ON LISON'S MODEL OF BIVALVE SHELL FORM, AND ITS BIOLOGICAL INTERPRETATION

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In the half-century that has elapsed since the publication of W. D'Arcy Thompson's classic study *On Growth and Form*, there have been several attempts to explain rigorously the phenomenon of shell growth in the Mollusca (Huxley, 1932; Lison, 1949; Owen, 1953; Yonge, 1952; Stasek, 1963) and Brachiopoda (Rudwick, 1959; Krans, 1965). Apart from the comprehensive and undeservedly neglected paper of Lison (1949), all these authors have used essentially the same approach as that of Thompson (1942, p. 756), though refining this approach in detail. It is my belief that Thompson's work entails certain *a priori* assumptions which, although intuitively plausible, are not valid, and that the application of these assumptions results in a confusion, rather than a clarification, of understanding of shell growth.

VARIANTS OF THE THOMPSON VECTOR MODEL

Thompson assumed that the bivalve shell might be considered as the result of a certain pattern of growth forces. These growth forces are represented at any point on the mantle edge by a series of vector components in arbitrarily defined reference directions. Such reference directions, or axes, are usually defined in intuitively satisfactory directions. Commonly one direction is defined to coincide with the hinge axis of the shell, one lies in a plane of median symmetry (if present), while the third is at right angles to the other two. The choice of these reference directions has varied from one author to another (see Fig. 1), but the following may be taken as typical:

Radial component of growth

Defined by Owen (1953, p. 59) as 'radiating from the umbones and acting in the plane of the generating curve'. Stasek (1963, p. 220) has pointed out that species with interumbonal growth (such as *Arca*) cannot be said to have a radial component of growth if lying *in* the plane of the generating curve is a requisite part of the definition. He amended Owen's definition to 'radiating from the umbones'.
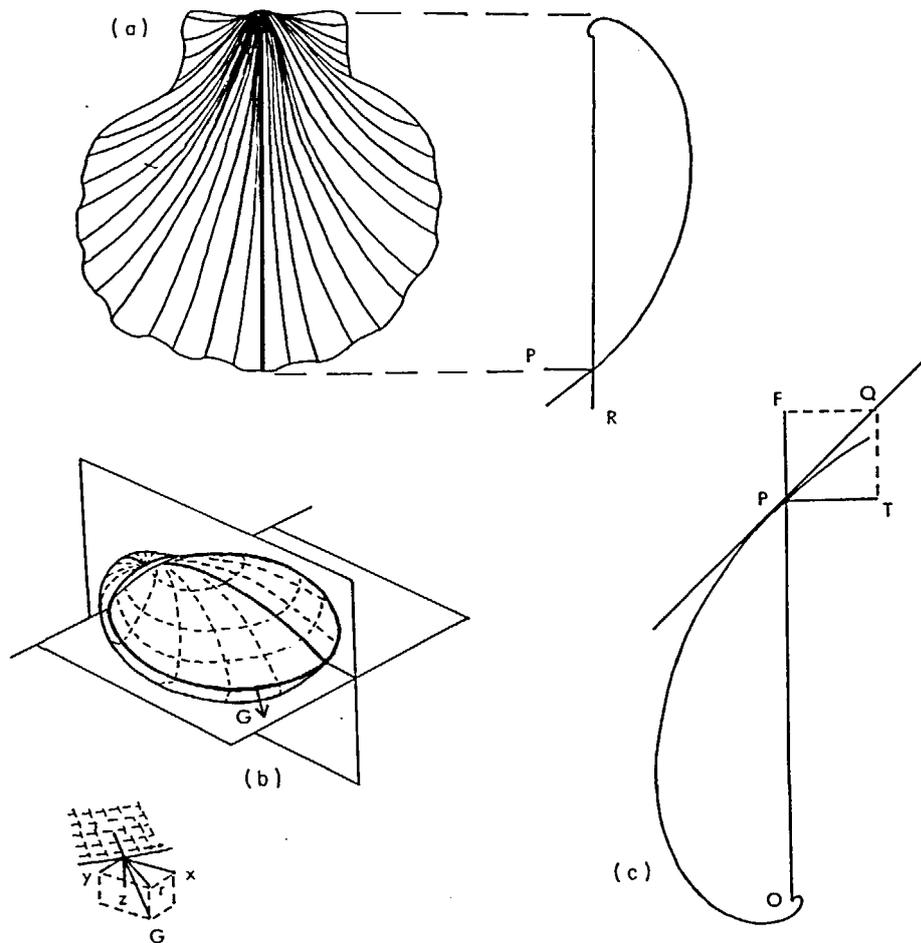
Fig. 1.   (a) Right valve of *Pecten maximus* and section through the plane of median symmetry
to illustrate the use of growth vectors. After Owen (1953). P, Transverse component; R, radial
component. (b) View of a rectimarginate brachiopod shell to show component growth rates
at one point on the dorsal valve edge. After Rudwick (1959). G, Actual rate of growth;
r, radial component; x, anterior component; y, lateral component; z, vertical component.
(c) After Thompson (1942), p. 756. 'Dynamical aspect of the equiangular spiral'. Growth
at point P is resolved into a force (F) acting radially and a force (T) acting transversely.
PQ, Tangent at point P.

Transverse component of growth

Defined by Owen (1953, p. 59) as 'acting at right angles to the plane of the
generating curve (represented by the valve margin)'.

Tangential component of growth

Defined by Owen (1953, p. 59) as 'acting tangentially to, and in the plane of, the

generating curve'. Thompson himself only considered the growth of a shell model based on a planispiral median plane of *Pecten* type. Lison (1949, p. 44) was the first writer to point out that an explanation of shell growth in asymmetrical bivalves such as venerids required a component of growth additional to those initially proposed by Thompson.

CRITICISM OF THE THOMPSON MODEL

Both Lison and Stasek have criticized the Thompson model of shell growth.

Lison suggested that it is unsatisfactory for two main reasons. First, it necessitates the assumption of a complex set of forces acting within a molluscan individual. Moreover, the absolute value of these forces must differ at different points on the commissure of the shell. Secondly, he maintained that the pole of the spiral, as represented by the umbo of the shell, has no biological developmental implications; it is merely a convenient point on which to centre a system of coordinates. 'Any theory that attributes to the pole an active role in the mechanism of the development of the shell, either as a centre of forces ('centre de traction')—as D'Arcy Thompson suggested—or even simply as a centre of influence or organization, is dangerous' (Lison, 1949, p. 45; free translation).

Stasek (1963, p. 218) also stressed that growth vectors of the Thompson type should not be construed as 'forces affecting the shape of the shell', and that such vectors are only of use in so far as they describe the directions taken by the generating curve during growth.

LISON'S MATRIX MODEL

For the purpose of a geometrical treatment of shell form, Lison (1949, p. 47) introduced the concept of a matrix. He defined this as 'all regions of an organism that secrete a substance becoming rigid from the moment of its secretion...' (free translation).

In most of Lison's treatment of form, and in what follows below, the matrix is considered as a two-dimensional secreting sheet coincident with the plane of the commissure* of the particular shell form under consideration. The resultant form is then, of course, a solid 'valve' without the mantle and body cavity of a living bivalve. (In a living species the formation of the body cavity may be explained by introducing modifications of rate and direction of shell secretion at points away from the margin of the shell.) Nonetheless, this in no way detracts from the validity of the concept when it is used as a means for explaining (or predicting) the geometry of the external shell surface.

Consider a circular matrix over which secretion of shell material is taking place. Assume that secretion is uniform over the matrix and that the matrix maintains

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* The plane of the commissure is the theoretical plane of gross symmetry between the two valves of the shell; it is coincident with the plane of contact of the two valves in the case of the simple shell forms being discussed in this paper.

its initial size during secretion. Let the secretion rate be dG and area of the matrix A. Then, during time dt, a right circular cylinder of volume $A.dG.dt$ will be generated. A profile view of this cylinder will have the form of a rectangle (Fig. 2a).
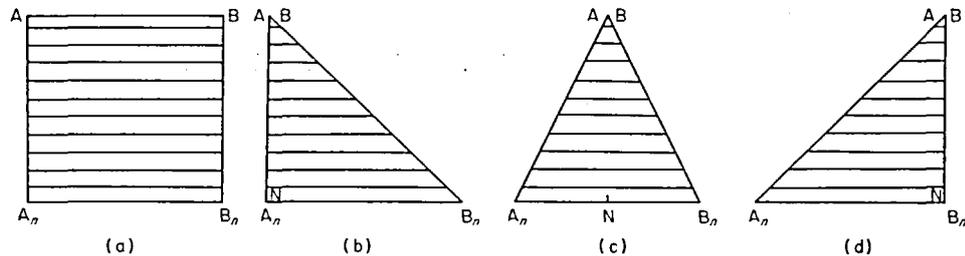

Fig. 2.   To show the different overall form resulting from secretion at a constant rate over a matrix AB when the point of stacking (directive normal point) is varied. (a) Matrix AB secretes growth increments of constant area. (b), (c) and (d) Matrix AB secretes growth increments of constantly increasing area; position of directive normal point is varied. AB, Initial dimensions of matrix; A_nB_n, final dimensions of matrix; N, directive normal point. After Lison (1949).

Suppose now that the matrix, as it secretes, is expanding at a certain constant rate. Then the edifice formed by secretion throughout the time of growth is conical—triangular in profile, Fig. 2(c)—and can be considered to be built of a series of disks stacked one on top of the other. As Lison took great trouble to point out, using this as a basic model it is possible to generate cones of a given base area and height (and hence volume) but differing in shape depending on what point the stacking of successive growth increments takes place. This point of stacking was termed by Lison the *directive normal point*. If the successive growth increments are stacked about the mid-point of the matrix, the profile of an isosceles triangle results (Fig. 2c). If they are stacked about one end or other of the matrix, profiles of right-angled triangles result (Figs. 2b and d) and, of course, all intermediates between these two extremes are possible.

We may now introduce an additional factor and thus adapt the model to simulate more closely the actual growth of bivalved shells. (It should perhaps be noted that model shown by Fig. 2(c) above already approximates to the shape of the adult shell of a limpet-like mollusc.)

Suppose that secretion rate decreases linearly from one end of the matrix to the other (Fig. 3). Then successive growth increments are no longer rectangular in profile, but triangular. The edifice of secretion through time still has a triangular shape though two sides of the triangle are now curved. Moreover, under the conditions we have assumed, the locus during growth of any point on the matrix is a logarithmic spiral (for rigorous proof of this see Lison, p. 52 *et seq.*). As in the previous model, different types of stacking of successive growth increments result in different shell shapes. Lison's elegant figures, redrawn here as Fig. 3, speak for themselves.
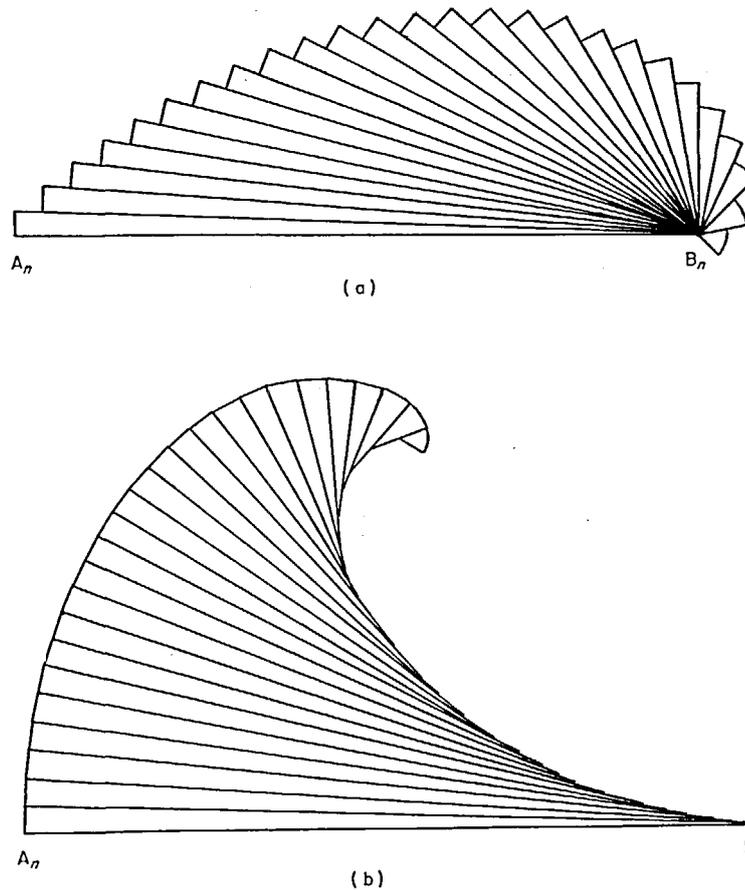
FIG. 3.   To show the different overall form resulting from secretion at a constant gradient over a matrix AB when the directive normal point is varied. Lettering as for Fig. 2; directive normal point is at B_n in (a), at A_n in (b). The figure is constructed of successive sectorial increments of constant arc length and successive radii h, $2h$, $3h$, . . . , nh. Secretory activity is assumed to fall uniformly from a maximum at A_n to 0 at B_n. The profile of (a) simulates a venerid style bivalve shell; that of (b) simulates a shell of exaggerated arciform style. After Lison (1949). See p. 274.

APPLICATION OF LISON'S MODEL

Given a bivalve with a planar commissure, gnomonic growth of the shell can only take place by secretion of wedges of shell material which taper towards the umbonal side of the shell (i.e. towards the point of minimum secretion). It is an unavoidable consequence that, depending on the way the wedges of shell material are stacked, shells of differing profile may be produced. 'Stacking', of course, represents successive growth increments of the shell. A unique shell form may be generated for any given combination of shape of generating curve, position of directive normal point, gradient

of secretion across the matrix and relation between the increase in size of the matrix and its secretory activity (Lison, 1949, p. 59).

Let us now replace, in Lison's model, the concept of 'matrix' with the concept of 'mantle'. As, in the model, the matrix grows in absolute size during time, so in actuality the area of mantle lining the shell of a mollusc increases during life.

It has been suggested that proliferation of mantle cells takes place all over the mantle surface, but modern opinion (Mutvei, 1964; Beedham, 1965) favours the mantle margin, and the periostracal groove in particular, as the main generative site for the new epithelial cells.

Now it is obvious that a model such as Fig. 2(c) could be explained by proliferation of mantle cells in the centre of the matrix, or by proliferation around the edge of the matrix, or indeed by proliferation of cells anywhere on the matrix. The model itself gives no indication as to which of the alternative *interpretative* ideas is correct. However, for purposes of conceptual convenience and in the light of what has been said above, I shall here assume that proliferation of mantle cells does in fact take place mainly at the mantle edge. It should be noted that the validity of the geometrical model is in no way dependant on this assumption. One may now seek an interpretation of gnomonic growth of different shapes of generating curve in terms of different rates of proliferation of epithelial cells at various points on the mantle edge.

BIOLOGICAL INTERPRETATION

In order to interpret correctly the growth of the bivalve shell it is essential to distinguish clearly between mantle growth (i.e. actual proliferation of mantle cells) and shell secretion (i.e. the secretion of the total set of mantle cells during a given period of time). It should be made quite clear that the validity of the interpretation that follows rests to a large extent on the validity of the assumption that the mantle edge is in fact the main generative site for new epithelial cells.

Consider the matrix AB in Fig. 4. Over a given period of time it may be considered to secrete a certain amount of shell in direction Y. This gives rise to the stippled field on the diagram. Meanwhile, there has been lateral introduction of new mantle cells which have themselves been responsible for the secretion of the small black field on the diagram, again in the direction Y.

In a living bivalve this process is more or less continuous and the new mantle cells are assumed to be supplied by continuous generation in the periostracal groove (G) of the mantle edge.

All versions of the vector model would seem to imply loosely that a path on the surface of the shell, such as PP′ (Fig. 4), is a secretion path, or has some similar fundamental significance. It can be seen from the figure that this is not so; the path of *secretion of the shell* is along PQ. Paths of shell secretion, as opposed to paths of mantle expansion or epithelial generation, can only be traced in full on sections cut through the shell.

In the vector model the vector PP′ is resolved into a component ('radial') in

direction X, and a component ('transverse') in direction Y. But the radial component of this 'growth' is due to proliferation of mantle cells, while the transverse component is due to the secretion of shell material by the set of presently existing mantle cells. The edifice formed by shell growth is thus the resultant of two basically different components, *only one of which is concerned with shell secretion per se*.
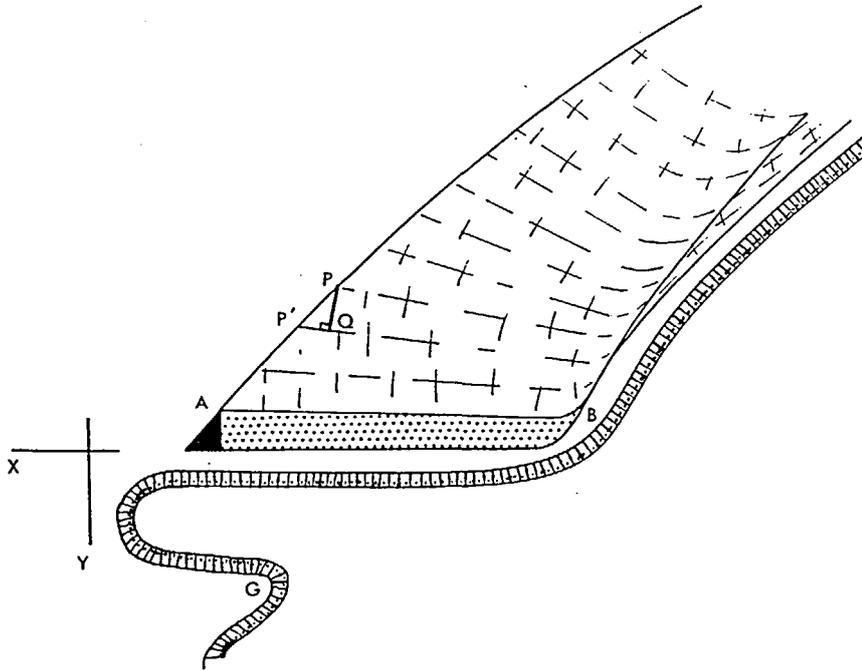

FIG. 4.   To illustrate actual mode of secretion and 'growth' of a bivalve shell. PQ, Path of shell secretion; PP', line of radial ornament, AB, secretory matrix; G, point of generation of new mantle cells; X, direction of extension of the mantle; Y, direction of shell secretion at the current commissure. See text for full explanation.

THE TANGENTIAL GROWTH COMPONENT

Modern authorities (Wilbur and Owen, 1964) have questioned the feasibility of Lison's model of shell growth. Lison's model is not only theoretically valid (in spite of certain reiterated statements to the contrary), but also allows predictions to be made which correspond strikingly with actual shell form and, most important of all, is amenable to meaningful biological interpretation. Measurements taken from a *Pecten* shell and compared with predicted measurements based on Lison's geometrical model agree to within less than 3 per cent and generally to within less than 1 per cent (Lison, 1949, p. 22).

In a shell such as *Pecten*, perhaps the simplest of shell forms to consider, it is obvious and well established that the median sector of the right valve approximates

to a logarithmic planispiral, and that sectors to either side of it are either dextral or sinistral turbinate logarithmic spirals. Lison noted that in most bivalves it is possible to recognize some axis about which the valve is growing in a plane *logarithmic spiral*. He designated as the *directive plane* that plane which passes through the common pole (usually the umbo) of the set of spirals defining the shell surface, and which contains a logarithmic planispiral. In a simple form such as *Pecten*, the axis of coiling of the set of shell spirals is coincident with the hinge line; the directive plane bisects the valve and makes an angle of 90° both with the axis of coiling and with the plane of the commissure.

The result of considering shell form in this fashion is that all points lying to one side or the other of the directive plane describe turbinate spirals. These turbinate spirals necessarily (in the Lison model) have spiral angles of greater magnitude than the angle of the definitive planispiral. The absolute value of any spiral angle is determined by the fact that its projection into the plane of the planispiral must have the same spiral angle as the planispiral.

The directive plane may theoretically make any angle between 0° and 90° with the plane of the commissure. In the latter case (e.g. *Pecten*) it is situated symmetrically in the centre of the shell; in the former (e.g. some gastropod opercula) it is coincident with the plane of the commissure.

In most bivalves, even those possessing a marked 'tangential component' (*Dosinia, Codakia*), the angle rarely drops below about 15°. Owen's statement (1953, p. 70) that 'in members of the Chamidae and Glossidae, the magnitude of this tangential component is such that *all* growth curves are turbinate spirals; i.e. *there is no "directive plane"* ' is misleading, for it implies that Lison was in ignorance of this fact. On the contrary, Lison himself was well aware that there were certain rare cases in the Bivalvia of shell forms without directive plane; in fact he specifically drew attention to them and even cited *Isocardia cor* as an example of this rare type of bivalve shell (Lison, 1949, p. 62). His treatment of such turbinate forms is included with his geometrical model of gastropod shell growth. For reasons of simplicity and brevity I have not summarized Lison's treatment of gastropods in this paper, but it should be noted that it is merely a simple and logical extension of his treatment of form in the Bivalvia.

However, Owen was correct in drawing attention to the fact that shell forms such as *Venus* possess (in Owen's terminology) a 'tangential growth component', and to emphasize that these bivalves are morphologically distinct from turbinate gastropod shells. As the term 'turbinate' is generally applied without distinction to any shell whose generating spiral is not confined to one plane, it seems to me useful to have a term to describe those bivalves that reach this condition by a different process of growth to that of the typical turbinate gastropod shell. I propose that these bivalves be termed *pseudo-turbinate*.

In order to explain the growth of pseudo-turbinate shells, we must recall that it was earlier demonstrated, after Lison, that vastly different shell shapes could be attained with the same basic 'building blocks', if these blocks were stacked about a directive normal point that varied its position on the matrix. Models of this sort

will serve to explain all types of bivalve except those that are pseudo-turbinate. However, it is obvious that we can generate further variants of shell form by keeping the directive normal point fixed and pivoting the matrix about it during stacking. The result is then a pseudo-turbinate shell. The more the matrix is pivoted during stacking, the greater the pseudo-turbinateness of shell model produced, i.e. the smaller the angle between the directive plan and the plane of the matrix.

The cause of this pivoting is, needless to say, not a tangential growth force affecting the shape of the shell. It arises from the growth of an opisthodetic ligament, and it should be noted that most, if not all, of those shells said to have a 'tangential growth component' possess an opisthodetic ligament. The ligament, like other external shell structures, grows spatially by accretion. In order to maintain overall shape its growth path approximates to a logarithmic spiral (of which a straight line is a limiting case). In a typical opisthodetic bivalve the growth of the external shell surface extends from the posterior end of the ligament to a point under the umbones at the anterior end of the ligament. The anterior end of the ligament may be taken as a fixed point; the posterior end of the ligament is then growing spatially away from this point. It inevitably follows that the sector of mantle edge that is secreting the external shell surface is slowly but consistently translated round the shell edge in an anterior direction, i.e. in terms of geometrical analysis, the generating curve pivots within its plane as the shell grows, and a 'tangential component' of growth has appeared. Other factors being equal, the tighter the logarithmic spiral of the ligament itself, the more 'tangentially affected' is the shape of the shell.

The interpretation just outlined was first suggested by Bernard (1895), and that it is basically correct is supported by the correlation of different types of opisthodetic ligament with different types of shell morphology. When the ligament is short it has very little effect on the turbinateness of the shell (Cardiidae, Trigoniidae); when it is long and straight, it again has very little effect (Mytilidae); but when the ligament is long and curved we find that its effect is at a maximum (Veneridae, Lucinidae, Cardiacea).

It is clear that the geometrical models of shell growth proposed by Lison may lead, in the light of more modern anatomical knowledge, to an understanding of the *actual* way in which a bivalve shell grows. However, a basic distinction must be made between the biological factors that control shell form, and the resultant geometrical characteristics of that shell form.

Given the basic facts of shell secretion and the limiting factors of molluscan physiology, shell form is a result of : (a) the shape of the shell generating curve, (b) the gradient of secretion of calcium carbonate across the shell generating curve, and (c) the rate of generation of new mantle cells around the shell generating curve. These three properties being known for any animal it is then possible to predict unambiguously the shape that its shell will have. The fact that the resultant shell shape closely approaches certain rigorous geometrical models is not an indication that shell growth is governed by the mathematical equations involved; one must strongly emphasize that it is merely an inevitable result of the mode of growth of the animal concerned.

The derivation of simple equations describing shell form, together with much interesting discussion on their use and development, may be found in Lison (1949). These equations are basic to any studies of molluscan shell form, and they have in no way received the attention from later workers that is their due.

THE PARADOX OF INTERUMBONAL GROWTH

Lison clearly understood the implications of his geometrical model even if he did not interpret it in quite the fashion outlined above. For it is a most interesting paradox that the ligamental area of a theoretical shell which grew according to the model represented in Fig. 3(b) would represent the locus of points of *no secretion* of shell material.

It should be stressed that Fig. 3 depicts two arbitrary limiting cases of theoretical shell form; in Fig. 3(a) the directive normal point coincides with the umbonal end of the matrix (B_n), and in Fig. 3(b) with the ventral end (A_n). (It would be geometrically possible for the directive normal point to fall outside the matrix; such a model is used by Lison to interpret some gastropod and cephalopod shell forms.) Accordingly, the first case can be interpreted (in terms of the biological model outlined above) as due to 'displacement' of successive growth increments entirely in a ventral direction, i.e. primary introduction of mantle cells takes place at the ventral end of the matrix. In the second case, since the directive normal point coincides with the ventral end of the matrix, all 'displacement' is in a dorsal direction, i.e. primary introduction of mantle cells is at the dorsal end of the matrix at the growing edge of the ligamental area (or interarea). No actual bivalve or brachiopod grows strictly according to the model illustrated in Fig. 3(b). The vast majority of such shell forms approximate to a model somewhere between the extremes of Fig. 3(a) and (b). Presumably the introduction of new epithelial cells then takes place at both the dorsal and ventral growing edges of the matrix model. Or, in a living bivalve, introduction of epithelial cells occurs, in a precisely determined pattern, at points all round the commissure.

THE PARADOX OF GNOMONIC ASYMMETRY

Lison pointed out (1949, p. 80) that in a shell such as *Solen* one has the impression that the rate of shell growth *sensu lato* is far greater at the posterior end of the shell than it is ventrally opposite the umbo. Using the above interpretation, this may readily be explained along the following lines.

The apparently faster rate of 'growth' at the posterior end of the shell may be considered as due entirely to the more prolific introduction of mantle cells and to their subsequent secretion. It is not due to a faster rate of secretion of shell material or to a larger 'growth force' governing deposition of shell material. Deposition of shell, *per se*, at the posterior end of the mantle (as elsewhere on the shell) proceeds at a constant rate for any particular point. In a shell with directive plane at right angles to the commissure, this rate depends on the distance of the point (in projection if necessary) from the point of minimum or no growth on the matrix, i.e. generally speaking, from the umbo (Fig. 5). Paradoxically then, a point such as Q (Fig. 5) has

a *lower* absolute shell secretion rate than a point such as R. The introduction of new epithelial cells, is of course, proceeding faster at Q than at R, and this results in the maintenance of the attenuated shape of the shell.
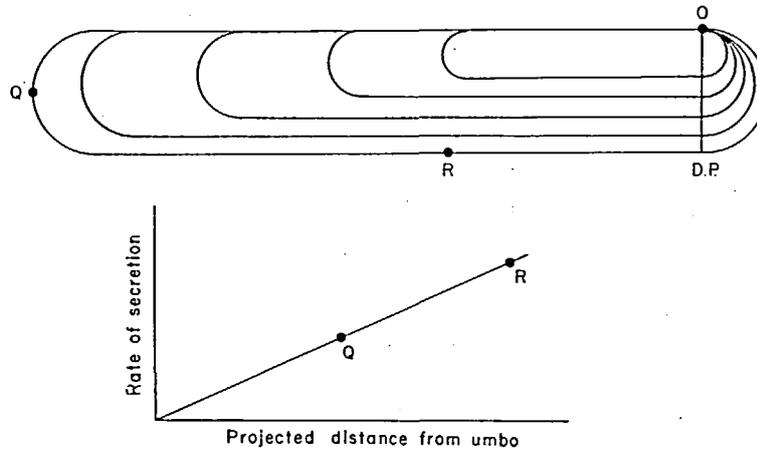
FIG. 5.   To illustrate relative rates of shell secretion in an asymmetrical shell with a vertical directive plane. DP, Directive plane; Q, point on posterior shell margin; R, point on ventral shell margin. See text for full explanation.

A similar line of argument may be followed for any markedly inequilateral shell forms. Any apparent differential growth in the plane of the commissure is due to the increase in size of the generating curve during life, and this may be interpreted as due to the differential proliferation of mantle cells at different points on the mantle edge.

IMPLICATIONS OF THE MODEL

The acceptance of this model of cell proliferation and shell secretion carries certain implications:

(1) During the life of the organism any given mantle cell changes from secreting periostracum to secreting outer shell layer (ectostracum), then middle shell layer (mesostracum) and ultimately inner shell layer (endostracum).

(2) Lines of radial ornament on the valve surface may be taken to mark the tracks of homologous points on the mantle edge. They should *not* be taken to mark the direction of actual shell secretion.

(3) The often drawn two-dimensional logarithmic planispiral may be considered as a 'map' of the constantly changing direction of shell secretion at the mantle edge. For, at any point P, the actual direction of shell secretion may be inferred by constructing the radius vector of the spiral at that point (Fig. 6). The Lison model then predicts that shell secretion at P is taking place at right angles to the radius vector, i.e. at right angles to the current commissure of the shell. My own observations lead me to conclude that this is so for a great many different groups of bivalves (Fig. 7).
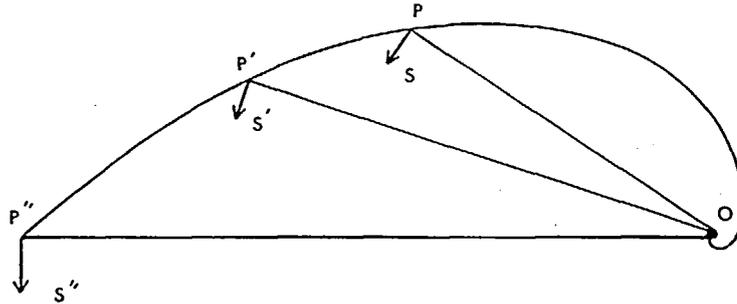
FIG. 6.   Reconstruction of directions of shell secretion in the directive plane of an idealized planispiral shell. O, Origin of spiral; P, P', P″, successive positions of a point on the mantle edge; OP, OP', OP″, radius vectors; S, S', S″, inferred directions of shell secretion.

In order for the model to predict accurately the shape of the external surface, it is only necessary that secretion be at right angles to the radius vector at the limiting edge of the shell. The topography of the inside of the valve edge, and the space in the interior of the shell, may be regarded as a result of rates and directions of secretion differing from those of the secretion taking place at the valve edge.
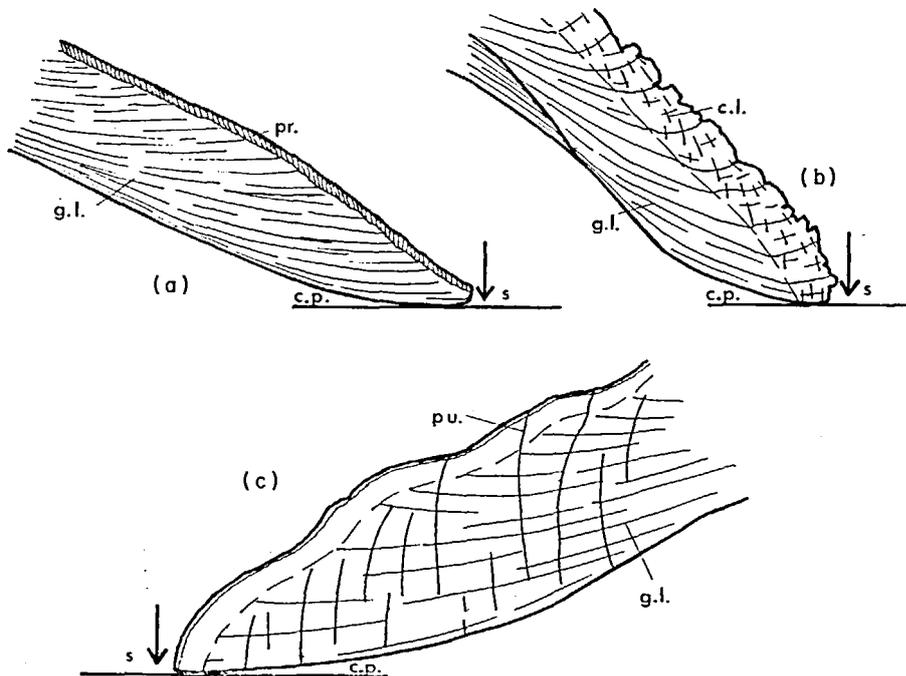
FIG. 7.   Camera lucida sketches of transverse sections of the growing edges of various bivalves. (a) *Unio pictorum* (L.), Recent, Cambridgeshire, ×7. (b) *Venus fasciata* (Da Costa), Recent, Cullercoats, ×6. (c) *Terebratula biplicata* Sow., Cretaceous, Red Chalk, Hunstanton, ×36. . c.p., Plane of commissure; s, direction of shell secretion at the commissure; g.l., growth lines; pr., prismatic shell structure; c.l., crossed lamellar shell structure; pu., punctae.

APPLICATION OF THE MODEL TO THE BRACHIOPODA

Although Lison developed his model of shell growth primarily to explain form in the Mollusca, it can easily be applied to any group of animals which grow by accretion, and whose external shell surface therefore has logarithmic spiral form. To apply the model biologically, the only additional prerequisite is that shell secretion at the mantle edge be perpendicular to the plane of the commissure. Even if this should not be so, it would be easy to adapt the geometrical model to a case where secretion is not precisely at 90° to the plane of the commissure, provided only that secretion was at a *constant* angle to the commissure throughout life.

The shell structure of brachiopods does not appear to be as simple as that of the Bivalvia, but to explain the external morphology of the shell it is only necessary to consider the detail of secretion at the actual mantle edge. It is generally accepted that the fibres of the external primary shell layer in brachiopods are normal to the shell surface (Williams and Rowell, 1965, p. H11). In thin sections of *Terebratulina* and *Terebratella (Waltonia)* lent to me by Dr R. Cowen, there are clear indications of growth lines in the primary shell layer which make an angle with the shell surface (Fig. 7). Assuming that fibrous shell structure reflects shell secretion directed along the long axis of the fibres, in the case described by Williams and Rowell (1965) one would expect growth lines to be parallel to the shell surface, not making an angle with it. Although it is difficult to see any fibrous structure in the primary shell layer of either of the genera I have examined, the growth lines are unambiguously marked and it is a reasonable assumption that shell secretion took place at right angles to the growth lines. This being the case, the growth lines may be taken to mark the position of former commissure planes and Fig. 7 shows the striking structural analogy that exists between the Bivalvia and certain Brachiopoda. It would seem likely, then, that the Lison model of shell form is applicable to at least some Brachiopoda.

In some recent work on Devonian brachiopods, Krans (1965, p. 101) concludes that direction of shell growth at the shell edge is everywhere radial. The obvious implication that shell secretion is also everywhere radial is, to my mind, erroneous. Krans's suggestion is conceptually merely a variant on the Thompson–Owen type of vector analysis. All such conceptions of shell growth seem to me to suffer from their failure to clearly distinguish the two concepts of shell secretion and mantle growth from the generalized concept of shell growth as a whole.

SUMMARY

Previous attempts to explain the growth and form of the bivalve shell are reviewed. Special attention is paid to the work of Lison, and it is concluded that, in spite of published opinions to the contrary, his work represents a major contribution to our understanding of bivalve shell form. Analyses of shell form in terms of vector components fail to distinguish between the fundamentally different processes of shell secretion *sensu stricto*, and epithelial cell generation. The Lison model enables these two processes to be clearly conceptually differentiated, and a meaningful biological interpretation of shell growth results. A short section dealing with the 'tangential
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growth component' introduces the definition of a pseudo-turbinate shell. It is postulated that the absolute rate of shell secretion at any point on the commissure of a bivalve shell is determined by the distance of that point, in projection if necessary, from the point of minimal secretion on the commissure. Implications of the acceptance of this model of bivalve growth are discussed, and it is suggested that the model is applicable to at least some Brachiopoda.

ACKNOWLEDGMENTS

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