CHAPTER VII

THE GILLS

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The gills of the oyster and other bivalves perform several important functions. They play a major part in respiration to which the mantle contributes a minor share. They maintain a steady current, filter the water, and collect food particles which are sorted and separated from detritus and other materials in suspension. They serve for the dispersal of sex cells at the time of spawning, and are used for the incubation of fertilized eggs in the larviparous species. The effectiveness of these functions is dependent on coordinated performance of the gill apparatus and on the contractions of the adductor muscle.

ANATOMY OF THE GILLS

Within the class of bivalves the structure of the gills varies in an increasingly complex series of modifications. The simplest of these is one pair of plumlike single gills or ctenidia with two rows of flattened filaments on each gill. This primitive type, present in the order Protobranchia (fig. 115, A), is found in *Nucula, Yoldia, Leda, Solenomya,* and others. More complex structure (fig. 115, B) occurs in the ark shells (Arcidae), scallops (Pectinidae), oysters (Ostreidae), sea mussels (Mytilidae), and other families of Filibranchia. This type is characterized by long and slender filaments kept in place by patches of interlocking cilia. In some of the bivalves of this group, including edible oysters, the gill lamellae are plaited into vertical folds and the reflected plates of the gills are completely united with the mantle and visceral mass. These were formerly designated as a separate order of Pseudolamellibranchia.

The highest degree of complexity is found in the gills of fresh-water mussels (Unionidae), cockles (Cardiidae), clams (Veneridae), and many other mollusks of the order Eulamellibranchia. In these bivalves the lamellae are joined by bars of connective tissue, the filaments are firmly connected by vascular junctions, and the entire gill has the appearance of a perforated, leaflike organ (fig. 115, C).

In the order Septibranchia (*Poromya, Cuspidaria*) the gills are degenerate. They are modified into perforated, muscular partitions between the two pallial chambers, and the gill filaments are greatly reduced (fig. 115, D).

The oyster gills consist of four folds (demibranchs or plates) of tissue suspended from the visceral mass. Two folds on each side of the body arise from a common ridge or gill axis, which is composed of connective tissue and muscles (fig. 73, g.m.). In a cross section made at right angles to the axis of the gill, each demibranch is V-shaped, with the two branches of the V forming its ascending and descending lamellae. The descending lamella arises from the gill axis; its opposite number is the ascending lamella. The two outer ascending lamellae, one on each side of the body, are fused with the mantle. The two inner demibranchs are joined together at

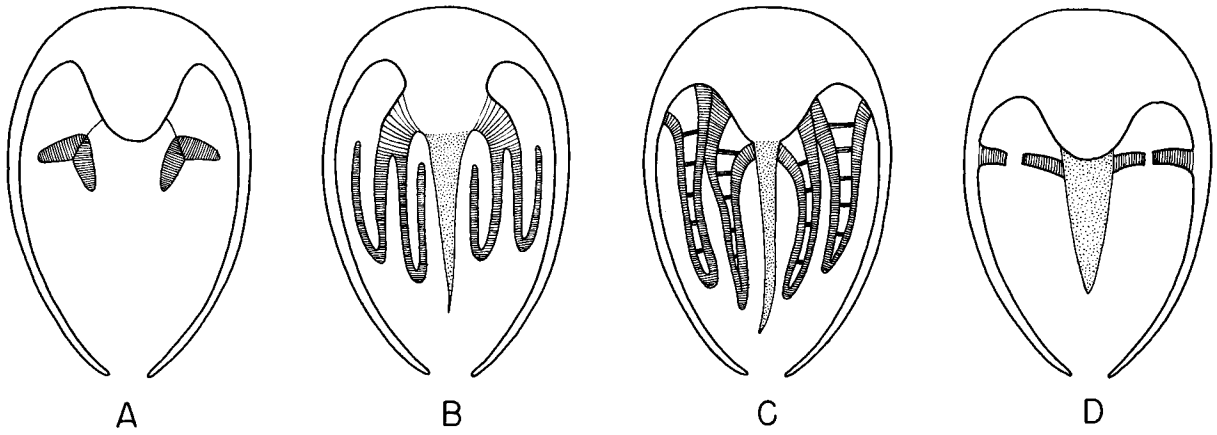

FIGURE 115.—Diagram of the four types of bivalve gills according to A. Lang (1900). A—Protobranchia type (*Nucula, Yoldia, Leda,* and others); B—Filibranchia type (Pectinidae, Ostreidae, Mytilidae, and others); C—Eulamellibranchia type (Unionidae, Cardiidae, Veneridae, and others); D—Septibranchia type (*Poromya, Cuspidaria*).

the central axis of the gills under the common afferent vein (fig. 73, c. af. v.). The section across all four demibranchs resembles two W letters joined together at the center.

Along the entire length of the gill runs the interlamellar space, which in places is divided by the interlamellar partitions or septae into a series of vertical compartments called the water tubes. The septae end close to the junction of the demibranchs and the visceral mass, so that the upper portion of the interlamellar space forms a continuous channel along the horizontal axis of each demibranch. This condition is found only at the upper (dorsal) part of the body at the level of the stomach and above it (fig. 116, *A*). At approximately the level of the heart the entire gill structure has only three points of attachment, in the center at the visceral mass and at each side where the gills fuse with the mantle (fig. 116, B.).

The entire chamber system of the gills can be visualized as four passages which at the level of the heart merge into two epibranchial chambers. The

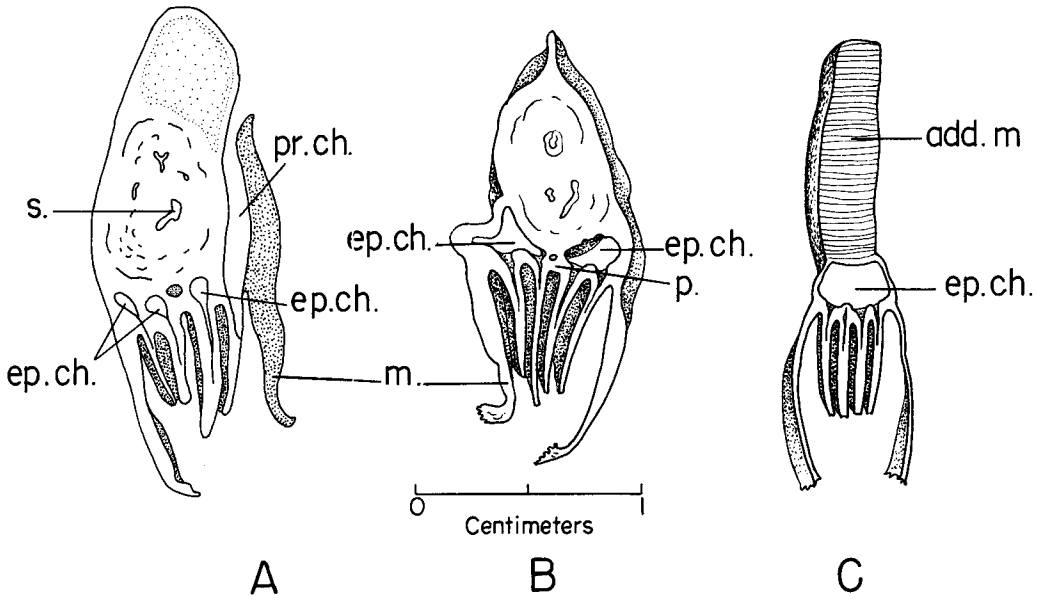

FIGURE 116.—Transverse sections of 1-year-old *C. virginica* (diagram drawn from sectioned and stained preparations). A—Section at the level of the stomach, s.; four epibranchial chambers at the base of the gills, ep.ch., and promyal chamber, pr.ch., at right. B—Section near the level of the heart, two epibranchial chambers, ep.ch., are separated by the pyloric process, p. C—Section at the level of the adductor muscle below the heart, common epibranchial chamber, ep.br.ch. Bouin, hematoxylin-eosin.

latter in turn lead to a common epibranchial chamber which, through the cone-shaped cloaca, opens to the outside.

There are no partitions, valves, or any other features for regulating the flow of water inside the chamber system. The current is maintained solely by the beating of the ciliary epithelium of the gills and of the lining of the chambers. Below the level of the heart the fusion of the gills with the median axis is lost and the two chambers, separated here by the pyloric process of the visceral mass (fig. 72, py.p.), merge together to form a commom epibranchial chamber (figs. 72 and 116, ep.br.ch.). This leads to a wide cone-shaped exhalant chamber or cloaca (fig. 72, cl.) which can be examined by forcing apart the posterior end of the valves and focusing a beam of light on its inner surface. The water tubes appear as large, round holes (fig. 72, w.t.).

PROMYAL CHAMBER

In oysters of the *Ostrea* type all the water collected by the gills is discharged through a single opening of the cloaca. In *Crassostrea*, however, the exhalant system is modified by the presence of an asymmetrical space on the right side of the body called the promyal chamber (fig. 116, pr.ch.). This irregularly shaped pocket between the mantle and the visceral mass extends in a dorsoposterior direction from the level of the pericardium to a wide outside aperture which may be seen by forcing the valves apart and examining the space between them. Openings of the water tubes similar to those found on the inner wall of the cloaca are visible inside the chamber (fig. 75)

The promyal chamber was first observed by Kellogg (1892), who suggested that the water from the gills may be discharged through it. Stafford (1913) showed the chamber in one of the illustrations of his book but did not refer to it in the text. The full anatomical significance of the promyal chamber in *C. virginica* was described by Nelson (1938) and by Elsey (1935) for *C. gigas*.

The position occupied by the promyal chamber makes it apparent that water from the dorsoanterior part of the right demibranch is discharged through this chamber and does not pass through the cloaca. After releasing carmine suspension near the gills of an actively feeding oyster (*C. virginica*), one can observe some of the red discolored water being expelled through the promyal chamber while the principal stream is passing through the cloaca. In spawning males the sperm shed from the right gonoduct is frequently discharged through the promyal chamber.

In assessing the relative importance of the promyal chamber in the movement of water through the gills, Nelson (1938) states that out of 36 water tubes in the right demibranch of *C. virginica* the first 14, comprising more than half the length of the demibranch, are in free communication with the promyal chamber. The remaining 22 water tubes discharge water into the narrowed portion of the epibranchial chamber beneath the adductor muscle or into the cloaca. In the absence of measurements of the amount of water discharged through the promyal chamber, it is impossible to state what percentage of the total output is discharged through the chamber. From anatomical evidence it may be concluded that the greatest part of the water used for ventilation of the gills leaves through the cloaca and only a minor portion through the promyal chamber.

Relative dimensions of the different parts of the exhalant system of the gills can be demonstrated clearly by casts made with plaster of Paris or with latex. Before being injected, the oyster should be completely narcotized. The material used for injection is then forced through both the cloaca and the promyal chamber while the oyster is gently and frequently tapped to permit good penetration to the very ends of the water tubes. When all the passages are full the valves are pressed together and tied with a string. The material is permitted to set for 24 hours before the shells are opened and the soft parts of the oyster removed.

The various parts of the water exhalant system of *C. virginica* are shown in figure 117, which represents the cast of the inner gill chambers viewed from three different angles. The promyal chamber (fig. 117, left, pm. ch.) occupies an irregular area on the right side of the visceral mass and ends in an aperture almost twice as large as the opening of the cloaca (cl.). The relation between the promyal chamber and the two demibranchs of the right side is shown in the central drawing (fig. 117) of the cast viewed from the left side. The right and left demibranchs are separated by a septum (s.) in the upper portion of the posterior side of the gills (fig. 117, right). Most of the inner spaces of the gills are in direct connection with the cloaca; less than one-half of the right demibranch empties into the promyal chamber.

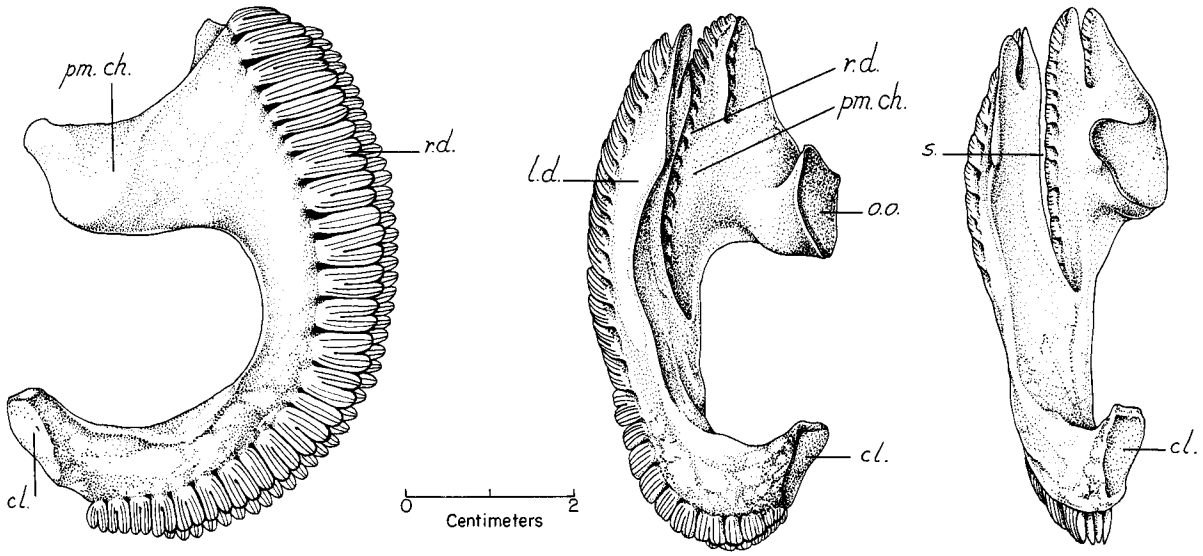

FIGURE 117.—Water exhalant system of the gills of *C. virginica*. Plaster of Paris cast of a large specimen. Left—view from the right side. Center—view at sharp angle from the left. Right—view from the posterior side of the gills. cl.—cloaca; l.d.—left demibranch; o.o.—outside opening (aperture) of the promyal chamber; pm. ch.—promyal chamber; r.d.—right demibranch; s.—septum separating the right and left demibranchs.

The relative size of the promyal chamber is variable. In some specimens it extends over three-fifths of the length of the gills and forms a spacious pocket (fig. 118). The exhalant system of *C. gigas* (fig. 119) is similar to that of *C. virginica*. In the specimens I examined, the promyal chamber extends approximately one-half the length of the gill, and the funnel-shaped cloaca was much wider than in *C. virginica*. In *O. edulis* the promyal chamber is absent and the entire system of water tubes, epibranchial chambers, and cloaca is symmetrical (fig. 120). In comparison with *C. virginica* and *C. gigas*, the cloaca of *O. edulis* is much broader and longer, which is probably the result of the almost circular shape of the body. The water tubes are shorter than in *Crassostrea*.

The promyal chamber also has been described for the Australian rock oyster, *Ostrea* (*Crassostrea*) *cucullata*, Born (*C. comercialis* I. and R.), and in *Ostrea* (*Crassostrea*) *frons* L. from the mangrove roots in Florida (Nelson, 1938).

Oysters of the *Crassostrea* type inhabit and thrive in the brackish and muddy coastal waters, which are less suitable for the mollusks of the *Ostrea* type. It has been implied by some investigators (Elsey, 1935; Nelson, 1938) that the tolerance to muddy waters is due to a superior cleaning mechanism which is somehow associated with the presence of the promyal chamber and prevents

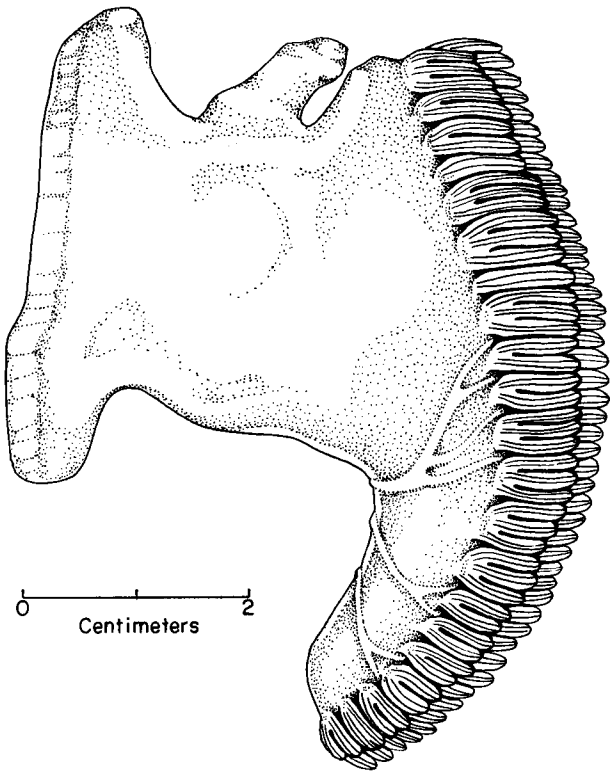

FIGURE 118.—Cast of the water exhalant system of a very large *C. virginica*. Note the extent of the promyal chamber along the gill axis and the impression made by the distended pallial arteries at the lower end of the right demibranch.

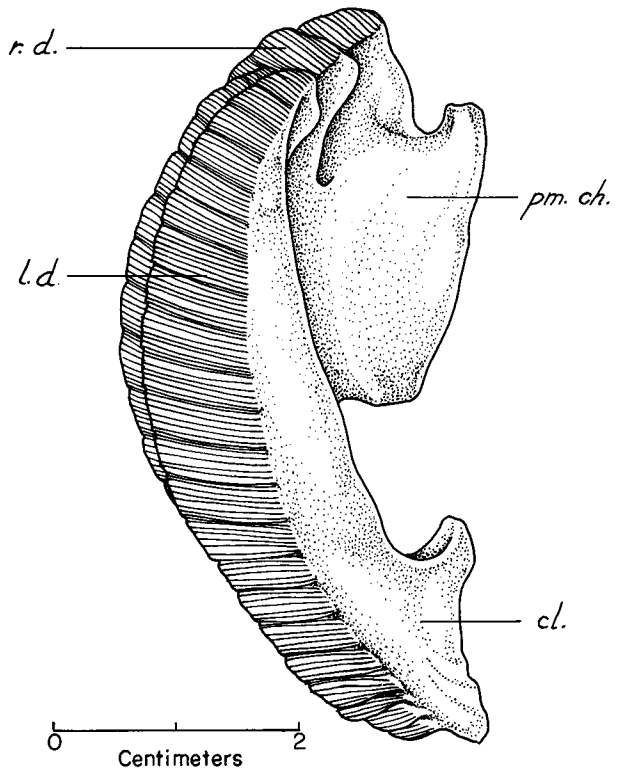

FIGURE 119.—Cast of the water exhalant system of the gill of *C. gigas* viewed from the left side. cl.—cloaca; l.d.—left demibranch; pm. ch.—promyal chamber; r.d.—right demibranch.

the accumulation of sediment in the pallial cavity. No evidence has yet been presented to corroborate this view. The physiological significance of the chamber is not known beyond the fact that it provides an additional outlet for the discharge of water through the gills. Elsey (1935) remarks that in *C. gigas* the promyal chamber allows a free passage of water when the gonads distend before spawning and encroach into the branchial space, partially closing the water tubes. Sections of the visceral mass of *C. virginica* with fully developed gonads do not show any "encroachments" into branchial space. The latter remains unobstructed, and the water tubes fully open. At present it is difficult to see what structural and physiological advantages are gained by the presence of a promyal chamber in *Crassostrea* oysters.

GILL LAMELLA

Each lamella of a gill consists of a great number of tubular filaments arranged at right angles to the axis of the gill. At the edge of the plate the filaments are reflected on themselves and continue upward along the plane of the ascending lamella. The filaments forming the gill-lamella do not lie smoothly on one plane; they are arranged in a series of transverse folds or plicae that give the surface of the gill a plaited appearance noticeable to the naked-eye. A transverse section (fig. 121) shows the arrangement of filaments in alternating grooves and ridges. The number of filaments on a single fold of an adult *C. virginica* is not constant. In my preparations it varied from 10 to 16 per fold.

There are three types of filaments that can be distinguished by their position, shape, and dimensions. The larger, or principal filaments (fig. 121, p.f.), are located at the bottom of the groove between the plicae. In cross section they have a triangular shape with two bulky chitinous rods forming two sides of this triangle. The rods are fused at the apex but are separated at the base, which contains a narrow blood vessel. The two transitional filaments (t.f.), one on each side of the principal one, are smaller and differ in shape from the ordinary filaments (o.f.), which form the rest of the plica. Sometimes the difference is insignificant. In general the ordinary filaments seen on cross section are elongated, club-shaped units.

Throughout their length the filaments of each plica are joined at the bases by regularly spaced interfilamentar junctions (if.j.), which consist of narrow bands of vascular connective tissue. The free portions of the filaments surround the oval-shaped openings, called ostia or fenestrae (o.), through which the water enters the inside passages of the gill. Numerous muscle fibers follow the interfilamentar junction and extend along both sides of the plica to its distal part (if.m.). At intervals, the two lamellae of each demibranch are connected by the partitions (interlamellar septa) made of connective tissue (il.s.) which run across the plate from one lamella to the other. These partitions are more numerous toward the distal (free) edge of the demibranch and diminish toward the base of the gill, where they are found only at about every sixth plica. The interlamellar junctions contain numerous muscle fibers, blood vessels, and nerves. The muscle fibers are arranged in three systems: the longitudinal muscles (l.m.) seen in cross section extend vertically from the proximal to the distal end of the lamellae; the transverse muscles (tr.m.) go from one side of the lamellae to the other; and the tangential

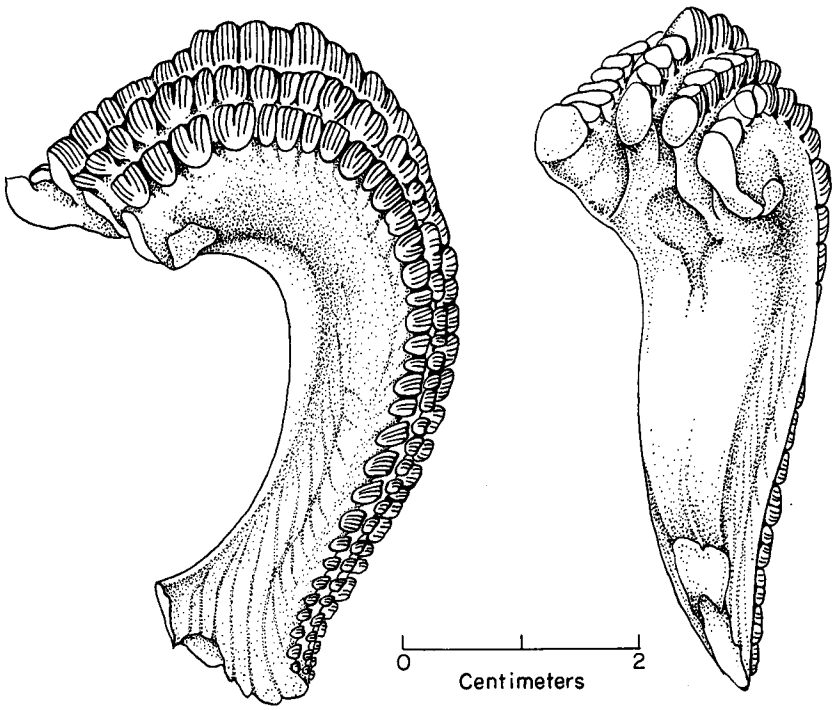

FIGURE 120.—Inner cast of the water exhalant system of the gills of *O. edulis*. Right—viewed from posterior side; Left—viewed from left side.

interlamellar muscles (il.m.) underlie the surface epithelium of the junction between the ascending and descending lamellae. At both ends of the junction near the location of the principal filaments the muscles branch off and form well-pronounced bands underlying the chitinous rods. It can be deduced from the pattern of distribution of the interlamellar muscles that their contractions bring the plicae of the two sides of the demibranch together, constrict the blood vessels, and reduce the diameter of the water tubes.

SKELETON

A framework of chitinous rods forms a scaffolding which supports the entire gill structure. The skeleton can be isolated from the tissues by brief treatment with a weak solution of sodium hydroxide, which does not affect the chitin. Structural elements cleared by this method are shown in figure 122. The skeleton of each filament resembles a ladder with the horizontal rungs slightly curved on one side and joined to the vertical elements by knobs of chitin. On both sides the supporting ladderlike unit of each filament is joined by cross pieces to the next units, forming a continuous framework. The vertical and horizontal bars surround the openings (ostia) between the filaments (o.). Each skeleton unit supports two adjacent filaments. The vertical bars correspond to the walls of the two adjacent filaments, while the horizontal members (the rungs of the ladder) are embedded in the tissue of the interfilamentar junctions. Two purposes are accomplished by such a pattern. The gill acquires rigidity and at the same time provides strong support for the delicate, sievelike membrane through which water passes into the water tubes. Heavy rods support the principal filaments (fig. 123). At the base of the gills the skeleton rods form massive V-shaped arches embedded in fibrous connective tissue (fig. 124).

THE FILAMENTS

The structural unit of the gill is a tubular filament of ciliated epithelium supported by skeleton rods. The central part of the filament is occupied by a space which is periodically filled with blood as the gill plates expand and contract. Connective tissue underlies the proximal part of the filament which consists of nonciliated, almost cuboid cells, tightly packed in a two-cell layer. The distal part of the filament is covered with ciliated cells (fig. 125). Bulky mucous cells occur at irregular intervals and discharge their

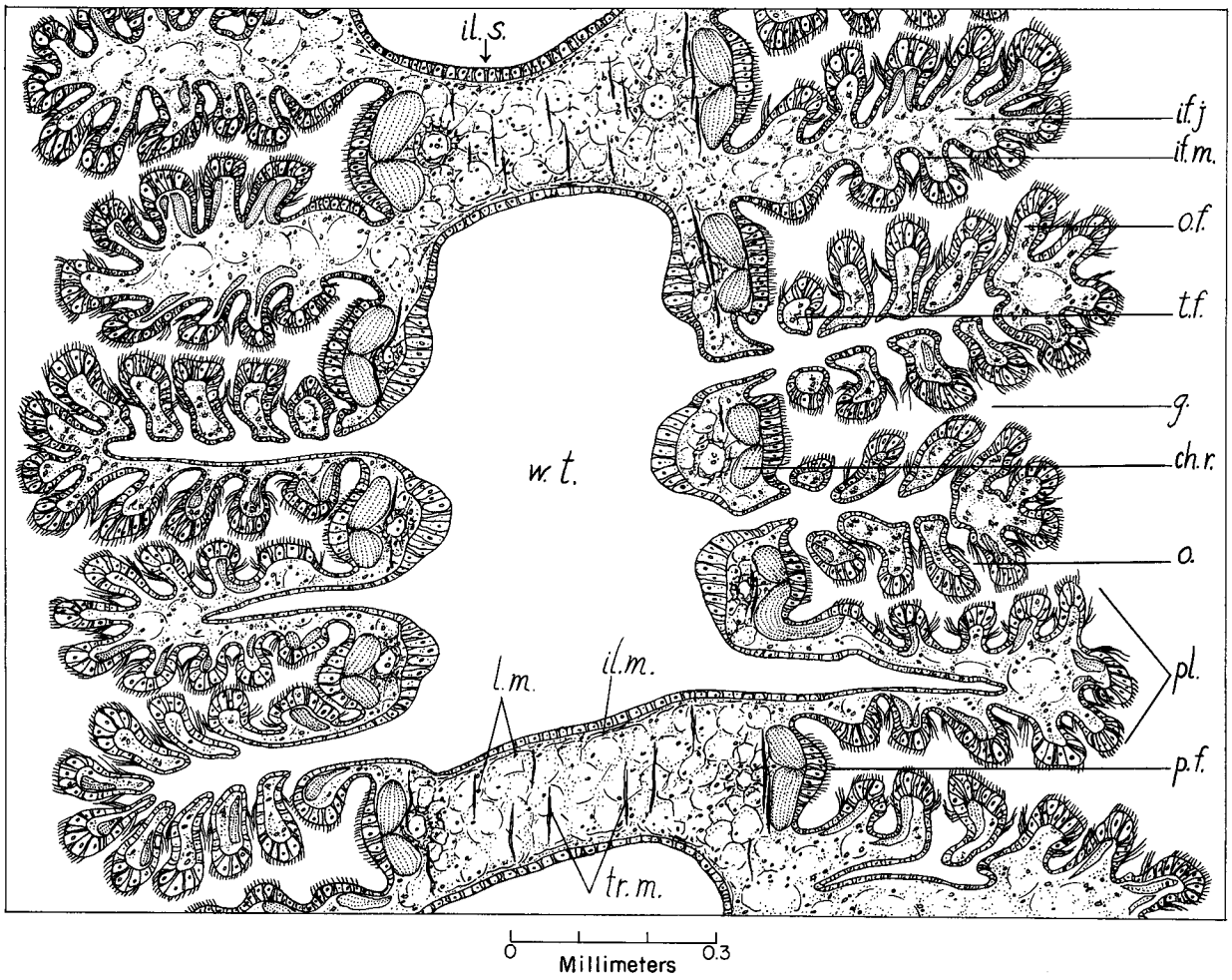

FIGURE 121.—Transverse section of the demibranch of *C. viriginica*. Kahle fixation, hematoxylin-eosin. ch.r.—chitinous rods; g.—groove; if.j.—interfilamentar junction; il.m.—interlamellar muscles; il.s.—interlamellar septum; l.m.—longitudinal muscles of the interlamellar septum; o.—ostium; o.f.—ordinary filament; p.f.—principal filament; pl.—plica; t.f.—transitional filament; tr.m.—transverse muscle of the interlamellar septum; w.t.—water tube.

content to the surface of the gills. The secreted mucus spreads over the gill plates and entangles the particles which settle on them. At the distal edge of the gill the filaments are fused together to form a terminal groove along which food is conveyed toward the mouth. The principal filaments differ from the others by their larger size and nontubular appearance. At the base of each filament there is a blood vessel located in a space between the chitinous rods. The epithelial cells are slightly larger than those of the ordinary filaments and have longer cilia (fig. 126).

OSTIA

Ostia or fenestrae, the oval-shaped open spaces between two adjoining filaments (figs. 121 and 125, o.), are framed by two vertical and two horizontal skeleton bars covered with epithelium. Their configurations and dimensions vary, depending on the degree of contraction of the filamental musculature and the distention of blood spaces. In an actively feeding oyster the contraction and expansion of the ostia regulate the passage of water through the gills. This can be observed on the surface of a gill exposed by cutting off a piece of shell. The dimensions of the ostia are somewhat correlated to the size of the oyster ova which pass through the gills during spawning (see ch. XIV, p. 303). In a viviparous *O. lurida* the ostia are large, varying from 90 by 45 μ in contracted state, to 180 by 60 μ when fully expanded. The ova of this species average 90 μ in diameter. In *C. gigas* and *C. virginica*, which have smaller eggs,

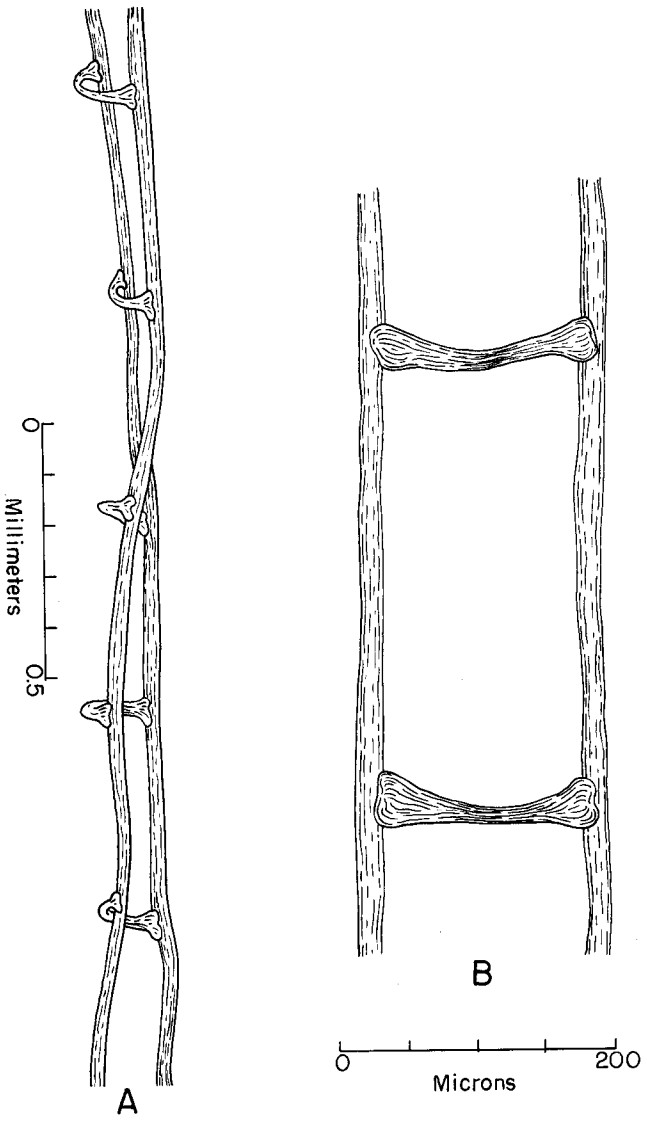

FIGURE 122.—Side view (A) and front view (B) of a skeleton of ordinary gill filaments of *C. virginica*. Soft tissues removed by sodium hydroxide. Unstained preparation, whole mount.

the ostia are approximately only one-third the dimensions of those in *O. lurida*.

CILIARY TRACTS

The surface of the filament is covered by several different ciliary tracts. Cells of uniform size on the outer surface bear the frontal cilia, which are relatively small and beat parallel to the surface of the filament (fig. 125, fr.c.). They are flanked on each side by a single laterofrontal cell (lf.c.) of larger size with a blade-shaped cilium, which according to Atkins (1938) occurs in the family Ostreidae and is somewhat different from the laterofrontal cells of other bivalves. In fixed and stained preparations this wide and curved cilium is frequently frayed. The shape of the cilium and the presence of the basal granules, typical for normal ciliated cells, both indicate that the laterofrontal cilium is formed by the fusion of ordinary filaments, a view which is confirmed by studies made with the electron microscope (see p. 132). The laterofrontal cells of *C. virginica* are fairly large and cone-shaped; their relatively small nuclei are located at the narrow, proximal end of the cell; and the protoplasm is devoid of granules and deeply stained with hematoxylin. The laterofrontal cilia of gills preserved in a relaxed state extend toward their opposing numbers on the adjacent filament and touch their tips. In a contracted gill they are bent and almost undistinguishable from the cila of the frontal cells. The length of the laterofrontal cila on sectioned and stained preparation varies from 11 to 15 μ. Accurate measurements, however, are difficult because of the bending of the cilia which do not remain fully extended even in completely narcotized cells. In *O. edulis*, according to Atkins (1938), the length of the laterofrontal cilia varies from 14 to 25 μ. The

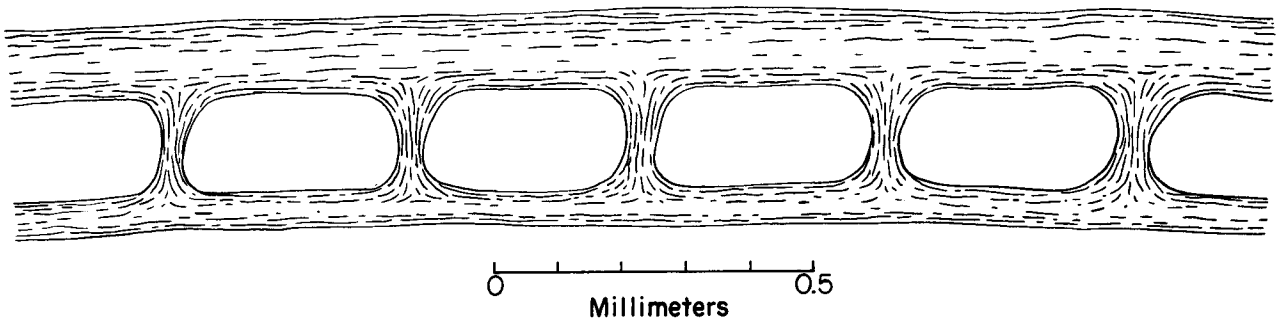

FIGURE 123.—Chitinous rod of the principal filament of *C. virginica*. Soft tissues removed by sodium hydroxide. Unstained preparation, whole mount.

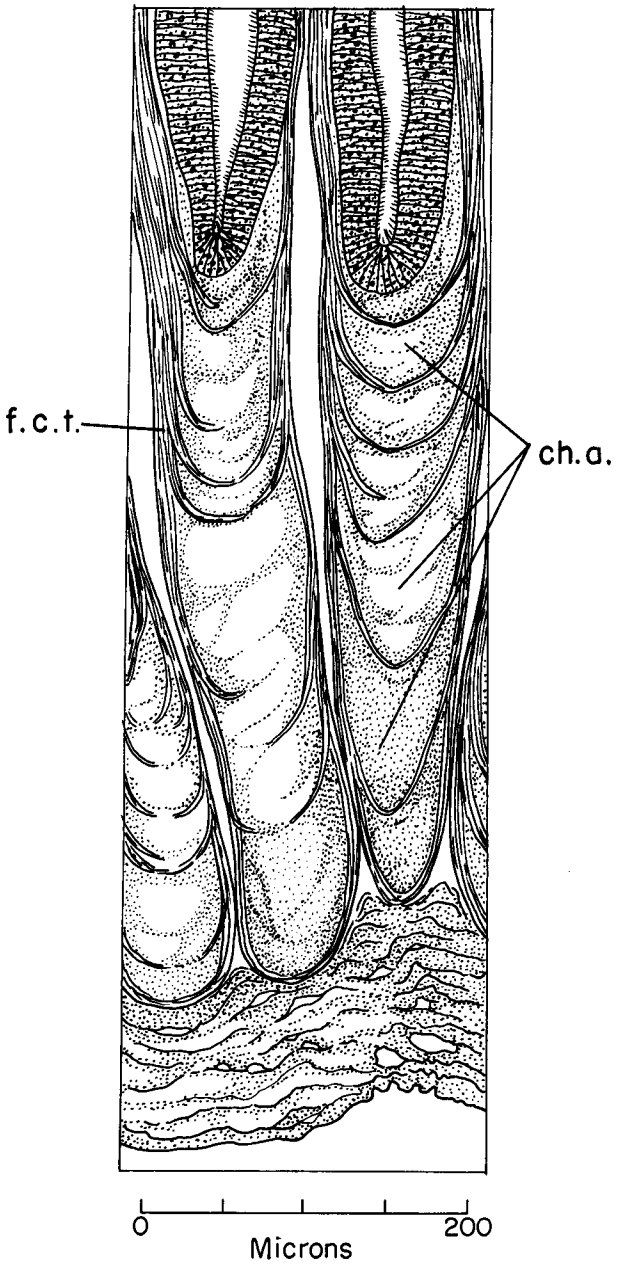

FIGURE 124.—Longitudinal section near the base of the gill of *C. virginica*. Chitinous arches, ch.a., are embedded in fibrous connective tissue, f.c.t. Osmic acid fixation, iron hematoxylin.

frontal and laterofrontal cilia of the principal filaments have the same structure as those of the ordinary filaments, differing only in their greater size. A short distance below the cell surface each cilium terminates in a basal body, a tiny granule from which a pair of rootlets extends deeper into the protoplasm and becomes undistinguishable near the nucleus (figs. 126 and 127).

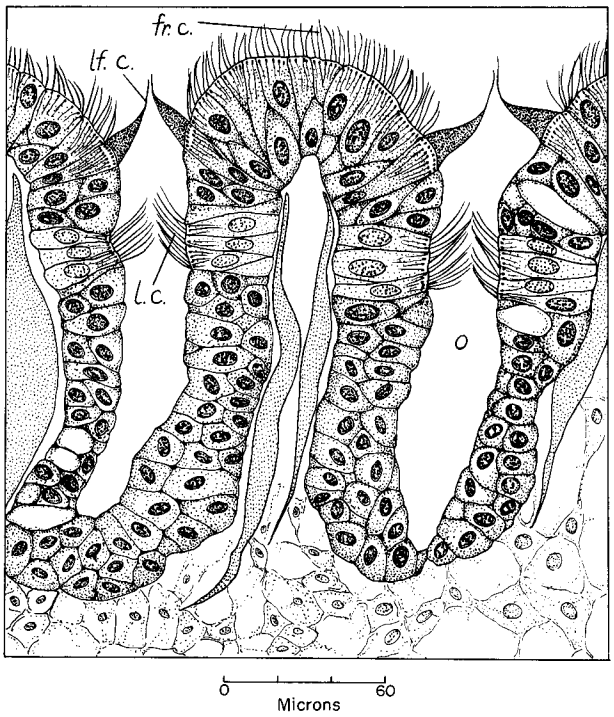

FIGURE 125.— Transverse section through ordinary filament of *C. virginica*. Vertical chitinous rods (stippled areas) and blood space are at the center. fr.c.—frontal cilia; lf.c.—laterofrontal cilia; l.c.—lateral cilia; o.—ostium. Kahle fixation; hematoxylin-eosin.

Besides the frontal and laterofrontal cilia, Atkins (1938) distinguishes in *O. edulis* the "fine frontal" and "paralaterofrontal" cilia, which run on both sides of the central portion of the frontal tract (fig. 127, f.f.c., para l.f.c.). He states (1938, p. 367) that: "Subsidiary laterofrontal cilia are present in Ostreidae, but are very difficult to distinguish even in the living gill." I was unable to identify these cells in sectioned preparations or in the living gill filaments of *C. virginica* examined under high power. The frontal cilia of this species appeared to be of uniform length along the entire cross section of the tract (fig. 125).

Beneath the laterofrontal cilia of the filaments there is a group of six large cells, four of them broad and two narrow, which bear large, stout cilia about 17 to 18 μ in length. These are the lateral cilia (fig. 125 and 127, l.c.), which bend forward slightly toward the outer surface of the filament and touch the cilia of the opposite group.

TERMINAL GROOVE

The free edge of a demibranch formed by the concrescence of the ascending and descending lamellae is a shallow trough called the terminal

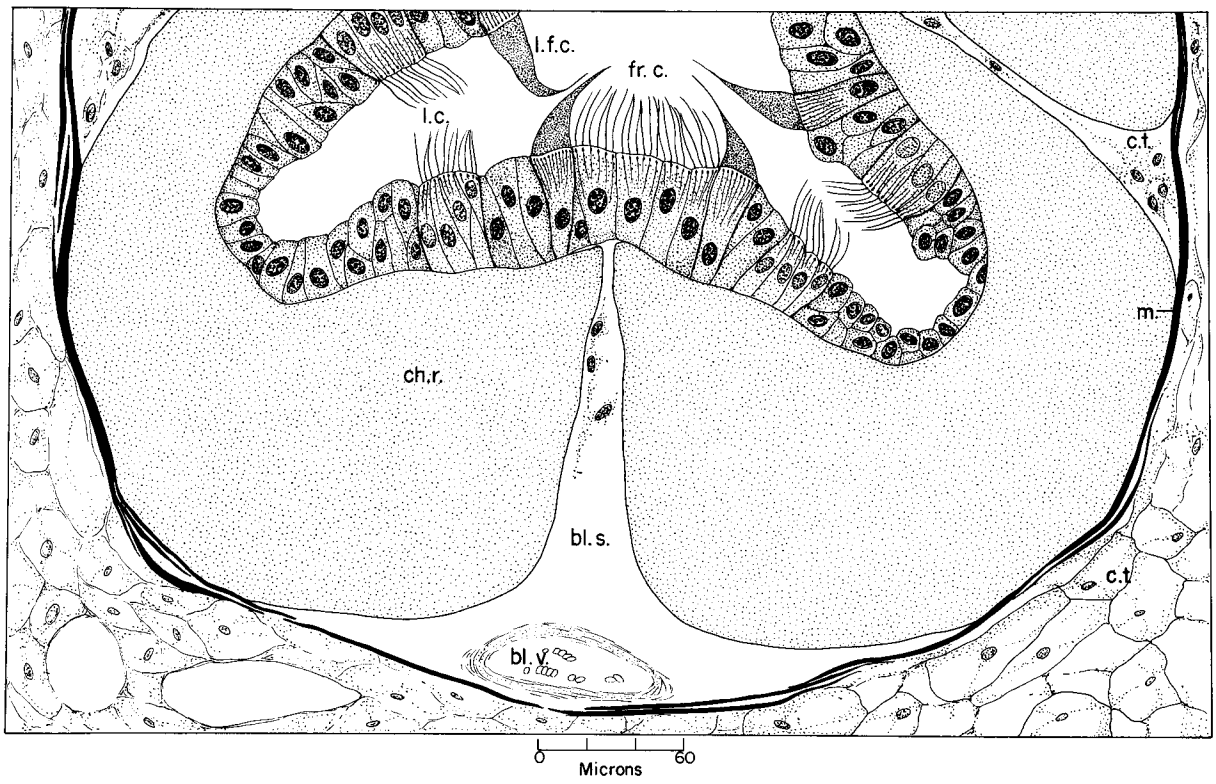

FIGURE 126.—Transverse section of the principal filament of the gill of *C. virginica* drawn from the same preparation as in figure 125. Note the well-developed muscle fibers, m., under the large skeleton bars, ch.r.. c.t.—connective tissue; bl.v.—blood vessel; bl.s.—blood space; fr.c.—frontal cilia; lf.c.—laterofrontal cilia; l.c.—lateral cilia; m.—muscle.

groove. This depression at the border of the gills extends their entire length. The epithelial lining of the terminal groove consists of columnar ciliated cells with large cilia and numerous mucous and eosinophilic cells. The epithelium rests on a basal membrane. Transverse muscle fibers extend between the two sides of the groove. During feeding the grooves are open, the condition which is shown in figure 128. Their contraction brings the edges together and closes the groove. In this way the oyster discards some of the material which was collected by the surface of the gill. The rejected particles entangled in mucus are dropped to the inner surface of the mantle and are discharged. The direction of the ciliary beat along the four terminal grooves is always toward the labial palps and the mouth.

THE MUSCLES OF THE GILLS

The gills of an actively feeding oyster contract and expand at frequent, although irregular, intervals. This behavior is difficult to notice in an intact oyster, but it can be observed in an oyster in which much of the valve has been cut off without injuring the adductor muscle and the gills. The mantle at the exposed area rolls up and leaves the gills in full view, and if carefully performed, the operation has no visible ill effect on the function of the gill.

The most conspicous movements which can be seen with the naked eye are the muscular contractions at the bases of the gills and the corresponding changes in the position occupied by the demibranchs. These four structures may stand apart like stiff leaves of a wide open album or they remain parallel, touching one another like the pages of a closed book. There is also a lateral movement of the filaments which brings them together or pushes them apart. This movement frequently occurs independently of the contractions of the demibranchs and may be limited to a small portion of the plica. Both types of movements affect the opening of the ostia, which are widely stretched when either the four demi-

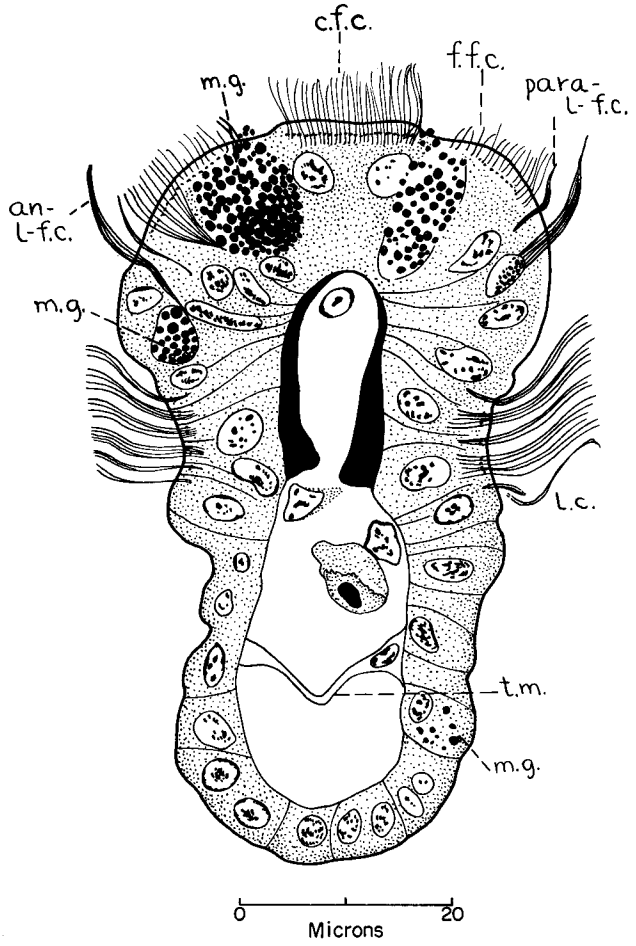

FIGURE 127.—Cross section of the filament of the gill of *O. edulis*, according to Atkins, 1938. an.l.fc.—anterior laterofrontal cilia; c.f.c.—central frontal cilia; f.f.c.—fine frontal cilia; para l.fc.—paralaterofrontal cilia; m.g.—mucous gland; l.—lateral cilia; t.m.—transverse muscle fiber. Chitinous rods are shown as black areas under the epithelium.

branchs or only a group of filaments stand apart and are constricted when the latter are drawn together.

Changes in the position of the demibranchs depend on two distinct systems of muscles located at the gill axis above and below the skeletal arches. In general the muscle fibers follow the configuration of the arches. The larger bands located inside the arches are the flexor muscles, which are attached to the inner sides of the two arms of an arch (fig. 129, f.). Their contraction brings the two adjacent demibranchs together. The smaller bands at the base of the arch (ex.) are the extensor muscles, which cause the demibranchs to stand apart. The action of the two bands shown in the

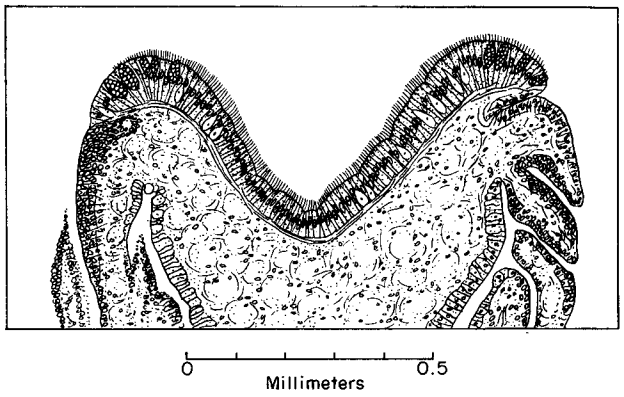

FIGURE 128.—Terminal groove at the edge of a demibranch of *C. virginica*. Longitudinal section of the demibranch. Bouin, hematoxylin-eosin.

figure is antagonistic. The extensor bands are smaller, probably because the elasticity of the chitinous arches pushes the demibranchs apart and this springlike action means that less force is required of the extensor muscles than of the flexor bands.

Other muscle bands of the gills, although less conspicuous than the flexors and extensors of the arches are, nevertheless, of great importance in regulating the transport of water through the complex gill apparatus and in facilitating the exchange of blood inside the gill filament. Water tubes of the gill can be constricted by the contraction of the muscles underlying the epithelium of the interlamellar septa and extending from one lamella to another (fig. 121, il.m.), while the contraction of the transverse muscles of the interlamellar septa compresses the blood vessels. The contraction of the longitudinal muscles of the septa (fig. 121, l.m.) results in the withdrawal and shortening of the entire demibranch. This reaction occurs spontaneously but can also be induced by stimulation. The contraction of the interfilamental muscles (if.m.) brings together the vertical rods of the gill skeleton, causes the curving of the crossbars, and constricts the blood space of the filament, forcing blood into the pallial veins.

Contractions affecting only part of the gill cause the blood to oscillate inside the gills. Because of the open nature of the lamellibranch circulatory system the direct return of blood from the gills to the auricles cannot be accomplished by the pumping action of the heart. Contractions involving the entire gill apparatus are needed to complete the renewal of blood.

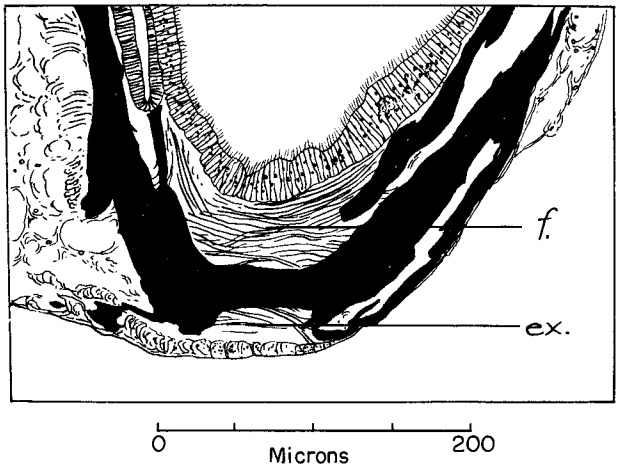

FIGURE 129.—Longitudinal section through the base of a demibranch of *C. virginica*. Kahle, Mallory triple stain. ex.—extensor muscles; f.—flexor muscles. Pieces of the skeleton arch are shown in black.

CILIATED CELLS

The structure and function of vibratile elements of the cells have been the object of numerous investigations beyond the scope of this book. The reader is, therefore, referred to comprehensive reviews of the problem of ciliary motion made by Gray (1928) and more recently by Atkins (1938) and Brown (1950). Several theories based on studies of the structure and action of cilia fail to give a satisfactory explanation of ciliary motion, which at present still remains a biological mystery.

Cilia examined in transmitted light or viewed on a dark background in reflected light appear to be optically homogenous. In polarized light they are birefringent (Schmidt, 1937). Observations with the light microscope disclose the presence of an axial filament (axoneme) surrounded by a thin sheet of cytoplasm (Wenyon, 1926). As a rule, the cilia emerge from tiny basal granules near the cell surface and penetrate through the cuticle, which under the light microscope appears as a thin homogenous membrane. Studies of the role and origin of basal bodies in various ciliated cells have resulted in a great number of speculations. Experiments by Peter (1899) showed that in small fragments of a crushed protozoan the cilia continued to beat as long as they were in organic connection with the adjacent pieces of cytoplasm. He deduced from this observation that the ciliary mechanism is located near the surface of the cell. Similar results were obtained with lateral cells stripped away from the filaments of *Mytilus* gills. The cilia that were removed from the basal granules remained motionless while those connected with them continued to beat (Gray, 1928). The microdissection technique in more recent years supports these findings. It was demonstrated that in the ciliated cells of the gills of *Anodonta* the motion of the cilia ceases when the cell is cut transversely in the immediate region of the basal granules. Transverse cuts made at any level within the proximal two-thirds of the cell had no effect on ciliary motion, but if the cut was made across the zone occupied by the fibrillae or rootlets in the distal third of the cell, the coordination of the ciliary motion was destroyed although the cilia continued to beat. These observations seem to support the validity of the theory, advanced independently by Henneguy (1897) and Lenhossék (1898), that the basal granule, homologous and sometimes identical with the centrosome of the mitotic figure, is the center which controls the activity of the cilium.

FINE STRUCTURE OF THE CILIA

With the advance of electron microscopy considerable progress has been made in the study of the fine structure of cilia. It has been discovered that throughout the plant and animal kingdoms, regardless of the position of the organism on the evolutionary level and irrespective of the organs studied, cilia have a common structural pattern. The cilia of the gill epithelium of the oyster are no exception to this rule. Thin sections of the frontal and lateral cells of the filaments fixed in buffered osmic acid and examined under the electron microscope show a structure which is undistinguishable from that of the cilia of vertebrates, protozoa, or the tails of spermatozoa. The cilium consists of a protoplasmic matrix in which are embedded 11 filaments; 2 single filaments are at the center and 9 double ones are arranged in a ring on the periphery. The central pair is connected to the peripheral ring by radial trabeculae or spokes. Short pieces of dense material join the outer filaments to the membrane (fig. 130), which binds more osmium and is, therefore, darker than their interior, making the cilia appear tubular (Fawcett, 1958). The two central filaments are oval shaped in cross section. The plane in which these filaments are oriented is similar for all the cilia of the cell and is thought to be perpendicular to the direction of the ciliary beat (Fawcett, 1958).

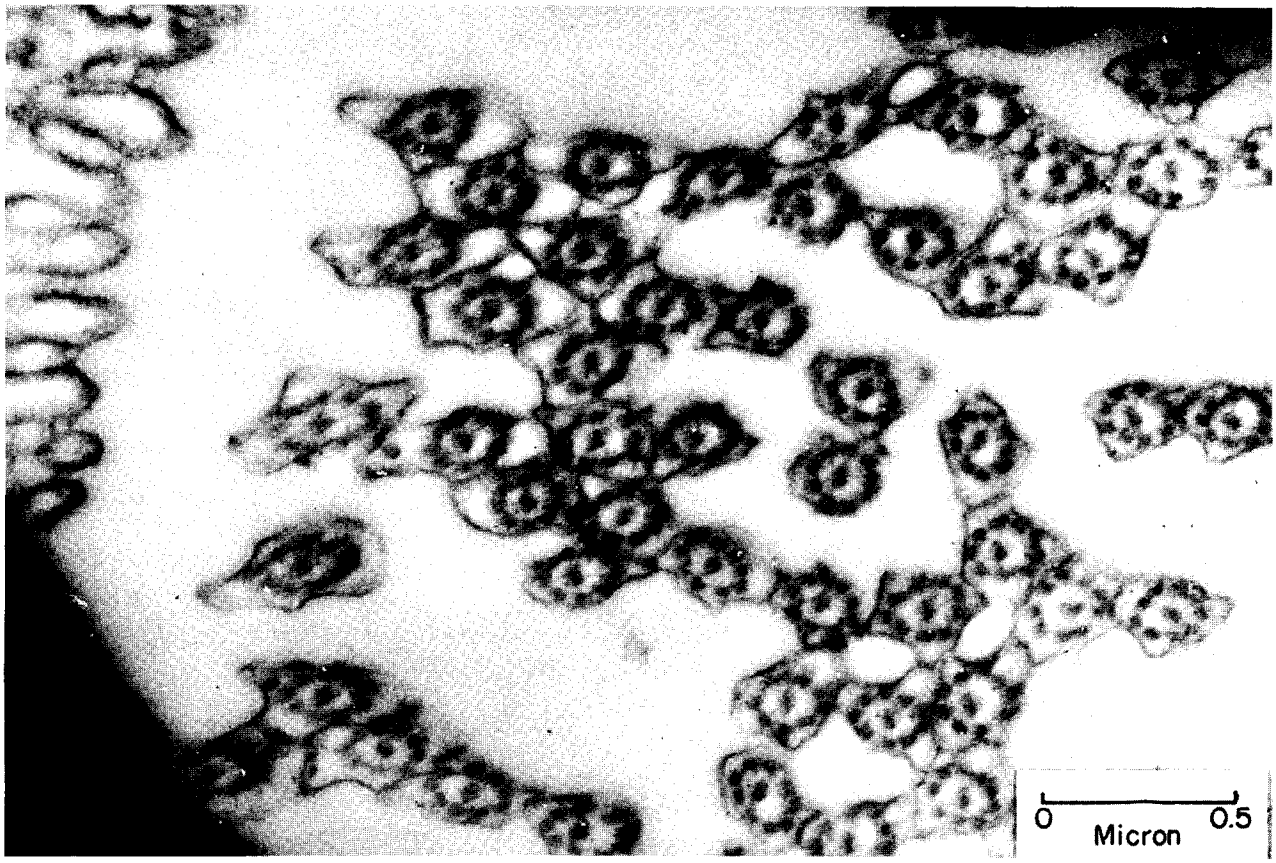

FIGURE 130.—Cross section of the group of frontal cilia of the gill of *C. virginica*. Microvilli of the cell surface are seen at the bottom. Electron micrograph. Buffered osmic acid 1 percent.

The orientation is apparent in the electron micrograph (fig. 131) of a longitudinal section of the distal part of the lateral cell of the filament of *C. virginica* and on transverse sections of the frontal cilia (fig. 130). Because the latter cilia are curved in the direction of the beat, they were cut transversely and appear in the micrograph a short distance above the cell surface. Their oval-shaped axial filaments are oriented parallel to the surface of the cell, i.e., in the direction of ciliary beat. The membranelike laterofrontal cilia consist of several individual cilia embedded in a protoplasmic membrane, but each element retains the typical structure of a single cilium (fig. 131).

The basal corpuscles of cilia are arranged in rows (fig. 132), and the central part of each is surrounded by denser cortex, giving the appearance of an empty central cavity. In the longitudinal section (figs. 131 and 132) they are elongated with a pair of rootlets arising from each proximal end. Rootlets of the cilia of the clam, *Elliptio complanatus*, have a periodic striation of about 750 Å. Similar periodicity appears in electron micrographs of oyster cilia made in the course of my studies, but the picture is not as clear as that published by Porter and Fawcett (see DeRobertis, Nowinski, and Saez, 1954, p. 382).

The distribution of rootlets follows a precise pattern. Each rootlet of a pair turns at an acute angle and crosses over the rootlet of the adjacent corpuscle. The rootlets may be followed further down the cytoplasm toward the nucleus (not shown in the micrograph); some of them cross the second rootlet emerging from the other side of the same corpuscle as can be seen at the center and left side of figure 132. The crossed rootlets are in close contact with each other, but it is not clear whether or not they are fused. Apparently direct communication between the basal corpuscles is lacking.

The question of whether the rootlets are simply the anchoring structures of the cilia or play an active part in its movement remains unanswered.

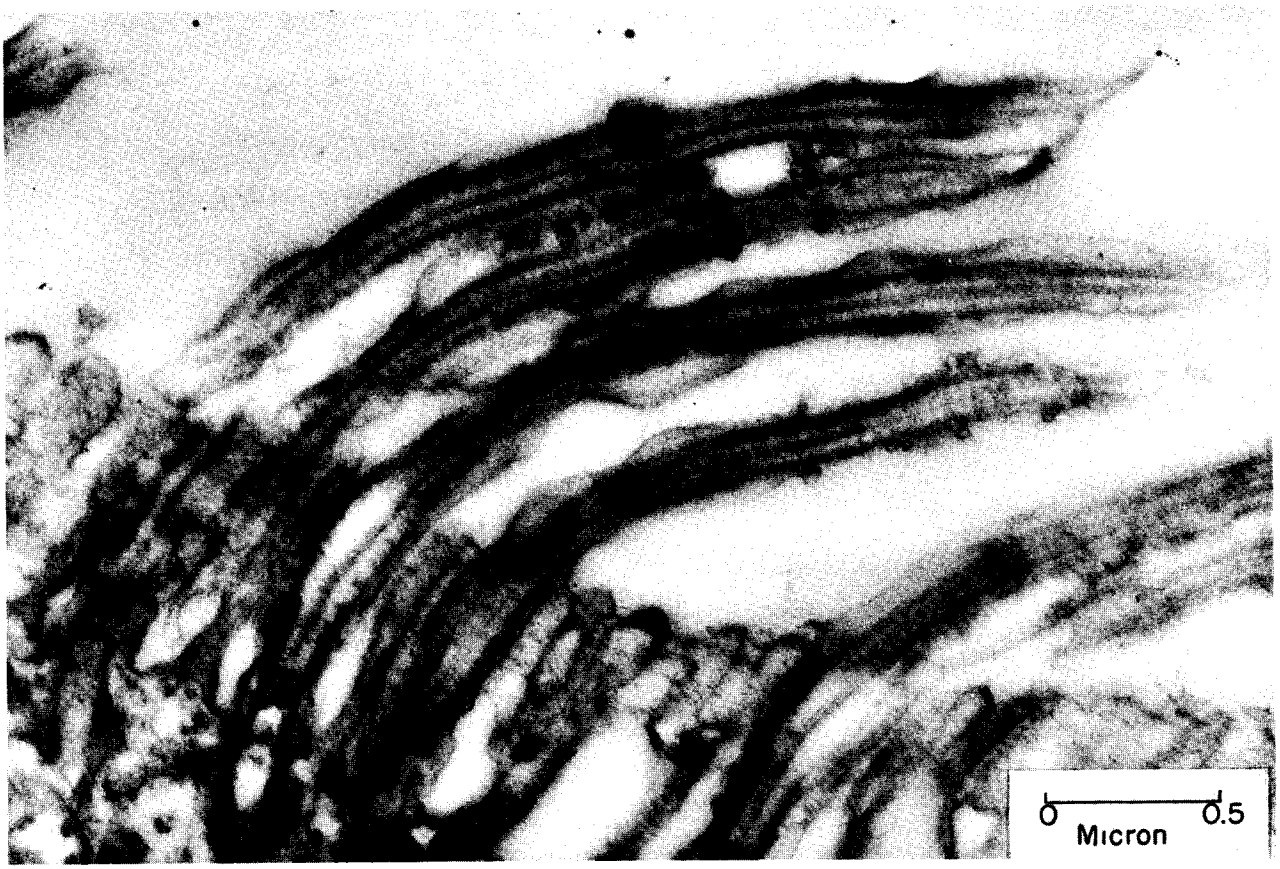

FIGURE 131.—Longitudinal section of the distal portion of laterofrontal cell of the gill of *C. virginica*. Since the plane of section passes at the middle of the cilium only single axial and two peripheral filaments can be seen. The basal corpuscle and the beginning of rootlets are at the lower part of the micrograph. Electron micrograph. Buffered osmic acid 1 percent.

There is the possibility that they may represent a coordinating mechanism of the ciliary epithelium. The fact that the rootlets of the two adjacent corpuscles cross each other is in favor of this view, which was advanced by Grave and Schmitt (1925) on the basis of their observation of the cilia of fresh-water mussels made with the light microscope. Exploration with the electron microscope gives additional support to their hypothesis which, however, requires further corroboration.

The free surface of the ciliated cell appears as a thin homogenous layer, devoid of visible structure, when examined in the light microscope. In reality this layer consists of fingerlike processes called microvilli (figs. 130 and 132), which are found in various tissues; they are considered a device to increase the surface of the cell. Their number has been estimated as high as 3,000 per single cell of intestinal mucosa, and there is no doubt that numerous fingerlike processes greatly increase the surface area of the gill and facilitate the exchange of gases and ions. In figure 132 the layer of microvilli, about 0.5 μ in thickness, rests upon the plasma membrane of the cells. The cytoplasm under the membrane contains numerous mitochondria.

The complex ultrastructure of the ciliated cell of the oyster gill is shown diagrammatically in figure 133, which represents a reconstruction of the principal features seen on electron micrographs. The diagram is based on a large number of micrographs and summarizes our present knowledge of the dimensions and arrangement of the various parts which comprise the ciliated apparatus of the oyster gill.

Although the mechanism of ciliary motion is not known, studies of the ultrastructure of the cilia suggest that the molecular organization of both cilia and myofibrillae of the muscle cells are homologous and that the mechanism of their contraction is similar. This conclusion gains further support from biochemical studies which