# A simple shell model: applications and implications

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**KEY WORDS.** Gastropods, shell, model.

**ABSTRACT.** A simple computer-assisted, non-mathematical procedure for emulating sagittal sections of Gastropod shells is described. Examples illustrate that the final "shell" shapes can largely be predicted from the values of the construction parameters. The problem of the meaning of traditional descriptions of the shape of shells is briefly addressed.

## 1. INTRODUCTION

Coiled shells are the hallmark of most living Molluscs and all Brachiopods, amounting to about half of all non-arthropod invertebrates. They also constitute a large proportion of all fossils. The fascination long exerted on biologists, mathematicians and other artists by the regular shapes of shells is reflected in a copious literature and an abundant iconography. As it could be expected, many mathematical models have been proposed to explain or imitate the growth of coiled shells. Most of these models have been reviewed by MEINHARDT (1995) and STONE (1996). For many years, the standard tool for the geometrical analysis of coiled shells has been the model developed by the eminent palaeontologist D.M. Raup in a series of papers culminating in his well-known 1966 synthesis.

A simple, operational model of coiled shells has been recently developed (TURSCH, 1997a). The model was intended as a probe for biological studies rather than for realistic simulation of specialised structures, so it could be kept very easy. It has several advantages over other shell models. Amongst others, it rests upon independent parameters and can simulate shells with non-isometric growth (for instance Gastropods with concave or convex spires) without having to postulate *ad hoc* changes in the shell parameters (which amounts to make constants vary). The basic shape of the shell (this does not account for spines, sculpture, etc.) is entirely determined by the construction parameters.

One short paragraph in the original paper stated that the outcomes of the construction are largely predictable by comparing the values of the parameters. Detailed examples will now be given.

Some conchologists have been made insensitive to the joys of mathematics. Yet they can easily produce rough simulations of sagittal shell sections without using any equation at all, by using a small computer equipped with one of the many drawing programs now in common use. The step by step procedure (very summarily outlined in TURSCH, 1997a) will be described here. It is particularly suited for simulating the shells of multi-coiled Gastropods.

A computer program that automatically generates "shells" can easily be derived from the model. If one aims at the mass production of shell models, the use of such a program will save several minutes on every construction. If one aims at understanding the role of the individual parameters and appreciating how these parameters do interact, then the step by step, hands-on procedure is certainly more informative.

Understanding shell parameters can be of importance for evaluating the descriptions of the shape of shells, which are at the very foundations of mollusc taxonomy. Let us consider the two shells depicted in Fig. 1. The obvious difference in their aspect would ordinarily be described by listing differences in the states of a series of traditional shell characters. These may be the general outline of the shell, the height of the spire, the shape and orientation of the aperture, the convexity of the whorls, etc. In works of taxonomy, the question of whether the characters in this list are independent of each other or are not is very rarely raised, if ever. It might be instructive to see how these different traditional characters relate to differences in shell parameters.

This paper is about shapes and relies heavily on illustrations. For the study of shapes, one drawing speaks better than a thousand words, a bunch of equations or a few pages of computer program listing.

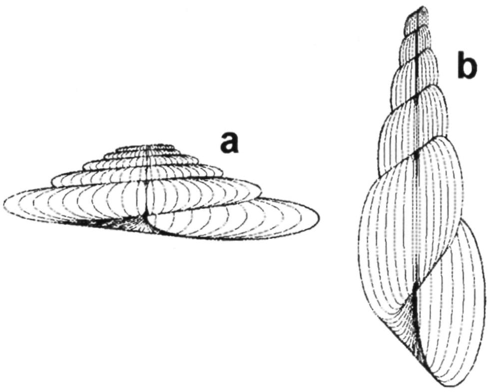



**Figure 1.** The problem of shell description. How do these two shells differ? (see text § 1).

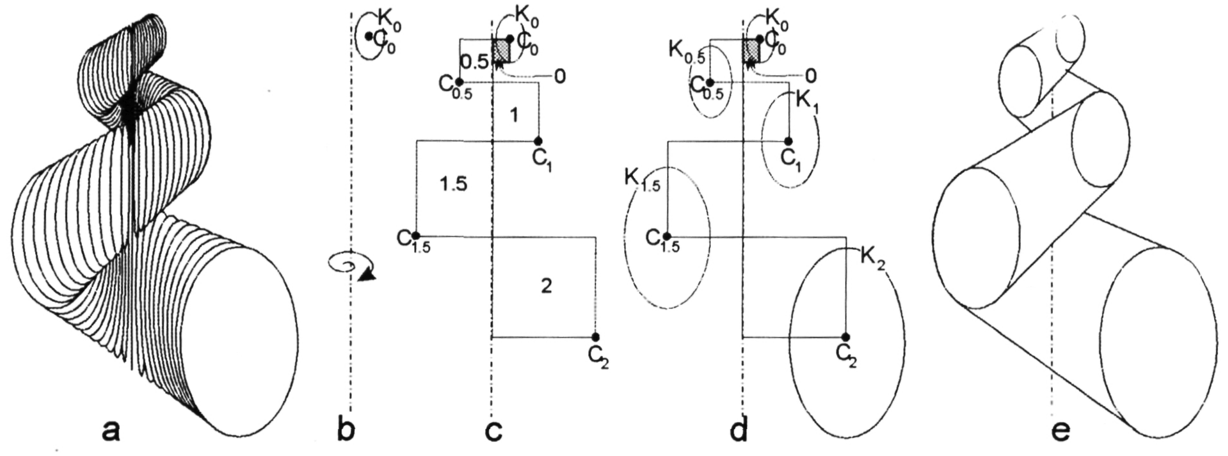



**Figure 2.** The shell model: general principle (see text § 2.1).

## 2. THE MODEL

### 2.1. Generalities

As in most other shell models, the "shell" is the surface of revolution produced by a regularly growing generating curve (the shell aperture) effecting a helico-spiral motion along an axis (the coiling axis). The generating curve $K_0$ is, as usual, taken to be an ellipse because the aperture of most shells can be approximated by (or inscribed in) this shape.

To simulate the sagittal section of a shell (such as the shell in Fig. 2, a) one first has to position in relation to a coiling axis a starting ellipse $K_0$ of suitable shape and size (Fig. 2, b).

One then determines where the centre of the generating curve $K_0$ will be located at each subsequent half-volution (Fig. 2, c). $C_0$ is the centre at the start and $C_{0.5}$, $C_1$, $C_{1.5}$, $C_2$, ...., $C_n$ are the centres after 0.5, 1, 1.5, 2, ..., $n$ revolutions. The position of these successive centres are found by building the successive rectangles "*0.5*", "*1*", "*1.5*", etc. They are all simply derived (by the use of appropriate parameters) from an essential element in the starting configuration: rectangle "*0*" (darkened in Fig. 2, c and d). Obtaining rectangle "*0*" will be explained in detail in § 3.1.1.

The starting figure $K_0$ is then "grown" by an appropriate factor to obtain $K_{0.5}$, $K_1$, $K_{1.5}$, $K_2$, etc., each of which is the placed on its calculated centre $C_{0.5}$, $C_1$, $C_{1.5}$, $C_2$ (Fig. 2, d).

If so desired, sutures can be drawn and the aspect of the whorls can be simulated by joining the edges of $K_{0.5}$, $K_1$, $K_{1.5}$, $K_2$, etc. with appropriate lines (Fig. 2, e).

The suitably positioned ellipse $K_0$, the three points $C_0$, $C_1$, $C_2$ and three growth parameters do completely determine all the construction, no matter the number of whorls.

### 2.2. Parameters

The parameters of the model have been defined in TURSCH (1997a). This has to be repeated here, to make the construction procedure comprehensible.

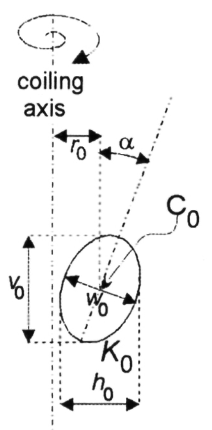



**Figure 3.** Parameters for shaping and positioning the generating curve $K_0$ (see text § 2.2.2).

#### 2.2.1. Parameters determining the starting conditions

The size and proportions of the starting ellipse $K_0$ (see Fig. 3) are determined by its smallest diameter $w_0$ (here always equal to 1) and its ellipticity $e$ (the ratio of its longer axis to the shorter).

The spatial orientation of the ellipse $K_0$ in relation with the coiling axis is described in the complete model (see TURSCH, 1997a) by three angular parameters $\alpha$, $\beta$ and $\delta$. In the simplified, rough simulation presented here, the generating ellipse $K_0$ is always *co-planar with the axis*, so parameters $\beta$ and $\delta$ will be neglected. Parameter $\alpha$ is the angle of the long axis of $K_0$ with the coiling axis.

Parameter $q$ is defined as:

$$q = r_0 / (h_0/2) \quad \text{so} \quad r_0 = q.(h_0/2)$$

Particular case: if angle $\alpha = 0$ then

$$h_0 = w_0 \quad \text{and} \quad r_0 = q.(w_0/2)$$

If angle $\alpha = 0$ and if $K_0$ is tangent to the coiling axis (a common case) then $r_0 = (w_0/2)$ and $q = 1$.

### 2.2.2. Parameters positioning the centre after one volution

Positioning the centre $C_1$ amounts to determining $d_0$ and $r_1$ (see Fig. 4). Parameter $p$ has been defined as

$$p = d_0 / (v_0/2) \quad \text{so:} \quad d_0 = p.(v_0/2)$$

Particular case: if angle $\alpha = 0$ then

$$v_0 = e.w_0 \quad \text{and} \quad d_0 = p.(ew_0/2)$$

Parameter $\mathcal{R}$ (the rate of ***R***adial expansion) has been defined as

$$\mathcal{R} = r_1 / r_0 \quad \text{so} \quad r_1 = \mathcal{R}.r_0$$

Parameter $\mathcal{R}$ applies to all subsequent whorls, so

$$\mathcal{R} = r_1 / r_0 = r_n / r_{n-1} \qquad (1)$$

### 2.2.3. Parameters positioning the centre after two volutions

Positioning point $C_2$ (see Fig. 4) amounts to determining $d_1$ and $r_2$.

Parameter $\mathcal{L}$ (the rate of ***L***ongitudinal expansion) has been defined as

$$\mathcal{L} = d_1 / d_0 \quad \text{so} \quad d_1 = \mathcal{L}.d_0$$

This parameter applies to all subsequent whorls, so

$$\mathcal{L} = d_1 / d_0 = d_n / d_{n-1} \qquad (2)$$

$r_2$ depends on parameter $\mathcal{R}$ defined here above:

$$r_2 = \mathcal{R}.r_1$$

### 2.2.4. Growth of the generating curve

This amounts to determining $w_1$, the diameter after one revolution.

The growth of the generating curve after one volution determines parameter $\mathcal{W}$ (the rate of ***W***horl expansion)

$$\mathcal{W} = w_1 / w_0$$

One will notice that $\mathcal{W}$ is the same as Raup's parameter *W*. This parameter applies to all subsequent whorls, so

$$\mathcal{W} = w_1 / w_0 = w_n / w_{n-1} \qquad (3)$$

### 2.2.5. Subsequent volutions

Each subsequent centre $C_n$ is placed in relation to the preceding centre $C_{n-1}$ by direct application of parameters $\mathcal{R}$ and $\mathcal{L}$ [see expressions (1) and (2)]. The size of each subsequent motive $K_n$ is simply that of the previous motive $K_{n-1}$ multiplied by parameter $\mathcal{W}$ [see expression (3)].

### 2.2.6. Remarks

The internal definition of $\mathcal{L}$ (the only originality in this otherwise obvious model) allows one to dodge the problem of having to select a point of origin for the helico-spiral. The position of this point in relation to $K_0$ determines much of the shape of the resulting surface of revolution, a difficulty that has plagued previous models.

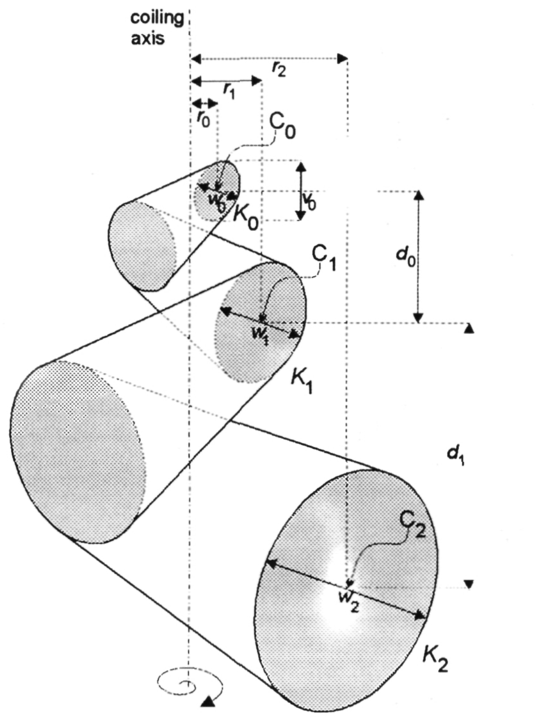



**Figure 4.** Construction: parameters for developing shell whorls (see text § 2.2.1).

The parameters of the model are of two very distinct kinds (see TURSCH 1997a). Parameters $q$, $p$, $e$, and $\alpha$ are fixed ***initial conditions***, and it is tempting to speculate that they reflect an embryonic *répertoire* (see TURSCH 1997a). Parameter $p$ only sets the pitch of the first volution. Parameter $q$ is defined from an initial distance $r_0$ and is useful for model construction and analysis convenience. In contrast, parameters $\mathcal{W}$, $\mathcal{R}$ and $\mathcal{L}$ are ***expansion rates***. They just selectively amplify the starting parameters during growth, as long as $n$ (the number of volutions) has not reached its final value.

## 3. APPLICATIONS

**Drawing program requirements.** The program should be able to draw lines, rectangles, ellipses and circles. It should also be able to group, move, rotate, mirror and scale objects (by stretching vertically and horizontally) by a given percentage. Most of the recent drawing programs allow these operations.

**Graphic conventions.** The step by step graphic constructions are made mostly by stretching and moving selected elements. In each step, the copy of a starting element (thick lines, light shading) is stretched horizontally by *x*% and vertically by *y*% (indicated by **H**= *x*%; **V**= *y*%). It is then moved as indicated by arrows to yield a resulting element (very thick lines, dark shading). This is often the starting element for the next step. For typographic facility, square roots are indicated in the text as: $p^{0.5}$.

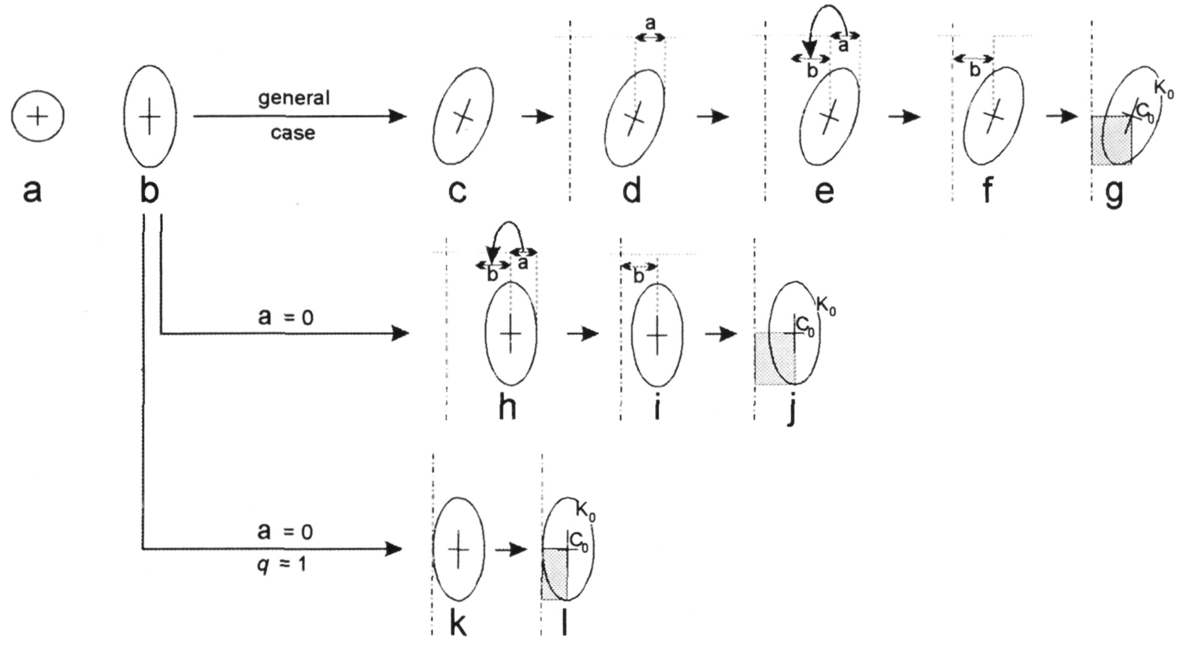
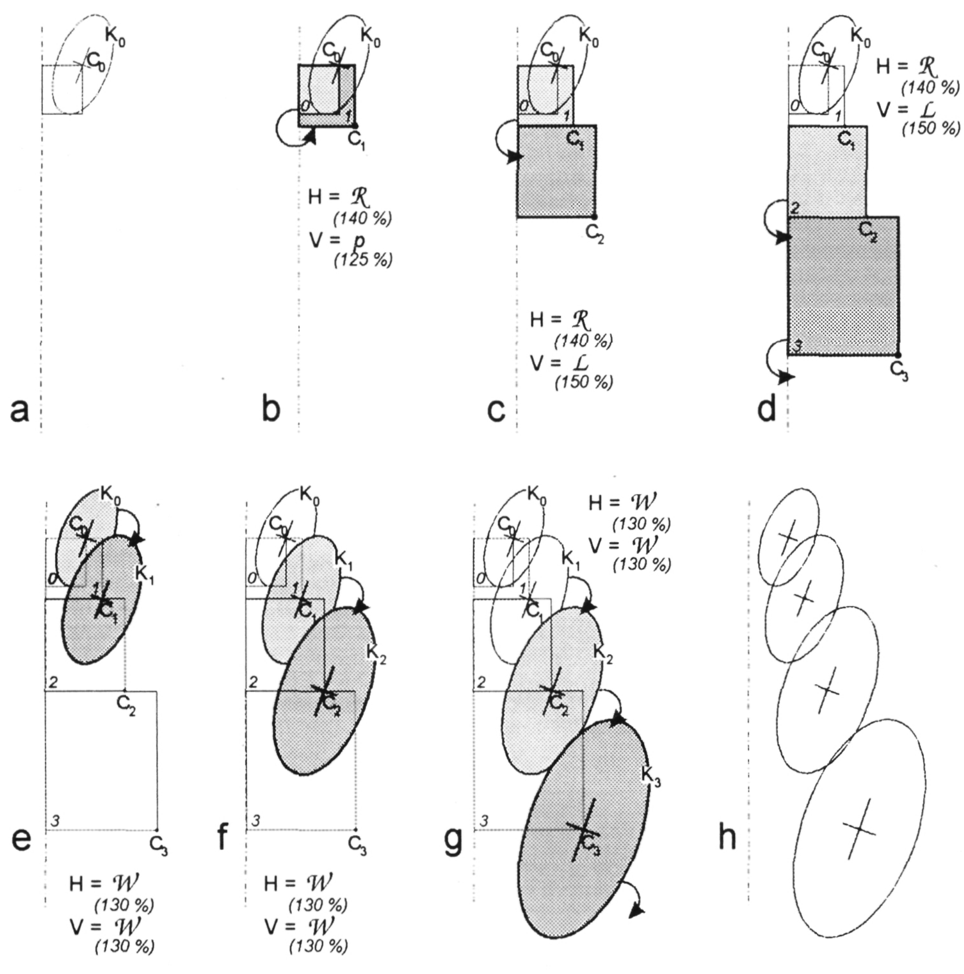



**Figure 5.** Construction: generating and placing the starting elements (see text § 3.1).




Parameters

$e$ = 2.00 ; $\alpha$ = 20 ; $q$ = 1.5 ; $p$ = 1.25 ; $\mathcal{W}$ = 1.30 ; $\mathcal{R}$ = 1.40 ; $\mathcal{L}$ = 1.50 ; $n$ = 3

**Figure 6.** Construction of sagittal half sections (see text § 3.2).

### 3.1. Construction: starting elements

All constructions require the same first steps: the positioning of the starting ellipse $K_0$ and the construction of rectangle "*0*".

**3.1.1. Starting ellipse**

*Parameters needed*: *e*, *q* and α. Let us take as example: $e = 2$; $q = 1.5$; $\alpha = 20$.

**a.** Draw two crossed lines (see Fig. 5, a). From their intersection as a centre, draw a circle of diameter $w_0$ (this has necessarily an ellipticity $e = 1$). With the command "*group*" (or similar) associate the lines with the circle into one single picture (the position of the centre will be needed to allow accurate positioning during the remainder of the construction). $w_0$ will be the length unit.

**b.** This figure is now stretched vertically by 200 % (in order to obtain an ellipse with the desired ellipticity $e = 2$) (see Fig. 5, b).

**c.** Rotate the ellipse by an angle α (in this case 20°) (see Fig. 5, c).

**d.** Draw the coiling axis and any line perpendicular to the axis (see Fig. 5, d). Build segment a.

**e.** Stretch horizontally a copy of segment a by 150 % (because $q = 1.5$) to obtain segment b, which is then placed as shown (see Fig. 5, e).

**f.** Position the ellipse at a distance b from the coiling axis (see Fig. 5, f). The generating curve $K_0$ is now fully positioned, with its centre $C_0$ marked by intersecting lines.

**g.** Erase all unnecessary features. Draw rectangle "*0*" (see Fig. 5, g). This will be the stepping stone for the remainder of the construction.

**3.1.2. Particular cases**

**a.** The construction is simplified if $\alpha = 0$ (ellipse parallel to the axis). Segment **a** (see Fig. 5, h) is now the half diameter $w_0/2$ of the ellipse. The next two steps (see Fig. 5, i and j) are straightforward.

**b.** Things are especially simple if $\alpha = 0$ and $q = 1$ (a very common case). All one has to do is then to bring directly the ellipse tangent to the axis (see Fig. 5, k) and draw rectangle "*0*" (see Fig. 5, l).

**c.** One will note that if $e = 1$ then α is indeterminate (rotating a circle by any amount yields the same circle).

*TIPS*: Make the starting ellipse small enough because it might grow very much (your computer program can "*zoom*" on small features). Most shells can be simulated by placing the starting ellipse tangent to (or very close to) the axis.

### 3.2. Construction: sagittal half sections

These constructions are very fast and extremely simple because no calculation at all is needed. Sagittal half-sections most often contain enough information to grasp the final shape of the whole "shell". All parameters are set in advance. The recipe is illustrated step by step in Fig. 6.

**3.2.1. Starting elements**

The starting elements (Fig. 6, a) are obtained as described in § 3.1, illustrated in Fig. 5. In this example: $e = 2$; $q = 1.5$; $\alpha = 20$.

**3.2.2. Centre after first volution.**

*Parameters needed*: $\mathcal{R}$ and *p*. In this example $\mathcal{R} = 1.4$, $p = 1.25$.

The position of centre $C_1$ (Fig. 6, b) is found by stretching a copy of rectangle "*1*" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 125% (because $p = 1.25$).

**3.2.3. Centre after second volution.**

*Parameters needed*: $\mathcal{R}$ and $\mathcal{L}$. In this example: $\mathcal{R} = 1.40, \mathcal{L} = 1.5$.

The position of centre $C_2$ (Fig. 6, c) is found by stretching a copy of rectangle "*1*" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 150% (because $\mathcal{L} = 1.5$). This new rectangle (rectangle "*2*") is placed as shown in Fig. 6, c. The remainder of the positioning of the subsequent centres is now repetitive.

**3.2.4. Centres of subsequent volutions**

Parameters needed: $\mathcal{R}$ and $\mathcal{L}$, as above.

The position of centre $C_3$ (Fig. 6, d) is found by stretching a copy of rectangle "2" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 150% (because $\mathcal{L} = 1.5$). This new rectangle (rectangle "3") is then placed as shown. For a "shell" with n volutions, the same procedure is repeated until one obtains rectangle "n", determining the position of centre $C_n$.

**3.2.5. Generating curve after one volution**

*Parameter needed*: $\mathcal{W}$. In this example: $\mathcal{W} = 1.30$.

Figure $K_1$ is obtained (see Fig. 6, e) by stretching a copy of the starting ellipse $K_0$ horizontally and vertically by 130% (because $\mathcal{W} = 1.30$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point $C_1$. The "growth" and the positioning of the generating curve at the subsequent volutions are now repetitive.

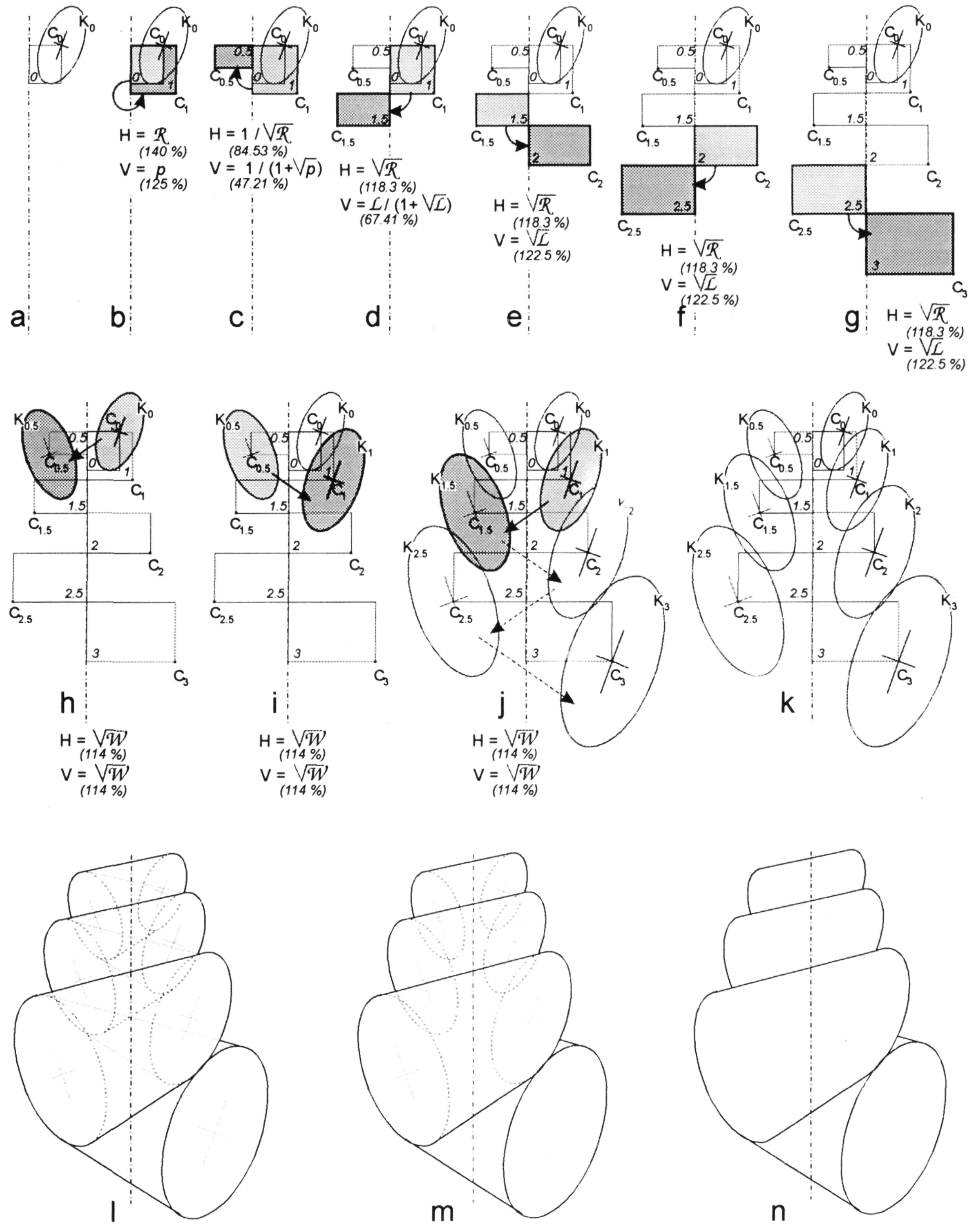
**3.2.6. Generating curve at subsequent volutions**

Parameter needed: $\mathcal{W}$, as above.

Figure $K_2$ is obtained (see Fig. 6, f) by stretching a copy of the starting ellipse $K_1$ horizontally and vertically by 130% (because $\mathcal{W} = 1.30$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point $C_2$. The "growth" and the positioning of the generating curve at the subsequent volutions is now repetitive (see Fig. 6, g). For a "shell" with *n* volutions, the same procedure is repeated until one obtains ellipse $K_n$, centred on $C_n$.

### 3.3. Construction: sagittal full sections

All parameters are set in advance. The procedure now entails the construction of the "shell" at each half-volution. Two steps do require simple transformations of the parameters.




Parameters: $e = 2.00$ ; $\alpha = 20$ ; $q = 1.5$ ; $p = 1.25$ ; $\mathcal{W} = 1.30$ ; $\mathcal{R} = 1.40$ ; $\mathcal{L} = 1.50$ ; $n = 3$

Derived values: $1/(1+\sqrt{p}) = 0.4721$ ; $\sqrt{\mathcal{W}} = 1.140$ ; $\sqrt{\mathcal{R}} = 1.183$ ; $1/\sqrt{\mathcal{R}} = 0.8453$ ; $\sqrt{\mathcal{L}} = 0.6441$ ; $\mathcal{L}/(1+\sqrt{\mathcal{L}}) = 0.6441$

**Figure 7.** Construction of sagittal full sections (see text § 3.3).

**3.3.1. Starting elements**

As for sagittal half-sections (§ 3.2), the starting elements (Fig. 7, a) are obtained as described in § 3.1 and illustrated in Fig. 5. In this example: $e = 2$; $q = 1.5$; $\alpha = 20$.

**3.3.2. Centre after first volution**

This step is the same as for sagittal half-sections (see § 3.2.2).

*Parameters needed*: $\mathcal{R}$ and $p$. In this example $\mathcal{R} = 1.4$, $p = 1.25$.

The position of centre $C_1$ (Fig. 7, b) is found by stretching a copy of rectangle "*1*" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 125% (because $p = 1.25$).

**3.3.3. Centre after 0.5 volution**

*Parameters needed*: $\mathcal{R}$ and $p$. One has to calculate the values of $\mathcal{R}^{0.5}$ (here: 1.183) and $1/(1+ p^{0.5})$ (here: 0.4721).

The position of centre $C_{0.5}$ is found by stretching a copy of rectangle "*0*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 47.21% [because $1/(1+ p^{0.5}) = 0.4721$]. This new rectangle (rectangle "*0.5*") is placed as shown in Fig. 7, c.

**3.3.4. Centre after 1.5 volution**

*Parameters needed*: $\mathcal{R}$ and $\mathcal{L}$. One has to use $\mathcal{R}^{0.5}$ (in this example: 1.183) and $\mathcal{L}/(1+\mathcal{L}^{0.5})$ (here: 0.6741).

The position of centre $C_{1.5}$ is found by stretching a copy of rectangle "*1*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 47.21% [because $\mathcal{L}/(1+ \mathcal{L}^{0.5}) = 0.4721$]. This new rectangle (rectangle "*1.5*") is placed as shown in Fig. 7, d.

**3.3.5. Centre after two volutions**

*Parameters needed*: $\mathcal{R}$ and $\mathcal{L}$. One has to use $\mathcal{R}^{0.5}$ (in this example: 1.183) and $\mathcal{L}^{0.5}$) (here: 1.225).

The position of centre $C_2$ is found by stretching a copy of rectangle "*1.5*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 122.5% (because $\mathcal{L}^{0.5}= 1.225$). This new rectangle (rectangle "*2*") is placed as shown in Fig. 7, e.

**3.3.6. Centres of subsequent volutions**

*Parameters needed*: $\mathcal{R}^{0.5}$ and $\mathcal{L}^{0.5}$, as above.

The position of centre $C_{2.5}$ (Fig. 7, f) is found by stretching a copy of rectangle "*2*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 122.5% (because $\mathcal{L}^{0.5}= 1.225$). This new rectangle (rectangle "*2.5*") is placed as shown. For a "shell" with $n$ volutions, the same procedure is repeated until one obtains rectangle "$n$", determining the position of centre $C_n$ (see Fig. 7, g).

**3.3.7. Generating curve after 0.5 volution**

*Parameter needed*: $\mathcal{W}^{0.5}$. In this example: $\mathcal{W} = 1.30$ and $\mathcal{W}^{0.5}= 1.14$.

Figure $K_{0.5}$ is obtained (see Fig. 7, h) by rotating a copy of the starting ellipse $K_0$ by an angle $-\alpha$, then stretching it horizontally and vertically by 114% (because $\mathcal{W}^{0.5} = 1.14$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point $C_{0.5}$. The "growth" and the positioning of the generating curve at the subsequent volutions are now repetitive.

**3.3.8. Generating curve at subsequent volutions**

*Parameter needed*: $\mathcal{W}^{0.5}$, as above.

Figure $K_1$ is obtained (see Fig. 7, i) by "rotating a copy of the ellipse $K_{0.5}$ by an angle $-\alpha$, then stretching it horizontally and vertically by 114% (because $\mathcal{W}^{0.5} = 1.14$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point $C_1$. The "growth" and the positioning of the generating curve at the subsequent volutions is now repetitive (see Fig. 7, j). For a "shell" with $n$ volutions, the same procedure is repeated until one obtains ellipse $K_n$, centred on $C_n$.

The procedure might look more difficult than it really is. With a little practice, once the derived values have been established, steps a to k (in Fig. 7) are easily effected in less than 5 minutes.

**3.3.9. Final image**

The final image (Fig. 7, k) can now be made up by masking hidden parts, drawing sutures and delineating the shape of whorls (for instance as in Fig. 7, l, m or n). Whorl resorption occurs in many Gastropods. According to the desired type of model, one can elect to have the "aperture" mask the previous whorl or not.

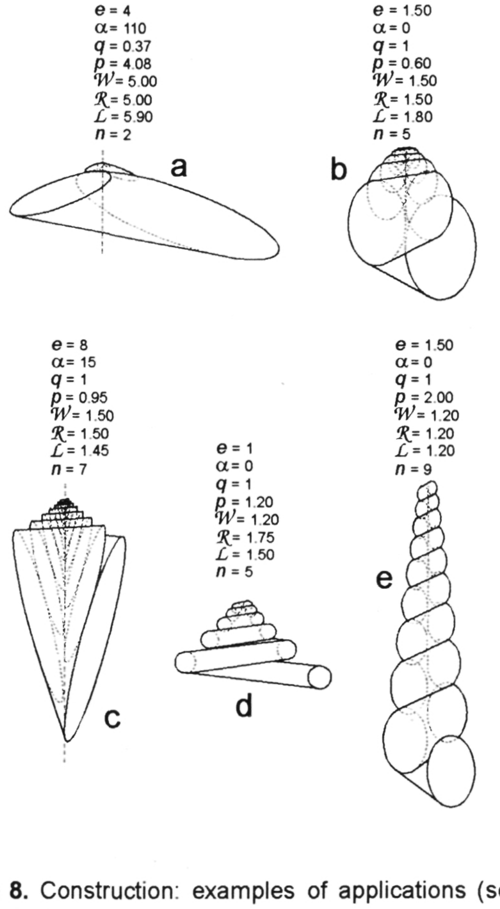



**Figure 8.** Construction: examples of applications (see text § 3.3.9).

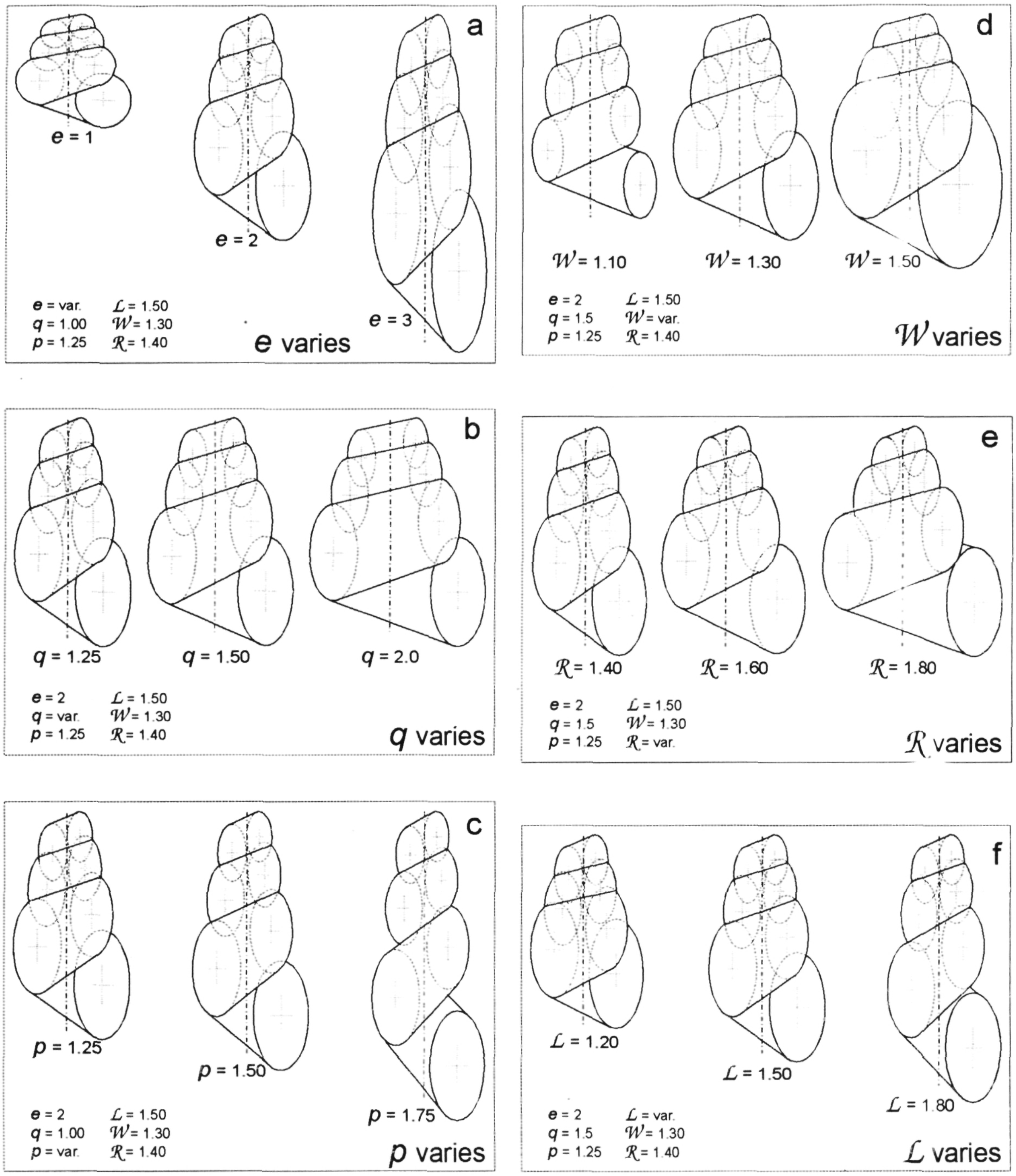



**Figure 9.** Shape variations due to changes in a single parameter (see text § 4.1).

Rather realistic renditions of many existing shells are easily produced by the graphic construction described here above (see Fig. 8, illustrating a few familiar cases). For even more realism, the shape of the starting ellipse could be modified, for instance by adding or substracting suitable features. With so many variables, it would take a very long time to produce a given "shell" by experimenting with arbitrary combinations of parameters. The task is very much simplified if one understands how each individual parameter acts and how given combinations of parameters do affect the final shape.

## 4. THE CONTROL OF SHAPE

Easy "rules of construction" can be deduced from the model. Some are given here under as examples. Many more could be found by an interested reader.

### 4.1. Effect of individual parameters

Examples of the changes resulting from the variation of individual parameters are shown in Fig. 9. The effect of the expansion parameters $\mathcal{W}$, $\mathcal{R}$, and $\mathcal{L}$ are quite predictable. One will notice that the final shape is extremely dependent from the initial conditions $q$, $p$ and $e$.

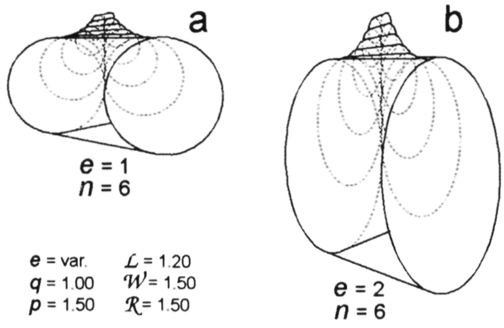



**Figure10.** Parameter ***e*** affects not only the shape of the body whorl but also the shape of the spire (see text § 4.1).

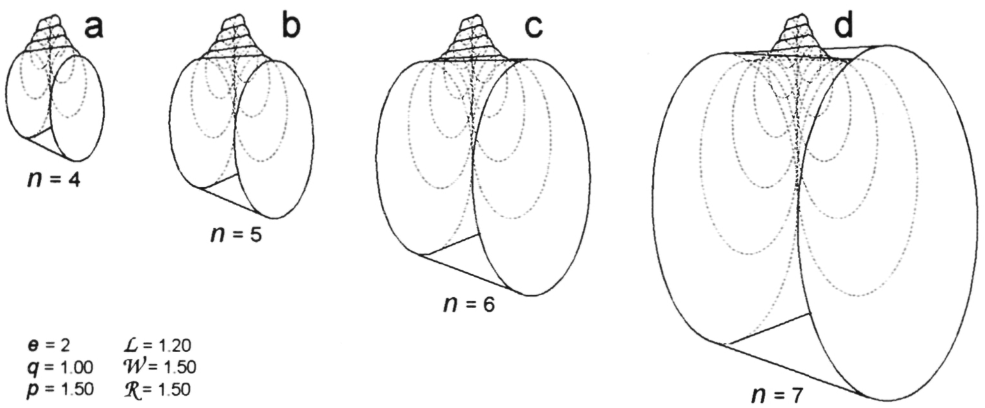



**Figure 11.** Non-isometric growth without change in shell parameters. The shape of the shell varies with the number of whorls *n*. (see text § 4.1).

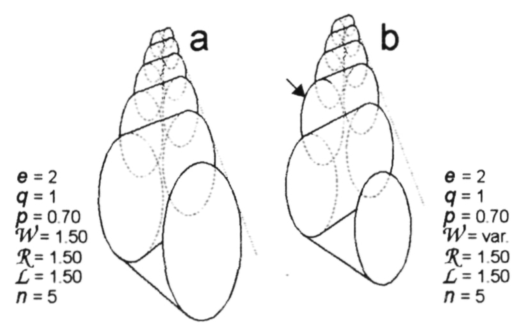



**Figure 12.** Non-isometric growth by abrupt change of a shell parameter. The construction of shell **a** yields shell **b** if at whorl 2.5 (marked by an arrow) one changes the value of *W* from 1.5 to 1.2 (see text § 4.1).

Fig. 10 shows that *e* (the ellipticity of the generating curve) influences not only the shape of the body whorl but also the shape of the spire. Some more dramatic effects of parameter *e* will be shown in § 4.3.

The shape of many shells (most shells, according to VERMEIJ 1993) does vary during growth. In contrast to others, this model can produce "shells" with non-isometric growth (see Fig. 11) without having to modify progressively the values of parameters. It is thus quite important to specify a value for *n* (the number of whorls).

Abrupt changes in the value of parameters do happen during the growth of some real shells (for an example, see TURSCH 1997b). This can of course be easily emulated in this step by step procedure by modifying any of the expansion parameters 𝒲, ℛ, or ℒ at any desired point of the construction (for an example, see Fig. 12).

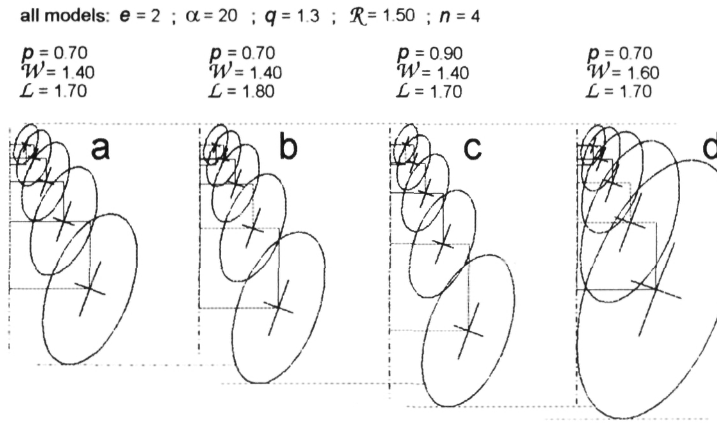



**Figure 13.** General features of the shell are affected by individual variations of several parameters. For instance, all other parameters kept constant, the length of a given shell (a) is modified by a change of $L$ (b), of $p$ (c) or $W$ (d). (see text § 4.2).

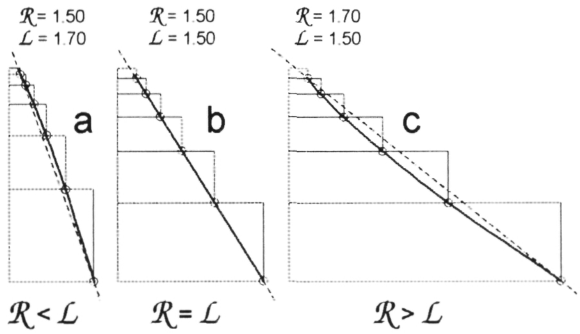



**Figure 14.** The relation of $R$ to $L$ determines the alignment of the centres (see text § 4.2.1).

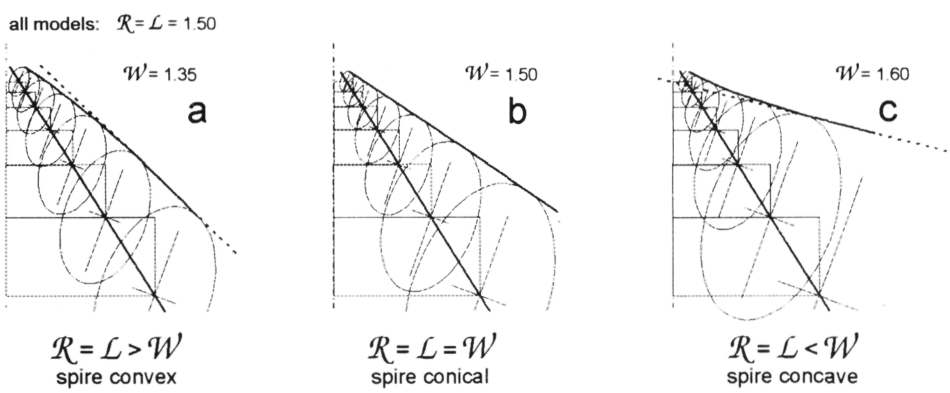



**Figure 15.** If $R = L$ then the value of $W$ determines the shape of the spire (see text § 4.2.2).

General features of the shell are affected by individual variations of several parameters. For instance, the total length depends on both the rate at which the centre of the aperture moves "down" the coiling axis (the compounded effects of $p$ and $\mathcal{L}$) *and* the growth rate of the aperture ($\mathcal{W}$). Therefore, all other parameters being the same, individual variations of $p$, of $\mathcal{W}$ or $\mathcal{L}$ will affect the total length of the "shell" (see Fig. 13). In the same way, the diameter (at any moment of growth) depends on both the growth rate of the aperture ($\mathcal{W}$) *and* the rate at which the centre of the aperture moves away from the coiling axis ($\mathcal{R}$).

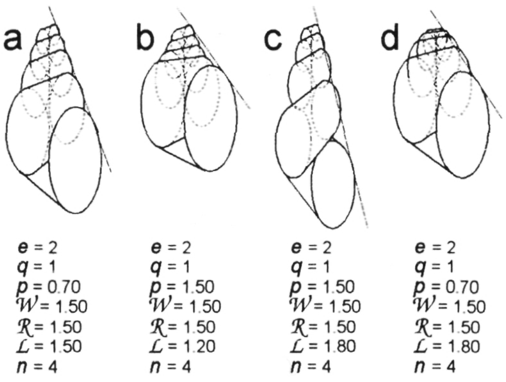



**Figure 16.** If q = 1 and *W* = *R* then all the whorls are tangent to the coiling axis (see text § 4.2.2).

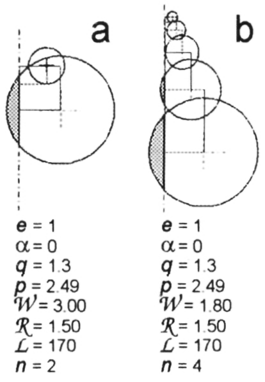



**Figure 17.** If *W* > *R* then fabricational problems may occur (see text § 4.2.2).

## 4.2. Effect of combinations of parameters

By their definition, all the parameters are completely independent from each other (this was not the case of the parameters in the classical model of RAUP 1966). However, the shape of the final "shell" depends very much on the interaction of these independent parameters.

### 4.2.1. Parameters $\mathcal{R}$, $\mathcal{L}$ and $\mathcal{W}$

If $\mathcal{R} = \mathcal{L}$ then, in sagittal view, all the centres are aligned on a straight line. The revolution of the centre of the generating curve takes place on a conical surface (see Fig. 14, b). If $\mathcal{R} < \mathcal{L}$ the surface of revolution of the centres will be convex (see Fig. 14, a); if $\mathcal{R} > \mathcal{L}$ it will be concave. (see Fig. 14, c). Note: these relations determine only the positions of the centres, not the outline of the shell.

If $\mathcal{R} = \mathcal{L} = \mathcal{W}$ then growth will be isometric, leading to shells with true conical spires (see Fig. 15, b). If $\mathcal{R} = \mathcal{W} \neq \mathcal{L}$ then growth will be non-isometric, the shape of the shell varying during growth (see § 4.1). If $\mathcal{R} = \mathcal{L} > \mathcal{W}$ the spire will be convex (Fig. 15, a). If $\mathcal{R} = \mathcal{L} < \mathcal{W}$ the spire will be concave (Fig. 15, c).

### 4.2.2. Parameter *q*

If $q = 1$ then the generating curve $K_0$ is tangent to the coiling axis (see the definition of $q$).

If $q = 1$ and $\mathcal{W} = \mathcal{R}$ then all the whorls are tangent to the coiling axis, whatever the values of the other parameters. This is a very common case in real Gastropods, as illustrated by the few examples in Fig. 16.

If $q = 1$ and $\mathcal{W} = \mathcal{R} = \mathcal{L}$ then all the whorls are tangent to the coiling axis and the shell is conispiral (Fig. 16, a).

If $\mathcal{W} > \mathcal{R}$ and if the number of volutions is not limited, the whorls will ineluctably increase beyond the coiling axis. If $q = 1$, this overlap will occur right at the start of the construction. If $q > 1$ it may happen either at the start (Fig. 17, a) or after a few volutions (Fig. 17, b), depending on the values of the other parameters. This does not necessarily constitute an insurmountable fabricational constraint. In real shells, the problem may be solved in various ways, for instance by the resorption of previous whorls or by changes in the angular parameter β (not treated here, but see TURSCH 1997a).

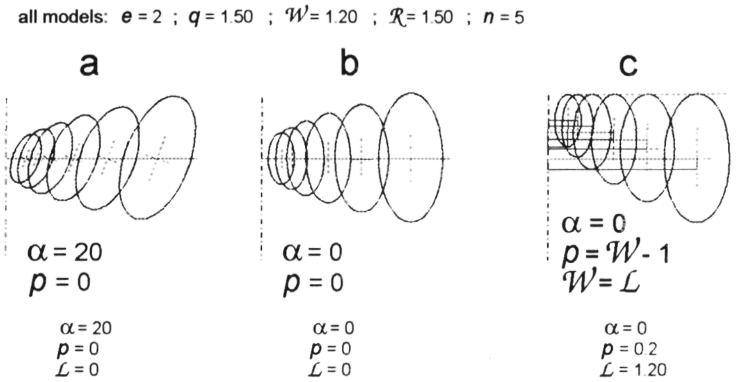



**Figure 18.** The construction of isostrophic and discoidal "shells" (see text § 4.2.3 ).

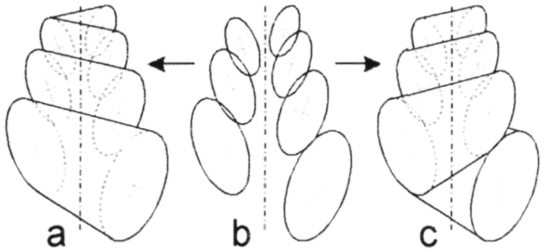



**Figure 19.** Dextral end sinistral shells (see text § 4.2.4).

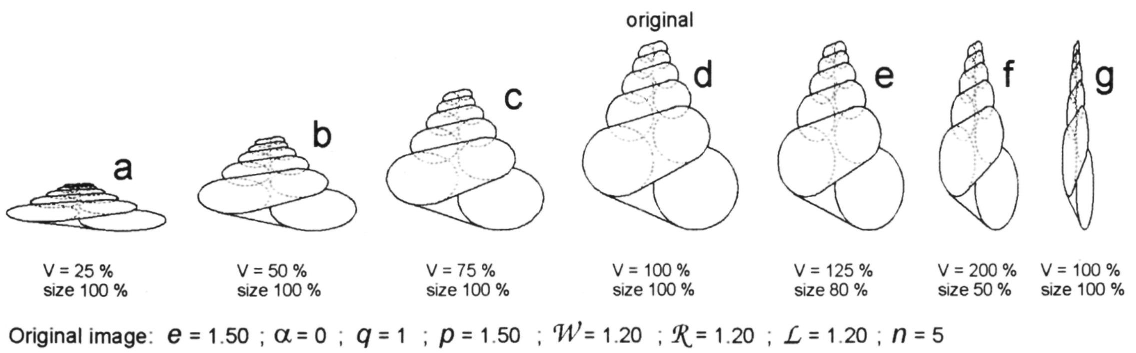



**Figure 20.** The stretching of whole images. The case $\alpha = 0$ (see text § 4.3).

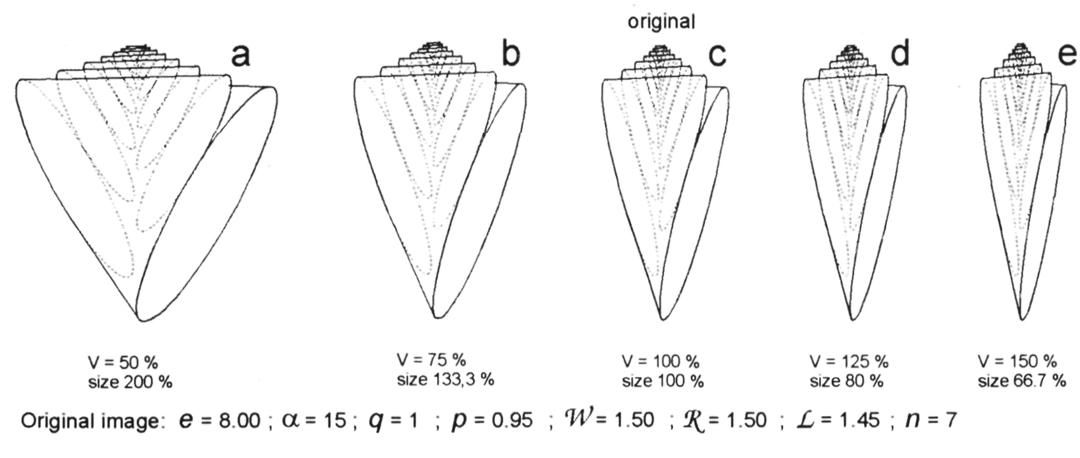



**Figure 21.** The stretching of whole images. The case $\alpha \neq 0$ (see text § 4.3).

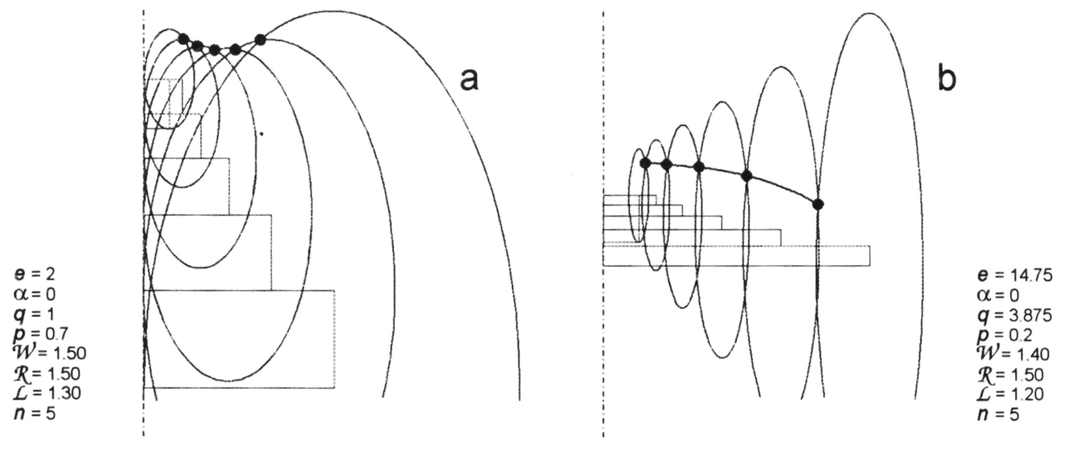



**Figure 22.** The problems of the suture (see text § 5.1).

**4.2.3. Parameter *p***

If $p = 0$ then $\mathcal{L}$ is indeterminate (its value is irrelevant for the construction). All the centres are located in the same plane, perpendicular to the coiling axis (Fig. 18, a).

If $p = 0$ and $\alpha = 0$ then the "shell" is *isostrophic* (has a plane of symmetry) (Fig. 18, b). Note that the word "planispiral" has been avoided here, as it can be taken in different meanings (see COX 1955, ARNOLD 1965).

$p = \mathcal{W}$ -1 and $\mathcal{W} = \mathcal{L}$ and $\alpha = 0$ is the condition for the "shell" to be *discoidal* (Fig. 18, c).

**4.2.4. Dextral and sinistral "shells"**

The observant reader will have noticed that the model does not specify the direction of coiling. Both dextral and sinistral "shells" can be obtained from the same construction (see Fig. 19). Sinistral shells (of entirely different nature) can be obtained by assigning negative values to parameter $p$ or to parameter $\mathcal{L}$. Note: one has then to take the negative square root of the absolute value.

### 4.3. Modification of completed models

Once a model has been completed, it is easy to modify its shape by stretching the whole image (all parts having been linked into one single image by using the command "group"). This generates very rapidly "shells" of various shapes. But what is one then really doing?

If $\alpha = 0$ in the original image, then vertical or horizontal stretching modifies only parameter $e$. An example of related images obtained by vertical stretching is given in Fig. 20. The magnitude of the observed changes in shape fully confirms the conclusions of § 4.1. Stretching "shells" does of course change their sizes. Many will have to be reduced or enlarged accordingly, to allow better comparison of shapes.

If $\alpha \neq 0$ in the original image, then vertical or horizontal stretching does modify the value of both parameters e and $\alpha$, as shown in Fig. 21.

## 5. IMPLICATIONS

### 5.1. Suture

The suture has been often used in shell morphometry because it is mostly easy to observe and lends itself well to a variety of measurements. However, the suture is a feature of much more complex nature than conchologists generally assume.

The suture is the locus of the outermost points belonging to two consecutive whorls. Determining the equation of the suture in terms of shell parameters is far from being elementary. Conversely, attempting to deduce the shell parameters from the suture would be extremely difficult (if possible at all).

Careful examination of sutures can nevertheless give most useful information. Abrupt changes in the aspect of the suture often indicate abrupt changes in parameters (for an example, see TURSCH 1997b: 98).

The example depicted in Fig. 22, a shows that the suture does not necessarily describe a regular helico-spiral: it starts by going "down" then goes "up" (this condition, although uncommon, is met in some real shells with a sunken spire, such as *Oliva concavospira* Sowerby, 1914). The revolution surface on which the suture is inscribed is also not easily deduced from the surface of revolution of the centres or even from the profile of the spire. This can be seen on the example of Fig. 22, b. In this sagittal section, the suture goes "down" the axis while the spire goes "up".

Small differences in shell parameters can produce large differences in the aspect of the suture and more work is definitely needed to clarify the properties of this familiar shell feature.

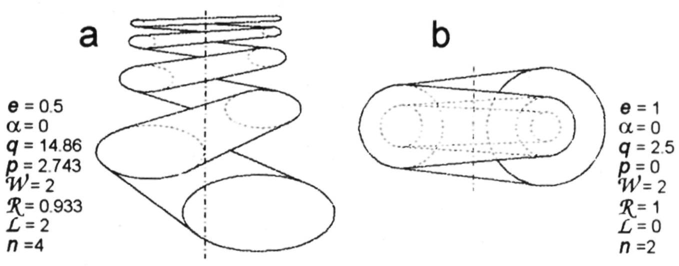



**Figure 23.** Two examples of "impossible shells" (see text § 5.2).

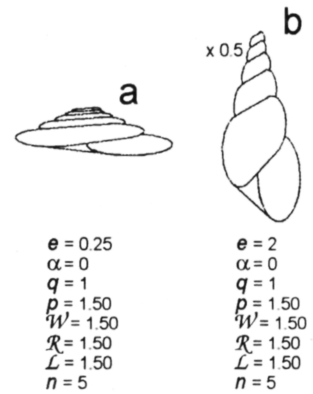



**Figure 24.** Shell parameters *vs.* traditional characters of shape. Variation of one single parameter (see text § 5.3).

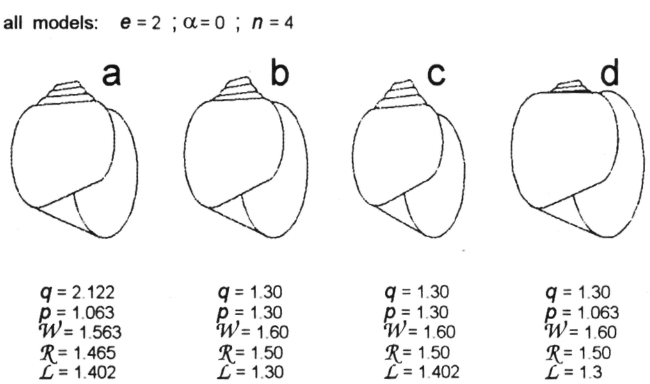



**Figure 25.** Shell parameters *vs.* traditional characters of shape. Variation of several parameters (see text § 5.3).

## 5.2. "Impossible shells"

Besides imitating known shells, the model can also produce "shells" that we can not (not yet? not anymore?) have in our collections. Many strange shapes are possible and only two examples will be given here. Some of these constructions meet obvious fabricational problems (for instance the "shell" in Fig. 23, b), some others seem perfectly feasible (see Fig. 23, a).

Accumulating a collection of such "impossible shells" is amusing but is not only a game. It constitutes an excellent tool for finding and maybe explaining the "forbidden avenues" of evolution in the "shell morphospace" (this is the set of all possible outcomes from a given geometrical/mathematical model). The interest of this classic problem in evolutionary biology has been recently emphasised by DAWKINS (1996).

## 5.3. Shell parameters *vs.* traditional characters of shape

The basic shape of shells (and of their parts) is usually described by a series of traditional characters (general outline of the shell, height of the spire, shape and orientation of the aperture, convexity of the whorls, etc.). The correlation between shell parameters and the conventional shell descriptions raises a number of questions.

**Example A.** "Shells" **a** and **f** in Fig. 20 are exactly the same as the shells depicted in Fig. 1. On the one hand, these shells have a completely different aspect, reflected by large differences in many traditional characters of shape. On the other hand, the two shells are very closely related in terms of shell parameters. They differ only by parameter $e$, as can be seen in Fig. 24 where all their parameters of the two shells are now given.

**Example B.** Conventional descriptions of the two closely matching "shells" **a** and **b** in Fig. 25 would be extremely similar, yet these two "shells" differ by the values of no less than five parameters. The smallness of the variation of each parameter does not justify the observed similarity. Let us modify shell **b** by changing only parameter $\mathcal{L}$ by the same amount. One then obtains shell **c**, of noticeably different shape (see Fig. 25). Modifying only parameter $q$ leads to shell **d**, of quite different aspect. The similarity is due to another cause: the effects of the variations in individual parameters nearly cancel each other. In real shells, this would be a nice case of convergence (possibly a case of sibling species).

Example A raises an immediate question. Do the different traditional shell characters really represent distinct characters? Example B shows that the traditional descriptors of basic shape do not necessarily reflect differences in shell parameters.

Example A shows that the conventional characters of shape are certainly correlated. All are entirely determined by the parameters of the model. All can change simultaneously by modifying one single parameter. Traditional descriptors of basic shape only *appear* to be independent. This illusion is simply due to the reductionistic way by which we describe a complex structure. We proceed by dividing it in arbitrary, smaller parts then describing these parts in succession.

The shell parameters being completely independent, one could be tempted to consider that each of them is a shell character. This would raise a serious problem. Indeed, we would then be compelled to consider that the very different shells **a** and **b** are more closely related than the very similar shells **b** and **c**. Fortunately, this does not happen. Shell parameters do not satisfy the conditions required for characters measuring phyletic similarity. They cannot be absent (thus precluding evolutionary novelty); there are no "primitive" and no "derived" parameters.

The very fact that we can (most often) recognise species by their shells establishes that the shell parameters, albeit mathematically independent, are *biologically* correlated. So there is no "description vs. parameters" paradox if one considers that it is the *whole set* of shell parameters that constitutes one single, numerical shell character. This holistic approach of shells reminds of the notion of "*morphological integration*" of NEMESCHKAL (1991).

It is the very same shell character that conventional descriptions attempt to convey (this time with words instead of figures). If the growth of the shell is regular (with constant parameters) then the whole set of the many traditional shell "characters" describing the basic shape of the shell and of its parts constitutes one single character.

It is not suggested that the whole set of shell parameters is controlled by one single gene! Most probably, these parameters do not even exist in nature as separate entities. They are parts of a model that *describes* the growth, not of natural law that *causes* a particular type of growth.

## 5.4. Deriving parameters from real shells

This paper concerns the building of conceptual "shells" from a set of predetermined parameters. What does it imply about the reverse operation: deriving parameters from real shells?

In the simple case of regular growth, the minimum requirements for finding all the parameters are: the correct positioning of the coiling axis, the determination of the co-ordinates of the centres at least at 3 accurately determined positions, the determination of the increase of the generating surface between at least at 3 accurately determined positions.

These very simple requirements are fraught with problems because small experimental errors in measurements may lead to serious discrepancies. A reliable, accurate method for exact positioning of the axis has yet to be published. Determination of the position of the centres is anything but evident, especially if the generating curve is not a true ellipse (it rarely is). Further problems arise because, in contrast to real shells, the theoretical shell model is an immaterial surface, without any thickness. One should also note that the same difficulties will be met with all other helico-spiral shell models.

Similar shells may differ by a number of parameters (see § 5.3.B), so really accurate determination of their values seems *a priori* quite difficult. To estimate shell parameters, graphic simulations are possibly more operational than shell measurements.

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