forma et functio, volume 4, 1971, page 319–325

The Geometry of Shell Sculpture

Die Geometrie von Schalenstrukturen

La Géométrie de la Coquille

GEERAT J. VERMEIJ

Author's address: G. J. Vermeij, Department of Biology, Yale University, New Haven, Connecticut 06520, USA

(Received/Eingegangen: April 7, 1971)

Abstract: Elements of spiral sculpture on the shells of molluscs and brachiopods are the result of deflections from the overall smooth form of the generating curve along the axes of a three-dimensional rectangular coordinate system. The nature and degree of expression of these deflections are functions of the shape of the generating curve at any fixed instant in time, as defined by the partial derivatives $\partial x/\partial y$, $\partial x/\partial z$, and $\partial z/\partial y$; and of the direction of growth of all points of the generating curve in a cylindrical coordinate system as defined by the parameters $\partial z/\partial r$, $\partial z/\partial \theta$, and $\partial r/\partial \theta$. Ontogenetic changes in the geometrical properties of shells are accompanied by ontogenetic changes in sculpture.

Zusammenfassung: Spiralige Strukturelemente auf den Schalen von Mollusken und Brachiopoden sind Abweichungen der überall glatten Form eines erzeugenden Kurvenstücks längs den Achsen eines dreidimensionalen rechtwinkligen Koordinatensystems. Art und Ausmaß dieser Abweichungen sind Funktionen der Größe des erzeugenden Kurvenstücks zu einem beliebigen festen Zeitpunkt und der Wachstumsrichtung aller Punkte des erzeugenden Kurvenstücks in einem zylindrischen Koordinatensystem. Erstere sind definiert durch die partiellen Ableitungen $\partial x/\partial y$, $\partial x/\partial z$ und $\partial z/\partial y$, letztere durch die Parameter $\partial z/\partial r$, $\partial z/\partial \theta$ und $\partial r/\partial \theta$. Ontogenetische Änderungen der geometrischen Relationen der Schalen werden von ontogenetischen Änderungen der Schalenstruktur begleitet.

Résumé: Les constituants de la sculpture spiralée des coquilles de mollusques et de brachiopodes résultent de la déflection de la courbe génératrice unie sur les axes d'un système tridimensionnel de coordonnées rectangulaires. La nature et l'importance de ces déflections sont fonction de la forme de la courbe génératrice à chaque instant, définie par les dérivées partielles $\partial x/\partial y$, $\partial x/\partial z$, et $\partial z/\partial y$, et de la direction de croissance des divers points de la courbe génératrice durant l'ontogénèse dans un système de coordonnées cylindriques définie par les paramètres $\partial z/\partial r$, $\partial z/\partial \theta$ et $\partial r/\partial \theta$. Au cours de l'ontogénèse, tout changement des propriétés géométriques s'accompagne de changements dans la sculpture.

Introduction

Peculiarities of shell sculpture in molluscs and brachiopods have been widely used by systematists as taxonomic characters, but they have received relatively scant attention from the functional morphological point of view. The work of THOMPSON (1942), OWEN (1953), RUDWICK (1959, 1968), STASEK (1963a, b), RAUP (1966, 1967), and VERMEIJ (1970, 1971), among others, has provided a geometrical framework in which shells of widely differing morphology can be compared, thereby laying a foundation for defining strategies of adaptation in quantitative terms. The geometrical basis of shell sculpture has been directly considered only by RUDWICK (1959) and to a lesser extent by VERMEIJ (1970).

Both THOMPSON (1942) and RAUP (1966) analyzed shell coiling by the use of an idealized model in which the center of an expanding generating curve rotates about an axis, tracing a logarithmic spiral on the surface of a right circular cone. The properties of shell coiling may then be expressed in terms of four parameters (RAUP, 1966):

1. The shape S of the generating curve;
2. The rate of translation T of the center of the generating curve along the axis of rotation;
3. The rate of expansion W of the generating curve; and
4. The ratio D between the distance from the axis to a point on the generating curve closest to the axis and the distance from the axis to the diametrically opposite point on the generating curve.

The principal limitations of the model are that the values of T and W are composites for a range of values for each point on the generating curve, and that S is a complex of theoretically independent parameters. Although RAUP's (1966) model serves well in defining the coiling characteristic of higher molluscan and brachiopodan taxa (RAUP, 1966, 1967, VERMEIJ, 1971), it does not of itself provide a sufficient framework for a detailed geometrical and sculptural analysis of a particular shell.

In the present paper, a model of shell geometry based on three parameters describing the shape of the generating curve and three parameters describing the direction of growth of the generating curve is employed to express shell sculpture in geometrical terms. The treatment of a sculptural element as a deflection or anomaly in an otherwise smooth curve is based on the analysis of RUDWICK (1959), and to a lesser extent on those by OWEN (1953) and STASEK (1963b).

Three-dimensional analysis

Consider an orthostrophic dextral conispirally coiled shell in an x, y, z rectangular coordinate system with the axis of coiling along the positive part of the Z-axis and the apex at the origin. Rotate the shell around the axis of coiling so that the plane of the generating curve will come to lie perpendicular to the y, z plane, i. e., so that its intersections with the x, y and x, z planes are straight lines parallel to the X-axis. The portion of the plane enclosed by the generating curve will in most cases lie in the first octant. The slope of the generating curve at a given point on the curve at any fixed instant in time can be expressed in terms of three partial derivatives, $\partial x/\partial y$, $\partial x/\partial z$, and $\partial z/\partial y$. Since the generating curve lies in a plane, and since that plane is perpendicular to the y, z plane, it follows that $\partial z/\partial y$ is a constant. Geometrically, $\partial z/\partial y$ is equal to the cotangent of the angle E between the plane of the generating curve and the axis of coiling of the shell (see Fig. 1): $\partial z/\partial y = \cot E$. The other two partial derivatives can then vary freely between 0 and infinity, and their respective values determine the shape of the generating curve.

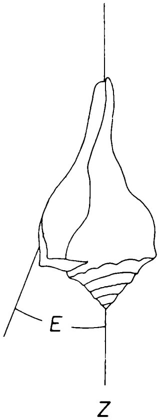

Figure 1

Angle E between the axis of coiling Z and the plane of the generating curve

Bild 1

Winkel E zwischen der Windungsachse Z und der Ebene des erzeugenden Kurvenstücks

A sculptural feature which is carried continuously or at regular intervals by a restricted segment of the generating curve through successive generating curves during growth will be called a spiral feature. Such a spiral feature manifests itself as a localized anomaly or deflection from the overall smooth form of the generating curve (RUDWICK, 1959). We may distinguish three types of deflection according to whether their orientation is parallel to the X-, Y-, or Z-axis respectively. For example, a z-deflection is one whose orientation is parallel to the Z-axis.

The degree of expression of spiral sculptural elements will depend on the type of deflection that gives rise to them and on the values at each point on the generating curve of $\partial x/\partial y$, $\partial x/\partial z$, and $\partial z/\partial y$. Fig. 2 illustrates the effect of slope of a curve in the x, y plane on the degree of expression of x- and y-deflections. When $dy/dx = 0$, y-deflections are maximally expressed, while x-deflections are completely suppressed; when $dy/dx \to \infty$, y-deflections are suppressed and x-deflections are strongly developed. In three dimensions, if $\partial x/\partial z = 0$ (i. e., if a tangent plane to the generating curve at a given point is perpendicular to the X-axis), then a sculptural element arising from an x-deflection will be maximally expressed, while an element arising from a z-deflection will be completely suppressed.

We now consider the sculptural properties of two contrasting geometries, most characteristically developed in the Gastropoda, based on the value of $\partial z/\partial y$.

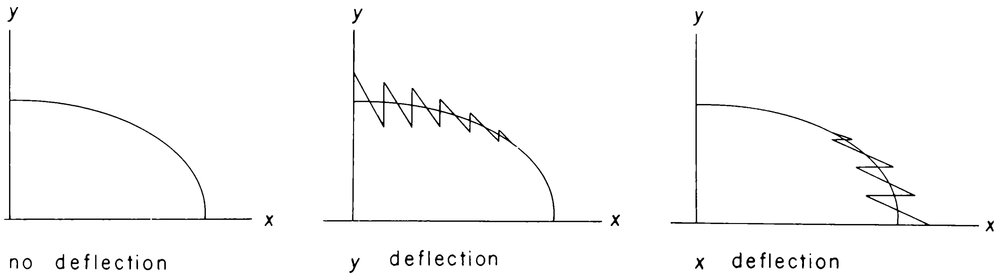

Figure 2. Effect of slope of a curve in the x, y plane on degree of expression of x- and y-deflections

Bild 2. Neigung der Kurve in der xy-Ebene in Abhängigkeit von den Abweichungen der x- und y-Koordinaten

Type 1, $\partial z/\partial y < 1$. This category includes those gastropods in which the angle E between the coiling axis and the plane of the generating curve is greater than 45°. Typical examples of this trochiform geometry are to be found in most conispirally coiled archaeogastropods, in some "lower" mesogastropods, and in many stylommatophoran pulmonates (VERMEIJ, 1971). Since $\partial z/\partial y$ is small, $\partial x/\partial z$ will generally be large along most of the length of the generating curve, and x-deflections will be of limited occurrence. If the juncture between the outer lip and the preceding whorl forms a smooth transition, i. e., if the suture is indistinct, then $\partial x/\partial y$ will be relatively large near the suture, and x-deflections might be expected; however, since increments of both x and z are large as compared to the increment of y along this portion of the generating curve, the slope $\partial x/\partial z$ will in extreme cases tend to the indeterminate form 0/0, and x-deflections will not occur on the generating curve near the point of contact with the preceding whorl. On the other hand, z-deflections could be expected to occur along most of the generating curve except in the region adjacent to the suture discussed above. Empirical observations indicate that many sculptured trochiform shells are characterized by well-developed ribs on the base (anterior portion of the whorl), and by a comparative paucity of strong sculpture on the upper (posterior) part of the whorl, suggesting that the spiral elements in these forms are mostly the result of z-deflections. In such archaeogastropods as *Monodonta* and *Turbo* and in many littorinid mesogastropods, where E is approximately 45°, strong sculpture resulting from x-deflections is often developed on the upper portion of the whorls, while the base is relatively devoid of sculpture.

Another consequence of low $\partial z/\partial y$ values is the absence of y-deflections. In this connection it is interesting that anterior siphonal canals or notches and labial spines, all of which are y-deflections, do not occur in trochiform shells unless the trochiform geometry is attained during the final stages of ontogeny, as in the nassariid neogastropod *Cyclope neritea* (VERMEIJ, 1971).

Type 2, $\partial z/\partial y > 1$. This category consists of those gastropods in which the angle between the axis of coiling and the plane of the generating curve is less than 45°. Typical examples include most "higher" mesogastropods, neogastropods, and basommatophoran pulmonates

(VERMEIJ, 1971). In these forms, $\partial x/\partial z$ will be small except in a restricted anterior region and sometimes in areas near the suture, and x-deflections can occur over most of the generating curve where the latter is not in contact with the preceding whorl. In the restricted anterior portion of the generating curve where $\partial x/\partial z$ becomes very large, the value of $\partial z/\partial y$ is usually too large to permit development of z-deflections. In *Melo diadema* (Volutidae), *Melongena corona* (Melongenidae), and a number of other neogastropods and "higher" mesogastropods, however, backwardly projecting spines probably resulting from z-deflections occur on a sharp bend of the posterior part of the generating curve, where a sudden increase in $\partial x/\partial z$ takes place just to the right of the juncture with the preceding whorl.

In gastropods of type 2, sculpture on upper portions of the whorls is often well-marked, and tends to be strongest towards the posterior part of the whorl. This type of sculpture is often expressed as one or two prominent spiral ridges or spiral rows of knobs near the shoulder of the whorl, as in many Strombidae, Cassididae, Thaisidae, and Vasidae. The increasing degree of expression of spiral sculpture in a posterior direction may be related to a corresponding decrease in the values of both $\partial x/\partial y$ and $\partial x/\partial z$.

In contrast to the type 1 geometry, the type 2 condition does allow for the expression of such y-deflections as siphonal canals or notches and labial spines (VERMEIJ, 1971). Empirical observations suggest that these y-deflections are usually more or less anterior in position, where $\partial x/\partial y$ tends to be large.

Nothing in the geometrical model developed here requires shells of type 2 to exhibit any type of deflection, and indeed many smooth type 2 species are known; it is, however, significant that the type 2 geometry poses no a priori restriction on the development of x- and y-deflections. On the other hand, while the type 1 geometry allows for the expression of z-deflections, it generally restricts the development of x- and y-deflections. From this point of view, as well as from other considerations (VERMEIJ, 1971), the type 2 geometry allows for a much greater morphological diversity than does the type 1 geometry.

We now consider the special case of planispiral coiling, a mode of coiling characteristic of most shelled cephalopods, brachiopods, and certain gastropods. With this type of geometry, in which $\partial z/\partial y \to \infty$, (i. e., the generating curve is perpendicular to the x, y plane), all three deflection types can occur on the same shell. In the immediate vicinity of the plane of symmetry $y = 0$, the slope $\partial x/\partial z = 0$ or is very small, and x-deflections may occur. On either side of this plane, $\partial x/\partial z$ becomes very much greater, especially in laterally compressed shells, and z-deflections can replace x-deflections as the morphological basis for spiral sculpture. Finally, y-deflections may occur on any portion of the generating curve, since both $\partial x/\partial y$ and $\partial z/\partial y$ are infinitely large. Mesozoic ammonoids in particular have taken full advantage of the potential sculptural diversity inherent in their planispiral coiling, and a wide variety of apertural embelishments, most of which are based on y-deflections, has been evolved by these and other planispiral groups.

The discussion thus far has dealt with the types and degree of expression of deflections as a function of the shape of the generating curve at some fixed instant in time. As RUDWICK (1959) has pointed out, however, shell form and sculpture are also a function of the direction of growth of the generating curve during ontogeny. In theory, the direction of growth of a point on the generating curve as it sweeps through space about an axis is independent of the slopes $\partial x/\partial y$, $\partial x/\partial z$, and $\partial z/\partial y$ at that point of the generating curve at any instant in time.

In order to investigate the effect of growth direction on sculpture in coiled shells, consider a shell with dextral orthostrophic conispiral coiling in an r, θ, z cylindrical coordinate system with the axis of coiling along the positive part of the Z-axis and the apex at the origin. The plane of the generating curve is free to rotate in a counterclockwise direction about the Z-axis, expanding as it does so. The direction of growth of any one point of the generating curve may then be expressed in terms of the following three parameters:

1. translation rate $T = \partial z/\partial r$;
2. expansion rate $W_r = \partial r/\partial \theta$; and
3. expansion rate $W_z = \partial z/\partial \theta$. Each point on the generating curve will generally possess unique values of each of these three parameters.

Since the generating curve lies within a plane, and since therefore all points of the generating curve sweep through the same angular increment $\Delta\theta$ as during time increment Δt, it follows that the values of the growth parameters depend on the r and z coordinates of each point on the generating curve. Thus, the value of $W_r = \partial r/\partial \theta$ will be much greater for a point on the generating curve far from the axis of coiling than for a point close to the axis.

If $\partial r/\partial \theta$ is very large and $\partial z/\partial r$ very small, then x-deflections will be poorly or not at all expressed, since they are oriented in a radial direction within the plane of the generating curve. Similarly, if $T = \partial z/\partial r$ and $W_z = \partial z/\partial \theta$ are very small, any z-deflection that may be present will be strongly expressed. The greatest development of y-deflections will occur when the radial growth increment Δr and the vertical growth increment Δz are both very large in comparison to the angular growth increment Δz are both very large in comparison to the angular growth increment $\Delta\theta$.

In the limpet-like thaisids *Drupa aperta, Purpura patula,* and *Concholepas concholepas,* the siphonal notch is broad and poorly developed despite the high $\partial z/\partial y = 2.6$ value, because points on the generating curve in the proximity of the notch have large W_r and W_z values. Numerous other cases are known where growth parameters counteract the effect of shape of the generating curve on the degree of expression of deflections.

RUDWICK (1959) has shown that if growth in the planispirally coiled brachiopods takes place only in a direction perpendicular to the plane of the commissure between the valves i. e., if the radial growth component is 0, then a vertical or y-deflection whose orientation is also perpendicular to the plane of the commissure will be completely suppressed as seen from the outer shell surface, while a radial or x-deflection would be maximally expressed. Similarly, if growth takes place only in a radial direction within the plane of the generating curve (commissure), x-deflections would be suppressed as seen from the outer shell surface and y-deflections would be maximally expressed. The sculptural differences between the two valves of brachiopods and inaequivalve bivalves can to a large extent be traced to differences in the direction of growth of the valves (see also STASEK, 1963b).

In the idealized logarithmically coiled shell, both the shape of the generating curve and its overall direction of growth will remain constant during ontogeny (THOMPSON, 1942). As STASEK (1963b), RAUP (1966), and many others have pointed out, however, the strict time-constancy of form is adhered to only by very few animals with accretionary skeletons. Variation in any or all of the parameters is the rule rather than the exception, and brings with it ontogenetic changes in sculpture. For example, juvenile specimens of the West Indian thaisid *Purpura patula* have relatively small $\partial r/\partial \theta$ values over most of the generating curve, and possess a sharply nodose shell. Adult shells, having a much broader aperture and correspondingly greater $\partial r/\partial \theta$ values over most of the generating curve, possess sculpture which is much more weakly developed and sometimes even obsolete. In this case, the ontogenetic increase of $\partial r/\partial \theta$ along most of the generating curve and to a much lesser extent the ontogenetic rounding of the aperture result in a decrease in the degree of expression of the x-deflections which give rise to the nodose sculpture.

It may be concluded that the apparent sculptural complexity evident in many molluscs and brachiopods at any one stage in growth and in ontogeny is often directly related to the geometry of the generating curve and to the direction of skeletal growth. The shell geometry itself may, however, be complex; indeed, certain assumptions in the mode presented here, such as the requirement that the generating curve lies entirely within a plane, are not valid in the case of many brachiopods and molluscs (RUDWICK, 1959; STASEK, 1963b), and add to the complexity of the geometrical analysis of shell form. Details of ontogenetic changes in sculpture as related to shell geometry are lacking for most molluscs and many brachiopods; their elucidation may shed new light on the functional significance of sculptural features.

References

OWEN, G.: The shell in the Lamellibranchia. Q. Jl microsc. Sci. 94, 57–70 (1953).

RAUP, D. M.: Geometric analysis of shell coiling: general problems. J. Paleont. 40, 1178–1190 (1966).

RAUP, D. M.: Geometric analysis of shell coiling: coiling in ammonoids. J. Paleont. 41, 41–65 (1967).

RUDWICK, M. J. S.: The growth and form of brachiopod shells. Geol. Mag. 96, 1–24 (1959).

RUDWICK, M. J. S.: Some analytic methods in the study of ontogeny in fossils with accretionary skeletons. J. Paleont. 42, 35–49 (1968).

STASEK, C. R.: Orientation and form in the bivalved Mollusca. J. Morph. 112, 195–214 (1963a).

STASEK, C. R.: Geometrical form and gnomonic growth in the bivalved Mollusca. J. Morph. 112, 215–229 (1963b).

THOMPSON, D. W.: On Growth and Form. London, Cambridge: University Press 1942.

VERMEIJ, G. J.: Adaptive versatility and skeleton construction. Amer. Nat. 104, 153–160 (1970).

VERMEIJ, G. J.: Gastropod evolution and morphological diversity in relation to shell geometry. J. Zool. 163, 15–23 (1971).