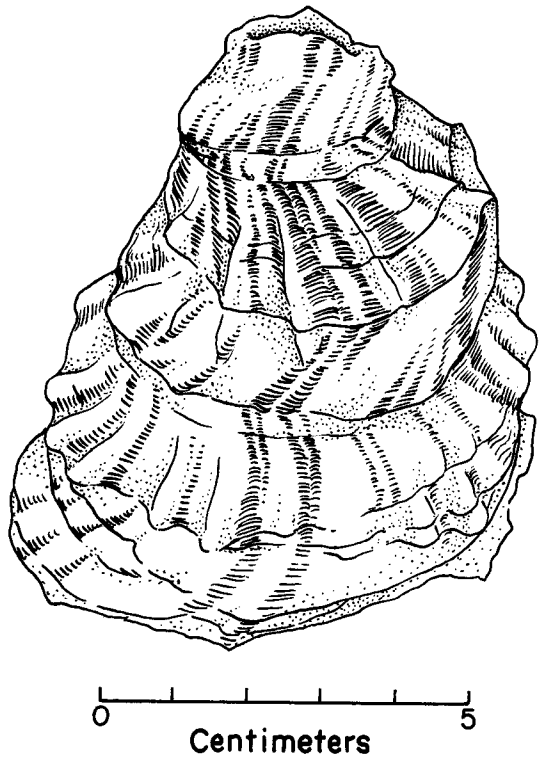

FIGURE 36.—Shell of an adult *C. virginica* showing periodic changes in the direction of the principal axis of growth. Note the zigzag line of pigmented bands in the middle of the valve. Actual dimensions: 8.5 by 6 cm. (3.25 by 2.5 inches).

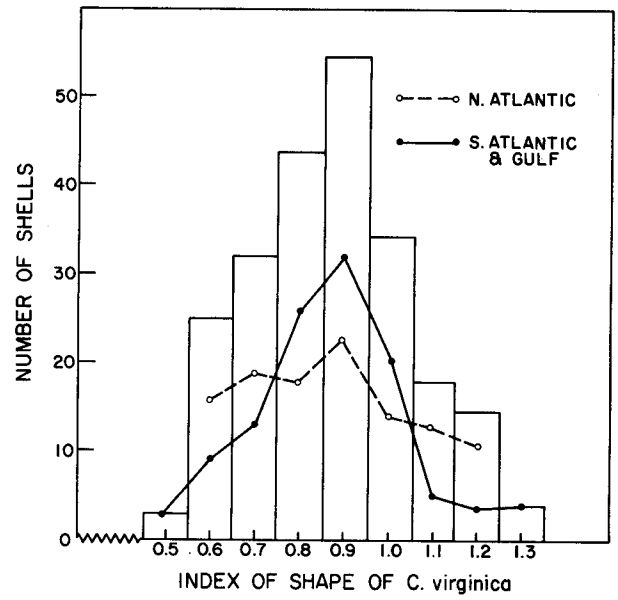

FIGURE 37.—Histogram of the distribution of the index of shape $\frac{\text{(height+width)}}{\text{length}}$ of shells of *C. virginica* from the Atlantic Coast. Frequency distribution of the index of North Atlantic oysters (open circles) and South Atlantic oysters (points) are shown by two separate curves.

terminations of the effect of local conditions on growth and shape of shells.

CHALKY DEPOSITS

The glossy, porcelainlike inner surface of an oyster shell is frequently marred by irregularly shaped white spots which consist of soft and porous material of different appearance and textture than the surrounding shell substance. These areas are called "chalky deposits". They are very common in *C. virginica* and *O. edulis*. Since the first record of their presence in edible oysters made by Gray (1833) they have been mentioned frequently by many biologists. Recent review of the literature on the subject is given by Korringa (1951).

The exact location of chalky deposits is of interest since some speculations regarding their role and origin are based on the position they occupy on the shell. Orton and Amirthalingam (1927) assumed that chalky material is formed in the places where the mantle loses contact with the shell. No experimental evidence in support of this explanation was presented by the authors or by Ranson (1939–41), who fully accepted the theory without making additional studies and stated positively that chalky deposits are formed wherever there is a local detachment of the mantle from the valve.

Considering the possibility that the mantle may be more easily detached from the valve if the oyster is placed with its lower (cuplike) side uppermost, Korringa (1951) made a simple field experiment. In one tray he placed 25 medium sized *O. edulis* in their normal position, with their cupped valves undermost; the other tray contained an equal number of oysters resting on their flat valves. At the end of the growth season he observed no significant differences in the deposition of shell material in the oysters of the two groups.

To determine whether chalky deposits are formed in places of partial detachment of the mantle, I performed the following experiment: Small pieces of thin plastic about 1 cm.^{2} were bent as shallow cups and introduced between the mantle and the shell of *C. virginica*. In 10 oysters the cups were inserted with the concave side facing the mantle, in another 10 oysters the position of the cup was reversed, i.e., the concave side faced the valve. The oysters were kept for

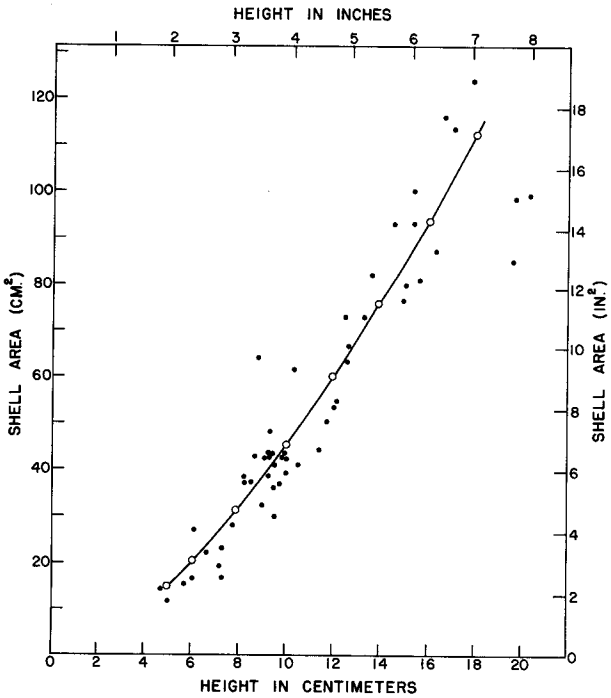

FIGURE 38.—Shell area in cm.² plotted against height of shells in cm. Inch scales are on top and on the right.

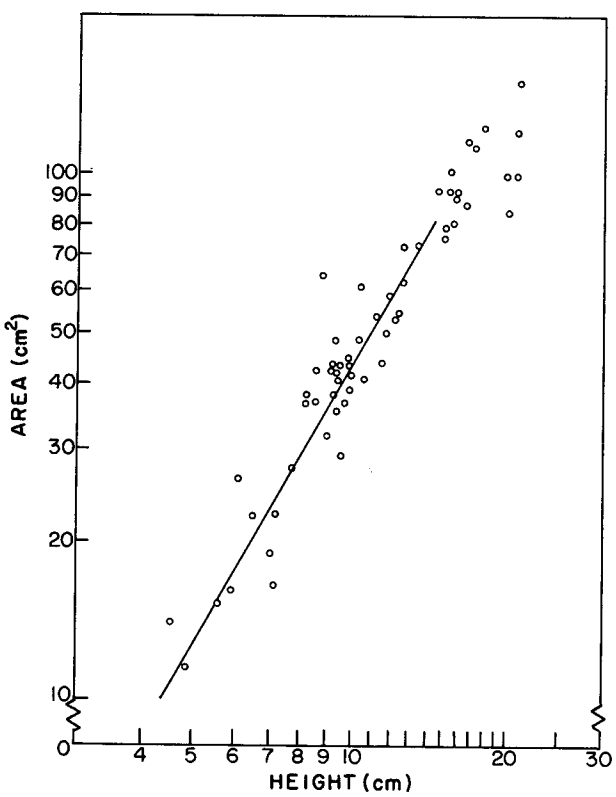

FIGURE 39.—Logarithmic plot of shell area against shell height.

55 days in running sea water in the laboratory. During this time they fed actively and had considerable shell growth along the margin of the valves. After their removal from the shells the cups were found to be covered with hard calcite deposits on the sides facing the mantles. No chalky material was found on cups or on the surface of valves adjacent to the area of insertion. On the other hand, conspicuous chalky areas were formed along the edge of the shell in places where the opposing valves were in close contact with each other (fig. 40). It is clear from these observations that the detachment of the mantle from the inner surface of the shell does not result in the deposition of chalky material and that such deposits may be laid in the narrowest space of shell cavity where the two valves touch each other.

Suggestions that chalky deposits result from secondary solution of calcium salts of the shell (Pelseneer, 1920) or that their formation is somehow related to the abundance of calcareous material in the substratum (Ranson, 1939–41,

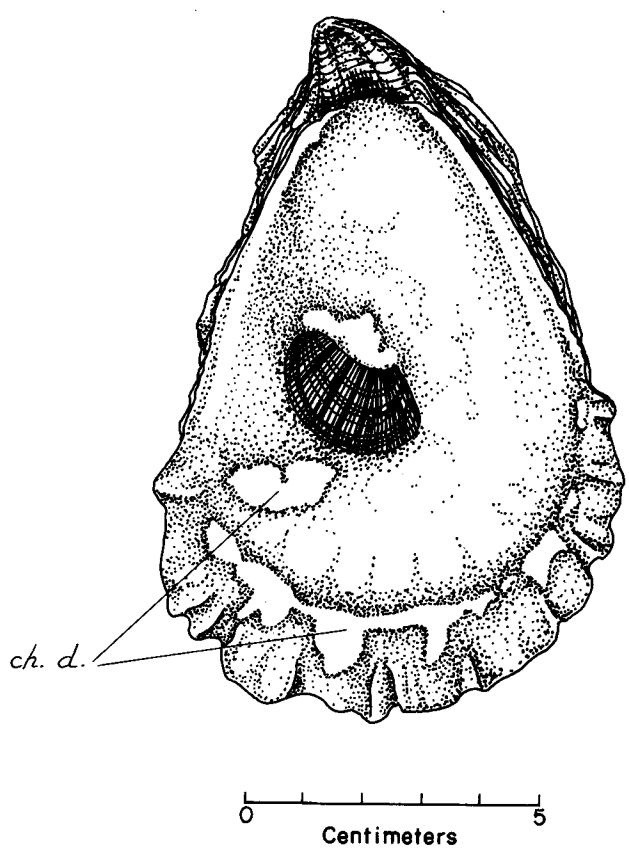

FIGURE 40.—Chalky deposits (ch. d.) on the newly formed shell at the edge of the valve, and near the muscle attachment.

1943) are not supported by evidence. The inner surface of bivalve shells may become slightly eroded due to the increased acidity of shell liquor when the mollusk remains closed for a long time, but the erosion is, however, not localized; it occurs over the entire shell surface. As to the effect of the abundance of lime in the substratum on the formation of chalky deposits, one must remember that the concentration of calcium salts dissolved in sea water is fairly uniform and that calcium used for building of shells is taken directly from the solution (see p. 103). Under these conditions the abundance of calcium carbonates in bottom deposits cannot have any effect on the formation of shell.

Chalky areas of shell do not remain unchanged. They become covered by hard substance and in this way they are incorporated in the thickness of the valves (fig. 41).

Korringa's theory (1951) that the oyster deposits chalky material ". . . when growing older, in its efforts to maintain its efficiency in functioning" and that ". . . where possible the oyster always uses soft porous deposits when quite a lot of shell volume has to be produced . . ." is based on the assumptions: (1) that chalky deposits most frequently develop in the area posterior to the muscle attachment, (2) that the layers of chalky material are more numerous in cupped than in flat oysters, (3) that in the area of the exhalant chamber (in the posteroventral quadrant of the shell) the oyster attempts to decrease the distance between the two valves by rapid deposition of shell material, and (4) that chalky material is used by the oyster "as a measure of economy, as a cheap padding in smoothing out the shell's interior." The validity of these assumptions with reference to *C. virginica* was tested by studing the relative frequency of the occurrence of chalky deposits on the left and right valves and by estimating the extent of these deposits in different parts of the valves. The collection of shells studied for this purpose comprised several hundred adult specimens from various oyster beds along the Atlantic and Gulf coasts. For determining the distribution of chalky areas the inner surface of the valves was arbitrarily divided into four quadrants shown in figure 42 and designated as follows: A—dorsoposterior; B—dorsoanterior; C—ventroposterior; and D—ventroanterior. The following five classes corresponding to the degree of the development of chalky deposits in each quadrant were established:

No deposits within the quadrant	0
1 to 25 percent of the area covered with deposits	1
26 to 50 percent of the area covered with deposits	2
51 to 75 percent of the area covered with deposits	3
76 to 100 percent of the area covered with deposits	4

With a little practice it was easy to select the correct class by visual examination. The first question was whether there is any difference in the frequency of occurrence and extent of chalky deposits on right and left valves. For this purpose the entire surface of the valve was examined and classified. Chalky deposits were found as often on the right as on the left valve of *C. virginica*. This is shown in table 3 which summarizes the observations made on 472 shells collected at random at oyster bottoms along the

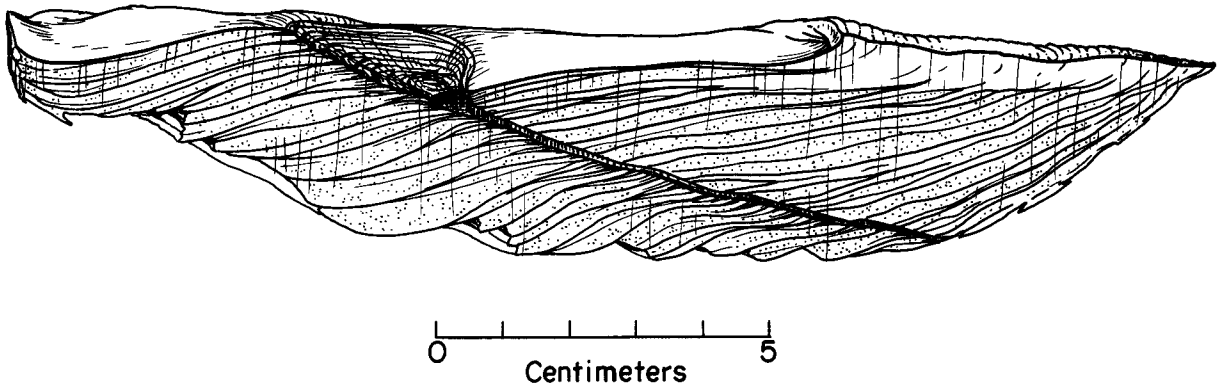

FIGURE 41.—Left valve of an old *C. virginica* cut along the principal axis of growth. Chalky areas on both sides of the hypostracum (dark platform for the attachment of the adductor muscle) are enclosed in the thin layers of hard crystalline material. Hinge on the right. Natural size.

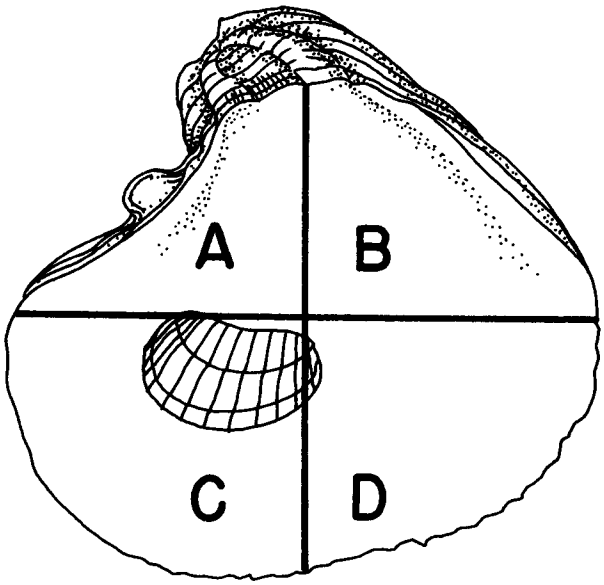

FIGURE 42.—Four arbitrary quadrants of the inner surface of shell used for estimating the distribution and extent of chalky deposits.

Atlantic Coast from Long Island Sound to Georgia. Nearly one-half of the total number of valves examined (48 percent of left and 53 percent of right valves) were free of the deposits. (The percentage of oysters without chalky deposits was not determined because in many shells of the collection the valves had separated and could not be arranged in pairs.) In about 25 percent of the total number of shells the chalky deposits cover less than one-quarter of the valve area. Larger deposits occurred in diminishing number of shells; those covering more than three-quarters of available space (class 4) comprised less than 3 percent of the total number examined.

There was no particular area on the valve surface where chalky deposits were formed more often than in any other place. The differences in the frequency of their occurrence in different quadrants of a valve were not significant.

In *O. edulis*, according to Korringa, chalky deposits form more often in deep (cupped) shells than in flat ones and can be found principally in the area in front of the cloaca, quadrant C according to our terminology. No such differences in the place of formation or in the type of shell could be observed in *C. virginica*.

TABLE 3.—*Percent of valves of* C. virginica *with chalky deposits*

Item	Area of valve covered by chalky deposits			
	Class 1 (1–25 percent)	Class 2 (26–50 percent)	Class 3 (51–75 percent)	Class 4 (76–100 percent)
Left valve	25.9	13.6	9.8	2.8
Right valve	24.9	12.1	8.4	1.5

From the observations on oysters of Prince Edward Island, Medcof (1944) concluded that chalky deposits are normal parts of shells and that they have "functional importance" in preserving "a size relationship between meats and shell cavity" and in regulating "the curvature of the inner face of the shell throughout the oyster's life." There could be no argument about the first conclusion that chalky deposits are normal parts of the oyster shell. The fact that they appear during the first weeks of the oyster's life confirms this statement. The second conclusion that they preserve the curvature of the shell is impossible to prove without careful study of a large number of shells. In comparing the contours of the shells of New England and Chesapeake Bay oysters with and without chalky deposits, I failed to notice any significant difference between the two groups.

Japanese investigators (Tanaka, 1937, 1943) found great variability in the distribution of chalky deposits in *C. gigas* and *C. futamiensis*. Large porous areas may be found in the shells of these species near the anus, in front of the labial palps, or near the gonads. There seems to be no evidence that they occur primarily in one particular place of the valve. These observations agree with my observations on *C. virginica*.

CHAMBERING AND BLISTERS

The French word "chambrage" or chambering has been used by European biologists to describe shallow cavities, mostly in the cupped valves of *O. edulis*. The cavities are usually filled with sea water and putrified organic material. In the museum specimens these spaces are dry and filled with air. Sometimes only one chamber is found, but occasionally an entire series of cavities may be present. The chambers may be invaded by tube-forming annelids living in the oyster (Houlbert and Galaine, 1916a, 1916b). The successive layers of shell material in the chamber are not in contact with each other but surround an empty space. This gives the impression that the body of the oyster had shrunk or retracted and occupies only a small portion of shell space. This view is generally accepted by European oyster biologists

(Korringa, 1951; Orton, 1937; Orton and Amirthalingam, 1927; Worsnop and Orton, 1923), who agree that chambering is caused by the shrinkage of the body, withdrawal of shell-forming organ, and deposition of partitions. Salinity changes were suggested by Orton as one of the principal causes of chambering, and shrinkage due to spawning was also considered by Korringa as a probable factor. These conditions have not been reported for *C. virginica*. I did not find any evidence that chambers or blisters in the American oyster are associated with shrinkage or other body changes.

It is interesting to add that some taxonomists of the middle of the past century (Gray, 1833; Laurent, 1839a, 1839b) were so puzzled by the presence of chambers that they compared chambered oyster with *Nautilus* and even suggested the possibility of some family relation between the latter genus and *Ostrea!*

An interesting shell structure consisting of a series of chambers near the hinge end is found in the Panamanian oyster, *O. iridescens*. The location of chambers and the regularity at which they are formed as the shell grows in height can be seen in figure 43 representing a longitudinal section of the valve made at a right angle to the hinge. This type of chambering is obviously a part of a structural plan of the shell and is not a result of an accidental withdrawal of the oyster body or of an invasion by commensals. Arch-forming septae of the chambers apparently contribute to the strength of the hinge and at the same time require relatively small amounts of building material. What advantage *O. iridescens* obtains from this type of structure is of course a matter of speculation.

Chambers found in *C. virginica* consist of irregular cavities containing mud or sea water. Such formations are called blisters. Blisters can be artificially induced by inserting a foreign object between the mantle and the shell (see p. 105). They are also caused by the invasion of shell cavity by *Polydora* (see p. 422) or by perforations of the shell by boring sponges and clams (p. 420).

STRUCTURE OF SHELL

For more than a hundred years the structure of the molluscan shell was an object of research by zoologists, mineralogists, and geologists. Several reviews of the voluminous literature (Biedermann, 1902a, 1902b; Bøggild, 1930; Cayeux, 1916; Haas, 1935; Korringa, 1951; Schenck, 1934; Schlossberger, 1856) deal with the problem from different points of view. Recently these studies have been extended by the use of X-ray and electron microscope. The methods, especially those of electron microscopy, opened entirely new approaches particularly with reference to the structure of the organic constituents of the shell (Grégoire, 1957; Grégoire, Duchâteau, and Florkin, 1950, 1955; Watabe, 1954).

Terminology of molluscan shells is somewhat confusing depending whether the emphasis is placed on morphological, crystallographical, or mineralogical properties. The names of different

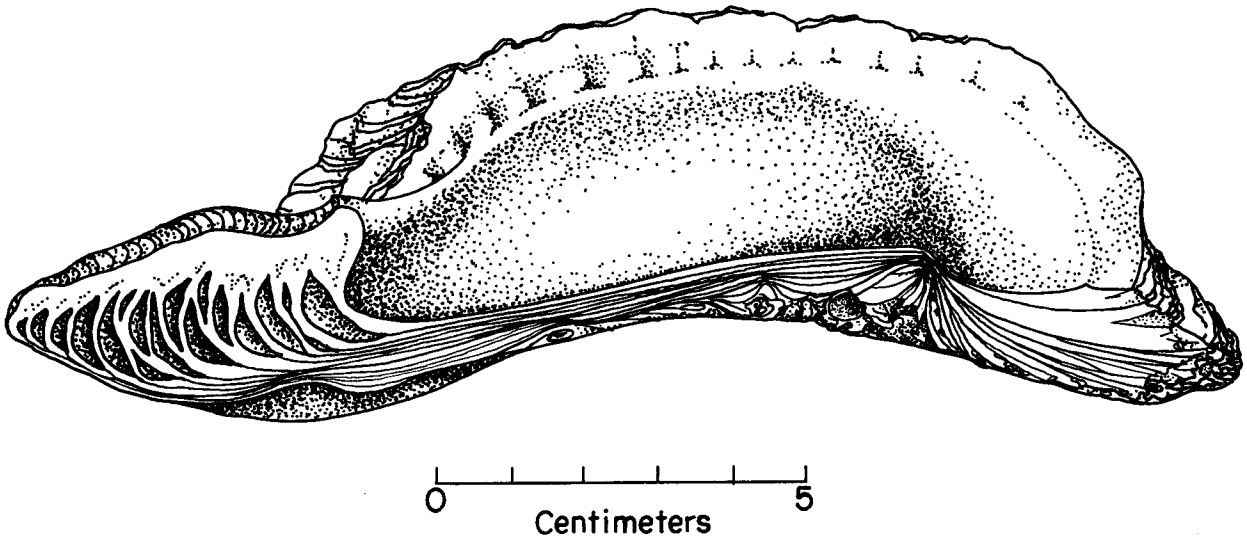

FIGURE 43.—Shell of *O. iridescens* cut at right angle to the hinge. Note a series of empty chambers at the hinge area. Specimen from the Gulf of Panama.

layers of shell described in this chapter are those which are found in more recent biological publications (Korringa, 1951; Leenhardt, 1926).

The shell of the oyster consists of four distinct layers: periostracum, prismatic layer, calcite-ostracum, and hypostracum. The periostracum is a film of organic material (scleroprotein called conchiolin), secreted by the cells located near the very edge of the mantle. The periostracum is very poorly developed in *C. virginica* and cannot be found in old shells. It covers the prismatic layer which can be best studied by removing from the edge of an oyster a small piece of newly formed shell. Microscopic examination reveals that the prismatic layer is made of single units shown in figure 44. Each prism consists of an aggregate of calcite crystals (Schmidt, 1931) laid in a matrix of conchiolin which after the dissolution of mineral constituents in weak hydrochloric acid retains the general configuration of the prisms (fig. 45). The double refraction of the walls of empty prisms is pronounced and causes slight iridescence noticeable under the microscope. In a well-formed layer the prisms are wedge-shaped and slightly curved (fig. 46). Conchiolin adhering to the prisms can be destroyed by boiling in potassium hydroxide solution and the prisms separated (Schmidt, 1931). Their shape and size are very variable.

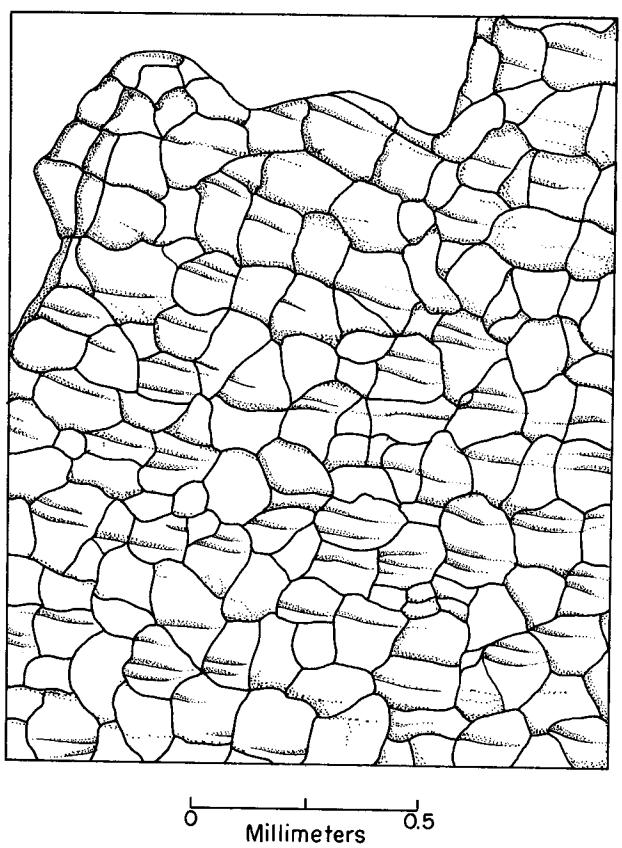

FIGURE 44.—Prismatic layer at earlier stages of calcification. *C. virginica.*

The optical axes of the prism are, in general, perpendicular to the plane of the prismatic layer, but in places they are irregularly inclined toward it.

Calcite-ostracum, called also a subnacreous layer (Carpenter, 1844, 1847), makes up the major part of the shell. The layer consists primarily of foliated sheets of calcite laid between thin membranes of conchiolin. The separate layers are irregularly shaped with their optical axes in accidental position (Bøggild, 1930). In a polished, transverse section of the shell of *C. virginica* the folia are laid at various angles to the surface (fig. 47). This layer is frequently interrupted by soft and porous chalky deposits (upper two layers of fig. 47) which appear to consist of amorphous material. It can be shown, however, that chalky deposit is formed by minute crystals of calcite oriented at an angle to the foliated lamellae of the hard material.

Hypostracum is a layer of shell material under the place of the attachment of the adductor muscle. In the shells of *C. virginica* the layer is pigmented and consists of aragonite (orthorhombic calcium carbonate, $CaCO_3$).

For many years oyster shells were considered to be composed entirely of calcite (Bøggild). Recently Stenzel (1963) has discovered that on each valve of an adult *C. virginica* aragonite is present as padding of the muscle scar, in the imprint of Quenstedt's muscle, and in the ligament.

As the oyster grows the adductor muscle increases in size and shifts in the ventral direction. The new areas of attachment become covered with aragonite while the older, abandoned parts are overlaid with the calcite. The progress of the muscle from hinge toward the ventral side can be clearly seen on a longitudinal section of the shell where it can be easily distinguished by its darker color and greater hardness of the secreted material (fig. 48).

ORGANIC MATERIAL OF THE SHELL

After the removal of mineral salts of the shell by weak acids or by chelating agents, such as sodium versenate, the insoluble residue appears in the

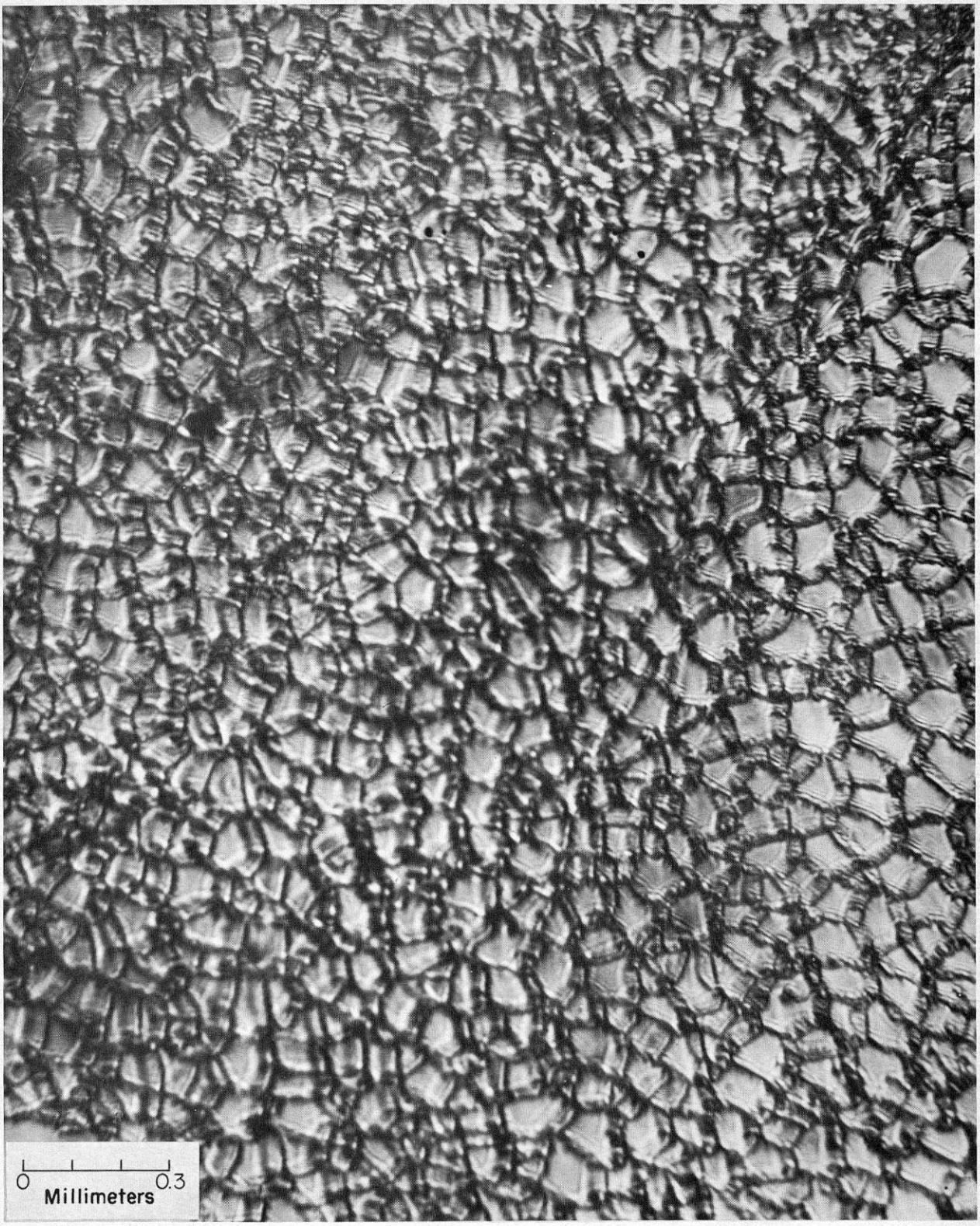

FIGURE 45.—Photomicrograph of a thin piece of prismatic layer after the dissolution of calcium carbonate in weak acid, *C. virginica*. The walls retain the shape of the prisms and are iridescent.

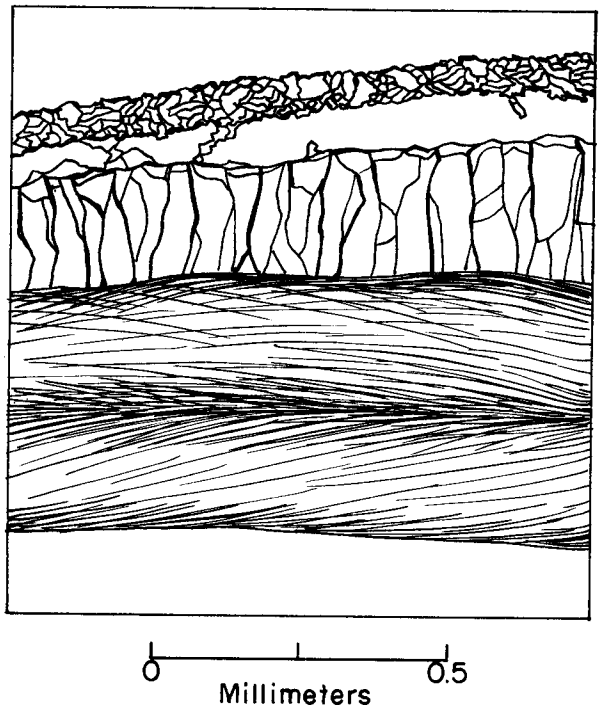

FIGURE 46.—Cross section of a piece of young shell of *C. virginica* (mounted in bakelite and ground on a glass wheel with carborundum, about 80 x). Periostracum (top line), prismatic layer (middle), and calcite-ostracum (lower).

form of thin, homogenous sheets of organic material kept together like pages of a book. This substance, discovered in 1855 by Fremy, is known as conchiolin. The name is applied to the organic material insoluble in water, alcohol, ether, cold alkaline hydroxides, and dilute acids. In the literature it appears also under the names of conchin, periostracum, epidermis, and epicuticula. Conchiolin is a scleroprotein, the structural formula of which has not yet been determined. The elementary analysis of conchiolin of *O. edulis* (Schlossberger, 1856) is as follows: H, 6.5 percent; C, 50.7 percent; N, 16.7 percent. Wetzel (1900) found that conchiolin contains 0.75 percent of sulfur and Halliburton (quoted from Haas, 1935) assigned to it the following formula: C_{30}, H_{48}, N_9, O_{11}, which also appears in the third edition of "Hackh's chemical dictionary" (Hackh, 1944). Similarity of conchiolin to chitin leads many investigators to an error in ascribing chitinous composition to structures which were found insoluble in alkaline hydroxides and dilute acids. Thus, the presence of chitin was reported in the shell and ligament of *Anodonta*, *Mya*, and *Pecten* (Wester, 1910). The application of the Schulze's test for chitin (intense violet coloration after treatment for 24 hours in diaphanol [chlorodioxyacetic acid], followed by a solution of zinc chloride and iodine), does not confirm these findings (Lison, 1953).[4]

To the naked eye and under the light microscope the conchiolin appears as amorphous, viscous and transparent material which hardens shortly after being deposited. Using the electron microscope technique, Grégiore, Duchâteau, and Florkin (1955) found that the conchiolin of gastropods and bivalves consists of a fine network with many meshes of irregular shape and variable dimensions. This is, however, not the case in oyster shells. Conchiolin of the genus *Ostrea* lacks meshes and under the electron microscope is of uniform appearance (personal communication by Grégoire).

Cross sections of decalcified shells of *C. virginica* show a distinct difference between the staining properties of the conchiolin of the prismatic and calcite-ostracum layers. On the cross sections of shell shown in figure 49 the two parts can be recognized by the typical foliated appearance of the calcite-ostracum and the meshlike structure of the prismatic layer. In the preparation stained with Mallory triple dye the organic matter of the walls of the prisms are stained reddish-brown while the foliae of the calcite-ostracum are bluish. Differential staining indicates the difference in the chemical composition of the two parts.

The amount of conchiolin in the oyster shell was studied by several investigators. As early as 1817 Brandes and Bucholz estimated that organic material of the shell constitutes about 0.5 percent of the total weight. Schlossberger (1856) found 6.3 percent of organic matter in the prismatic layer of the oyster but only from 0.8 to 2.2 percent in the calcite-ostracum. According to Douvillé (1936), the albuminoid content of the oyster shell is 4.8 percent.

According to the determinations made by A. Grijns for Korringa (1951), the conchiolin content of the prismatic layer of *O. edulis* varied from 3.4 to 4.5 percent against the 0.5 to 0.6 percent in the calcite-ostracum. The conchiolin content was calculated from the percentage of N (by Kjeldahl method) multiplied by 6.9. The results of my determinations of the weight of organic material

[4] Inasmuch as the same reaction is obtained with cellulose and tunicine, additional tests should be made using Lugol solution and 1 to 2 per cent sulphuric acid (H_2SO_4). With this test chitin is colored brown, while cellulose and tunicine are blue.

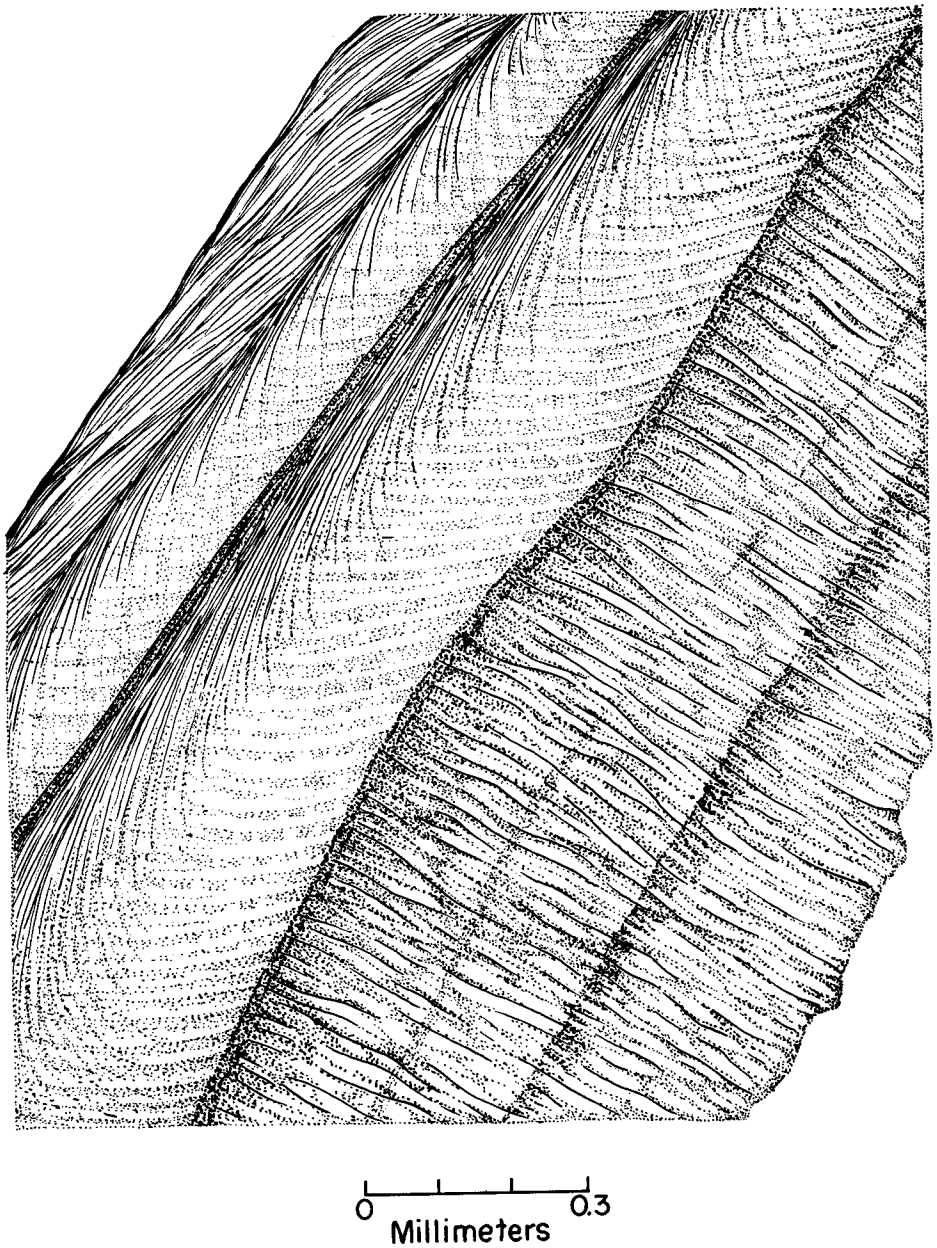

FIGURE 47.—Cross section of the shell of adult *C. virginica* embedded in bakelite and polished on a glass wheel with carborundum. Two upper layers consist of chalky deposits.

after decalcification of the calcite-ostracum of *C. virginica* shells from Long Island Sound and Cape Cod waters are in agreement with those given for *O. edulis*. The content of conchiolin in my samples varied from 0.3 to 1.1 percent with the mode at 0.6 percent. For these analyses 23 pieces of shell were taken from 16 adult oysters not damaged by boring sponge. The samples varied in weight from 0.5 to 15 g.

Higher percentage of conchiolin in the prismatic layer may be expected because this layer represents the new growth of shell which has not yet completely calcified.

The role played by conchiolin in the deposition of calcium salts in the form of calcite or aragonite presents a very interesting problem which has not yet been solved. Recent electron microscope studies of pearl oyster shells made by Grégoire show that the organic material in which aragonite crystals are laid (Grégoire, Duchâteau, and Florkin, 1950) is arranged as a series of bricklike structures. No such arrangement has been de-

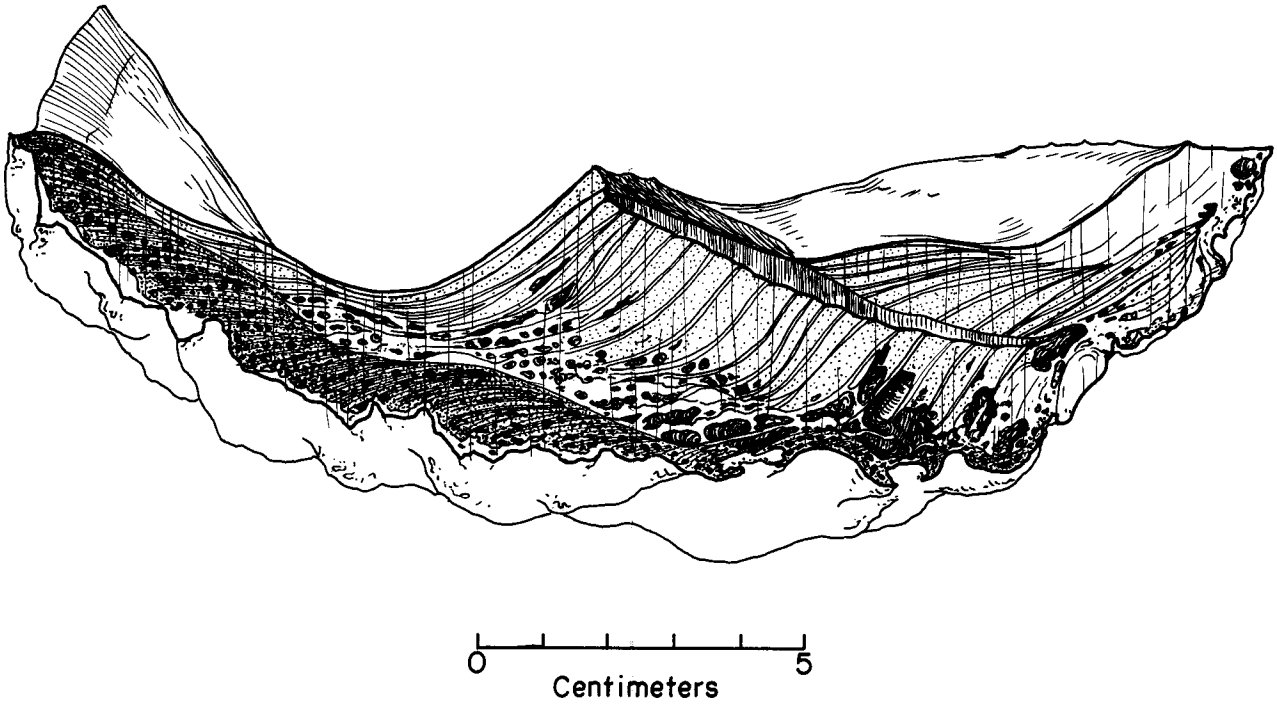

FIGURE 48.—Left valve of *O.* (*Alectryonia*) *megodon* cut along the principal axis of growth. Hypostracum (dark striated layer) forms a pronounced platform for the attachment of the adductor muscle, and can be traced to its original position in the young oyster (right). Chalky deposits are regularly arranged between the layers of calcite. Also see fig. 41.

scribed for calcite shells. Present knowledge of the chemistry of the organic constituents of the shell is inadequate. It seems reasonable to assume that conchiolin like other proteins is not a single chemical substance common to a large number of organisms, but that it differs specifically from animal to animal and may even vary in the different parts of the same shell.

The analysis of amino acids obtained by hydrolysis of conchiolin prepared from decalcified shells showed (Roche, Ranson, and Eysseric-Lafon, 1951) that there is a difference in the shells of the two species of European oysters, *O. edulis* and *C. angulata* (table 4).

TABLE 4.—*Amino acids from the conchiolin of two species of oysters*

[In parts of 100 parts of protein according to Roche, Ranson, and Eysseric-Lafon (1951)]

Amino acids	*Crassostrea angulata*	*Ostrea edulis*
Arginine	0.45	2.90
Histidine	----------	0.65
Lysine	3.55	4.30
Glycine	15.70	15.70
Leucine	0.51	----------
Tryptophane	----------	0.48
Tyrosine	3.27	3.05
Valine	0.95	----------
Cystine	----------	0.98
Methionine	1.77	1.62

Taking advantage of the fact that both calcite and aragonite are present in the two distinct layers of shell of the fan oyster (*Pinna*) and of the pearl oyster (*Pinctada*), the French investigators (Roche, Ranson, and Eysseric-Lafon, 1951) attempted to determine whether there is a difference in the chemical composition of the organic material of the two layers of the shell of the same species. They found that tyrosine and glycine occur in higher concentrations in the prismatic layer than in the nacreous part of shells. In the prismatic layer of calcite portion the content of tyrosine varies between 11.6 and 17.0 percent and that of glycine between 25 and 36 percent. In the nacreous part made of aragonite the concentration of tyrosine was from 2.8 to 6.0 percent and that of glycine varied between 14.9 and 20.8 percent. The significant differences in the contents of the two amino acids in the two parts of the shell may provide a clue for further studies of the role of the organic component on the mineral form in which the calcium carbonate is deposited by the mantle.

MUSCLE ATTACHMENT

The place of attachment of the adductor muscle or muscle scar is the most conspicuous area of the

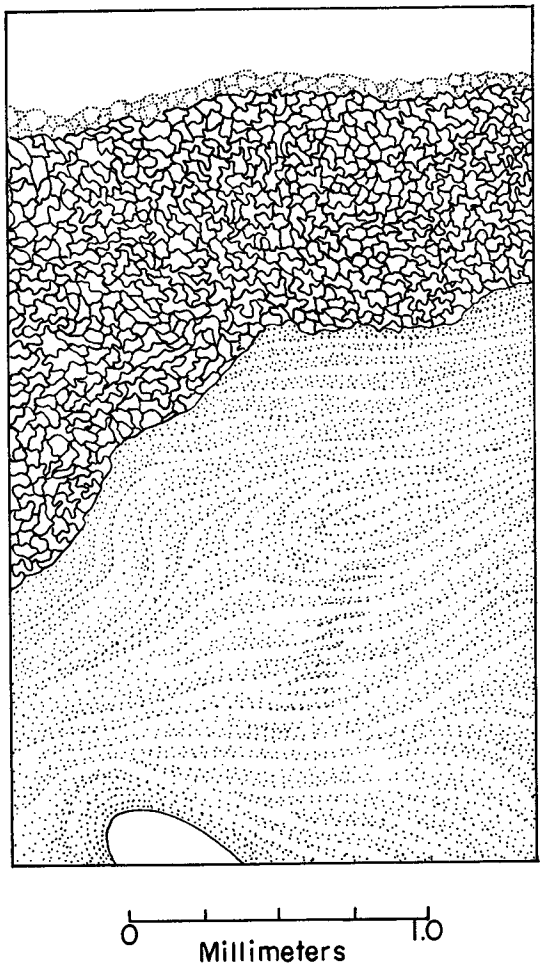

FIGURE 49.—Cross section of shell of an adult *C. virginica* after decalcification in weak acid, Mallory triple stain. Conchiolin of the prismatic layer is reddish-brown; that of calcite-ostracum is bluish.

oyster shell. In *C. virginica*, *C. angulata*, and many other species this area is highly pigmented; in *O. edulis*, *C. gigas*, pigmentation is either absent or very light.

The muscle scar in *C. virginica* is located in the posteroventral quadrant of the shell (figs. 15, 21, 33). To a certain extent the shape of the scar reflects the shape of the shell, being almost round in broad and round oysters and elongated in narrow and long shells. The area of scar is slightly concave on the side facing the hinge and convex on the opposite, i.e., ventral side. Curved growth line, parallel to the curvature of the ventral edge of the valve, can be seen on the surface. They are most pronounced in the ventral part of the muscle impression. Size and shape of the scar is variable and often irregular (fig. 50). The outlines of the impressions shown in this figure were obtained in the following manner: the periphery of the impression was circumscribed with soft pencil; a piece of transparent Scotch adhesive tape was pressed on the impression and the outline was lifted and mounted on cross-section paper; the area occupied by the impression was measured by counting the number of squares. Using this method, I obtained the replicas of muscle impressions from 169 shells taken at random from various oyster beds of the Atlantic and Gulf Coasts. The impressions are arbitrarily arranged in four series (A–D) according to their shape and size. The impression areas of round and broad shells are shown in the two upper rows, A and B; those of long and narrow shells are arranged in the two lower rows, C and D.

It may be expected that the larger is the shell the greater is the area of muscle impression. The relationship, as can be seen in fig. 51, is rectilinear although the scatter of plotted data is considerable and the variability increases with the increase in size. The ratio of muscle impression area to shell surface area varies from 8 to 32 with the peak of frequency distribution at 16 to 18 (fig. 52).

A small oval and unpigmented area on the

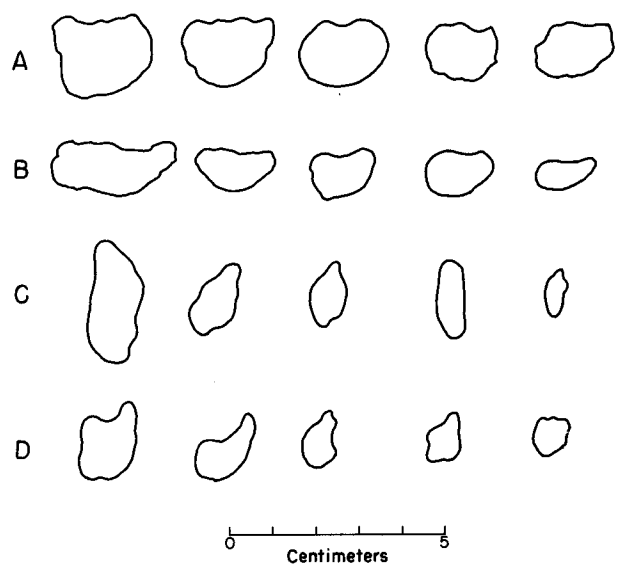

FIGURE 50.—Variations in shape and size of muscle scars on the shells of *C. virginica*. Rows A and B show the types of scars normally found on broad and rounded shells, the length of which is almost equal to or exceeds the height. Rows C and D are the scars often found on long and narrow shells in which the height exceeds the length. Replicas of scars were made from shells collected at random.

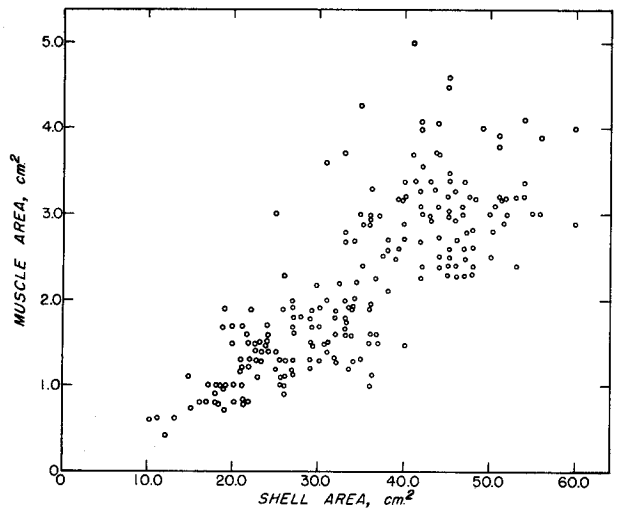

FIGURE 51.—The relationship between the area of muscle scar and the area of the shell of *C. virginica*.

dorsal half of each valve is the imprint of a vestigial muscle in the mantle, discovered in 1867 by Quenstedt in the valves of the early Jurassic oyster, *Gryphaea arcuata* Lamark, and found by Stenzel (1963) in *C. virginica*. In my collection of living *C. virginica* the imprint is hardly visible (figs. 15, 21, and 22). Slight adhesion of the mantle to the valve indicates the location of this area which Stenzel calls "imprint of Quenstedt's muscle."

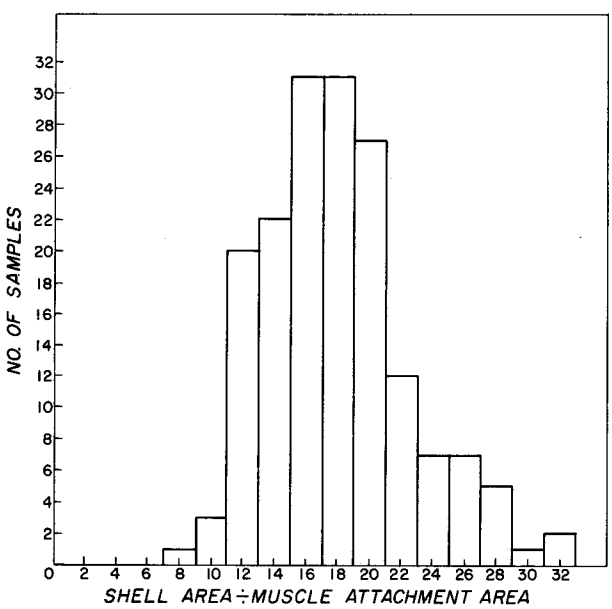

FIGURE 52.—Frequency distribution of the ratio of muscle scar area vs. shell area in the shells of *C. virginica* of Atlantic and Gulf States.

TABLE 5.—*Chemical composition of oyster shells in percent of shell weight*

[From Hunter and Harrison, 1928]

Constituents	Sample 1	Sample 2
Al	0.045	0.043
Ca	38.78	38.81
Cu		0.0025
Fe	0.11	0.09
Mg	0.183	0.189
Mn	0.009	0.009
P_2O_5	0.075	0.073
SiO_2	0.570	0.580
Zn		0.0009
Cl	0.0034	0.0035
CO_3	[3] 57.19	
Fl		
N	0.196	0.196
As		
Organic matter [1]	1.41	1.51
Water [2]	0.27	0.28

[1] Loss above 110° C. Ignited.
[2] Loss to 100° C.
[3] Average for samples 1 and 2.

CHEMICAL COMPOSITION

The oyster shell consists primarily of calcium carbonate, which composes more than 95 percent of the total weight of the shell. The balance is made up by magnesium carbonate, calcium sulfate, silica, salts of manganese, iron, aluminum, traces of heavy metals, and organic matter. Several analyses of oyster shell found in the literature are incomplete, particularly with reference to trace elements. Analysis made for the U.S. Bureau of Fisheries by the Bureau of Chemistry of the Department of Agriculture and published in 1928 (Hunter and Harrison, 1928) is given in table 5.

Dead oyster shells buried in the mud of the inshore waters of Texas and Louisiana are extensively dredged by commercial concerns primarily for the manufacture of chicken feed. Analysis of these shells as they are received at the plant after thorough washing in sea water is given in table 6.

The calcium carbonate content of these shells is probably lower than in live oysters due to their erosion and dissolution of lime in sea water. The chloride content is affected by the retention of

TABLE 6.—*Chemical composition of mud shells received at the plant of Columbia-Southern Corporation at Corpus Christi, Tex.*

[Percent of constituents in samples dried at 110° C.]

Chemical	Percent
$CaCO_3$	93.88
SO_4 as $CaSO_4$	0.48
$MgCO_3$	0.88
SiO_2	1.40
$Al_2O_3+Fe_2O_3$	0.32
Cl as NaCl	0.27
Na_2O (other than NaCl)	0.46
Loss at 500° C	1.60

(Analysis supplied by Columbia-Southern Corporation and copied with their permission.)

these salts in the shells after thorough washing with sea water of greatly variable salinity. The percent of silica, aluminum, and iron, which are also higher than in the analyses of shells of live oysters, is at least in part influenced by the efficiency of plant operations in removing mud from the surface of the shells.

Chemical composition of shells of *O. edulis* is not significantly different from that of *C. virginica*. Table 8 gives the results obtained by European scientists. The data quoted from various sources are taken from Vinogradov (1937).

A much more detailed analysis of dead oyster shells dredged from the bottom of Galveston Bay 8 miles east of San Leon was made recently by the Dow Chemical Company (Smith and Wright, 1962). The shells were scrubbed in tap water with a nylon brush, rinsed in distilled water, dried at 110° C., and ground in a porcelain mortar. With the kind permission of the authors the results are given in table 7. Additional 19 elements were sought but not found at the following sensitivity limits:

10 p.p.m.—arsenic, barium.

1 p.p.m.—antimony, chromium, cobalt, germanium, gold, lead, lithium, mercury, molybdenum, nickel, vanadium, and zirconium.

0.1 p.p.m.—beryllium, bismuth, cadmium, silver, and tin.

The authors remark that traces of clay entrapped within the shell may have influenced the findings for titanium, manganese, copper, or zinc; and that individual variations in silicon, iron, and aluminum were due to contamination not removable by washing. It appears feasible that these variations may have been caused by spicules of boring sponges and algae infesting the shells.

TABLE 7.—*Composition of* C. virginica *oyster shell dredged from Galveston Bay, according to Smith and Wright (1962)*

Constituent	Concentration	Constituent	Concentration
	Percent		*P.p.m.*
Calcium (CaO)	54.6	Organic Carbon as CH_4	400
Carbon (CO_2)	43.5	Chlorine (Cl)	340
Sodium (Na_2O)	0.32	Aluminum (Al)	200
Magnesium (MgO)	0.33	Iron (Fe)	180
Sulfur (SO_3)	0.16	Phosphorus (P)	116
Silicon (SiO_2)	0.16	Manganese (Mn)	110
Strontium (SrO)	0.12	Fluorine (F)	54
Moisture (H_2O)	0.58	Potassium (K)	30
		Titanium (Ti)	12
Total of major constituents	99.8 %	Boron (B)	5
		Copper (Cu)	3
		Zinc (Zn)	2
		Bromine (Br)	1
		Iodine (I)	0.5

TABLE 8.—*Chemical composition of shells of* O. edulis *(in percent of ash residue)*

Constituent	Sample 1	Sample 2	Sample 3	Sample 4
$CaCO_3$	98.60	97.65	96.54	97.00
$Ca_3(PO_4)_2$	1.21			
$MgCO_3$		0.312	0.9125	trace
P_2O_5		0.52	0.058	0.09
$(Al, Fe)_2O_3$		trace		0.03
Fe_2O_3	0.0719			
$CaSO_4$		1.456		2.00
SiO_2	0.813			
Organic matter		0.50	0.5–4.5	

According to Creac'h (1957), all shells of *O. edulis* and *C. angulata* contain traces of phosphorus. The French biologist found that the phosphorus content is variable. Expressed as P_2O_5, it varies in *C. angulata* from 0.075 to 0.114 percent. There is a significant difference in the phosphorus content in various parts of the shell. The amount of phosphorus per unit of volume of shell material is lower in the chalky deposits than in the hard portion of the shells. Thus, in laying a chalky deposit the mollusk utilizes from 2.4 to 2.6 times less phosphorus than is needed for secreting the same volume of harder shell substance.

The presence of small quantities of strontium in calcareous shells of mollusks is of particular interest because of its apparent relation to aragonite. The marine organisms containing calcium carbonate as aragonite have relatively higher strontium content than those having calcite shells. The relationship between the two elements is expressed as strontium-calcium atom ratios (Thompson and Chow, 1955; Trueman, 1944; and Asari, 1950). In *C. virginica* and *C. gigas* the strontium-calcite ratio x 1,000 varies between 1.25 and 1.29. *Ostrea lurida* from California has a lower strontium content, the ratio being 1.01. The percentages of Ca, Sr, CO_2, and organic matter in the shells of three species of oyster and in *Mya arenaria*, in which the content is the highest among the bivalves, given by Thompson and Chow (1955), are summarized in table 9. The

TABLE 9.—*The percentage of calcium and strontium in the shells of oysters and soft shell clam*

[According to Thompson and Chow, 1955]

Species	Calcium	Strontium	Carbon dioxide	Organic matter	Atom ratio Sr/Ca x1,000
O. lurida	38.6	0.085	42.5	1.68	1.01
C. virginica	33.7–37.8	0.92–0.107	41.8–42.4	2.16–2.34	1.25–1.29
C. gigas	34.6–36.2	0.097–0.100	32.6–42.5	1.33–1.71	1.26–1.28
M. arenaria	38.6–38.8	0.181–0.246	42.2–42.3	2.22–2.44	2.16–2.91

salinity and temperature of the water have apparently no influence on Sr/Ca, which remains fairly constant in calcareous shells. The possible role of strontium in the mineralization and formation of shell is discussed in chapter V.

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