

ON THE BIOLOGY AND RELATIONSHIPS OF
THE LAMELLIBRANCH *XYLOPHAGA*
DORSALIS (TURTON)*

By R. Denison Purchon, Ph.D.

University of Bristol

(Text-figs. I-I6)

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INTRODUCTION

Xylophaga dorsalis (Turton) is a lamellibranch specialized for boring into timber in the sea. It occurs chiefly in floating timber, and probably for this reason and because of its much smaller economic importance it has never been studied in the same detail as many species of *Teredo* which do great damage to wooden ships and pier piles. The relationships of the genus *Xylophaga* are also obscure. Although it never bores into stone it has hitherto been included in the Pholadidae together with *Pholas* and other genera which are exclusively rock borers.

Specimens of *Xylophaga dorsalis* were obtained from Plymouth, and others, in two heavily-colonized pieces of driftwood, from Cullercoats and from Millport. The anatomy of the species has been studied in detail since it has never as yet been adequately described. The ciliary mechanisms in the mantle cavity were examined under the binocular microscope after the application of powdered carmine and of fine carborundum powder. Duboscq Brasil was found to be the most suitable general fixative. Sections were cut at thicknesses of from 3 to 8 μ and were stained in Delafield's haematoxylin and erythrosin.

* Owing to Dr R. D. Purchon's absence from this country on active service, this paper, which represents the greater part of the thesis he presented for the degree of Doctor of Philosophy, has been prepared for publication by Prof. C. M. Yonge.

In addition the ciliary currents and ctenidia of *Teredo megotara* Hanley and *T. norvegica* Spengler, the latter obtained from Port Erin and from Millport, were examined. This was done primarily for comparative purposes and to determine the effect of the modification of the feeding mechanisms due to the wood-boring habit upon the ciliary currents in the mantle cavity. These mechanisms have never previously been studied and new observations are recorded.

Work on *T. megotara* was carried out at the Marine Biological Station, Plymouth, in August 1937. The author wishes to express his gratitude to Dr S. Kemp, F.R.S., and members of the staff at Plymouth for the facilities provided. The remainder of the work was conducted in the Department of Zoology, University of Bristol, at the suggestion and under the direction of Prof. C. M. Yonge.

HABITAT AND HABITS OF *XYLOPHAGA DORSALIS*

Xylophaga dorsalis resembles members of the Teredinidae in its habit of boring into timber and not into stone. It is typically found in driftwood and only occasionally in fixed structures such as dock gates. It is usually, although not always, present in wood uninfected by *Teredo*. The animal which damages submarine telegraph cables and is known to cable repairers as "Teredo" is actually *Xylophaga*. Its ability to live in the gutta-percha sheath of these cables indicates that it cannot be completely dependent on wood as a source of nutriment. This matter will be discussed later.

The shell of a fully-grown *X. dorsalis* is of much the same size as that of *Teredo norvegica* the greatest antero-posterior dimension being about 10 mm. But, unlike the latter, it almost completely encloses the animal. Owing to the globular shape of the animal the borings of *Xylophaga dorsalis* are much less extensive than those of the Teredinidae. They are usually 2-3 cm. long and open to the exterior by a small pore, unless the surface wood has been broken away. Shell valves have been obtained from driftwood with an antero-posterior length of slightly over 1 in. These are probably shells of *X. praestans*. The accessory plates differ markedly in shape from those of *X. dorsalis*, and to each pair is attached a large transparent horny median plate. No such structure has been recorded in *X. dorsalis*. The excavations made by these large specimens were several inches long (Fig. 1 a).

Xylophaga does not line its burrow with a calcareous deposition as do *Teredo* and *Bankia*, nor does it possess pallets with which to close the opening of the burrow.

Being globular in shape it might be supposed that when *Xylophaga* releases its attachment by means of the foot to the forward end of the burrow it would roll about in the cavity. But this cannot occur, nor can the animal withdraw far from the boring end of the burrow, because the posterior end of the burrow is tightly packed with faecal pellets.

As shown in Fig. 2*a*, the exhalant siphon differs from that of other lamelli-branches in that it opens at the base of the siphonal process, on its dorsal side close to the posterior margins of the shell valves (s). The opening, which is oval, entire and devoid of tentacles, lies well within the burrow (ES). The faecal

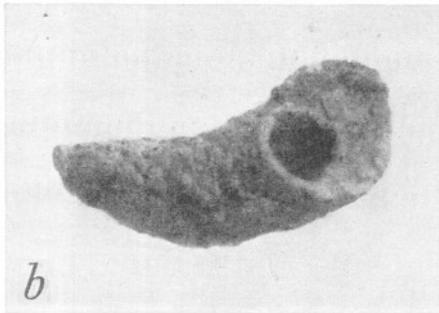
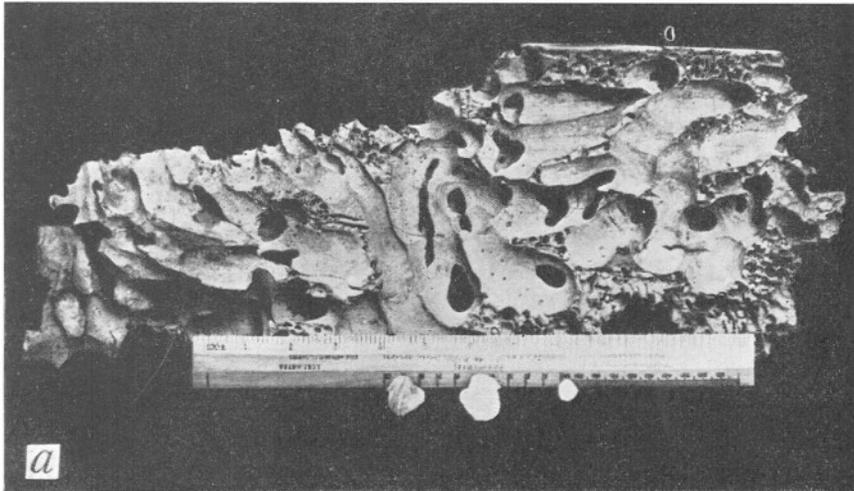


Fig. 1. *a*, Piece of wood bored by large specimens of *Xylophaga*, probably *X. praestans*. This sample was obtained by Messrs Neale and West, Trawler owners of Cardiff, and is now in an exhibition case in the Technical College, Cardiff. *b*, Faecal concretion taken from the posterior end of a burrow of one of the large specimens of *Xylophaga*.

pellets are not expelled with sufficient force to carry them out of the burrow and so accumulate at its posterior end as a compact mass, consolidated with mucus, which surrounds the siphonal process through which the exhalant water current passes. The presence of this faecal accumulation prevents any extensive movements of the animal.

The inhalant siphon (Fig. 2*a*, IS) is elongate, tubular and delicate. It may extend for as much as 1 cm. from the surface of the wood. The circular aperture is fringed with about six delicate tentacles (Figs. 2*a*, 6*b*, IS).

It is often possible to tell almost at a glance whether wood is colonized by *Teredo* or by *Xylophaga*, as in the former the siphons arise in pairs and in the latter they arise singly, being exclusively inhalant. The dorsal surface of the inhalant siphon possesses a pair of longitudinal lappets which are crenate for

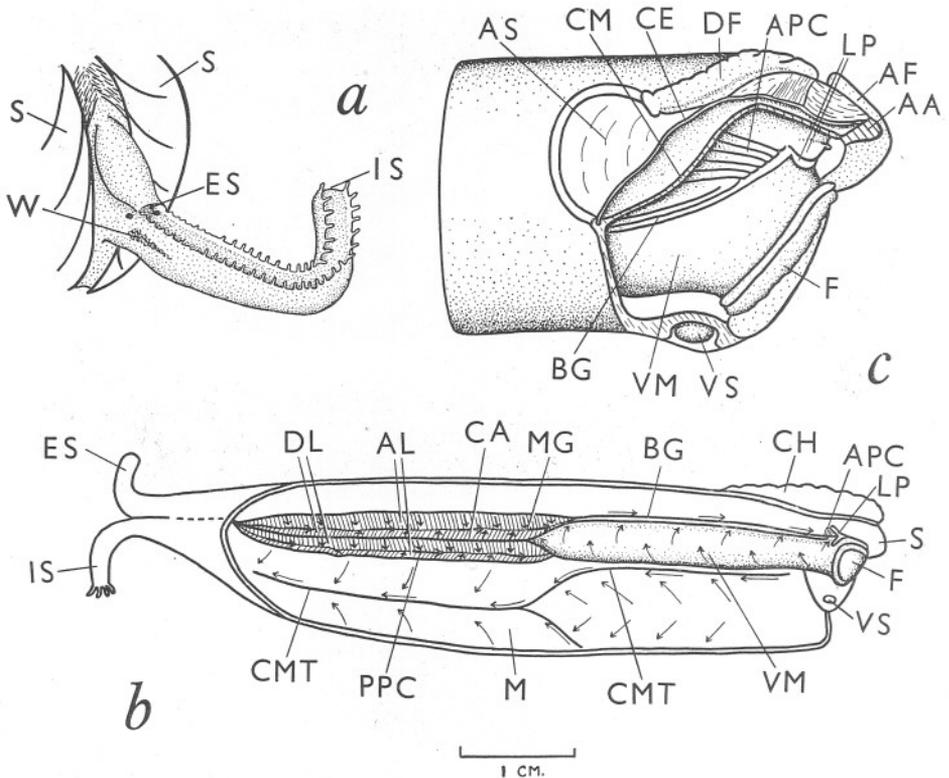


Fig. 2. *a*, *Xylophaga dorsalis*: posterior end of the shell valves and the siphonal process: ES, exhalant siphon; IS, inhalant siphon; S, shell; W, wedge-shaped mass of mucous glands. *b*, *Teredo norvegica*: mantle cavity opened laterally to show the course of the ciliary currents: AL, ascending lamella of ctenidium; APC, anterior portion of ctenidium; BG, branchial groove; CA, ctenidial axis; CH, cephalic hood; CMT, ciliated mantle tract; DL, descending lamella of ctenidium; ES, exhalant siphon; F, foot; IS, inhalant siphon; LP, labial palps; M, mantle; MG, marginal groove; PPC, posterior portion of ctenidium; VM, visceral mass; VS, ventral articulation of shell: other lettering as before. *c*, *Teredo navalis* (after Lazier): anterior portion of the mantle cavity opened to show the structure of the anterior portion of the ctenidium and the labial palps: AA, anterior adductor; AF, anterior pallial fold; AS, auricle of shell; CE, cut edge of shell; CM, cut edge of mantle; DF, dorsal pallial fold. Other lettering as before.

the proximal third of their length and then bear fine tentacles (Figs. 2*a*, 6*b*). They probably represent the original lateral walls of an elongated exhalant siphon which was attached throughout most of its length to the inhalant siphon, but the orifice of which has migrated backwards to the position which it now occupies. These fimbriated lappets support the sides of the cavity through the

faecal mass along which the exhalant water current passes. The dried remains of the siphonal process in a faecal concretion from the large specimens which were probably *X. praestans* suggest that in this species the siphonal process is similarly modified (Fig. 1*b*).

It is curious to observe that, although both Adams (1853-8) and Jeffries (1865) examined *Xylophaga* in sufficient detail to record the two longitudinal pectinated ridges which ornament the dorsal surface of the siphonal process, they erred in stating that the siphonal process was divided at its distal end into distinct inhalant and exhalant tubes. A similar error was made by Forbes & Hanley (1853) and by Pelseneer (1906), and erroneous illustrations are given by the first three of these authors. Forbes & Hanley, however, were made aware of their mistake by a Mr Cocks, as is recorded in Volume II of their work (pp. 375-6).

Near the base of the siphonal process a pair of opaque white spots can often be seen, one on each side of the opening of the exhalant siphon (Fig. 2*a*). Below each of these lies a thin but conspicuous wedge of mucous glands which have an opaque bubbly appearance (Figs. 2*a*, 6*b*, *w*). These may act as organs of temporary attachment (*Teredo* is weakly attached to the calcareous lining of its burrow at the base of the siphonal process), or they may exude mucus which assists in consolidating the faecal mass in the posterior end of the burrow.

Water expelled from the exhalant siphon passes slowly through the burrow and disperses at its mouth. Water is collected by the inhalant siphon about 1 cm. from the opening of the burrow and so a supply of fresh water is ensured.

It is difficult to observe the way in which *Teredo* clings to the end of its burrow, because when the burrow is opened the animal retreats from the boring end. Miller (1924), however, succeeded in observing *Teredo* making boring movements by dissecting open the burrow and covering the opening by a thin strip of glass which was stuck down at the edges by vaseline. After a short time the animal expanded and returned to the boring end of the burrow. Miller observed boring operations by means of a binocular microscope before the animal had covered the strip of glass with a deposition of calcium carbonate.

Unlike *Teredo*, however, *Xylophaga* maintains its grip on the end of the burrow while the latter is being opened, and there is no difficulty in observing the mode of attachment. Suction doubtless plays an important part in the attachment of the foot, but it was frequently observed that when a specimen of *X. dorsalis* was being removed from its burrow with the foot firmly attached, this could be prised slowly from the wood by a needle. Attachment of the foot thus continues after suction can no longer be maintained. There appears to be a sticky secretion which assists attachment. The adhesive surface of the foot is roughly circular and is bounded by a conspicuous ridge. Median to this ridge, the surface of the foot bears two lateral crescentic opaque patches one on each side; in the centre of the foot the surface is not opaque. The ridge which

surrounds the adhesive surface of the foot bears a conspicuous opaque raised disk in a median dorsal position (Fig. 6*b*, OF). Serial sections of the foot show that mucoid glands are present close to the epidermis in the regions which appear opaque externally. These glands are probably derived from the byssus apparatus, and presumably it is a sticky secretion from these glands which assists in fastening the foot to the boring end of the burrow. Sections through the foot of *Teredo* show that it also possesses mucoid glands which may assist in attachment.

CILIARY MECHANISMS IN THE MANTLE CAVITIES OF
TEREDO AND *XYLOPHAGA*

Teredo norvegica Spengler

The ctenidia.

Sigerfoos (1908) has shown that, in the post-larval development of *Bankia* (*Xylotrya*) *gouldi* Bartsch, the ctenidium, which is composed of only one demibranch, becomes separated into two portions of unequal size due to the great broadening of the tenth or eleventh filament. The ctenidium is also divided into two portions in *Teredo*, the number of filaments in the anterior portion (Fig. 2*b*, APC) varying in different species. In *T. navalis* L. (Lazier, 1924) there are five anterior gill filaments (Fig. 2*c*, APC). In *Teredo*, as in *Bankia*, only one demibranch is present on each side of the animal. Ridewood (1903) and also Atkins (1937*b*) considered this to be the inner demibranch; but it has been shown elsewhere (Purchon, 1939) that in *Teredo* and in *Xylophaga* it is the *outer demibranch* which remains.

The ciliary mechanisms in the mantle cavity of *Teredo* have been compared with those of the closely related rock-borers in the family Pholadidae, of which American species in the genera *Pholadidea*, *Zirphaea* and *Barnea* were examined by Kellogg (1915). In the Pholadidae the ctenidia are each composed of *two complete demibranchs* (Kellogg, 1915).

Both Ridewood (1903) and Sigerfoos (1908) considered that in *Teredo* and *Bankia* the anterior portion of the gill consisted of *descending* filaments. The afferent branchial vein travels in the ctenidial axis and, bearing this in mind, consideration of the figures given by Sigerfoos (1908) for *Bankia* makes it evident that in the anterior portion of the gill the descending lamella is represented by the inner wall of the branchial groove, and that the filaments present actually form the *ascending lamella* of the gill. The same holds good for *Teredo*.

The anterior portion of the ctenidium lies close to the labial palps at the sides of the foot (Figs. 2*b*, 4, APC). The posterior part is situated for the most part posterior to the visceral mass (Fig. 2*b*, PPC). These two portions of the gill are connected by the branchial groove (Fig. 2*b*, BG), which is an extension of the marginal food groove (Fig. 2*b*, MG). In *T. norvegica*, as in *T. navalis* (see Ridewood, 1903), owing to the ventral position of the gill axis, the descending lamellae pass outwards almost horizontally (Fig. 3*g*) instead of downwards

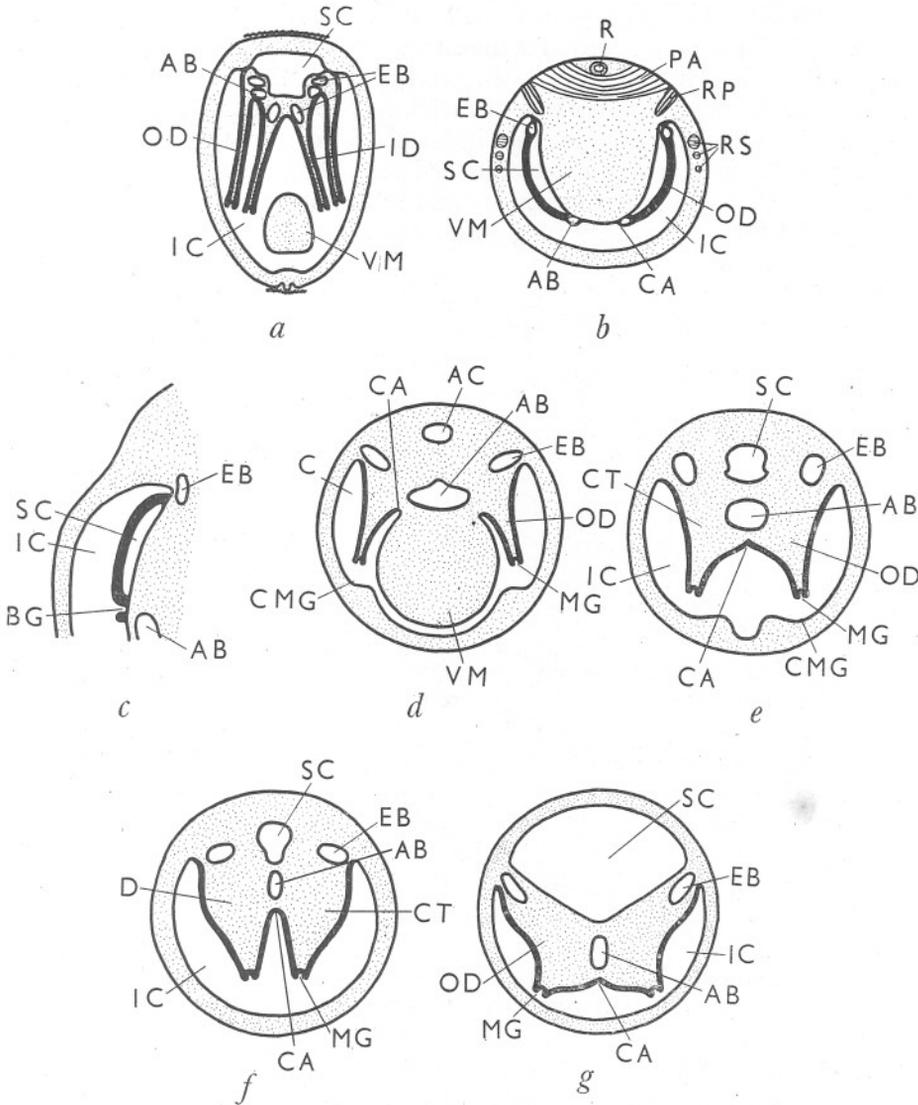


Fig. 3. Diagrammatic transverse sections through the soft parts of various rock-boring and wood-boring lamellibranchs.

a, *Barnea parva*.

b, *Xylophaga dorsalis*.

c, *Teredo norvegica*, through the anterior portion of the ctenidium.

d, *Bankia gouldi* (after Sigerfoos), through the posterior end of the visceral mass.

e, *B. gouldi* (after Sigerfoos), through the posterior portion of the ctenidium.

f, *Teredo megotara*, through the posterior portion of the ctenidium.

g, *T. navalis* (after Ridewood), through the posterior portion of the ctenidium.

AB, afferent branchial vein; AC, anal canal; CMG, ciliated mantle groove; CT, ctenidium; EB, efferent branchial vein; IC, infra-branchial cavity; ID, inner demibranch; OD, outer demibranch; PA, posterior adductor; R, rectum; RP, retractor pedis muscle; RS, retractor muscles of siphonal process; sc, supra-branchial cavity. Other lettering as before.

as in *Bankia gouldi* (Fig. 3, *d, e*) and in *Teredo megotara* (Fig. 3*f*). In *T. norvegica* the anterior portion of the ctenidium is composed of ten ascending filaments, of which the tenth is shorter than the others in the specimens examined. Occasionally one of the filaments may be broader near the marginal groove than elsewhere as is the case in filament two (Fig. 4).

The ctenidial axes are situated in a dorso-lateral position opposite the visceral mass, but near the posterior end of the visceral mass they approach the median line, where they fuse, as do the afferent branchial vessels. The

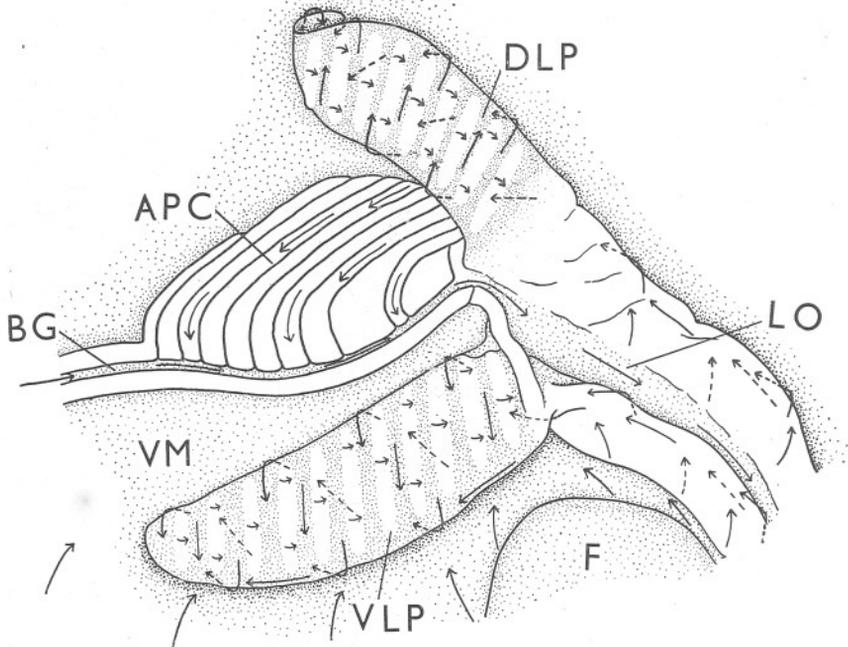


Fig. 4. *Teredo norvegica*: anterior portion of the ctenidium and the labial palps: DLP, dorsal labial palp; LO, lateral oral groove; VLP, ventral labial palp. Other lettering as before.

posterior portions of the ctenidia thus lie side by side and their descending lamellae arise from a common axis (Fig. 3 *e, f, g, CA*). The ctenidia are flat and homorhabdic; upon both portions of the ctenidium the cilia beat downwards into the marginal groove. In the marginal food grooves and in the branchial groove the cilia beat forwards, and all particles which enter them are driven towards the base of the labial palps (Figs. 2*b, 4*).

As summarized by Atkins (1936, 1937*a*) there are two main types of ctenidial sorting mechanisms in the Lamellibranchia whereby large particles are rejected and small particles are passed to the mouth. In the first of these, large particles pass down the lamellae along the crests of the plaeae into the marginal

groove, whence they are eventually rejected; small particles, however, pass upwards in the grooves of the plicae and forwards along the ctenidial axes, or along the upper borders of the ascending lamellae, towards the mouth (Arcidae, Anomiidae, *Pecten*, *Ostrea*, etc.). In the second type both large and small particles pass down the ctenidium, but the small particles are allowed to pass forwards in the marginal food groove, while large particles are prevented—in some forms—by the presence of fan-like groups of large guarding cilia (*Pinna*, *Thracia*, *Musculus*, *Montacuta*, etc.).

Close examination of the ctenidia of *Teredo norvegica* showed that no such sorting mechanisms occur; all particles placed on the ctenidia passed down into the marginal food groove whence they are all passed forwards to the base of the labial palps (Fig. 2*b*, LP; Fig. 4, DLP, VLP). There is no ciliary current in the longitudinal direction either along the ctenidial axis or along the dorsal borders of the ascending lamellae.

The labial palps.

Deshayes (1845-8) and Quatrefages (1849) probably worked upon *T. norvegica*; they both figured animals with long strap-shaped labial palps, and *T. norvegica* is the only species in European waters which answers to such a description.

Of the species under consideration, the labial palps of *T. norvegica* exhibit the least reduction in size and complexity; those of *Bankia gouldi* are, according to Sigerfoos (1908), reduced to small ridges on the sides of a slight groove approaching the mouth. In *Teredo navalis* (Fig. 2*c*, LP) Lazier found "that the dorsal palps are small and inconspicuous but quite distinct, whilst the ventral palps are reduced to slightly raised ciliated patches". The labial palps of *T. megotara* are also greatly reduced; they will be described in due course.

The labial palps of *T. norvegica* are relatively large strap-shaped organs which hang freely in the mantle cavity just in front of the anterior portion of the ctenidium (Fig. 4). In comparison with the labial palps of a typical lamellibranch they are greatly reduced, although they are the largest yet recorded in the Teredinidae. Their outer surfaces are smooth, and their inner, opposed, surfaces possess eleven indistinct transverse ridges (Fig. 4). The ciliary mechanisms on the palps are complex, and can best be understood by close reference to the figure (Fig. 4). On the inner surfaces the current in the grooves is directed towards the lower edge and over this on to the outer surface. Along the free lower edge the current is towards the tip of the palp and away from the mouth. On the transverse ridges the cilia beat across the palp towards the mouth. On the outer surface the cilia beat obliquely backwards and upwards towards the free upper edge of the palp and over this on to the inner surface as shown by broken arrows in Fig. 4.

When extremely small quantities of carmine particles are applied to the palps, the grooves between the ridges become occluded. The particles are

therefore carried by the cilia on the ridges towards the mouth. When a little more carmine is added the grooves open and the ridges become less distinct. The most prominent ciliary activity is now that in the transverse grooves. Material passed forwards from the branchial groove is picked up by the palps and passed down one of the transverse grooves on to the outer surface. Here it passes obliquely upwards and backwards on to the inner surface again. A large mass of carmine quickly forms, and this circles the palp and slowly moves backwards to the tip of the palp where it is transferred to the mantle and passed backwards in a rejection current to the base of the inhalant siphon. The labial palps therefore exercise quantitative selection, and only few and fine particles are allowed to reach the mouth.

The walls of the lateral oral groove are well defined and possess powerful rejection currents. Small quantities of carmine travel down the centre of the groove to the mouth; but if a suspension of carmine is added here, it is seen that on the walls of the lateral oral groove ciliary currents pass downwards and backwards on both surfaces. Those on the inner surfaces pass over on to the outer surfaces and thence on to the outer surface of the labial palps.

The visceral mass and the mantle.

Lazier (1924) found that in *T. navalis* the ciliation of the mantle was restricted to two narrow strips opposite the marginal and branchial grooves. In *T. norvegica* the ciliation of the mantle can be divided into two distinct types. The first consists of groups of cilia scattered over the major part of the visceral mass and the mantle. The second consists of a pair of ciliated mantle tracts (Fig. 2*b*, CMT) which in the anterior region of the mantle cavity lie close to the branchial grooves. As shown in Fig. 2*b*, they approach the mid-ventral line opposite the posterior end of the visceral mass and thence pass backwards as a single tract to the base of the inhalant siphon. Throughout these tracts the cilia beat backwards.

As shown in Fig. 2*b*, the scattered groups of cilia on the mantle beat towards the ciliated mantle tracts and assist in keeping the surface of the mantle clean. The cilia on the mantle tracts beat powerfully, and by their action skeins of mucus are drawn from the general surface of the mantle and incorporated in the stream passing backwards to the base of the inhalant siphon. This action tends to mask the activity of the scattered groups of cilia.

In the vicinity of the labial palps the scattered cilia on the visceral mass beat forwards and particles borne in these currents are collected by the palps (Fig. 4). This is probably for the collection of stray wood fragments formed during boring operations. The cilia on the remainder of the visceral mass beat towards the branchial grooves, though it is probable that under normal conditions material collected by these cilia is passed to the ciliated mantle tracts (Fig. 2*b*).

The surface of the visceral mass and of the mantle which bears the scattered groups of cilia appears to consist of a shallow syncytial epithelium. This bears

groups of long cilia which arise from distinct basal granules arranged in a plate close to the surface (Fig. 5*a*). The junction between each basal granule and its cilium can be distinguished, as also can a series of fine fibres passing inwards in the form of a spindle from the basal granules to the base of the syncytium. No lateral cell walls can be distinguished, but a certain rather regular patchiness of the cytoplasm is suggestive of cell demarcation.

Near the anterior gill filaments, this syncytium gradually becomes deeper, and lateral cell walls can be distinguished, and each cell in this region possesses a group of long cilia. This suggests that the great elongation of the visceral mass and of the mantle has been accompanied by a stretching of the epithelial layers as well as by a proliferation of the cells comprising the epithelium.

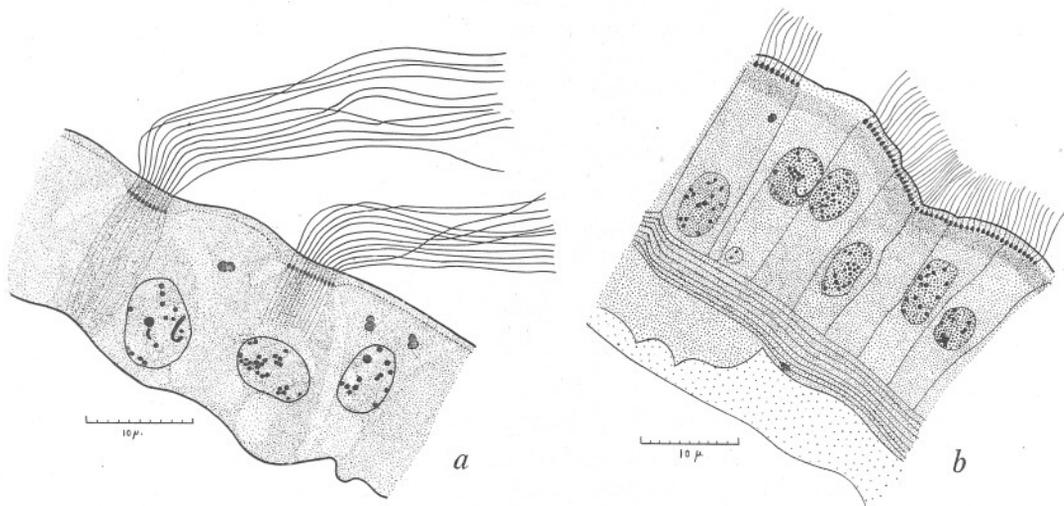


Fig. 5 *Teredo norvegica*: *a*, section through the epithelium of the visceral mass. *b*, section through the ciliated mantle tract.

There is often a slight but distinct delay before particles laid upon the visceral mass are set in motion by this scattered series of cilia, and it is possible that these cilia are under some distant control. There is a close resemblance between the spindle here described, passing from the plate of basal granules, and a spindle figured by Carter (1926), who established that certain cilia in the veliger larvae of various Nudibranchia are under nervous control.

The epithelium forming the ciliated mantle tracts differs markedly from that covering the general surface of the mantle (Fig. 5*b*). The cells are deep and columnar with distinct lateral walls. The nuclei are similar to those found in the syncytium covering the general surface of the mantle. The cytoplasm is a little more densely aggregated close to the surface, which is evenly covered with short cilia arising from a regular layer of basal granules. Very occasionally a cell is encountered which bears no cilia. There is no fibrous spindle arising

from the basal granules in these cells. Many mucous glands occur in the ciliated mantle tracts.

Similar mantle tracts have been described in *Pinna* (species not determined) by Stenta (1902), in *Pinctada vulgaris* by Herdman (1904), in *Cardium*, *Mytilus*, *Ostrea* and *Pecten* by Orton (1912), and in *Arca tetragona* and *Glycymeris glycymeris* by Atkins (1936).

In *Teredo norvegica*, as in *T. megotara* and in *T. navalis* (see Lazier, 1924), the mantle is of the same thickness throughout, but in *Bankia gouldi* (see Sigerfoos, 1908) the mantle is greatly thickened median to the ciliated mantle tracts, as shown in Fig. 3 *d, e*, CMG, forming well-defined "ciliated mantle grooves". Sigerfoos considered that in *B. gouldi* the mantle grooves are closely opposed to the free edges of the ctenidia and that, under the combined effect of the cilia in the marginal food grooves and in the mantle groove, food particles collected from the water are driven forwards to the mouth. But it is improbable that the cilia of the mantle groove in *B. gouldi* beat forward.

The ctenidia.

Teredo megotara Hanley

The anterior portion of the ctenidium is composed of seven ascending filaments, as shown in Fig. 6 *a*, APC. The posterior portion of the ctenidium resembles that of *Teredo norvegica* in all respects save its appearance in transverse section. The ctenidial axis occupies the normal position and the ctenidium is V-shaped when seen in transverse section (Fig. 3 *f*). The ciliary currents on the ctenidium are similar to those of *T. norvegica*.

The labial palps.

In *T. megotara*, which closely resembles *T. navalis* (see Lazier, 1924), reduction of the labial palps has been carried further than in *T. norvegica*. Both the upper and lower palps are triangular (Fig. 6 *a*, DLP, VLP), and they differ from those of other lamellibranchs (save *T. navalis*, as described by Lazier (1924), and *Xylophaga dorsalis*, which will be described later) in that the *inner* as well as the outer surfaces are *smooth*.

The application of carmine particles and of carborundum powder revealed that no sorting takes place on the palps, all material being passed to the mouth. The ciliary currents on the outer surfaces pass material backwards and downwards and over the free edges of the palps on to the inner surface. On the opposed surfaces the currents are directed forwards and upwards to the lateral oral groove. In Fig. 6 *a* the direction of the ciliary currents on the outer surfaces is indicated by broken arrows. Material passed forwards by the branchial groove enters the lateral oral groove at the base of the palps and is rapidly borne to the mouth. Particles which fall on the visceral mass close to the labial palps pass towards these and are incorporated in the food current.

The labial palps often suffer shock following dissection, as the removal of the shell valve jerks the apophysis slightly, and this is situated in an intucking of the mantle below the palps. On such occasions the mucous string arriving

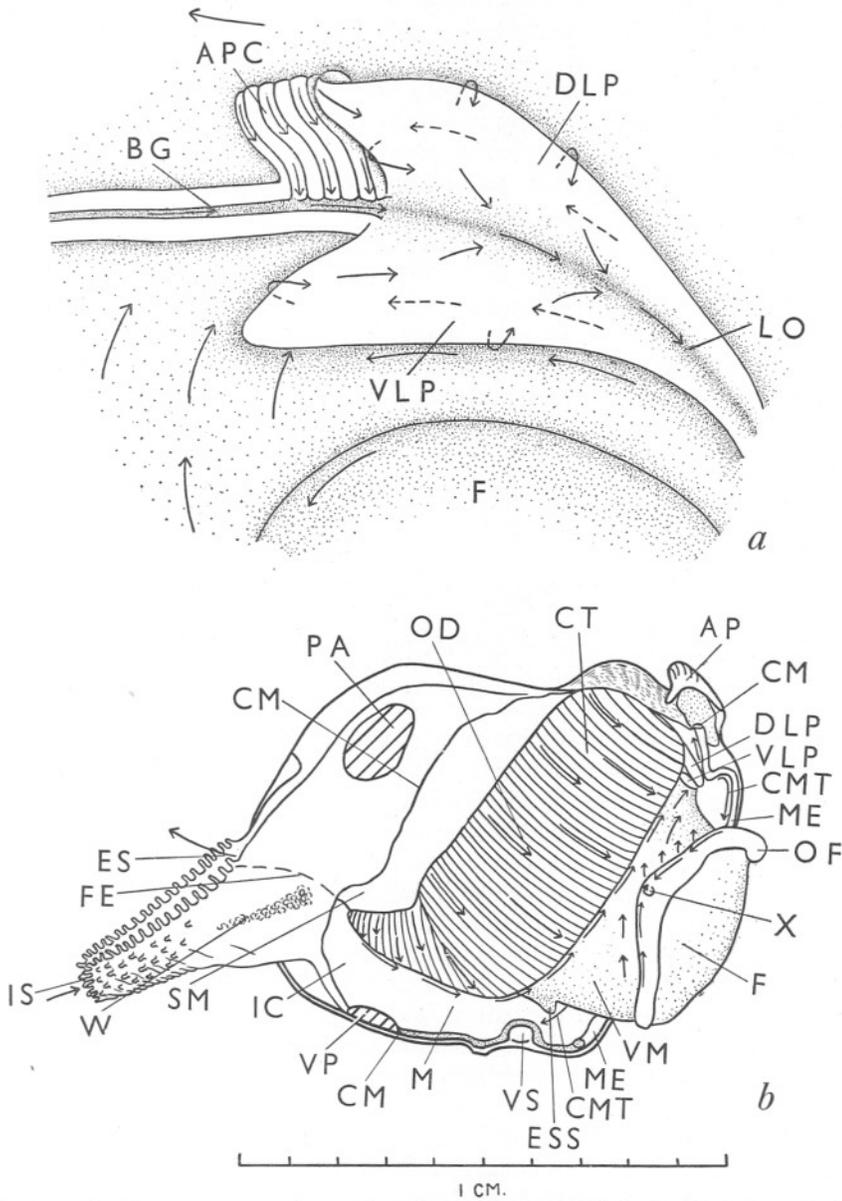


Fig. 6. *a*, *Teredo megotara*: anterior portion of ctenidium and labial palps: lettering as before. *b*, *Xylophaga dorsalis*: ciliary currents in the mantle cavity: AP, accessory plate; ESS, blind end of style sac; FE, floor of the exhalant siphon; ME, mantle edge; OF, opaque disk of foot; SM, suspensory membrane of ctenidium; VP, ventral pallial muscle; W, wedge-shaped mass of mucous glands; X, vortex in the ciliary currents on flank of the foot. Other lettering as before.

from the branchial groove is not accepted, due, it is thought, to some lack of continuity in the action of the cilia. This was not a normal rejection mechanism of the palps. When carmine is laid on the posterior portion of the ctenidia it travels up the branchial grooves on both sides of the visceral mass and, at the same time that material is being rejected by the palps on the dissected side, it can be seen, by moving the foot to one side, that the palps on the other side are accepting the food stream, passing both carmine and even carborundum powder along the lateral oral groove towards the mouth.

Thus no selective activity is displayed by the labial palps in *Teredo megotara*. There remains the selection displayed by rejection mechanisms of the mantle. If large quantities of carmine are added they become entangled as they pass along the marginal food groove, or along the branchial groove, with the mucous threads on the ciliated mantle tracts, and are then drawn away from the food stream by the superior strength of the rejection mechanisms.

The visceral mass and the mantle.

The ciliary mechanisms on the visceral mass and on the mantle are similar to those described for *T. norvegica*.

Xylophaga dorsalis (Turton)

The ctenidia.

The ctenidium is a large but delicate organ placed obliquely on the side of the visceral mass, as illustrated in Fig. 6*b*, OD. The posterior ends of the two ctenidia meet in the mid-ventral line near the origin of the inhalant siphon. The ctenidium is flat and homorhabdic and possesses no marginal groove. It is greatly reduced and consists of the direct lamellae (not divided into descending and ascending lamellae) of the *outer* demibranch (Purchon, 1939). The ctenidial axis runs along the ventral margin of the lamella (Fig. 3*b*, CA). The afferent branchial vein runs in the ctenidial axis (Fig. 3*b*, AB), and the efferent branchial vein traverses the dorsal margin of the lamella (Fig. 3*b*, EB).

The major portion of the ctenidium is broad and in life is held well away from the visceral mass by the large quantity of water that is held in the supra-branchial cavity. At the posterior end the filaments are much shorter than they are in the middle of the ctenidium (Fig. 6*b*). The ciliary currents are all directed downwards towards the ctenidial axis and forwards along it to the labial palps (Fig. 6*b*). The ctenidia possess no sorting mechanisms.

The labial palps.

The upper labial palp is a small spindle-shaped organ, the outer surface of which is fused to the visceral mass throughout its length (Fig. 7*a*, DLP). It is fleshy and tapers considerably distally. The lower palp is still smaller and is flat, and the outer surface is free from the visceral mass to a slight extent along its lower border. It forms a broad platform extending from the ctenidium to the mouth and is partially overhung by the upper palp (Fig. 7*a*, VLP).

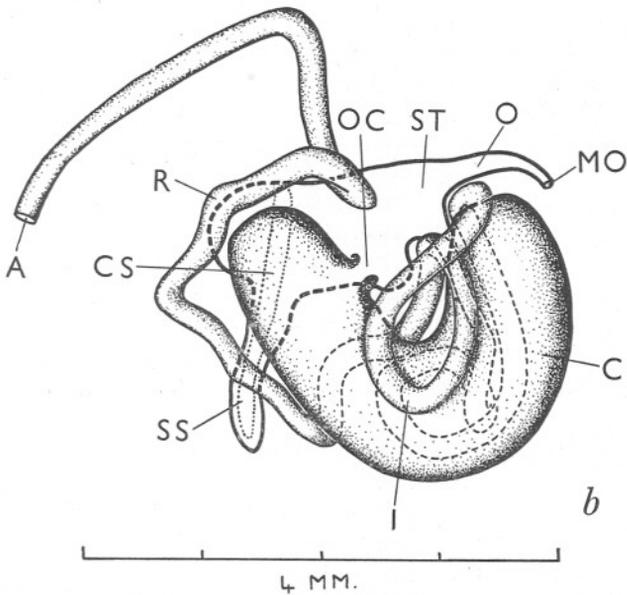
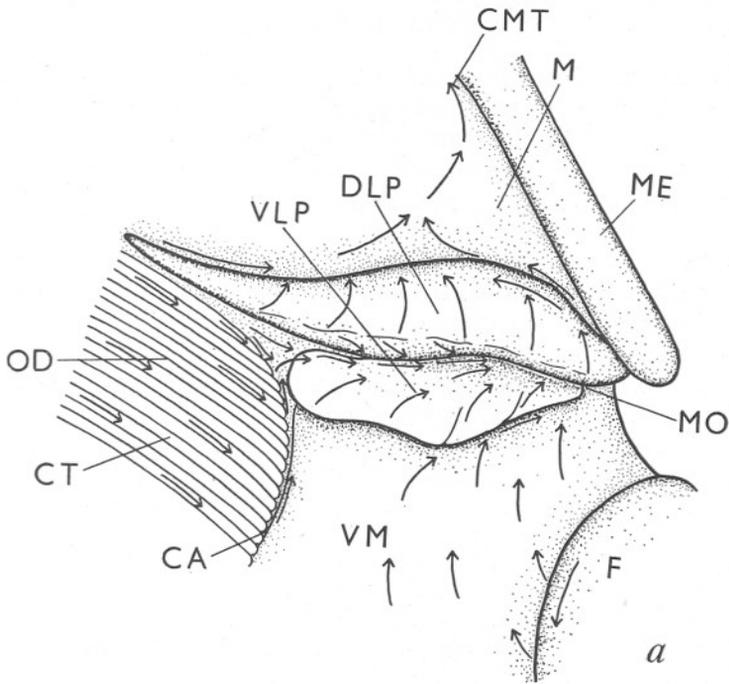


Fig. 7. *Xylophaga dorsalis*: a, labial palps and adjacent organs of the right side, upper palp turned slightly upwards to expose ciliary currents on the inner surface: MO, mouth. b, alimentary canal reconstructed from serial sections: A, anus; C, caecum; CS, crystalline style; I, intestine; O, oesophagus; OC, opening of caecum into stomach; SS, style sac; ST, stomach; R, rectum. Other lettering as before.

The sorting mechanism on the palps is greatly reduced. On the lower palp the currents, as shown in Fig. 7a, carry particles upwards and forwards to the mouth (MO). Along the innermost strip of the exposed, free surface of the upper palp the cilia also beat in the direction of the mouth; but over the greater extent of its surface the cilia beat outwards, away from the oral groove and on to the mantle, where rejected material is removed by the ciliated mantle tract which arises close to the upper palp (Fig. 7a, CMT).

Small quantities of carmine are accepted by the palps and passed to the mouth, but slightly larger quantities come under the influence of the outward-beating cilia on the upper palp. All particles are then drawn out of the lateral oral groove and transferred to the ciliated mantle tract. In Fig. 7a the upper palp has been turned slightly upwards in order to expose the ciliary currents on its inner surface. The labial palps in *Xylophaga* retain to a certain degree the power of quantitative selection.

The visceral mass and the mantle.

On the sides of the visceral mass the cilia beat upwards towards the labial palps as in *Teredo norvegica* and *T. megotara* (Figs. 6b, 7a). On the ventral region of the visceral mass no ciliation was observed. On the latero-dorsal flank of the foot the cilia beat upwards. At x the cilia impart a clockwise spin to material, which quickly collects there. This mass is removed from the foot by the ciliated mantle tract.

The major portion of the mantle is unciliated, particles being efficiently removed, under normal conditions, by the ctenidia. A ciliated mantle tract arises close to the upper labial palp as already described (Fig. 7a, CMT) and passes downwards close to the mantle edge until it is opposite the point at which particles collect on the sides of the foot (Fig. 6b, x). Here the mantle tract leaves the mantle edge and passes diagonally downwards to the mid-ventral line where it meets the mantle tract of the opposite side (Fig. 6b, CMT). A common mantle tract passes backwards from this point to the base of the inhalant siphon (as in *Teredo* and *Bankia*, the mantle lobes are completely fused in the mid-ventral line; Fig. 6b, CM). The ventral region of the mantle anterior to the point where the two mantle tracts unite is weakly ciliated, and particles falling here pass slowly backwards into the ciliated mantle tracts.

THE MORPHOLOGY OF THE ALIMENTARY CANAL AND
DIGESTION OF WOOD BY *XYLOPHAGA*

The anatomy of *Bankia gouldi* has been described by Sigerfoos (1908) and the morphology of the alimentary canal of *Teredo navalis* by Lazier (1924). The only contribution to our knowledge of *Xylophaga* was made by Potts (1923). Working upon an unidentified species of *Teredo*, he discovered that the digestive diverticula were of two types, one of which was specialized for the ingestion and intracellular digestion of wood fragments. He was unable to find any specialized area of the digestive diverticula in *Xylophaga*, and

concluded that the development of this specialized phagocytic region of the digestive diverticula in *Teredo* was associated with "the great development of the capacity for digesting wood (which was already possessed by *Xylophaga* to some extent) and a very rapid rate of growth". He concluded that *Xylophaga*, which possesses a caecal diverticulum of the stomach, has a limited capacity for digesting wood. No evidence was given in support of these views. Harington (1921) demonstrated the presence of a cellulase in the digestive diverticula of *Teredo norvegica*. Sawdust was digested, producing glucose, but not pure cellulose in the form of filter paper. The digestion of wood by *T. navalis* was demonstrated by a different technique by Dore & Miller (1923) and Boynton & Miller (1927). Chemical analyses were made of the faecal pellets of *T. navalis* and also of the wood through which the same specimens were boring. It was shown that wood loses up to 80% of its cellulose and 15-56% of its hemicellulose during its passage through the gut of the animal. Potts (1923) reared specimens of *Teredo* (species undetermined) from an early age to maturity in water freed from plankton, and concluded that the animal is more or less independent of plankton. The work of Roch (1932) supported his conclusions.

In the Lamellibranchia food normally passes through the alimentary canal in a slow steady stream so far as external conditions permit. The rhythmical production of large quantities of wood fragments in the Teredinidae and in *Xylophaga* by boring operations therefore involves corresponding modifications in the mode of digestion and the provision of a mechanical contrivance whereby the spasmodic entrance of material into the alimentary canal is converted into a slow steady stream. The functions of the caecum—a diverticulum of the stomach only possessed by wood-boring molluscs—are possibly to provide a reserve of food upon which the animal may live after it has exhausted the supply of available timber or ceased to bore, and, more probably, to release these fragments into the stomach in a slow and continuous stream.

In the rock-boring molluscs of the family Pholadidae, the products of their boring activities are not passed through the alimentary canal. The morphology of the alimentary canal of a small specimen of *Barnea parva* (Pennant) was examined so that a comparison could be drawn between the alimentary canal of *Xylophaga* and that of a typical member of the Pholadidae. The alimentary canal of *Xylophaga* was also compared with that of *Teredo navalis* as described by Lazier (1924).

In *Xylophaga* the mouth is an oval aperture situated between the labial palps just below the anterior adductor muscle (Figs. 7 a, b, MO). The oesophagus is wide but greatly flattened dorso-ventrally; it is considerably shorter than that of *Barnea parva* (Fig. 8, O). Its inner surface is smooth anteriorly but strongly ridged posteriorly; it is lined by a ciliated columnar epithelium. The oesophagus passes through the digestive diverticula and opens into the anterior end of the stomach.

The stomach (Figs. 7 b, 9 a, b, ST), which is situated to the left of the

median line, has an irregularly oval cavity, the surface of which is lined for the most part by the gastric shield (Fig. 9a, gs). The stomach of *Xylophaga* is relatively larger than that of *Barnea*. The stomach of *Teredo navalis* also is enlarged (Lazier, 1924). The stomach is lined by a ciliated columnar epithelium; the cilia are of various lengths, the longest ones being situated ventral to the gastric shield close to the point at which the crystalline style bears upon it.

The digestive diverticula consist of a number of small tubules which surround the oesophagus and lie close to the surface of the visceral mass at its anterior end. Two broad ducts open into the anterior end of the stomach (Fig. 9 a-c, DD). These ducts extend upwards under the umbonal beaks of

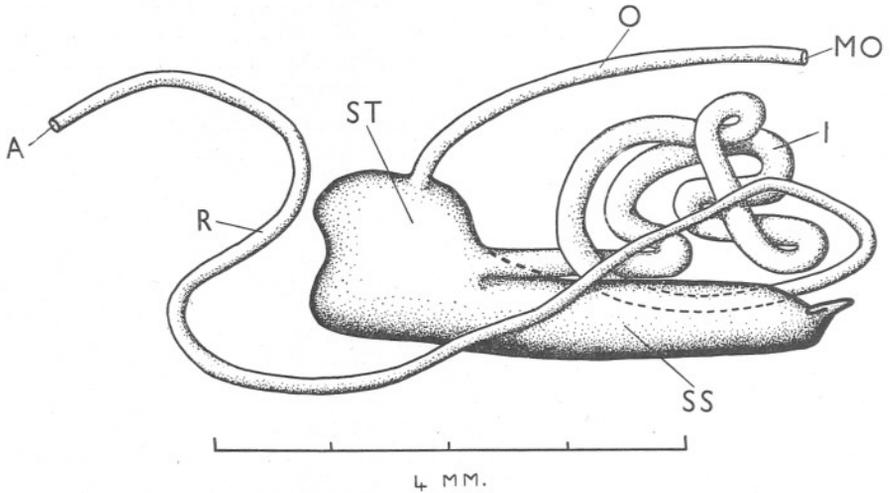


Fig. 8. *Barnea parva*: alimentary canal, reconstructed from serial sections. Lettering as before.

the shell valves, surrounding the intucking of the mantle within which the shell ligament is situated (Fig. 9 a, b, IM, L). Cilia have not been observed in sections either in the digestive diverticula (although seen in living tissue by Potts (1923) and Yonge (1926a)) or in their ducts, nor have phagocytes been observed in these regions. The cells forming the digestive diverticula are small and cuboid; they normally contain large numbers of very small spherical granules of a pale yellow colour. No evidence has been produced regarding the ingestion of particles, although this may be assumed in the light of previous data (Yonge, 1926a). Wood fragments have never been recorded either in the digestive diverticula or in their ducts, thus confirming the statement of Potts (1923) that in *Xylophaga* the digestive diverticula are not specialized for the ingestion of wood particles.

At the posterior end of the stomach the style sac enters on the right side (Fig. 7b, ss). This is small, and the crystalline style reduced (Figs. 7 b, 9 a, c, cs) when compared with that of *Barnea parva* (Fig. 8). Nelson (1918), who

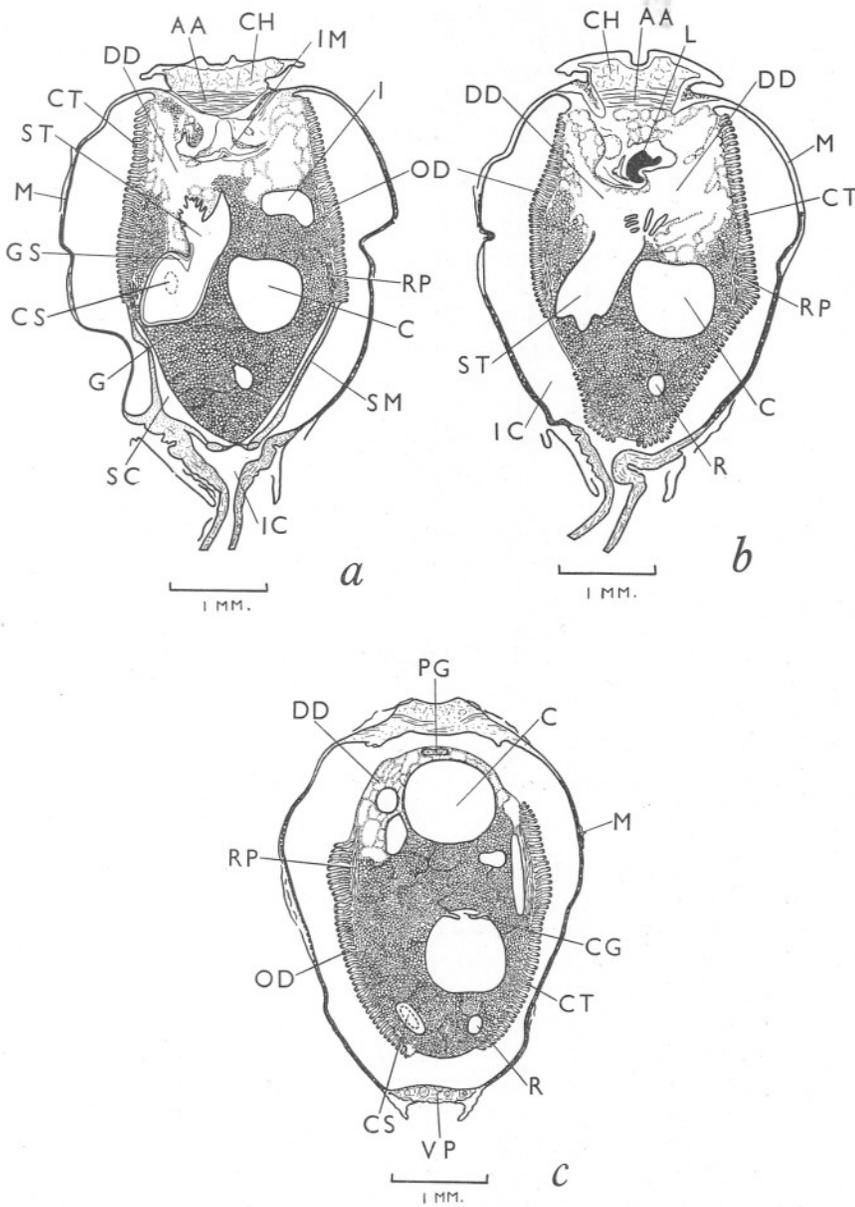


Fig. 9 *Xylophaga dorsalis*: horizontal sections through the whole animal, *a* cut slightly above *b*, and *b* above *c*: CG, ciliated groove of caecum; DD, digestive diverticula; G, gonad tubules filled with ova; GS, gastric shield; IM, intucking of mantle; L, ligament; PG, pedal ganglion. Other lettering as before.

did not personally examine *Teredo*, referred to the style, which he described as being much smaller than that of *Pholas* and of *Martesia*.

In *Xylophaga*, as in all members of the Adesmacea, e.g. *Teredo* and *Barnea*, the style sac is completely separated from the intestine. The blind end of the sac of *Xylophaga* closely approaches the surface of the visceral mass in the mid-ventral line and forms there a slight but distinct projection into the infra-branchial cavity (Fig. 6*b*, ESS). The sac is lined by the typical ciliated epithelium. The head of the crystalline style projects across the stomach diagonally (Figs. 7*b*, 9*a*, CS) and bears upon a concavity in the gastric shield on the left side of the upper border of the stomach (Fig. 9*a*, CS).

The caecum also opens into the stomach on its right side anterior to, and at the same level as, the style sac. The caecum is a U-shaped cylinder, the opening into the stomach being on the posterior limb and not quite terminal (Fig. 7*b*, OC). The distal limb of the caecum passes close under the adhesive surface of the foot and closely approaches the oesophagus (Fig. 7*b*). Sigerfoos (1908) states that in a young specimen of *Bankia gouldi* the caecum is similarly disposed, but in an adult specimen, as in *Teredo navalis* (see Lazier, 1924), the caecum is directed backwards. The inner surface of the caecum bears two conspicuous ridges seen in transverse section in Fig. 9*c*, CG. These enclose a ciliated channel which extends downwards from the opening of the caecum along its inner wall, round the bend and for a short distance up the ascending limb. Although not determined, it is probable that the cilia in this channel beat towards the stomach and that by this means a slow continuous stream of wood fragments is conveyed from the distal limb of the caecum into the stomach.

On the opposite side of the caecum to the ciliated channel the epithelium is columnar and the surface may bear cilia or may be distended into little colourless bubbles. In this region phagocytes may often be found squeezed between the epithelial cells, or at the base of the epithelium. The remainder of the epithelium lining the caecum is shallow and bears no cilia. Phagocytes have never been seen in this region. In serial sections the caecum is usually distended with wood fragments amongst which phagocytes occasionally occur. In some cases, however, phagocytes are abundant in the lumen, which is then almost entirely filled with bacteria. Phagocytes also occur occasionally in the stomach, though never in the digestive diverticula or in their ducts. Bacteria form a large percentage by volume of faeces in the rectum. When the caecum is heavily laden with wood shavings it is difficult to determine whether bacteria are present, but in some serial sections it appears as if bacteria are present as well as wood fragments.

Lazier (1924) showed that in *T. navalis* the caecum is apparently not ciliated but possesses a conspicuous two-coiled typhlosole capable of writhing movements. He thought that wood fragments were moved in and out of the caecum by muscular activity of the typhlosole and of the caecum walls. No such typhlosole occurs in *Xylophaga*.

The orifice between the stomach and the caecum in *Teredo navalis* resembles that of *Xylophaga* in possessing two lateral infoldings of the wall, this arrangement presumably providing for simultaneous ingress and egress of wood fragments. The right fold in *Teredo navalis* is continuous with the caecal typhlosole. In *Xylophaga* the two folds are continuous with the ridges which lie on the inner wall of the caecum.

The opening from the stomach into the intestine in *Xylophaga* is situated at the anterior end of the stomach on the left side of the ventral wall. The course of the intestine is complicated and can best be understood by reference to Fig. 7*b*. The intestine coils once on the left side of the stomach, rises and passes over the distal extremity of the caecum, coils once on the right side of the caecum and returns to the left side below the stomach. It then passes behind the style sac and merges into the rectum which passes forwards and upwards to the pericardium. The rectum travels upwards through the pericardium and, unlike that of *Teredo*, penetrates the ventricle.

Typically, lamellibranchs possess a typhlosole which extends throughout the intestine. Such a typhlosole is found in *Barnea parva*. Sigerfoos (1908) found that in *Bankia gouldi* the typhlosole extends throughout the intestine. According to Lazier (1924) *Teredo navalis* possesses a typhlosole only in the anterior portion of the intestine, which is greatly dilated in this region. A typhlosole has also been noted in certain portions of the intestine of *T. norvegica*, though the whole of the intestine has not been examined. In *Xylophaga dorsalis* no intestinal typhlosole is present; for this reason it is difficult to determine at which point the intestine passes into the rectum. In spite of the absence of an intestinal typhlosole, the faeces are well consolidated. They are extruded into the supra-branchial cavity and accumulate, as already described, in the posterior end of the burrow.

The absence in *Xylophaga* of a portion of the digestive diverticula specialized for the intra-cellular digestion of wood fragments (Potts, 1923) has led to a general belief that this species is incapable of digesting wood (Yonge, 1937, 1938).

Evidence is here produced which suggests that *Xylophaga* may be able to derive some nutriment from the wood through which it bores. It must be emphasized, however, that *Xylophaga* under certain circumstances is certainly independent of wood as a source of food. Specimens of *Xylophaga* living in the gutta-percha sheaths of submarine telegraph cables must subsist entirely upon plankton or other matter suspended in the water. Such specimens must penetrate metal wrappings before entering the gutta percha, unless they attack the cables only at points where the metal casings have been damaged. An outer wrapping of brass tape is now used to prevent such damage.

In order to determine whether *Xylophaga* possesses a cellulase, approximately twenty-four individuals of various sizes were extracted in sea water after grinding up with clean silver sand. The extract was diluted to 30 c.c. with clean sea water and divided into three equal parts. The substrate consisted of

fine sawdust previously treated three times with boiling water to remove any soluble sugars. The experiment and two controls were incubated at 30° C. for 14 days and the glucose present then estimated by the technique used by Boyland (1928). Full details are given in Table I.

TABLE I

Experiment	10 c.c. extract + 0.2 g. sawdust	4.725 g. glucose
Control 1	Ditto boiled	3.213 g. glucose
Control 2	Ditto without substrate	3.517 g. glucose

The glucose present in control 1 represents that originally present in the extract, that in control 2 represents this amount together with any produced by autolysis during the period of the experiment. The somewhat greater quantity of glucose present in the experiment indicates, although not with any certainty, the possibility of a cellulase. Further experiments with greater numbers of animals are necessary before this point can be settled.

If *Xylophaga* is capable of digesting wood the question arises as to where digestion takes place. In *Teredo* it was shown by Potts (1923) that wood is ingested in regions of the digestive diverticula specialized for this purpose. He also showed that these are absent in *Xylophaga*, a fact which the present investigation has confirmed. It is not impossible that the bacteria found in the caecum may feed on the wood and then be ingested by the phagocytes, which, as originally shown by Yonge (1926*a*, 1926*c*), play so great a part in the digestive processes of the Lamellibranchia. Further work is indicated on the nature of these bacteria and their presence in other wood-boring species. Final decision on the capacity of *Xylophaga* to digest wood will have to await the results of such work.

SEX CHANGE AND SEXUAL DIMORPHISM IN *XYLOPHAGA*

It is known that hermaphroditism occurs in *Bankia gouldi* (see Sigerfoos, 1908), *Teredo norvegica* (see Yonge, 1926*b*) and *T. navalis* (see Coe, 1933, 1934, 1935, 1936). To determine its possible occurrence in *Xylophaga dorsalis*, smears were made of the gonads of ninety-six specimens, while large numbers of specimens of many different sizes were sectioned to show the condition of the gonads. The greatest antero-posterior dimension of the shell of each individual examined was recorded, and the results obtained are given in Table II.

TABLE II. THE RELATION BETWEEN SIZE AND SEX IN *XYLOPHAGA DORSALIS*

Antero-posterior length of shell in mm.	Number of males	Number of hermaphrodites	Number of females
0-3	16	1	1
3-4	9	1	7
4-5	15	—	13
5-6	7	—	6
6-7	3	—	3
7-8	4	—	6
8-9	—	—	3
9-10	—	—	1

It will be seen that, of eighteen specimens not exceeding 3 mm. in length, all were males with the exception of one hermaphrodite and one female. A second hermaphrodite specimen was present in the next size group, while the remaining animals between 3 and 8 mm. long were fairly evenly divided between males and females. The four specimens which exceeded 8 mm. in length were all females.

X. dorsalis appears, therefore, to be a protandric hermaphrodite. The young specimens are male, change to the female sex occurring when they reach a length of about 3 mm.; but this change may apparently be delayed, and therefore animals of medium length are about evenly divided between the sexes.

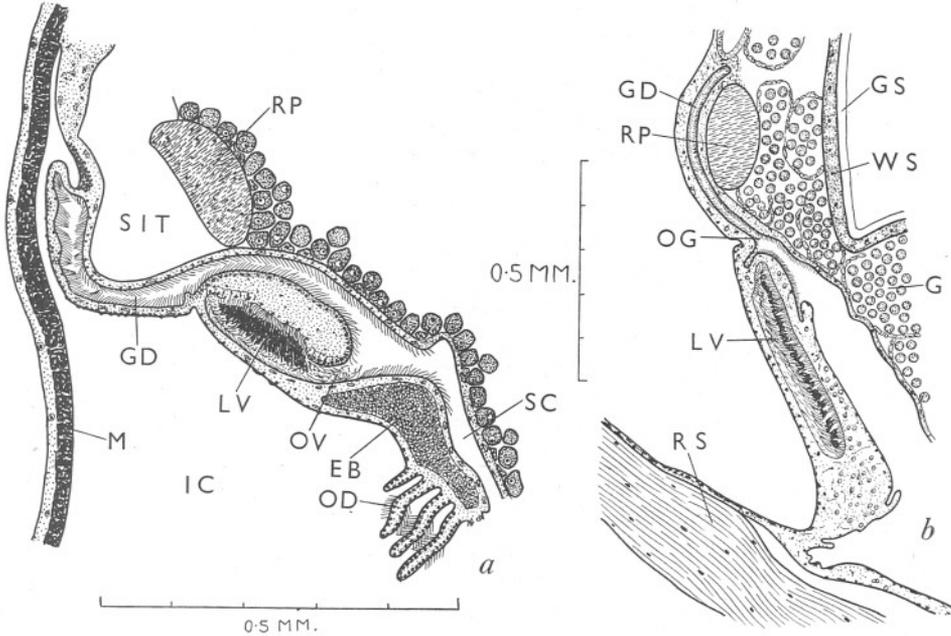


Fig. 10. *Xylophaga dorsalis*: *a*, transverse section through the vesicula seminalis: GD, genital duct; LV, lumen of vesicula seminalis; SIT, split in tissues. *b*, longitudinal section through the vesicula seminalis: OG, opening of genital duct; WS, wall of stomach. Other lettering as before.

It is possible that individuals may undergo more than one change in sex, so that the largest size groups may consist of individuals which are female for the second time. Coe (1933-6) believes that such alternation of sexes occurs in *Teredo navalis*.

Examination of serial sections of various specimens confirmed these observations. In Fig. 12 *a* is shown the appearance of the gonad in a hermaphrodite individual 3 mm. long. The lumina of the gonadal tubules are filled with spermatocytes and ripe spermatozoa, whilst the walls of the tubules are lined with developing oogonia of various sizes. It is less easy to demonstrate a

change of sex from female to male because this is thought to occur relatively quickly (Coe, 1933). Evidence has been obtained, however, from serial sections of an individual 5 mm. long, of a change of the gonad from female to male. In this animal the tubules were filled with spermatocytes and spermatozoa, with no signs of oogonia. The animal, therefore, was in the male phase. In its genital ducts, however, a small number of ripe ova was found, and since there was no sign of change of sex in the gonads, it was concluded that these ova were formed in a female phase prior to the existing male phase. This may be regarded as presumptive proof that a second change of sex, from female to male, may occur. Since the largest specimens examined were all females, it is possible that a further change of sex may occur.

In *Xylophaga* the genital duct is short, passing round the retractor muscle of the foot (Fig. 10 *a, b*, RP) and opening at the base of the suspensory membrane of the gill into the supra-branchial cavity anterior to the opening of the kidney duct (Fig. 10 *a*, GD; Fig. 10 *b*, GD, OG). It is lined by a ciliated epithelium which extends for a short distance over the suspensory membrane of the gill. Situated in the suspensory membrane close to the genital opening is a cylindrical cavity with an anterior opening. The cavity is lined by a ciliated epithelium which is continuous with that extending from the genital duct over the suspensory membrane. The opening of this ciliated pocket is directed ventrally (Fig. 10 *a*, OV) and is situated close to the genital opening. The lumen of this organ (Fig. 10 *a, b*, LV) is filled with spermatozoa, which are tightly packed and orientated with their heads pointing towards the ciliated epithelium lining the cavity. Irregularly disposed spermatozoa can be seen at the orifice of the organ (Fig. 10 *a*, OV), and these may have been entering or leaving the organ.

It is considered that the organ is a vesicula seminalis, and that it is loaded with spermatozoa when these are discharged at the end of the male phase of the gonad. No other records of such an organ in the Lamellibranchia have been found, and it is possible that *Xylophaga* is peculiar in the possession of a pair of vesiculae seminales. *X. dorsalis* presumably shares this distinction with other members of the genus, e.g. *X. praestans*, *X. indica*, and *X. globosa*.

The vesiculae seminales are present in specimens of all sizes, even in the smallest ones examined, in both sexes, and always contain a considerable quantity of spermatozoa. The method by which they are filled with spermatozoa will be discussed later. Whether self-fertilization occurs in *Xylophaga* to the exclusion of cross-fertilization is difficult to determine, but it appears certain that the possession of these organs renders self-fertilization possible.

Xylophaga is peculiar among the Lamellibranchia not only in the possession of vesiculae seminales, but also for the development of an unusual glandular organ in the supra-branchial cavity. This "accessory genital organ", as it will be here called, is found in a fully developed condition in the male phase only, thus making *Xylophaga* one of the few recorded cases of external sexual dimorphism in the Lamellibranchia. It lies suspended from the posterior surface of the posterior adductor muscle (Fig. 11) and when fully developed

consists of a large fleshy peduncle (Fig. 11c, PE) which expands distally into a broad, slightly bilobed blade or lamella (Fig. 11c, LA). The dorsal border of the peduncle encircles the rectum close to the anus. The blade is pressed closely against the posterior and lateral surfaces of the visceral mass. Fig. 11c shows the organ removed from the visceral mass, and in it the two lobes of the blade are pressed close to one another. In serial sections, the fully developed organ more or less completely occludes the supra-branchial cavity.

The posterior surface of the blade, and that of the peduncle, are sparsely ciliated, the weak ciliary currents being directed upwards towards the posterior adductor muscle. The anterior surface of the blade, which is closely pressed

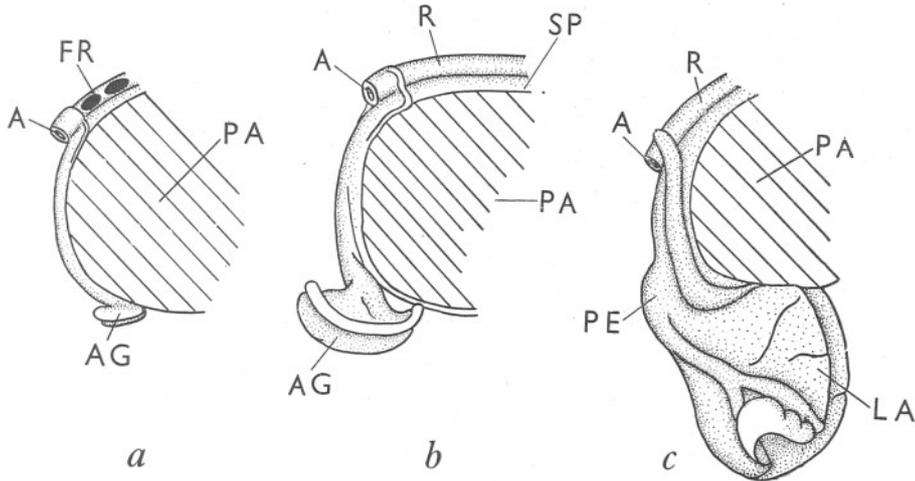


Fig. 11. *Xylophaga dorsalis*: the accessory genital organ in various stages of development, seen from the right side: a, small, from a female; b, medium, from a female, or hermaphrodite; c, large, from a male: AG, accessory genital organ; FR, faeces in rectum; LA, lamella, or blade, of accessory genital organ; PE, peduncle of accessory genital organ; SP, dorsal surface of posterior adductor. Other lettering as before.

against the visceral mass, is composed of a very shallow unciliated epithelium (Fig. 12 b, c). The cilia on the posterior surface of the blade, are seldom visible in sections.

The organ is of very variable size, being fully developed only in male specimens; occasionally it is of an intermediate size in female specimens—suggesting a recent change of sex—but it is always medium in size in hermaphrodite specimens. Data on this matter are summarized in Table III, which indicates the intimate relationship between the size of this accessory genital organ and the sex of the individual.

Serial sections through the accessory genital organ show that it is glandular, the posterior surface being composed of mucoïd cells. This layer occupies about a third of the thickness of the blade (Fig. 12b). No glands open on to the anterior surface. The remainder of the lamella is composed of a glandular

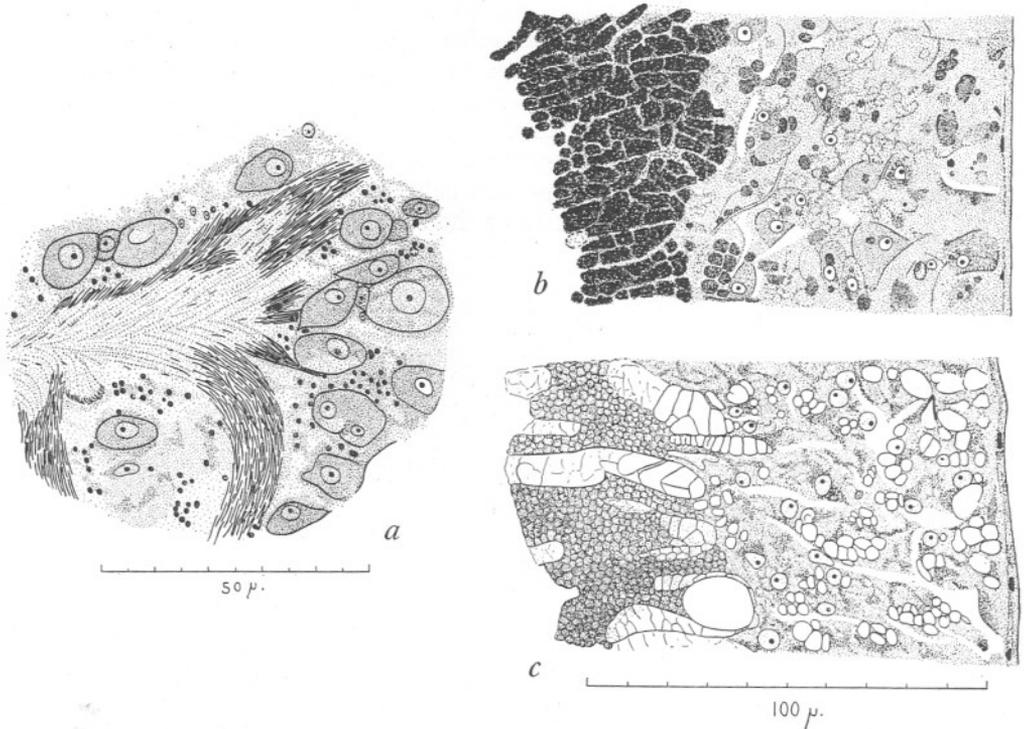


Fig. 12. *Xylophaga dorsalis*: transverse sections: *a*, through the gonad during the initial change from the male to the female phase; *b*, through the blade of the accessory genital organ, seen here in a ripe condition; *c*, through the blade of the accessory genital organ, in a spent condition.

TABLE III. THE RELATION BETWEEN THE SIZE OF THE ACCESSORY GENITAL ORGAN AND THE SEX OF THE ANIMAL

Antero-posterior length of shell in mm.	Size of accessory genital organ			
	Large	Medium	Small	Absent
0-3	16 ♂	I ♀	—	I ♀
3-4	7 ♂	2 ♂, I ♀	3 ♀	3 ♀
4-5	13 ♂	2 ♂, I ♀	3 ♀	9 ♀
5-6	7 ♂	—	I ♀	4 ♀
6-7	3 ♂	—	2 ♀	I ♀
7-8	4 ♂	—	3 ♀	3 ♀
8-9	—	—	—	I ♀
9-10	—	—	I ♀	—
Total	50 ♂	4 ♂, 2 ♀, 5 ♀	13 ♀	22 ♀

tissue which is for the most part stained but lightly with Delafield's haematoxylin. The cells are roughly fusiform in shape, and are shown in transverse section in Fig. 12 *b, c*. Their nuclei are easily distinguished, for they have a distinct nuclear membrane and a large central nucleolus. The secretion arises close to the nucleus, and when first formed consists of a lightly stained packet which later acquires darkly stained walls surrounding unstained contents. The number of these packets of secretion increases until finally a reticulate mass of bubbly appearance is formed. The secretion must pass to the posterior surface of the blade, which is deeply folded close to the peduncle. In these folds strands of mucus are frequently seen. Comparison of a number of series of sections shows that the organ secretes as a whole. Either the posterior surface is loaded with secretion or all the secretion has been discharged, leaving the cells at the posterior surface empty (Fig. 12 *c*). When the organ has secreted it presumably commences to degenerate.

It is probable that when spermatozoa are discharged from the gonad duct, owing to the pressure of the ripe gonads, they are forced past the openings of the vesiculae seminales, and fall upon the posterior surface of the supra-branchial organ. It is at this stage that the accumulation of mucus is discharged, and in it the spermatozoa become entangled. By the action of the cilia upon the posterior surface of the blade and peduncle the spermatozoa are driven upwards and conveyed to the openings of the vesiculae seminales. The spermatozoa are then passed into the lumina of these organs by the cilia on the suspensory membranes. Evidence has been found which supports this theory. In one series of sections both spermatozoa and spermatocytes were found entangled in mucous threads on the posterior side of the blade. The presence here of spermatocytes indicates that the spermatozoa were those produced by the animal itself, and were not foreign spermatozoa collected from the inhalant current.

When the vesiculae seminales are fully loaded the function of this accessory genital organ has been completed, and its degeneration commences. Residual sperm in the gonads may either be discharged or resorbed.

With the degeneration of the accessory genital organ the volume of the supra-branchial cavity is greatly increased and at the same time the animal changes to the female phase. It is not known whether *Xylophaga* incubates its larvae; but this occurs in some species of *Teredo* (Hatschek, 1880; Calman, 1919), and in view of the probable value of such a habit to animals inhabiting driftwood, it is probable that the same is true of *Xylophaga*. If so there is now available space for the larvae in the supra-branchial cavity. As shown in Table III, the accessory genital organ is present in all males whatever their size; thus if the animals do change sex more than once it must be redeveloped during the second male phase.

The possession of both these organs is probably of great survival value to *Xylophaga*. The animals live in isolated communities in driftwood, and the chance of fertilization might be slight were eggs and sperms discharged freely

into the sea. The retention of the sperms produced during the male phase will ensure fertilization of eggs produced during the later, female phase and so overcome this danger. Sigerfoos (1908) recorded that in male specimens of *Bankia gouldi* there is a great development of mucous glands in the roof of the supra-branchial cavity, but there is no record in any species of *Teredo* of any glandular organ. It is by no means impossible that *Bankia* and *Teredo* may also possess vesiculae seminales which have hitherto been overlooked.

THE SYSTEMATIC POSITION OF *XYLOPHAGA*

Consideration of the shell features of *Xylophaga* led systematists to the conclusion that, although these superficially resembled those of the Teredinidae, the genus was more nearly related to the Pholadidae, in which it has accordingly been included (Adams, H. & A., 1853-8; Paetel, 1890; Pelseneer, 1906; Thiele, 1926). But examination of the anatomy of *Xylophaga* gives no support to this view. Whilst showing affinities both with the Teredinidae and the Pholadidae, *Xylophaga* also possesses certain specialized characters of sufficient importance to justify the creation of a new family for its inclusion.

In the following important points *Xylophaga* has undoubted affinities with the Pholadidae.

With the exception of the siphonal process, the animal is entirely covered by the shell valves (Figs. 2a, 6b), its burrow is never lined with a calcareous deposition, nor does the animal possess pallets as do the members of the Teredinidae. *Xylophaga* possesses a pair of accessory plates (Fig. 6b, AP), though their absence in the Teredinidae is probably due to reduction. The rectum of *Xylophaga* passes through the ventricle (Fig. 13a, R), which it does not in the Teredinidae. Finally, the visceral ganglia occupy their normal position in *Xylophaga*, on the ventral surface of the posterior adductor muscle. In the Teredinidae, owing to the great elongation of the visceral mass, these ganglia are displaced backwards and lie far behind the posterior adductor.

The above are outweighed, however, by the following affinities between *Xylophaga* and the Teredinidae.

Xylophaga bores normally in wood (Fig. 1a), never in stone; its shell in its general appearance and fragility is not unlike that of *Teredo*. The ctenidia of *Xylophaga* (Figs. 3b, 6b) and of the Teredinidae (Figs. 2b, c, 3, 4) are composed of only one demibranch (Atkins, 1937b; Ridewood, 1903). This is in each the outer demibranch (Purchon, 1939). In addition there are no ctenidial sorting mechanisms in *Teredo* or in *Xylophaga*.

The labial palps in the Teredinidae have undergone various degrees of reduction (Fig. 2c, LP; Figs. 4, 6a, DLP, VLP) and may possess no ciliary sorting mechanisms; those of *Xylophaga* (Figs. 6b, 7, DLP, VLP) are also greatly reduced and have poor powers of selection. The ctenidia of the Pholadidae possess both inner and outer demibranchs, their labial palps are highly organized and the ciliary mechanisms on the ctenidia and the palps are highly developed (Kellogg, 1915). The alimentary canal of *Xylophaga* possesses

modifications similar to those in the Teredinidae for the acceptance of large quantities of wood fragments produced spasmodically. The oesophagus is short, the stomach is large and bears a conspicuous caecum within which wood shavings are stored. The style sac and the crystalline style are reduced in size (Fig. 7*b*, ss, cs)—contrast the large style sac of *Barnea* (Fig. 8, ss) and of

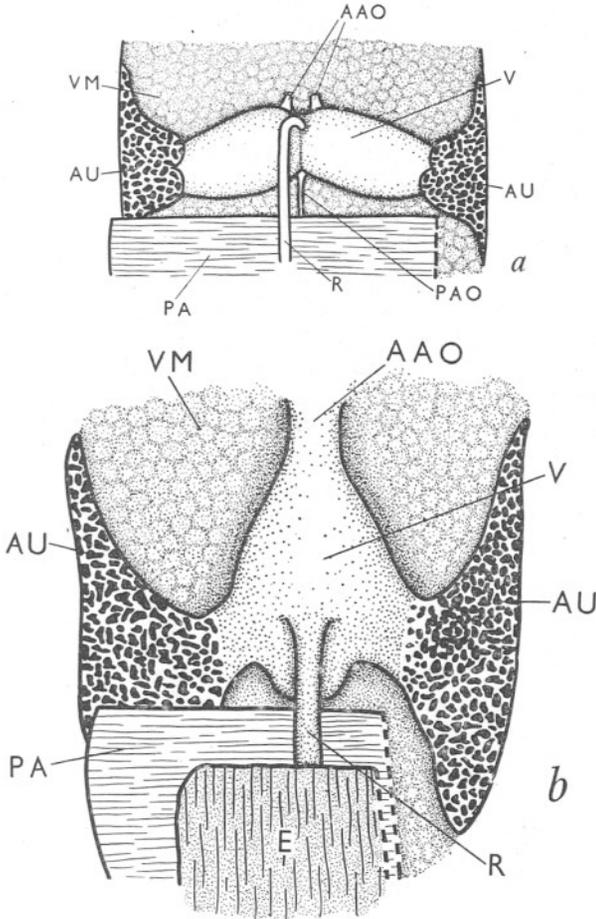


Fig. 13. Dorsal view of the organs in the pericardium. *a*, *Xylophaga dorsalis*; *b*, *Barnea parva*: AAO, anterior aorta; AU, auricle; E, epithelium of the siphonal process; PAO, posterior aorta; v, ventricle. Other lettering as before.

Martesia (see Nelson, 1918). The intestinal typhlosole has undergone various degrees of reduction in the Teredinidae (Sigerfoos, 1908; Lazier, 1924); it is absent in *Xylophaga*, but well developed in *Barnea*, a member of the Pholadidae.

It has been shown that various members of the Teredinidae are protandric hermaphrodites (Sigerfoos, 1908; Yonge, 1926*b*; Coe, 1933-6), and *Xylophaga*

also is a protandric hermaphrodite. This condition has never been demonstrated for any member of the Pholadidae. Various members of the Teredinidae incubate the larvae (Sigerfoos, 1908; Calman, 1919), and it is not improbable that *Xylophaga* also incubates its larvae, though this remains to be proved.

Finally, the structure of the ventricle of *Xylophaga* more nearly resembles that of *Bankia gouldi* (see Sigerfoos, 1908) than that of *Barnea parva*—in spite of the fact that it is traversed by the rectum. The ventricle of *Xylophaga* is short from front to back (Fig. 13*a*, v), it possesses two delicate anterior aortae which pass downwards into the visceral mass from a short median lobe which lies in front of the rectum (Fig. 13*a*, AAO), and a single posterior aorta (Fig. 13*a*, PAO) which passes under the posterior adductor muscle. The ventricle itself is short from back to front and is produced laterally into two conspicuous lobes which communicate with the auricles (Fig. 13*a*, AU). The ventricle of *Barnea parva* (Fig. 13*b*, v) is unlike that of *Xylophaga*; it possesses the typical fusiform shape, long in the antero-posterior plane, in which the rectum traverses the ventricle (Fig. 13*b*, R). The heart of *Bankia gouldi* (Sigerfoos, 1908) is deeply bilobed. In the young individual (Fig. 14*a*) the auricles are not attenuated, nor is the ventricle drawn out in the antero-posterior axis; it is more deeply lobed than that of *Xylophaga*. It is also morphologically upside down. Owing to the great length of the adult animal, the heart when fully developed (Fig. 14*b*) is quite unlike that of *Xylophaga*. The anterior and posterior aortae arise close to one another at the anterior end of the heart (Fig. 14*b*, AAO, PAO), and the auricles, which are greatly attenuated, communicate with two posterior lobes of the ventricle. In *Bankia gouldi* the ventricle of a young specimen, 2 mm. in length, is laterally bilobed, as it is in *Xylophaga*. This is doubtless a modification due to the globose shape of the two animals. In larger specimens of *Bankia gouldi* the antero-posterior elongation of the body necessitates a departure from the laterally expanded ventricle of the young animal.

There remain a number of characters in which *Xylophaga* differs both from the Teredinidae and from the Pholadidae. These characters show such a high degree of specialization that it is proposed to transfer *Xylophaga* from the Pholadidae and place it alone in a new family in the order Adesmacea, more closely related to the Teredinidae than to the Pholadidae.

Although it is typical of a member of the Adesmacea that the shell bears an apophysis upon which the retractor muscles of the foot are inserted, as in *Pholadidea penita* Conrad (Lloyd, 1897) (Fig. 14*c*, SA) and in *Teredo norvegica* (Fig. 14*e*, SA), *Xylophaga* possesses no shell apophysis (Fig. 14*d*), and the retractor muscles of the foot are inserted upon the shell in the primitive position, anterior to the insertion of the posterior adductor muscle. The siphonal process of *Xylophaga* is specialized, the exhalant siphon being reduced and opening within the burrow (Figs. 2*a*, 6*b*, ES). While there is some slight evidence that *Xylophaga* may resemble the Teredinidae in the possession

of a cellulase, it certainly possesses no regions of the digestive diverticula exclusively specialized for wood ingestion.

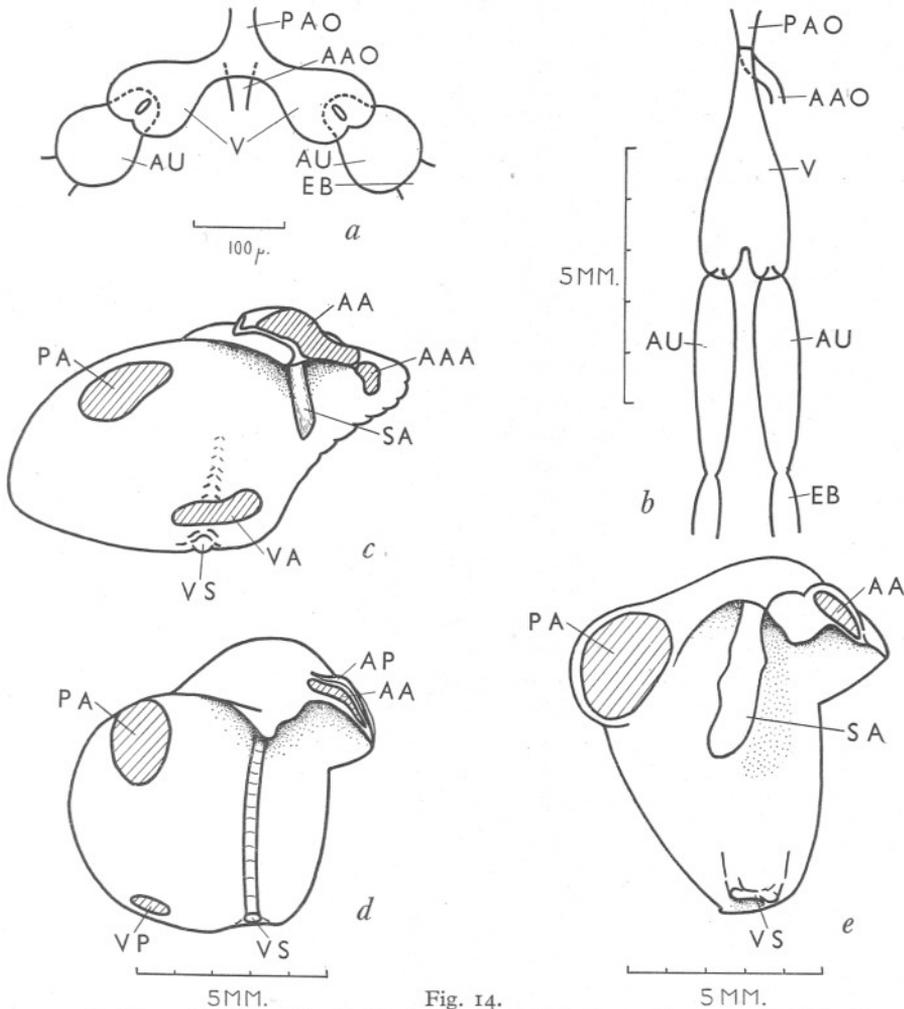


Fig. 14.

a, *Bankia gouldi* (after Sigerfoos): dorsal view of the heart of a young individual.
b, *Bankia gouldi* (after Sigerfoos): dorsal view of the heart of an adult individual.
c, *Pholadidea penita* (after Lloyd): shell and musculature.
d, *Xylophaga dorsalis*: shell and musculature.
e, *Teredo norvegica*: shell and musculature.
 AAA, accessory anterior adductor; SA, shell apophysis; VA, ventral adductor. Other lettering as before.

Apart from shell characters, the most important differences between *Xylophaga* and the Teredinidae are the modifications in the reproductive system which render self-fertilization possible, namely, the vesiculae seminales

and the accessory genital organ, the presence of which appears to be correlated with the isolated life of the colonies of *Xylophaga*. Consideration of the shell and musculature of *Xylophaga* suggests possible homologies with regard to the pallets and pallet muscles of the Teredinidae. Lloyd (1897) showed that in *Pholadidea penita* (Fig. 14c) in addition to the anterior and posterior adductor muscles, there are auxiliary adductor muscles; of these the accessory anterior adductor (Fig. 14c, AAA) was probably split off the anterior adductor (Fig. 14e, AA). Close to the ventral articulation of the shell (Fig. 14c, VS) is a ventral adductor muscle (Fig. 14c, VA).

In *Xylophaga* no division of the anterior adductor (Fig. 14d, AA) has occurred. At the postero-ventral border of the shell, behind the ventral articulation of the shell is a ventral pallial muscle (Figs. 6b, 14d, VP) composed largely of longitudinal fibres, but also possessing a few transverse and dorso-ventral muscle fibres. In *Teredo norvegica* (Fig. 14e) the postero-ventral adductor, or ventral pallial muscle is present. In all other members of the Teredinidae the postero-ventral margin of the shell is emarginated.

It is suggested that the pallets in the Teredinidae are derived from this postero-ventral corner of the shell valves, and that the pallet muscles of the Teredinidae, the ventral pallial muscle of *Xylophaga*, and the ventral adductor of *Pholadidea* are homologous.

With regard to the accessory plates possessed by all members of the Pholadidae (not shown in Fig. 14c) and also by *Xylophaga* (Fig. 14d, AP), in the Teredinidae an anterior pallial fold, similar to that which in the Pholadidae bears the accessory plates, extends forwards over the shell valves in an antero-dorsal position (Fig. 2c, AF). It is therefore probable that the absence of accessory plates in the Teredinidae is secondary.

It is proposed to call the new family to which the genus *Xylophaga* is to be transferred, the Xylophaginidae. The affinities of the families in the order Adesmacea may then be summarized as follows:

	<i>Adesmacea</i>	
Common origin	{ Xylophaginidae Teredinidae Pholadidae	} Wood-boring Lamellibranchia Rock-boring Lamellibranchia

The affinities of *Xylophaga* are shown in tabular form in Table IV.

DISCUSSION

If it be assumed that the absence of a shell apophysis and the insertion of the pedal retractor muscles upon the shell in *Xylophaga* are primitive characters it follows that *Xylophaga* departed from the common stock of the Adesmacea before the development of the shell apophysis, as shown below in Fig. 15.

On this theory it is evident that reduction of the ctenidium to a single demibranch in the Xylophaginidae and in the Teredinidae occurred separately, which is quite possible, and that either the caecum of the stomach was also separately evolved in these two families, or that the absence of the caecum in

the Pholadidae is due to reduction. This is inherently improbable and it is therefore contended that the absence of the shell apophysis in *Xylophaga* is secondary and *not primitive*.

The implications of this second and more probable view are shown in Fig. 16. The common stock of the Adesmacea was rock-boring, and from this arose a wood-boring stock which was to evolve into the Xylophaginidae and Teredinidae. With the evolution of a wood-boring habit a stomach caecum

TABLE IV. THE AFFINITIES OF *XYLOPHAGA*

<i>Affinities with the Teredinidae</i>	<i>Specialized characters</i>	<i>Affinities with the Pholadidae</i>
Bores chiefly in wood, and never in stone	No shell apophysis; pedal retractor muscles inserted upon shell in primitive position	Body enclosed by shell valves
Proportions, sculpture, and fragility of shell valves	Reduction of exhalant siphon	Two accessory plates
Ctenidia possess outer demi-branch only and no ctenidial sorting mechanisms	Faecal accumulation in burrow	No pallets
	Method of wood digestion: by bacteria?	No calcareous lining to burrow
		Rectum passes through ventricle
Labial palps greatly reduced	—	—
Products of boring activity passed through alimentary canal	Vesiculae seminales and accessory genital organ permit self-fertilization	Visceral ganglia in normal position
Short oesophagus; conspicuous stomach; caecum to stomach; small style sac; intestinal typhlosole absent	—	—
Possible digestion of wood?	—	—
Ventricle laterally bilobed	—	—
Alternation of sex	—	—
Possible incubation of larvae	—	—

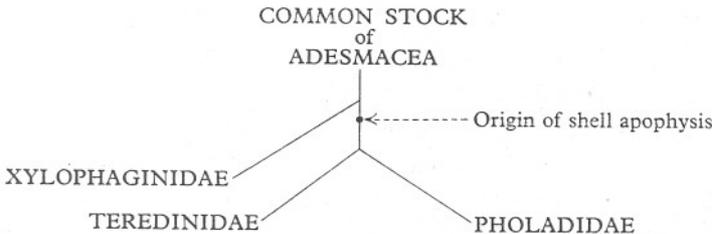


Fig. 15.

was formed as a device converting the spasmodic production of large quantities of wood fragments into a slow steady stream passing through the alimentary canal. Due to the pelagic life in driftwood, the animals seldom, if ever, encounter the heavy sedimentation and turbidity which must be endured by rock-dwelling animals. The ctenidia and labial palps were thus reduced in structure and in function.

The wood-boring stock then divided into the Xylophaginidae and the Teredinidae. In the former the shell apophysis was lost, and the insertion of the pedal retractor muscles moved back to the primitive position; the exhalant

siphon was also greatly reduced. The accessory genital organs were evolved. In the Teredinidae, elongation of the body occurred with the accompanying modifications in the anatomy set down in Fig. 16. It has not been possible to make any suggestion as to the reason for the reduction of the exhalant material in the posterior end of the burrow.

The reduction of the ctenidium in the Teredinidae and in the Xylophaginidae to a single demibranch, and the complete loss of ctenidial sorting mechanisms seem best related to the absence of turbidity in the open sea. The same explanation may be offered for the reduction of the labial palps. Where there is no danger of the mantle cavity or the alimentary canal becoming filled with sediment it is not surprising to find a corresponding reduction in the ciliary sorting and cleansing mechanisms. It is recorded that *Teredo megotara* usually

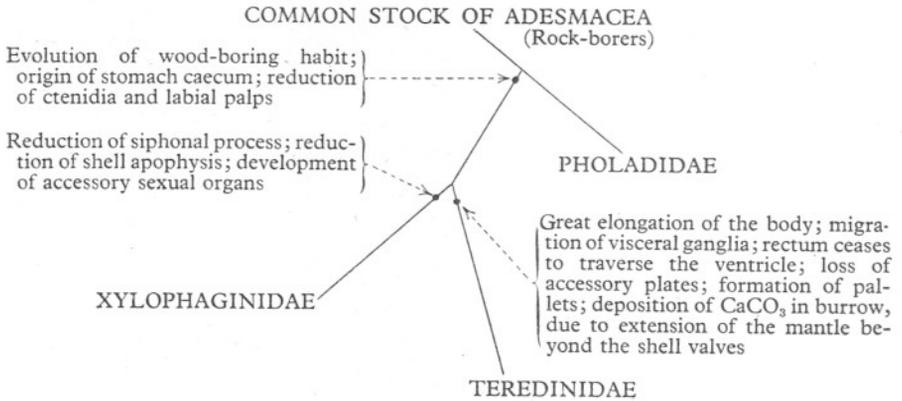


Fig. 16.

occurs in driftwood (Calman, 1919) and that *T. navalis* is intolerant of estuarine water. In these species the reduction of the labial palps has been carried to an extreme; in *Xylophaga* also, the palps are greatly reduced. *Teredo norvegica*, however, is the most common shipworm in European waters on piers or lock gates where the turbidity may be high. In this species the labial palps show least reduction.

The caecum of *Teredo* and of *Xylophaga* has been considered to be a mechanical contrivance, storing wood fragments while they are accumulating rapidly during boring operations, so that a strain is not placed upon the remainder of the alimentary canal. It is here considered that the caecum is also a contrivance to convert the spasmodic arrival of large quantities of material into a slow steady stream through the intestine. In other words, the caecum is as much a constant level reservoir as a safety valve.

The evidence obtained from the single experiment upon the digestive enzymes of *Xylophaga* suggests that this animal may be able to digest certain constituents of wood. Further evidence is required on this matter, and it must

be borne in mind that *Xylophaga* can live in the absence of wood. In the ship-worms, as noted by Nelson (1918) and Lazier (1924), the style sac and crystalline style are small when compared with those of rock-boring lamelli-branches of a similar size (see Figs. 7b, 8, ss, cs). This is also true of *Xylophaga*. If the wood-boring lamelli-branches are all capable of digesting cellulose or hemicellulose the animal may be largely independent of digestive enzymes from the style.

If *Xylophaga* is capable of digesting wood it is important to know how this is carried out. Potts has shown that regions of the digestive diverticula, specialized for the intracellular digestion of wood fragments, do not occur in *Xylophaga*; it is possible that wood is digested by the bacteria which have occasionally been found in the alimentary canal. It would be interesting to know whether bacteria are also present in the caecum of *Teredo*. It could be postulated that wood digestion by bacteria is primitive and its intra-cellular digestion in *Teredo* a later development.

Protandric hermaphroditism has now been demonstrated in all genera of wood-boring lamelli-branches. This condition, however, has not been recorded for any member of the Pholadidae. Incubation of larvae, which is known to occur in *T. navalis* (see Calman, 1919), has not been recorded for *Xylophaga*, but owing to the exceedingly heavy colonization of driftwood by small individuals in the samples obtained, it seems highly probable that the larvae are incubated until a late stage of development. Examination of a sample collected in the summer would in all probability settle this point. Whenever the establishment of young individuals upon a suitable substrate is a question of hazard modifications may be expected in the reproductive system. Such is the case in fluviatile, or commensal lamelli-branches, where the larvae are incubated in the supra-branchial cavity. *Xylophaga* possesses certain modifications which render self-fertilization possible. These modifications are believed to be without parallel in the Lamelli-branchia. A pair of vesiculae seminales store spermatozoa formed during the male phase, and an accessory genital organ in the supra-branchial cavity is thought to assist in this process by directing the sperm by ciliary activity to the openings of these organs. Grobben (1892) recorded in *Cuspidaria* a pair of internal glandular organs associated with the genital apertures in male specimens. These organs are of unknown function. With this exception, *Xylophaga* is apparently unique amongst the Lamelli-branchia in the possession of accessory genital organs functional only in the male phase. These modifications and developments in the reproductive system, if, as appears probable, they render the fertilization of ova more likely, will be of the greatest survival value.

SUMMARY

The exhalant siphon of *Xylophaga* is greatly reduced and its opening is situated within the burrow. Faeces accumulate in the posterior end of the burrow in a compact mass.

The ctenidia and labial palps of *Teredo*, *Bankia* and *Xylophaga* are modified and reduced, unlike those of the Pholadidae. The ctenidia are flat and homorhabdic and possess no ciliary sorting mechanisms; they consist of the outer demibranch only.

The ctenidia of *Xylophaga* are composed of a direct lamella; those of *Teredo* and *Bankia* are divided into anterior and posterior portions connected by a branchial groove which is an extension of the marginal food groove of the gill. The number of filaments in the anterior portion of the gill varies according to the species, and is of assistance in identification.

The labial palps of *Teredo norvegica* are least reduced; in *Xylophaga dorsalis* reduction is greater, though selection of food material is still exercised. The greatest reduction has occurred in *Teredo megotara* and in *T. navalis* where there is no selection.

The ciliated mantle tracts in *Teredo* and in *Xylophaga* play an important part in limiting the quantity of food particles passed from the ctenidia to the mouth.

The alimentary canal of *Xylophaga* is modified in a similar way to that of *Teredo* for the passage through it of large quantities of material. The stomach is enlarged and possesses a conspicuous caecum; the style sac is reduced; there is no typhlosole; the rectum passes through the ventricle.

The caecum probably serves both as a safety valve and as a mechanism to ensure a slow steady stream of wood particles through the intestine. Bacteria and phagocytes may occur in the lumen.

Xylophaga may derive some nourishment from wood, but there is no region of the digestive diverticula specialized for ingestion of wood particles.

Xylophaga is a protandric hermaphrodite; possibly more than one change in sex occurs.

A pair of vesiculae seminales lies in the suspensory membrane of the ctenidium, close to the openings of the genital ducts. They are filled with spermatozoa during the male phase. A ciliated, glandular organ is present in the supra-branchial cavity during the male phase only. This accessory genital organ probably directs spermatozoa into the vesiculae seminales.

The presence of these two structures renders self-fertilization possible and this may be of great survival value to a species which lives in isolated communities.

It was not determined whether *Xylophaga* incubates larvae in the mantle cavity, but this is regarded as probable.

The relationships of *Xylophaga* are discussed and it is concluded that the genus should be removed from the family Pholadidae and placed in a new family in the same order (Adesmacea) but more nearly related to the Terebinidae than to the Pholadidae. It is proposed to name this family the Xylophaginidae.

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LIST OF ABBREVIATIONS USED IN FIGURES

A	Anus	L	Ligament
AA	Anterior adductor	LA	Lamella (or blade) of accessory genital organ
AAA	Accessory anterior adductor	LO	Lateral oral groove
AAO	Anterior aorta	LP	Labial palps
AB	Afferent branchial vein	LV	Lumen of vesicula seminalis
AC	Anal canal	M	Mantle
AF	Anterior pallial fold	ME	Mantle edge
AG	Accessory genital organ	MG	Marginal groove
AP	Accessory plate	MO	Mouth
APC	Anterior portion of ctenidium	O	Oesophagus
AS	Auricle of shell	OC	Opening of caecum into stomach
AU	Auricle (of heart)	OD	Outer demibranch
BG	Branchial groove	OF	Opaque disk of foot
C	Caecum	OG	Opening of genital duct
CA	Ctenidial axis	PA	Posterior adductor
CE	Cut edge of shell	PAO	Posterior aorta
CH	Cephalic hood	PE	Peduncle of accessory genital organ
CM	Cut edge of mantle	PG	Pedal ganglion
CMG	Ciliated mantle groove	PPC	Posterior portion of ctenidium
CMT	Ciliated mantle tract	R	Rectum
CS	Crystalline style	RP	Retractor pedis muscle
CT	Ctenidium	RS	Retractor muscles of siphonal process
DD	Digestive diverticula	S	Shell
DF	Dorsal pallial fold	SA	Shell apophysis
DL	Descending lamella of ctenidium	SC	Supra-branchial cavity
DLP	Dorsal labial palp	SIT	Split in tissues
E	Epithelium (of the siphonal process)	SM	Suspensory membrane of ctenidium
EB	Efferent branchial vein	SP	Dorsal surface of posterior adductor
ES	Exhalant siphon	SS	Style sac
ESS	Blind end of style sac	ST	Stomach
F	Foot	V	Ventricle
FE	Floor of exhalant siphon	VA	Ventral adductor
FR	Faeces in rectum	VLP	Ventral labial palp
G	Gonad tubules	VM	Visceral mass
GD	Genital duct	VP	Ventral pallial muscle
GS	Gastric shield	VS	Ventral articulation of shell
I	Intestine	W	Wedge-shaped mass of mucous glands
IC	Infra-branchial cavity	WS	Wall of stomach
ID	Inner demibranch	X	Vortex in the ciliary currents on flank of foot
IM	Intucking of mantle		
IS	Inhalant siphon		