CHAPTER II

MORPHOLOGY AND STRUCTURE OF SHELL

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APPEARANCE AND PRINCIPAL AXES

The body of the oyster is covered with two calcareous valves joined together by a resilient ligament along the narrow hinge line. The valves are slightly asymmetrical. The left one is larger and deeper than the right one, which acts as a lid. Under normal conditions the oyster rests on the left valve or is cemented by its left valve to the substratum. The difference between the right (flat) and left (cuplike) valve is to a certain degree common to all the species of oysters which have been sufficiently studied. Orton's (1937) statement with reference to *Ostrea edulis* that: "In life the flat or right valve usually rests on the sea bottom and is often referred to as the lower one" is an obvious oversight.

In *C. virginica* the left valve is almost always thicker and heavier than the right one. When oysters of this species are dumped from the deck of a boat and fall through water they come to rest on their left valves. I observed this many times while planting either small oysters not greater than 2 inches in height, or marketable adults of 5 to 6 inches. In the genus *Ostrea* the difference between the two valves is not great, it is greater in the genus *Crassostrea*, and extremely pronounced in the oyster of uncertain systematic position from Australia which Saville-Kent (1893) has called "*Ostrea mordax* var. *cornucopiaeformis*." [2]

[2] I am indebted to H. B. Stenzel for calling my attention to this species and for several suggestions regarding the morphological terminology used in this chapter.

The oyster is a nearly bilaterally symmetrical mollusk with the plane of symmetry passing between the two valves parallel to their surfaces. In orienting any bivalve it is customary to hold it vertically with the narrow side uppermost (fig. 15). The narrow end or apex of the shell is called the umbo (plural, umbos or umbones) or beak. A band of horny and elastic material, the ligament (fig. 16) joins the valves at the hinge on which they turn in opening or closing the shell.

In many bivalves the hinge carries a series of interlocking teeth, but these structures are absent in the family Ostreidae. The hinge consists of the following parts: a projecting massive structure within the right valve, the buttress, according to Stenzel's terminology, supports the midportion of the ligament and fits the depression on the left valve. The tract made by the buttress during the growth of the shell along the midportion of the ligamental area is the resilifer. On the left valve the resilifer is the tract left on the depression. The central part of the ligament is called resilium.

The pointed end of the valve or the beak represents the oldest part of a shell. In old individuals it reaches considerable size (fig. 17). The beaks are usually curved and directed toward the posterior end of the mollusk although in some specimens they may point toward the anterior. In the majority of bivalves other than oysters the beaks usually point forward. The direction and degree of curvature of the beaks of oysters as well as their relative proportions vary greatly as can be seen in figure 18, which represents different shapes found in old shells of *C. virginica*. Very narrow, straight, or slightly curved beaks of the kind shown in figure 18–1 are usually formed in oysters which grow on soft, muddy bottoms. Extreme development of this type can be seen in the narrow and slender oysters growing under overcrowded conditions on reefs (fig. 19). Other forms of beaks (fig. 18, 2–4) cannot be associated with any particular environment. In fully

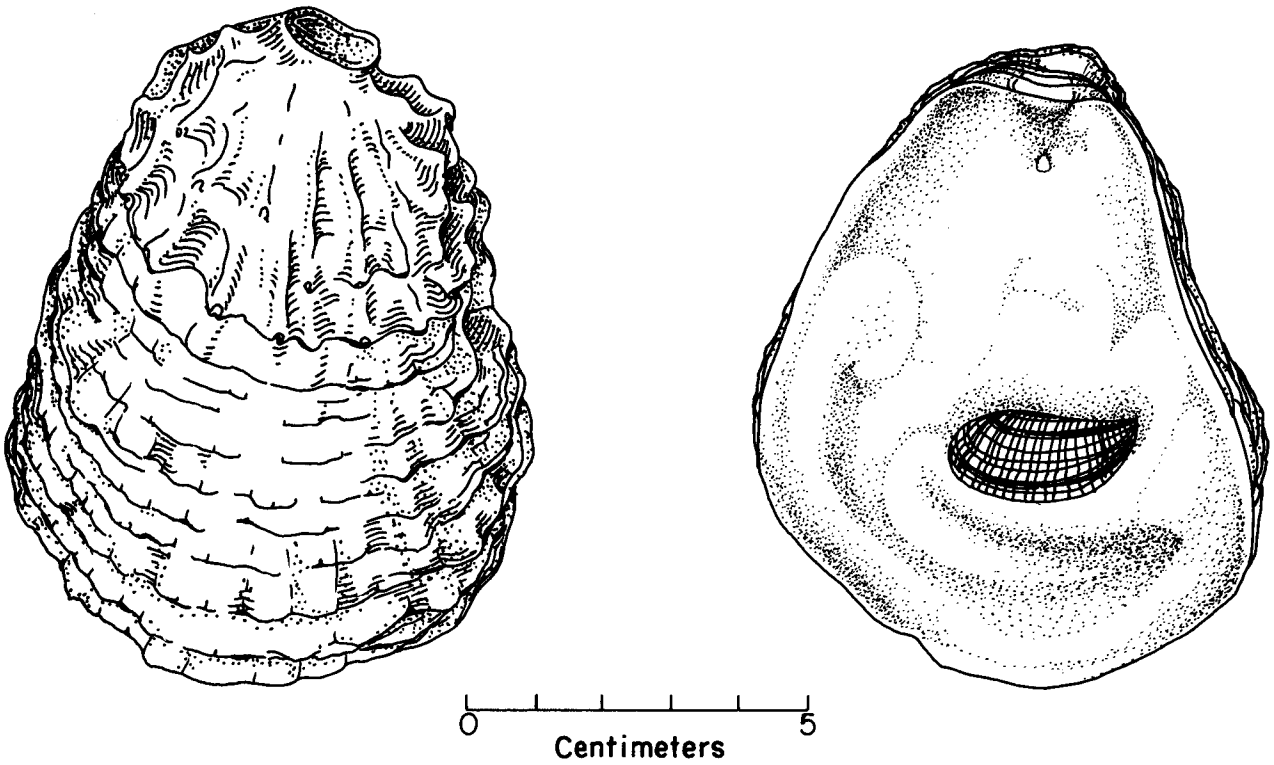


FIGURE 15.—Blue Point oyster (*C. virginica*) from Great South Bay, Long Island, N.Y. The size of this 5-year-old oyster is about 10 x 6.6 cm. (4 x 3 inches). The shell is strong and rounded; its surface is moderately sculptured. Left—outside surface of left valve. Right—inner surface of right valve. Small encircled area under the hinge on the inner surface of right valve is an imprint of Quenstedt's muscle.

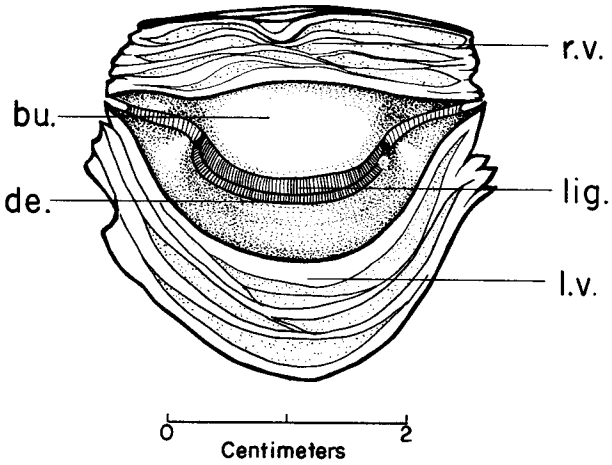


FIGURE 16.—Cross section below the hinge of an adult *C. virginica*. Left valve at bottom, right valve at top of the drawing. The buttress of the right valve fits the depression on the left valve. The two valves are connected by a ligament (narrow band indicated by vertical striations) which consists of a central part (resilium) and two outer portions. Slightly magnified. r.v.—right valve; bu.—buttress; de.—depression or furrow on left valve (l.v.); lig.—ligament.

grown *C. virginica* the pointed end of the upper (flat) valve is always shorter than that of its opposite member (fig. 17). The angle between the two beaks determines the greatest extent to which the valves can open for feeding or respiration and is, therefore, of significance to the oyster.

If the oyster shell is oriented in such a way that both of its valves are visible and the beaks point up and toward the observer, the flat valve with a shorter, convex resilifer is the right one and the cuplike valve with the longer concave resilifer is the left one. The dorsal margin of the oyster is the beak or hinge side, the ventral margin the opposite. If viewed from the right (flat) valve with the hinge end pointing away from the observer the anterior end of the oyster is at the right side of the valves and the posterior is at the left.

The posterior and anterior parts of the oyster shell may also be identified by the position of the muscle impression, an oval-shaped and highly pigmented area marking the attachment of the adductor muscle on the inner side of each valve.

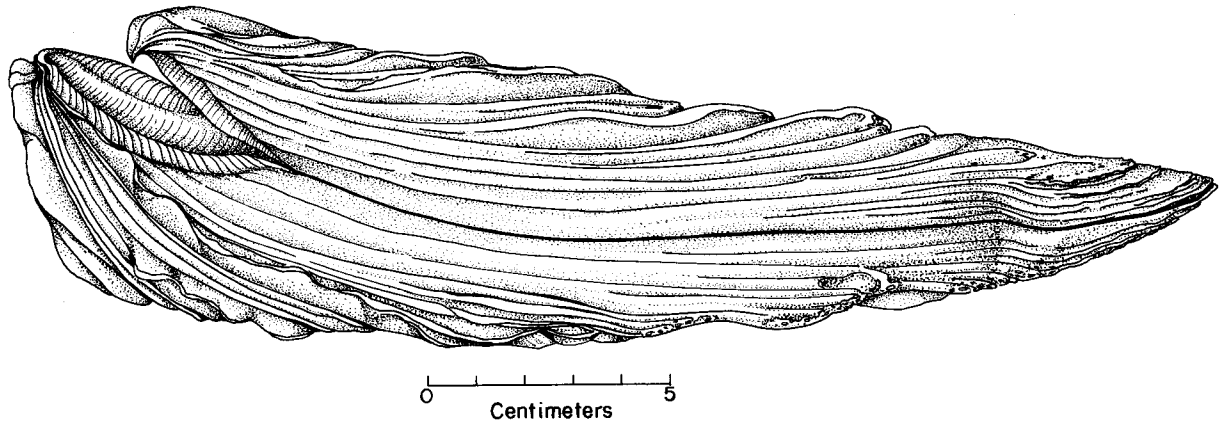


FIGURE 17.—Side view of a very old and large *C. virginica* from Stony Creek, Conn. Notice the curvature of the beak, the depressed resilifer on the lower valve and the protruding resilifer on the upper one. The angle between the beaks determines the maximum movement of the upper valve. Dimensions: height—25.5 cm. (10 inches) and width—6.4 cm. (2.5 inches).

The muscle impression is asymmetrically located closer to the posterior end of the valve. This area of the attachment of the adductor muscle has been called the "muscle scar." Some malacologists prefer to use the expression "muscle impression" or "area of attachment" (Stenzel, personal communication) because the word "scar" usually means the mark left by healing of an injury. The proposed change in terminology does not seem to be desirable because the name "muscle scar" has been so well established in scientific and popular writings that its abandonment may cause confusion.

The three principal dimensions of bivalves, including oysters, are measured in the following manner (fig. 20): height is the distance between the umbo and the ventral valve margin; length is the maximum distance between the anterior and posterior margin measured parallel with the hinge axis; and width is the greatest distance between the outsides of the closed valves measured at right angles to the place of shell commissure.

In many popular and trade publications on shellfish the word "length" is used instead of "height", and the word "width" is employed to designate the length of the oysters. To avoid confusion the scientific rather than popular terminology is used throughout the text of this book.

The shape of oyster shells and their proportions are highly variable and, therefore, are, in some cases, of little use for the identification of species. The variability is particularly great in the species of edible oysters (*C. virginica, C. gigas, C. angulata,* and *C. rhizophorae*) that have a wide range of distribution, thrive on various types of bottom, and are tolerant to changes in salinity and turbidity of water. Certain general relationships between the shape of the oyster shell and the environment are, however, apparent in *C. virginica.* Oysters growing singly on firm bottom have a tendency to develop round shells ornamented with radial ridges and foliated processes (figs. 4, 15). Specimens living on soft, muddy bottoms or those which form clusters and reefs are, as a rule, long, slender, and sparsely ornamented (figs. 19, 21).

The thickness and strength of the valves of *C. virginica* are highly variable. Shells of oysters grown under unfavorable conditions are often thin and fragile (Galtsoff, Chipman, Engle, and Calderwood, 1947). Likewise, so-called "coon" oysters from overcrowded reefs in the Carolinas and Georgia are, as a rule, narrow and have light shells (fig. 19). Heavy and strong shells are not typical for any particular latitude. They can be found on hard, natural bottoms throughout the entire range of distribution of *C. virginica.* I have in my collection shells from Prince Edward Island, Cape Cod, Delaware Bay, Louisiana, and Texas which in shape and strength of valves are indistinguishable from one another. Sometimes the growth of shells in length (in anteroposterior direction) equals or exceeds the growth in height. Such specimens, one from Texas and one from the waters of Naushon Island off the Massachusetts coast, were found in sticky mud. As can be seen

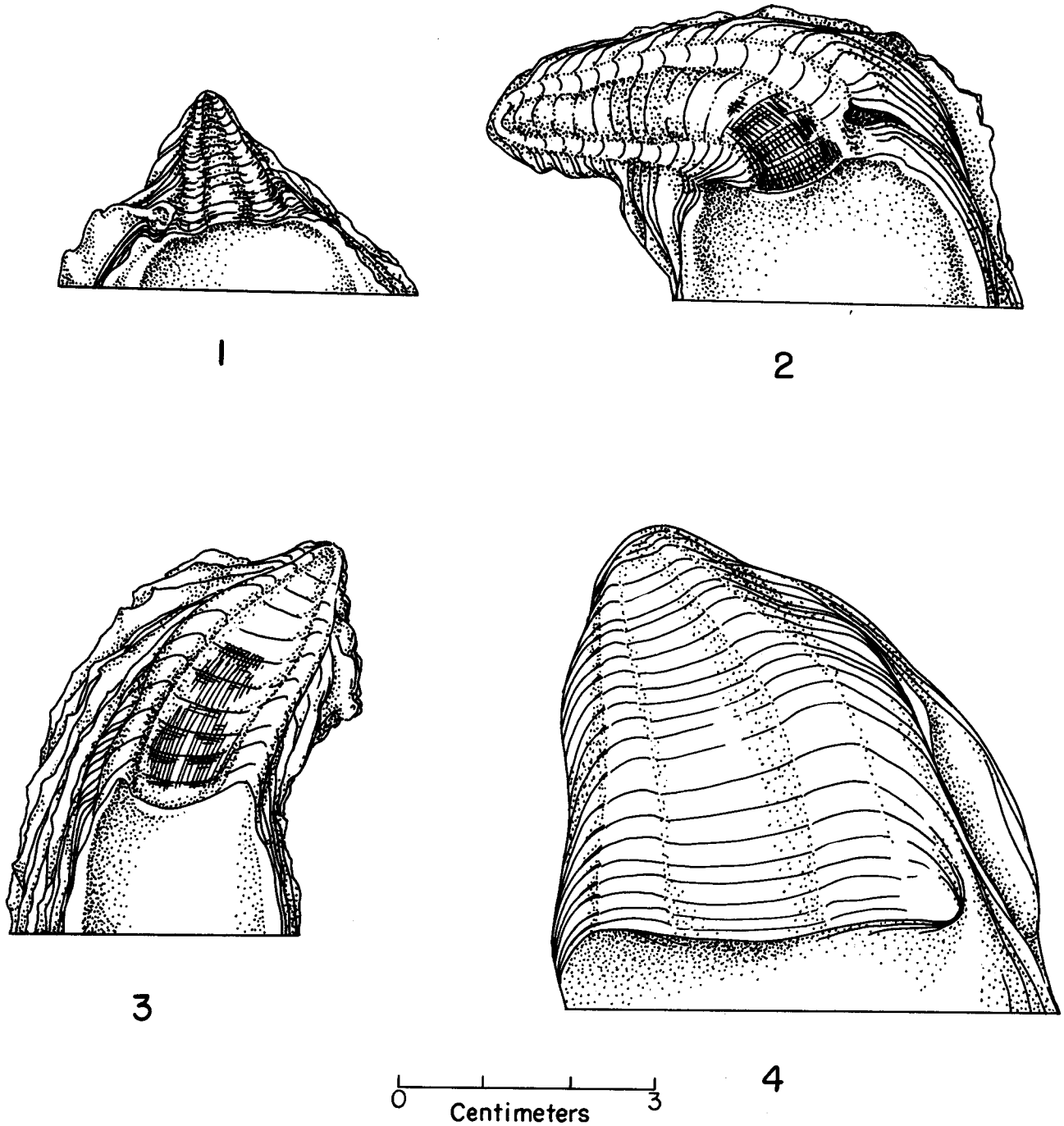


FIGURE 18.—Four shapes of beaks on left valves of old oysters, *C. virginica*. 1—narrow, short and almost straight; 2—strongly curved to the posterior; 3—of medium width, pointed forward; 4—very broad and slightly curved to the posterior.

from figure 22, the shells are almost identical in shape and size.

Oysters are frequently marketed under specific brands or trade names such as Blue Points (fig. 15), Cotuits, Chincoteagues, and others which imply the existence of local varieties different in size and shape of shells. There is no evidence, however, to substantiate this claim. So-called "Blue Points" characterized by round shape, strong shell, and medium size may be found,

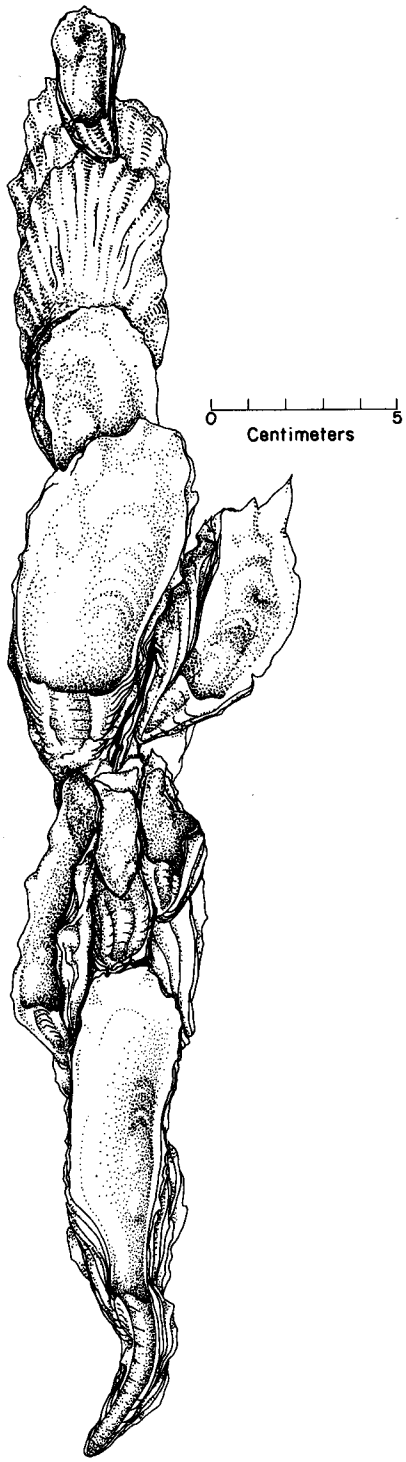


FIGURE 19.—Several generations of oysters, *C. virginica*, growing vertically on muddy bottom of Altamaha Sound, Ga. Notice the very long and narrow beak of the lowermost shell.

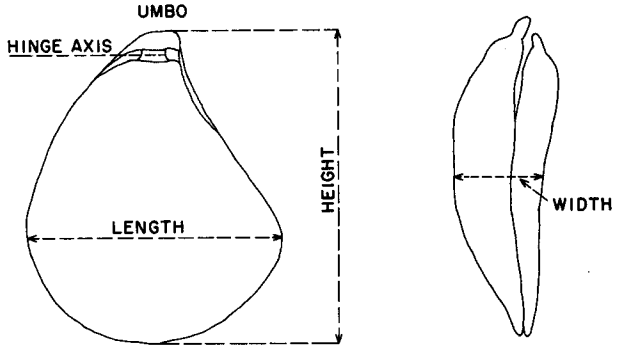


FIGURE 20.—Diagram showing the correct method of measuring the height, length, and width of oyster shells.

for instance, in any part of the coast where oysters grow singly on hard bottom and are not crowded. As a matter of fact, in past years "Blue Points" sold in retail stores actually were taken from the Chesapeake Bay and North Carolina. This is also true for "Cotuits" and other popular brands.

That the shape of oysters cannot be associated with any particular geographical location is best shown by the fact that all the kinds represented in trade, including long and narrow "coon" oysters which are regarded as being typical for the tidal areas of the South Atlantic States, are found in various bays and estuaries of Cape Cod, Mass. The only shell character that appears to be associated with the geographical distribution of the species is the pigmentation of the interior surfaces of the valves. In North Atlantic oysters the inner surface is unpigmented or very lightly pigmented (outside of the place of attachment of the adductor muscle), while in South Atlantic and Gulf oysters the dark brown or reddish pigmentaton of the valves is more pronounced.

DIMENSIONS

Oysters (*C. virginica*) of marketable size usually measure from 10 to 15 cm. (4 to 6 inches) in height; depending on the place of origin an oyster of this size may be 3, 4, or 5 years old.

As a rule, oysters do not stop growing after reaching certain proportions but continue to increase in all directions and, consequently, may attain considerable size. Such old and very large oysters are usually found on grounds undisturbed by commercial fishing. The largest oyster in my collection was found in the vicinity of Boothbay Harbor, Maine. Its dimensions were as follows:

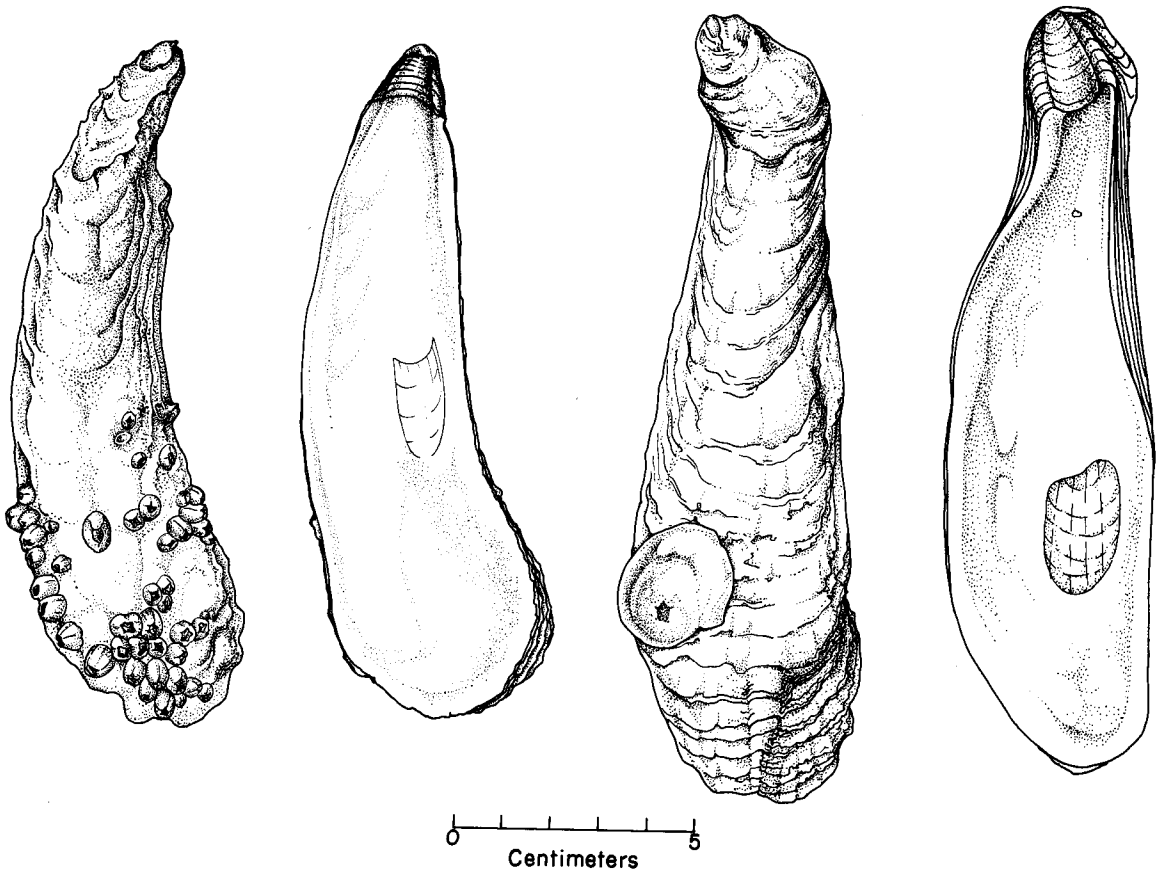


FIGURE 21.—Shells of *C. gigas* (left) and *C. virginica* (right) grown on soft, muddy bottom. Note the remarkable similarity in the shape, size, and sculpture of the two species of oysters. The *C. gigas* was obtained from the northern part of Puget Sound and the *C. virginica* from Georgia. The shells of the two species can be distinguished by the absence of pigmentation of the muscle impression in *C. gigas* and by its lighter shell material.

height—20.6 cm. (8.1 inches); height of left and right beak—5.5 cm. (2.1 inches) and 4.5 cm. (1.75 inches) respectively; length of shell—9.7 cm. (3.8 inches); maximum width (near the hinge)—6.5 cm. (2.6 inches). The total weight was 1,230 g., the shell weighing 1,175 g., the meat 35.8 g., and the balance of 19.2 g., representing the weight of sea water retained between the valves. Apparently the largest oyster recorded in American literature is the giant specimen from the Damariscotta River, Maine, reproduced in natural size by Ingersoll (1881, pl. 30, p. 32). This shell is 35.5 cm. (14.3 inches) in height and 11 cm. (about 4.4 inches) in length.

SHAPE OF SHELLS

The shells of many gastropods and bivalves are spiral structures in which the convolutions of the successive whorls follow a definite pattern. The spiral plan is frequently accentuated by ridges, furrows, spines and nodules, or by pigmented spots which repeat themselves with remarkable regularity. A spiral structure is not restricted to mollusk shells. As a matter of fact, it is very common throughout the animal and plant kingdom as well as in architecture and art. Examples of a great variety of spirally built organisms and structures are given in the beautifully illustrated books entitled "Spirals in nature and art" and "Curves of life" (Cook 1903, 1914). As the title of the second book implies, Cook is inclined to attach some profound significance to the kind of curves found in animal and plant forms. This view, inherited from the philosophers of the 18th and 19th centuries, considers the spiral organic structures as a manifestation of life itself. The influence of this philosophy persisted among some scientists until the thirties of the present century. It can be found, for instance, as late as 1930 in the writings of a French physiologist, Latrigue (1930)

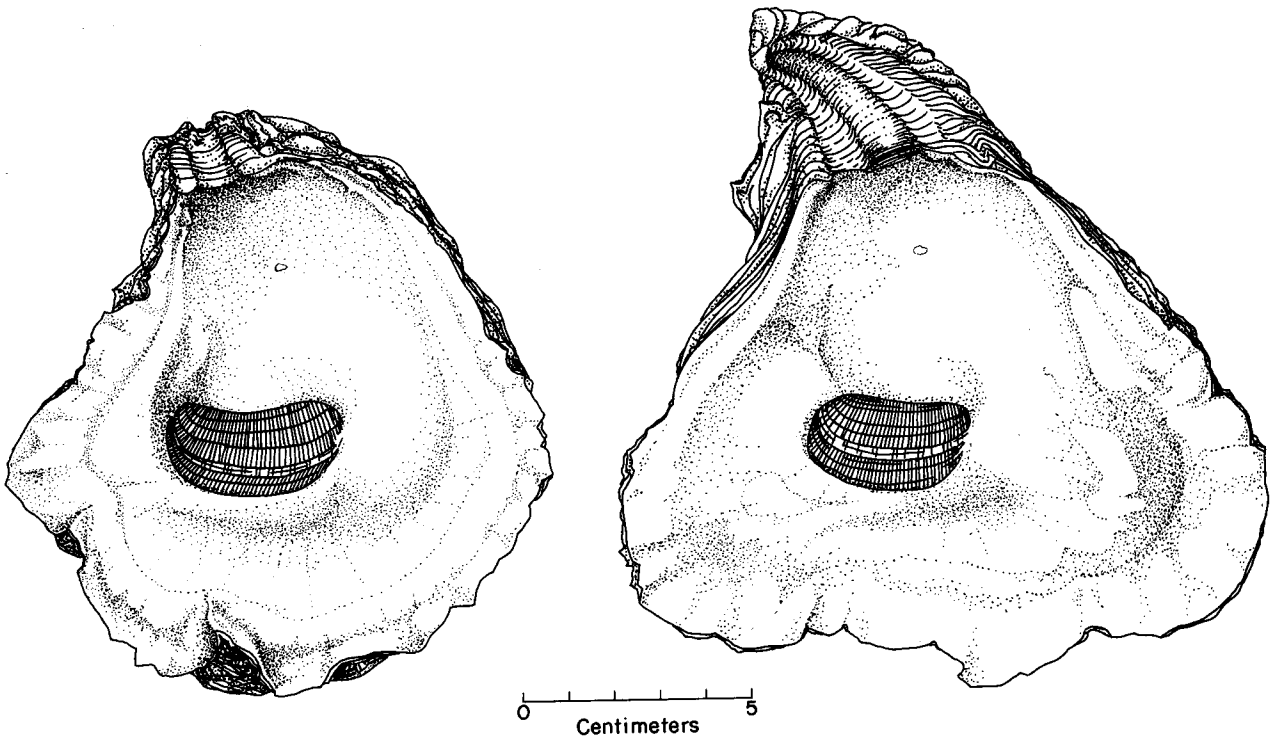


FIGURE 22.—Two left shells of *C. virginica* grown on sticky mud. On the left side is the oyster from Karankawa Reef in Matagorda Bay, Tex.; on the right is the oyster from Hadley Harbor, Naushon Island, near Woods Hole, Mass. The dimensions of the Texas oyster are 13 by 11.5 cm. (5.1 by 4.5 inches) and for the Hadley Harbor oyster 15.5 by 14.5 cm. (6.1 by 5.7 inches).

who in the book, "Biodynamique générale," attributes mysterious and not well-defined meaning to the "stereodynamics of vital vortex." These speculations contributed nothing to the understanding of the processes which underlie the formation of shells and other organic structures.

In the earlier days of science the geometric regularity of shells, particularly that of gastropods, had been a favored object for mathematical studies. Properties of curves represented by the contours of shells, as well as those seen in horns, in flower petals, in the patterns of distribution of branches of trees, and in similar objects, were carefully analyzed. An excellent review of this chapter of the history of science is given in a well-known book "On growth and form" (Thompson, 1942) in which the reader interested in mathematics and its application to the analysis of organic forms will find many stimulating ideas.

Among the array of curves known in mathematics, the kind most frequently encountered in the shells of mollusks is the logarithmic or equiangular spiral (fig. 23). The latter name refers to one of its fundamental characteristics, described by Descartes, namely, that the angle between tangent PG (fig. 23) and radius vector OP is constant. Another property of this curve which may be of interest to biologists is the fact that distances along the curve intercepted by any radius vector are proportional to the length of these radii. D'Arcy Thompson showed that it is possible to apply the mathematical characteristics of curves to the interpretation of the growth of those shells which follow the pattern of a logarithmic spiral. According to his point of view, growth along the spiral contour is considered as a force acting at any point P (fig. 23) which may be resolved into two components PF and PK acting in directions perpendicular to each other. If the rates of growth do not change, the angle the resultant force, i.e., the tangent PG, makes with the radius vector remains constant. This is the fundamental property of the "equiangular" (logarithmic) spiral. The idea forms the basis of Huxley's (1932) hypothesis of the interaction of two differential growth ratios in the bivalve shells and also underlies Owen's (1953) concept of the role of the growth components determining the shape of the valves.

Another important characteristic of the growth of bivalves pointed out by Thompson is that

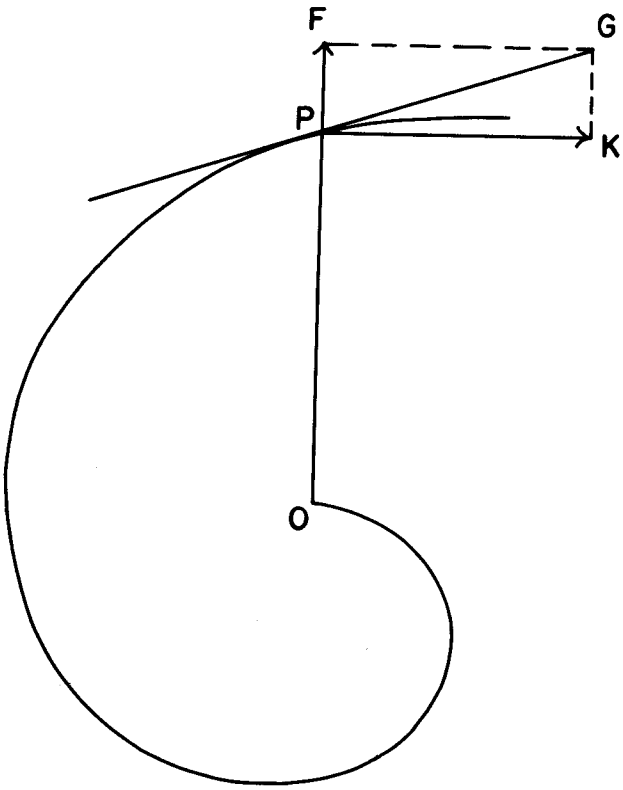


FIGURE 23.—Logarithmic or equiangular spiral. Explanation in text.

increase in size is not accompanied by any change in shape of the shell; the proportions of the latter remain constant, and the shell increases only in size (gnomonic growth). This general rule holds true for many free-moving gastropods and bivalves. It is not, however, applicable to sessile forms like oysters, in which the shape of the shell changes somewhat with size, particularly at the early stages of growth, and is greatly modified by contact with the substratum upon which the mollusks rest. The plasticity and variability of attached forms are probably associated with their inability to escape the effects of proximate environment.

The contour of oyster shell may be either circular (young *C. virginica*, *O. edulis*) or elongated and irregular. Spiral curvature may be noticed, however, on a cross section of the lower (concave) valve cut along its height perpendicular to the hinge. The curve can be reproduced by covering the cut surface with ink or paint and stamping it on paper. The upper valve is either flat or convex.

The curvature of bivalve shells is sometimes called conchoid. The term may be found in general and popular books dealing with bivalve shells, but the author who introduced it in scientific literature could not be traced. The Greek word "conchoid", derived from "conch"—shell and "eidos"—resembling or similar to, implies the similarity of the curve to the contour of a molluscan shell.

The curve is symmetric with respect to the 90° polar axis (fig. 24). It consists of two branches, one on each side of the fixed horizontal line CD to which the branches approach asymptotically as the curve extends to infinity. The curve, known as conchoid of Nicomedes, is constructed by drawing a line through the series of points P and P_1 which can be found in the following way: from the pole O draw a line OP which intersects the fixed line CD at any point Q. Lay off segments $QP=QP_1=b$ along the radius vector OP. Repeat the process along the radii originating from the pole O and draw the two branches of the curve by joining the points. The curve has three distinct forms depending on whether "a" (a distance OQ from the pole to the point of intersection of the polar axis with the fixed line CD) is greater, equal to or less than b. The formula of the curve if $b<a$, is $r=a \sec \theta \pm b$, where r is the locus of the equation and $\sec \theta$ is secant of the vectorial angle θ.

Sporn (1926) made a detailed mathematical analysis of the conchoid curve and considered that the curvatures of bivalve shells conform to this geometrical type. Lison (1942) rejected this conclusion as not supported by observations and experimental evidence. He quite correctly stated that Sporn's work deals exclusively with abstract mathematical analyses of curves which in reality are not those found in molluscan shells. If one cuts a bivalve shell at any angle to the plane of closure of the valves, one obtains the curved lines of the two valves (fig. 25) which only remotely resemble the conchoid of Nicomedes and touch

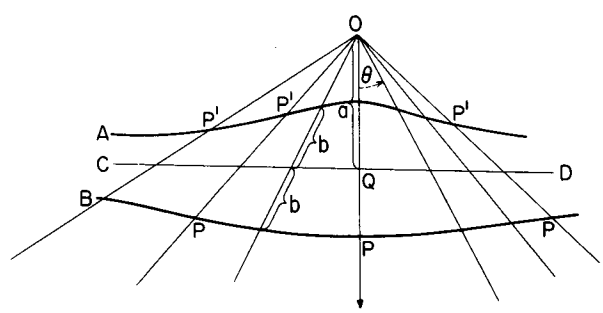


FIGURE 24.—Construction of the conchoid curve of Nicomedes. Explanation in text.

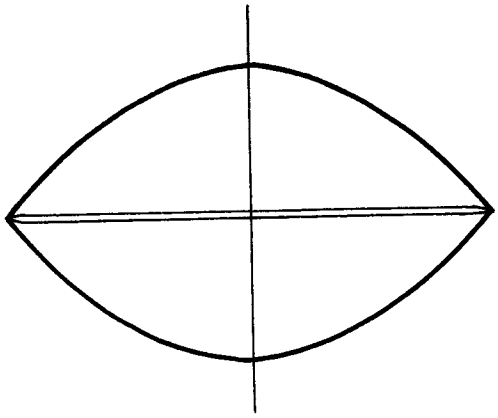


FIGURE 25.—Cross section of two valves of *Cardium*. The similarity with the conchoid in figure 24 is superficial.

each other at the ends. The two branches of conchoid (C and D) join together only in infinity (fig. 24).

Lison pointed out that the shape of the shell may be considered as a whole series (ensemble) of arches, the curvatures of which are described by logarithmic spirals of the same parameter which have a common origin at the umbo. The latter is their common pole. The arches terminate at the edge of the valve. The contour of the valve edge, frequently called the "generating curve", is usually confined to one plane parallel to the plane of opening and closing of the shell.

Among many spirals that can be drawn on the surface of a shell only one is completely confined to a single plane. This spiral was called by Lison the "directive spiral"; its plane is the "directive plane" of the shell. All other spirals which can be easily noticed on the shell surface as ridges, furrows, or as pigmented bands deviate to the right or left depending on which side of the directive plane they are located (fig. 26).

By mathematical analysis of the curved surfaces of various bivalve species Lison arrived at the general equation [3] of a valve. He observed that by itself such an equation may not be helpful to biologists unless it can be used for comparing the shape of the individuals of the same species or in making comparison between the different species. Lison stated that in practice it is not necessary to make the involved mathematical computations. It is sufficient to compare certain "natural" characteristics of shells, namely, the directive plane described above, the plane of closure of valves (or commissure plane), and the angle of

[3] General equation of a valve as given by Lison (1939) is as follows: $\sigma=\sigma_0 p x$; $\omega=\omega_0+\alpha$; $z=z_0 e^{p\alpha}$ in which p is a constant and σ_0, ω_0, and z_0 are the functions which express on cylindrical coordinates the form of the free edge of the valve when the directive plane is located within the xy and the origin of the coordinates is at the umbo. (Translation by Paul S. Galtsoff.)

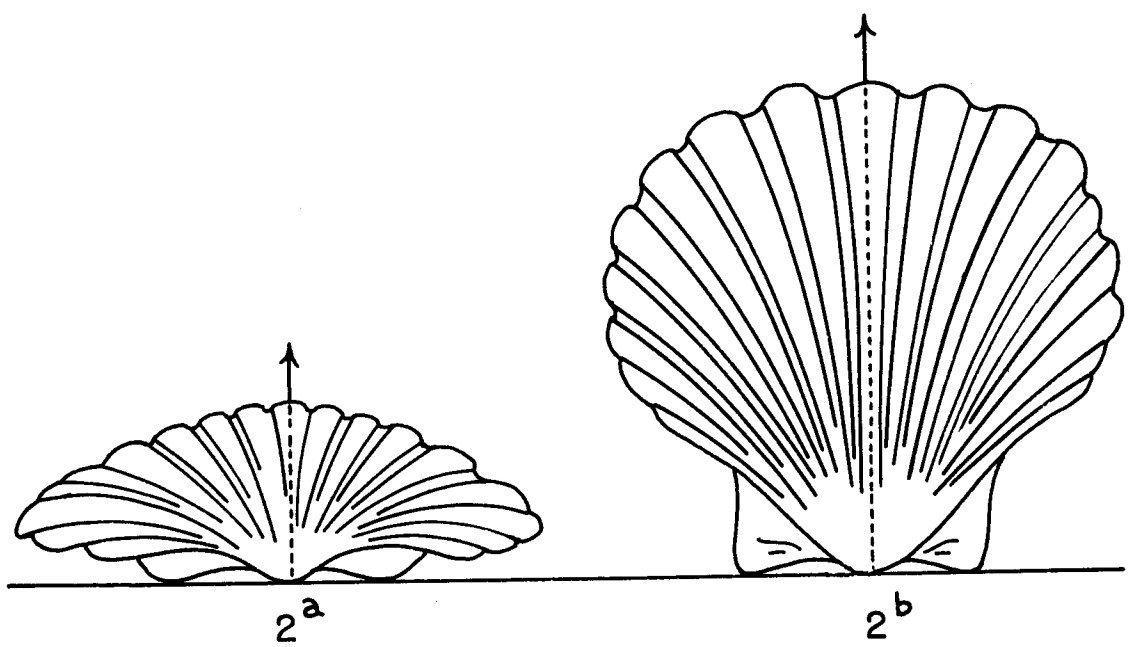


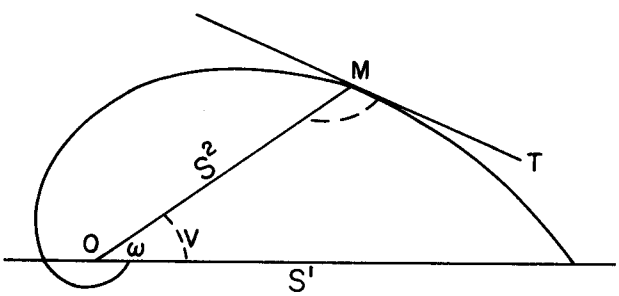
FIGURE 26.—Directive plane of scallop shell, *Pecten*, viewed from hinge end 2a, and from the broad side 2b. The arrows indicate the directive plane. (After Lison, 1939.)

incidence. The plane of closure of the valves originates at the umbo and passes between the edges of the two opposing valves when they are closed and touching each other. The angle of incidence, as defined by Lison, is the angle between the plane of closure and the directive plane. In round and symmetrical shells of scallops, pearl oysters, and other bivalves the directive plane is perpendicular to the plane of closure and the angle of incidence is 90° (fig. 26). In the shells of *Cardium orbita*, the directive plane forms an acute angle of 81° and is much smaller in elongated shells such as *Fimbria fimbriata* and *Trapezium oblongum*. The comparison between the shells can easily be made by recording the contours at the free margins of the valves and determining the angle of incidence.

To determine the shape of logarithmic spiral of the valve the shell may be sawed along the directive plane (fig. 27) and the section oriented with the umbo O at lower left. If S_1 and S_2 are respective lengths of the two radii the value of parameter p can be computed by using the fundamental equation of logarithmic spiral,

$$P = \frac{\log. S_1 - \log. S_2}{\omega}$$

(logarithms in this equation are natural, to base e).



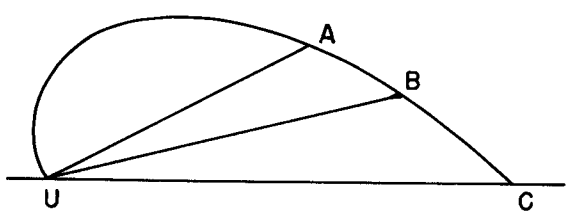


FIGURE 27.—Valve of a shell sawed along the directive axis describes a plane logarithmic spiral. According to Lison (1942). OM—radius vector; T—tangent; O—umbo; V—angle between the two radii.

In résumé, Lison attempted to prove that the form of the shell in which the generating curve is confined to one plane is determined by three conditions: (1) the angle of the directive spiral, (2) the angle of incidence, and (3) the outline of the generating curve.

Further attention to the problem of the shape and formation of the bivalve shell was given by Owen (1953). In general he accepted Lison's conclusions and stated that "the form of the valves should be considered with reference to: (a) the outline of the generative curve, (b) the spiral angle of the normal axis, and (c) the form (i.e., plani-spiral or turbinate-spiral) of the normal axis." The normal axis is considered by Owen with reference to: (1) the umbo, (2) the margin of the mantle edge, and (3) the point at which the greatest transverse diameter of the shell intersects the surface of the valves. Thus, it can be seen from this statement that Owen's "normal axis" does not coincide with Lison's directive plane except in bilaterally symmetrical valves (fig. 28). According to Owen's view, the direction of growth at any region of the valve margin is the result of the combined effect of three different components: (a) a radial component radiating from the umbo and acting in the plane of the generating curve, (b) a transverse component acting at right angles to the plane of the generating curve, and (c) a tangential component acting in the plane of the generating curve and tangentially to it. The turbinate-spiral form of some bivalve shells is due to the presence of the tangential component which in plani-spiral shells may be absent or inconspicuous. Likewise, the transverse component may be greatly reduced or even absent in the valve. Thus, from this point of view the great variety of shell forms may be explained as an interaction of the three components (fig. 29). Owen's point of

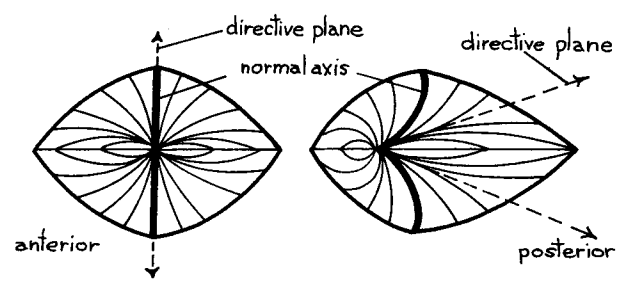


FIGURE 28.—Comparison of directive plane of Lison with normal axis (Owen). A—shell not affected by tangential component; B—shell affected by tangential component.

view is basically similar to Huxley's hypothesis (1932) of differential length growth and width growth of molluscan shells. Owen correctly points out an error in Lison's interpretations that the lines of equal potential activities involved in the secreting of shell material at the edges of the valves are parallel to each other. This is obviously not the case since all lines of growth of the lamellibranch shell radiate from a common node of minimum growth near the umbo. For this reason the comparison of bivalves can be more conveniently made by using radial coordinates as has been shown by Yonge (1952a, 1952b).

The mathematical properties of shell surfaces are of interest to the biologist because they may provide clues to understanding the quantitative aspects of the processes of shell formation. It can be a priori accepted that any organism grows in an orderly fashion following a definite pattern. The origin of this pattern and the nature of the forces responsible for laying out structural materials in accordance with the predetermined plan are not known. The pattern of shell structure is determined by the activities at the edge of the shell-forming organ, the mantle. At the present state of our knowledge it is impossible to associate various geometrical terms which describe the shape of the shell with concrete physiological processes and to visualize the morphogenetic and biochemical mechanisms involved in the formation of definite sculptural and color patterns. The solution of this problem will be found by experimental and biochemical studies which may supply biological meanings to abstract mathematical concepts and equations. Experimental study of the morphogenesis of shells offers splendid opportunities for this type of research.

GROWTH RINGS AND GROWTH RADII

Nearly 250 years ago Réaumur (1709) discovered that shells grow by the accretion of material secreted at their edges. Since that time this important observation has been confirmed by numerous subsequent investigations. The rings on the outer surfaces of a bivalve shell, frequently but incorrectly described as "concentric", represent the contours of the shell at different ages. Rings are common to all bivalves but are particularly pronounced on the flattened shells of scallops, clams, and fresh-water mussels. Depending on the shape of the shell, the rings are either circular or oval with a common point of origin at the extreme dorsal side near the umbo (figs. 30 and 31). The diagrams clearly show that the rate of growth along the edge of the shell is not uniform. It is greater along the radius, AD, which corresponds to the directive axis of Lison, and gradually decreases on both

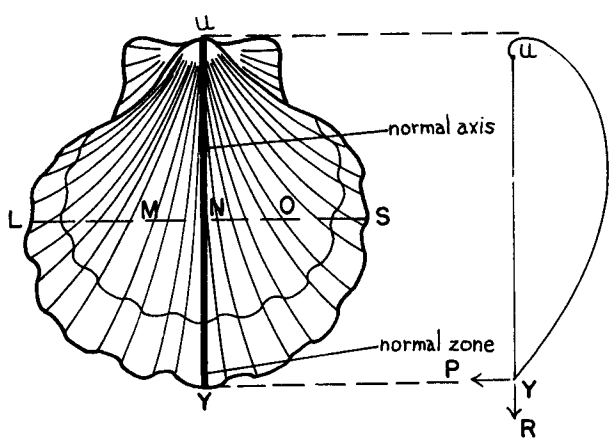


FIGURE 29.—Normal axis and the two growth components in the shell of scallop. LS—plane perpendicular to the plane of the generating curve; N—turning point of the concave side of the shell shown at right; M and O—auxiliary radii; P—transverse component; R—radial component; UY—normal axis. From Owen (1953).

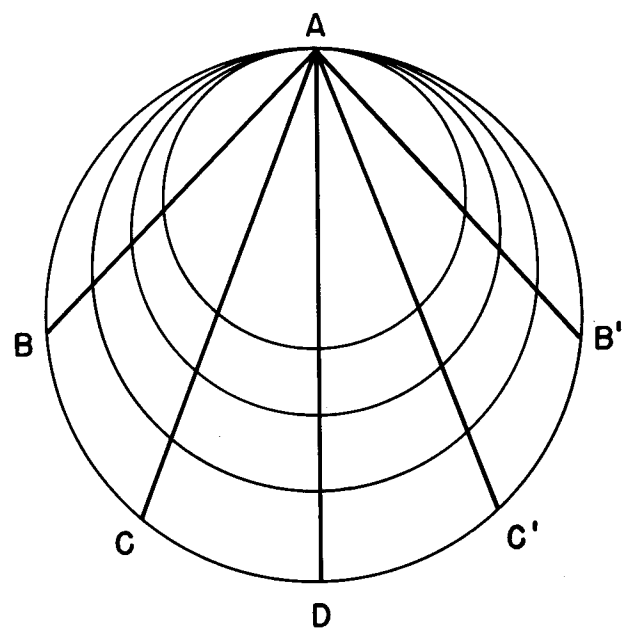


FIGURE 30.—Diagram of a circular bivalve shell of the kind represented in *Pecten*, *Anomia*, and young *C. virginica*. Radii extending from the umbo to the periphery of the generating curve are proportional to the rate of growth at the edge of a circular shell Radius AD corresponds to the directive axis of Lison.

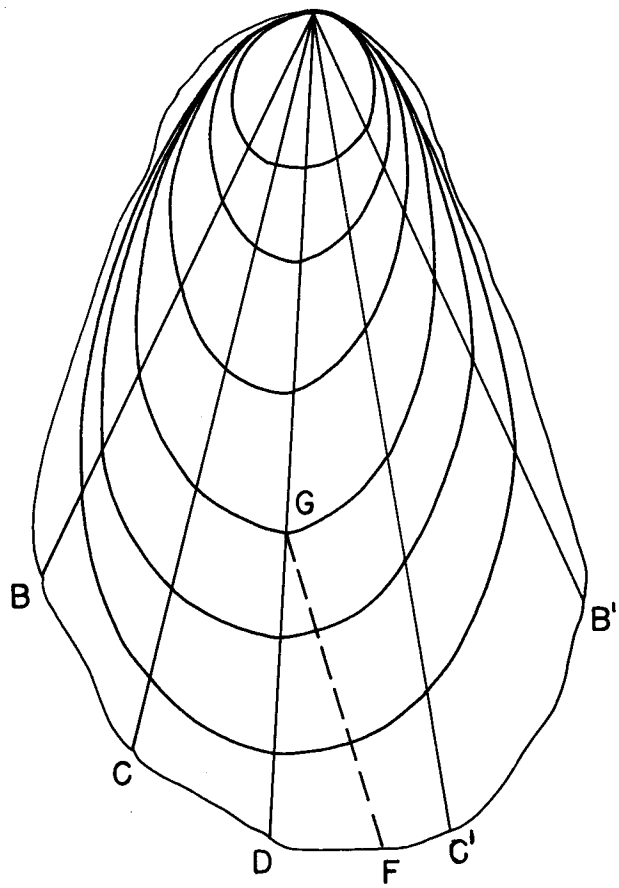


FIGURE 31.—Diagram of a shell of adult *C. virginica*. Radii extend from the umbo to the periphery of the generating curve. The principal axis AGF shows the change in the direction of growth at G. The length of radii is proportional to the rate of shell growth at the edge.

sides of it along growth radii AC, AB, and AC_1, AB_1.

Circular shells in *C. virginica* may be found only in very young oysters (fig. 32a). Within a few weeks after setting the shell becomes elliptical, and as elongation (increase in height) continues the principal vector of growth shifts to one side (fig. 32b).

A series of curves noticeable on round shells (fig. 32) clearly illustrate the differential rate of growth along the periphery of the valve, which increases in size without altering in configuration. Thompson (1942) found an interesting analogy between this type of growth, radiating from a single focal point (the umbo), and the theorem of Galileo. Imagine that we have a series of planes or gutters originating from a single point A (fig. 30) and sloping down in a vertical plane at various angles along the radii AB, AC, AC_1, and AB_1 which end at the periphery of a circle. Balls placed one in each gutter and simultaneously released will roll down along the vectors B, B_1, C, C_1, and D. If there is no friction or other form of resistance, all the balls will reach the periphery at the same time as the ball dropping vertically along AD. The acceleration along any of the vectors, for instance, AB, is found from the formula $t^2=2/g$ AD where t is time and g is acceleration of gravity.

A similar law, involving a more complex formula, applies to cases in which the generating curve is nearly elliptical, for instance, in the shells of adult oysters. The rate of growth at different sectors of the periphery of the shell obviously has nothing to do with the acceleration of gravity, but the similarity between the length of the radii which represent the rate of growth along a given direction of the shell and the acceleration along the vectors in the theorem of Galileo is striking. It appears reasonable to expect that the Galileo formula may be applicable to the physiological process taking place near the edge of the valve. One may assume, for instance, that the rate of physiological activities is affected by the concentration of growth promoting substances or by enzymes involved in the calcification of the shell and that these factors vary at different points of the mantle edge in conformity with Galileo's formula. Experimental exploration of the possibilities suggested by mathematical parallelism may be, therefore, profitable in finding the solution to the mystery of the formation of shell patterns.

CHANGES IN THE DIRECTION OF PRINCIPAL AXES OF SHELL

The principal axes of shells of *C. virginica* are not as permanent as they are in clams, scallops, and other bivalves in which the shape of the valves remains fairly constant and is less affected by environment than in the oyster. The plasticity of oysters of the species *Crassostrea* is so great that their shape cannot be determined geometrically (Lison, 1949). This inability to maintain a definite shape is probably the result of the sedentary living associated with complete loss of the power of locomotion.

In some species of oysters the shells are circular or nearly circular. In such cases the ratio of the height of the valve to its length is equal to

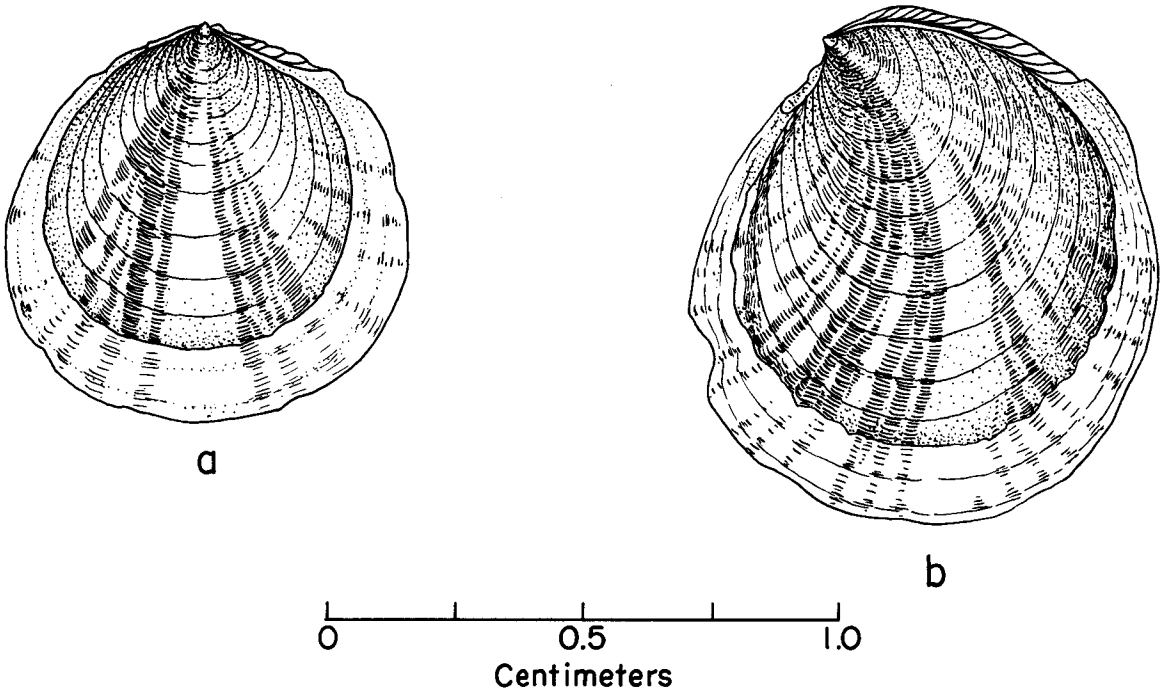


FIGURE 32.—Two small *C. virginica* growing attached to tar paper. Maximum dimension of shell: a—0.85 cm.; b—1.0 cm. At b the principal axis curves to the left.

1.0, as, for instance, in *C. rivularis* (fig. 8) and *O.* (*Alectryonia*) *megodon* Hanley (fig. 3) (Olsson, 1961). Oysters of the latter species from the Pacific Coast of Central and South America grow singly, in vertical position, cemented to the rocks by their left valves. The specimens I collected on Pearl Islands, Gulf of Panama, measured 17 to 18 cm. in height and 16 to 17 cm. in length. The European flat oyster, *O. edulis* (fig. 9) usually forms rounded shells in which the length exceeds the height. Small, noncommercial species, *O. sandwichensis* of the Hawaiian Islands and *O. mexicana* from the Gulf of Panama, are almost circular with the tendency to extend in length rather than in height. Crowded conditions under which these species thrive attached to rocks in a narrow tidal zone greatly obscure and distort the shape of their shells.

Small *C. virginica* growing singly on flat surfaces without touching each other are usually round (fig. 32). In a random sample consisting of 100 single small oysters (spat about 6 weeks old) varying from 5 to 15 mm. in height and growing on tar paper, the height/length ratio varied from 0.6 to 1.2. Nearly half of them (49 percent) were perfectly round (H/L ratio=1); in 30 percent the ratio was less than 1; and in 21 percent the length exceeded the height.

In small single oysters less than 10 mm. in height the principal (normal) axis of growth is clearly marked. All other radii symmetrically oriented on both sides of the principal axis are indicated by the pigmented bands on the surface of the shell. The newly deposited shell, discernible at the periphery of the oyster, forms a band which is wider at the ventral edge of the shell and slightly narrows anteriorly and posteriorly (fig. 32a). With the growth of the oyster its principal axis is shifted to the side, curves, and is no longer confined to one plane. The curvature of the valve becomes a turbinate-spiral. Gradually the oyster becomes slightly oval-shaped and asymmetrical.

The change in the direction of the principal axis of growth is not associated with the environment since it takes place only in some of the oysters growing under identical conditions. Occasionally oysters are formed in which the pigmentation along the principal axis is so pronounced that the dark band which marks its position may be mistaken for an artifact (fig. 33) while the secondary axes are not visible. The shells of adult *C. virginica* usually curve slightly to the left (if the oyster is placed on its left valve and viewed from above). Frequently, however, inverted specimens are found in which the growth

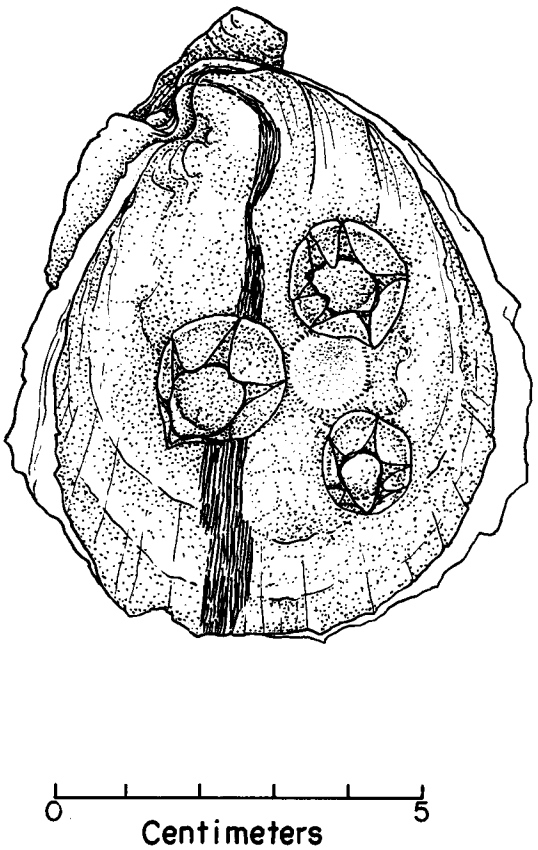


FIGURE 33.—Principal axis of growth of a *C. virginica* from Chatham, Mass., is deeply marked by a pigmented band.

has shifted into the opposite direction (fig. 34). The "normal" oyster (the right side of the figure) is curved to the left while in the inverted specimen, shown on the left of the figure, the shell curves to the right. Such "right-handed" oysters are probably common in all oyster populations since they were found in Texas, Chesapeake Bay, Narragansett Bay, and Great Bay, N.H. In every other respect the inverted specimens are normal and had typically cupped left valves with well-developed grooved beaks. There is no evidence that inversion was caused by mechanical obstruction or some unusual position on the bottom.

Complete inversion in bivalves was described by Lamy (1917) for *Lucina*, *Chama*, and several species of the subgenus *Goodallia* (fam. Astartidae). It consisted in the appearance of structures, typical for the right valve, on the left valve and vice versa. In the case of *C. virginica* the structural elements remain unaffected and the inversion is limited to the contours of the valves.

The once established principal axis of growth does not always remain unchanged. Occasionally old oysters are found in which the direction of growth had undergone sudden changes of about 90°. The change shown in figure 35 took place when both oysters were about 6 to 7 years old.

The instability of the principal axis of growth may be even more pronounced. My collection has an oyster (*C. virginica*) found on the banks of a lagoon near Galveston, Tex., in which the principal axis, clearly indicated by pigmented bands on the surface of the valves, changed its direction at the end of each growing period. The resulting zigzag line is clearly visible in the specimen (fig. 36).

DIMENSIONAL RELATIONSHIPS OF SHELL

Shape of a bivalve shell is often expressed as a ratio between its height and length or by some other numerical index. Lison (1942) pointed out that the shape of an oyster shell cannot be expressed in precise geometrical terms, presumably because of its great variability. The "index of shape" determined as a ratio of the sum of height and width of a shell to its length was used by Crozier (1914) in studying the shells of a clam, *Dosinia discus*. For the mollusks ranging from 2 to 7 cm. in length collected near Beaufort, N. C. this index varied from 1.24 to 1.28 indicating that the increase of the species in height and width was directly proportional to the increase in length. Such regularity is not found in the shells of adult *C. virginica* taken at random from commercially exploited bottoms. For the entire range of distribution of this species in the Atlantic and Gulf states the index of shape varied from 0.5 to 1.3. The histogram (columns in figure 37) shows nearly normal frequency distribution with the peak of frequencies at 0.9. No significant differences were found in the index of shape in the northern and southern populations of oysters examined separately. The boundary between the two groups was arbitrarily drawn at the Virginia-North Carolina line. The two curves connecting the frequency points on figure 37 indicate that in the southern population the index of shape extends from 0.5 to 1.3, while in the northern oysters it varies from 0.6 to 1.2. The difference is probably not very significant, but it may be due to a greater percentage of wild oysters on commercially exploited natural bottoms of the southern states.

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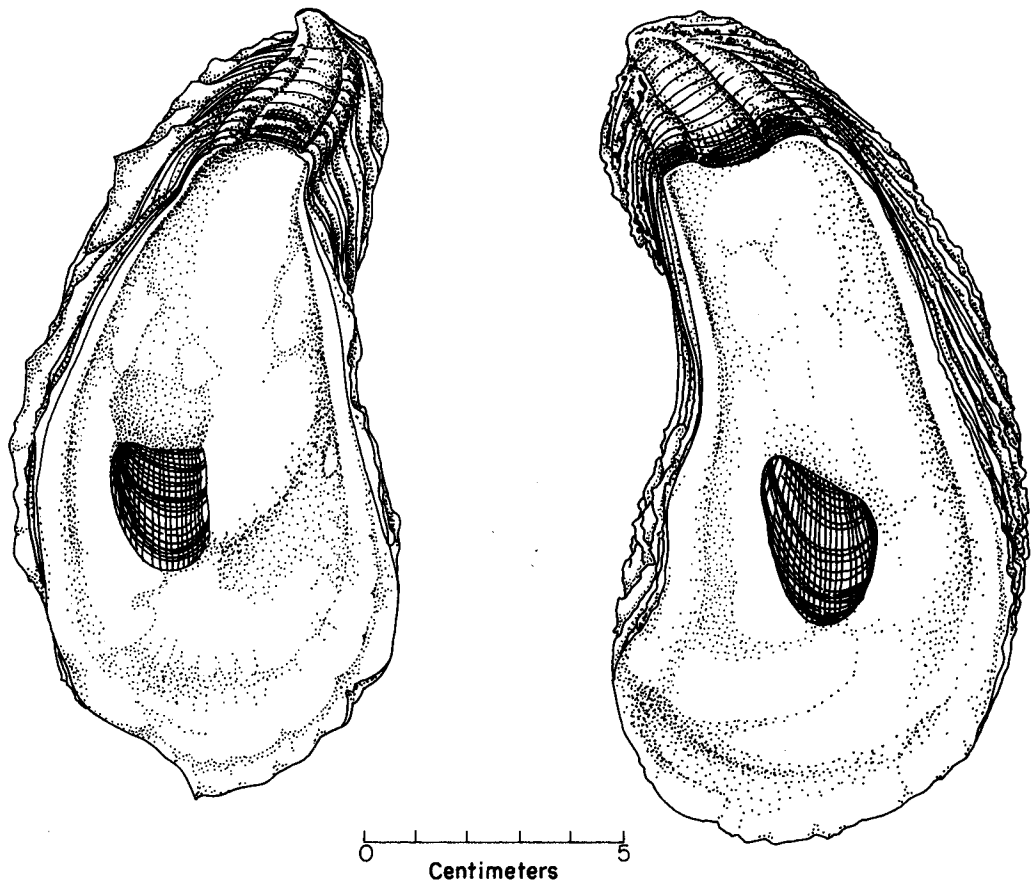

FIGURE 34.—Left valves of the two large *C. virginica* from Narragansett Bay, R.I. On the right is a "normal" oyster; its shell curves to the left. On the left side is an inverted oyster; its shell curves to the right.

Most of the oysters from the North Atlantic and Chesapeake states were taken from bottoms on which oysters are regularly planted for cultivation. There are no significant differences in the mean, mode, and median of the two groups (table 1). Contrary to the conditions found by Crozier in *Dosinia discus*, the "index of shape" of *C. virginica* is highly variable.

SHELL AREA

Information regarding the approximate area of an oyster shell of known height may be useful to oyster growers who want to determine in advance what percentage of the bottom area set aside for planting will be covered by oysters of known size. Since the oystermen usually know the number of oysters of various sizes needed to make up a bushel, the information given below may be used in determining in advance whether the area of the bottom is sufficient to provide space for their additional growth.

TABLE 1.—*Index of shape* $\left(\frac{height+width}{length}\right)$ *of oysters taken by commercial fishery*

Locality	Mean	Standard deviation	Mode	Median
Northern grounds	0.87	0.05	0.94	0.09
Southern grounds	0.87	0.02	0.94	0.9

It is self-evident that the area of the valve increases proportionally to the increase in its linear dimensions. For determining the area a piece of thin paper was pressed against the inner surface of the right (flat) valve and the outlines were drawn with pencil. The area was measured with a planimeter. The outlines of small shells were placed over graph paper and the number of millimeter squares counted.

The relationship between the height and shell area (fig. 38) is represented by an exponential curve of a general type $y=ax^b$ which fits many empirical data. The y in the formula is the shell area, and the x is the height. The parabolic nature of the curve is demonstrated by the fact

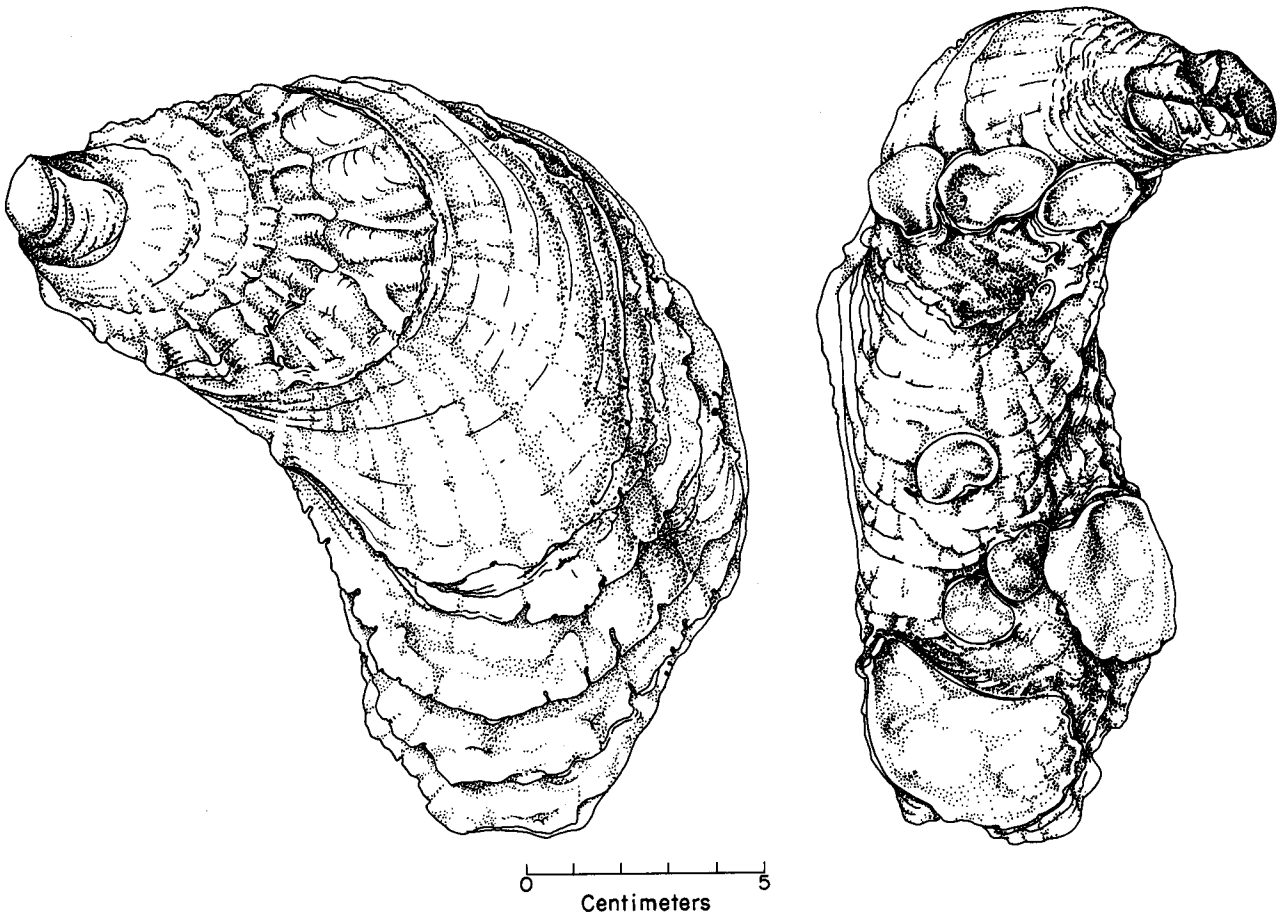

FIGURE 35.—Two upper (right) shells of old *C. virginica* from Chesapeake Bay (left) and Matagorda Bay, Tex. (right). The direction of growth changed suddenly about 50° to the left in the Chesapeake oyster and about 75° to the right in the Texas oyster.

that the log/log plot (fig. 39) fits a straight line. The numerical values of factors a and b were found to be equal to 1.25 and 1.56 respectively. The formula reads, therefore, $y=1.25x^{1.56}$. As a convenience to the reader who may be interested in finding directly from the curve the average area occupied by a shell of a given height, the data computed from the equation can be read from the curve in figure 38. The measurements are given both in centimeters and inches. The data refer to the random collection of live oysters from the coastal areas between Prince Edward Island, Canada, and the eastern end of Long Island Sound (table 2).

The relationship between the height and area of the upper valve of *C. virginica* is in agreement with the findings of other investigators (Newcombe, 1950; Nomura, 1926a, 1926b, 1928) who concluded that in several marine and fresh-water bivalves and gastropods the dimensional relationships can be adequately expressed by the formula of heterogenic growth, $y=bx^k$. According to Nomura's (1926a) interpretation of the growth of the clam *Meretrix meretrix*, the constant b in this formula represents the effect of the environment while k is a factor of differential growth. Nomura's conclusions may be applicable to other bivalves, and if confirmed by further studies this method may become useful for quantitative de-

TABLE 2.—*Height and shell area of northern oysters computed by using the equation* $y=1.25x^{1.56}$

Height		Area	
Cm.	*Inches*	*Cm.²*	*In.²*
5	1.97	15.4	2.39
6	2.36	20.5	3.18
8	3.15	32.3	5.01
10	3.94	45.4	7.04
12	4.72	60.3	9.35
14	5.51	76.7	11.9
16	6.30	94.5	14.6
18	7.09	113.5	17.6
20	7.87	133.8	20.7

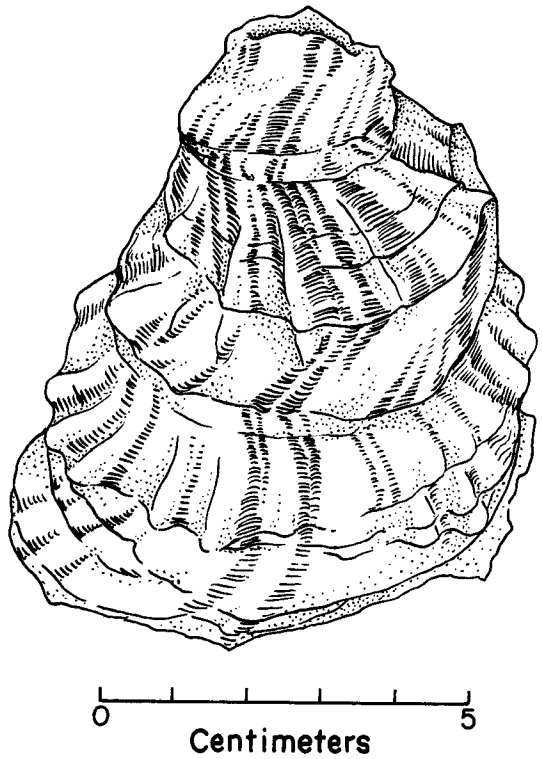

FIGURE 36.—Shell of an adult *C. virginica* showing periodic changes in the direction of the principal axis of growth. Note the zigzag line of pigmented bands in the middle of the valve. Actual dimensions: 8.5 by 6 cm. (3.25 by 2.5 inches).

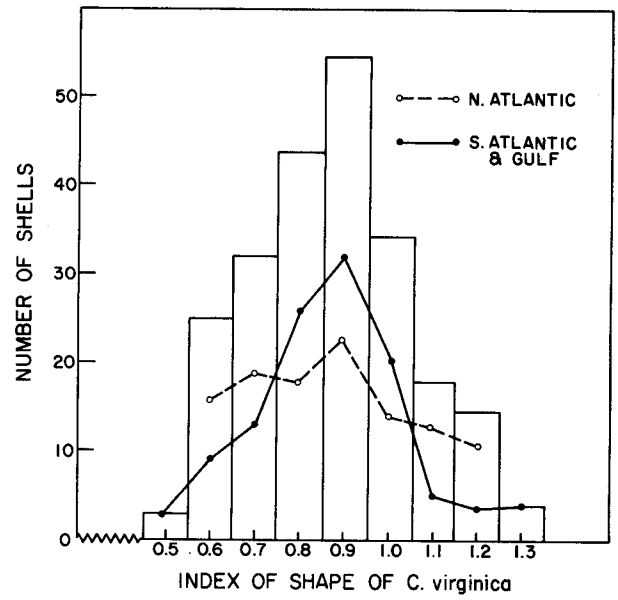

FIGURE 37.—Histogram of the distribution of the index of shape $\frac{\text{(height+width)}}{\text{length}}$ of shells of *C. virginica* from the Atlantic Coast. Frequency distribution of the index of North Atlantic oysters (open circles) and South Atlantic oysters (points) are shown by two separate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

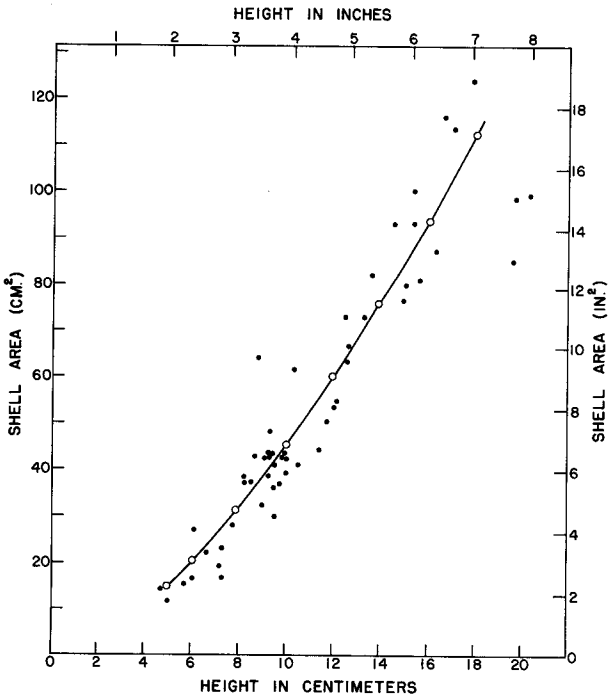

FIGURE 38.—Shell area in cm.² plotted against height of shells in cm. Inch scales are on top and on the right.

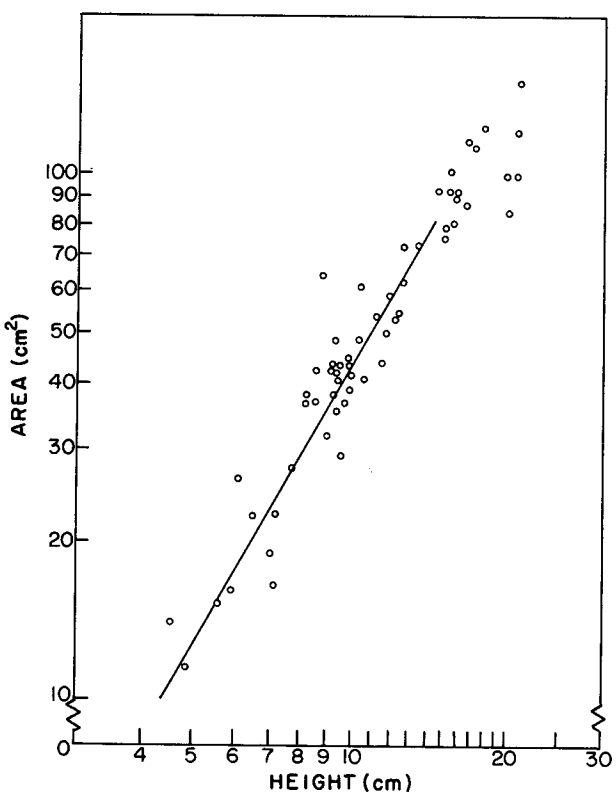

FIGURE 39.—Logarithmic plot of shell area against shell height.

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,

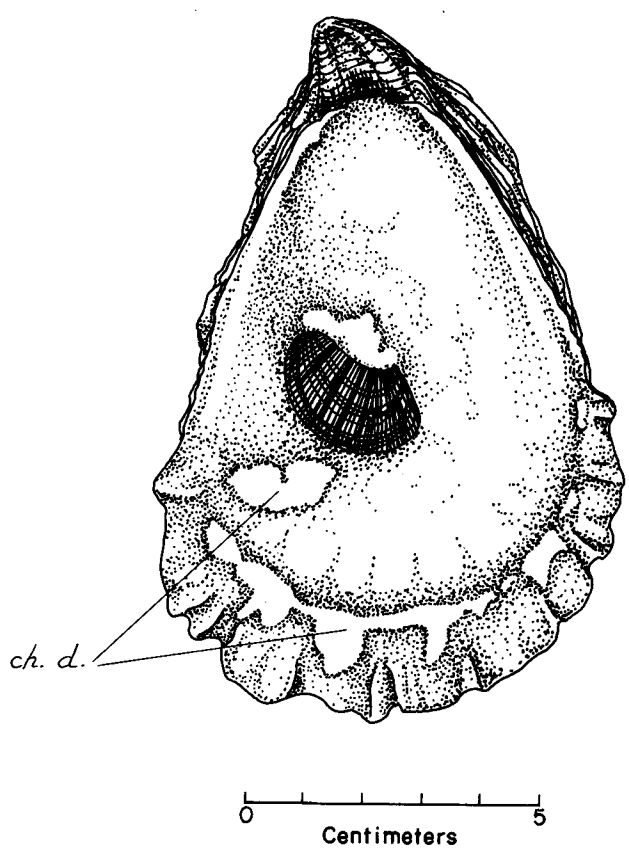

FIGURE 40.—Chalky deposits (ch. d.) on the newly formed shell at the edge of the valve, and near the muscle attachment.

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

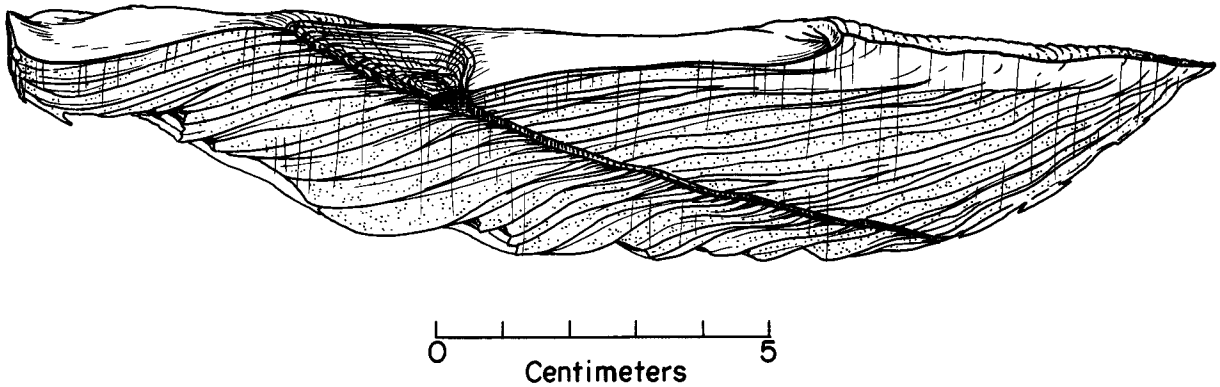

FIGURE 41.—Left valve of an old *C. virginica* cut along the principal axis of growth. Chalky areas on both sides of the hypostracum (dark platform for the attachment of the adductor muscle) are enclosed in the thin layers of hard crystalline material. Hinge on the right. Natural size.

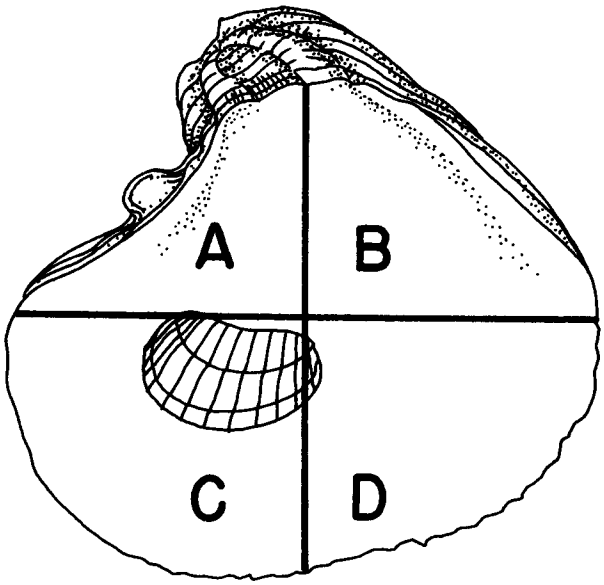

FIGURE 42.—Four arbitrary quadrants of the inner surface of shell used for estimating the distribution and extent of chalky deposits.

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

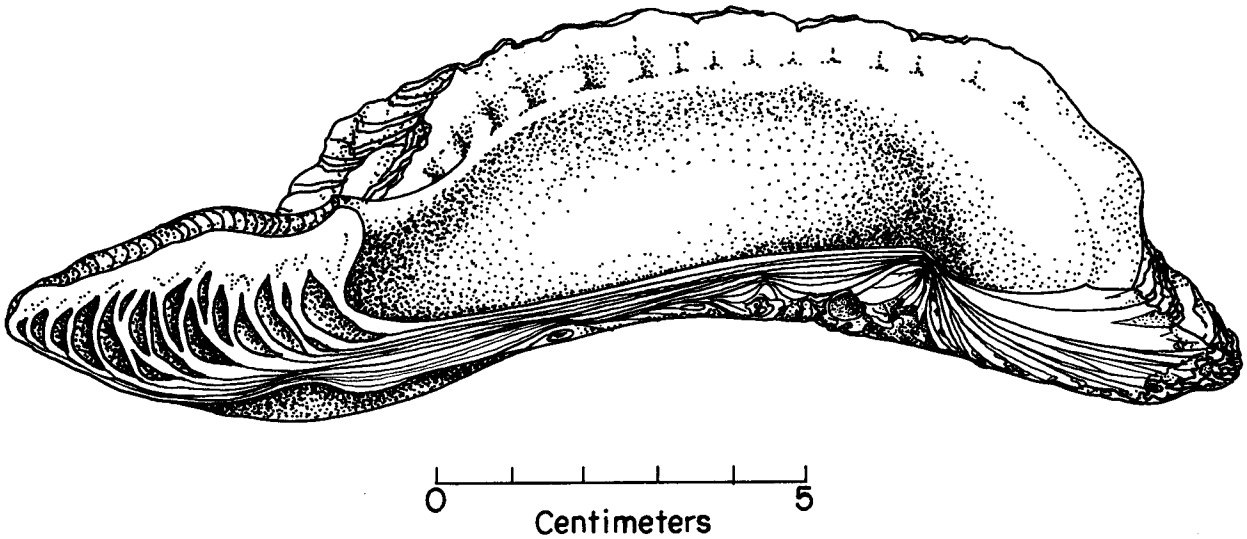

FIGURE 43.—Shell of *O. iridescens* cut at right angle to the hinge. Note a series of empty chambers at the hinge area. Specimen from the Gulf of Panama.

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.

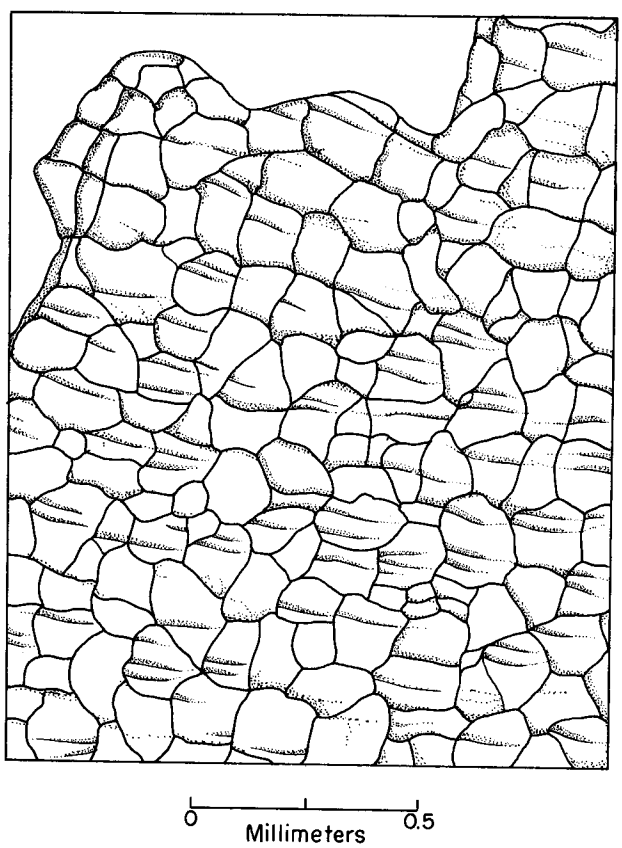

FIGURE 44.—Prismatic layer at earlier stages of calcification. *C. virginica.*

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

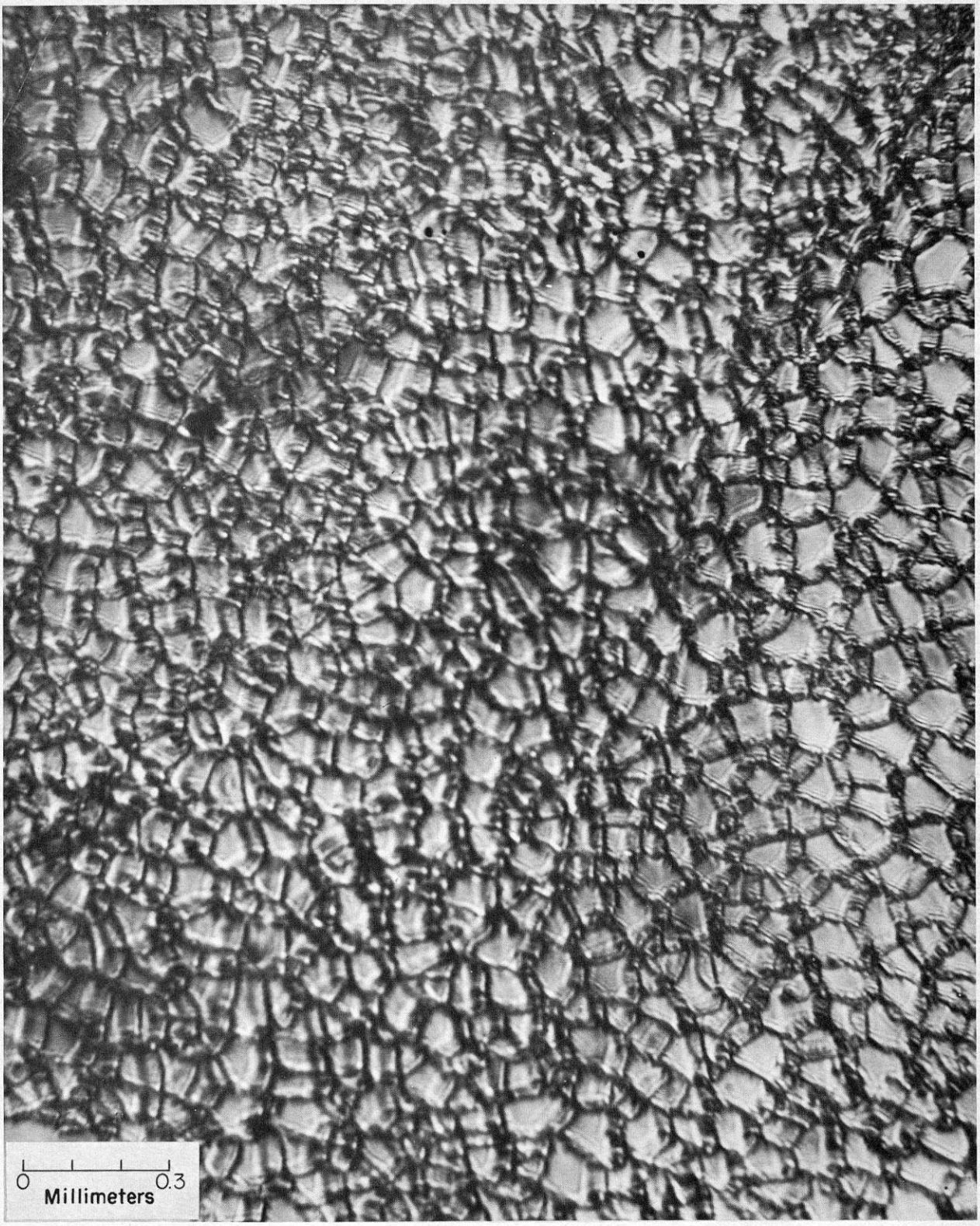

FIGURE 45.—Photomicrograph of a thin piece of prismatic layer after the dissolution of calcium carbonate in weak acid, *C. virginica*. The walls retain the shape of the prisms and are iridescent.

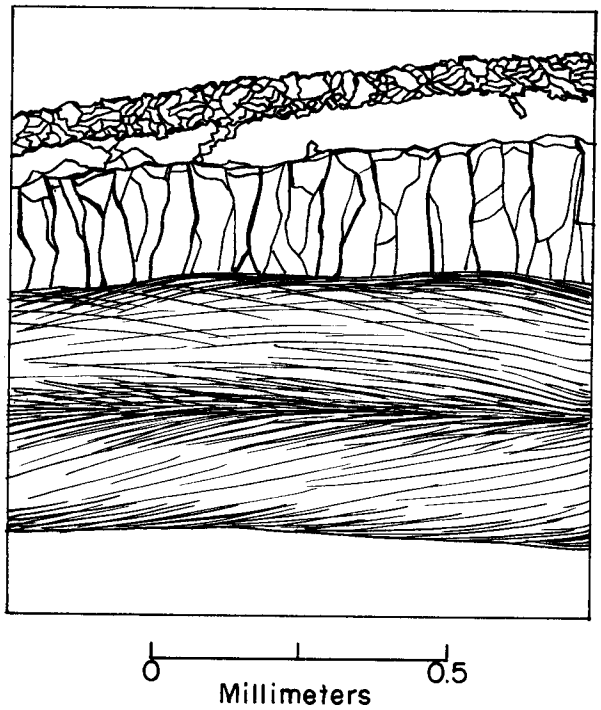

FIGURE 46.—Cross section of a piece of young shell of *C. virginica* (mounted in bakelite and ground on a glass wheel with carborundum, about 80 x). Periostracum (top line), prismatic layer (middle), and calcite-ostracum (lower).

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.

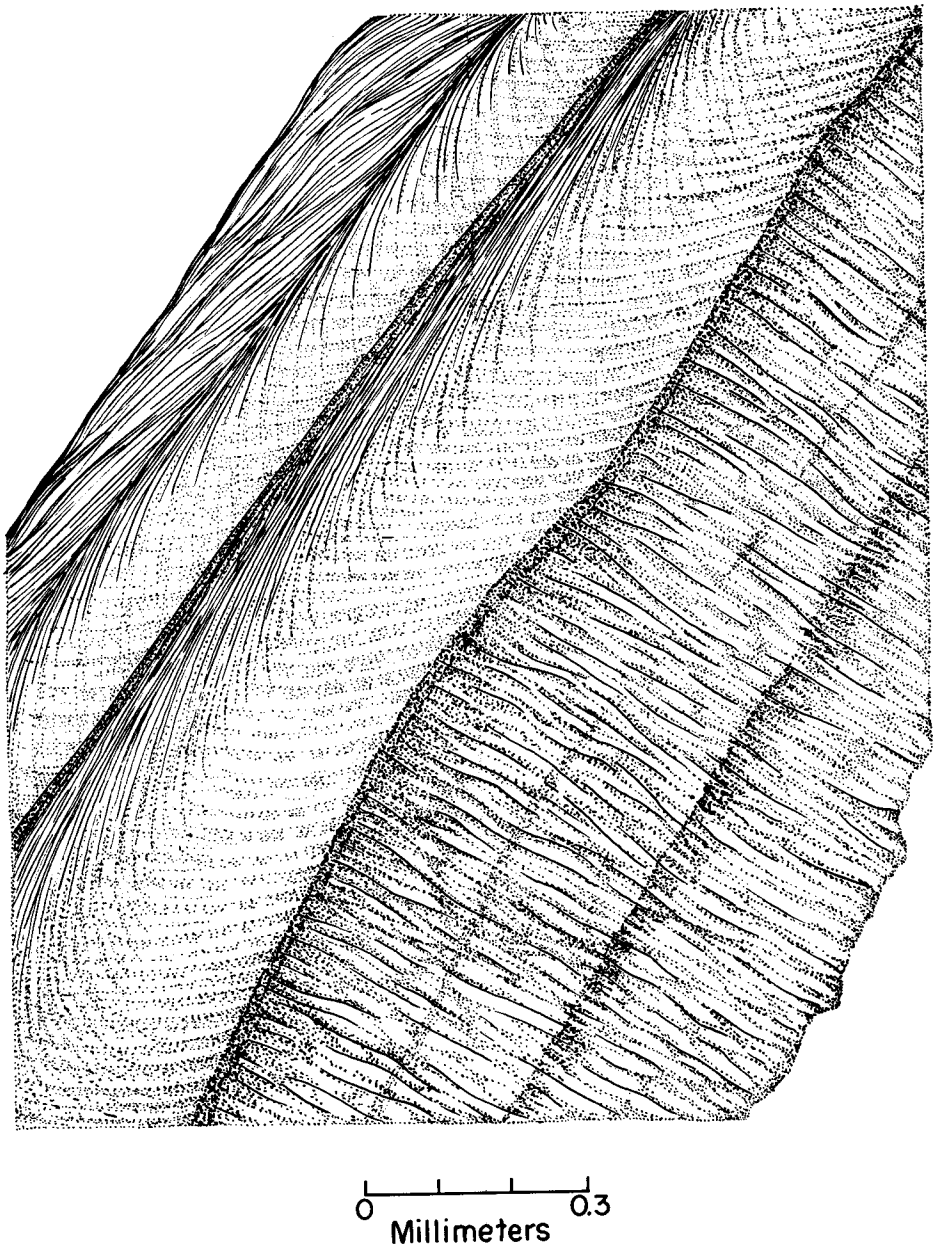

FIGURE 47.—Cross section of the shell of adult *C. virginica* embedded in bakelite and polished on a glass wheel with carborundum. Two upper layers consist of chalky deposits.

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-

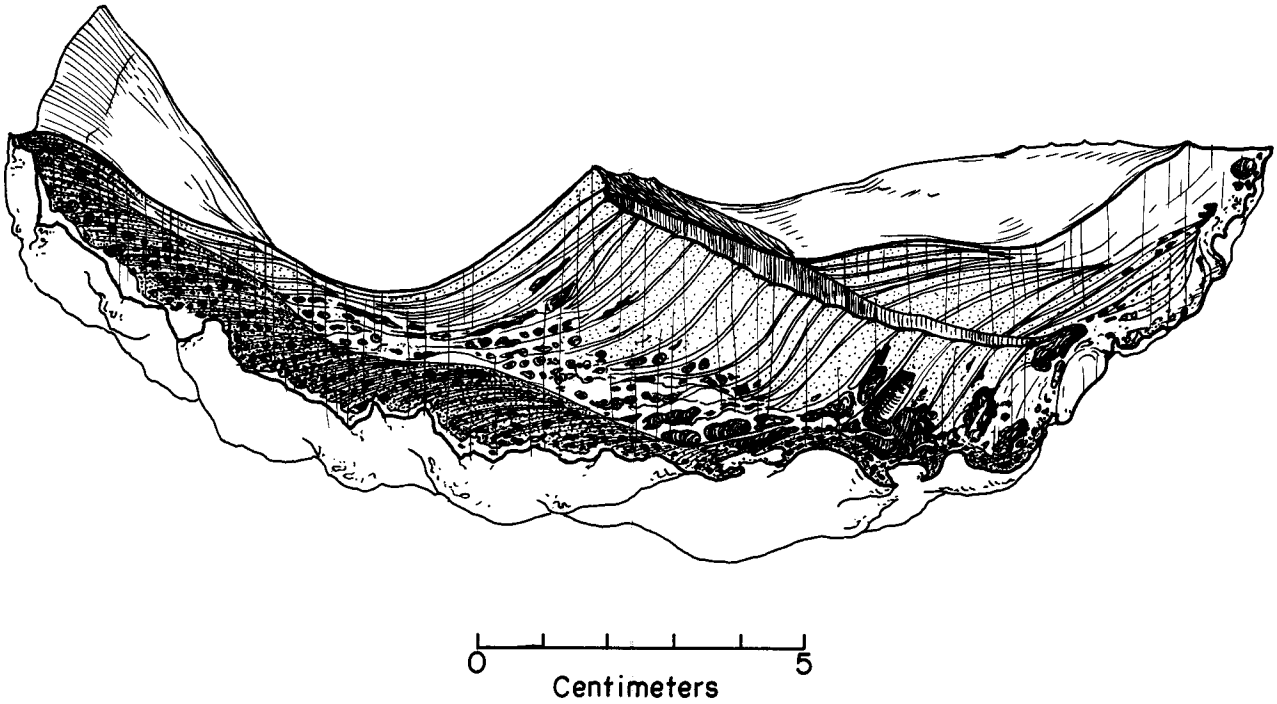

FIGURE 48.—Left valve of *O.* (*Alectryonia*) *megodon* cut along the principal axis of growth. Hypostracum (dark striated layer) forms a pronounced platform for the attachment of the adductor muscle, and can be traced to its original position in the young oyster (right). Chalky deposits are regularly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

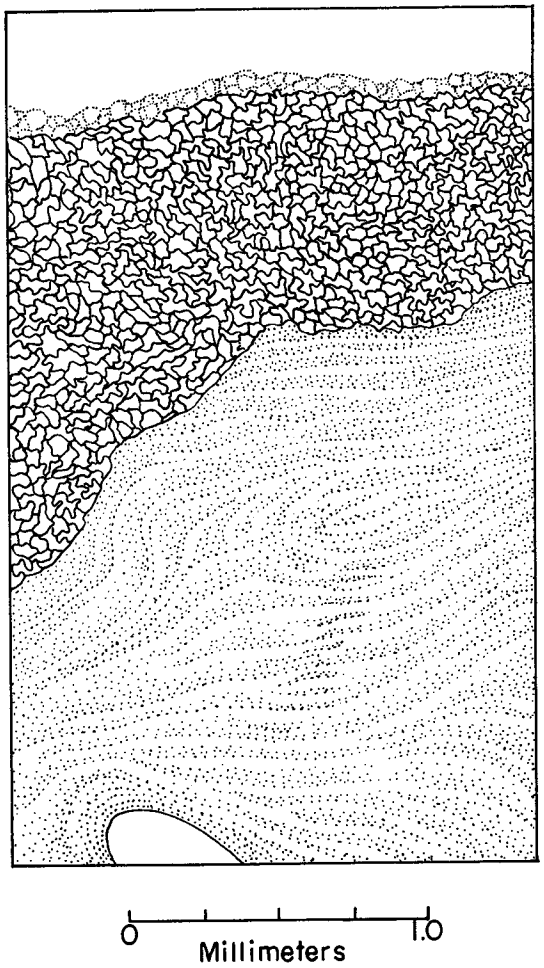

FIGURE 49.—Cross section of shell of an adult *C. virginica* after decalcification in weak acid, Mallory triple stain. Conchiolin of the prismatic layer is reddish-brown; that of calcite-ostracum is bluish.

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

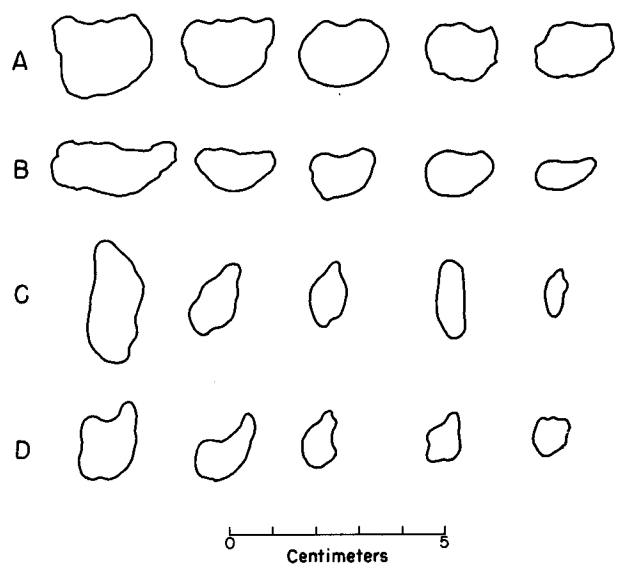

FIGURE 50.—Variations in shape and size of muscle scars on the shells of *C. virginica*. Rows A and B show the types of scars normally found on broad and rounded shells, the length of which is almost equal to or exceeds the height. Rows C and D are the scars often found on long and narrow shells in which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

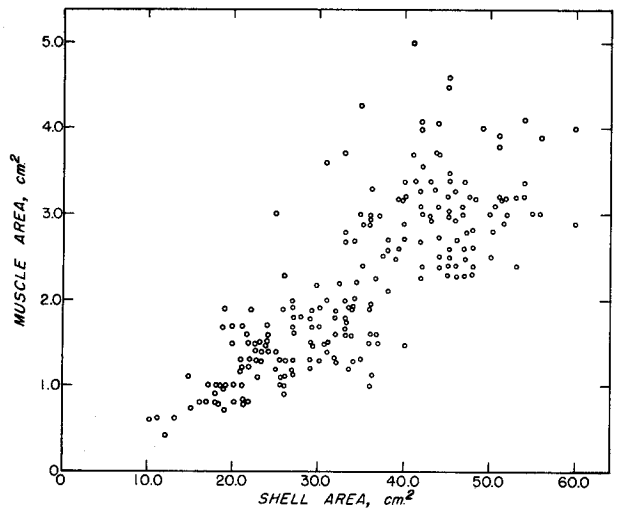

FIGURE 51.—The relationship between the area of muscle scar and the area of the shell of *C. virginica*.

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."

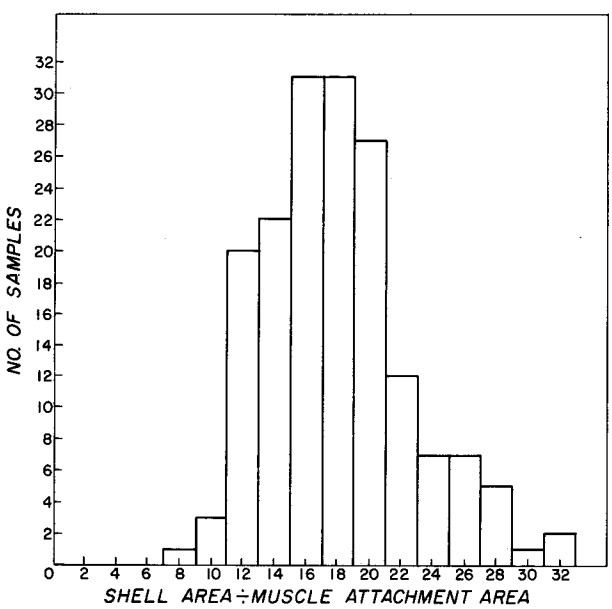

FIGURE 52.—Frequency distribution of the ratio of muscle scar area vs. shell area in the shells of *C. virginica* of Atlantic and Gulf States.

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.

BIBLIOGRAPHY

ANTHONY, R.
1905. Influence de la fixation pleurothétique sur la morphologie des mollusques acéphales dimyaires. Annales des Sciences Naturelles: Zoology, série 9, tome 1, pp. 165–396.

ASARI, TAMIYA.
1950. Geochemical distribution of strontium. VII. Strontium contents of shells. Journal of the Chemical Society of Japan, vol. 71, pp. 156–158.

BIEDERMANN, W.
1902a. Untersuchungen über Bau und Entstehung der Molluskenschalen. Jenaische Zeitschrift für Naturwissenschaft, Neue Folge, Band 29, pp. 1–164.
1902b. Ueber die Bedeutung von Krystallisationsprozessen bei der Bildung der Skelette wirbelloser Tiere, namentlich der Molluskenschalen. Zeitschrift für allgemeine Physiologie, Band 1, pp. 154–208.

BØGGILD, O. B.
1930. The shell structure of the mollusks. Det Kongelige Danske Videnskabernes Selskabs Skrifter, raekke 9, bind 2, part 2, pp. 233–326.

BRANDES, RUDOLPH, und PROFESSOR BUCHOLZ.
1817. Analyse der Austerschalen (*Ostrea edulis*). Neues Journal der Pharmacie für Aerzte und Apotheker, vol. 1, pp. 204–214.

CARPENTER, WILLIAM B.
1844, 1847. On the microscopic structure of shells. Report of the British Association for the Advancement of Science, 14th Meeting, 1844, pp. 1–24; *ibid.* 17th Meeting, 1847, pp. 93–134.

CAYEUX, LUCIEN.
1916. Introduction à l'étude pétrographique des roches sédimentaires. Mémoire pour servir à l'explication de la carte géologique détaillée de la France. Ministere des Travaux Publics, Paris, vol. 1 and 2 (Atlas), 524 pp.

COOK, THEODORE A.
1903. Spirals in nature and art. John Murray, London, 200 pp.
1914. Curves of life. Holt Co., New York, 479 pp.

CREAC'H, PAUL V.
1957. Variations physiologiques du phosphore total de la coquille de *Gryphaea angulata* Lmk. Revue des Travaux de l'Institut des Pêches Maritimes, tome 21, fascicule 3, pp. 415–430.

CROZIER, WILLIAM J.
1914. The growth of the shell in the lamellibranch *Dosinia discus* (Reeve). Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere, Band 38, pp. 577–584.

DOUVILLÉ, HENRI.
1936. Le test des lamellibranches: sa formation dans l'*Ostrea edulis*. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, tome 203, pp. 965–968.

FREMY, E.
1855. Recherches chimiques sur les os. Annales de Chimie et de Physique, série 3, tome 43, pp. 47–107.

FRIZA, FRANZ.
1932. Zur Kenntnis des Conchiolins der Muschelschalen. Biochemische Zeitschrift, Band 246, pp. 29–37.

GALTSOFF, PAUL S.
1955. Recent advances in the studies of the structure and formation of the shell of *Crassostrea virginica*. Proceedings of the National Shellfisheries Association, vol. 45, August 1954, pp. 116–135.

GALTSOFF, PAUL S., WALTER A. CHIPMAN, Jr., JAMES B. ENGLE, and H. N. CALDERWOOD.
1947. Ecological and physiological studies of the effect of sulphate pulp mill wastes on oysters in the York River, Virginia. [U.S.] Fish and Wildlife Service, Fishery Bulletin 43, vol. 51, pp. 59–186.

GRAY, JOHN EDWARD.
1833. Some observations on the economy of molluscous animals, and on the structure of their shells. Philosophical Transactions of the Royal Society of London for the year 1833, part 1, vol. 123, pp. 771–819.

GRÉGOIRE, CHARLES.
1957. Topography of the organic components in mother-of-pearl. Journal of Biophysical and Biochemical Cytology, vol. 3, No. 5, pp. 797–808.

GRÉGOIRE, CHARLES, GH. DUCHÂTEAU, and M. FLORKIN.
1950. Structure, étudiée au microscope électronique, de nacres décalcifiées de Mollusques (Gastéropodes, Lamellibranches et Céphalopode). Archives Internationales de Physiologie, vol. 58, pp. 117–120.
1955. La trame protidique des nacres et des perles. Annales de l'Institut Océanographique, nouvelle série, tome 31, pp. 1–36.

HAAS, F.
1935. Bivalvia. Teil 1. Dr. H. G. Bronns Klassen und Ordnungen des Tierreichs. Band 3: Mollusca; Abteilung 3: Bivalvia. Akademische Verlagsgesellschaft, Leipzig, 984 pp.

HACKH, INGO W. D.
1944. Hackh's chemical dictionary. 3d ed. Revised by Julius Grant. Blakiston Co., Philadelphia, Pa., 925 pp.

HOULBERT, C., and C. GALAINE.
1916a. Sur le chambrage des huîtres et sur l'infection possible des chambres par le fait d'une Annélide tubicole parasite de la coquille. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, tome 162, pp. 54–56.

HOULBERT, C., and C. GALAINE.
1916b. Sur les causes du chambrage et sur l'entretien raisonné des bancs d'huîtres naturels. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, tome 162, pp. 301–304.

HUNTER, ALBERT C., and CHANNING W. HARRISON.
1928. Bacteriology and chemistry of oysters, with special reference to regulatory control of production, handling, and shipment. U.S. Department of Agriculture, Technical Bulletin No. 64, 75 pp.

733-851 O—64——4

HUXLEY, JULIAN S.
1932. Problems of relative growth. Méthuen and Co., London, 276 pp.

INGERSOLL, ERNEST.
1881. The oyster-industry. *In* The history and present condition of the fishery industries, 251 pp. Tenth Census of the United States, Department of the Interior, Washington, D.C.

KORRINGA, P.
1951. On the nature and function of "chalky" deposits in the shell of *Ostrea edulis* Linneaus. Proceedings of the California Academy of Sciences, series 4, vol. 27, No. 5, pp. 133–158.

LAMY, ED.
1917. Coquilles sénestres chez les Lamellibranches. Bulletin du Muséum National d'Histoire Naturelle, Paris, tome 23, pp. 489–493.

LATRIGUE, ALFRED
1930. Biodynamique générale fondée sur l'etude du tourbillon vital d'ether. G. Doin and Co., Inc., Paris, 60 pp.

LAURENT, J. L. M.
1839a. Observations sur la structure de la coquille de l'huître commune (*Ostreaedulis* Linn.). Annales Francaises et Étrangères d'Anatomie et de Physiologie, Appliquées à la Médecine et à l'Histoire Naturelle, tome 3, pp. 53–55.
1839b. Résultats d'observations faites sur la coquille de l'huître commune (*Ostrea edulis* L.). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, tome 8, pp. 135–136.

LEENHARDT, HENRY.
1926. Quelques études sur *Gryphea angula*. (Huître du Portugal). Annales de l'Institut Océanographique, nouvelle série, tome 3, fascicule 1, pp. 1–90.

LISON, LUCIEN.
1939. Forme et méchanique du développement des coquilles de Lamellibranches. Annales de la Société Royale Zoologique de Belgique, tome 70, pp. 9–32.
1942. Caractéristiques géométriques naturelles des coquilles de Lamellibranches. Bulletin de la Classe des Sciences, Académie Royale de Belgique, série 5, tome 28, pp. 377–390.
1949. Recherches sur la forme et la méchanique de développement des coquilles des Lamellibranches. Mémoires, Institut Royale des Sciences Naturelles de Belgique, série 2, fascicule 34, pp. 1–87.
1953. Histochimie et cytochimie animales. Principes et méthodes. 2d ed. Gauthier-Villars, Paris, 607 pp.

MEDCOF, J. C.
1944. Structure, deposition and quality of oyster shell (*Ostrea virginica* Gmelin). Journal of the Fisheries Research Board of Canada, vol. 6, No. 3, pp. 209–216.

MOYNIER DE VILLEPOIX, R.
1892. Recherches sur la formation et l'accroissement de la coquille des Mollusques. Journal de l'Anatomie et de la Physiologie Normales et Pathologiques de l'Homme et des Animaux, pp. 461–518; *ibid.*, pp. 582–674.

NEWCOMBE, CURTIS L.
1950. An analysis of certain dimensional relationships of the Virginia oyster, *Crassostrea virginica* (Gmelin). American Naturalist, vol. 84, No. 816, pp. 203–214.

NOMURA, EKITARO.
1926a. Further studies on the applicability of $a=kb^x$ in expressing the growth relations in molluscan shells. Science Reports of the Tôhoku Imperial University, series 4, Biology, vol. 2, No. 1, pp. 63–84
1926b. An application of $a=kb^x$ in expressing the growth relation in the freshwater bivalve, *Sphaerium heterodon* Pils. Science Reports of the Tôhoku Imperial University, series 4, Biology, vol. 2, pp. 57–64.
1928. On the relation between weight and dimensions in the bivalves *Tapes philippinarum* and *Cytherea meretrix*. Science Reports of the Tôhoku Imperial University, series 4, Biology, vol. 4, no. 3, pp. 113–124.

OKEN, LORENZ.
1847. Elements of physiophilosophy. Ray Society, London, 209 pp.

OLSSON, AXEL A.
1961. Mollusks of the tropical Eastern Pacific particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). Panamic-Pacific Pelecypoda. Paleontological Research Institution, Ithaca, N.Y. Norton Printing Co., Ithaca, N.Y., 574 pp.

ORTON, JAMES H.
1937. Oyster biology and oyster-culture, being the Buckland Lectures for 1935. Edward Arnold and Co., London, 211 pp.

ORTON, JAMES H., and C. AMIRTHALINGAM.
1927. Notes on shell-depositions in oysters. Journal of the Marine Biological Association of the United Kingdom, vol. 14, pp. 935–953.

OWEN, G.
1953. The shell in the Lamellibranchia. Quarterly Journal of Microscopical Science, vol. 94, part 1, pp. 57–70.

PELSENEER, PAUL.
1920. A propos de la formation et de la composition chimique de la coquille des mollusques. Annales de la Société Royale Zoologique et Malacologique de Belgique, tome 51, pp. 70–74.

QUENSTEDT, F. A.
1867. Handbuch der Petrefakenkunde. Laupp, Tübingen, 2d ed., p. 598.

QUILTER, H. E.
1891. On the molluscan shell and periostracum. Conchologist, vol. 1, pp. 5–8.

RANSON, GILBERT.
1939–41. Les huîtres et le calcaire. Bulletin du Muséum National d'Histoire Naturelle, Paris, série 2, tome 11, pp. 467–472; *ibid.* tome 12, pp. 426–432; *ibid.* tome 13, pp. 49–66.
1943. La vie des huîtres. Histoires Naturelles-1, Collection dirigée par Jean Rostand. Gallimard, Paris, 261 pp.

DERÉAUMUR, M.
1709. De la formation et de l'accroissement des coquilles des animaux tant terrestres qu'aquatiques,

soit de mer soit de riviere. Histoire de l'Académie Royale des Sciences avec les Mémoires de Mathématique et Physique, pp. 475–520. [Reprinted as a separate: Académie Royale des Sciences Paris, Mémoires, pp. 364–400.]

DERÉAUMUR, M.
1716. Eclaircissemens de quelques difficultés sur la formation et l'accroissement des coquilles. Histoire de l'Académie Royale des Sciences avec les mémoires de mathématique et physique, pp. 384–394. [Reprinted as a separate: Academie Royale des Sciences Paris, Année 1716, Mémoires, pp. 303–311.]

ROCHE, JEAN, GILBERT RANSON, AND MARCELLE EYSSERIC-LAFON.
1951. Sur la composition des scléroprotéines des coquilles des Mollusques (conchiolines). Comptes Rendus des Séances de la Société de Biologie et de ses Filiales, tome 145, pp. 1474–1477.

SAVILLE-KENT, W.
1893. The great barrier reef of Australia: its products and potentialities. W. H. Allen and Co., Ltd., London, 387 pp.

SCHENCK, HUBERT G.
1934. Literature on the shell structure of pelecypods. Bulletin du Musée Royal d'Histoire Naturelle de Belgique, tome 10, No. 34, pp. 1–20.

SCHLOSSBERGER, J.
1856. Zur näheren Kenntniss der Muschelschalen, des Byssus und der Chitinfrage. Liebigs Annalen der Chemie, Band 98, pp. 99–120.

SCHMIDT, W. J.
1931. Über die Prismenschicht der Schale von *Ostrea edulis* L. Zeitschrift für Morphologie und Ökologie der Tiere, Band 21, pp. 789–805.

SCHULZE, P.
1922. Über Beziehungen zwischen pflanzlichen und tierischen Skelettsubstanzen und über Chitinreaktionen. Biologisches Zentralblatt, Band 42, pp. 388–394.

SMITH, R. A., and E. R. WRIGHT.
1962. Elemental composition of oyster shell. Texas Journal of Science, vol. 14, No. 2, pp. 222–224.

SPORN, E.
1926. Über die Gesetzmässigkeiten im Baue der Muschelgehaüse. Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen, Band 108, pp. 228–242.

STENZEL, HENRY B.
1963. Aragonite and calcite as constituents of adult oyster shells. Science, vol. 142, No. 3589, pp. 232–233.
Oysters. *In* Treatise of invertebrate paleontology. Part N—Mollusca, 6 (Bivalvia). [In press.]

TANAKA, KOJIRO.
1937. On the chalky deposits in oysters. Fishery Investigation, Imperial Fishery Experimental Station, Tokyo, Supplementary Report No. 4, No. 46, pp. 36–44. [English translation by the Atlantic Biological Station, St. Andrews, Canada, 1953.]

TANAKA, KOJIRO.
1943. On the effect of the concentration of salt on the chalky deposits in oysters. Suisan Kenkyushi (Journal of Fisheries), vol. 38, No. 12, pp. 222–224. [English translation by the Atlantic Biological Station, St. Andrews, Canada, 1953.]

THOMPSON, D'ARCY W.
1942. On growth and form. 2d ed. Cambridge University Press, Cambridge, England, 1116 pp.

THOMPSON, THOMAS G., and TSAIHWA J. CHOW. 1955. The strontium-calcium atom ratio in carbonate-secreting marine organisms. Deep-Sea Research, vol. 3, suppl., pp. 20–39.

TRUEMAN, E. R.
1944. Occurrence of strontium in molluscan shells. Nature, vol. 153, No 3874, p. 142.

VINOGRADOV, A. P.
1937. The elementary chemical composition of marine organisms. Composition of shells of Lamellibranchiata. Translation in Memoirs, Sears Foundation for Marine Research, No. 2, 1953, pp. 303–309.

WATABE, NORIMITSU.
1954. Electron microscopic observations of the aragonite crystals on the surface of cultured pearls. I. Report of the Faculty of Fisheries, Prefectural University of Mie, vol. 1, No. 3, pp. 449–454.

WESTER, D. H.
1910. Über die Verbreitung und Lokalisation des Chitins im Tierreiche. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere, Band 28, pp. 531–558.

WETZEL, G.
1900. Die organischen Substanzen der Schaalen von *Mytilus* und *Pinna*. Hoppe-Seyler's Zeitschrift für physiologische Chemie, Band 29, pp. 386–410.

WORSNOP, EDITH, and JAMES H. ORTON.
1923. The cause of chambering in oysters and other lamellibranchs. Nature, vol. III, No. 2775, pp. 14–15.

YONGE, C. M.
1952a. The monomyarian condition in the Lamellibranchia. Transactions of the Royal Society of Edinburgh, vol. 62, part II, pp. 443–478.
1952b. Observations on *Siliqua patula* Dixon and on evolution within the Solenidae. University of California Publications in Zoölogy, vol. 55, pp. 421–438.

ZANDER, ENOCH.
1897. Vergleichende und kritische Untersuchungen zum Verständnisse der Jodreaktion des Chitins. Pflügers Archiv für die gesammte Physiologie des Menschen und der Thiere, Band 66, pp. 545–573.