

# Control of Gastropod Shell Form Via Apertural Growth Rates

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**ABSTRACT** This paper discusses and corrects ideas in Løvtrup and Løvtrup (*J. Morphol.* 197:53–62, '88) on how differential growth rates around the aperture cause the gastropod shell to coil at particular angles. The relationship between position relative to the shell apex and growth rate is derived. This lets us understand what information on relative growth rates around the aperture is sufficient to determine the shape of the logarithmic spiral that these growth rates generate. I argue that differential growth rates could not be physiologically controlled precisely enough to regulate apical angle; they passively follow, not actively direct, shell shape.

Molluscan shells have long been described as logarithmic helicospirals, a curve the shape of which we can manipulate by altering few parameters. One aspect of shape is whether shells coil in a plane perpendicular to the coiling axis (planispiral) or whether successive whorls are displaced along the axis, forming a turbinate shell. The recent paper of Løvtrup and Løvtrup ('88) in this journal considers which of the parameters that affect this aspect could be developmentally controlled by growth processes at the aperture. This is a first step in identifying the physiology of shell shape regulation; it may help in understanding why some combinations of shell characters are rare; and comparisons based on such parameters represent better the true divergence between shell forms. Unfortunately some of Løvtrup and Løvtrup's later arguments are logically flawed.

On page 60 they quote D'Arcy Thompson ('17), who asserted that bovid horns (also logarithmic spirals) are planispiral only when the points where growth is a maximum and minimum lie on a diameter of the generating curve. (The generating curve is the outline of the tube sectioned in a plane containing the coiling axis; very similar, therefore, to the shape of the aperture, which may be slightly inclined to this plane.) In their work, and elsewhere in this paper, "growth" or "growth rates" refers to the amount of shell secreted and is thus measured along the spiral trajectory of the shell. Løvtrup and Løvtrup provide geometrical arguments that, whether umbilicate or not, turbinate logarithmic spirals with circular generating curves, do indeed have the points of maximum and minimum growth on *different* diameters, and that the position of the point of maximum growth is simply related to the apical angle of the shell ( $\beta$  in Fig. 1). They go on to say that a turbinate shell must

have these points on the same diameter, but that, as this is impossible, a "core" replaces the coiling axis. They claim that this umbilicus does allow these points to lie on the same diameter, although I do not understand how this could be. It is also to allow this, they argue, that in real shells the generating curve deforms from the circular outline of their model.

Much of this argument I will not discuss further because I fundamentally fail to understand why a shell must avoid having points of maximum and minimum shell deposition on different diameters (Løvtrup and Løvtrup: p. 60). What does require comment is their misjudgement of the relationship between the position of these points and the apical angle. This is necessary because one of their main conclusions is valid and potentially important: growth rates around the aperture are theoretically capable of directing the shape of the shell. Later in this paper I cast doubt on whether this is a practical means of developmental regulation (the alternative is for the position of the mantle to control growth *direction*); but first I explore the real geometrical relationship between shell shape and the pattern of differential growth rates.

## POSITION OF MAXIMUM AND MINIMUM GROWTH RATE

Løvtrup and Løvtrup's ('88) Figure 14 (my Fig. 1) misplaces the position of maximum growth, putting it at point B, a simple function of the apical angle. Maximum growth rate must occur on or below point A, not above. Consider two points symmetrically below and above A and thus equidistant from the coiling axis. Look-

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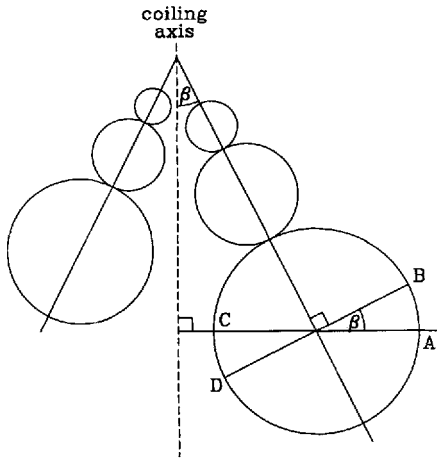


Fig. 1. Section down the coiling axis of a logarithmic spiral with circular generating curve and apical angle  $\beta$ . Adapted from Løvtrup and Løvtrup ('88).

ing along the axis both move the same distance about the axis in one revolution, but in a direction parallel to the coiling axis the point below must move further (Fig. 2). Using a similar argument the point of minimum growth must lie at or above C (Fig. 1). The precise position of the maximum and minimum is actually a complex function of the expansion rate and the relative size of the aperture, as well as the apical angle (see Appendix A).

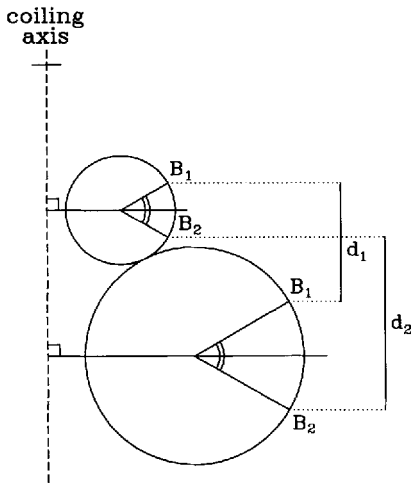


Fig. 2. The same section as Figure 1 (omitting the left-hand side). The distance  $d_1$ , moved in one revolution parallel to the coiling axis by point  $B_1$ , is less than  $d_2$ , the corresponding distance for  $B_2$ .

Nevertheless, as is shown in Appendix A, they are correct that an expanding shell growing isometrically with a circular generating curve will grow planispirally if, and only if, the maximum and minimum points are on a diameter. This result may even appear intuitive but it must not be freely extrapolated to generating curves of other shapes. For less symmetrical shapes, whether the points of maximum and minimum growth lie on a diameter is immaterial and is not what determines whether the curve is planispiral. Thompson ('17) also does not make this limitation explicit.

Consider the triangular aperture in Figure 3. Maximum growth will clearly occur at point B, as it both has the largest radius of rotation and moves furthest parallel to the axis. Conversely, the minimum growth rate must occur at C. Line CB is not a diameter, yet, depending on the relative growth rate elsewhere, for instance at P, the shell can be turbinate or planispiral.

LOCI OF POINTS OF EQUAL GROWTH RATE

What aspects of growth rate distribution do determine apical angle? Consider a point  $(r, z)$  on the surface of a logarithmic spiral.  $r$ , the distance from the coiling axis, increases as an exponential function of the number of revolutions  $(t)$ .

$$\therefore r = Ae^{it}, \text{ where } A \text{ and } i \text{ are constants.}$$

$z$  is the distance from the apex measured parallel to the axis. Since growth is isometric,

$$z = br$$

where  $b$  is a constant ( $\cot^{-1}(b)$  is the apical angle for that point—see Fig. 7).

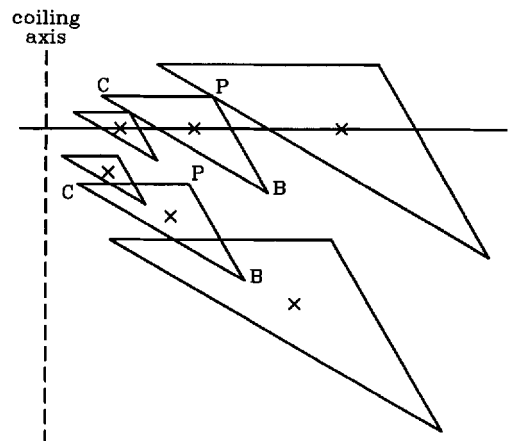


Fig. 3. Superimposed sections, down their coiling axes, of two shells with the same triangular generating curves. Their apical angles differ, yet the points of maximum and minimum growth rate (B and C) are identical.

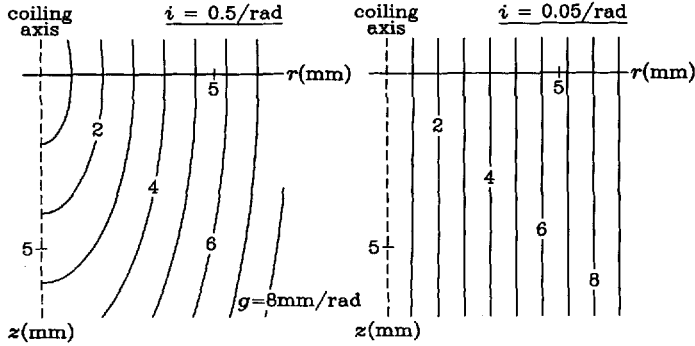


Fig. 4. Elliptical contours of equal growth rate ( $g$ ) for points on a logarithmic helicospiral. The loci for two values of  $i$ , the expansion rate, are shown, but the value for the left-

hand diagram is unrealistically high: the range of  $i$  in the British terrestrial snail fauna is 0.008/radian to 0.12/radian (from Cameron [81], using  $i = [\ln W]/[2\pi]$ ).

Growth rate is considered as the length of shell laid down per angle of revolution about the coiling axis. This length is the distance moved by a point on the aperture as the shell grows, measured along the curve of its trajectory, i.e. the arc length. It is a standard result in differential geometry that

$$\begin{aligned} (d(\text{arc length}))^2 &= (dr)^2 + (rdt)^2 + (dz)^2 \\ \therefore (d(\text{arc length}))^2 &= (irdt)^2 + (rdt)^2 + (birdt)^2 \\ &\text{since } dr = dr/dt \times dt \text{ and } dz = dz/dr \times dr \\ \therefore \left[ \frac{d(\text{arc length})}{dt} \right]^2 &= (i + 1)r^2 + i^2z^2 \end{aligned}$$

So for a particular growth rate,  $g$ ,

$$g^2 = (i^2 + 1)r^2 + i^2z^2$$

The locus of points with equal growth rate is therefore an ellipse with center at the origin.

This means that for particular values of  $i$  (the expansion rate) we can draw, on a section containing the coiling axis, a system of concentric elliptical contours where growth rates are equal (Fig. 4). The outline of an aperture can lie anywhere on Figure 4 and we can read from the contours the relative growth rates at different points on the aperture. Note that we cannot alter the apical angle that the centre of the aperture makes without change in these relative growth rates. Thus if apical angle were regulated by other developmental processes, a by-product of any change in apical angle that left aperture shape unaffected would be a change in the pattern of growth rates.

Conversely, if we specify the expansion rate ( $i$ ) and the two ratios linking growth rates at three specified points around an aperture (and specify that the aperture is coplanar with the coiling axis), there is generally only one position at which

the aperture can sit to match the contours. We can then read from the diagram the consequent orientation of the coiling axis relative to the aperture and the apical angle of the shell resulting from such a pattern of growth rates. Rigorous control of growth rates would thus determine growth direction.

We can now also understand how defining the position of the maximum and minimum growth rate does not necessarily determine the apical angle (discussed on page 260). Figure 5 shows how the triangular aperture of Figure 3 can be moved around the diagram, making various apical angles, without changing the points of maxi-

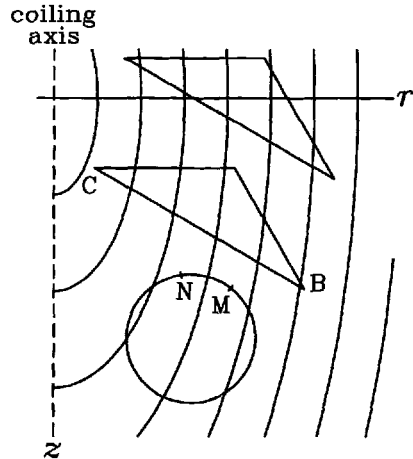


Fig. 5. The generating curve of Figure 3 can sit anywhere in this quadrant of the growth-contour map (see Fig. 4) without the sites of maximum and minimum growth (B and C) changing. But the circle cannot sit anywhere where growth is a maximum at M and a minimum at N.

imum and minimum growth. It also shows that we cannot specify these points to be just anywhere on the outline. For instance, if the maximum growth on the circular aperture occurs at M, whatever the aperture's position on the diagram or the shape of the ellipses, minimum growth cannot occur at N. Thus, if the aperture is rigid and in a plane containing the coiling axis, only certain patterns of growth rate are possible and growth rate at any particular point is constrained by growth rates elsewhere.

Return now to the original problem of when it is that the points of maximum and minimum growth lie on a diameter of a circle. As can be grasped from Figure 6, the ellipses never make tangents with a circular aperture at points on the same diameter, unless the circular aperture lies symmetrically over the coiling axis, impossible in three dimensions, or unless it lies over the horizontal axis, thus forming a planispiral. This would also be the case if the elliptical loci became circular, but  $(i^2 + 1) > i^2$ , so circular loci would imply an infinitely large value of  $i$ , i.e., expansion outwards without rotation, which is nonsensical with a circular aperture orientated in this plane. Another possibility is for  $i = 0$ , no expansion, when the elliptical loci become straight lines parallel to the coiling axis. In such

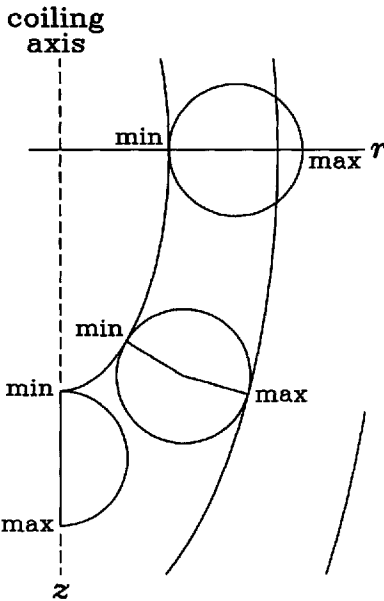


Fig. 6. Sites of maximum and minimum growth around a circular generating curve positioned at three different apical angles. Three contours of equal growth rate are also shown (see Fig. 4).

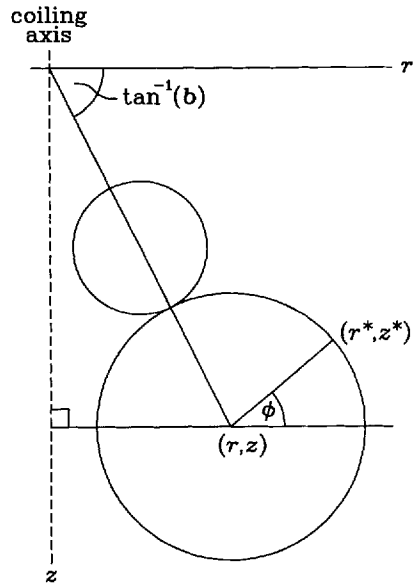


Fig. 7. The same section as Figures 1 and 2, showing terms used in text.

a staircase-like helix, the points furthest from, and nearest to, the coiling axis are sites of maximum and minimum growth, regardless of pitch.

DISCUSSION

Having explored the geometrical relationship between differential growth rate and apical angle, and recognized that the former could thus be the physiological process that directs the latter, I will now question how powerful such developmental control could be. To use an analogy, the usual way to build a wall is with parallel courses of bricks. So one might think that it is the bricks' rectangular shape and consistent size that makes a wall vertical and flat-topped. In fact, it is the builder's use of a plumb line and spirit level that controls these attributes and he could make an equally vertical wall if some of the bricks were malformed, or even by selecting irregular stones.

When expansion rate and the shape of the generating curve are fixed, growth rate around the generating curve must indeed determine the orientation of the coiling axis and apical angle. But equally, if instead it were orientation of the coiling axis and apical angle that were fixed, particular patterns of growth rates could still be accommodated by an altered expansion rate, a rotation or distortion of the generating curve, or just an inclination of the aperture out of the plane of the coiling axis without altering its shape in cross-section.

In most snails each whorl has to attach to the shell one revolution earlier, and often only a specific region of the preceding whorl appears suitable as a site of attachment. The possibility exists that the body follows this part of the preceding whorl like a car follows the asphalt (Hutchinson, '89). If this were not to be disrupted, differential growth could exert only a severely constrained influence on how the shell coils. Either the distortions to the aperture mentioned in the preceding paragraph would occur and/or growth rate would largely have to respond passively to accommodate active positioning of the shell, accurately spaced away from the preceding whorl by the width of the body. Similarly with aperture shape we can envisage other mechanical constraints that might limit how much this responds to patterns of growth rates: in the short term, the new shell is constrained to fit onto the old aperture; and we might suppose that the body would resist the deformation necessary to secrete, or withdraw inside, certain novel shapes of aperture that growth rates might require, especially if the latter were perturbed by damage.

Without experiment we therefore need to consider further to what extent growth rates either direct shell characters or have to accommodate to the demands of other shell parameters. Regulation of shape by mechanical processes is at least easier to conceive of than the unknown means by which shell secretion would need to be kept accurately tuned along the mobile, deformable strip of mantle edge. It is hard to envisage every mantle cell on a complex outline "knowing" physiologically even the correct speed to advance just so as not to lag behind its neighbor. I consider it much more likely that a limited capability of the mantle edge to deform holds back mechanically those local regions of mantle that tend to rush ahead in shell production, so ensuring the smooth aperture edge that we observe. (Excess production might instead be turned to local thickening.) It is in just the same way that other mechanical forces acting on the mantle edge, such as a reluctance of the body to part company with the preceding whorl, could force growth rates to assume patterns unrelated to the growth rate potential of the tissue.

Using the formulae derived in Appendix A, I have quantified just how accurately growth rates would have to be controlled in order to regulate apical angle. It turns out that quite exceptional accuracy is required. The data in Cameron ('81) suggest that *Trichia striolata* is typical of British pulmonates in its expansion rate and size of

umbilicus, which give values of  $i = 0.068$  and  $M = 0.415$ , if we assume a circular generating curve (these parameters are defined in Appendix A). Consider the growth rates when the center of the generating curve is 10 mm from the coiling axis. In the planispiral case (apical angle  $0^\circ$ ) maximum growth occurs, as we know, at  $\phi$  (see Fig. 7) =  $0^\circ$ , and minimum growth at  $\phi = 180^\circ$ . When the apical angle is  $45^\circ$ , maximum growth rate is 14.2 mm/radian and occurs when  $\phi = -0.19^\circ$ . The growth rate at  $\phi = 0^\circ$  is only  $2.2 \times 10^{-5}$  mm/radian less than the maximum. Considering still an apical angle of  $45^\circ$ , minimum growth rate occurs when  $\phi$  is only  $0.45^\circ$  short of  $180^\circ$ , so the maximum and minimum points miss being on a diameter by just  $0.26^\circ$ . Minimum growth rate is 5.9 mm and growth rate at  $\phi = 180^\circ$  is only  $1.3 \times 10^{-4}$  mm/radian more. Nor do patterns of growth elsewhere on the generating curve alter much: the points half way between the sites of maximum and minimum growth grow, in the planispiral case, at 0.7070 the maximum rate, and in the turbinate case, at 0.7081 and 0.7075 the maximum rate. It thus seems extremely implausible that a snail could directly control relative growth rates accurately enough to regulate the apical angle between  $0^\circ$  and  $45^\circ$ , let alone within the narrower limits observed in nature.

Bovid horns appear a more likely case of differential growth directing shape, since the flexible mantle is replaced by a horn-secreting annulus supported by a rigid bony boss, and coiling is not constrained by the need for consecutive whorls to attach. However, I will again quantify the accuracy of growth rates required to regulate apical angle, using parameter values estimated from the horn of a domestic sheep (*Ovis aries*):  $i = 0.19$ ,  $M = 0.21$ , apical angle =  $62^\circ$ . If the horn were circular in section, the points of maximum and minimum growth still would lie only  $1.59^\circ$  off a diameter. The points half way between the sites of maximum and minimum growth grow at 0.8424 and 0.8415 the maximum rate. The ragged surface of the horn of the sheep does not suggest that the regulation is therefore precise enough to control the apical angle, although relative growth rates could well control the tightness of coiling. An alternative is that it is the curved bony core within the base of bovid horns that moulds the horn extruded around it (Thompson, '17).

Curly hair is a clearer example of a spiral, although not an expanding one, in which growth rates could well dominate mechanical constraints in determining the tightness of coiling. But for apical angle to be regulated in this way, the

elliptical loci of equal growth rate must appear less like straight lines, requiring larger expansion rates and generating curves. So perhaps Løvtrup and Løvtrup's idea might be most applicable to the bivalves, in which these characteristics are most developed.

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APPENDIX A

Figure 7 is a section down the coiling axis of a logarithmic spiral with a circular aperture. ( $r, z$ ) are the co-ordinates of the aperture center, measured relative to the apex of the spiral. ( $r^*, z^*$ ) are the co-ordinates of a point on the periphery making an angle  $\phi$  with a radius perpendicular to the coiling axis.

Growth is isometric, so  $z = br$  and  $R$  (the radius of the aperture) =  $Mr$ , where  $M, b$  are constants.

$$r^* = r + R \cos \phi = (1 + M \cos \phi)r$$

$$z^* = br - R \sin \phi = (b - M \sin \phi)r$$

Let  $r = Ae^{it}$  (logarithmic spiral), where  $A$  is a constant,  $t$  the number of revolutions, and  $i$  a measure of the rate of expansion radially.

$$\therefore dr^* = dr^*/dr \times dr/dt \times dt = (1 + M \cos \phi)irdt$$

and

$$dz^* = dz^*/dr \times dr/dt \times dt = (b - M \sin \phi)irdt$$

It is a standard result that

$$[d(\text{arc length})]^2 = (dr^*)^2 + (r^*dt)^2 + (dz^*)^2$$

$$\therefore [d(\text{arc length})]^2 = [(1 + M \cos \phi)irdt]^2 + [(1 + M \cos \phi)rdt]^2 + [(b - M \sin \phi)irdt]^2$$

$$\text{growth rate} = \frac{d(\text{arc length})}{dt}$$

$$= r[(i^2 + 1)(1 + M \cos \phi)^2 + i^2(b - M \sin \phi)^2]^{1/2}$$

At those points around the aperture where growth rate is a maximum or minimum,

$$\frac{d(\text{growth rate})}{d\phi} = 0$$

$$\therefore \frac{r[-2M \sin \phi(i^2 + 1)(1 + M \cos \phi) - 2Mi^2 \cos \phi(b - M \sin \phi)]}{2[(i^2 + 1)(1 + M \cos \phi)^2 + i^2(b - M \sin \phi)^2]^{1/2}} = 0$$

$$\therefore Mr[M \sin \phi \cos \phi + (i^2 + 1) \sin \phi + bi^2 \cos \phi] = 0 \quad (A1)$$

If two solutions exist on a diameter, this is true also for  $\phi + \pi$ .

$$\therefore Mr[M \sin(\phi + \pi) \cos(\phi + \pi) + (i^2 + 1) \sin(\phi + \pi) + bi^2 \cos(\phi + \pi)] = 0$$

$$\therefore Mr[M \sin \phi \cos \phi - (i^2 + 1) \sin \phi - bi^2 \cos \phi] = 0 \quad (A2)$$

Adding Equations A1 and A2,

$$2M^2r \sin \phi \cos \phi = 0$$

This is only true if

- $r = 0$  or  $M = 0$  (trivial cases);
- or  $\cos \phi = 0$ , but this is never a solution to (A1);
- or  $\sin \phi = 0$ , which is a solution to (A1) when  $bi^2 \cos \phi = 0$ .

The latter is true either when  $i = 0$ , the limiting case of a non-expanding helix, or when  $b = 0$ , the planispiral, thus the only case of an exponentially expanding helix where maximum and minimum growth rates occur on exactly opposite sides of a circular aperture.