THE ANATOMY, HABITS, AND EMBRYOLOGY OF YOLDIA LIMATULA, SAY.

A DISSERTATION SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS UNIVERSITY, FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

by

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THE ANATOMY, HABITS, AND EMBRYOLOGY OF YOLDIA LIMATULA, SAY.

Along the coast of Maine, where Yoldia limatula is very abundant, and grows to be especially large, specimens are widely distributed. Their principal habitat, however, is in the shallow coves and inlets, where the tidal currents sweep by without entering. Here, soft mud has accumulated, and is constantly being added to, by the decay of plants and animals swept in from the surrounding sea and land. They are most abundant in water from one to five fathoms deep, and probably never occur above low tide mark.

During the two seasons of my stay at Casco Bay Maine, Prof. C. B. Wilson generously allowed me the free use of his equipment, which was of great value to me. Previous to this, specimens from Woods Holl, Mass., were furnished me through the kindness of Dr. W. K. Brooks, Mr. Richard Rathburn and Dr. James L. Kellogg Most of these specimens were collected by Mr. Vinal Edwards.

My own work, like the work of Drs. Mitsukuri(11) and Kellogg(7) upon this animal, has been carried on under the direction of Dr. Brooks who has for many years manifested a great in-

terest in this rather peculiar lamellibranch. It is a pleasure to acknowledge my indebtedness to him. I wish publicly to acknowledge my indebtedness to my wife, who has materially aided me in securing, tending and preserving specimens.

ANATOMY AND HABITS.

The distinctive characters for the genus Yoldia as given by Verrill and Bush (21) are : "shell nearly smooth, compressed, lanceolate, gaping, more or less prolonged and tapering posteriorly, with a well defined wide rostrum, generally without carinations. The external ligament is marginal, feebly developed, continuous under the beaks and not much differentiated from the general epidermis. The Chondrophore is large, concave, and projects within the margin. The pallial sinus is large and deep. The siphon-tubes and posterior pallial tantacle are long. The palpal tentacles are long and tapered ; in life they may extend nearly to the end of the expanded siphon."

SHELL.

Figures 1 and 2.

To the above characters of the shell will be added a few others, part of which, no doubt, are common to all the species of the genus, while others are specific.

When the animal is taken from the mud in which it lives, the anterior portion of the shell is jet black. Posteriorly it gradually assumes olive green. The black is no doubt a stain, as it bleaches out in animals kept in aquaria, and the shell assumes a rather uniform olivaceous tint, somewhat streaked along some of the more prominent lines of growth with yellow or brown.

On each valve, two more or less pronounced radial stripes extend from the beak to the ventral margin, one anterior, the other posterior, figure 1. The margin of the mantle opposite the extremity of each of these stripes is specially modified and sensitive. Internally, near the dorsal margin of each valve are two rows of toxodont teeth, one extending anteriorly and the other posteriorly from the cartilage pit, figure 2. Near the cartilage pit these teeth are very small and closely placed. They attain their greatest length about midway along each row, and become short and rather widely separated at the ends furth~~e~~est from the cartilage pit.

Internal markings are rather obscure. Beside the foot and adductor muscle scars, and the pallial line with its deep and broad sinus, there is on each valve a rather distinct, curved line, extending from the ventral margin of the anterior adductor muscle scar, nearly to the cartilage pit. Dissection shows that this line marks the limit of the genital mass and digestive gland.

Tryon(20) refers to this mark on the right valve, and thinks it is caused by the loop of the intestine that extends forward, on the right side, very near the shell. That this view is wrong is shown by there being similar markings on both valves.

MANTLE.

Figures 1 and 3.

The mantle lobes are free along their ventral borders, and are ciliated in patches on their inner surfaces. They are modified to form the siphons, the marginal tentacles, an unpaired, very much elongated tentacle situated near the base of the siphons, a flattened expansion opposite the extremity of each posterior shell stripe, and a rounded projection opposite the extremity of each anterior shell stripe. These will be treated in turn. There are also two pairs of apparently glandular patches, one situated ventral to the anterior adductor muscle and the other ventral to the base of the siphons.

Siphons-- The oldest specimens reared from eggs have not begun to develop siphons. The youngest specimen collected with a dredge (about 1/2 m m. long) had already formed the exhalent siphon.

This siphon, figure 11, seems to have been formed by the union of the margins of the mantle lobes, followed by their growth into a tube and the withdrawal of the tube between the

mantle lobes. In withdrawing the tube its dorsal surface, corresponding to the dorsal surface of the united mantle lobes, is drawn in, forming a complete septum. A ridge on each mantle lobe indicates where the point of union of the mantle margins has been drawn along its inner surface.

The ventral surface of the base of this siphon arches dorsally, figure 12, the ridges on the mantle lobes near its base thicken and finally fuse. Thus a second tube is formed lying ventral to the exhalent siphon, figure 13. The wall separating the two siphons remains arched upward for some time, but subsequent growth straightens it. Even in the adult the line of fusion along the ventral side of the inhalent siphon remains distinct, figure 14, and offers little resistance to splitting. Although the inhalent siphon is formed between the mantle lobes, at the base of the exhalent siphon, it may morphologically be considered marginal in formation, as it is formed by thickenings of, and growth from, ridges that seem to have been carried back from the margin. The adult siphons are united along their whole length, figures 1 and 3, and may be extended beyond the shell to a distance considerably exceeding the shell's length. Normally the inhalent siphon is shorter, broader, and has thicker walls

than the exhalent siphon, but they are frequently rendered of equal length by injury. Both siphons, figure 14, have between their outer and inner layers of epithelium, large bundles of longitudinal muscle fibers, separated by sheets of radial muscles. A few circular fibers lie near the epithelium but they are not numerous. The siphons are extended by forcing blood into the spaces hollowed out in the connective tissue. If the siphon of a young specimen is examined with a moderately high power of the microscope, small, conical papillæ will be seen projecting from its surface, figure 15. Each papilla bears at its tip a long, rigid filament. Older specimens show similar papillæ, but instead of bearing single elongated filaments, several shorter filaments are borne on the tip of each. Similar papillæ are found in various places on the mantle and its modifications. They probably correspond to the "pinselzellen" of Flemming(5) later described by Dorst(4) and Rawitz (17).

Siphonal tentacle and marginal tentacles,-

The youngest specimen collected with a dredge, shows a little rounded knob, figure 11, st. lying on one side, between the mantle and the siphon. This knob, the rudiment of the siphonal tentacle, is an outgrowth from the line of union of the

mantle with the base of the siphon, which line, as has been shown, seems morphologically to be a portion of the mantle's margin.

During the development of the siphons the tentacle is carried ventrally and in the adult, comes to lie nearly opposite the ventral border of the inhalent siphon. This unpaired tentacle was first described by Brooks (1) and has frequently been referred to since. Pelseneer$^{(14)}$ found that it occurred on either the right or left side of Yoldia isonota, an observation that also holds true for Y. limatula. From its position and innervation Pelseneer(14) was led to conclude that it might be compared to the osphradium of gastropods, but this conclusion does not seem to be borne out by a further knowledge of the subject. Another organ corresponding in innervation and position to the osphradium of other lamellibranchs, is present and will be described later.

When extended, figures 1, 3 and 10, st. the siphonal tentacle is a long and slender filament, gradually tapering to its free extremity, and generally lying loosely coiled on the bottom of the aquarium, or on the surface of the mud in which the animal lives. Throughout its length it is set with small conical papillāē, figures 6 and 7, such as have already been described for the siphons. Each papilla, like the papillāē on the

adult siphon, bears a cluster of filaments at its tip.

When retracted the tentacle presents a series of transverse wrinkles, figure 6. Beneath the layer of epithelium, figure 8, ep. run strands of longitudinal muscle fibers, lm. imbedded in connective tissue. On the side of the tentacle nearest the mantle lobe to which it is attached, inside the muscle layer, is a large nerve, tn, which can be easily traced to the tentacle's tip. This nerve is a branch of the pallial nerve. It is not given off directly opposite the base of the tentacle, but some distance above it, and the two nerves continue along, side by side, until the tentacle is reached. The appearance of the two nerves lying side by side, is quite like that of a ganglion and has, no doubt, been mistaken for one. On the side of the tentacle opposite the nerve, also within the muscle layer, is a more or less definite blood space, bs.

Extension of the tentacle seems to be accomplished solely by forcing blood into this space. In favorable cases blood corpuscles can be seen moving along it when the tentacle is being extended.

If considerable force is exerted in extendeing the tentacle, swellings, figure 7, may occur in it. Such swellings are

filled with blood and disappear when the pressure is removed. When the muscles of the tentacle contract, the blood is forced back, and the blood-space may be completely obliterated.

The tentacles that fringe the postero-ventral margins of the mantle, have, beneath their epithelium, both longitudinal and transverse strands of muscle fibers, and generally several blood spaces. While branches of the pallial nerves have not been traced into these tentacles, such branches can be traced to their bases, and there can be no doubt that the tentacles are supplied by fibers from these nerves.

Each tentacle has at least one papilla and frequently there are several papillāe upon its surface. In development the tentacle is preceded by a single sense papilla which is carried out by the growth of the mantle near its base, into a conspicuous projection. As this projection grows, other sense papillāe make their appearance on its sides, and the papilla at its tip may or may not retain its position. In a few cases the tentacles divide or branch. This is most common with the tentacles fringing the posterior expansions of the mantle, soon to be described.

Considering the origin, structure, and inervation of the siphonal tentacle and the marginal tentacles, there can be

but little doubt that the siphonal tentacle is a greatly enlarged and specialized marginal tentacle.

Both structure and experiment agree in assigning to these tentacles a tactile function. The siphonal tentacle is not, as might be supposed, the most sensitive to touch of any of the organs. It seems to be rather more sensitive than the marginal tentacles, about as sensitive as the expansions of the mantle opposite the extremities of the posterior shell stripes, and rather less sensitive than the projections opposite the extremities of the anterior shell stripes, the foot, and the siphons. It may be moved about with a pencil-point without causing much disturbance, but if it be pressed slightly, moved quickly, or jarred, it is quickly withdrawn, and the withdrawal may be accompanied by the partial or complete retraction of the siphons, the closing of the shell, and, in some cases, by the activity of the foot. It seems especially sensitive to sudden movements or jars, and its special function may lie in this direction, in enabling the creature to detect the approach of enemies, of which flounders seem to be among the most dangerous.

If a vessel, containing several specimens partially buried in the mud, is not disturbed for some hours and is then jarred, all will generally disappear with astonishing rapidity.

Whether the stimulus is transmitted through the siphonal tentacle or not, has not been determined, but its position, coiled on the surface of the mud, suggests the possibility.

All of the experiments that were tried to determine the function of the tentacle resulted in failure, inasmuch as specimens in which the tentacle had been removed, seemed to be as sensitive to jars as uninjured specimens. It may be remarked, however, that the jars of a small vessel, can at best bear only a slight resemblance to jars affecting the surface of the mud on the bottom of the ocean, such as would be caused, for instance, by the swimming of a flounder.

Posterior expansions of the mantle,-

These expansions, figures 1, 3 and 10, pe., lie opposite the extremities of the posterior shell stripes. They consist of flat, somewhat triangular extensions of the edges of the mantle. The anterior border of each is fringed with tentacles, resembling the ordinary marginal tentacles, but more frequently branched, and usually they have a rather larger proportion of sense-papillae. The inner surfaces of the expansions are very densely ciliated. Near the base of each is a fold or ridge, along the side of which such dirt as gains access to the mantle chamber is swept. This dirt is swept back over the ex-

pansions and so out of the cavity. The rich nervous supply comes as branches of the pallial nerves.

Anterior projections of the mantle.-

The antero-ventral margins of the mantle may be protruded a short distance beyond the margin of the shell, figure 1, and seems to aid in cleaning the foot when it is withdrawn from the mud. These margins are destitute of tentacles but are well supplied with sense-papillāē.

Arising from each margin, opposite the extremity of the anterior shell stripe, is an oblong projection, figure 1, a e. This projection carries a row of sense-papillāē, and is ciliated on either side, figures 16 and 17. Branches of the anterior pallial nerves can be traced very near, and they undoubtedly enter, these projections. Enlarged pallial muscles, figure 17, pm. act as their retractors.

These organs are very sensitive to mechanical stimulation, and probably serve as tactile organs, but their function is not known. They are placed so near the edges of the retracted foot that it is easy to think that they may serve some function in connection with it, but no observations were made that support this surmise or that give a clue to any other function.

FOOT.

Figures 3, 5 and 9, f.

The foot, figure 3, f, is very large and powerful. During development its sides grow out into two muscular flaps, that lie side by side, and are capable of being extended laterally so that their inner sides form an almost flat or arched surface, figure 9. It is this part of the foot that is called the sole.

Notwithstanding its being a rigid muscular organ, known to be adapted for burrowing (7) and executing movements with remarkable rapidity (1 and 21), this part of the foot ~~it~~ is still referred to as a "creeping sole" (10-12-15 and 21).

The free margins of the flaps are thin, and are fringed with flattened papillae that are very sensitive to touch. There are four pairs of foot muscles, one posterior and three anterior. The posterior foot muscles, figure 3, pfm, are inserted on the shell, just in front of the posterior adductor muscle and very near the bases of the teeth. They are very large and send all of their fibers forward, along the sides of the foot, to be distributed to its anterior and ventral portions. Their function is to retract the foot.

The anterior foot-muscles, afm, are inserted on the

shell just behind the anterior adductor muscle and very near the bases of the teeth. Of these muscles there are three pairs. The anterior pair pass ventrally and posteriorly, along the sides of the foot, and are distributed to its posterior portion. The middle pair pass ventrally, between the pair just mentioned, and are distributed to an intermediate portion. The posterior pair pass ventrally and anteriorly, between both of the preceding pairs and are distributed to the anterior and ventral portion of the foot, including the muscular flaps.

These three pairs of muscles are undoubtedly used in producing the varied and energetic movements of the foot. Beside these special foot muscles which together form a large part of its outer walls, there are transverse strands of muscle fibers extending from one wall to the other. Large blood spaces are hollowed out between these strands.

Movements of the foot are always very rapid and are remarkably diversified. The movements of burrowing consist of thrusting the closed foot, which is wedge-shaped, ~~anteriorly~~ deep into the mud, reflecting its margins to form an anchor, and then withdrawing it. These movements follow each other in quick succession and enable an animal to bury itself with great rapidity. When the animal is placed upon its side, the closed foot is bent

back under the shell, its margins are reflected, and it is then withdrawn. If these movements are executed on mud, the lower, reflected margin of the foot buries itself, and gives the necessary purchase for the animal to right itself. If instead, they are executed on a smooth, hard surface, where no purchase can be obtained, these movements are likely to be replaced by leaping movements.

The leaping movements consist of bending the foot back under the shell, turning the shell nearly on its dorsal margin, planting the surface of the expanded "sole" on the bottom, and giving a quick downward movement.

If the foot does not slip, the shell is generally turned end for end and thrown some inches. If the foot slips, as more frequently happens in smooth-bottomed aquaria, it shoots forward ~~out anteriorly~~ with wonderful rapidity and causes a posterior movement. Other movements are common but will not be described. It seems very hard to imagine that the foot could possibly be used as a creeping organ, and its present function, for which its structure so admirably fits it, is to burrow~~ing~~ in soft mud.

BYSSAL GLAND.

Figures 4 and 5 bg.

In none of the specimens that came under my observa-

tion, did this organ seem to be functional. The youngest specimen collected with a dredge shows a small pouch, lined with epithelium, which opens into the posterior end of the groove that separates the muscular flaps of the foot. The gland receives a rather large nerve from each pedal ganglion, and often contains a few fine threads. These threads have never been seen protruding from the ~~glands~~ duct.

ALIMENTARY CANAL.

Figures 4 and 5.

The rather broad and long oesophagus opens into the dorsal end of a capaceous stomach, figure 4, sto. which extends from near the dorsal margin of the animal, well into the foot. The stomach is divided transversely by a well marked constriction, and internally by a prominent ridge, formed by elongated epithelial cells. Above this ridge the epithelial cells are rather slender, carry cilia, as do the other epithelial cells of the alimentary canal, stain deeply, and have the appearance of secretory cells. Below the ridge the epithelial cells are broader and stain less deeply.

From the ventral end of this portion of the stomach, the intestine bends back along its posterior side, ascends to a

point just beneath the pericardium, makes a forward turn, comes very near the surface on the right side, follows the edge of the genital mass and digestive gland nearly to the anterior adductor muscle, then turns dorsally and posteriorly, gradually assumes a median position again, passes through the ventricle, and opens into the mantle chamber at the base of the exhalent siphon, just behind the posterior adductor muscle. The intestinal epithelium is composed of short, deeply-staining cells, which are frequently arranged in longitudinal ridges. One of these ridges, rather more prominent than the others, occupies the position of the typhlosole.

DIGESTIVE GLANDS.

The digestive glands consist of a pair of racemose glands, the ducts from which open into the stomach near its dorsal end. The lobes are very numerous and form a rather compact mass, in the dorsal region of the body, which laterally overhangs the dorsal part of the foot.

LABIAL PALPS.

Figures 3 and 5, lp.

The palps of the adult animal are very large, figure 3, lp. Each united pair is suspended from the body wall by a thin

membrane, containing a few muscle-fibers, which is attached to the body wall beneath the overhanging digestive gland. The palps are triangular in shape and have their inner surfaces ciliated and thrown into a series of ridges and grooves, that do not extend quite to their free margins. Large blood spaces follow along the bases of many of these ridges. The supposition that the large expanded palps, serve in respiration, seems probable.

Each outer palp is supplied with a long appendage, figure 3, pap, which originates from its posterior end, near its dorsal margin, and can be extended far beyond the posterior margin of the shell.

In young specimens, this appendage is flat and is entirely confined to the external palp, figure 5, pap. As it grows, it folds longitudinally so as to form a groove on its inner side, and, at the same time, twists so that it may appear like a continuation of the united dorsal margins of the outer and inner palps.

Each palp appendage is supplied with longitudinal muscles, figure 18, lm, a large nerve, pn, that is continued into it from the dorsal margins of the palps, and a continuous blood space, bs, lying beside, and morphologically ventral to it. Under favorable conditions, blood corpuscles may be seen moving

along this space, when the appendage is being extended. Other blood spaces occur in the connective tissue of the appendage, but they are much smaller and anastomose freely.

The epithelium lining the groove formed by the longitudinal folding of the appendage, is densely covered with cilia.

The animal while feeding, figure 10, is slightly tipped ventrally from the perpendicular, and frequently has about one third of its posterior end above the mud. While in this position, the palp-appendages are thrust out of the shell and one, at least, bends over and inserts its tip in the mud. The cilia lining its longitudinal groove immediately begin to elevate the mud, which is rich in living organisms. The stream of particles passing along the groove is large enough to be distinguished at a distance of some feet. In this way, foraminifers, ostracods, and even small lamellibranchs, and gastropods, together with the smaller forms and mud, are passed along the groove, finally between the palps, and so on into the mouth. Thus we find that Mitsukuri's surmise(11), based on finding sand in the grooves of the palp-appendages of preserved specimens, was right. The palp appendages are food collectors.

GILLS.

Figures 3, 19 and 20.

Although the gills have been well treated by Mitsukuri, (11) Kellogg(7), and others, some additional facts both on the structure and function of these organs, seem to make it allowable to go over the already rather familiar ground.

Each gill, figure 3, g, consists of a double series of rather broad, flat plates, placed laterally edge to edge, and antero-posteriorly with their flat surfaces opposed.

This double series of plates is suspended from the body wall by a thin muscular membrane. Anteriorly the gills pass beneath the overhanging digestive glands, on the under sides of which the plates become gradually smaller and smaller, and finally fade away. The extreme anterior ends are continued as ridges. These ridges seem to represent continuations of the suspensory membranes rather than gill plates, and point to the probable origin of the membranes as folds from the body wall.

Posteriorly the gills likewise become smaller, and are finally attached to the wall that separates the inhalent ~~and~~ from the exhalent siphon.

With the exception of a few of the plates at the extreme anterior ends of the gills, which are sometimes much distorted

and swollen, all of the plates are alike in shape and structure. Laterally the plates of each gill lie opposite each other. Generally in the length of each gill, one or more plates are interpolated on one side or the other, figure 20, ip, and thus the plates are made to alternate for a short distance, but they soon become opposite again.

The plates on the two sides of each gill are separated from each other except below, where they are fused, either leaving a connecting ridge, as frequently happens anteriorly, or a smooth intermediate portion, as is generally the case further back.

Each plate is also joined to the suspensory membrane, figure 19 su, above, and to two longitudinal muscles, llm and ulm, that are continuous the length of the gill. Each plate is hollow and may be likened to a loosely folded sheet of paper, leaving a space between ; which space is traversed by a few fibers of connective tissue. The unshaded line, y, figure 19, represents where the wall has been cut in separating the plate from the plate lying in front of it. The opposite wall of the plate is continuous, in a like manner, with the wall of the plate lying behind. Along each side of the ventral portion of each plate,

lying just inside, and closely applied to the wall, is a chitinous rod or plate, figure, 19, cr., These rods are much heavier near the median line, become thinner laterally, and finally disappear. Furthermore the chitinous rod on each side of each plate is continuous with the chitinous rod of the opposing side of the plate adjoining. Each rod, might then be described as hairpin shaped, with two prongs, each of which extends along the inner side of the wall of one side of one plate. Each plate receives one prong from each of two hairpin shaped rods, figure 20 cr.

Many of the muscle fibers of the suspensory membrane are continued down along the inner surface of the anterior wall of each plate, fig. 19 mp. These were supposed by Mitsukuri (11) to be chitenous rods but they were later shown by Kellogg (7) to be muscles. They start from the suspensory membrane as bundles of fibres, which branch and spread out as they descend. ~~into a fan shape.~~ Many of the fibers apparently find insertion in the wall of the plate itself, but not a few are extended to the chitenous rods and are inserted over their surfaces. Kellogg, (7) no doubt rightly, ~~connected~~ referred movements of the plates, which are common in the gills of mutilated specimens, and in the excised gills themselves, to these muscles.

It can be seen in young specimens, where the gills can

be watched through the transparent shell, that these movements are not common. The normal function of these muscles will be made apparent later, in connection with the special function of the gills.

Each plate bears cilia along its ventral margin, and for a short distance along each side, but not over its general surface.

The cilia between the plates are arranged in lines, one or two lines on each side of each plate. Near the ends of the chitinous rods, the cilia on the edges of the plates disappear, and those between the plates become modified, as described by Kellogg(7) for holding the plates together. They do not seem to be hooked, but are very numerous, rather stout, and ~~fully~~ freely intermingle with the cluster on the adjoining plate. The area covered by these cilia is rather limited, and above them the plates are not ciliated. The cilia of the gills seem to drive water between the plates and aid in lowering the gills.

Each gill has two, rather large bundles of muscles running its entire length, one above, figure 19, ulm, and one below, llm. The lower bundle is somewhat crescent shaped in cross section, the concave surface being directed upward and forming part of the ventral wall of a large blood space, lbs, that is also continuous the length of the gills. These longitudinal muscles were supposed by Mitsukuri(11), whose material was poorly preserv-

ed, to be fibrous tissue, but there seems to be no doubt that they are muscles. Their contraction cause the gills to shorten, a common movement, already described by Kellogg (7), and a movement necessarily of service in their special function.

The cavities of the plates on the two sides of each gill open freely ~~fully~~ into each other, and the cavities of all of the plates are put into communication through the blood space, lbs, which is continued upward between the plates as a narrow slit reaching to the upper longitudinal muscle. Above this muscle, at the base of the suspensory membrane, is another blood space, ubs, also running the length of the gills, separated from the blood spaces between the muscular walls of the suspensory membrane only by occasional strands of connective tissue. This space communicates laterally with the cavities of each of the gill plates ~~cavities~~. Mitsukuri (11) supposed that these blood channels were connected with some definite blood circulation (in Nucula.)

In Yoldia there seems to be no evidence that the blood follows a very definite course. The continuous longitudinal spaces seem to be the means of equalizing pressure throughout the gills, by allowing a free movement of the blood to different parts as circumstances demand.

Should the blood be confined in any part of the gills when pressure is applied, the walls of the plates would probably

be ruptured, but with these continuous cavities the pressure must necessarily remain nearly equal in all the plates.

Before bringing the discussion of the structure of the gills to a close, reference will be made to Kellogg's (7) opinion that the plates of each gill are alternate and not opposite.

His opinion is based on horizontal sections taken below the upper longitudinal muscle, in which position the inner edges of the plates are alternate. This seems to be due to bending caused by the pressure of blood in them. Horizontal sections through the bases of the gills, or just beneath the upper longitudinal muscle, as well as whole specimens, show the plates to be opposite as a rule.

It will be remembered that the gills are suspended by muscular membranes, which probably represent folds of the body wall. They are composed of wide plates that are sufficiently wide to span the space between the foot and the mantle and, behind the foot, unitedly to span the mantle-chamber itself. Anteriorly they gradually diminish in size and finally disappear. Posteriorly they are attached to the wall that separates the inhalent and exhalent siphon. The mantle chamber is thus divided by a movable partition, into a ventral chamber, opening through the inhalent siphon and a dorsal chamber, opening through the exhal-

ent siphon.

In young speciemns the movements of the brown gills are visible through the shell. They are gradually pressed ventrally, probably by the blood forced into them, possibly aided by the powerful cilia, which, as Kellogg (7) has pointed out, are so powerful in their action, as frequently to cause excised gills to move about in the water. As the gills descend the water passes between the plates. After reaching their greatest ventral depression the gills may remain quiet for a longer or shorter time. Then comes a quick contraction of the suspensory membranes, accompanied by a vigorous discharge of water through the exhalent siphon, as the chamber dorsal to the gills diminishes, and a corresponding influx of water through the inhalent siphon, as the chamber ventral to the gills enlarges. During this exchange, the siphons are made quite rigid, probably by having blood forced into them. The movements of the siphons accompanying the movements of the gills are very conspicuous and have been mentioned by Brooks (1).

The movements of the gills are more or less rhythmic, the time varying with the needs of the animal. Thus the rhythm is much faster after a disturbance that has caused all movements to be suspended for sometime, than when no such disturbance has occurred.

The currents of water are probably for respiratory purposes, and to keep the mantle-chamber clear of the dirt that is constantly finding its way in, more especially the fāeces, which, being so largely composed of sand and other heavy particles, would otherwise drop into, and soon clog,this chamber.

It seems to be a justifiable suggestion that the contraction of the gills may aid in the movements of blood as well as movements of water.

The blood spaces of the plates, and especially of the suspensory membranes are considerably diminished in size during each contraction and, as the openings where the spaces of the suspensory membranes communicate with the auricles, are guarded by ridges that probably act as valves, each contraction must modify the blood supply.

A little study will show how admirably the gills are fitted for the function of pumping water.

In shape they exactly fit the mantle chamber, in which they form a moveable partition. Contact is insured by the pressure of the blood inside the plates, and by the soft dorsal projections. These projections must act much like the leather on the plunger of a suction pump, making good contact when there is pressure from above but not hindering its descent.

~~As the gills lie at rest before the contraction of the~~

When the gills are expanded

suspensory membranes, the plates are loosely opposed and allow water to pass freely between them. In this position the gills are much longer than during contraction, and lie in a curves, figure 3, g. When the suspensory membranes contract, the longitudinal muscles, figure 19, ulm, and llm, also contract, the gills are shortened, and the plates more closely opposed.

Each plate is rendered rather rigid ventrally chitinous rods that are so disposed as to allow flexibility ; and many of the muscle fibers of the plate are attached to these rods in such a way as to insure an even strain and keep the plate from bending ventrally when pressure is applied.

Experiments were tried to determine, if possible, the part taken by the gills in the collection of food. For this purpose both mutilated and uninjured specimens were used. No definite results were reached, but in no case was Kellogg's observation (7), that the gills are extremely active food collectors, confirmed. Considering the remarkable activity of the palps as collectors of food, such activity for the gills seems rather unnecessary, and it would also seem that the pumping action of the gills would seriously interfere with their normally performing such a function.

EXCRETORY ORGANS.

Figures 4 and 23.

In the adult animal the excretory organs are very extensive. They consist of many loops, the walls of which are much sacculated. They lie ventral to the pericardium and are continued into the foot along the posterior side of the stomach, figure 4, ex. The inner, pericardial, opening of each excretory organ, is separated from the outer, mantle chamber, opening by a very short space.

Figure 23 is a drawing of a wax model of the ends of the left excretory organ and genital duct, seen from the ventral side.

The inner end, i e, opens into the pericardium ~~of which a portion of the wall~~, p c, is ~~shown~~, by a rather large opening, turns abruptly towards the middle line of the body, crosses the outer end, o e, and is continued anteriorly close to the pericardium. After passing through the many sacculated loops already mentioned, the tube again comes near the pericardial wall, enlarges, runs alongside the anterior turn of the inner end, narrows down again and opens into the mantle chamber through an an antero-posteriorly elongated opening, mco, just posterior to the point where the outer and inner ends of the tube cross.

The genital duct, gd, following the course of the cerebro-visceral commissure, turns ventrally when almost in contact with the inner end of the excretory organ, meets the outer end and opens with it. The common opening of the excretory ~~opening~~ organ and genital duct is, as has been noticed, elongated in an antero-posterior direction, figure 65, mco, and may represent a fusion of the two rather than an opening of one into the other.

As has been seen, the condition described by Pelseneer(15) viz : the genital duct opening into the excretory organ near its pericardial opening, is not borne out by these observations.

In material that is not well preserved, it not unfrequently happens that the walls of the genital duct and the inner end of the excretory organ, are ruptured in sectioning, at the point where they come in contact, thus placing their cavities in communication.

It may be well to state in passing that the genital ducts of Nucula proxima open into or with the outer end of the excretory organs in a manner similar to that just described for Yoldia limatula.

GENITAL GLANDS.

These, when distended with their products are very extensive. They push in between the kidneys, below the pericardium,

between the stomach and intestine nearly to the pedal ganglia, and surround the digestive glands as well as dip in between their lobes. The opening of the genital duct, figure 23, gd, has already been described in connection with the excretory organ.

The sexes are separate and, when the genital products are abundant, they may easily be distinguished by the color of the genital mass surrounding the digestive glands. This portion is chocolate brown in females and yellow in males.

NERVOUS SYSTEM.

Figures 4 and 5.

The cerebral ganglia fig. 4, cg. united in front of the oesophagus by a very broad commissure, which differs very little in structure from the ganglia themselves, lie just posterior to the ventral side of the anterior adductor muscle. Each ganglion is almost circular in transverse section and gradually tapers posteriorly into the cerebro-visceral commissure. So gradually does this tapering take place, that it is impossible to determine where the ganglion ends and the commissure begins. Even in structure there is only a difference in degree, there being proportionally more nuclei in the ganglion than in the commissure. Posteriorly each commissure gives place, in the same gradual way, to a visceral ganglion. The visceral ganglia, vg, lie anterior to the

ventral side of the posterior adductor muscle, and almost equal the cerebral ganglia in size. The commissure connecting these ganglia is also very broad and, like the cerebral commissure, tends to share the structure of ganglia.

The pedal ganglia, pg, are rounded bodies and are apparently larger than either the cerebral or visceral. They lie very close together and are connected by a very broad commissure.

The cerebro-pedal, unlike the cerebro-visceral commissures are not surrounded by nuclei and show ordinary commissural structure.

Although a great many specimens of widely differing ages have been examined, the double origin of each cerebro-pedal commissure from the cerebral ganglia, has not been observed. Neither is a separation into cerebral and pleural ganglia evident. It is true that the cerebral ganglia are not quite smooth and, in some places, the outer layer of nuclei dips into the fibrous layer, but this seems to be accounted for by the origin of nerves in the immediate vicinity. The only place that can be looked upon as a constriction, lies between the origin of the large anterior pallial nerve, on the outer dorsal surface of the ganglion, and the origins of the cerebro-pedal commissure, the large palpal nerve, and a small ~~foot-muscle~~ nerve supplying muscles of the foot, all of which leave the ganglion

together, on the inner, near the ventral side, of the ganglion. The origin of the cerebro-pedal commissure is entirely anterior to this depression. The bulgings at the bases of the nerve seem sufficient to account for the irregularity.

Each cerebral ganglion gives rise to several nerves. A large nerve passes forward, under the anterior adductor muscle, branches,and supplies the anterior portion of the corresponding mantle lobe. Another large nerve passes down to the dorsal margins of the palps, follows them posteriorly and is finally continued the whole length of the palp appendage. Of the smaller nerves, one supplies the anterior adductor muscle and another passes to the body wall.

Each visceral ganglion gives rise anteriorly to a small osphradial nerve, and posteriorly to a nerve that branches almost immediately. Sometimes these branches originate as separate nerves. One of them sends a small nerve to the posterior adductor muscle and another below the adductor muscle to the postero-dorsal portion of the mantle. The main nerve bends ventrally and is distributed to the siphons. The other nerve passed ventrally, beside the nerve just described, sends a large nerve to the siphonal tentacle~~s~~, on the side where this tentacle is present, and is continued to supply the postero-ventral margin of the mantle.

Several branches are given to the posterior extension of the mantle.

Each pedal ganglion gives rise to a nerve that runs directly to the byssal gland, and to six or more nerves that supply the muscles of the foot. Frequently one nerve and sometimes several nerves may run up the cerebro-pedal commissure for some distance before issuing to be distributed to the muscles of the foot.

The nerve that supplies the otocyst issues from the cerebro-pedal commissure but, judging from the direction of the fibres in the commissure, probably has its origin in the cerebral ganglion.

OTOCYSTS.

Figures 4, 21 and 22.

The otocysts are rather large and, as Kellogg(7) has pointed out, each contains a single large otolith, which plainly shows concentric structure. The epithelial cells of the otocysts carry rather long and slender cilia. In adult specimens there is a well defined canal connected with each otocyst. Pelseneer(15) describes this canal as opening at the surface of the foot and gives a figure indicating the position of its opening.

I have found that, by the careful dissection of specimens preserved in formaline, the cerebro- pedal commissures, with the otocysts, otocystic nerves, and otocystic canals, all held

together by connective tissue, can be removed. Study of these preparations, of which I have made nearly 30, shows the usual form of the otocystic canals to be cylindrical and of a uniform size for about three-fourths the length of the otocystic nerves, figure 21, ot, at which point there is nearly always a swelling, beyond which there continues a thin strand of fibrous tissue, probably connective tissue. At the distal end of the swollen portion of each canal there is generally, probably always, a wall that can easily be seen in dissected preparations, and has been verified in sections. This wall is the rounded end of the otocystic canal.

Sometimes one or more little closed ~~patches~~ pouches are found, lying in the strand of tissue that is continued on past the swollen portion of the canal.

Two such pouches are shown in figure 22, which represents the distal swollen portion of a canal and part of the continuing strand of tissue. These pouches, when found, show the same structure that is shown by the canals, and like them are lined with numerous very long cilia.

It seems to me that these walls and pouches show conclusively that in each of the several cases the whole canal has been removed and, in this species, that the canals do not reach the surface of the foot.

In Nucula proxima there is a strand of tissue passing from each otocyst to the surface of the foot. This corresponds in position to the canal described by Pelseneer(15) for Nucula musculus, and is probably an open canal, but I have not had time to demonstrate this point.

In Yoldia limatula, the strand of tissue, with the series of pouches which it sometimes encloses, seems to indicate that these canals have undergone, and perhaps are still undergoing, degeneration.

The otocystic nerves lie alongside the canals and seem to send fibers to their walls. In fact it is difficult to demonstrate that the nerves reach the otocysts other than through the walls of the canals.

OSPHRADIUM.

On the inner side of each suspensory membrane of the gills, lying just beneath the visceral ganglion of the corresponding side, is a rather large patch of modified epithelium which probably represents an osphradium.

This epithelium is supplied by a rather large nerve, figure 4, on, that leaves the corresponding visceral ganglion pretty ~~well forward.~~ near its front end.

CIRCULATORY SYSTEM.

The heart, figure 4, h, is situated just posterior to the beaks of the shell, and very near the dorsal margin. The cavity of each auricle is connected with the blood spaces of the corresponding gill, through a slit in a muscular partition that projects dorsally into the cavity of the auricle. The arrangement of this partition is such as to tend to stop the backward flow of blood into the gills. The ventricle is perforated by the intestine. Where the ventricle joins each auricle, there is a marked constriction and, internally, a muscular septum perforated by a single opening. When the ventricle contracts, this septum probably contracts and more or less completely closes the opening in it.

Two blood vessels leave the ventricle, one anteriorly on the left side of the intestine, the other posteriorly, beneath the intestine.

EMBRYOLOGY.

The eggs of Y. limatule, are about .15 m m. in diameter, of a chocolate brown color and very opaque. They are laid ~~free~~ in the water and are not encumbered by any kind of envelope. The polar bodies are lost soon after they are formed. The first cleavage, which takes place about two hours after the eggs are

fertilized, results in the formation of subequal blastomeres, figure 24.

In the next cleavage, figure 25, the smaller blastomere divides equally and the larger unequally. The eight celled stage is formed by a cleavage at right angles to the two preceding planes of cleavage, and the two sets of four cells each come to lie in the position indicated by figure 26, the last division being in the plane of the paper.

One of these cells is considerably larger than the other seven and, with the beginning of the next cleavage, begins to be somewhat surrounded by other cells, figure 27. The small cell formed by the unequal division of this large cell, figure 28, becomes a surface cell. What becomes of similar cells in later divisions has not been determined, but, from sections, it appears probable that the next small cell cut from the large cell, figure 29, crowds in over the tip of the large cell and divides into two, figure 37.

About this time the outer cells, or at least part of them, acquire cilia, figure 30, and the embryo rolls around on the bottom of the dish. It finally rises to the surface and swims freely.

Just what internal changes take place during this interval is rather hard to determine. Surface cells in the region

of the blastopore become especially active, dividing and crowding in around the large internal cell, which now divides into nearly equal cells, figure 39.

Most of the outer cells now take on a decidedly different appearance from the internal cells.

There is a rather densely staining layer of protoplasm against the outer wall of each cell, but the remainder of the cell is occupied by vacuolated protoplasm. These vacuoles become larger with age.

Beside the vaucolated cells, there is a group of cells, figures 38 and 39 cg, and figure 40, ap, which are largely surface cells and later give rise to the cerebral ganglia and the apical plate. The apical plate, figure 40, ap, is already distinguishable.

Whether there is a general migration of surface cells into the interior is doubtful, but it is certain that their number is reduced. The reduction is probably not more than is accounted for by the pushing in of those around the blastopore, and the setting aside of the group from which the cerebral ganglia and apical plate arise.

The embryo now elongates, figure 31, the apical plate acquires a tuft of apical cilia, ac, and the outer, vacuolated cells, which will hereafter be referred to as test cells, arrange

themselves into five rows that surround the embryo. Frequently the fifth, last, row of test cells, is not complete on the dorsal side at this stage but this does not long remain so. Occasionally a sixth more or less complete row is present. The blastopore and the apical plate occupy nearly opposite ends of the embryo, but for some time the blastopore may be twisted around somewhat to one side. The position of the group of cells from which the cerebral ganglia are formed, is indicated in the external view of the embryo by a depression, x, where the cells of the first, or anterior row of test cells, are pushed away from the second row. As later stages show this to be the ventral side of the embryo, it is easy to determine that the blastopore is always twisted toward the same, that is, the dorsal side.

The test cells are distinctly rounded and the cilia on each of the three intermediate rows are collected into a band. The embryo now swims in more or less definite lines, rotating the while upon its longitudinal axis. The rotation is quite rapid but is not always in the same direction, there being frequent changes. During activity the apical cilia are bunched together into a sort of whip, which lashes vigorously from side to side, and always precedes the embryo in its movements.

Inside the test the cells in the region of the blastopore are still actively undergoing division and are quite small,

figure 41.

The cells of the apical plate, ap, and those from which the cerebral ganglia arise, cg, are separated externally by test cells, but internally are, and continue to be, connected by cells that do not take part in the formation of other organs.

The other internal cells have increased in number, and their origin can no longer be determined. At a little later stage, figure 42, the dorsal internal cells are arranged in a layer, sg, that represents the beginning of the formation of the shell gland. Other cells soon arrange themselves over the remainder of the surface inside the test and, together with the shell gland, form a new ectoderm. This ectoderm probably is formed from cells originally surface cells. If this view is true, the original surface cells give rise to at least three groups : those that remain at the surface, acquire cilia, and become differentiated as test cells ; those that form the cerebral ganglia and apical plate ; and those that form the new ectoderm inside the test.

In the stage of which figure 42 represents a section, a space seems always to be present in about the same position.

This space probably represents the beginning of the lumen of the midgut.

The embryo continues to elongate, figure 32, becomes cylindrical, and the test cells flatten and become less distinct from one another. Between about the 32nd hour and about the 70th hour, there is no appreciable change in the external appearance of the embryo and, as the test cells are quite opaque, few internal changes can be followed in living specimens.

The test, which is now fully formed, is composed of large vacuolated cells, figure 44, t, the nuclei of which are almost, if not quite, in contact with the inner walls. Just beneath each band of cilia the protoplasm stains very deeply. Just inside the test, between it and the new ectoderm, are, frequently, scattered nuclei, lying in a very thin film of protoplasm. Their significance is not known.

The shell gland becomes more definite, the lumen of the midgut, figure 43, mg, becomes surrounded by a definite wall of rather large cells, and an invagination, std, extends into the mass of cells from the ventral side of the blastopore. This invagination is the beginning of what I have called (4) the ventral tube, but, as it has since been found that it is formed as an ectodermal invagination that does not at first communicate with the midgut there seems to be no reason to give it a special name, and it will hereafter be referred to as the stomodæum.

The stomodǣum elongates and soon establishes communication with the midgut, figures 40, and 48. It lies along the ventral side of the embryo, just inside the test, and is joined, but is not enclosed by, the layer of ectoderm, figure 49, std. The shell gland becomes slightly invaginated, figures 44, and 45, sg, but it very soon arches upward preparatory to protruding laterally to form the mantle, figure 49. The midget becomes prolonged posteriorly, and the mass of cells from which the cerebral ganglia form arch inward and form two pouches that open to the surface. The pouches lie side by side, figure 46, and generally open to the exterior together. Sometimes, however, they open between different test cells, figure 47, and seem to be only slightly connected with each other. In other cases only one of the pouches opens to the exterior and this opening may be small. In some cases it may not be present at all.

The walls of the pouches are rather thick but each is composed of a single layer of cells.

The shell gland folds out at the edges and most of the dorsal cells assume the character of mantle cells. Only those near the edges remain especially large and glandular. This is accompanied by the ectodermal thickenings that form the pedal ganglia, figure 59 pg, and the invaginations that form the

otocysts, figure 56, ot. The next stage shows the otocysts apparently completely closed off, lying very close to the clefts that separate the mantle from the body wall.

The formation of the mantle and shell is accompanied by a slight lateral compression and a corresponding dorso-ventral widening of the embryo. The test cells become very much thinner and the vacuoles, nearly or quite disappear, but the cilia remain as described and the movements of swimming are not altered. Several new organs make their appearance.

Cleared whole mounts show some of the internal organs, but throughout it is necessary to resort to reconstructions from the study of serial sections, to get the relationship of the different parts.

The body of the embryo now lies between the shell valves and these are enclosed in the test. The foot, figures 33, 55, and 61, f, is formed by a rapid increase of cells between the mid-gut and the stomodǣum. The anterior adductor muscle, figures 33, 55, and 56, aa, is formed at a corresponding time (about 35 hours) and consists of a few muscle fibers which stretch from one shell valve to the other. It is left, by the growth of the embryo, separated from the rest of the body, except at its ends, which penetrate the mantle, and are attached to the shell. The

posterior adductor muscle. figures 33 , and [illegible], pa, does not appear until some hours later. It is always surrounded by other tissue. The digestive glands, figures 33, 62, and 63, are formed as evaginations from the anterior end of the midgut, which is now extended posteriorly nearly to the blastopore. The visceral ganglia appear as groups of nuclei, the position of which suggests ectodermal origin. The cerebral pouches have moved some distance dorsally and posteriorly into the interior of the embryo, and are situated at the end of a single pouch, figures 33 and 58, r, which opens to the exterior between the test cells at the point where the pouches were originally formed. The paired pouches are thus brought to lie in the interior, as diverticula of a single elongated pouch. As they are carried into the interior, the cells forming their walls divide rapidly, push in, and fill up their cavities, and a commissure is formed connecting the two masses of cells. The relation of the unpaired pouch to the cerebral ganglia has been shown by three succeeding transverse sections of the same embryo. Figure 58 shows the external opening of the un-paired pouch, figure 59 shows the anterior portion of the cerebral ganglia, cg, with the laterally compressed unpaired pouch, r, lying beneath them, and figure 60 shows the commissure connecting the ganglia.

Having described the formation of the various organs attention will be given to the embryo's appearance.

Further than the lateral compression and the corresponding dorso-ventral widening; there has been little change in the embryo's external appearance, but the internal appearance is greatly altered.

Inside the test a shell has been formed, the two valves of which gape ventrally. The anterior adductor muscle, figure 33, aa, is quite large and, being isolated from the general mass of the body, is very conspicuous. The posterior adductor muscle, pa, as yet consists of very few fibers and is enclosed in other tissue. It is not easily seen in whole mounts. The apical plate ap, is connected with the ventral end of the group of cells that form the wall of the unpaired pouch, r. This group of cells forms a distinct stalk which runs dorsally and posteriorly to connect with the anterior part of the body. The midgut, mg, and the stomodaeum, std, are widely separated by the foot, f. The stomodaeum opens to the exterior through the blastopore, bl, and the posterior end of the midgut almost reaches it but does not open. #

\# Observations since my publication in the Johns Hopkins University Circular (4) have not revealed the actual opening, up to the time the test is cast away.

The stomodaeum is often attached to the anterior, and to part of the ventral margins, of the foot, but its posterior end, figure 61, std, lies free between the mantle lobes, sometimes almost, if not quite, in contact with the test, sometimes raised well above it. The anterior end of the midgut is enlarged to form the stomach, which communicates with the liver-pouches. Most of the tissue dorsal to the intestine has been used in forming the mantle, which is now separated from it by a large space. This space extends to, and around, the anterior adductor muscle anteriorly, and nearly to the margin of the shell posteriorly. The cerebral, pedal, and visceral ganglia, with their commissures, have been formed. The otocysts, figure 61, ot, have apparently been entirely closed off, and each contains an otolith, which stains deeply with haematoxylin and, a little later, plainly shows concentric structure.

As the otocysts have never been open to the exterior, development having taken place inside a closed test, the otoliths cannot be foreign particles.

The only places where the outer test is attached to the body of the embryo lying inside it are, around the blastopore, the apical plate, and the opening of the unpaired pouch, figure 33, r. The embryo still swims rapidly but has periods of rest.

This condition of the embryo is reached in from 90 to 120 hours. It now stops swimming, settles to the bottom, the apical cilia shrivel, and the test cells break apart and frequently go to pieces at once. The process of casting the test generally begins with the posterior row of cells and works forward. It generally takes but a very few minutes. Casting includes, beside the test, the stalk which extends from it to the cerebral ganglia, the apical plate and its connection, and the stomodaeum from the blastopore to the position of the definitive mouth. These parts, together with a few adhering test cells, that are no longer stretched flat but have rounded up, may not sever their connection for a half hour or more, figure 34, but they finally break off just below the cerebral ganglia, and casting is complete.

Until about the time that the test is cast, the shell valves remain gaping ventrally and the tissues of the body extend completely across from valve to valve. When the shell is finally closed by the contraction of the adductor muscles, there is no longer sufficient space for the organs in their original position. The principal change of importance due to this crowding, takes place in the pouches of the digestive glands, which are forced into the space dorsal to the alimentary canal, and, in

all of the specimens examined, seem to undergo changes that result in the formation of large cells, figures 33, 34, and 35, Z, that are not arranged in any definite manner.

It was thought possible that this appearance was due to poor preservation, an explanation that very naturally suggests itself, but the large cells appear in living as well as preserved specimens. Reformation of the liver pouches is accompanied by the disappearance of these cells.

The anterior adductor muscle soon becomes enclosed by the forward growth of the body. For a few hours a space may remain between it and the cerebral ganglia but this soon disappears. The foot, which at first is capable of only feeble movements, grows quite rapidly, and is soon very active. Locomotion is chiefly effected by the means of long and powerful cilia, which are arranged along the sides of the foot, figures 35, and 36, and are very active whenever the foot is thrust out of the shell.

These enable the animal to glide over the surface on which it lies, but do not enable it to rise. For some hours after the test is cast, the foot shows no indication of the modification which is later generally known as the sole, figure 53. The first indication of this modification is a groove which appears along the middle line of the ventral surface of the foot,

figure 53. This groove deepens, apparently by the growth of the parts on each side, figure 54, and gives rise to a "sole" resembling that of the adult, figures 2, and 9. The movements of the foot now closely resemble those of the adult, but locomotion is still materially aided by the powerful cilia along its sides.

The formation of the "sole" is accompanied by the growth of the postero-ventral portion of the foot into a more and more prominent portion resembling a heel. The use of this outgrowth is not evident. It remains in the adult as a small projection, just behind the opening of the byssal gland ; an organ that makes its appearance about a day after the test is cast, but does not seem to secrete threads.

About the time that the test is cast away, a thickening makes its appearance on the inside of each mantle lobe, near its posterior border, figures 34 and 35 g.

This thickening, the rudiment of the gill, acquires cilia and grows anteriorly so as to project over the mantle-surface. A constriction appears near the middle of each gill, figure 36, g, deepens, and divides it into almost equal lobes. Beneath its epithelium, following the curve of its anterior margin, is a chitinous bar, the two ends of which lie near the ends of the lobes, figure 36, cr.

Figures 50 and 51 represent longitudinal sections of a gill, taken in the planes indicated in figure 38. The chitinous bar is cut in one, but the plane of the other lies below it. These sections show the gill to be rather evenly ciliated. Later stages, after the lobes have elongated, show the cilia to be confined to the side next to the mantle. The third lobe is formed from the ventral lobe, which broadens and then constricts in the manner detailed above. Other lobes are formed in a similar manner.

The alimentary canal elongates, bends ventrally, and the stomach enlarges. In from two to four days after the test is cast, the liver pouches reappear. At first they do not have very definite walls, but they gradually become well defined, and it is noticeable that the large scattered cells disappear at a corresponding time. The two pouches are no longer symmetrical, the left being prolonged posteriorly, fills up the space between the dorsal end of the stomach and the intestine, figures 36 and 66. The greater development of the left liver lobe at this early date, very likely affects the future position of the intestine, a loop of which comes to lie on the right side of the animal, very near the shell.

About the 25th day, a ridge, corresponding in position

to the outer labial palps, appears as an outgrowth from the body wall. The palps have not attained any considerable development in any of the embryos reared from eggs.

The ganglia are all distinct in whole mounts as well as in sections. At first the cerebral ganglia are much larger than either of the others, figure 33, but the pedal ganglia grow rapidly, and soon come to equal if not to exceed them in size, figure 36. No division into cerebral and pleural ganglia has been observed.

GENERAL REMARKS.

ANATOMY.

Since Mitsukuri's (11) paper appeared in October 1881, much has been written on the anatomy, ~~and its significance,~~ of members of this group. Pelseneer (15) has called attention to certain characters, in support of the supposition that the group is primitive. Possibly influenced by the desire to make the case as strong as possible, he has allowed some errors to creep in. Thus he says on page 272 :

" The least specialized lamellibranchs : In demonstrating the phylogenetic development of the [illegible], part 2, IV, 6, p. 246, I have shown that the most primitive of these organs are

found in the Nuculidae and Solenomyidae. On the other hand several recent authors have considered either *Avicula*, or *Meleagrina* and *Arca*, as representing the most ancient forms of this group.

But, it is to be noticed that *Avicula* and *Meleagrina* have already lost their anterior adductor (this in itself is not a sign of great antiquity) and further that these free forms have their gills more specialized than the Nuculidae and Solenomyidae. It is not only by the appearance of their respiratory apparatus. but by the existence of all the following common characters, that are not found in other Lamellibranchs (include here *Avicula, Meleagrina* and *Arca*) that these two families are undebateably shown to be the most archaic of all :

1. Hypobranchial gland situated dorsally, between the mantle and the gills.

2. Foot has a ventral "creeping" disc (not existing in others except *Pectunculus*).

3. Gills far posterior, have free, flat filaments, without reflected lamellae, analagous to the bipectinate gills of Amphineura, Cephalopoda, Rhipidoglossus, and Euthyneura.

4. Heart posterior, has auricles in contact with the gills only by their anterior extremities and not along their whole axes.

5. Absence of a posterior aorta.

6. Kidneys glandular throughout their extent, without internal partitions, or communications between them.

7. Genital glands opening into the pericardial extremities of the kidneys.

8. Pleural ganglia still distinct from the cerebral, and pleuro-pedal connectives arising by distinct origins from the cerebro-pedal.

9. Visceral ganglia little developed, much smaller than the cerebral."

It is not my intention to enter into theoretic considerations until my studies on other numbers of the group are more complete, but so far as Yoldia limatula is concerned the foregoing statement is not accurate.

Of Pelseneer's numbered statements, numbers 2, 5, and 7 are wholly wrong and I can do no better than refer the reader to what has already been said under these heads (see pages 13, 37 and 30). Number 3 I have not been able to confirm.

The theoretic value of the gills is, for the present, rendered doubtful inasmuch as they have a special function that accounts for their shape and structure. Here there remains the choice of two views, viz, that they have been modified in a

primitive type or that they have been modified from the ordinary type.

Continuing from the quotation given above Pelseneer says : "These common characters teach, at the same time the mutual relations of the Nuculidāē and Solenomyidāē which should be united into a common group, contrary to the ideas up to the present time, which have placed the latter family with the Solenidāē, near the Lucinidāē, under the Anaticinacēā, etc.

If, on the other hand, comparisons be made between the two families Nuculidāē and Solenomyidāē, it is proved that :

1. With Nucula, the mantle is entirely open ventrally, between the two adductors, and that the margins are simple, without tentacles.

2. With the Nuculidāē (Leda, Yoldia, etc) one sees again that the retractors of the foot (columellaires), form a almost continuous series (without specialization), between the two adductors.

3. In the Nuculidāē, the digestive tube presents a pharyngeal cavity where two glandular pockets open.

4. With Nucula the heart is dorsal to the rectum.

5. In Nucula the pleural ganglia reach their maximum separation from the cerebral, in the sense that the cerebro- and

pleuro-pedal connectives are still separated for a part of their extent.

6. With the Nuculidæ, the otocysts open freely to the outside.

One can conclude from this that the Solenomyidæ are less primitive than the Nuculidæ, and that *the Lamellibranchs actually the most archaic are represented* by the latter family and *specially by Nucula.*"

In this, reference is made directly to Yoldia only in number 2, and the statement here made does not hold good. The foot muscles of Yoldia are surely among the most highly developed of any to be found in the Lamellibranchia, and the only reason they occupy so much of the dorsal margin is because of their enormous size. Numbers 3 and 6, which refer to the Nuculidæ in general, do not seem to hold good with this species.

EMBRYOLOGY.

The most striking peculiarities in the development of Yoldia are connected with the formation and disappearance of the test.

I find similar tests in the embryos of two species of Nucula (N. proxima and N. delphonodonta), in both of which cases

the tests are cast. In the former, the eggs are thrown free in the water and the embryos closely resemble those of Yoldia, but are considerably smaller. In the latter species, the embryos are much larger and are somewhat modified by being carried in a mucous case, which is attached to the posterior end of the shell.

Outside the group, so far as I have been able to learn, Dondersia is the only other Mollusk whose embryo is known to be provided with a similar test.

Comparing the embryo of Yoldia with Pruvot's (16) account of the embryo of Dondersia, we find that the fully formed tests of both are composed of five rows of cells, all of which bear cilia. Counting from the anterior, the cilia on the third row of cells in the test of Dondersia, and the second, third, and fourth rows of cells in the test of Yoldia, are long and collected into bands which surround the embryos. The body of the embryo of Dondersia protrudes posteriorly during development. No such protrusion takes place with Yoldia. Each is provided with an apical plate, and, in either case, the test is finally cast off. Internal changes in the embryos of Dondersia not being known, further comparisons are denied us.

The young embryos of Dentalium as described and figured by Lacaze-Duthiers (9) and Kowalevsky (8) bear a certain resem-

blance to those of Dondersia and Yoldia. This is largely due to three or more rows of cells, each bearing a band of cilia. At this stage, these ciliated cells form the greater portion of the surface of the embryo. As the body elongates posteriorly, these cells are crowded forward to form the velum, but this does not seem to be cast off.

A somewhat similar resemblance is noticeable in the case of the embryos of Patella as figured and described by Patten (13). In either Dentalium or Patella, if we imagine the velum to be stretched posteriorly over the shell-gland dorsally, and the foot ventrally, so as to enclose the body, the oesophagus will be pulled out into a long narrow tube ventral to the foot, and the position of the blastopore will correspond to its position in Yoldia. Furthermore the position of the foot and shell gland will correspond, and the alimentary canal will necessarily be bent in the same way.

In a similar manner, if we imagine the cells of the velum of a typical lamellibranch larva to be drawn posteriorly over the shell, there will be the same relation of parts. The same seems to be true of the larvae of gastropods if we take into account the twisting that accompanies development in these forms.

Thus we may perhaps trace an homology between the test

of Yoldia and the velum of other forms. In this connection it is of interest to notice that in a few forms the velum is known to be cast away.

This has been observed by Heath# for Chiton, Sigerfoos (19) for Teredo, and Mrs. Drew [1] for Cardium.

Wilson (22) has described a similar casting of the cells of the velum for Polygordius.

It seems quite possible that the embryo of Yoldia represents a rather primitive form, and that the typical molluscan larvāe may have been developed from an ancestor approaching it in form and structure. If this is true, the probability is that Yoldia and its relatives, when compared with other lamellibranchs, would represent a comparatively recent departure from the primitive molluscan form and, in such a case, it is more likely that organs which now show high specialization, have been developed from the more primitive than from the highly complex.

\# Dr. Heath has kindly allowed me to notice this point although his observations are not yet published.

[1] This work has not been published. The species upon which the observations were made seems to be C. pinnulatum (Con.)

SUMMARY.

A brief statement of the chief points is as follows :

ANATOMY AND HABITS.

1. The mantle has two pairs of sense organs, figures 1. ae, and pe, one long unpaired tentacle, st, and a fringe of marginal tentacles. All of these organs are sensitive to mechanical stimulation. The unpaired tentacle seems to be homologeous to one of the ordinary marginal tentacles.

2. The foot, figures 3 and 9, f, is a highly ~~modified~~ specialized burrowing organ.

3. The palp-appendages, figures 3, 10 and 18, pap, are food-collectors. In the adult they are not assisted, to any considerable extent, by any other organ.

4. The gills, figures 3, 19 and 20, are used in pumping water, for which function they are well fitted by their structure. They probably serve in respiration but do not seem to aid in collecting food.

5. Each genital duct, figure 29, gd, joins the outer, not the inner, end of the corresponding excretory organ, very near its opening into the branchial chamber.

6. No division into cerebral and pleural ganglia has been

observed. Neither do the cerebro-pedal commissures seem to have a double origin.

7. The otocysts are not connected with the surface by canals. Canals, apparently in process of degeneration, figures 21 and 22, ot, are present in adults.

8. Both an anterior and a posterior aorta ~~is~~ are present.

EMBRYOLOGY.

1. The original surface cells seem to give rise to the test, the cerebral ganglia, the apical plate, and a new ectoderm, inside the test.

2. The cerebral ganglia, figures 46 and 47, are formed as invaginations from the surface.

3. The otocysts contain otoliths before the test is cast.

4. The test, the apical plate, the stalk connecting the test with the anterior portion of the body, and the stomodaeum from the blastopore to the position of the definitive mouth, are all cast away.

5. It seems that ~~the~~ typical molluscan larvae may have been developed from embryos resembling those of Yoldia.

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KEY TO LETTERS.

aa.	Anterior adductor muscle.
ac.	Apical cilia.
ae.	Anterior projection of the mantle margin.
afm.	Anterior foot muscle.
ap.	Apical plate.
bg.	Byssal gland.
bl.	Blastopore.
bs.	Blood space.
cg.	Cerebral ganglia.
cr.	Chit~~e~~inous rods.
cvc.	Cerebro-visceral commissure.
ec.	Ectoderm.
ep.	Epithelium.
es.	Exhalent siphon.
f.	Foot.

g.	Gill.
gd.	Genital duct.
h.	Heart.
ie.	Inner end of excretory organ.
ip.	Interpolated plate.
lbs.	Lower blood space.
ll.	Left lobe of liver.
llm	Lower longitudinal muscle.
lm.	Longitudinal muscle.
lp.	Labial palp.
mco.	Common opening of the excretory organ and genital duct into the mantle chamber.
mg.	Mid-gut.
mp.	Muscles of the gill plates.
oe.	Outer end of the excretory organ.
on.	Osphradial nerve.
ot.	Otocyst.
pa.	Posterior adductor muscle.
pap.	Palp appendage.
pc.	Pericardial wall.
pe.	Posterior expansion of the mantle margin.
pfm.	Posterior foot muscles.
pg.	Pedal ganglion.

pm.	Pallial muscles.
pn.	Palp nerve.
r.	Pouch leading to the cerebral ganglia.
rl.	Right liver lobe.
s.	Shell.
st.	Siphonal tentacle.
std.	Stomodæum.
sto.	Stomach.
t.	Test.
tn.	Tentacle nerve.
ubs.	Upper blood space.
ulm.	Upper longitudinal muscle.
vg.	Visceral ganglia.
x.	Depression at the point where the cerebral ganglia are formed.
y.	Cut wall of gill plate.
Z.	Large cells that appear when the liver is forced into the space dorsal to the intestine.

EXPLANATION OF FIGURES.

Fig. 1. Expanded adult specimen, seen from the right side.

Fig. 2. Left shell valve, seen obliquely from the dorsal margin.

Fig. 3. Adult specimen represented as seen from the right side, with the right shell valve and mantle lobe removed. The siphons are shown cut longitudinally.

Fig. 4. Same as the above with the right palp and gill removed, figured to show the relations of internal organs. The nerves leaving the ganglia are shown only on the left side. (~~Largely~~ Partially reconstructed).

Fig. 5. Specimen about 1 mm. long. Represented as a partially transparent object, seen from the right side, after the right shell valve and mantle lobe have been removed. (~~Largely~~ Partially reconstructed).

Fig. 6. Tip of a retracted siphonal tentacle.

Fig. 7. Portion of an extended siphonal tentacle, with a swelling caused by the pressure of the blood, seen as a transparent object.

Fig. 8. Transverse section of a siphonal tentacle.

Fig. 9. Anterior portion of the shell, and the reflected margins of the foot just before they are brought together and withdrawn into the shell.

Fig. 10. An animal as it appears while feeding.

Fig. 11. Posterior portion of a specimen about 1/2 mm long.

Fig. 12. Transverse section of a specimen about 1 mm. long, showing the thickening of the ridges leading to the base of the siphon, and the pushing in of the ventral wall of the exhalent siphon. Taken near the base of the siphon.

Fig. 13. Posterior portion of a specimen about 2mm. long.

Fig. 14. Transverse section of a specimen about 1 cm. long, taken through the bases of the siphons. One of the ridges is shown joining the inhalent siphon. The section also includes a portion of the wall attaching the exhalent siphon with the dorsal portion of the mantle.

Fig. 15. End of the exhalent siphon of a specimen .7 mm. in length.

Fig. 16. Projection of the mantle margin opposite the extremity of the anterior shell stripe, seen somewhat obliquely.

Fig. 17. Section of the anterior projection of the mantle margin.

Fig. 18. Transverse section of a palp appendage.

Fig. 19. A pair of gill plates seen from their anterior surfaces. The suspensory membrane, the walls of the plates joining the plates next in succession, the longitudinal muscles, and the basis of the chitinous rods are shown in section. These are all cut across in separating the pair of plates from the pair lying in front. (Drawn from a study of sections).

Fig. 20. Portion of a gill, seen from the ventral side.

Fig. 21. Otocyst with its canal and nerve, and a portion of the cerebro-pedal commissure. A nerve frequently leaves the commissure near to otocystic nerve and is distributed to the muscles of the foot.

Fig. 22. Portion of the extremity of an otocystic canal, showing ~~the~~ two closed pouches.

Fig. 23. Inner and outer ends of the left excretory organ and genital duct, seen from the ventral side.

Fig. 24. Two celled stage.

Fig. 25. Four celled stage.

Fig. 26. Eight celled stage seen from the animal pole.

Fig. 27. Eight celled stage. The cells preparing for the next cleavage.

Figs. 28 and 29. Later cleavage stages.

Fig. 30. Ciliated embryo about 20 hours old.

Fig. 31. Extrenal appearance of an embryo about hours old.

Fig. 32. External appearance of an embryo about hours old.

Fig. 33. Reconstruction of an embryo about 105 hours old. The outline and test cells were obtained from a whole mount. The cilia are indicated only at the margins.

Fig. 34. Reconstruction of an embryo that has just cast the test, represented with the right cell valve and mantle lobe removed. The stomodǣum and the stalk extending from the cerebral ganglia, together with adhering test cells, are still attached.

Fig. 35. Reconstruction of an embryo about 10 hours after casting. Represented with the left shell valve and mantle lobe removed.

Fig. 36. Reconstruction of an embryo about 12 days old. Represented with the right shell valve and mantle lobe removed.

Fig. 37. Section of an embryo about 10 hours old. The plane of the section lies through the blastopore.

Figs. 38, 39 and 40. Successive sections of an embryo about 13 hours old. Some of the surface cells are beginning to assume the character of test cells. The group of cells cg, figures 38 and 39, are connected with the cells ap, figure 40, by cells of the same character.

Fig. 41. Median vertical section of an embryo about 15 hours old.

Fig. 42. Median vertical section of an embryo about 22 hours old.

Fig. 43. Median vertical section of an embryo about 30 hours old.

Fig. 44. Median vertical section of an embryo about 36 hours old.

Fig. 45. Transverse section of an embryo about 35 hours old, taken near the third band of cilia.

Fig. 46. Transverse section of an embryo about 45 hours old, taken through the cerebral pouches.

Fig. 47. A similar section showing the pouches separate.

Fig. 48. Transverse section of an embryo about 45 hours old, taken where the stomodāeum joins the midgut.

Fig. 49. Transverse section of the same embryo a little further posterior.

Fig. 50. Section of the gill rudiment in the plane indicated by the line 50, figure 36.

Fig. 51. Section of the same gill rudiment in the plane indicated by the line 51, figure 36.

Figs. 52, 53 and 54. Transverse sections showing the formation of the "sole" of the foot.

Fig. 55. Median vertical section of an embryo about 95 hours old. (A portion of the stomodāeum was drawn from the next section).

Fig. 56. Transverse section of an embryo about 75 hours old, showing the invaginations that form the otocysts.

Fig. 57. Transverse section of an embryo about 70 hours old showing the forming pedal ganglia.

Figs. 58, 59 and 60. Successive transverse sections through the anterior portion of an embryo about 95 hours old.

Fig. 61. Transverse section of an embryo about 95 hours old, taken through the otocysts.

Fig. 62. Transverse section through the liver pouches of an embryo about 95 hours old.

Fig. 63. Horizontal section through the liver pouches of an embryo of the same age.

Fig. 64. Median vertical section of an embryo about 10 hours after casting.

Fig. 65. Transverse section of an embryo of the same age.

Fig. 66. Horizontal section through the dorsal portion of an embryo about 12 days old.

LIFE.

The writer of this thesis was born in Jasper County, Iowa, November 15th, 1868. He received his early educational training in the public schools of that state, and, in the year 1890 was granted the degree of Bachelor of Science at the State University of Iowa.

Three years have since been spent in teaching, and five years have been devoted to study in this University.

In the year 1897 he was awarded a [illegible] [illegible]ship and has since held a fellowship.

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