BIOLOGY AND ECONOMIC VALUE OF THE SEA MUSSEL Mytilus edulis.[1]

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Contribution from the U. S. Fisheries Biological Station, Woods Hole, Mass.

CONTENTS.

[1] After this report was completed and submitted to the Bureau but before it could be published Dr. Field's untimely death occurred in February, 1921. Consequently there was no opportunity for the author to review the final editorial corrections or to read the proof. The report was submitted to the faculty of Clark University, Worcester, Mass., in partial fulfillment of the requirements for the degree of doctor of philosophy.

INTRODUCTION.

The object of this report is to present as completely as possible the facts known concerning the biology and economic importance of the sea mussel *Mytilus edulis* Linn. and the possibilities of developing a mussel fishery in the United States. In a previous paper (Field, 1911) the food value of the sea mussel was demonstrated to be equal to or greater than that of any other commercial shell-fish on our coast, and the mussel beds of our eastern and western coasts were shown to constitute one of our great undeveloped marine food resources. The importance of this sea mussel as a valuable source of food supply was considered so great that a more exhaustive study of the life history, distribution, and the commercial possibilities of utilizing the species was considered advisable. The results of this investigation show the possibility of adding to our food supplies millions of pounds of wholesome flesh food annually.

The material entering into this report is based upon the review of an extensive literature verified and supplemented by a series of investigations carried on during seven summers for the United States Bureau of Fisheries at its biological station at Woods Hole, Mass., and by a reconnaissance of the mussel beds on a limited portion of the north Atlantic coast. A considerable portion of the work was done in the biological laboratories of Clark University.

SYSTEMATIC AND ECONOMIC RELATIONS OF MOLLUSKS.

The term mussel, as generally used, applies to either of two groups of bivalve mollusks one of which is restricted to salt and brackish waters, the other to a fresh-water habitat.

The marine species belong to the genus Mytilus and other allied genera of the family Mytilidæ. On our eastern coast there are five species of this family representing three genera, the most important of which is the common sea mussel, *Mytilus edulis* (fig. 100, opp. p. 128), which ranges from the Arctic Ocean to Cape Hatteras. The horse mussel, *Modiolus modiolus*, is next in importance, ranging from the Arctic Ocean to New Jersey. *Mytilus hamatus*, the hooked mussel, is found from Chesapeake Bay southward and on the Gulf coast. *Modiolus demissus* (*Modiola plicatula*), the plicated mussel, is a shallow water form found from Maine to Georgia. *Modiolaria nigra* is a northern form which inhabits the deeper waters from the Arctic Ocean to Cape Hatteras.

On our western coast the family is likewise represented by three genera and five species. *Mytilus edulis* occurs from the Arctic Ocean to San Francisco. *Mytilus californianus* is common on the California coast. *Modiolus modiolus* and the straight horse mussel, *Modiolus rectus*, are also present on the California coast. *Modiolaria nigra* occurs from Arctic waters to San Francisco. The marine mussels are characterized by a byssus which is secreted from a gland located at the base of the foot.

The fresh-water mussels belong to the family Unionidæ represented by Unio, Anodonta, Quadrula, and other allied genera. They are particularly common in most of the rivers of the central United States. They secrete no byssus in the adult stage.

The phylum Mollusca comprises a great variety of forms; but there is a close relation between all the groups, which are merely modifications of the same type. It includes the chitons, Amphineura; snails, Gastropoda; mussels, clams, oysters, scallops, etc., Lamellibranchia; and the nautilus, devilfishes, and squids, Cephalopoda.

The characteristic feature of these animals is a ventral, muscular foot which usually serves for locomotion, but is much modified according to habit. The body is soft and moist and usually more or less covered with a shell which is generally either univalve or bivalve; the shell is secreted by a glandular fold of skin called the mantle. The shell often consists of three layers; an outer thick, tough portion, or periostracum; a middle prismatic layer, which is much thicker; and an inner mother-of-pearl, or nacreous layer, which is sometimes brilliantly iridescent. The adult forms show no sign of segmentation and the body cavity is more or less obliterated. The pericardium represents the chief portion of what is left of the true body cavity. Communication between the pericardium and the exterior is established through the nephridia. The respiratory organs consist of gills except in a few species, chiefly terrestrial, which possess a sort of lung. It is probable, also, that the mantle plays an important part in respiration. The nervous system consists of three ganglionic centers with connectives located respectively in the head, cerebral ganglion; in the foot, pedal ganglion; and on either side of the œsophagus, visceral ganglia. Sense organs of touch, sight, smell, and equilibrium may be present in the head region. In the development of the Mollusca segmentation of the egg is unequal and the larvæ pass through a free-swimming or trochosphere stage which is also the characteristic larval stage of the Annelida. There is also a probable relationship with the Polyzoa.

In distribution, we find the Mollusca occupying, in a general way, the whole surface of the earth at all latitudes and altitudes. They are found in the polar, temperate, and tropical regions; in the ocean; along the seashore; on land; and in fresh-water lakes, ponds, and streams. Certain snails of the suborder Stylommatophora have been found in mountains at a height of 15,000 feet; abyssal mollusks have been taken from a depth of 2,800 fathoms. There are pelagic species which are distributed over the surface of the sea, some live on the floating seaweed, while others descend many thousands of feet from the surface. It is within the Tropics, however, both on land and in the sea, that the Mollusca are most abundant both in numbers and varieties.

Protective markings of a striking nature are characteristic of many mollusks. Most of the pelagic species are colorless or tinged with blue. The nudibranchs, which are found on the floating sargassum weed, are beautifully marked with yellow and brown like the weed itself. Other species are green or red in color, similar to the algæ on which they live. The shellfish which live in the great depths beyond the reach of the faintest

ray of light are characterized by thin, colorless shells, a highly developed tactile sense, and the absence of visual organs.

The length of life and age of attaining sexual maturity vary considerably for different mollusks. Mytilus reaches the adult stage in one year. The fresh-water mussels, Anodontidæ, do not reach sexual maturity until they are 5 years old. Some mollusks, nudibranchs, and the cephalopod, Rossia, appear to live for one year only, while others, as Mytilus and the oyster, may live 10 or more years; the periwinkle, Littorina, has been known to attain an age of 20 years in captivity, and the Anodontidæ, which are remarkable for their long life, may reach an age of 25 or 30 years.

The Mollusca is an old group whose fossil representatives are found in all Paleozoic deposits upward. As a group it has met the changing conditions of the world most successfully, as is clearly demonstrated by its present abundance and wide distribution. More than 28,000 living Mollusca have been described up to the present time, more than half of which are Gastropoda.

The economic importance of the Mollusca is very great indeed. The group includes species of negative as well as of positive value. In the former class may be mentioned the so-called shipworm, *Teredo navalis*, a boring lamellibranch whose habits are extremely destructive to the bottoms of wooden ships, to wharf piles, and to other submerged wooden objects, which are riddled by its borings. To prevent the destructive inroads of the shipworm it is necessary to incase the bottoms of wooden ships with a metal sheath and to coat such wooden objects as spars, buoys, etc., with verdigris paint periodically every six months.

Among the gastropods are found many voracious species armed with rasping organs against which few shellfish are safe. They prey upon many species valuable to man, such as oysters, clams, scallops, mussels, etc., by boring holes through their shells and literally eating them alive. The destructive ravages of these snails on the commercial species of mollusks amount to many thousands of dollars yearly. The Cephalopoda are also carnivorous animals of very active and voracious habits. They dart into the schools of young fishes and feed upon them in great numbers. Young lobsters and other small crustaceans often fall prey to them.

Molluscan species of positive value to man are numerous and represent every class except the Amphineura. Most of the cephalopods are good to eat and are utilized extensively as food in some countries. Although not used as such in the United States, there is no reason why they should remain a neglected food product. Squid is the most valuable bait known in the cod fisheries and for this reason often brings fancy prices. When abundant it is used for fertilizer. The cuttlefish furnishes the cuttle bone which is used as a food for canary birds, and formerly its inky secretion was sold as India ink or sepia, which was used for drawing purposes.

The gastropods include species of food value, as, for example, the large, edible snail of Europe, the periwinkle, *Littorina littorea*, which is eaten by the ton in London, but, as yet, remains unknown as a food in this country. The abalone of our western coast is beginning to be appreciated as a food through the influence of the Chinese, who have developed the fishery into a business worth many thousands of dollars annually. Its shell is remarkable for its great beauty and was formerly used by the Indians for making their money. In Europe it is used for making buttons, studs, and buckles and for decorating purposes.

The class Lamellibranchia is the most important of all from the commercial standpoint. It includes the oyster, which furnishes the most valuable fishery of the nation, the receipts from this source alone amounting to one-third the total income derived from all the fisheries of the United States. The flesh of the oyster constitutes a most delicious morsel, and the shells are used in the construction of roads, as a food for poultry, as fertilizer, and as cultch for starting new oyster beds. About 25,000,000 bushels of oysters are utilized in the United States annually. Other valuable edible lamellibranchiate species are the clams Mya and Venus, which have made the New land clam-bake famous throughout the land, and the scallops, which are popular in every hotel and restaurant of our northeastern coast.

The fresh-water mussels of our inland waters furnish pearls of rare value and shells especially adapted for the button industry and for the manufacture of articles of much beauty. So great has been the demand in recent years for the important species that the resources have been greatly depleted. Fortunately, however, the United States Bureau of Fisheries has been able to take up the problem, and, by the application of scientific methods, it is now propagating mussels to provide for the increased demand.

Not only do the lamellibranchs yield products of commercial value, but in their daily functions they perform a service which has never been estimated in dollars and cents. Their habit of setting up currents of water which are continually filtered through the gill filaments serves to remove the bacteria and other microorganisms along with quantities of floating organic particles which, if left in the water, would lead to stagnation. They constitute, therefore, one of the great purifying agents of our lakes, ponds, and streams.

The United States Bureau of the Census reported the value of the mollusk fisheries of the United States for 1908 as follows:

Oysters	$15,713,000
Hard clams	1,317,000
Long clams	553,000
Scallops	317,000
Fresh-water mussel shells	392,000
Slugs and pearls	300,000
Sea mussels	11,600
Oyster and other shells	20,000
Squid	43,000
Cockles, winkles, conchs	35,000
Total	18,701,600

ANATOMY AND PHYSIOLOGY OF THE SEA MUSSEL.

THE SHELL.

DESCRIPTION.

The sea mussel has a general form which may be described as triangular ovate. Anteriorly, in the hinge region, the shell presents its greatest breadth; posteriorly, it becomes narrower and flattened. The posterior edge of the shell is nearly semicircular in outline; in the dorsal region it forms almost a straight line up to the beginning of the hinge, where it bends obliquely downward at an angle of about 45° to the umbo, which is located at the tip of the shell. From the sharp point of the umbo the ventral edge of

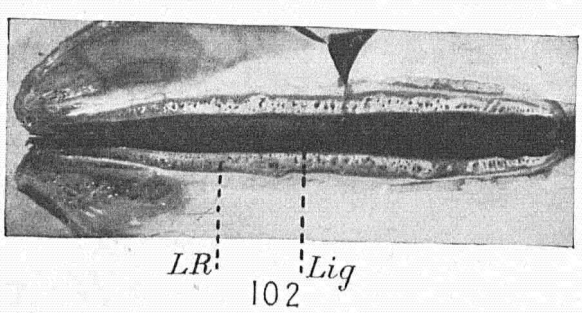
the shell extends backward in an almost straight line. In specimens of mussels growing on wharf piles in protected situations the ventral edge sometimes presents a slightly convex outline, while, on the other hand, mussels growing on the rocks or mud where they are subjected to swift currents and exposure often show a decidedly concave under surface.

The size of the adult mussel varies from 2 to 4 inches in length, from 1 to 2 inches in height, and from ¾ to 2 inches in breadth. Occasionally specimens 4½ inches long are found. The proportions of length to height and breadth vary with the age of the mussel. Individuals less than a year old show a length, breadth, and height which are to each other as 2.75 : 1.5 : 1; while in older ones they are to each other about as 2.25 : 1.15 : 1, indicating that in adults growth in breadth is proportionately more rapid than in length.

The color of the shell varies from violet or blue-black to a pale blue. When dried it takes on a brownish hue. This change of appearance is due to the hornlike covering of the shell, the periostracum, which is itself brown. The characteristic violet color of the shell comes from the thick prismatic layer which lies immediately below the thin periostracum and which contains a deep blue pigment. The general hue of the shell is therefore due to a combination of the brownish, transparent periostracum and the underlying layer of deep blue calcareous matter. This results in a variety of color variations according to the thickness and density of the periostracum and the amount and distribtion of the pigment in the prismatic layer of the shell. The arrangement of the pigment is in bands which run from the umbo in a radiating manner to the posterior end of the shell. Most commonly the stripes lie so closely together that it gives the shell surface a uniform dark blue color. Sometimes, however, the bands of color are few in number or entirely absent. In the latter case the mussel is colored a uniform brown or yellow-brown by the periostracum, while in the former case it is marked with alternate blue and brown bands which radiate from the umbo to the posterior edge of the valve.

The inner surface of the shell is divided sharply into two regions, an inner, glossy white or pinkish-white mother-of-pearl layer and an outer deep blue border about three-sixteenths of an inch wide. The line of demarcation between these two layers is sharp and may be either straight or serrated in outline. The blue layer is absent in the hinge region.

Six impressions which mark the attachment of muscles are conspicuous on the inner white surface: (1) The largest and most prominent is more or less circular in form and located posteriorly near the dorsal border. It marks the point of attachment of the posterior adductor muscle (fig. 104, *PAD*, opp. p. 132). (2) Running anteriorly from the dorsal edge of this impression is another, linear in form (fig. 104, *PRet*), which marks the point of attachment of the posterior retractor muscles of the foot and byssus. (3) A third, somewhat triangular impression lying just posterior to the impression of the posterior adductor muscle marks the insertion of the muscles of the anal membrane (fig. 104, *An*). (4) At the anterior end of the shell on the ventral border is an impression where the anterior adductor muscle is attached (fig. 104, *AAd*). (5) Just above it on the dorsal edge is another which marks the point of insertion of the anterior retractor muscles of the foot and byssus (fig. 104, *ARet*). (6) A long, narrow, linear impression extending along the lower edge of the shell from the impression of the anterior adductor muscle to that of the posterior adductor muscle and just inside the border of the nacreous layer forms the line of attachment for the pallial muscles (fig. 104, *Pal*).



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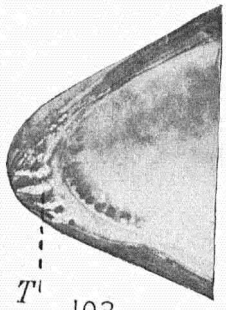

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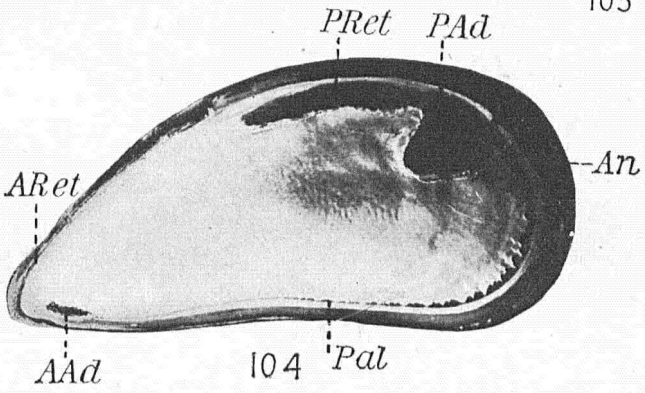

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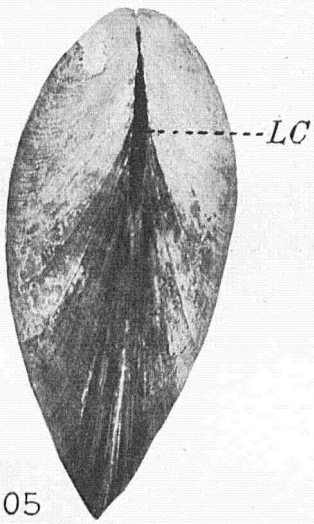

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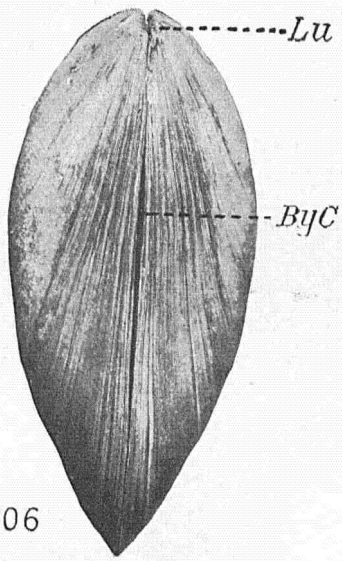


106

FIG. 102.—Interior view of hinge ligament. *Lig*, ligament; *LR*, ligament ridge.

FIG. 103.—Interior view of anterior end of a valve showing four hinge teeth, *T*.

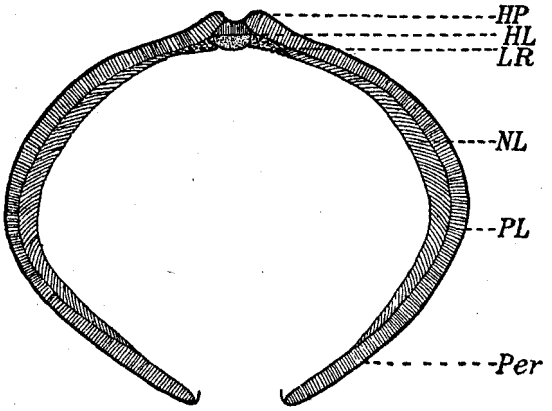
FIG. 104.—Inner surface of a valve showing muscle impressions. *AAd*, anterior adductor muscle; *An*, anal muscle; *ARet*, anterior retractor muscle; *PAd*, posterior adductor muscle; *Pal* pallial muscle; *PRet*, posterior retractor muscle.

FIG. 105.—Dorsal surface of a shell from which periostracum and ligament have been removed. *LC*, ligament cleft.

FIG. 106.—Ventral surface of a shell from which periostracum has been removed. *ByC*, byssus cleft; *Lu*, lunula.

The two valves are attached at their anterior dorsal edges by means of a hinge plate over which the periostracum extends from one valve to the other. Teeth are present at the anterior end of the hinge in numbers varying from one to six, the most common number being three or four. The teeth of one valve are so arranged that they fit into the depressions between the teeth on the opposite side. In size they are small, rarely over a millimeter in length, and in form they are conical pointed knobs or wedge-shaped lamellæ (fig. 103, *T*).

The ligament (fig. 102, *Lig*), a straight, brownish colored, elastic rod, lies between the two valves just beneath the hinge band and helps to unite the shell edges. In cross section it presents the form of an ellipse with its long diameter lying in a horizontal position. It is bounded laterally by parallel ridges, the ligament ridges (fig. 102, *LR*), which have a very characteristic structure. They are chalky white in color and perforated with numerous pores. Each ridge terminates in a fine point both anteriorly and posteriorly. The median surfaces are concave to fit snugly against the ligament when the shell is normally open; consequently when the valves are closed by contraction of the adductor muscles the ligament is compressed and its elasticity tends to counteract the action of the muscles (fig. 107). As a result, when the adductor muscles relax the ligament forces the shell open again. This explains why the shells of dead mussels are always open.



107

FIG. 107.—Cross section of a shell in hinge region in diagrammatic form to show relation of ligament to hinge plate and valves. *HL*, hinge ligament; *HP*, hinge plate; *LR*, ligament ridge; *NL*, nacreous layer; *Per*, periostracum; *PL*, prismatic layer.

The umbo is at the anterior end of the shell and forms a sharp beak, off the ventral side of which may be found, often hidden by the periostracum, a special structure called the lunula (fig. 106, *Lu*, opp. p. 132), which bears a definite relation to the hinge teeth. It consists of a series of semicircular furrows and ridges which run out peripherally from the teeth and terminate at the umbo. Each furrow corresponds to a tooth; and each ridge, to a depression between the teeth. The lunula is conspicuous only in individuals where the teeth are comparatively large in size and number.

When the valves of a normal shell are shut they form a complete closure. If, however, they are first treated with a solution of potassium hydroxide, which removes all the periostracum, it will be found when they are closed that there are two places where the edges fail to come in contact. On the ventral side in the middle of the shell there is a fissure through which the byssus may project, the byssus cleft (fig. 106, *ByC*). In the normal shell this cleft is hidden by a fold of the periostracum which incloses the marginal blood sinus. The structure is such as to act as a cushion which presses against the byssus when the shell is closed. Corresponding to the byssus cleft on the dorsal side in the hinge region is another opening between the valves, the ligament cleft (fig. 105, *LC*, opp. p. 132). In the complete shell this depression is covered externally by the periostracum and internally by the underlying ligament.

HISTOLOGY.

If the shell of the sea mussel is broken or cut in cross section, three distinct layers, sharply defined from each other, are visible to the naked eye: An outer, thin, cuticular layer, the periostracum; a middle violet-colored portion, the prismatic shell; and an inner glossy white or pink substance, which often reflects iridescent colors, the mother-of-pearl, or nacreous, layer. Under high magnification each of these parts shows a characteristic structure.

The periostracum generally covers the whole outer surface of the shell and extends over the free edge for a short distance over the inner surface where it terminates in a fold of the mantle border. It is a smooth, glossy cuticula, thinnest in the region of the umbo, where it is often completely worn off as a result of exposure at low tide and the action of strong waves and currents. The hinge of the shell is formed from the periostracum which extends over from one valve to the other. In cross section the periostracum presents three layers (fig. 111, *Per*, p. 136). The outer and inner portions consist of a clear, transparent, brownish substance which does not readily stain with any of the ordinary dyes. The middle portion is colorless and has an affinity for plasma stains. In the region of the mantle edge from which it is an outgrowth the layer consists of a single layer of cells, but as the outer surface of the shell is approached the cells disappear, leaving a series of cavities to mark the middle zone. The periostracum may, therefore, be divided into three distinct areas: An outer, middle or hollow, and an inner layer. The periostracum is attached to the layer of the shell lying immediately below it by means of trabeculæ which are embedded in the calcareous substance.

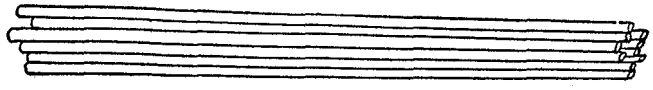
The blue portion of the shell or middle layer is composed of fine needlelike filaments of calcareous matter closely united into a single structure by an organic matrix of conchiolin (fig. 108, p. 135). When a valve is broken in cross section and examined with a hand lens this layer presents a series of alternate ridges and grooves with glistening surfaces which extend across the shell. With higher magnification it is possible to see that the prisms are long and almost straight and so arranged as to form an angle of about 45° with the outer shell surface (fig. 111, *PL*, p. 136). The pigment, which is more abundant on the peripheral surface of the layer, is deep blue or violet in color and is distributed in the form of parallel bands which run across the prisms at an angle of about 30° (fig. 112, *PB*, p. 136). Around the ventral and posterior borders of the shell there is no inner nacreous layer present, consequently the prismatic shell lies in direct contact with the outer fold of the mantle edge.

The nacreous or mother-of-pearl layer covers the inner surface of the shell out to the mantle line as a boundary. It is thickest in the anterior and middle regions and thinnest at the border. This is the only layer which continues to grow in thickness throughout the life of the mollusk. The nacreous and prismatic layers lie in direct contact with each other without any intervening substance to connect them. The structure of the nacre consists of a series of thin lamellæ with irregular edges placed one on the other with their surfaces lying horizontal to the surface of the shell. When seen in cross section of the shell under high magnification they appear as fine irregular parallel lines (fig. 111, *NL*, p. 136). If a portion of the nacreous layer is dried for some time or is treated with sodium hydroxide it becomes fragile and has a tendency to break up into flakes whose surfaces mark the line of cleavage between the separate lamellæ.

Microscopic examination of the flat surface of one of these flakes near its edge will show distinctly the leaflike layers with their irregular edges (fig. 109). The transverse plane of cleavage always follows the zigzag edges. A surface view of a single lamella under very high magnification reveals a fine network with meshes of a polygonal form (fig. 110).

The ligament when examined in cross section with an ordinary hand lens presents three distinct layers; the outer portion is marked by the dark brown periostracum, the middle part is composed of a yellow-brown homogeneous substance, while the inner layer is of the same color but marked with numerous horizontal dark brown lines. Under higher magnification four distinct and separate layers are visible.

The outermost layer consists of the periostracum (fig. 113, *Per*, p. 136), which is really not a part of the ligament proper, although it is fused so closely with it as to form



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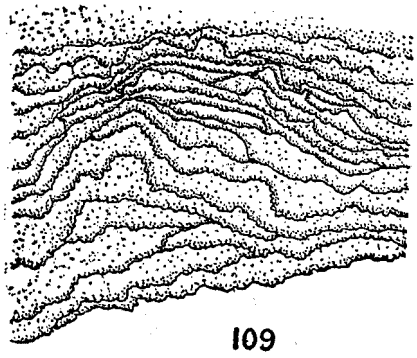

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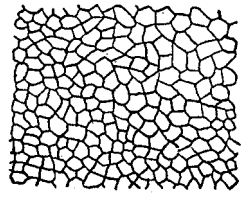


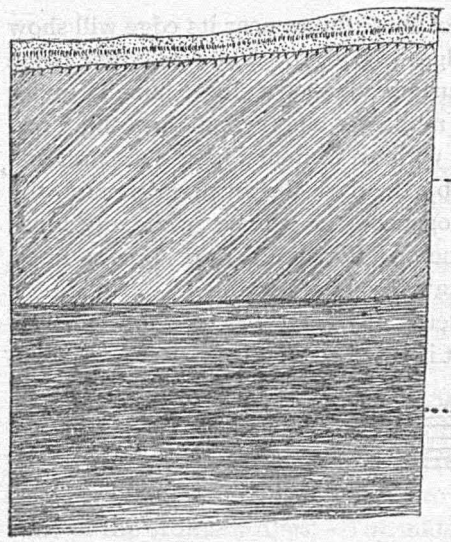
110

FIG. 108.—Transverse section through prismatic layer of shell, showing needlelike prisms, which are held together by an organic matrix of conchiolin. × 854.

FIG. 109.—Fragment of nacreous layer showing overlapping lamellæ. × 500.

FIG. 110.—Surface view of nacreous layer very highly magnified.

a unit body. What appears to be the middle layer under low magnification is divisible into two sharply separated parts when examined with stronger lenses. The outer portion of this layer presents a homogeneous structure similar to a film of gelatin, with a yellowish color often tinged with blue or green (fig. 113, *HyL*). The inner part of the middle layer is of a darker shade and strongly granular in appearance, due to an abundance of irregular masses of lime crystals, many of which are aggregated into starlike bodies. A few of these crystals may be seen scattered in the homogeneous layer close to its border next the granular layer (fig. 113, *GL*). The inner layer is distinguished from the others by its cross-striped appearance (fig. 113, *IL*). It is marked by numerous fine vertical lines across which there run at right angles many dark brown bands of varying width. Crystals of lime salts are present in small numbers scattered throughout the substance of this layer. The crystals may be readily removed by treating the sections



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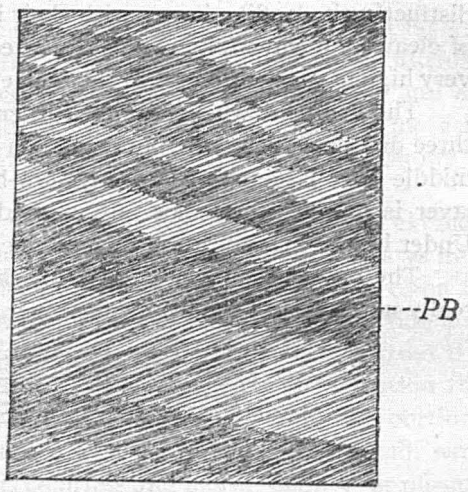

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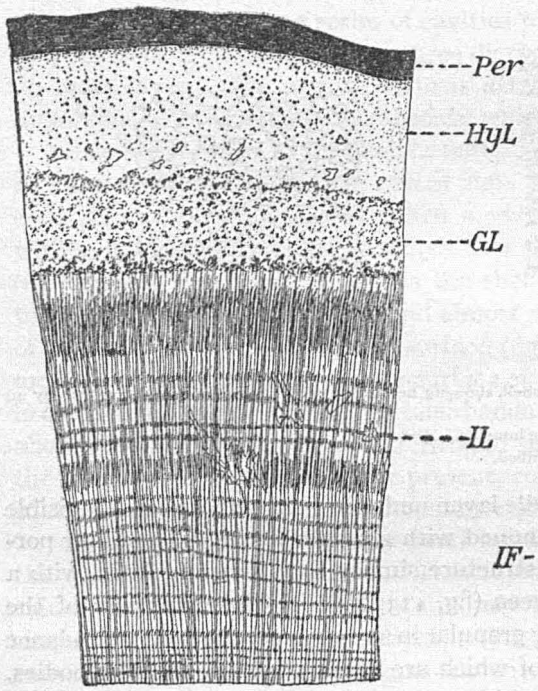

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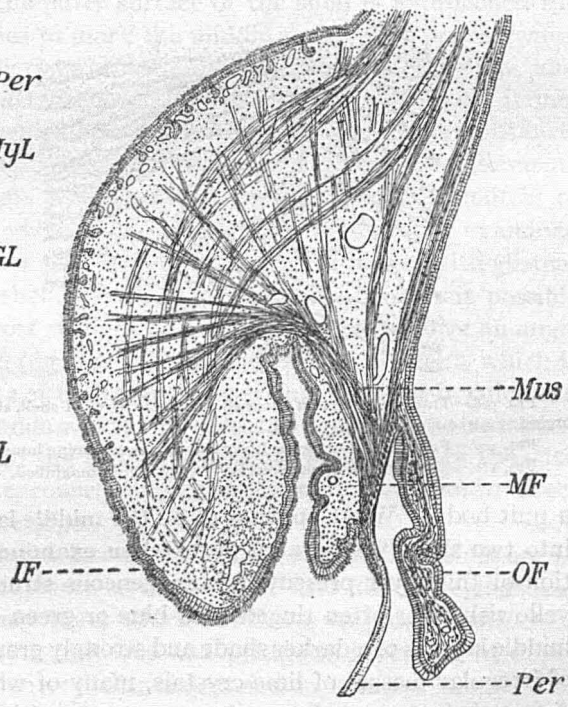


114

FIG. 111.—Cross section of piece of shell. × 50 approximately.

FIG. 112.—Section through prismatic layer. × 45.

FIG. 113.—Cross section through ligament. × 26.

FIG. 114.—Cross section through edge of mantle. × 35. Fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red.

ABBREVIATIONS.—*GL*, granular layer; *HyL*, hyaline layer; *IF*, inner fold; *IL*, inner layer containing a few groups of calcium crystals; *MF*, middle fold, showing origin of periostracum (*Per*) from its outer edge; *Mus*, muscle fibers; *NL*, nacreous layer; *OF*, outer fold; *PB*, pigmented bands; *Per*, periostracum; *PL*, prismatic layer.

with weak nitric or hydrochloric acid. The staining reactions of the decalcified sections of the ligament are characteristic; the middle layer has a tendency to take up the plasma stains, while the inner layer takes up the basic dyes.

FORMATION.

The periostracum is an outgrowth from a specialized portion of the mantle edge. If a cross section of the mantle is examined under low magnification it will be seen that the edge of the mantle is divided into three distinct folds which run parallel with its edge. They may be designated by their position as the outer, middle, and inner folds. From the outer surface of the middle fold the periostracum arises as a thin cuticula which is secreted by a layer of epithelial cells having characteristic, long, elliptical nuclei and fibrils which lie at an oblique angle with the surface of the periostracum. Numerous muscle fibers from the mantle terminate among these cells (fig. 114, *Mus*, p. 136). The youngest portion of the periostracum, which lies in contact with the secreting cells, is a thin, transparent, homogeneous structure, but as it extends out beyond the limits of the mantle edge it grows progressively thicker and becomes differentiated into the three layers which have already been described. The periostracum grows over the edge of the outer fold, beyond which it becomes attached to the outer surface of the prismatic layer of the shell.

The prismatic or blue layer of the shell is secreted by the low columnar epithelial cells which cover the outer surface of the outer fold of the mantle edge. As fast as the material is built up along the edge of the shell its outer surface comes in contact with the outgrowing periostracum, to which it becomes attached.

The epithelium of the outer mantle surface is composed of small cubical cells and gland cells which secrete the mother-of-pearl (fig. 114, p. 136). The process is continuous, so that as the animal grows older this layer continues to grow thicker, giving the shell the unusually firm and heavy character which is often noted in old mussels. Exposure to the rough action of waves and currents stimulates the cells to more rapid secretion.

The ligament arises from a layer of tall columnar epithelial cells which lies immediately below it.

ATTACHMENT TO THE BODY.

The whole outer surface of the fleshy part of the body is more or less intimately connected with the inner surface of the shell. The epithelium of the mantle forms a rather weak attachment, while the muscles adhere most tenaciously at their points of union with the shell.

The epithelial cells of the outer surface of the mantle lie in direct contact with the inner surface of the shell and are attached to it by the secretion of a soft, gummy substance from which the shell is being formed constantly. The attachment may be likened to that of a label pasted on a bottle.

In case of the muscle attachments, a very different type of adhesion is found. Here the epithelial cells of a highly specialized nature serve as anchoring organs. They are so intimately attached to the bundles of muscle fibers at their proximal ends that it is difficult to distinguish them from the contractile tissue without applying staining methods. Ordinarily muscle fibers stain more deeply than do the supporting epithelial cells. Distally the epithelial cells are embedded in the surface of the shell, making an attachment so strong that it is impossible to separate the mass from the shell without applying acid to dissolve away the calcareous substance in which they are firmly fixed.

CHEMICAL COMPOSITION.

The shell of the mussel consists of an organic base infiltrated with mineral salts, as has been shown above in the description of its histological structure.

The organic matrix is an albuminoid substance called conchiolin, the composition of which, according to Wetzel (1900), is carbon 52.3 per cent, hydrogen 7.6 per cent, nitrogen 16.4 per cent, and sulphur 0.65 per cent. It is readily obtained by mascerating the shells in hydrochloric acid and boiling the residue in sodium hydroxide in which the conchiolin remains undissolved. Treated with hot mineral acids it goes into solution. Wetzel (1900) found that the substance gives Millon's reaction, and from the decomposition products formed in boiling sulphuric acid he obtained glycocoll, leucin, and an abundance of tyrosine. He assigns this compound to a place between casein and egg albumin.

The inorganic constituents of the shell consist chiefly of calcium carbonate with which are present small quantities of sulphates, oxides, or carbonates of magnesium, iron, manganese, and silica. The following analysis by Mr. Adrian Thomas will serve to show the various elements and compounds:

Composition of the mussel shell.

	Per cent.
Calcium oxide	51.21
Magnesium oxide	.27
Iron and manganese oxides	.32
Silica	.11
Carbonates	37.33
Sulphates	1.02
Organic matter	8.05
Water	.58
Phosphates, chlorides, sulphides	Trace.

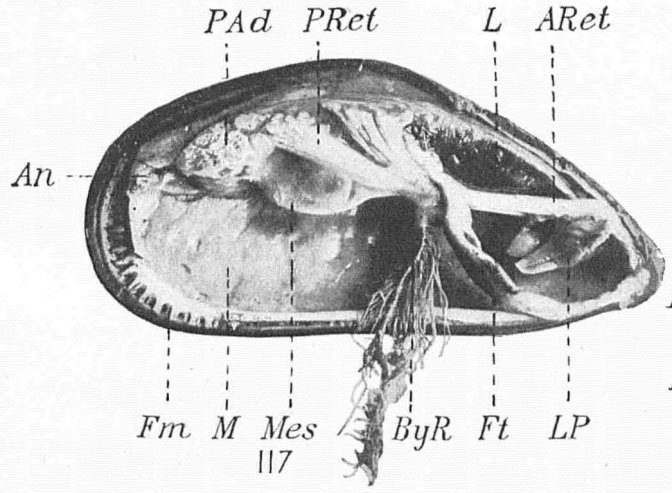
Traces of sodium and potassium which probably came from unremoved sea water were also detected.

THE MANTLE.

The mantle is a fold of integument which almost completely envelops the body. It is composed of the two lobes which lie symmetrically placed on the right and left sides of the body. They arise dorsally as an outgrowth of the body wall, cover the entire inner surface of the shell, and terminate in a free ventral border which is firmly attached to the edge of the shell by means of the pallial muscles. The free mantle edges unite anteriorly near the posterior edge of the anterior adductor muscle. At the posterior end of the shell they are joined together by a triangular-shaped band of deeply pigmented integument, the branchial membrane (fig. 115, *BrM*, opp. p. 138).

The exhalent syphonal opening (fig. 115, *Exs*, and fig. 116, *Exs*) lies just dorsal to the branchial membrane and is surrounded by a tough ring of heavily pigmented tissue. The mantle edges separate to pass on either side of this opening and converge forward to the apex of the shell, where they unite and terminate. Between the syphonal opening and their point of termination they are joined together by a continuation of the branchial membrane. The space between the mantle lobes lying just below the exhalent corresponds to the inhalent syphon of many lamellibranchs.

The structure of the mantle lobes in young animals is quite simple. In cross section they are thin and membranelike, consisting of an outer layer of simple epithelial cells, an



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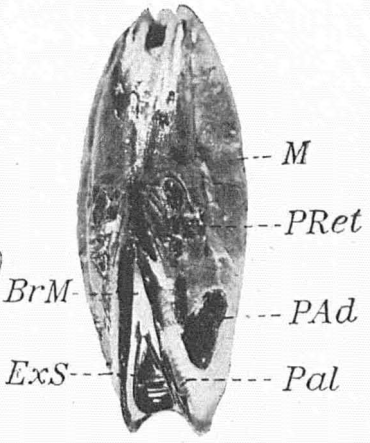

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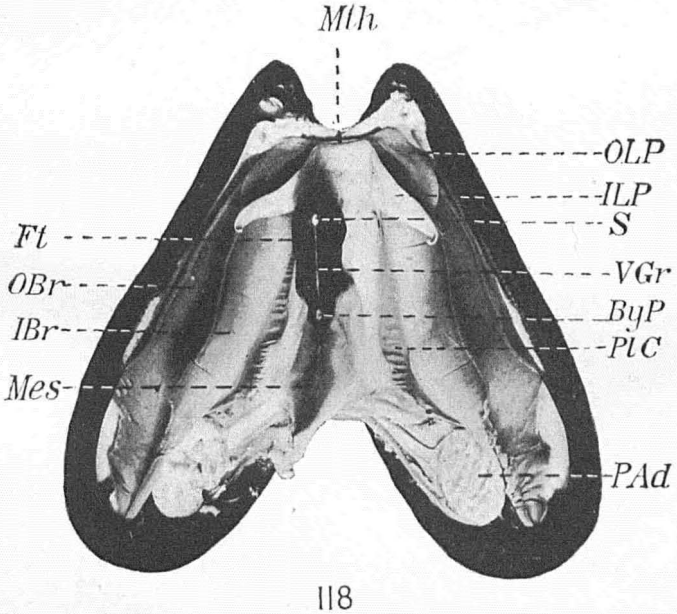

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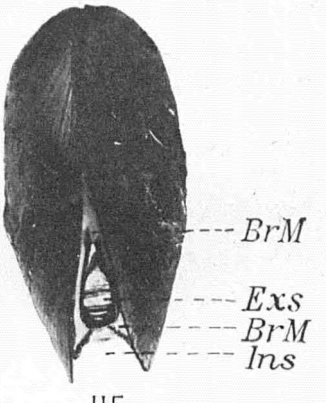

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FIG. 115.—Dorsal view of an adult mussel with valves open normally.

FIG. 116.—Dorso-lateral view of an adult mussel from which shell has been removed.

FIG. 117.—Median view of a mussel with right valve, right mantle lobe, and gills removed.

FIG. 118.—Ventral interior view of a mussel with anterior and posterior muscles cut and valves laid open.

ABBREVIATIONS.—*An*, anal muscle; *ARet*, anterior retractor muscle; lower *BrM* in fig. 115, main portion of branchial membrane, upper *BrM* in fig. 115 and *BrM* in fig. 116, extension of branchial membrane; *ByR*, byssus root bearing threads; *ByP*, byssus pit; *ExS* and *Exs*, exhalent syphon; *Fm*, fimbriæ of mantle; *Ft*, foot; *IBr*, inner branchial fold; *ILP*, inner labial palp; *InS*, inhalent syphon; *L*, liver; *LP*, labial palp; *M*, mantle; *Mes*, mesosoma; *Mth*, mouth; *OBr*, outer branchial lamella; *OLP*, outer labial palp; *PAd*, posterior adductor muscle; *Pal*, pallial muscles; *PlC*, plicate canals; *PRet*, posterior retractor muscle; *S*, sucker; *VGr*, ventral groove.

inner layer of ciliated epithelium, and a middle layer of supporting tissue, gland cells, nerves, and blood vessels. In adult animals this condition is profoundly modified by the development of the genital organs. Preliminary to the growth of the reproductive products the middle tissue layer of the mantle increases greatly in bulk, genital canals proliferate out through it up to the border of the pallial muscles, the blood supply is greatly increased, and fatty tissue is deposited. During the change the mantle increases in size from a thin membrane to a thick fleshy organ. The ratio in mantle thickness before and after the production of genital products may be as much as 1: 100.

The free edges of the mantle are different in structure from the rest of the organ. They are firmer and tougher and constitute the region of rigid attachment to the shell. Their edges, which are attached to the ventral and posterior borders of the shell, are divided into three parallel folds that run longitudinally. The inner fold (fig. 114, *IF*, p. 136) is much thicker than the others; anteriorly the edge is smooth, but toward the posterior region it becomes thicker and is fringed with tentacular processes of fimbræ (fig. 117, *Fm*, opp. p. 138). This region of the mantle edge is dark brown in color, due to the numerous pigment granules which fill the outer portion of the ciliated epithelial cells (fig. 165, *PgG*, p. 178). The interior of the fold is rich in muscle fibers which give to it considerable contractile quality. When the mussel is resting undisturbed in the water with its shell open, the inner fold of the mantle in the posterior region may extend some distance beyond the edge of the shell. A sudden change in light intensity by casting sunlight or a shadow over it or by applying some slight mechanical stimulus will cause it to be withdrawn and the shell closed.

The middle fold is narrower than the outer one but, like it, is richly supplied with muscle fibers (fig. 114, *Mus*). Its inner surface and free edge are lined with pigmented ciliated epithelium, while the outer surface is composed of fibers and simple epithelial cells which secrete the periostracum (fig. 114, *MF*).

The outer fold is the narrowest of the three. The upper part of its inner surface is covered with tall columnar epithelium, while the rest of its surface is bounded with epithelium of the low columnar type. The interior of the fold is richly supplied with muscle fibers. Ordinarily this fold is not visible because of the periostracum, which grows out from the outer surface of the middle fold across to the outer surface of the shell, where it is firmly attached (fig. 114, *OF*). The inner fold is therefore completely shut off from the exterior.

The space which is inclosed between the mantle lobes constitutes the pallial or mantle cavity. In it lie the foot, byssus, gills, mesosoma, and the visceral mass.

DIGESTIVE SYSTEM.

ANATOMY.

The alimentary tract of *Mytilus edulis* presents the characteristic specialized type of digestive organs found in the Lamellibranchia, consisting of an anterior mouth, œsophagus, stomach, a long complicated intestine, and a posterior anus together with two pairs of accessory mouth structures, the labial palps, which serve to convey food into the mouth, and a large digestive gland, the liver.

The mouth is situated between the anterior retractor muscles of the byssus just posterior to the anterior adductor muscle (fig. 118, *Mth*, opp. p. 138). When seen from in front or from below it appears as a transverse slit with distinct upper and lower lips

from the corners of which two pairs of triangular gill-like folds extend backward. These are the labial palps.

The labial palps arise as a prolongation of the lips on both sides of the mouth, forming a two-paired organ which is so situated that the upper pair lie externally to the lower pair when they are in normal position. They are therefore distinguished as outer and inner labial palps (fig. 118, *OLP* and *ILP*). The angle which is formed between the palps at their point of origin on each side marks the anterior termination of the gills and the position of the pigmented eye spots. In form the palps are long, smooth, triangular bands marked on the median side with transverse ridges which extend from the middle to the ventral edge of each palp. A single longitudinal ridge runs from the corner of the mouth to the tip of each palp and forms the line of demarcation between the smooth and ridged side (fig. 119). The inner palps are much broader at the base than are the outer ones and are continuous with the lower lip on their ridged side, while the smooth side is attached to the surface of the liver. The outer palps are continuous with the upper lips on their ridged side and attached to the inner wall of the mantle with the opposite side.

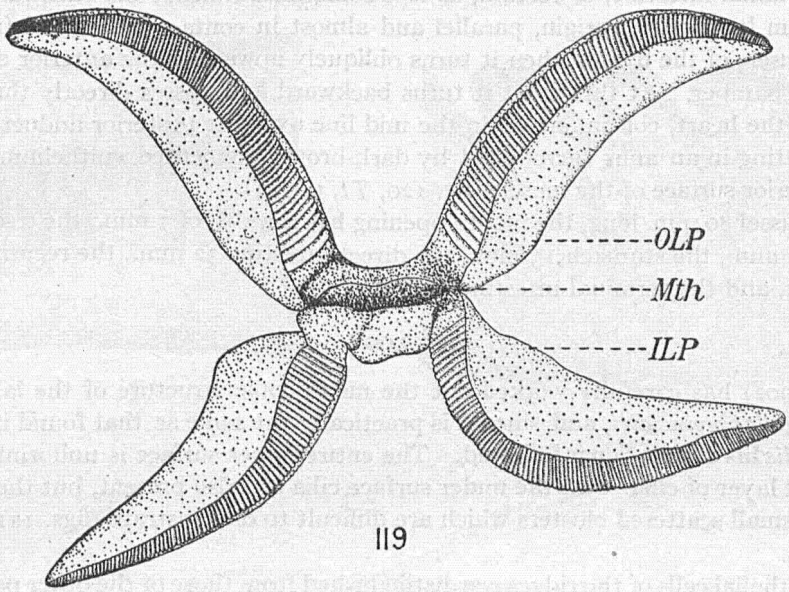
The œsophagus arises directly at the mouth opening and continues backward and upward, bending off slightly to the right of the median plane to enter the anterior end of the stomach.

The stomach is a small sac of irregular form, usually more or less elliptical, with small pockets sometimes present in the dorsal, lateral, or ventral walls. It is situated dorsally just below the middle region of the hinge ligament and lies chiefly on the right side of the body, completely surrounded by liver tissue (fig. 120, *St*). The ventral stomach diverticulum described by Sabatier (1877) was not found to be regularly present.

Numerous large canals open into the stomach from the liver. In *Mytilus galloprovincialis* List (1902) generally found 13 in all, 6 emptying in on the right ventral side, 4 on the left ventral side, 1 on the left wall, and 2 on the left dorsal wall. Sabatier states for *Mytilus edulis* that a number of gland canals empty into the stomach, without giving the number. Purdie (1887) says that in *Mytilus latus* the vessels empty into the under half of the stomach. In the author's observations there could be found no definite number nor regular arrangement to the liver canals. In number they varied from 8 to 14. A majority of these might open on either the right or left side or on the floor of the stomach.

The direct intestine arises from the posterior end of the stomach and passes backward almost on the mid line except in its posterior third, where it bends slightly to the left side and terminates in a blind sac or cœcum of the crystalline style on the dorsal surface of the posterior adductor muscle (fig. 120, *DI* and *Coe*, p. 141). When the animal is well nourished the direct intestine is almost filled with a transparent, gelatinous rod which extends its whole length from the stomach to the cœcum.

The recurrent intestine arises from the median side of the direct intestine at the point where it crosses the mid-dorsal region of the posterior adductor muscle. It runs transversely for a short distance to the right side of the animal and then turns directly forward to run parallel with the direct intestine as far as the posterior end of the stomach; at this point it bends gradually to the left, passing over the direct intestine and then downward and forward over the left side of the stomach almost to its anterior end, where the intestine suddenly makes a posterior loop. This bend marks the beginning of the terminal intestine.



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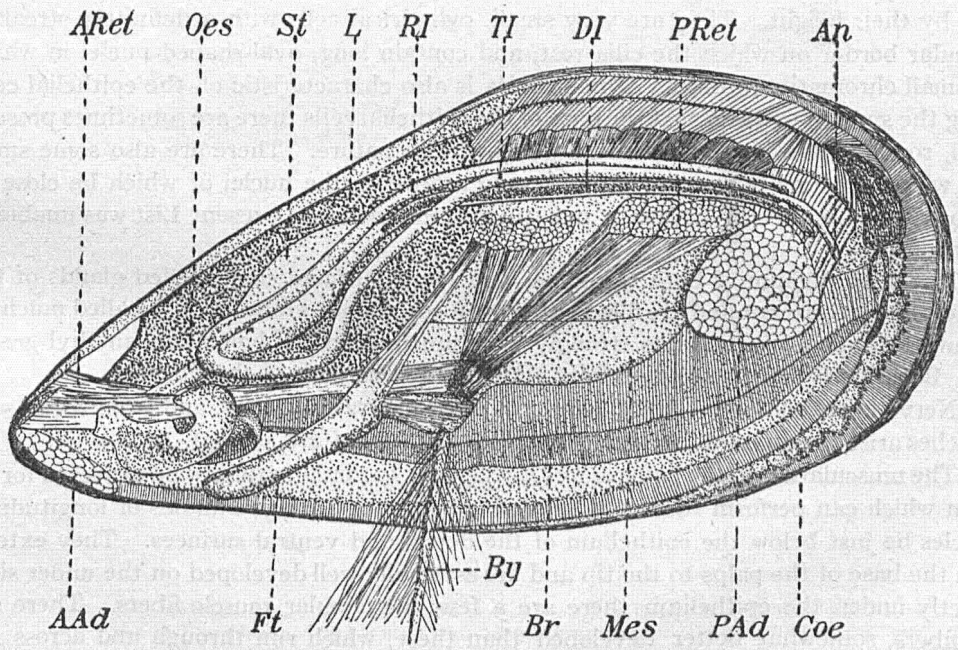

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FIG. 119.—Anterior view of mouth showing relation of lips to labial palps. *ILP*, inner labial palp; *Mth*, mouth; *OLP*, outer labial palp.

FIG. 120.—Digestive organs dissected out and shown in side view. *AAd*, anterior adductor muscle; *An*, anus; *ARet*, anterior retractor muscles; *Br*, gills; *By*, byssus; *Coe*, coecum of the crystalline style; *DI*, direct intestine containing the crystalline style; *Ft*, foot; *L*, liver; *Mes*, mesosoma; *Oes*, œsophagus; *PAd*, posterior adductor muscle; *PRet*, posterior retractor muscle; *RI*, recurrent intestine; *St*, stomach; *TI*, terminal intestine.

The terminal intestine, or rectum, as it is sometimes called, runs backward a short distance from its point of origin, parallel and almost in contact with the left anterior retractor muscle of the byssus, then it turns obliquely upward to the anterior end of the pericardial chamber. At this point it turns backward and passes directly through the ventricle of the heart, continuing on in the mid line over the posterior adductor muscle and terminating in an anus surrounded by dark-brown pigmented epithelium, situated on the posterior surface of the muscle (fig. 120, *TI*, p. 141).

In a mussel 80 mm. long, the mouth opening has a width of 7 mm., the œsophagus a length of 12 mm., the stomach 13 mm., the direct intestine 32 mm., the recurrent intestine 48 mm., and the terminal intestine 52 mm.

HISTOLOGY.

List (1902) has carefully worked out the microscopic structure of the labial palps of *Mytilus galloprovincialis*, and since it is practically the same as that found in those of *Mytilus edulis* his description is followed. The entire upper surface is uniformly covered with a thick layer of cilia. On the under surface cilia are also present, but they are distributed in small scattered clusters which are difficult to demonstrate (figs. 121 and 122, opp. p. 142).

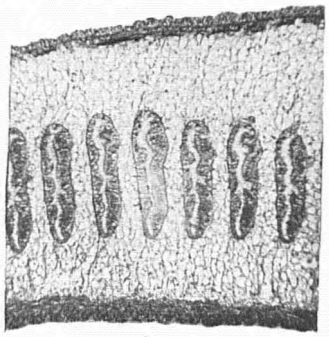
The epithelial cells of the ridges are distinguished from those of the other parts of the palp by their height. They are very small, cylindrical cells with a definitely streaked cuticular border on which the cilia rest, and contain long, oval-shaped nuclei in which are small chromatin granules. The cuticula is also characteristic of the epithelial cells lining the smooth surface. At the base of the epithelial cells there are sometimes present small, round cells which are perhaps ganglionic in nature. There are also some small cells with peripherally running protoplasmic processes, the nuclei of which lie close to the basal membrane. Whether or not special sense cells are present List was unable to determine.

In the epithelium of both the upper and lower surfaces single-celled glands of the beaker type are present and are filled either with eosinophile granules or so-called mucin—a slimy substance which stains strongly with mucin carmine, hæmalum, methyl green, etc. Both kinds of cells are especially abundant at the ends of the ridges.

Nerve fibers run over the surface of the palps in large numbers, and from these, side branches arise to supply each ridge with a fiber (fig. 160, *BuN*, p. 173).

The musculature of the palps is well developed, as would naturally be expected for an organ which can perform such complicated movements. Large bundles of longitudinal muscles lie just below the epithelium of the dorsal and ventral surfaces. They extend from the base of the palps to the tip and are especially well developed on the under side. Directly under the epithelium there are a few fine circular muscle fibers. There are also fibers, somewhat better developed than these, which run through and across the organ. Three sets of muscles are present on the rigid side of the palps. They consist of (1) fine, circularly running fibers which lie just below the epithelium (2) bundles of fibers which run from one ridge to the next, thus joining all of them together, and (3) fibers which run from the base of the epithelial cells of the ridges to the epithelium of the under side.

The epithelium of the lips is continuous with the ridged epithelium of the palps but differs from it by having taller ciliated cells. Below the epithelium of the lips



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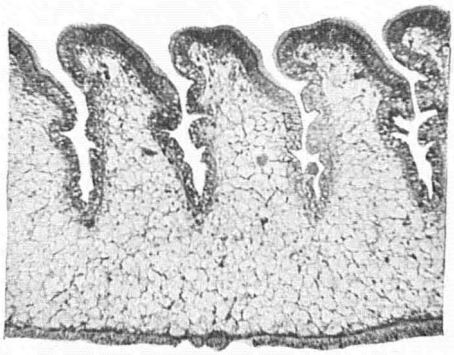

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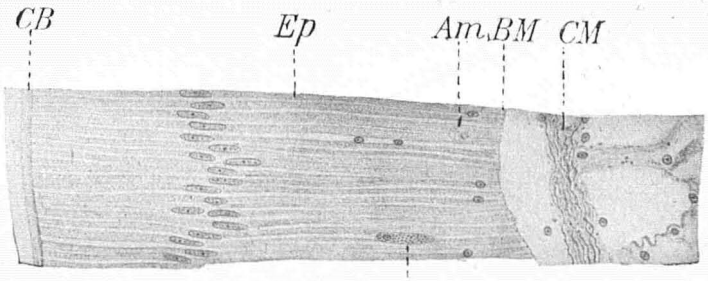

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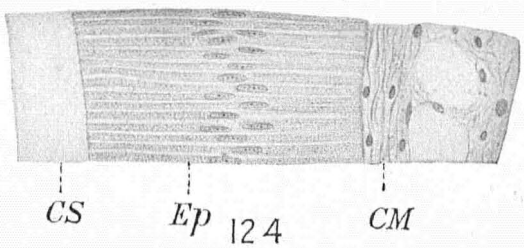

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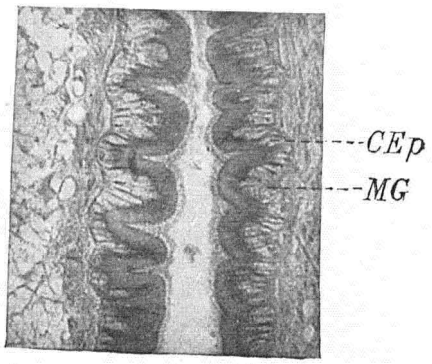
FIG. 121.—Photomicrograph of a longitudinal section through the smooth side of a labial palp. × 30. Fixed in Flemming fluid and stained with Delafield hæmatoyxlin. The centrally located ciliated canals are continuous with furrows shown in fig. 122.

FIG. 122.—Photomicrograph of a longitudinal section through the ridged side of a labial palp. ×30. Preparation same as fig. 121.

FIG. 123.—Section through the stomach epithelium. *Am*, amoebocyte; *BM*, basal membrane; *CB*, cuticular border; *CM*, circular muscles; *Ep*, stomach epithelium; *MG*, mucous gland. (After List, 1902.)

FIG. 124.—Section through the stomach epithelium in the posterior region. *CM*, circular muscles; *CS*, crystalline style substance; *Ep*, stomach epithelium. (After List, 1902.)



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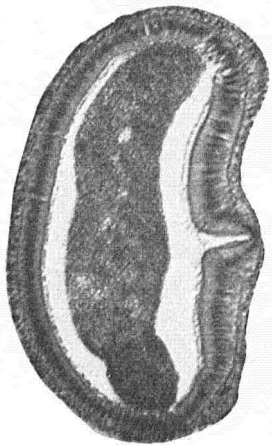

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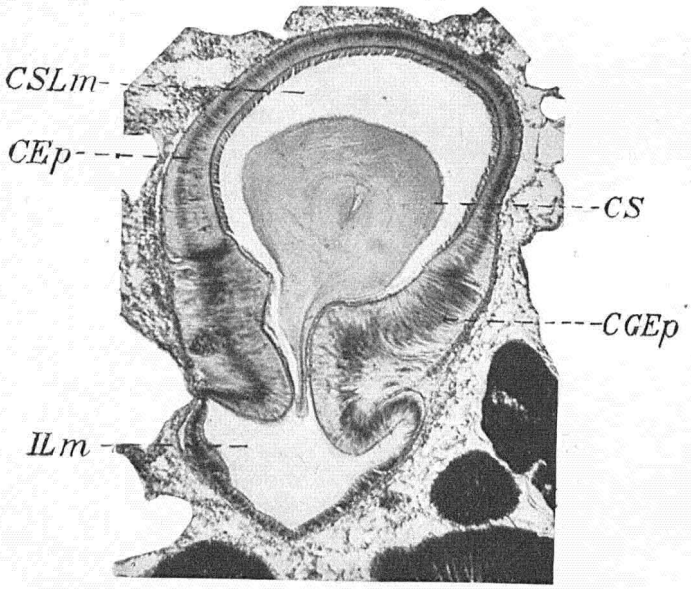

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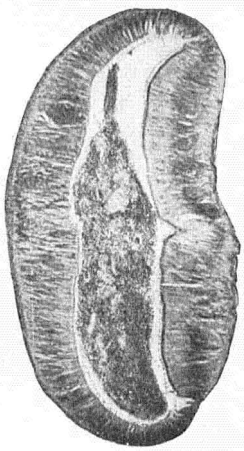

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PHOTOMICROGRAPHS. × 50.

FIG. 125.—Longitudinal section through œsophagus. Fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red. *CEp*, ciliated epithelium; *MG*, mucous glands.

FIG. 126.—Cross section through recurrent intestine. Preparation same as fig. 125. The lumen is filled with diatoms and detritus.

FIG. 127.—Cross section through terminal intestine. Preparation same as fig. 125.

FIG. 128.—Cross section through direct intestine. *CEp*, ciliated epithelium; *CGEp*, ciliated and glandular epithelium; *CS*, crystalline style; *CSLm*, crystalline style lumen; *ILm*, intestinal lumen

there is a thick layer of gland cells whose contents stain deeply with Delafield's hæmatoxylin. A second type of gland cell lies peripherally to these just below the epithelium or, in some cases, in the epithelium itself, as single cells filled with round granules which stain deeply with Bordeaux red or eosin.

The epithelium of the œsophagus is a continuation of that of the lips, but in the transition the surface changes from a smooth to a convoluted condition. The epithelium is of the columnar ciliated type similar to that on the lips except that in the basal region the gland cells increase greatly in number as the stomach is approached (fig. 125, *MG*, opp. p. 143). They are the type of gland cell which stains with hæmatoxylin. There are also small cells of irregular form containing yellow granules which lie scattered throughout the basal region of the epithelium in varying numbers. List (1902) thinks they are probably amœbocytes which were caught while wandering through the epithelium of the œsophagus where they were loading themselves with food material to be carried to assimilation organs in the manner suggested by the researches of Carazzi (1893) on the oyster.

The epithelium rests on a distinct basal membrane, below which there is a thin layer of circular and longitudinal muscle fibers. According to Sabatier (1877) the circular fibers form an inner layer in relation to the longitudinal muscles, but in the author's preparations the two sets of fibers seem to be intermingled.

The stomach has its inner surface thrown into numerous folds and prominences of various sorts in different individuals. Sometimes it gives rise to one or more pockets from the dorsal, lateral, or ventral walls.

The epithelium of the stomach is similar to that of the œsophagus except that it is higher and almost without any mucous gland cells (fig. 123, opp. p. 142). The cells are all ciliated, but the cilia are proportionately shorter. In many places, chiefly on the dorsal wall, they may be entirely covered with a homogeneous substance very similar to the crystalline style (fig. 124, *CS*, opp. p. 142). The basal membrane on which the cells rest varies in thickness in different places, being more strongly developed where the greatest folds appear and showing scattered nuclei lying within its substance.

Circular muscles lie immediately below the basal membrane, and, according to Sabatier (1877), external to these there is a layer of longitudinal fibers. This layer, however, the author could not demonstrate to his own satisfaction.

The direct intestine or tubular stomach, in the terminology of Sabatier (1877), arises from the posterior end of the stomach as a canal which at first is round in cross section, becoming oval in the middle region, the large end usually placed ventrally (fig. 128, opp. p. 143). Sometimes it is found in a dorsal position. Often the lateral walls of the canal project inward so as to divide the direct intestine into a dorsal and a ventral canal. In each case the larger lumen contains the crystalline style, the smaller one performing the usual functions of an intestine. The epithelium of the two regions is very different, that which lines the walls of the lumen occupied by the crystalline style being composed of low columnar cells covered with relatively heavy cilia, while that of the intestinal portion is lined with a columnar ciliated epithelium whose cells are much higher. The lateral walls form thick folds of very high cells which also carry a heavy coat of cilia. The wall lying opposite to the crystalline style cavity is lined with a relatively low columnar ciliated epithelium between the cells of which lie numerous gland cells of the beaker type.

The recurrent intestine is either round or elliptical in cross section at its posterior end. As it runs forward one side becomes flattened and develops a high columnar, ciliated epithelium which is parted in the middle by a longitudinal furrow (fig. 126, opp. p. 143). The walls which are continuous on either side with this thickened portion are composed of comparatively low epithelial cells, but as they pass around to the opposite side of the intestinal wall they become progressively higher, although they do not reach the height of those on the flat side. Between the epithelial cells there are scattered a few tall mucous cells. The epithelium is bounded externally with a basal membrane which is thickest on the side where the epithelial cells are highest. External to it there is a thin layer of circularly running fibers.

The terminal intestine is a continuation of the recurrent intestine and preserves the same semicircular outline of the latter with the very tall epithelium lining the flat side. The furrow, however, which divides this thickened portion into right and left halves is much deeper than that in the recurrent intestine, and the ciliated cells gradually become much lower (fig. 127, opp. p. 143). Mucous cells are distributed in considerable numbers between the epithelial cells. The basal membrane on which the ciliated cells rest is well developed and covered externally with a thin layer of circular muscle fibers.

The crystalline style as observed by Haseloff (1888) and List (1902) is composed of a somewhat firm, elastic substance of gelatinous consistency. In the fresh state it is perfectly clear and transparent. In cross section it shows a series of concentric layers, the central portion presenting a homogeneous structure, while that near the periphery is granular in appearance. According to List (1902) the crystalline style is formed from secretions produced by the high epithelial cells, in the side walls of the direct intestine. The secretion consists of granules which are molded into the surface of the crystalline style.

The liver occupies the anterior part of the visceral mass and completely surrounds the stomach and those portions of the intestine which lie anterior to the heart. The larger portion of the liver occupies the right side of the body. The organ is single and composed of numerous lobules which in turn are made up of elongated glandular acini. The discharging canals unite successively with the main canals which empty into the stomach by large openings that often cause irregularities in the walls. The number of main canals appears to vary between 8 and 15.

List (1902) says in regard to their structure that the main canals to the stomach are unevenly ciliated throughout, the epithelium being composed of two distinctly different elements of which each circles one-half of the canal when seen in cross section. On one side the columnar cells are lower and broader than those of the opposite side and contain numerous granules lying in their distal ends; the nuclei are large, each one containing a conspicuous necleolus. Cilia are absent. The epithelium lining the opposite side of the canal is composed of high columnar cells which bear long cilia arising from distinct basal bodies; the nuclei are small and contain numerous chromatin granules with or sometimes without a nucleolus. Externally the canal is surrounded by a well-developed layer of circular muscles (fig. 129).

The epithelium of the secondary liver canals is continuous with that of the main canals and differs from it in having a lining of broad, low columnar cells that contain large nuclei with a conspicuous nucleolus (fig. 130). The protoplasmic portion is further

characterized by the presence of numerous large granules which in the fresh tissue are yellowish or brown in color. The particular hue of the granules seems to depend upon the food of the animal according to List (1902). If the mussel is starved the liver granules become lighter in color, if fed with algæ they become green, and if given india ink or carmine they become black or red, respectively.

The granules contain albumin particles, fat droplets, and glycogen.

PHYSIOLOGY.

Erman (1833) believed that the function of the palps was to sweep into the mouth particles of floating food carried forward in the currents set up by the action of the ciliated gills. It was also considered that they might have a respiratory function.

Thiele (1886) thought that the chief function of the palps was to transfer food collected by the gills to the mouth. He pointed out that their structure and position clearly indicated this. The outer pair extend from the upper lip of the mouth to the outer pair

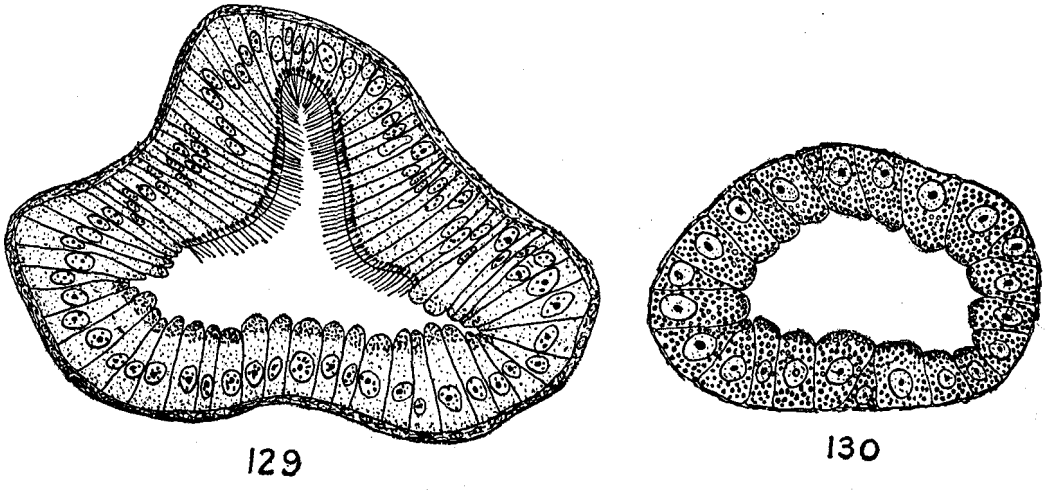


FIG. 129.—Cross section of a primary liver canal to the stomach. Fixed in Flemming fluid and stained with Delafield hæmatoxylin. × 575.

FIG. 130.—Cross section of a secondary liver canal. Preparation same as fig. 129. × 575.

of gills, while the inner pair reach from the lower lip to the inner pair of gills where they can pick up the food particles collected by these organs. The rich innervation of the palps suggests that they may possibly function as taste organs. List (1902) questions this latter theory on the ground that observations show it to be only slightly probable, as all foreign bodies which have been transported to the palps are taken into the mouth if they do not exceed a certain size. The experiments of Lotsy (1893), however, indicate that certain shellfish have the power of discrimination in the selection of food, for when clouds of diatoms from a culture were introduced near the ventral opening of the syphon of a clam they were immediately ingested, but when hashes of fish or shrimp were given they were refused or if ingested were forcibly ejected an instant later. Oysters, in a similar manner, exhibited the power of discrimination between different kinds of food which were given to them. How the mollusks were able to distinguish between the different kinds of food Lotsy does not attempt to explain. Anatomically, however, it seems likely that this center of discrimination is located in the palps.

The composition and function of the crystalline style was studied by Haseloff (1888), who found that alcohol causes it to become opaque and thinner. Nitric acid makes it turn yellow, and dilute hydrochloric acid prevents it from decomposing. It dissolves in ordinary water, but more readily in salt water. In 1 per cent acetic acid it dissolves completely in from two to three minutes. Treated for some time with sulphuric acid it takes on a violet color. Picric acid will precipitate a solution of crystalline style. If the solution is first treated with acetic acid and then with potassium ferrocyanide, a white flocculent precipitate is formed. From these reactions Haseloff concluded that the crystalline style is composed of albuminous matter and is therefore a reserve food material. This view is given additional support by the fact that if mussels are starved the structure will disappear in a few days, after which, if plenty of food is again supplied, the structure reappears.

Many different functions have been ascribed to the crystalline style. Heide (1684) and Cailliaud (1850) thought it was related to the reproductive organs. Meckel (1829) took it for a tongue. Garner (1841) believed it had something to do with the swelling up of the foot. Milne-Edwards (1859) ascribed to it the function of stirring up the food during digestion. Vulpian (1869) found that it contained some crystals of calcium oxalate and concluded from this fact that it must be connected with the urinary function. Sabatier (1877) described it as functioning to grind up and press the food against the intestinal wall. Krukenberg (1880) considered it as a pestle which forced the digested food as closely as possible to the absorbing epithelium as it passed along. Hazay (1881) and Haseloff (1888) considered it as a reserve food material, while Barrois (1890) believed it served only in helping to transport the food becoming dissolved in the stomach and surrounding the food mass with a slippery coat. He evidently considered it a substance similar to mucin and chondrin and therefore without any food value.

The best researches on the origin and function of the crystalline style since that of Haseloff (1888) have been made by Mitra (1901), who employed chemical methods, and List (1902), whose plan was to feed india ink to the shellfish and observe its effects on the organ. List found that the strong bristlelike cilia of the cavity in which the crystalline style lies swept the india ink particles around the rod in continuous rotations which moved gradually forward. When it was completely covered with ink, he was able to observe that the anterior end was being gradually dissolved in the stomach while the posterior end was being formed of new crystalline style substance free from india ink. Furthermore, the coating of ink which remained on the rod was in turn covered with a layer of the crystalline style material. List therefore concluded that the crystalline style is secreted in the direct intestine from the tall epithelium of the side walls and that it gradually moves forward to the stomach by a rotating movement set up by ciliary action. In the stomach it dissolves and, as List assumes, probably serves as a food substance.

The function of the crystalline style has been most satisfactorily demonstrated by Mitra (1901), who worked with fresh-water mussels. His analyses gave the following as the chemical composition of crystalline style: Water, 88 per cent (approximately); globulin, 12 per cent; salts, 1 per cent. The composition is similar to that of the pancreatic secretion of dogs and suggests that the crystalline style may function as a digestive ferment. Further experiments gave strong support to this assumption, for it was found that two styles if added to 30 minims of starch solution would completely

convert it into reducible sugar in about 3 hours, and if a solution of 7 styles in distilled water was added to 30 minims of the same starch solution it was transformed into a reducible sugar in about 20 minutes. Mitra concludes therefore that the crystalline style contains an amylolytic ferment. It acts upon raw starch and is able to convert glycogen slowly into sugar but appears to have no action on such protein matters as egg albumin, fibrin, or muscle fibers. He considers the protein matter (globulin) of the style and the ferment as identical substances and believes that the former in no way functions as a reserve food mass.

The conclusion to be drawn from the investigations recorded above is that the crystalline style originates from the tall columnar epithelium of the direct intestine and gradually moves forward with a spiral motion to the stomach, where it mixes with food and functions as a digestive ferment of starchy materials.

The experiments of List (1902) on the function of the liver show that the granular bodies in the liver cells take up nourishing materials (also carmine, india ink, iron, and litmus) in the form of very small particles until the granules are entirely filled; then the food materials emerge in the form of large particles which are removed by way of the main liver canals to the stomach and intestine. He demonstrated clearly that the characteristic color of the liver always depends upon the nature of the nourishment taken by the animal and concludes that the liver functions primarily as a storehouse of reserve food material.

CIRCULATORY SYSTEM.

HEART.

The heart lies in the mid-dorsal region just posterior to the upper extremity of the hinge where it is inclosed in a spacious pericardial cavity the walls of which are formed of a thin, transparent membrane that is continuous with the body wall (fig. 133, *PC*, p. 149). The floor of the pericardial cavity rests on the direct and recurrent intestines which run parallel to each other in this region. Laterally it is covered with a thin portion of the mantle that is usually free from any proliferations of the genital epithelium, while dorsally it is inclosed between the two bands of pallial muscles which are continuous with the mantle edge. In a mussel 8 cm. long the floor of the pericardial chamber is about 15 mm. long by 8 mm. wide, and the roof of the cavity which is shaped like an inverted V is about 5 mm. high. At the anterior extremity of its base the pericardial cavity opens into a wide duct that borders the anterior surface of the oblique vein and connects with the kidney. This wide duct was given the name *couloir* by Sabatier (1877) but may better be called the renipericardial canal (fig. 133, *RC*).

The heart is composed of a ventricle and two auricles. The ventricle is more or less elliptical in form and extends the whole length of the pericardial chamber. In a mussel 8 cm. long it has a length of 15 mm. and a breadth of 2 mm. when relaxed. When distended with blood the diameter becomes about 4 mm. The blood leaves the heart by a single aorta which leads off from it at the anterior extremity. The middle of the ventricle is traversed by the rectum which enters at the anterior end just above the aorta and passes out at the posterior extremity in the dorsal region, so that a blind sac is left in the posterior end of the ventricle.

The auricles are two large sacs which are symmetrically placed one on each side of the ventricle and connected with it by a short auriculo-ventricular canal (fig. 131,

AVC, p. 149) in which are valves that permit the blood to flow toward the ventricle only. On the other hand, the auricles communicate with large afferent oblique veins on their respective sides. The afferent oblique veins enter the auricles in the ventral anterior region where they greatly enlarge and become continuous with the walls of the auricles (fig. 133, *AOV*, p. 149). The walls of the auricles are covered with a brown colored, spongy tissue which presents a rough, irregular surface. These are the *pericardial glands* (fig. 131, *PG*), which are described under the excretory system. The auricles lie almost free in the pericardial cavity. They are attached to the floor and lateral walls of the chamber at their posterior extremities by numerous small blood vessels which empty directly into the auricles. Anteriorly the auricles are held in place by the afferent oblique veins with which they are continuous.

ARTERIAL SYSTEM.

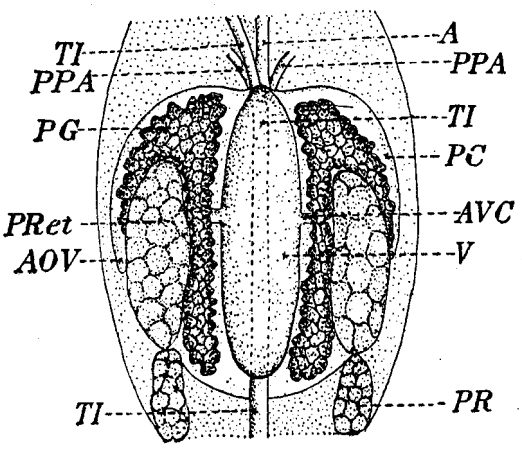
The blood leaves the heart by a single anterior aorta, from which it is distributed to the body through five channels which are as follows: (1) Three pairs of pallial arteries which supply the mantle and pallial muscles; (2) a pair of gastro-intestinal arteries which go to the stomach, intestines, posterior retractor muscles, posterior adductor muscle, lateral cavities, and mesosoma; (3) a single pericardial artery which carries blood to the walls of the pericardium, the direct and recurrent intestines, and the bordering genital glands; (4) three pairs of hepatic arteries which go to the liver; and (5) a pair of terminal arteries which furnish branches to the anterior parts of the body.

The aortic bulb marks the beginning of the aorta and gives rise to several of the most extensive arteries. It arises as a bulbous swelling from the anterior end of the ventricle immediately below and just anterior to the point where the rectum penetrates into the ventricle.

The *anterior aorta*, which is the largest of the arteries, arises from the anterior end of the bulb and runs forward on the dorsal surface of the body immediately below the hinge ligament (fig. 133, *A*, p. 149). When it reaches the point just below the anterior end of the hinge ligament it divides into two large right and left trunks that pass outward to the outer surface of the mantle and then bend sharply backward to supply numerous small vessels to the ventral anterior portion of the mantle. These are the *anterior pallial arteries* (fig. 133, *APA*). A very small artery continues forward and downward from the bifurcating point of the aorta to send out fine branches over the dorsal surface of the œsophagus.

A second pair of arteries of minor extent arise from the mid region of the anterior aorta and send branches to the anterior portion of the mantle folds. Because of their position the author has named them the *intermediate pallial arteries* (fig. 133, *IPA*). Sometimes two pairs of these intermediate pallial arteries are present.

The *posterior pallial arteries* are a pair of large vessels which arise from the ventrolateral surfaces of the aortic bulb. The trunks pass out to the surface where they fork into anterior and posterior vessels that in turn subdivide into numerous branches that supply the entire middle and posterior portions of the mantle and the posterior adductor muscle besides sending numerous small vessels into the liver (fig. 133, *PPA*). The main branches of the three pallial arteries give off many minor branches that continue to divide and subdivide into still smaller vessels which make a fine network throughout the whole mantle. The trunks that terminate at the periphery of the



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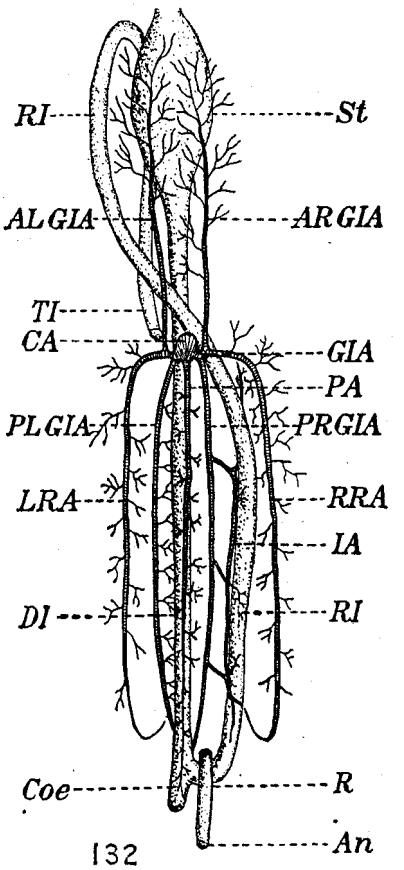

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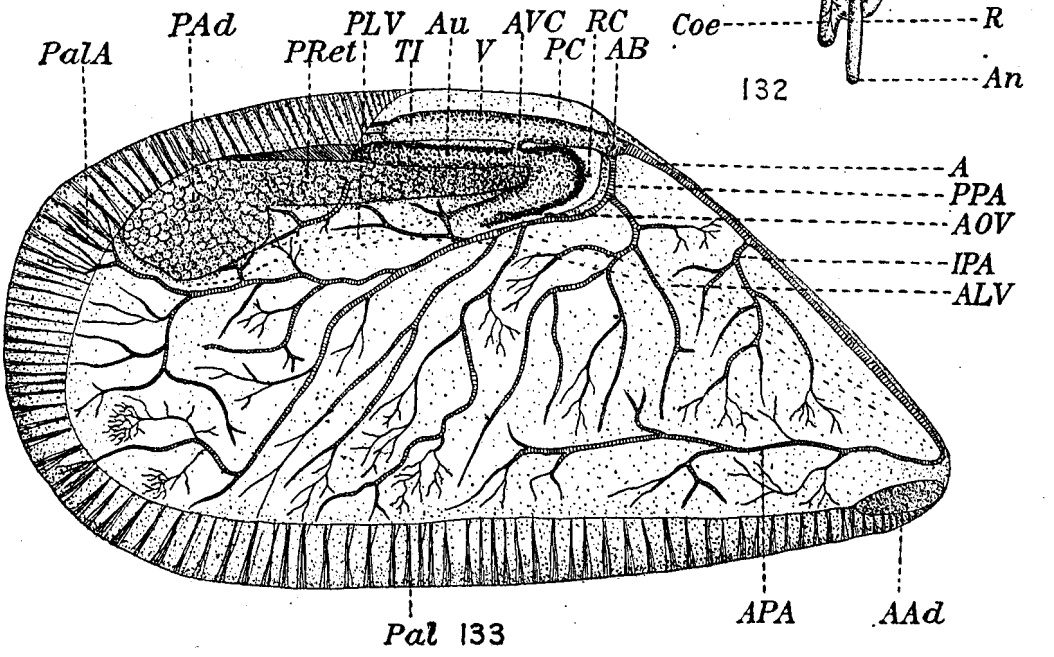


133

FIG. 131.—Dorsal view of heart exposed in the pericardium.

FIG. 132.—Gastro-intestinal arteries seen from above. From dissection of a specimen which had been injected with carmine-gelatin mass.

FIG. 133.—Lateral view of mantle showing arteries injected with carmine-gelatin mass.

ABBREVIATIONS.—*A*, aorta (fig. 131), anterior aorta (fig. 133); *AAd*, anterior adductor muscle; *AB*, aortic bulb; *ALGIA*, anterior left gastro-intestinal artery; *ALV*, anterior longitudinal vein; *An*, anus; *AOV*, afferent oblique vein; *APA*, anterior pallial artery; *ARGIA*, anterior right gastro-intestinal artery; *Au*, auricle; *AVC*, auriculo-ventricular canal; *CA*, coeliac artery; *Coe*, coecum; *DI*, direct intestine; *GIA*, gastro-intestinal artery; *IA*, intestinal artery; *IPA*, intermediate pallial artery; *LRA*, left recurrent artery; *PA*, pericardial artery; *PAd*, posterior adductor muscle; *Pal*, pallial muscles; *PalA*, arterial network of pallial muscles; *PC*, pericardial cavity; *PG*, pericardial gland; *PLGIA*, posterior left gastro-intestinal artery; *PLV*, posterior longitudinal vein; *PPA*, posterior pallial artery; *PRet*, posterior retractor muscle; *PRGIA*, posterior right gastro-intestinal artery; *R*, rectum; *RC*, renipericardial canal; *RI*, recurrent intestine; *RRA*, right recurrent artery; *St*, stomach; *TI*, terminal intestine; *V*, ventricle.

mantle break up into a fine lacunar network that envelops the pallial muscles (fig. 133, *PalA*).

The *gastro-intestinal arteries* are a pair of large vessels leading off to the right and left, respectively, from a very short thick trunk, the *cœliac artery*, that arises from the ventral surface of the arterial bulb (fig. 132, *GIA*, p. 149). They immediately divide into two branches, one of which passes forward sending out many small vessels to the stomach, recurrent intestine, terminal intestine, and liver; the other of which runs posteriorly supplying blood to the direct intestine, recurrent intestine, and surrounding tissues. The *anterior gastro-intestinal arteries* are more or less symmetrical in their course, while the posterior ones are not. The left *posterior gastro-intestinal artery* lies to the left of the direct intestine to which it sends a rich supply of blood. The right *posterior gastro-intestinal artery* lies on the right side of the direct intestine deeply imbedded in the tissues. To expose this artery to view it is necessary to remove the rectum and overlying tissues and move the recurrent intestine slightly to the right. The right *gastro-intestinal artery* is slightly larger than its corresponding vessel on the left side and further differs from it by giving off a large trunk, the *intestinal artery* (fig. 132, *IA*) that runs posteriorly along the recurrent intestine, giving off small branches that spread over it. In its course backward from the point of origin of the *intestinal artery* the *right posterior intestinal artery* gives off two or three short trunks from its right side that pass directly to the recurrent intestine, where they divide into small vessels that spread out over the surface of the intestine. This artery also furnishes several vessels that carry blood to the right side of the direct intestine and to the rectum.

The *recurrent arteries* (fig. 132, *RRA* and *LRA*) are a pair of long trunks that arise from the lateral sides of the *anterior gastro-intestinal* arteries immediately after their point of origin. They pass outward and then turn abruptly backward, passing over the median side of the posterior retractor muscles to the anterior wall of the posterior adductor muscle, where they turn downward and forward and give out numerous branches to the walls of the lateral cavities and the mesosoma.

The *pericardial artery* (fig. 132, *PA*) is a single median vessel that arises from the ventral side of the *cœliac trunk* between the points of origin of the *gastro-intestinal arteries*. It runs posteriorly on the middle part of the floor of the pericardial chamber terminating in the region of the anus. In its course it gives off numerous small vessels which go to the base of the pericardial chamber, the direct intestine, the recurrent intestine, and adjacent tissues.

The *hepatic arteries* consist of several pairs of short vessels, usually three in number, which branch off from the aorta at right angles and penetrate directly into the liver, where they divide into many branches that form a rich network throughout the gland.

The *terminal arteries* arise from the anterior end of the aorta which forks at a position about midway between the point of origin of the *intermediate pallial arteries* and the anterior extremity of the body. The two resulting branches continue forward and downward to the anterior extremity of the body, where they turn back sharply on their respective sides to form the anterior pallial arteries which traverse the lower edge of the mantle for about one-half its length. In their course the *terminal arteries* also give rise to small vessels that go to the anterior part of the liver, the genital glands of the

immediate region, the dorsal and lateral walls of the supra-œsophageal cavity, and to the anterior adductor and anterior retractor muscles.

The *anterior ventral artery* is a median trunk that arises from the *anterior aorta* ventral and slightly posterior to the point where the *terminal arteries* branch off. It runs forward in the middle of the floor of the supra-œsophageal cavity for about half its length and then turns sharply downward, crossing the œsophagus on its right side and continuing to the ventral body surface between the anterior retractor muscles. Here it turns backward and gives off in its course a large *pedal artery* to the foot besides a number of smaller vessels to the anterior and posterior retractor muscles and to the byssus organ.

The *tentacular arteries* are two anterior branches from the *anterior ventral artery*. The *dorsal tentacular* artery continues forward on the floor of the supra-œsophageal chamber from the angle where the *anterior ventral artery* turns downward and extends to the mid-dorsal region of the upper lip. There it forks into right and left branches that extend laterally to the dorsal palps on their respective sides. The vessels enter the basal region of the palps on their ribbed sides and pass transversely across to the smooth border, which they follow back to the distal extremity, giving off at right angles in their course numerous fine vessels which extend across the palp to its lower edge. The *ventral tentacular artery* branches off from the *anterior ventral* artery where it turns abruptly backward on the ventral side of the body. It runs forward slightly beneath the ventral surface between the anterior retractor muscles to the ventral surface of the lower lip, where it forks into right and left branches that go to the right and left inferior palps, respectively. The course of the vessels through the inferior palps is the same as that already described for the superior palps.

VENOUS SYSTEM.

The venous system collects the blood of the body into the 10 main groups of vessels through which it is conveyed to the heart. Briefly described, they are as follows: (1) A *marginal sinus* which extends around the border and receives the blood of the mantle, (2) a large number of *ascending pallial veins* on the inner face of the mantle which collect the blood of this organ, (3) a pair of *horizontal veins* which extend the length of the mantle just below the roots of the gills and receive the blood from the ascending pallial veins, (4) a pair of large *intermuscular veins* in the region of the muscles of the foot and byssus, (5) a pair of *mesosomal veins* which receive blood from the mesosoma, (6) *visceral veins* which conduct the blood from the liver, stomach, and intestines, etc., (7) *afferent branchial veins* and *efferent branchial veins* which carry blood to and from the gills, (8) a pair of *afferent longitudinal veins* which are closely associated with the kidney tissue and receive blood from the veins of the mesosoma and the branchial vessels from the horizontal veins by way of the plicate canals, and from the horizontal vein, visceral veins, intermuscular sinus, and branchial veins through the kidney, (9) a pair of *anastomosing veins* and the *transverse sinus* of the posterior adductor muscle which unite the horizontal veins with the longitudinal veins, and (10) a pair of *afferent oblique veins* which receive the blood from the longitudinal vein and conduct it to the heart.

The marginal sinus follows the free border of the mantle which is enveloped by the fold of periostracum that extends beyond the edge of the shell (figs. 134 and 135, *MS*,

p. 153). It receives blood from the area of the mantle lying close to the border through a network of fine vessels that empty into it throughout its course.

The *ascending pallial veins* are a series of vessels covering the internal face of the mantle extending upward, more or less parallel to each other, from the margin of the mantle to the horizontal vein that runs parallel and just below the line of attachment of the gills (fig. 134, *APV*). They result from the union of numerous fine capillary vessels that form a network all through the mantle and represent the principal channels by which the blood leaves the mantle.

The *horizontal veins* are paired vessels which follow a sinuous course the length of the mantle, parallel to and just below the roots of the gills (fig. 134, *HV*). Beginning anteriorly as a vessel of small diameter, each horizontal vein gradually increases in diameter as it runs backward. In the region of the posterior adductor muscle it reaches its maximum size and is quite conspicuous. Throughout its entire course it is connected with the ascending pallial veins which discharge their blood into it. Near the posterior end it receives the anastomosing vein and finally connects with the marginal sinus behind the posterior adductor muscle.

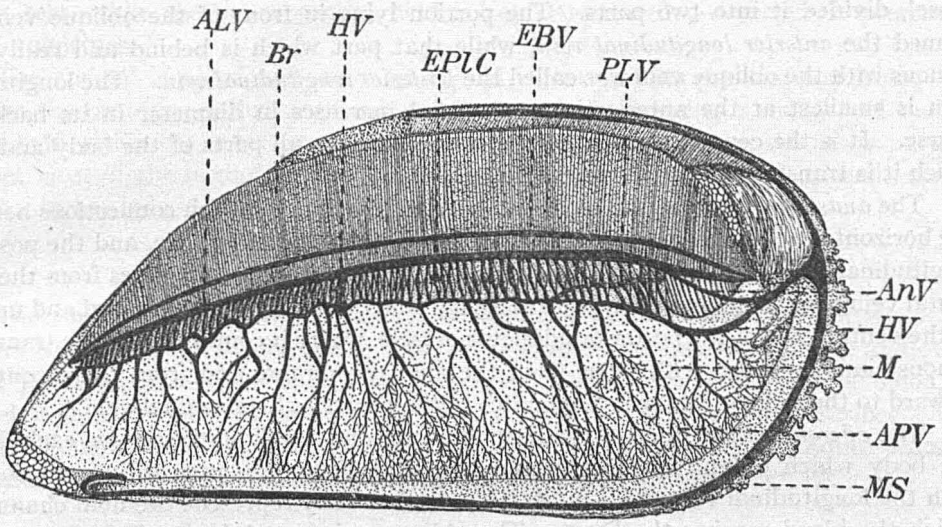
The *intermuscular sinus* is also a paired vessel. It arises between the palps at their point of attachment and extends back over the muscles of the foot and byssus in a series of cavities. One branch of the sinus lies between the anterior retractor muscles; a pair of vessels runs laterally to these muscles, extending back as far as the posterior adductor muscle; and still another pair goes between the posterior retractor muscles. In their course they receive veins from the liver, foot, kidney, and the mesosoma (fig. 135, *IMS*).

The *mesosomal veins* arise as three main trunks on each side of the mesosoma. A median vessel runs posteriorly close to the free border. Above it, two lateral vessels run backward and unite with it. The common trunk, thus formed, empties into a transverse sinus on the anterior ventral side of the posterior adductor muscle, which connects with the longitudinal vein and vessels of the kidney (fig. 135, *MV*).

The *visceral veins* include numerous small vessels which convey blood from the liver, stomach, intestines, etc., chiefly to the network of vessels within the kidney. The blood supply of the liver is particularly rich and involves a complicated mass of vessels which envelop the lobes. The blood from the dorsal and deeper parts of the liver is carried directly into the kidney, while that from the ventral portion and superficial area is conveyed to the kidney by way of the internal plicate canals (fig. 135, *IPlC*). A small amount of blood from the surface of the liver is carried off by small vessels that empty into the afferent vein of the gills.

The *branchial veins* on each side of the body consist of a single *afferent branchial vein* at the roots of the gills and a pair of *efferent branchial vessels* which border the free ends of the reflected filaments (fig. 134, *EBV*, and fig. 135, *ABV* and *EBV*). The afferent branchial vein is connected with vessels of the kidney from which blood is received and the efferent branchial veins open anteriorly into the anterior longitudinal vein near the base of the palps.

The *longitudinal veins* are paired vessels more or less enveloped by the kidney tissue. They extend from the base of the posterior adductor muscle to the anterior extremity of the gills. The position of the vessel on the right side of the body is indicated by a dotted outline in figure 133, *ALV* and *PLV*, page 149. Sabatier (1877), who named the



134

FIG. 134.—Interior view of right mantle with veins injected with Berlin blue-gelatin mass. Left mantle lobe with part of visceral organs has been removed and right branchial lamellæ reflected to expose external plicate canals and connecting veins. *ALV*, anterior longitudinal vein; *AnV*, anastomosing vein; *APV*, ascending pallial veins; *Br*, gills; *EBV*, efferent branchial vein; *EPlC*, external plicate canals; *HV*, horizontal vein; *M*, mantle; *MS*, marginal sinus; *PLV*, posterior longitudinal vein.

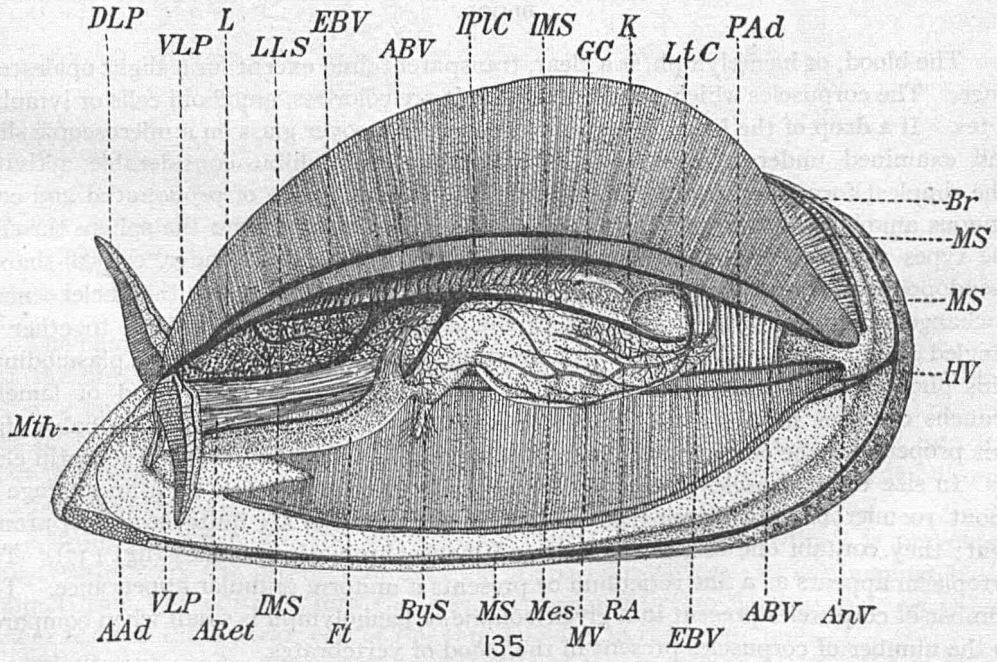


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FIG. 135.—Interior view of mantle cavity of an injected mussel with left branchial lamellæ reflected to expose foot and mesosoma. *AAd*, anterior adductor muscle; *ABV*, afferent branchial vein; *ARet*, anterior retractor muscles; *BySS*, byssus stalk; *DLP*, dorsal labial palp; *Ft*, foot; *GC*, genital canal; *IMS*, intermuscular sinus; *IPlC*, internal plicate canals; *K*, kidney; *L*, liver; *LLS*, left lateral sinus; *LtC*, lateral cavity; *Mes*, mesosoma; *Mth*, mouth; *MV*, mesosomal vein; *PAd*, posterior adductor muscle; *RA*, recurrent artery; *VLP*, ventral labial palp; other abbreviations same as in fig. 134.

vessel, divided it into two parts. The portion lying in front of the oblique vein was termed the *anterior longitudinal vein*, while that part which is behind and really continuous with the oblique vein was called the *posterior longitudinal vein*. The longitudinal vein is smallest at the anterior extremity and increases in diameter in its backward course. It is the central sinus that receives blood from all parts of the body and from which it is transferred directly to the heart.

The *anastomosing veins* are a pair of short trunks that establish connections between the horizontal vein, transverse sinus of the posterior adductor muscle, and the posterior longitudinal vein (fig. 134, *AnV*, p. 153). The vessel on each side arises from the horizontal vein near its junction with the marginal sinus, runs obliquely forward and upward to the ventral side of the posterior adductor muscle, where it connects with the transverse venous sinus and also with veins from the anal membrane, and from there continues forward to the kidney, where it terminates in the posterior longitudinal vein.

The *afferent oblique veins* of the heart are prominent oblique vessels on each side of the body which extend downward and backward from the pericardium to connect with the longitudinal vein (fig. 133, *AOV*, p. 149). They represent the final channel by which the blood reaches the heart. The oblique vein on each side is inclosed in the renipericardium canal, to which it is attached on the dorsal wall. The anterior and ventral surfaces are more or less covered with folds of kidney tissue similar to that of the pericardial glands which envelop the auricles and with which it is continuous. This portion of the oblique vein is free from any attachment and lies submerged in the fluid of the renipericardium canal.

BLOOD.

The blood, or hæmolymph, is a clear, transparent fluid except for a slight opalescent tinge. The corpuscles which are suspended in it are colorless, amœboid cells or lymphocytes. If a drop of the hæmolymph is placed under a cover glass on a microscopic slide and examined under a microscope, the lymphocytes exhibit considerable activity. The simplest form they assume is a sphere, but, being capable of pronounced and continuous amœboid movement, they take on all sorts of shapes from the sphere through the types with few pseudopodia to stellate forms with many slender, conical-shaped pseudopodia as shown in figure 136, *a*, *b*, *c*. During these movements the nuclei remain unchanged in form. When exposed to the air the amœbocytes collect together in tangled groups (fig. 136, *c*), after which the central mass runs together as a plasmodium. This phenomenon seems to be of great significance, for since the blood of lamellibranchs contains no fibrin and therefore is incapable of clotting, it is probable that this property of the corpuscles to form a plasmodium takes the place of the fibrin clot.

In size the corpuscles vary from 8 to 12 microns in diameter, with an average of about 10 microns. In histological preparations the nuclei are quite large and prominent; they contain one or two nucleoli and many chromatin granules (fig. 137). The cytoplasm appears as a fine reticulum or presents a uniform granular appearance. The number of corpuscles present in a given volume of hæmolymph is small when compared to the number of corpuscles present in the blood of vertebrates.

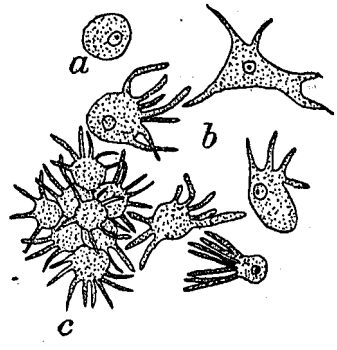
The fluid portion of the hæmolymph is an albuminous, salty liquid with an osmotic concentration equal to that of the sea water. When heated, a slight coagulation occurs. It is precipitated by picric acid, nitric acid, and mercuric chloride. It gives a decided

biuret test, while the xanthoproteic acid is not pronounced. Glycogen is present in small quantities.

The volume of blood present in an animal varies with its size and condition. By cutting the posterior adductor muscle, after thoroughly draining a shellfish of the sea water held within the mantle cavity, it is possible by gently pressing the fleshy parts to extract most of the hæmolymph. The quantity obtained from well-nourished mussels about 3 inches long is between 5 and 6 cc.

PHYSIOLOGY.

The function of the circulatory system is to carry dissolved food materials and oxygen to the various tissues of the body and to remove the carbon dioxide and other waste products of metabolism. This is accomplished by the circulation of blood, or hæmolymph, through the system of arteries and veins which have been described. Circulation is maintained by regular pulsations of the heart, which in the adult beats at the rate of 25 to 30 times per minute when the body temperature is 20° C.



136

137

FIG. 136.—Blood corpuscles drawn from life. ×560. *a*, contracted condition; *b*, showing pseudopodia formed during locomotion; *c*, tangled group of corpuscles.

FIG. 137.—Blood corpuscles drawn from histological section. ×560. Fixed in Gilson fluid and stained with Heidenhain iron hæmatoxylin.

The character of the heart beat is somewhat similar to that of the vertebrate. At first the auricles contract. This is followed immediately by a slight dilation of the posterior end of the ventricle, and then a wave of contraction moves forward rapidly over it. At the same time the ventricle contracts and discharges its blood into the aorta the auricles dilate with blood received from the oblique vein. This is followed by a period of rest, and then the process repeats itself.

The blood forced into the ventricle by contraction of the auricles is prevented from returning by the presence of auriculo-ventricular valves. In like manner blood pumped from the ventricle into the aorta is prevented from flowing back by valves present in both the anterior end of the ventricle and in the aortic bulb.

The blood flows from the aorta to the different organs of the body through a system of arteries which ultimately break up into a lacunar network of vessels that pervade all the tissues. The main arterial vessels lie on the outer surfaces of the mantle and run through the deeper parts of the body where the carbon dioxide accumulates in greatest

abundance. Becoming laden with the waste products of metabolism, the blood accumulates in the veins and sinuses which, for the most part, lie on the inner walls of the mantle and superficial parts of the body where a continuous flow of water is maintained over them by the cilia of the gills. This allows a ready interchange of gases with the sea water, whereby oxygen is absorbed by the blood and carbon dioxide eliminated. This process is continued further in the gills and plicate canals, as will be described below.

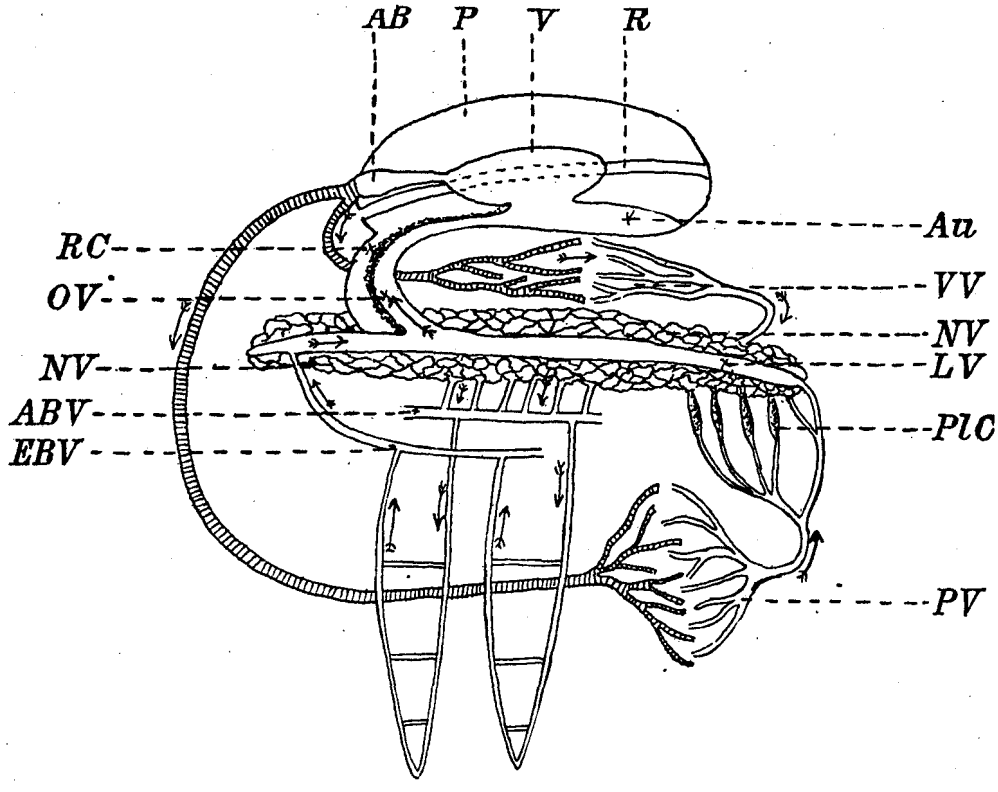


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FIG. 138.—Diagram of the circulatory system of *Mytilus edulis*. *Au*, auricle; *AB*, aortic bulb; *ABV*, afferent branchial vein; *EBV*, efferent branchial vein; *LV*, longitudinal vein; *NV*, nephridial veins; *OV*, oblique vein; *P*, pericardium; *PlC*, plicate canals; *PV*, pallial blood vessels; *R*, rectum; *RC*, renipericardial canal; *V*, ventricle; *VV*, visceral blood vessels.

The return of the blood to the heart may take place through several channels. Most of the blood from the visceral organs—stomach, intestines, liver, etc.—is discharged into the lacunar system of vessels in the kidney. The blood from the mantle may flow in small part into the posterior longitudinal vein and from thence be carried directly to the heart without penetrating the kidney tissue. Most of the blood from the mantle, however, passes into the kidney by way of the plicate canals, which have been mentioned before as a compact series of thin-walled ribbonlike organs extending the length of the mantle just below the roots of the gills (fig. 134, *EPlC*, and fig. 135, *IPlC*, p. 153). These canals contain a spongy reticulum of elastic fibers and externally are covered with

long actively beating cilia which keep up a constant flow of water. Sabatier (1874) was the first to recognize these as respiratory organs and noted how important it was for them to take on this rôle when the mantle was distended with genital products. This view is in harmony with the fact that when the mantle is filled with reproductive elements the plicate canals are distended with blood and are most prominent. A small amount of blood from the mantle may flow into the kidney without passing through the plicate canals.

In the kidney certain impurities are removed from the blood, as has been stated in the account of the excretory system.

The return of the blood to the heart from the kidney may be by two channels, either directly by way of the longitudinal vein and the oblique vein, or by way of the branchial vessels, anterior longitudinal vein, and the oblique vein. By far the greater part of the blood takes the first-mentioned course. The branchial circulation of Mytilus is very weak compared with that of many other lamellibranchs. Sabatier (1874) assigned three reasons to account for this: (1) The small caliber of the branchial vessels, (2) the feeble course of the blood which comes to the gills after traveling an extensive capillary network, and (3) the existence of more easy paths of return which allow the blood to reach the heart without traversing the gills.

A diagram of the general course taken by the blood in Mytilus is shown in figure 138.

MUSCULAR SYSTEM.

The muscles of *Mytilus edulis* fall naturally into five groups: (1) The adductors which close the valves, (2) the muscles of the foot, (3) the retractor muscles of the foot and byssus, (4) the pallial muscles which attach the mantle to the border of the shell, and (5) the anal muscles.

The adductor muscles are two in number, consisting of a small anterior adductor and a large, much more strongly developed, posterior adductor. The ratio in volume between the two muscles varies from 1:8 to 1:10. The posterior adductor (fig. 117, *PAd*, opp. p. 138; fig. 141, *PAd*, opp. p. 158) serves as the powerful muscle to close the valves and is located in the posterior dorsal region of the body where it runs across from one valve to the other. Its ends are firmly embedded in the round impressions of the shell which have already been described. The muscle itself is more or less cylindrical in form and is composed of numerous bundles of fibers which run parallel with each other across the space between the valves. Owing to the convexity of the shell the fiber bundles of the lower portion are about twice as long as those on the dorsal surface.

The anterior adductor (fig. 141, *AAd*) lies at the anterior end of the ventral edge of the shell. It extends across from one valve to the other as a thin band of fibers which is traversed on its midventral surface by a narrow pigmented membrane that arises from the union of the inner folds of the right and left mantle edges. The muscle terminates on the anterior ventral surface just inside the edge of each valve in the impression shown in figure 104, *AAd* (opp. p. 132).

The muscles of the foot are of two types, an outer circular layer of fine fibrils and an inner longitudinal layer composed of large bundles of fibers (fig. 145, *CM* and *LM*, opp. p. 159). The longitudinal muscles make up the bulk of the foot and run its entire length. They occupy chiefly the dorsal and lateral portions; in the ventral region they

are present as a single layer of small bundles. The circular layer surrounds the foot with a thin sheath of fibrils which lies just beneath the surface layer of pigmented, ciliated epithelium. Near the tip of the foot on the right and left sides the circular muscles give rise to numerous oblique muscles which run in various directions in such manner as to form a coarse network.

The purpose of this system of arrangement is obvious when the function of the foot is known. By contraction of the circular muscles the foot is thrust out as a long slender organ which may be directed in its course by the longitudinal and oblique muscles; contraction of the powerful longitudinal muscles with the synchronous relaxation of the circular muscles serves to draw the foot into a short, thick organ. The importance of these movements will be discussed later when the formation of the byssus and the movement of the mussel are described.

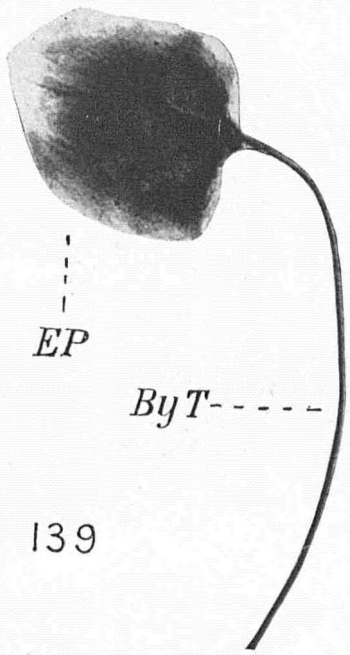
The anterior retractors of the byssus and foot (fig. 141, *ARet*, opp. p. 158) arise from the base of the byssus as a pair of cylindrical muscles which run forward on the ventral surface of the body (fig. 140, *ARet*, opp. p. 158) slightly diverging in the form of a letter V. They are inserted in elliptical impressions which lie on the dorsal anterior end of the shell parallel with the ligament. These impressions are about three times as long as they are broad, but are not symmetrical with each other, one usually being longer proportionately than the other. Although the name infers that these muscles are related to the foot, they really are not in the adult, for all the fibers terminate at the base of the byssus or are interwoven with the fibers of the posterior retractors of the byssus.

The posterior retractors of the foot and byssus may be described together since they are fused together in such close relation (fig. 140, *PRet*; fig. 141, *PRB*). Whereas the anterior retractors consist of a single cylindrical pair of muscles, those of the posterior retractors consist of several paired bundles which may vary in number from three to six or even more. They arise from the base of the foot and byssus as a single powerful muscle which divides up into separate bundles that spread out on either side in a fanlike manner and terminate in the impression of the valve which runs forward from that of the posterior adductor muscles parallel with the dorsal edge of the shell. The most posterior bundle runs directly over and in contact with the posterior adductor. The most anterior bundle arises from the base of the foot itself and properly constitutes the retractor of the foot (fig. 141, *PRB* and *PRF*).

The pallial muscles, or those of the mantle edge, are present on the ventral, posterior, and dorsal border of the mantle. They are composed of numerous small bundles of fibers which are separated a short distance from each other and run perpendicularly to the outer edge except in the region dorsal and anterior to the posterior adductor muscle where they slope backwards obliquely to the outer edge of the mantle (fig. 133, *Pal*, p. 149). The muscles are most strongly developed in the posterior region where the inner mantle fold is thicker and in the area about the anal syphon.

The anal muscles (fig. 117, *An*, opp. p. 138) are merely modified pallial muscles which arise from the wall of the anal syphon and are inserted in the shell impression which forms the triangular area on the posterior ventral edge of the impression made by the posterior adductor muscle.

With such a muscular system the sea mussel is wonderfully adapted for living in an environment where it is subjected to strong currents, the surge of the ocean, and other forces which exert great strains upon it. The pallial muscles firmly bind the edges of



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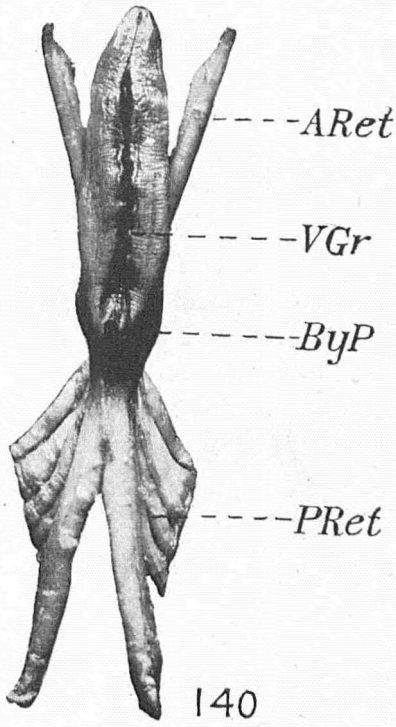

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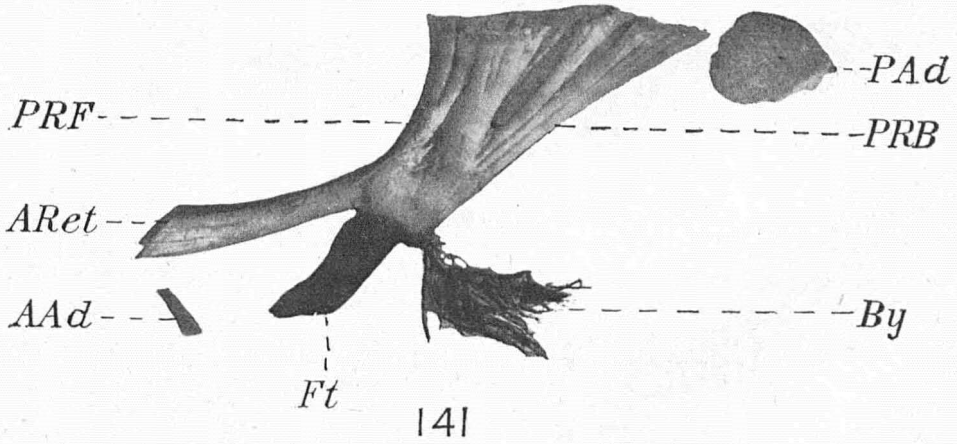

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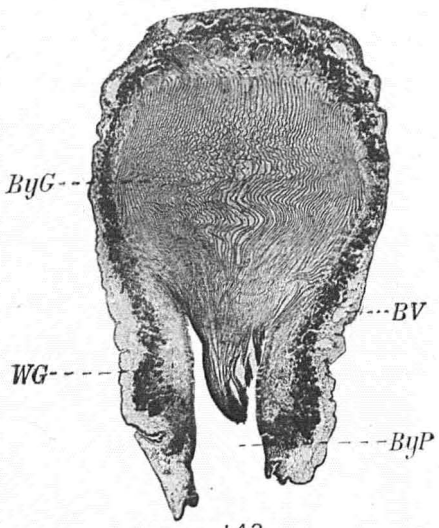
FIG. 139.—Photomicrograph of a byssus thread and end plate. × 10.

FIG. 140.—Ventral view of foot and retractor muscle.

FIG. 141.—Side view of adductor and retractor muscles.

ABBREVIATIONS.—*AAd*, anterior adductor muscle; *ARet*, anterior retractor muscles; *By*, byssus; *ByP*, byssus pit; *ByT*, byssus thread; *EP*, end plate; *Ft*, foot; *PAd*, posterior adductor muscle; *PRB*, posterior retractor muscles of byssus; *PRet*, posterior retractor muscles; *PRF*, posterior retractor muscles of foot; *VGr*, ventral groove.



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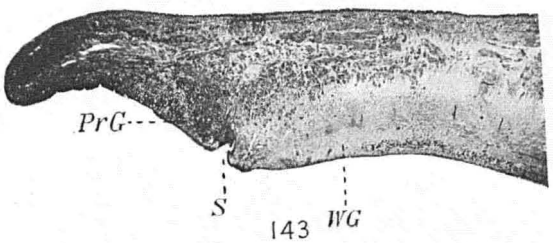

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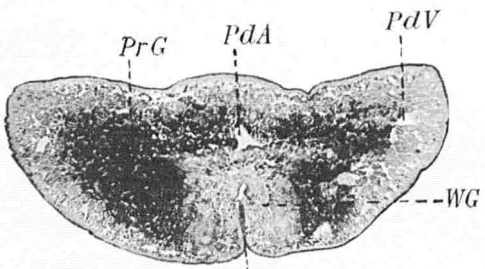

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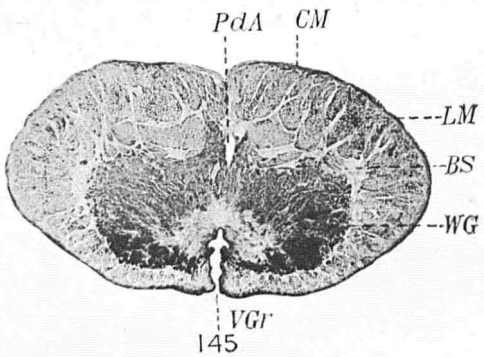


145

FIG. 142.—Photomicrograph of main byssus gland in cross section. × 8. Fixed in Gilson fluid and stained with Delafield hæmatoxylin.

FIG. 143.—Sagittal section through foot. × 6 approximately.

FIG. 144.—Cross section of foot taken just posterior to sucker.

FIG. 145.—Cross section of foot in the mid region. × 7 approximately.

ABBREVIATIONS.—*BS*, blood sinus; *BV*, blood vessels; *ByG*, glandular lamellae of byssus gland; *ByP*, byssus pit; *CM*, circular muscles; *LM*, longitudinal muscles; *PdA*, pedal artery; *PdV*, pedal vein; *PrG*, purple gland; *S*, sucker; *VGr*, ventral groove; *WG*, white gland.

the mantle to the shell, and the powerful retractors centered in the foot and byssus, which is the anchoring organ, are so firmly embedded in the calcareous walls of the shell that they can not be separated without tearing the muscles themselves. This enables the sea mussel to thrive in situations where no other shellfish can exist.

FOOT AND BYSSUS.

ANATOMY AND HISTOLOGY.

The foot is a muscular, glandular organ, tonguelike in form, with a deep longitudinal groove on the underside that terminates near the tip in a cuplike depression which serves as a sucker when the animal takes hold of a solid object. Posteriorly the groove becomes continuous with the byssus pit (fig. 118, *VGr* and *ByP*, opp. p. 138). When the foot is in a contracted state the groove forms an irregular line and its lips have crenated edges. As the foot becomes relaxed and extended, the groove and lips assume a straight form. The base of the groove is enlarged to make a closed canal leading from the byssus pit to tip of the foot when the lips are pressed together. This condition is readily seen in a cross section of the foot (fig. 145, *VGr*, opp. p. 159).

The entire surface of the foot is covered with a columnar, dark brown, pigmented, ciliated epithelium, the ciliated parts extending over the inner walls of the groove.

The portion of the foot which lies immediately below the epithelial covering is made up of numerous muscle bundles which have been described under the muscular system. Between the bundles numerous large blood spaces occur, as may be seen in a cross section of the organ (fig. 145, *BS*).

The central and ventral portions of the foot are filled with a mass of glandular tissue. Tullberg (1882) and Williamson (1907) have made quite thorough studies of the anatomy of the byssus glands and their results and terminology are used in the following description.

The byssus glands may be divided into two sets according to the region they occupy, (1) those of the foot and (2) those of the byssus pit which lies just behind the foot.

Two kinds of glands are distributed in the foot. The principal one is white in color and is therefore known as the white gland. It is of large size and occupies the middle region of the foot, inclosing the basal canal and extending more or less over the walls of the foot groove (fig. 145, *WG*). The white gland borders the groove for its whole extent and posteriorly continues backward to surround completely the byssus pit. The second type of the gland in the foot is known as the purple gland. It lies dorsal to the white gland and discharges its secretions into the cuplike depression at the end of the groove. It lies chiefly in the anterior region where it becomes much larger than the white gland. (See fig. 144, *PrG*, opp. p. 159.)

The glands of the byssus pit are also two in number. One set, as just described, represents a prolongation of the white gland which surrounds the opening of the byssus pit. Separated masses of glandular tissue of the same nature as the white gland occupy spaces between the muscle bundles and connective tissue of the walls of the byssus cavity (fig. 142, *WG*, opp. p. 159). The second set of glands is scattered through a series of thin lamellæ which are suspended from the dorsal wall of the byssus pit. They run parallel to the long axis of the body and hang down like the leaves of a book (fig. 142, *ByG*).

The origin of this very specialized type of molluscan foot which is found in Mytilus has been traced from the simple foot of Solenomya, which has a flat sole with a simple invagination but possesses neither groove nor byssus. Nucula and Leda have this same type of foot, but in addition there arises from the simple invagination a small lamella and a byssus is developed to a slight extent. The next step leads to the condition found in Mytilus where the invagination is differentiated into a cavity with a duct and the byssus with its glands is highly developed. Being no longer primarily an organ of locomotion, the foot has degenerated in size to a strap-shaped appendage without any sole. Its power of extension, however, is increased to serve the chief function of attaching the byssus. Parallel with this change from the primitive foot to the byssus-forming foot there is a modification of the pedal muscles which become attached to the byssus gland forming the retractors of the byssus.

The byssus is a bundle of tough threads secreted by the glands lying in the foot and byssus pit with which the animal anchors itself to convenient objects. It consists of a great number of very thin sheets or septa of byssal matter lying between the lamellæ which hang down into the byssus cavity. As the byssus septa grow downward they are molded together in the form of the cavity and pass outward through the external opening in the form of a solid rod, the so-called byssus root (fig. 117, *ByR*, opp. p. 138). Externally the root becomes a region of origin for numerous byssal threads which terminate in specialized endings, composed of a cementlike material capable of attaching them to solid objects with great firmness.

The byssus material is light to dark brown in color and appears to be made of numerous layers, one above the other, but when crushed or torn it breaks up readily into fine fibrils. Tullberg (1882) pointed out that the surface layer of the thread stained with carmine while the central portion did not and concluded therefore that it was a different substance. Williamson (1907), however, believes that the thread is homogeneous in character and that the reaction is due to the action of sea water in its surface. Tullberg (1882) further believed that the stem was enveloped with a rind, but Williamson (1907) pointed out that this was true only where the base of the threads enveloped it. The covering was nothing more than the numerous threads which were looped about it, for no rind was present where they were absent.

The attachment plates, or what Williamson calls the "buttons," are at the distal ends of the threads and serve as the direct medium of attachment for the byssus. They are gray in color and when stained with Bordeaux red or hæmatoxylin they show a typical alveolar structure with a byssal thread spreading out and terminating in the center. (See fig. 139, opp. p. 158.)

PHYSIOLOGY.

The foot serves as an organ of locomotion, and in conjunction with the glands of the byssus cavity it functions in producing the byssus and attaching the threads to favorable positions.

As a locomotor organ it is very effective in performing its functions, although considered degenerate anatomically. The author's attention was directed to the unusual locomotor powers of young mussels when he placed an incrusted mass of material covered with mussels of all sizes from 1 to 50 mm. in length in a glass battery jar under a tap of running sea water. Twenty-four hours later the very young mussels, which measured

from 1 to 4 mm. in length, were found attached in a mass about the upper edge of the jar. These same mussels, with other young ones of larger size, were placed in a glass dish containing sea water and kept under observation. In less than a minute most of them thrust out the foot and began to creep about. The foot was extended for a distance beyond its base nearly equal to the length of the animal itself. The tip of the foot was then attached by means of its sucker, and then by contracting its longitudinal muscles the body was drawn almost up to the point of attachment. Mussels 1½ mm. long extended the foot for a distance of 2 mm., those 5 mm. in length extended it 4 mm., while mussels 10 mm. in length thrust it out for a distance of 8 mm. before contracting it.

The young shellfish were able to creep up the perpendicular walls of the glass dish almost as well as they could over the bottom, but their powers for moving under difficult conditions did not reach their limit here. A number of individuals, having reached the surface of the water, continued on by creeping out on the underside of the superficial film similar to the habit of the pond snail. Some of them succeeded in traveling across the dish without falling, while others lost their hold and sank slowly to the bottom with their feet fully extended and moving about as if in search of an object on which to anchor themselves. The slow rate at which they sank suggested that they were possibly being supported by ciliary action on the foot.

Ascending a perpendicular wall and creeping on the superficial film of the water is accomplished by using the entire ventral groove as a sucker. By distending and contracting the foot and alternately attaching the posterior and anterior ends progression is accomplished. Sometimes the young shellfish would allow themselves to slide down the wall of the glass dish on the bottom of the foot, catching hold every few millimeters in the descent and then relaxing their hold again.

The rate of locomotion was determined by allowing the mollusk to creep over measured distances which varied from 1 to 10 cm. in extent. Specimens 4 to 5 mm. in length were used, and these covered the distance at rates varying from 1½ to 2½ cm. per minute. The usual and average rate was 2 cm. per minute.

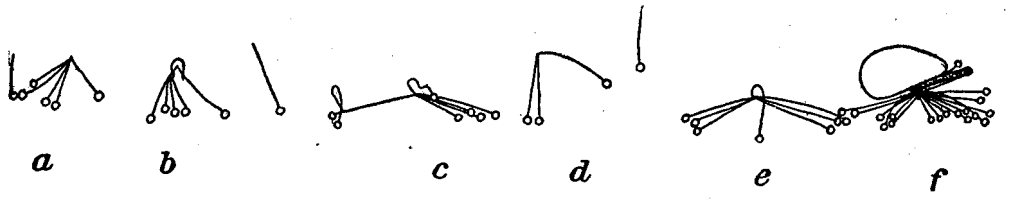
Before describing the functions involved in the formation of the byssus it will be well to state briefly the views which have been held in regard to its origin and nature. Von Nathusius-Königsborn (1877), Reichel (1888), and others took the view that the byssus grew from the animal's body, as does the cuticula of arthropods, and in like manner was shed from time to time. On the other hand, Müller (1837), Tullberg (1882), Jobert (1882), and Williamson (1907) have disproved the contentions of these writers by clearly demonstrating that the byssus arises as a glandular product. A few observations of the byssus-forming habit of the mussel are sufficient to convince one that this substance is a product of glandular secretion and not of cuticular growth.

The byssus stem, which represents the fused secretions from the cells of the epithelial walls of the glandular cells lying in the surrounding tissue, is molded into its characteristic form first by the cavity and then by the neck leading to the opening from which it passes out. Growth is continuous, but its rate probably depends upon the amount of strains the byssus has to bear, vigorous stimuli causing a more rapid secretion of material. Such growth is capable of producing a stem of cumbersome length, but the shellfish is able to avoid this by casting it off and starting a new one.

The threads are formed in the basal canal of the foot. When the mussel is in the act of producing a new thread the foot is extended and the depression near its tip placed

in contact with the object to which the thread is to be attached. According to Williamson (1907), the secretions pour out from the white gland so that they surround the stem and fill up the groove, the flow probably being caused by internal pressure attained by distending with fluid the lacunæ which exist between the muscles and about the glands. In the depression at the end of the foot ducts from the purple gland pour out a cementlike secretion which forms the attachment plate for the thread. The secretions are thick when first discharged and of fibrous character. As soon as they are in place the lips of the groove open and allow the sea water to enter, which hardens them. This results in the formation of a thread which at the proximal end loops the byssus stem and at the distal end is cemented to some solid object by means of the attachment plate. In color the new threads are a glistening white, but in a few hours' time they become yellowish, then brownish, and when old may be of a very dark-brown shade.

The rate at which the threads may be formed was determined with some specimens about 1 inch long and which were probably less than 1 year old. It is advantageous to use young mussels for these observations, because after being transferred to a dish of sea water they become active far more quickly than do older shellfish and the production of byssal threads begins within a few minutes after they have crept about.

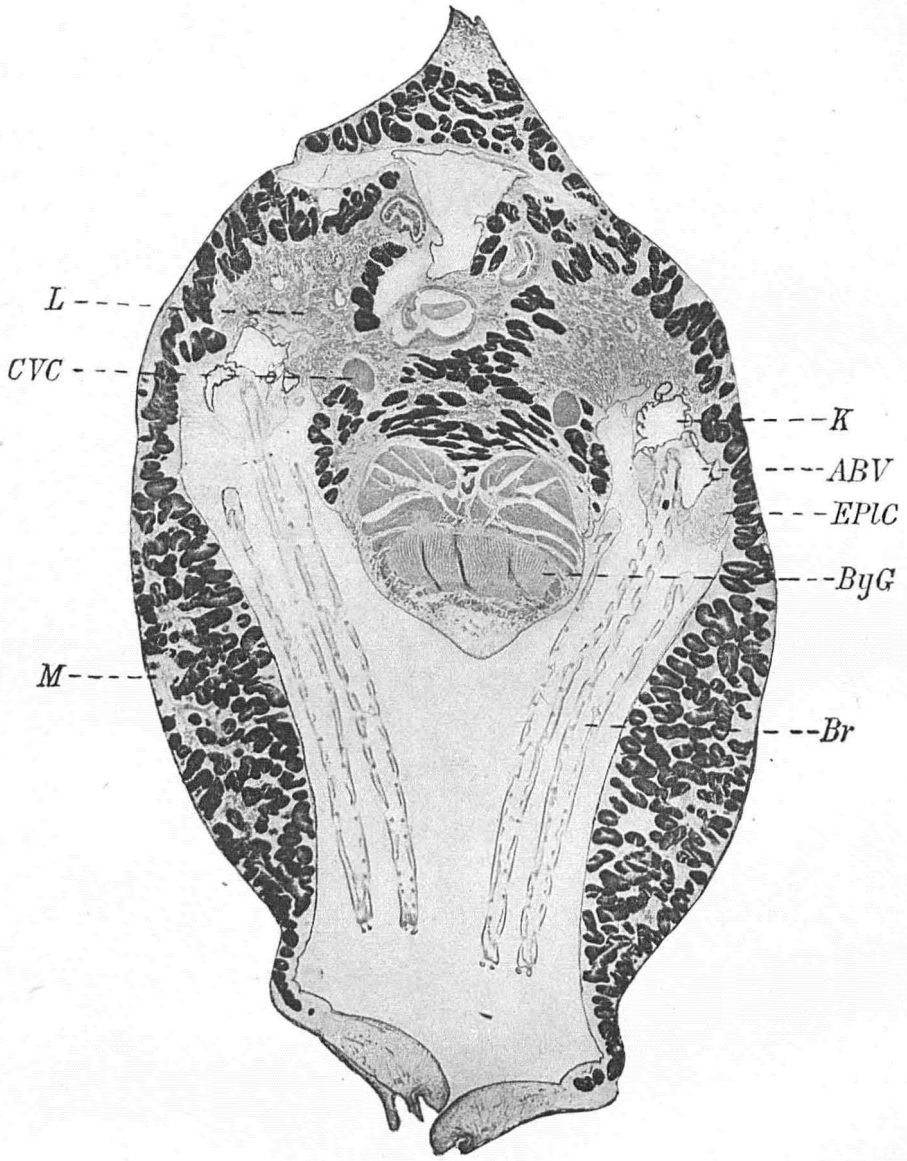


146

FIG. 146.—Tracing of a path of byssus threads left behind by a mussel 1 inch long during a period of three days.

In December, when the sea water was at a temperature of 45° F., two mussels, each 1 inch long, were placed in a 2-gallon battery jar containing sea water to a depth of 6 inches. In less than five minutes the shellfish began to creep about. When they came in contact with the side of the jar they promptly started to ascend the perpendicular wall and continued upward until they reached the surface of the water. There they stopped and began to attach themselves by means of byssal threads. The foot was extended and the cuplike depression at the end of the groove was pressed against the glass. The cavity of the depression appeared to become filled with a white cushionlike substance which flattened against the glass. With a strong hand lens the author tried to see what was taking place at this point of contact but could detect nothing. When, however, the foot was removed at the end of eight minutes a thread was found attached in this position by the usual attachment plate. The process was immediately repeated, this time the thread being formed and attached in three minutes. Then a third one was formed during the following five minutes. Four hours later this same mussel was found attached by 18 threads.

In another jar 14 young mussels were placed and left for a period of 3½ hours, when 4 of them were found attached to the side of the jar near the surface of the water with 10, 13, 15, and 16 threads, respectively.



147

Photomicrograph of a cross section taken through mid-body region of a 1-year-old mussel. Fixed in Gilson fluid and stained with Delafield hæmatoxylin. × 14.4. *ABV*, afferent branchial vein; *Br*, gills; *ByG*, byssus gland; *CVC*, cerebro-visceral commissure; *EPlC*, external plicate canals; *K*, kidney; *L*, liver; *M*, mantle filled with genital follicles.

Hescheler, in Lang (1896), states that most of the byssus-forming mussels are able to cast off the byssus and again replace it with a new one and many forms are able by alternately fastening threads forward and breaking off the old threads behind to move up a smooth, perpendicular glass wall. The sea mussel not only uses this method of movement on perpendicular glass surfaces but on horizontal surfaces covered with mud, as Williamson (1907) has described. Figure 146 represents a trail of byssus threads left by a mussel which was under the author's observation in the laboratory. It was in a glass dish half filled with sea water. The animal at first crept up the vertical side of the dish to the surface of the water, where it attached itself at *a*, then it started to move around the wall of the dish in the direction indicated by the letters *b*, *c*, *d*, etc., keeping just below the surface of the water. The distance of 7½ inches was covered in three days, at the end of which period the mollusk attached itself permanently with 18 threads and remained there until it died 10 days later, probably from starvation.

CHEMISTRY OF BYSSUS.

The composition of byssus is similar to that of the organic matter which is present in the shell. It is popularly spoken of as a horny or chitinous material, but in the opinion of Krukenberg (1886) it is closely allied to conchiolin, which forms the organic basis of the shell. According to Abderhalden (1908), it yields on hydrolysis glycocoll, tryosin, and proline in large amounts, besides alanine and aspartic acid. Treated with nitric acid the threads are stained yellow, which is a typical protein reaction. These results clearly indicate that byssus belongs in the albuminoid group and not in the class of chitin.

In regard to solubility, Winterstein (1910) states that the byssus threads are insoluble in boiling water, alcohol, ether, ammonia, dilute acids, or alkalis, but are slightly soluble in hot concentrated acetic acid or in concentrated mineral acids. The solution in acetic acid is precipitated by tannin or by mercuric chloride. According to Scharling (1842) and Schlossberger (1856), byssus is slightly soluble in potassium hydroxide. Byssus is classified by Hammarsten (1914) as a skeletin compound in the group of albuminoids.

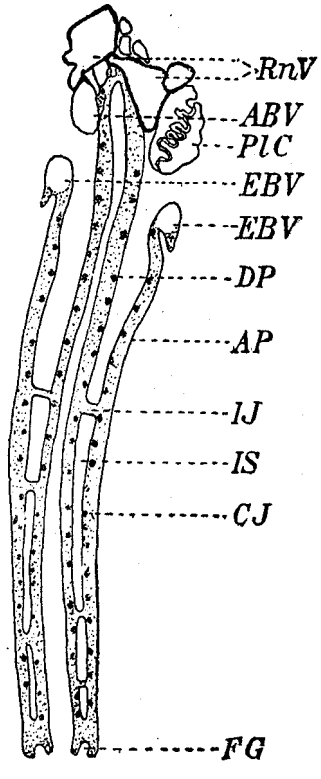
RESPIRATORY SYSTEM.

ANATOMY.

The organs of respiration in the Mollusca are usually the gills, but in the mussel, as in other lamellibranchs, the primary function of these organs seems to be the collection of food. The respiratory function is carried on only in part by the branchial apparatus. Aside from the gills, respiration takes place through the plaited membranes which extend across from the base of the gills to the mantle. To these folds Sabatier (1874) gave the name *Organes godronnes*. Respiratory exchange also takes place through the surface of the body, especially on the inner wall of the mantle.

The gills are suspended from the ventral side of the visceral mass on either side of the body (fig. 147, *Br*, opp. p. 163) and extend from the corners of the mouth to the branchial membrane (fig. 120, *Br*, p. 141). The posterior portion which extends from the ventral surface of the posterior adductor muscle to the branchial membrane is not attached to the body, but is supported by the large afferent branchial blood vessel which runs forward on its dorsal edge (fig. 135, *ABV*, p. 153). The right and left gills are most widely separated from each other in the middle of the body and from this point converge toward each other both anteriorly and posteriorly.

Our first knowledge of the finer structure of the gills of Mytilus is due to the careful work of Lacaze-Duthiers (1856), who studied both their constitution and development. The nomenclature which he introduced will be used in the description which follows. When observed in cross section the gills appear in the form of a narrow W suspended by the upper angle with the outer lamellæ terminating with a free edge in the mantle cavity (fig. 147, *Br*, opp. p. 163). This gives a branchial apparatus on each side of the body composed of two folds, each of which is made up of two lamellæ. The outer plates on each side are known as the right or left outer gill plates, and in like manner the inner plates are designated as the right or left inner gill plates (fig. 148). The separate lamellæ of each plate are known as the *descending portions*, which arise from the point of attachment of the gills and pass to the ventral edge, and the *ascending portions*, which arise from the ventral border and extend upward terminating with a free edge. The space inclosed between the ascending and descending lamellæ is known as the *interlamellar space* (fig. 148, *IS*).



148

Transverse section of a gill. *ABV*, afferent branchial vein; *AP*, ascending portion of gill lamella; *CJ*, ciliary junction; *DP*, descending portion of gill lamella; *EBV*, efferent branchial vein; *FG*, food groove; *IJ*, interlamellar junction; *IS*, interlamellar space; *PlC*, plicate canal; *RnV*, renal veins lined with kidney tissue.

In side view the gills are seen to be composed of numerous parallel filaments which lie one next to the other, with a slight interfilamentar space between them. They are cross-marked with fine, light-colored striations which form parallel lines running from the anterior to the posterior end of the gills.

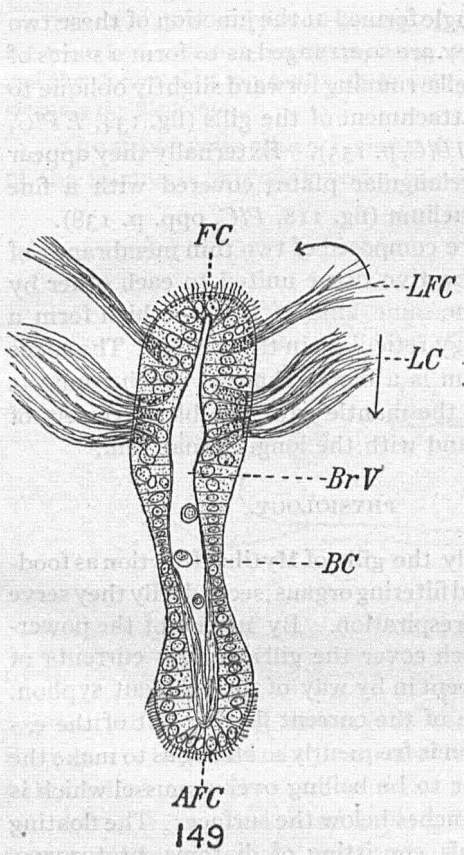
HISTOLOGY.

The filaments which make up the gills are composed of specialized groups of ciliated epithelial cells which surround a central canal or branchial blood vessel (fig. 149). In this cross section of a gill filament four types of cilia may be clearly distinguished: (1) Frontal cilia, which are relatively short (*FC*); (2) latero-frontal cilia, which are very long (*LFC*); (3) lateral cilia, also very long (*LC*); and (4) ab-frontal cilia, which are the least developed of all (*AFC*). Each group has a special function to perform, as will be explained later. Gland cells are also present in the latero-frontal region, according to Kellogg (1892). The author's own preparations do not show them unless the ciliated cells which bear the latero-frontal and lateral groups of cilia also function as gland cells. Their protoplasmic content is filled with fine granules which stain deeply with acid fuchsin when no other parts of the tissue take this dye. They have the appearance of gland cells, but at the same time seem to be nothing more than highly specialized ciliated cells.

Connections between the filaments are established by means of tufts of cilia which project from their anterior and posterior surfaces close to their interlamellar edge. These *ciliated junctions* occur at short intervals over the entire length of both the

ascending and descending limbs, varying in number from 15 to 30, according to the age of the specimen (figs. 148, *CJ*, p. 164; figs. 150, and 151, *CJ*).

The ascending and descending fibers of each gill are attached by cross partitions of tissue which have the form of bars. These structures were given the name *interlamellar junctions* by Peck (1877). (See fig. 148, *IJ*.) They are usually three or four in number, separated by some distance and not grouped as Peck figures them. According to this author they are composed of longitudinal elastic or muscular fibers



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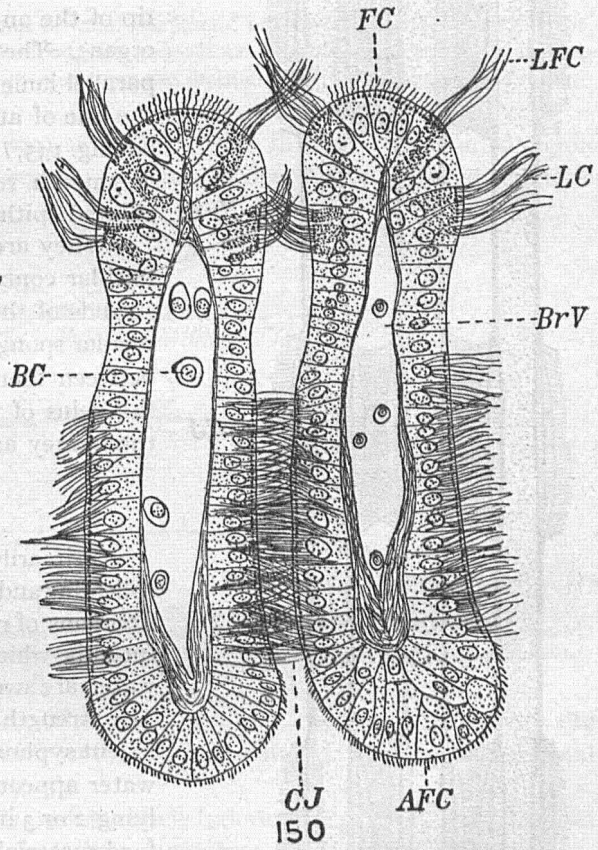

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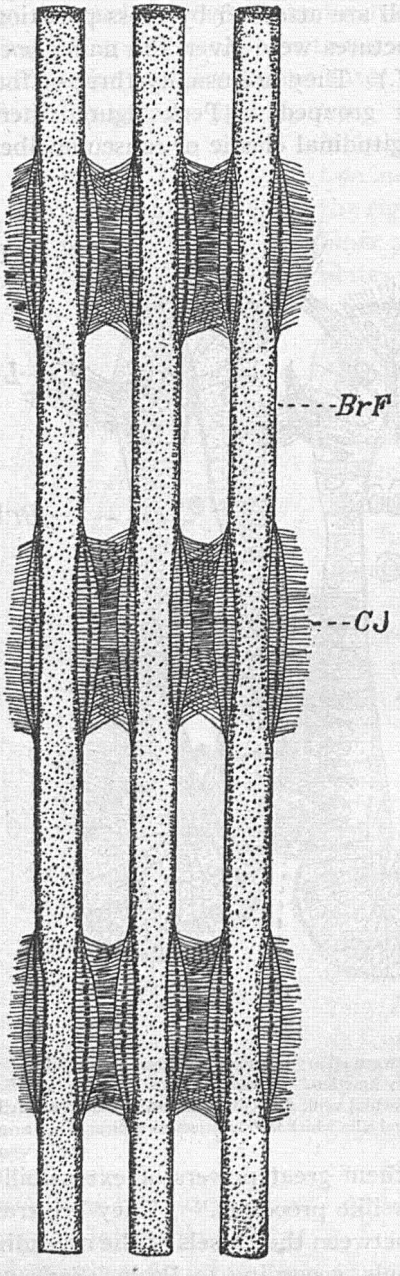
FIG. 149.—Transverse section of gill filament taken through the area between ciliary junctions. × 500.

FIG. 150.—Transverse section of two gill filaments taken through a ciliary junction. × 500.

ABBREVIATIONS.—*AFC*, abfrontal cilia; *BC*, blood corpuscle; *BrV*, branchial vein; *CJ*, ciliary junction; *FC*, frontal cilia; *LFC*, latero-frontal cilia which lash in direction indicated by arrow; *LC*, lateral cilia which lash in direction indicated by arrow.

surrounded by a layer of epithelium which gives them great powers of extensibility and contractibility. He speaks of them as "bellowslike processes." They are traversed by a canal which allows cross communication between the vessels of the ascending and descending limbs. The walls of the latter canals, according to Peck (1877), are lined with chitin, while those of the interlamellar junctions are not. Kellogg (1892) makes a similar statement but in addition says an endothelial lining is present. What these authors refer to as chitin is probably not that substance but conchiolin or some related compound.

The free ends of the filaments which form the ascending lamellæ are hook-shaped, with their anterior and posterior ends firmly attached to each other. This free edge is traversed for its whole length by the efferent branchial blood vessel (fig. 148, *EBV*), which increases in size toward the anterior end of the body.



151

FIG. 151.—Lateral view of a portion of a lamella showing three gill filaments. × 130. *BrF*, branchial filaments; *CJ*, ciliary junction.

The *plicate canals* or *Organes godronnes* of Sabatier (1874) are membranous structures which extend from the mantle to the base of the gills across the tip of the angle formed at the junction of these two organs. They are so arranged as to form a series of parallel lamellæ running forward slightly oblique to the line of attachment of the gills (fig. 134, *EPlC*, and fig. 135, *IPlC*, p. 153). Externally they appear as smooth triangular plates covered with a fine ciliated epithelium (fig. 118, *PlC*, opp. p. 138).

They are composed of two thin membranes of fibrillar connective tissue united to each other by strands of the same kind of tissue, which form a regular spongy reticulum in the cavity. The space between them is a blood channel which connects the veins of the mantle with the blood vessels of the kidney and with the longitudinal vein.

PHYSIOLOGY.

Primarily the gills of Mytilus function as food-collecting and filtering organs; secondarily they serve as organs of respiration. By means of the powerful cilia which cover the gills, strong currents of water are swept in by way of the inhalent syphon. The strength of the current flowing out of the exhalent syphon is frequently so strong as to make the water appear to be boiling over a mussel which is lying 2 or 3 inches below the surface. The floating food materials, consisting of diatoms, protozoans, and minute organic particles, are thus swept in by these food currents where they are filtered out and transported to the mouth. The currents of water, in addition to bringing in a constant supply of food, also carry the necessary oxygen for the respiratory exchange which takes place through the gills, plicate canals, and the mantle wall.

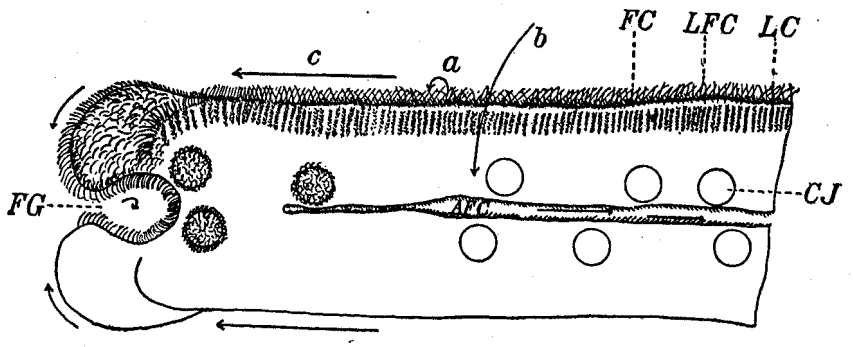
The action of the different sets of cilia in performing this function has been ably studied by Orton (1912). He found that the lateral cilia which lash across the length of the filaments are the chief cause of the inhalent current and that the frontal cilia which lash toward the free edge of the gill collect the food

particles and sweep them toward the food groove on the ventral edge (fig. 152). On the interlamellar or ab-frontal surface the cilia sweep upward or in just the opposite direction of the frontal cilia. They serve to help in producing the main current and in keeping the inner surfaces of the gills clean.

The long latero-frontal cilia are undoubtedly the straining mechanism. They project out from the sides of the filaments, forming a sieve, and lash relatively slowly across the middle of the frontal face of the filament (fig. 152; fig. 149, p. 165). Orton (1912) summarizes his results as follows:

> Thus Nucula and Mytilus have four kinds of cilia, the lateral cilia producing the main current, the frontal for collecting and transporting the food, the fronto-lateral which assists in food collecting and the ab-frontal or inner cilia which help in producing the main current, in collecting food, and in cleaning the filaments.

The gland cells which Kellogg (1892) says are present in the latero-frontal region of the filaments probably serve to secrete a mucus which cements the food particles



152

FIG. 152.—Longitudinal interfilamentary view of a living filament of the left outer lamella of the gill. × 84 approximately *a*, *b*, *c*, arrows indicating roughly the directions in which the latero-frontal, lateral, and frontal cilia, respectively, lash; *CJ*, ciliary junction; *FC*, frontal cilia; *FG*, food groove; *LC*, lateral cilia; *LFC*, latero-frontal cilia.

together in morsels of convenient size. These are swept by the frontal cilia into the food groove, in which they are carried forward by the cilia lining its walls to the labial palps, which transfer them into the mouth.

As an organ of respiration the gills perform their function incompletely. This was recognized by Sabatier (1874), who found that circulation took place within the filaments in a very imperfect manner. The defective circulation, according to this author, is due (1) to the small caliber of the branchial vessels, (2) to the weak current of the blood which flows to the gills after having traversed the kidney or other capillary network, and (3) to the existence of other and larger channels which allow the blood to return to the heart without traversing the gills.

The mantle serves as an organ of respiration when it is not distended with genital products. During the period of reproductive quiescence it is a thin-walled organ, with the blood vessels separated from the outside medium by a very thin layer of tissue. During reproductive activity, however, the walls of the mantle become thick and the blood vessels are covered with heavy layers of tissue in which metabolic activity is

accelerated by the formation of reproductive elements causing the production of large quantities of carbon dioxide. The respiratory function is greatly increased in the plicate canals at this time. They become enlarged and well filled with blood which flows through them from the mantle to the kidney and longitudinal vein. Being composed of thin convoluted membranes and covered externally with cilia which keep up a constant circulation of water, these organs are able to bring the blood into intimate relation with a rich supply of oxygen. They might well be termed the accessory gills.

EXCRETORY SYSTEM.

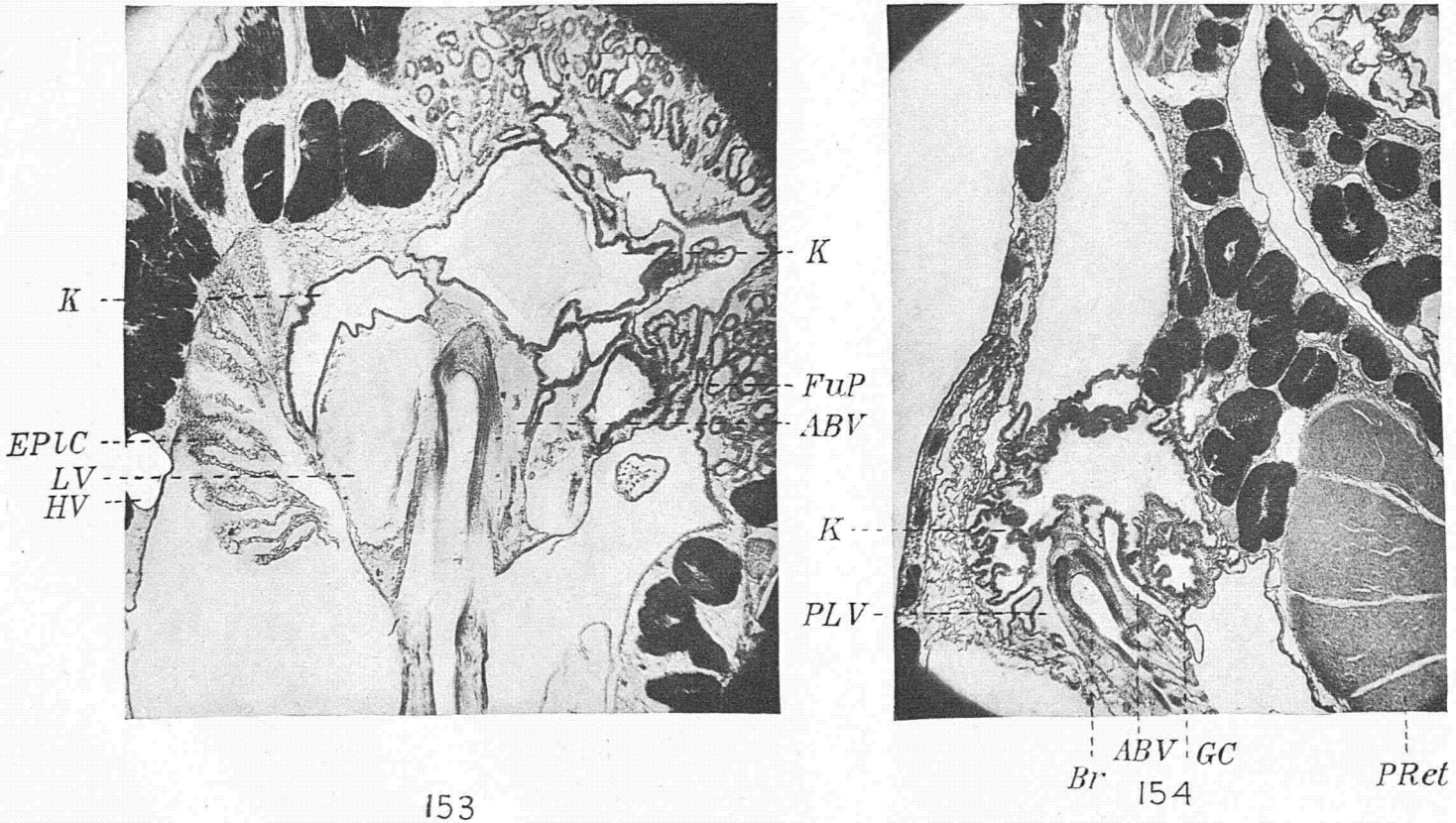
ANATOMY.

In the sea mussel the excretory system consists of two sets of organs, the kidney, or so-called organ of Bojanus, and a pair of pericardial glands which invest the outer walls of the auricles. If the posterior adductor muscle of the shellfish be cut and the valves laid open so that the gills lie flat on the mantle wall as is shown in figure 118 (opp. p. 138), the kidney may be seen as a dark brown band of tissue along the ventral body wall at the base of the gills, extending from the posterior border of the labial palps to the posterior adductor muscle (fig. 135, *K*, p. 153). Sabatier (1874) divided the kidney into two parts, (1) that which is independent of the blood vessels and (2) that which covers the walls of the great veins. The former type lies anteriorly on the lateral walls of the liver, where it is thrown into conical folds which extend across to the main canal of the kidney like the teeth of a comb. These folds are designated by Sabatier as the "fusiform pillars of the kidney" (fig. 153, *FuP*, opp. p. 168).

The second type of kidney tissue, or that dependent on the blood vessels, consists of plates of tissue which cover the walls of the great veins. This portion of the organ forms a long sac with numerous diverticula which cover the walls of the large longitudinal vein or line its cavity. As the central cavity of the kidney extends backward it increases both in size and in number of diverticula, as may be seen in figures 153, 154 (opp. p. 168), and 157 (opp. p. 169), which are cross sections taken at the anterior, middle and posterior regions of the body, respectively. The kidney discharges exteriorly through a small excretory pore located on a slight elevation at the base of the genital papilla on its posterior side (fig. 158, *EO*, opp. p. 169). It was first discovered by Lacaze-Duthiers (1854).

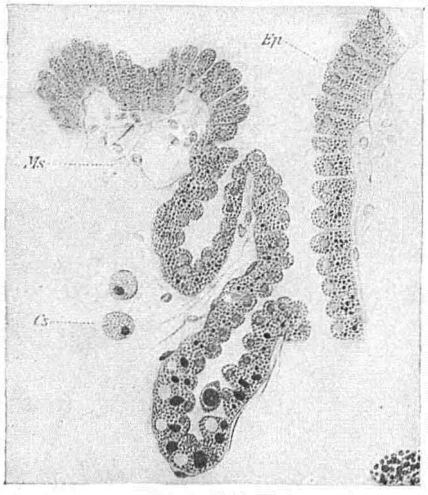
The pericardial glands, so named by Grobben (1888), but previously described by Sabatier (1877), are an extensive part of the kidney tissue which invests the outer walls of the auricles. The enveloping tissue consists of numerous small folds of various sizes which are dark brown in color similar to that of the kidney proper. Posteriorly the glands are attached to the wall of the pericardial cavity; while anteriorly each gland extends downward into the afferent oblique vein and becomes intimately attached to its walls.

The pericardial cavity, just anterior to the oblique vein, is in open communication with the collector canal of the kidney by what Sabatier (1874) termed a "couloir place," which consists of a spongy partition of kidney tissue through which are many fine openings that allow passage of the contents of the pericardial chamber into the kidney canal but render difficult any return backward (fig. 138, *RC*, p. 156).



153 154

Photomicrographs of transverse sections through the kidney in the middle region of the body (fig. 153) and in the posterior region of the body (fig. 154). *ABV*, afferent branchial vein; *Br*, gill; *EPIC*, external plicate canals; *FuP*, fusiform pillars of Sabatier; *GC*, genital canal; *HV*, horizontal vein; *K*, kidney; *LV*, longitudinal vein; *PLV*, posterior longitudinal vein; *PRet*, posterior retractor muscle.



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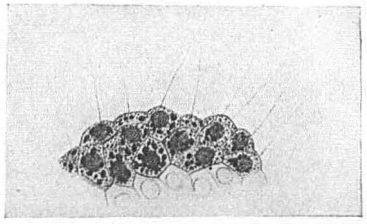

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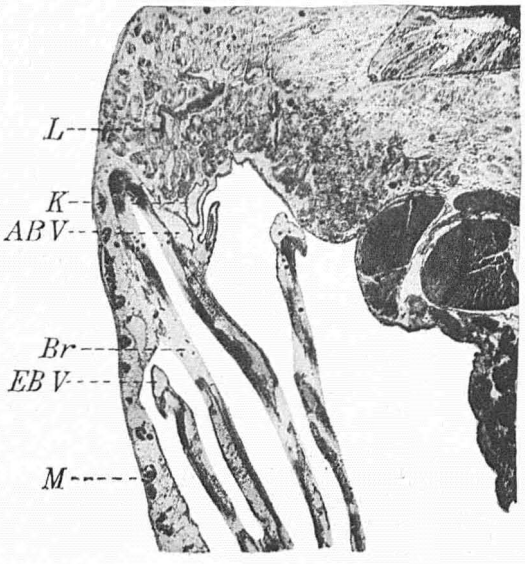

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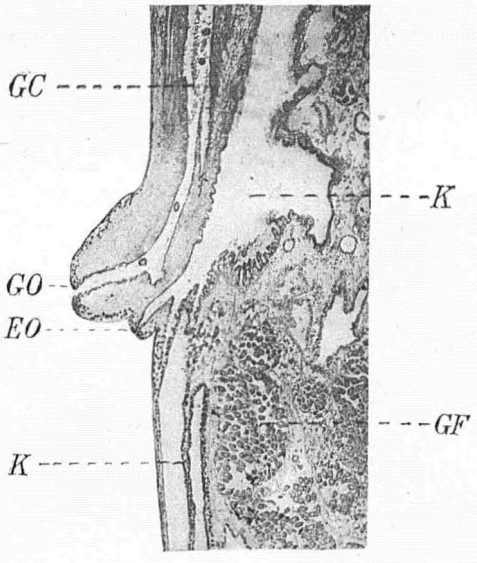


158

FIG. 155.—Transverse section through the pericardial glands. × 350 approximately. *CS*, blood corpuscle; *Ep*, epithelium of the pericardial gland; *Ms*, muscle fibers. (After Grobben, 1888.)

FIG. 156.—Pericardial gland epithelium drawn from life. × 490. (After Grobben, 1888.)

FIG. 157.—Photomicrograph of a transverse section taken through the anterior region of the kidney. *ABV*, afferent branchial vein, *Br*, gill, *EBV*, efferent branchial vein; *K*, kidney; *L*, liver; *M*, mantle.

FIG. 158.—Photomicrograph of a longitudinal section through the genital papilla. × 12. *EO*, excretory opening; *GC*, genital canal; *GF*, genital follicle filled with ova; *GO*, genital opening; *K*, kidney

HISTOLOGY.

The cells which make up the kidney tissue are of two types, as described by Sabatier (1874). One class is found in what he termed the free or independent part, as is best seen in the pillars of the kidney and the membrane which separates the kidney canal from the pericardial cavity. These form a pavement epithelium of nearly cubical cells, with the free edge presenting a convex surface. A large, round nucleus lies in the center or near the base of the cell. The cytoplasm is clear and transparent and often contains either few or numerous small greenish granules. In size these cells vary from 8 to 10 microns in diameter.

The second type of cell is found in that portion of the kidney which lines the wall of the veins. They form a columnar epithelium in which the cells may vary from 5 to 24 microns in height with a diameter of from 4 to 6 microns. The nucleus lies near the base of the cell. Between the nucleus and the distal end of the cells the transparent protoplasm is filled with numerous fine granules in which are often seen one or two large roundish bodies which are apparently nuclear concretions of a crystalline nature. The free edges of the cells present a decided convex surface.

The structure of the pericardial glands has been most thoroughly worked out by Grobben (1888). He pointed out that the glands consist of numerous small flaps or folds of different sizes which are dark brown in color and that they completely surround the auricles. The cells are of different shapes and sizes, some being low and broad, while others are tall, narrow, and cylindrical in form (fig. 155, opp. p. 169). The cells in most cases are more or less separated from each other, and where connection does exist between them it is in the basal region only. Exception to this rule occurs in the case of the very tall cylindrical cells, which are often so thickly crowded together that their entire side walls are in direct contact with those of the neighboring cells. Spaces, however, are often observed between them. The outer ends of the cells are convex and bear on the apex a single vibrating flagellum (fig. 156, opp. p. 169). The flagella are visible on the living cells, but when prepared histologically they disappear.

The cells contain nuclear concretions of various sizes and forms near their peripheral ends. In color these particles are brownish-green to black and highly refractive. It is to their presence that the dark shade of the gland is due. Sections through the glands show that the concretions are larger and more abundant in the cells lying in the deeper invaginations.

Grobben also occasionally observed pale, spherical bodies lying close to the refractive concretions and, in the deeper invaginated parts, vacuoles were found present in the cells (fig. 155). Whether or not the vacuoles exist in living cells the author was unable to determine.

In the lumen of the invaginated folds epithelial cells richly laden with concretions are often seen cut off from the epithelium (fig. 155). They contain their concretions molded either into a single large sphere almost the size of the cell body or as several large concretions which make up the greater part of the cell contents. These leave the pericardial cavity whole or in a disintegrated form by way of the opening to the kidney.

PHYSIOLOGY.

The function of the lamellibranchiate kidney and of the pericardial glands has been studied by Kowalevsky (1889), Letellier (1891), and Cuénot (1899). Their method in

all cases was to inject acid and basic dye substances and to observe their reactions in the organ where they were eliminated. Indigo carmine, for example, is discharged through the kidney and usually shows an acid reaction according to Cuénot; Kowalevsky and Letellier, on the other hand, state that it is usually neutral. Ammonium carminate is eliminated through the pericardial glands where, all the authors agree, the reaction is very acid. The strong reaction in this case was established by Letellier to be due to the fact that the pericardial glands secrete hippuric acid in the free state. He concludes that among certain lamellibranchs the urinary function is accomplished by means of two separate organs, (1) the kidney which lies below the heart serving to eliminate excess of water, urea, various nitrogenous bodies, phosphates, and possibly uric acid and (2) the pericardial gland which covers the auricles serving to extract the acid contained in the blood. This acid in at least two mollusks, Pecten and Cardium, was found to be hippuric acid. Kowalevsky assumes that the kidney, or organ of Bojanus, is analogous to the Malpighian corpuscles of vertebrates, which are neutral or basic in reaction, and that the pericardial glands are analogous to the convoluted tubules, which are acid.

NERVOUS SYSTEM.

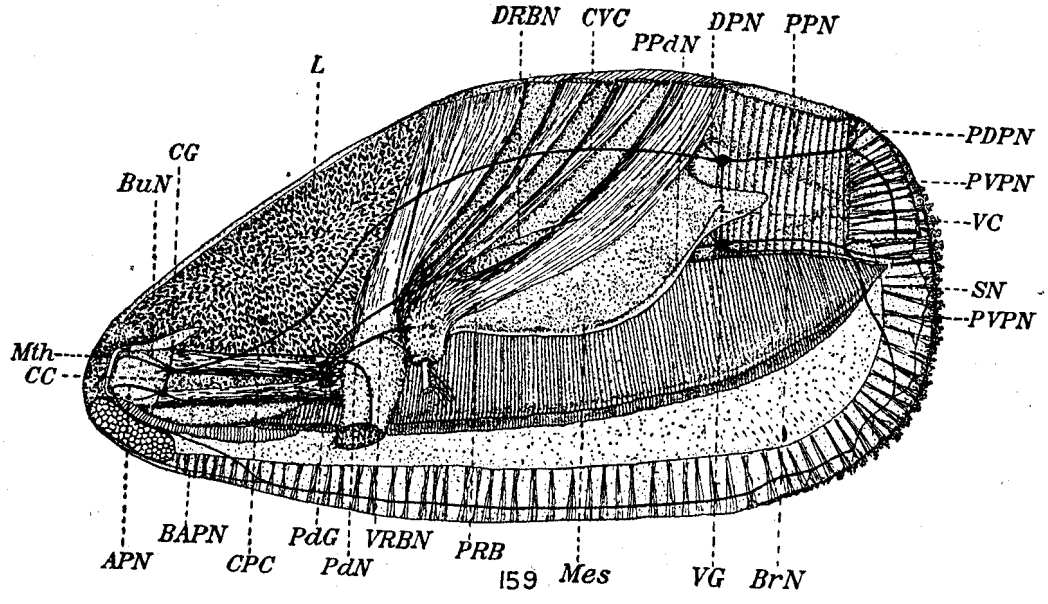
The central nervous system consists of three pairs of ganglia, symmetrically placed and connected by nerve commissures. The arrangement is strictly bilateral, one ganglion of each pair giving off nerves to its own particular side of the body. In *Mytilus edulis* the form of the nervous system is but slightly modified from the typical type found in the Lamellibranchia.

The *cerebral ganglia* are triangular bodies which lie with their apices pointing backward on the ventral side of the œsophagus just under the posterior edge of the lower lip (fig. 159, *CG*, p. 171). They are laterally placed so that in an adult mussel they are separated by a distance of 4 to 6 mm. In some specimens they are very conspicuous to the naked eye, owing to the presence of an orange-red pigment, while in others they are difficult to find, because the bright pigment is absent and their color is like that of the tissue in which they lie. The cerebral ganglia are united by the *cerebral commissure* which runs dorsally over the œsophagus (fig. 159, *CC*). Each ganglion gives rise to a large anterior trunk, the anterior pallial nerve, and a posterior trunk which contains the combined cerebrovisceral and cerebropedal nerves. Besides these there are two fine fibers, one of which supplies the labial palps and the other the eye.

The *anterior pallial nerve* (fig. 159, *APN*) arises from the outer anterior corner of the cerebral ganglion, runs forward and slightly outward over the anterior adductor muscle, to which it supplies a few fine fibers, and then turning backward it traverses the inner fold of the mantle edge, giving off along its course numerous side branches that form a network of fibers in the border of the mantle. A short distance posterior to the anterior adductor muscle the nerve trunk gives off a large branch (*BAPN*) that runs forward to the ventral side of the anterior adductor muscle.

The *cerebropedal* and *cerebrovisceral connectives* leave the posterior angle of the cerebral ganglion in a common trunk that passes backward and outward across the ventral side of the anterior retractor muscle. When it reaches the lateral side of the muscle the trunk divides into its two separate components. The cerebropedal con-

nective continues backward and around the anterior retractor muscle to its dorsal wall and terminates in the pedal ganglion (fig. 159, *CPC*). The cerebrovisceral connective at the point of bifurcation with the cerebropedal connective turns upward and continues in a posterior direction across the lateral surfaces of the posterior retractor muscles to its point of termination in the visceral ganglion (fig. 159, *CVC*). Along its course several delicate nerve branches are given off which go to the liver, intestines, genital glands, and kidney. Of these the last branch forward, the *anterior renal nerve* (fig. 163, *ARN*, p. 175) is the most prominent. The *otocyst nerve* is a very fine fiber that arises from the cerebropedal connective at its junction with the cerebrovisceral connective and continues a short distance backward to the otocyst (fig. 163, *OtN*).



159

FIG. 159.—Ventro-lateral view of the nervous system in a transparent total preparation of a mussel 10.5 mm. long, separated from the shell, mantle and gills removed from one side, and a portion of foot cut off. Fixed in strong Flemming fluid, exposed in 70 per cent alcohol to strong sunlight, dehydrated in alcohol and cleared in benzol and wintergreen oil. × 15. *APN*, anterior pallial nerve; *BAPN*, branch of anterior pallial nerve; *BrN*, branchial nerve; *BuN*, buccal nerve; *CC*, cerebral commissure; *CG*, cerebral ganglion; *CPC*, cerebropedal commissure; *CVC*, cerebrovisceral commissure; *DPN*, dorsal pallial nerve; *DRBN*, dorsal retractor byssus nerve; *L*, liver; *Mes*, mesosoma; *Mth*, mouth; *PdG*, pedal ganglion; *PdN*, pedal nerve; *PDPN*, posterior dorsal pallial nerve; *PPdN*, posterior pedal nerve; *PPN*, posterior pallial nerve; *PRB*, posterior retractor muscle of byssus; *PVPN*, posterior ventral pallial nerve; *SN*, syphonal nerve; *VC*, visceral commissure; *VG*, visceral ganglion; *VRBN*, ventral retractor byssus nerve.

The *buccal nerve* is a relatively fine fiber which arises from the anterior end of the cerebral ganglion and runs forward to supply the labial palps (fig. 159, *BuN*). Branches of the nerve enter the palps and run along the smooth edge as a loose bundle of fibrils from which single fibers run out laterally across the palp and penetrate the transverse ridges (fig. 160, *BuN*, p. 173).

The *optic nerve* arises from the cerebral ganglion just posterior to the buccal nerve as a very fine fiber and runs in an anterio-latero-dorsal course to the eye at the base of the first inner branchial filament (fig. 163, *OpN*, p. 175).

A few very fine nerves that are distributed about the mouth region are also given off from the median sides of the cerebral ganglion and from the cerebral commissure.

The *pedal ganglion* lies on the dorsal side of the anterior retractor muscles just in front of the posterior retractor muscles of the foot (fig. 159, *PdG*). The ganglia are more or less pear shaped with the apex pointing forward and uniting with the cerebropedal connective. In most specimens there is a heavy deposit of pigment which gives the ganglia a deep orange-red color. Unlike the other ganglionic centers, the pedal glanglia are fused together into a single mass, but the dual structure is shown by the distinct furrow which runs around the body and separates the stems which project forward to connect with the cerebropedal nerves. Three nerves arise from each ganglion.

The *pedal nerve* emerges from the ventral side of the pedal ganglion, passes backward over the anterior retractor muscle, penetrates the posterior retractor muscle of the foot, and then continues downward into the foot (fig. 159, *PdN*).

The *ventral retractor byssus nerve* arises from the posterior side of the ganglion and subdivides into several branches that supply the byssus organ and the anterior and posterior retractor muscles in that region (fig. 159, *VRBN*).

The *dorsal retractor byssus nerve* arises from the dorsal surface of the pedal ganglion and runs obliquely backward and upward, subdividing in its course into several branches that go to the posterior retractor muscles above the region supplied by the ventral retractor byssus nerve (fig. 159, *DRBN*).

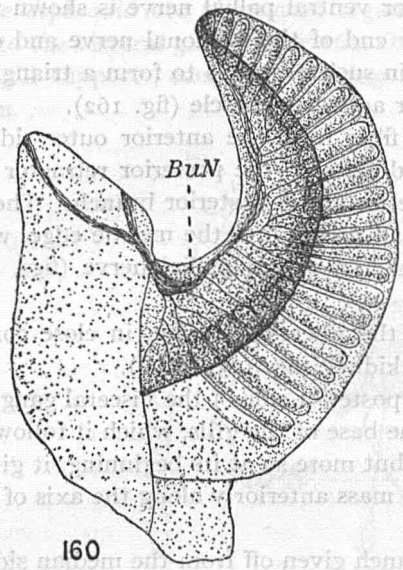
The *visceral ganglia* are situated on the anterior ventral surface of the posterior adductor muscle just under the epithelium. They lie just inside the line where the gills are suspended (fig. 159, *VG*), which places them some distance apart. A large *visceral commissure* (*VC*) connects them. Each visceral ganglion receives the cerebrovisceral connective at the anterior surface, while laterally and from behind several important nerves are given off.

The *posterior pallial nerve* arises from the posterior side of the visceral ganglion and runs backward and slightly outward across the ventral surface of the posterior adductor muscle (fig. 159, *PPN*). At the posterior ventral surface of the muscle it divides into two branches, one of which penetrates the mantle edge and runs dorsally (*PDPN*), whereas the other runs obliquely downward and backward some distance across the mantle before it enters the mantle edge (*PVPN*).

The *posterior dorsal pallial nerve* is the branch that arises from the posterior pallial nerve just behind the posterior adductor muscle, penetrates the mantle edge, and continues dorsally and anteriorly, giving off in its course many fine fibers to the surrounding tissues. It terminates in the mid-dorsal region in the trunk of the dorsal pallial nerve (fig. 162, *PDPN*).

The *posterior ventral pallial nerve* is the ventral branch of the posterior pallial nerve (figs. 159 and 162, *PVPN*). It runs downward and slightly backward until it penetrates the inner fold of the mantle edge, where it begins to give off numerous fine side branches that form a network of fibers throughout the inner and middle folds. In its course forward it becomes continuous with the anterior pallial nerve, forming what is commonly called the *pallial nerve* (fig. 162, *PN*).

The *syphonal nerve* arises from the posterior ventral pallial nerve, passes backward directly into the mantle edge, and then runs downward to unite again with the posterior ventral pallial nerve where the latter enters the mantle edge (fig. 162, *SN*). The syphonal nerves take their course through the region where the inner folds of the mantle edge are fused to form the anal syphon. The distribution of the side branches and



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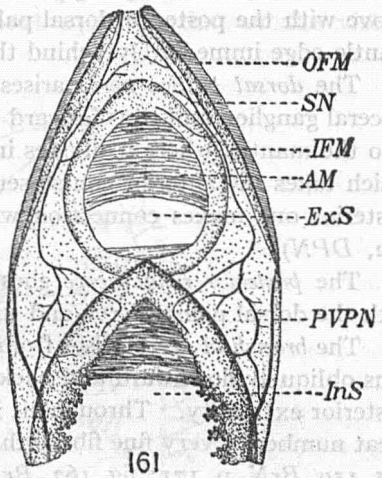

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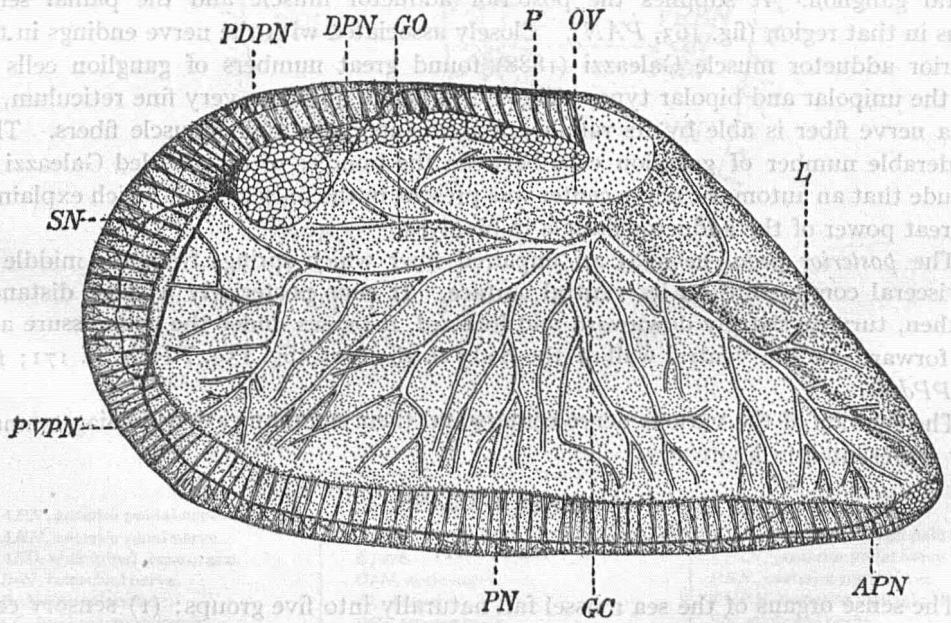

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FIG. 160.—View of labial palp in transparent preparation. Fixed in strong Flemming fluid, exposed in 70 per cent alcohol to strong sunlight, dehydrated, and cleared in benzol and oil of wintergreen. *BuN*, buccal nerve and its branches which run between the ridges.

FIG. 161.—Posterior view of the area surrounding the syphonal region showing the innervation of the anal syphon. Preparation same as fig. 160. *AM*, anal membrance; *ExS*, exhalent syphon; *IFM* inner fold of the mantle; *InS*, inhalent syphon; *OFM*, outer fold of the mantle; *PVPN*, posterior ventral pallial nerve; *SN*, syphonal nerve.

FIG. 162.—Lateral view of mussel with shell removed showing distribution of genital canals and pallial nerves. *APN*, anterior pallial nerve; *DPN*, dorsal pallial nerve; *GC*, genital canal; *GO*, position of the genital opening on the ventral wall inside the mantle; *L*, liver; *OV*, oblique vein; *P* pericardium; *PDPN*, posterior dorsal pallial nerve; *PN*, pallial nerve; rest as in fig. 161.

relation of the syphonal nerve to the posterior ventral pallial nerve is shown in figure 161. A short branch springs from the upper end of the syphonal nerve and connects above with the posterior dorsal pallial nerve in such a way as to form a triangle in the mantle edge immediately behind the posterior adductor muscle (fig. 162).

The *dorsal pallial nerve* arises as a fine fiber from the anterior outer side of the visceral ganglion and runs forward and upward between the posterior retractor muscles into the mantle, where it divides into an anterior and a posterior branch. The branch which takes the anterior course sends out small nerves into the mantle edge, while the posterior one makes connection with the posterior dorsal pallial nerve (figs. 159 and 162, *DPN*).

The *posterior renal nerve* goes out from the visceral ganglion in close connection with the dorsal pallial nerve and supplies the kidney (fig. 163, *PRN*).

The *branchial nerve* arises from the outer posterior side of the visceral ganglion and runs obliquely downward and backward to the base of the gills, which it follows to the posterior extremity. Throughout its course, but more so at its beginning, it gives off a great number of very fine fibrils that run in a mass anteriorly along the axis of the gills (fig. 159, *BrN*, p. 171; fig. 163, *BrN*).

The *posterior adductor nerve* is a small branch given off from the median side of the visceral ganglion. It supplies the posterior adductor muscle and the pallial sense organs in that region (fig. 163, *PAN*). Closely associated with the nerve endings in the posterior adductor muscle Galeazzi (1888) found great numbers of ganglion cells of both the unipolar and bipolar type. They form in the muscle a very fine reticulum, so that a nerve fiber is able by its ramifications to innervate many muscle fibers. This considerable number of ganglion cells between the bundles of muscles led Galeazzi to conclude that an automatic nerve center was present in the muscle itself which explained the great power of the adductor muscle in bivalves.

The *posterior pedal nerve* is an unpaired fiber which springs from the middle of the visceral commissure on its ventral surface. It runs posteriorly a short distance, and then, turning sharply downward and forward, it passes under the commissure and runs forward on the ventral wall of the body to the foot (fig. 159, *PPdN*, p. 171; fig. 163, *PPdN*).

The relation of the various nerve centers and their communications is diagrammatically represented in figure 163.

SENSE ORGANS.

ANATOMY.

The sense organs of the sea mussel fall naturally into five groups: (1) sensory cells in the epidermal layer, (2) a pair of osphradia, (3) a pair of abdominal sense organs, (4) a pair of otocysts, (5) a pair of eyes and extensive areas of light receptive epithelium.

The sensory cells of the epidermal layer are present in scattered groups or as single elements in the wall of the mantle cavity. The groups of cells which are sometimes referred to as the *pallial sense organs* (fig. 164, p. 178) are particularly abundant on the ventral epithelium of the posterior adductor muscle. The single sense cells, first described by Flemming (1870) as *pinselzellen* (fig. 167, p. 178), are scattered all over the inner walls of the mantle.

The *osphradia* are pigmented organs of dark brown color which lie ventral and lateral to the visceral ganglia (fig. 169, *Os*, p. 178). They extend as far as the inner side of the gill supports, each one covering an area about equal to that of the visceral ganglion.

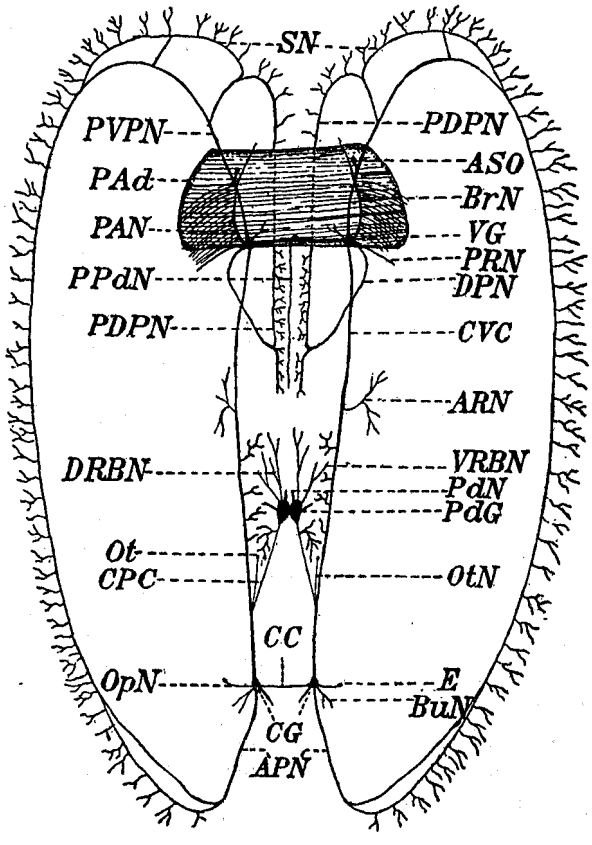


FIG. 163.—Diagrammatic representation of the nervous system of *Mytilus edulis*.

APN, anterior pallial nerve.
ARN, anterior renal nerve.
ASO, abdominal sense organ.
BrN, branchial nerve.
BuN, buccal nerve.
CC, cerebral commissure.
CG, cerebral ganglia.
CPC, cerebropedal commissure.
CVC, cerebrovisceral commissure.
DPN, dorsal pallial nerve.
DRBN, dorsal retractor byssus nerve.
E, eye.
OpN, optic nerve.
Ot, otocyst.
OtN, otocyst nerve.
PAd, posterior adductor muscle.
PAN, posterior adductor nerve.
PdG, pedal ganglion.
PdN, pedal nerve.
PDPN, posterior dorsal pallial nerve.
PPdN, posterior pedal nerve.
PRN, posterior renal nerve.
PVPN, posterior ventral pallial nerve.
SN, syphonal nerve.
VG, visceral ganglion.
VRBN, ventral retractor byssus nerve.

The *abdominal sense organs*, first described by Thiele (1889) in Arca, were found by List (1902) to be present in some form or other in all species of the Mytilidæ. In *Mytilus edulis* they lie on the ventral posterior side of the posterior adductor muscle just outside of the gill supports. A microscopic cross section of a mussel taken through the posterior adductor muscle just behind the visceral ganglion will show the relative

position of the osphradia and abdominal sense organs (fig. 169). The osphradia are always found on the inner side of the gill supports, while the abdominal sense organs are on the outer side. List (1902) finds these organs best developed in *Modiolaria marmorata* and *Modiolus barbaratus*, well formed in *Lithophagus lithophagus*, and less developed in *Mytilus galloprovincialis*.

Otocysts were first observed in Mytilus by von Ihering (1876), the position, size, and innervation of which he described briefly. List (1902) found the otocyst present in all the Mytilidæ of the Mediterranean region as a paired, symmetrical organ, which he states is always a pear-shaped pustule lying directly under the body epithelium between the two connectives which bind the cerebral ganglion with the pedal ganglion, on the one hand, and with the visceral ganglion, on the other. In *Mytilus edulis* the organ occupies this same position in the angle formed by the union of the cerebrovisceral and cerebropedal connectives. It lies approximately over the point where the œsophagus joins the stomach. In gross structure the otocyst is an oval body, which in mussels about 5 cm. long has a length of from 150 to 200 and a breadth of from 125 to 135 microns. The smaller end points anteriorly and gives off a canal having a diameter of 25 to 30 microns, which runs forward just beneath the epithelium for a distance of 700 to 1,000 microns, where it opens to the exterior in a funnel-shaped invagination. In very thin specimens a fine white nerve can be traced forward from the oval part of the body as far as the junction of the cerebropedal and cerebrovisceral connectives.

In favorable material it is possible to isolate the otocyst sufficiently from its surrounding tissues so that it can be observed in a living condition under the mircoscope. To do this it is necessary to select animals whose sex glands are spent or undeveloped and which have been starved for several days. The animals should then be narcotized with a saturated solution of chloretone in sea water or with cocaine to bring about complete relaxation of the muscles. Then it is possible with small, sharp scissors or with a clean scalpel to cut around the area occupied by the otocyst, strip it off with the epithelium, and spread it out in a drop of water on a microscopic slide where it may easily be examined under the microscope. Under these conditions the otocyst appears as an oval body with a long, slender handle. It is a hollow structure, the walls of the oval part of the body being several times thicker than the wall of the canal and forming a clear, thick outer zone which stands in sharp contrast with the dark inner zone, in which vibrating cilia may be seen distinctly (fig. 173, p. 180). The walls of the canal are comparatively thin, and within its lumen the effects of active ciliary movement are visible, the effective stroke of the cilia being inward.

The visual organs of the sea mussel are of two types, consisting of a pair of well-developed direction eyes and of pigmented epithelial cells of the mantle edge capable of responding to changes in light intensity. Lovén (1848) first pointed out that Mytilus possessed an eye in the larval stage. Lacaze-Duthiers in his studies failed to note the fact at all, but Wilson (1887) observed that an eye was present in larvæ that had reached the four branchial filament stage. After such authors as Balfour, Fischer, and Lang had stated that the eyes were lost before the adult condition was reached, Pelseneer (1899) announced that the eyes persisted in the adult mussel. List (1902) found that in all the Mytilidæ studied by him, the larval eye was retained throughout life and that in all the species it occupied the same position. It is always found at the base of the first anterior inner gill filament on its lateral side (fig. 168, *E*). Ordinarily it is hidden

from view between the pair of labial palps. It is most easily made accessible for observation by laying the two gills apart and following up the inner gill support to its anterior end, where a little dark spot which represents the eye may be easily observed, especially if use is made of an ordinary hand lens. It is an invaginated cup, oval in form and consisting of epithelial cells filled with coarse granules of a dark-brown pigment (fig. 166).

In the larval mussel the eye occupies this same position at the base of the inner first anterior gill filament. In young specimens that have been fixed in toto the pair of eyes stand out distinctly under the microscope as large, pigmented oval spots.

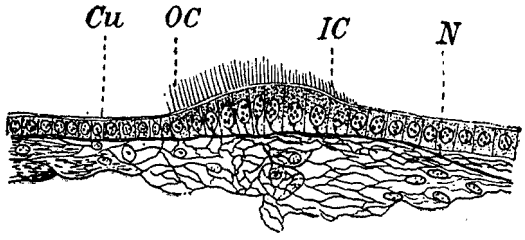
In addition to this pair of complex direction eyes, the sea mussel has a wide area of its body, extending the whole length of the free mantle edge and over the entire surface of the anal membrane and the foot, covered with brown densely pigmented epithelial cells, which are capable of being stimulated by light. Sometimes spots of the pigmented epithelium are present on the lips, although their presence in this position is unusual.

HISTOLOGY.

The *pallial sense organs*, which are most commonly found on the ventral epithelium of the posterior adductor muscle, consist of small groups of cells that are so related as to form little sense hills (fig. 164, p. 178). The surrounding epithelium consists of cubical cells covered with a relatively thick cuticula and bearing no cilia. The outer cells of the pallial sense organs are slightly taller than the epithelial cells, and as one passes from the periphery to the center of the sense body the cells become taller, the central cells being about twice as high as those of the surrounding epithelium. They are furthermore characterized by being ciliated, the cilia of one side of the elevation being much longer than those of the opposite side. The longest cilia are about as long as the tallest cells. The nuclei are large and contain several large chromatin granules, and each nucleus gives off from its base a nerve fiber. These fibers pass down into the connective tissue below, where they unite into a trunk that apparently runs to the visceral ganglion.

The *pinselzellen* of Flemming (1870), which are scattered over the epidermal layer of the mantle cavity, differ but little in form and size from the epithelial cells which surround them. Sometimes they are narrower or their outer ends flare outward. They are tall, columnar cells with a height about three times their breadth. They contain large oval or elliptical nuclei in which are several chromatin granules. Their most characteristic feature is the group of long cilia which extends from the outer end of the nucleus to a distance beyond the surface cuticula equal to the total length of the cell. (See fig. 167, p. 178.) These cilia stain deeply with iron hematoxylin. Dakin (1909) in his studies on Pecten found these same epidermal sense cells and states that each one is connected with a nerve fiber. The author has failed to demonstrate any nerve connection in Mytilus.

The *osphradium* is conspicuous because of its large columnar cells and nuclei which stand out in sharp contrast to the small cubical epithelial cells that surround it. The organ extends on either side of the body from a point ventral to the visceral ganglion to the inner side of the gill support and is one layer of cells thick. (See fig. 172, p. 180.) Numerous fine nerve fibers arise from the basal portion of the organ and run into the



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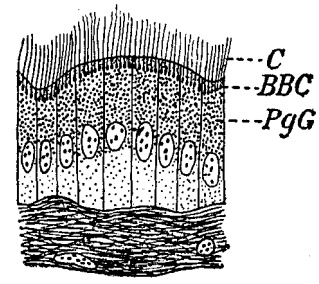

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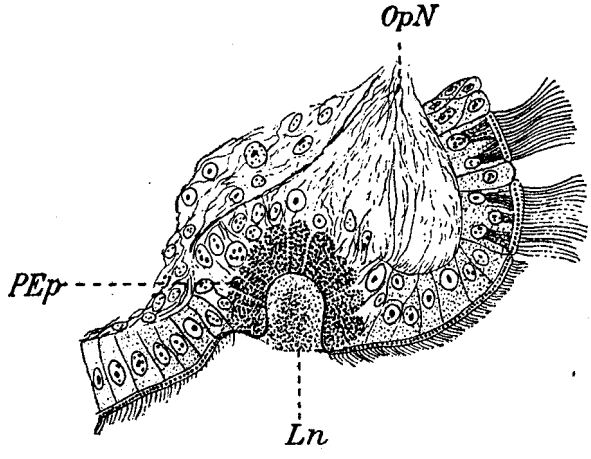

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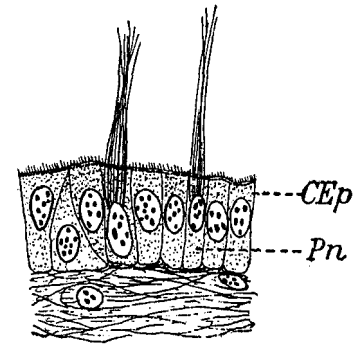

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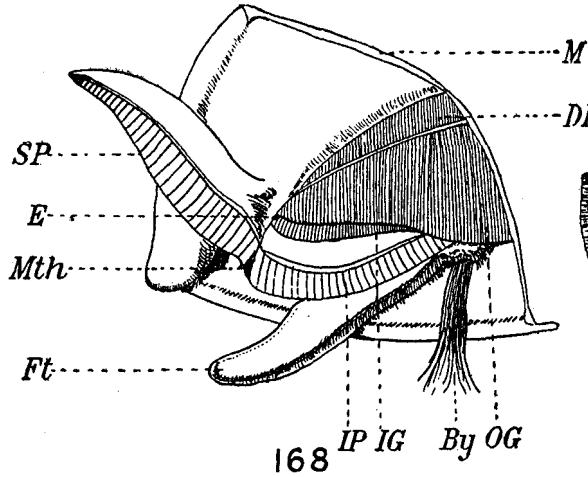

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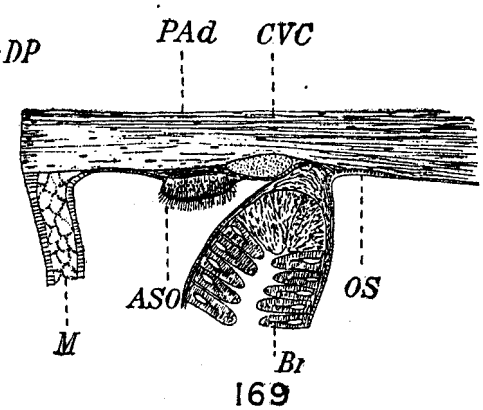


169

FIG. 164.—Cross section through a pallial sense organ. × 575. Fixed in Gilson fluid and stained with Delafield hæmatoxylin. *Cu*, cuticula; *IC*, inner cilia; *N*, nerve supplying the sense organ; *OC*, outer cilia.

FIG. 165.—Cross section of anal epithelium. × 1,000. Preparation same as fig. 164. *BBC*, basal bodies of cilia; *C*, cilia *PgG*, pigment granules.

FIG. 166.—Transverse section through eye of young mussel 15 mm. long. × 500. Fixed in Flemming fluid and stained with Heidenhain iron hæmatoxylin and congo red. *Ln*, so-called lens; *OpN*, optic nerve; *PEp*, pigmented epithelium of eye cup.

FIG. 167.—Cross section through body epithelium containing two pinselzellen of Flemming. × 1,000. Preparation same as fig. 166. *CEp*, ciliated epithelium, *Pn*, pinselzellen of Flemming.

FIG. 168.—Lateral view of anterior end of gills with superior palp reflected to show position of eye at base of first filament of inner gill lamella. *By*, byssus; *DP*, descending portion of outer gill lamella; *E*, eye; *Ft*, foot; *IG*, inner gill lamella; *IP*, inferior palp; *M*, mantle; *Mth*, position of mouth; *OG*, outer gill lamella; *SP*, superior palp. (After Pelseneer, 1899.)

FIG. 169.—Cross section passing through posterior adductor muscle to show positions of abdominal sense organ and osphradium in relation to roots of gill. × 50. Preparation same as fig. 166. *ASO*, abdominal sense organ; *Br*, gill; *CVC*, cerebrovisceral commissure; *M*, mantle; *OS*, osphradium; *PAd*, posterior adductor muscle.

visceral ganglion. The cells are devoid of cilia, which differentiates the osphradium from all the other sense organs.

The structure of the *abdominal sense organ* is similar to that of the pallial sense organ, but it is larger and more complex. It forms a sense hill from three to four times as high as the contiguous epithelium, from which it arises with a steep slope. The transition from the body epithelium to the sense epithelium is sudden, without any cells of an intermediate character intervening. A characteristic feature of the organ is that it is several cells thick. The distal ends of the cells show distinct striations and are covered with a thick cuticula. The innervation of the abdominal sense organ comes from a side branch of the principal posterior pallial nerve. The nerve enters at the base of the sense organ and sends out numerous branches which spread throughout its structure, some of which connect with or surround the nuclei, while others, passing the length of the cells, penetrate the cuticula and project out some distance as tactile hairs. (See fig. 171, p. 180.)

The *otocyst*, when examined under the microscope, is found to lie just under the body epithelium between the cerebropedal and cerebrovisceral connectives. The main body of the otocyst, which is oval in form, is made up of several layers of cells, which inclose a cavity containing numerous small irregularly-shaped particles varying from 1 to 4 microns in diameter and which, on account of their insolubility in acid, are probably silicious in character. The anterior and posterior walls are thicker than the others, and the nuclei of their cells are longer. The cavity is lined with a layer of epithelium, each cell of which bears a long tuft of cilia. (See fig. 173.)

The *otocyst canal* is made up of a single layer of more or less cubical cells containing small spherical nuclei. These cells bear very fine cilia that, in the beginning of the canal at least, slope inward, preventing the passage outward of any of the contents of the otocyst. The anterior end of the canal opens to the exterior in the bottom of a funnel-shaped pit formed by an invagination of the body epithelium. The cells which form this pit are arranged in concentric layers. The whole otocyst is inclosed in a homogenous, structureless substance which is thickest about the oval-shaped portion.

The *otocyst nerve*, carrying an abundance of fibers, arises from the cerebropedal connective just posterior to its junction with the cerebrovisceral connective and passes backward just under the otocyst canal into the main body of the sense organ.

Microscopic examination of the eyes of *Mytilus edulis* reveals the fact that they are formed from an invagination of the ciliated body epithelium. This gives a cuplike depression whose walls are formed from the transformed epithelial cells of the body. These cells have lost their cilia and are filled, especially toward the periphery, with rather coarse granules of brown pigment (fig. 166, p. 178). The transition from optic epithelium to body epithelium is abrupt, but the two groups of cells are covered with a continuous layer of cuticula. Mucus or some other crystalline secretion fills the optic cup and is thought by some to constitute a lens.

A very delicate nerve arises from the cerebral ganglion and passes directly back to the eye, where it breaks up into numerous fibrillæ that spread over and enter the optic epithelium.

The *pigmented epithelium*, covering the mantle edge and other parts of the body, is composed in most part of columnar ciliated, epithelial cells which are partially filled with fine, brown granules. These granules lie for the most part in the region distal to the nuclei (fig. 165, p. 178).

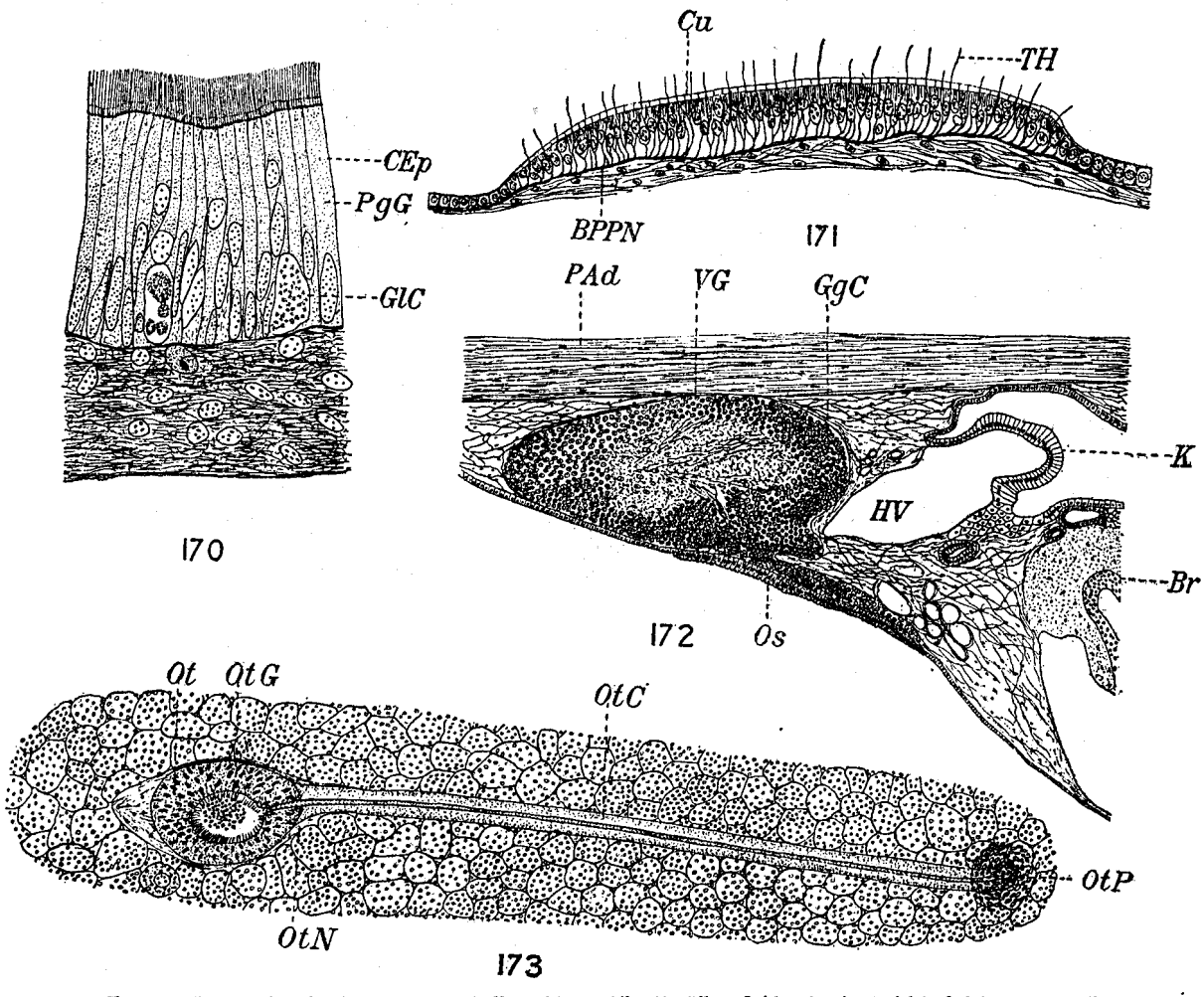


FIG. 170.—Cross section of a pigment spot on the lips. × 750. Fixed in Gilson fluid and stained with Delafield hæmatoxylin. *CEþ*, ciliated epithelium; *GlC*, gland cell; *PgG*, pigment granules.

FIG. 171.—Cross section through an abdominal sense organ. × 375. Preparation same as fig. 170. *BPPN*, branch of posterior pallial nerve; *Cu*, cuticula; *TH*, tactile hair.

FIG. 172.—Cross section passing through visceral ganglion and osphradium. × 100. Fixed in Flemming fluid and stained with hæmalum and congo red. *Br*, gill; *GgC*, ganglion cells; *HV*, horizontal vein; *K*, kidney; *Os*, osphradium; *PAd*, posterior adductor muscle; *VG*, visceral ganlion.

FIG. 173.—Lateral view of otocyst drawn from a living preparation. × 100. *Ot*, main body of otocyst; *OtC*, otocyst canal; *OtG*, otolith granules; *OtN*, otocyst nerve; *OtP*, otocyst pit containing the external opening.

Round, pigmented spots found on the lips of some mussels are similar in character to the pigmented cells of the mantle edge, except that the cells are taller and more irregular in form. In size the cells vary from 38 to 40 microns in length by from 2 to 3 microns in width. The pigment granules are finer than those of the cells on the mantle edge, are more abundant, and extend into the basal regions of the cells. At the distal ends of the cells the granular group tapers out to a point (fig. 170, p. 180). Each cell bears many cilia that arise from a layer of basal bodies which stain deeply with hæmatoxylin. The cilia are about 7 microns in length. The nuclei which lie at the proximal ends of the cells are long and narrow and filled with fine chromatin granules. The portion of the cells distal to the nuclei is filled with finely granulated, yellowish-brown pigment. Large gland cells more or less oval or elliptical in outline occur at frequent intervals, between the proximal ends of the pigmented cells (fig. 170, *GlC*, p. 180).

PHYSIOLOGY.

The functions of the various sense organs just described in Mytilus remain undetermined up to the present time. Literature on the subject is of a speculative nature, but a brief review of it may be worth while.

In regard to the *sensory cells* scattered throughout the epidermal layer, Dakin (1909) says they seem to be stimulated by very slight movements in the water. He also ventures the assumption that in addition to being tactile organs they may be olfactory in function.

Concerning the function of the *osphradium* there is no experimental evidence. Because of its similarity to the osphradium of gastropods such authors as Lankester (1883) and Pelseneer (1888) have assumed that it is olfactory in function.

The *abdominal sense organ*, according to Dakin (1909), functions to test the quality of the incoming water either as an olfactory or as a gustatory organ; but since this sense is usually ascribed to the osphradium, it is difficult to understand why these two organs should be placed side by side. Since the histological structure is so remarkably like that of the lateral line organs described by Eisig (1887) in the Capitellidae, Thiele (1889 and 1890) assumes that they are homologous with the lateral line not only of the chætopods but of fishes, and therefore probably function to perceive wave movement or vibrations in the water. He considers furthermore that they may be olfactory in function.

No literature on the function of the *otocyst* in Mytilus has been found, but it may be assumed that, as in other invertebrates, it serves as an organ of orientation.

Neither has the author been able to find any references to the physiology of the eyes or pigmented epithelium of the mussel. A single series of experiments performed September 6, 1912, furnishes all the data the author has. Some mussels, whose mantle edges were expanded from between the open valves, were lying in a trough of running water in the laboratory, so situated that a number of them were subjected to the direct light of the sun while the others were shaded. When the hand was held so as to cast a shadow on the mantle fringe a rather quick response followed. The mantle edge contracted decidedly and sometimes was completely withdrawn, followed by closing of the valves. A similar response was obtained from the mussels lying in an expanded condition in the shade when direct sunlight was reflected with a small mirror onto the mantle edge. Response came, however, only when there was a decided change in the intensity of the light one way or the other. This would indicate, therefore, that the pigmented epithelium of the mantle edge is a light receptor, but at best is a very crude sense organ.

REPRODUCTIVE SYSTEM.

ANATOMY.

The reproductive system consists of numerous ducts which branch throughout nearly the entire body, giving off in turn smaller branches which terminate in pockets or follicles. The greater part of the system occupies the mantle lobes, which are filled almost exclusively with reproductive tissue just prior to spawning. It also fills the mesosoma, penetrates through the tissues just below the pericardial chamber, lines the walls of the lateral cavities, and spreads over the outer surface of the liver. Practically every part of the body with the exception of the gills, muscles, and foot is covered or occupied by the genital organs. This is well shown by a cross section taken through the middle of the body of a mussel 1 year old which was about to spawn for the first time. (See fig. 147, opp. p. 163.)

The main genital ducts lie near the outer surface of the mantle lobes and converge to a point of common union which lies just below the pericardium. In general there are five principal canals which meet at this point: (1) A main branch which supplies the anterior region of the mantle and the surface of the liver, (2) and (3) two lateral branches which supply the mid region of the mantle, (4) a posterior branch which connects with the hinder parts of the mantle, and (5) a dorsal branch which supplies the area between the posterior adductor muscle and afferent oblique vein and the dorsal body wall (fig. 162, *GC*, p. 173).

From the point of union of these several ducts, the main genital canal thus formed on each side of the body penetrates the mantle to its inner surface, where it turns backward and runs on the ventral body wall just inside and parallel with the attached edge of the inner gills to the genital papilla on which it opens to the exterior. The genital papilla lies a short distance in front of the posterior adductor muscle in the angle formed at the base of the mesosoma with the inner gill. A median branch from the common genital canal connects with the mesosoma on each side of the body.

HISTOLOGY.

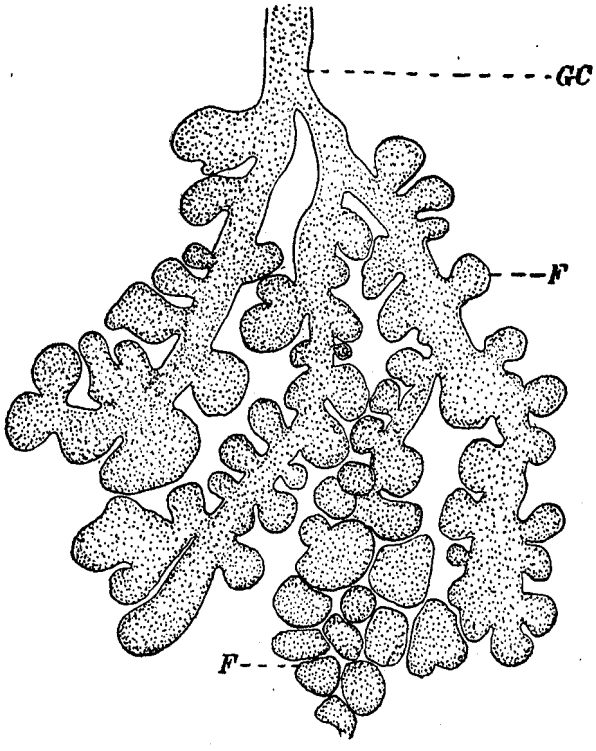
If the mantle of a mussel which has almost finished spawning is treated with Gilson's fluid or some other suitable fixing solution and then stained with borax-carmine, dehydrated, and cleared, preferably in oil of wintergreen, the minor canals and the follicles connected with them can be seen easily under the microscope when examined with low-power lenses.

In male animals, the follicles are small outgrowths from the sides of the canals. They are of almost uniform size, very numerous, and situated about the same distance apart (fig. 174).

In the female the arrangement of the canals is the same as in the opposite sex, but the follicles are larger, much less numerous, and more variable in size.[2] In some cases they appear to be lateral outgrowths of the genital canals, while in others they form the blind ends of the ducts (fig. 175).

[2] The relative sizes of the follicles shown in figures 174 and 175, according to the magnifications given in the legends, do not correspond with the description in the text and suggest that a mistake was made in the figures given for the magnification of either figure 174 or 175, or both.

In both sexes the follicles are lined with germinal epithelium, the minor genital ducts are bordered with germinal epithelium on one side and ciliated epithelium on the other (fig. 177, p. 184), and the main canals have their walls thrown into longitudinal ridges which are covered entirely with columnar ciliated epithelium. They are surrounded by a thin layer of fine muscle fibers which increase in number toward the genital orifice. The opening on the papilla has two distinct lips which may completely close it when they are brought together by muscular action (fig. 162, *GO*, p. 173).



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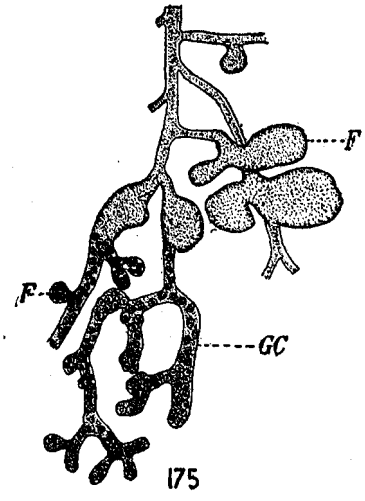


175

FIG. 174.—Terminal branches of a minor genital canal in a male mussel showing follicles which are lined internally with germinal epithelium and filled with genital products. × 25.[2] Drawing made from a total preparation which was fixed in Gilson fluid, stained with borax-carmine, dehydrated in alcohol and cleared in oil of wintergreen. *F*, follicles; *GC*, a minor genital canal.

FIG. 175.—Branching genital canals and follicles in a female mussel. × 23.8.[2] Preparation same as fig. 174. *F*, follicles, smaller ones with transparent walls showing ova contained within; *GC*, minor genital canals also filled with ova.

The ova and spermatozoa arise from the germinal epithelium lining the follicles and minor genital canals. Before the germ cells begin to grow the epithelium is membranous in character and composed of very small cells. As the ova develop, their area of attachment increases greatly in thickness (fig. 177, *GE*, p. 184). Their nuclei are very prominent, containing large, conspicuous nucleoli, and are surrounded by a thin layer of

[2] The relative sizes of the follicles shown in figures 174 and 175, according to the magnifications given in the legends, do not correspond with the description in the text and suggest that a mistake was made in the figures given for the magnification of either figure 174 or 175, or both.

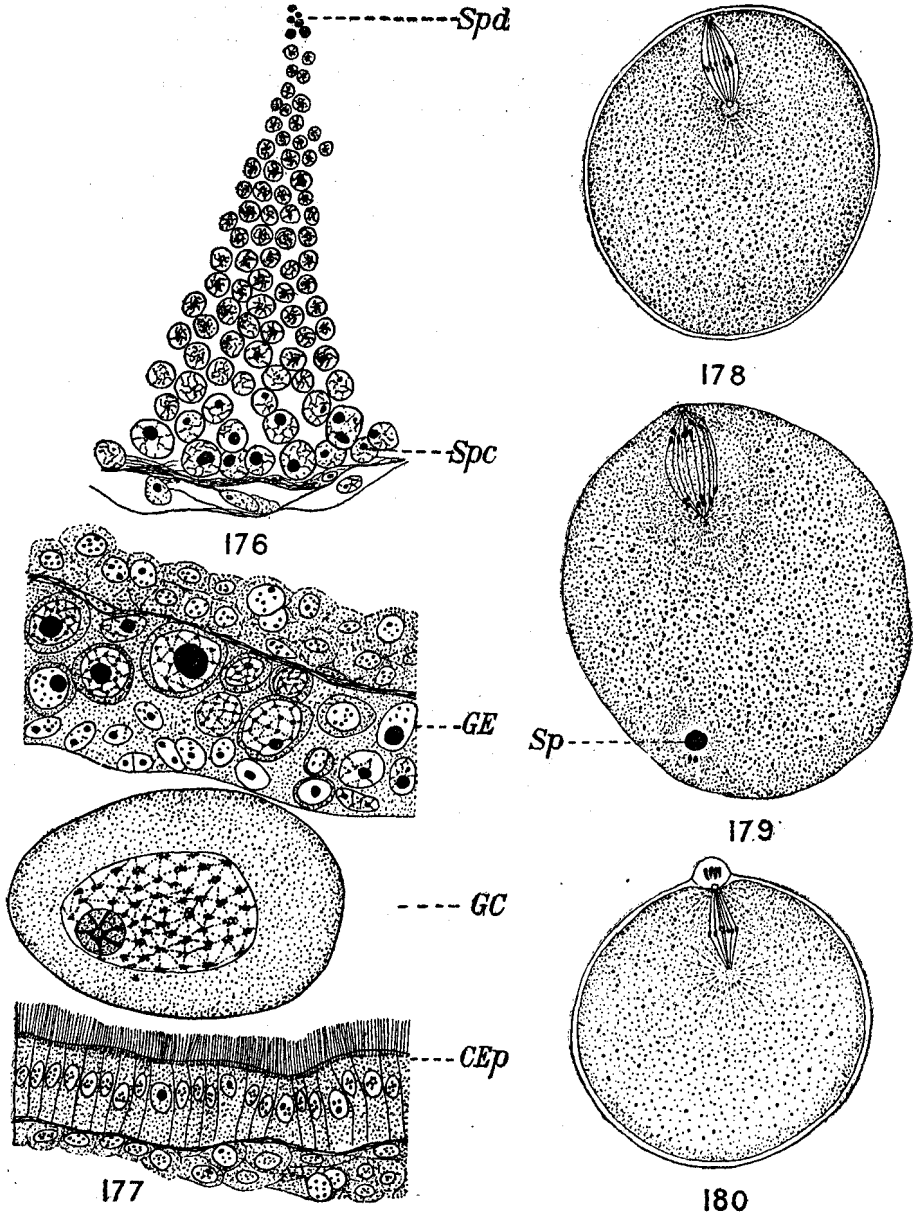


FIG. 176.—Sector from a male follicle prepared on April 1. × 900. Fixed in Flemming fluid and stained with Heidenhain iron hæmatoxylin. *Spc*, sperm mother cells or spermatocytes on wall of follicle; *Spd*, spermatids in center of follicle.

FIG. 177.—Longitudinal section through a minor genital canal of a female mussel. × 765. Preparation same as fig. 176. *CEp*, ciliated epithelium which lines one side of canal only; *GC*, genital canal, containing a ripe ovum; *GE*, germinal epithelium containing developing ova.

FIG. 178.—Longitudinal section through a freshly laid egg that has not been fertilized. The spindle of the first polar body is formed and does not pass beyond this stage normally unless the egg is fertilized. Fixed in Bouin fluid and stained with Heidenhain iron hæmatoxylin and congo red.

FIG. 179.—Longitudinal section through an egg showing the condition which follows immediately after impregnation. × 900. Head of spermatozoon, *Sp*, enlarges greatly as it migrates toward center of cell. At same time spindle of first polar body passes into anaphase stage and process of maturation continues rapidly from this time on until completed. Preparation same as fig. 176.

FIG. 180.—Longitudinal section through an egg showing spindle of second polar body which is formed immediately after first polar body is extruded. Preparation same as fig. 178.

cytoplasm. As fast as the ripe ova are formed they burst out into the follicles and canals which they come to fill so tightly that they are compressed into a characteristic, polygonal form. A cross section of either the mantle or mesosoma at the height of the breeding season will show how completely these organs are filled and distended with eggs (fig. 215, opp. p. 226).

The sperm follicles just previous to the reproductive period, when seen in cross section, are irregularly circular in outline, from 300 to 800 microns in diameter. They are almost completely filled with sperm mother cells and spermatozoa, the latter occupying the central portion. The peripheral region of the follicle is occupied with large sperm mother cells, which consist of nuclei surrounded with only a film of cytoplasm and containing one or two large nucleoli. Passing toward the center of the cavity, the nuclei become smaller and the contained chromatin is in the form of threads, which indicates that the cells are in the active process of division. In no preparations, however, was a single mitotic figure observed. In the center of the follicle spermatids and spermatozoa were present which were very small compared with the mother cells and which stained uniformly deep blue or black with iron hematoxylin (fig. 176, p. 184). Later in the season when the ripe products are ready to be liberated, the follicles present a different appearance. They are densely filled with spermatozoa, which appear as minute, round dots arranged in bands or lamellæ which converge toward the center, or they may be so arranged as to make a coarse network (fig. 220, opp. p. 227).

The number of follicles which are contained in the mantle of a mussel depends upon the age and size of the animal. In small specimens just approaching maturity a single follicle will fill the space between the outer and inner walls of the mantle, while in large specimens, 3 or more inches long, the same space may accommodate a series of 6 to 8 follicles (fig. 220).

PHYSIOLOGY.

When the genital products are first formed, they are mature to all appearances, morphologically, but physiologically they are immature, for when such eggs and spermatozoa are mixed together fertilization fails to take place. The spermatozoa have tails but make no movement, and the eggs, though containing a well-developed germinative vesicle, fail to form the spindle of the first polar body when they come in contact with the sea water as is normal for mature ova. Both elements are perfectly inert. Before reaching functional activity they must undergo a period of rest which apparently lasts for several weeks. As they reach the stage of functional activity they begin to crowd out into the main canals and are swept onward by strokes of the powerful cilia which line one side of the canals (fig. 177, *CEp*). They are forced up close to the genital opening, which is closed by two lips of tissue and furthermore sealed by a plug of granules and minute pigmented cells which are reddish brown in color.

The expulsion of the reproductive elements begins suddenly and takes place rapidly. The first sign is when the plug of pigmented granules is discharged. This is followed, in the male, by a continuous stream of milt which renders the water milky for a distance of several feet from the spawning individual. The discharge may continue for half an hour, with little or no interruption. In the female the process is similar, except that the eggs usually are expelled while sticking together in the form of rods, which may be from 3 to 5 mm. in length. They represent the form into which they were molded together while in the oviduct. The eggs flow out in a continuous stream and in quiet

water settle to the bottom in a pink or reddish mass. The ova, which are clustered together in the shape of rods, soon fall apart and assume the normal spherical or oval form. The process sometimes continues until nearly all the genital products are removed; sometimes the process is incomplete and occurs periodically from two to three days apart; and sometimes the animals fail to expel any of the elements. In the latter case the eggs and spermatozoa degenerate and are absorbed by the tissues of the body.

The normal stimulus which starts up the act of spawning still remains an unsolved problem. Ripe specimens were transferred from cold to warm water and vice versa, from water of high density to that of low density and back again; they were exposed to the air from one to three hours and then submerged, subjected to swift currents and then still water, but in no case was there positive evidence that it influenced the act of spawning. Rough handling, such as shaking them up and down in a bucket of water or stirring them about vigorously with the hand, caused spawning to take place within a few minutes to an hour later, but this can not be called a normal stimulus. It is a common belief that the presence of spermatozoa in the water stimulates the female to the act of spawning, but the author could not verify this statement. Often the females spawned before the males began to liberate sperm, and isolated individuals in filtered sea water were observed to deposit eggs in great quantities on several different occasions. On the other hand, sometimes the trough in which quantities of ripe mussels were kept would be milky with sperm and not a female would show a sign of laying an egg. The following day, when very few or no spermatozoa were present, a dozen or more females might spawn. The nature of the spawning stimulus, therefore, remains doubtful.

EMBRYOLOGY.

GERM CELLS.

The early history leading up to the formation of the germ cells could not be worked out from any of the author's slides, although histological preparations were made from material collected every two weeks during the year. Dividing cells were rarely observed, but it was clearly evident that the sexual elements arise from the epithelial lining of a vast number of canals that proliferate throughout the whole body. The germ cells begin to form early in the winter and reach maturity by early spring or late summer, according to the temperature of the water and, possibly also, the amount of available food. On our Atlantic coast the spawning season begins in April and continues on through the summer well into September. At the Woods Hole (Mass.) Biological Station, the author has secured spawning individuals every week throughout the season from June 20 to September 15.

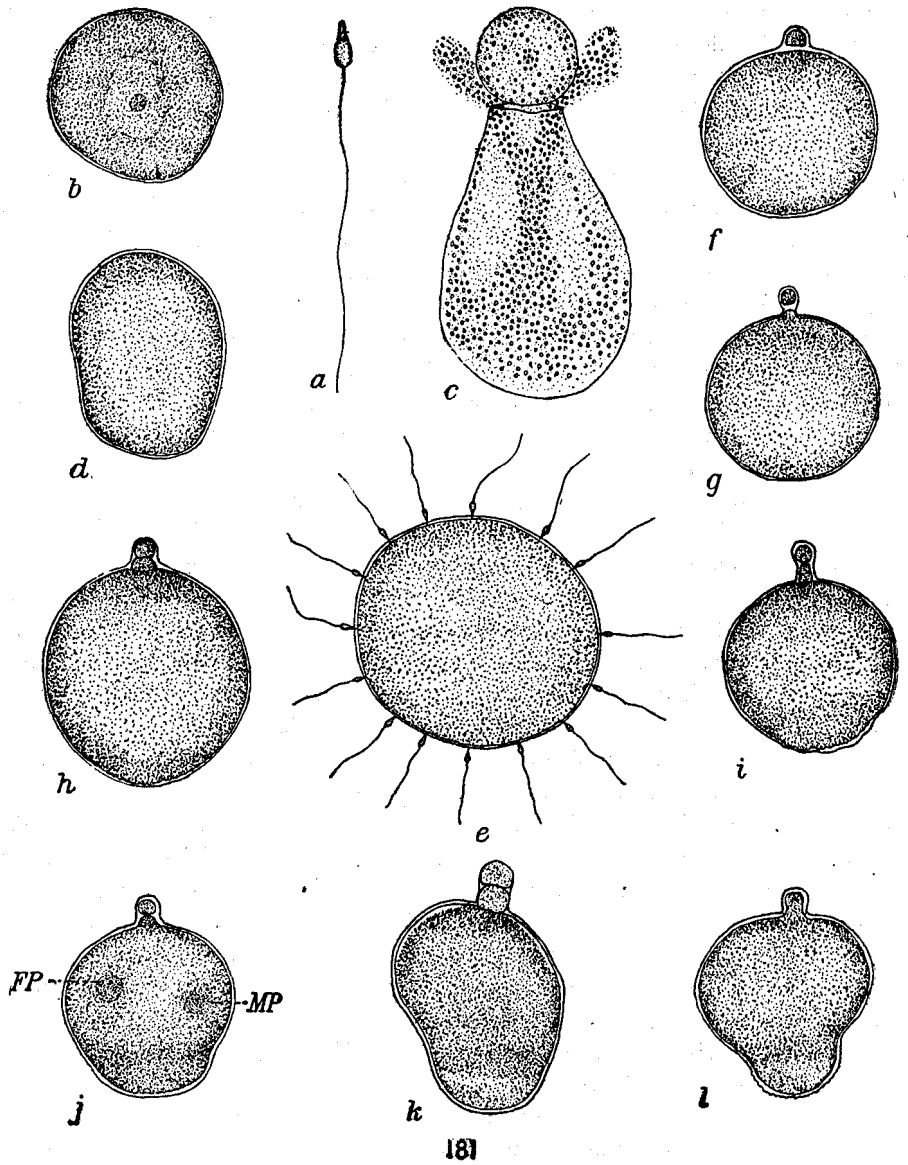
The number of germ cells liberated is something enormous, but that is to be expected when we consider that practically the whole body functions as a genital gland. In figure 147 (opp. p. 163) the genital follicles filled with their products are shown to occupy almost the entire portion of the mantle, the floor of the pericardial region, the wedge-shaped mesosoma, and the outer walls of the liver. A male mussel discharges a stream of milt that in a few minutes' time will render milky all the water in a trough 10 feet long, 1½ feet wide, and 3 inches deep. Figures can not be used to express the countless numbers of fertilizing elements that swarm in the water under these conditions.

The number of eggs spawned by a female mussel at a given time can be determined fairly accurately by determining the size of the egg and the volume liberated. The eggs average about 0.07 mm. in diameter, and the volume liberated at single intervals is from 2 to 4 cc. If the eggs were placed side by side in a line it would require 142 to make a centimeter, and 142 such lines, or 20,164, to cover a square centimeter with eggs one layer thick. A cubic centimeter would contain 142 layers, or 2,863,288 eggs, if placed one directly upon another. As a matter of fact, however, this does not occur, for the eggs settle in the depressions formed between those of the layer beneath, which results in adding some 500,000 more to the total number. But owing to the various errors that occur in making the measurements, such as the presence of foreign matter and the buoying property of the water, which prevents the eggs from coming into actual contact with each other, it probably more closely approximates the truth to assume that there are 2,863,288 eggs to the cubic centimeter. This would mean, therefore, that a mussel during a single act of spawning liberates from 5,000,000 to 12,000,000 eggs. By comparing the volumes of water displaced by the mantle and mesosoma of large mussels 3½ to 3¾ inches long, before and after spawning had occurred, the author found the difference to be a little less than 10 cc., which would indicate that large specimens are capable of producing as high as 25,000,000 eggs.

The spermatozoa are pin-shaped bodies when observed under the low power of the microscope. Under high magnification the head appears as an oval body, with the small end terminating anteriorly in a conical protuberance. At the base of the conical structure are two small, doubly refractive bodies that stain deeply with janus green in the living element. A long slender vibrating tail projects from the opposite end of the head (fig. 181*a*, p. 188). In size the head measures 5 microns long and has a width of 2.5 microns. The tail has a length of 35 microns.

The egg, before leaving the follicle, is more or less spherical in form, with a diameter of 0.07 mm. With transmitted light its color is a pale brownish-yellow. A distinct vitelline membrane no less than 1 micron in thickness envelops the egg, while the center is occupied by a large germinative vesicle containing a conspicuous nucleolus (fig. 181*b*, p. 188). The portion of the egg outside the germinative vesicle is filled with fine yolk granules that render the egg more or less opaque, especially after the germinative vesicle breaks down, which occurs at the time of spawning (fig. 181*d*).

No microphile is visible in the ovarian egg, but if the egg is slightly crushed under a cover glass, it becomes balloon-shaped and an opening appears at the tapering end. Yolk granules flow out from this point of exit, constantly vibrating with the Brownian movement. If pressure continues to be applied to the cover glass the nucleus will also slip out through the opening (fig. 181*c*). The ripe egg, just before it is expelled from the main oviduct, or immediately after it comes in contact with the sea water, undergoes considerable change internally. While externally it retains a form that varies between a long oval and an imperfect sphere, internally the germinative vesicle breaks down and forms the spindle of the first polar body (fig. 178, p. 184). This explains why no nucleus is visible in the freshly laid egg, as noted by Wilson (1887) and Williamson (1907), rather than the presence of abundant deutoplasmic granules to which they attributed the fact. Unless fertilized within three or four hours after extrusion, the eggs die without passing beyond the stage of the first polar spindle.



181

a. Spermatozoon. Note oval head bearing conical protuberance (at base of which are two doubly refractive bodies) and long, slender tail. × 1,185.

b. Ovarian egg removed from mantle. Imperfect sphere with an external membrane. Germinative vescicle with large nucleolus visible. × 375.

c. Ovarian egg slightly crushed under cover glass showing escaping nucleus and yolk granules. × 375.

d. Ripe egg immediately after being shed. No definite form. Germinative vescicle has disappeared. × 375.

e. Egg a few minutes after fertilization. Perfectly spherical. Spermatozoa acting against it cause it to roll about. × 450.

f. Egg 20 minutes after fertilization, showing protrusion of first polar body. × 375.

g. Egg 10 minutes later, showing appearance of second polar body just below first. × 375.

h. Another egg showing a stage 5 minutes later. The two polar bodies are distinctly separated from egg proper which has now become elongated. Cytoplasmic border at vegetative pole is beginning to take on an irregular outline and to withdraw from cell wall. × 375.

i. Egg 2 minutes later, showing increased activity at nutritive pole. Wavy outline of cytoplasm is more pronounced. Cell membrane opposite to it is wrinkled and beginning to draw away from egg. × 375.

j. Egg 10 minutes later, showing continued protuberance of nutritive pole, contents of which become more transparent than rest of egg. Male pronucleus, *MP*, clear spot near nutritive pole; female ptonucleus, *FP*, similar body near formative pole. × 375.

k. Egg 10 minutes later. Unsymmetrical pear form. Pronuclei have fused and disappeared. × 375.

l. Egg 2 minutes later. Pear form more symmetrical. Nutritive pole contains finer granules, and is therefore more transparent. × 375.

MATURATION AND FERTILIZATION.

That fertilization of the mussel egg takes place in the water has been observed by McIntosh (1885) and Wilson (1887), while Scott (1901), who studied mussels kept in tanks, believes that impregnation of the eggs occurs in the branchial chamber of the mother. According to his observations, "the embryos flow from the female in a slow distinct stream." Of the hundreds of spawning mussels which have been under the author's observation, not one to his knowledge has discharged fertilized eggs into the water. The eggs are discharged in short rodlike masses, which have been described in the chapter dealing with the reproductive system. If the water is quiet they settle to the bottom and the eggs fall apart, forming a brick-red to pinkish mass, according to the amount of pigment present, which is variable. If the locality is subject to the influence of currents or wave action, the eggs flow away and are more or less widely scattered over the bottom. Spermatozoa are generally liberated into the water at the same time that eggs are being shed, and with their long, rapidly vibrating tails, they are able to locomote with surprising rapidity. They are attracted to the eggs, about which they cluster in large numbers, with their conical pointed heads pressing against the vitelline membrane and the tails beating so that the egg keeps twisting around with a spiral motion (fig. 181*e*). Normal freshly laid eggs permit but one spermatozoon to enter, whereas stale or anesthetized eggs allow many to penetrate the cell wall.

As soon as the spermatozoon enters the egg, rapid changes begin to occur in both bodies. The spermatozoon loses its tail and the head begins to increase greatly in size as it moves toward the center of the egg, leaving a clear path behind it (fig. 179, *Sp*, p. 184). The spindle of the first polar body, which has remained stationary at the end of the prophase period since the egg was first deposited, now becomes active again. The chromosomes in the equatorial region divide and migrate toward their respective poles (fig. 179), and at the same time the egg, which hitherto has had no definite form, becomes a regular sphere. When the eggs assume the spherical form it is a pretty sure sign that impregnation has occurred.

The first polar body appears in from 18 to 20 minutes after the eggs and spermatozoa are mixed together, provided the sperms are in an active state (fig. 181*f*, p. 188). Wilson (1887) states that the polar cells appear four hours after mixing ova and sperm, which indicates that his material was abnormal or that the water was very cold. For several years the author has been repeating the experiment with the uniform result that in sea water at about 68° F. the first polar cell appears within 20 minutes after the eggs are discharged and mixed with spermatozoa.

Ten minutes after the appearance of the polar cell a second polar cell is extruded behind the first (fig. 181, *g* and *h*, p. 188), after which the egg remains quiescent, to all external appearances, for a period of about 20 minutes.

At the end of this period the vitelline membrane on the side of the egg opposite to the polar bodies becomes wrinkled, and the margin of the cytoplasm adjacent to it takes on an irregular and wavy outline (fig. 181, *h* and *i*, p. 188). This end of the egg, which represents the vegetative or nutritive pole, now begins to protrude itself in such a way as to give the egg a pear shape, the stalk of the pear including the nutritive pole and the broad end the formative pole. At the same time, two clear spots are usually visible in the granular cytoplasm, which represent the male and female pronuclei (fig. 181*j*, p. 188).

The pronuclei move toward each other, fuse, and disappear during the following 10 to 15 minutes.

CLEAVAGE AND FORMATION OF GERM LAYERS.

The pear shape of the cell becomes more pronounced, and one side of the broad end increases more rapidly in size than does the opposite side (fig. 181*k*, p. 188). At the same time the cytoplasm becomes less dense at the vegetative pole, which permits more light to pass through and therefore makes this region appear brighter and less granular than the rest of the egg.

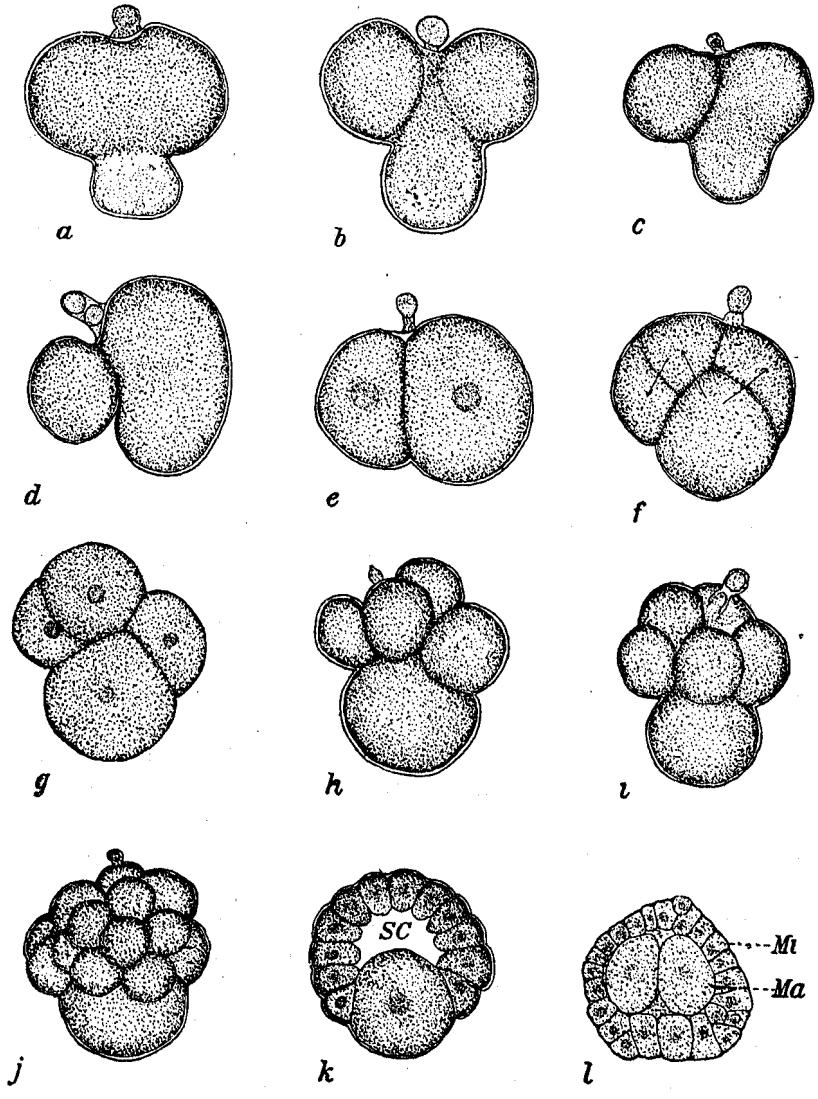
One or two minutes later the opposite side of the egg bulges rapidly, making the pear shape more symmetrical, as is shown in figure 181*l* (p. 188). The sides continue to protude outward, a depression appears at the formative pole, and a constriction begins to form about the proximal end of the nutritive pole (fig. 182*a*). Then two planes of constriction appear as shown in figure 182*b* and, to all external appearances, a body of three nearly equal cells results. This, however, is really not the case, for during the next 10 minutes radical changes occur in the egg. One of the apparent cells fuses with the one that corresponds to the nutritive pole, as shown in figure 182, *c* to *e*, resulting ultimately in two cells of very unequal size. The large one is known as the macromere, and the small one as the micromere. The nuclei are visible as clear round spots in the center of the two cells. During the next 10 minutes two more micromeres result. The first one of these is given off from the macromere, and almost at the same time the second one results from the division of the original micromere, as shown in figure 182, *f* and *g*.

From this point on, cell multiplication through the division of the micromeres and the giving off of new micromeres from the macromere is very rapid. The stages represented in figure 182, *h* to *j*, are passed through in about half an hour. The result is a macromere almost covered with a cap of micromeres and a small segmentation cavity inclosed by the group of cells. The relation of the cells to the segmentation cavity at this stage is best seen in an optical section represented in figure 182*k*.

As cell division proceeds, the ectodermal cells become smaller and ultimately completely envelop the macromere, which finally divides into two equal cells (fig. 182*l*). These two cells are apparently the forerunners of the mesoderm.

Figure 183*a* (p. 193) shows a later stage where the embryonic cells have become more uniform in size. The first polar body has, in the meantime, divided so that three polar cells are visible at this stage. Very fine cilia develop on the exposed surface of the cells at this time, and by their vibrations cause the embryo to move slowly about. The period of development from fertilization to the free swimming embryo requires normally 4½ to 5 hours.

Internal changes are difficult to follow in the living material from this stage on. Up to the end of the twenty-fourth hour the principal changes observed are the rapid multiplication of cells, the extraordinary growth of cilia over the outer surface of the body, and the development of a long flexible flagellum, which is composed of several filaments. This flagellum is situated on the anterior end of the body and is held forward like an antenna as the trochophore propels itself rapidly through the water by means of the cilia (fig. 183*c*, p. 193).



182

FIG. 182.—Egg at various stages. × 375.

a. Egg at stage 4 minutes later than 181*l*. Three nearly equidistant furrows have formed, separating formative poleinto two masses and setting nutritive pole off as single mass.

b. Two minutes later. Nutritive pole has enlarged to form macromere. Left mass at formative pole is about to be cut off as first micromere.

c. One minute later, showing fusion taking place between macromere and yolk mass to right of formative pole. First micromere is now completely separated by a furrow.

d. Two minutes later, showing continuation of same process.

e. Ten minutes later with macromere and micromere in resting stage. Their nuclei are visible as clear spots in centers of the cells.

f. Ten minutes later. Macromere has given off a second micromere, and first micromere has divided into two as indicated by arrows.

g. Three minutes later.

h. Twelve minutes later.

i. Two minutes later.

j. Fifteen minutes later, showing cap of micromeres gradually growing down over macromere.

k. Optical view of a little later stage, showing segmentation cavity, *SC*.

l. Few minutes later. Macromere now completely surrounded by micromeres, *Mi*, and has divided into two equal cells, *Ma*, that are apparently forerunners of the mesoderm.

Figure 183*b* (p. 193) shows an embryo of this same stage that was placed in a dilute solution of glycerine and water. The solution was not strong enough to destroy the organism through osmotic action, but served to stupefy and render it more transparent. The invagination process of gastrulation was occurring as represented, and mesodermal cells were scattered throughout the segmentation cavity. A typical invagination gastrula is formed in the mussel, therefore, as in the oyster, after first starting as an epibolic gastrula.

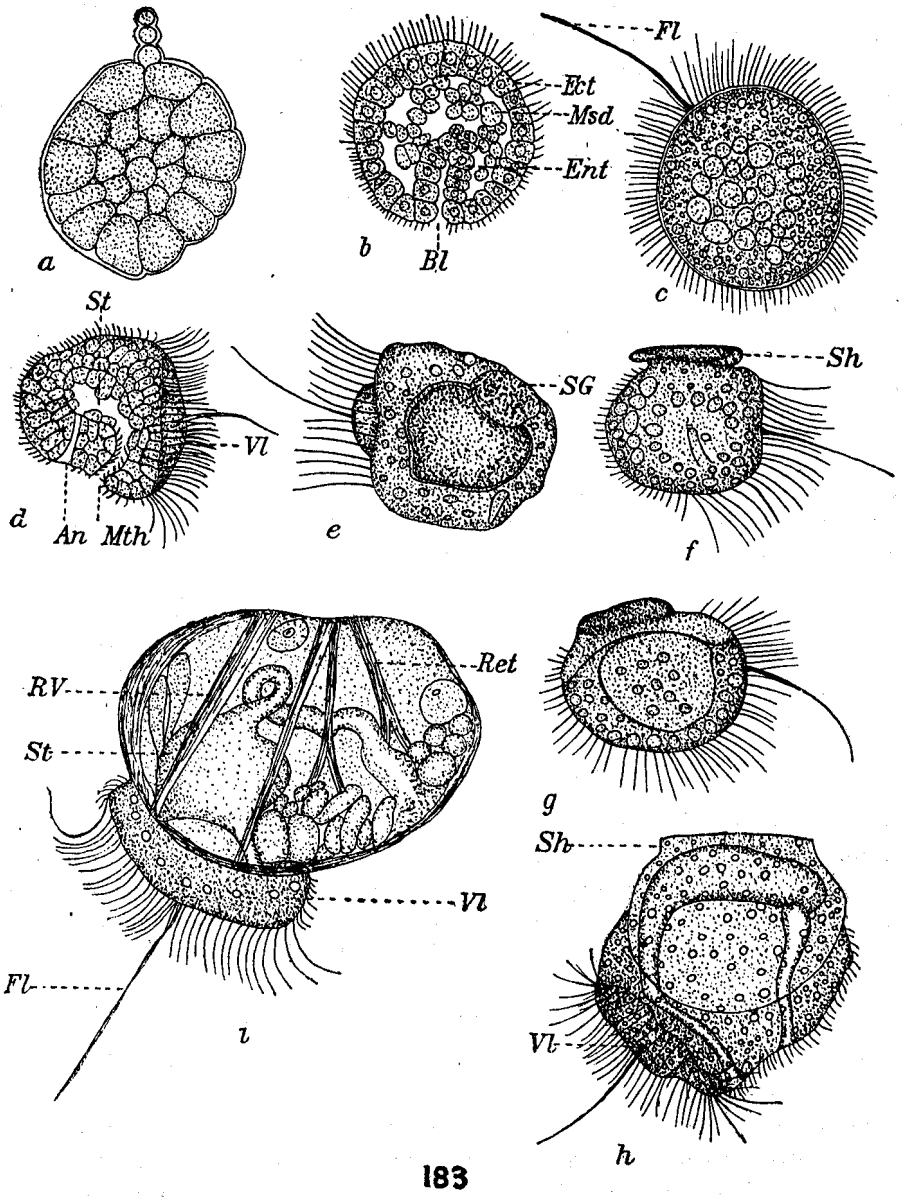
Observations on the living eggs during cleavage and formation of the germ layers would lead to the conclusions that the ectoderm arises from the cleavage of the first micromeres formed, the entoderm from an invagination of the micromeres that come to lie in the region of the vegetative pole, and the mesoderm from the macromere that is ultimately surrounded by the micromeral cells.

DEVELOPMENT OF THE TROCHOPHORE LARVA.

When the developing Mytilus larva has reached the age of about 20 hours, it begins to enter on a stage very characteristic of the free-swimming larvæ of the Lamellibranchia and which so closely resembles the trochophore larva of the Annelida that it has been designated by the same name. The cilia, already weakly developed over the entire surface of the larva, become very prominent. The body gradually elongates and at the anterior pole, just in front of the mouth, a zone of very large cilia is formed which encircles the apical plate. The similarity to the annelidan trochophore is still further emphasized by the flexible flagellum that protrudes from the center of the apical plate, as shown in figure of embryo 42 hours old (fig. 183*d*). At this stage the larvæ become very active swimmers. The flagellum is carried forward and appears to serve as a tactile organ, while the body cilia beat with the effective stroke backward in such a way as to drive the larva forward with a spiral, clockwise motion.

The fate of the blastopore could not be determined.. It apparently disappears in the region later occupied by the proctadeum. At about the fortieth hour of development the digestive tract appears in well-defined form (fig. 183*d*). The stomadeum arises as an invagination of the ectoderm just behind the apical plate and is lined with well-developed cilia which beat with the effective stroke inward. It connects with the anterior end of the stomach. The stomach, when it first appears, has an oval form and is lined with large cells. At the same time the stomadeum is formed the proctadeum arises a short distance behind the mouth and connects with the posterior region of the stomach.

The shell gland is observed, immediately following the formation of the digestive tract, as a thickened portion of the ectoderm in the posterior dorsal region (fig. 183*e*, *SG*). The cells are glandular in character and continue to grow anteriorly until they cover the mid-dorsal line. Two or three hours later the beginning of the embryonic shell is visible as a thin integument over the dorsal surface of the gland (fig. 183*f*, *Sh*). When first secreted it is unpaired, but as growth continues over the sides of the larva a median dorsal dividing line is formed which separates the shell into right and left valves (fig. 183h, *Sh*). This line of division corresponds to the hinge line of the adult shell. During the next few hours the growth of the shell is the most conspicuous change observed in the larva. At the age of 69 hours the valves are almost large enough to inclose the fleshy parts completely (fig. 183*i*).



183

a. Optical section of embryo 4 hours old. First polar body has divided making a total of three polar cells which still adhere to embryo. Macromeres shown inclosed within the blastula (*Ma* in fig. 182*l*) have multiplied into smaller cells which more or less fill the segmentation cavity. Cilia, too fine to be shown in the drawing, are developed and embryo begins to rotate slowly.

b. Optical section of embryo 20 hours old, showing formation of gastrula and origin of germ layers. Epibolic process of gastrulation shown in fig. 182, *h* and *l*, now becomes typical embolic process which results in formation of entoderm, *Ent*, and a blastophore, *Bl*. *Ect* is ectoderm; the mesoderm cells, *Msd*, which are scattered throughout the segmentation cavity, are derived from the macromeres originally inclosed by epibolic process. Cilia are well developed and trochophore larva swims about actively.

c. Trochophore larva 24 hours old, showing flagellum, *Fl*.

d. Trochopore larva 42 hours old, showing formation of digestive tract and apical plate. *An*, anus or proctadeum; *Mth*, mouth or stomadeum; *St*, stomach; *Vl*, apical plate, anlarge of velum.

e. Trochophore larva 45 hours old, showing shell gland, *SG*.

f. Trochophore larva 48 hours old, showing first formation of shell.

g. Another larva 48 hours old, showing further growth of shell.

h. Trochophore larva 69 hours old, showing straight hinge shell, *Sh*; anlage of velum, *Vl*; and digestive tract.

i. Trochophore larva 5 days old with well-developed velum, *Vl*, and retractor muscle fibres, *RV*; *Fl*, flagellum; *St*, stomach. Actual size of lavra 91.4 by 68.5 microns.

Jackson (1888) observed that in the oyster this first formed shell was strikingly different from that which immediately succeeds it and which is retained throughout the rest of its life. It is different in form, composition, and histological structure and covers different organic soft parts. He considered it to be the homologue of the protoconch of cephalous mollusks and the periconch of Dentalium and has named it therefore the *prodissoconch* (early double shell). For the adult double shell, which is believed to be homologous with the adult single shell of cephalous mollusks, he has suggested the name *dissoconch* (double shell). The age at which the dissoconch begins to form could not be determined by the author, for it was impossible to keep larvæ growing normally in the laboratory for more than five days. Specimens showing the developing dissoconchs had to be collected from the open sea, where it was impossible to estimate their age with any degree of accuracy.

The velum becomes the organ of locomotion when the prodissoconch incloses the body. It is formed from the apical plate with its encircling zone of cilia and the surrounding tissue. It keeps its location in the anterior region, where it grows relatively very large. Retractor muscle fibers, which have their origin in the dorsal region of the valves, are inserted into the velum and provide for the contraction and withdrawal of the organ into the cavity between the valves (fig. 183*i*, *RV*, p. 193). When fully protruded, the velum projects laterally, considerably beyond the margins of the shell, especially when the valves are nearly closed. Its large, vibrating cilia make it a powerful locomotor organ, by means of which the larva is able to swim with great rapidity in any direction or to creep on solid surfaces under the water. The velum is also highly sensitive and may be withdrawn with a sudden jerk the instant it is touched by a foreign object.

TRANSITION TO THE ADULT.

The metamorphosis of the larva into the adult is characterized by the degeneration of the velum, which is the most prominent organ of the trochophore stage, a marked advance in the number and complexity of the internal organs, and a decided change in the external form of the animal. In describing this transition the development of the organs will be considered separately as nearly as possible in the order in which they appear.

MANTLE.

The mantle has its origin in the shell gland which first grows to cover the whole dorsal surface of the trochophore larva. This is indicated by the extent of the prodissoconch shell shown in figure 183, *e* to *g* (p. 193). Lateral folds of the shell gland are then formed, which grow downward as the right and left mantle lobes. These develop so rapidly that before the end of the trochophore stage is reached they come to envelop the entire body except when the velum is extended. The result is a decided change in the shape of the animal from a cylindrical to a laterally compressed form (fig. 183, *e* to *i*, p, 193).

SHELL.

The origin and development of the embryonic cuticular shell, or prodissoconch, have been described above. Later the calcareous, prismatic shell, or dissoconch, which is characteristic of the adult mussel, develops. It begins as a limy glandular secretion from the mantle that is deposited in two centers symmetrically placed on the right and

left sides of the body, where they may be seen lateral to the stomach and inside the prodissoconch at the stage when the larva has attained a length of 0.274 mm. (fig. 184, *Dis*, p. 197). The dissoconch continues to grow rapidly in size by further deposition of calcareous matter. By the time the young mussel has reached a length of 0.512 mm. the prismatic shell can be seen extending far beyond the limits of the prodissoconch (fig. 187, *Dis*, p. 198). At this stage the form of the developing mussel is undergoing a radical change from the more or less circular, straight hinge-line embryonic shell to the triangular ovate form of the adult (figs. 187 and 188, p. 198). This is accomplished by growth taking place most rapidly in the ventral and posterior directions. The prodissoconch persists as the covering, periostracum, of the umbones and is shown in its final position in the 0.72 mm. stage (fig. 188, *Pds*).

ALIMENTARY ORGANS.

In the trochophore larva it has been shown that the œsophagus is large and leads from the posterior border of the velum to the stomach. The intestine is short and straight, leading directly from the posterior end of the stomach to the anus, which, at this stage, is located a short distance behind the oral opening. During the transition from the larva to the adult the intestine increases in length, which results, first, in a bending to the left with the formation of a loop. The portion anterior to the loop grows directly backward to form the direct intestine, while the loop continues to lengthen in the anterior direction on the left side of the stomach until it reaches the œsophagus. This results in the formation of the recurrent and the terminal portions of the intestine (fig. 188, *RI* and *TI*, p. 198).

When the larva is about 0.27 mm. long the liver appears as a pair of diverticula composed of large, loosely aggregated endodermal cells from the anterior lateral walls of the stomach. In a short time they become tinged with a brownish pigment, which is characteristic of the gland and makes it stand out distinctly from the other tissues, (fig. 184, *L*, p. 197). By the time the embryo has attained a length of 0.72 mm. the liver tissue has grown to envelop the stomach completely (fig. 188, *St*).

The labial palps, to all appearances in total preparations, are developed the same way in Mytilus as Meisenheimer (1901) observed them in *Dreissensia polymorpha*. They arise from the cerebral pit, after the fundaments of the cerebral ganglia have been laid down, by a flattening of the tissue into two lateral bands of ciliated epithelium above and at the sides of the mouth (fig. 187, *LP*, p. 198). From these, the superior and inferior palps are developed by growth from the upper and lower edges, respectively.

MUSCLES.

As the end of the larval period approaches the various systems of muscles, characteristic of the adult, develop in rapid succession. According to Wilson (1887) the pallial muscles appear first as a band of considerable width running round the entire margin of the valves before the embryo is 0.134 mm. long, or about 12 days old. Then the anterior adductor muscle is formed from a group of large mesoblast cells which appear in the anterior region (fig. 184, *AAd*, p. 197). This is followed immediately by the development of the posterior adductor muscle from a similar group of mesoblast cells in the posterior dorsal region (fig. 184, *PAd*). At this stage the anterior adductor is

much larger than the posterior adductor muscle, but as development proceeds it becomes narrower and finally much smaller than the posterior adductor muscle.

The foot, which is a muscular glandular organ, appears next as a hollow outgrowth of ectodermal cells into which there grows a large mass of mesodermal tissue from immediately behind the velum (fig. 185, *Ft*, p. 197). At this stage of development specimens are 0.36 mm. long and show three or four gill papillæ. In its early appearance the foot is wedge-shaped, but as growth continues it becomes long, slender, and highly contractile, and is covered with fine cilia (figs. 187 and 188, *Ft*, p. 198). During this development a deep invagination occurs on the posterior ventral side of the foot, which results in the formation of the byssus gland (fig. 188, *ByT*).

As soon as the foot begins to take on form the posterior retractor muscle of the foot and byssus can be seen running from the base of the foot back over the posterior adductor muscle to the shell where it is inserted (figs. 185 and 186, *PRet*). At this stage the young mussel has attained a length of 0.385 mm.

The anterior retractor muscle of the foot and byssus is the last one developed. The smallest specimen in which it was observed was 0.512 mm. long (fig. 187, *ARet*).

GILLS.

The development of the gills was worked out first by Lacaze-Duthiers (1856) and more recently by Rice (1908). According to these investigators a papilla arises on each side of the body between the mantle and median visceral mass when the larva is about 0.3 mm. long, or approximately at the stage shown in figure 184. New papillæ arise behind these in succession and grow downward to form the branchial filaments (figs. 185–188, *BrF*). The free ends of the filaments are thickened, and as they increase in number the anterior and posterior faces of the succeeding swollen tips fuse together making a continuous membrane of the sheet of filaments. As the filaments continue to grow they are reflected inward to form the ascending lamellar leaf. At the same time interfilamentar junctions are developed by the interlocking of some specially long cilia which hold the adjacent filaments together firmly. Immediately following this stage, in fact before the ascending lamella is well formed, there arises, just outside and parallel with the first series, a similar row of papillæ which grow downward to form the filaments of the descending lamella of the outer gill. As growth continues they bend outward and are reflected upward to produce the ascending lamella of the outer gill. The outer branchial filaments begin to appear when the mussel is about 1.4 mm. long and possesses 20 of the inner gill filaments. In specimens that had reached a length of 1.6 mm. Rice (1908) found 25 filaments in the inner gill and 15 in the outer one.

KIDNEY.

The first sign of the kidney is a mass of small mesodermal cells immediately in front of the posterior adductor muscle in specimens 0.36 mm. long (fig. 185, *K*, p. 197). The anterior end of the mass grows forward, finally forming a pair of longitudinal canals which lie on either side of the body at the roots of the gills (fig. 188, *K*).

NERVOUS SYSTEM.

The ganglionic centers arise independently from thickenings of the ectoderm and become connected later by commissural fibers which grow out from them. Wilson

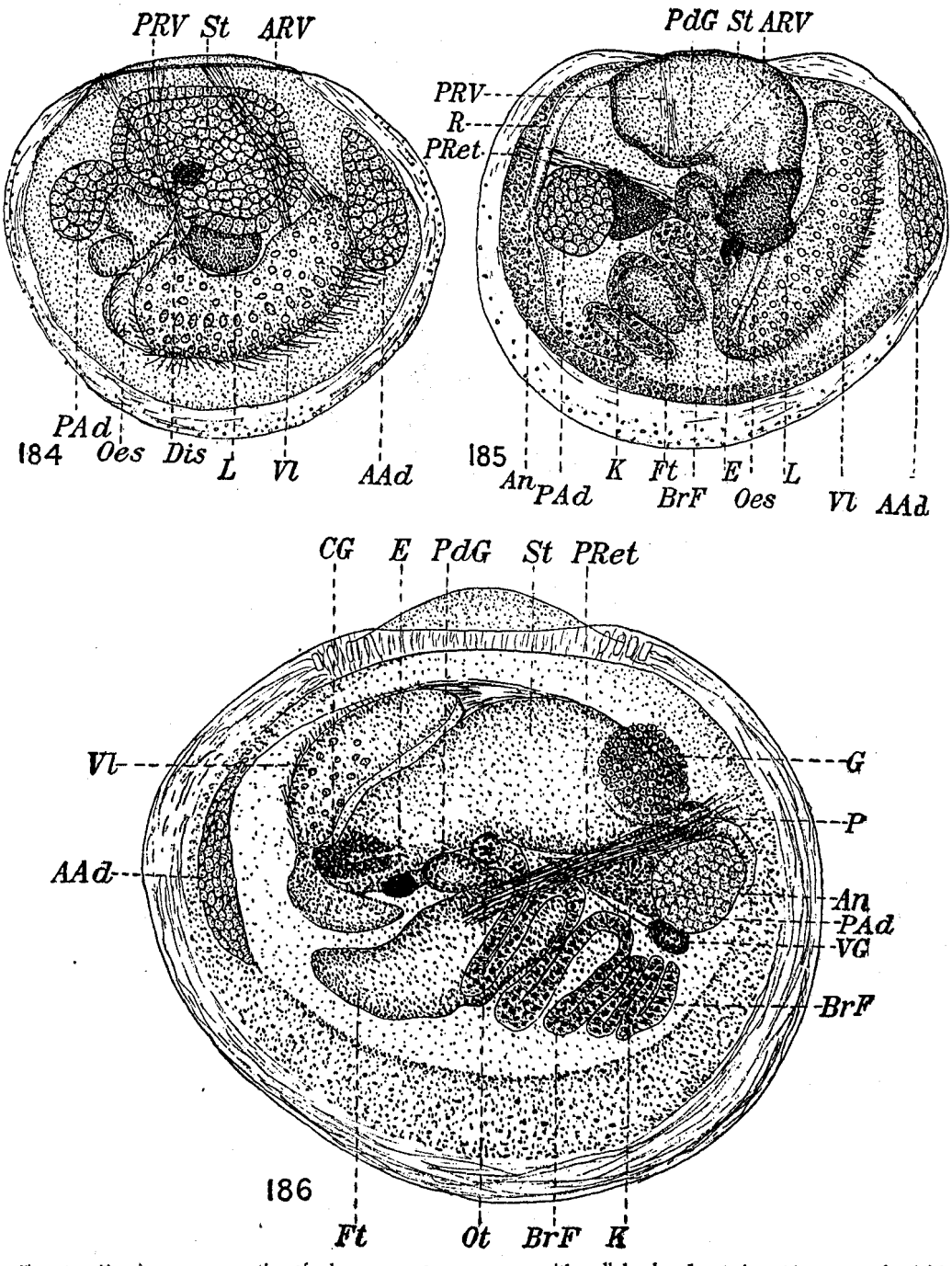
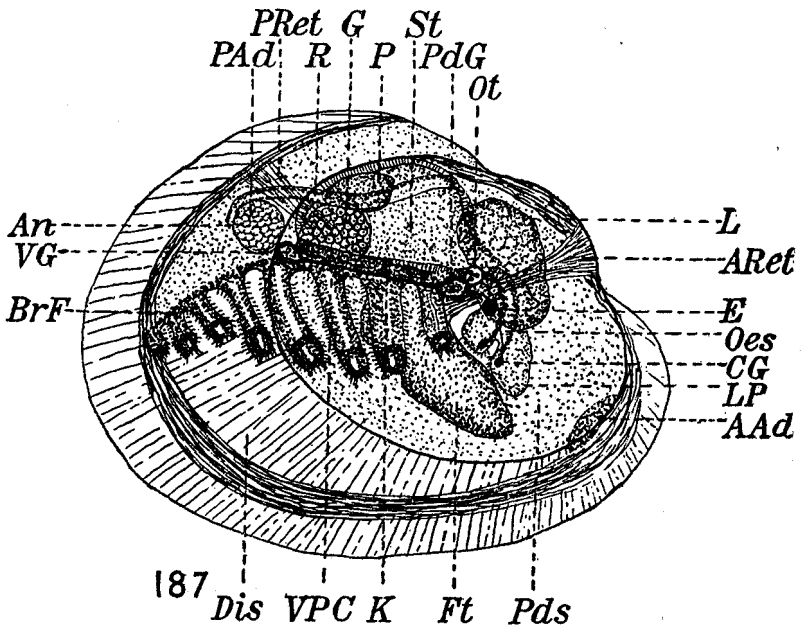


FIG. 184.—Transparent preparation of a larva, 0.274 by 0.260 mm., with well-developed anterior adductor muscle, *AAd*, and posterior adductor muscle, *PAd*. Liver, *L*, and prismatic cell or dissoconch, *Dis*, just appearing. *ARV*, anterior retractor muscle of velum; *Oes*, œsophagus; *PRV*, posterior retractor muscle of velum; *St*, stomach; *Vl*, velum.

FIG. 185.—Transparent preparation of a larva, 0.360 by 0.260 mm., showing first appearance of foot, *Ft*; four branchial filaments, *BrF*; eye, *E*; pedal ganglion, *PdG*; posterior retractor muscle of foot and byssus, *PRet*; and kidney, *K*. *An*, anus; *R*, rectum; other abbreviations same as in fig 184.

FIG. 186.—Transparent preparation of a larva, 0.385 by 0.329 mm., showing first appearance of cerebral ganglion, *CG*; visceral ganglion, *VG*; otocyst, *Ot*; pericardium, *P*; and genital gland, *G*. The velum is degenerating, the anterior adductor muscle is reduced in relative size, and the foot has undergone considerable growth. Other abbreviations same as in figs. 184 and 185.



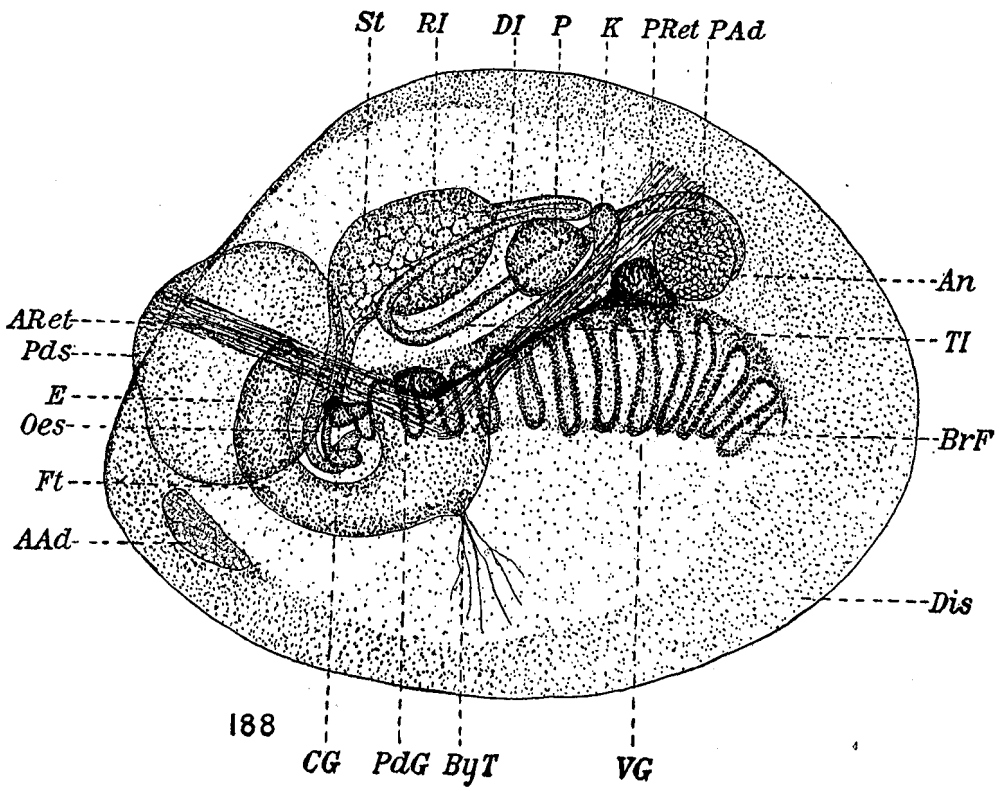


FIG. 187.—Transparent preparation of a young mussel showing relation of prodissoconch, *Pds*, or larval shell, to dissoconch, *Dis*, or adult shell. Anterior retractor muscle, *ARet*, beginning of the labial palps, *LP*, and commissural nerve, *VPC*, appear at this stage. The velum has degenerated and disappeared. Other abbreviations same as in figs. 185 and 186.

FIG. 188.—Transparent preparation of a young mussel, 0.72 mm. long, showing the prodissoconch, *Pds*, which is destined to cover the umbo; the well-developed liver which has come to envelop the stomach, *St*, completely; the looping of the intestine to form the direct intestine, *DI*, the recurrent intestine, *RI*, and the terminal intestine, *TI*. Byssus threads, *ByT*, extending from byssal gland, are present for the first time, and the kidney, *K*, pericardium, *P*, and gills, *BrF*, show considerable advance in development over the previous stage figured. Other abbreviations same as in figs. 185, 186, and 187.

(1887) observed that the cerebral ganglion is the first to be formed in the trochophore larva at the base of the velum in the cerebral pit. Next in order the pedal ganglion is formed. It is readily distinguished as a large group of cells situated at the base of the anterior edge of the developing foot in specimens 0.36 mm. long (fig. 185, *PdG*, p. 197). The visceral ganglion appears later on the anterior ventral edge of the posterior adductor muscle, where it is readily seen in mussels 0.385 mm. long (fig. 186, *VG*, p. 197). At the same time a commissural nerve can be seen growing forward from the visceral ganglion. In specimens 0.512 mm. long commissures are completely established between the visceral and pedal ganglia and between the cerebral and pedal ganglia (fig. 187, p. 198). The direct connection between the visceral and pedal ganglia is soon lost, however, for the commissural nerve grows forward to terminate in the mid region of the cerebropedal commissure which is the adult condition (fig. 163, p. 175).

SENSE ORGANS.

A pair of direction eyes appears at the time the first gill papillæ are formed. The position they occupy corresponds to what will be the base of the first anterior inner gill filament. They are formed from a cuplike invagination of ectodermal cells which later become filled with a mass of dark brown granules that make the eyes appear as conspicuous dark round spots in specimens rendered transparent (figs. 185 and 186, *E*, p. 197).

Shortly after the eyes are developed a pair of otocysts arise as ectodermal invaginations just dorsal to the eyes. The invagination proceeds backward to a position where the capsules with their contained otoliths lie dorsal to the pedal ganglion (fig. 186, *Ot*). As growth of the animal continues the pedal ganglion shifts backward, leaving the otocyst inclosed in the angle formed by the union of the cerebropedal and cerebrovisceral commissures (fig. 163, *Ot*, p. 175).

The osphradium and the abdominal and pallial sense organs are clearly modifications of the body epithelium, but at just what period the transition takes place was not determined.

PERICARDIUM.

The pericardium is first seen when the young mussel reaches a length of 0.385 mm. It arises from a mass of mesodermal cells around the terminal intestine just dorsal to the posterior adductor muscle (fig. 186, *P*, p. 197). As the intestine lengthens, the pericardium migrates forward to the mid-dorsal region of the body (figs. 187 and 188, *P*, p. 198). Pulsations of the heart were noted by Wilson (1887) as first visible in embryos 0.65 mm. long, possessing 10 or 11 gill papillæ.

GENITAL ORGANS.

The genital organs begin to form after the animal has almost completed its metamorphosis. According to the author's assumption, based on the observations of Ziegler (1885) on *Cyclas cornea*, the paired mass of mesodermal cells, which appears just dorsal and anterior to the posterior adductor muscle, in close relation to the pericardium when the embryo is 0.385 mm. long, is the forerunner of the reproductive system (fig. 186, *G*, p. 197). This position corresponds to the external opening of the genital system in the adult. At this stage the further course of development from the cell group was lost. In the next stage of the author's series, which was 0.72 mm. long, no trace of the cell groups could

be seen in total preparations rendered transparent, which led to the conclusion that in the interval between the 0.512 mm. and the 0.72 mm. stages a sudden change in the activity of these cells occurs which results in a rapid proliferation to form the series of reproductive canals that ramify throughout the body tissue. This latter condition was observed in sections of specimens 1 mm. long.

The age at which the various organs appear during the later metamorphosis can be stated only approximately, since it was impossible to carry normally developing embryos beyond the first week. All the stages represented beyond figure 183*i* (p. 193) were drawn from specimens [3] collected in Casco Bay near Harpswell, Me., during the month of August, which offers no clue as to age, since the reproductive process is more or less continuous throughout the summer. Matthews (1913), however, was able to rear mussel larvæ in the laboratory by feeding them on cultures of Nitzachia, and she succeeded in keeping them alive for months. Metamorphosis in these artificially reared mussels appears to have taken place more rapidly in proportion to increase in size than in normally grown specimens. The artificially reared larvæ, for example, measured 0.31 by 0.24 mm. when at the five-gill filament stage, whereas normal larvæ of the same stage measure 0.385 by 0.320 mm. On the basis of Matthews's observations it is probable that the stage represented in figure 184 (p. 197) is approximately 6 weeks old; that in figure 186 (p. 197), 2 months old; while that in figure 188 (p. 198) is not more than 10 weeks old.

GROWTH.

The rate of growth which takes place in the mussel after it reaches the attachment stage depends upon several factors, the chief one of which is abundance of food. If food is scarce, growth is retarded regardless of all other conditions. On the other hand, if diatoms, Protozoa, and spores of algæ are abundant in the water which flows over the beds and at the same time mud, sand, and filamentous algæ are absent, growth will take place rapidly. These conditions are further influenced by the rate and volume of the currents flowing over the beds and by the length of time the mussels are exposed to the air during each tide. Large volumes of water moving slowly supply food most advantageously to the mollusk, and where the beds are not exposed the food is continuously brought to the shellfish without interruption. For this reason the largest and best mussels are found in beds where the water covers them to a depth of from 6 to 15 feet.

Salinity of the water is thought by some observers to influence the rate of growth. Brandt (1897) noted that in Kielwight the mussel grows to a length of 4½ inches, while in the Gulf of Bothnia, where the salinity of the water is less, the mussel only attains a size of about 1 inch. In the Kaiser Wilhelm Canal, where the salinity of the water decreases from east to west, he found that the ripe mussels in the fresher parts were only about half the size of those growing in the saltier regions.

Under ideal conditions the mussel will increase about an inch in length annually for the first two or three years, and then the rate of growth gradually diminishes. Mussels, however, do not frequently find such situations, so that the average rate of growth as actually found on the natural beds is much less. Ordinarily the time required for the shellfish to attain a length of 3 inches is five to seven years.

[3] The author is indebted to Dr. Edward L. Rice, of Ohio Wesleyan University, for these specimens.

Williamson (1907) made observations on the growth of some mussels which he kept in the laboratory for one to two years. He divided them into three sets, according to size, and designated them as A, B, and C. Lot A consisted of individuals 0.3 inch long, lot B of specimens 1 inch in length, and those of lot C measured about 1.5 inches in extent. Individuals of the A group, on the average, doubled their length during the first year, but owing to the artificial conditions they assumed a peculiar form, which was described roughly as barrel-shaped. At the end of the second year the increase in size was very slight. The greatest growth observed during the entire period was three-eighths inch; the least, one-eighth inch. Lot B gained from one-sixteenth to five-sixteenths inch the first year; at the end of the second year the total gain in length was from one-eighth to three-eighths inch. Lot C did least well of the three. During the two years five out of the seven specimens died. Of the remaining two, one showed an increase of one-eighth inch in length, while the other exhibited no growth at all.

The above experiments were performed under such artificial conditions that the results appear to be of little value. In order to find out the actual rate of growth under normal conditions, the author selected five groups of mussels which were located in different environments and situated where they were least likely to be disturbed. Five specimens were selected from each group and measured for three successive summers. During this period two of the experimental groups disappeared. The three remaining ones, however, represent a variety of situations and show some interesting results.

Table 1 shows the record of specimens kept on Pine Island, Woods Hole, Mass. They were firmly attached by byssal threads to a rocky bottom which was kept perfectly free from mud by a very swift tidal current that swept over it. The shellfish were so situated that they were exposed at low tide for a period of from two to three hours daily.

TABLE 1.—RATE OF GROWTH OF MUSSELS ON PINE ISLAND, WOODS HOLE, MASS., IN MILLIMETERS.

Number.	1910		1911		1912		Average per year.	
	Length.	Height.	Length.	Height.	Length.	Height.	Length.	Height.
1	47.2	27.2	49	27.5	51	28	1.9	0.4
2	38	20.5	44	22	46	23	4	1.2
3	56	31	63	32.5	65	33	4.5	1
4	50.5	25	54	26	56.3	26.1	2.9	.5
5	48	24	50.3	24.5	52.8	24.8	2.4	.4
Total average growth per year							3.1	.7

Table 2 represents the growth of mussels which were attached to one of the piles of the Government wharf at Woods Hole, Mass. They occupied a position slightly below the level of low-tide mark and were exposed only at very low tides. A moderately strong current of water which was rich in food materials flowed over them. Slack water prevailed for about three hours each day. In this situation it will be observed the mussels grew more than twice as fast as those on Pine Island.

TABLE 2.—RATE OF GROWTH OF MUSSELS ON WHARF PILE, WOODS HOLE, MASS., IN MILLIMETERS.

Number.	1910		1911		1912		Average per year.	
	Length.	Height.	Length.	Height.	Length.	Height.	Length.	Height.
1	63	36	69.5	36.8	72.9	37.5	4.9	0.7
2	50	30.8	61.7	34.5	66.6	35.4	8.3	2.3
3	67	34.7	77.5	39	84.1	40.6	8.5	2.9
4	64.5	36.1	67.6	37.5	72.2	39.3	3.8	1.6
5	52	28	65.5	31	73	33.8	10.5	2.9
Total average growth per year							7.2	2.1

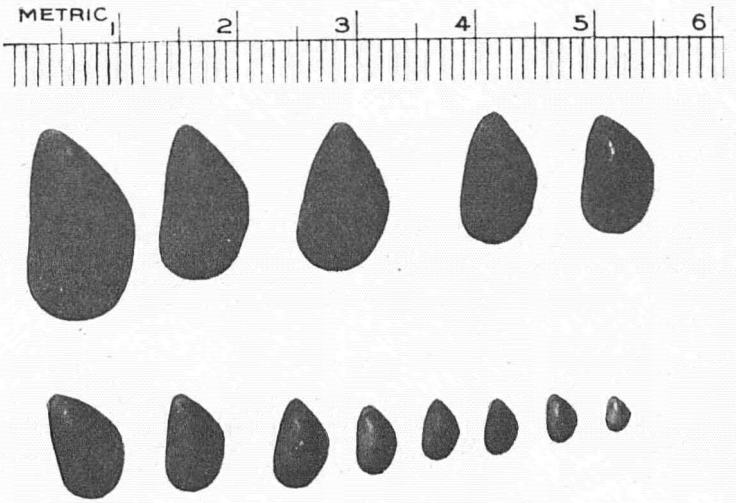
Table 3 indicates the rate of growth of mussels on a mud bottom at the mouth of Menemsha Pond, Marthas Vineyard, Mass. A rather strong tidal current of water, rich in food matter, swept back and forth over them with but a few minutes of slack water prevailing at each turn of the tide. They were exposed only when the tides were extremely low. Algæ and eelgrass grew about them to considerable extent, but they were at no time covered with the vegetation. In this situation growth took place at about three times the rate of that in the Pine Island mussels.

TABLE 3.—RATE OF GROWTH OF MUSSELS IN MENEMSHA POND, MARTHAS VINEYARD, MASS., IN MILLIMETERS.

Number.	1910		1911		1912		Average per year.	
	Length.	Height.	Length.	Height.	Length.	Height.	Length.	Height.
1	71.5	35	80	40	89.5	41	9	3
2	72.5	34.8	81.5	39.7	89.7	41.1	8.6	3.1
3	78	35	83	36.1	90	38	6	1.5
4	67.2	32.5	76.3	37	82.4	39.2	7.6	3.3
5	61.3	31	71	34.8	79	36.7	8.9	2.9
Total average growth per year							8.6	2.7

Comparison of these results with those of Williamson (1907) show that they are almost identical. The least amount of growth observed, 4 mm. or one-seventh inch, compares favorably with Williamson's one-eighth inch minimum increase, while the 10.5 mm., or nearly seven-sixteenths inch, compares well with his three-eighths inch maximum growth.

These results, however, should not be taken to mean that the rate of growth of the sea mussel is from one-fourth to one-half inch per annum, for specimens are often found which show an annual growth of 1 inch or more. It is not uncommon to find mussels 3 inches long on beds which are from three to four years old. Orton (1914) reports that the Plymouth (England) mussels attain a length of from 1⅝ to 2 inches the first year and when 18 months old average 2 inches long. In France, where they are cultivated on wooden frames, the mussels attain a length of from 1¾ to 2 inches in from 12 to 15 months. At Woods Hole, Mass., ropes on fish traps put out in April and taken in the last of August were found covered with young mussels, many of which were nearly three-fourths of an inch long and which could not have been more than 4 months old (fig. 189). Less rapid growth has been found to occur in the older shellfish. Wright (1917), after careful examination, has shown for the mussels of Cardigan Bay that the



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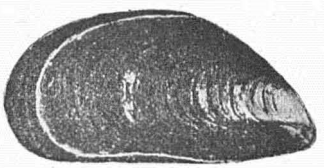

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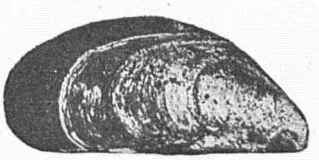

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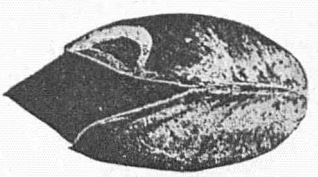

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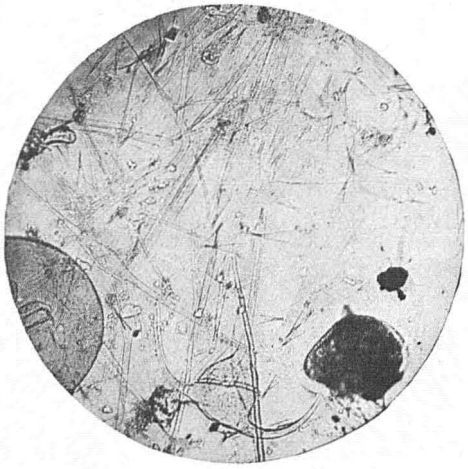
FIG. 189.—Growth stages of young mussels which collected on the rope of a fish trap put out in Buzzards Bay near Woods Hole, Mass., in April and taken up the last week in August. The largest individuals were nearly three-fourths of an inch long and could not have been more than 4 months old.

FIGS. 190 and 191.—Side views of young mussels showing amount of growth, indicated by area outside the light colored growth line, which took place in transplanted specimens at Morecambe, England, during a period of seven months.. (After Bjerkan, 1911.)

FIGS. 192 and 193.—Lateral and dorsal views of an old mussel showing growth, indicated by the new shell area, that was stimulated by transplanting after it had remained almost stationary in size for years. (After Bjerkan, 1911.)



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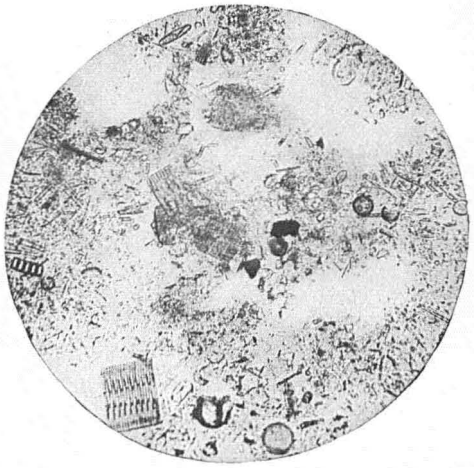

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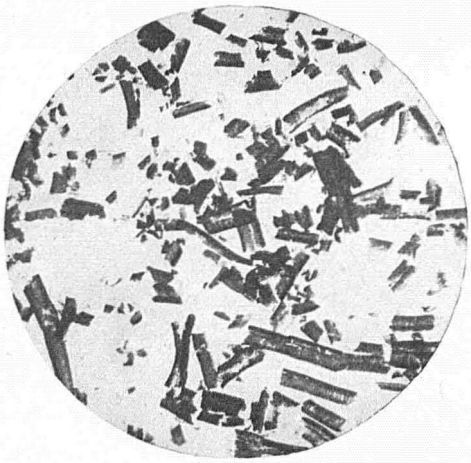

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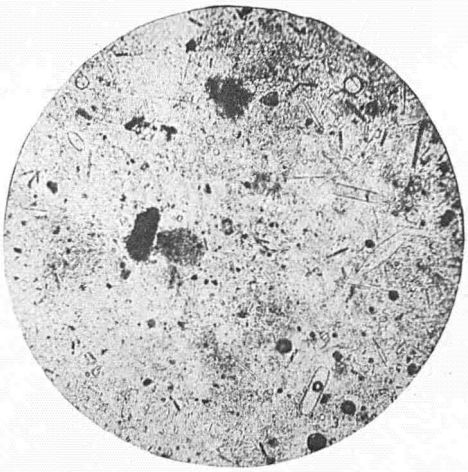

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FIG. 194.—Photomicrograph of a bit of tow material collected over a mussel bed near Woods Hole, Mass.

FIG. 195.—Photomicrograph of a bit of material from the stomach contents of a mussel. Plankton organisms and detritus are present in about equal amounts.

FIG. 196.—Photograph of the fresh fecal discharges of a mussel which was cast out in ribbonlike form. Slightly enlarged.

FIG. 197.—Photomicrograph of the feces of a mussel after the ribbonlike discharges have disintegrated. Note the finely divided state of the material compared with that of the stomach contents.

average increase in length made by 2-inch specimens, between March 30 and November 15 of the same year, is nine-sixteenths of an inch.

It appears, therefore, that in both Europe and America the growth rate of mussels under favorable conditions amounts to 1 inch annually for the first two years, after which the rate decreases gradually in the third year and rapidly thereafter. However, as will be described later, the transplanting of old individuals which for a long time have exhibited no growth to a new environment will cause rapid growth to start again (figs. 192 and 193).

FOOD OF THE SEA MUSSEL AND ITS SIGNIFICANCE.

In a former paper (Field, 1911) the author stated that the food of the mussel consisted of microscopic plants and animals and gave a list of 29 species of diatoms and 9 species of Protozoa which were found in the stomachs of mussels taken in the vicinity of Woods Hole, Mass., In the light of more recent research, which is discussed later in this section, his attention was turned to the fact that the food organisms mentioned do not form more than one-half of the bulk of material actually ingested and that the remaining matter, which was considered not worth reporting, may be of prime importance in the nutrition of the mussel. Other observers also have noted the same conditions in the stomachs of different species of shellfish, and likewise also have disregarded the mud-like contents as of no food value. Lotsy (1893), who examined the stomach contents of oysters, reported that he found in addition to the diatoms "a quantity of decaying organic matter at least equal in amount." Quahogs, soft clams, and ribbed mussels living in the same vicinity as the oysters had the same proportion of things in their stomachs. He asserted, however, that the decaying organic matter went through the alimentary tract unchanged. Moore (1913), discussing the food of the oyster, states:

> It appears that finely divided organic débris, or detritus, which constitutes the major part of the material ingested, plays a more important röle in the oyster diet than has been conceded.

In the stomach of the mussel this detritus is present in relatively the same proportion as has been reported for the oyster. Figure 194 is a photomicrograph of a sample of plankton tow taken over a mussel bed on Pine Island near Woods Hole, Mass., August, 1915. Figure 195 is a photomicrograph of the stomach contents of a mussel on this bed. A comparison of the two pictures shows that the mussel feeds exclusively on fine particles of detritus and the smaller plankton organisms. The larger organisms and those with long spinous processes, as well as the coarser particles of decaying organic matter, are excluded almost entirely from its diet. The feces are discharged in flat ribbonlike segments of varying lengths, which are shown somewhat enlarged in figure 196. After lying on the bottom a few hours they fall apart into the separate fine particles of which they are composed. These are shown in the photomicrograph, figure 197. It reveals the diatom shells empty and, in most cases, finely broken and the detritus ground to a fine powder.

In an attempt to determine the daily quantity of material ingested by the mussel, measurements were made of the volume of feces cast off each day by a group of 3-inch mussels which were thoroughly washed and placed in a trough having a clean, white bottom. Sea water to a depth of 4 inches was kept flowing over the shellfish, but the current was not permitted to become swift enough to carry away the excrement. Each

day for three days the discharged feces were carefully picked up with a pipette and placed in a graduate with a few drops of formalin to prevent decomposition. When the material had settled completely the quantity was read off. The observed result was that 75 mussels discharged a daily average of 3,065 c. mm. of digested matter, or 40.8 c. mm. for each individual. This means that the volume of solid food actually consumed by a 3-inch mussel is not less than 40.8 c. mm. per day and probably is considerably more. This brief series of observations is too limited to form the basis of any conclusions as to the amount, kind, and quantity of food utilized by the mussel, but it suggests a means for solving the problem. What is required is that the observations of this sort be made to cover a long period and be supplemented with chemical analyses of stomach contents and feces to show the quantity of carbon and nitrogen absorbed in a given time.

Whether or not the phytoplankton and detritus constitute the entire food of the mussel we do not know at present, but that there must be an enormous supply of food materials available in the sea is demonstrated in a most striking way to one who witnesses the appearance and rapid growth of a bed of sea mussels on vast areas of the sea bottom, sometimes hundreds of acres in extent. In three years time this shellfish may attain a length of 3 inches and cover the ground to the amount of more than a bushel to the square yard. This phenomenal growth indicates that the mussel must be fed from some great and constant source of food supply for, according to the well-known physical laws, neither matter nor energy can be created or destroyed. The source of the enormous amount of matter and energy represented in a 3-year-old mussel bed presents a most interesting problem upon which much light has been thrown but which, as stated above, has not been completely solved. To appreciate the principles it is necessary to compare the conditions of life as they are found on land and in the sea.

On the land the most conspicuous form of life is vegetation. Almost everywhere the land presents a vast expanse of verdure consisting of green plants of all sizes from the minute algæ to the giant trees. They represent a particularly important organization in that, as distinguished from animals, they have the power of uniting solar energy, water, the common salts of the earth, and gases of the air into the food principles which supply not only the needs of the plants themselves but provide also for the existence of all forms of animal life. The animals are, for the most part, herbivorous. Carnivora are necessarily few in number, for if it were not so they would soon destroy the Herbivora and thus bring about their own extinction. Green plants, therefore, furnish the ultimate source of food supply for terrestrial organisms.

In the ocean, life conditions are found to be quite different, although, as we shall see, the relations are the same in principle as for those on land. Vegetation, however, is as inconspicuous in the sea as it is conspicuous on the land. A fringe of seaweed may be found along the coast and some rather extensive masses of algæ, such as the Sargasso sea, may be found floating in the middle of the ocean; but taken as a whole the ocean is barren of visible vegetation. Under these conditions there can be very few or no animals that correspond to the terrestrial Herbivora. A few fishes may browse on the seaweeds which fringe the shore or float in the water, but they are not numerous. Most of the marine animals commonly seen are carnivorous and voracious beasts of prey. The larger species devour the smaller ones, and these in turn feed upon those smaller

than themselves. Furthermore, animal life swarms in the sea in incredible multitudes. The naturalists of the *Challenger* expedition reported that the waters of the equatorial Pacific contained great banks of pelagic animals through which the vessel sailed. Chiercha wrote that the equatorial calms of the Atlantic are rich beyond all measure in animal life and that the water often looks and feels like coagulated jelly. The *Challenger* expedition reported having encountered banks of copepods a mile thick and on one occasion to have steamed for two days through a dense cloud formed of a single species, one found distributed from the Arctic regions to the Equator. Brooks (1893) states that he cruised for more than two weeks, from Cape Hatteras to the Bahama Islands, surrounded continually, night and day, by a vast army of dark-brown jelly fishes, *Linerges mercutia*, whose dark-brown color made them very conspicuous in the clear water. They were so abundant that nearly every bucketful of water dipped up contained some of them, and at noon, when the sun was overhead, they could be seen through a well in the middle of the vessel drifting by at all depths down to 50 or 60 feet, which was as far as sufficient light would penetrate to make them visible. The area explored covered more than 50,000 square miles, in which they were everywhere in equal abundance. Of the fishes Prof. Brooks says: "Herring swarm like locusts and a herring bank is almost a solid wall." Goode tells of a school of mackerel which was estimated to contain a million barrels and of another which was a windrow of fish half a mile wide and at least 20 miles long. In the bays and estuaries beds of sea mussels are often found covering hundreds of acres of bottom and containing 4,000 to 6,000 bushels to the acre.

How this vast multitude of animals can be supported in a region destitute of visible vegetation has been a problem of investigation since the microscope came into use, and it is interesting to note that the first contribution on the subject was written October 16, 1699, by the old pioneer, Antony van Leeuwenhoek, who ground lenses and made the microscopes with which he opened up a new field of investigation. After observing many of the minute organisms which were discovered in fresh water by means of his microscope, he came to the following conclusion:

> If it be then asked, to what end such exceedingly minute animalcules were created, no answer can readily be given which seems more agreeable to the truth than that, in like manner as we see constantly the bigger kinds of fish feed on the smaller; as, for example, the codfish preys on the haddock and other smaller kinds of fish; the haddock again on the whiting; these on still smaller fishes, and among the rest on shrimps; and shrimps on still more minute fishes; and that this gradually prevails among all the kinds of fish; so that, in a word, the smaller are created to be food for the larger. Again, if we consider the nature of our sea, abounding with fish, yet having nothing at the bottom of it save barren sand stored with various shellfish, yet destitute of every green herb; and if we, moreover, lay it down for a truth that no fish can be supported on water alone, there will not remain a doubt that the smaller fishes are destined by nature to be subsistence for the larger.

It is evident from Leeuwenhoek's illustrations that his use of the expression "smaller fishes" refers to what we now recognize, in general, as plankton, which includes both animal and vegetable organisms, particularly of the groups Protozoa and Protophyta.

Peck (1896), in his splendid paper on The Sources of Marine Food, gives us an excellent example of the food relations described by Leeuwenhoek. Reporting on the stomach contents of the squeteague, he says:

> On the morning of July 23 there was taken a large specimen whose stomach contained an adult herring. In the stomach of the herring were found two young scup (besides many small crustacea), and

in the stomach of one of these scup were found copepods, while in the alimentary tract of these last one could identify one or two of the diatoms and an infusorian test among the mass of triturated material which formed its food. This is an instance of the universal rule of this kind of food: The squeteague captures the butterfish or squid, which in turn have fed on young fish, which in their turn have fed upon the more minute crustacea, which finally utilize a microscopic food supply.

These microscopic organisms constitute an unfailing, ultimate food supply and, without it, the larger animals of the ocean, whose chief business is to devour each other, would soon exterminate themselves. It consists of single-celled plants and animals, chief among which are the diatoms and radiolarians. According to Peck these two groups alone may be regarded as the great primary food supply for the larger marine animals. The diatoms, in particular, may be said to constitute the pastures of the sea.

How these minute organisms can support such a large and extensive fauna may be readily understood when their habits are known. In the first place they exist in the ocean in countless myriads. Brandt (1902) describes a haul made in Kiel Bay with a net having a mouth area of 0.1 square meter which was lowered down to a depth of 20 meters and then hauled up. It was found to contain 3,173,000,000 diatoms, 500,000 peridinians, and 15,000 copepods. He estimated that this represented not more than one-third the total number of organisms in the column of water, owing to the escape of the smaller and more abundant species through the pores of the net and the fact that all the water entering the net did not pass out through the pores of the silk. According to his calculation the number of diatoms per liter would be about 6,000,000. Kiel Bay is particularly rich in plankton organisms, so these observations may be taken to represent a maximum value. For a minimum value we may take the observations of Lohman (1903), who examined the water of the Mediterranean Sea off Syracuse, which is poor in plankton. He found that 1 cubic meter of the water contained 2,082,740 Protophyta, 325,510 Protozoa, 17,415 Metazoa, 785,000,000 bacteria. Moore (1907) made careful measurements of the number of diatoms in the waters of Matagorda Bay, Tex., and found from 13,250 to 70,500 to the liter. The west Baltic was found by Hensen to contain about 457,000 diatoms per liter at the time of maximum abundance, and according to Johnstone (1908) the number of diatoms that inhabit the North Sea or the Baltic beneath every square meter of surface is between one and four millions. It is evident, therefore, that they represent the most abundant organisms in the sea, numbering anywhere from thousands to millions per liter of water. They occur in all parts of the world and are more abundant in the temperate than in the tropical seas. They appear in maximum numbers in the spring and fall of the year.

In structure a diatom is a minute, single-celled plant surrounded by a cell wall of cellulose and inclosed in a flinty case which is often most elaborately sculptured. Pelagic forms have thinner shells, and the characteristic ornamentations are less prominent. Some possess organs for suspension, such as buoying vesicles, enlarged flattened surfaces, projecting hairs, lamelliform outgrowths, or secretion of mucilaginous filaments. The outside case is always made up of two valves, one of which fits over the other like the cover of a pill box. The interior of the cell is filled with cytoplasm containing a nucleus usually located in the center. Colored bodies, called chromatophores, are present in the cytoplasmic contents, often as two large plates which lie parallel and extend nearly the whole length of the cell, or as numerous, small, oval bodies like those common in the higher plants. They contain chlorophyl, but the green color is disguised by the

presence of a golden-brown pigment called diatomin. In addition to these structures, one or more conspicuous oil droplets are often visible within the cell.

The function of the chromatophores is a subject that deals with one of the most fundamental principles of marine food supply, for it is through these bodies that the plant is able, in the presence of sunlight, to convert inorganic materials into organic compounds which may be utilized as food.

The chemical elements required for the nourishment of the plant are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, calcium, silicon, iron, and chlorine. If all of these elements were present in the ocean in unlimited quantities there would be no limit to the quantity of plankton organisms that might be produced. The limited presence of a single one of these elements, however, is sufficient to limit plankton production. According to von Leibig's "Law of the Minimum," a plant requires a certain number of foodstuffs if it is to continue to live and grow, and each of these food substances must be present in a certain proportion. If one of them is absent the plant will die; and if it is present in minimal proportion the growth will also be minimal. This will be the case, no matter how abundant the other foodstuffs may be. With the exception of nitrogen, silicon, and phosphorus compounds, the foodstuffs necessary for the support of plants are exceedingly abundant in the sea. The quantity of marine plants, therefore, fluctuates in relation to the proportions of these rarer but indispensable foodstuffs. The water of the warmer seas is lower in its nitrogen content than that of the colder seas, and in accord with these conditions we find a much richer plankton population in the latter region. Brandt (1898) showed that the lakes which Apstein (1896) found richest in plankton also contained the greatest amount of inorganic nitrogen. In the Bay of Kiel, where silicic acid was proportionately the least abundant of the required foodstuffs, Raben (1905) found that the increase and decrease in the number of diatoms ran parallel with the amounts of silicic acid present.

The myriads of diatoms scattered throughout the sea represent so many chemical laboratories in which the solar energy is utilized to combine the air, water, and salts of the sea into the three food principles—proteins, fats, and carbohydrates—upon which all animals are dependent. This is one reason why they have been considered as important for the support of the animals of the sea as the grasses, vegetables, and fruits are for the terrestrial fauna.

Diatoms are peculiar in that many of them possess the power of movement. They may glide slowly over a solid substratum or over moist surfaces which serve as a fulcrum for movement. The direction of motion is usually along a more or less curved path and may be reversed. How the locomotor energy is developed was explained by Siebold in 1849, who demonstrated a streaming movement of external protoplasm which undergoes a periodic reversal of direction. This was shown by the fact that particles of sand or indigo adhering to the upper valve of a fixed diatom are moved alternately backward and forward from one pole to the other. It has more recently been shown by O. Müller that the protoplasm exudes through the polar furrow on each of the valves, streams along the crevice of the raphe to its termination at the median nodule, where each stream returns to the interior, and travels back internally. The result of the movement of these extracellular masses of protoplasm is to create friction against the surrounding media and cause a forward movement of the organism in the opposite direction. The extracellular layer of protoplasm is extremely thin, and if it moves at

a rate of 3 mm. per minute it will produce a velocity of movement of about 1 mm. per minute.

Light has a slight effect on the response of diatoms. In general the chlorophyllous forms appear to be positively phototropic, while the colorless ones are negative. The orienting action, however, is feeble, and the oscillating forms follow irregular paths toward or away from the light. In the presence of light of moderate intensity negative forms creep into the mud.

The minimum temperature which diatoms can withstand varies considerably with the species. Some have been reported to withstand $-200°$ C., but, in general, actively vegetating forms are killed by freezing at -8 to $-10°$ C. In southern Newfoundland, where the Labrador current mingles with the warm water of the Gulf stream, a great mortality of a certain species, *Cosinodiscus radiatus*, has been taking place, for in this region enormous quantities of the dead shells are found covering the bottom.

Reproduction is by means of simple cell division or by the formation of what is called an auxospore. In the first case the nucleus and protoplasm divide into two parts, the valves separate, and a new valve develops within each of the old. The valves, once formed, are fixed in size which determines that each successive generation will become smaller. This constant decrease in size is compensated for by the formation of the auxospore. In doing this the diatom leaves its shell, swells up to the maximum size, and secretes a continuous membrane about itself. Within this there is first formed a single valve, like one of the original ones, and soon after a second one fitting into it. Sometimes the naked protoplast of two cells may escape and fuse together as one, in true sexual union. From the cell thus produced a diatom is either formed at once or after a preliminary division of the protoplast. The rate at which this process takes place varies with the conditions, but, on the whole, we know it must be exceedingly rapid in order to keep almost every part of the sea in the constant condition of a living broth. Being bathed in a uniform medium containing dissolved nourishment and subject to the full benefit of the sunlight without being exposed to extreme changes of temperature, growth and reproduction become so rapid that they pass beyond our powers of conception. As the late Prof. Brooks has written:

> Their vegetative power is wonderful past all expression. Among land plants, corn, which yields seed a hundredfold in a single season, is the emblem of fertility, but it can be shown that a single marine plant, very much smaller than a grain of mustard seed, would fill the whole ocean solid in less than a week if all its descendants were to live. This stupendous fact is almost incredible, but it is capable of rigorous demonstration, and it must be clearly grasped before we can understand the life of the ocean.

This wonderful productive power, together with their chemical composition, show that they occupy an exceedingly important place in the economy of nature. Brandt (1898) analyzed several samples of plankton. One, consisting chiefly of Chaetoceros, gave the following composition: Albumin, 10 to 11.5 per cent; fat, 2.5 per cent; carbohydrate, 21.5 per cent; and ash, 64.5 to 66.0 per cent (50 to 58.5 per cent SiO_2). Another sample, consisting of *Ceratium tripos*, had a very different composition, as follows: Albumin, 13 per cent; fat, 1.3 to 1.5 per cent; carbohydrate, 80.5 to 80.7 per cent; and ash, 5.0. As Brandt points out, these results compare very favorably with those of analyses of land crops.

PERCENTAGE COMPOSITION OF THE DRY SUBSTANCE OF LAND CROPS.

	Protein.	Fat.	Carbo-hydrate.	Ash.
Ordinary meadow hay	8.7	1.7	83.6	5.8
Good meadow hay	13.6	3.2	75.0	8.2
Rye (grain)	12.8	2.3	82.3	2.1
Peas	26.4	2.2	68.2	3.1
Potatoes	8.4	.8	87.2	3.6

Because of their silicious skeletons, the diatoms show a small proportion of protein with a high percentage of ash. Samples, however, containing many such Protozoa as Ceratium will have a composition similar to rye or good meadow hay. It is on this evidence that many persons have concluded that diatoms and, to some extent, such Protozoa as the peridineans, represent the ultimate source of marine food supply. As Moore (1910) has remarked, it is this invisible vegetation of our bays and estuaries which, useless to man in its original state, is annually converted into oyster flesh worth $18,000,000. In fact there is good evidence for believing that the total value of our entire fisheries products is derived, in large measure, from this source. So great is the economic value of this group of plants that it has been made a subject of important investigation by the Governments of many nations, including England, France, Germany, Denmark, and the United States.

The most recent advances in methods for determining quantitatively the available amount of these food organisms in the water, such as are utilized by the oyster, have been made by Moore (1910), who devised a bottle which has a capacity of a little more than a liter and can be filled in such a way as to "inclose a vertical column of the stratum lying between 2 inches and 12 inches above the bottom, and as the currents do not flow over the beds in horizontal strata, but roll over and over, the specimen is regarded as a fair sample of that in which the oysters are bathed." A liter of this sample is concentrated in 10 cc. of water by filtration through sand or precipitation in an Erlenmeyer flask after the addition of a little formalin. The filtrate is then agitated and a measured quantity transferred to a Rafter cell, where the organisms are listed and counted by species and a calculation made of the total number of each per liter. Careful measurements of the length, breadth, and thickness of each species are made based on Van Heurch's "c. d. m." (0.01 millimeter) as a unit of measurement, the unit of volume being the cube of this, "cu. c. d. m." (0.000,001 cubic millimeter). By this means a fairly accurate measurement of the actual bulk of the organisms present in a given volume of water can be made.

Using this method in connection with careful measurements of the stomach contents of oysters and the amount of water they are able to filter, Moore (1913) was forced to the surprising conclusion that "the volume of living food is insufficient to account for the actual growth of the oyster, making no allowance for the requirements of the other vital activities." Such investigators as Pütter, Petersen, Blegvad, and Jensen are of the same opinion and claim to have found other equally important sources of food supply for the marine fauna. Pütter (1907 and 1908) maintains that the sea is an immense reservoir of foodstuffs in the form of dissolved organic carbon and nitrogen compounds on which many marine animals actually feed as saprozoic creatures. His investiga-

tions on the metabolism of several marine animals showed that it would be impossible for the plankton organisms that could be consumed to provide the required amount of carbon or nitrogen. He found surprisingly large amounts of organic matter dissolved in the sea water. His results have been checked up by Raben (1915), who found an average of 12.25 mg. of organic combined carbon per liter in the Bay of Kiel, while in water from the Baltic it amounted to 3 mg. per liter. Compared with the amount of organic substance present in the form of living organisms, these results are very high. The total amount of the organic combined carbon in the plankton at Laboe in Kiel Bay was found by Lohman (1908) to vary between 12.7 and 189.8 mg. per 1,000 l. of sea water. As an estimate of the maximum amount of organic matter in the form of plankton that may be found in the ocean, we may refer to the phenomenal haul made in the Bay of Kiel referred to by Brandt (1898), which contained 0.19 mg. of protein, 0.05 mg. of fat, 0.43 mg. of carbohydrate, or a total of 0.67 mg. per liter. Raben (1905), who analyzed water from the same vicinity, found the mean value of organic combined carbon in dissolved form to be 12,250 mg. per 1,000 l., or about 60 times as much as that ordinarily present in the form of plankton organisms and nearly 20 times as much as that present in the plankton when at its maximum. Pütter's view is that the plankton organisms are only of secondary importance in the nutrition of marine animals, just as insects are to insectivorous plants which depend primarily on the photosynthesis of starch to supply their needs. The facts presented by Pütter present some ground for his hypothesis, but the actual utilization of these dissolved organic compounds as food by marine animals remains undemonstrated.

Another great source of marine food supply has been suggested by Petersen (1890), who expressed the idea that the abundance of fish on the Danish coasts was due chiefly to Zostera, which is better known to fishermen as eelgrass. Petersen and Jensen (1911) tried to show that, in all probability, the plants of the eelgrass belt and not the plankton organisms should be regarded as the main sources of the organic matter of the sea bottom in Danish waters. Their reasoning is based on the fact that the quantity of carbon in a series of bottom samples is directly proportional to the amount of Zostera vegetation and not to the quantity of plankton present.

The study was continued in greater detail and published by Jensen in 1914. He showed that the eelgrass plays an important part in the production of organic matter in the sea. In all the Danish waters he found fragments of eelgrass deposited in greater or less quantities, for the most part in very fine particles as detritus. In this detritus he found comparatively few diatom shells. Much of the detritus particles were too small to be identified by the microscope as of eelgrass or plankton origin. By chemical means, however, Jensen was able to determine the source of the organic matter in the sea bottom. He found that the eelgrass cells contain a considerable quantity of starchlike substances known to the chemists as pentosans, whereas those of diatoms are composed mainly of silica and those of peridineans of fairly pure cellulose. By comparing analyses of various bottom samples of organic matter with those of eelgrass and diatoms the following conclusions were reached:

(1) In the more sheltered waters the organic matter of the sea bottom is to a preeminent degree formed by eelgrass. (2) In the more open waters, at least half of the organic matter is probably formed by eelgrass. (3) In the deepest waters the organic matter is probably formed chiefly by the plankton organisms.

Calculations on the production of phytoplankton and eelgrass per square meter of surface have been attempted, but what has been done so far approaches a mere approximation only. In regard to the phytoplankton, Hensen (1887) figured that 1 square meter of surface produces annually 15 to 18 grams of dry organic matter exclusive of the phytoplankton consumed by the surface fauna. The total annual production of phytoplankton he estimated to be 150 grams per 1 square meter. Jensen, by very careful calculations, estimated that in the Danish waters about 100 grams of organic matter per square meter are produced each year by the phytoplankton. For eelgrass the percentage of dry organic matter produced annually per square meter he found to be 1,920, 1,120, and 344 grams in good, moderate, and bad localities, respectively. Eelgrass beds cover about one-seventh of the area studied (between the Skaw at the most northern tip of Denmark and the Baltic Sea), which means that the annual production of eelgrass per square meter of the water as a whole is 120 grams of organic matter. Comparing the production of eelgrass and plankton on a basis of Jensen's calculations we see that eelgrass produces 120 grams of organic matter per square meter, while the plankton produces 100 grams.

Now the question arises, How much of the organic matter from each source is deposited on the sea bottom? Undoubtedly much of the matter of the plankton dissolves following the death of the organisms due to the action of bacteria. Admitting that a portion of the eelgrass material is similarly lost, it is evident that the plankton organisms, with their relatively far greater surface, are in a much higher degree liable to destruction than the eelgrass. Furthermore, a large part of the plankton is devoured by the plankton fauna, which would lead one to believe that but a limited portion of plankton production is deposited on the sea bottom. These calculations are supported by the results of chemical analyses of the organic matter in the sea bottom. Jensen has done this and states his conclusions as follows:

> In the more sheltered waters the organic matter of the sea bottom is derived almost exclusively from the Zostera (eelgrass); in the more open waters it is possible that the plankton organisms may play a not altogether important part as a source of the organic matter of the bottom.

The transformation of nitrogen during the decomposition of eelgrass and its relation to the nitrogen content of the organic matter in the sea bottom was also investigated by Jensen. He found that the green eelgrass is as rich in nitrogen as peas or beans, which contain about 3 per cent. As the eelgrass decomposes the percentage of nitrogen decreases until it is as low as 0.88 per cent, then as decomposition continues it rises again up to 1.39 per cent. Analyses of the organic matter in the sea bottom indicate that the average amount of nitrogen present is 4 per cent. Thus it is evident that the organic substances of the sea bottom contain a greater proportion of nitrogen than the eelgrass.

Why the organic matter in the sea bottom is so much richer in nitrogen than the eelgrass, from which it is formed chiefly, is readily explained by Jensen. As has been shown the amount of nitrogen in the green eelgrass is greater than that in the early stages of decomposition. Later the amount of nitrogen increases, becoming much greater than in the green eelgrass. The diminution in nitrogen during the first stages may be due to the fact that a portion of the nitrogenous protoplasm is dissolved in the sea water as the cells die. The increase in proportion of nitrogen in the final stages of decomposition may be due to two causes—(1) either by the destruction of nonnitroge-

nous substances in the sea bottom to a greater extent than is the case with the nitrogenous matter or (2) by the fixation of inorganic or free nitrogen by bacteria.

It has been established beyond all doubt that nonnitrogenous substances of the sea floor are to a very considerable extent destroyed by bacteria, at least one step in the process being the fermentation of the pentoses. Another is the formation of methane from the fermentation of cellulose. On the other hand, it is probable that the nitrogenous substances are acted upon to a lesser degree, due to the fact that they are comparatively easily transformed into humic compounds, which are less easily destroyed.

It is also possible that the excremental action of the fauna contributes to render the bottom richer in nitrogen. The nitrogenous portion of the bottom is indigestible, while the nonnitrogenous matter contains considerable quantities of digestible pentosans. Hence, when fed upon in the form of detritus by such organisms as mussels and oysters, the nonnitrogenous matter would be removed and the nitrogenous portion returned to the bottom. This was well illustrated by comparing the composition of oyster excrement, which consisted of almost pure detritus, with bottom samples taken at the same place where the oysters were found. The nitrogen of the bottom samples amounted to 0.187 per cent, while that of the excrements was 0.71 per cent.

That nitrogenous matter of the bottom can also be increased by the fixation of inorganic nitrogen through the action of bacteria is likewise probable. The nitrogen may be taken from the ammonia or nitrates dissolved in the water or from the free nitrogen, which is also present in solution. Bacteria such as Azotobacter and Clostridium, which perform this function, are of common occurrence on the bottom, and a considerable amount of nitrogen fixation has been shown to take place where the vegetation is abundant.

In addition to the above sources of nitrogen, it should be mentioned that the fauna itself, by dying and forming detritus, also serves to increase the amount of nitrogen in the sea floor.

A determination of the total quantity of detritus and plankton in sea water was also attempted. Ten-liter samples of sea water from various localities were carefully filtered and the total quantity of detritus and plankton measured. It was first weighed and dried at 100° C. and then weighed again. Samples were also subjected to microscopical examination to determine the amounts of detritus and plankton organisms present. The results were that nearly all the samples showed a greater proportion of detritus than plankton. The weight of the dry matter in the residue varied between 9.6 and 72.3 mg. per 10 l. of sea water. No relation could be shown to exist between the weather conditions and the amount of detritus in the water. The conclusion to be drawn from these results is that sea water is rich in the quantity of detritus it contains.

The next question which arises is, What value does this organic matter of the sea bottom possess as a source of nourishment for the benthos or bottom fauna?

Having assumed that the organic matter of the sea bottom forms a source of nourishment for the majority of the fauna living in and near the bottom, Jensen considered it advisable to investigate the question as to how far suitable nourishment for such fauna can be shown to exist among the substances of which the sea floor is composed. Since eelgrass contributes most of the organic matter of the bottom, it was natural to examine quite closely the chemical composition of this weed. It was found to compare favorably with the composition of the common fodder grasses. Proteinw as

found present to the amount of 7.5 per cent and pentosan to the amount of 8 to 9 per cent. No fat determination was made. When eelgrass is treated with pancreatin, from 23 to 26 per cent of the nitrogen is digested. Since the eelgrass contains 7.5 per cent proteins, of which about one-fourth is digestible by pancreatin, the amount of digestible proteins contained may be put at 1.08 per cent. Decomposed eelgrass contains less nitrogen and is less digestible. For example, black eelgrass (dead) was found to contain 1.39 per cent nitrogen, of which but 6.6 per cent was digestible. These figures should, however, in all probability mainly be taken as minimal.

Experiments on the digestible nitrogenous compounds in the sea bottom brought out the fact that there is only a very small amount of proteins in the bottom which is digestible with pancreatin. In fact, the amount is so small as to be very nearly within the limits of possible error. The analyses for the top layer, however, give such positive results that it is justifiable to conclude that the uppermost layer of the bottom really does contain a certain amount of proteins digestible by pancreatin. In the upper layer from 44 to 68 mg. of digestible proteins per 100 square cm. are found, which means that the amount of digestible proteins per square meter is approximately 5 g.

On the other hand, digestible nonnitrogenous compounds in the sea bottom consist of a fairly considerable amount of material in the form of pentosans, amounting to from 0.3 to 1.0 per cent. This is an important fact, for there is reason to suppose that the bottom fauna is able to digest pentosan. It has been well established that herbivorous animals utilize pentosan as a food, and Biederman and Moritz (1899) showed that gastropods were able to digest pentosan. It is probable, therefore, that bivalves also can digest pentosan and that the considerable amount of pentosan present in the sea bottom besides other possible substances (hemicellulose generally) plays an important part as nonnitrogenous nourishment for a great portion of the bottom fauna.

In support of Jensen's observations, Blegvad (1914) has made an interesting study of the food of the commonest and most widely distributed bottom-inhabiting animals in the various communities of the Danish waters. His report is based on the analysis of stomach contents. Three main sources of nourishment for the bottom fauna of the sea were determined: (1) Plants—fresh growing plants of the benthos formation, chiefly eelgrass which in the Danish waters produces about 8,232,000 kilograms annually. In course of time, this decays and falls to pieces, forming (2) detritus. This includes dead or dying organisms or portions of them, whether vegetable or animal in origin, as are found in suspension (or solution in the sea water) or deposited upon the bottom. Most of this detritus is of eelgrass origin. (3) Animal or carneous food, or the third source, includes all living animals found in the sea, together with their carrion, save where these are to be reckoned as forming part of the detritus as just defined.

The plankton, heretofore considered as of greatest significance, he does not list as an important source of food. Whereas previous observers have emphasized the great importance of plankton, Blegvad emphasizes the importance of detritus. He furthermore questions Pütter's (1908) theory to the effect that the carbon compounds present in solution in the sea water are of very extensive importance as food for certain animals of the bottom fauna. At least it must for the present be regarded as unproved. It is possible, however, that some organisms may live on dissolved organic matter, and so for the sake of convenience Blegvad classifies dissolved organic matter under detritus.

The commonest animal forms in Danish waters are classified into three groups according to their mode of feeding: (1) Herbivores, which include certain gastropods, two echinoderms and some Crustacea. (2) Pure detritus eaters, which comprise all the Lamellibranchia, Holothurians, Sipunculidæ, Cumacea, Diptera larvæ and Ascidiæ, two gastropods, Balanoglossus, Amphioxus, ostracods, Bryozoa, Porifera, and Foraminifera. The great mass of material in the alimentary tracts of these animals is detritus and when analyzed chemically it corresponds to that on the ocean floor. Plankton organisms are only incidentally present. These observations led Blegvad to make the extreme statement: "The living phytoplankton is thus of no importance at all as a food for the bottom fauna." (3) Purely carnivorous animals, including a few Polychæta, some gastropods, some Crustacea, some echinoderms, coelenterates, nemerteans, planarians, and pantopods, constitute the last group. Quite a large number of animals are both carnivores and detritus feeders.

The Danish investigations tend to show the vast importance of detritus as a food for the fauna on the sea bottom. To use Blegvad's words:

> Detritus forms the principal food of nearly all the invertebrate animals of the sea bottom, next in order of importance being plant food from fresh benthos plants. The value of the live phytoplankton in this connection is absolutely minimal, amounting in any case to nothing more than an indirect significance through the medium of the plankton copepods.

This view is given some support by the recent researches of Mitchell (1917), who presents evidence that oysters can utilize fragments of seaweed (*Ulva lactuca*) as food.

That detritus is formed so abundantly in the shallower waters of the ocean and constitutes such an important source of food supply for most of the bottom-inhabiting animals is of great significance in its bearing on the coming science of sea farming. If the investigators of the Danish biological station are right in their conclusions concerning the importance of detritus as food for the benthos fauna, then we shall have to revise our methods of determining the available oyster, mussel, or clam food supply in the waters of a given locality. It also means that the available fields for the cultivation of oysters or other shellfish may be more fertile than we have ever dreamed in the past. The knowledge of the rôle played by detritus in its relation to the benthos fauna helps us to understand better the phenomenal growth which often takes place in many mollusks. For example, many mussel beds are known to yield on an average 2,000 bushels per acre annually, and experiments have shown that 1 bushel of seed clams planted in a barren flat will yield 10 bushels of marketable clams one year later. This serves to show what splendid opportunities for increased food production lie within our reach. Between the plankton organisms and the detritus there is an inexhaustible ultimate food supply which can be quickly and readily converted into a form available for human consumption. A partial solution of the serious problem of increasing the food production of the Nation lies in the appropriation of this vast resource for conversion into mussels, clams, and oysters. Mussels planted in protected situations, where the water currents will bring them an abundance of these materials, will produce flesh food at a rate far in excess of any resource on which we have depended in the past. Cultivating the ocean promises to yield the fisherman far greater returns, with less expense of time and energy, than the farmer is able to derive from the land. Each new discovery in marine biology is making it more clear that for the comfort and economy of the Nation we ought to be doing more in the scientific development of our fisheries.

ENEMIES AND PARASITES.

The sea mussel, as are all the smaller marine species of animals, is preyed upon by a host of enemies. The destructive forces with which it has to compete are so numerous it seems almost incredible that the species can maintain itself so successfully. From the moment the egg is laid to the end of its life, dangers of various sorts threaten it constantly from every side. Inanimate as well as animate forces unite in working toward the destruction of this mollusk. The animate forces which act against the life and welfare of the mussel may be divided into the active enemies, which include the predacious animals, and the passive, which comprise a number of sedentary organisms that intercept the food supply or cause depositions of silt which interfere with the digestive processes or smother the mollusk.

The following account does not by any means include all the enemies of the sea mussel. It serves merely to show some of the tremendous forces with which the species has to contend in order to maintain itself.

INANIMATE DESTRUCTIVE FORCES.

A slight change of current may cause a deposition of sand over the beds which may be acres in extent and smother the mussels out of existence. Some years ago such a wholesale extinction by this agency took place in Menemsha Pond, Marthas Vineyard, Mass. The bed, a photograph of which was published in a previous paper of the author (Field, 1911), was in perfect condition in August, 1911, but when visited in July, 1912, nothing but a barren flat of white sand was visible at low tide. Investigation revealed the presence of the decaying shellfish about 4 inches below the surface. Exposure at low tide to the frost of winter proves fatal to enormous numbers. The young larval mussels succumb to sudden falls of temperature and are often swept up on the shore by winds, waves, and tidal currents to perish by the millions.

ACTIVE ENEMIES.

STARFISH.

The starfish *Asterias forbesii* and *A. vulgaris*, are the arch enemies of the sea mussel. The former species ranges from Massachusetts Bay southward to the Gulf of Mexico and is abundant south of Cape Cod. *A. vulgaris* ranges from North Carolina to Labrador, but is abundant only north of Cape Cod. The starfish feed upon almost any kind of mollusk, but the sea mussel constitutes their favorite food. The method of feeding is to seize the shellfish in such a position that the mouth of the starfish comes to lie opposite the opening of the shell (fig. 203, opp. p. 216). Then by attaching its numerous tube feet to the opposite valves it sets up a constant pull, which in the case of a large starfish has been shown by Schiemenz (1896) to equal more than 2½ pounds. The starfish can rest by shifting its work from one set of muscles to another, while the mussel, relying only on its single set of adductors, becomes exhausted and succumbs to the weaker but tireless pull of the enemy. When the valves open, the starfish turns its stomach inside out and envelops it about the soft parts of the prey and digests them outside its own body. This accomplished the starfish withdraws its stomach and moves on in search of another victim. Young starfish, especially, have voracious

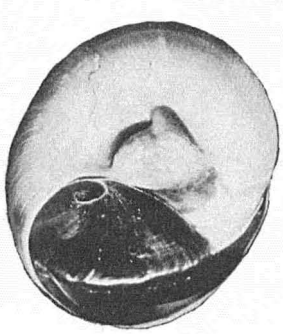
appetites; specimens less than a quarter of an inch in diameter were observed stripping the young mussels, little less than their own size, from wharf piles. Every starfish picked up was found in the act of eating a Mytilus. The larger starfish move back and forth across the mussel beds in regular armies, up and down the wharf piles and rocks where the mollusks grow, feeding on them at a rate which it is difficult to estimate.

The mussel, which heretofore has not been of sufficient commercial value to be cultivated, has escaped the attention of the fisherman who would be the most capable of estimating the depredations of its enemies. For the oyster, however, whose every enemy is watched by the jealous cultivator, we have been able to learn more of the devastating habits of the starfish. In Connecticut waters alone it was estimated in 1888 that this echinoderm destroyed $631,500 worth of oysters after not less than 42,000 bushels of the starfish had been removed from the beds. If mussels are a more favorite food of the starfish, what must be the destruction wrought on the unprotected beds of this shellfish? The answer must be up in the hundreds of thousands of bushels. Mead (1903) states that some mussel beds which had recently disappeared were probably destroyed by starfish. Lebour (1907) states that a whole bed of mussels at the mouth of the river Tyne, England, completely disappeared owing to the ravages of this animal.

DRILLS.

The oyster drill, *Urosalpinx cinerea*, is a small snail commonly found on mussel and oyster beds where it plays havoc with these bivalves, doing damage which undoubtedly amounts to thousands of dollars yearly. So great has been its injury to the oyster beds that the United States Bureau of Fisheries has recently started a special investigation to determine the possibility of protecting the oyster beds from its depredations. T. E. B. Pope, who has been carrying on these investigations for the Bureau, finds that the drills are abundant on the oyster beds where the salinity is above 1.010, and that a single female is capable of producing about 100 young each season. Its method of attack is like that of the winkles, Lunatia and Neverita. With a powerful radula it is capable of drilling holes through shells of almost any thickness, but it prefers to prey upon thin-shelled forms, such as mussels and young oysters. The time required to perforate shells was found by Mr. Pope to be for oysters about 1½ inches long, two days; 2½ inches long, 4 days; 3½ inches long, 6 days; 4 inches and over, 7 days. The perforation is made at no particular point on the shell, but is generally somewhere near the middle of the valve. When completed the proboscis is thrust through the opening to the soft parts on which the snail feeds. One drill was seen to kill five young oysters in succession without taking any rest between its attacks. The author's experiments with drills kept with mussels in a trough of running sea water demonstrated that the time required for the snail to perforate the shell of a mussel less than an inch long was about 18 hours, while for large ones the time varied from 24 to 36 hours. Figure 201 (opp. p. 216) shows a drill and a shell which was perforated by it.

The dog-whelk, *Purpura lapillus*, is another species of drill similar in appearance to Urosalpinx, but somewhat larger and more powerful. Its favorite food is the sea mussel, which it attacks even more voraciously than does the oyster drill. It does not cover such a wide area as the latter species, being confined to the rocky shallow waters; consequently it is limited to doing much less harm than the oyster drill, which ranges over



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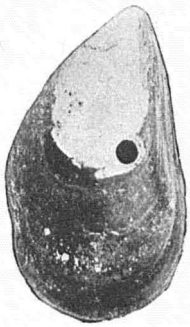

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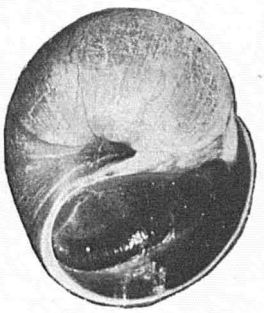

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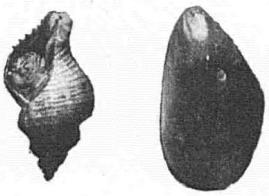

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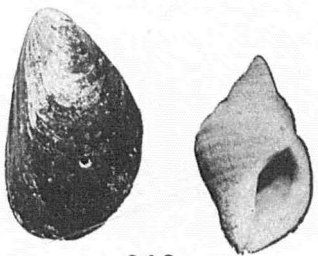

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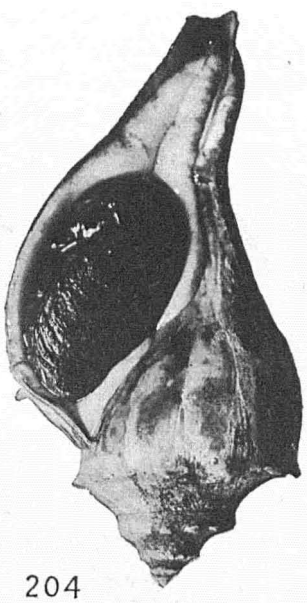

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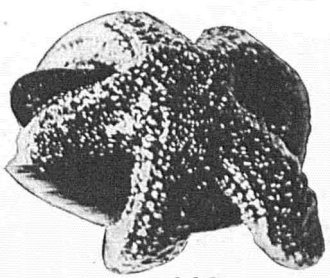

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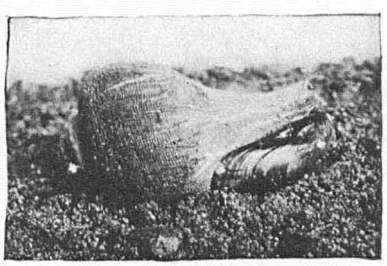


205

FIG. 198.—The winkle, *Neverita duplicata*.

FIG. 199.—Valve of a sea mussel which has been perforated by one of the winkles, *Neverita duplicata* or *Lunatia heros*.

FIG. 200.—The winkle, *Lunatia heros*.

FIG. 201.—The oyster drill, *Urosalpinx cinerea*, and a mussel shell it had perforated.

FIG. 202.—The dog whelk, *Purpura lapillus*, and a mussel shell it had perforated.

FIG. 203.—The starfish, *Asterias forbesii*, attacking a mussel.

FIG. 204.—The conch, *Busycon carica*.

FIG. 205.—The conch, *Busycon canaliculata*, feeding on a mussel.

both rocky and sandy bottoms. The dog-whelk drills a hole from one and one-half times to twice the diameter of that made by Urosalpinx and makes it in any part of the shell, even through the umbo (fig. 202, opp. p. 216). The time required to make the perforation varies from one to two days, according to the age of the mussel. On the rocky shore off Sandwich, Mass., near the opening of the Cape Cod Canal, the author found the Purpuras in great abundance on the scattered mussel beds, where the perforated shells of the latter mollusk could be picked up by the handful. It was amazing to see the destructive work that was being carried on by hundreds of these snails which could be seen adhering to mussels here and there busily engaged at their deadly work. They preferred the young shellfish which were about half an inch long. In one case two snails were found clinging to the opposite sides of a young mussel. Further examination revealed that both animals had perforated the shell at the same time and were competing for the maximum share of the prize within. They eat the softer parts of the body first, leaving the edges of the mantle and adductor muscles to the last.

The snails, *Lunatia heros* and *Neverita duplicata*, sometimes called winkles, are common all along our eastern coast as far south as Cape Hatteras and constitute an important enemy of the mussel. The two species are much alike in habit and appearance and may be easily confused. They are most readily distinguished by the thick, dark lobe, which nearly covers the wide umbilicus, which is characteristic of the space ventral to the opening of the shell of *Neverita duplicata* (fig. 198), but absent from that of *Lunatia heros* (fig. 200). The latter species seems to frequent deeper waters than does the former. They attack mussels and other mollusks with their rasping tongues, which bear chitinlike teeth, and bore holes 3 to 6 mm. in diameter through the side of the shell (fig. 199). The proboscis is then inserted through the opening and the contents devoured. Quantities of mussel shells perforated by these predacious mollusks have been dredged up by the steamer *Fish Hawk* in Vineyard Sound, which demonstrate their destructive powers.

The best measure of the devastation worked by *Neverita duplicata* on shellfish was made by Mead and Barnes (1903). Their experiment was to invert an ordinary orange box, which has two compartments, over a clam bed and sink it into the soil after clearing away the surface débris. A single Neverita was placed in each compartment. A fortnight later the contents of the box was examined. In one compartment neither snail nor any perforated shells were found, while in the other the single Neverita was found 5 inches below the surface of the ground with the perforated shells of eight clams as witnesses of its voracity. This would indicate that the normal appetite of these snails is satisfied with a clam or mussel once every two or three days. Snails which the author kept in captivity with mussels during July and August refused to eat at any time during that period.

OTHER GASTROPODS.

The conchs or winkles, *Busycon carica* (fig. 204, opp. p. 216) and *B. canaliculata*, are supposed to be greater enemies of mussels, oysters, and clams than they really are. Ingersoll (1887) states that these snails seize oysters with the concave under surface of the foot and by muscular action crush the shell into fragments, then feed upon the flesh thus exposed. He gave the estimate of one planter who believed that one winkle was able to destroy a bushel of oysters in a single hour. Colton (1908), who carried

on a long series of experiments on the feeding habits of these creatures, came to a very different conclusion. He found that they spend about 65 per cent of the time buried in the sand. They may eat two oysters a day on two successive days, but this is invariably followed by a long period of several days to months during which the animal remains buried in the sand. The method of attack is to crawl on top of an oyster, mussel, or clam and wait for the victim to open its valves; then, rotating its shell on the axis of the columella to the proper position, to thrust its own shell between the valves of the prey, introduce its proboscis, and with its radula tear out the flesh of the victim.

These observations are in harmony with those of the author who, during the summer of 1917, kept an individual of each of the two species of Busycon in an aquarium with several mussels. During a period of six weeks five mussels only were eaten, three of them being consumed during the night. The method of attack, as observed, was somewhat different from that described by Colton (1908), but the principle was the same. On one occasion the author saw one of the conchs creep up to a mussel which was lying on its side with the valves open. Moving very slowly it thrust the edge of its foot between the valves and then inserted the edge of its shell in such a manner as to pry the valves open so that the proboscis could be inserted. After feeding on its victim for a few minutes the snail turned the mussel over onto its back and forced the prolonged portion of its shell between the two valves, in which position it held the bivalve until every particle of the flesh was eaten (fig. 205).

Ilyanassa obsoleta is a gastropod often found on the mussel beds, especially where they are located on protected muddy flats. The author has never seen anything to indicate that it is an enemy of the mussel, but the observations of Belding (1910) suggest that it belongs to the class of predatory mollusks. He observed that these snails are active enemies of the scallop, forcing themselves in between the open valves of the unwary shellfish to form a wedge while other members of their species creep in and feed on the victim. If this is true for the scallop, it undoubtedly holds for the mussel also.

FISHES.

Fishes of various species depend upon the mussels for their food supply. Killifish, cunners, scup, and tautog greedily strip them from wharf piles, seaweed, and from the beds. The squeteague, flounders, and cod also eat them in great quantities. Vidal (1871) states that young eels are very destructive enemies. He says they dart in between the open valves into the mantle cavity, where they gnaw the muscles free from the shell, so that the valves can not remain closed, and then devour all the soft parts of the shellfish. The fact that mussels constitute the best bait known next to squid indicates how they rank as a food for fish.

BIRDS.

Birds, such as herring gulls, night herons, crows, and ducks, find this mollusk a desirable morsel. At Menemsha Pond, Marthas Vineyard, Mass., the author has seen herring gulls, *Larus argentatus*, apparently eating mussels. They would seize the shellfish, which were about 2½ inches in length, in their bills and shake them to break their byssal threads which bind them together. When frightened the gulls would seize a

string of the mussels and fly off with them, but they never succeeded in carrying their burden more than a hundred yards without dropping it. The gulls would then return and make other attempts to carry them off. Laughing gulls, *Larus atricilla*, which were also present on the beds, were never seen to pick up mussels, but it may be that they were feeding on the very young ones, which at the time of the observations were from 5 to 8 mm. in length. The author was not able to kill any of the birds to examine their crops for shellfish, but judging from their behavior it is reasonable to assume that they were feeding upon mussels. Black ducks, *Anas obscura*, were several times seen on the Menemsha mussel beds feeding over places where the young shellfish were particularly abundant. L. L. Dyche (*in* Field, 1910a, p. 165), at the New York meeting of the American Fisheries Society in 1910, said:

> The eider ducks eat the small ones, about an inch in length, and you will find the ducks oftentimes full of these mussels clear to the throat; I do not believe I would be exaggerating if I should say there was a pint in each.

MAMMALS.

Mammals of various sorts depend upon the mussels as a source of food. The common gray rat, *Mus decumanus*, and the muskrat, *Fiber zibethicus*, often eat them. Ingersoll (1887) states that seals, especially young ones, feed largely upon the Arctic mussel, but that the mammal which preys most extensively upon them is the walrus. According to Mr. Dyche:

> They constitute the sole food of the walrus. The walrus crushes and spits out the shell and swallows the mussel. I have killed from 24 to 30 walruses and have found in the stomach on occasions a ball containing two quarts of pieces of shell and other material from sea mussels. Seals eat squid and small fish, but the only thing that the walrus feeds on in the north is the sea mussel.

PASSIVE ENEMIES.

The passive enemies include a large number of plant and animal forms which do not attack the mussel directly but by their habits intercept the currents, causing deposition of silt, which interferes with the nutrition of the mollusk; or they may so envelop the shellfish as to cut off their food supply and even suffocate them; or they may come into direct competition for the food substances in the water.

EELGRASS.

Eelgrass, *Zostera marina*, is one of the most destructive weeds which grows in profusion on the sheltered beds. It not only intercepts the currents which bear the food supply of the mollusk but causes very often such a heavy deposition of silt that the mussels are smothered or even completely buried beneath it. Their decomposing bodies then form the richest kind of fertilizer on which the eelgrass thrives.

ALGÆ.

Algæ of various species are oftentimes present in great abundance on the beds or on the mussels which encrust wharf piles, buoys, etc. The most common species found associated with the mussels are *Fucus vesiculosus, Laminaria saccharina, Chorda filum, Champia parula, Enteromorpha erecta, Rhabdomia tenera*, and *Ulva lactuca.*

INVERTEBRATES.

Invertebrates in great variety and abundance swarm over and in the mussel beds. The ascidians, Molgula, Cynthia, and Amorecium; numerous Bryozoa; sea anemones, *Metridium marginatum* and *Sagartia luciæ;* hydroids, Eudendrium and Tubularia; and sponges grow on the mussels themselves, especially where they are attached to wharf piles (fig. 99, opp. p. 127; fig. 206, opp. p. 220). On the beds other species find it advantageous to take up a similar position on the mussels. In some localities, as at Sandwich, Mass., barnacles, *Balanus* sp?, cover the beds so completely as to hide the shellfish. Lamp shells, *Anomia glabra,* and boat shells, *Crepidula fornicata,* also have the habit of attaching themselves to the mussels and competing with them for their food supply. The same is true of the little sea anemone, *Sagartia luciæ,* which is very abundant on the Menemsha mussel beds. Worms of various sorts, Nereis, Lepidonotus, and others, burrow beneath and between the mollusks, and on their shells *Hydroides dianthus* often secretes its limy tubes.

The ribbed mussel, *Modiolus demissus* (*Modiola plicatula*), common clam, *Mya arenaria,* hard-shell clam, *Venus mercenaria,* oyster, *Ostrea virginiana,* and the scallop, *Pecten irradians,* are often associated with the mussel, and the periwinkle, *Littorina littorea,* is nearly always present on the exposed beds in great numbers, especially if eelgrass or algæ is present in abundance. Crabs, Carcinus, Cancer, Libinia, and Panopeus, hermit crabs, *Bupagurus longicarpus,* and the king crab, *Limulus polyphemus,* run about over the beds in the shallow, protected estuaries, while in the mantle cavity of the mussel a little crab, *Pinnotheres maculatum,* finds its abode. Some authorities say the relation between the two species is symbiotic, while others claim it is parasitic, the crab occupying this position to collect the food particles swept in by the ciliarv currents of the mollusk.

PARASITES.

Polydora ciliata.

Parasites in the mussel are apparently few in number, only one having been described previously by Lebour (1907), who found a boring annelid, *Polydora ciliata,* which burrows through the shell, making a hole about the size of a pin. It causes pearly excrescences to grow over the internal surface of the shell which prevents muscular development and oftentimes almost destroys the posterior adductor muscle. It furthermore often interferes with the production of the genital products wherever the calcareous ridges press against the mantle. This results in giving the shellfish an unsightly appearance, which renders it unfit for market.

Haplosporidium mytilovum, n. sp.

A new species of sporozoan parasite was recently discovered while the author was studying the maturation of the Mytilus egg. This protozoan occurs in the egg, and its presence there gives rise to a phenomenon suggesting the formation of a chromatin vesicle which for a long time the author took to be a normal process in the development of the egg. The peculiar condition was observed by several prominent zoologists who offered different explanations for its presence. It was finally identified for the author through the kindness of Dr. Gary N. Calkins, of Columbia University, as a probably new species of the genus Haplosporidium. In its vegetative state it is amœboid in

FIG. 206.—A group of living mussels whose shells are encrusted with Bryozoa, barnacles, sea anemonies, and serpulids.

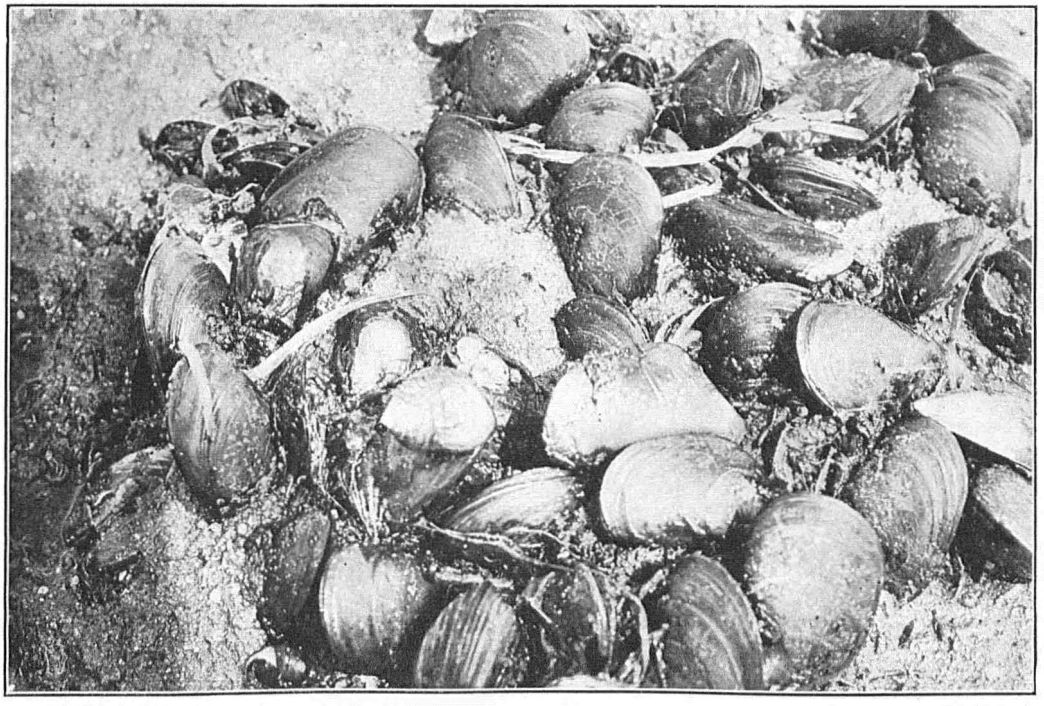
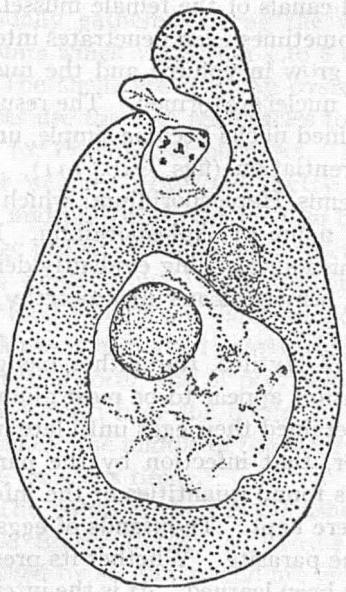


FIG. 207.—Vertical view of mussels on a natural bed, showing the characteristic position they assume with the anterior end buried in the sand and the posterior or syphon end projecting well above the level of the bottom.



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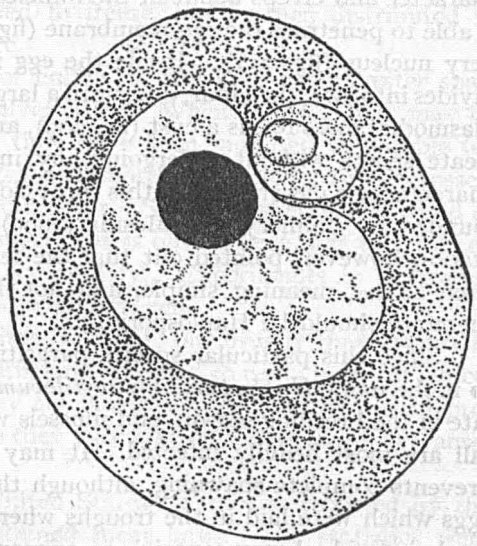

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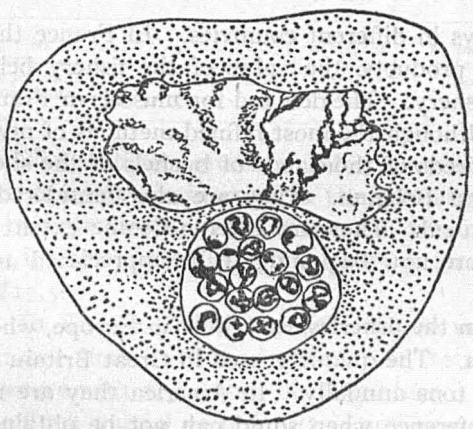

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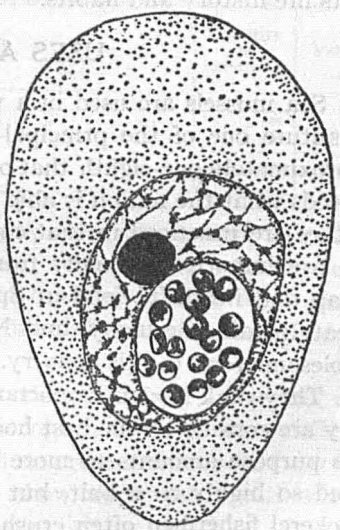

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FIG. 208.—A sporozoan parasite, *Haplosporidium mytilovum*, new species, in its vegetative stage, shown penetrating the wall of a mussel egg.

FIG. 209.—*Haplosporidium mytilovum* encysted in the cytoplasm of a mussel egg where it is undergoing a period of growth.

FIG. 210.—A later stage than fig. 209, showing multiplication of nuclei within the cyst. The cyst is in the cytoplasm just below the egg nucleus.

FIG. 211.—A group of spores of *Haplosporidium mytilovum* encysted within the nucleus of a mussel egg.

All figures are fixed in Gilson fluid and stained with Heidenhain: iron hæmatoxylin. × 1500.

character and creeps about in the follicles and genital canals of the female mussel. It is able to penetrate the egg membrane (fig. 208) and sometimes even penetrates into the very nucleus (fig. 211). Inside the egg it begins to grow in volume and the nucleus divides into two, then four, etc., until a large number of nuclei are formed. The resulting plasmodial mass forms a cyst (fig. 209), and the contained nuclei become simple, uninucleate spores without undergoing any internal differentiation (figs. 210, 211). This characteristic clearly places this protozoan in the genus Haplosporidium, which was founded by Caullery and Mesnil (1899) under the name of Aplosporidium. Lühe (1900), however, pointed out that the term was a misnomer, being evidently derived from ἁπλους, meaning simple, and not from ἀπλους, which means unseaworthy, and therefore should be Haplosporidium.

Since this particular species parasitizes the egg of Mytilus, the author has given to it the name *Haplosporidium mytilovum*. The parasites appear to be most abundant late in the breeding season, and mussels which have retained their eggs until late in the fall are most heavily infected. It may be, however, that infection by the parasite prevents complete spawning, although the author has found quantities of the infected eggs which were laid in the troughs where mussels were kept. Thousands of eggs in a single individual may contain one or more cysts of the parasite. Whether its presence does any more injury than to destroy the eggs has not been learned. It is the intention of the writer to investigate the organism further and publish a more complete description of its life history and habits.

USES AND COMMERCIAL VALUE.

Sea mussels are used in a variety of ways in different countries. In France they constitute one of the principal marine food products, the value of the fishery being approximately one-eighth that of the oyster fishery. The demand for mussels in France exceeds what the nation is able to produce, although the most refined methods of myticulture are practiced in that country. Hundreds of thousands of bushels of the shellfish are imported annually from Holland and Belgium. They are also considered a cheap and healthful food in Spain and Portugal. They are eaten to some extent in Great Britain, Germany, and Norway, and are now beginning to be appreciated as a wholesome food in this country.

They rank next in importance as a bait in the fisheries, especially in Europe, where they are considered the best hook bait known. The quantity used in Great Britain for this purpose amounts to more than 100,000 tons annually. In America they are not rated so highly as a bait, but are given preference when squid can not be obtained. Mackerel fishermen often crush mussels and throw them overboard to attract the fish to their boats.

As a fertilizer they constitute another useful and important product. Where the beds are exposed to the deposition of silt the mussels are gradually smothered to death, while new generations are constantly becoming attached to the layers above. The result after a number of years is a thick layer of blue, ill-smelling matter called mussel mud, which is rich in lime, sulphur, and nitrogen. It is considered one of the best fertilizers known, especially for carrots and onions. A writer from Essex County, Mass. (*in* Ingersoll, 1884, p. 621), stated that for 30 years he had seen it applied to lands where onions had been grown with a yield varying from 300 to 600 bushels per acre. The material

is usually gathered during the winter, allowed to freeze, and is then distributed in amounts which vary from 4 to 8 cords per acre.

The shells are used by oyster planters for cultch on which to catch oyster spat. Artists use them as receptacles for gold and silver paint. When polished they may be used for ornamental purposes. In this form they have been mounted on marble for paper weights. Buttons, pretty needle books, scent bottle holders, earrings, crosses, pins, and pin cushions have also been made from them. Since the shell is composed of a large proportion of albuminous matter, the suggestion is offered here that the cracked shells would probably make a valuable food for poultry. Experiments to determine their food value from this standpoint ought to be undertaken.

Mussels also yield pearls which are sometimes of value, but usually they are small, of irregular form, and of poor color, selling in England for from 50 cents to $1 an ounce. When formed near the border of the shell they are blue-black in color, but when produced near the middle of the inner shell surface they may take on the beautiful character of the nacreous tissue.

The value of the mussel fishery in the United States for 1908 is reported by the United States Bureau of Census on the contained meat basis. The statistics were furnished by six States and are given in Table 4.

TABLE 4.—QUANTITY AND VALUE OF SEA MUSSELS MARKETED IN THE UNITED STATES IN 1908.

	Quantity in pounds.	Value.		Quantity in pounds.	Value.
New York	8, 175, 000	$8, 200	Rhode Island	3, 500	$100
California	68, 000	1, 600	Massachusetts	1, 100	100
New Jersey	287, 000	1, 400			
Connecticut	7, 200	200	Total	8, 541, 800	11, 600

The statistics given in Table 4 are for the year 1908, since which time there has been considerable increase in the consumption of mussels. The present quantity used probably exceeds several times the amount indicated in the above table, for a single firm in New York during the year 1912 reports having handled 50,000 bushels, valued at $17,500.

In Europe the mussel fisheries are much better developed and of far greater importance than in this country. The statistics of the European fisheries were difficult to secure with any degree of completeness, and what is here presented is to be regarded as only a partial record. It is sufficient, however, to show the great wealth which lies in this fishery.

TABLE 5.—QUANTITY AND VALUE OF MUSSELS MARKETED IN EUROPE.

Country.	Year.	Quantity in pounds.	Value.	Country.	Year.	Quantity in pounds.	Value.
France	1909	90, 044, 010	$559, 276	Germany	(?)	370, 100	$2, 375
Belgium	1906	56, 129, 356	255, 133	England	1911	[1] 3, 519, 860	15, 125
Netherlands	1910	3, 737, 481	23, 300				
Ireland	1908	(?)	15, 510	Total			882, 994
Portugal	1909	(?)	12, 275				

[1] Returns from Grantees of Mussel Fishery Orders.

Lankester, in his article on the Mollusca, published in the Encyclopedia Britannica, states that in 1873 the mussels exported from Antwerp alone to Paris to be used as a human food were valued at $1,400,000. If this production still continues, the total yearly value of the mussel fishery for Belgium and France alone equals nearly $2,000,000.

Owing to the food shortage in Europe caused by the war, the boiling and salting of mussels in Holland for German consumption has developed into a large and valuable industry. According to the Seafood Journal for February 12, 1917:

> Up to a month or two ago these humble shellfish which abound in the shallow waters of the Scheldt delta were retailed for local consumption and constituted a cheap popular food. They have now suddenly disappeared from the market, and instead of being eaten are salted down in great quantities and bought up for Germany. Some of the workmen's families that have taken up the new occupation are earning about $6 a day, for them a princely wage.

Consul Frank W. Mahin, of Amsterdam, also states in Commerce Reports No. 61, Washington, D. C., Thursday, March 14, 1918, page 963, that—

> Mussels abound in the vicinity of Texel, an island at the mouth of the Zuider Zee. They have been eaten more or less, but now it is probable they will become very popular. Samples of smoked mussels have been received from Texel, which are pronounced "uitstekend" (substantially, "delicious"). Smoked and salted, the mussel is said to resemble smoked meat (similar to American dried beef), but tenderer and fatter.

These facts serve to show how important and valuable the mussel fishery is to Europe and suggest the possibilities of developing an equally great food-producing industry in this country from the abundance of natural mussel resources at our disposal and the vast unutilized areas along our shores that are especially adapted for the cultivation of this particular shellfish.

CHEMICAL COMPOSITION AND NUTRITIVE VALUE.

Chemical analyses made by Atwater (1892), Atwater and Bryant (1906), and Alsberg, whose account is published in Field (1911), show that the sea mussel not only contains the same kinds of nutrients as other shellfish but contains them in greater abundance. These nutrients are: (1) Protein, which forms the nitrogenous basis of blood, muscle, connective tissue, etc., and supplies energy to the body; (2) carbohydrates; (3) fats, which may be stored up as fat or consumed for fuel; and (4) mineral matters or ash, which are used chiefly in the formation of bone. The energy-yielding power of a nutritive substance is measured in terms of its fuel value, which refers to the number of calories of heat equivalent to the energy that the body is supposed to obtain from 1 pound of the thoroughly digested food. A calorie as here used equals approximately the amount of heat required to raise the temperature of 1 pound of water 4° F. According to the factors of Rubner, the fuel value of each pound of protein or carbohydrate is equivalent to 1,860 calories of energy, while that of fat is equal to 4,220.

Table 6 shows the comparative composition and fuel value of the mussel and several shellfish most commonly found on the market. Of the five species the mussel ranks first, second, and third, respectively, in the yield of carbohydrate, fat, and protein, while in the total production of nutrients it surpasses all the others. Its superiority over the oyster in this respect amounts to 365 per cent, and over the round and long clams to 220 per cent and 11 per cent, respectively. The lobster most nearly approaches

the mussel in fuel value, but even this occupies a lower rank. The general excellence of the mussel is due chiefly to the fact that there is little waste in the animal as a whole. It is in the same class with the long clam, where the amount of edible material supplied exceeds 50 per cent. The oyster, on the other hand, is at its greatest disadvantage in this respect, for its heavy shell makes the percentage of refuse amount to more than 81 per cent.

TABLE 6.—COMPARATIVE COMPOSITION AND FUEL VALUE OF CERTAIN SHELLFISH.[1]

Species.	Refuse.	Water.	Protein. N×6.25.	Fat.	Carbohydrate.	Ash.	Total nutrients.	Calories of fuel value per pound.
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	
Sea mussels	46.7	44.9	4.6	0.6	2.2	1.0	8.4	50
Lobsters	61.7	30.7	5.9	.7	.2	.8	7.6	141
Long clams	41.9	49.9	5.0	.6	1.1	1.5	8.2	136
Round clams	67.5	28.0	2.1	.1	1.4	.9	4.5	68
Oysters	81.4	16.1	1.2	.2	.7	.4	2.5	41

[1] Data from Langworthy (1905).

The relative value of food substances from the standpoint of economy can not be determined from their chemical composition alone. It is necessary to know the actual cost of the food principles supplied and the proportion which the body is able to metabolize.

In regard to the palatability of the sea mussel little need be said aside from the fact that the flesh is tender and of fine quality and the flavor is superior to clams and equal to that of the oyster. This statement is based on the testimony of a hundred or more persons who reported on the comparative merits of these shellfish.

Metabolism experiments made by Dr. D. D. Van Slyke, assisted by Dr. W. M. Clark and Dr. C. B. Bennett, and reported in Field (1911) demonstrated that the rate of digestion and proportion of nutrients supplied to the body approximate very nearly those of steamed beef, which is considered very digestible. It is unfortunate that we have no similar data for the clam, oyster, and lobster flesh.

The above evidence, however, is sufficient for drawing the conclusion that the sea mussel is not only as palatable as the oyster, but is now the cheapest and most nutritious shellfish which can be placed on the market.

SEASONAL CHANGES IN STRUCTURE AND FOOD VALUE.

Mussels, like oysters, undergo a series of structural and physiological changes during the year which render them prime for market during one season and of very poor quality in another. These changes are caused primarily by the reproductive activities of the animal and secondarily by the rhythmic changes in the amount of food organisms present in the water.

It has been shown that by far the greater part of the mussel's body is devoted to the production of genital products. Just before the spawning season the mantle and mesosoma are greatly distended with reproductive tissue. It also covers the pericardium and often envelops completely the outer walls of the liver. When in this state the shellfish are of maximum nutritive value, most palatable, and most attractive in appearance.

In Narragansett Bay and Long Island Sound mussels usually reach this condition in the late winter or early spring, while in the more open waters of the ocean, such as along the south shore of Long Island, they do not attain it until June or July.

Following the maximum development of genital tissue there is a shedding of the reproductive elements that leaves the body in a shrunken condition and with a comparatively large and conspicuous dark-green liver. Such shellfish are unattractive in appearance and undesirable for use as food. This change takes place in the mussels of Narragansett Bay and Long Island Sound during the months of June and July, or sometimes as late as August, according to the depth of the water in which the beds lie. Those in shallow water subject to the higher temperatures, direct rays of the sunlight, and wave action are the first to spawn, while those in very deep water are the last to begin the process, or they may even retain the genital products throughout the season and absorb them as reserve food. Such mussels are nearly always in good condition.

Mussels on the south shore of Long Island put on flesh and mature their reproductive elements in the late spring and early summer, coming into prime just as the Narragansett Bay and Long Island Sound mussels go out of season. They continue in marketable condition until the latter part of September.

From Narragansett Bay and Long Island Sound, on one hand, and the south shore of Long Island, on the other, there may be obtained a continuous supply of marketable mussels from March to October. This fact is of much significance, for since the mussel season supplements that of the oyster it offers an opportunity to oystermen to keep their expensive equipment busy the year round in case a mussel industry is established.

The series of structural changes which occur during the year are illustrated in the photomicrographs of cross sections taken through the mantles of mussels from Woods Hole, Mass., during the months of December, January, April, June, and August (figs. 212 to 220). The figures are all represented on a uniform scale of 30 diameters magnification, so that the relative thickness and condition of the mantle at the different seasons may be compared at a glance.

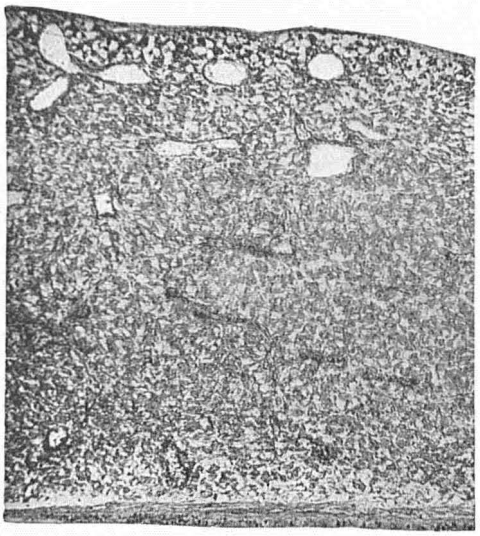
On December 1 the mantle of a female mussel was found to be composed of a rather uniform reticular tissue, with blood vessels running just below the outer surface and small genital canals and follicles extending to a slight extent throughout the middle and inner side (fig. 212). On the same date the mantle of a male mussel was found to be thinner, but the follicles were much more completely formed and were filled with developing spermatozoa (fig. 213).

Six weeks later the mantle of a female mussel was found to be thinner than that of the specimen examined December 1, but the genital canals and follicles were more numerous and better developed (fig. 216). On the other hand, the mantle of a male mussel taken on the same date was thicker than that of the male specimen examined on December 1, and the tissue was firmer and less vacuolated (fig. 217).

During the next three months considerable increase in growth was found to have taken place in the tissue as well as the formation of large numbers of genital cells in both the female (fig. 219) and the male (fig. 220).

The maximum development was found in the middle of June when the female mantle in particular was distended with the reproductive products (fig. 214).

Shortly following this condition, spawning takes place and practically all of the genital elements are shed, which results in a decided shrinkage of the mantle and other



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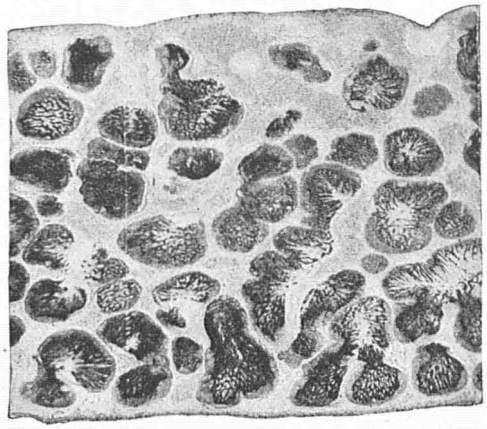

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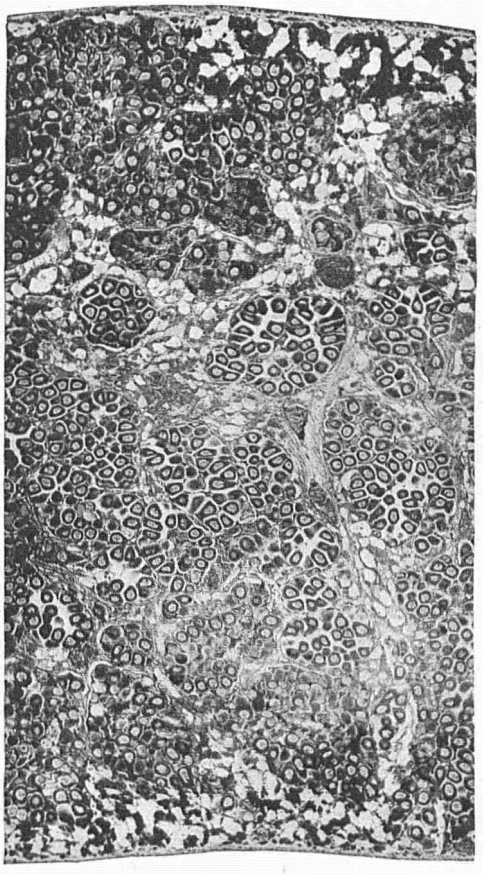

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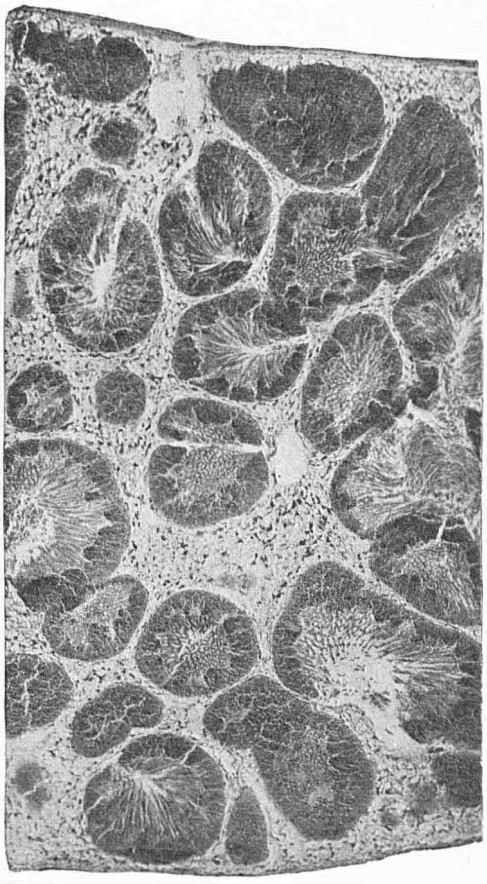

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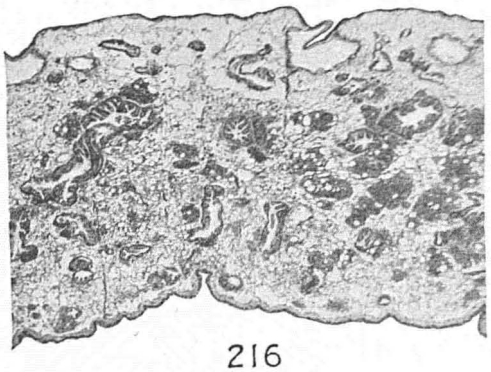
Cross sections through the mantles of mussels collected at Woods Hole, Mass. All figures are photomicrographs of material fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red. × 30.

FIG. 212.—From a female mussel collected on December 1.

FIG. 213.—From a male mussel collected on December 1.

FIG. 214.—From a female mussel collected on June 16.

FIG. 215.—From a male mussel collected on June 16.



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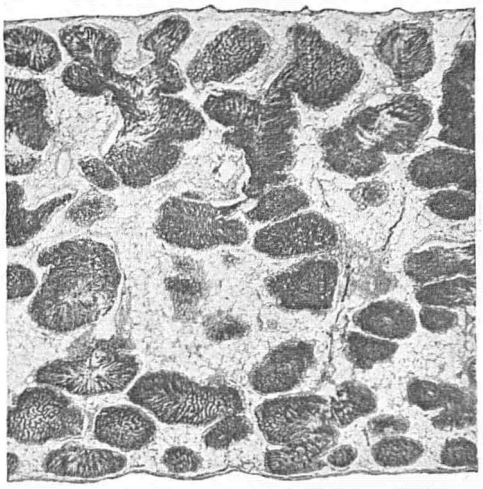

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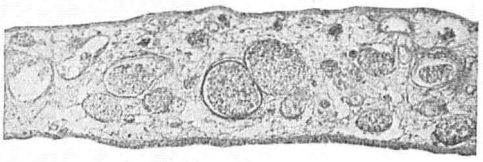

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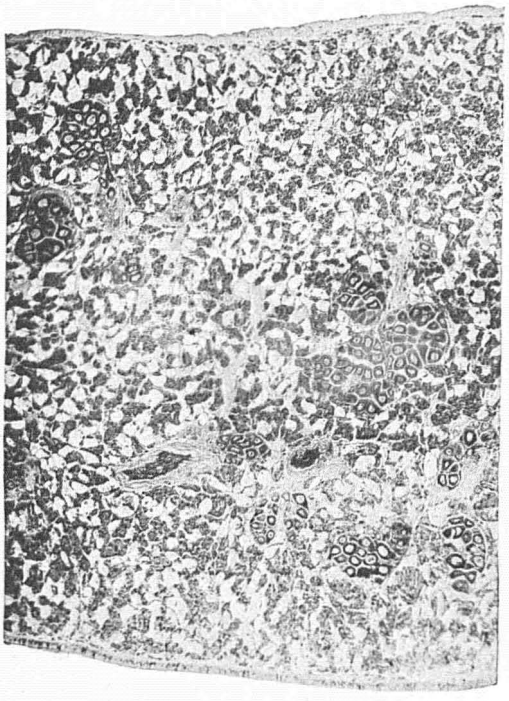

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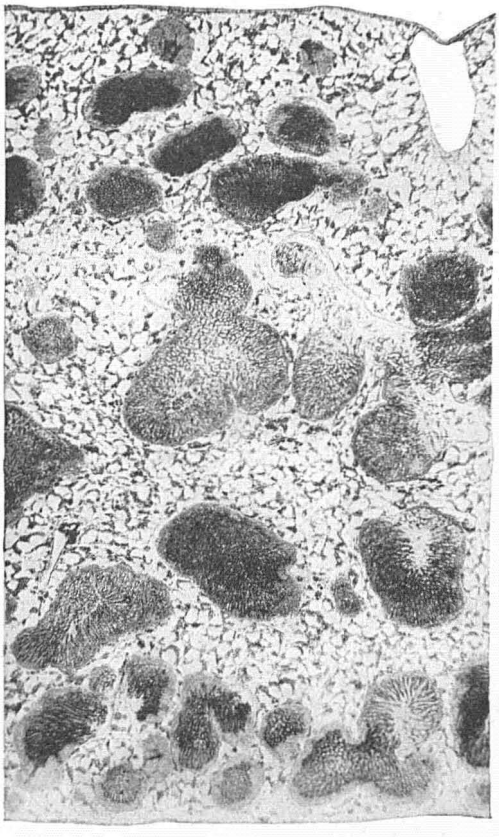

220

Cross sections through the mantles of mussels collected at Woods Hole, Mass. All figures are photomicrographs of material fixed in Gilson fluid and stained with Delafield hæmatoxylin and congo red. × 30.

FIG. 216.—From a female mussel collected on January 12.

FIG. 217.—From a male mussel collected on January 12.

FIG. 218.—From a female mussel collected on July 16 after spawning had taken place.

FIG. 219.—From a female mussel collected on April 27.

FIG. 220.—From a male mussel collected on April 27.

parts of the body pervaded with genital tissue (fig. 218). An idea of the relative food values of a mussel before and after spawning is shown in a most striking manner by comparing figures 214 and 218.

WHEN MUSSELS ARE UNFIT FOR FOOD.

While advocating the use of mussels for food, the author has often encountered persons who protest against so using them on the ground that they are a dangerous product which can never be eaten with safety. But having eaten them for years himself and knowing many other persons who have been doing the same thing without ever experiencing disagreeable symptoms, the author is convinced that the idea of their possessing any poisonous qualities is false. However, to say that they are never poisonous would be as wrong as to say that oysters, clams, or lobsters are never toxic. When infected with disease-producing germs, ptomaines, or other injurious substances any of these shellfish are a menace to human life if ingested; and the record of suffering and fatalities which appears in the medical journals and daily papers serves to show how important it is to select these foods with care. A study of mussels as a human food shows that they are a most wholesome shellfish and that they are no more dangerous to eat than are oysters, clams, or lobsters, provided the same care is used in selecting them.

The purpose of this section is to show the causes and symptoms of poisoning which have resulted from eating unwholesome mussels, with the hope that similar occurrences may be averted in the future. The subject may be considered under two heads—diseases resulting from eating mussels taken from polluted waters, and diseases resulting from ingesting poisonous substances secreted in the body of the mussel itself

MUSSELS AND TYPHOID FEVER.

Buchan (1910) collected some very important data on the relation of mussels from polluted waters to typhoid fever. The results of his paper are based on evidence collected at Birmingham, England, between June 1, 1904, and June 1, 1909, during which period there were 855 cases of typhoid fever, of which 124, or 14.5 per cent, were attributed as due most probably to mussels and 32 to other shellfish.

Investigations demonstrated that several of the sources from which mussels were supplied to Birmingham were polluted with sewage. Bacteriological examinations of mussels taken from the Birmingham market showed that the number of microorganisms to a single mussel varied from 2,000,000 to 1,000,000,000. The most common number was between 10,000,000 and 100,000,000 per mussel, which is considered high. Where the number reaches 1,000,000,000 it undoubtedly indicates gross pollution. In 5 samples the *Bacillus coli communis* was actually isolated, while evidence of its presence was found in 26 other cases. Since the *Bacillus coli communis* is so closely associated with the *Bacillus typhosus* it is reasonable to infer that the presence of this germ in mussels means the possible and probable pollution by the typhoid bacillus. Sewage pollution was also indicated by the presence in large numbers of the *Bacillus enteritides sporogenes* and of numerous *streptococci.* The investigations of Johnstone (1912) further show that there is abundant epidemiological evidence that enteric fever has been transmitted by mussels.

The above evidence proves that mussels may be carriers of typhoid fever in the same way as oysters or clams if taken from waters polluted with sewage. The problem of protection in each case is the same. Either the sewage must be purified before it is allowed to flow into waters where the shellfish are propagated or the law should forbid the marketing of shellfish taken from polluted waters. Some writers have advocated transplanting oysters and mussels from regions of sewage contamination to clean waters for a period sufficient to allow them to be freed from any pathogenic germs. The practicability of this method, however, is doubtful, for as Klein (1905) has demonstrated, cockles infected with typhoid organisms and thereafter kept in clean sea water frequently changed allowed the bacilli to multiply, and bacilli in mussels similarly treated were still plentiful after seven days. Johnstone (1909) found that mussels taken from polluted beds and placed in sea water half a mile from the nearest discharging sewer were able to rid themselves of 93 per cent of intestinal bacteria in four days, but that a further period of eight days did little if anything to effect a further reduction.

Wright (1917) describes a type of purification tank that is being erected under the supervision of the Lancashire and Western Sea Fisheries Committee in order to remove as much risk as possible from the consumption of polluted mussels in Great Britain.[4]

> They are solidly built concrete structures, in several compartments, on the wooden grids of the floor of which the mussels are placed, in layers not exceeding three deep. They are designed to fill over the top at about high water of neap tides, when the mussels will rest under a depth of about 2 feet of clean sea water. As the fecal matter is ejected, it falls through the gratings on to the cemented floor beneath, which slopes away to outlet pipes of large diameter. The water is allowed to escape when the tide is low, and carries, as it flows out, the excretory products. Exhaustive tests (bacteriological and others) are carried out before the site of the tank is decided upon, in order to insure the purity of the water gaining access to it. The shellfish remain in the structure for the space of 48 hours, and they are then put into bags bearing the lead seal of the committee, to show that they have undergone treatment.

PTOMAINES.

Another source of danger in utilizing sea mussels for food is from the ptomaines and other poisons which often occur in shellfish. The cause of prejudice which has grown up against this mollusk is due to the fact that fresh mussels which exhibited no signs of decomposition have on several occasions fatally poisoned groups of persons who ate them at a particular time. Aurel Krause (1885), in Flinkit-Indianer, Jena, reports that in 1799 a company of soldiers stopping at Peril Way, near Sitka, Alaska, ate of these mollusks and that in less than two hours 100 men died in great pain. This incident is doubtless the same one referred to by Dall (1870) and Petroff (1884). The place and date in the two accounts are the same, but according to Dr. Dall the victims were Aleut hunters from Unalaska and Kodiak instead of soldiers. It was this calamity which gave the place its name of Peril (in Russian Pogibshi) Strait. In this case the poisoning was supposed to have been caused by ptomaines generated in the liquor of the mussels which had been exposed to the sun for a long period. The Aleuts of that region informed Dr. Dall that mussels which were not exposed at low tide were always safe to eat.

[4] A method of purification which has been used for three years at Conway, in Wales, and proved to be commercially successful is briefly summarized in the Fisheries Service Bulletin No. 61, June 1, 1920, p. 3. "This method consists essentially in placing the shellfish on wooden grids in vats of 40,000 gallons capacity, cleansing them with water from a hose, and allowing them to stand in sterilized sea water for 24 hours, then cleansing with the hose again, followed by immersion in sterilized sea water for another period of 24 hours, after which water containing 3 parts per 1,000,000 of available chlorine is run over the shellfish and allowed to stand 1 hour. The shellfish are shipped in sterilized sealed bags."

PECULIAR POISONS.

A class of poisons different in some respects from that of the ptomaines has appeared in the sea mussel at various times in certain restricted localities. In some cases large groups of people have been suddenly stricken with severe illness after eating this shellfish and death has often quickly followed. The most prominent case of this sort occurred at Wilhelmshaven, Germany, October 17, 1885, when 19 persons were taken severely ill after eating *Mytilus edulis*. Four of the people died. Consternation followed this event and numerous investigators began to study the nature and effects of the poison. The result has been an extensive and most valuable literature, knowledge of which should protect us from again falling into the fatal error of eating poisonous mussels of this type.

Netter and Ribadeau-Dumas (1907b) published a table showing the fatal cases of poisoning which have been known to result from the ingestion of such mussels. In modified form it is as follows:

Author.	Locality.	Month.	Year.	Number of sick.	Number of deaths.
Vancouver (1798)	North America	(?)	1793	3	1
Combe (1828)	Leith	June	1827	30	2
Crumpe (1872)	Tralee	(?)	(?)	3	3
Crumpe (1872)	Tralee	(?)	1872	1	(?)
Virchow (1885)	Wilhelmshaven	Oct. 17	1885	19	4
Schmidtmann (1888)	Wilhelmshaven	September	1887	3	1
Permewan (1888)	Liverpool	August	1888	3	1
Cameron (1890)	Dublin	June 30	1890	7	5
Hill (1899)	Richard Surrey	Jan. 8	1895	1	1
Thesen (1902)	Christiania	May	1901	5	2
Rolfe (1904)	Avonmouth	June	1904	2	1
Netter and Ribadeau-Dumas (1907)	Calais	May 23	1907	13	2
Boinet, Ed. (1911)	Paris	(?)	1911(?)	2	2
Total				92	25

The symptoms which follow the ingestion of poisonous mussels may be one or more of three distinct types.

(1) The erythematic form is the lightest in which the toxine takes effect. The symptoms are similar to those which appear in many persons after eating strawberries, pineapple, or fish, when red spots appear on the body. This is also frequently accompanied by a swelling of the face and abdomen and sometimes with a sense of suffocation.

(2) The choleratic form is more severe in its effects. A few hours after ingesting poisonous mussels diarrhea and vomiting appear, which last for from 24 to 36 hours. The symptoms are similar to those of the dry-weather cholera, which appears periodically at Trieste, Austria, and with which cases of mussel poisoning have been confused.

(3) The paralytic form is the worst, being rapid in its action and often fatal. It was this form of poisoning which occurred at Wilhelmshaven. On that occasion the physician Schmidtmann (1888) made a study of the subject from the clinical and etiological standpoint, while Virchow (1885) investigated it from the standpoint of pathology.

The symptoms as described by Schmidtmann (1888), Permewan (1888), Cameron (1890), and others, indicate that there are three stages to the paralytic form of poisoning.

The first signs are a prickling or burning sensation in the hands or feet, a constriction of the pharynx, mouth, and lips, and a sensation in the teeth similar to that produced by acid substances. The lips become numb, and this condition gradually passes

down over the arms. A consciousness of lightness and that objects have no weight comes over the patients; they believe that they can fly.

The second stage is marked by a feeling of restlessness and fear. No rise of bodily temperature takes place, but the pulse rate is quickened to a frequency of 80 to 90 per minute. The pupils of the eyes are dilated and reactionless, there is a feeling of giddiness, and the patients speak in a weak voice and with difficulty. They hold themselves in an upright position with great pain. The secretion of urine is suspended or passed with pain and great effort.

The third stage follows with vomiting and cramps and sometimes, but rarely, with diarrhea. The pulse grows feeble, and the limbs become cold. The condition of restlessness increases with a feeling of suffocation. Through it all the senses remain intact. Finally the body becomes cold, the patient sinks into a state of unconsciousness, and death follows in a quiet sleep. Cameron (1890) states that some of his patients appeared to have died from asphyxiation, their faces being intensely livid. In some cases the symptoms do not begin to show themselves until 12 hours after eating the poisonous shellfish, while in others death has resulted within 2 hours after the meal.

Rolfe (1904), who had two patients afflicted with the paralytic type of poisoning under his observation, noticed that hot strong coffee had a marked beneficial effect upon the pulse and general condition. He reports that the patient which gave least promise of getting well drank coffee and survived, while the other took no coffee and died.

The autopsies made by Virchow (1885) established the facts that as a general rule there is an accentuated rigor mortis in the bodies of persons who die from this form of poisoning; the cardiac and arterial blood is dark in color and viscous in consistency except where the arteries are more exposed to the action of oxygen, in which places it is clear red. The most pronounced alterations appeared in the omentum and the large intestine, which with the stomach were strongly hyperemic. The mucosa of the small intestine was likewise strongly injected with blood and covered with mucous swellings. The spleen was swollen, and the liver presented a congested condition.

The characters of the mussels which cause this type of poisoning are different from those of the normal shellfish. Schmidtmann (1888) observed a nauseating odor to the broth prepared from them. The mussels had a yellow color and the shells were unusually thin and fragile. while the liver was darker than the ordinary and very brittle.

SOURCES OF POISON.

Wolff (1886), Schmidtmann (1888), Lustig (1888), Thesen (1902), and Netter et Ribadeau-Dumas (1907) determined that the poison was confined entirely to the liver, but how it gets into the organ is still a theoretical matter. Wolff (1886) believed that the poison was secreted as the result of a disease and stored up in the liver. The change in volume, color, and consistence of the liver and of variation in toxicity supports this view. Schmidtmann (1888) established the fact, however, that the toxic mussels are found only in certain special restricted localities, where the water is in a stagnant condition, and that if removed to open, freely circulating water of the sea they lose their poisonous qualities in less than four months. And, on the other hand, if harmless mussels are transferred to the stagnant waters of the inner harbor of Wilhelmshaven they develop toxic properties in from two to three weeks. This would suggest that

there was some injurious compound present in the water which was taken up by the mussel and stored in the liver.

To test this, Thesen (1902) placed some mussels in weak solutions of strychnine, curare, and the poison of mussels. He was confident that at the end of a certain time these poisons were taken up by the liver. Schmidtmann's (1888) evidence supports this view. He observed that harmless mussels placed in the suspected Wilhelmshaven basin became more toxic the longer they remained there. After 24 hours they developed sufficient poison to kill a rabbit in 1½ hours, after 48 hours in 12 minutes, after 72 hours in 4½ minutes, and after 96 hours in from 2 to 4 minutes. Mussels which were capable of killing rabbits in a few minutes, after being placed in the open water of the sea for a period of 8 hours, were unable to cause the death of rabbits in less than 1½ hours. But all efforts to isolate the mussel poison in a preformed condition from the stagnant water met with negative results.

Lindner (1888) assumed that the poison was produced by certain Protozoa which he found present in considerable numbers in the toxic mussels. Popular opinion has attributed the production of the poison to various sources. Some think it is due to the absorption of copper salts which come from the metal sheaths of ships; others believe that it comes from the eggs of starfish which are consumed by the mollusk. This view is evidently without foundation, for there is apparently no authentic record of starfish eggs being poisonous or ever being found in the mussel. It has also been assumed without reason that the poison comes from the little crab, *Pinnotheres maculatum*, which lives in the mantle cavity. It has also been accredited to the byssus.

The most plausible explanation of the origin of the poison is contributed by Lustig (1888), who studied the subject from the bacteriological standpoint. He obtained some mussels from Genoa and Trieste which exhibited all the physical characters of the poisonous variety. A sample of them which was fed to a cat and a rabbit produced vomiting which was followed by death in less than 24 hours, accompanied with the characteristic anatomical features of enteritis. From the livers of these mussels he obtained, by Koch's method, cultures of two microorganisms, one of which proved to be pathogenic. The latter organism is a straight, slender bacillus varying from 0.8 to 1.0 micron in length. It stains with gentian violet, fuchsin, methyl violet, and Grams method. In old cultures the bacilli unite into a spiral form. They liquefy gelatin. Twenty-four hours after infection they produce rather large colonies, having a funnel form with a dense whitish mass at the center similar to that of the bacillus of Finkler and Prior.

Test-tube inoculations show a bubble of gas on the surface of the gelatin at the end of 12 hours, and at the end of 24 hours the gelatin at this point is liquefied into the funnel form. The depression continues to deepen by liquefaction, until at the end of 8 hours more all the gelatin is dissolved into a cloudy, grayish liquid, on the surface of which there is a delicate green ring. The cultures give off a nauseating odor. The bacillus grows readily on agar-agar at a temperature of 16 to 20° C. and on potatoes at ordinary room temperature. The potato culture takes the form of a yellow film. It also develops well in sterilized milk or bouillon.

To show the relation of this organism to the Mytilus poison, Lustig performed a series of feeding experiments and of injections on rabbits and guinea pigs. From some 24-hour gelatin cultures he transferred by means of a sterilized platinum needle about 4 to 6 drops to small cubes of sterilized potato which were preserved in sterilized glass

receptacles. The infected portions of potato were fed to rabbits and guinea pigs in doses of three cubes to each individual. The animals were then isolated and allowed nothing more to eat. All the rabbits, eight in number, died within 12 hours. Of these, two died in two hours after having suffered from severe diarrhea. Of the guinea pigs, four in number, two survived and two died.

An autopsy demonstrated the same conditions which have been described for persons who have succumbed to the effects of mussel poisoning, and microscopic examination of the cardiac blood and of the intestinal contents revealed the presence of the bacillus in question.

After these results of natural infection he injected from 15 to 20 drops of 24-hour cultures into the skin of rats and rabbits, but both cutaneous and subcutaneous injections proved to be without effect. However, if injected into the peritoneum in small quantities it produced death in rabbits and guinea pigs in from 8 to 24 hours. The clinical and pathological phenomena presented by these animals were the same as of those naturally infected. An injection of these bacteria into the blood vessels of the ears of four rabbits produced no harmful results. Cultures from the alimentary tracts of animals which died as a result of these infections if taken within 24 hours after death are just as capable of infecting other animals when ingested as are the original cultures from the mussel liver. As the cultures grow older they become less virulent in their effects and after a few hours cause nothing more serious than diarrhea when injected into the peritoneum.

Lustig admits that the above evidence is not complete enough to definitely prove this organism to be the cause of the poison which is sometimes found in the mussel liver. It is very suggestive, however, and calls for further research when the opportunity presents itself again. Other investigators, Netter et Ribadeau-Dumas (1907), who secured some of these poisonous mussels at Calais, France, were unable to isolate a specific germ.

CHEMISTRY OF MUSSEL POISON.

The chemical nature of the poison classes it with the ptomaines according to Schmidtmann (1888), while Virchow (1885) is inclined to group it with the alkaloids. Our first knowledge of its chemical properties was furnished by Salkowski (1885), who extracted the poison by means of alcohol. He found that alcoholic solutions of non-poisonous mussels were almost colorless, while those from the diseased livers of poisonous mussels were golden yellow in color and if treated with warm concentrated nitric acid gave a grass-green color. He furthermore found that the activity of the poison is not affected by heat up to 110° C. but that it is destroyed by warm sodium carbonate.

Mytilotoxin is a poisonous compound which Brieger (1886, 1888, 1889) succeeded in isolating from the livers of toxic mussels. Its formula according to his determinations is $C_6 H_{15} NO_2$. This compound, Brieger claims, is the specific curare-like active toxin of the sea mussel.

The method of extracting the mytilotoxin is as follows: Several hundred of the pathologic mussels are heated in water with some hydrochloric acid, and the mixture is then filtered. The poisonous compound is in the filtrate as hydrochloric mytilotoxin. This filtrate is evaporated to dryness, and the residue is dissolved in alchool. The alcoholic solution is neutralized with sodium carbonate, then acidified with nitric acid, and

gradually precipitated with phosphomolybdic acid. The first precipitate which comes down contains albumin bodies and color substances, while that which is precipitated later contains the mytilotoxin. This latter precipitate is dissolved in a solution of lead acetate, slightly warmed and filtered. The filtrate is treated with hydrogen sulphide to remove the lead and then evaporated after adding some hydrochloric acid. The residue is dissolved in alcohol and reprecipitated with platinic chloride. The filtrate then contains the mytilotoxin which may be precipitated by means of gold chloride after first removing the platinum with hydrogen sulphide.

The mytilotoxin forms a double gold salt which crystallizes into minute cubes having the composition $C_6H_{16}NO_2AuCl_4$. They have a melting point of 182° C. With the ordinary alkaloid reagents mytilotoxin gives oily precipitates only. It was further found that when the hydrochloric mytilotoxin is distilled with potassium hydroxide trimethyl amine $N(CH_3)_3$ is produced. Brieger therefore says that mytilotoxin is a quaternary base and its power to paralyze the motor apparatus is no longer surprising since it has been demonstrated by Glause and Luchsinger (1884) that all trimethylammonium bases produce muscarin effects.

If the hydrochloric acid extract of poisonous mussels is boiled with some sodium hydroxide a nauseous odor is liberated. Brieger recommends therefore that this method be used as a test for mussels which may be under suspicion.

In addition to the mytilotoxin Brieger found several other substances of a basic nature, some of which are poisons. Among these is the nonpoisonous betain—oxyneurin, trimethylglycin, $(CH_3)_3$. NOH. CH_2. CO_2H. The mytilotoxin may arise from the betain by introducing the radical CH_3, which may be represented by the following formula: $(CH_3)_3$. NOH. $CH(_3)$. CO_2H. This relationship, however, is not at all clear.

In support of the above observations, Cameron (1890), in attempting to extract an alkaloid from some poisonous mussels which came under his observation, clearly proved the presence of a leucomaine which was obtained in crystals visible under the microscope. These crystals corresponded to those described by Brieger and were considered as identical with them.

On the other hand, Thesen (1902), who investigated a large number of poisonous mussels from the haven of Christiania, was unable by the Brieger method to identify the poison with that of Brieger's mytilotoxin. Griffiths (1890), who studied a case of mussel poisoning at Dublin, Ireland, states that the effects were undoubtedly due to the action of alkaloids (ptomaines) which were developed by the action of microbes in the muscles of the shellfish. The poisonous compounds formed, he says, are all members of the pyridine and hydropiridine organic bases. We are therefore still uninformed as to the exact nature of the mussel poison, and further research on this subject should be encouraged.

Jourdain (1891) believes that mytilotoxin is always present in Mytilus and that other ptomaines are always present in other shellfish, such as the oyster, which often causes poisoning of a serious nature. The quantities of these toxines present, however, is rarely ever sufficient to be injurious.

Mytilocongestine is a toxic substance which has been extracted from the bodies of *Mytilus edulis* by Richet (1907, 1907a). It is analagous to the congestine which he obtained from the bodies of Actinians, and was therefore given the name of mytilocongestine. It is prepared by grinding up frozen mussels with sand and water; the product is filtered

as quickly as possible and precipitated with three times its volume of alcohol. The precipitate is dissolved in water, filtered, and reprecipitated with alcohol. This precipitate is collected on the filter and washed with alcohol and then allowed to dry. A white powder is obtained which browns a little in the air and which almost completely dissolves in water. When precipitated again the substance is obtained in pure form, but naturally the quantity is very small, scarcely more than 5 g. from 24 kg. of mussels.

When injected intravenously into dogs it produces diarrhea, bloody stools, rectal pain, vomiting, prostration, and decrease of arterial pressure. Autopsy reveals an intense hemorrhage of the mucous digestive lining, including the stomach and rectum. The poison produces the phenomenon of anaphylaxis; that is, the animal can withstand a comparatively heavy dose at the first injection, but a short time after that it becomes extremely sensitive and dies when injected a second time with a small fraction of the original amount. The difference in sensitiveness to the mytilocongestine between normal and anaphylactic dogs was found to be about 1:25, while in an extreme case it was 1:100.

CONCLUSION.

What has been stated above furnishes no evidence to support the assumption that the sea mussel is a dangerous food, but it sounds a warning that it is just as capable as the oyster or any other shellfish of transmitting typhoid fever if it is taken for consumption from waters polluted with sewage containing the germs of this disease; and that if taken from water so stagnant that it makes the fishes and eels which inhabit it lose almost all their vitality, as was the case at Wilhelmshaven, then it is apt to contain a poison which is rapid and severe in its effects. It should be borne in mind, however, that mussels possessing this poisonous quality are very rarely met with, and to the knowledge of the author have never been discovered on either the Atlantic or Pacific coasts of the United States.

Finally, let it be noted that all sea mussels which have been found unwholesome or dangerous to human health have come from waters polluted with sewage, from stagnant basins, or were exposed to the heat of the sun for such a long period that ptomaines were able to develop in the liquid held within the shell. On the other hand, mussels from pure water subject to the ebb and flow of the tides have always been found wholesome and delicious articles of food. If selected and marketed with due regard for the facts already mentioned, it is probable that their use in this country will never be accompanied by the disasters which have occurred in certain localities of Europe.

CULTIVATION OF MUSSELS.

In the past few years there has been considerable talk of the sea farms of the future. It has been predicted that the fisherman will grow his oysters, clams, lobsters, etc., under artificial cultivation in a manner similar to that employed by the farmer in raising his crops. The idea, however, is not new, for centuries ago, in the year 1235, a shipwrecked sailor was rescued at the point of Escale, about a mile and a half from Esnandes, France, where, in order to earn a livelihood he devised a system of myticulture that has yielded wonderful results. The method proved so successful that it has been continued to the present day in this locality, where it gives support to 3,000 or more inhabitants of the villages Esnandes, Marsilly, and Charron. If one should visit this locality in the Bay

of Aiguillon he would find hundreds of men and women busily engaged day and night, whenever the tide permits, attending to their mussel farms. The spectacle of the army of mussel culturists going to and from their work is said by Coste (1883) to be most curious and grotesque, impossible to portray. With their peculiar types of foot canoes, which will be described later, they glide back and forth over the slippery surface of the mud like a flock of birds driven by the tide, in and out of the mazes formed by the 6,000 palisades which cover the marsh. They speak of the various operations of the industry in agricultural terms, such as sowing, planting, transplanting, weeding, pruning, and harvesting.

Patrick Walton, the founder of the method of mussel cultivation now practiced in France, was a native of Ireland and a sailor by trade. In the fall of 1235 his ship was driven by a northeast gale onto the rocks at the point of Escale near the port of Esnandes. Of the three sailors aboard the ship, Walton was the only one saved, and that was due only to the timely help offered by the fishermen who lived on the coast. Having lost practically everything that he possessed, and being without means for returning home, there was nothing to do but look for a means of subsistence in that place. Previous to his arrival the French fishermen had made poor success at earning a livelihood from the sea, but Walton with his great ingenuity was able to devise a means which not only gave him bountiful support but has proved a lasting legacy to all the inhabitants of that coast.

With the mind of an investigator Walton, seeing the great lake of mud before him, examined it to see if it could be turned to any profit. The problem of getting over the mud through which it was impossible to walk was solved by the invention of his "acon," or foot boat. This device is made of a plank about 10 feet long by 2½ feet wide bent up in front to form the prow. The sides and stern are each composed of straight boards about 1½ feet wide. The boat is further reinforced by a shelf in the stern and a narrow thwart close to the bow. A board may extend across the middle to serve for a seat or it may be replaced by a wooden stool. A paddle and short pole complete the equipment. When the boatman wishes to travel over the mud flats he faces the prow of the boat, puts his left knee on the bottom, and thrusting his right leg, incased in a long sea boot, over the side of the boat, pushes it along (fig. 221, 4*B*, opp. p. 236). By this means he is able to glide over the mud at a very rapid rate. Coste (1883) says the speed attained with one of these boats is equal to that of a trotting horse. With this foot boat the inventor was able to explore every part of the marsh. He could propel it over the mud by means of his foot, through shallow water by means of the short pole, and when deeper water was reached he could use the paddle.

The first thing which attracted Walton's attention was that a large number of land and sea birds were in the habit of skimming over the water in the evening. He promptly determined to catch them as an object of trade. In order to do so he invented a second device, the "alluret," a large net 1,000 to 1,200 feet long and 10 feet wide suspended in a vertical position on stakes driven into the mud for a distance of 3 or 4 feet. Birds flying into its meshes became entangled and were held securely. After his nets had been up a short time Walton discovered that young mussels were attached to the stakes in great numbers. He observed that they grew more rapidly than those on the mud and furthermore were better flavored. With this new discovery

he began putting down more stakes in various places and watched for the result. These also, in turn, became covered with growing colonies of mussels. Continuing his observations, he soon concluded that the young of native mussels could be collected and profitably raised under artificial conditions. The result of his investigations was the establishment of the bouchot system of mussel culture for which France has become famous.

The bouchot system as finally perfected by Walton consists of rows of stakes arranged in the form of a V, with its apex pointing toward the sea or the direction from which the strong waves and tide come. This arrangement is to protect the structure from the destructive action of the wind, waves, and ice. The stakes are trunks of trees 6 to 12 inches in diameter and from 10 to 15 feet in length. They are placed from 2 to 3 feet apart and driven into the mud for about half their length. Then branches of osier or chestnut are twisted back and forth between the posts in horizontal rows about 20 inches apart from the top to within a foot of the bottom. If placed closer together than this they are apt to accumulate mud and cause deposition of silt. Walton left an opening from 3 to 4 feet wide at the apex of the two wings where traps were placed to catch the fish which went out with the tide, thus making the structure serve a double purpose.

The length of the wings depends on the size of the area covered by the tide, which is about one-fourth of the distance between the extreme limits of high and low tides. At the present time in the Bay of Aiguillon they are about 250 yards in length but are no longer arranged in the historic V form. According to Herdman (1894) they are now arranged at right angles to the shore in parallel rows about 30 yards apart, as is shown in figure 221, 4.

The bouchots are arranged in three series, according to the particular function each is to perform. One set consists of large solitary stakes placed about 1 foot apart out in deep water where they are uncovered only by the lowest tides. These serve for the collection of spat and are known as the bouchots d'aval, or low crawls (fig. 221, 2).

The second series of bouchots is placed halfway between tide marks and serves for the growth and fattening of the mussels. Several rows of crawls, each with a separate name, may enter into this series. The general term applied to this group is the bouchots batards, or false crawls (fig. 221, 3).

The third series of bouchots is in the upper limits between tide marks where they are exposed several hours each day during low water. These crawls are known as the bouchots d'amont and serve to inure the mussels to exposure and consequently make them keep longer and fresher than those from the lower rows (fig. 153, 4).

The method of working the bouchots is to collect seed mussels and transfer them successively from the lower to the higher bouchots at the proper times. The spat is liberated in the Bay of Aiguillon during February and March and is caught on the low crawls which are situated in an ideal position for the preservation and growth of the young shellfish, since they are rarely exposed to the air. When such an event does occur it is for a short time only. When the set of spat first appears the young mollusks are smaller than a grain of flaxseed and are called *naissan*. The young mussels grow rapidly so that by July they reach the size of an ordinary bean. In this condition they are termed *renouvelain*. They are then ready for transplanting.

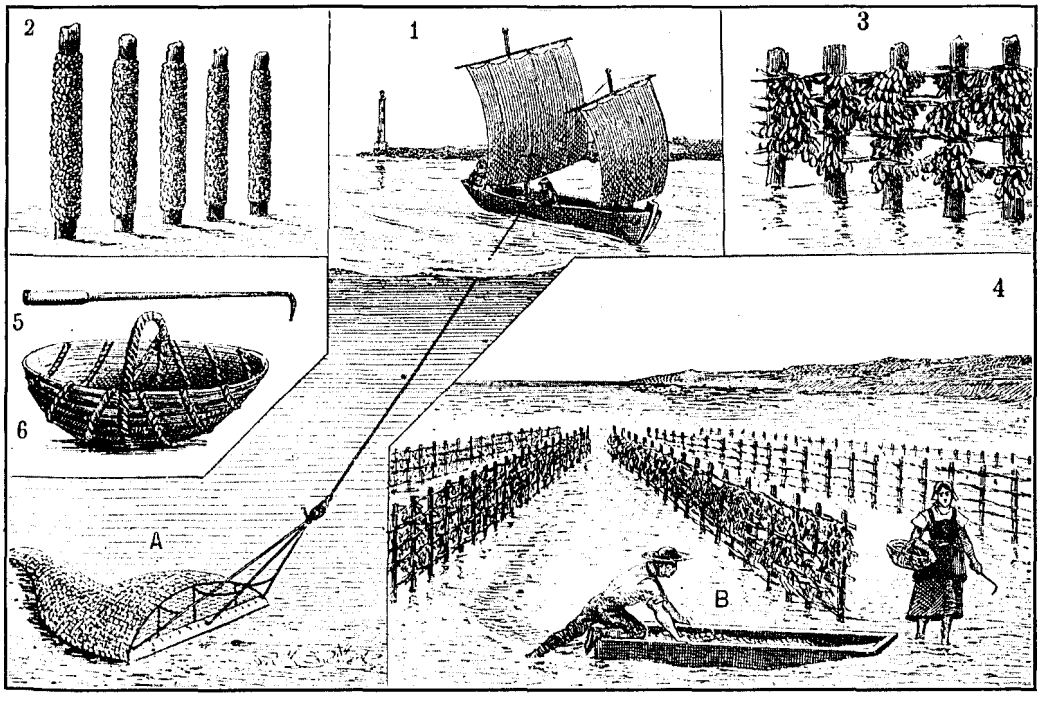

FIG. 221.—Cultivating mussels in France. 1, Method of collecting mussels by means of a dredge, *A*; 2, bouchot d'aval; 3, bouchot batard covered with mussels; 4, view of a series of bouchots d'amont showing mussels under cultivation and mussel fisherman operating his acon, *B*, which is used for transporting mussels over the mud flats; 5, iron hook used in collecting seed mussels; 6, basket for receiving mussels. (After Nouveau Larousse Illustré Dictionnaire Universal Encyclopédique, Paris.)

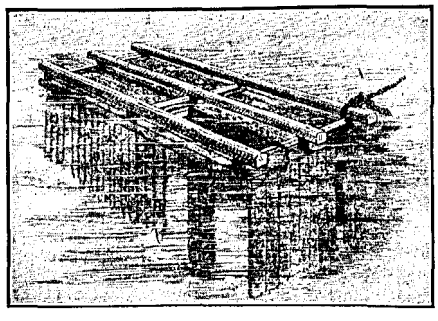

FIG. 222.—A raft collector for catching spat and rearing mussels. (After Fraiche, 1883.)

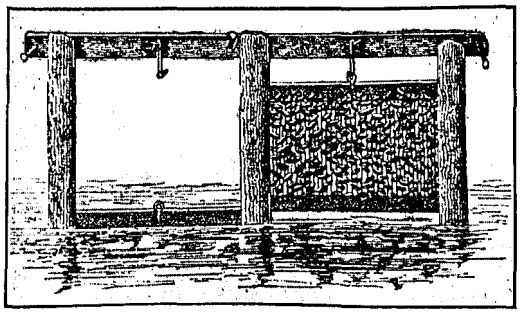

FIG. 223.—A claie or movable wooden frame used for growing mussels in the Lamotte canal near Marseilles. (After La Grande Encyclopédie, Paris.)

The seed mussels are collected by means of a hook set in a handle like the one shown in figure 221, 5. A characteristic type of basket (fig. 221, 6) is used to receive them and is filled with the young shellfish to the limit of its capacity. When the baskets are filled they are transported by means of the "acon" to the bouchots batards, where parcels of the young mussels are tied to the wickerwork of the frames by means of old netting. The shellfish immediately begin to attach themselves to the wooded structures by means of their byssal threads, so that by the time the netting has rotted or washed away, they are firmly united to the crawls.

The rate of growth in this position is very rapid, and in a few months they become so crowded as to almost hide the frames. It then becomes necessary to transplant them again, this time to the next series of crawls lying nearer the shore. The mussels are attached by the same method used in the first transference, but are not fastened so securely, since they are able at this stage to attach themselves to the bouchots much more quickly. After one year's treatment on the crawls the mussels reach a length of 1¾ to 2 inches, which is marketable size.

The net returns from an investment in a series of bouchots has been published by Fraiche (1863) and Coste (1883), showing that it is approximately 11½ per cent. To quote from Coste, the production and value of cultivated mussels in the Bay of Aiguillon is as follows:

> A bouchot well stocked, furnishes generally, according to the length of its wings, from 400 to 500 loads of mussels; that is to say, about 1 load per meter. The load is 150 kilograms, and sells for 5 francs. One bouchot, therefore, produces a crop weighing from 60,000 to 75,000 kilograms, and valued at 2,000 to 2,500 francs; from which it follows that the crop of all the bouchots united would weigh about 30,000,000 to 37,000,000 kilograms, which at the figures already given would be worth about 1,000,000 to 1,200,000 francs. These figures and the abundant crops from which they result give an idea of the food supplies and of the great benefits that may be derived from a similar industry, if, instead of being confined to only one portion of the Bay of Aiguillon, it should be extended to the whole of it, and carried from the locality where it originated to all the coasts and salt water lakes where it could be successfully carried on. In the meantime the prosperity which it secured to the three communes of which it has become the patrimony will remain as an end worthy of effort; for, thanks to the precious invention of Walton, wealth has succeeded to poverty, and since the industry has been developed here no healthy man is poor. Those whose infirmities condemn them to idleness are cared for in most generous and delicate manner by the others.

Other methods of mussel cultivation have been suggested and are being used in France. Fraiche (1863) states that this shellfish can be raised in claires or artificial reservoirs the same as oysters, especially in places where the abundance of mud and silt renders oyster culture impossible. The settling basins of the oyster claires in particular can be utilized for this purpose, if proper care is taken to exclude the mussel spat from the inner reservoirs during the season of reproduction.

A modification of the bouchot method of myticulture is employed in a part of the Lamotte Canal near Marseille. This canal is one of the branches which puts the sea in connection with Berre Lake and is traversed back and forth continually with the tidal waters, which contain great quantities of diatoms and Infusoria, making it an especially rich place for the cultivation of mussels. Because of the slight rise and fall of the tide in this stream, it is impossible to use here the bouchot system of culture. In place of it, claies, or movable wooden frames, are placed vertically between grooved stakes on

which they can rise and fall by means of a floating axis. The grooved stakes are mounted with a crosstree bearing a ring on the underside. The frame is surmounted with a hook so that it can be raised from the water and hung on the ring of the crosstree above (fig. 223, opp. p. 236). With this device the mussel culturist can at any time gather, replenish, wash, or do any necessary work at his convenience, and when through, return the frame to the water.

The capacity of one of these claies is about 10,000 mussels, weighing from 660 to 880 pounds. The young mussels are collected on the shores of Berre Lake and placed on the claies by the same method employed in fixing seed mussels to bouchots. When of sufficient size they are marketed without any further transplanting.

Still another means for collecting spat and rearing mussels is by means of the raft collector (fig. 222, opp. p. 236) recommended by Fraiche (1863). It consists of a raft from which hang planks or frames in a vertical position. It is anchored in a region where mussels are spawning and when covered with spat is towed to a breeding basin where the rearing can take place without any further care than to see that no mud accumulates on the frames. The chief objection to this contrivance is that the planks or frames decay rapidly, often causing an entire loss of the harvest. This difficulty can not be remedied, as some have thought, by replacing the wood with metal, because spawn will not set on it.

Myticulture is also practiced in Italy, especially in the vicinity of Taranto, where mussels are raised to supply the southern markets of the peninsula as far north as Rome. Here the shellfish are cultivated on ropes made from rushes or "alfa" suspended in the water from stakes, which are placed from 20 to 30 feet apart, depending on the depth of the water. The ropes are hung over the mussel beds close to the shellfish in order to catch the free-swimming young. Six months after a set of spat has occurred the ropes are taken up and all the shellfish on them which have attained the size of an almond are removed. The smaller ones are left to grow until the following season, when they will have attained sufficient size for food purposes. The larger mussels selected are interlaced, either singly or in bunches, into ropes which are then suspended vertically in the water from a main rope extending between two stakes planted out in deep water. Parks are also utilized in the culture of mussels by this means, some of them extending 2,600 to 2,925 feet into the sea. Bouchon-Brandely (1883) states that the yearly yield of such a park is 40,000 to 50,000 pounds, worth from $880 to $1,100.

In Germany the Bay of Kiel contains extensive areas where mussels are raised by artificial means. The method employed there is to drive stakes into the bottom and leave them there for a period of three to five years, during which time they become covered with mussels of marketable size. They are then taken up, stripped of the shellfish, and replaced by others. About 1,000 stakes are planted annually in this locality, from which the yield of mussels amounts to about 800 tons.

The systems of myticulture which have been described above are especially adapted for regions where the bottom is composed of mud too soft to support a bed of mussels and where there is considerable rise and fall of tide over large areas. Where the bottom is hard or covered with only a thin layer of mud and where silt is not being deposited too rapidly, a much more economical method of cultivation is merely to transplant the mussels from crowded situations to more extensive areas where food is abundant. It is in this manner that mussels are grown for market in England and for that reason it

is often spoken of as the British method to distinguish it from the bouchot system or French method. The practice is to collect young mussels from salt water and sow them on artificial beds in favorable localities. The best regions for planting are rich estuarine flats where there is plenty of sand and gravel covered with mud rich in diatoms, Infusoria, and spores of algæ. Care is taken to avoid planting the beds where they will be uncovered at low tide or subject to the ill effects of floods, gales, shifting sands, or frost. Furthermore, the individuals should not be placed so near together that one must lie on another. In this crowded condition the food supply is cut off from a large number of the shellfish and death or arrested development results, destroying the good effects of transplanting.

Harding (1883) and others believe that the spat will not mature in anything but pure sea water, but that for fattening the full-grown mussel brackish water of the density 1.014 is the most suitable. It is very doubtful, however, if brackish water is advantageous in perfecting the development of the mussel. The finest mussels ever seen by the author were cultivated in the water of the open ocean where there was no dilution with fresh water. In Menemsha Pond, Marthas Vineyard, Mass., where the mussels are fat and of unusually large size, the specific gravity of the water varies from 1.021 to 1.023. In this particular locality the author has found many individuals which exhibited an annual growth of an inch in length for the first three years of their existence. In Oyster Bay and Long Island Sound first-class mussels of excellent quality are grown in water where the density varies from 1.017 to 1.018. In these localities there is some dilution of the sea water, but not to the extent recommended by Harding.

The advantages of the bed system of cultivation are now being recognized in other countries. Bjerkan (1910) is recommending this method in Norway and figures samples of transplanted shellfish to show the splendid results obtained. Figures 192 and 193 (opp. p. 202) are views of an old mussel which had shown little or no signs of growth for years, but when transplanted added on the new portion of the shell, which is conspicuously shown in the photograph. Figure 191 (opp. p. 202) represents the exceptional growth which took place in a young mussel during a period of seven months after being transplanted at Morecambe, England.

Some of the progressive fishermen in this country have also recently put the transplanting method into practice with great success in certain regions of Long Island Sound. In one case a fisherman was paid by an oysterman to remove great quantities of mussels which were growing on and about his oyster beds. The fisherman carefully planted them at the mouth of Oyster Bay and three years later dredged them up by the hundreds of barrels, which he marketed in New York City at $1.25 per barrel. After paying all his expenses he found that he had left a net profit of $0.75 per barrel. For two months he was able to ship 100 barrels a day, which will indicate the income he was able to derive from the business. It is needless to say that this man is still cultivating mussels.

For harvesting the mussels a rake or dredge is used. In England the rake is recommended as the better instrument to employ for the reason that it does not crush the shells nor stir up sand over the bed. In size it has a breadth of about 18 inches, with teeth 1 inch apart. It has a handle 20 to 25 feet long and a wire net bag attached behind it for holding the catch. The mussels are sorted by means of a riddle, which is a sieve having a 1-inch iron mesh. After the mussels have been separated by hand

they are sifted in the riddle. The large ones are taken for the market and the small ones replanted.

The yield from a crop of mussels properly cared for is something enormous and difficult to comprehend. In agriculture, corn is considered one of the most prolific and valuable of farm products, producing on the maximum 246 bushels to the acre. If marketed at $0.75 per bushel, the farmer realizes $184.50. However, when compared with a crop of mussels this yield appears small. Harding (1883) estimates for the English beds that the average yearly production is 108 tons per acre, worth at least $262. George A. Carman reports that the artificially planted mussel beds in the vicinity of New York produce from 4,000 to 6,000 bushels per acre, which at the market price of $0.40 per bushel amounts to from $1,600 to $2,400. Allowing three years for the growth of these beds, it leaves an annual average income of from $500 to $800 per acre. Furthermore, the time and labor required to plant and care for an acre of mussels is almost nothing compared with that expended by the agriculturist in raising his grain.

To the question, "which is the better method to use for cultivating mussels in the United States, the bouchot system or the bed system?" it is safe to answer that the latter is the only reasonable and practical one to attempt. There are probably few, if any, places on our coast where the bouchot could be utilized, and even if there were such places the cost of building materials and of labor are so high compared with the value of the shellfish that the method would prove unprofitable. On the other hand, we have thousands of acres along our shores that are adapted for mussel beds, with plenty of seed with which to plant them. The experiment of transplanting, as described above, has been tried, and it has proved not only successful but exceedingly profitable. Cultivation by means of the bed system is therefore the one to be recommended for use in this country.

DURATION OF MUSSEL BEDS.

One of the important facts brought out from the study of mussel beds is that, in general, they are short lived. Vast areas of bottom suddenly become covered with countless numbers of the shellfish, and three or four years later little or no trace of the bed can be found. George A. Carman, of Canarsie, N. Y., reported one bed in Jamaica Bay from which he took fine healthy mussels on one occasion and, on returning for a second load about 10 days later, found that practically all of the mussels were dead. A number of the Long Island oystermen stated that in their experience the average life of a mussel bed was three to four years.

In the course of the reconnaissance conducted during the summer of 1917 more than 3,000 acres of mussel grounds which had been reported on the best of authority were found to contain nothing but dead shells or no traces of mussels ever having been present. These reports included two beds on the north side of Long Sand Shoal, aggregating about 600 acres in extent, one in Fishers Island Sound between Latimer Reef and Eel Grass Ground of 500 acres, one at the mouth of Fort Pond Bay of 1,000 acres, one in Orient Harbor of 50 acres, and one off Sandy Hook of considerably more than 1,000 acres. In the case of the Sandy Hook bed, which bordered the south side of the Main Channel and Gedney Channel from a point 1 mile east of bell bouy 5 on the Main Channel to light buoy (Occ. W) 5 on Gedney Channel, a distance of nearly 2 miles, George A. Carman had reported finding a dense growth of 2¾-inch mussels in the fall of 1916

which he thought would be ready for the 1917 market. With his services as a guide, a series of dredgings was made the entire length of the bed, with the result that not a single large mussel was taken. A heavy set of young mussels from three-eighths to three-fourths of an inch long, however, was found to cover the entire territory. The explanation for the complete disappearance of the old bed was that during the heavy storms of the winter the tidal currents and wave action had been strong enough to strip the shellfish from the bottom and carry them to distant points.

Other causes which account for the damage or destruction of beds are freshets, shifting sand and ice, freezing of mussels exposed at low tide, depredations of starfish, drills, and other enemies, and suffocation from the mussels' own excrement. It is well known that mussel beds collect great quantities of mud, but few persons have realized that this mud, in large part, represents the excrement discharged by the mussels themselves. To determine roughly the quantity of waste matter which is thrown off by mussels daily, twenty-five 3-inch mussels were placed in a clean trough of slowly running sea water where the body discharges could be collected with a pipette from time to time. During a period of 72 hours the excrement given off measured 3,065 c. mm. Its composition, as revealed by the microscope, was diatom shells and detritus. This means that where mussels of this size lie no thicker than 500 to the square yard they discharge not less than 20 cc. of feces daily, and if this rate is maintained throughout the year the result would be an annual deposit of 7,000 cc., or about 1 peck, of the muddy matter per square yard. Viallanes (1892), making similar observations, states that in proportion to the numbers covering the same area of ground the mussel will deposit 3 times as much material as a Portuguese oyster and 18 times as much as a French oyster. Knowledge of this fact makes it easy to understand how a mussel bed, in a few years time, can build up a thick layer of mud and be destroyed by its own waste products.

Under natural conditions a uniform supply of mussels can not be depended upon, for, as past history has shown, there are years when they are exceedingly abundant and others when they are very scarce. The problem of maintaining a large and constant supply can be easily solved, however, by transplanting the young shellfish from exposed natural beds to favorable grounds in protected bays and estuaries as is now being practiced in Cold Spring Harbor. Minimum waste will occur where cultivated beds are completely cleaned up when ready for market and promptly planted again with seed mussels. The mortality rate will be low on beds that are permitted to stand not more than three years. Hard bottom is the most convenient ground on which to grow and handle a crop of mussels, but the shellfish will thrive equally well on mud bottoms which are unfit for oyster culture. The chief objection to raising mussels on mud is that it increases the cost of gathering and preparing them for market.

EFFORTS TO DEVELOP A MUSSEL INDUSTRY IN THE UNITED STATES.

Recognizing the importance of the extensive sea-mussel beds on the north Atlantic coast as a valuable source of food supply and the fact that as a nation we are failing to utilize them through ignorance or unreasonable prejudice, the Bureau of Fisheries undertook a limited publicity campaign in the spring of 1914 to acquaint the people of Boston and vicinity with the food qualities of this little-known shellfish. A 5-page pamphlet for public distribution was issued March 24, 1914, under the title "Sea

Mussels: What They Are and How to Cook Them," U. S. Bureau of Fisheries Economic Circular No. 12. It bears the photograph of a sea mussel on the first page, states briefly the magnitude of the sea mussel industry in Europe, points out the close relationship of mussels to clams and oysters, and shows that as a food they are delicious, nutritious, wholesome, and cheap when properly collected, handled, and prepared. The account concludes with a list of 18 recipes furnished by the French chef of a prominent Boston hotel. Some placards, 14 by 20 inches in size, were printed in heavy type with the words:

SEA MUSSELS

A CHEAP AND NUTRITIOUS FOOD

Recommended by

U. S. BUREAU OF FISHERIES

These were loaned to reputable fish dealers to put in their store windows, with the understanding that they should market mussels collected from waters knows to be free from pollution. In some cases this card of indorsement, with a hundred of the economic circulars, was all that was necessary to start a fish dealer in the mussel business. This was especially true in localities populated with English or French people, who possessed knowledge of their importance as a food in Europe.

Another method employed to get the shellfish before a large class of persons was to serve them on the tables of many first-class hotels, restaurants, and clubs. Boston offered the best opportunity for starting such a campaign, for in one of her leading hotels there was a French chef, Charles Doucot, whose enthusiasm for the mussel knew no bounds when he learned that the species could be procured on the New England coast. He had served them formerly in his father's Paris restaurant and was eager to be the pioneer in getting them introduced into the Boston hotels and eating houses. The Bureau arranged to furnish mussels without charge to every first-class hotel, club, and restaurant in Boston on the condition that they be given a prominent place on the menu card and the patrons urged to order them. The success of the plan surpassed expectations, largely due to the energetic support given the movement by Mr. Doucot, who was then president of the Boston Chefs' Club. In this influential position he persuaded the chefs of practically every first-class hotel, club, and restaurant in Boston to put sea mussels on their bills of fare. The newspapers appreciated the importance of the propaganda and with the active support of Mr. Doucot devoted considerable space from day to day to the campaign and the merits of the mussel as a food.

To bring the food value of the mussel to the attention of another large class of people who do not commonly eat at hotels and restaurants, the Bureau placed a barrel of the shellfish in each of the Boston police stations for free distribution to members of the force. As was expected, the chief topic of conversation on the following day, as the men went over their beats, was concerning the qualities of the "new sea food." The plan proved very successful in bringing the food to the attention of the general public for a short time.

In Lowell, Mass., the Bureau developed a market for mussels quickly by cooperating with the Y. M. C. A. in its educational lecture course. An agent of the Bureau arranged

for a dinner in the association building at which mussels were made the conspicuous feature. The dinner, which was well attended, was followed by an illustrated lecture on the biology and economic importance of the sea mussel. The event was well advertised beforehand, and briefs were furnished to the newspapers of the city. The fish dealers were prepared with a fresh supply of mussels, a sufficient quantity of economic circulars containing the recipes for cooking them, and the placards bearing the recommendation of the Bureau of Fisheries. Persons who purchased mussels were presented with a circular. As a consequence the whole city was eating or talking about mussels on the day following this active campaign. Similar dinners, followed by a lecture, were given in one of the large Worcester churches and the Brockton (Mass.) Y. M. C. A.

The general result has been to create what promises to be a permanent and growing demand for this shellfish. In Boston a year after the campaign many dealers who never handled them before were selling mussels and were getting higher prices than had prevailed previously. In Worcester several of the markets experienced a growing mussel business, and the conditions were apparently the same in Lowell. Brockton seems to be the only place where the people could not be persuaded to eat them. A Providence dealer reported a considerable increase in his mussel sales, which he attributed to the publicity given the campaign by the newspapers. Pushcart venders in Boston have been selling them, and doubtless many other parties not known to the Bureau have taken up the business. The demand on the Narragansett Bay beds, which were hundreds of acres in extent, was so heavy during the campaign that the Bureau was lead to believe it unwise to continue the publicity work further until new sources of supply were found available.

In the summer of 1917 the writer was directed by the Bureau to make a reconnaissance of the mussel beds on a limited portion of the north Atlantic coast, with the object of locating positively beds which were sufficiently large and productive to support a commercial fishery and to collect data concerning their areas, depth of water over the beds, abundance, size, and quality of the shellfish, and also to consult with local fishermen to ascertain if they would engage in the fishery for mussels provided there should be a market for them. The territory examined included Plymouth Harbor, Mass.; Narragansett Bay, R. I.; and the north and south shores of Long Island, N. Y. Approximately 3,715 acres of mussel beds were located and charted. Of this area it was estimated that about 1,000 acres of the shellfish, containing not less than 2,000,000 bushels, were ready for the immediate market and that 1,500 acres would yield 1,000,000 bushels of seed mussels less than 1 inch long. The rest of the area was occupied by old beds which were depleted or mixed with such a great quantity of dead shells and trash as to make working them unprofitable commercially. The survey was necessarily incomplete owing to the brief time allotted for it, but was sufficient to show that for the time there was an abundant supply of mussels available immediately for the market besides vast quantities of seed mussels which could be transplanted to favorable situations and made ready for future needs.

In the year 1914, while the Bureau of Fisheries was engaged in placing the merits of the fresh sea mussel as a food before the public in Boston and vicinity, an oyster company in Providence was conducting some important experiments on the preservation of mussels by pickling and canning. Splendid samples in the form of canned mussels, pickled mussels, deviled mussels, or Muscello, and mussel cocktail were produced. The

materials used were of excellent quality and they were put up in a most attractive manner. Except for minor defects, such as using wrong proportions of vinegar and spices in their preparation, which could be readily corrected, the products were of superior quality and promised to find a good market if properly advertised. But unfortunately the president of the packing company grew pessimistic about the possibilities of the business and stopped the packing of mussels without making any serious attempt to put them on the market.

The method employed in handling the shellfish for canning purposes as worked out by this company is recorded here because of its historic importance in marking the first step toward developing a mussel-canning industry in the United States.

For collecting mussels the same equipment is employed as in the oyster fishery, since the shellfish grow under essentially the same conditions as oysters, on the bottom and in water of varying depths from between tide marks to 100 feet. In Narragansett Bay most of the beds lie in from 10 to 60 feet of water. The principal difference in character between mussel and oyster beds that has to be taken into consideration in harvesting methods is that in the former the shellfish lie together much more thickly, are firmly attached to each other by byssus threads in the form of a carpet, and often accumulate much mud, while in the latter the shellfish are loosely distributed over a clean, hard bottom.

The type of oyster boat shown in figure 224 furnishes the most efficient means of collecting mussels. It is propelled by a gasoline or kerosene engine and carries two 5 to 7 bushel oyster dredges that are operated by power and manipulated from the pilot house. They are situated on the forward deck, one on each side of the boat. To operate the dredges successfully on a mussel bed requires both skill and experience, for if not enough warp is let out the dredge will slip over the surface of the shellfish, which are woven together, without picking them up, while, on the other hand, if too much warp is let out the dredge will plunge deep into the mud and fill with it to greater extent than with mussels. This involves a waste of time, labor, and energy to separate the mussels from the mud, which is accomplished by alternately raising the filled dredge from the water and dropping it back again. Two men are stationed on the deck to receive and empty the dredges as fast as they come up. Properly manipulated on a good bed of mussels, a boat equipped with two 7-bushel dredges can take on a load at the rate of 150 bushels per hour.

The mussels thus collected and brought to port are bound together in tangled masses and mixed with dead shells, mud, and much débris. A device for tearing the individuals apart and separating them from the foreign matter was devised from a standard coal screen over which there was made to play jets of water, as shown in figure 225. Mussels dumped into one end of the revolving screen are tumbled about, torn apart, and freed from débris by the running water.

After this preliminary treatment the shellfish are shoveled upon a shelf where they are rapidly culled by hand (fig. 228) and then given a final washing in a cylindrical screen which revolves, partially submerged, in a tank of water (fig. 226). After this cleansing they are placed in wire baskets, such as shown to the right in figure 226, and transferred to a steam chest or process kettle (fig. 227) which holds about 15 of the bushel baskets. When filled, the lid of the kettle is clamped in place, and this completes the preparation for cooking.

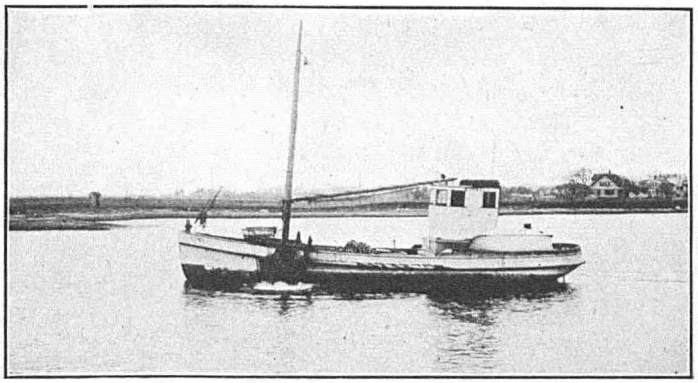

FIG. 224.—Oyster boat dredging up mussels in Narragansett Bay.

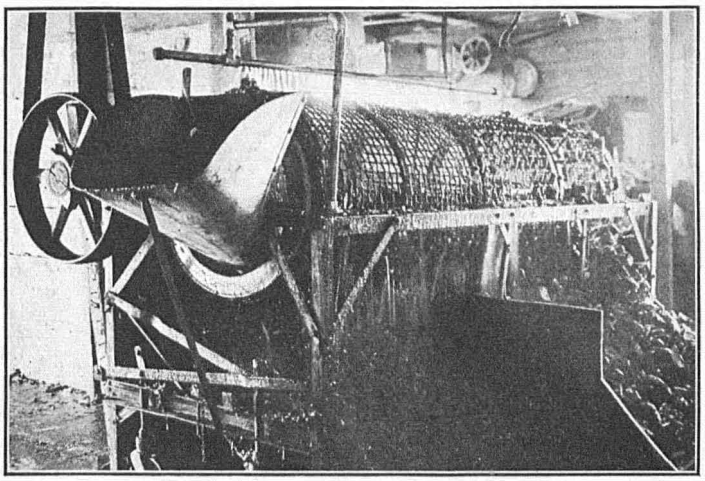

FIG. 225.—Modified coal screen used for cleaning and separating mussels.

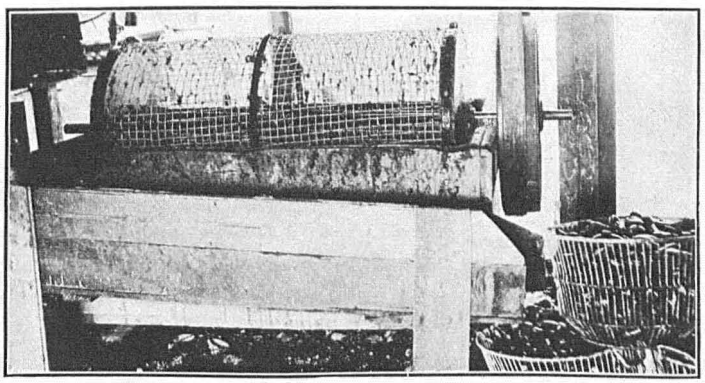

FIG. 226.—Revolving screen cylinder in tank of water used for final cleansing of mussels. Wire baskets for holding mussels are shown at right.

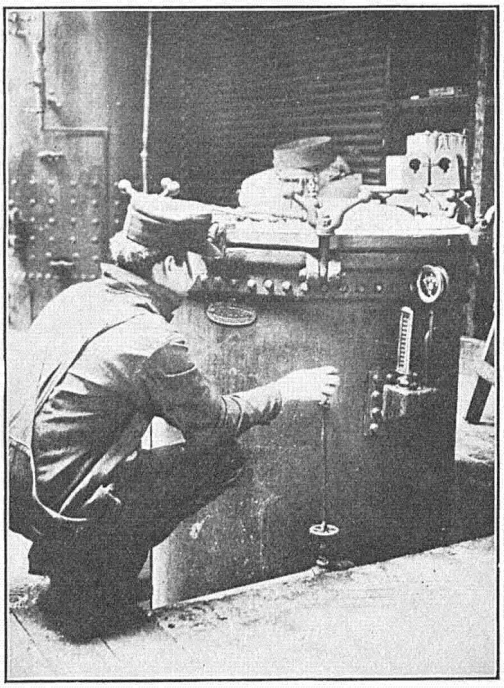

FIG. 227.—Steaming mussels in a process kettle.

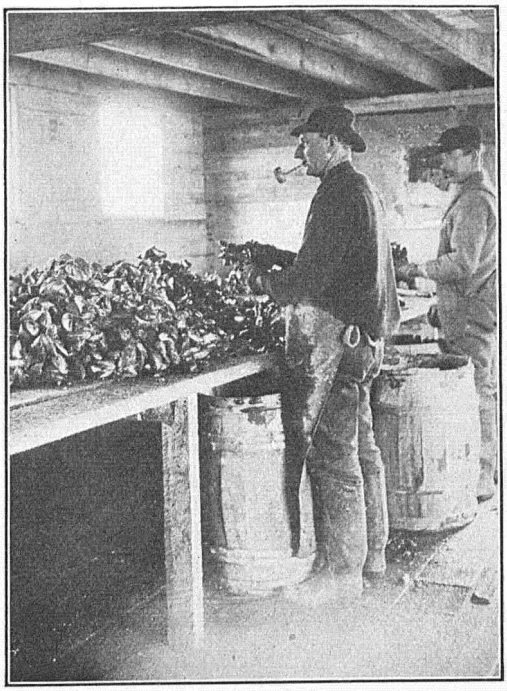

FIG. 228.—Culling mussels by hand.

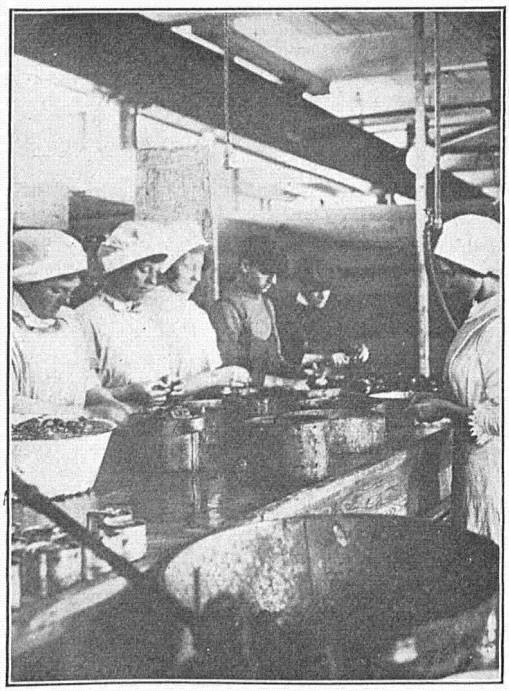

FIG. 229.—Girls shucking steamed mussels which are to be canned or pickled.

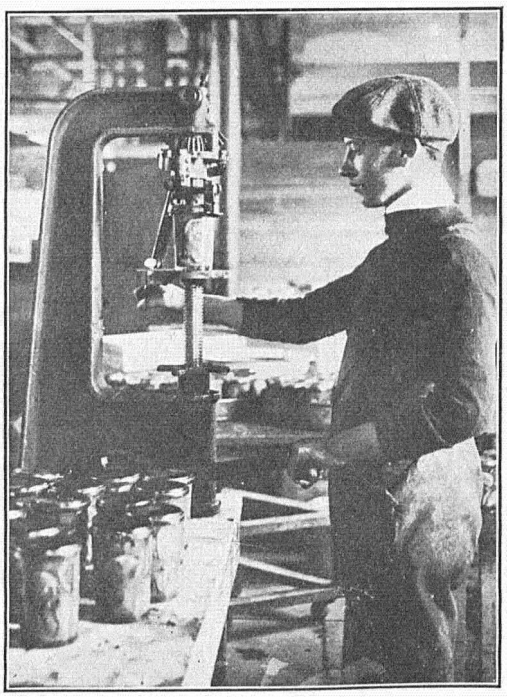

FIG. 230.—Sealing glass jars which have been packed with picked mussels.

The mussels are cooked with steam, which is turned gradually into the bottom of the kettle by an operator who watches the thermometer closely to see that the temperature does not rise above 100° C. or 212° F. Turning live steam directly against the shellfish or cooking them at a temperature higher than the boiling point of water hydrolyzes protein compounds in the shell and flesh, transforming them into products possessing a disagreeable odor and flavor. Some investigators, however, claim to have steamed out mussels under pressure at temperatures much higher than 212° F. without injuring the delicacy of flavor. They assert, moreover, that cooking at high temperatures is absolutely essential to the successful handling and preservation of the shellfish. The process is complete when the shells open and the flesh becomes readily detached. The proper length of time during which the shellfish must be steamed to obtain the desired results varies with the temperature employed and the quantity of material introduced at a given time.

When cooked to the proper degree, the baskets of mussels are removed from the process kettle and allowed to cool until they can be handled with comfort with the bare hands. Then they are taken to a shucking room, where girls and boys dexterously take out the meats and remove the byssus. The waste matter is dropped into barrels under the table and the meats collected in metal measures (fig. 229).

The mussel meats, after being measured, are packed in glass jars or tin cans with enough of the body liquor, which collects in the bottom of the process kettle, to nearly fill the receptacles. The filled jars or cans are next transferred to a machine which crimps on the covers air-tight without the use of solder (fig. 230). They are then packed in a crate and processed in the steam chest for about half an hour at a temperature varying between 240 and 280° F. Except for labeling, this completes the process of canning.

Mussels, after being steamed and shucked, can be pickled by placing them in a solution of 1 part strong vinegar and 2 parts water. White wine vinegar is best to use as a preservative. The flavor can be improved to suit the taste by the addition of a little spice, vegetables, such as carrots and onions, or slices of lemon. The pickled form can be canned and, if processed, will keep for a long time without deteriorating. Care must be exercised not to get too much spice in the mixture, for the strength continues to increase with age, especially where peppers are employed. Submerged in pickling liquor in wooden tubs of 5 to 10 gallons' capacity, mussels will keep well for weeks and are conveniently handled in this form for the immediate trade.

At the beginning of 1918 several prominent firms took active steps to put large quantities of mussels on the market in fresh or preserved form. With extensive advertising and a well-organized propaganda in its favor, there is every reason to believe that the result will be the establishment of a new and valuable fishery that will rank second only to that of the oyster, and at the same time add millions of pounds of flesh food to our annual food supply.

SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS.

1. The sea mussel *Mytilus edulis* Linnæus is a bivalved mollusk closely related to clams and oysters and is one of the most abundant shellfish on our north Atlantic and north Pacific coasts.

2. The anatomy and physiology of the different systems of organs have been described.

3. The sexes are separate and mature their products at the end of the first year. Single females may spawn from 5,000,000 to 12,000,000 eggs annually. A ciliated larva is formed 4½ hours after fertilization, and when 10 weeks old possesses nearly all the organs of the adult. Under favorable conditions growth amounts to about 1 inch per year for the first three years. After that the rate is much reduced. A mussel bed represents one of the greatest organizations in nature for making flesh food by a short and rapid process.

4. The food of the mussel is practically unlimited, consisting of plankton organisms (chiefly the smaller diatoms and Protozoa) and detritus. It is possible that some of the dissolved organic carbon and nitrogen compounds are absorbed directly from the medium in which the shellfish are bathed.

5. Destructive agencies operating against the mussel are storms, shifting sands, extensive growths of eelgrass and other seaweeds which smother them, and a host of predacious enemies, including starfishes, conchs, winkles, oyster drills, dog-whelks, numerous fishes, gulls, ducks, rats, muskrats, seals, and walruses. A parasite, *Haplosporidium mytilovum*, which is described as a new species, destroys enormous numbers of mussel eggs.

6. In European countries mussels are prized as a food and hundreds of millions of pounds are consumed annually. In France the value of the fishery is second only to that of the oyster. Although exceedingly abundant in many places along our shores, very limited quantities have been eaten in this country up to the present time. Some use has been made of them for bait and fertilizer.

7. In chemical composition and nutritive value the mussel ranks equal to or superior to any other shellfish. The flesh is tender, palatable, and easily digested. The cost of production and marketing is less than for any other shellfish.

8. Marketable mussels are generally in season when oysters are out of season. Narragansett Bay and Long Island Sound mussels are usually in prime condition from March to June, while those on the south shore of Long Island are best from June to September.

9 Fresh mussels only, taken from pure water subject to the ebb and flow of tides and free from sewage contamination, should be eaten.

10. Mussels are cultivated extensively in France, Italy, Germany, and England, where they yield large returns. At the time of preparing this report cultivation by the bed system was being practiced successfully on a small scale in Cold Spring Harbor, L. I., and in the vicinity of New York with an annual yield of 2,000 to 3,000 bushels per acre. Thousands of acres of unutilized bottom on our north Atlantic coast are adapted to the culture of mussels.

11. Natural mussel beds, under normal conditions, last from two to four years. Unless utilized commercially before the end of this period they are destroyed by natural enemies or by physical forces.

12. That the mussel beds on our north Atlantic and north Pacific coasts, if utilized, are capable of yielding millions of pounds of wholesome, palatable flesh food annually is established beyond question. The time has come when we can no longer afford to waste this great natural resource by failure to utilize it.

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