It follows that the effect of the weight of suspended sediment upon the motion of deeper water masses cannot be neglected in any part of the ocean where the nepheloid zone is present.

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## Theoretical Morphology of the Coiled Shell

Abstract. *In studying the functional significance of the coiled shell, it is important to be able to analyze the types that do not occur in nature as well as those represented by actual species. Both digital and analog computers are useful in constructing accurate pictures of the types that do not occur.*

Mathematical models are being used in an increasing number of morphological studies. In such studies, equations are written which describe in idealized form a morphological character or set of characters common to a group of organisms. Morphological differences can thus be expressed by differences in the values of variables in the equations. One advantage of this approach is that it puts each morphological type in a conceptual framework which makes possible comparison with all other possible types.

Applications of mathematical models to morphological problems have been confined mostly to the description of naturally occurring species. Too little use has been made of the fact that the models are equally useful for treating morphological types not found in nature. As will be shown, the types that do not occur are important in interpreting observed morphology.

The mathematical model used to describe the coiled shell has recently received particular attention (*1–3*). Coiling is found in such diverse invertebrate groups as the Mollusca (bivalves as well as univalves), Brachiopoda, and Foraminifera. The coiled shell may be thought of geometrically as a tapered, hollow tube, open at the larger end and coiled about a fixed axis. During growth, addition of shell material takes place principally at the margin of the open end.

Within this framework, shell form can be expressed in terms of several variables (*3*). The four most important are: the shape of the generating curve ($s$) (equivalent to the cross-sectional shape of the tube) (*4*), the rate of increase in the size of the generating curve per revolution ($w$), the distance between the generating curve and the coiling axis ($d$), and the rate of movement or translation of the generating curve along the axis per revolution ($t$). Other factors become important as we consider particular biologic groups (*5*), but the four variables just listed serve to approximate the basic form of most shells.

The four variables can be combined to define a "four-dimensional" space which contains most of the theoretically possible shell forms. When the geometries of naturally occurring species are plotted in this space, it becomes evident that it is not evenly filled. Evolution has favored some regions while leaving others essentially empty. In the empty regions we are presumably dealing with forms which are geometrically possible but biologically impossible or functionally inefficient. The correct explanation of such empty regions may provide keys to the ultimate interpretation of the morphology of actually occurring shell forms. It is often easier to explain the absence of forms than their presence. For example, inspection of regions devoid of bivalves reveals a fundamental limit of bivalve coiling: for the bivalve hinge to be efficient, successive coils cannot overlap (that is, the inner margin of the generating curve must be exposed). In a different vein, it has been suggested that a basic factor governing the morphology of coiled cephalopods is the hydrodynamic efficiency of the shell (*6*). An integral part of any test of this hypothesis should be an analysis of efficiency, or lack of efficiency, of geometric forms *not* used by the cephalopods.

To study the empty regions effectively, it is imperative that we be able to construct (graphically) the nonexistent types. A method of construction in which an IBM 7090 computer and a Calcomp X-Y plotter was to be used was proposed by one of us (D.M.R.) in

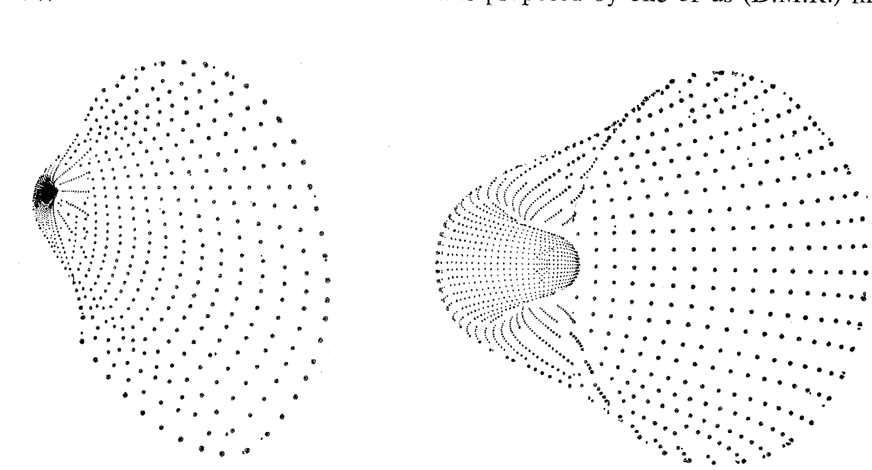

Fig. 1. Printed output of Calcomp X-Y plotter showing coiling geometries generated by a digital computer (IBM 7094).

1962 (*2*); but it produced only a cross-section of the hypothetical shell. The digital method was expanded recently to produce perspective views (Fig. 1). The principal changes from the original program are as follows. First, the coordinates of points used to outline the shell are computed at intervals of 5° of revolution about the axis, instead of 180°. Before being plotted, the points are projected to the plane of the plotting surface. Second, all the computed points are scanned to remove those which would not be seen when the hypothetical shell is viewed from the "front." Also in the new program, $t$ is redefined as the ratio of vertical to horizontal movements (along and away from the axis, respectively) of the center of the generating curve. The new $t$ is thus zero in forms where translation is absent (the planispiral forms).

The output of the X-Y plotter is a scatter of points which represents the shell in isometric perspective. Further elaboration of the program could include plotting of stereographic pairs (*7*).

The digital method has the disadvantage that it is relatively costly in terms of computer time. A much cheaper and nearly as rigorous method has been developed in which a standard PACE TR-10 analog computer and oscilloscope are used. A circle is generated which is traced rapidly enough to appear solid and whose offset from both vertical and horizontal axes can be controlled. The circle (simulating the generating curve) is rotated about the vertical axis (simulating the coiling axis) by multiplying the horizontal signal by $\cos \omega T$, where $T$ is time and $\omega$ is radian frequency. During the rotation, both horizontal and vertical signals are made to decay exponentially by multiplying each by $e^{-\alpha T}$, where $\alpha$ is a function of $w$, the rate of expansion of the generating curve. The circle thus becomes smaller as it rotates and simulates the shell growth process in reverse (that is, starting from the larger end). Translation ($t$) is introduced by varying the vertical offset of the initial circle. The relative distance ($d$) of the generating curve from the coiling axis is established by the initial horizontal offset.

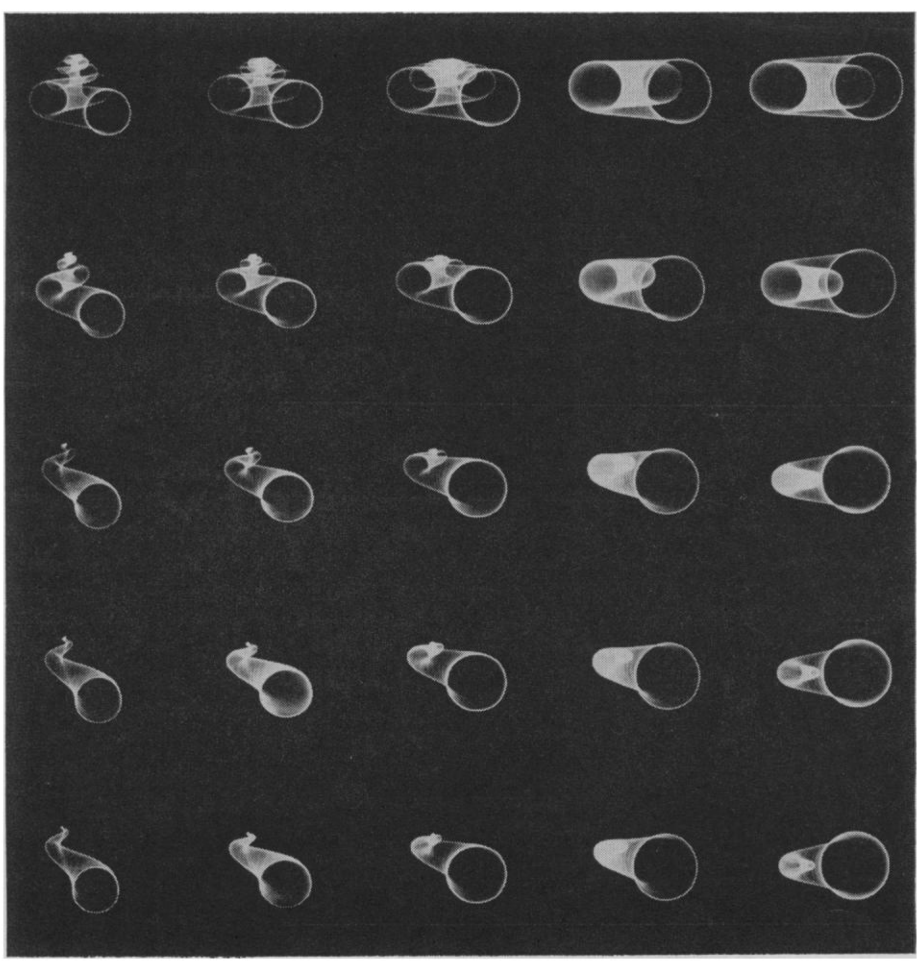

Fig. 2. Oscilloscope photographs showing coiling geometries generated by an analog computer (PACE TR-10).

To simulate the change in shell thickness during growth, the intensity of the image is varied as a function of the size of the circle. To improve perspective, the intensity is varied also as a function of the simulated position of the image in the $z$-direction, normal to the plane of the screen. (The intensity control necessitates the use of additional amplifiers.) The resulting trace on the oscilloscope is recorded photographically as a composite exposure (5 to 10 seconds).

Results obtained with the analog computer are shown in Fig. 2. The shell forms in this figure cover but a small part of the total four-dimensional space. Rate of translation ($t$) increases to the left and rate of expansion of the generating curve ($w$) increases downward; the other two parameters, $s$ and $d$, are held constant. Although a simple circle was used for the generating curve in Fig. 2, the addition of appropriate function generators would allow essentially complete freedom in choice of shape.

The two methods of graphical construction provide means of exploring the entire spectrum of possible shell forms. Series such as that in Fig. 2 can be used as a format for analysis of the functional significance of variation in coiling.


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