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THE GEOMETRY OF COILING IN GASTROPODS

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The geometrical form of coiled invertebrate shells has long attracted the attentions of zoologists and mathematicians. Coiling is exhibited, to varying degrees, in such diverse groups as the Brachiopoda, Foraminifera, and Mollusca. Most of the work in this field has been directed, however, at the gastropods and coiled cephalopods. Among the early references to the geometry of gastropods are the studies of Réamur,[1] Mosely,[2, 3] Naumann,[4] and Blake.[5] These and other works of the same period have been ably digested and summarized by D'Arcy Thompson.[6]

The principal thesis of Thompson's work is that growth in coiled forms follows rather rigid mathematical laws. According to Thompson, a fundamental characteristic of the coiled shell is that, as growth proceeds, "... the curve traced in space is, in all cases, an equiangular [logarithmic] spiral ..." [7] Many of the basic differences between species are ascribed to differences in the angle of this spiral. Additional characteristics considered to be fundamental were presented as follows: (1) the apical angle (the vertex angle of a cone enveloping the spire of the snail), (2) the shape of the generating curve (which may be thought of, in most instances, as the whorl cross section), and (3) the angle of retardation (expressing the rate of growth of the inner as compared with the outer part of each whorl).[8] The measurement of these three parameters and of the angle of the equiangular spiral should, in Thompson's view, suffice to describe the basic form of any coiled gastropod.

Thompson's scheme for describing the gastropod shell does not consider such morphologic features as ornamentation, growth lines, or the form of the protoconch: it is intended only to include the basic shape upon which the complete morphology is built. As such, it is an idea which should be exceedingly attractive to the zoologist and paleontologist. From the viewpoint of pure description, it represents an attempt to diagnose shell form in terms of truly natural parameters, related to growth, rather than in terms of rather arbitrary characters such as width of body whorl or spire height.

Beyond simple description, the possibilities for fruitful application of this kind of approach to the study of gastropod evolution are manifold. But Thompson's generalizations have not been widely used by the zoologists and paleontologists actively working with problems of comparative morphology in gastropods. This is to be expected in that some of the basic parameters (the angle of retardation, in particular) are difficult or impossible to measure in most specimen material. Furthermore, there appear to be several basic fallacies in Thompson's reasoning. For example, the measured value of the apical angle is very sensitive to minor changes in configuration of the generating curve, or whorl cross section. Such changes often do not affect the basic form of the shell but do have a profound effect on Thompson's diagnosis of its geometry because the apical angle is one of his basic parameters and is also used in the calculation of the angle of the equiangular spiral. Another example involves the use of the "sutural angle," the angle formed by the axis of coiling and the projection (in the plane of the axis) of a suture between two successive whorls. This angle is used in Thompson's calculations and is assumed to be constant for a given snail. This assumption is invalid, however, because as the whorl enlarges, the sutures must diverge, bringing about a progressive change in the sutural angle: this can be observed readily in many specimens.

In the literature since Thompson, there are several noteworthy papers on the geometry of coiling but these studies represent only extensions of Thompson's work and have the same shortcomings. There still remains a paucity of application of geometric characteristics to practical problems of gastropod systematics and evolution.

In the present paper, a fresh approach to the general problem of morphologic description of coiled gastropods is considered. The objectives are practical rather than theoretical, and the descriptive scheme which is proposed should be evaluated on the basis of its direct applicability to gastropod morphology, fossil and Recent.

The Nature of the Coiled Shell.—Perhaps Thompson's most significant contribution to gastropod geometry was to emphasize a few characteristics of shell form which may be built upon in the formulation of a workable analytical scheme. For the present purposes, the most important of these are as follows:

1. *In a single individual, the shape of the generating curve remains constant throughout growth.* With relatively few exceptions, the shape of the whorl cross section remains unchanged during the development of the snail (not considering the protoconch). As a result, the body whorl of a young individual has the same shape as that of an older individual except where a pronounced lip is formed in maturity.

2. *In a single individual, the rate of expansion of the generating curve is approximately constant.* If a series of whorl widths is measured at regular intervals on a single specimen, some variation in the ratios of successive widths is observed; the variation may even be correlated with growth. But at the species and genus level, such minor variations cease to be significant, and the average ratio (defined as w, where successive measurements are separated by one full revolution about the axis) may be used to contrast differing basic shell forms.

3. *In a single individual, the relative amount of overlap of one whorl on the preceding one is approximately constant.* In some forms, such as *Conus*, a given whorl almost completely overlaps the previous one, as measured in a direction parallel to the axis of coiling. Near the other extreme, there is almost no overlap in the height dimension of whorls of *Epitonium.* For any individual, however, the overlap is nearly constant.

4. *In a single individual, a constant ratio relates size of generating curve to the distance between the axis of coiling and a given point on the generating curve.* The axis is considered as a straight line which bisects the apical angle. In some forms, the whorl is never in contact with the axis of coiling: these are the umbilicate gastropods. More generally, however, the whorl is in contact with the axis or overlaps it slightly. In each case, the relation between whorl and axis remains constant throughout growth.

The four generalizations presented above simply reflect the fact that there is rarely much variation in coiling characteristics during growth of an individual gastropod. A young form has a shell which is essentially a scaled-down replica of the shell of an older form. However, the several characteristics show marked variation from genus to genus. Often, the differences between two quite distinct morphological types are caused by variation in only one of these characteristics.

As an example, the effects of changing only the amount of overlap of successive whorls are shown in a series of hypothetical gastropods in Figure 1. In this figure, the shape of the generating curve, the rate of expansion of this curve, and the distance from the curve to the axis (relative to the size of the curve) have been held constant; only the amount of overlap has been changed. The effects of increasing overlap are (1) increase in apical angle, (2) change in the shape of the aperture, and (3) marked decrease in the length-width ratio of the whole shell; in short, the whole morphologic aspect is changed simply by altering the amount of whorl overlap.

At this point, it is important to make a distinction between the shape of the generating curve and the shape of the aperture. Thompson defined the generating curve as a closed curve which increases its dimensions continuously as it revolves

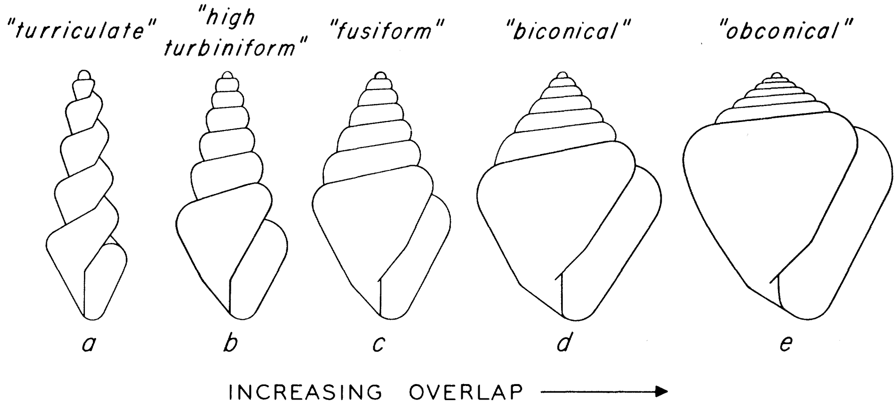

FIG. 1.—Effects on gastropod morphology of changes in amount of whorl overlap.

about a fixed axis (the axis of coiling). In forms such as the one in Figure 1*a*, the shape of this curve is observable: it is nearly equivalent to the aperture or to a cross section of any whorl. But as the amount of whorl overlap increases, part of the outline of the generating curve becomes obscure. In fact, the gastropod represented in Figure 1*e* does not utilize the entire generating curve; rather, only the outer part is actually deposited by the organism. The aperture in this case is enclosed between the inner surface of the body whorl and the outer surface of the previous whorl and reflects the generating curve only along its outer margin.

In Figure 2, the effects of changing the rate of whorl expansion are shown by

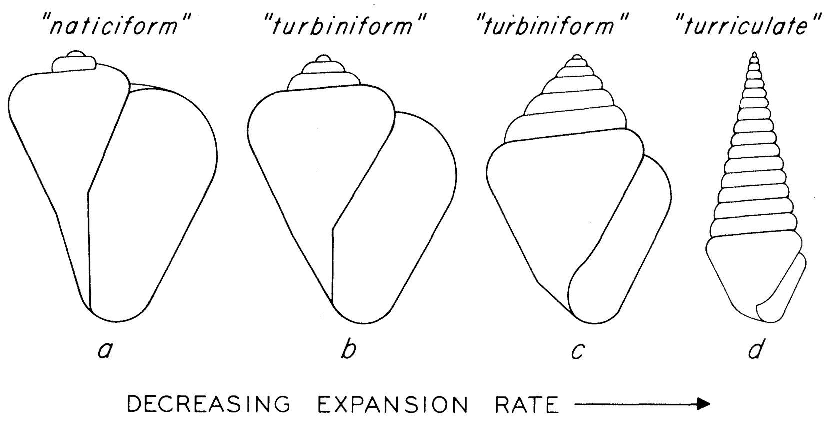

FIG. 2.—Effects on gastropod morphology of changes in rate of whorl expansion.

another series of hypothetical gastropods. As in the previous case, all other coiling characteristics have been held constant. In Figure 2*a*, one complete revolution of the generating curve causes a 300 per cent increase in the dimensions of the generating curve; the increase per revolution is only 10 per cent in Figure 2*d*. Here again, the change in one fundamental characteristic of the shell produces a marked change in over-all appearance. Note also, by comparing Figures 1 and

2, that a given value of the apical angle can be produced by more than one combination of the basic parameters.

The Description of Gastropod Morphology.—It is implied, above, that the basic coiling form of the gastropod can be defined through only four parameters (not the same four that Thompson used): shape of the generating curve, rate of expansion of this curve, amount of overlap between successive whorls, and the position of the whorl relative to the axis. This possibility may be tested by describing the appropriate characteristics on actual specimens and then attempting to reproduce the form of each specimen by purely mechanical means. An example of this procedure is illustrated in Figure 3. The species chosen is *Ecphora quadricostata* (Say), of Miocene age (and, incidentally, the first fossil ever described from the New World[9]). Figure 3*a* is an artist's sketch of the specimen and Figure 3*b* represents the scheme here proposed to describe coiling form.

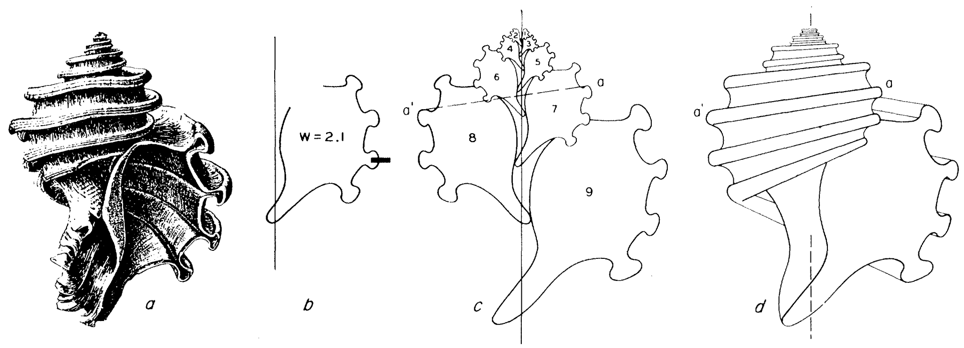

FIG. 3.—Reconstruction of basic form of gastropod from its coiling characteristics. 3*a*, drawing of *Ecphora quadricostata*[10]; 3*b*, basic coiling characteristics; 3*c*, *d*, reconstruction of morphology from 3*b*.

In Figure 3*b*, the vertical line indicates the axis of coiling, that is, the axis about which the generating curve revolves. The outline to the right of this axis is that portion of the generating curve which may be observed in the species, and the position of the curve relative to the axis is shown. The tick-mark on the generating curve represents the point of contact with the succeeding whorl (which would be the suture) and thus indicates the amount of overlap. Finally, the rate of whorl expansion (w) is shown by a number which indicates the ratio between *any* dimension of one whorl and the same dimension of the preceding whorl (the two measurements being separated by 360 degrees of rotation.) In this case, the dimension used was the distance between two of the prominent ribs on the generating curve, but any other convenient dimension could have been used. (In most species, the distance between successive sutures along a line through the apex of the shell proves to be the most favorable dimension.) All characteristics shown in Figure 3*b*, except the value of w, were obtained with a camera lucida.

The remaining sketches in Figure 3 show the procedure for reproducing *Ecphora*. First, an axis of arbitrary length is drawn. Next, replicas of the generating curve are drawn in varying sizes by using the lens and ground glass assembly of a portrait camera. The size of the first (and smallest) generating curve is purely arbitrary, and sizes of succeeding copies are determined by the expansion rate (w). The size (x) of the generating curve is related to the number of revolutions (y) about the axis in the following manner: $x = w^y$. The size of the generating curve which is second from the top on the right-hand side of the axis (#3 in Fig. 3c) is w times the size of the preceding generating curve on the same side (#1), #5 is w times #3, and so on. Following the same relation, a given generating curve on the left-hand side of the axis (#2, for example) is larger than the preceding one on the *right* (#1) by a factor of the square root of w.

The series of generating curves may then be distributed along the axis in such a way that they maintain a constant distance from the axis (relative to their respective sizes) and that their vertical position reproduces the amount of overlap indicated by the tick-mark on the outline of the generating curve.

The result of the above (Fig. 3c) is essentially a cross section of *Ecphora*. A perspective drawing (Fig. 3d) may be constructed readily from this cross section by connecting like points (such as a and a') on outlines of the generating curve which are 180 degrees apart.

It should be emphasized that the complete reconstruction of the gastropod form (Fig. 3c, d) serves only to demonstrate the validity of the system. Figure 3b suffices to describe *E. quadricostata*.

The basic description of a wider variety of gastropod forms is shown in Figure 4. In forms like *Conus*, only a part of the generating curve may actually be observed,

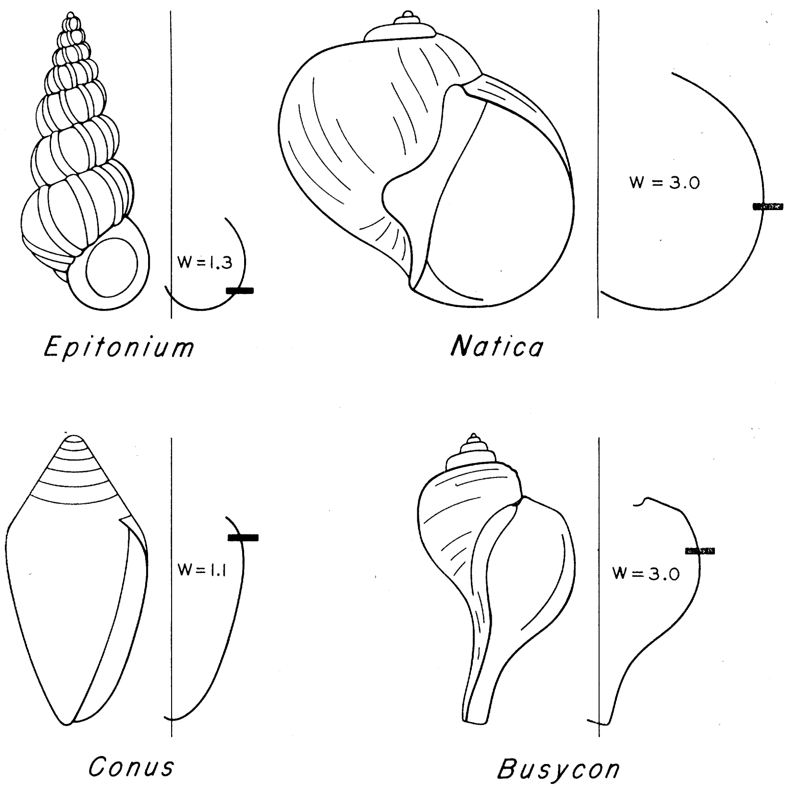

FIG. 4.—Basic coiling characteristics of several common gastropods.

but this does not detract from the feasibility of description of the basic geometry. Also, features of ornamentation such as are commonly observed in *Epitonium* would not be found in the reproduction of its coiling form.

It is concluded from the above that the basic description of morphology (excluding ornamentation, etc.) can be accomplished with one calculated ratio (w) and a line drawing showing the other critical elements (as in Fig. 3*b*). Four parameters are used, and it should be noted that the shape of the generating curve is the only one which has been carried over from Thompson's list of four fundamental characteristics.

Applications.—It is not suggested that the proposed scheme should replace conventional procedures in morphologic description. Only the basic coiling form is encompassed by the method. This basic form should be expressed by as simple and consistent a scheme as possible, however, and thus the present proposals may lead to more efficiency in description. Other areas of possible application are as follows:

Ontogenetic studies: Variation in coiling form during growth has long been known. This variation represents departure from the generalizations set forth above; striking examples are those species which have coeloconoid shells, that is, those which exhibit a concave spire in lateral profile. It can be shown (through series of measurements) that ontogenetic variation in gastropod coiling is explicable in terms of systematic and regular changes in one or more of the four basic parameters. The definition and measurement of these parameters provide a convenient tool with which to study this variation.

Phylogeny and evolution: Figures 1 and 2 suggest that spectra of gradation exist between morphologic types which are generally distinguished by terms such as "turriculate," "turbiniform," and "biconical." The recognition of gradational series in zoological or paleontological material would be much more readily accomplished by description in terms of the basic parameters of coiling. Evolutionary series may thus be recognized which have been obscured by the conventional methods of description. A fundamental question here is whether the four parameters that have been defined have genetic reality and would thus be expected to change independently and in a regular fashion. This question can be answered only after more is learned from studies of gastropod genetics and work with comparative morphology in evolving lineages.

Ecology: It is tempting to relate coiling form to the gastropod environment. It will be noted, for example, in Figure 2, that the surface area of shell material deposited by the organism relative to the volume of the shell bears an inverse relation to the whorl expansion rate. This suggests that an increase in expansion rate tends toward the conservation of calcium carbonate. Because of this, the geographic distribution of certain combinations of coiling characteristics might be related to ecologic factors bearing on carbonate metabolism, such as temperature and salinity. There is, indeed, a suggestion of such a correlation with water temperature in western Atlantic marine snails, but further study is necessary for confirmation.

Conclusions.—As stated in the introduction, the main objective of the present study is to devise a system of description which may be applied readily to a wide range of gastropod types. For this reason, the treatment lacks mathematical elegance. Although much more precision could be added to the system, it is doubtful whether the purely qualitative aspects could ever be removed. The shape of the generating curve, for example, is generally irregular enough to greatly hinder mathematical description. Furthermore, the complete generating curve, as a closed curve, can rarely be seen, and thus its position relative to the axis of coiling is difficult to define mathematically. Finally, the departures from regularity observed in ontogeny discourage completely rigorous analysis of gastropod geometry.

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[6] Thompson, D'A., *On Growth and Form* (New York: Macmillan Co., 1942), pp. 748–849.

[7] Thompson, *ibid.*, p. 812. The defining characteristic of this spiral (as a plane figure) is that the angle formed by a tangent to the spiral and a radius (at the point of tangency) is constant. The size of the constant angle controls, therefore, the shape of the spiral.

[8] The reader is referred to Thompson (*ibid.*, pp. 798–805) for a fuller discussion of the angle of retardation.

[9] Lister, M., *Historia sive synopsis methodicae Conchyliorum* (London, 1685), Plate 1059, Figure 2.

[10] Martin, G. C., *Maryland Geological Survey*, Miocene Volume, Plate 52, Figure 1 (1904).

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*PROLONGATION OF THE LIFE SPAN OF KOKANEE SALMON (ONCORHYNCHUS NERKA KENNERLYI) BY CASTRATION BEFORE BEGINNING OF GONAD DEVELOPMENT**

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The present investigation was undertaken as an initial approach to the problem of the nature of the post-spawning death of Pacific Coast salmon. The regularity with which all five species of this salmon die after their first reproduction, no matter whether the normal life cycle of the species is 2, 3, or 4 years, strongly suggests a causal relationship between the spawning act and subsequent death. However, it is also possible that the life span of each species is biologically fixed and that spawning constitutes the final phase. Would prevention of spawning extend the salmon's life cycle? An attempt to answer this question was made by castrating a number of sexually immature kokanee and observing them over a period of years. Unoperated controls of the same hatch were maintained under the same environmental conditions.