

XLIV.—*Notes on the Embryology, Anatomy, and Habits of Yoldia limatula, Say.* By GILMAN A. DREW*.

IN this short abstract attention will briefly be called to some points of interest in the development, anatomy, and habits of *Yoldia limatula*, a member of Pelsner's order Protobranchia. A more detailed description will follow at a later time.

EMBRYOLOGY.

The eggs are about .15 millim. in diameter, of a chocolate-brown colour, 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 results in the formation of subequal blastomeres. Subsequent divisions give rise to an epibolic gastrula in which there may be as many as sixty outer ectoderm-cells. Some of the ectoderm-cells wander into the interior, the entoderm-cells divide, and at one side of the resulting cell-mass a narrow tube appears, which opens to the exterior through the blastopore. As it has not been determined whether this tube is ectodermal or endodermal in origin, whether it represents a stomodæum or a primitive gut, it will throughout this description be referred to as the ventral tube.

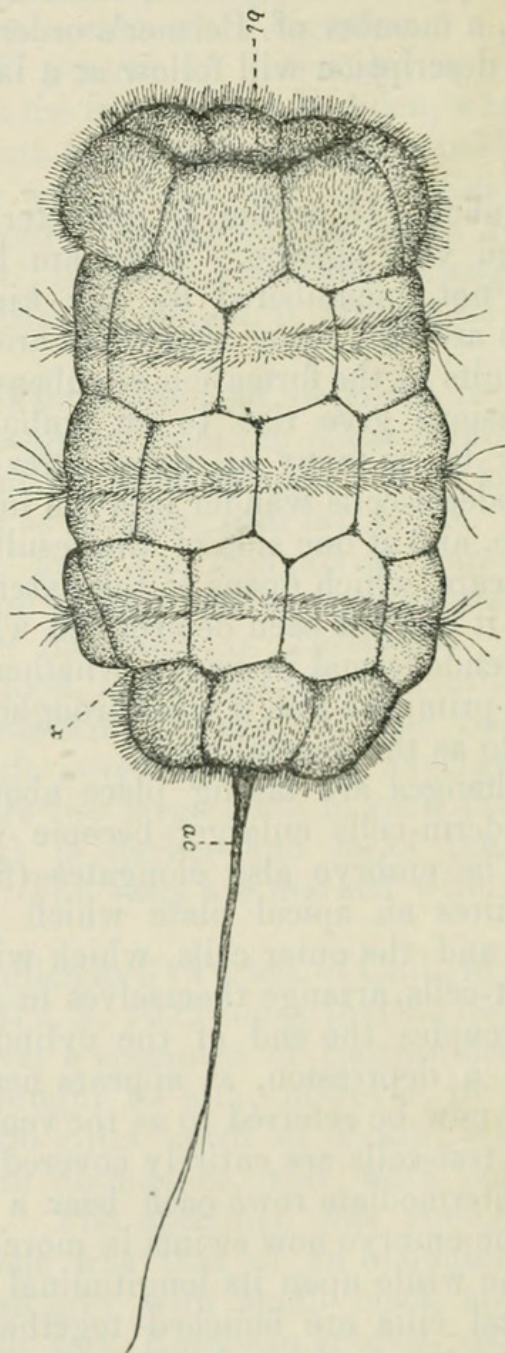
While these changes are taking place about forty-two of the surface ectoderm-cells enlarge, become vacuolated, and acquire cilia. The embryo also elongates (fig. 1), becomes cylindrical, acquires an apical plate which bears a tuft of apical cilia, *ac*, and the outer cells, which will hereafter be referred to as test-cells, arrange themselves in five rows. The blastopore, *bl*, occupies the end of the cylinder opposite the apical plate, and a depression, *x*, appears near the anterior end of what may now be referred to as the ventral side. The two end rows of test-cells are entirely covered with fine cilia, and the three intermediate rows each bear a band of much longer cilia. The embryo now swims in more or less definite lines, rotating the while upon its longitudinal axis. During activity the apical cilia are bunched together into a sort of whip, and always precede the embryo.

Inside the test a new ectoderm is formed, probably from the ectoderm-cells that wander in. At the age of about forty hours a few of these ectoderm-cells elongate and give rise to the shell-gland, which spreads over the dorsal portion of the

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embryo, but never forms a distinct invagination. At most it is only slightly concave when viewed from above, and soon becomes arched outward. These changes are accompanied by the formation of the mid-gut, a term that is not intended

Fig. 1.

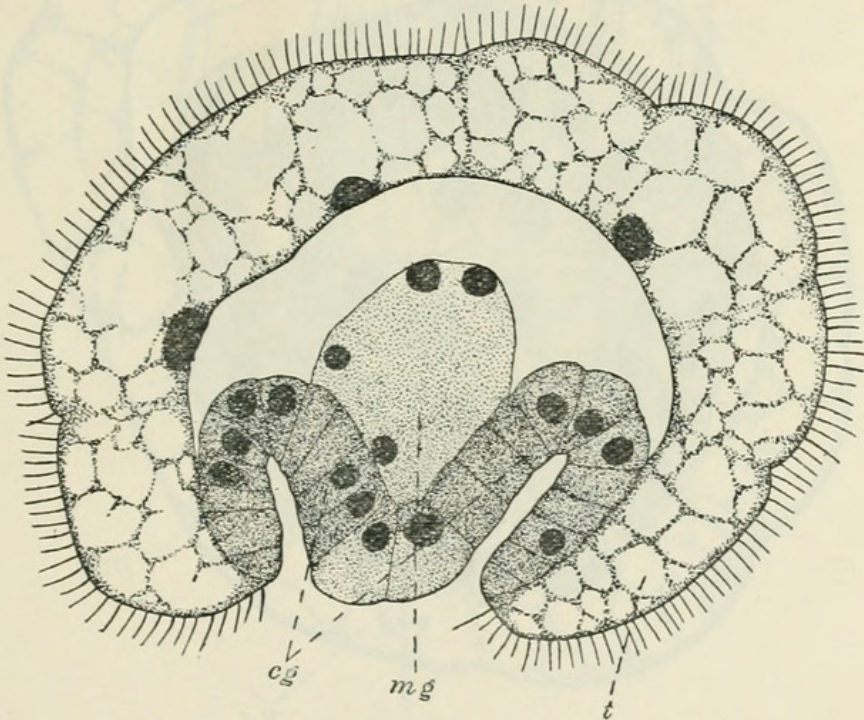


External appearance of an embryo of forty-four hours.
ac, apical cilia; *bl*, blastopore; *x*, ventral depression.

to include the ventral tube, which is of unknown origin. From the beginning it is connected with the ventral tube, formed, as it were, as a continuation of the anterior extremity of the ventral tube.

From a time preceding the formation of the apical plate a few cells of ectodermal origin have occupied an anterior position. These cells extend ventrally to the depression x (fig. 1), and push in between the test-cells. It was apparently from cells connected with this group that the apical plate was formed, and now, at about forty hours, other cells from this same group form two thick-walled pouches, which open to the exterior between the test-cells. These are the rudiments of the cerebral ganglia. Fig. 2 represents a transverse section of an embryo of fifty-eight hours, taken through

Fig. 2.



Transverse section of an embryo of fifty-eight hours, taken through the depression x , fig. 1. *cg*, pouches which form the cerebral ganglia; *mg*, wall of the anterior end of the mid-gut; *t*, test.

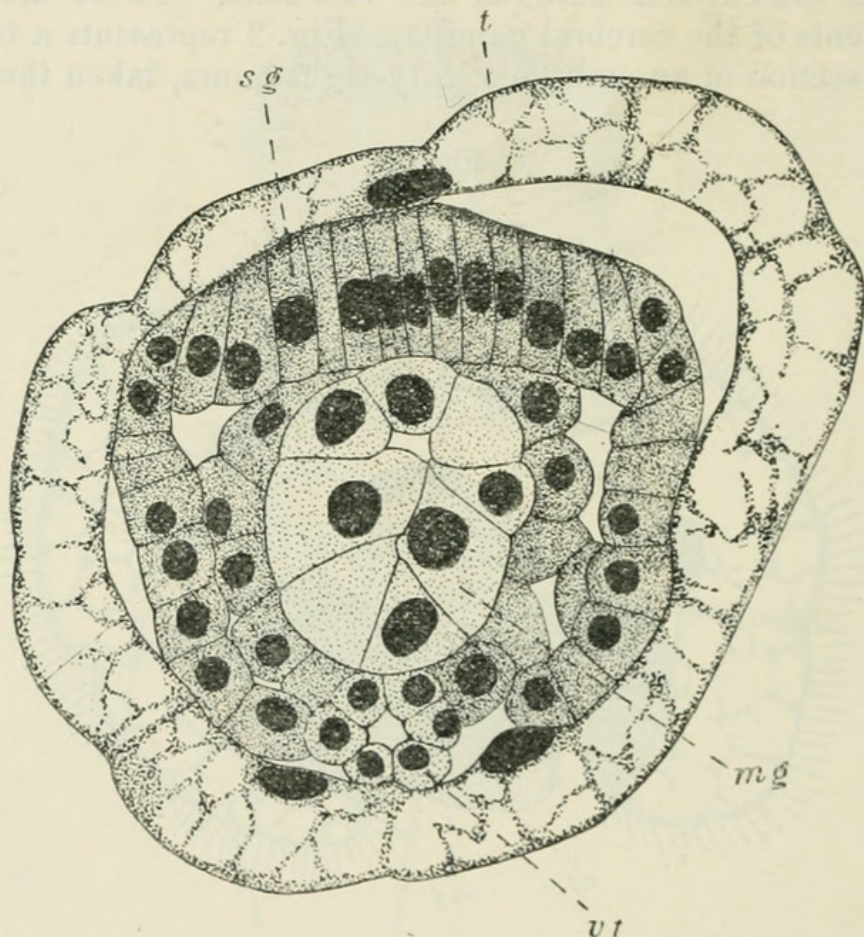
the depression x (fig. 1). The test, *t*, is shown to be composed of large vacuolated cells, the walls between which are no longer very distinct. As this section cuts the anterior row of test-cells, they are uniformly covered with cilia. The rudiments of the cerebral ganglia, *cg*, appear as two thick-walled pouches. The wall of the anterior end of the mid-gut, *mg*, appears in section.

Fig. 3 represents a transverse section of another embryo at a corresponding stage, taken just in front of the second band of cilia. The shell-gland, *sg*, has become arched upward, and is on the verge of protruding laterally to form the

mantle. The mid-gut, *mg*, and the ventral tube, *vt*, are both shown in cross-section.

This stage is of interest in showing the beginnings of the ectodermal thickenings that form the pedal ganglia and the ectodermal invaginations that form the otocysts.

Fig. 3.



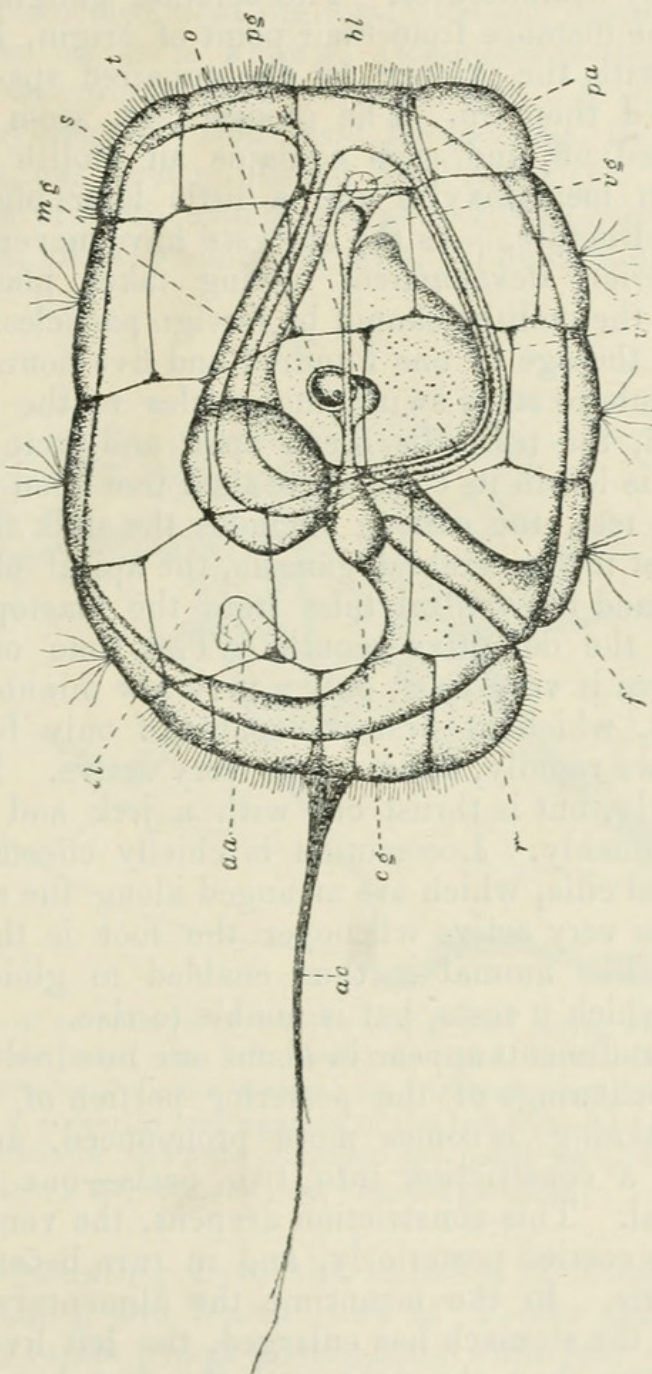
Transverse section of an embryo of fifty-eight hours, taken just in front of the second band of cilia. *mg*, mid-gut; *sg*, shell-gland; *t*, test; *vt*, ventral tube.

As the shell-gland spreads out into the mantle, the embryo becomes slightly compressed laterally, the foot appears, and the visceral ganglia may be distinguished.

Fig. 4 represents a reconstructed embryo of one hundred and five hours. The test-cells, *t*, are now very flat and much thinner than at an earlier stage. The shell, *s*, indicated in outline, is well formed. The anterior adductor muscle, *aa*, occupies a rather isolated position. The posterior adductor muscle, *pa*, has just made its appearance. The foot, *f*, is pretty well formed, and has running over and united to its

tip the ventral tube, *vt*, which opens to the exterior through the blastopore, *bl*, and is continuous with the mid-gut, *mg*.

Fig. 4.



Reconstruction of an embryo of one hundred and five hours; cilia indicated only at the margins. *aa*, anterior adductor muscle; *ac*, apical cilia; *bl*, blastopore; *cg*, cerebral ganglia; *f*, foot; *ll*, left liver-lobe; *mg*, mid-gut; *ot*, otocyst; *pa*, posterior adductor muscle; *pg*, pedal ganglion; *r*, pouch extending from the cerebral ganglia to the exterior; *s*, shell; *t*, test; *vg*, visceral ganglion; *vt*, ventral tube.

The embryo at this stage has acquired an anus, which has broken through into the upper part of the blastopore. The

liver, of which the left lobe, *ll*, is indicated, has made its appearance as evaginations of the mid-gut. The cerebral ganglia, *cg*, pedal ganglia, *pg*, and visceral ganglia, *vg*, are connected by commissures. The cerebral ganglia have been carried some distance from their point of origin, but are still connected with the exterior by the unpaired space, *r*, which has followed them in. The otocysts, *ot*, seem to be completely closed off, and each contains an otolith that stains deeply with hæmatoxylin 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.

At about the age of one hundred and five hours, or a little later, the embryo stops swimming, settles to the bottom, the cilia shrivel, the test-cells break apart and go to pieces, and the animal is left in its clear white shell free upon the bottom. Beside the test, the casting includes the stalk that extends from the test to the cerebral ganglia, the apical plate and its connexion, and the ventral tube from the blastopore to the position of the definitive mouth. The time occupied by these changes is very brief, only a very few minutes at most.

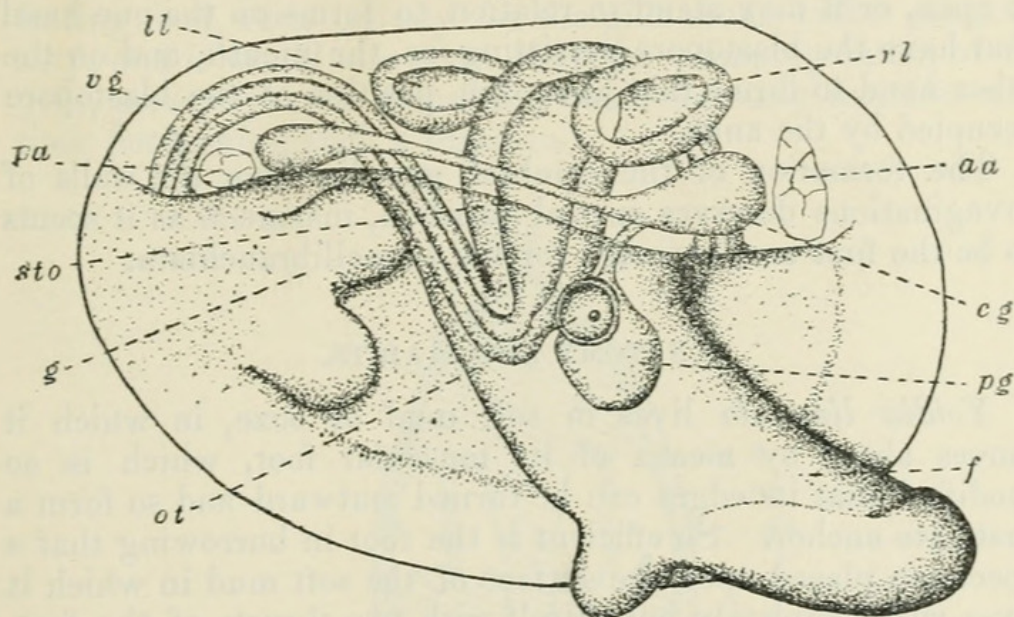
The foot, which at first is capable of only feeble movements, grows rapidly, and is soon very active. It is never moved slowly, but is thrust out with a jerk and withdrawn quite as suddenly. Locomotion is chiefly effected by long and powerful cilia, which are arranged along the sides of the foot, and are very active whenever the foot is thrust out of the shell. The animal is thus enabled to glide over the surface on which it rests, but is unable to rise.

The gill rudiments appear in about one hundred and fifteen hours as thickenings of the posterior portion of the mantle. Each thickening becomes more pronounced, and is soon divided by a constriction into two parts—one dorsal, the other ventral. This constriction deepens, the ventral portion broadens, is carried posteriorly, and in turn becomes divided into two parts. In the meantime the alimentary canal has lengthened, the stomach has enlarged, the left liver-lobe has become larger than the right, and the foot has acquired a "sole," which roughly corresponds in shape and movements with the "sole" of the adult. Locomotion is still materially aided by the long and powerful cilia. Fig. 5 represents a reconstruction of an embryo twelve and a half days old, as seen from the right side, with the right shell-valve and the mantle-lobe removed. The powerful cilia of the foot and gill and the fine cilia that cover the surface of the body and project into the lumen of the alimentary canal have not been

indicated. The lettering will enable the reader to identify the different parts.

The most striking peculiarities in the development of *Yoldia* are connected with the formation and disappearance of the test. So far as is known, *Dondersia* is the only other mollusk whose embryo has a locomotor test. A short account of the embryology of *Dondersia banyulensis*, illustrated by three figures, has been published by Pruvot (7). The fully formed tests of both *Dondersia* and *Yoldia* consist of five rows of cells, all of which bear cilia. The cilia on the third

Fig. 5.



Reconstruction of an embryo of twelve and a half days, seen from the left side, with the left shell-valve and mantle-lobe removed. *aa*, anterior adductor muscle; *cg*, cerebral ganglion; *f*, foot; *g*, gill; *ll*, posterior prolongation of the left liver-lobe; *ot*, otocyst; *pa*, posterior adductor muscle; *pg*, pedal ganglion; *rl*, right liver-lobe; *sto*, stomach; *vg*, visceral ganglion.

row of cells (counting from the anterior) of *Dondersia* and the second, third, and fourth rows 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 apical cilia, and in either case the test is finally cast off.

The young larva of *Dentalium*, as figured and described by Lacaze-Duthiers (4) and Kowalevsky (3), bears a certain resemblance to those of *Dondersia* and *Yoldia*. This is largely due to three or more rows of cells, each of which bears a band of cilia. At this stage these cells form the

greater part of the external surface of the embryo. As the body of the larva elongates posteriorly these cells are crowded forward to form the velum, which, however, does not seem to be cast off.

Through these forms we may, perhaps, trace an homology between the test of *Yoldia* and the velum of other forms. In this connexion it is interesting to notice that in a few forms the velum is known to be cast away. This was observed by Sigerfoos (8) for *Teredo* and by Wilson (9) for *Polygordius*.

The condition presented by the mouth and anus both opening through the blastopore is interesting. It may be that the blastopore offers the only available place for the anus to open, or it may stand in relation to forms on the one hand that have the blastopore persisting as the mouth, and on the other hand to forms that have the position of the blastopore occupied by the anus.

The formation of the cerebral ganglia from the walls of invaginations deserves special mention, inasmuch as it seems to be the first case reported for the Lamellibranchiata.

ANATOMY AND HABITS.

Yoldia limatula lives in soft mud or ooze, in which it moves about by means of its muscular foot, which is so modified that its edges can be turned outward and so form a first-rate anchor. So efficient is the foot in burrowing that a specimen placed upon the surface of the soft mud in which it lives will completely bury itself with two thrusts of the foot. The foot is very sensitive and is moved with wonderful rapidity. In every way it shows itself to be nicely adapted for burrowing. It seems very hard to imagine that it could possibly be used as a creeping-organ.

From the posterior part of each external palp there arises an elongated appendage, known as the palp-appendage, which can be protruded to a distance considerably exceeding the length of the shell. This appendage is folded longitudinally to form a groove that runs from its tip to its point of attachment.

When the animal is feeding the shell is slightly tipped ventrally from the perpendicular, and about two-thirds of its anterior end is buried in the mud. The palp appendages are thrust out of the shell, and one at least bends over and inserts its tip into 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.

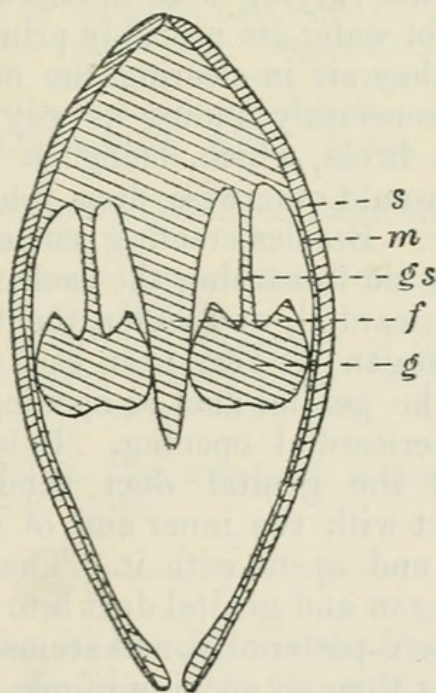
In this way foraminifers, ostracods, and even small lamelli-branchs and gastropods, are passed along the groove, between the palps, and finally into the mouth.

Thus we find that Mitsukuri's surmise (5), based on finding sand in the grooves of the palp-appendages of preserved specimens, was right. The palp-appendages are food-collectors.

Experiments were tried to determine if possible the part taken by the gills in collecting food. No definite results were reached, but in no case was Kellogg's observation (2) that the gills are extremely active food-collectors confirmed.

Considering the remarkable activity of the palps in collecting food, such activity for the gills seems rather unnecessary, and it would also seem that the pumping action of the gills, presently to be described, would seriously interfere with their performing such a function.

Fig. 6.



Diagrammatic transverse section of an adult animal, taken just in front of the posterior adductor muscle. *f*, foot; *g*, gills; *gs*, gill suspensory membrane; *m*, mantle; *s*, shell.

It is well known that each pair of gills is suspended from the body-wall by a membrane, but little or no attention has been given the fact that this membrane is muscular. As the gills are composed of wide plates, they are sufficiently broad to span the spaces between the foot and the mantle-lobes (fig. 6), and behind the foot unitedly to span the entire

mantle-chamber. Anteriorly the gills gradually diminish in size and finally disappear. Posteriorly they are attached to the wall that separates the two siphons. 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 exhalent siphon.

In young specimens, in which the brown gills are visible through the shell, the movements of the gills may be observed. They are gradually pressed ventrally, probably by the blood forced into them, the water passing between the gill-plates as they descend. This is followed by a quick contraction of the suspensory membranes (fig. 6, *gs*), accompanied by a vigorous discharge of water through the exhalent siphon as the dorsal chamber diminishes, and a corresponding influx of water through the inhalent siphon as the ventral chamber enlarges. The movements of the siphons accompanying the movements of the gills are very conspicuous, and have been mentioned by Brooks (1). The movements are more or less rhythmic, the time varying with the needs of the animal.

The currents of water are probably primarily for respiratory purposes, but they aid in clearing the mantle-chamber from the dirt that is constantly finding its way in, and more especially from the fæces, which, being so largely composed of sand and mud, would otherwise drop into and soon clog the mantle-chamber. Besides creating currents of water, these movements may aid in causing the exchange of blood.

The inner, pericardial, and outer, mantle-chamber, ends of each excretory organ lie very near each other. Pelsner (6) has described the genital duct as opening into the excretory organ near its pericardial opening. In all the cases that I have examined the genital duct bends ventrally, when almost in contact with the inner end of the excretory organ, meets the end and opens with it. The common opening of the excretory organ and genital duct into the mantle-chamber is elongated antero-posteriorly, and seems to represent a fusion of the two rather than an opening of one duct into the other.

No distinct separation into cerebral and pleural ganglia has been observed.

The otocystic canals have not been traced to the exterior, but they are distinctly visible near the otocysts. Their meaning is not clear to me, as the otocysts seem to be entirely closed off at an early age.

In closing, attention will be called to two sensitive areas on each mantle-margin. These lie opposite the extremities of shell-stripes that run from the beaks to the ventral margin, one anterior, the other posterior. The anterior area is in the

form of an elliptical projection, and the posterior area is a flat expansion. Both, especially the anterior projection, are quite sensitive to mechanical stimulation. They are both entirely distinct from the organ of special sense described by Brooks (1). Their special functions remain to be determined.

My thanks are due to Dr. W. K. Brooks, who has directed this work, and I wish publicly to acknowledge my indebtedness to my wife, who has materially aided me in securing, tending, and preserving specimens.

Zoological Laboratory, Johns Hopkins University,
Baltimore, May 1, 1897.

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XLV.—*On some new Mammals from the Neighbourhood of Mount Sahama, Bolivia.* By OLDFIELD THOMAS.

THE British Museum has purchased from Mr. Gustav Garlepp a small series of mammals obtained by him at Esperanza, a “tambo” in the neighbourhood of Mount Sahama, Bolivia, while collecting birds for Count von Berlepsch. The specimens prove to be of considerable interest, as there are among them examples of no less than five new species, one of these representing a new genus.

Mr. Garlepp informs me that “the mammals were all taken at an altitude of 4000 metres in the ‘Puna’ region—that is to say, on the high plateau between the Coast



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