CHAPTER XIII

THE NERVOUS SYSTEM

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The nervous system of the oyster is relatively simple. The visceral and cerebral ganglia are joined by the cerebro-visceral connectives; the U-shaped cerebral commissure goes around the esophagus; the circumpallial nerve travels along the mantle's edge; and a number of nerves originate from the ganglia and extend to different parts of the body. The pedal ganglia, well developed in many other bivalves, and the cerebro-pedal connective are absent. These retrogressive features are associated with the sedentary mode of life of the oyster and the loss of the organ of locomotion (foot). In the evolution of bivalves this simplification of the anatomy represents an adaptive change and cannot be regarded as a primitive trait (Jhering, 1877).

The only organs of sense in the oyster are the tentacles, along the edge of the mantle, and the pallial organ inside the cloaca. The tentacles are highly sensitive to changes in illumination; they contract if a shadow passes in front of a feeding oyster, or a beam of light is focused on them. They also detect the presence of minute quantities of various drugs, chemicals, excessive amounts of suspended particles, and changes in temperature and composition of sea water. The function of the pallial organ is not well understood; the organ is probably concerned with the detection of mechanical disturbances in the surrounding water.

The eyes found in freely moving bivalves, such as scallops, are absent in adult oysters but are present in fully grown larvae.

There is no major control center (brain), and in this sense the nervous system is decentralized. The integration of its various parts is accomplished by the interconnections of the ganglia through the cerebro-visceral connectives, cerebral commissure, and the larger nerve trunks. All these parts contain groups or nuclei of nerve cells and have a structure similar to that of the ganglia.

In oysters the two visceral ganglia are fused into a single organ. Its double origin is clearly visible on tangential sections.

The distribution of nerves in bivalves was studied by many zoologists of the 19th century (Garner, 1837; Duvernoy, 1854; Jhering, 1877; Rawitz, 1887, Babor, 1896; Pelseneer, 1891; Freidenfelt, 1896; Gilchrist, 1898) who described the principal topographic features of the nervous system of various species. The nerves of the European oysters were quite accurately depicted in the old paper of Duvernoy; a general description of the nerve system of *O. chilensis* was given by Dahmen (1923); of *C. angulata* by Leenhardt (1926), and of *O. cucullata* by Awati and Rai (1931).

METHODS

Anatomical dissection of the nervous system of the oyster is rather difficult. The nerves are small, unpigmented, and are embedded in connective tissue. In fully ripe or in so-called "fat" oysters even the principal nerves of the visceral mass are hidden under a thick layer of gonad or are covered by large quantities of glycogen. The lean and watery specimens usually found shortly after spawning are most suitable for dissection. Immersion in 10 percent nitric acid, followed by washing and clarification in glycerol, may be useful because the nerve tissue is stained by the acid a light brown color. The entire nervous system may be stained in toto by using the following procedure: oyster tissue preserved in 95 percent ethyl alcohol or in 5 percent formalin is transferred into 1 percent aqueous solution of potassium hydroxide (solution No. 1) for 1 to 3 days. The specimen is then placed in solution No. 2 made of 1 part glacial acetic acid, 1 part glycerol and 6

parts of 1 percent chloral hydrate solution, and is left in it for about 24 hours. The tissue is then transferred into solution No. 3 consisting of 1 part of Ehrlich acid hematoxylin, 1 part of glycerol and 6 parts of 1 percent chloral hydrate solution. After several days in this mixture the preparation is destained in the solution No. 2 for about 12 to 24 hours and cleared in glycerol. Time of staining and destaining may be modified depending on thickness and condition of tissues. In successful preparations the dark purple nervous tissue is visible against the semitransparent visceral mass. In my experience the method proved to be capricious and not entirely reliable.

In a live oyster the nerves appear as thin, white threads which can be traced for some distance in very thin oysters containing no glycogen. Oysters starved for 4 to 6 weeks in filtered sea water were found to be very suitable for nerve study. Dissection of the nervous system must be supplemented by reconstruction of ganglia and nerves through examination of serially sectioned material.

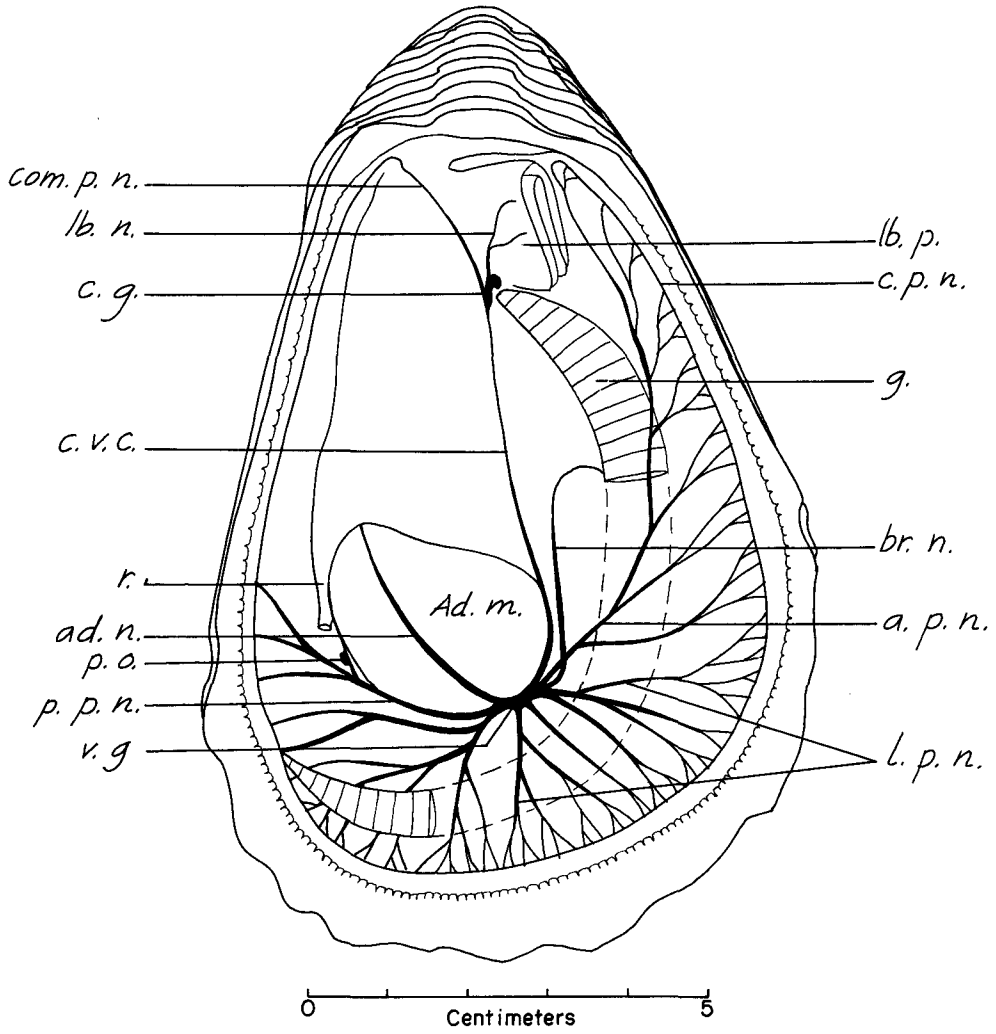

FIGURE 253.—Diagram of the nervous system of *C. virginica* seen from the right side. Dorsal and ventral ends of the gills are shown under the mantle; the middle portion of the gill has been cut off; the middle portion of the branchial nerve is indicated by the dotted line. Ad.m.—adductor muscle; ad.n.—adductor muscle nerve; a.p.n.—anterior pallial nerve; br.n.—branchial nerve; c.g.—cerebral ganglion; c.p.n.—circumpallial nerve; com.p.n.—common pallial nerve; c.v.c.—cerebro-visceral connective; g.—gills; lb.n.—labial nerve; lb.p.—labial palps; l.p.n.—lateral pallial nerves; p.o.—pallial organ; p.p.n.—posterior pallial nerve; r.—rectum; v.g.—visceral ganglion. The cerebral commissure is not visible.

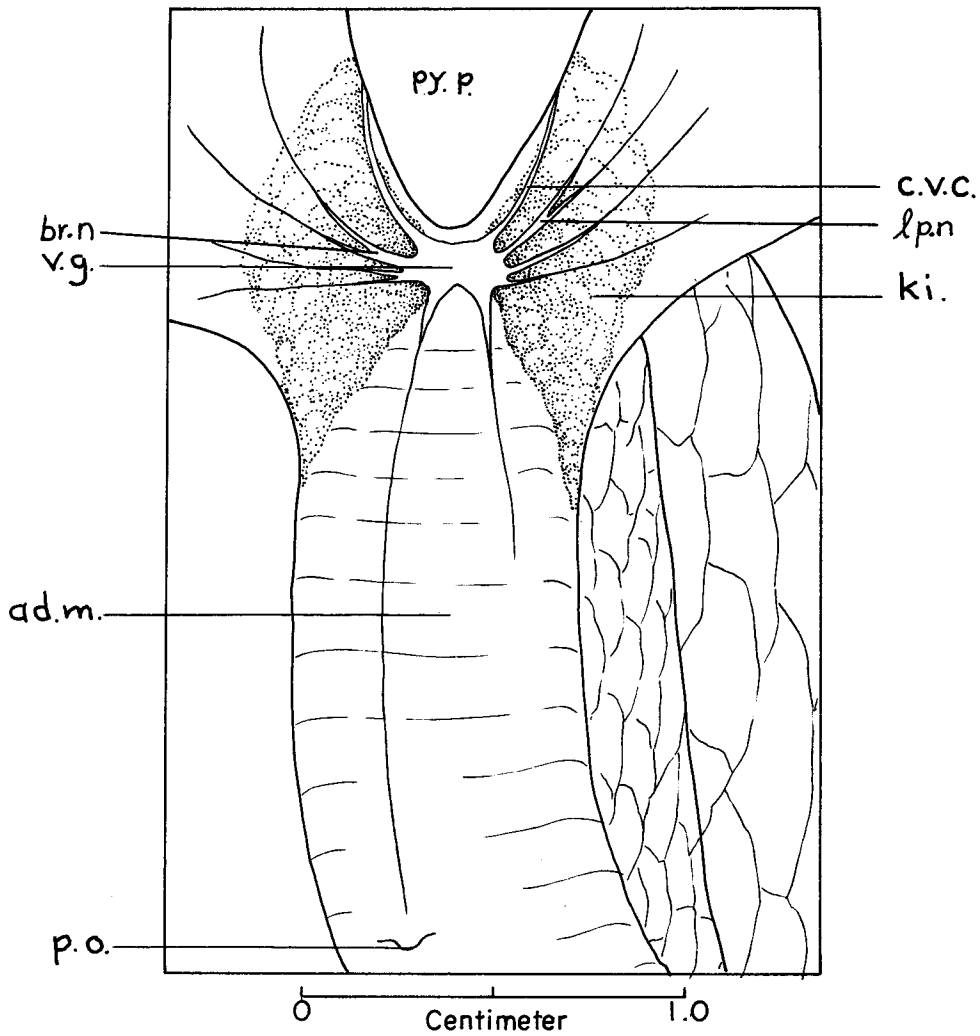

FIGURE 254.—Visceral ganglion of a large *C. virginica* seen through the epibranchial chamber. ad.m.—ventral side of the adductor muscle; br.n.—branchial nerve; c.v.c.—cerebro-visceral connective; ki.—kidney; l.p.n.—labial palp nerve; p.o.—pallial organ; py.p.—pyloric process; v.g.—visceral ganglion. The oyster was fully narcotized and the adductor muscle completely relaxed. Drawn from life.

ANATOMY

The visceral ganglion, the largest unit of the nervous system, is a wedge-shaped structure embedded on the anteroventral side of the adductor muscle in a depression formed by the junction of the translucent and opaque parts of the muscle. To see the ganglion in its natural position one must cut off the wall of the epibranchial chamber and lift the tip of the pyloric process. The location of the ganglion in such a preparation, examined from the right side of the oyster, is shown in figure 253. The entire ganglion can be examined in situ in an intact oyster. For this purpose the oyster is narcotized until the valves gape, and a beam of light is directed into its cloaca with the oyster's posteroventral end held toward the observer; when the pyloric process is raised slightly with a probe, the ganglion becomes visible as a white or sometimes slightly yellowish flat organ (fig. 254). In the preparation from which the drawing was made the muscle was completely relaxed and the gaping distance between the valves measured about one-half inch.

The visceral ganglion is highly developed in all Ostreaceae (Rawitz, 1887). The right and left components, fused into a single organ, are distinguishable, and the ganglion appears to consist of three parts, one central section and the two

lateral sections from which emerge six pairs of nerves. In some bivalves the ganglion and the nerves are pigmented, but not in the oyster.

The pair of cerebral ganglia of the oyster (fig. 253, c.g.) is located at the bases of the labial palps. The position of these small organs is slightly asymmetrical in relation to the palps, with the left ganglion slightly lower than the right one. Because of such asymmetry, only one ganglion is usually seen in the transverse sections of the visceral mass made at the level of the bases of the palps. In large and thin ("poor") oysters the cerebral ganglia may easily be located, but in "fat" specimens they are not usually clearly visible.

The narrow cerebral ganglion of each side is bent at a sharp angle: this gives it the appearance of a saddle sitting over the basal membrane of the epithelium of the palps (fig. 255). The cerebral commissure emerges from the end of the ganglion (c.com.) and makes an inverted U-shaped loop which passes dorsally over the esophagus and connects with the ganglion of the opposite side.

The following nerves emerge from the anterior side of the visceral ganglion: The cerebro-visceral connectives rise from the anterior side of the ganglion and soon are buried in the connective tissue of the visceral mass (figs. 253, 254, 255, c.v.c.); next to the connectives and slightly dorsal to their roots are the anterior pallial nerves (a.p.n.), which run forward through the kidney, pass across the pericardium wall toward the dorsal part of the body and along their course give off branches extending to the central part of the mantle. Two branchial nerves (figs. 253, 254, br.n.), arise near the roots of the cerebro-visceral connective and run parallel to it for a short distance. These nerves are more easily recognizable than the others because they form a convex curve and enter the gill axis on each side of the body accompanied by the efferent blood vessels. The two distinct branches of the lateral pallial nerves originate from the extreme points on the sides of the visceral ganglion. The outer branch (upper in fig. 254) almost immediately enters the mantle, while the inner branch (lower in fig. 254) divides into numerous smaller nerves which establish contact with the circumpallial nerve (fig. 253, c.p.n.). The posterior pallial nerve (fig. 253, 255, p.p.n.) runs from the ventral end of the ganglion along the ventral side of the adductor muscle as far as the rectum and divides into smaller branches

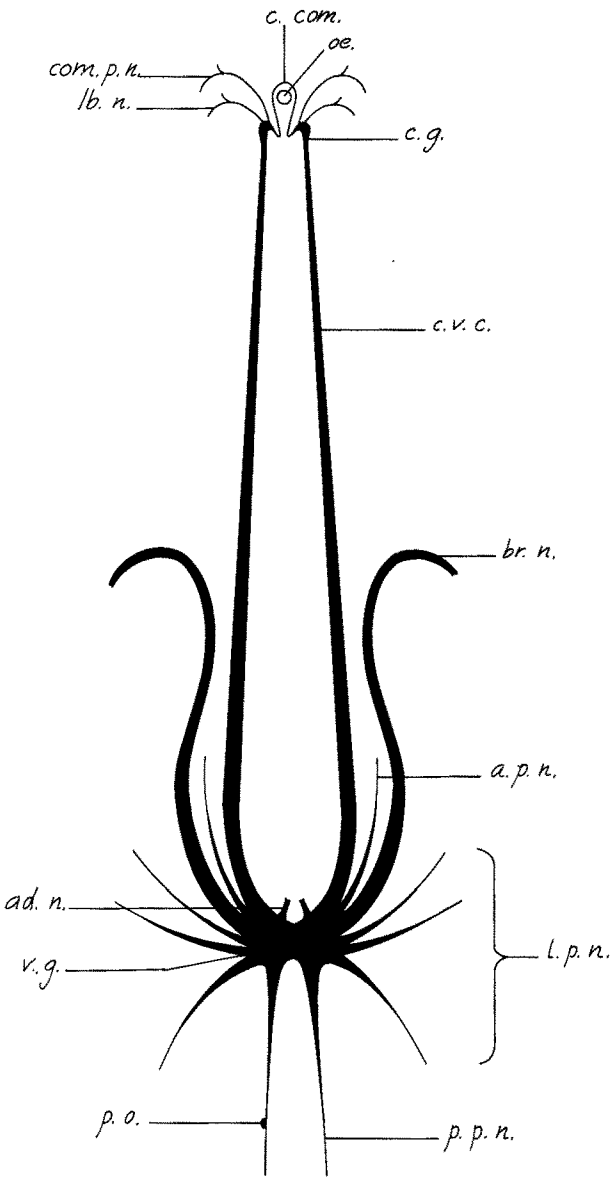

FIGURE 255.—Diagram of the nervous system of *C. virginica* seen from the anterior side. ad.n.—adductor muscle nerve; a.p.n.—anterior pallial nerve; br. n.—branchial nerve; c.g.—cerebral ganglion; c. com.—cerebral commissure; com.p.n.—common pallial nerve; c.v.c.—cerebro-visceral connective; lb.n.—labial nerve; l.p.n.—lateral pallial nerves; oe.—esophagus; p.o.—pallial organ; p.p.n.—posterior pallial nerve; v.g.—visceral ganglion.

which penetrate the mantle. The pallial organ (fig. 255, p.o.) is located along the course of this nerve. A pair of adductor nerves arises from the dorsal side of the ganglion and immediately enters the muscle tissue (fig. 255, ad.n.). They are not visible from the ventral side of the muscle.

Except for the pair of cerebro-visceral connectives, only a few nerve trunks originate from the cerebral ganglia. The common pallial nerve (figs. 253 and 255, com.p.n.) enters the mantle of the corresponding side and establishes connection with the dorsal portion of the circumpallial nerve. The labial nerves (lb.n.) branch to the four labial palps.

The circumpallial nerve (fig. 253, c.p.n.) is a fairly large nerve trunk which runs parallel to the edge of the mantle. Throughout its course it is accompanied by the circumpallial artery and supplies numerous branches to the tentacles and makes connections to the radial nerves which extend from the base of the mantle to its edge (see: fig. 86 in chapter V). The circumpallial nerve is connected anteriorly with the cerebral ganglia and posteriorly ends in the visceral ganglion. Stimuli received anywhere on the mantle may be transmitted to the entire nervous system of the oyster by this circular nerve. Because of this arrangement the oyster may respond to stimuli as a whole in spite of separation of its nerve centers.

The cerebral and visceral ganglia also are joined by a pair of relatively broad and long cerebro-visceral connectives (fig. 253, 255, c.v.c.), which constitute the main nerve trunks through which communication is maintained with all the parts of the body.

MICROSCOPIC STRUCTURE

The ganglia are formed of a central core or the neuropile, tightly packed bundles of nerve fibers, and the cortex made of several layers of nerve cells. This arrangement gives the ganglia a resemblance to the white and gray matter of the central nervous system of vertebrates. A layer of loose connective tissue forms the outer sheath of the molluscan ganglia.

The visceral ganglion is a relatively large, wedge-shaped structure embedded on the ventral side of the adductor muscle in the depression between its two parts (fig. 256). In the oyster the ganglion is completely fused but its paired origin is clearly seen on a tangential section (fig. 257).

The cortex is made of a continuous layer of nerve cells. Scattered nerve cells also occur in the neuropile. The ventral side of the ganglion facing the epibranchial chamber is covered with a unicellular layer of epithelium.

The nerve cells which in the oyster and other bivalves form the cortex were described by Rawitz (1887), whose paper remains the major contribution to the histology of the molluscan nervous system. To obtain the entire nerve cells with their axons Rawitz macerated small pieces of ganglia in 25 percent ethyl alcohol for 4 to 5 hours or in an aqueous solution of potassium bichromate (from 0.025 to 0.1 percent) for 8 to 24 hours.

Individual nerve cells of the oyster are either pear- or club-shaped with one, two, or several processes extending from their bodies. These processes give rise to fine fibrillae which enter the neuropile. Depending on the number of the processes, the cells are called unipolar (fig. 258, a, b), bipolar (e), and multipolar (c, d). The unipolar cells are more abundant than the other two types. The apolar cells, i.e., those without the processes, have not been found in bivalves, according to Rawitz.

The size of nerve cells varies. The multipolar cells are usually the largest; their dimensions, without the processes, range from 14.5 μ by 5 μ to 20 μ by 8 μ. The unipolar and bipolar cells are smaller, varying in size from 12.5 μ by 4 μ to 14 μ by 6 μ. The tapered ends of the cells give rise to the nerve fibers, which enter the neuropile where they combine with other nerve fibers to form several compact bundles. Single bipolar and unipolar cells are scattered throughout the neuropile, but do not aggregate into distinct nuclei or groups. The protoplasm of the nerve cell is dense and is deeply stained with Ehrlich's and Delafield hematoxylin.

The nerve cells and their axons are supported by a framework of connective tissue cells which descend from an outer sheath of the ganglion. These cells were observed first by Freidenfelt (1897). Bochenek (1906) and Jakubski (1912, 1913) described the supporting elements in the ganglia of *Anodonta*, *Pinna*, and several gastropods, tunicates, and echinoderms, and regarded them as typical glia cells. Jakubski distinguished three groups of glia cells: (1) Star-shaped flat cells with oval nuclei and thin processes which continue as neuroglia fibers were found in the outer sheath of the ganglion, (2) spindle-shaped cells with a pointed nucleus usually have two outgrowths and are most common in the inner portion of the ganglion for which they form a supporting framework; and (3) "neuropile glia cells", which occur singly, scattered through the neuropile. Jakubski

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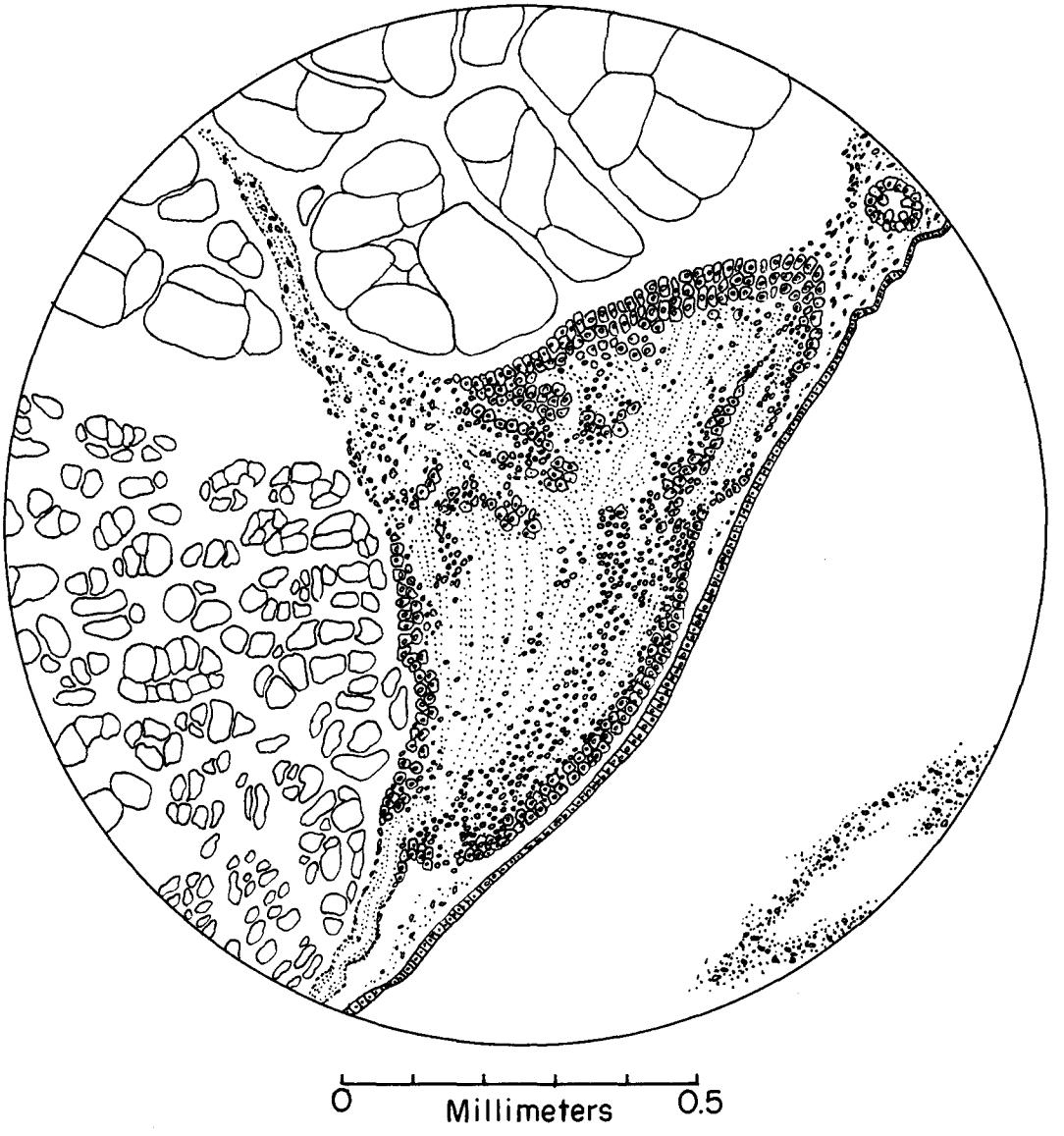

FIGURE 256.—Visceral ganglion of *C. virginica*. Transverse section at the right angle to the fibers of the adductor muscle. Bouin, hematoxylin-eosin.

(1912) pointed out that the interstitial elements of the neuropile do not isolate the nervous elements, while in the nerves and in the commissures the glia cells surround a number of nerve fibrillae which form distinct tracts. Of the three different types of glia cells described by Jakubski, the narrow, spindle-shaped cells could be seen in the preparation of the ganglia of *C. virginica* stained with Delafield and iron hematoxylin. Nissl granules were described in the multi-polar nerve cells at the ends of siphons in *Mya* (Piéron, 1941).

The nerve fibers which form the neuropile are clearly noticeable in sections of the visceral ganglion (fig. 256); some of them cross the ganglion, while others enter the viscero-cerebral connective on the same side where they emerged.

Rawitz (1887) described in detail the pathways of these fibers in the visceral ganglion of *Mytilus*. He found that in each half of the ganglion approximately one-quarter of the fibers originates from the nerve cells of the same section; one-quarter arises from the opposite half; one-quarter is derived from the cerebro-visceral connective of the corresponding side; and one-quarter originates in the cerebro-visceral connective of the opposite side. It is difficult to determine these pathways in the

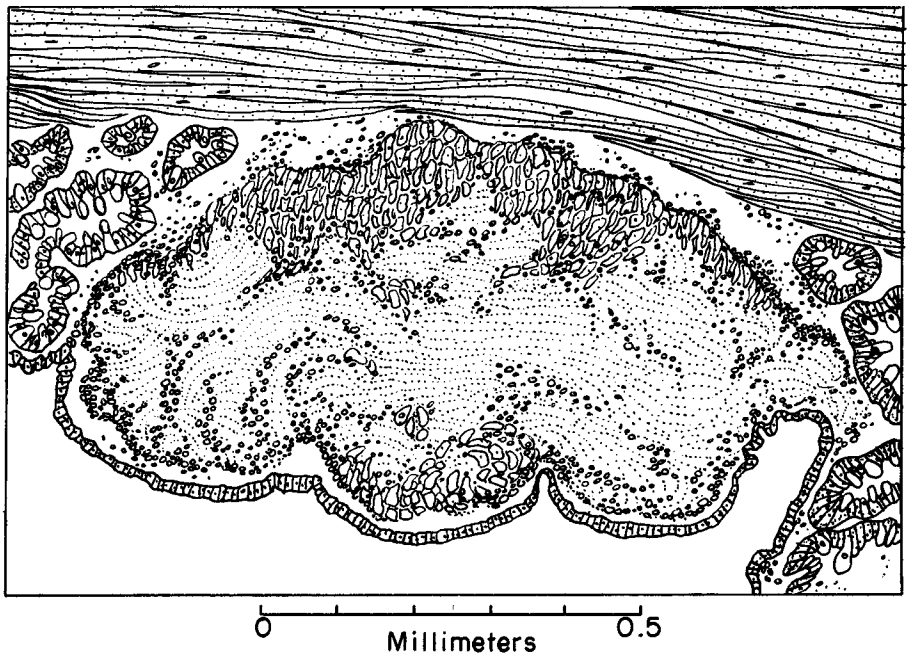

FIGURE 257.—Visceral ganglion of *C. virginica*. Tangential section. Bouin, hematoxylin-eosin.

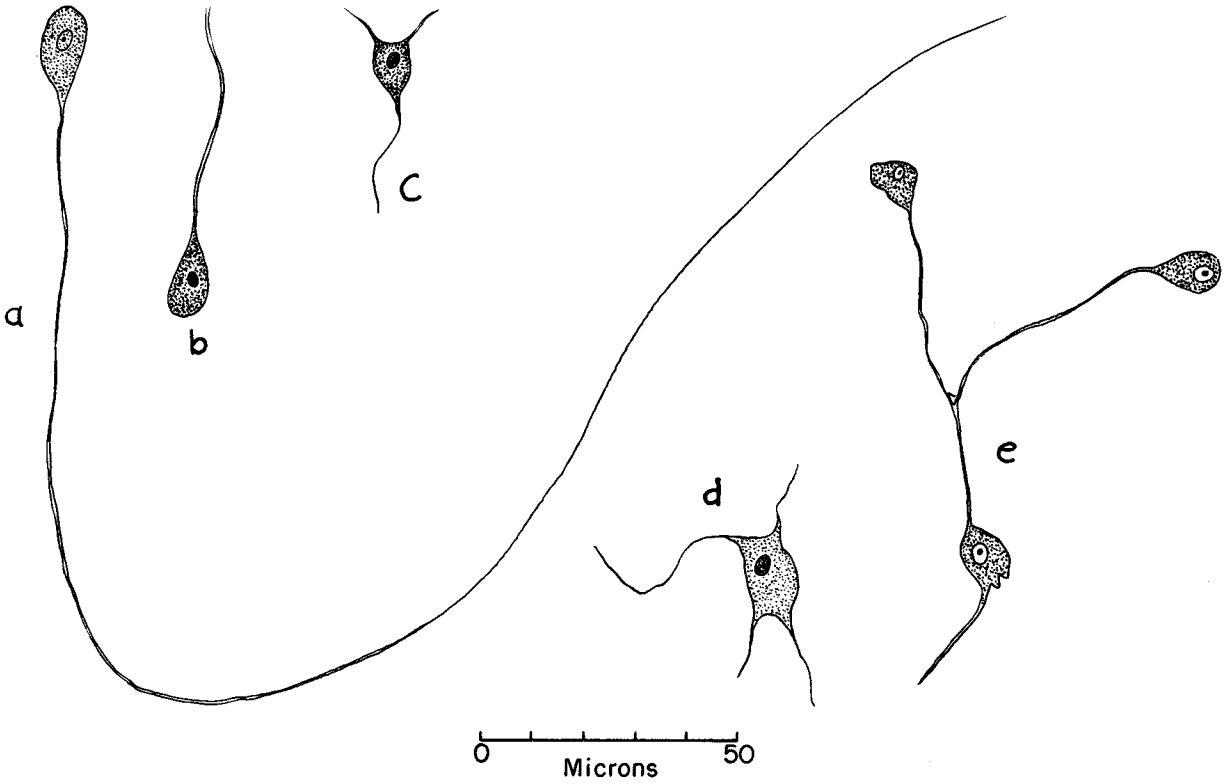

FIGURE 258.—Nerve cells isolated from the visceral ganglion of *O. edulis*, according to Rawitz (1887). a, b,—unipolar cells; c, d,—multipolar cells; e,—bipolar cells.

sectioned material of the oyster ganglia. The crossing of some fibers from the right to the left side and their extension into the connective can be seen, but there is no way to estimate the relative abundance of these fibers. There is not enough evidence to establish with certainty which fibers run from the nerve cells of the connective into the ganglion and which follow the opposite direction.

The tissues of the cerebral ganglion are less compact than those of the visceral ganglion, and the entire organ is rather indistinctly separated from the underlying connective tissue (fig. 259). The cerebral ganglia are located on each side of the oyster directly under the surface epithelium but separated from it by a thin layer of connective tissue fibers. The inner part of the cerebral ganglion (fig. 260) consists of bipolar cells of medium size. The outer layer, corresponding to cortex, is made up of large unipolar and multipolar nerve cells with dense protoplasm, stained dark with hematoxylin. Loose connective tissue covers the ganglion on the outer side. The entire organ is less compact than the visceral ganglion.

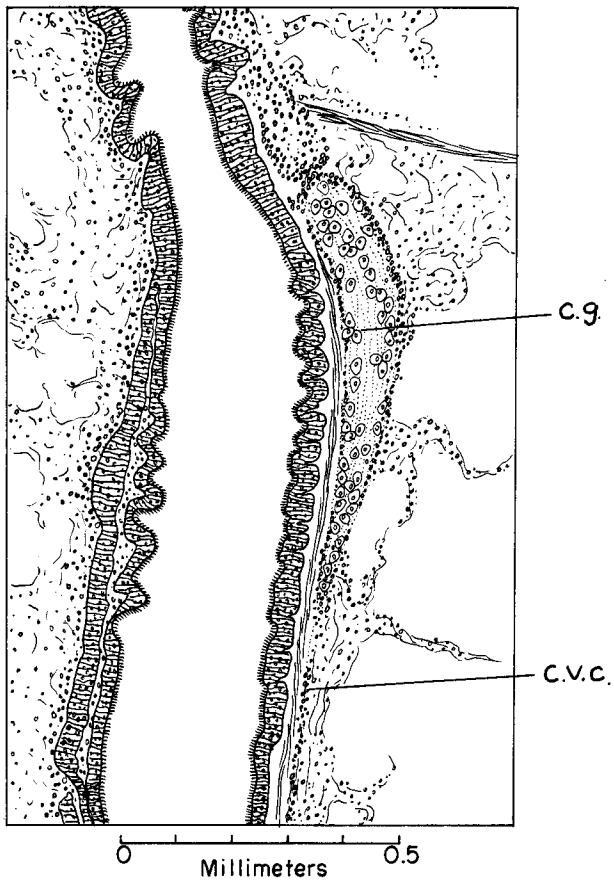

FIGURE 259.—Longitudinal section of a portion of the cerebral ganglion, (c.g.) at the base of the labial palps of *C. virginica;* c.v.c. the beginning of the cerebro-visceral connective. Kahle, hematoxylin-eosin.

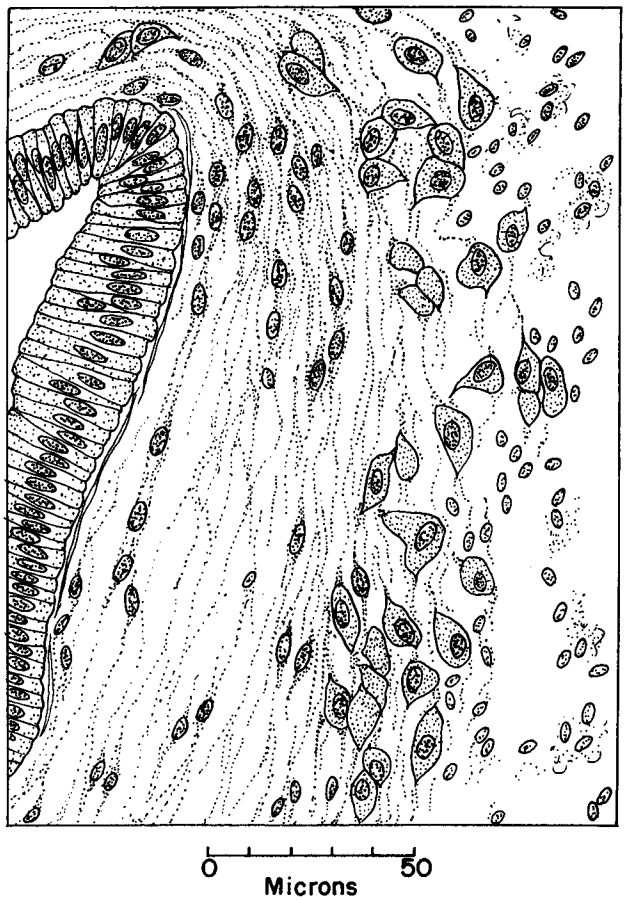

FIGURE 260.—Small portion of a longitudinal section of the cerebral ganglion of *C. virginica* under the epithelium of the base of the labial palps. Large unipolar and multipolar nerve cells form a cortex layer. Medium sized bipolar nerve cells and nerve bundles occupy the central part of the ganglion. Loose connective tissue covers the structure (right side of the drawing). Kahle, hematoxylin-eosin.

The structure of the cerebro-visceral connective is similar to that of the ganglia (fig. 261). A thick layer of large nerve cells surrounds the neuropile, which is divided into several bundles. There is no well formed sheathing, but small connective tissue cells are found along the periphery of the ganglion and are scattered throughout its entire structure.

A similar pattern of ganglionic structure repeats itself in many nerves emerging from the ganglia. This plan of organization is found in the circumpallial, branchial, and many other nerves.

The circumpallial nerve is surrounded by a sheath of connective tissue fibers (fig. 262). The

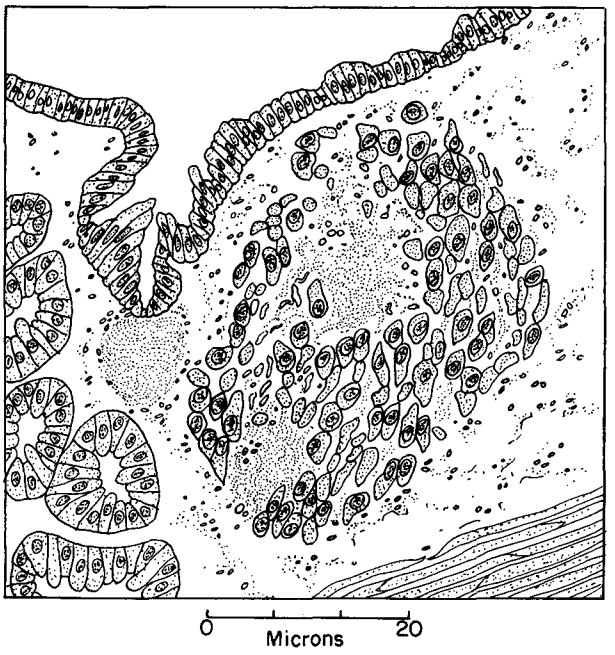

FIGURE 261.—Transverse section of the cerebro-visceral connective of *C. virginica*. Large aggregation of nerve cells on the periphery. Kidney tubules on extreme left. Kahle, hematoxylin-eosin.

nerve cells are predominantly at the periphery. Along its entire course the nerve gives rise to numerous branches which at regular intervals enter the tentacles and terminate at their surface in a number of small fibers which can be seen in gold-impregnated preparations (fig. 86, ch. V).

Small peripheral nerves such as the branchial nerves (fig. 263) and the radial nerves of the mantle (fig. 264) are made of bundles of fibers with occasional small nerve cells between them. The sheath of these nerves consists of a narrow layer of spindle-shaped connective tissue cells. A well-developed nerve net, visible in gold-impregnated sections (fig. 87, ch. V), is found over the entire mantle.

The anatomical and histological picture describes an intercommunication system which connects all the organs and parts of the oyster. Stimulus received, for instance, at the dorsoanterior part of the mantle and transmitted to the cerebral ganglia may reach the visceral ganglion either through the cerebro-visceral connective or directly via the numerous nerve branches which extend from the edge of the mantle and are connected by the circumpallial nerve. Stimuli transmitted to cephalic ganglia may reach the visceral ganglion through one of the connectives and vice versa. Thus, in spite of the absence of a central nervous system, the nervous reactions of the oyster are well integrated.

The major movements of the oyster are limited to the contraction and relaxation of the adductor muscle. Muscular contraction may be provoked either by the stimulation of the receptors of the tentacles and mantle or by impulses which originate from the internal organs. An example of the latter type of stimulation is found in the spawning reaction of the female. It consists of a series of rhythmic contractions of the adductor muscle associated with the release and dispersal of ova by the sexually mature oyster but in the immature specimen it cannot be induced by drugs, mechanical, electric, or thermal stimuli. The reaction is fully discussed in chapter VIII, page 172.

THE PALLIAL ORGAN

The only sense organs of the oyster are the tentacles of the mantle edge and the pallial (also called abdominal) organ. The structure and innervation of the tentacles have been already discussed in chapter V, page 85. The pallial organ is a very small structure attached to the anterior side of the adductor muscle inside the exhalant chamber of the gills. In order to see the organ the wall of the cloaca and of the epibranchial chamber must be dissected and the two sides drawn apart in the manner shown in figure 236 in chapter XI, page 259. The pallial organ is a small, colorless protuberance marked on the drawing by the letters pal.or.

The structure was discovered by Thiele (1889) in a number of bivalves iucluding *O. edulis*. In the European oyster the organ was described as a comma-shaped protuberance ("kommaformige Erhebung") with the pointed end turned to the right and the concave side oriented toward the posterior end. The organ on the right side is well developed but on the left side is small and degenerate. The description and illustration published by Thiele apply to *C. virginica*. In this species the pallial organ on the right side is also better developed while on the left side it is much smaller and frequently absent. A similar condition is found in *O. cucullata* (Awati and Rai, 1931).

The structure of the pallial organ of *C. virginica* is revealed in a series of sagittal sections (fig. 265). The rounded surface of the organ is covered by elongated epithelial cells with hairlike cilia which are longer than the cell bodies. This type of cell

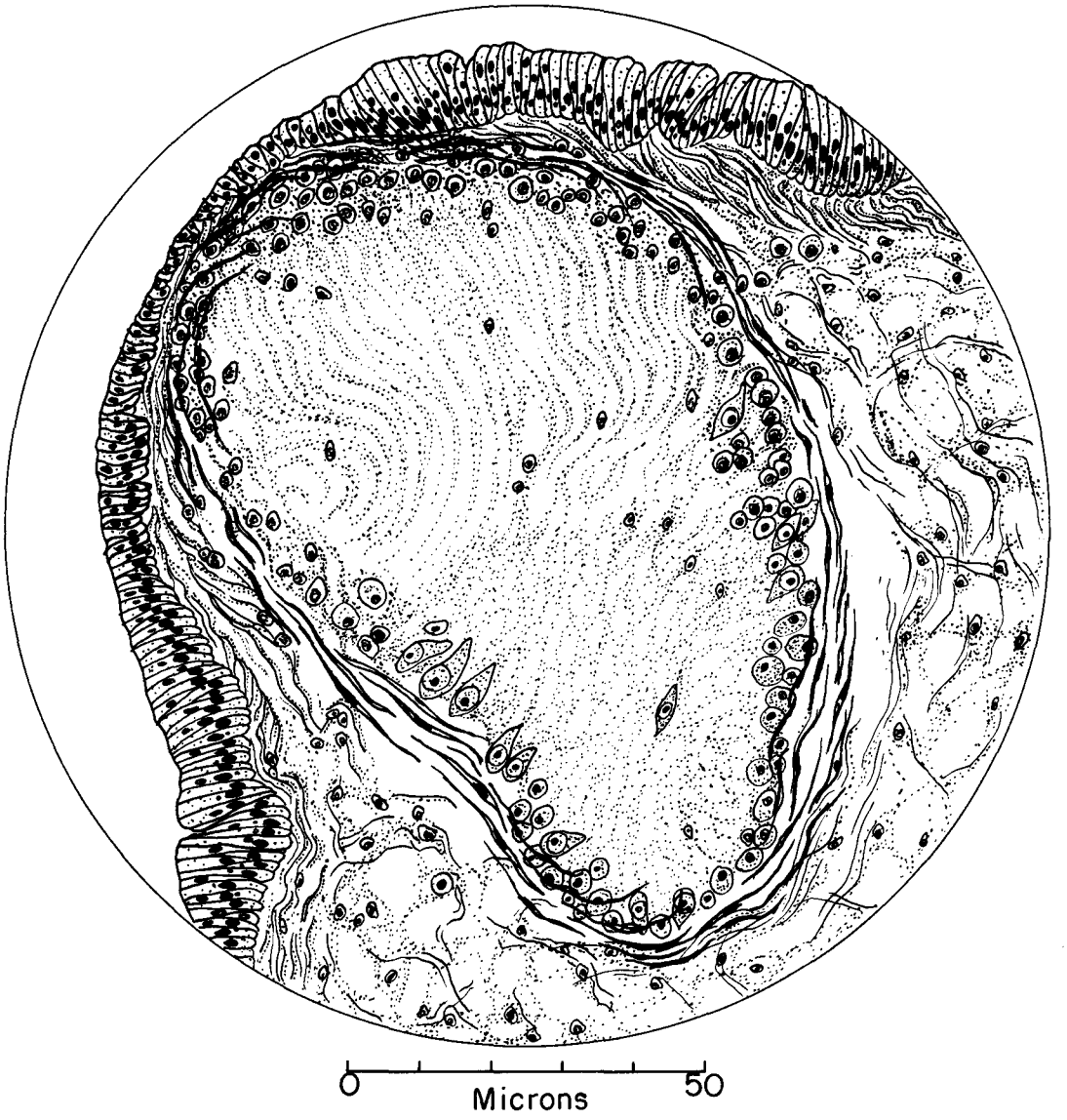

FIGURE 262.—Cross section of the circumpallial nerve of *C. virginica*. Kahle, hematoxylin-eosin.

closely resembles the so-called brush cells (Pinselzelle) described by Flemming (1884) in the sense organs of various mollusks. Thiele (1889) found such cells in the pallial organs of *Pinna, Avicula Arca, Lima,* and other bivalves. The epithelium of the pallial organ of *C. virginica* consists of two layers of cells: the deeper one is made of cells with globular nuclei, while in the surface layer the cells and their nuclei are oval-shaped (fig. 266). This observation is in agreement with the descriptions given by Thiele. The epithelial layer of the pallial organs of *Lima inflata* and *L. hians* is made, however, of a single layer (Studnitz, 1931). Thiele remarks that the cilia in *Arca noae* and *Lima* are motionless. It seems reasonable to assume that this may be true for the pallial organs of oysters. Unfortunately, the location of the pallial organ inside the exhalant chamber of the gills makes it impossible to study the function of the organ without inflicting serious injury to the surrounding tissues and nerves. From the histological picture it appears that stiff, hairlike cilia on the surface transfer the stimuli to the nerve endings and to the nerve trunk. Figure 266 represents a small section of the epithelial covering of the pallial organ of *C. virginica* examined at high magnification. Here the surface layer contains many sensory cells recognizable by their narrow

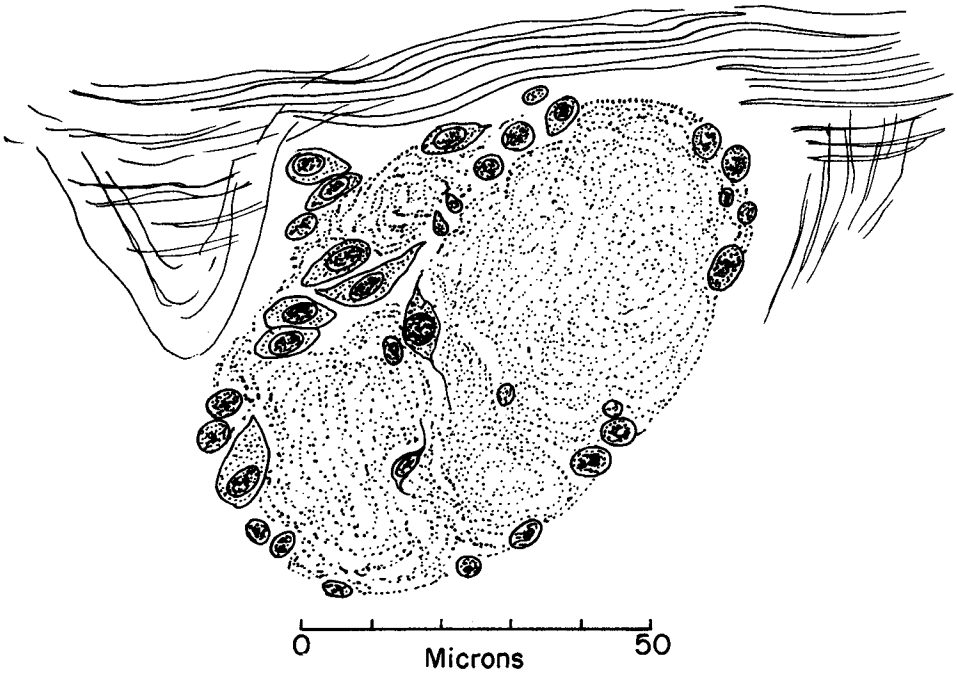

FIGURE 263.—Transverse section of branchial nerve of *C. virginica*. Gill muscles are above the nerve. Kahle, hematoxylin-eosin.

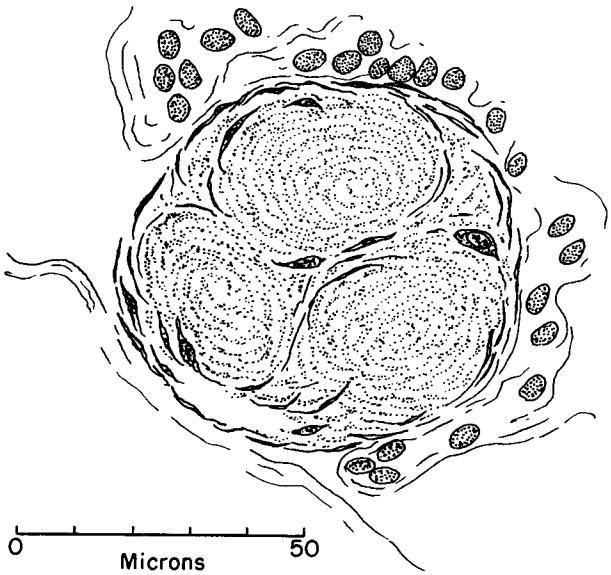

FIGURE 264.—Radial nerve in the mantle of *C. virginica*. The sheathing of connective tissue forms the periphery. Here the nerve consists of three distinct nerve trunks. Blood cells are scattered in the connective tissue of the mantle. Kahle, hematoxylin-eosin.

bodies and long processes which extend from the surface of the organ deep into the underlying connective tissues. The nuclei are elongated, and the cells are deeply stained with iron and alum hematoxylin. A large nerve trunk, shown in figure 265, sends its branches to the surface of the pallial organ. The nerve entering the organ is a branch of one of the posterior pallial nerves which emerge from the visceral ganglion. Typical vesicular connective tissue forms the core of the organ.

There has been no experimental study of the pallial organ, and its physiology is not well understood. Elsey (1935) expressed the opinion that its primary function is the regulation of respiratory current. Haas (1935) thought that in *Lima* the pallial organ is primarily concerned with chemical testing of water, and this view is repeated by Franc (1960) in his review of Bivalvia.

The long, stiff cilia seem to be more suitable for detecting mechanical disturbances than for responding to chemical stimuli. The organs of chemical taste in the oyster are the tentacles of the mantle. Because of their location at the edge of the mantle they are the first ones to come in contact with the irritating or poisonous substances in water and give the oyster a signal to prevent its access into the pallial cavity. It appears unreasonable that an organ of chemical taste should be located inside the water transporting system near its end. Dahmen (1923) and Awati and Rai (1931) think that the pallial organ in bivalves is primarily the organ for detection of

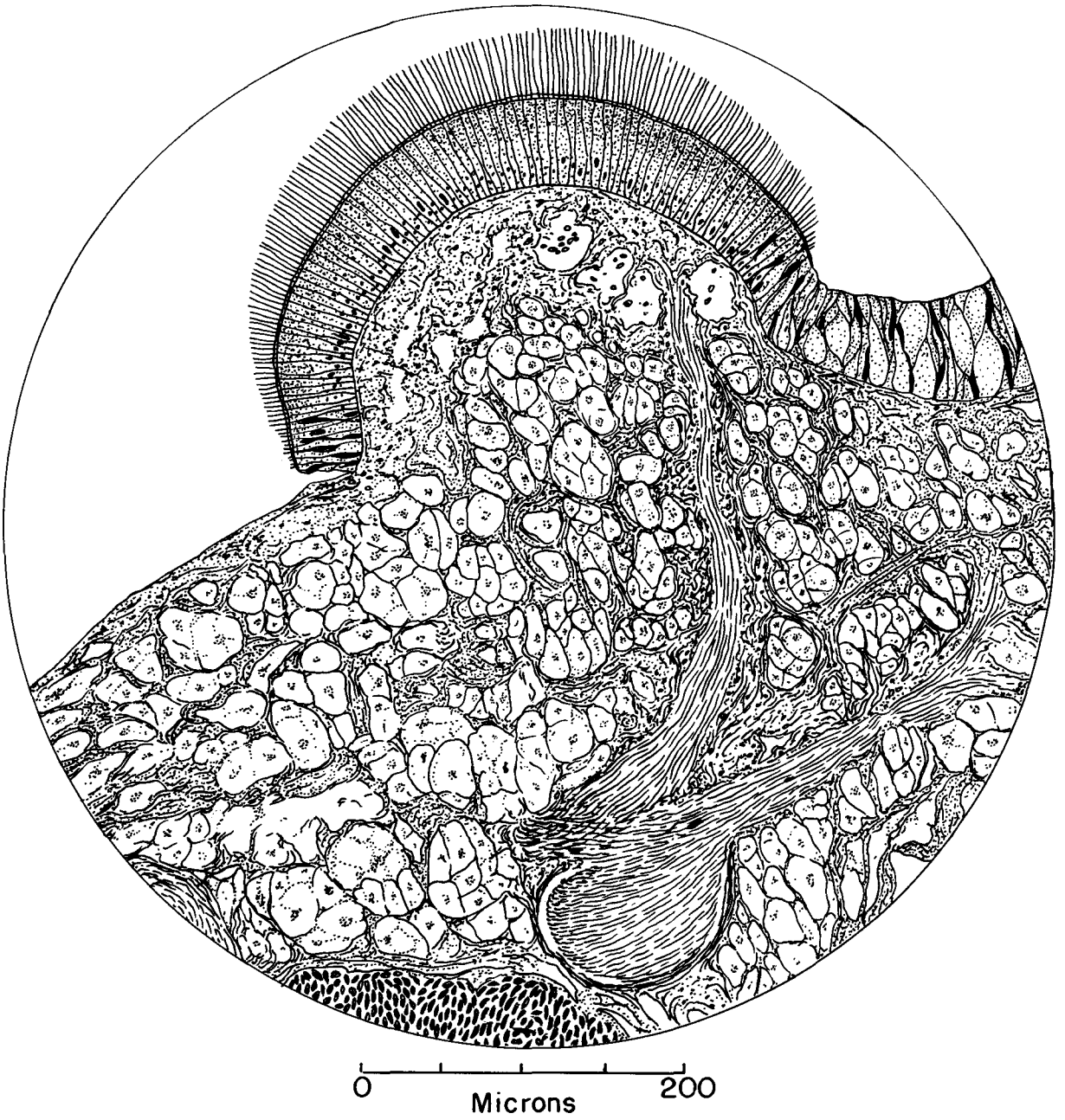

FIGURE 265.—Sagittal section of the pallial organ of *C. virginica*. Long ciliated cells rest on semiglobular protuberance of connective tissue richly supplied with blood vessels and ramifications of the posterior pallial nerve. Kahle, hematoxylin-eosin.

mechanical disturbance in the surrounding water. A final answer to the enigma of the pallial organ must await results of physiological studies which so far have not been undertaken.

A different type of pallial sense organ of the spat of *O. edulis* was described by Cole (1938), who found a thin-walled spherical and pigmented sac projecting from the inside mantle surface near its border, about one-third of the length of the free edge from the mouth. The cavity of the sac contains a comparatively large noncalcareous and nonsiliceous concretion which stains visibly with eosin. There are no cilia inside the sac, which is covered by very attenuated epithelium. Cole remarks that the organ is suitably constructed and in a favorable position

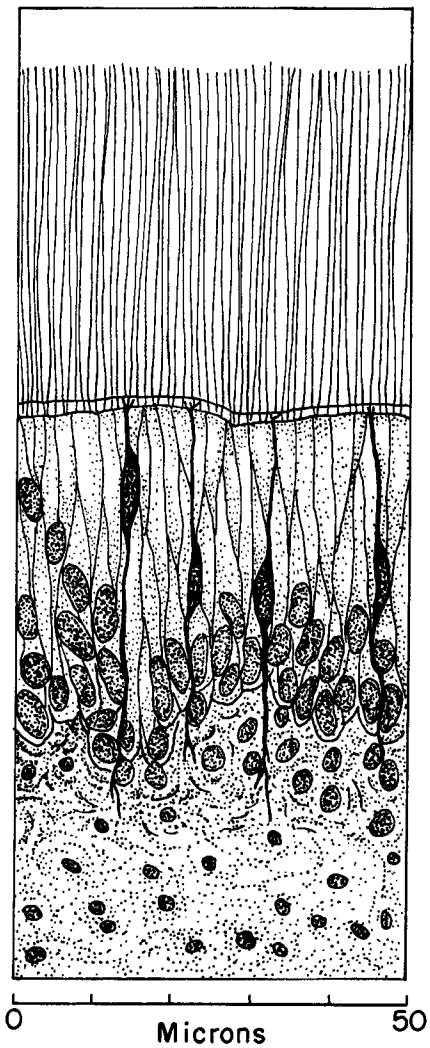

FIGURE 266.—Section of a small part of the ciliated covering of the pallial organ of *C. virginica* showing sensory cells between the ciliated epithelial cells. Kahle, iron hematoxylin.

for receiving and reacting to vibration. He found that this organ is fully developed in 4- to 5-day-old spat. It is not known whether the organ is present in adult *O. edulis* or in *C. virginica*.

SENSORY STIMULATION

Very little experimental work has been conducted on the physiology of the nervous system of the oyster. Most of the research on neurophysiology of other bivalves (*Pecten*, *Mytilus*, *Mya*, and *Anodonta*) dealt with the action potentials, tonus of the adductor muscle (see: ch. VIII), and stimulation of the siphons of *Mya* (Hecht, 1919a, 1919b, 1920a, 1920b; Piéron, 1941) and *Pholas* (Hecht, 1928). From a study of the action potentials along the nerve trunks of the siphon of the soft shell clam, Piéron calculated that the velocity of the transmission of stimuli along the nerve of this mollusk is of a magnitude of several meters per second. The value is probably common to other bivalves.

Neuro-secretory cells are present in a number of marine bivalves (*Nucula*, *Anomia*, *Mytilus*, *Modiolus*, *Chlamys*, *Lima*, *Donax*, *Arcopagia*, *Mactra*, *Cardium*, *Venerupis*, *Venus*, and *Paulora*) and probably may be found in other genera including the oyster (Gabe, 1955). These cells are typical small neurones of the cerebral and visceral ganglia but are absent in the pedal ganglia (Lubet, 1955). The amount of secretion they contain varies with the season and is apparently related to or parallels the sexual cycle for it increases with the maturation of sexual products (see: ch. XIV, page 312).

Sensory stimulation of the tentacles of the oyster by chemicals was studied by Hopkins (1932a, 1932b). He measured their sensitivity by determining with a stopwatch the latent period, i.e., the time elapsed between the application of a chemical and retraction of a tentacle or a group of them. The method is very simple. The mantle is exposed by cutting off a portion of shell, and the oyster is placed in sea water running at a constant speed through a rectangular tank with two communicating parts, one of them shallow and the other several inches deeper. Water in the taller part is kept at a constant level. The oyster is placed in the shallow portion of the tank, and a vessel containing the solution to be tested floats in the taller part. A three-way stopcock is mounted on the wall separating the two parts of the tank, one branch of the stopcock is bent horizontally and ends in a capillary nozzle placed a short distance in front of the tentacles. The two other branches are fitted with flexible rubber tubing at the end; one is lowered into sea water, the other into the floating vessel with the test solution. At the beginning of the test the stopcock is turned to deliver a constant, gentle stream of sea water to the tentacles, which remain in a relaxed state as long as the current and temperature of the water are constant. The stopcock is turned abruptly, and the sea water is suddenly replaced by the solution to be tested. The total time from the turning of the stopcock to the observed retraction of the tentacles is measured with the accuracy of one-tenth of a second. Before making a test the time required for a test solution

to pass from the container to the tip of the nozzle is recorded by using a colored solution and the value obtained is subtracted from the total time measured, giving the duration of the actual latent period. Since the vessel in the deeper part remains afloat, the level from which the solution is withdrawn remains constant and consequently there is no change in the velocity of current striking the tentacles.

All parts of this simple apparatus may be built of plastic. The following precautions should be taken: 1) the nozzle in front of the oyster must be firmly mounted and placed on a solid stand to avoid mechanical disturbance when turning the stopcock; 2) water and test solutions should be kept at equal and constant temperature; and 3) levels from which the sea water or the test solution are delivered to the tentacles should be constant in order to avoid a change in the velocity of current.

This method was satisfactorily used in the Woods Hole laboratory in testing the reaction of oysters to various organic compounds and contaminants.

Sensory stimulation of tentacles by inorganic salt solutions depends on the chemical composition of the substance used and its concentration. The relationship between the concentration of a given substance and the latent period, presented in Hopkins' papers, indicates that the effect, considered as the reciprocal of the latent period, is directly proportional to concentration. Sometimes a secretion of mucus covers the tentacles and impedes the reaction. In such cases Hopkins found it necessary to subtract a constant from the latent period values.

The range of latent period values in Hopkins' experiments varied from a fraction of a second to about 15 seconds. By using 0.5 M solutions of several inorganic salts Hopkins arrived at the conclusion that sensory stimulation is primarily the function of cations, which he listed in the following order of effectiveness: $K > Na > NH_4 > Li$.

Tentacles respond also to chemical stimulation by various organic compounds such as quinine sulphate, cumarin, etc. An odorous compound such as cumarin is detected by the oyster in a concentration of 0.0004 percent. The oyster responds also in a measurable reaction to a 0.004 percent solution of quinine sulfate. This concentration is one-eighth of the strength of the solution of quinine that can be detected by man's tongue (Hecht, 1918).

Cane sugar has little stimulating effect on the tentacles (Hopkins, 1932b). Tests with fructose (in sea water) that I made in the Woods Hole laboratory gave the following results:

0.05 percent	No reaction in 1 minute.
1.0 percent	Latent period 8 to 12 seconds in four out of 10 trials.
5.0 percent	Latent period 4 to 8.4 seconds.

Arabinose is more effective:

50 mg./l	Latent period 26 to 49 seconds in five out of 10 trials.
100 mg./l	Latent period 12 to 34 seconds in all 10 trials.
5.0 percent	Latent period 5 to 8 seconds in all 10 trials.

An interesting reaction was observed when diluted sea water (one part fresh water + three parts sea water) was used. The inner lobe of the mantle curled up, but the tentacles were not affected. The gradual curling ended in a sharp contraction of the adductor muscle. Normal sea water added to the edge of the nantle in a control experiment produced no such result.

A similar protective reaction was observed when the extracts of the meat of the oyster drill (*Urosalpinx cinerea*) and of the stomach of the starfish (*Asterias forbesi*) were used. The tentacles reacted strongly in contact with the undiluted juice of *Urosalpinx* with the latent periods of 1.5 to 3.6 seconds. These experiments suggest that sensory mechanism of the oyster may be sufficient to detect the close proximity of carnivorous gastropods.

The mechanism of sensory stimulation has not been adequately studied and is not fully understood. Its biological significance is, however, apparent. The warning received by the tentacles is transmitted through the circumpallial nerve of the mantle to the ganglia. If stimulation is sufficiently intense either a part or the entire mantle is withdrawn, the entrance to the gills is closed, and the ensuing contraction of the adductor firmly closes the shell. The three steps outlined can be observed under experimental conditions; they constitute the three distinct phases of the defense reaction of the organism.

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