The bio-geometry of mollusc shells

Sean H. Rice

Abstract.—The shells of gastropods and cephalopods grow by production of new material, by the mantle, at the lip of the shell. I derive a model of shell form that allows us to describe the morphology of a shell in terms of independently definable biological parameters. These are (1) the relative rates of shell production at different points around the aperture, (2) the total amount of shell produced per time interval, (3) the growth rate of the aperture, (4) aperture shape, and (5) the orientation of the animal within the shell. Describing shell form in these terms allows us to see what biological changes must occur in development in order to change one shell morphology into another and what constraints are associated with particular morphological transformations. The model shows that it is developmentally easy to derive a slightly coiled limpet shell from that of a high-spired ancestor, but difficult to take the next step to a fully conical limpet. Many, if not most, real gastropod shells are not conical but rather have a convex or concave profile. I show that these forms result from a decoupling of shell production rates from the growth rate of the animal within the shell. The model also shows how truly different forms, such as vermetid snails and heteromorph ammonites, escaped the confines of spiral growth—sometimes by rotating the body within the shell, and sometimes by taking up a growth strategy that does not constrain them to coil. This model is compatible with shell morphometric models that have been widely discussed in the literature but strives toward a different goal: understanding the relationships between the various biological processes involved in shell development.

Sean H. Rice. Department of Ecology and Evolutionary Biology and Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520. E-mail: sean.rice@yale.edu

Introduction

Gastropod molluscs are one of the most diverse groups of metazoans, with over 100,000 extant and fossil species described. Seemingly at odds with this diversity is the fact that the external morphology that they present to the world, their shells, appear elegantly simple in basic design. This simplicity has inspired researchers for over a century (Moseley 1838; Thompson 1968) to describe gastropod shells in geometric terms.

Interest in the developmental processes that construct these shells has more than an aesthetic basis. The considerable interest that has arisen in recent years concerning the relationship between developmental and evolutionary mechanisms has pointed out the need for model systems with which to study how selection acts on the processes by which organisms are built. Ideally, such a model system would involve a highly diverse group of organisms for which we can study both the selective pressures acting on phenotypes in particular environments and the developmental mechanisms by which those phenotypes are

built. I shall argue that gastropods provide just such a system.

In the last 30 years, a number of researchers have formulated mathematical models of gastropod shell form (Raup 1966; Okamoto 1988; Ackerly 1989a; Savazzi 1990; Stone 1995). While these models differ with respect to the kind of coordinate systems used (some using a fixed, external, coordinate system while others invoke a moving reference frame), all are based in some way on moving a "generating curve" through space so as to trace out the shape of a shell. In each case, the goal is to construct a set of equations that allow us to describe a variety of shell forms in terms of a small number of parameters.

My goal in this paper is *not* to devise another scheme for doing shell morphometrics, but rather to identify some of the important *biological* factors influencing shell form and to begin to investigate how these interact. Ultimately, we would like to be able to look at two different shells of related species and describe what biological processes must have changed in order to derive both of them from a common ancestor.

In order to do this, I will first describe a "morphometric" model of shell growth that is similar to those cited above (as it must be, since the geometry of helices and tubes is not at issue). Rather than use the parameters of this descriptive model as comparators of shell form (as other modelers have), I use the model to derive a set of terms, such as the pattern of shell production around the aperture, that have independent biological meaning and are closer to the actual developmental determinants of shell form. The relation between these new parameters, which can be interpreted in terms of physiological or developmental processes, and shell form constitutes a simple developmental model. The rest of the paper is concerned with applying these results to understand the developmental changes underlying the evolution of limpets, irregular shells, and heteromorph ammonites.

Describing Shell Growth

Shell material is laid down by a strip of cells running along the outer fold and outer epithelium of the mantle (Wilbur and Saleuddin 1983). What we are after is a model of shell growth that is based on the behavior of these cells during ontogeny. First, though, we must devise a description of shell form. In principal, any of a number of shell models could serve this purpose. I present a model below that is structured so as to facilitate the derivation of the developmental parameters that are the focus of the rest of the paper. This model follows the trajectory of a point on the aperture (similar to Checa 1991).

New shell must be added as the animal inside grows. In the simplest case (I will consider others later), the rate at which new shell material is produced is proportional to the growth rate of the aperture (which is itself related to the growth rate of the animal within the shell); if the animal is not growing, it need add no new shell. Letting A be the diameter of the aperture (I shall refer to this as "aperture size;" any linear measure will do as I will assume that aperture shape remains constant), we write the rate of shell production, $\sigma_{\mu,t}$, at a position μ on the aperture at time t as
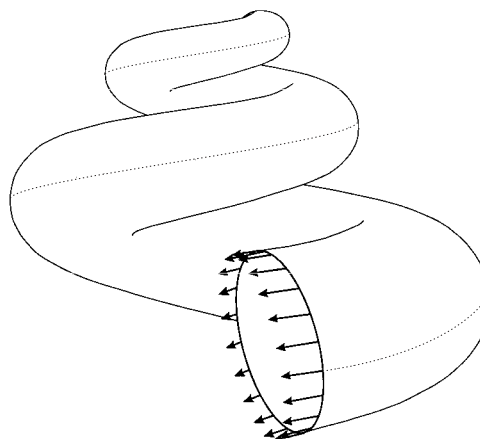

FIGURE 1.   A shell showing the trajectory of a point u on the aperture. The vectors illustrate the rates at which new shell material is being laid down at each point.

$$\sigma_{\mu,t} = \sigma^*_{\mu} \frac{dA}{dt} \qquad (1)$$

where σ_{μ}^* is characteristic of the point μ on the aperture and will allow us to compare relative rates of shell production at different points.

If the relative rates of shell production at different points around the aperture remain constant, and the absolute rate scales as the growth rate of the animal, then the trajectory (see Fig. 1) of a chosen point on the aperture is determined by the growth of the aperture and the rate of shell production there and at nearby points on the aperture. If a shell is growing isometrically, then each point on the aperture follows a "generalized helix." A useful result from differential geometry is that for a generalized helix there exists, somewhere in space, a vector that makes a constant angle with respect to the curve (Nutbourne and Martin 1988). On a gastropod shell, this vector points the same direction for all trajectories; it is the direction of the coiling axis. Invoking a coiling axis is a convenience that is not necessary, since we could parameterize our equations in other ways (Okamoto 1988; Ackerly 1989a), I use it because it facilitates calculating the pattern of shell production and will provide a useful way to derive the developmental parameters discussed below from measurements on an actual shell. All that this derivation requires is that during a short time inter-

val, dt, the path of a point on the shell follows a generalized helix. Later, I will consider kinds of growth that do not produce a constant coiling axis but are nonetheless amenable to the analysis presented below.

Let W be the distance of a point on the aperture from the coiling axis (measured in the same units as aperture diameter). Note that this is different from Raup's "W", which is the rate at which this distance increases for the center of the generating curve. Because each trajectory makes a constant angle with respect to the coiling axis,

$$\frac{dW}{dt} \propto \sigma \tag{2}$$

(since W and σ are measured for the same point on the aperture, I drop the subscript). Define ϕ as the angular position around the coiling axis, relative to the starting point. The change in ϕ over the time interval dt satisfies $\text{Tan}(d\phi) \propto (\sigma\, dt)/W$. However, since $d\phi$ is arbitrarily small, $\text{Tan}(d\phi) = d\phi$, so,

$$\frac{d\phi}{dt} \propto \frac{\sigma}{W}. \tag{3}$$

Since σ is proportional to dA/dt (eq. 1), $dW/dt \propto dA/dt$; so $W \propto A$. Substituting this and equation 1 into equation 3, and letting γ be a constant, we get

$$\frac{d\phi}{dt} = \gamma \frac{1}{A} \frac{dA}{dt}. \tag{4}$$

The constant γ is the same for every trajectory on the shell and measures the degree to which the shell is coiling. Strictly, if we project the trajectory of a point on the aperture into a plane that is normal to the coiling axis (what we would see if we were looking straight down on the shell), γ is the curvature of the projected trajectory divided by the rate at which it is elongating. A more intuitive definition of γ appears when we integrate equation 4 to get

$$\phi_t = \gamma \ln\left(\frac{A_t}{A_0}\right) \tag{5}$$

where A_0 is the initial aperture size, set whenever we start following growth. Here we see that γ measures the change in position around

the coiling axis as the aperture grows by a factor of $e = 2.718$, and the shell completes one full coil in the time that it takes for the aperture to grow by a factor of $e^{2\pi/\gamma}$. Equation 5 also confirms that the curve is a logarithmic spiral, since W, the distance from the coiling axis, is proportional to aperture size (A) while ϕ, the angle around the axis, is proportional to $\ln(A)$.

Given this, we can draw a shell in a space defined by the coiling axis. We can write the trajectory of a point on a shell, as a function of aperture size (A), in a space with axes (i, j, C) where C is the coiling axis, as

$$i_{\mu,A} = \frac{\sigma^*_{\mu} A}{1 - \gamma} \{\cos[\gamma \ln(A/A_0)]$$
$$+ \gamma \sin[\gamma \ln(A/A_0)]\} G_1$$
$$j_{\mu,A} = \frac{\sigma^*_{\mu} A}{1 - \gamma} \{\sin[\gamma \ln(A/A_0)]$$
$$+ \gamma \cos[\gamma \ln(A/A_0)]\} G_1$$
$$C_{\mu,A} = \sigma^*_{\mu} A G_2 \tag{6}$$

(see Appendix 1). G_1 and G_2 are, respectively, the sine and cosine of the angle between the trajectory and the coiling axis (or any vector normal to the coiling axis). This allows us to construct a visual way to study the different factors that influence shell form.

From the above equations, we can calculate the distance, $W_{\mu,t}$, of a point on a growing aperture from the coiling axis as $W_{\mu,t} = (i_{\mu,t}^2 + j_{\mu,t}^2)^{1/2}$ or

$$W_{\mu,t} = \frac{\sigma^*_{\mu} A_t G_1}{\sqrt{1 + \gamma^2}}. \tag{7}$$

We can now define a system of cylindrical coordinates based on the position along the coiling axis, C, and distance from that axis, W. More importantly, we can calculate the rate of shell production, σ, at any point in this space from equations 1 and 6:

$$\sigma^2 = r^2(1 + \gamma^2)W^2 + r^2 C^2 \quad \text{where} \quad r = \frac{1}{A} \frac{dA}{dt} \tag{8}$$

One way to visualize this is to draw contours of equal shell production in a space defined by W and C. From equation 8, these con-
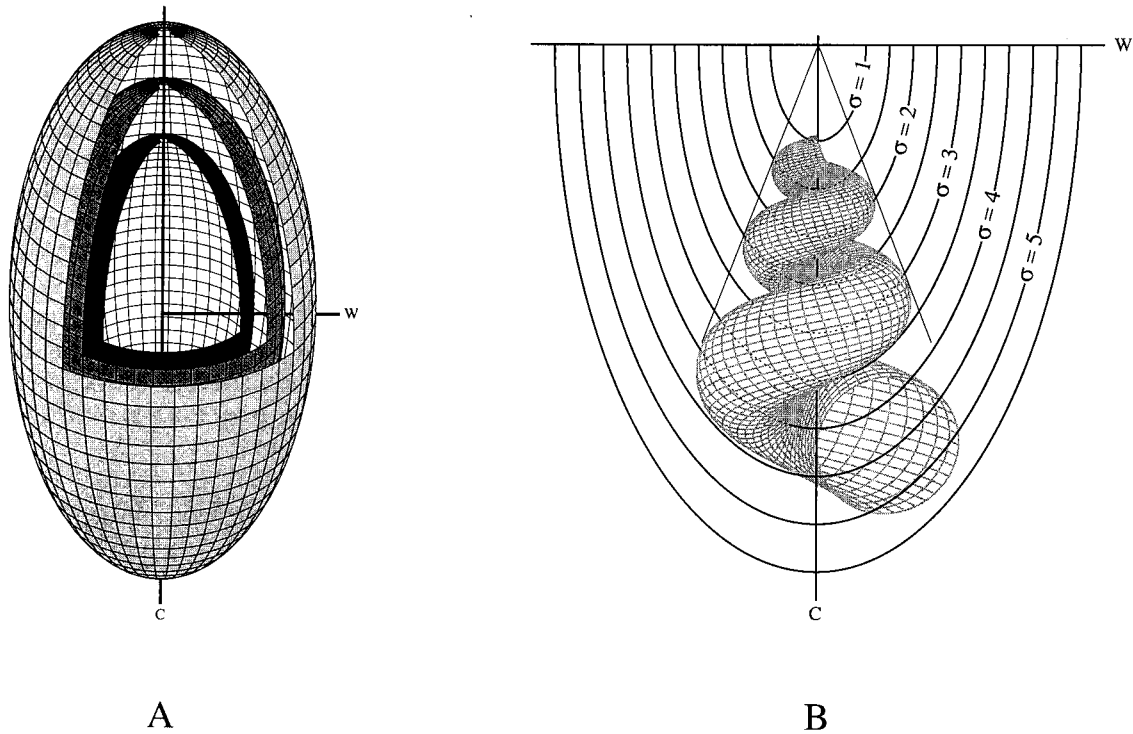
<center>A   B</center>

FIGURE 2. Contours of equal rates of shell production in a space defined by the coiling axis, C, and distance from that axis, W. A, Full three-dimensional surfaces, each of which represents the set of points with a particular value of σ (see equation 8 in the text). These surfaces are symmetrical around the C-axis. B, A slice of the same space illustrating how the origin is defined relative to a shell and how the rates of shell production can be read off at each point on the aperture. In this example, γ = 2.

tours are ellipses (Fig. 2) (similar to those in Hutchinson 1990). Figure 2A shows elliptical surfaces corresponding to three different values of σ (derived by setting a value for σ in equation 8 and solving for all values of W and C that correspond to it). Since these surfaces are symmetrical under rotation around the C axis, a two-dimensional representation (Fig. 2B) captures the geometry and shows how we could place a shell in this space and read off the rates of shell production at each point on the aperture by noting which σ contour that point lies on. In Appendix 2, I use this construction to show how to calculate shell production rates for an actual specimen. The larger the value of γ, the more tightly coiled the shell and the more elliptical the contour surfaces. If γ = 0, as for a conical limpet, then the contours corresponding to those in Figure 2A are spheres and there is no distinct coiling axis.

Alternatively, specifying the shape of an ap-

erture and the rates of shell production at each point around it is sufficient to reconstruct the contours in Figure 2. We can thus define a new set of terms that, together, specify shell form. These are (1) the pattern of shell production (the relative rates at different points around the aperture) (2) the total amount of shell produced per time interval, (3) the growth rate of the aperture (r in equation 8), (4) aperture shape, and (5) the orientation of the animal within the shell (this last parameter is only significant if it changes during growth; this will be important when we consider irregular shells). These specify shell form as well as do the parameters in equation 6. The relation between these new parameters and shell form constitutes a simple developmental model— allowing us to describe shell form in terms of the biological factors that contribute to shell growth, rather than purely abstract parameters such as γ or the parameters in the equa-
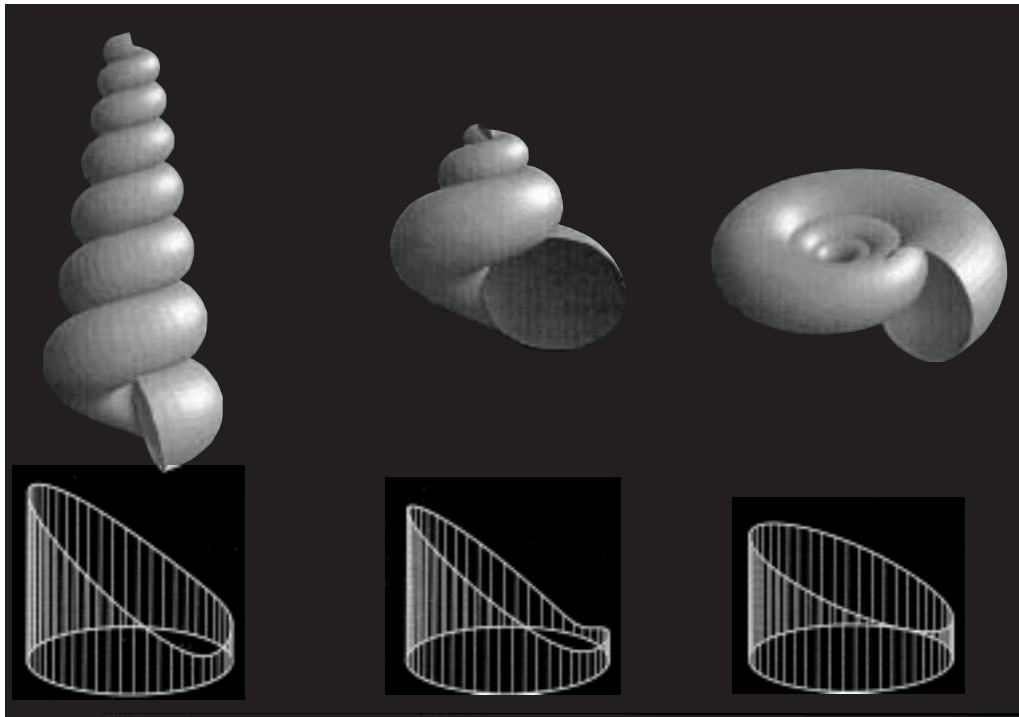
FIGURE 3. Three shells along with their corresponding aperture maps. The vertical lines on the aperture maps are analogous to the vectors around the aperture in Figure 1 and represent the rates of shell production at different points around the aperture. The largest values, on the left in each aperture map figure, correspond to the outer lip of the growing shell where the rate of deposition is highest.

tions of Raup (1966), Okamoto (1988), Ackerly (1989a), Illert (1990), or Stone (1995).

Another way to think of this is to note that the shell production parameters listed in the previous paragraph have independent physiological interpretations, whereas most of the parameters in equation 6 or the other models cited have no meaning other than as descriptors of shell shape. We can thus start to relate changes in shell form to physiological changes such as a reduction in the total amount of energy devoted to shell construction (which would change parameter 2 above and will be important in the discussion of the evolution of limpets, below) or the different metabolic demands on different cells around the mantle.

Developmental Parameters

We can now begin to investigate the interaction between various biological processes during shell construction. Here are the principal factors that I will consider.

The Aperture Map.—The aperture map for a particular shell represents the relative rates of new shell production for each point around the aperture. The idea was first discussed by Huxley (1932). Figure 3 shows some shells and their corresponding aperture maps (for each map, the high point on the left corresponds to the part of the aperture farthest from the coiling axis; compare with Figure 1). From these, we can see what changes in production rates would have to take place in order to derive any of these shell forms from any other.

The aperture map is most significant as a determinant of shell form for shells in which the inner edge of the aperture is on or close to the axis of coiling. If this is not the case, then very different shells may have very similar aperture maps (Hutchinson 1990). I will discuss this further below when considering irregular shell forms.

For closed-coiled shells, where successive whorls are in contact with one another, the aperture map clearly must change drastically at the point of contact with the existing shell. Some snails truncate shell production at this point, only secreting a nacre layer along the

surface of the previous whorl. Others continue to produce a thick shell fused to the old whorl. In the figures, I have ignored this truncation to facilitate comparison of the shapes of different maps. Appendix 2 shows how to calculate the aperture map from measurements on a shell.

Total Shell Production.—Since the aperture map only describes the relative rates of shell production, we need to consider also the total amount of new material produced. This changes as the animal grows. I will argue below that this is probably more evolutionarily flexible than the map itself. This parameter can sometimes change when the aperture map does not, producing a predictable morphological change.

Growth Rate.—So long as shell production scales with the growth rate of the aperture (assumed in equation 1), and the aperture scales with the rest of the animal inside the shell, the actual pattern of growth of the animal has no effect on shape. If shell production scales differently, though, then different growth trajectories yield different shapes. I show below that this is important in the production of shells that do not form perfect conical spirals.

Aperture Shape.—This is, in principle, an infinite-dimensional character and in fact varies widely among gastropods. The model presented here could be used to investigate the relationship between any change in aperture shape and the other developmental parameters discussed. It does not, however, address the biology determining aperture shape (see Morita [1991] for a mechanical discussion of aperture shape and Checa [1991] for a model that allows differential growth of different parts of the aperture).

Orientation of the Animal within the Shell.—Rotation of the body within the shell reorients the coiling axis. This is roughly fixed throughout the growth of most gastropods, but will emerge as an important factor in allowing the growth of some distinctly non-snail-like forms.

The parameters listed above are clearly not the only biological determinants of shell form. For one thing, the model discussed here does not address the formation of sculpture on shells, a distinct developmental process that

clearly has great ecological and evolutionary significance (Vermeij 1987). Nevertheless, a model based on these factors provides a starting point for a careful study of how variation in some underlying developmental processes translates into morphological variation. It also illustrates just how elaborate such processes are. Even for a structure as "simple" as a coiled shell, the basic parameters listed above interact in distinctly non-additive ways.

The model describes the relationship between these parameters. By itself, it tells us nothing about how much variation exists in natural populations. We can, however, make some educated guesses. The following is an example of one such guess; it is based purely on theoretical results and thus ultimately will require an empirical verification.

The growth rate of an animal can be thought of as a single, global parameter that is known, from breeding experiments, to harbor much quantitative variation, in everything from fruit flies to farm animals. This means that natural populations harbor many genetic variants that influence the overall growth rate of the organism rather than only the growth of some particular part, and is one reason that we sometimes see allometric relationships between closely related species that are similar to those found within each species. Similarly, the total amount of new shell produced (as opposed to the relative production rates at different points) can probably likewise be treated as a single variable that may be influenced by a number of genes that contribute to overall metabolic rate.

By contrast, changing the *pattern* of shell production (the "shape" of the aperture map) would require many different, yet coordinated, changes in a number of different parts of the mantle. Another way to look at this is to say that the aperture map is a many-dimensional character in the sense of Rice (1990). (Mathematically, six pieces of information are necessary to specify the map.) As Rice (1990) argues, such high-dimensional characters should evolve more slowly than low-dimensional ones.

We thus might reasonably guess that changes in form that require alterations in the shape of the aperture map will be more dif-
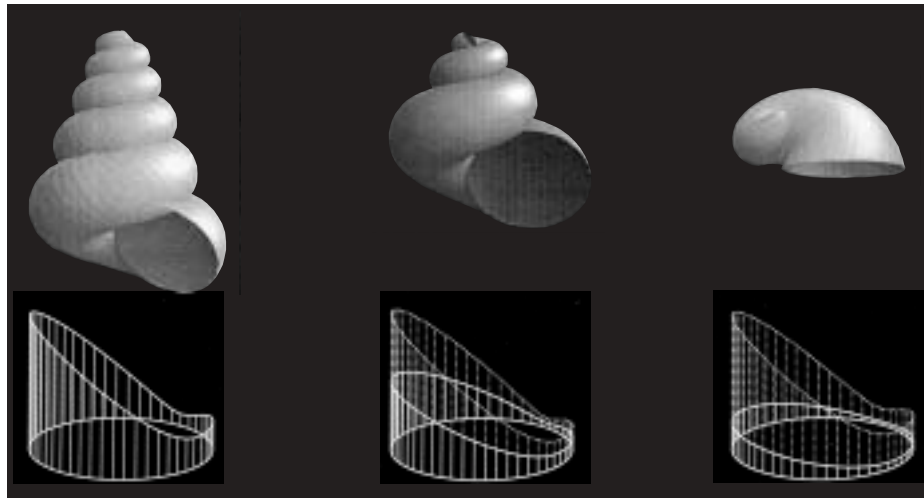
FIGURE 4. Deriving a coiled limpet from a high-spired shell. The shells in the middle and on the right produce new material at one-half and one-fifth the rate of the one on the left. The dotted lines show what these aperture maps would look like when scaled up, to facilitate comparison of the *relative* rates of shell production.

ficult to achieve in evolution than those that simply require a change in one of the global rate parameters. This latter change would be an example of heterochrony, while changing the map requires a fundamental restructuring of a developmental process.

Regular Shells

So long as the aperture map and shape remain constant, and shell production is proportional to growth rate, then the shell forms a perfect conical spiral. Given a particular form, we can now ask what other forms might easily be derived from it. I will illustrate this with a case for which we can say something about the selective forces involved.

One trend that appears repeatedly in gastropod phylogeny is the evolution of a limpet body form from a high-spired ancestor (Abbot 1986). I define a "limpet" here as a gastropod with a cap-like shell that is uncoiled or only slightly coiled and that pulls the shell over it while attached to a surface rather than retreating behind an operculum, I thus include such organisms as *Crepidula* among "limpets." Two properties of limpets make them particularly successful in ephemeral and disturbed environments. Because relatively little shell material needs to be produced (relative to soft body mass), limpets can grow very quickly compared to highly coiled snails.

A second consequence of reducing the amount of shell produced is that the surface area of the foot becomes larger relative to the surface area of the shell. This is a particular advantage in intertidal environments where strong currents and wave action put a premium on tenacity (Branch 1985).

Figure 4 shows a sequence of shells leading from a high-spired shell to a coiled limpet-like form. Below each shell is its corresponding aperture map. Note that while the absolute amount of shell material produced per time is lower for the limpet-like form, the pattern of shell production is identical for all three shells. A basic limpet body form, with a large foot relative to shell surface area, can thus be attained simply by globally reducing the amount of shell material produced, other factors held equal.

Most familiar limpets, however, do not look like the one in Figure 4, having a conical shape instead. Figure 5 shows the comparison between a coiled limpet and a truly conical one. Note that this transition requires a substantial change in the aperture map. We can thus see that while the shells of the coiled limpet and the conical one are perhaps functionally similar, they are developmentally quite different. We can also see that, in terms of the developmental changes that must occur, it is much easier to derive a slightly coiled limpet from a
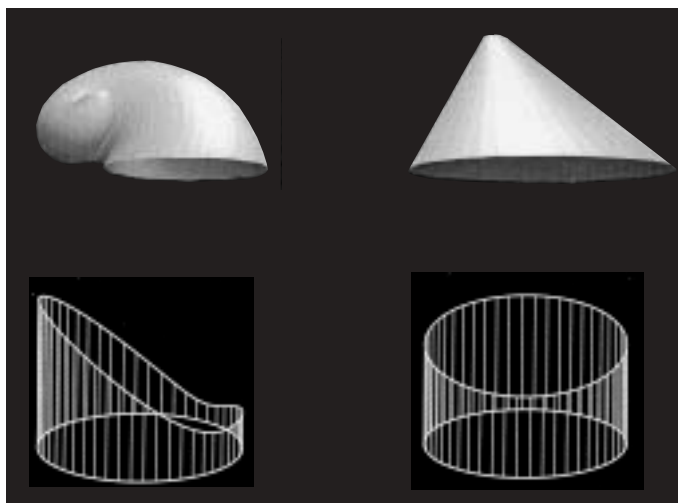
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FIGURE 5. Comparison of a coiled limpet and a purely conical one. Note that these two forms, which might be functionally similar, are developmentally quite different.

high-spired (snail-like) ancestor than it is to go all the way to a completely conical limpet.

In order to see why this is so, consider the shell growth space discussed above (Figure 2A), in which the contours of equal shell production are ellipses. The plane that contains the aperture slices this space, and it is from this slice that we read off the aperture map (Figure 6). Recall that the eccentricity of the ellipses in the shell growth space is determined by how much the shell coils, and reducing the degree of coiling causes the contours to expand horizontally. Figure 6 shows how the relative rates of shell production can be kept constant as we reduce the degree of coiling, so long as the total amount of shell produced also declines (think of each figure as a slice of a space like that in Figure 2A; A through C are slices that include the coiling axis, D is the slice defined by the plane of the aperture). As we move from Figure 6A to 6B to 6C, the value of γ is reduced (corresponding to reduced coiling), causing the contours to become less elliptical. The contours do this by expanding horizontally. Thus, the actual rate of shell production at any point not on the coiling axis goes down. We are most interested in the shape of the contours, so I have drawn in those contours that have the same horizontal scale with respect to the aperture size. Thus, the outer contour in 6B actually

corresponds to a value of σ similar to the second contour from the middle in 6A.

Figure 6D shows the shape of the contours in the plane of the aperture for each case. These are the same, even though the actual values of σ on each contour are smaller as we go from A to B to C. Thus the aperture map (the relative rates of shell production) stays the same through this uncoiling process, even though the total amount of shell produced decreases. This strategy only works to a point, though, after which further uncoiling requires a change in the shape of the aperture map (Fig. 7).

We might interpret the last result to imply that when selection favors a limpet-like body form, we should most often see the appearance of coiled limpets rather than conical ones. A preliminary study of gastropod phylogeny (Rice and D. Lindberg unpublished) shows that this is in fact the case: partly coiled limpets have arisen at least 14 different times, while conical forms appear to have arisen 4 times. The current preponderance of conical limpets reflects not the number of times that this form has appeared, but rather the great success of a few groups (particularly the Patellogastropods) after they had acquired this form. The success of these few groups suggests that the conical limpet form is no less functional than the slightly coiled form, which has not led to as much in-
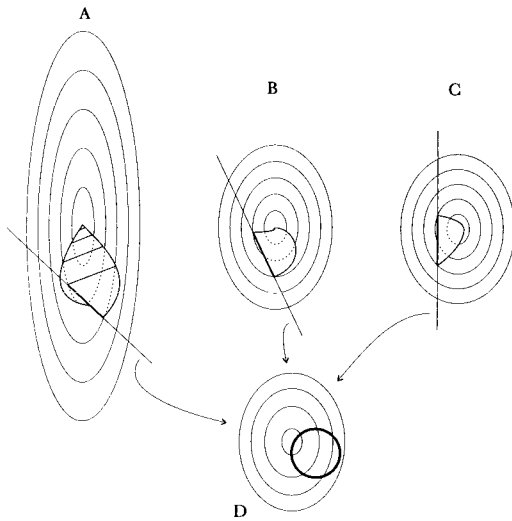
FIGURE 6. Shell production diagrams showing how the shape of the aperture map can remain constant as the shell uncoils, so long as the overall amount of shell material produced goes down (compare with Figure 4). A, B, and C show slices along the C-axis of spaces like that in Figure 2A. D shows the slice in the plane that contains the aperture. By changing the tilt of the aperture relative to the shell, the shape of the contours in the plane of the aperture, and thus the aperture map, can be kept constant even though the total amount of shell being produced is reduced. This only works to a point, though, beyond which further uncoiling requires a change in the aperture map.

crease in species numbers even though it has arisen more frequently.

This last point highlights the different roles played by developmental and environmental (selection) processes in evolution. In this case, development influences the probability that a particular phenotype will arise; selection influences its fate once it has arisen.

Nearly Regular Shells

So far, I have assumed that total rate at which new shell material is laid down is proportional to the growth rate of the animal within the shell. This condition, combined with a constant aperture map, produces a perfectly conico-spiral shell, regardless of the actual growth of the animal. We can easily imagine other rules for shell production, though, that might lead to different kinds of shapes. Modeling this requires that we represent both shell production and aperture growth as separate functions of time (Appendix 1).

This is important, since many (if not most)

shells deviate from the conico-spiral ideal (Vermeij 1993). For example, consider the case in which the total rate of shell production is proportional to the *size* of the aperture, rather than the rate at which it is growing (Appendix 1). In this case, the shape of the resulting shell is a function of the growth curve of the aperture.

Figure 8 illustrates the results of varying the growth function followed by the aperture while making the rate of shell production proportional to aperture size, rather than growth rate. When the aperture grows exponentially, we still get a perfect cone, since here the size of the aperture is proportional to its growth rate. Other growth functions, however, produce different shell forms.

Linear growth of the aperture results in a shell that slopes down, with an outline that is more parabolic than conical. This pattern of convex sloping sides to the shell is very common. If the aperture stops growing altogether, but the animal continues to produce new material, the shell forms a helix that maintains constant distance from the coiling axis. Thus, a logistic type growth function, with initial exponential growth followed by a relatively constant aperture size, produces the beehive-shaped shell of *Cerion*.

Given this, it is not at all surprising that most of the shells that one looks at are not perfect conical spirals. Though linking shell production to growth rate seems logical at first glance, many factors could alter the balance. Most snails house their gonads in the upper whorls, calling for more space there when the animal becomes reproductive. Also, the apex of the shell may be damaged by predators or wave action, necessitating a shift forward even if the body is not increasing in size.

Though these nearly regular shells deviate somewhat from the conico-spiral ideal (an ideal for shell modelers, not gastropods), they are all readily identifiable as snails. There are some shell forms, though, that seem truly to break the rules, and one test of the theory presented here must be its ability to shed light on how some forms escape the confines of traditional shapes and develop radically different shells.
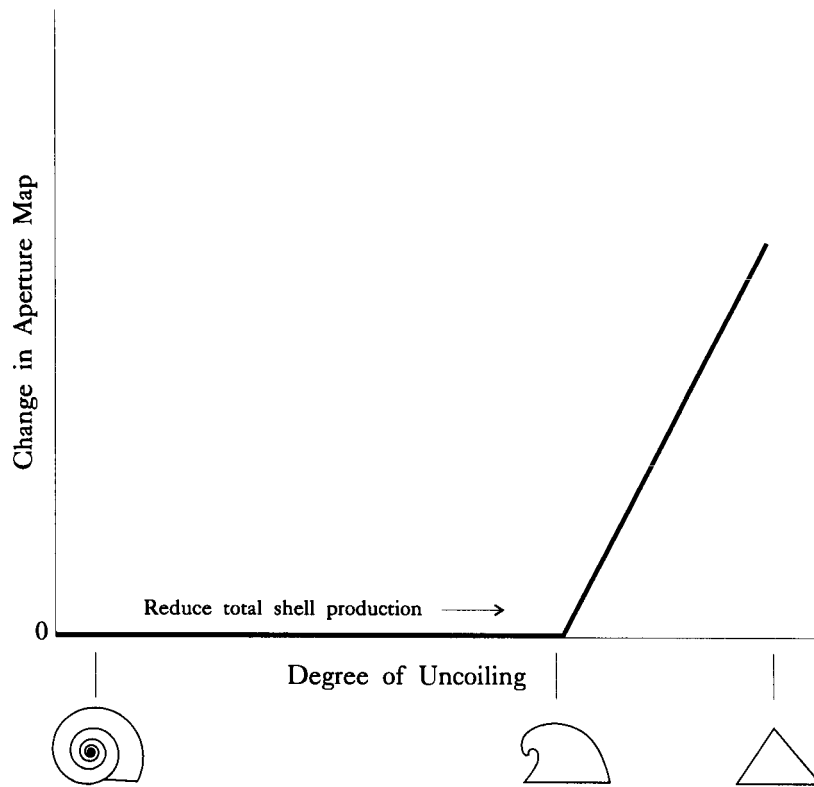
FIGURE 7. Schematic diagram showing how the aperture map must change in the evolution of a limpet from a high-spired ancestor. A substantial amount of uncoiling can be achieved with no change in the map, simply by reducing the absolute rates of shell production but keeping the relative rates nearly constant. How far this process can go is determined by the initial angle of inclination of the aperture. When the plane of the aperture is parallel to the coiling axis, no further uncoiling is possible without a change in the aperture map.

Heteromorph and Freeform Shells

A number of ammonites exhibited complex growth forms that often changed direction at specific stages. Lumped together as "heteromorphs," these animals clearly had found ways to break the rules followed by most shelled molluscs.

Figure 9 shows two views of a specimen of *Didymoceras*, a heteromorph that began life as a conico-spiral and then abruptly switched to a different growth pattern. At first glance, this would appear to require a radical change in the pattern of shell deposition. In fact, neither the aperture map nor growth rate need change at all during the growth of this animal; all that is needed is for the animal to rotate its body within the shell.

Figure 10 illustrates the consequences of such a rotation. At the start of the fourth coil, the aperture map begins to rotate clockwise (relative to an observer inside the shell looking out). This has the effect of shifting the axis of coiling and causes the shell to grow downward. After rotating through an angle of 1.2 radians, the aperture map begins to rotate back (counterclockwise). This is what would happen if each point around the mantle lip continued producing new shell material at the same relative rate that it always did, but the entire mantle rotated—as though the animal twisted itself first one way, then the other. The black line represents the strip of shell laid down by a particular point on the mantle.

Some confirmation that this story describes what *Didymoceras* actually did is provided by sculpture on the shell. The specimen in Figure 9 has two rows of knobs (shaded in the figure) running along the outer part of each whorl. As the shell begins its aberrant growth, these knobs follow the same kind of trajectory
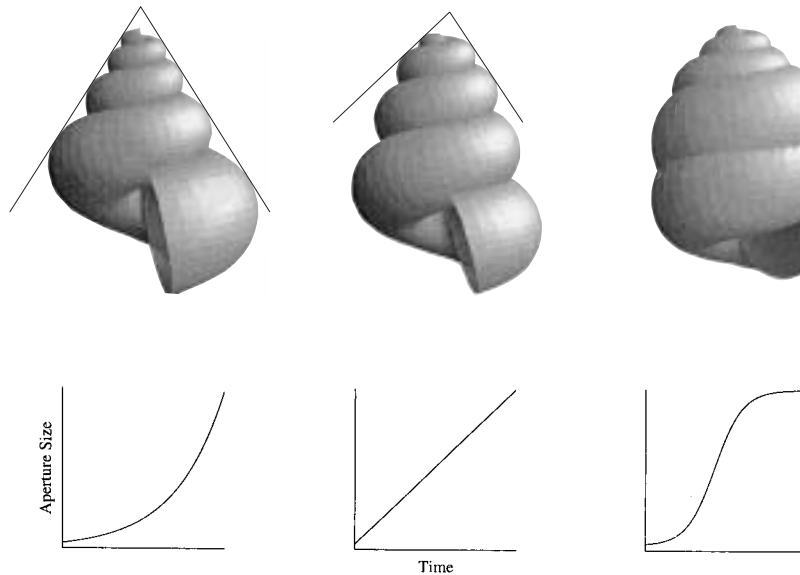
FIGURE 8.   Shells resulting from different growth functions when the rate of new shell production is proportional to aperture size (rather than growth rate). When the aperture (and, by inference, the animal inside) grows exponentially, a perfectly conico-spiral shell results. Linear growth (or any function for which the ratio of growth rate to body size decreases as size increases) produces a shell with convex sides. A sigmoid growth function builds a shell that at first expands, then coils straight down the axis.

shown by the black line in Figure 10—rotating first to the outside of the loop and then ending up on the bottom. This is exactly the path that would be taken by the mantle tissue underlying the knobs in the upper whorls if the animal rotated as hypothesized. Of course, we don't know that the knobs were produced by

the same part of the mantle throughout growth, but this seems likely and would make sense of both the distinctive form of the shell and the path taken by sculpture on it.

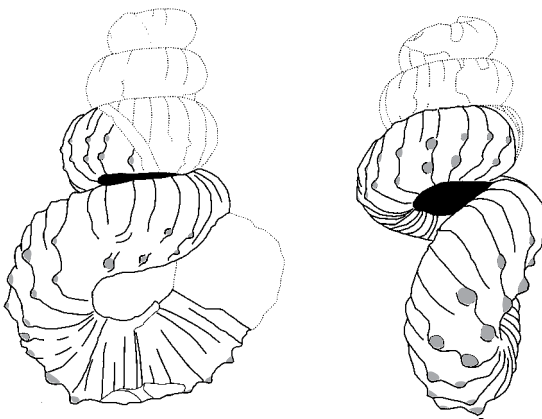A similar process may have been used by

FIGURE 9.   A composite specimen of *Didymoceras* (Yale Peabody Museum specimens 6092 and 35001) showing the final coil and sculpture on the shell. The solid lines (specimen 6092) show the last regular whorl and the region in which the animal appears to have rotated within its shell. Note the path followed by sculptural knobs (shaded).
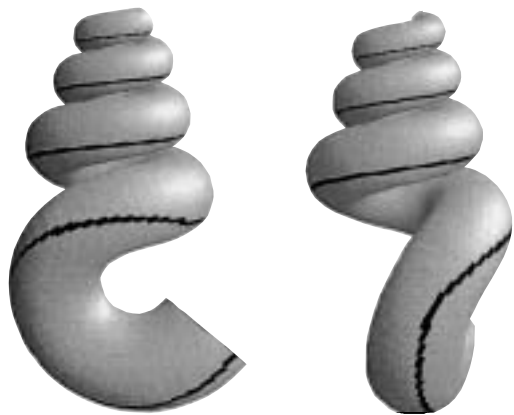

FIGURE 10.   Approximation to *Didymoceras* generated with a constant aperture map and growth rate. Rotating the entire aperture map (corresponding to the animal rotating within the shell) changes the axis of coiling. This is what would result if, at the beginning of the fourth whorl, the animal began rotating through an angle of 1.2 radians, finished this rotation at the middle of the fourth whorl, then began rotating back. The black line tracks the strip of shell laid down by a particular segment of the mantle.
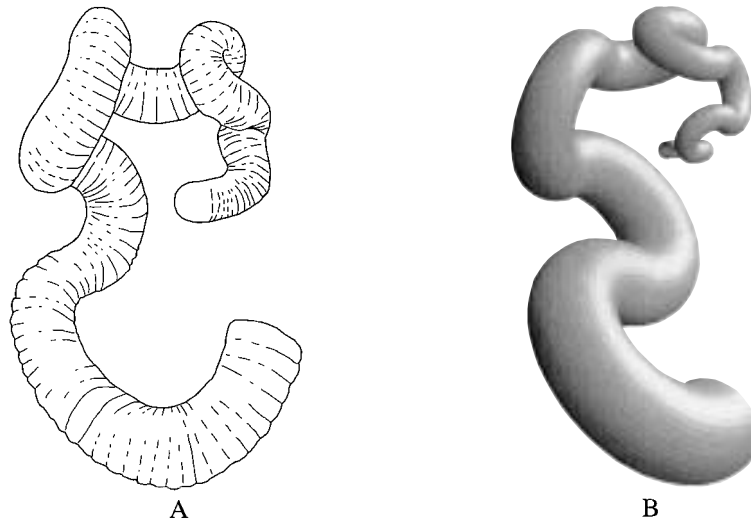
FIGURE 11. A, The heteromorph ammonite *Nipponites* (after Klinger 1981). B, Approximation to *Nipponites*, generated with a constant aperture map and growth rate, in which the animal rotates within the shell by 2 radians every 0.6 whorl. The last rotation is through an angle of 2.9 radians.

another heteromorph, *Nipponites* (Figure 11). This shell has no fixed axis of coiling and never approximates a helical spiral. Figure 11 shows a reconstruction of *Nipponites* and of a theoretical shell produced by repeatedly rotating the aperture map. Note that this is similar to what *Didymoceras* would look like if it began its back-and-forth rotations at the first whorl, instead of waiting until the last.

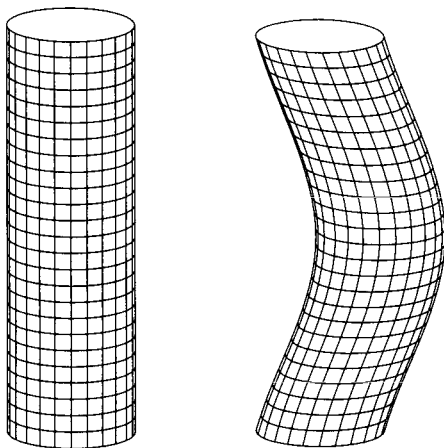This trick of rotating the entire animal with-

FIGURE 12. Two tubes with the same flat "aperture map" but different shapes. These can shear to one side or the other because the aperture is not growing and the rate of "shell" production is the same all around the aperture.

in the shell may explain how some Vermetids shift the coiling axis after they settle (Ackerly 1989b). Thus, the tricks used by *Didymoceras* and *Nipponites* are not so radical as one would guess. In addition to making sense of an otherwise confusing form, this result hints that the rarity of the *Nipponites* type shape is not a consequence of developmental constraint; it was an easy shape for loosely coiled ammonites to attain. Not all Heteromorphs are so easily explained; some clearly changed all growth parameters at certain stages in ontogeny. It is interesting, though, that some of the most bizarre looking forms are among the easiest to generate.

There is another way that a shell can attain irregular form without any change in the aperture map. To see how, we must add one detail to the model as presented so far.

The aperture map and growth rate determine shell form *almost* everywhere. The one exception is when the aperture is not expanding at all and shell material is being produced in a symmetrical pattern around the aperture. At this point in growth parameter space, the shell can "shear" in directions along which the aperture map is flat, as shown in Figure 12. More importantly, as we approach this point, the aperture map becomes less and less
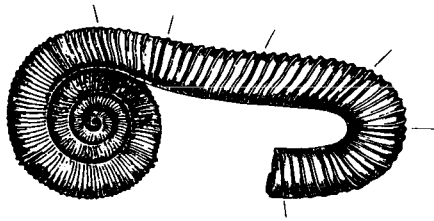
FIGURE 13. *Macroscaphites* redrawn and modified from Thompson (1968). Note the progression (expressed as change in the angle of the sculptural ribs) of the upper lip during the straight phase of growth. The straight lines indicate the plane of the aperture, as inferred from sculpture.

of a constraint on shell form, as a wide range of shapes can be produced with extremely small changes in the pattern of shell production. (This is not a problem for limpets, since their aperture growth rate is so high as to stabilize shell form even with a "flat" aperture map.)

This shearing effect may be at work in the growth of vermetid "worm snails." Though these exhibit a variety of growth patterns (Gould 1994; Savazzi 1996), many begin life tightly coiled, then undergo a period of "uncoiling" followed by freeform growth, in which form is determined largely by the surface on which the animal is growing. In some species, such as *Vermicularia pelucida*, this happens gradually after settling, resulting in the first couple of whorls being loosely coiled but still following a smoothly spiral trajectory. This breaks into freeform growth when the shell becomes sufficiently loosely coiled corresponding to a sufficiently flat aperture map. (Note that the previous arguments for the evolutionary conservatism of the aperture map do not apply to changes during development.)

The shearing process discussed above can be seen clearly in the heteromorph *Macroscaphites* (Figure 13). This animal follows a planispiral ammonite pattern for a few whorls, then suddenly grows out straight for a time, after which it goes through another tight coil. *Macroscaphites* is sculptured with regularly spaced ridges that allow us to estimate shell production rates (assuming that the spacing of ridges corresponds to growth rates). We can thus study a growth process that took place during the Cretaceous and has no modern analogue.

Though the aperture map must change somewhat during the growth of *Macroscaphites*, this change is minimized by the shearing process described above. Along the straight section of the shell, the upper (in the picture) part of the shell is still growing at a higher rate than the lower part, just as the outer lip of the whorl was growing faster than the inner lip when the shell was coiling. Eventually, the upper lip of the aperture has grown so far out ahead of the lower lip that the animal allows another, tight, coil to take up the difference. Note that, as it comes out of that last coil, the inner and outer lips have again come into line.

Discussion and Conclusions

The goal of this paper is to describe shell form in terms of parameters that have independent developmental or physiological meanings. Though I began with a mathematical description similar to traditional shell models (Raup 1966; Okamoto 1988; Ackerly 1989a; Illert 1990; Savazzi 1990; Stone 1995), I do not use this as an end in itself, but rather derive from it a set of descriptors that relate shell form to *other* aspects of physiology and development. These are the following: the shape and growth rate of the aperture, the total rate at which new shell material is produced, the relative rates of shell production at different points around the aperture (the aperture map), and the orientation of the animal within the shell. (A similar approach, starting with a description of shape and deriving other biological parameters from this, has been used by Løvtrup and Løvtrup (1988), who studied one aspect of the aperture map, and Checa (1991), whose model is useful if the aperture changes shape during growth.)

To illustrate the consequences of this approach to modeling, consider the sequence of shells in Figure 4. In terms of Raup's (1966) parameters, the partly coiled limpet on the right differs from the high-spired form by having a lower rate of translation down the coiling axis and a greater whorl expansion rate relative to aperture size. In terms of Okamoto's (1988) model, the limpet has a lower generalized torsion and curvature. Other models provide similar geometric descriptors. These are perfectly good mathematical descriptions of the

differences between the shapes, but note that that is all that they are. Translation down a coiling axis and generalized curvature have no clear biological interpretation except in the context of shell form.

By contrast, the model presented here shows that the shell on the right can be derived from the one on the left simply by reducing the total amount of shell material produced (holding aperture growth rate constant). The rate at which new shell material is produced is a physiological parameter that could be studied quite independently of shell form, and related to other aspects of the animal's biology, such as total energy budget or resource allocation. Thus, rather than just describing the difference between the shapes, we have taken a step toward explaining it in terms of other, independently measurable, aspects of the animal's biology.

This becomes significant when we consider the perfectly conical limpet in Figure 5. The model shows that deriving this form from a highly coiled ancestor requires more than just a uniform reduction in shell production—it calls for a change in the relative rates of shell production at different points around the aperture. Thus we can see that a kind of physiological change is necessary for the evolution of a perfectly conical limpet that is not necessary for the evolution of a partly coiled limpet. The degree to which this constrains limpet evolution depends on the genetic ease with which this more elaborate physiological change could be achieved. Though this model does not address this genetic question, it sets the stage for it to be studied.

In a sense, this model describes the "natural logic" (cf. "natural history") of shells. Natural logic here refers to the relationships that must hold between different developmental and physiological processes and between these and phenotype. When combined with natural history (the actual attributes of the animal and its environment), this describes the opportunities and constraints that evolution has to work with.

This approach does not contradict other shell coiling models. Morphometric descriptions such as those cited above are still the best way to describe shell form in terms of a small number of easily measured parameters. Rather, the model presented here complements such models by allowing us to relate changes in their parameters to other aspects of the animal's biology, and to make testable predictions about which aspects of morphology will change together.

Stone (1995, 1996) presents a computer model that allows one to draw shells that are not perfectly conical, such as those in Figure 8. This model still describes shell form in terms of rate of horizontal expansion, rate of vertical translation, and so forth, but allows these terms to vary allometrically as the program proceeds. While this allows one to draw shells such as the irregular forms in Figure 8, it does not allow us to see that these forms arise from a difference in the rate at which shell production increases and the rate at which the aperture grows—something that the model presented here makes clear. Understanding this is significant if we wish to answer questions about the evolution of these forms.

Okamoto (1988) and Illert (1990) devise algorithms that reproduce the various forms of heteromorph ammonites. This is achieved by pulling a generating curve through space along a trajectory that is defined by a function specifying its curvature and torsion, a similar approach is used by Ackerly (1989a). While this produces an image that resembles *Nipponites* (for example), it does not make it clear that the animal could build such a form simply by rotating its body within the shell (though Illert and Pickover [1992] show that *Nipponites* can be described by a model with a complex value of the torsion parameter, which could be thought of as a rotation of the coordinate axes, though they do not interpret it in this way). Using the model presented here, we can see that *Nipponites* and *Didymoceras* could have achieved their unique forms without devising any really new growth rules. Beyond simply describing the shape, this model leads to a hypothesis about what the animal was doing that in turn makes a testable prediction about the path taken by sculpture on the shell. Figures 9 and 10 show that this prediction is upheld by *Didymoceras*.

Another difference between the approaches

is apparent when the models fail to describe a particular form. Because Raup's model was parameterized in terms of the angular position of the aperture around a coiling axis, it could not describe a truly conical limpet. This was never taken to mean that such limpets are doing anything biologically novel, though, only that we need a new set of parameters (which other authors provided). By contrast, when the biological model presented here fails, as it does with a flat aperture map and no aperture growth, it tells us something interesting about biology, namely, that these parameters no longer constrain shell form and the animal can take up freeform growth.

In one sense, the model presented here does not resolve the problem of how shells grow, but simply shifts the question to another level. To a first approximation, we can break up the study of development into two levels. The first is the level at which gene products interact to determine the behavior of cells and tissues. The second level is that at which cells and tissues interact to build a phenotype. Almost all current research in development focuses on the first level; this paper concerns the second.

It should be clear that, even for the simplest of phenotypes, this second level of development is rather complex. Even if we knew everything about which genes are involved in development and how they are regulated, we would still be a long way from knowing how most phenotypes are built.

For the mollusc case (at least concerning shell form), it is the first level that is missing. What we do not know is how the aperture map is determined at the cellular level, and without this knowledge, we can only make guesses (as I have done) as to the degree to which it constrains phenotypic evolution.

A model system for the study of developmental evolution should be one for which we have some understanding of both the processes by which phenotypic characters are constructed and the selective regimes acting upon them. Numerous authors have investigated components of the selective forces acting on gastropod shells (Vermeij 1987), largely through the study of their structural properties when attacked by various predators. Thus with a developmental model of shell form, this group should emerge

as an excellent model system for the rigorous study of phenotypic evolution.

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Appendix 1

The shape of a trajectory in three space can be described exactly by specifying two values on it, the curvature (κ) and torsion (τ). Curvature measures the degree to which the trajectory curves ($\kappa = 0$ for a straight line) and torsion measures the degree to which the trajectory refuses to live in a plane (strictly, it measures the rate of change of the plane in which a short segment of the trajectory lies as we move along the trajectory). Note that this is a geometric description of a curve and is completely unrelated to the developmental event called "torsion" that characterizes gastropods. For a thorough discussion of these terms, see Nutbourne and Martin (1988), or see Okamoto (1988) for an application to shell form.

For a generalized helix, $\kappa \propto \tau$ and the curve makes a constant angle with respect to some direction (Nutbourne and Martin 1988). This angle, θ, is given by

$$\theta = \text{Arctan}\left(\frac{\kappa}{\tau}\right). \tag{A1}$$

For a trajectory on a shell, this is the angle made by the trajectory and the coiling axis, as shown in Figure A1.

We define the coiling axis as **C**, and imagine the trajectory projected into a plane normal to **C**. Now define two axes, **i** and **j**, which lie in this plane such that **i** is in the direction of the projected curve where it starts and **j** is normal to **i**.

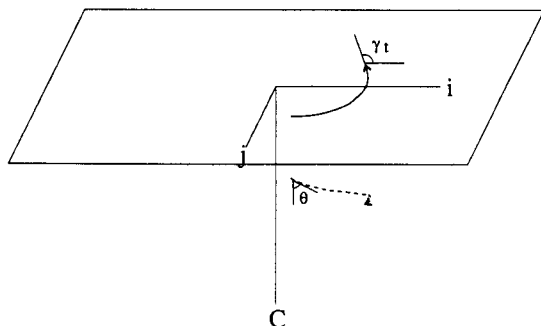If the pattern of shell production around the point of interest

FIGURE A1. Formalism for describing the trajectory. The dashed curve is the real trajectory, the solid curve is its projection in the (i, j) plane.

on the aperture does not change, then in a short time interval, dt, the angle between the direction of growth and the **i** axis changes by γdt. γ is the curvature of the projected trajectory divided by the rate at which it is elongating. The actual trajectory on the shell is growing at a rate $\sigma_{u,t}$, so the projection grows at a rate $\sigma_{u,t}\sin(\theta)$.

From this, we can write down the differential equations defining the trajectory in the space with axes **i**, **j**, and **C** as

$$\frac{di_u}{dt} = \sigma^*_u \frac{dA}{dt} \cos(\phi)\sin(\theta)$$

$$\frac{dj_u}{dt} = \sigma^*_u \frac{dA}{dt} \sin(\phi)\sin(\theta)$$

$$\frac{dC_u}{dt} = \sigma^*_u \frac{dA}{dt} \cos(\theta) \tag{A2}$$

where

$$\sin(\theta) = \frac{\kappa}{\sqrt{\kappa^2 + \tau^2}}, \qquad \cos(\theta) = \frac{\tau}{\sqrt{\kappa^2 + \tau^2}}.$$

These equations can be rewritten to eliminate the time differential:

$$\frac{di_u}{dA} = \sigma_{u,0}\cos(\phi)\sin(\theta)$$

$$\frac{dj_u}{dA} = \sigma_{u,0}\sin(\phi)\sin(\theta)$$

$$\frac{dC_u}{dA} = \sigma_{u,0}\cos(\theta). \tag{A3}$$

Solving these yields equation 6.

The fact that γ is the same for all trajectories on a given shell follows from the fact that every point on the aperture completes one trip around the coiling axis in the same amount of time as every other point.

If the rate of shell production scales with the size of the aperture (rather than its growth rate), as for the shells in Figure 8, then the growth equations change to

$$\frac{di_u}{dt} = \sigma^*_u A_i\cos(\gamma t)\sin(\theta)$$

$$\frac{dj_u}{dt} = \sigma^*_u A_i\sin(\gamma t)\sin(\theta)$$

$$\frac{dC_u}{dt} = \sigma^*_u A_i\cos(\theta). \tag{A4}$$

The shell on the left in Figure 8 is built by letting $A_t = A_0 e^{rt}$. Such exponential growth produces a conical spiral since $dA/dt \propto A$, so σ is still proportional to dA/dt.

Substituting $A_t = A_0(1 + rt)$ into equation A4 produces the middle figure in Figure 8, for which the aperture grows linearly with time. The shell on the right of Figure 8 results from letting the shell grow exponentially (as above) for a few whorls, then holding aperture size constant by setting $r = 0$.

The heteromorph shells in Figure 10 were produced by following the growth equations given in the text, but rotating the entire frame of reference around the aperture at specified times. Specifically, the entire frame was rotated around a vector normal to the plane containing the aperture and situated in the center of the aperture. This is equivalent to having the animal rotate within the shell.

Appendix 2

There are two ways to calculate the aperture map from measurements on a shell. In each case, we are only calculating rel-
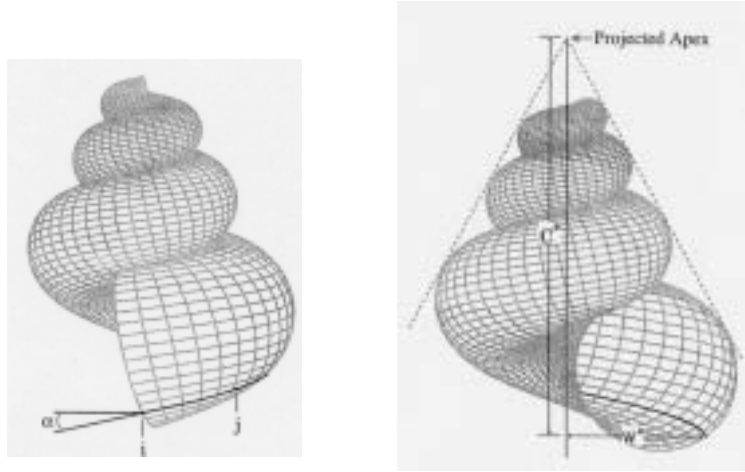
FIGURE A2.   Measurements used in calculating the aperture map for a specimen.

ative rates of shell production; absolute rates could only be found by watching the shell grow. However, we can find the shape of the aperture map and the rate of shell production relative to aperture growth rate. These, along with aperture shape, are the principal determinants of shell form discussed in the text.

The first, and most awkward, approach requires shells with visible growth lines. Here, one can directly measure the distance between these lines to estimate the amount of shell material produced at each point during the same time period. This is difficult for small shells, but is the only option for truly irregular shells such as some heteromorph ammonites.

For approximately regular shells, for which one can estimate a coiling axis and a "projected apex" (Schindel 1990) (Figure A2) for a couple of whorls, there is an easier way. Schindel (1990) describes practical methods for locating the axis of coiling and the projected apex of the shell.

Setting $Z = (1 + \gamma^2)$, we can rewrite equation 8 as

$$\sigma_i^2 = r^2\, Z\, W_i^2 + r^2\, C_i^2$$

where σ_i is the rate of shell production at a point i, W_i is the distance of that point from the coiling axis, and C_i is the distance along the coiling axis of the point from the projected apex (see Figure A2). r, the growth rate of the aperture, is a constant at each point around the aperture. As discussed above, γ is the same for every point on the aperture (since each point has traced a path with the same number of coils) so Z is also a constant that can be calculated as follows (refer to Figure A2).

Choose a point on the aperture and measure its distance from the coiling axis and projected apex, calling these W^* and C^*, respectively. Measure the angle α between the trajectory of the chosen point and the plane normal to the coiling axis (Figure A2). A good choice for this point will often be the lowest point on the aperture, since it facilitates measuring α and minimizes

the effects of measurement error on the calculations below. With these values, we calculate Z as

$$Z = \frac{C^{*2}}{W^{*2}}\, \frac{1}{\tan^2(\alpha)}. \tag{A5}$$

Once this is calculated for a single point, the same value of Z can be used to calculate σ_i/r for any other point, given values of W and C, as

$$\frac{\sigma_i}{r} = \sqrt{ZW_i^2 + C_i^2} \tag{A6}$$

This gives the shape of the aperture map.

We can also calculate the actual rate of shell production at a point relative to aperture growth (as mentioned in the text with respect to the evolution of limpets). To do this, measure the values of C for two homologous points, i and j, on the same trajectory for which the value of α is known (Figure A2). The distance, s, along the shell between these is given by

$$s = \frac{C_i - C_j}{\sin(\alpha)}$$

Assuming that the aperture shape did not change over this interval, the change in aperture size can often be estimated by measuring whorl height at points i and j as A_i and A_j, respectively. The per-size growth rate is then

$$\frac{\Delta A}{A} = \frac{A_i - A_j}{A_j}.$$

The ratio of s to $\Delta A/A$ is what changes in the sequence leading to a half-coiled limpet in Figure 4.

If the plane of the aperture is close to parallel with the coiling axis, then W and C can be measured directly from a photograph or drawing of a shell. If the aperture is inclined at an angle, then it is necessary to look at the shell from different angles in order to get correct values of W.