Control of Gastropod Shell Shape; The Role of the Preceding Whorl

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I propose that a snail uses the shape of the preceding whorl as a cue to dictate where upon it the new whorl attaches. The consequent constant difference in orientation between successive whorls can generate the domed outline that is commonly observed. This "road-holding" model is considered more representative of growth processes than models that generate logarithmic helicospirals, but I consider how the curve of the shell just *behind* the aperture might also act as a cue, to line up the shell-secreting mantle. I discuss why it might be that shells dome less as they grow, and suggest a set of biologically more meaningful measurements with which to compare shells.

1. Introduction

A gastropod shell is in structure a rolled-up cone. This normally expands and coils regularly, so that the outline closely follows a logarithmic helicospiral, its dimensions increasing exponentially each revolution (Fig. 1 shows some examples in cross-section). Growth occurs only at the open end of a shell but, by following such a spiral, the shape of the whole shell is unaltered however many whorls grow. Furthermore, each band of new shell added is the same shape (gnomic growth) or, viewed as a continuous process, the shell deposition rates around the aperture remain in constant ratios to each other (Thompson, 1917).

So many molluscs follow more or less this simple shape that, by altering the few parameters that determine a logarithmic spiral, Raup (1966) generated the appearance of a large portion of the molluscan shell radiation. In his model the shell was traced out by the path of a generating curve expanding and revolving about the coiling axis; when a circular generating curve overlaps on successive whorls, a lunulate aperture is produced (Fig. 1). Raup used one parameter (W) to describe the proportional increase in the shell radius each revolution; a second (D) fixed the relative distance of the generating curve from the coiling axis, and thus the extent of overlap with the preceding whorl; a third (T) described its translation rate parallel to the coiling axis (Fig. 1); further parameters would be necessary to describe the shape of the generating curve. Other workers have used these, or similar parameters, to describe and compare variation even within a species (e.g. Newkirk & Doyle, 1975), because they are geometrically independent and together fully describe a perfect logarithmic spiral.

Inevitably real shells are not quite as isometric as a perfect logarithmic spiral. Outlines of *Conus* show that during ontogeny W and T change progressively (Kohn
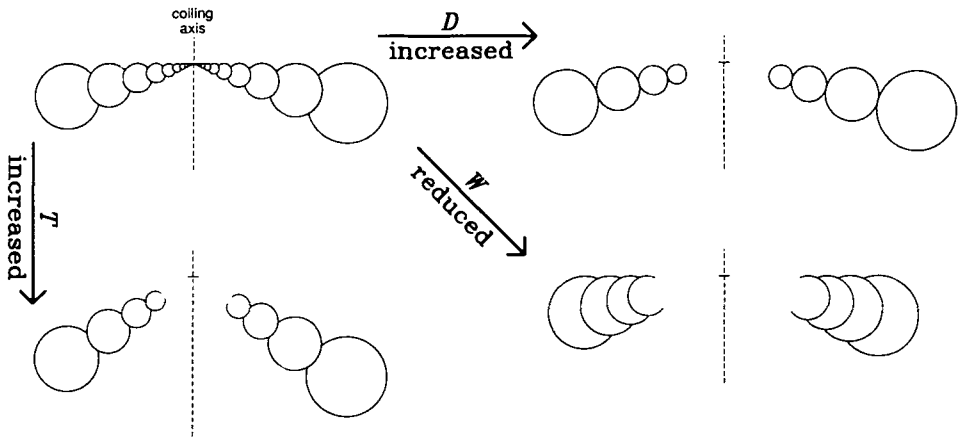
FIG. 1. Sections down the coiling axis of perfect logarithmic helicospirals. Each differs from the top left-hand spiral by the setting of just one parameter.

& Riggs, 1975). Figures 2(a–c) show similar alterations to the log-spiral parameters of a terrestrial pulmonate. These data stem from my own research on *Trichia hispida* (L.) in which I have found that a section down the coiling axis (Fig. 3) gives much more insight into developmental processes than does the exterior alone, besides enabling accurate measurements of all dimensions of even the smallest whorls. This species also exhibits a trend that is especially common in terrestrial snails (Gould, 1968; Vermeij, 1980): the outline of the spire is not triangular but domed [Fig. 3(a)].

Although the log-spiral's attractive simplicity would be lost, the model could be elaborated to model this doming as an allometric increase in *T*, decrease in *W* (Vermeij, 1980), and/or change in shape of the aperture (Gould, 1968). But, as the sections in Fig. 3 show, the doming appears to be associated with a changed inclination of the long axis of the generating curve to the coiling axis, leading me to propose a quite different model of gastropod growth.

2. A New Model of Spiral Coiling

Retain from the log-spiral model the constant shape of the aperture and its exponential increase, but suppose that, instead of the aperture following a predetermined trajectory in space, its inner edge between the sutures is directed to attach consistently to homologous sites on the preceding whorl. How this can generate doming is shown in Fig. 4(a) and compared with the generation of a similar spire outline by a modified log-spiral [Fig. 4(c)].

In this new model, growth is not gnomic (the shape of the whole shell alters with each increment and succeeding increments are relatively more tightly coiled for their size); but the developmental rule is simple and invariant [in geometrical terms, repeated application of a similarity transformation generates the view in section,
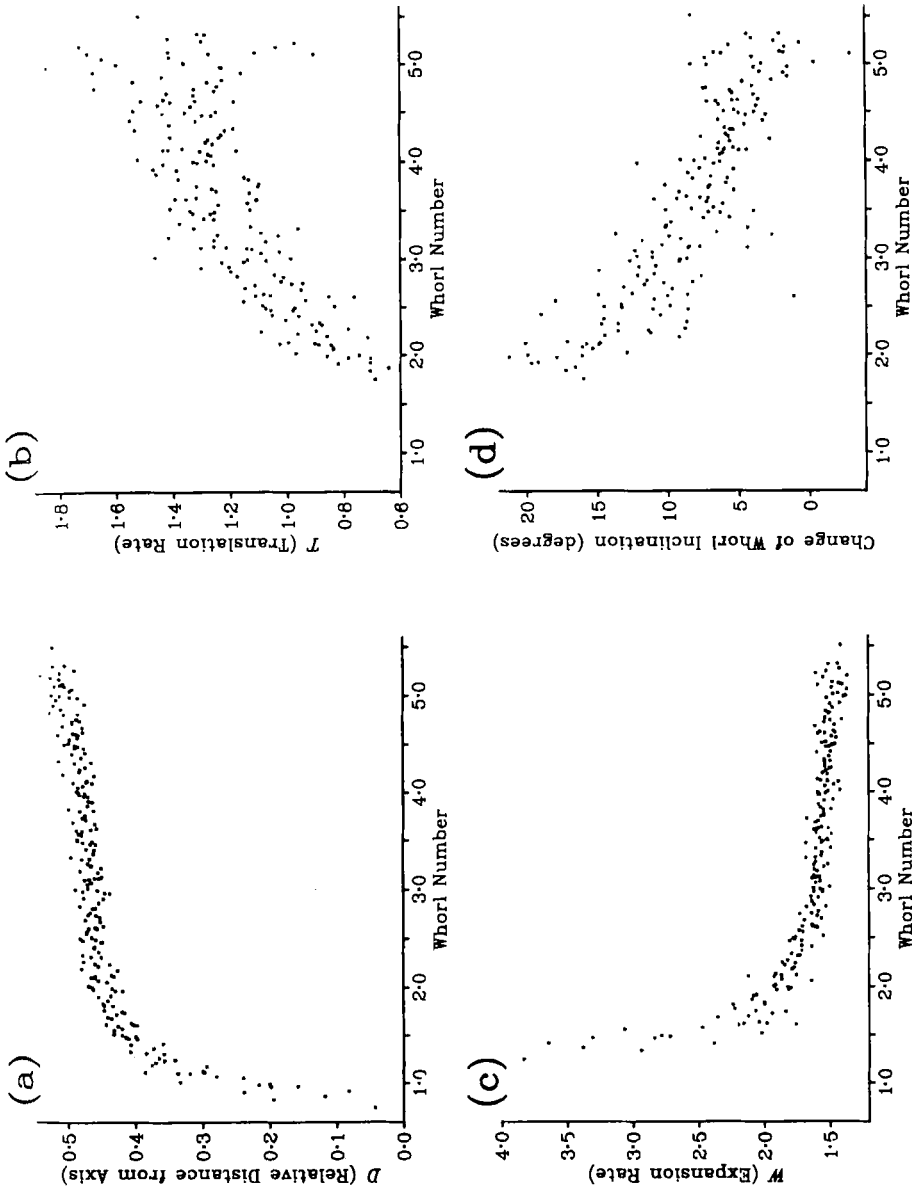
FIG. 2. Growth parameters measured from sections (down the coiling axis) of 25 adult *T. hispida*, all from the same site. Whorl number is based on the number of revolutions from the protoconch, but since the protoconch is not distinct, the starting values were set for each shell by the volume of its first 1·5 revolutions. The change of whorl inclination in (d) is angle *a* in Fig. 3(a). The position of the coiling axis is calculated from the centre of area of the whorl cross-sections but other parameters are based on ellipses fitted by a least-squares technique to each cross-section's outline.

$D = (R_n - r_n)/(R_n - r_n)$, where $R_n =$ the distance of the ellipse centre from the coiling axis and $r_n =$ geometric mean of the major and minor semi-axes.
$T = (Y_n - Y_{n-1})/(R_n - R_{n-1})$, where $Y_n =$ distance, parallel to the coiling axis, from the apex to the ellipse centre. The suffix $n - 1$ refers to measurements made one revolution behind those with suffix n.
$W = (R_n/R_{n-0.5})^2$.
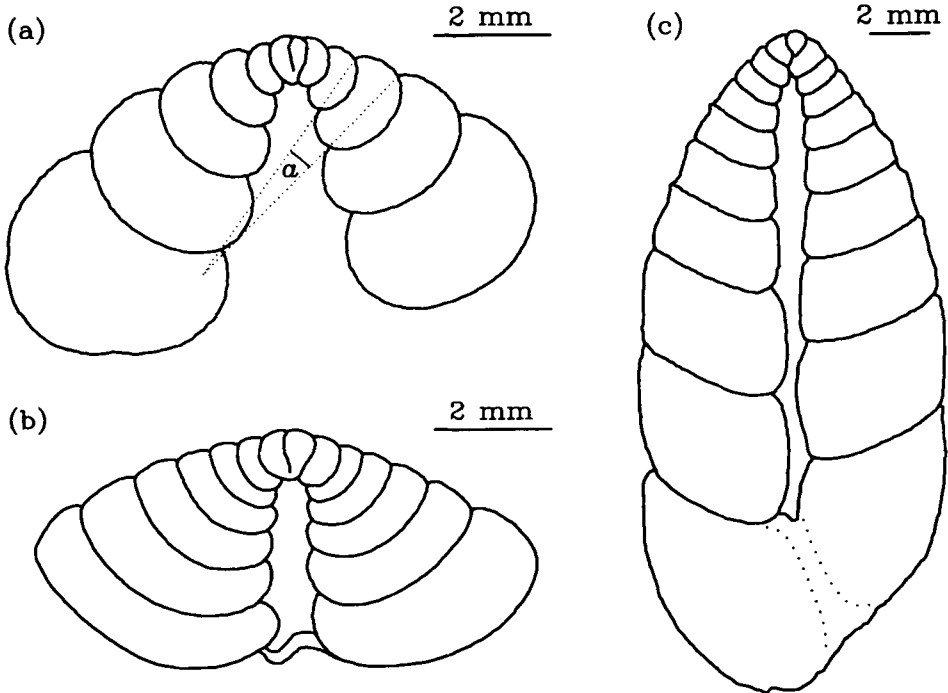
(a)

(c)

2 mm

2 mm

(b)

2 mm

FIG. 3. Sections down the coiling axis of (a) *Trichia hispida*, (b) *Oestophorella buvinieri*, (c) *Cerion glans*. The angle *a* is the change in inclination of the line joining inner and outer sutures.

Fig. 4(a)]. *D*, *W* and *T* may change during ontogeny, but this is incidental. The logarithmic spiral is a special case of the new model, in which successive whorls attach such that they remain parallel in orientation. To describe where the next whorl goes, the same number of parameters need be set in both models, because the position of attachment determines the translation rate as well as the change of orientation (in conjunction with the aperture shape, which both models have to describe). However, to describe the whole shell, the new model requires an extra parameter, setting the initial orientation of the generating curve.

3. Biological Realism of the Two Models

(A) MECHANISMS OF GROWTH REGULATION

The road-holding model

The chief attraction of this new model is that it seems likely to reflect the *biological* processes guiding shell growth. The portion of the old whorl to which the new whorl attaches is often relatively flat (seen in cross-section, Fig. 3) and provides an obvious "road" for the mantle, poking out from the aperture, to follow. I will therefore christen this new model the "road-holding model". Many shells, especially when immature, have a sharply angled periphery [Figs. 3(b, c)] and this keel might provide an even more helpful "railway line" for the outer suture to track thereby also
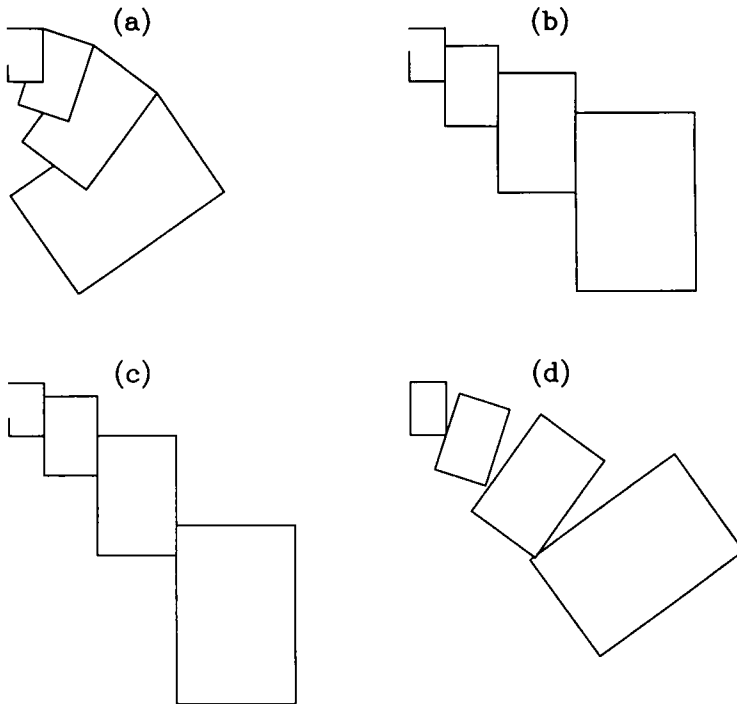
FIG. 4. Sections down the coiling axis of hypothetical shells with a rectangular generating curve (right-hand side only shown). (a) is generated by the road-holding model (same site of attachment); (b) log-spiral model; (c) log-spiral model with increasing translation rate; (d) log-spiral model with the same consistent change in inclination of the aperture as in (a).

engineering a shell with sutures that are only shallowly indented, possibly advantageous in resisting predation). Many tropical sea shells (e.g. *Strombus gigas*, the queen conch) have massive spines which may be similarly tracked and must certainly limit where the mantle can reach to deposit new shell. When whorl outlines are more rounded, so long as they are not circular, the curvature of a particular portion will still be distinct and could be tracked by the matching outline of the mantle. But we can make a testable prediction that in such snails shell shape regulation is less precise.

It seems implausible that the snail could accurately feel, from the way that its soft body is bent, where its body lies one revolution before. That is why I emphasise that it is the *shape* of the *shell* that is followed, as the only cue of where the preceding whorl lies. In the parlance of embryologists working on much smaller-scale phenomena, this is a process of contact guidance.

Three alternative mechanisms to generate a logarithmic spiral

Are there alternative mechanisms for constructing the trajectory of a logarithmic spiral, without reference to the preceding whorl? I can suggest three techniques. The first, favoured by Løvtrup & Løvtrup (1988), is rigidly to maintain the shape

and inclination of the aperture, so that constant asymmetries in the rates of shell deposition around the aperture produce a logarithmic spiral. But, as I discuss elsewhere (Hutchinson, in press), it seems impossible for relative growth rates to be maintained sufficiently accurately.

Even if the snail cannot, via its convoluted body, directly relate the position of the apex to that of the aperture, it could theoretically extrapolate from the curve of the last whorl where the coiling axis and apex lay, and then direct its shell-secreting mantle the correct distance away from them. But, at least in umbilicate shells, accurate estimation of the coiling axis's position seems implausible.

A third technique is to ignore the coiling axis but regulate the constant shallow angle that the new band of shell makes with the band to which it attaches (α in Fig. 5). Although small deviations in this angle affect the spiral's shape dramatically, this mechanism is plausible, because the body "extruded" from the aperture is preset in approximately the correct curvature, which could be finally adjusted by slight isometric expansion. The mantle could thus be *lined up* by the shell behind the aperture. Figure 5 illustrates this lining-up process maintaining the expansion rate away from the axis; it is even simpler to regulate similarly the translation rate parallel to the axis, since the "floor" and "ceiling" of the inside of a logarithmic spiral are flat, inclined at constant angles to the vertical.

Regulation of distance from the coiling axis

In one respect the road-holding model is almost bound to be right and the lining-up model wrong. If the preceding whorl suddenly swelled or narrowed, the next whorl would surely follow; I cannot imagine it obstinately ceasing growth because its true path was blocked, nor blindly continuing along the same spiral despite having lost all contact with the preceding whorl. Okamoto (1988a) studied some unusual ammonites that do coil regularly out of contact with earlier whorls, but the whorls of most snails attach to their predecessors. Think of bending a piece of wire into a
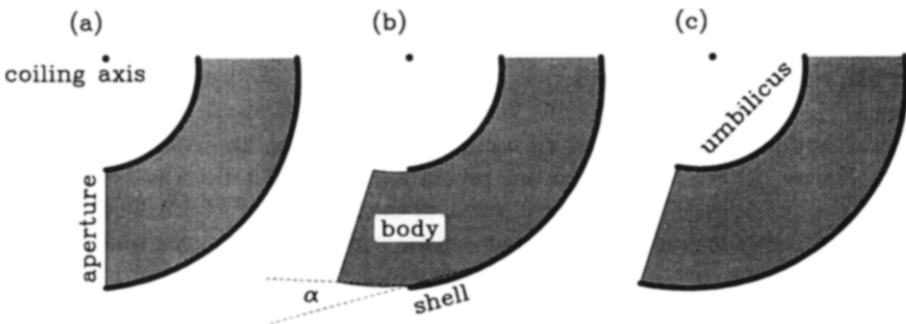

FIG. 5. Mechanism for regulating angle α, that which a new band of shell makes with the old aperture. The outer whorl is shown sectioned perpendicular to the coiling axis, with the body protruding (b) to lay down a new band of shell (c). The body protruded from the aperture is preset in approximately the right curvature (once it has undergone slight isometric expansion).

spiral—it is much easier to wrap it round something than to separately bend each section to the correct curvature. In just the same way, the strand of silk forming the capture spiral of a spider's web is spaced away from the preceding revolution by the spider using its legs as calipers (Vollrath, 1987).

In snails the first few whorls exhibit the process most clearly. Figure 1 shows log-spiral shells that have expanded steadily from nothing. By the time that the aperture is the size of the initial whorl of a real snail, it is a long way from the axis, much further than the radius of the protoconch about which a real snail coils. The shells in Fig. 1 thus look peculiar because real shells, by road-holding around the protoconch, start to coil more closely to the axis than expected by extrapolation from their subsequent growth parameters. The initially low values of D [Fig. 2(a)] are a symptom of this nucleating effect.

Regulation of translation rate

Given this constraint that successive whorls must be in contact, there is still a continuous choice where to attach the next whorl and it is this that we are primarily attempting to model. So, which does the snail maintain, the curvature and translation rate of the shell behind, or the curvature (in a perpendicular plane) of its inner margin, matching that of the preceding whorl? To appreciate the distinction, consider rolling up a carpet that has started to coil at an angle; frustratingly, it is impossible to get the ends square because it is *lined up* by the carpet just behind. Now consider instead a cable being neatly coiled on a drum; it follows the course dictated by the preceding coil—the road-holding model.

Particularly in keeled snails, the preceding whorl seems too true and available a cue for the snail to ignore. It has the advantage of damping any perturbations that occur and is much less likely than the outer whorl to mislead by being damaged. But it is quite possible that both mechanisms act concurrently; in a shell coiling regularly they need conflict little, or not at all if their parameter settings exhibit allometry, so that they could correct each other's mistakes.

(B) THE GENERATING CURVE AND APERTURE SHAPE

The lack of biological realism in the log-spiral model is emphasised when we consider alterations to the coiling parameters of real shells. In Figs 6(a–b), we see how the logarithmic spiral models a change in translation rate, T. The new aperture has an increased area and a different shape, and the shape of some of its outline (shown dotted) is guesswork, because this part of the generating curve was not realised in the original shell (a problem encountered by Heath, 1985). It seems biologically quite inappropriate to thus preserve the shape and size of the generating curve at the expense of those of the aperture.

With the road-holding model the aperture is not constrained to remain parallel to its orientation one revolution earlier, so a sudden change in translation rate can be modelled as the mantle merely directing the sutures to follow a new "road" on the preceding whorl. The new band of shell, although oriented differently, is
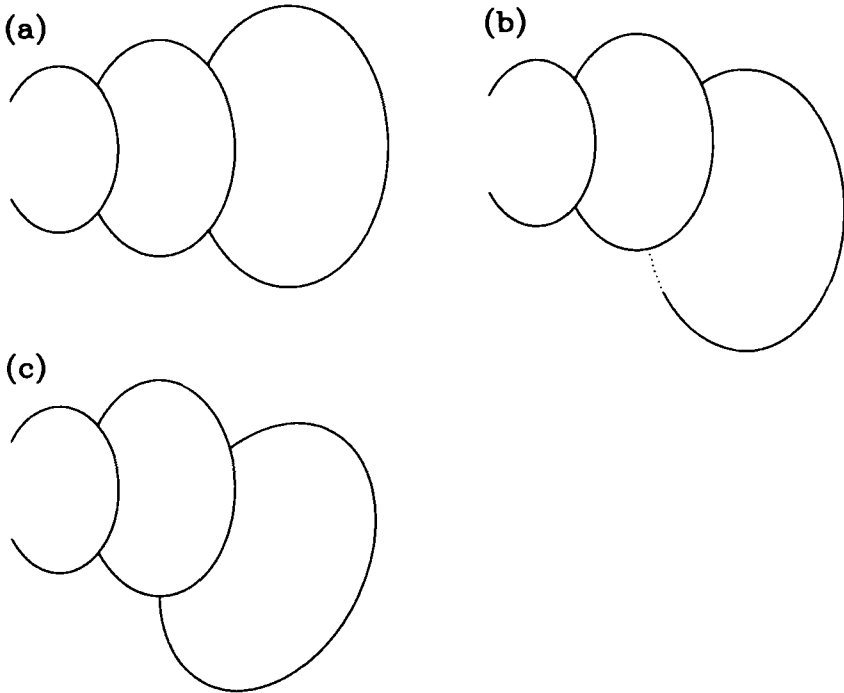
(a)

(b)

(c)

FIG. 6. Suppose (a) to be a section down the coiling axis of a real shell. With the log-spiral model, simulation of a change of translation rate requires some of the outline to be guessed (shown dotted) and produces a very altered aperture shape (b), compared with a simulation of the same change in translation rate based on road-holding principles with an altered site of attachment (c).

identical in outline, and the shape and area of the aperture as a whole need alter little [Fig. 6(c)].

(C) INCLINATION OF THE APERTURE

Another attraction of the road-holding model is how easily it accounts for the obvious ontogenetic change in inclination of the long axis of the whorl cross-section, becoming more perpendicular to the coiling axis (Fig. 3). (Workers often appear to treat whorl measurements made parallel or perpendicular to the coiling axis as homologous from whorl to whorl, but it seems obtuse to thus regard this rotation instead as a distortion, with the body's orientation to the coiling axis remaining constant; perhaps this could be proved by mapping the homologous points some-times provided by spiral bands of pigment.) We could introduce such rotation into the log-spiral model, by rotating the generating curve about its centre which follows the original path [Fig. 4(d)]; but Fig. 4(d) has a concave, not domed, outline to the spire. Doming is caused by the position of attachment lying closer to the axis, not, by itself, the change in orientation of the aperture. A log-spiral model would have

to be modified in both respects, dispelling further its chief attractions, simplicity and isometry.

4. Modifying Influences

The road-holding model not only accounts for this change in orientation of the whorls, but predicts that the change in inclination of the line joining the inner and outer suture (*a* in Fig. 3) should be constant. The prediction is not borne out in *T. hispida*—*a* decreases as these lines on successive whorls become more parallel [Fig. 2(d)]. This is equally a problem for a log-spiral model, but with the road-holding model we can perhaps understand why the allometry occurs.

One explanation could be that the shape of the aperture has also altered. If the new whorl still attached to the homologous points on the old whorl, a change in aperture shape would directly affect the inclination of the next whorl. The effect may be greater if the developmental program defines "same point on the preceding whorl" by some criterion other than homology, for instance relative to the site of a particular curvature. Further work is required to identify such a rule and to test whether application of the same rule to the altered aperture shapes would indeed result in the inclination changing less.

Another factor may be more important. Doming causes the radius of the shell to become progressively smaller, relative to the size of the whole shell. The road-holding model would predict the same to be true for the relative size of the umbilicus [as in fact is generally observed in land snails (Goodfriend, 1986), although in *T. hispida* the tendency is overcome by the aperture becoming rounder]. Quite possibly there are anatomical constraints in a species as to how tightly the whorl can coil, mechanically counteracting the tendency for the new whorl to follow the same "road" on the old whorl. If a doming snail grew more whorls, the change of inclination would certainly have to stop eventually, otherwise even portions of the same whorl half a revolution apart would interfere.

This factor is particularly evident in the complex allometry of *Cerion* [Fig. 3(c)]. The roof domes just as with *T. hispida*, but eventually this causes constriction of the umbilicus and, in order to grow further, the succeeding whorls simply must lie parallel to each other. Note that it is the initially large umbilicus that allows the doming. I suggest that the reason why doming is rare in marine snails (Gould, 1968) might be little to do with the roof outline itself, but the virtual absence of an umbilicus in the young shell. This in turn depends on whether the first whorl coils planispirally or more turbinately; in land snails, selective pressures which might decide the latter include packing considerations inside the egg, which most marine snails lack.

5. The Place of Road-holding in a Synthetic Framework

The real situation thus seems more complex than the simple road-holding model idealised in Fig. 4. My view of the influences determining where new shell is laid can be formalized by a crude equation of three terms:

Shell shape at revolution $\phi = ss(\phi)$

$$= f[ss(\phi - 2\pi), ss(\phi - \delta\phi), \text{physiology}]$$

The first term, $ss(\phi - 2\pi)$, incorporates the road-holding model and states that shell shape depends on the shell shape one revolution earlier. The second term, $ss(\phi - \delta\phi)$, admits that the mantle may be lined up by the shell behind the aperture and that the new band of shell is constrained to attach to, and thus diverge only gradually from, the present aperture. The reluctance of the shell to coil too tightly could also be modelled by such a term, as a function of the shell's curvature leading up to the aperture. The third term, "physiology", is there to include influences independent of earlier shell shape. For instance, many apertures change shape at maturity, often quite suddenly (Fig. 3). This can occur at various shell sizes, presumably subject to environmental influences.

Possible another term incorporating more diffuse measures of shell shape may be necessary. Okamoto (1988a) explains the convoluted outline of a heteromorph ammonite as due to regulatory responses to changes in life orientation, determined by the balance of the shell (see also fig. 7 of Bayer, 1977). Perhaps in some gastropods also the weight distribution of the whole shell affects how it is held relative to the mantle, and thus its subsequent shape. But the purpose of my simple equation is only to emphasise that more realistic models must include, amongst others, a $(\phi - 2\pi)$ term, previously ignored.

Such a term gives rise to a difference equation. Others (e.g. Bayer, 1977) have suggested modelling shells with difference equations, but the time difference envisaged was one growth band, not one revolution; theirs is just a version of the lining-up model. Shells do grow in discrete increments, but this is no justification for modelling each increment as linear rather than curved. The advantage of their difference equations over differential equations appears merely to be computational simplicity. (Linear increments do correctly predict a decrease in the convexity of some bivalves as a growth rate slows (Bayer, 1978), but the fit with the theory is not shown to be quantitative. McGhee (1978) shows that the size of the increment has little effect on convexity.)

6. When Does Road-Holding Occur?

Much of the more recent work on shell shape has concerned bivalves and brachiopods (e.g. Savazzi, 1987; McGhee, 1980) whose few coils and high expansion rates make the road-holding model irrelevant. Other work has been directed at cephalopods (e.g. Bayer, 1977). Their usually planispiral shape does also not immediately suggest the importance of road-holding, paradoxically perhaps because it is so effective in keeping the shell planispiral. Certainly road-holding seems unavoidable in those ammonites with sharp keels and considerable whorl overlap, which "ride" the preceding whorl like a monorail. In the much rarer cephalopod and gastropod species in which successive whorls do not touch, road-holding can play no part. Measurements of the coiling of such shells may still fit a logarithmic model (Okamoto, 1988a), but whether less well than normal shells has not been quantified. (I have stressed the regulatory benefits of the road-holding model, but the bizarre shapes of some of these shells with disjunct whorls emphasise that the

need to attach somewhere on the preceding whorl is a severe restriction on morphological diversity.)

In turbinate gastropods the relative importance of the $(\phi - 2\pi)$ and $(\phi - \delta\phi)$ terms is less clear cut. We need actually to test whether the *position* of the *inner* margin of the new whorl really is a function of the *shape* of the *outer* margin of the preceding whorl. If the inner margin were orientated relative to the point on the previous whorl furthest from the coiling axis, both the $(\phi - 2\pi)$ and $(\phi - \delta\phi)$ terms would be involved. Some terrestrial snails may be variable enough for carefully measured cross-sections to provide the critical data; but most measurements in terrestrial snails are somewhat correlated with size or maturity, which makes detection of other independent correlations difficult.

A more rigorous approach would be to manipulate the outline of the penultimate whorl by attaching ramps of different shapes in various positions. The converse, manipulation of the present whorl, risks too many other, stress-related consequences. But sometimes such damage occurs naturally and can result in the new shell going off at a new angle, riding rough-shod over the penultimate whorl's outline [Fig. 7(b)]. It appears that lining-up by the shell behind has overridden any road-holding program [although it could be that the body has been damaged so that it is a road-holding program that is giving the wrong instructions; Oldham (1931) found snails stressed by mite infestations to grow similarly scalariform]. We know not on how many other occasions following damage, road-holding might instead have steered an errant whorl into line, as suggested by Figs 7(d–e). Similarly, Stelfox (1968) breeding for scalariformity, complained that promising new-born shells "had
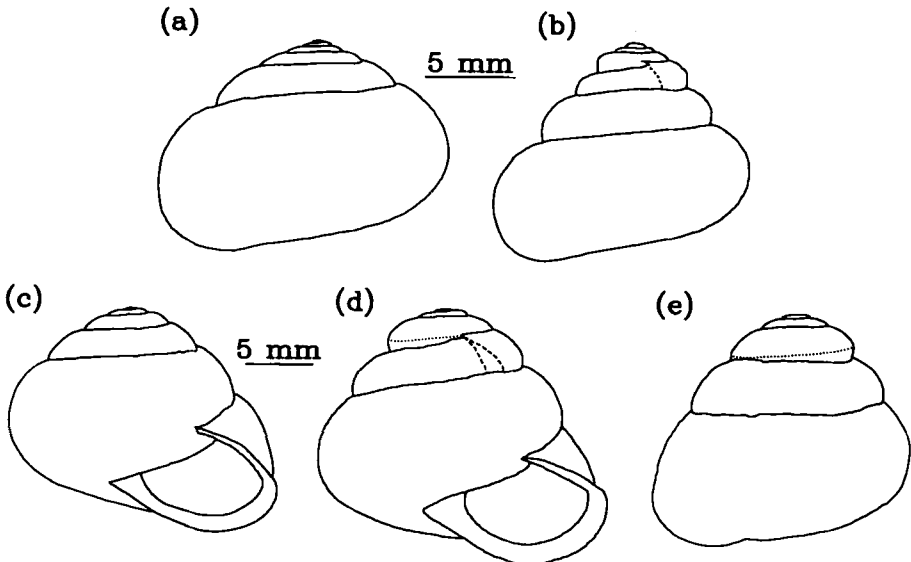

FIG. 7. (a) normal *Monacha cantiana*; (b) scalariform *M. cantiana* from the same site, coiling at a new angle following damage; (c) normal *Arianta arbustorum*; (d, e) two views of a scalariform *A. arbustorum* from the same site, somewhat corrected in its deviation.

the uncanny knack of correcting the spire during growth", not something that lining-up could achieve.

7. Applying the Road-holding Model

How is the road-holding model of value to us? Its role is probably not in comparisons between larger taxa (cf. Raup, 1966), but nearer the species level and through ontogeny, with reference to real specimens. We have already seen that obedience to a constant developmental rule eliminates the need to put forward involved allometric explanations for why doming occurs. Once the road-holding model is considered the null case, it is different allometric changes that we have to explain, or even opposite ones, such as a *reduction* in the degree of doming with size—earlier authors were trying to explain why it should *increase* (Gould, 1968; Vermeij, 1980). This may mean that different selective pressures are recognized as important. Also, in imitation of Raup's classic work (1966, 1967) with the logarithmic spiral, we could generate an array of new shapes and ask why some of them have not been produced by nature.

But the primary importance of this model is in suggesting new measurements with which we should compare shells. Raup (1961) claimed that the log-spiral model "represents an attempt to diagnose shell form in terms of truly natural parameters, related to growth, rather than in terms of rather arbitrary characters such as width of body whorl or spire height". It was a positive step to consider *growth* processes, since increments to the shell should be simpler to interpret when they change than the cumulative product of such changing increments. But according to the road-holding model, Raup's growth parameters are equally arbitrary, complex products of the characters that the snail can alter directly.

For instance, Raup defines the expansion rate, W, in terms of the relative increase in radius each revolution. This will alter if the shell domes (later whorls are added more ventrally, and less laterally), yet no change to the angular rate of increase in area of the aperture need be occurring. Others have already realized (e.g. Vermeij, 1980) that W and the translation rate parallel to the axis, T, will be inversely correlated, "to maintain contact of the aperture and coiling axis" (Newkirk & Doyle, 1975), so these authors' discussions are encumbered with alterations to two parameters, rather than one, when the site of attachment to the preceding whorl shifts or the aperture becomes relatively smaller. Instead, the road-holding model suggests that one parameter should describe the expansion rate of the aperture in terms of area, and another its position relative to the last whorl. Each seems likely to be under more direct biological control, and not directly affected by changes in the other. For similar reasons, I further propose that we should measure expansion rate with respect to the arc length traversed along the preceding whorl, rather than per angle of rotation—if the shell were unrolled, this measure would be the taper of the cone.

Both models require a description of aperture shape. As Okamoto (1988*b*) observed, "Any fixed co-ordinate system is no more than an artificial framework imposed upon the coiling pattern"; we would therefore not wish to measure parallel

and perpendicular to the coiling axis, as is standard practice (Cox, 1960: 126). Of more relevance to what the snail can sense, and direct its shape towards, is a *moving* framework dictated by the aperture itself, perhaps most simply relative to the line joining the inner and outer suture. Unlike the point on the aperture furthest from the axis, the sutures are always recognizable as homologous from whorl to whorl or shell to shell, making it more likely that the measurements based on them will be also.

Løvtrup & Løvtrup (1988) shared a similar concern about biological reality—that the translation rate, or apical angle, in the log-spiral model was not described by a measurement related to a process at the mantle edge. The most basic achievement of the road-holding model is to say that the change in orientation between successive whorls is such a measurement. To portray even more exactly the growth process, we could instead describe where on the old whorl is the point of attachment. Ideally we would like to judge this position in the same way as does the snail. However, this would effectively mean elucidating the developmental rules—rather too much to expect of routine taxonomy.

Unfortunately, the spire's shape is not fully described by parameters such as the change in whorl orientation unless we measure also the starting conditions (for instance the initial orientation to the coiling axis), which can be measured only on sections that are laborious to grind down. And the one whorl which can be measured without sectioning, the last one, is the most untypical in its coiling parameters. It is easy to estimate Raup's translation rate averaged over the whole shell without sectioning it, but this is impossible for the average change in whorl orientation. Arbitrary characters such as spire angle may reveal little about the growth processes but they can indicate whether patterns of allometry differ overall. They represent simply aspects of shape that are most apparent to us, and they may also be the characters of direct adaptive value. So, for practical purposes, we cannot always let theory restrict comparisons between shells to our new growth parameters. But recognition of what sort of parameters are under more direct biological control, will facilitate interpretation of the measurements that we can make.

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