CHAPTER XII

THE EXCRETORY SYSTEM

End products of bivalve catabolism are excreted by the nephridia, pericardial glands, wandering phagocytes, and the mantle epithelium. The urinary function, which is the principal activity of the excretory system, is performed by the paired nephridia situated on either side of the visceral mass near the heart. The pericardial glands, as the name indicates, are located on the wall of the pericardium but in the oysters and some other species are represented by special cells on the outer wall of the auricles. The wandering phagocytes may be found throughout the tissues of the visceral mass and the gills. They accumulate on the surface of the body by diapedesis and are discarded. Mucus or goblet cells of the surface epithelium are, in addition to their primary function of secreting mucus, involved in excretion and carry within their bodies various granules which contain pigments and heavy metals (see: ch. XVII).

The principal part of the excretory system of bivalves is similar to that of annelids. It consists of a pair of tubular nephridia (fig. 244, 1. neph., r. neph.) which retain direct communication with the pericardium and sex glands on one side and open to the outside through a short passage. The coelom of bivalves is reduced to two separate spaces, the pericardial cavity and the inside of the gonad tubules. The ducts leading from the nephridia and gonads open to the outside either independently or through a common reno-gonadial vestibule.

Comprehensive reviews of the anatomy and histology of the excretory system in mollusks may be found in the papers of Odhner (1912), Strohl (1924), Haas (1935), Spitzer (1937), and Franc (1960).

ANATOMY OF THE EXCRETORY SYSTEM

The excretory organ of the oyster occupies an indistinctly outlined triangular area on either side of the visceral mass. On the surface its location is marked by light brownish pigmentation. The organ consists of a central part which lies between the pericardium and the adductor muscle and two branches or limbs which extend along both sides of the body. The right limb is slightly longer than its opposite member. Excretory tissues are found directly under the surface epithelium; they are surrounded by branchial vessels and numerous blood sinuses.

The relation between the different parts of the excretory system, the heart, and the adductor muscle is shown diagrammatically in figure 244.

Each nephridium of a bivalve is bent into a U-shaped tube which forms many convoluted branches penetrating the surrounding tissues. The narrow central part of the excretory system extends across the body from one side to the other and contains a narrow and twisted inter-nephridial passage (i.r.p.) which connects the two limbs. Fingerman and Fairbanks (1958) think that this passage "does not appear to be present in *Crassostrea virginica*." Reconstruction of the structure of this area from serially sectioned material shows that there is a communication between the right and left nephridia although the passage is narrow and greatly twisted (fig. 245) and, therefore, appears in the preparations as a series of circles and irregular cylinders. Examination of a number of consecutive sections shows an uninterrupted connection between the right and left nephridia.

The nephridium of each side begins inside the pericardium by the reno-pericardial opening (fig. 244, r.p.o.), which leads through a ciliated funnel, the nephrostome and a short reno-pericardial canal (fig. 244, r.p.c., and fig. 246), to the body of the kidney. Both limbs of the kidney are formed

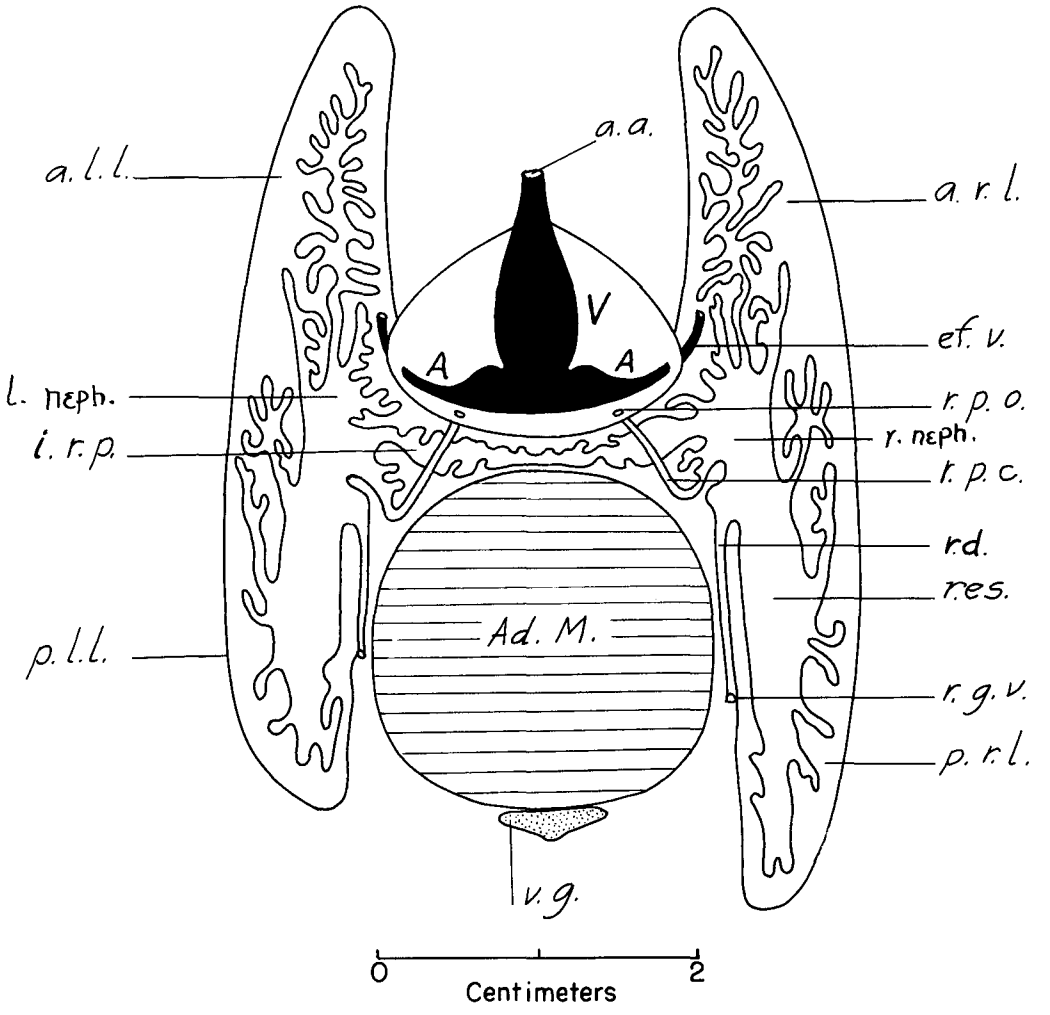

FIGURE 244.—Diagram of the excretory system of *C. virginica* based on examination of a series of transverse sections. Viewed from the anterior side. Gonads and their ducts, blood vessels, and blood sinuses are not shown. The pericardium wall is dissected and pulled down. A—auricle; a.a.—anterior aorta; Ad.M.—adductor muscle; a.l.l.—anterior left limb; a.r.l.—anterior right limb; ef.v.—efferent vein; i.r.p.—internephridial passage; l. neph.—left nephridium; p.l.l.—posterior left limb; p.r.l.—posterior right limb; r.d.—renal duct; r. neph.—right nephridium; res.—reservoir; r.g.v.—reno-gonadial vestibule; r.p.c.—reno-pericardial canal; r.p.o.—reno-pericardial opening; V—ventricle; v.g.—visceral ganglion.

by numerous branching and twisted tubules lined with excretory cells.

Much of the posterior limb of the kidney is occupied by a wide vesicle or reservoir (fig. 245, R.) for the storage of urine. A short renal duct (fig. 244, r.d., and fig. 247) leads from the reservoir to the outside and opens into the reno-gonadial vestibule, a shallow indentation on the surface of the pyloric caecum, behind the opening of the gonad (fig. 247). Numerous anastomosing tubules of the nephridia form a spongy tissue which extends into the visceral mass (fig. 248). Odhner (1912) pointed out that regardless of the apparent complexity of the nephridia, it is always possible to distinguish the two limbs or branches of the excretory system.

Topography and relationship of the excretory and reproductive systems vary greatly within the class of bivalves. Certain topographical features, however, remain constant. One of them is the position of the renal opening in relation to the cerebro-visceral connective. Lacaze-Duthiers (1855), one of the early students of molluscan anatomy, pointed out that the renal opening (also called "nephroprokt") is always located beyond the cerebro-visceral connective. Pelseneer (1891) at-

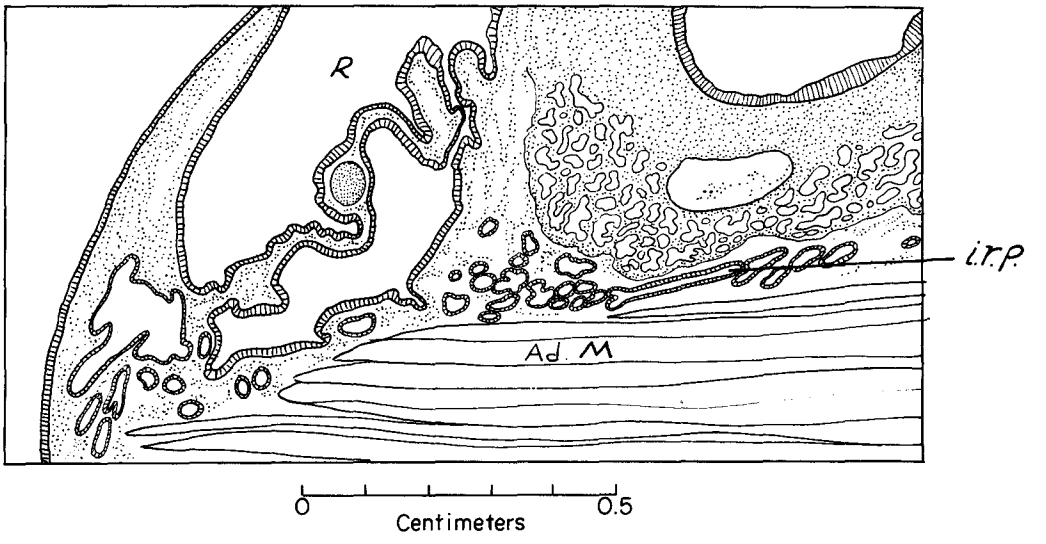

FIGURE 245.—Camera lucida drawing of a left portion of the central part of the excretory organ of *C. virginica* seen on cross section. The beginning of the inter-nephridial passage (i.r.p.) at the junction with the reservoir, R, is on the left side; Ad.M.—adductor muscle. Bouin, hematoxylin-eosin.

tached considerable importance to this morphological relationship for which he coined the term "ektaxial."

In the absence of a generally accepted anatomical terminology for the excretory system of bivalves, considerable confusion exists in the literature because of the great variety of names and descriptive terms applied to identical parts. The nephridium was discovered in 1817 by Bojanus (1819) who mistook it for the organ of respiration. Since then the excretory system of mollusks has been known in zoological literature as the organ of Bojanus. There seems to be no advantage in the continued use of this name, because the organ is frequently called kidney, nephridium, renopericardial or nephropericardial passage (Renopericardialgang, in German), and nephridial sac in cephalopods. The dorsal limb of the nephridium may be called the proximal part, inner limb, pericardial part, inner sac, excretional part, anteroposterior limb, and kidney sac. The ventral (or distal) limb is also known as outer sac, efferent part, and kidney passage. The reservoir is sometimes referred to as vesicle and bladder. The reno-pericardial opening is called nephrostome, nephridial funnel, and "Nierenspitze" or kidney syringe (Haas, 1935).

HISTOLOGY

The glandular nephridial tubes of the oyster are lined with a special epithelium; the cells are characterized by clear cytoplasm and absence of granules. Three kinds of epithelial cells are found in the different parts of the excretory system. In the tubules of the anterior limb the cells are of medium size, cylindrical, and vacuolated (fig. 249). The lining of the internephridial passage and of the tubules originating from its wall is made of short, almost cubical cells with inconspicuous vacuoles (fig. 250). In places the epithelium lining is two or three cells deep. Tall columnar cells with large terminal vacuoles are found primarily in the tubules of the posterior limb and in the reservoir (fig. 251 and fig. 252). The cells are about seven to nine times longer than their width. The vacuoles have no granules visible under the light microscope; they appear to contain liquid as if they are ready to burst. Some of the vacuoles seem to be empty, and many separated vacuoles are found in the lumen.

The lining of the reservoir consists of columnar cells of different heights; some of them are twice or three times taller than the others and protrude into the lumen (fig. 252). The epithelium rests on a basal membrane with a well-developed layer of circular muscles which extends to the renal duct. There is no organized sphincter for the control of the flow of urine. The contraction of the bladder in response to the fluid flowing into it from the pericardial cavity was observed by Fingerman and Fairbanks (1958).

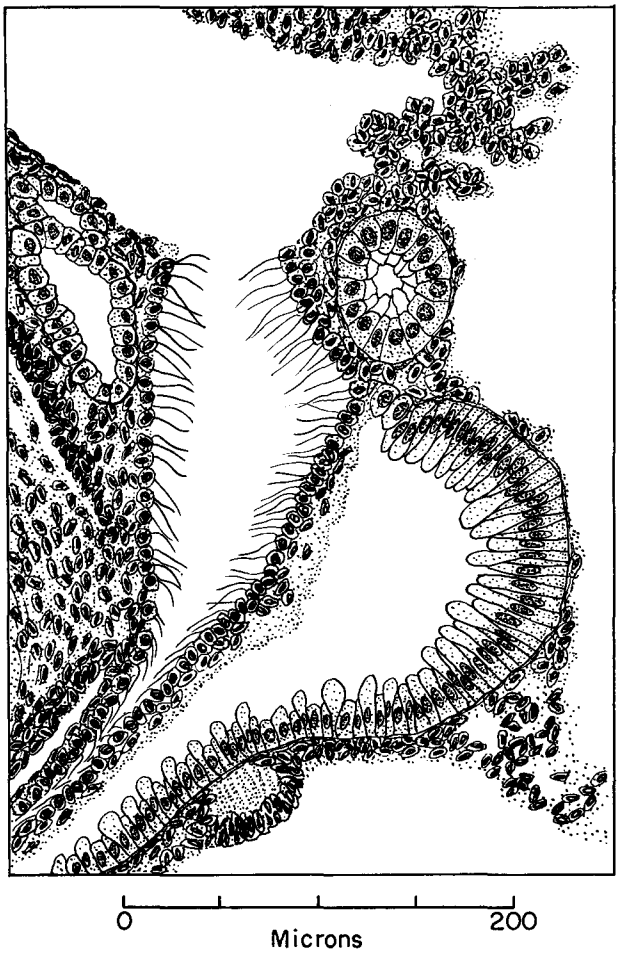

FIGURE 246.—Longitudinal section through the reno-pericardial opening and reno-pericardial canal, which connects the inner part of the kidney with the auricle in *C. virginica*. Part of the auricle at upper left and the adjacent portion of the kidney at lower right. Bouin, hematoxylin-eosin.

The epithelium of the reno-pericardial passage and of the renal duct is ciliated (fig. 246 and fig. 247).

PHYSIOLOGY

No comprehensive account of the biochemical and physiological processes of excretion in bivalves can be written at present because of the inadequate state of our knowledge, however, a review is possible.

During the past three-quarters of the century many studies have been made of the function of the organ of Bojanus and of the role of the pericardial glands. Most of these investigations were carried on for gastropods, cephalopods, and fresh-water mussels. The reader is referred to the review of this subject found in the papers of Marchal, 1889; Letellier, 1889; Cuénot, 1900; Fosse, 1913; Turchini, 1923; Delaunay, 1924, 1931, 1934; Spitzer, 1937; and Franc, 1960. Very little work has been done, however, with marine bivalves and particularly with oysters for which physiological studies of the excretory system present considerable technical difficulties. The nephridial organs of oysters do not form a sharply outlined unit. They are surrounded by delicate and loose connective tissue which contains numerous blood vessels with very thin walls and spacious sinuses. Consequently, it is very difficult to obtain a sample of the liquid from the various parts of the kidney system without contaminating it with blood or with the sea water which surrounds the organ. Such difficulties are not encountered in the studies of land snails and cephalopods.

An experimental approach to the study of the function of nephridia was made by Grobben (1888), Kowalevsky (1890), and Emeljanenko (1910) who injected various dyes in the foot, mantle, or visceral mass of the mollusk. It was shown by this method that the excretory organs of bivalves excrete indigo-carmine and that ammonia carmine injected in physiological solution is concentrated in the pericardial glands. In *Ostrea* the carminates are concentrated in the walls of the auricles, while in *Pecten maximus* they are spread throughout the connective tissue (Cuénot, 1900).

Attempts to determine the rate of filtration of fluid into the pericardium of fresh-water Unionidae were made by Turchini (1923) and Picken (1937). Picken studied the hydrostatic and colloid osmotic pressure of the body fluid. He supposed, probably correctly, that the pericardial fluid is a filtrate of the blood through the wall of the heart. His observation that the pericardial fluid of *Anodonta* is isotonic with blood seems to support this view.

On the basis of the experiments by these authors and by Robertson (1949, 1953), the following course of urine formation may be visualized: The blood is filtered through the wall of the heart into the pericardium, and this fluid, together with the secretion of the pericardial glands, passes through the reno-pericardial opening into the nephridial tubes. The secretion from the tubules is added to the liquid. Its final composition will depend on how far and how rapidly the secretion and possibly the reabsorption of certain constituents proceed in the secretory epithelium.

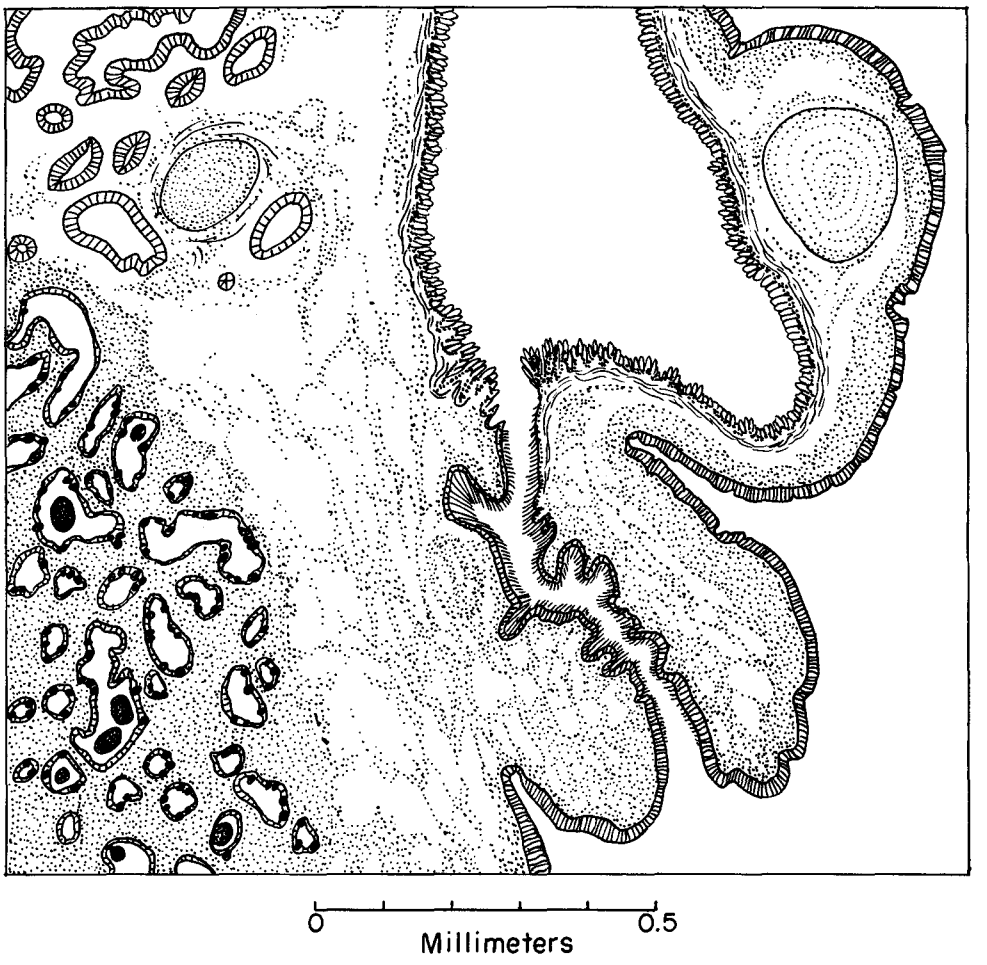

FIGURE 247.—Section through the reservoir and renal duct of the right nephridium *C. virginica*. Gonad at the lower left corner and cerebro-visceral connective at the upper right corner. Bouin, hematoxylin–eosin.

The experimental procedures for separate collection of blood, pericardial fluid, and urine from the reservoir are uncertain, both because the tissues are fragile and because a rich supply of blood is received by the nephridia directly from the visceral sinuses. Prosser (1950, p. 36) states correctly that urine volume cannot, therefore, be calculated from the rate of accumulation of the pericardial fluid; neither can the composition of urine be inferred from an analysis of the fluid collected from the interior of the kidney.

The rate of filtration of blood from the ventricular wall into the pericardium was studied in *Anodonta* by Picken (1937) using the following method: A hypodermic needle of 1.5 mm. bore was inserted in the pericardial wall previously exposed by cutting off the adjacent portion of the shell. A length of about 2 cm. of glass tubing was sealed to the hypodermic needle, which was tilted so that there was a difference of about 0.5 cm. in the levels at each end of the needle. The fluid from the pericardium dropping through the needle was collected for periods of 5 minutes at 10-minute intervals. The average rate of filtration determined in this manner was about 25 ml. in 4 hours. The method probably gives a higher rate of blood filtration than occurs under normal conditions because of a loss of pressure inside the pericardium resulting from the puncture of the wall. Furthermore, it does not necessarily follow that the rate of the discharge of fluid by the kidney is controlled by the rate at which the pericardium fills up with blood. The method does not seem applicable to the oyster because of the position of the excretory organs on the oyster body and the inherent technical difficulties.

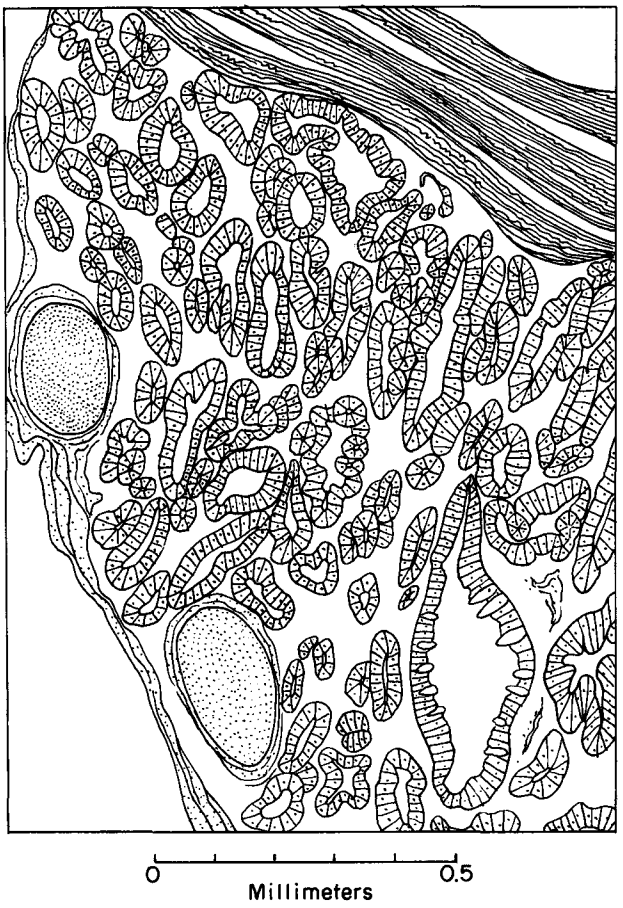

FIGURE 248.—Tightly packed and twisted blind tubules of the excretory organ of *C. virginica* form "spongy" tissue which extends on both sides into the visceral mass. Adductor muscle at upper right. Bouin, hematoxylin–eosin.

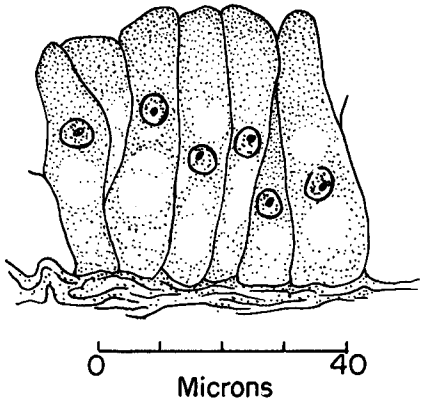

FIGURE 249.—Medium-sized cylindrical epithelial cells lining the lumen of the nephridial tubules of the anterior limb of *C. virginica*. Oil immersion. Kahle, hematoxylin–eosin.

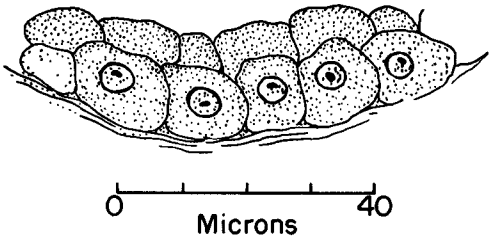

FIGURE 250.—Cubical cells of the epithelium lining of the inner wall of the internephridial canal of *C. virginica*. Oil immersion. Kahle, hematoxylin–eosin.

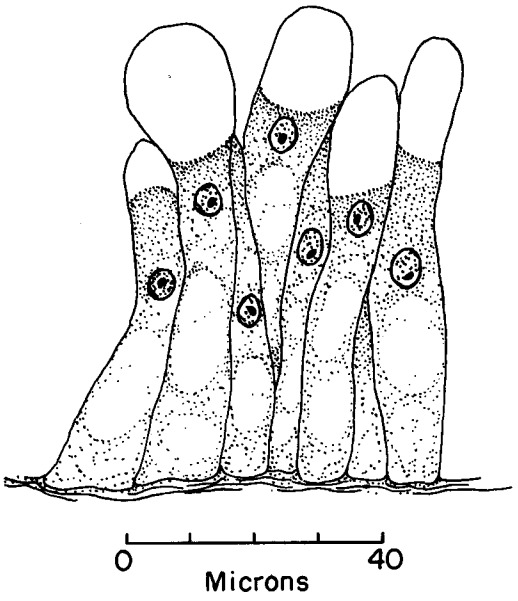

FIGURE 251.—Tall columnar cells of the lining of the tubules of the posterior limb of *C. virginica*. Oil immersion. Kahle, hematoxylin–eosin.

THE WASTE PRODUCTS

Relatively little is known about nitrogen excretion in the oyster or in other marine bivalves. As in other organisms the waste products are various nitrogenous compounds. The presence of a low concentration of ammonia, the principal nitrogenous product of amino acid breakdown in mollusks (0.051 mg. per 100 ml.) was demonstrated by Florkin and Houet (1938). In the excreta of the marine clam (*Mya arenaria*) ammonia comprises 21.5 percent of the total nonprotein nitrogen (Delaunay, 1924), and in *Mytilus* the figure varies from traces to 10.8 percent (Spitzer, 1937). Small quantities of urea amounting to 4.5 percent of the nonprotein nitrogen excreted in different forms were found in *Mya* and only traces of it in *Mytilus*. No uric acid was found in the latter species

(Spitzer, 1937) and only traces were reported in *Mya*. In both organisms amino acids in the excreted material amounted to 18 percent in *Mya* and from 17 to 35 percent in *Mytilus*.

Two different methods were used in the studies of nitrogen secretion. The nephridia with adjacent tissues were ground with sand and extracted with distilled water, and the extracts analyzed; alternately, the entire animals were placed in small quantities of distilled water, kept at 16° to 18° C. for a period of time varying from 24 to 72 hours, and the metabolites accumulated in the water were analyzed. It appears from the experiments in which both fresh-water and marine bivalves were used that uric acid is not present in the nephridia of *Anodonta, Unio, Mytilus*, and *Mya* (Spitzer, 1937; Przylecki, 1922a). Przylecki found that in *Anodonta* up to 60 percent of the total excreted nitrogen is represented by ammonia, and that the amount of ammonia excretion may be greatly increased by placing the animals in acidified water for a short time. He also found that urease, the enzyme which converts urea into ammonia, is present in abundance in *Mytilus edulis* and *Helix* (Przylecki, 1922b). In a study of the urinary functions in bivalves Letellier (1887, 1889) arrived at the conclusion that in the nephridia of *Mytilus, Anodonta,* and *Cardium* urea takes the place of the uric acid; and Marchal (1889) was not able to find uric acid in the excretion of 50 mussels he tested. Spitzer (1937) demonstrated, however, the presence of uric acid in the middle intestine of *Unio* and *Mytilus*. Delaunay (1931) found traces of uric acid in *Mya arenaria* and small quantities of it in the products of nitrogen excretion in the Portuguese oyster *Crassostrea* (*Gryphaea*) *angulata*.

Among the identified nitrogenous metabolites excreted by *Mya arenaria* and *Mytilus edulis* the largest proportion belongs to the amino acids. Next in importance is ammonia, followed by purine, urea, and uric acid. The numerical values expressed in grams of nitrogen of a given compound per total nitrogen in excreta are given in table 32.

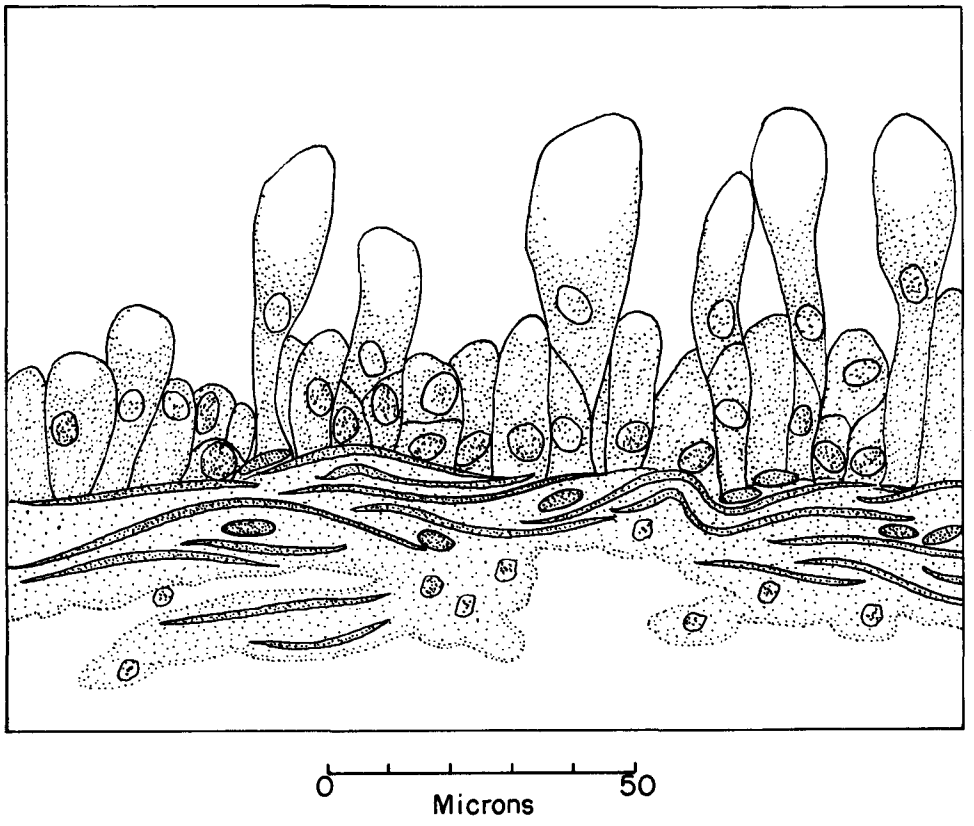

FIGURE 252.—Columnar cells of the lining of the kidney reservoir of *C. virginica*. Basal membrane with a well-developed layer of circular muscles. Oil immersion. Kahle, hematoxylin–eosin.

Baldwin (1935) suggested that the enzyme arginase may be involved in the elaboration of both urea and uric acid in gastropods. He found no evidence of its presence in *Mytilus edulis* or *Pecten opercularis* although the enzyme was found in fresh-water *Anodonta*. Brunel (1938) points out that many investigations have shown that uric acid and allantoine (the product of oxidation of uric acid) are not found in bivalves, and Needham (1935) considers that its absence in that class and its presence in land snails are adaptations to terrestrial life by uricotelic organisms, which often can not find sufficient water for their needs and avoid toxemia by converting poisonous ammonia into the insoluble and relatively innocuous uric acid. The body of a marine bivalve is, as a rule, permeable to water and to small molecules. Consequently, the ammonia formed during catabolism easily escapes by diffusion into the external environment.

TABLE 32.—*Excretion of nitrogen in three species of bivalves in grams of nitrogen per total nitrogen excreted*

[From Handbook of biological data, 1956, Spector, ed., p. 43]

Species	Amino acid N	Ammonia N	Purine N	Urea N	Uric acid N	Unidentified N
Crassostrea angulata	13.2	7.2	----------	3.2	1.6	75
Mya arenaria	18	21.5	5	4.3	Trace	51
Mytilus edulis	17–36	Trace-11.4	Trace-16	Trace	--------	39–79

OSMOREGULATION

It is generally considered that marine bivalves have little power of osmoregulation when placed in diluted sea water (Morton, 1958), and can prevent loss of salts only by closing their valves. There is, however, an indication that the excretory system may serve as an osmoregulating organ. Kumano (1929) reported almost complete agreement between the ionic concentrations of the blood and pericardial fluid of *O. circumpicta* and the sea water in which the oyster was kept. The exception was reported only for magnesium and sulfate ions, which were higher in the blood by 11 and 7 percent respectively than in the sea water. The corresponding values for the pericardial fluid were 5 percent higher for magnesium and 2 percent lower for sulfate.

Robertson (1949, 1953) found that marine bivalves and gastropods (*Pecten, Mya, Ensis, Pleurobranchus, Neptunea*) accumulate potassium and calcium and eliminate sulphate to a small degree. The range of values expressed in percentage of ionic concentration in the surrounding sea water was as follows: sodium, 97 to 101; calcium, 103 to 112; magnesium, 97 to 103; chlorine, 99 to 101; sulphate, 87 to 102.

Robertson defined ionic regulation as the maintenance of ionic concentrations in the body fluid differing from those found in a passive equilibrium with the external medium. Accordingly, he made an analysis of a body fluid obtained from a mollusk and determined its ionic concentration. A second determination was made using the same fluid after it had been dialyzed in a collodion sac against the original sea water. The results reproduced in table 33 show that *Mytilus* and *Ostrea* exert little ionic regulation in their coelomic fluid or plasma, apart from the accumulation of potassium. Magnesium remains within 3 to 4 percent of the equilibrium while calcium sometimes exceeds this by a few percent. The accumulation of sulphates by *Mytilus galloprovincialis* was regarded by Robertson as a rare feature in marine invertebrates. The protein content of blood plasma was found to be low (0.2 to 0.3 percent) in *O. edulis* and significantly higher in *M. galloprovincialis*.

TABLE 33.—*Ionic concentrations in plasma as percentage of concentrations in dialyzed plasma (according to Robertson, 1953)*

[Data based on pooled samples]

	Na	K	Ca	Mg	Cl	SO_4	Protein mg./ml.
Ostrea edulis	99.5	129.1	100.6	102.3	99.8	99.7	0.2
Mytilus edulis	100.0	134.7	99.5	99.5	100.5	98.2	0.3
M. galloprovincialis	100.9	120.8	106.6	96.5	98.6	120.0	0.8

The suggestion that some sort of osmoregulation is present in *C. virginica* was made by Fingerman and Fairbanks (1957, 1958), who placed Louisiana oysters in sea water of three different salinities. After periods up to 14 days, samples were taken from the ventricles, the pericardial cavity, the reservoir of the excretory system, the secretory portion of the nephridia, and the mantle. The authors claim that at the highest concentration of 515.6 milliequivalents of chloride per l. all fluids were hypotonic and at low salinities (161.7 milliequivalents of chloride per l.) all body fluids were hypertonic to the environment. The original data are not given, and the results are presented as average differences. The "t" test of significance ranging in the values of P

from 0.20 to 0.50 seems to indicate that the differences are not significant. The authors' conclusion can not, therefore, be accepted without further confirmation.

The relative significance of the nephridia, pericardial glands, and phagocytes in excretion can not be evaluated at present. The three different systems probably supplement one another by eliminating different waste products. Histochemical studies show, for instance, that phagocytes play the major role in the accumulation, storage, and discharge of iron and copper. Undoubtedly the phagocytes heavily loaded with dark granules contain other substances besides heavy metals which are discarded by the organism. On the other hand, other tissues also are involved in the process of excretion. For instance, the epithelia of the gills, of the edge of the mantle, and of the labial palps under certain conditions store iron. My observations on *C. virginica* indicate that iron is excreted by the epithelium of the mantle, and Stauber (1950) found that India ink injected into the ventricle is distributed by the phagocytes to all parts of the organism and is eliminated through the epithelium of the alimentary tract, digestive diverticula, palps, mantle, and pericardium. Nephridia and shell-forming parts of the mantle are not, however, the routes of migration of these cells. Observations made by Kowalevsky (1890) and Cuénot (1900) showed that if a mollusk with pericardial glands is injected with a mixture of indigo carmine and ammonia carmine, the latter is concentrated in the cells of the pericardial glands, while the indigo goes into the nephridia. These separations lead some investigators to designate the different cells as "carmineathrocytes" and "indigoathrocytes" (Strohl, 1924), terms which have not been accepted by biologists. The affinity of these cells to special dyes does not necessarily indicate that they participate in the normal process of excretion.

Pigmentation may be considered as a certain phase of excretion. Green oysters of Long Island Sound develop dark green pigment as the result of absorption and storage of copper by the phagocytes (Galtsoff and Whipple, 1931). Schiedt (1904) considered that the development of black pigment in the mantle of oysters exposed to strong illumination is also a product of excretion. His finding was not in agreement with the observations of Faussek (1899) on pigmentation on the mantle of *Mytilus* with partially removed shells.

Excretion through diapedesis is undoubtedly of great importance to the mollusk, but its exact role is not fully understood.

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