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

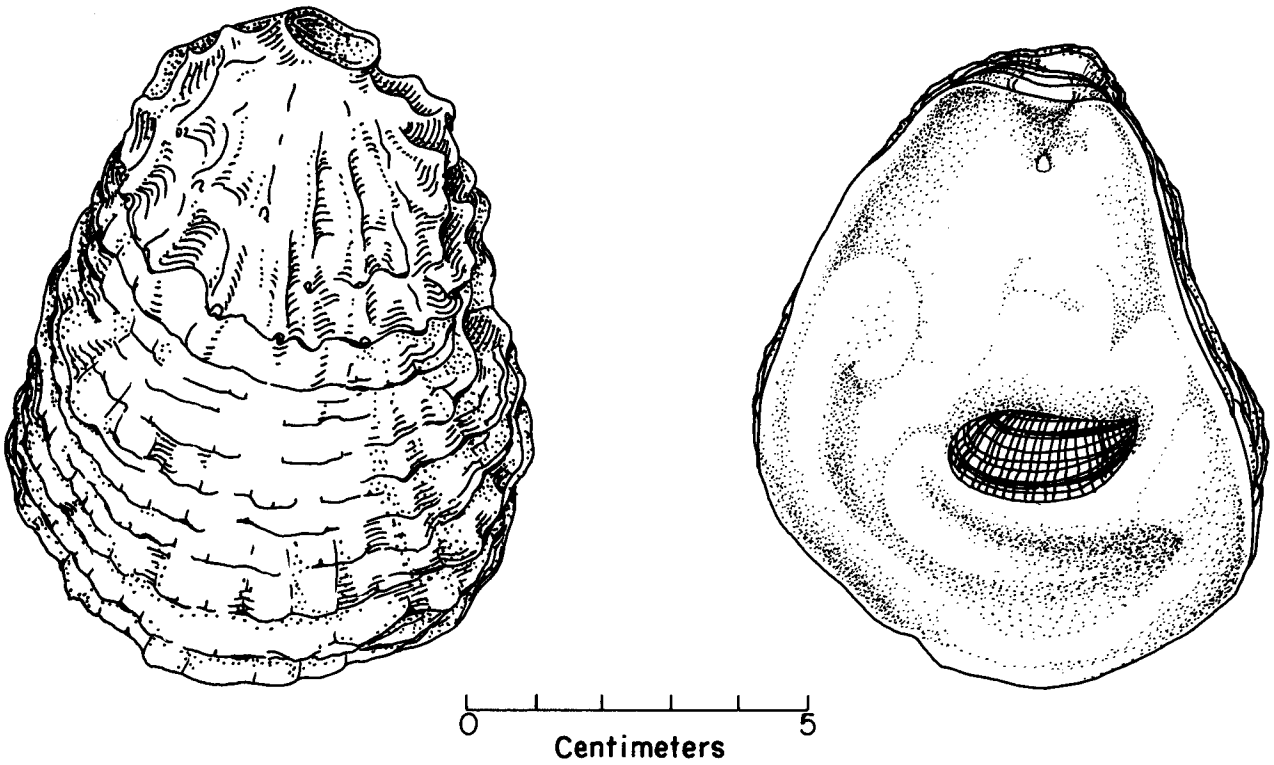


FIGURE 15.—Blue Point oyster (*C. virginica*) from Great South Bay, Long Island, N.Y. The size of this 5-year-old oyster is about 10 x 6.6 cm. (4 x 3 inches). The shell is strong and rounded; its surface is moderately sculptured. Left—outside surface of left valve. Right—inner surface of right valve.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

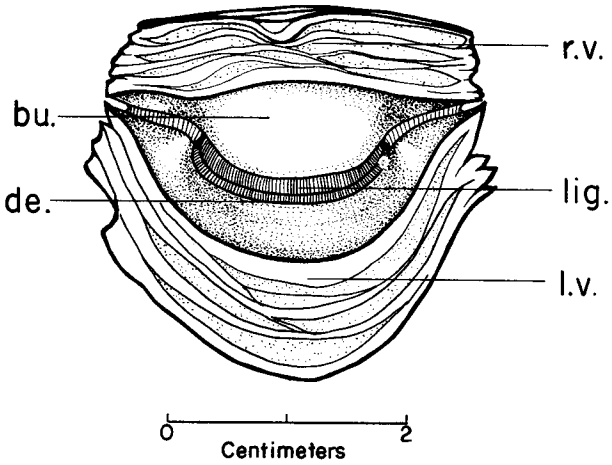


FIGURE 16.—Cross section below the hinge of an adult *C. virginica*. Left valve at bottom, right valve at top of the drawing. The buttress of the right valve fits the depression on the left valve. The two valves are connected by a ligament (narrow band indicated by vertical striations) which consists 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.

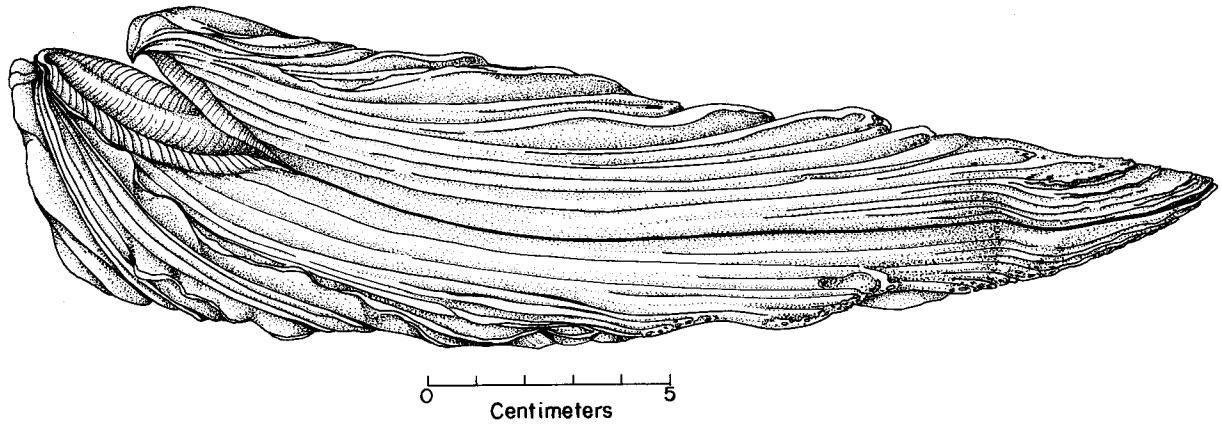


FIGURE 17.—Side view of a very old and large *C. virginica* from Stony Creek, Conn. Notice the curvature of the beak, the depressed resilifer on the lower valve and the protruding resilifer on the upper one. The angle between the beaks determines the maximum movement of the upper valve. Dimensions: height—25.5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

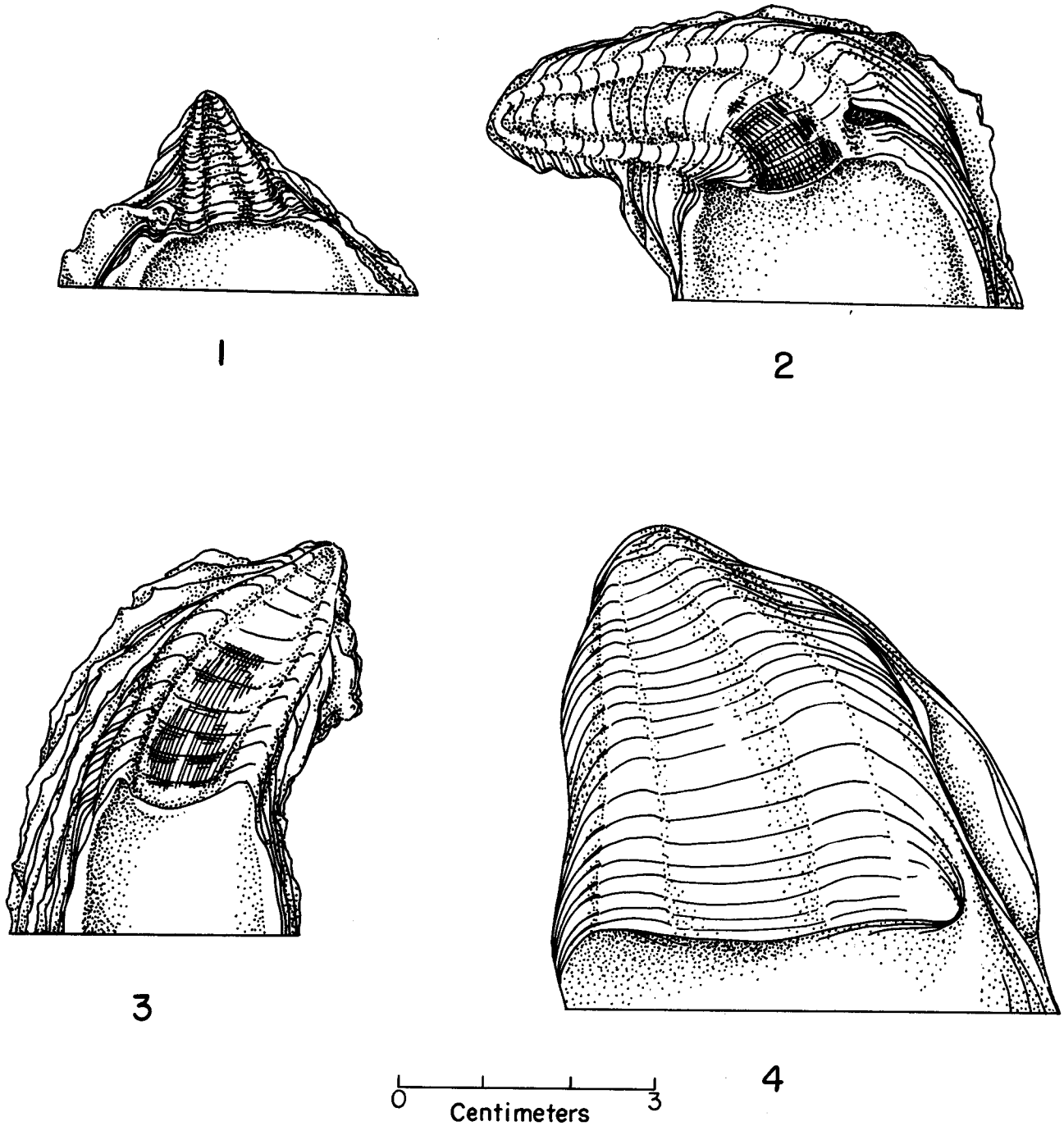


FIGURE 18.—Four shapes of beaks on left valves of old oysters, *C. virginica*. 1—narrow, short and almost straight; 2—strongly curved to the posterior; 3—of medium width, pointed forward; 4—very broad and slightly curved to the posterior.

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,

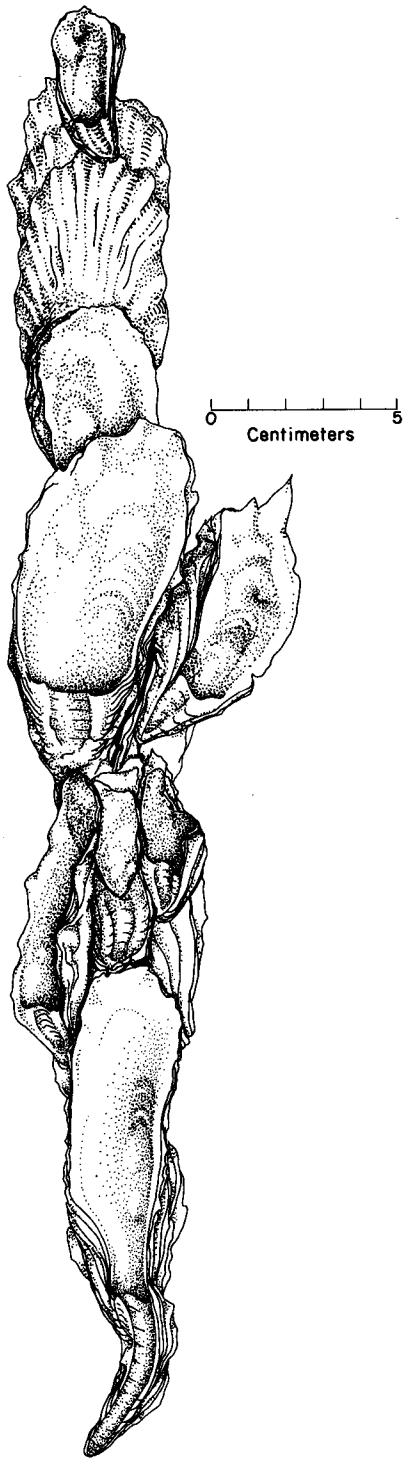


FIGURE 19.—Several generations of oysters, *C. virginica*, growing vertically on muddy bottom of Altamaha Sound, Ga. Notice the very long and narrow beak of the lowermost shell.

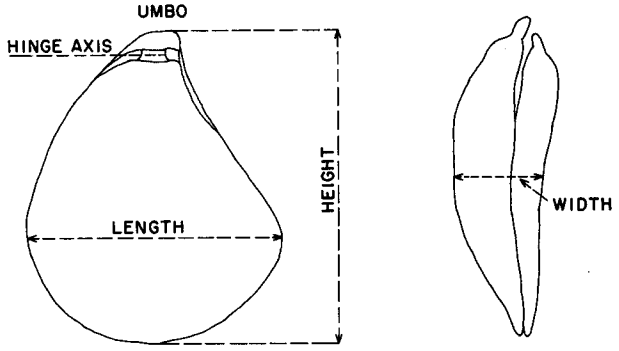


FIGURE 20.—Diagram showing the correct method of measuring the height, length, and width of oyster shells.

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:

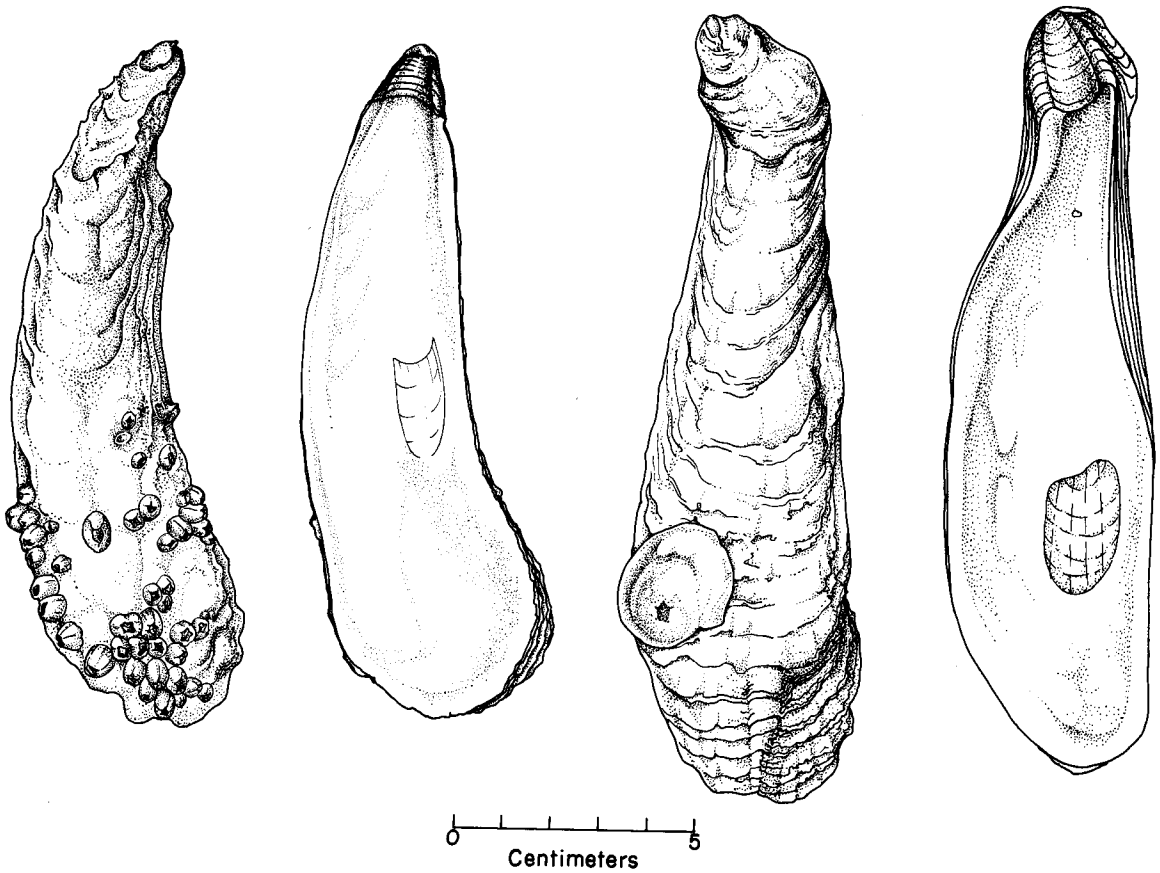


FIGURE 21.—Shells of *C. gigas* (left) and *C. virginica* (right) grown on soft, muddy bottom. Note the remarkable similarity in the shape, size, and sculpture of the two species of oysters. The *C. gigas* was obtained from the northern part of Puget Sound and the *C. virginica* from Georgia. The shells 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)

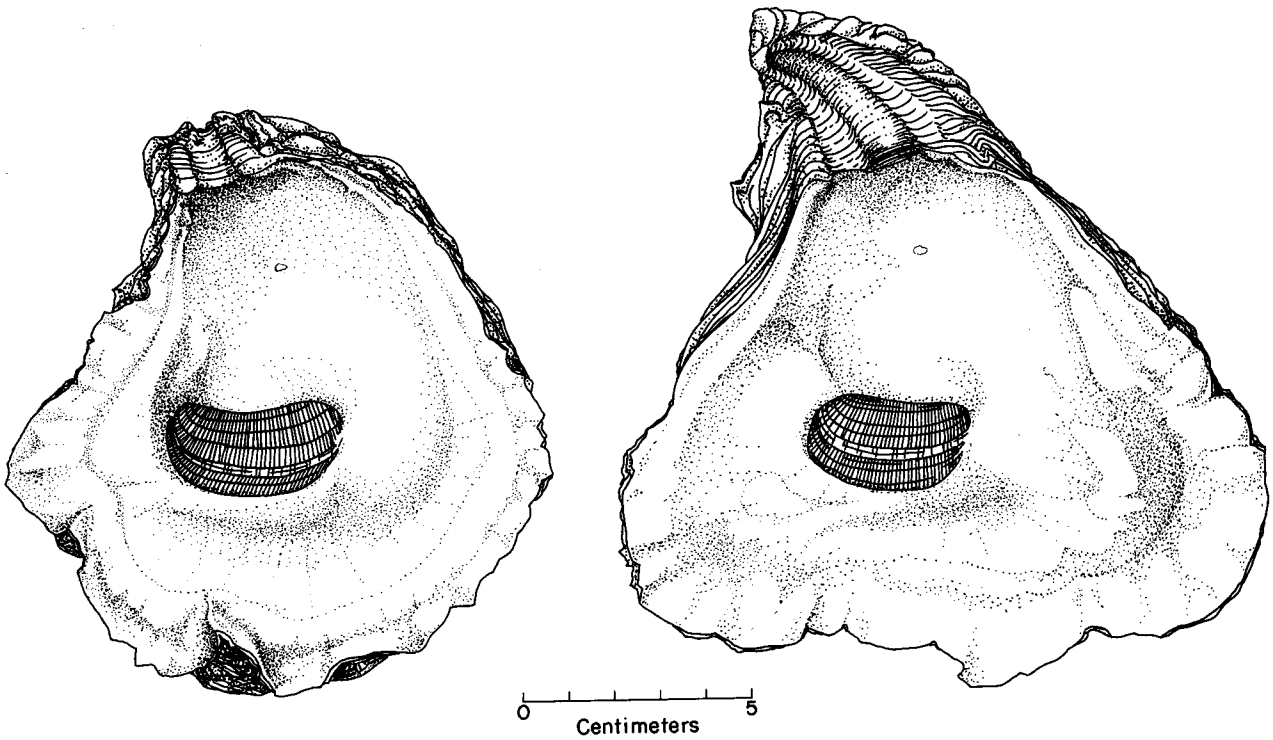


FIGURE 22.—Two left shells of *C. virginica* grown on sticky mud. On the left side is the oyster from Karankawa Reef in Matagorda Bay, Tex.; on the right is the oyster from Hadley Harbor, Naushon Island, near Woods Hole, Mass. The dimensions of the Texas oyster are 13 by 11.5 cm. (5.1 by 4.5 inches)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

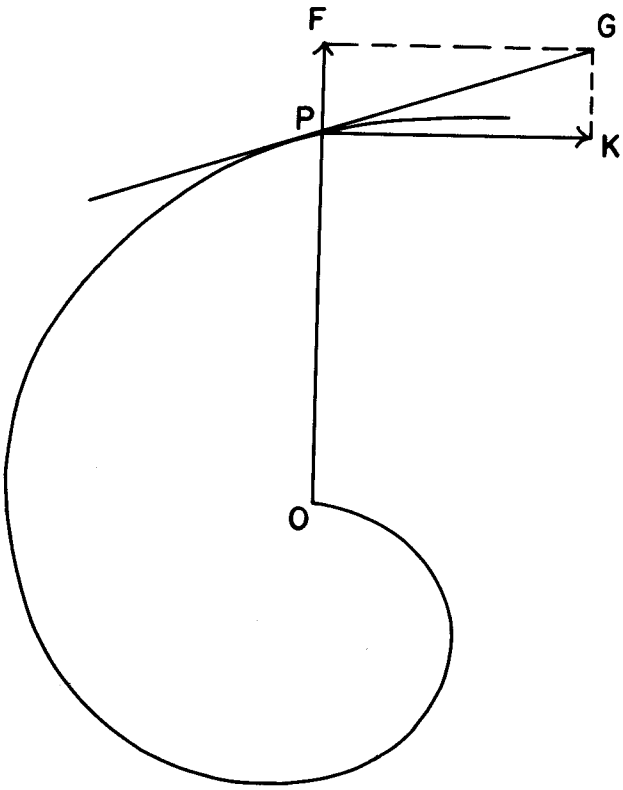


FIGURE 23.—Logarithmic or equiangular spiral. Explanation in text.

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

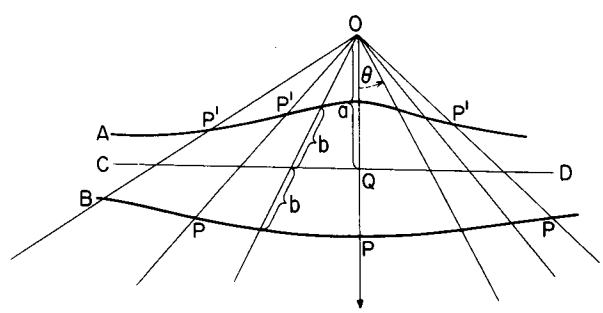


FIGURE 24.—Construction of the conchoid curve of Nicomedes. Explanation in text.

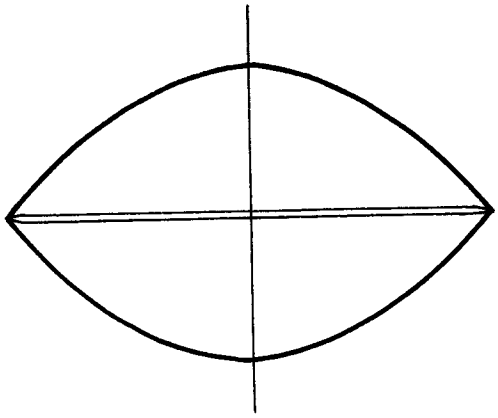


FIGURE 25.—Cross section of two valves of *Cardium*. The similarity with the conchoid in figure 24 is superficial.

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.)

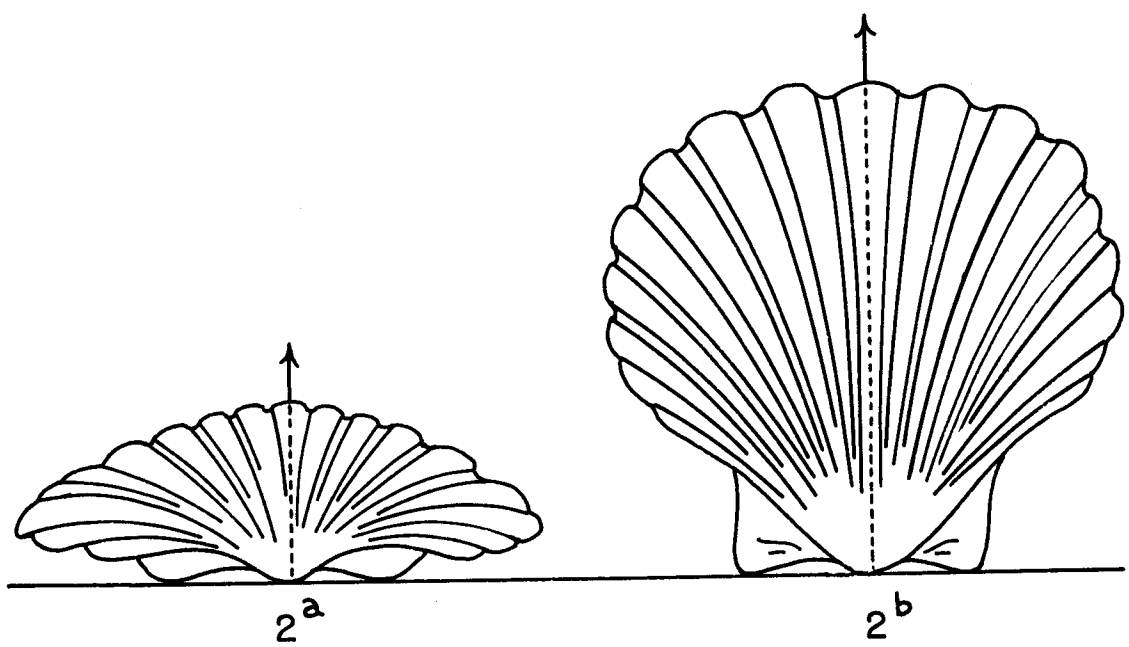


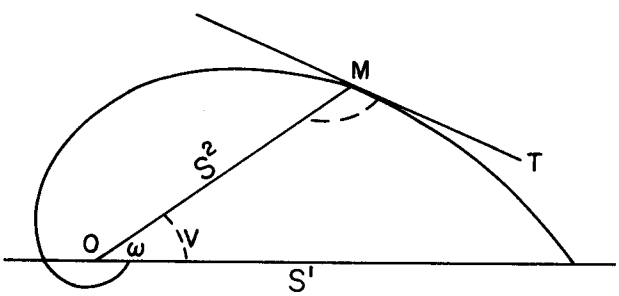
FIGURE 26.—Directive plane of scallop shell, *Pecten*, viewed from hinge end 2a, and from the broad side 2b. The arrows indicate the directive plane. (After Lison, 1939.)

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).



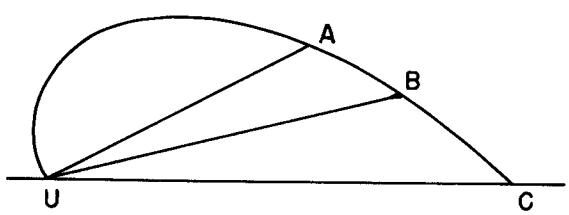


FIGURE 27.—Valve of a shell sawed along the directive axis describes a plane logarithmic spiral. According to Lison (1942). OM—radius vector; T—tangent; O—umbo; V—angle between the two radii.

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

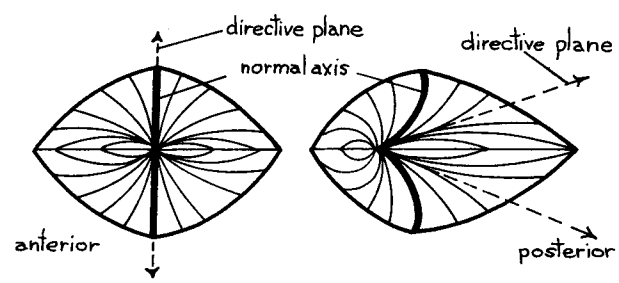


FIGURE 28.—Comparison of directive plane of Lison with normal axis (Owen). A—shell not affected by tangential component; B—shell affected by tangential component.

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

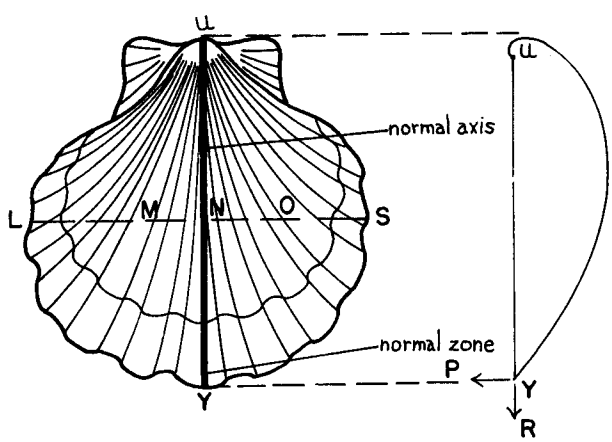


FIGURE 29.—Normal axis and the two growth components in the shell of scallop. LS—plane perpendicular to the plane of the generating curve; N—turning point of the concave side of the shell shown at right; M and O—auxiliary radii; P—transverse component; R—radial component; UY—normal axis. From Owen (1953).

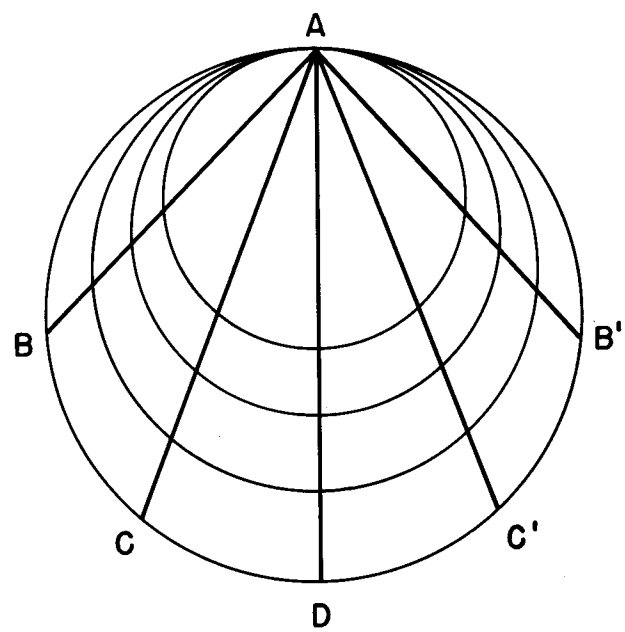


FIGURE 30.—Diagram of a circular bivalve shell of the kind represented in *Pecten*, *Anomia*, and young *C. virginica*. Radii extending from the umbo to the periphery of the generating curve are proportional to the rate of growth at the edge of a circular shell Radius AD corresponds to the directive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

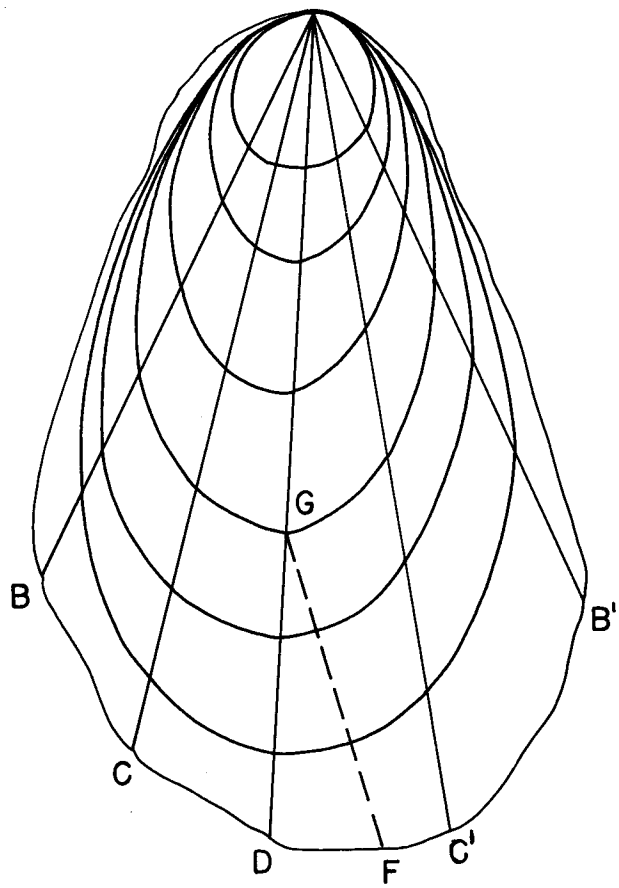


FIGURE 31.—Diagram of a shell of adult *C. virginica*. Radii extend from the umbo to the periphery of the generating curve. The principal axis AGF shows the change in the direction of growth at G. The length of radii is proportional to the rate of shell growth at the edge.

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

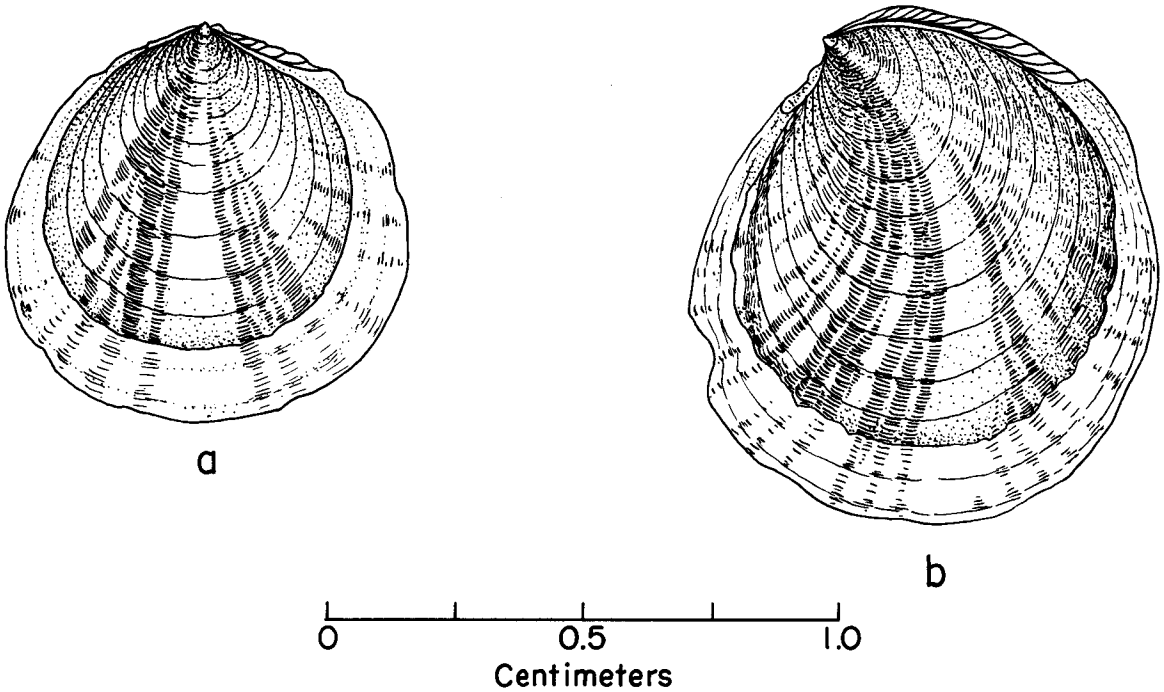


FIGURE 32.—Two small *C. virginica* growing attached to tar paper. Maximum dimension of shell: a—0.85 cm.; b—1.0 cm. At b the principal axis curves to the left.

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

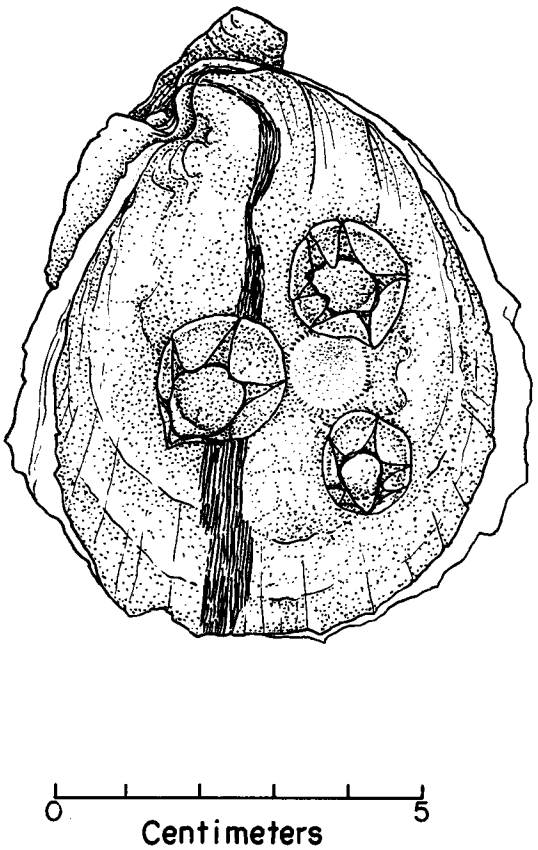


FIGURE 33.—Principal axis of growth of a *C. virginica* from Chatham, Mass., is deeply marked by a pigmented band.

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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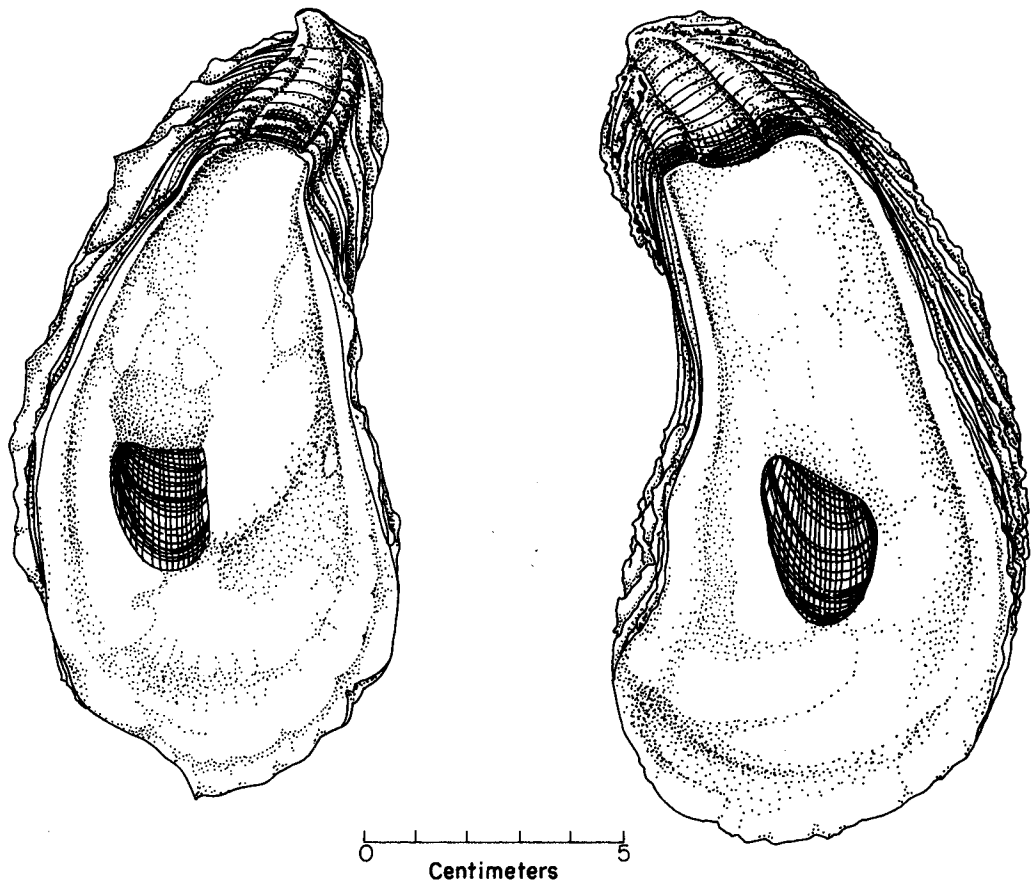

FIGURE 34.—Left valves of the two large *C. virginica* from Narragansett Bay, R.I. On the right is a "normal" oyster; its shell curves to the left. On the left side is an inverted oyster; its shell curves to the right.

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

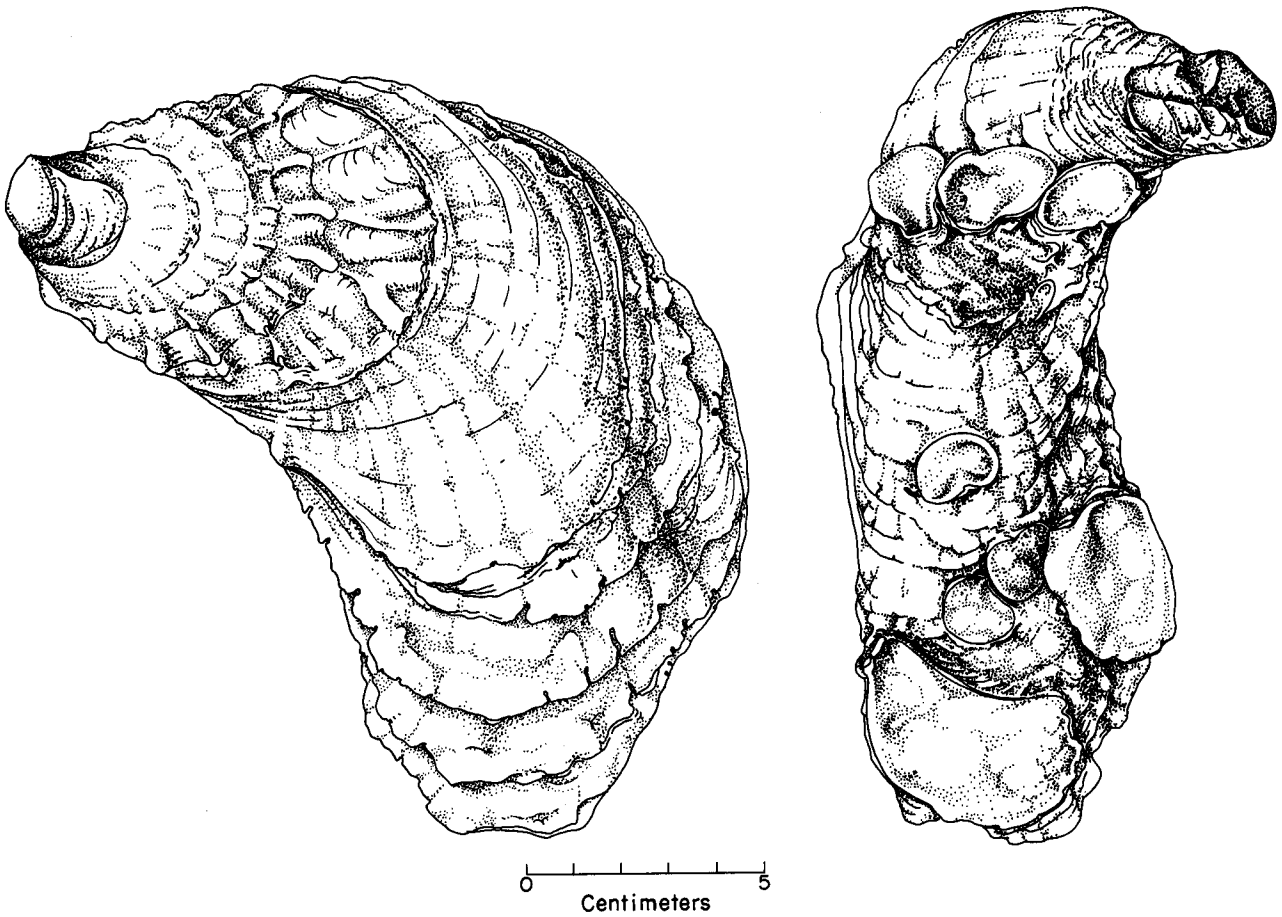

FIGURE 35.—Two upper (right) shells of old *C. virginica* from Chesapeake Bay (left) and Matagorda Bay, Tex. (right). The direction of growth changed suddenly about 50° to the left in the Chesapeake oyster and about 75° to the right in the Texas oyster.

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