Univ. Iowa. Studies in Natural History 11(9):1-16 1926

A STUDY OF TRITOGONIA TUBERCULATA, THE PISTOL-GRIP MUSSEL

DAVID T. JONES

The incentive to study certain animals comes, not because of their utility, but because their uniqueness arouses curiosity. The blade-beaked skimmers (Rhynchopidæ), duck-billed platypus (*Ornithorhynchus*), the dog's head butterfly (*Zerene cæsonia*) are familiar examples. Among mollusks, the buckhorn or pistol-grip, *Tritogonia tuberculata* (Barnes), likewise never fails to arouse curiosity. Children wonder "what is the matter with it" and usually regard it as a freak. The noticeable feature about the shell is the surface, studded with protuberances which makes the name "pistol-grip" applicable. Call speaks of the surface as "nodulous," while Baker calls the prominences "tear-like pustules." Simpson[1] regarded this shell as peculiar enough to merit a separate genus *Tritogonia*. Ortmann[2] thinks it resembles the Quadrulas enough in internal anatomy to be called *Quadrula tuberculata* (Barnes). As to the pustulate surface, he calls attention to the fact that *Quadrula lachrymosa* (Lea), the maple-leaf is scarcely less pustulose. Walker,[3] however, as late as 1918, is content to let it remain aloof in its own genus *Tritogonia*.

Simpson gives two species and one variety of *Tritogonia* for the United States. In distribution *Tritogonia tuberculata* is confined to the Mississippi Valley and Gulf drainages. Call[4] gives its range as "Western New York to Minnesota, Iowa and Nebraska; to Kansas and central Texas; to Georgia and Alabama. The species was originally described from Wisconsin." In most older works it goes under the name *Unio tuberculatus* (Barnes), which name dates from 1823.

Economic reports on *Tritogonia tuberculata* for the most part consider it along with other shells. It is used to a certain extent

1 Synopsis of the Naiades, p. 608.

2 Families and Genera of the Najades, p. 254.

3 A Synopsis of the Classification of the Fresh Water Mollusca of North America, p. 45.

4 The Unionidæ of Arkansas, p. 55.

in the pearl-button industry. Coker[5] reports it as having "white nacre of good texture and quality, but is often spotted. It is thinnish at the tip and has a very rough back; some shells have a pinkish tinge." Baker[6] reports that the Salt Fork and Sangamon species (Illinois) are of good quality for buttons, and calls attention to the fact that "abnormalities and pearly growths due to injuries or parasitism are rare in specimens of this species examined." Call reports the nacre as usually white, but often blotched in large specimens with irregularly distributed, brownish spots. He says that more than half the specimens from the Cahaba River, Alabama, have purple nacre.

The following extracts from descriptions bring out the main features of the shell and animal.

Ward and Whipple[7]—"All four gills serving as marsupia. Shell large, solid, rhomboid, truncated posteriorly in the male, elongated with a strong posterior ridge, sexes dissimilar in shape, the posterior region being rounded or subcompressed in the female; hinge complete, surface pustulose, except on the extended portion of the female." Walker—"Epidermis dark olive, hinge plate rather narrow; pseudocardinals strong, rugged; laterals long and straight, near to the pseudocardinals." Simpson—"Well developed lunule filled with epidermal matter. . . . . Inner gills much larger than outer, generally free from abdominal sac."

The periostracum is thin and tough, not scaling readily; the prismatic layer thin, and the nacreous layer thick. All three layers enter into the composition of the nodules. On the inside of the shell the nacre is smooth showing no conformity to the rough exterior except slight undulations in the posterior region, and an arched furrow corresponding to the umbonal ridge. The latter is sometimes so great as to pull the mantle away from the shell, thus breaking the pallial line as in fig. 3. The nodules are irregular, but often elongate and pointed radially in the opposite direction from the beak. Back of the posterior umbonal ridge especially of the short shells, the nodules are extremely large and united in huge folds.

A good start has been made on the ecology of *Tritogonia tuberculata* in the Fisheries Bureau Report on "Natural History and

[5] Fresh-water Mussels and Mussel Industries, p. 27.
[6] Fauna of the Big Vermillion River, p. 33.
[7] Fresh Water Biology, p. 998.

Propagation of Fresh-Water Mussels[8]." There *Tritogonia tuberculata* is recorded as being found in sand, sand and gravel, gravel, mud and sand, soft mud over firm bottom, mud, and clay and sand. Authorities disagree as to which kind of bottom *Tritogonia tuberculata* prefers, some believing "mud" or "mud over firm bottom", while others believe "gravel". Drew[9] records it as common, especially on muddy bottoms. Baker found the largest specimens "on a mud bottom although it also lives on sand and gravel bottom." The specimens on which this article is based were brought up by the sand pump from the sand bed in Iowa River just south of Benton Street bridge at Iowa City, Iowa. Somewhere in the neighborhood of fifteen specimens were secured during the period from September through December, 1925. When rock and gravel were pumped up with the sand they seemed to be the most plentiful. They were thrown out very irregularly, more than half the number being secured on two days between which several weeks intervened. As the intake of the sand pump was swinging across the river in ever-lengthening arcs, this would hint at gregariousness. Single specimens were secured while the pumping was confined to the middle of the stream, but the two groups were struck when pumping was approaching shore, yet in deep water and current. Coker, Shira, and co-workers record *Tritogonia tuberculata* as occuring in little or no current, fair or good current, and strong or swift current. Two authorities think it prefers the second situation; one, the last. While *Tritogonia tuberculata* seems to prefer a current, it can live in still water. Of the group on which this article is based, one was kept alive from the latter part of September to the first of the following December in a vessel in which the water was changed once a day or once in two days. *Tritogonia tuberculata* outlived other species (*Quadrula plicata*, *Q. pustulosa*, and *Lampsilis gracilis*) kept under similar conditions. Of the other forms *Quadrula plicata* seemed to approach the endurance of *Tritogonia tuberculata*.

As this study was made in the fall there was no opportunity to observe glochidia for *Tritogonia tuberculata* is a summer breeder.[10] Simpson, quoting Kelly, in "Synopsis of the Najades" says that

[8] Coker, Shira, Clark, and Howard, p. 106.
[9] Unios of Iowa, Vol. 2.
[10] Coker and others. Natural History and Propagation of Fresh Water Mussels.

the form with the compressed shell, having the expanded flap behind, is the female. Very little seems to be known of the life history of this species. Coker, Shira, and associates give an illustration of a glochidium, and observed the growth made by a medium sized specimen from July 31, 1911 to Nov. 14, 1913 during which there was an increase in length of 0.36 inch. Baker, in Salt Fork at Homer Park, Ill., found large males 115 mm. long and females 145 mm. long, together with young specimens 46 mm. long.

Tritogonia tuberculata has been and is yet reported as common in regard to numbers throughout its range. In the region of Iowa City the following are the most common mussels in the order of their abundance, judging from what the sand pumps throw up and from the shell piles along the shore.

1. Quadrula plicata (*Q. undulata* is less common than *Q. plicata* and is usually not distinguished from it.)
2. Symphynota complanata
3. Lampsilis gracilis
4. Lampsilis ligamentina
5. Anodonta grandis
6. Quadrula pustulosa
7. Tritogonia tuberculata
8. Lampsilis ventricosa
9. Lampsilis anodontoides
10. Obliquaria reflexa
11. Plagiola donaciformis
12. Lampsilis alata
13. Quadrula trigona
14. Lampsilis capax
15. Pleurobema æsopus
16. Quadrula coccinea
17. Lampsilis recta—1 live specimen and 1 valve found
18. Quadrula metanevra—1 specimen—Coralville
19. Lampsilis subrostrata—1 specimen—near Amana
20. Quadrula ebenus—1 valve
21. Quadrula lachrymosa?—1 valve.

The following living mussels were thrown out of the same sand bed where the specimens of *Tritogonia tuberculata* were secured. These are given in the order of their abundance.

1. Quadrula plicata
2. Lampsilis gracilis
3. Anodonta grandis
4. Quadrula pustulosa
5. Tritogonia tuberculata
6. Lampsilis anodontoides
7. Quadrula trigona—1 specimen
8. Pleurobema æsopus—1 specimen.
9. Symphynota complanata—1 specimen.
10. Lampsilis recta—1 specimen.

Shimek's "Keys to the Mollusca of Iowa" were used in classification. Drew's "Unios of Iowa" Vol. 2, Coker's "Freshwater mussels and the mussel industries of the United States" and other articles were used as checks on identification.

I wish to thank Dr. Gilbert L. Houser and Dr. Frank A. Stromsten for the facilities provided in the laboratories of Animal Biology of the State University of Iowa where this study was made, as well as for the helpful suggestions offered.

Tissues for sectioning[11] were fixed in Bouin's picro-formol, Carnoy's fluid, Chrom-aceto-formaldehyde,[12] and Chrom-oxalic acid.[13] The paraffin method for delicate objects was used. All sections were cut 10 micra thick except one thick free-hand section through the edge of the mantle to show the calcareous bodies in the connective tissue. For a detailed study of cell structure it would be better to cut still thinner. Sections through the visceral mass were floated out in warm water immediately after cutting to prevent curling. Delafield's hematoxylin and erythrosin were used as stains, although mucin tests were made with thionin also. The calcareous nature of structures was tested by adding glacial acetic acid to freshly-stained sections and observing changes under the low power of the compound microscope. Permanent sections were cleared in

[11] See Guyer for technique unless specifically stated.

[12] Formula used in Laboratories of Animal Biology, S. U. I.

Chromic Acid, 1%	640 cc.
Glacial Acetic	40 cc.
Pure Formaldehyde	320 cc.
	1000 cc.

Wash out in water.

[13] Formula used in Laboratories of Animal Biology, S. U. I.

Oxalic Acid, 8% aq. sol.	800 cc.
95% Alcohol	600 cc.
Chromic Acid, 1% aq. sol.	600 cc.
	2000 cc.

Mix in the order as named.

xylol and mounted in balsam. Outlines of drawings of microscopic sections, except figures 8, 9, 14, and 21 were made by the aid of the projecting microscope. Figures 8, 9, and 14 were made under oil immersion.

The ligament in *Tritogonia tuberculata* extends from the beaks posteriorly about half the length of the hinge teeth. It is low, usually not rising above the level of the dorsal part of the valves. Anterior and posterior to the ligament lie the anterior and posterior lunules respectively. The former has more epidermal matter and is better developed. Both lunules and the ligament have a heavy outer layer corresponding to the periostracum of the valves.

The interior of each valve, if normal, is a mirror-image of the other, except for the teeth. The cardinal teeth, normally two in each valve, are large and jagged, the most anterior cardinal in the left valve being usually largest. The broad, smooth, flattened junction between the cardinals and hinge teeth is well developed in both valves. On the right valve it frequently bears a rudimentary third cardinal. There are two hinge teeth in the left valve and one tooth in the right. Of the former, the ventral tooth is usually highest in its posterior extent. The hinge teeth are quite straight but do not run parallel with the dorsal border of the shell.

Both anterior and posterior adductor scars are well impressed, the former being deeper. Continuous with its inner border is the scar of the anterior retractor pedis. The impression of the protractor pedis, immediately posterior to the anterior adductor, is especially deep. The posterior retractor pedis scar, near the dorso-anterior border of the posterior adductor, is very superficial.

The pallial line normally extends from the lower outer portion of the anterior adductor scar around to the outer border of the posterior adductor scar. It does not run parallel to the border, especially in the posterior part, but continues its oval course without following the posterior bulge of the margin. Some mantle vessel, probably the peripheral artery of the mantle, has impressed a groove in the nacre, starting where the pallial line meets the anterior adductor scar, then curving outward and running posteriorly close to and parallel with the margin of the valve. This groove becomes fainter as it proceeds posteriorly. A slight pearly ridge, obliquely dorsal to the depression which corresponds to the umbonal ridge is noticeable in some shells.

The mantle closely invests the inner surface of each valve. It is attached at the muscle scars by the piercing strands of the muscles, and at the pallial line also by muscular strands. The mantle is thin and barely transparent except the portion distal to the pallial attachment, which forms a thickened muscular edge. The right and left lobes of the mantle are fastened together between the two siphons in the region of the posterior termination of the gills. At the exhalant siphon there is little modification of the mantle, but at the inhalant the margin is much thickened, and the inner part is modified into papillæ, called siphonal tentacles or fimbriæ. These are most robust near the center of the siphonal opening. There are from seven to fourteen large fimbriæ on each side of the siphon and twice that many small ones. The two lobes of the mantle meet near the posterior ends of the hinge teeth. A thickened fold of the mantle (fig. 4x) lying dorsal to the hinge teeth continues as thin sheets over the hinge teeth of both right and left valves. Between the bases of the cardinal teeth the mantle is thickened, and again becomes very thin over the jagged portion of the cardinals.

The function of the mantle in secreting the shell is an interesting study. The edge of the mantle is modified, not only at the inhalant siphon, but to the lesser degree all around. In cross-section it shows an outer, a middle, and an inner lobe (fig. 11). The periostracum is secreted from a groove at the junction of the outer and middle lobes. This groove is lined ventrally by a mound of tall columnar epithelium and dorsally by cuboidal epithelium (fig. 13). The periostracum seems to come off of the latter as a secretion. The cells of this groove are not pigmented as is the neighboring epithelium. This apparatus makes an excellent histological study. Without using a lens the periostracum can be seen stretching over the outer fold to the edge of the valve, in specimens where the mantle has been undisturbed. The origin of the prismatic layer and nacreous layer is not so evident. Since the periostracum is the outer layer, and is laid down first, the other two layers would have to be formed by the outer lobe of the edge or the outer epithelium of the mantle. No histological evidence was found as to the origin of these two. Parker and Haswell make the statement that the prismatic coat is also formed by the edge of the mantle and the nacreous coat by the whole outer surface of the mantle. The outer epithelium consists of tall columnar epithelial cells (fig. 14) resting on a homogeneous basement membrane under which are the muscle cells and connective tissue. The inner epithelium is similar but contains more mucous cells, many of which are subepithelial (fig. 12). The inner lobe of the edge of the mantle contains much amorphous material which stains blue with hematoxylin. In the middle, connective-tissue layer of the mantle, large masses of granules calcareous in nature were found. These disintegrate least in thick sections.

A process, no less interesting than the activities of the mantle edge, is going forward in the region of the hinge teeth and cardinal teeth. Drew, in "Unios of Iowa", Vol. 1, gives sections through the teeth, showing the undulating layers of nacre deposited by the mantle. Coker and co-workers, in "Natural History and Propagation of Fresh-Water Mussels", say that hypostracum is laid down by the ends of the muscles in place of nacre. Since the muscles retain the same relative position on the shell during the life of the animal they must migrate to keep up with shell growth. Thus a layer of hypostracum extends in a tapering vein through the nacre from the beak to each muscle scar and to the pallial line. Considering the process of enlargement of the teeth by the mantle as going forward over these earlier deposits of hypostracum, the explanation of the growth of this part of the shell becomes as interesting as the marginal growth. It is interesting to note that the thickest part of the mantle, which is in the region of the inhalant siphon, produces the thinnest part of the shell. A fold of the mantle, covering the anterior ends of the gills and the liver, is contained in the umbonal cavity which in *Tritogonia tuberculata* lies under the flattened junction of cardinal and hinge teeth.

The outer gills are attached to the mantle. Keber's organ, a light brown body, lies along the mantle dorsal to the junction. The gills are generally considered as modified folds of the mantle. There are four gills, one pair on each side of the central, visceral mass. The outer gill in *Tritogonia tuberculata* is much shorter than the inner one, as shown in fig. 5. Each gill is composed of two lamellæ with an intervening series of water tubes. The lamellæ are connected by interlamellar junctions between water tubes. Each lamella is finely striated vertically on its outer surface by ridges and grooves. These ridges are the gill filaments. There are ten to the millimeter in one specimen studied. In this specimen, interlamellar junctions showed through the lamella so they could be counted from the outside. There were twelve of these to

one centimeter. Fig. 17 shows a cross section of the dorsal portion of the gills. The filaments cut in section are margined with ciliated epithelium. Spaces, called ostia, open between filaments and communicate with the water tubes. Thus water, admitted through the inhalant siphon, circulates from the mantle cavity through the ostia, through water tubes, to super-branchial chamber, and out at the exhalant siphon. Through the substance of the lamella and interlamellar junctions run many blood vessels. Schwanecke, in 1913, worked out the relations of these vessels in *Anodonta*. He finds that the venous net or reticulum lies vertically near the outer edge of the lamella and extends into each gill filament. The arterial net is represented by a vertical network of vessels near the water tubes. Between these two nets there are connectives. The larger arteries come in through the interlamellar junctions. Supporting rods are found in the filaments. In the dorsal portion of the gill, mucous material was found. Masses of mucous material seem quite common in the mantle and certain parts of the body. Sometimes they are amorphous, sometimes goblet cells, or long subepithelial mucous cells. The last case is best illustrated in the long subepithelial mucous cells in the ventral portion of the foot (fig. 16).

The visceral mass consists of two parts;—the visceral mass proper and the muscular foot which curves over the visceral mass ventrally and anteriorly. The foot in the *Tritogonia tuberculata* is narrower and projects more anteriorly than the foot in mussels of the *Lampsilis* type. A specimen kept in an aquarium quickly buried itself in the sand on the bottom when the water became stagnant, instead of pulling itself over the surface as *Lampsilis gracilis* and *Quadrula plicata* did. The foot in *Tritogonia tuberculata* seems to be very efficient, although it is less frequently protruded than in the Quadrulas. Above the foot is the visceral mass proper which in cross-section projects downward in longitudinal midline into the foot (fig. 21). Transverse muscles pass through the visceral mass from the muscles of the foot on one side to those on the other. Most of the visceral mass proper is composed of reproductive organs which give it a spongy appearance. In the visceral mass are imbedded parts of other systems as described below. Dorsal to the visceral mass lie the organs of Bojanus, kidneys or nephridia, two tubes one on each side consisting of a ventral glandular and smooth dorsal portion. They lie just dorsal to the internal gill and lower, more internal, and more posterior than Kebér's organs (fig. 4). A section through the folds of the glandular portion (fig. 15) shows that these folds are made up of a single layer of columnar epithelium, beneath which is a thin layer of connective tissue. Under this are large spaces containing many leucocytes.

Dorsal to the organs of Bojanus, and in midline, is the heart, composed of a tubular ventricle and two flaplike auricles (fig. 4). The ventricle is folded around the rectum, thus enclosing it. The pericardium (fig. 5) covers this organ loosely leaving a large pericardial space.

The nervous system consists of three pairs of ganglia. In *Tritogonia tuberculata* the nervous system is white. In two of the species dissected, namely *Symphynota complanata* and *Pleurobema æsopus*, this system had a salmon colored tinge which set it off markedly from the surrounding tissues and facilitated dissection. In *Tritogonia tuberculata* the cerebral ganglia lie on the ventro-posterior surface of the anterior adductor muscle, the visceral ganglia on the ventral surface of the posterior adductor, and the pedal ganglia in the muscles of the anterior foot region in midline near the junction of the visceral mass proper with the muscles of the foot (fig. 4). The first two pairs are connected by commissures (fig. 21) and the pedal are connected to the cerebral ganglia by commissures. In a cross-section through the pedal ganglia and anterior foot region, the nerve cells were torn apart in sectioning by transparent, elongate capsules, which were themselves shattered by the razor. Some of these contained coarse, granular bodies which stained deep blue with hematoxylin. These parasitic sporocysts (fig. 9) seemed to be confined to the ganglia as the surrounding muscles were free of them. Except for lacking the long flattened tail, they resemble the sporocysts of gregarines which Helen P. Goodrich illustrated in a recent number of the Quarterly Journal of Microscopical Science.[14]

The labial palps are four in number and lie one pair on each side of the visceral mass. They are joined dorsally for a greater part of their length. The approximated sides of labial palps are furrowed vertically by lateral furrows (figs. 6, 7, and 10). These furrows and the ridges between are lined with columnar, ciliated

[14] Quarterly Journal of Microscopical Science. Vol. 69, Part IV, Oct. 1925, Plate 49, page 628, fig. 10.

epithelium which rests on connective tissue. Grooves project into the ridges on either side of the furrows. These grooves are very regularly arranged in *Tritogonia tuberculata*. Many blood vessels run through the connective tissue of the palp. The outer epithelium rests on a heavy basement membrane of homogeneous structure. The labial palps are united and fastened to the visceral mass for about one-half their length as shown in figure 5. However, the labial palps are joined together posterior to this and are attached to the mantle for about five-sixths of their length, the posterior one-sixth being free. In this region, where they are joined to the mantle but not to the visceral mass, there is a distinct dorsal furrow which extends dorsally to the ventral margin of the inner gill. This furrow is lined with columnar epithelium (fig. 8) which has very large cilia. Many goblet cells also occur in this region. The two pairs of labial palps meet at the mouth, thus forming upper and lower lips.

The mouth opening is small. It leads into a short esophagus which gradually enlarges and opens to the right into a sac-like stomach which continues as a blind pouch anteriorly. Both esophagus and the stomach are surrounded by the liver. The intestine leads obliquely, from the ventral part of the stomach, in a U-shaped loop ventro-posteriorly through the mass of reproductive organs to the ventral part of the visceral mass proper, then curving dorsally to the postero-dorsal portion of the visceral mass. This U-shaped portion is sometimes called the crystalline style portion, as under certain conditions it contains the crystalline style. From here the intestine bends sharply on itself, curving to the right and posteriorly. It descends parallel to the ascending ramus of the U until it reaches the most ventral portion of the visceral mass; thence it continues anteriorly along the ventral margin of the visceral mass until under the stomach, then curves sharply on itself, turning to the right and running posteriorly, crossing to the right of the descending ramus of the U. This part is known as the thin-walled portion. After crossing to the right it curves between the two rami of the U as the rectum, and passes into the pericardium and the ventricle of the heart where it takes a horizontal course posteriorly, finally running dorsal to the posterior adductor and terminating in the anus which is bordered by scalloped folds. Starting in the last ascent of the intestine, or in the rectum, is a ventral fold, the typhlosole. The intestine is small in the crystalline style portion. The thin-walled portion and rectum are much more enlarged. The coiling of the intestine is remarkably uniform in the different species of mussels examined. Variations were noted in *Tritogonia tuberculata* in the anterior extent of the intestine in the ventral portion of the visceral mass, and in the nearness of approach to the stomach of the typhlosolic portion of the rectum (fig. 4).

A cross-section of the rectum in the region of the ventricle (fig. 20) shows an inner lining of ciliated, columnar epithelium with many goblet cells. The typhlosole is composed of connective tissue. The basement membrane of the epithelium is most pronounced here.

The liver, greenish in color, closely surrounds the esophagus and stomach and extends dorsally with the anterior portion of the gills into that fold of the mantle which goes into the beak of the shell (fig. 4). It is a compound tubular gland as shown by cross-section (fig. 18). The larger ducts are lined by folded epithelium composed of slender, ciliated, columnar cells and goblet cells. Some of these folds are caused by actual folding while others are formed by elongation of the cells. The tubes are lined with secreting epithelium, composed of large cuboidal or columnar cells.

Tritogonia tuberculata structurally presents a peculiar shell, some peculiarities of the gills, and a narrower and more anteriorly projecting, blade-like foot than most freshwater mussels. It is hardy, it can endure still water, and is of some economic value. This combination recommends further investigation of its life history from the viewpoint of mussel culture. Dr. Frank A. Stromsten suggests that an investigation of the correlation between lime content of water and type of shell might be well worth while in the transplantation of mussels. It would be interesting to have data from certain parts of Iowa where streams flow over relatively little limestone, and then similar data from limestone regions of our state, and notice the difference in thickness and texture of the shells of mussels from the two areas. Professor Shimek finds snail collecting better in limestone regions than in sand dune areas, even though the latter be wooded. Some similar correlation might be found in mussel distribution. Mr. George Potter brought some mussels from the Okoboji and Little Sioux regions, an area of comparatively little limestone and near the headwaters of the drainage systems. I notice that his specimens of *Symphynota complanata*

are much more fragile than those we find here in the Iowa River. The number of species varies with different localities, and the individuals of one species vary likewise with locality. The whole question is one that calls for data which could be collected easily.

BIBLIOGRAPHY

Allen, W. R.—1914. The food and feeding habits of freshwater mussels. Biol. Bull., 27, pp. 127-139.

1921. Studies in the biology of freshwater mussels. Biol. Bull., 40, pp. 210-241.

Baker, F. C.—1922. The molluscan fauna of the Big Vermillion River, Ill. Ill. Biol. Monog., Vol. 7, No. 2.

Brück, A.—1914. Die Muskulatur von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 110, S. 481.

Call, R. E.—1895. A study of the Unionidæ of Arkansas with incidental reference to their distribution in the Mississippi Valley. Trans. Acad. Sci. St. Louis, 7, pp. 1-65, 21 plates.

Churchill, E. P., and Lewis, S. I.—1923. Food and feeding in freshwater mussels. Bull. Bur. Fish., Vol. 39, p. 439.

Coker, R. E.—1917. Fresh-water mussels and mussel industries of the U. S. Bull. Bur. Fish., Vol. 36, pp. 11-90.

Coker, R. E.; Shira, A. F.; Clark, H. W.; and Howard, A. D.—1920. Natural history and propagation of fresh-water mussels. Bull. Bur. Fish., Vol. 37, p. 77.

De Kay, J. E.—1843. Natural history of New York. Part 5, Mollusca.

Drew, G.—1890. Unios of Iowa. Vol. 1, Anatomy and histology; Vol. 2, Description of species. Thesis, State University of Iowa. (Not published).

Edmundson, C. H.—1920. The reformation of the crystalline style in *Mya arenaria* after extraction. Jour. Exp. Zool., Vol. 30, pp. 259-291.

Fernau, W.—1914. Die Niere von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 110. I Teil, Morphologie der Niere, S. 253; II Teil, Die Histologie der Niere, S. 303; III Teil, Die Nierentätigkeit, Bd. III, S. 569.

Gutheil, F.—1912. Uber den Darmcanal und die Mitteldarmdrüse von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 99, S. 445-537.

Guyer, M. F.—1922. Animal Micrology.

Hatschek, B., und Cori, C. J.—1896. Elementarcurs der Zootomie. *Anodonta mutabilis* Cless, S. 39.

Hebers, Karl—1913. Entwicklungsgeschichte von *Anodonta cellensis* Schröt. Zeit. wiss. Zool., Bd. 108, S. 1.

Howes, G. B.—1885. An atlas of practical elementary biology, p. 61.

1902. Atlas of practical elementary zootomy. Pl. 20-22.

Howard, A. D.—1922. Experiments in the culture of fresh-water mussels. Bull. Bur. Fish., Vol. 38, p. 63.

Huxley, T. H., and Martin, H. N. Revised by Howes, G. B., and Scott, D. H. —1892. A course of elementary instruction in practical biology. The freshwater mussel (*Anodonta cygnæa*) p. 20.

Jaffé, G.—1921. Die Pericardialdrüse von *Anodonta cellensis* (Schröt). Zeitschr. wiss. Zool., Bd. 119, S. 67.

Kellogg, J. L.—1890. A contribution to our knowledge of the morphology of lamellibranchiate mollusks. Bull. Bur. Fish., 10, p. 389.

Krug, C.—1922. Morphologie und Histologie des Herzens und Pericards von *Anodonta cellensis*. Zeitschr. wiss. Zool., Bd. 119, S. 155.

Lee, A. B.—1905. The microtomist's vade-mecum.

McMurrich, J. P.—1894. Textbook of invertebrate morphology, p. 326.

Nelson, T. C.—1918. On the origin, nature, and function of the crystalline style of lamellibranchs. Jour. Morph., Vol. 31, pp. 53-111. Has an exhaustive bibliography on the crystalline style.

Ortmann, A. E.—1912. Notes on the families and genera of the Najades. An. Carnegie Mus., Vol. 8, pp. 222-365.

Parker, T. J., and Haswell, W. A.—1910. A textbook of zoology, Vol. 1, p. 680.

Plenk, H.—1925. Zum Bau der Muskelfasern von *Anodonta*. Zeitschr. wiss. Zool., Bd. 125, S. 249.

Pratt, H. S.—1916. Manual of invertebrates.

Rassbach, R.—1912. Beiträge zur Kenntnis der Schale und Schalenregeneration von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 103, S. 363.

Retzius, G.—1892. Das sensible Nervensystem der Mollusken. Biologische Untersuchungen (Stockholm). Neue Folge IV, Tafel IV-VI, S. 11.

Schneider, K. C.—1902. Lehrbuch der vergleichenden Histologie der Tiere. *Anodonta mutabilis*, S. 536, Litteraturverzeichnis S. 954.

Schwanecke, H.—1913. Das Blutgefässsystem von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 107, S. 1.

Shimek, B.—1915-1918. Keys to the mollusca of Iowa. Appendix to plant geography of the Lake Okoboji region. Bull. Lab. Nat. Hist., S. U. I., Vol. 7, No. 2, p. 75 and p. 80.

Siebert, W.—1913. Das Körperepithel von *Anodonta cellensis*. Zeitschr. wiss. Zool., Bd. 106, S. 449.

Simpson, C. T.—1900. Synopsis of the Naiades, or pearly fresh-water mussels. Proc. U. S. Nat. Mus., Vol. 22, pp. 501-1044.

Splittstoesser, P.—1913. Zur Morphologie des Nervensystems von *Anodonta cellensis* Schröt. Zeitschr. wiss. Zool., Bd. 104, S. 388-466.

Sterki, V.—1907. Note on *Tritogonia tuberculata*. Nautilus, 21, p. 48.

Vogt, C., und Yung, E.—1888. Lehrbuch der praktischen vergleichenden Anatomie. Blattkiemer—*Anodonta anatina*. Bd. 1, S. 735.

Walker, B.—1918. A synopsis of the classification of the fresh-water mollusca of North America, north of Mexico. U. of Mich. Mus. of Zool. Misc. Pub., No. 6.

Ward, H. B., and Whipple, G. C.—1918. Freshwater biology.

Weisensee, H.—1914. Die Geschlechtsverhältnisse und der Geschlechtsapparat bei *Anodonta*. Zeitschr. wiss. Zool., Bd. 115, S. 262.

Wetekamp, F.—1914. Bindegewebe und Histologie der Gefässbahnen von *Anodonta cellensis*. Zeitschr. wiss. Zool., Bd. 112, S. 433-522.

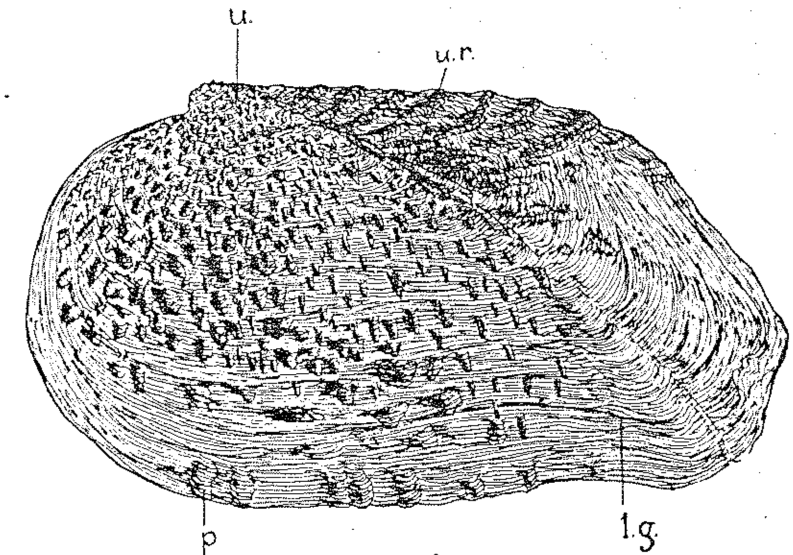
PLATES

PLATE I

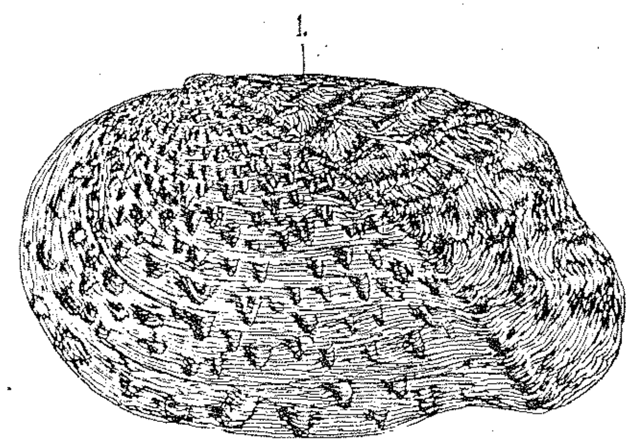
Key to figure 1. Elongate form of *Tritogonia tuberculata*
- u. umbo
- u.r. umbonal ridge
- p. pustule
- l.g. line of growth

Key to figure 2. Short form of *Tritogonia tuberculata*
- l. ligament

PLATE I



1



2

PLATE II

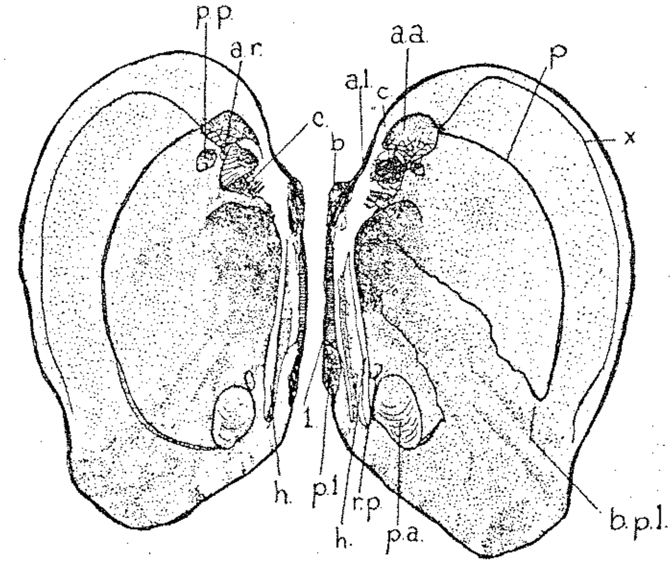
Key to figure 3. Interior of valves. *Tritogonia tuberculata*

- p. pallial line
- p.p. protractor pedis scar
- a.r. anterior retractor pedis scar
- r.p. posterior retractor pedis scar
- p.a. posterior adductor scar
- a.a. anterior adductor scar
- b.p.l. break in pallial line
- x. groove probably representing peripheral artery of mantle
- l. ligament
- p.l. posterior lunule
- a.l. anterior lunule
- b. beak
- c. cardinal teeth
- h. hinge teeth

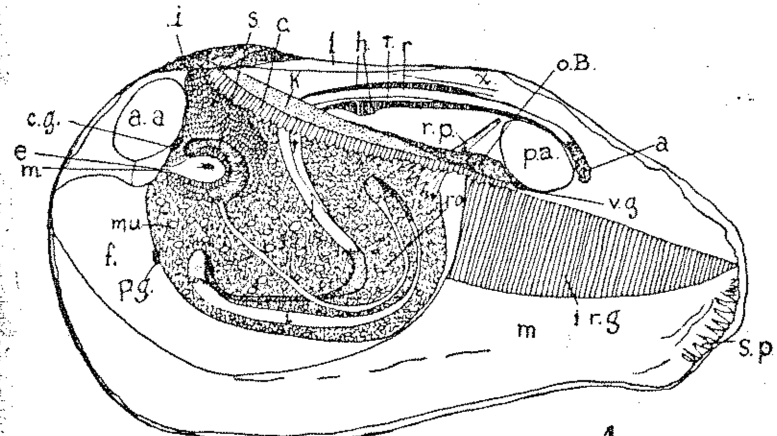
Key to figure 4. Conventionalized section through visceral mass in right valve

- li. liver
- a.a. anterior adductor
- r.p. posterior retractor pedis
- p.a. posterior adductor
- s.p. siphonal papilla
- h. heart
- l. ligament
- x. fold of the mantle above the hinge teeth
- c.g. cerebral ganglion
- p.g. pedal ganglion
- v.g. visceral ganglion
- K. Keber's organ
- o.B. organ of Bojanus
- r.o. reproductive organs
- m. mouth
- e. esophagus
- s. stomach
- i. intestine
- t. typhlosole
- r. rectum
- a. anus
- f. foot
- i.r.g. inner right gill
- m. mantle
- c. cut edge of outer left gill
- mu. transverse muscles of visceral mass

PLATE II



3



4

PLATE III

Key to figure 5. Internal structures shown in the right valve. Left valve and left fold of mantle removed
- a.a. anterior adductor muscle in section
- p.a. posterior adductor muscle in section
- p.p. protractor pedis
- r.p.a. anterior retractor pedis
- r.p.p. posterior retractor pedis
- s.b.c. superbranchial chamber
- e.s. exhalant siphon
- i.s. inhalant siphon
- v.m. visceral mass
- f. foot
- s.t. siphonal tentacle or papilla=fimbria
- l. ligament
- b. beak
- i.l.g. inner left gill
- o.l.g. outer left gill
- m. mantle
- a.l. anterior lunule

Key to figure 6. Detail of vertical section of a labial palp
- r. ridge
- g. groove
- e. epithelium
- b.m. basement membrane
- c.t. connective tissue
- c. cilia

Key to figure 7. Detail of vertical section of ventral furrow at junction of labial palps
- v.f. ventral furrow
- l.f. lateral furrows

Key to figure 8. Detail of epithelium from ventral portion of dorsal furrow of labial palps
- b.m. basement membrane
- g. secreting goblet cell
- m. mucous cell
- c. cilia
- w. wandering cell

Key to figure 9. Detail of fragment of pedal ganglia
- n. nerve cells
- p. parasitic sporocysts

PLATE III

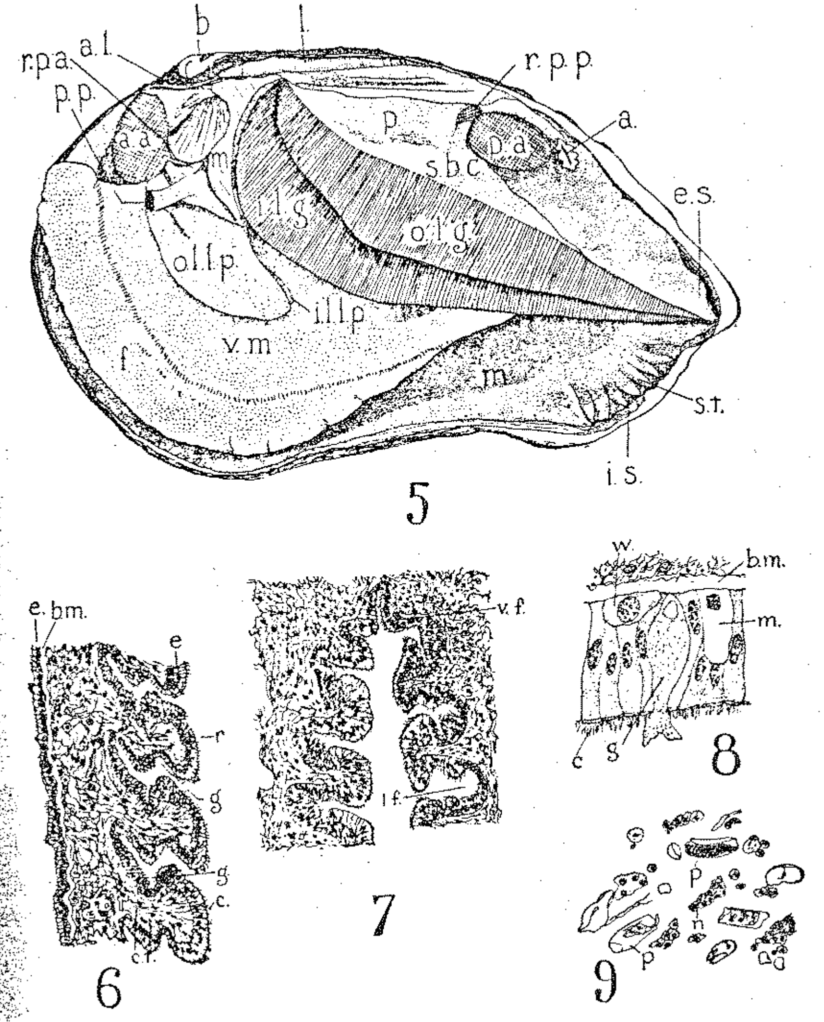
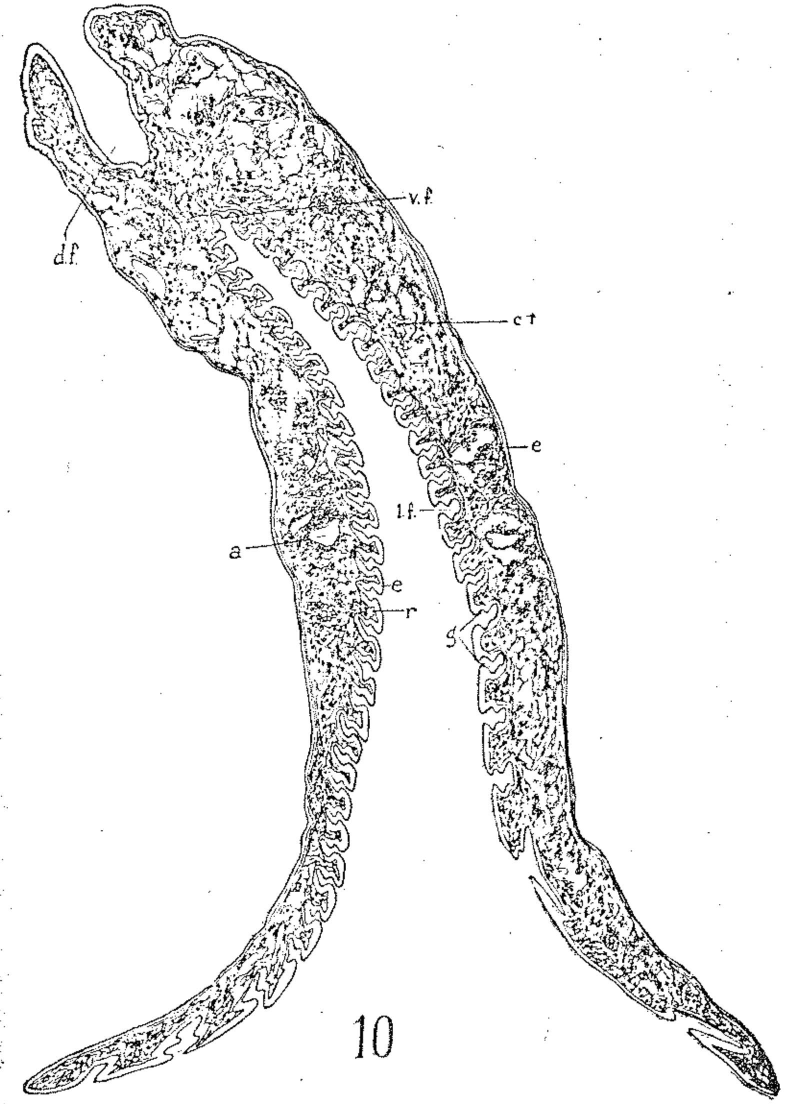


PLATE IV

Key to figure 10. Vertical section through labial palps

d.f.	dorsal furrow
c.t.	connective tissue with cut ends of small bloodvessels
e.	epithelium
a.	labial palp artery
r.	ridge
g.	grooves
v.f.	ventral furrow
l.f.	lateral furrow

PLATE IV



10

PLATE V

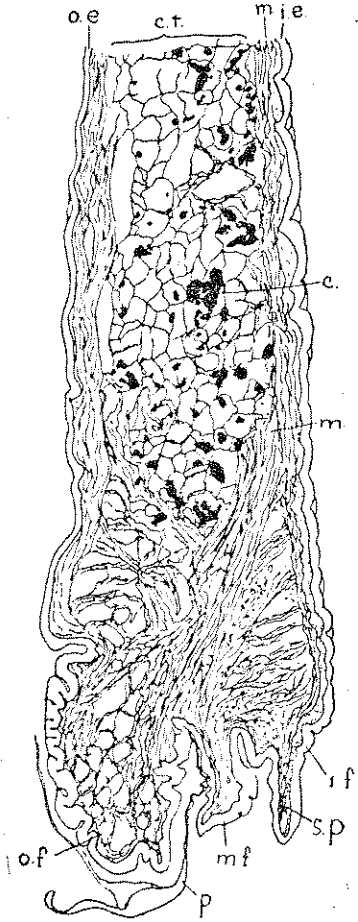
Key to figure 11. Free-hand transverse section through edge of mantle
- o.e. outer epithelium
- c.t. connective tissue layer
- m. muscles
- i.e. inner epithelium
- i.f. inner fold
- s.p. siphonal papilla
- m.f. middle fold
- o.f. outer fold
- p. periostracum
- c. masses of calcareous granules

Key to figure 12. Detail of inner lobe of mantle—10 micra thick
- m. mucous material

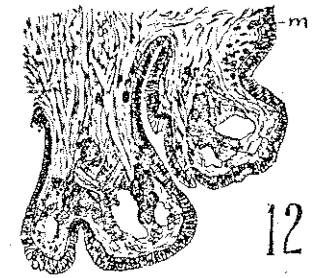
Key to figure 13. Detail of groove secreting periostracum—10 micra thick
- p. periostracum
- pi. pigment in epithelium
- o.f. outer fold
- m.f. middle fold

Key to figure 14. Detail of layers on outer side of mantle. Oil immersion
- e. epithelium
- b.m. basement membrane
- m. muscle cells
- w.c. wandering cells
- c.t. connective tissue
- t.m. transversely cut muscle cells

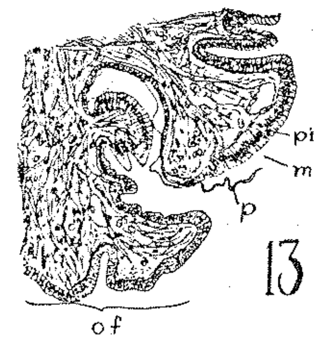
PLATE V



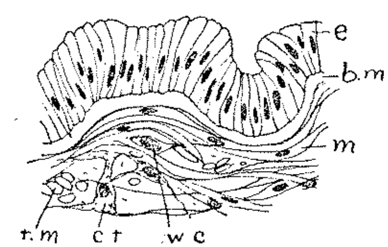
11



12



13



14

PLATE VI

Key to figure 15. Cross-section through folds of the wall of the glandular portion of the organ of Bojanus

- l. leucocyte
- e. epithelium
- c. connective tissue

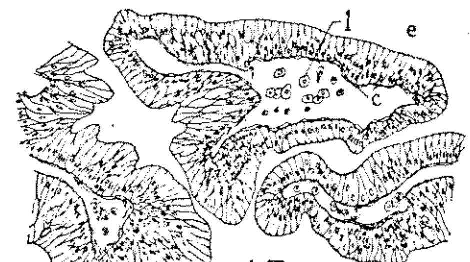
Key to figure 16. Epithelium of the ventral part of foot

- e. epithelium
- s. sub-epithelial mucous cells
- m. muscles
- c. connective tissue

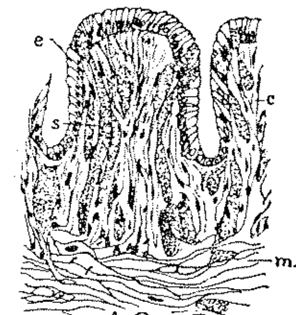
Key to figure 17. Cross-section through dorsal portion of gills

- a.n. arterial net
- v.n. venous net
- c. connecting vessels between arterial and venous nets
- w.t. water tube
- i.l.j. interlamellar junction
- la. lamina of gill
- i.a. interlamellar artery
- os. ostium
- f. filament
- e. ciliated epithelium
- r. supporting rods
- m. mucous material

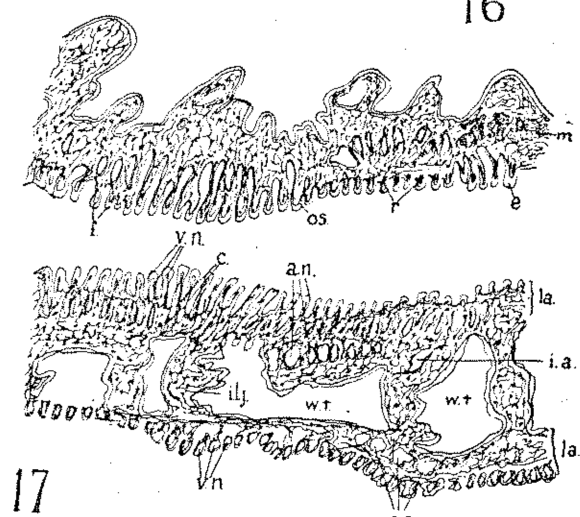
PLATE VI



15



16



17

PLATE VII

Key to figure 18. Cross-section through liver
- t. tubules
- d. duct

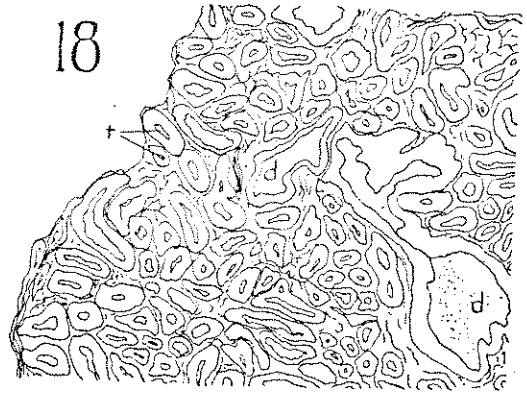
Key to figure 19. Detail of figure 18
- t. tubule
- d. lumen of duct
- e. ciliated epithelium of duct
- g. goblet cell

Key to figure 20. Cross-section of rectum in region of the heart
- t. typhlosole
- c. connective tissue
- e. ciliated epithelium
- r. lumen of rectum

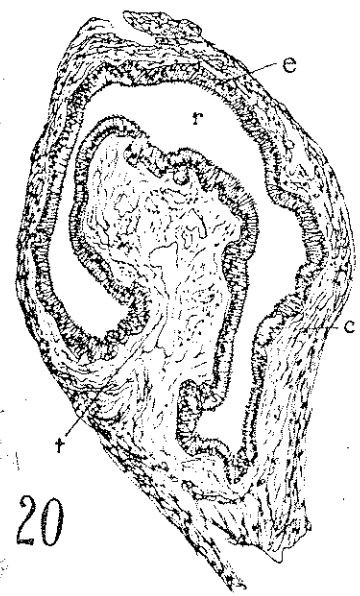
Key to figure 21. Conventionalized cross-section through visceral mass
- n.c. nerve commissure
- o.B. cut ducts of glandular portion of organ of Bojanus
- i. intestine
- t. typhlosole
- r.o. reproductive organs
- t.m. transverse muscles of foot and visceral mass
- m. muscles of the foot
- e. folded epithelium and subepithelial mucous cells

PLATE VII

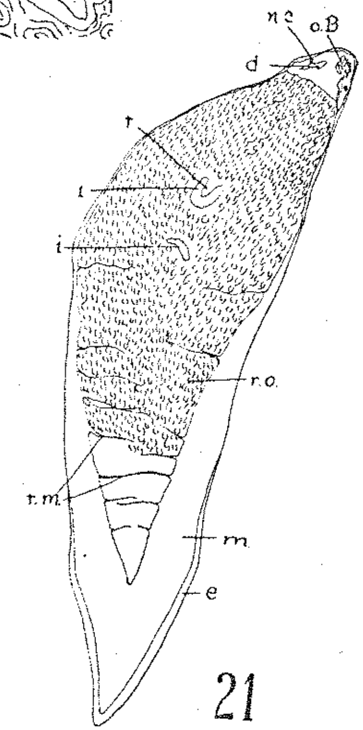
18



19



20



21