctenidia.

The Shell and the Accessory Plates

The morphological features of the shell valves and observations on the changes that take place during its growth have been described in earlier papers, (Srinivasan 1959, 1962).

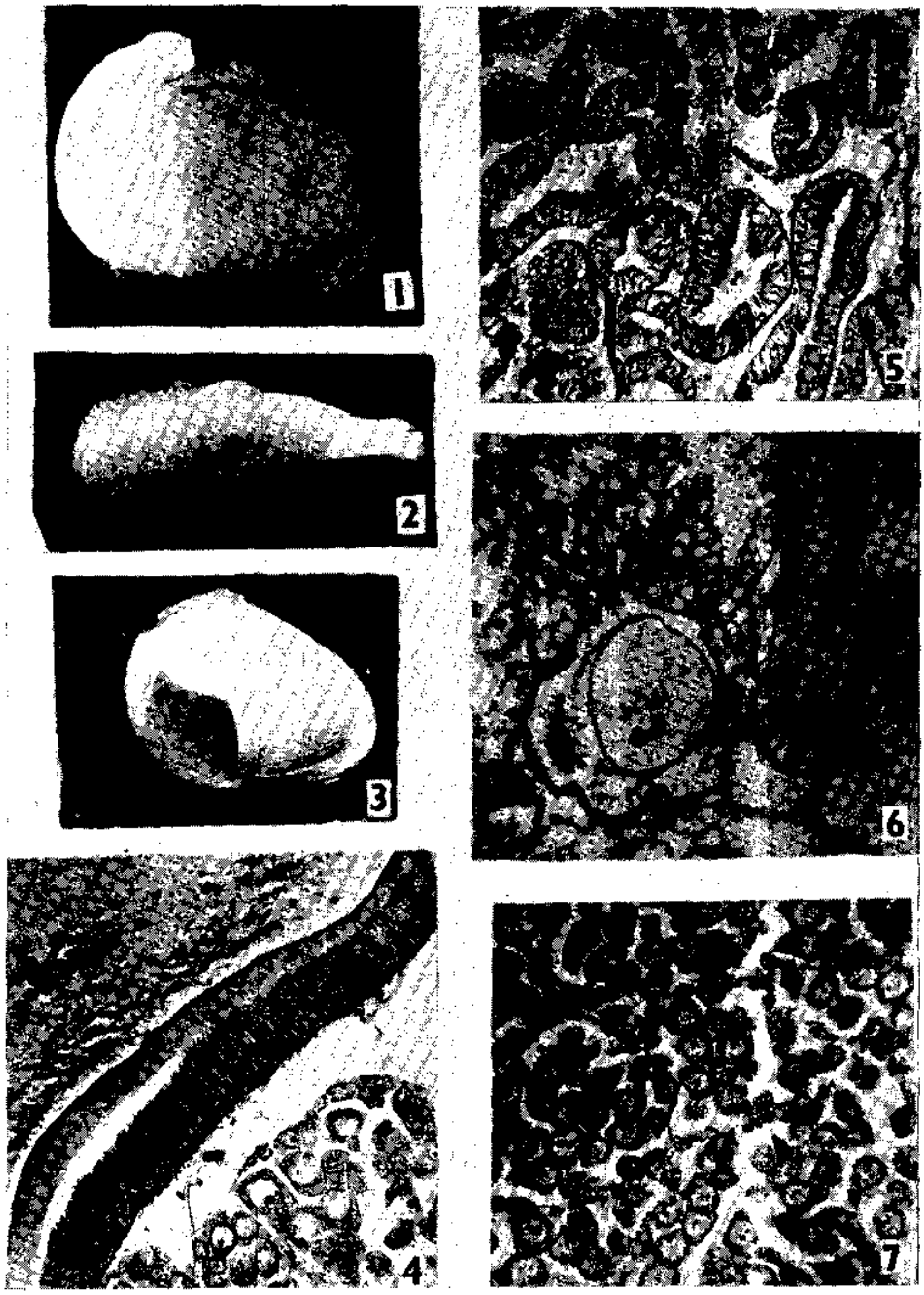
The Internal Anatomy

The adductor muscles.

The anterior adductor muscle is smaller in size than the posterior adductor evidence being taken from their insertional scars on the shell valves. This is in contrast to the conditions found in other pholads (Purchon, 1955) where the anterior adductor is comparatively larger than the posterior adductor and is attached partly on the reflection of the shell and partly over the flange. The muscle consists of coarse muscle strands stretching transversely across the anterior part of the body. The rectum travels above the posterior adductor muscle. The kidney is applied to the ventral face of the adductor. It is also a compact bundle and has striated fibres.

From their position of attachment on the valve and their size, it is seen that these two muscles contract alternately (Purchon, 1955). The large size of the posterior adductor suggests that the valve can be brought together more vigorously in the posterior region than in the anterior region and this is responsible for the outward thrust of the valves at the anterior side. The accessory ventral adductor muscle lies behind the ventral end of the sulcus. It is found as one piece on the posterior of the umbonal ventral sulcus.

In young specimens in which when the foot persists, in addition to the abovementioned muscles three more muscles, occur relating to the movements of the visceral and pedal mass. The anterior retractor muscle takes its origin on the



FIGS. 1, 2, 3. Adults and young specimens of *M. fragilis* with and without the shell valves.
FIG. 4. Transverse section through the epithelium of the stomach. (Photomicrograph).
FIG. 5. Transverse section through a part of the digestive diverticula (Photomicrograph).
FIG. 6. Transverse section through the renal organ showing the folded inner glandular layer and the cuticular lining over the inner surface of the duct of the proximal limb. (Photomicrograph).
FIG. 7. Section of the gonad in the female phase showing ova. (Photomicrograph).

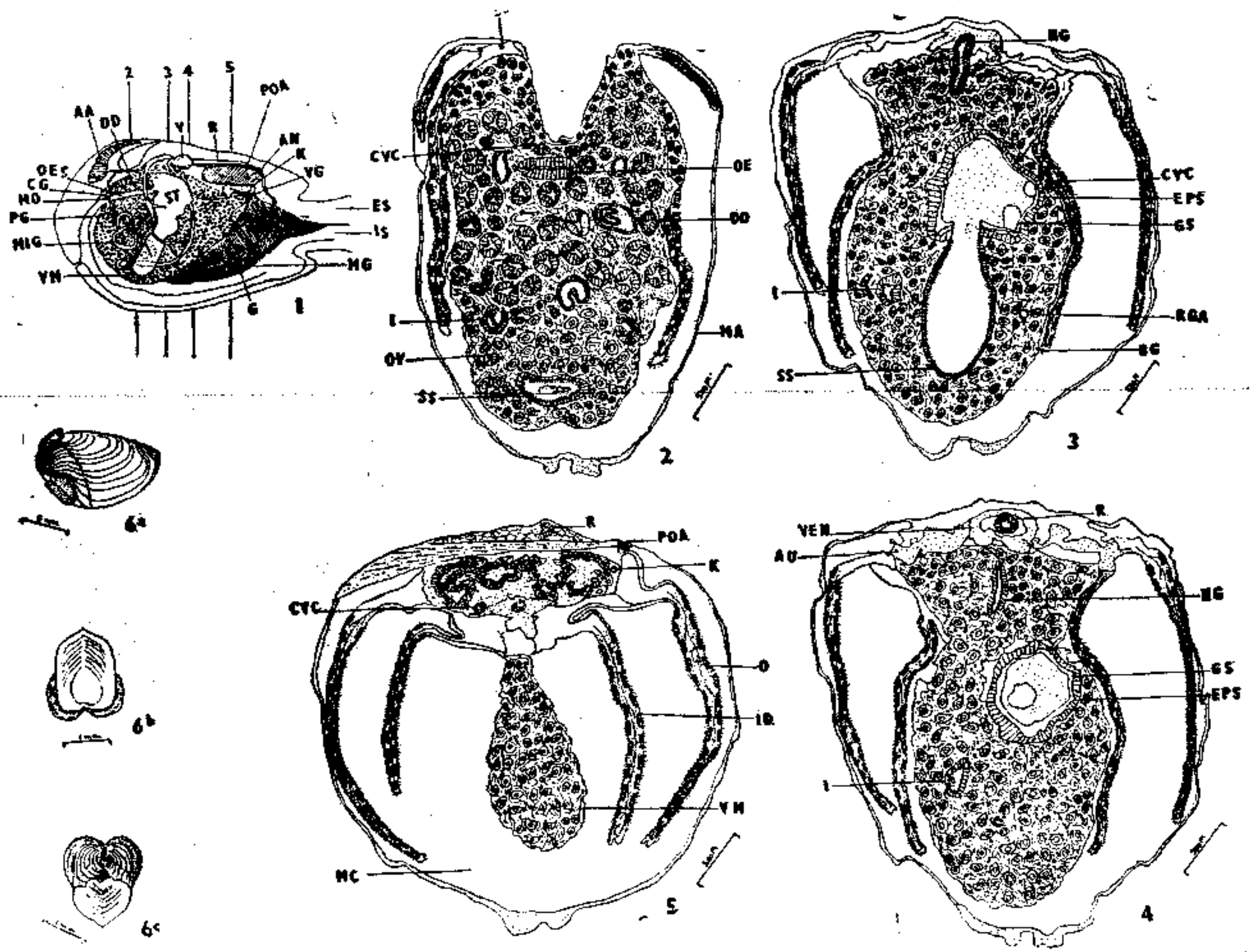


FIG. 1. The general disposition of the organs in the mantle cavity.
FIGS. 2-5. Series of transverse sections of an adult animal along the lines indicated in fig. 1.
FIG. 2. Section through the oesophagus, the intestines and the style-sac passing through the line marked '2' in fig. 1.
FIG. 3. Section through the hind gut, the stomach and the style-sac passing through the line marked '3' in fig. 1.
FIG. 4. Section through the rectum, ventricle, auricles and the stomach passing through the line marked '4' in fig. 1.
FIG. 5. Section through the posterior adductor, the renal organ and the gonads passing through the line marked '5' in fig. 1.
FIG. 6a. Side view of the young shell of *M. fragilis*. b. Dorsal view of the Mesoplax of the young shell of *M. fragilis*. c. Ventral view of the Mesoplax of the young shell of *M. fragilis*.

shell valves, anterior to the base of the apophysis and spreads out as it passes downwards and becomes inserted on the antero-dorsal surface of the visceral mass. The posterior retractor muscle passes through the posterior adductor and the excretory organs and enters the visceral mass. The pedal retractor takes its origin from the ventral face of the apophysis and spreads over the sides of the foot. In adults in which the foot has degenerated and the pedal gape closed these three muscles also disappear.

The Alimentary Canal

The course of the alimentary canal is shown in Fig. 7. The mouth opening is a median elliptic transverse aperture situated behind the anterior adductor muscle and bounded laterally by the two pairs of labial palps (Fig. 8). The labial palps, though small, are very distinct structures, the ventral ones being smaller than the dorsal ones. The oesophagus is moderately long and enters the stomach antero-dorsally. The stomach is a fairly large sac lying in the middle of the visceral mass.

The stomach gives rise to the intestine or midgut which coils twice in the anterior part of the visceral mass and passes backwards along the right side of the style sac. It emerges into the hind gut which passes through the substance of the ventricle and runs over the dorsal surface of the posterior adductor as the rectum.

Labial palps.

The dorsal labial palps are fleshy small broadly triangular organs like those of *P. loscombiana*, the outer surface of these are fused to the visceral mass throughout their length as in *Xylophaga dorsalis*. The ventral palps are still smaller, the outer surface of these are free from the visceral mass to a slight extent. They form a broad platform extending from the ctenidium to the mouth. The external palps of the two sides are joined together in front of the mouth and the inner palps united behind it. The outer surface of the labial palps are smooth while their inner surfaces possess distinct ciliated transverse ridges. The marginal groove of the inner demibranch passes between the bases of the labial palps and carries particles into the lateral oral groove.

Oesophagus.

The oesophagus of *M. fragilis* (Fig. 2, Fig. 7) is moderately long measuring about 1.15 mm. in a specimen of 10 mm. long. It is dorsoventrally flattened and its inner surface is strongly ridged. It is lined by a layer of connective tissue with strands of muscle fibres and blood sinuses passing between them. Next to the connective tissue lies the basement membrane which is followed by the columnar ciliated epithelium.

Stomach.

The stomach is a dorsoventrally elongated sac into the middle of which the oesophagus opens. The intestine which leaves the stomach starts a little below the oesophagus and runs forwards. On either side of the oesophagus are two pockets or caecae of the stomach into which open the two ducts of the digestive diverticula of the anterior side. The digestive diverticula of the left side of the stomach open separately into a pouch on the left side of the middle part of the stomach directly opposite the opening of the oesophagus. On the posterior wall of the stomach is a small hollow appendix. The dorsal region of the stomach is wide and is known as the ' dorsal hood ' which has on its inner wall a number of grooves. The ventral region of the stomach forms the narrower style sac containing the style.

The stomach is lined by an epithelium which is ciliated except near the opening of the dorsal hood. In this region there is a layer of cuticle called 'the gastric shield' (Pl. I, Fig. 4 ; Fig. 3 ; Fig. 11) secreted by the underlying epithelium (Photomicrograph I). The gastric shield not only covers the right and left sides of the middle part of the stomach, but has its dorsal edge projecting into the lumen for the play of the style (vide infra). In sections it stained red with acid fuchsin of Mallory. The epithelium underlying the gastric shield is formed of slender columnar cells possessing elongated nuclei in the basal third of the cytoplasm. In *Martesia*, the stomach bears all the six diverticula, which have been noted in *B. parva*, *B. candida* and *P. loscombiana* (Graham, 1949 ; Purchon, 1955).

Digestive diverticula.

The digestive diverticula which in lamellibranchs provide extensive surface for intracellular digestion and absorption (Yonge, 1926 d) occur in *M. fragilis* as numerous small blind tubules the major part of which lie anterior to the stomach. They occupy the ventral and posterior regions of the stomach and communicate with it by ducts. Sections through the digestive diverticula show that this gland consists of a large number of blind tubules packed together with connective tissue. Each tubule (Pl. I, Fig. 5 ; Fig. 2 ; Fig. 14) is of thick walled columnar cells surrounding a lumen which appears triradiate in cross-sections. In some the lumen shows four or five arms and as many crypts.

The crypts are lined by groups of cells which stain dark brown with Mason's Trichrome and have round nuclei. The wall of the tubule between these crypts are of lightly staining columnar cells which contain vacuoles with particles within. The occurrence of these two types of cells within the tubules and the absence of cells suited for intracellular digestion suggest that the digestive diverticula of *M. fragilis* is of the unspecialized type like those found in other pholads, like *Xylophaga* (Purchon, 1941). Transverse sections of a tubule (Fig. 14) show that each is composed of thick walled columnar cells, forming a round or oval cavity with three to five crypts. The unspecialized nature of the digestive diverticula is further evidenced by the structure of the ducts. These are lined by granular, non-vacuolated ciliated cells with oval nuclei. Under this epithelium lies a basement membrane surrounded by connective tissue supported by circular fibres. These histological features supported by the fact that cellulase is absent suggest that the digestive diverticula of *M. fragilis* is not specialized for cellulose digestion. The histological differences recorded by Sigerfoos (1908), Potts (1923), Yonge (1926d), Nair (1957) who have studied Teredines like *Bankia gouldi*, *Teredo navalis* and *Bankia indica* which are proved to be capable of feeding on timber, thus become more significant.

The dorsal hood.

The dorsal hood or pouch (Fig. 12), is an evagination of the anterior dorsal wall of the stomach which projects outwards into the digestive diverticula. Examination of live specimens taken fresh from timber samples shows that the dorsal hood contains food items like diatoms, copepods etc., whereas after the live specimens have been kept in filtered seawater for a few days, the dorsal hood is empty of all food items. It is probable that this part of the stomach acts more as a storage organ and does not participate actively in digestion as has been suggested for *P. loscombiana* by Graham (1949).

A finger-like hollow appendage measuring about 3.5 mm. in length is borne by the stomach on its posterior side (Fig. 12) situated more on the right than on the left. It contains particles of grit useful in triturating the food.

Style-sac.

The style-sac is a wide thin walled bag-like ventral extension of the stomach turned forwards into the visceral mass (Figs. 3, 7). Section of the stomach at the place where the style-sac rises will show that the wall of the stomach is produced inwards to form a circular ledge marking the junction between the style-sac and the stomach. Though the style-sac is a projection of the stomach, the flattened epithelium of the stomach gives place to a lining of the columnar epithelium. These columnar cells (Fig. 10) are ciliated the cilia measuring 14 μ and have a dual role of both secreting the substance of the crystalline style and moving the style (Nelson, 1918) by its cilia. In *Martesia* these cilia, however, do not extend inwards through the bases of cells as has been described for *Ostrea edulis* (Yonge, 1926b).

The Crystalline style.

The crystalline style (Fig. 9) is a club-shaped mass of gelatinous consistency and is transparent. It is about 4 mm. long and is larger than those of *Bankia* and *Xylophaga*. Its lower end is broad while the upper tapering end projects into the lumen of the stomach and abuts against the dorsal part of the gastric shield. Sections of *M. fragilis* passing through the crystalline style when stained with Mason's trichrome stained green as in the case of cuticular protein derivatives. Ganapathi and Nagabushanam (1956) found in extracts of the crystalline styles of *M. striata* enzymes like amylase, maltase and lactase though not cellulase.

Intestine.

The intestine starts on the antero-ventral wall of the stomach and passes obliquely forwards coils twice on itself and then runs backwards on the right side of the style-sac, (Fig. 7), emerges into the hind gut towards the pericardium and runs over the dorsal surface of the posterior adductor as the rectum (Fig. 4) which passes through the pericardium penetrating the ventricle. In this respect it differs from *Bankia*. Sections passing through the intestine (Fig. 13) show the presence of a typhlosole which is a dorsal fold of the gut wall having its origin in the right caecum of the stomach and travels down the right anterior side of the stomach and passes extending into the intestines. This gastro-intestinal fold is covered by the columnar ciliated cells as in the rest of the intestinal epithelium. A ciliary sorting area consisting of transverse ridges extends across the roof of the stomach ending near the opening of the right caecum. It will be seen from the foregoing account that the alimentary system of *M. fragilis* recalls that found in *B. parva* and *P. loscombiana* in the general disposition of the various organs connected with the digestive tract and other external morphological features. The details of the stomach and digestive diverticula are noteworthy.

The course of food particles through the alimentary canal.

The course of food particles was studied with the help of carmine. The particles entangled in mucus pass up the oesophagus in a single string and are carried to the base of the gastric shield. Here they come under the influence of the cilia of the gastric epithelium which are spread uniformly over the area. They beat vigorously and keep the particles moving. Larger particles fall on the sorting area of the dorsal hood. The cilia over the crests of the folds of the sorting area beat transversely whereas on the groove they beat backwards rejecting the material into the intestinal groove. The intestinal typhlosole which starts from the right caecum is ciliated and possesses numerous mucus secreting glands exuding large quantities of mucus. The larger particles are separated from the food stream and taken away by the cilia of the typhlosole into the intestine.

Besides these movements, the food particles in the stomach entangled in mucus becomes wound about the head of the style which is rotated in a clockwise direction by the cilia of the style-sac (Nelson, 1918). The style is pushed forward into the stomach and the gastric shield protects the gastric mucosa against the abrasive action of the head of the rotating style. The cortical layers of the head of the style slowly dissolves away liberating the enzymes. There is an extracellular digestion in the stomach and small particles of the food are taken by the ciliated ducts of the digestive diverticula and passed on to the tubules. Purchon (1955) is of the opinion that food particles are taken from the stomach to the tubules of the digestive diverticula by changes in the concentration of the digestive diverticula and stomach. The movement of materials in the intestine are by cilia of the epithelium and the currents move towards the anus. Here they come under the influence of the exhalant current and are ejected out through the exhalant siphon.

The Excretory System

The excretory organs of *M. fragilis* are paired symmetrically placed glandular pouches which lie ventral to the posterior adductor, and extend anteriorly over the dorsal side of the visceral mass (Fig. 15). In a specimen measuring 10 mm., the kidney measure 1.5 mm. in length and 1 mm. in breadth. Each nephridium is a U-shaped tube both apertures of which are anterior. One limb of the U-shaped organ of Bojanus is wide and glandular and has its opening into the floor of the pericardium. There are simple longitudinal folds on the walls of the glandular limb. This limb has its glandular lining increased by being thrown into longitudinal folds. The non-glandular limbs of the U which serves as the external duct has a very low ridge on its floor. This limb crosses down to open through the external anal opening at the junction of the mantle and the gill near the posterior tip of the visceral mass.

While the histology of the renal organ has been studied in some detail in *Bankia indica* (Nair, 1957), a similar study in the various pholads has not been attempted. The wall of the glandular part of the kidney consists of an outer thin connective tissue (Fig. 17), a middle basement membrane and an inner glandular layer which is thrown into folds (Pl. I, Fig. 6). The glandular layer is composed of tall cells measuring about 0.052 mm. in length and 0.117 mm. in breadth. These cells stain light blue in Mallory and pink in Delafields'. Each cell of this layer contains a very large vacuole with the protoplasm situated near to the cell bases, towards which end the rounded nucleus is also to be found. The free surfaces of the cells facing the lumen of the gland bear delicate cilia like processes. These have been considered by Dakin (1909) as some fibrous exudation from the epithelium.

The Circulatory System

The circulatory system in this small bivalve was mainly studied by dissections of specimens into which borax carmine dissolved in hot water was injected with a minute needle into the ventricle and auricles of the heart. The heart enclosed in the pericardium lies between the visceral mass and the posterior adductor. The pericardium (Fig. 4) measures about 2.31 mm. in length and 1.31 mm. in breadth, in an animal measuring 10 mm. in length and 4.5 mm. in breadth. Its ventral wall lies over the kidney while anteriorly and posteriorly it is in contact with the visceral mass. The sides of this transparent sac are free and the chambers of the heart are visible through them. In *Xylophaga* however, the ventricle is produced laterally into two conspicuous lobes (Purchon, 1941). The ventricle is oval-shaped and measures about 1 mm. in length and 0.77 mm. in breadth. It is slightly constricted forming two well-marked unequal divisions and is traversed by the rectum as in *B. parva*. Sections through the wall of the ventricle is composed of a layer of epithelial cells on the outer side, resting on a delicate basement membrane of connective tissue. Lying against the latter are muscle fibres staining blue in Mallory's. These muscular trabaculae run across the cavity of the ventricle in all directions thus reducing the size of the ventricular cavity.

The ventricles communicate on each side with the auricles by horizontal slits, which are bounded by thickened tissue, acting as valves. The auricles are two large triangular chambers one on each side of the ventricle, the apices of which are uppermost. The base of the auricles open into the efferent branchial vein which brings blood from the ctenidia and mantle to the heart. In *Bankia* and other teredines owing to the great length of the adult animals the auricles are elongated and lie behind the ventricle in the form of narrow cylindrical chambers, and are of the same length as the ventricles. The walls of the auricles are thin and possess glandular epithelial walls.

The anterior aorta (Fig. 16) arises from the dorso-anterior edge of the ventricle above the rectum, and passes into the digestive gland. It continues forward and distributes blood to the rest of the visceral mass, the gills and the mantle. In all, the anterior aorta gives off the following arteries :—

(1) the anterior adductor artery ;

(2) the oesophageal artery ;

(3) the hepatic artery ;

(4) the gastric artery ;

(5) the renogonidial artery which supply the anterior adductor muscle, the oesophagus, the digestive diverticula, the stomach, the gonads and the renal organs respectively. The anterior adductor artery besides supplying the adductor muscle also serves the labial palps and the mantle. Further there are two arteries supplying the midgut and an artery supplying the crystalline style. The renogonidial artery gives off a branch which supplies the hind gut. The posterior aorta leaves the ventricle below the intestine and running all the length of the posterior adductor continues as the siphonal artery after branching off an artery to the posterior adductor muscle.

The three sinuses namely the muscle sinus, the renal sinus and the visceral sinus are the only features of venous system that are easily traceable in *Martesia fragilis*. Of these the muscle sinus is the smallest and is situated on the ventral side of the adductor muscle. The renal sinus surrounds the kidney on either side. The visceral sinus is the largest and extends between the palps and the siphons. The rest of the venous system consisting of the veins draining the blood from the gills, kidney, gonads, liver, stomach are too inconspicuous.

It will be seen from the above account that the heart, pericardium and the main blood vessels resemble those of the pholads described by Egger (1887) and Purchon (1955) differing in minor details of size and form. Their differences from teredine borers are however more marked and obvious.

The Nervous System

The cerebral, pedal and the visceral ganglia are the only nerve centres which are well differentiated, (Fig. 1 and Pl. II, Fig. 18). Of these the cerebral ganglia are white and lie in loose connective tissue on either side of the mouth. Five main nerves namely the anterior pallial nerve, the cerebral commissure, the anterior adductor nerve, the cerebro-pedal connective and the cerebro-visceral connective are given off from each ganglion. The anterior pallial nerve leaves the anterior margin of the cerebral ganglion and passes out to the margin of the mantle around the pedal aperture. The two cerebral ganglia are connected by the cerebral commissure passing over the anterior end of the oesophagus. A small nerve from the cerebral ganglia runs upwards towards the anterior adductor muscle. The cerebro-pedal connectives are very short nerves which arise from behind the cerebral ganglia and run towards each other, slightly towards the surface.

The pedal ganglia are very close to the mouth, nearest to the surface. They are fused along their length and the pedal commissure is indistinguishable. The nerve cells are greyish blue when alive but easily stained deeper blue in haematoxylin or Mallory's.

Observations of the sections showed that both the cerebral and the pedal ganglia have similar structure, a cortex of ganglion cells with processes passing into a core, which is made up of nerve fibres. These fibres stain dark blue in Mallory. The cerebro-pedal connectives enter into the ganglia into the foot where they break into numerous branches supplying the muscles as found in *P. loscombiana* (Purchon, 1955).

The lower end of the cerebral ganglia gradually pass into the cerebro-visceral connectives (fig. 15) which pass backwards and travel very close to the line of attachment of the ascending lamella of the inner demibranch. At the posterior end of the visceral mass it passes ventral to the renal organ. Along its course, five branches are given off which supply the visceral mass innervating the intestine, digestive diverticula, gonads and kidney.

The two visceral ganglia which lie on the postero-ventral surface of the renal organ are the largest in the nervous system. They are enclosed in a close fitting capsule similar to the condition found in *M. striata* and *P. loscombiana* (Purchon, 1955, 1956). In sections of the ganglion it was found that the ganglion cells are for the most part grouped over the surface forming the cortex. The main part of the ganglia is made up of transverse series of fibres with scattered nerve cells. The visceral ganglion gives rise to four important nerves. The cerebro-visceral connective terminates in the antero-lateral corners of the visceral ganglion and travels to the anterior region. There is a transverse connective between the cerebro-visceral connectives which is swollen and forms the accessory visceral ganglion. Similar ganglion occurs in *M. striata* and other pholads except in *Z. crispata* where it is only a simple connective. The accessory visceral ganglion in *M. striata* is also invested with a fibrous capsule (Purchon, 1956). Two very prominent nerves arise

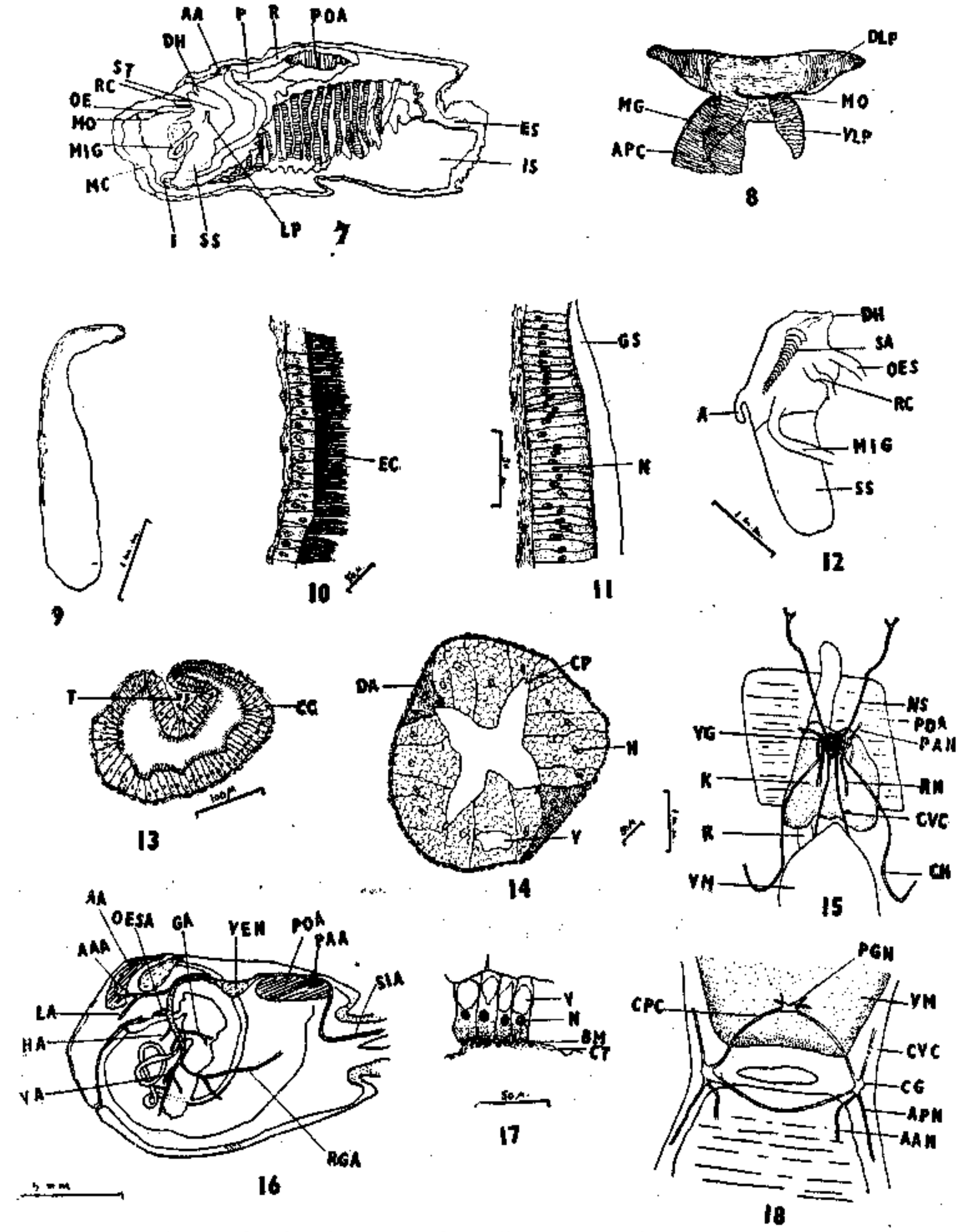


FIG. 7. Diagram showing the course of the alimentary canal.
FIG. 8. Anterior part of the ctenidium and the labial palps.
FIG. 9. The crystalline style.
FIG. 10. Transverse-section through the epithelium of the Style-sac.
FIG. 11. Transverse-section through the stomach epithelium below the gastric shield.
FIG. 12. Right side view of the external surface of the stomach.
FIG. 13. Transverse-section through the intestine showing the typholosole.
FIG. 14. Transverse-section through a tubule of the digestive diverticula.
FIG. 15. Showing the position of the visceral ganglia and the associated nerves.
FIG. 16. Diagram showing the arterial system.
FIG. 17. Transverse-section through the epithelium of the glandular portion of the renal organ.
FIG. 18. Showing the position of the cerebral and pedal ganglia and the associated nerves.

close to the entrance of the cerebro-visceral connectives passing out almost at right angles to the cerebro-visceral connective. These are the ctenidial nerves which enter the ctenidial axis along which they pass. They travel above the afferent branchial vessel along its entire length. Small nerves from the visceral ganglion pass into the posterior adductor and a larger pair travels posteriorly to the siphonal process in which they develop small ganglia before breaking up into a number of small nerves. A pair of nerves from the cerebro-visceral connective run towards the ventral wall of the renal organ to which it serves.

A comparison of the nervous system of *M. fragilis* with those of the rock-boring pholadids (Purchon, 1955) and wood-boring *Teredo* shows, that while there is close similarity in the general disposition and distribution of the various nerves with the former, in the latter, differences were noted in the disposition of the various nervous ganglia. The visceral ganglia in *Teredo* is situated posterior to the posterior adductor m[illegible]nlike *M. fragilis*.

The Reproductive System

The gonads in *M. fragilis* consist of branched ramifying tubules, which when mature form creamy white masses. During the breeding season the branching tubules increase in size and the tubules from the sides meet and extend over the entire visceral mass. The gonads open separately by two ducts into the suprabranchial cavity, dorsal to the renal aperture, on the postero-dorsal end of the visceral mass. Though both the ovary and the testis are of the same colour, the ovary is distinguishable since it occupies the greater part of the visceral mass.

The male gonad consists of thickly packed spermatozoa, which are extremely minute bodies developing from the germinal epithelium of the follicles. They have a large circular head and a protoplasmic long flagellum. The ova (Pl. I. Fig. 7) are large cells developed from the germinal epithelium of the follicles. Some have a rounded shape while others are polyhedral. They measure about 25 to 27 μ with a large circular nucleus which is highly granular enclosing a clearly visible nucleolus. Some cells have two nucleoli. In Mallory the nucleolus stained red and the cytoplasm light blue, while in haematoxylin and Eosin the nucleolus stained dark blue and the cytoplasm pink. The ovum is surrounded by a vitelline membrane.

As has been reported by Ganapathi and Nagabushanam (1953) for *M. striata* the present form also is protandric hermaphrodite. Out of 96 specimens ranging from 1-15 mm. in length examined in the laboratory it was found that the gonads were not of appreciable development till the forms attained a length longer than 4 mm. Out of 29 specimens 4-8 mm. long examined 15 were males and a smaller number of about 12 were females two being indeterminate. 28 of older specimens which attained a length of 8-12 mm. were examined and 15 were females while 7 were indeterminate suggesting a larger number in the hermaphrodite condition and only 6 were males. Among the largest forms examined from 12-18 mm. length 18 out of 25 were females only 2 were indeterminate, the rest being males. These figures suggest a change from the male condition to the female condition during the growth from 4 mm. to 18 mm. This sex change however is not accompanied by any change in structure as has been noted by Purchon (1941) in *Xylophaga*. The factors which may influence in the duration of the male phase and which may determine the change to the female are being studied.

REMARKS

From the foregoing account of the anatomy of *M. fragilis* it is seen that while it resembles the other pholads in all essential features it shows certain unique characteristics. The shell and the associated parts are modified during young stages for boring into wood but in later stages the pedal gape gets closed up with the formation of the callum and thereby the animal loses the ability to bore into wood. This is in contrast to the condition reported in teredines and other pholads like *Xylophaga* where the animals are able to bore throughout their life.

Although *M. fragilis* is known to bore into wood the significance of this is not certain but from the anatomical study of the digestive system it would appear, that structures like the large wood storing caecum found in teredines and *Xylophaga* specialized for storing wood particles associated with the digestion of wood, are totally absent. It may be inferred that the animal is not dependent on wood as a source of nutrition.

A comparison of the anatomy of the digestive system with that of *Xylophaga* and the teredines would suggest a gradation. The teredines being most specialized for digesting wood while *Xylophaga* shows a less specialized condition. *M. fragilis* though boring into wood do not show any specialized features for the digestion and absorption of wood. On the other hand it is seen that it possesses a well developed ciliary mechanism which is adapted for feeding on planktonic organisms as in the rock-boring pholads. In these respects it shows marked differences from teredines and *Xylophaga* in which the ctenidia are reduced and consist of only the outer demibranch and the ciliary sorting mechanisms presenting unspecialized features.

These observations suggest that *M. fragilis* though a wood-borer has none of the adaptations for subsisting on wood, on the other hand shows a well developed plankton feeding mechanism as in the rock-boring pholads. The significance of the wood boring habit while not being of digestive importance suggests that it may be for protection during young stages when they possess adaptive features for boring into wood. That the animal can also live even when it is denied the access to wood has been shown by experimental observations during the above studies, indicating that both in the young and adult stages these forms can live outside wood for varying periods and feed exclusively on plankton. These observations support the suggestion made above that *M. fragilis* in its anatomical characteristics is more like the rock-boring pholads than either *Xylophaga* or the wood-boring teredines.

SUMMARY

1. The external features and the characteristics of the shell in the young stages when it bores into wood and the changes undergone on the attainment of the adult condition are described. It is shown that the adults are incapable of boring into wood.

2. The anatomical features of the alimentary system together with certain histological observations are described. It is seen that the large wood storing caecum such as those found in teredines and *Xylophaga* is absent. Instead an appendix is found which is useful as a storage organ for unwanted large fragments.

The specialized diverticula for the intra-cellular digestion of wood is absent in *M. fragilis*, and it is considered that the animal may not be able to digest wood.

3. The anatomy of the respiratory system is described. It shows close resemblance to those of other pholads.

4. A comparison of the essential characteristics in the anatomy of the animal is made with other pholads and the wood-boring teredines.

5. The results are discussed.

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KEY TO LETTERING OF FIGURES

A	Appendix
AA	Anterior aorta
AAO	Anterior adductor
AAA	Anterior adductor artery
AAN	Anterior adductor nerve
APC	Anterior portion of ctenidium
APN	Anterior pallial nerve
AN	Anus
AU	Auricle
BM	Basement membrane
CC	Columnar cells
CG	Cerebral ganglion
CN	Ctenidial nerve
CP	Crypts
CPC	Cerebro-pedal commissure
CT	Connective tissue
CVC	Cerebro-visceral connective
DA	Darkly staining area
DD	Digestive diverticula
DH	Dorsal hood
DLP	Dorsal labial palp
EC	Epithelial cells of style sac
ES	Exhalent siphon
EPS	Epithelium of the stomach
C	Ctenidium
GA	Gastric artery
GS	Gastric shield
HA	Hepatic artery
HG	Hind gut
I	Intestine
ID	Inner demibranch
IS	Inhalent siphon
K	Kidney
LA	Labial artery
LP	Duct to left pouch
MA	Mantle
MC	Mantle cavity
MG	Marginal groove
MIG	Midgut
MO	Mouth opening
N	Nucleus
NS	Nerve to siphons
O	Outer demibranch
OES	Oesophagus
OESA	Oesophagial artery
OV	Ovary
P	Pericardium
POA	Posterior adductor
PAA	Posterior adductor artery
PG	Pericardial groove
PGN	Pedal ganglion
PAN	Posterior adductor nerve
R	Rectum
RC	Duct to right caecum
RGA	Renogonidial artery
RN	Renal nerve
SA	Sorting area
SC	Suprabranchial chamber
SIA	Siphonal artery
SS	Style sac
ST	Stomach
T	Typhlosole
V	Vacuole
VA	Visceral artery
VEN	Ventricle
VG	Visceral ganglion
VLP	Ventral labial palp
VM	Visceral mass

* Not referred to in original.