
ANATOMY AND PHYSIOLOGY OF THE WING-SHELL
ATRINA RIGIDA



By Benjamin H. Grave

Assistant Professor of Zoology, University of Wyoming

CONTENTS.

	Page.
Introductory.....	411
Shell.....	412
Mantle.....	413
Burrowing.....	414
Regeneration and growth of shell.....	414
Mantle gland.....	416
Labial palps.....	417
Gills.....	418
Structure of the filaments.....	421
Course of the circulation in the gills.....	422
Respiratory current.....	424
Food-bearing currents.....	425
Circulatory system.....	425
Arterial system.....	426
Venous system.....	427
Adductor muscles.....	428
Retractor muscles of the foot.....	428
Visceral mass.....	429
Foot and byssus.....	429
Kidney.....	429
Digestive tract.....	431
Nervous system.....	432
Sense organs.....	435
Otocysts.....	435
Osphradium.....	436
Summary.....	436
Bibliography.....	437
Explanation of plates.....	438

ANATOMY AND PHYSIOLOGY OF THE WING-SHELL *ATRINA RIGIDA*.^a



By BENJAMIN H. GRAVE,
Assistant Professor of Zoology, University of Wyoming.



INTRODUCTORY.

Atrina rigida (Dillwyn) occurs along the eastern coast of America from the northern shore of South America as far north as Cape Hatteras. At Beaufort, N. C., where most of the observations reported in this paper were made, this species is confined to shallow water near low-tide mark, occasionally being exposed during unusually low tides. Another species, *Atrina serrata* (Sowerby), is found in the deeper water of the inlet. The largest specimen found measured 14 by 9 by 3 inches, but the average size is only about 11 by 8 by 2½ inches.

This mollusk is not without an economic interest and value. The black pearls formed in *Atrina* and *Pinna*, and produced in considerable numbers, have been used in the manufacture of brooches and other articles of jewelry, and there is no reason why they should not be used more extensively. They are usually spherical in shape and quite smooth.

The pearls are not found in all specimens, but as many as ten have sometimes been found in a single individual. At a rough estimate I should think pearls would be found in about one-fifth of the individuals. This was about the proportion as regards those examined during the preparation of this paper.

The byssus has been used extensively in the manufacture of various articles, such as shawls, caps, waistcoats, gloves, purses, etc. The following quotation from Simmonds's Commercial Products of the Sea gives in a few words the extent to which the byssus has been used in the past, as well as its present standing as a commercial product:

The ancients made this [the byssus] an article of commerce, greatly sought after, and the robes formed of it, called "tarentine," were very much in esteem. * * * * *

^a Dissertation submitted to the Board of University Studies of the Johns Hopkins University in conformity with the requirements for the degree of doctor of philosophy.

I am indebted to Prof. W. K. Brooks for the suggestion that I undertake the study of the anatomy of *Atrina*. My thanks also are due especially to Prof. E. A. Andrews, under whose direction this work has been done and who has offered many helpful suggestions and stimulated my interest in biological study. I am indebted to the Commissioner of Fisheries for the use of a table at the fisheries laboratory at Beaufort, N. C., during the summers of 1908 and 1909; to H. D. Aller, director of the laboratory, for many conveniences while there and for assistance in procuring material; to Prof. G. A. Drew for counsel and suggestions; and to Prof. William H. Dall, of the Smithsonian Institution, for the determination of the species and the free use of his library.

Even in the present day the fiber is utilized, but more for its rarity than anything else. The women comb the *lana* [byssus] with very delicate cards, spin it, and make from it articles which are much esteemed for the suppleness of the fiber and their brilliant burnished gold luster.

A considerable manufactory is established at Palermo; the fabrics made are extremely elegant and vie in appearance with the finest silk. The best products of this material are, however, said to be made in the Orphan Hospital of St. Philomel, at Lucca.

This byssus forms an important article of commerce among the Sicilians, for which purpose considerable numbers of *Pinna* are annually fished up in the Mediterranean from the depth of 20 to 30 feet.

Under normal conditions *Atrina* occupies one position during its entire life—nearly buried in the mud, with its anterior end downward. The enormous byssus extends deep into the mud and attaches to shells and coarse pebbles. Specimens are most easily collected in calm weather at low tide, when they can be seen extending an inch or less above the surface of the mud.

In the following discussion, although the continuity is thereby interrupted, it seems advisable to treat the organs under separate headings, passing briefly over those which have yielded nothing of particular interest. To avoid repetition the anatomy and physiology of the organs will be treated together. The general anatomy is shown in figures 16 and 20.

Since every species is adapted to its peculiar mode of life certain anatomical features are better understood when their function is known. It has therefore been my purpose to study habits and function as well as anatomy.

SHELL.

The shell valves are large in comparison with the size of the body, and they are united to each other along one side by a hinge ligament which extends in a straight line from their anterior to their posterior ends. The hinge ligament is more or less calcified, so that it is not greatly different from the other parts of the shell. The outer surface of each shell is studied with spines, which are distributed in rows radiating from the anterior pointed end as a center to the posterior end. Primary, secondary, and tertiary rows of spines may be distinguished in the shell of a large specimen. The portion of the shell which lies posterior to the adductor^a consists of a single layer in contrast to the typical lamellibranch shell, which has three layers, easily distinguishable by difference in structure or material. It apparently corresponds to the middle or prismatic layer of the typical lamellibranch shell, being composed of prisms which lie at right angles to the surface. When the surface is examined with a compound microscope it appears honey-combed, while a transverse section, obtained by grinding, looks not unlike a lot of quartz crystals corded like wood. (See fig. 1.) It is possible to dissolve out the lime salts with acid, leaving behind only the organic matrix. This matrix resembles cork in many respects, but when examined histologically it is seen to have the same gross structure as the shell before treatment with acid, except that the chambers formed by the organic matrix are now empty.

^a I refer here to the posterior adductor muscle, and unless otherwise stated further references to the adductor may be taken to mean the posterior adductor.

The portion of the shell in the region of, and anterior to, the adductor is composed of two layers, there being a second or nacreous layer of the ordinary type deposited upon the inner surface of the prismatic. This layer is secreted by the general surface of that part of the mantle which lines the shell in these regions. The outer layer frequently wears through, or becomes brittle and broken, on the older portions of the shell, leaving the nacreous layer exposed. A discussion of experiments on the growth and regeneration of the shell will be found at the end of the next section.

MANTLE.

The mantle is a muscular membrane, the folds of which adhere closely to the shell, but are attached to it only at a single point just ventral to the adductor muscle. The muscles which control the ventral and posterior portions of the mantle are attached here and radiate from this point as divisions and subdivisions of a single bundle. Another bundle of muscle fibers is located near the dorsal part of the body. It is not attached to the shell at any point, but is inserted into the mantle itself. This bundle of mantle muscles also divides and subdivides into smaller and smaller bundles and is distributed to a portion of the posterior part of the mantle. (Fig. 16, pl. XLVIII.) It is thus seen that there is no pallial line in the shell for the attachment of the mantle muscles, though that is so common among lamellibranchs. Since the muscles are attached so high up, the mantle margin can be withdrawn a considerable distance from the edge of the shell; in fact, it can be withdrawn nearly to the adductor. After being contracted the mantle again expands by creeping outward upon the shell, to which it adheres closely. This result can not be brought about at once. At least half an hour is required for the mantle to again reach the edge of the shell after having been fully contracted. There are no siphons, but the two lobes of the mantle are united posteriorly by an intermantle septum at the place where siphons might be expected to occur. This structure consists of two prominent ridges, one on each mantle lobe, which stretch across posterior to the gills to meet each other in the mid line. Each mantle ridge is continued anteriorly, though reduced in size, and forms the place of attachment for the upper borders of the reflexed lamellæ of the outer gills.

On account of the position assumed by *Atrina*, only the posterior portion of the mantle is exposed to frequent sensory stimulation. Connected with this fact we find that the edge of each mantle lobe has a row of short sensory tentacles, which decrease in size and gradually disappear toward the anterior end. This part of the mantle is thick and muscular, as an adaptation to burrowing. A deep narrow passage or groove, formed by the development of two tall ridges on the inner surface of the mantle, is also correlated with burrowing. (Fig. 16, D, pl. XLVIII.) This groove lies parallel to the edge of the mantle and extends from the region of the foot to the intermantle septum,

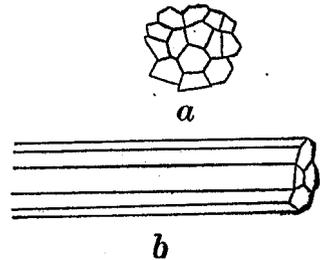


FIG. 1.—The shell. a, Surface view; b, transverse section showing prismatic structure.

where it approaches the edge of the mantle. The cilia within this groove beat toward the posterior to produce currents that continually remove foreign bodies from the mantle chamber. Any large particle of dirt or sand which enters the mantle chamber soon finds its way into this ciliated passage and is carried forthwith to the exterior.

BURROWING.

In order that *Atrina* may maintain its position in the mud throughout life, it must burrow more or less. The bottom about it is sure to be shifted considerably by the tides, thus tending to uproot or cover up fixed objects on its surface. This shifting of the bottom was observed last year on the very beds where *Atrina* was found most abundant. During the summer of 1908 these beds were covered by eel grass, while a year later this grass had entirely disappeared and the character and depth of the bottom had changed to a noticeable extent. *Atrina* while undisturbed in its natural surroundings was never seen to burrow. But the method of burrowing was frequently observed when the animal was removed and again partially buried with the anterior end downward. The shell valves were opened wide by the relaxation of the adductor muscle, and the edges of the posterior part of the mantle lobes were brought together firmly to prevent the escape of water in this direction. Then followed the contraction of the adductor, forcing water from the mantle chamber at the anterior end. The force of the expelled current makes the water fairly boil, washing up quantities of sand and mud from beneath. This process was usually repeated several times at intervals of four or five seconds and then there followed a period of rest during which the sand and mud which had entered the mantle chamber during the burrowing movements was removed through the ciliated groove. This heavy material was expelled over the posterior edge of the shell in surprisingly large quantities in a short time. This accomplished, the burrowing movements were resumed. The settling of the specimen was very gradual, but in the course of an hour one could see that it had sunk 3 or 4 inches. Although the ciliated groove is of service in removing solid particles which enter the mantle chamber with the respiratory current, I think it is an especial adaptation for removing the heavier bodies which enter the mantle chamber during burrowing movements.

A number of *Atrina* individuals were laid upon their sides to see if they would bury themselves. The results were practically negative, for although they were left for weeks in this position not one made any attempt to bury itself. They seemed to thrive as well in this position as in any other, and none were seen to make movements which could be construed as an attempt to assume the normal position. Mr. Charles Hatsel, official collector at Beaufort, in whose charge certain experiments were left during the winter, reported that one specimen buried itself as far as the box in which it was kept would permit.

REGENERATION AND GROWTH OF SHELL.

Atrina is a particularly good subject for experiments upon the growth and regeneration of the shell because of the great rapidity with which this is produced. When one breaks a piece from the posterior or ventral edge of the shell, the mantle in this region becomes particularly active in mending the breach, a strip one-tenth of an inch in width

often being produced in twenty-four hours, the amount varying in different specimens between one-eighth and one-twelfth. In one instance a hole which measured approximately one-half by three-fourths of an inch was cut in the shell of a vigorous young *Atrina* with the result that it was repaired in three days. Experiments performed to determine what parts of the mantle are capable of producing shell go to show that this power belongs only to the very edge and is probably confined to a small portion of modified epithelium located in a groove in the edge of the mantle.^a (Fig. 2, a.) When a notch was formed in the shell by breaking out a piece, the edge of the mantle was quickly applied to the bottom of it with the result that it was soon built up even with the general level of the edge of the shell. When holes were cut in the shell at a great distance from the edge to see if other portions of the mantle could produce shell, it was found that the mantle edge was drawn back to these places and remained there until they were repaired. Although conclusive proof that only the edge of the mantle can produce shell is lacking, there is abundant evidence that *Atrina* generally repairs all injuries to the shell with this part of the mantle, and it seems safe to assume that shell formation is confined to this portion.^a

As stated in a previous section, the outer surface of the shell bristles with spines, which are distributed in rows. They have the same prismatic structure as the shell and like it they are secreted by the edge of the mantle. When fully formed, they are between one-half and three-fourths of an inch in length, and, except that they are slightly broader at the base than at the top, have the shape of a half tube, the hollow side of which faces the edge of the shell. During the growth period of one of these spines a little fold or tongue of the mantle edge extends beyond the shell and fits into the hollow surface of the spine. In time the shell, by its growth at the edge, extends beyond the spine so that the mantle no longer comes into contact with it. This mode of formation accounts for the fact that the spines are hollow and open toward the growing edge of the shell. There is no visible differentiation of the mantle edge in the form of permanent folds to which the formation of the spines is due. The edge of the mantle opposite a row of spines does not seem to differ from that located between two rows. The tongues which creep out into the spines are not permanent structures, but are formed by a local expansion of the mantle.

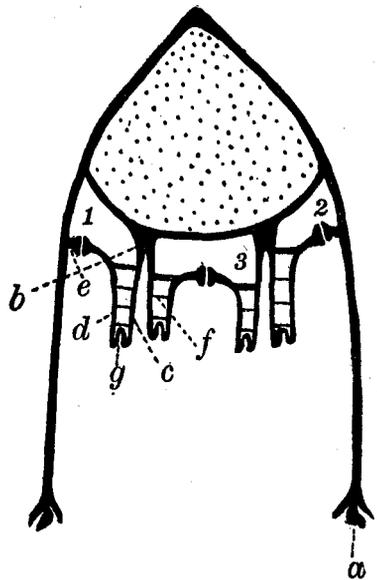


FIG. 2.—Diagrammatic cross section of the body anterior to the adductor muscle. a, Modified epithelium which secretes shell; b, suspensory membrane; c, descending lamella of outer gill; d, reflected lamella; e, longitudinal ridge on the mantle to which the gill is attached by means of interlocking cilia; f, vascular interlamellar septum; g, longitudinal groove in edge of gill. 1, 2, and 3, suprabranchial chambers.

^a This refers only to the prismatic layer. The second layer, which is laid upon the inner surface of the shell at the anterior end, is secreted by the whole of the epithelium of the mantle of this region.

Measurements to determine the rate of growth of *Pinna* under natural conditions revealed slower growth than had been anticipated. In seven weeks' time some specimens increased one-half inch in length with corresponding increase in breadth. The greater number grew only about one-fourth of an inch in this time and the oldest specimens showed no growth. It is impossible to estimate from these figures the time required for an individual to reach maturity, but the fact is revealed that when they reach a certain age growth ceases.

At the suggestion of Professor Andrews I endeavored to discover whether the calcium salts used in shell formation are taken directly from the sea water or whether they are taken from the blood. The results are not satisfactory, but I give them for what they are worth: A notch was cut in the shell of a young specimen and the broken edges were filed until they were quite smooth. The specimen was then placed in artificial sea water which lacked only the calcium salts. This water was kept aerated by compressed air. The specimen applied the mantle edge to the broken place in the shell and kept at work for several hours without accomplishing much. During the first experiment, which was continued for twenty-four hours, only about one-tenth as much shell was produced as would have been formed under normal conditions. However, enough was produced to be plainly visible and when it was removed and examined under the microscope it showed normal structure and effervesced when hydrochloric acid was added.

Several similar experiments were tried, but no perceptible growth of shell was obtained. In the first experiment the chemicals used were not "C. P." and may have had some calcium in them, and this may account for the lack of uniformity in the results. It was impossible to keep the specimens in good condition for twenty-four hours in this artificial sea water and on this account I think it unwise to draw hard and fast conclusions from the experiments. The method seems worth trying under more favorable conditions. Recently the question has been raised as to whether animals which live in a water medium can take nourishment from it through the general body surface. It seems quite possible that lamellibranchs take the lime salts from the water directly rather than indirectly from the digestive tract. If lamellibranchs elaborate shell from calcium salts in the blood, their supply must be continually replenished, judging from the above experiments, which indicate that these specimens could not make much headway from stores already present in the body.

MANTLE GLAND.

● A large muscular structure, which appears from its connections to have been developed from the mantle, lies in the cloacal chamber. It resembles the foot in many respects and, like it, can be extended by blood pressure. When extended it becomes slender and may reach a length of nearly 6 inches, but when contracted it is short and thick. Upon its tip it bears a large mucous gland. (Fig. 16, M, pl. XLVIII.) This peculiar organ is not commonly found in lamellibranchs, being confined to the Pinnidæ. Many specimens were examined in their natural habitat and in the laboratory for the purpose of learning

its function. So long as a specimen is undisturbed this glandular structure is likely to lie quietly in the cloacal chamber, but when the mantle is irritated, for example by breaking off part of the shell, it becomes active and moves about in every conceivable direction. It was frequently pushed far down into the branchial chamber toward the point of irritation. When grains of sand were put upon the mantle this muscular gland sometimes succeeded in brushing them off after several trials and much aimless maneuvering. While this organ is moving about the glandular tip is usually kept pressed against the mantle and appears to be sweeping its surface. It seems to be a "swab" for the purpose of freeing the mantle of any foreign body which may lodge upon it.

Just why the Pinnidæ need such a structure is difficult to determine, since other lamellibranchs get on without it, the cilia on the inner surface of the mantle being equal to the task of keeping it clean. The position assumed by *Atrina* is one of disadvantage for removing débris. It has been pointed out that great quantities of dirt and sand do enter the mantle chamber, and this must all be raised vertically to the edge of the shell for expulsion, so that structures especially adapted to this purpose are to be expected. The mantle gland is probably such a structure.

The mantle gland is much less compact in structure than the foot. On the outside there is an epithelial covering which is glandular only at the tip of the organ. Here the cells are very much elongated and they contain a large amount of secretion in the form of granules. Immediately beneath the epithelium there is a band, or cylinder, of longitudinal muscle fibers. They are attached to the organs at the base of the gland for support. Many of them spread out over the adductor, into which they are inserted. They are so distributed in the gland that they can control the direction of its movement provided that they do not all contract at the same time. The shortening of the gland is also brought about by the contraction of these muscles. The central part of the gland is composed of very open connective tissue and a few transverse muscle fibers.

LABIAL PALPS.

The palps consist of two thin muscular lamellæ which extend across the anterior end of the body, one above and the other below the mouth. Their outer ends are roughly triangular in shape and lie alongside the body. The epithelium lining the palps is continuous with that of the mouth and Drew (2) has aptly likened these structures to a pair of drawn-out lips. They are essentially alike in many lamellibranchs but vary greatly in size and shape in different species. In *Atrina* they are comparatively large and consist of two well-defined portions. That part which lies near the mouth is narrow and is lined by a smooth ciliated epithelium, while the outer triangular portion is broad and is lined by an epithelium that is thrown into a series of prominent ridges and grooves large enough to be plainly seen without magnification. Posteriorly the palps inclose the anterior ends of the gills, and it is their function to transport the food collected by these organs to the mouth. An extra projecting membrane is present on the ventral border of the inner palp, which folds up over the outer. (Fig. 16, pl. XLVIII.)

GILLS.

There are two large gills on each side of the body which extend parallel to its longitudinal axis from the neighborhood of the mouth almost to the posterior extremity of the mantle. (Fig. 16, pl. XLVIII.) They are attached to the body by a suspensory membrane in the usual manner. The gills are much alike except that the inner one of each pair is somewhat broader than the outer and hence reaches below its fellow. They are pointed at the extremities and anteriorly are inclosed by the palps. Each gill consists of two lamellæ which lie close together; or perhaps it is more correct to think of it as being composed of a single lamella which has been folded upon itself. According to this conception, the gill consists of a direct and a reflexed lamella, the two being continuous at the free edge of the gill. Various anatomical and embryological studies, especially those of Lacaze-Duthiers (8) and Peck (12), show this to be the correct interpretation. The two lamellæ are united to each other merely by blood vessels which pass from the one to the other. The interlamellar space is not partitioned off into definite parallel water tubes by continuous septa, but is undivided except for the scattered blood vessels which traverse it. The only place where there is anything resembling true interlamellar septa is at the upper borders of the gills where nonvascular, or only partially vascular, strands bind the two lamellæ together. At the outer free edge of the gill they are bound firmly together by lacunar connective tissue and by a continuous plate or cord of muscle whose fibers run longitudinal to rather than transverse to the gill. By its contraction the gill is shortened and folded. A large nerve lies immediately above this muscle, but I have made no attempt to study its distribution.

Each gill is attached to the suspensory membrane by one lamella only, as is common among lamellibranches. The inner lamella of the outer gill and the outer lamella of the inner gill are attached to the suspensory membrane as far back as the adductor muscle. From this point they are attached to each other. The outer lamella of the outer gill is attached to a ridge on the mantle (the same as that mentioned above). The inner lamellæ of the inner gills of the two sides are united to each other, except at the extreme anterior, where for a space of half an inch or so they are attached to the sides of the byssal apparatus which with the foot extends ventrally at this point. The attachments of the gills, together with the intermantle septum, thus cut off a system of supra-branchial passages from the general mantle cavity. A section across the body shows that there are three of these, which are diagrammatically represented in figure 2 (1, 2, and 3). A section taken posterior to the visceral mass would show only a single supra-branchial passage, the three having been thrown together at the termination of the suspensory membranes. This single supra-branchial passage lies below and posterior to the adductor muscle, and for distinction might be called the cloacal chamber.

The direct lamellæ are outgrowths from the suspensory membrane, and hence there is a firm organic union between them. On the other hand, the attachment of the upper borders of the reflexed lamellæ to the neighboring parts and of the ridges on the mantle to each other, to form the intermantle septum, is merely an interlocking of cilia so that they can be torn apart without doing the slightest injury to the animal. Only

a slight pull is necessary to separate them. In this way the branchial and suprabranchial chambers can be thrown together. In fact, the animal can maintain them separate or throw them together apparently at will. These unions commonly show an interlocking of the epithelial cells as well as the cilia, and sometimes the epithelium of the opposed surfaces is thrown into a series of ridges and grooves, thus producing a firmer union. Although Lacaze-Duthiers (8) and Peck (12) have described forms in which there is a weak union between the upper borders of the reflexed lamellæ and the mantle, they did not describe the actual mode of union. Their purpose in the description was to show the transition between those forms which have the mantle edge free and those which have it permanently united to the neighboring parts. Grobben (5) has shown that this weak union is by means of interlocking cilia, and he considers it to be universal among the *Aviculidæ*. He states also that when the opposed surfaces are forcibly separated they will reunite in a short time if undisturbed. The evidence upon which this assumption was based was his observations on the gill of *Mytilus*. Here he found, what Lacaze-Duthiers had already described, that the ciliary interfilamentar connectives would reform after being separated. Stenta (14) demonstrated that the reflexed lamellæ of the gills of *Pinna* and *Solen* would reunite to adjacent parts after being separated from them, and I have confirmed the same for *Atrina*. I separated the gill from its attachment to the mantle for a distance of 2 inches. When examined several hours later it had effected a union. Stenta thinks that this type of union between the gills and mantle is of much more general occurrence than has been supposed, suggesting that it may occur in those forms in which the gills have been described as free. He maintains that in life they are never separated unless by accident, but he is probably in error, because I observed the mantle gland, which normally lies in the cloacal chamber, extending far down into the branchial chamber. This could not take place so long as the gills retained their connection with each other.

When magnified sufficiently each lamella is seen to be thrown into a series of folds (grooves and ridges). These structures are barely visible to the unaided eye as a series of parallel lines running across the gill perpendicular to its base. Each ridge (fig. 3) is composed of from 10 to 12 hollow filaments which are slightly separated from each other. The latter are bound together at regular intervals by tubular interfilamentar connectives which are somewhat larger than the filaments and run at right angles to them. These two sets of tubules thus form a trelliswork in which the spaces between are the ostea through which water enters the gill from the branchial chamber. (Fig. 4.) The one or two filaments which occupy the summit of the ridge differ somewhat from the others in that they contain numerous goblet cells whose sticky secretion entangles minute organisms as they are carried over the gills in the respiratory current. The filaments and ridges of one lamella do not pass directly over into those of the other, but gradually decrease in size and disappear as they approach the edge of the gill. There is a deep groove with smooth walls in the edge of each gill which is lined by ciliated epithelium. (Fig. 2, *g*.) There is no fusion of filaments due to crowding as has been described by Rice for *Cardium* and other forms (13).

The grooves which lie between the ridges just described are not filamentous in structure but are lined by a continuous finely ciliated epithelium, below which there is a large crescent shaped rod of chitinous material for giving rigidity and elasticity to the gill. (Fig. 3, *c*.) Running along the floor of each groove within the cavity of the gill there is a large blood vessel. Each is connected with the similar vessels which lie next

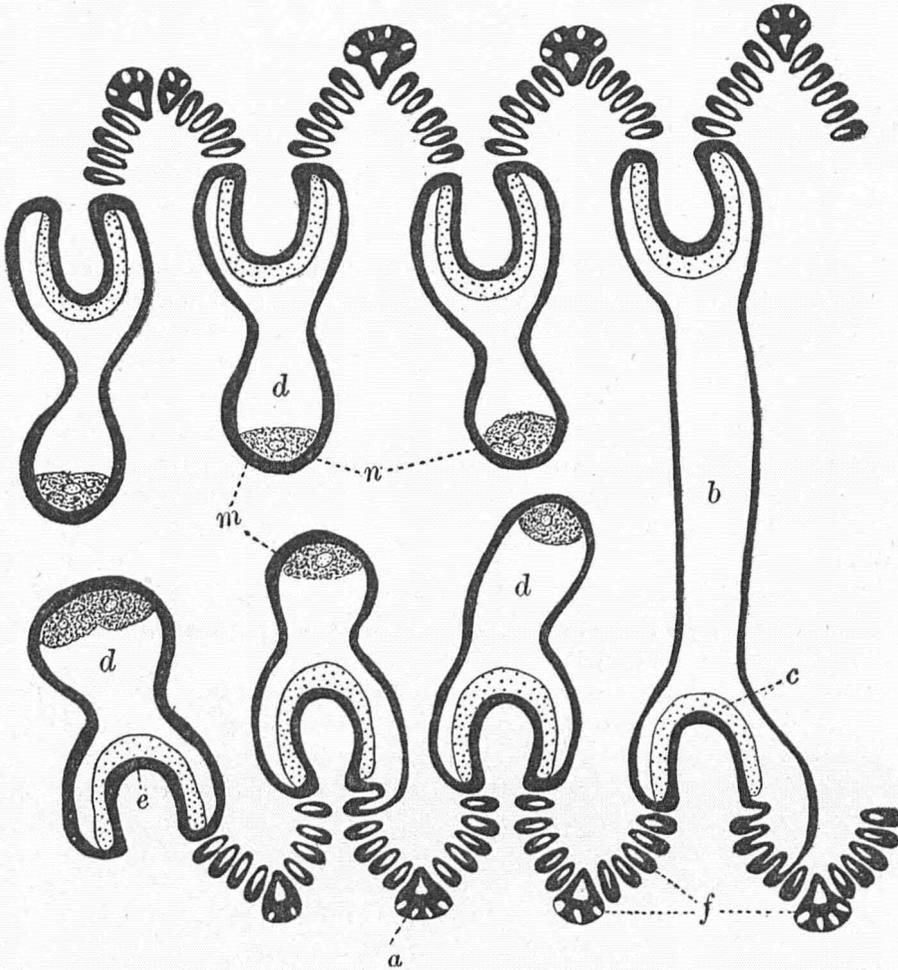


FIG. 3.—Transverse section of gill highly magnified. *a*, Modified filament containing glands; *b*, vascular interlamellar connective; *c*, chitinous supporting rod; *d*, large blood vessel; *e*, epithelium; *f*, filaments; *m*, muscles; *n*, nerves.

to it, at regular intervals, by smaller tubes which are the interfilamentary connectives already described as binding the filaments together. All of these structures are hollow and the cavities of all are in open communication. Thus when blood enters the gill it penetrates every part, including the filaments and interfilamentary connectives. (Fig. 4.) It is common to regard the structures which occur between two folds of the lamella as

a large modified filament, or as a single filament with its subsequent development of subfilamentar lacunar tissue, and there is some evidence that this is correct, viz, the epithelium lining the ciliated groove is continuous with that of the blood vessel. (Fig. 3, e.) At the edge of the gill also the resemblance becomes much more striking where it assumes clearly the appearance of a filament.

STRUCTURE OF THE FILAMENTS.

The structure of the individual filaments is best made out in cross sections such as that represented in figure 5. Each is composed of a simple epithelium which is lined by a very thin layer of chitinous material resembling a cuticle. (Fig. 5, c). Peck (12) considers this lining cuticle to be modified lacunar tissue. Sometimes protoplasmic

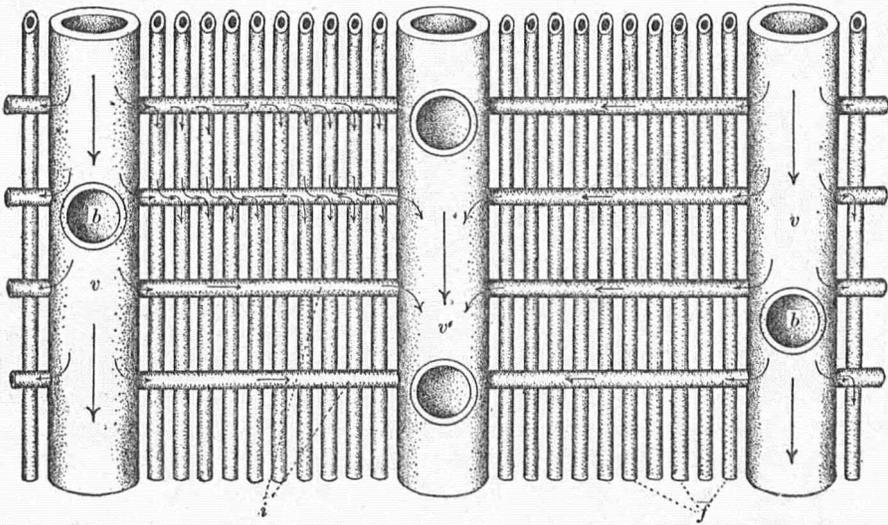


FIG. 4.—Diagrammatic drawing of a bit of the gill. *b*, Interlamellar connectives; *f* filaments; *i*, interfilamentar connectives; *v* and *v'*, large blood vessels. The arrows indicate the direction of the flow of the blood.

corpuscles can be seen lying upon its inner surface but none have been detected within it. There are no transverse bridges of this material such as are uniformly present in the filaments of the lower forms (*Arca*, *Mytilus*, and *Pecten*). It has commonly been supposed that the septum in these forms divides the cavity of the filament into two blood channels—the one afferent the other efferent—and this view seems well founded. Drew (2) by use of injections found that in *Pecten* this bridge had no such physiological significance. He has therefore suggested that it may serve to prevent the walls of the filament from spreading under the pressure of the inclosed blood which might close the incurrent ostia of the gill. He thinks that further study of gills of similar structure might throw light upon this interesting point. The gill of *Atrina* is made up on exactly the same plan as regards the shape of the filaments and amount and kind of interfilamentar connectives and yet there is no septum dividing the blood channel

into two parts. It seems better to regard this structure as a partition which divides the blood space of the filament into two blood channels because it is known to serve this purpose in *Arca* (1). In *Pecten*, where the circulation of the blood has been changed from the original type, it no longer serves this function but remains as a functionless membrane.

The outer surface of each filament is ciliated and three cells on each side have a tuft of long cilia. (Fig. 5). The latter point outward and are usually regarded as having a straining function, preventing food particles from entering the interlamellar cavity with the water currents. If the usual interpretation be correct they have nothing to do with the production of water currents.

The larger blood channels of the gill (fig. 3, *d*) show a structure similar to that of the filaments. There is a one-layered epithelium on the outside which is ciliated for the most part and contains numerous goblet cells (probably mucous secreting cells). Lining the epithelium inside the vessel there is more or less of lacunar tissue which has retained its primitive character. It contains scattered nuclei and its lacunar nature is easily made out. I find no evidence of an endothelium, which has been described by Bonnet (1) and Menegaux (9). The vessels frequently contain bundles of muscle fibers and nerves which run from the attached border to the free border of the gills. Their distribution has not been studied, but figure 3 shows their position.



FIG. 5.—Transverse section of a filament highly magnified. *c*, Cuticle lining the blood space.

COURSE OF THE CIRCULATION IN THE GILLS.

Before giving the course of the circulation in the gills it will be necessary to describe certain vessels which carry the blood to and from these organs, and since the circulation is the same for the two sides it will be necessary to describe it in but one. A very large vessel, which we will call X, arising from the kidney, passes posteriorly along the line of junction of the two gills as far as their extremities. (Fig. 20, X, pl. L). It gives off numerous branches, to the right and left, which pass through the interlamellar septa to the upper borders of the reflexed lamellæ. These lateral vessels open into one which runs along the upper border of the lamella. The latter which will be called vessel Y in further descriptions, is a distributing vessel made necessary, it would seem, because the main vessel from the kidney takes its origin near the middle of the gills, and hence no blood could pass from it to their anterior portions except through some such arrangement. Every other one of the larger vessels of the reflexed lamella (fig. 4, *v*), which lie at the reentrant angles of the folds, connects directly with vessel Y. Every alternate one (fig. 4, *v'*) ends blindly at the upper border of the lamella. This was proved not only by the study of sections but by injections as well. In the same way one-half of the larger vessels of the direct lamella end blindly while the other half connect with an efferent vessel which runs along its upper border carrying the blood back to the heart

after being aerated in the gills. The latter is a T-shaped vessel, one arm of which lies in the suspensory membrane and carries blood from the anterior half of the gills, while the other arm lies immediately below the vessel X and collects the blood from the posterior portions of the gills. The two arms of the vessel flow together just anterior to the kidney and form a rather wide tube disposed at right angles to them. (Fig. 9, *a*.) This tube is perhaps an inch and a half in length and connects directly with the auricle.

From these connections it is clear that the blood enters the gills through the reflexed lamellæ and leaves them through the direct. When a starch mass was injected into the vessel X the afferent vessels of this gill were injected and the course of the blood was made out with certainty. The mass first distends vessel X and then passes to Y, through the interlamellar septa, filling it from end to end. The mass now enters the vessels of the gill which communicate with vessel Y and passes toward the gill's free margin. (See fig. 20, pl. L.) Half of the vessels of this reflexed lamella are thus filled. Some of the mass flows across to the opposite lamella through the interlamellar connections and fills half of its vessels. (Figs. 3 and 4, *b*.) Examination shows that only those which end blindly above are filled with the mass, so that none of the injection mass finds its way into the efferent vessels of the gills. By injecting through the auricle, or the T-shaped vein which carries the blood from the gills, it is possible to fill all the vessels of the gills not already filled by injecting from the kidney. The mass first enters the direct lamellæ and spreads across to the other. I have a preparation in which the afferent vessels are injected with a black mass and the efferent with a yellow one, which brings out the relationship between them quite clearly. It is evident that provision is made for making the blood pass through the smaller vessels of the gill before returning to the heart.

We may conclude from evidence obtained from the injections and anatomical studies that the blood enters the gill through every alternate vessel of the reflexed lamellæ, from which part of it spreads to the right and left in the interfilamentar connectives and filaments (fig. 4, *i* and *f*), finally finding its way into the neighboring vessels of the same lamella. These vessels (fig. 4, *v'*) end blindly above so that it must yet pass across to the opposite lamella through the interlamellar connectives before finding its way out of the gill to the heart. On the other hand part of the blood on entering the gill passes at once across to the opposite lamella through the interlamellar connectives into vessels which end blindly above. From these it spreads laterally, right and left, in the interfilamentar connectives and filaments of this lamella and finally into the neighboring vessels which open freely above into the vein which leads back to the heart. The general course of the blood in the gill is therefore outward in the reflexed lamella and the opposite in the direct, and the vessels are so connected that it must pass through a capillary system in one lamella or the other before leaving the gills.

The relationship of vessels just described holds good for all parts of the gills, except a narrow strip at their outer free margin. Here it is different and for completeness must be briefly described. Here the transverse vessels (interlamellar connectives), are very numerous and lie side by side. In the mid-line between the lamellæ they

fuse and their cavities intercommunicate, forming a sort of irregular sinus. Here all the vessels of the two lamellæ seem to be in open communication, but the starch mass was not forced into them sufficiently to show this. If one can rely upon sections, this is true. Blood which does not find its way across to the direct lamella before reaching the edge of the gill does so here by passing through one of the very numerous transverse vessels which are present in this region. As has already been said, these intercommunicate, and this may be an adaptation to take care of the extra amount of blood which flows through the gills during muscular activity or when the heart beats rapidly from any cause, supposing that the capillaries are not sufficient to accommodate it at such times. Only a very small part of the blood passes around the edge of the gill. As has been stated already, the filaments disappear at the edge of the gill, but it is possible to trace vessels to the edge where they communicate with irregular spaces which pass around to the opposite lamella.

It is clear that the blood does not pass, as a whole, down one lamella and up the other, as is the case in *Pecten tenuicostatus*, as described by Drew (2). All the vessels of the outer lamella of this form are afferent, and all of those of the inner lamella are efferent. He found none ending blindly and no cross connections. On the other hand, Johnstone (6), studying *Cardium edule*, found that half of the vessels of each lamella are afferent and half are efferent. He implies that the efferent vessels of each lamella open separately into the main efferent vein, but he does not make this plain, and his figures 24 and 30 are inconsistent. If we imagine the efferent vessels of the outer lamella as ending blindly above, and give them many cross connections with those of the opposite lamella, we have practically the arrangement found in *Atrina*, although the gills of the two forms differ considerably in other respects. As regards circulation the gill of *Atrina* is therefore intermediate between those of *Cardium* and *Pecten*, but is more nearly like *Cardium*.^a

RESPIRATORY CURRENT.

The respiratory current in *Atrina* is remarkably strong. When specimens are as much as 6 inches below the surface a very considerable agitation of the water directly above them is perceptible when the respiratory current is running full force. In fact, the water fairly boils. The mantle, being open, may admit water at any point ventral to the inter mantle septum and it is expelled dorsal to this structure. While the respiratory current is flowing the edges of the mantle are brought quite close together, so that objects of any considerable size are prevented from entering the mantle chamber. It was found difficult to get admission even for powdered carmine. The sensory tentacles detect solid objects in the water and the mantle closes, preventing their entrance. When one shell is partially removed and the mantle lobe folded back the respiratory current within the mantle chamber can sometimes be seen. Powdered carmine shows strong

^a Bonnet describes a different circulation for the gill of *Pinna nobilis*, a form so closely related to *Atrina* that one would expect to find no fundamental differences in the circulation. Menegaux finds the work of Bonnet incorrect. His description of the anatomy of the gill for *Pinna* agrees very closely with mine for *Atrina*, but he gives a different description of the course of the circulation through it. I am inclined to think they are the same.

currents sweeping anteriorly in the ventral part of the mantle chamber, turning dorsally between and over the outer surface of the gills. The inflow of the water seems to be due in part to the action of the fine cilia of the inner surface of the mantle, but the gills, much of whose inner and outer surfaces are ciliated, are evidently the seat of the great pulling force.

FOOD-BEARING CURRENTS.

The respiratory current entering the mantle chamber carries with it many small objects in suspension, including minute living organisms. These are not allowed to pass through the gills, but are filtered out and passed in slow moving currents toward the mouth. These food-bearing currents are easily followed when powdered carmine, suspended in water, is dropped upon the gills. The particles of carmine are seen to move outward to the free border of the gill, where they enter the longitudinal groove in its edge and pass toward the anterior, finally reaching the palps, between which they continue to the mouth. These respiratory currents and food-bearing currents have long been known, and they seem to be much the same in all lamellibranchs. It was thought until recently that so long as water was flowing into the mantle chamber the lamellibranch had no choice but to receive the food, strained from it, into its digestive tract. In 1900 J. L. Kellogg (7) showed that when food was not desired it could be turned aside in the palps and deposited by them into backward-moving currents in the mantle, through which it was carried directly or indirectly to the exterior. Stenta (14), working independently upon many forms, including *Pinna*, came to the same conclusions. In *Atrina* I found the food-bearing currents turned aside at about the middle point of the palps at the anterior end of the corrugated portion. Here it moves outward to the edge of the palps and then posteriorly to their tips, where it leaves them to enter the ciliated canal of the mantle, which transports it to the exterior. Whether lamellibranchs can exercise choice in their food, accepting only the part which is desirable, is not known. C. Grave (3) compared the contents of the digestive tract of oysters with diatoms found in the water above their beds and came to the conclusion that they have the ability to choose. J. L. Kellogg read a paper before the American Society of Zoologists in December, 1909, in which he stated that it is not the nature of the food but the quantity of it which causes lamellibranchs at times to reject it. When great quantities of food material are carried to the palps by the gills they reject it. In this case it passes outward in the grooves of the corrugated portion of the palps to their outer borders and then posteriorly to their tips. It then enters the backward-moving currents in the mantle chamber and is expelled.

CIRCULATORY SYSTEM.

In order to get a good injection of the blood vessels it was necessary to narcotize the specimens. Otherwise they would contract to such an extent as to make the relation of the parts unintelligible. This was done by placing them in a large pan of sea water and adding alcohol slowly until dead, which required from six to eight hours. By this means they remained expanded and the vessels were relaxed sufficiently to allow easy penetration of the injecting fluid.

ARTERIAL SYSTEM.

The arterial system is not bilaterally symmetrical, so that a description of the arteries of each side will be necessary.

The heart lies in the pericardium just anterior to the adductor muscle and mantle gland. It consists of a heavy walled ventricle and two thin walled auricles. (Fig. 17, *h*, pl. XLIX.) The latter are elongated in the direction of the longitudinal axis of the body and are attached at one extremity to the tissue covering the retractor muscle and at the other to the adductor. They receive the blood from the gills through a short tube which lies external to the retractor muscle. (Fig. 17, *t*, pl. XLIX, and text fig. 9, *a*.)

The ventricle is a saddle-shaped structure into which the auricles open on either side. It gives off an anterior and a posterior aorta. The latter soon gives rise to a large branch which passes dorsally to the right of the rectum and enters the mantle. This artery divides into two equal branches at the posterior dorsal angle of the mantle, one branch going to the right mantle lobe, while the other goes to the left.

The arteries of the left mantle are represented in figure 17, plate XLIX, the right mantle lobe having been removed and its artery being therefore shown cut off. The mantle artery branches very profusely. It will be noted that there are two parallel arteries connected by numerous anastomoses. The outer and smaller of the two is distributed to the edge of the mantle, the other branches mostly in the opposite direction, and supplies the greater part of the mantle. This posterior mantle artery meets and joins with a similar one from the anterior end of the body.

The posterior aorta gives rise to a second branch, which is distributed to the rectum and mantle gland, then, bending abruptly ventrally, it enters the adductor muscle. A small branch continues over the anterior face of the adductor and goes to the region of the visceral ganglia and kidneys. (Fig. 18, pl. XLIX.)

The anterior aorta is much the larger of the two. On the right side (fig. 17, pl. XLIX) it gives rise to five branches which go to the reproductive organ and liver. Three small branches go to the dorsal part of the mantle where they spread anteriorly and posteriorly in the midline. At the anterior end of the visceral mass the aorta gives off a branch which passes forward over the anterior retractor muscle. Three arteries arise from this branch; one to the outer palps, one to the middorsal line of the mantle, and one to the anterior adductor muscle. It then passes over the anterior adductor and at the extreme anterior end of the body divides into two equal branches, one of which goes to the right mantle lobe and the other to the left. These two branches join with the similar mantle arteries which arise from the posterior aorta.

The aorta after giving off the artery, which has just been described as passing above the anterior retractor muscle, bends ventrally and divides into a number of arteries which are distributed to the inner palps and byssal apparatus and foot. Those which go to the byssus are paired, right and left; but those to the left side are not represented in the figure.

The arteries given off from the aorta on the left side of the body are represented in figure 18, plate XLIX, and are three in number. All three are distributed to the digestive

tract, to some extent, as well as to the reproductive organ and liver. The middle one lies deep within the visceral mass and follows closely the coils of the intestine. The most anterior one, besides giving branches to the stomach and liver, gives one to the byssal apparatus and posterior retractor muscles of the foot (fig. 18, *a*, pl. XLIX). Other arteries shown in this figure have already been described as belonging to the right side of the body. The main branches of the arteries are constant in number and portion, but the smaller ones are not so constant. There is so much variation in these as to be confusing to one who is studying them. The figures were drawn after dissecting several specimens, so that they may fairly be considered typical.

VENOUS SYSTEM.

The venous system, unlike the arterial, seems to be absolutely symmetrical, so that a description of one side will suffice for both. The venous blood enters the kidney from the visceral mass through a large vein which runs diagonally over the surface of the posterior retractor muscle of the foot. This vein brings blood from nearly all parts of the body, including the foot, byssus, liver, reproductive organ, and digestive tract. (Fig. 19, *v*, pl. XLIX.) There is no venous sinus below the pericardium into which the blood collects previous to entering the kidney. The blood enters the kidney, as stated above, through a large vessel which breaks up into a closed capillary system. After bathing the glandular cells of the kidney the blood is collected into a large vein which transports it to the gills to be aerated.

The blood from the adductor muscle, and probably also the mantle gland, drains into a sinus located on the ventral surface of the adductor. This sinus communicates with the vein to the gills on each side just as it emerges from the kidney, and hence the blood from the adductor and mantle gland does not enter the kidney, but goes directly to the gills. Since this sinus communicates with both sides it is possible to inject the veins of both sides from one point.

Besides the sinus just mentioned there is another at the base of the foot. Those organs which are extended by blood pressure therefore have sinuses in their immediate vicinity.

After traversing the gills the blood is returned to the heart by two vessels, one of which lies in the suspensory membrane and carries the blood from the anterior half of the gills, the other bears the same relation to the posterior half of the gills as the first to their anterior portion. These two vessels flow together to form a single short wide tube which runs at right angles to them and communicates with the auricle. This tube lies just anterior to the adductor muscle and runs over the outer surface of the retractor muscle. (Text fig. 9, and fig. 16, pl. XLVIII.) Just before entering the auricle it receives a vein from the mantle. The latter is formed by the union of two mantle veins, one from their anterior and the other from their posterior portions.^a

^a A number of small vessels from the palps enter the distributing vessel of the gills. The direction of the flow of the blood in these vessels was not determined, but it is probably toward the gills. They may therefore be considered as part of the venous system.

It will be noted that the blood which goes to the mantle passes through one capillary system before returning to the heart, that to the adductor and mantle gland passes through two, while that to the body proper passes through three, viz, those of the body, kidney, and gill. In this respect as well as in general plan the circulation seems to be similar in many lamellibranchs. The walls of the veins in general are not so well defined as those of the arteries. When a starch mass which had been strained through fine bolting cloth was injected into the veins, it soon spread out among the tissues, showing that the blood is not confined in a closed system of vessels. The arteries, however, divide into extremely small branches, so that it was impossible to force the injection mass to their ends.

ADDUCTOR MUSCLES.

There are two adductor muscles, the anterior of which is small and practically useless so far as could be made out. The posterior adductor is large and powerful and is situated near the middle of the shell. It is composed of two distinct kinds of fibers as indicated by a difference in color. The ventral two-thirds is darker than the dorsal one-third. No attempt was made to distinguish physiological differences in these parts, but various opinions have been given. Von Jhering (15) experimented upon *Pecten* to determine the difference in function of the two kinds of fibers. He cut the dark portion and found that the remaining white portion contracted only very slowly, but it prevented the valves from opening widely under the influence of the hinge ligament. He next cut the white portion of another specimen and found that the remaining dark portion was capable of very rapid contraction, but it could not hold the valves closed for any considerable time. It also allowed the valves to gape widely. He therefore concluded that it is the function of the white portion to keep the valves from gaping widely and to hold them closed for a long time when occasion demands. The dark portion, according to his view, is the real muscle to which the contractions are due. J. L. Kellogg (7) holds the opposite opinion, that it is the white portion which is contractile, and that the dark part is for the purpose of keeping the valves tightly closed.

In *Atrina* the mantle muscles are white and are capable of rapid contraction, while the anterior adductor and foot retractor muscles, which are also white, scarcely contract at all. The white muscle fibers of lamellibranchs may therefore be quick or sluggish in their contractions. Von Jhering is the only investigator who has isolated the two kinds of fibers to test them, and his results seem conclusive, although Pelseneer (11) and Kellogg have opposed his view.

RETRACTOR MUSCLES OF THE FOOT.

There are two pairs of foot retractors, one posterior and the other anterior. The latter is so situated that the foot would be extended by its contraction rather than retracted, but it is customary to call this pair of muscles retractors. As a matter of fact none of these muscles has any considerable power of contraction. Their function seems rather to be to support the body. They suspend it in the manner of a hammock.

(Fig. 19, pl. XLIX.) The anterior retractors are cylindrical and composed of white fibers. At one end they are inserted into the anterior surface of the foot, while at the other they are attached to the shell just posterior to the anterior adductor muscle. (Fig. 19, *ar*, pl. XLIX.) The posterior retractor muscles appear large in the drawings, being attached at one end to the base of the foot and at the other to the shell just anterior to the posterior adductor muscle. (Fig. 19 *pr*, pl. XLIX.) This structure in reality consists of two parts, the byssal apparatus and the muscle proper. These retractor muscles have become very much reduced. They no longer serve to retract the foot, but have taken on a new function, that of supporting the byssus.

VISCERAL MASS.

The main body of the visceral mass is approximately cone shaped, with the apex at the anterior end. It is slightly flattened dorso-ventrally and at the posterior end there is a slender horn which projects back below the pericardium between the posterior retractor muscles. Its hindermost extremity rests upon the adductor muscle. (Fig. 18, pl. XLIX, and fig. 9, *m*.) The visceral mass includes the digestive and reproductive organs. The liver, which surrounds the stomach, fills the anterior part. The reproductive organs fill the remainder of the space not occupied by the coils of the intestine. The sexes are separate and are easily distinguished by the color of the reproductive organ, which shows through the thin body wall. The testis is white, as shown in figure 16, plate XLVIII, while the ovary is orange red. The main duct, which carries the reproductive elements to the exterior, opens into the kidney very near the renal aperture. (Fig. 6, *g*.) Fertilization of the eggs takes place after they are extruded into the water.

FOOT AND BYSSUS.

The foot is cone shaped and is attached to the anterior end of the visceral mass. At its base a large opening, from which the byssus protrudes, is to be found. (Fig. 16, pl. XLVIII.) From this point a groove extends along the ventral surface of the foot to a point near its tip. (Fig. 15, *g*.) The byssal gland is situated in the floor of this groove and is continued back of the foot into the posterior retractor muscles. The foot can be protruded, and it is probably of service in attaching the byssus.

KIDNEY.

The kidneys are two in number, and each consists of a glandular and a nonglandular portion. They lie between the gills on the ventral side of the body, just anterior to the abductor muscle. They hang down into the central suprabranchial chamber as two dark colored bags and are very conspicuous organs, requiring no dissection to expose them. (Fig. 20, K, pl. L.) Each is in open communication with the pericardial chamber above and each opens below into the suprabranchial chamber by a large tube, which ends at the summit of a papilla. The glandular portion forms the prominent sac mentioned above and lies about midway between the two extremities of the kidney. For convenience of description the kidney may be divided into three portions: First, a

tube (*a*, fig. 6) which opens into the pericardium; second, a short tube (*b*) which opens to the exterior; third, a central pouch (*c*) into which the tubes *a* and *b* open at their inner ends. This central pouch is large and irregular in shape. One branch of it extends upward over the posterior retractor of the foot and ends beneath the pericardium. (Fig. 6, *e*.) This portion of the kidney is probably homologous with a kidney-like organ which Grobben (5) found in a number of lamellibranchs extending as a fold into the pericardium and connected below with a large sinus, which he believed to belong to the kidney. In *Atrina* it is plainly a branch of the main kidney.

The glandular portion (fig. 6, *h*) is located at the posterior and outer end of the main pouch. It is quite extensive and is colored dark brown on account of the reddish brown excretory material which is inclosed by its cells. All other parts of the kidney appear colorless and thin walled.

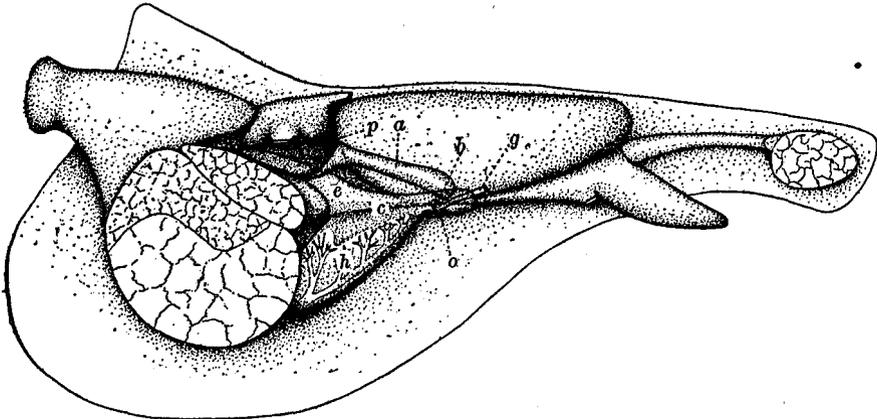


FIG. 6.—Drawing of the kidney in position, showing three well-marked parts, a tube (*a*) opening into the pericardium, a tube (*b*) opening to the exterior, and a large central pouch (*c*) into which tubes *a* and *b* open at their inner ends; *e* represents a prolongation of pouch *c* which extends upward beneath the pericardium; *g*, the genital duct; *h*, the glandular portion of the kidney; *p*, the pericardium.

It will be noticed that this kidney differs considerably from the usual type, which is typically a coiled tube. In the form under consideration it may once have been a true coiled pouch. Its transformation may have come about by the fusion of the two branches of the central loop to form the single large pouch.

While working with living specimens I frequently saw quantities of yellowish-brown material expelled from the kidneys. When examined under the microscope this material proved to consist of very numerous vacuolated cell-like bodies, which were filled with yellowish-brown or reddish-brown globules of excretory matter. Each excreted body had a tuft of extremely long cilia which were still active. (Fig. 7.) After collecting and fixing some of this excreted matter I stained it with iron-alum hæmatoxylin to see if there were nuclei present. None were found and I believe that none are thrown off. Paraffin sections of the glandular portions of the kidney show the epithelial cells to be greatly vacuolated and filled with this excretory matter. (Fig. 8.) The vacuole is located in the outer end of the cell and there is very little protoplasm

surrounding it. The nucleus is seen in the basal end of the cell and is surrounded by dense protoplasm. Certain cells show a constriction below the vacuole, as if they were in process of being divided. Other cells show this process farther advanced, and appear as if they were drawn out by some force which was stretching them into two. The nuclei in these cells are to be seen in the basal half, and it appears also that very little cytoplasm is thrown off with the vacuole. This method of excretion, although uncommon, is not especially wasteful, as would appear from the statements of investigators who have written upon this subject and maintained that the entire cells are excreted in the mollusks studied by them. Of course this may take place in some; but excretion in *Atrina* is not of that wasteful character.

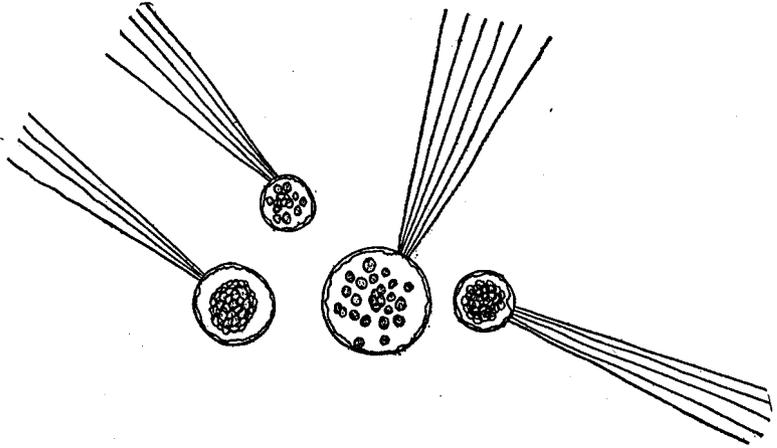


FIG. 7.—Bodies excreted from the kidney, formed by the pinching off of the vacuolated tips of the cells. Note the tuft of long cilia on each and the concretions of waste material within the vacuole.

DIGESTIVE TRACT.

The stomach is a large asymmetrical pouch which adheres closely to the dorsal wall of the visceral mass. On the left side it is attached to the ventral wall by a strand of muscle tissue. The ducts of the liver open into it at two points, one on the right and one on the left. (Fig. 9, *d*.) A part of the epithelium lining the roof of the stomach is differentiated as a conspicuous gland which forms a prominent ridge within the cavity of the stomach. The anterior end of the crystalline style adheres closely to this gland.

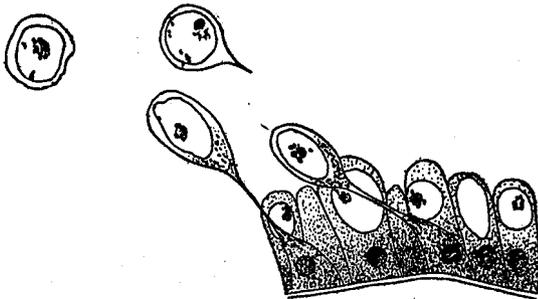


FIG. 8.—Section of the glandular portion of the kidney showing the formation and excretion of vacuoles by constriction.

The intestine originates at the posterior end of the stomach and passes to the extreme posterior end of the visceral mass, where it bends sharply to the right and passes anteriorly as far as the stomach. It then makes a large loop and again passes posteriorly, traverses the ventricle and mantle gland, to end behind the adductor muscle (Fig. 9.)

The part of the intestine nearest the stomach possesses a feebly developed typhlosole, while the remainder has it very strongly developed. A large crystalline style lies in

the part of the intestine which has the typhlosole feebly developed. This crystalline body is largest near the stomach and tapers gradually to a point and ends just beyond the first bend of the intestine, where the typhlosole becomes prominent. The latter structure is much swollen and gelatinous at this point, so that it almost obliterates the cavity of the intestine.

Several theories have been advanced to explain the nature of the crystalline style. Mytra (10) seems to have shown pretty conclusively that it contains an enzyme which will digest starch. He thinks it is a secretion from the liver. Pelsener (11) has held for a long time that its function is that of protection. He thinks it forms a protective coat for the intestine and surrounds rough particles of sand and diatom shells which might otherwise injure the delicate tissues. I find a structureless coat or cuticle of

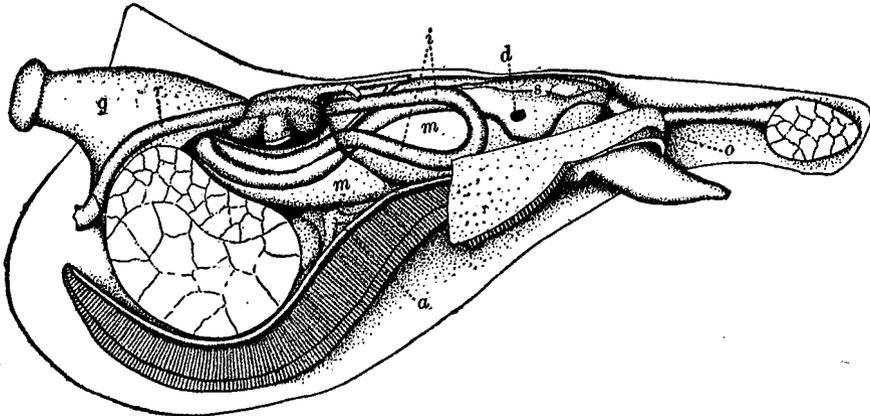


FIG. 9.—Drawing of the digestive system in position. *g*, Mantle gland; *m*, visceral mass; *o*, mouth; *s*, stomach; *d*, opening of liver ducts into stomach; *i*, intestine; *r*, rectum.

some kind lining a considerable part of the wall of the intestine. This may be formed from the crystalline style and may serve to protect the epithelial lining of the intestine.

NERVOUS SYSTEM.

The central nervous system consists of three pairs of ganglia which are connected by nerve tracts, or commissures, in the usual way. One member of each pair of ganglia is situated on the right side of the body and the other directly opposite it on the left. Each ganglion supplies nerves to tissues situated on its own side of the body only, and since those of the right and left are alike in number and distribution they will be described as coming off in pairs. The pedal ganglia are fused more or less to form a single mass, but the line of separation is plainly discernible. (Fig. 10, *pg.*) They are situated at the base of the foot and they give off three pairs of nerves posteriorly which are distributed to the byssal apparatus and retractor muscles of the foot. They also give rise to one pair of nerves from their lower anterior surfaces, which penetrate the foot.

The cerebral ganglia are situated wide apart, there being one on each side of the esophagus. They are connected by a nerve ring which passes over the esophagus. (Fig. 10 and 12, *cc*.) They give off a number of nerves, usually seven pairs, to the palps. A very large nerve leaves the anterior end of the ganglion and passes parallel to the cerebral connective for a short distance and then bends outward and enters the mantle. Just before it enters the mantle it gives off a branch, which continues forward for a short distance above the anterior retractor muscle of the foot. This branch then bends outward and ventrally, penetrates the tissue of the retractor muscle, from which it finally emerges and enters the anterior adductor. (Fig. 12.) The mantle nerve having entered the mantle divides into a number of branches, all of which unite with the circumpallial nerve, to be described later. Each cerebral ganglion communicates with the corresponding pedal ganglion by a short, thick connective. A complete nerve ring is thus formed around the esophagus. (Fig. 10.)

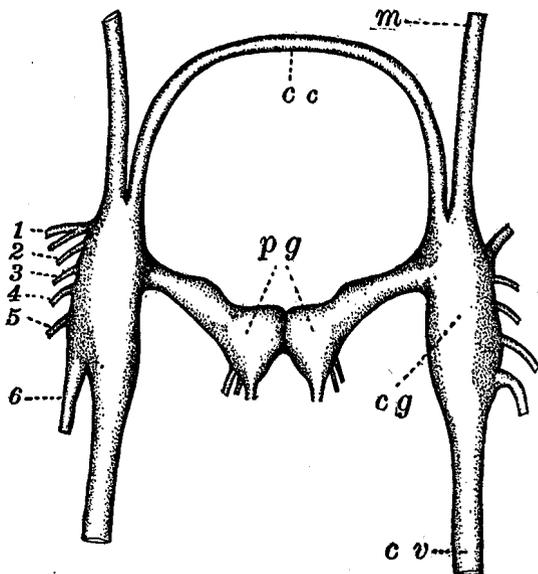


FIG. 10.—Drawing of the cerebral and pedal ganglia with their connectives. *cg*, Cerebral ganglion; *pg*, pedal ganglia; *cv*, cerebro visceral connective; *cc*, cerebral connective; *m*, nerve to mantle and anterior adductor; 1, 2, 3, 4, 5, and 6, nerves to the palps.

The visceral ganglia are situated on the ventral face of the adductor, just posterior to the kidney. They lie near together and are connected by a very thick commissure which contains many nerve cells. (Figs. 11 and 12, *vg*.) A large cerebro-visceral connective passes through the kidney and visceral mass between the cerebral and visceral ganglia. (Fig. 12, *c*.) The visceral ganglia give off four pairs of nerves to the posterior, which pass over the ventral surface of the adductor. (Fig. 19, 1, 3, 3, and 4.) Three of these finally bend outward and enter the mantle. Their course in the mantle may be seen in figure 12, 1, 2, and 3. Most of the branches of these nerves unite with the circumpallial nerve, but a few from the most anterior of the three lose themselves in the tissue of the mantle. The fourth pair of nerves, described above as lying on the ventral surface of the adductor, does not reach the mantle, but passes near the rectum and enters the muscles of the mantle gland. Judging from their close connection with the

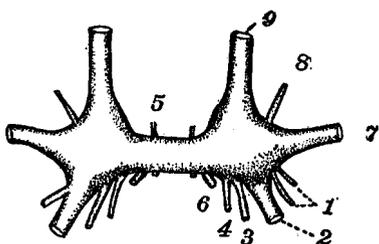


FIG. 11.—Drawing of the visceral ganglia. 1, 2, and 3, nerves to the mantle; 4 and 5, to mantle gland; 6, to adductor; 7, to gills; 8, to kidneys; 9, the cerebro visceral connective.

muscles of this organ, one is led to believe that they are distributed to the muscles only. Another pair of nerves which arises from the visceral connectives (fig. 11, 5) passes on the surface of the adductor in the opposite direction from those just described and enters the tissue of the mantle gland. These nerves are most likely distributed to the glandular

portion of this structure, since they do not seem to be closely associated with muscles. The other nerves which belong to the visceral ganglia are the following: A pair of large nerves which penetrate the adductor muscles (fig. 11, 6), a large pair to the posterior portions of the gills (fig. 11, 7), and a pair of very small nerves (fig. 11, 8), which are distributed to the kidneys. I have been unable to find the nerves to the anterior part of the gills. These nerves, however, arise from the visceral ganglia, as can be proven by experimental methods. If the gills are isolated from the cerebral and pedal ganglia by cutting all possible connectives, they will still contract when the posterior part of the mantle is stimulated. The anterior part of the gills will contract under these conditions, even after the large nerve to the posterior part of these organs has been cut. It is therefore evident that the nerve supply of the gills comes entirely from the visceral ganglia.

The circumpallial nerve lies near the edge of the mantle, to which it gives off numerous small nerves. (Fig. 12, *cp*.) It runs entirely around the mantle, passing across the mid line at either end, and thus forms a complete ring. Although it seems to contain

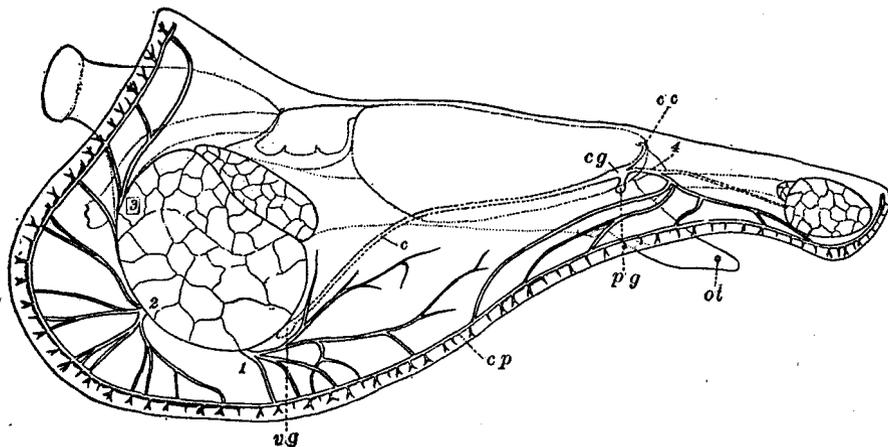


FIG. 12.—Drawing to show distribution of mantle nerves. *cg*, Cerebral ganglion; *pg*, pedal ganglion; *cc*, cerebral connective; *c*, cerebrovisceral connective, *cp*, circumpallial connective; 1, 2, and 3, mantle nerves from the visceral ganglion; 4, mantle nerves from the cerebral ganglion; *ot*, otocyst.

many nuclei it has no motor nerve cells. If the nerves from the cerebral and visceral ganglia are cut the mantle is paralyzed. The nuclei which might be mistaken for nerve cells probably belong to the nerve sheath.

A number of experiments were performed to determine which parts of the body are supplied with nerves from each ganglion. The experimental and anatomical evidence agree and there seems to be little if any overlapping. Each ganglion seems to supply its own definite regions of the body. The visceral ganglion controls the posterior part of the mantle, posterior adductor muscle, gills, mantle gland, and kidneys. The cerebral ganglia control the anterior part of the mantle, the palps, anterior adductor, and anterior retractor muscles. The cerebral and pedal ganglia together control the foot, posterior retractor muscle, and byssus. The nerves to the viscera and heart were not discovered. A more complete account of the experimental study of the nervous system of this form is given in a paper published in the Johns Hopkins University circular for June, 1909 (4). The most interesting feature of this work was the discovery of reflexes. For example,

when the mantle is stimulated gently opposite the anterior end of the gills, the anterior part of the gills contract, while the posterior part of these organs remains quiet. A stronger stimulus causes the whole of the gills, as well as other parts, to contract.

SENSE ORGANS

OTOCYSTS.

The otocyst in *Atrina* is located very near the tip of the foot and has therefore a very unusual position. (Fig. 12, *ot.*) It varies greatly in size in different specimens and may be a degenerating organ. In some specimens it was found to be an extremely

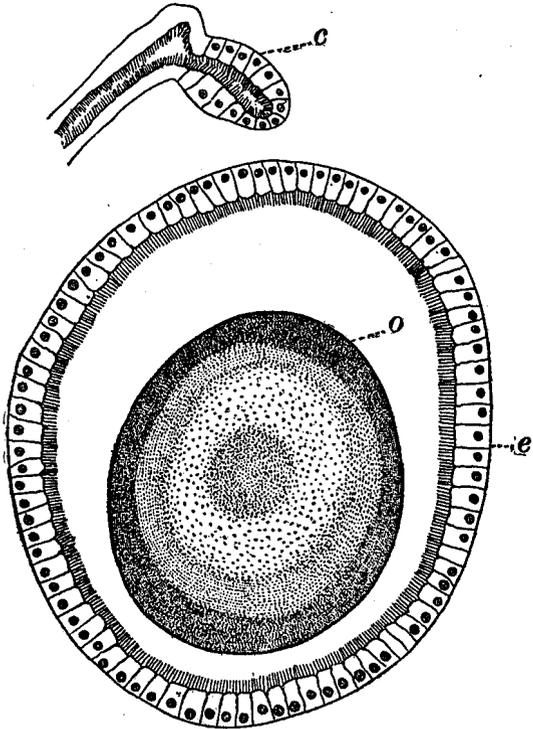


FIG. 13.—Drawing of a transverse section of one lobe of the otocyst, outlined with a camera lucida. *c*, Ciliated tube connecting the otocyst with the exterior; *e*, ciliated epithelium forming the wall of the otocyst; *o*, otolith showing concentric structure.

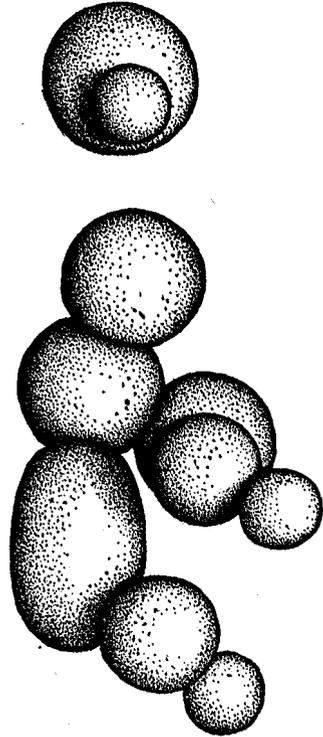


FIG. 14.—Reconstruction of the compound otocyst from a series of sections.

small sac lined by ciliated epithelium containing no otolith. In others it is a large lobed structure with an otolith in each lobe. The otoliths (fig. 13, *o*) show a concentric structure. Figure 14 represents a reconstruction of the otocyst from a series of sections, and shows that in this specimen there were two or three otocysts in place of one, the usual number. There are three ciliated canals leading in toward the otocysts from the outside and although they could not be traced into the otocysts they came so near that there is scarcely any doubt but that they are the tubes formed by the invagination of the ectoderm, which gave rise to the otocysts. (Figs. 13 and 15, *c*.) The evidence indicates therefore that there are three otocysts in this specimen formed by independent

invaginations of the ectoderm. Some of the numerous lobes seen in figure 14 were formed by division of the original otocysts. Some of the lobes are completely separate from the rest while the cavities of others communicate with those of their neighbors. If there is a nerve connected with the otocyst, it was not discovered.

OSPHRADIUM.

The osphradium consists of a small patch of sensory epithelium situated directly ventral to the visceral ganglion at the origin of the branchial nerve. (Fig. 20, *o*, pl. L.)

It is large enough to be seen without magnification and appears to be colorless. When examined under the microscope, however, its cells are seen to contain a yellow pigment. Nerve fibers are distributed to the osphradium from a ganglionic mass which surrounds the base of the branchial nerve. This nervous tissue appears to be a part of the visceral ganglion, but Pelseneer insists that the osphradium receives its nerve supply from the cerebro-visceral commissure and hence from the cerebral ganglion. I have no preparations to show that this is the case. This sense organ is said to be used for testing the purity of the water, whatever that may mean.

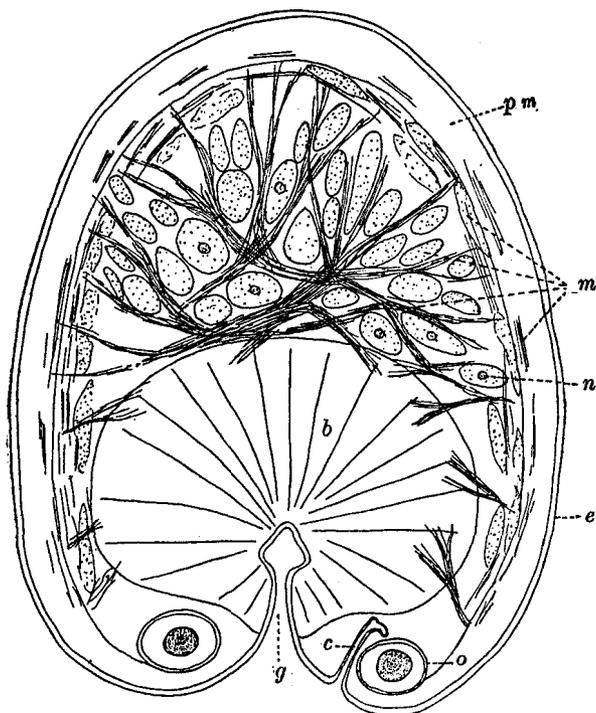


FIG. 15.—Drawing of transverse section of the foot showing the position of the otocyst. (Outlined with camera lucida.) *b*, Byssal gland; *g*, ventral groove in the foot; *m*, circular and transverse and longitudinal muscles; *n*, nerves; *o*, otocyst; *c*, ciliated tube which has given rise to the otocyst by invagination from the ectoderm; *p m*, undifferentiated mesoblast.

SUMMARY.

1. The arterial system of the two sides is not symmetrical, as may be readily seen by a comparison of figures 17 and 18, which represent the arteries of the right and left sides, respectively.

2. The venous system lacks the "sinus venosus" which is commonly present in lamellibranchs and which receives the blood from all parts of the body previous to entering the kidney. This sinus or a substitute for it is a necessary part of the mechanism described by Menegaux for extruding the foot and other organs whose movement is due to blood pressure.

3. The blood in traversing the kidney passes through a closed capillary system.

4. The blood which enters the gills must pass through a capillary system before emerging again.

5. There is no pallial line but the mantle is attached to the shell at a single point just ventral to the adductor muscle. As a consequence the mantle can be withdrawn a considerable distance from the edge of the shell. After being contracted the mantle again reaches the edge by creeping outward upon the shell.

6. The spines on the outer surface of the shell are formed by little tongues of the mantle which creep out into them during their growth period.

7. The mantle gland which Menegaux calls the "appendice" is probably a "swab" for keeping the mantle free from dirt.

8. The kidney excretes vacuoles containing quantities of concretions, but little protoplasm and no nuclei are thrown off.

9. Each ganglion supplies a definite region of the body and there is little overlapping. Reflex arcs were shown to exist.

10. The otocyst is located in the end of the foot far from the pedal ganglion and is a variable structure, sometimes consisting of as many as eight lobes and sometimes of only one. In one instance three separate ciliated tubes connecting them with the outside were discovered. This indicates that they have arisen from three separate invaginations of the ectoderm. This is the first instance of this sort found in lamellibranchs above the Protobranchia.

BIBLIOGRAPHY.

1. BONNET, R.
Der Bau und die Circulationsverhältnisse der Acephalenkieme. *Morphologisches Jahrbuch*, bd. 3, 1877, p. 283-322.
2. DREW, G. A.
The habits, anatomy, and embryology of the giant scallop (*Pecten tenuicostatus*, Mighels). *University of Maine Studies*, no. 6, September, 1906, 71 p., 17 pl.
3. GRAVE, C.
Investigations for the promotion of the oyster industry of North Carolina. Report U. S. Fish Commission 1903, p. 247-341, pl. 1-x, 1 map, 1905.
4. GRAVE, B.
Pinna seminuda. *John Hopkins University Circular No. 6*, June, 1909, p. 46-51.
5. GROBBEN, C.
Zur kenntniss der anatomie und morphologie von *Meleagrina* sowie der *Aviculidæ*. *Im Allgemeinen Denkschrift der k. Akademie der Wissenschaft, Mathematisch-Naturwissenschaftliche Klasse*, bd. 69, 1901, p. 487-496.
6. JOHNSTONE, J.
On the structure and life history of the common cockle, with an appendix on the Lancashire cockle fisheries. *Proceedings and Transactions of the Liverpool Biological Society*, vol. 14, 1900, p. 178-261, pl. 1-vi and map.
7. KELLOGG, J. L.
A contribution to our knowledge of the morphology of the lamellibranchiate mollusks. *Bulletin U. S. Fish Commission*, vol. 10, 1890, p. 389-436, pl. LXXIX-XCIV, text fig. 1-3.
The ciliary mechanism in the branchial chamber of the Pelecypoda. *Science*, n. s., vol. XI, 1900, no. 266, p. 172-173.

8. LACAZE-DUTHIERS.
Mémoire sur le développement des branchies des mollusques acephales lamellibranches. *Annales des Sciences Naturelles, Zoologie, sér. 4, t. 5, 1856.*
9. MENEGAUX, A.
Recherches sur la circulation dans les lamellibranches marines. Besançon, 1890, 291 p., 56 fig.
10. MITRA, S. B.
The crystalline style of Lamellibranchia. *Quarterly Journal of Microscopical Science, vol. 44, 1901, p. 591-602.*
11. PELSENEER, P.
Contribution à l'étude des lamellibranches. *Archives de Biologie, t. XI, 1891, p. 147-312, 2 fig., pl. 6-23.*
12. PECK, R. H.
The minute structure of the gills of lamellibranch Mollusca. *Quarterly Journal of Microscopical Science, vol. XVII, 1877, p. 43-66, pl. IV-VII.*
13. RICE, E. L.
Fusion of filaments in the lamellibranch gill. *Biological Bulletin, vol. II, 1900, no. 2, p. 71-80, text fig. 1-8.*
14. STENTA, M.
Zur Kenntniss der Strömungen im Mantelraum der Lamellibranchiaten. *Arbeiten aus den Zoologischen Institut der Wien, bd. 14, 1903, p. 211-240, 2 fig., taf.*
15. VON JHERING, H.
Ueber Anomia. *Zeitschrift für wissenschaftliche Zoologie, bd. 30, sup. hft. 1, p. 13-27, pl. II.*

EXPLANATION OF PLATES.

PLATE XLVIII.

Fig. 16. Drawing of a specimen natural size to show the relative position and appearance of the various organs. One shell valve, one mantle lobe, and the posterior half of the gills of one side have been removed. P A, posterior adductor; A, anterior adductor; C, posterior retractor of the foot; P, palps; G, gill; F, foot; B, byssus; M, mantle gland; R, rectum; K, the portion of the kidney which communicates with the pericardium; T, testis; D, ciliated canal of the mantle which carries débris from the mantle chamber.

PLATE XLIX.

Fig. 17. Drawing of the arteries of the right side of the body and of the left mantle lobe, the shell, right mantle lobe, gills, and kidneys having been removed. *h*, heart; *t*, tube which carries the blood from the gills to the auricle, here shown cut off just below the auricle; *v*, anterior aorta; *p*, posterior aorta; *m*, mantle artery; *g*, cerebral and pedal ganglia; *op*, and *ip*, arteries to the outer and inner palps, respectively.

Fig. 18. Drawing of the arteries of the left side of the body, the shell, left mantle, gills, posterior retractor muscles of the foot and kidneys having been removed; *m*, visceral mass; *a*, artery to the retractor muscles which have been removed. The distribution of the other arteries is easily made out in the drawing. Only the main trunk of the mantle arteries is shown here, but they are similar to those represented in figure 17.

Fig. 19. Drawing of the principal veins of the right side of the body, the shell, right mantle lobe, and gills having been removed. *pr*, posterior retractor muscle of the foot; *ar*, anterior retractor of the foot; *v*, the large venous trunk which enters the kidney and breaks up into capillariæ; 1, 2, and 3, veins from the foot and byssal apparatus, they receive blood from a large sinus which lies just at the base of the foot; *k*, the vein which gathers the blood from the kidney and carries it to the gills. It is here shown cut off at the point where it entered the gills.

PLATE I.

Fig. 20. Semidiagrammatic drawing of a specimen, ventral side up, to show the veins which enter the kidneys and those which emerge from them. The shell, part of the left mantle, and the gills of the left side have been removed. One kidney is cut open to show that the large vein upon entering the kidney breaks up into capillaries. F, foot; G, gill; G', the upper border of the reflexed lamella of the gill; K, kidney; O, osphradium; 1, 2, and 3, mantle nerves from the visceral ganglion which lies upon the adductor muscle at the posterior end of the kidneys; 4, nerve to mantle gland; V, vein entering the kidney (the same as the vessel labeled V in fig. 19); x, the vessel which carries the blood from the kidney to the gills; y, the vessel which receives the blood from vessel x and distributes it to all parts of the gill.

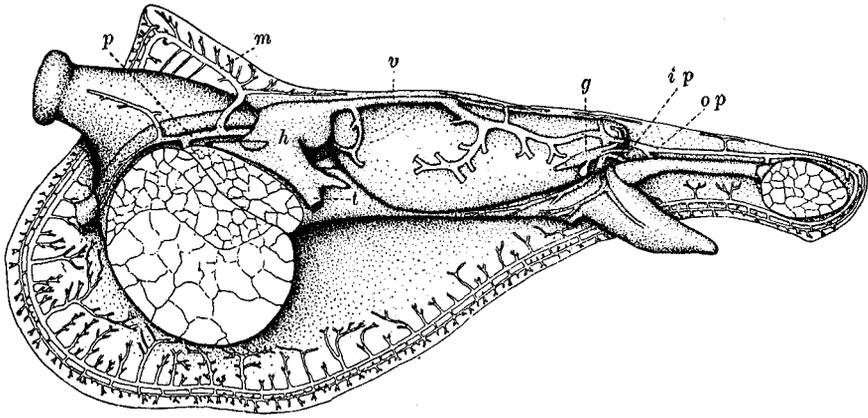


FIG. 17.

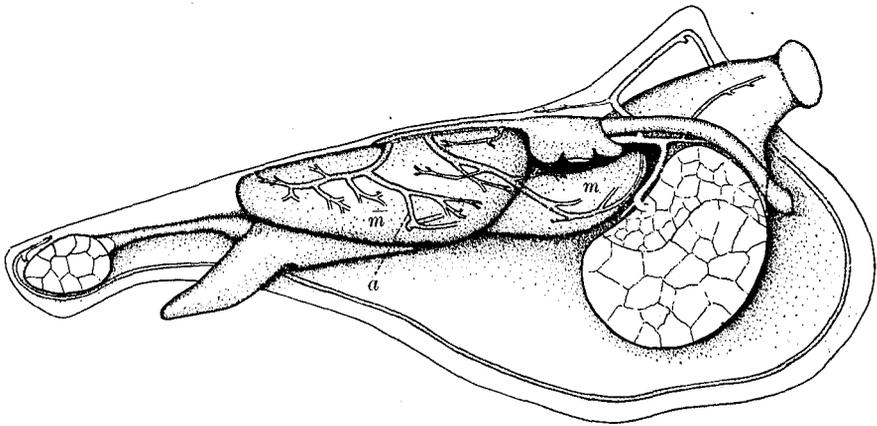


FIG. 18.

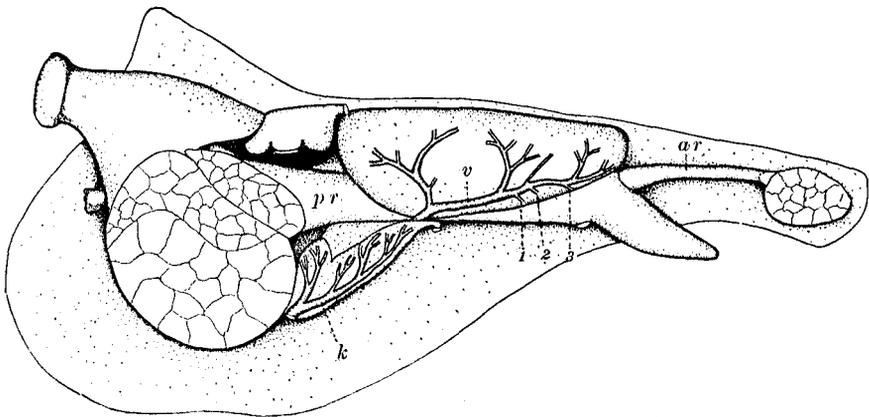


FIG. 19.

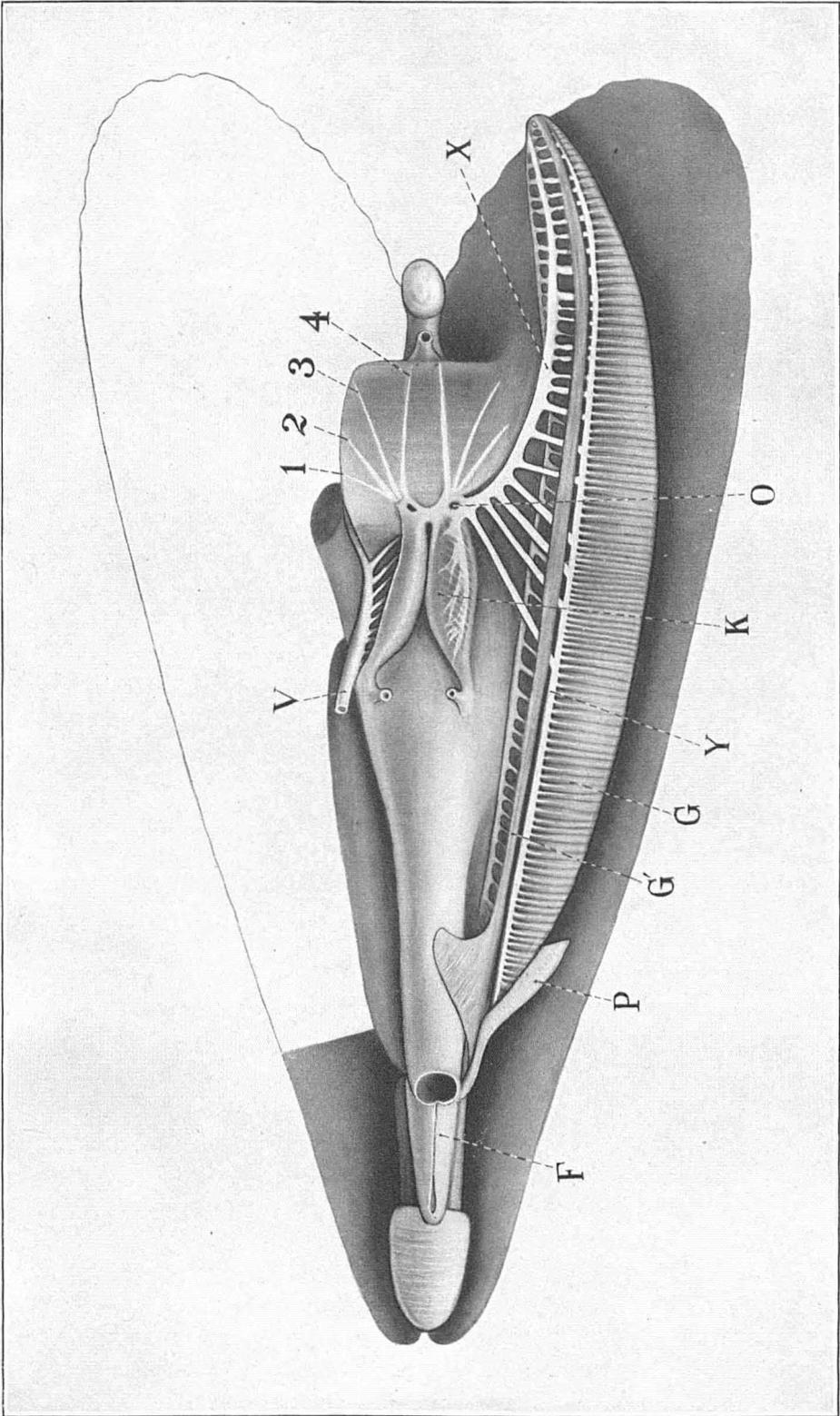


FIG. 20.