The Mathematical Form of Seashells

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1 Introduction

Seashells fascinate us. They have been used for decorations and as symbols of status and good fortune throughout history.[1] In India, fossilized ammonites from the Himalayas were seen as symbols of the god Vishnu and were gifted in matrimony.[2] In the seventeenth century, Robert Hooke studied seashells and considered the fossilized ammonites to be a window into the Earth's past (see Figure 1).[3] In Sri Lanka, trumpets made of conch shells are sounded to usher in auspicious beginnings. The varied and beautiful forms, patterns, and constitutions of seashells provide a window into the biology of the organisms that have created them and the ecologies within which they have thrived.[1,4]

Figure 1: Ammonite shell engravings based on drawings by Robert Hooke, published in 1705 in *The Posthumous Works of Robert Hooke* (Richard Waller, Ed.). |

[1] See *Fascinating Shells* by A. Salvador, The University of Chicago Press, 2022.

[2] See *Ammonites* by N. Monks and P. Palmer, Smithsonian and The Natural History Museum (London), 2002

[3] See the online article, *Robert Hooke*, by W. B. Ashworth, Jr., published by the Linda Hall Library in Missouri on February 29, 2016; also see *The Curious Life of Robert Hooke* by L. Jardine, HarperCollins, 2004.

[4] See *A Natural History of Shells* by G. J. Vermeij, Princeton University Press, 1993.

This essay explores the mathematics of seashell forms. While the topic has been explored in the past[5], my goal in this essay is to provide a systematic pedagogical derivation of the equations that govern the forms of seashells.

2 Deriving the Mathematical Form of Smooth Seashells

Fundamentally, a transverse cross section of a seashell can be modeled by an ellipse (of which the circle is a special case, of course). The movement of this (two-dimensional) ellipse along a curve in three-dimensional space gives rise to a tubular structure, which can be considered to result in an observed seashell. The two-dimensional ellipse that governs the transverse cross section is known as the generating curve ($\mathcal{G}$), and the three-dimensional space curve along which the center of the ellipse moves, the structural curve ($\mathcal{S}$). The structural curve, then, serves as an invisible spine of the seashell. In order to manage the complexity, let us break the derivation of the mathematical form of seashells into multiple steps: We will first derive the form of the structural curve; second, we will derive the form of the generating curve in a special orientation; third, we will give a general orientation to the ellipse in three-dimensional space using the Euler angles. These three steps result in realistic but smooth seashells. As a fourth step, we will add nodules to the smooth shells resulting in further realistic seashell models.

In the discussion to follow, the coordinate systems we set up are right-handed; that is, the thumb of the right hand points in the positive Z-direction when the rest of the fingers are curled from positive X- to positive Y-direction. The global[6] coordinate system $\{\mathcal{O}, X, Y, Z\}$ that we will use in this essay is shown in Figure 2.

2.1 The Form of the Structural Curve

The structural curve "runs" lengthwise along a shell and it is generally observed that it takes the shape of a spiral when viewed from a certain perspective. This spiraling nature of the shell is associated with its uneven growth. When projected onto a two-dimensional plane, a special feature of this spiral is that the angle between the radial line from the center of the spiral to a given point on it and the tangent to the spiral at that point is a constant and is independent of the point chosen.

[5] A pioneer in studying the mathematics of biological form is D'Arcy Thompson whose work first appeared in 1917; see *On Growth and Form*, Dover, 1992. Mathematical models of seashells have been explicitly studied by many researchers. They have even been modeled in the era of early personal computers by M. B. Cortie; see his article, Digital Seashells, in *Computers & Graphics*, Vol. 17, No. 1, pp. 79-84, 1993. I have relied on some of the parameters given by Cortie in his article for modeling seashells in this essay.

[6] We use the term "global" to distinguish this coordinate system from a "local" coordinate system that will be introduced later.

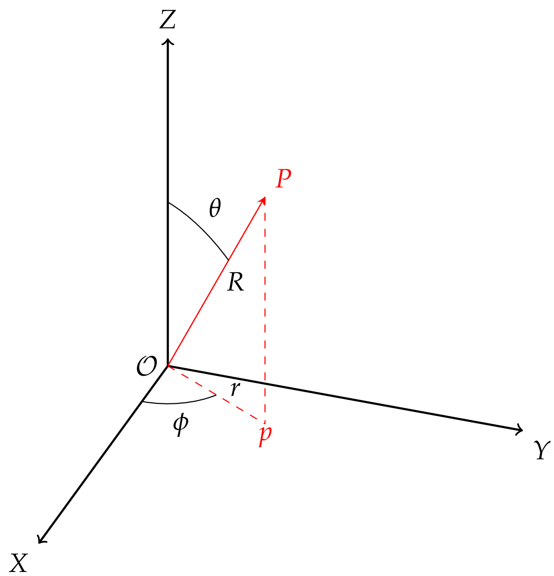

Figure 2: The right-handed global cartesian coordinate system $\{\mathcal{O}, X, Y, Z\}$. The axes are orthogonal to each other. The arbitrary point P can be marked with the spherical polar coordinates $\{R, \theta, \phi\}$, where R is the radial distance from the origin $\mathcal{O}$, and θ and ϕ are the co-latitude and the azimuthal angles, respectively. The projection of P on the XY plane is p and the radial distance from the origin to p on the XY plane is r.

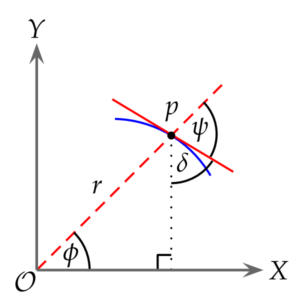

Figure 3: The projection of the structural curve $\mathcal{S}$ (blue) on the XY plane. The radial distance to point p from the origin $\mathcal{O}$ is r. The radial direction (dashed, red) to point p makes an angle ϕ with the positive X-axis. ψ is the angle between the radial direction to point p and the tangent (solid, red) to the curve at point p. The structural curve is such that ψ remains a constant at any point on it. δ is the angle between the tangent at point p and the line through p that is perpendicular to the X-axis. | Drawing by AD.

Let us assume that the structural curve is projected onto the XY plane with the property stated above (see Figure 3). Then, for an arbitrary point p on this curve, $X = r\cos\phi$ and $Y = r\sin\phi$. Note that unlike in a circle where r is constant along the curve, here r depends on the angle ϕ; thus, $r = r(\phi)$. Now consider the angle ψ, which is the angle between the radial direction to point p from the origin and the tangent to the curve at point p. It is a special property of the structural curve to be considered that the angle ψ remains a constant along the curve. Considering the angle δ shown in Figure 3, it is clear that

$$\delta = \pi - [(\pi/2 - \phi) + \psi] = (\pi/2 - \psi) + \phi.$$

It is also clear that $\tan\delta = dX/dY$. But,

$$\frac{dX}{d\phi} = r'\cos\phi - r\sin\phi, \quad \frac{dY}{d\phi} = r'\sin\phi + r\cos\phi, \quad \text{where} \quad r' = \frac{dr}{d\phi}.$$

Therefore,

$$\tan[(\pi/2 - \psi) + \phi] = \frac{r'\cos\phi - r\sin\phi}{r'\sin\phi + r\cos\phi}.$$

The left hand side of the last expression is

$$\tan[(\pi/2 - \psi) + \phi] = \frac{\tan(\pi/2 - \psi) + \tan\phi}{1 - \tan(\pi/2 - \psi)\tan\phi} = \frac{\cot\psi + \tan\phi}{1 - \cot\psi\tan\phi}.$$

We therefore have,

$$\frac{\cot\psi + \tan\phi}{1 - \cot\psi\tan\phi} = \frac{r'\cos\phi - r\sin\phi}{r'\sin\phi + r\cos\phi},$$

which, after a few algebraic steps (using the relations $2\sin\phi\cos\phi = \sin 2\phi$, $\cos^2\phi - \sin^2\phi = \cos 2\phi$), reduces to

$$(r'\cot\psi + r)\sin 2\phi - (r' - r\cot\psi)\cos 2\phi = 0.$$

For this relation to hold for all $\phi \geq 0$, the two brackets must simultaneously vanish. This implies that

$$r'\cot\psi + r = 0 \quad \text{and} \quad r' - r\cot\psi = 0.$$

Focusing on the second expression, it implies that $dr/d\phi = r\cot\psi$, which can be integrated. Thus, noting that ψ is a constant,

$$\int_{A_X}^{r} \frac{dr}{r} = \cot\psi \int_0^{\phi} d\phi \implies \ln\left(\frac{r}{A_X}\right) = \phi\cot\psi \implies r = A_X\exp(\phi\cot\psi).$$

Similarly, the first expression yields $r = A_x \exp(-\phi \tan \psi)$. The parameter A_x is akin to an amplitude in the sense that it determines the value of r where the curves intersect the X-axis; that is, the value of r when $\phi = 0$. Both these plane curves make a constant angle $0 < \psi < \pi/2$ between the radial direction to a point on the curve and the tangent to the curve at that point. The form $r = A_x \exp(\phi \cot \psi)$ takes on a prominent spiral shape for larger ψ; alternatively, the form $r = A_x \exp(-\phi \tan \psi)$ takes on a prominent spiral shape for smaller ψ. Since larger ψ angles are often relevant for seashells, let us take the form $r = A_x \exp(\phi \cot \psi)$ as fundamentally determining the structural curve of a seashell. Given that $r = A_x \exp(\phi \cot \psi)$ results from the expression $\ln(r/A_x) = \phi \cot \psi$, this spiral form is often called a logarithmic spiral. Note that in $r = A_x \exp(\phi \cot \psi)$, A_x and ψ are parameters, and ϕ is a variable. That is, ϕ varies for fixed A_x and ψ. Figure 4 shows a spiral on the XY plane plotted according to the form $r = A_x \exp(\phi \cot \psi)$.

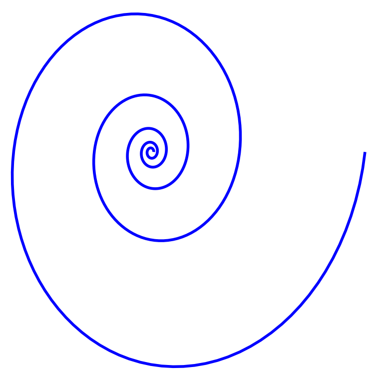

Figure 4: A spiral on the XY plane generated according to $r = A_x \exp(\phi \cot \psi)$ where $A_x = 5$ (arbitrary length units), $\psi = 82°$, $\phi = [0, 10 \times 180°]$.

The reader may pause here to appreciate the self-similarity of the spiral shown in the above figure. This means that the figure looks the same no matter at what length scale it is viewed. In other words, regardless of whether we zoom in or out, the spiral pattern looks the same.

We arrived at the form of the spiral by considering the projection of the structural curve of the seashell on the XY plane. This form can be simply extended to the three-dimensional space by replacing A_x by A, which is the radial distance to the point on the three-dimensional spiral when $\phi = 0$. (A_x is then the projection of A on the X-axis when $\phi = 0$.) We can thus summarize the form of the structural curve in three-dimensional space as follows:

Form of the Structural Curve of a Seashell

In three-dimensional space, the structural curve ($\mathcal{S}$) of a seashell, which acts as its invisible spine takes the shape of a spiral given by,

$$\mathcal{S}: \quad R_s = A\exp(\phi\cot\psi); \quad A > 0, \quad 0 < \psi < \pi/2, \quad \phi \geq 0, \tag{1}$$

where R_s is the radial distance to a point on $\mathcal{S}$ from the origin $\mathcal{O}$ of the global coordinate system $\{\mathcal{O}, X, Y, Z\}$, ϕ is the azimuthal angle between the X-axis and the projection of the radial direction on the XY plane, and ψ is the constant angle between the radial direction to a point on $\mathcal{S}$ and the tangent to $\mathcal{S}$ at that point. Hence, the structural curve of the seashell is determined by the two parameters A (length) and ψ (angle), and the angular variable ϕ.

The projection of the three-dimensional structural curve onto the XY plane results in a self-similar logarithmic spiral.

2.2 The Form of the Generating Curve: special orientation

The generating curve of a seashell determines its cross-sectional shape and expands as the organism responsible for the shell grows. Before including any growth factor, let us first model the bare cross section as an ellipse whose center O moves along the structural curve $\mathcal{S}$. Furthermore, let us take the plane of this ellipse to coincide with the plane that results from connecting the origin $\mathcal{O}$ of the global coordinate system $\{\mathcal{O}, X, Y, Z\}$, the origin O of the ellipse, and the projection of O on the XY plane, which is point A (see Figure 5).

If the polar coordinates of the center of the ellipse are $O = \{R_s, \theta, \phi\}$, then its global cartesian coordinates are simply,

$$\begin{aligned} X_O &= R_s \sin\theta\cos\phi, \\ Y_O &= R_s \sin\theta\sin\phi, \\ Z_O &= R_s \cos\theta. \end{aligned}$$

(Here, and elsewhere in the essay, the subscript s signifies the structural curve.) Let us now place a local cartesian coordinate system $\{O, x, y, z\}$ at the center of the ellipse such that the axes of this coordinate system are parallel to the corresponding axes of the global $\{\mathcal{O}, X, Y, Z\}$ coordinate system (see Figure 6).

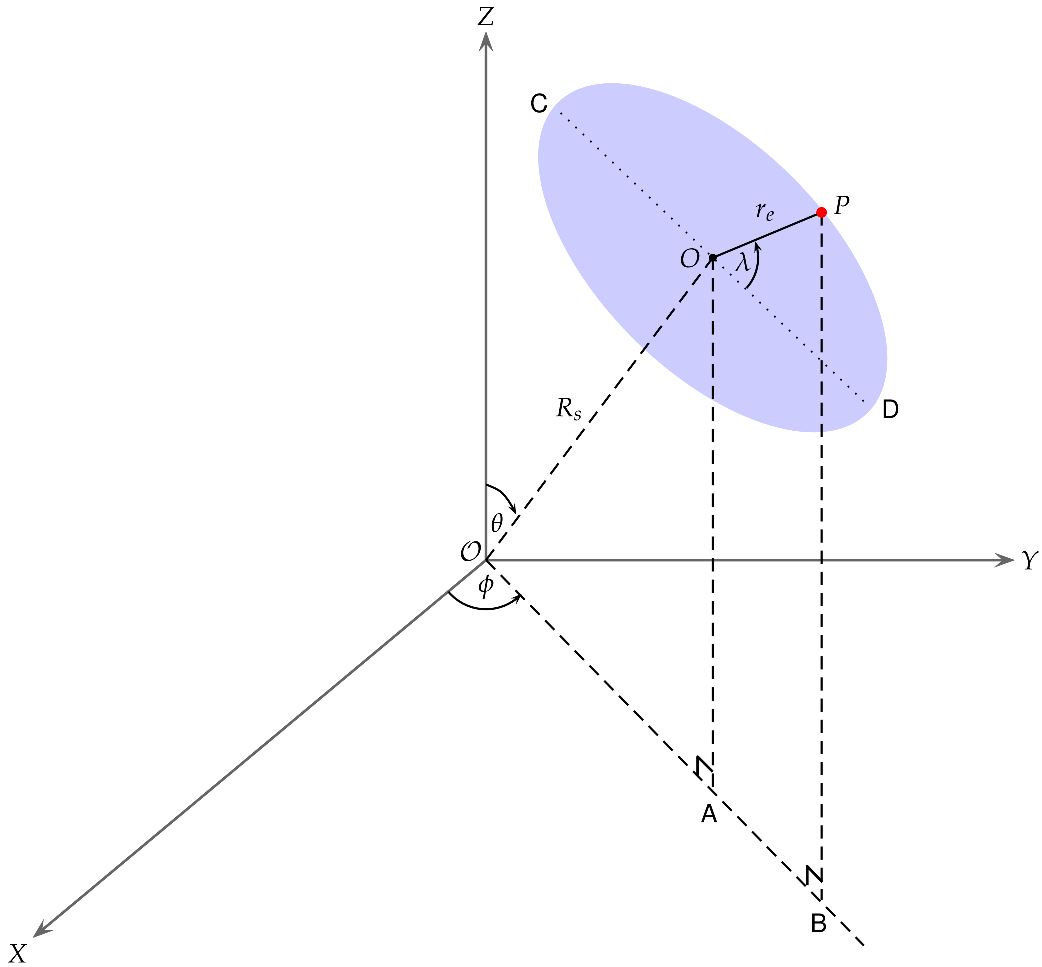

Figure 5: The ellipse that represents the generating curve $\mathcal{G}$ of a seashell. (At this stage, the ellipse or the cross-sectional area of the seashell is assumed to be not growing.) The center $O = (R_s, \theta, \phi)$ of the ellipse moves along the structural curve $\mathcal{S}$. The major axis of the ellipse is CD. The semi-major and semi-minor distances of the ellipse are a and b, respectively. The plane of the ellipse coincides with the plane $\mathcal{O}$AO where A is the projection of O on the global XY plane. (Note that A is the point p in Figure 3.) An arbitrary point $P = (r_e, \lambda)$ on the ellipse makes an angle λ to the major axis at distance r_e from O. The projection of P on the global XY plane is B. CD $\parallel$ $\mathcal{O}$B. | Drawing by AD.

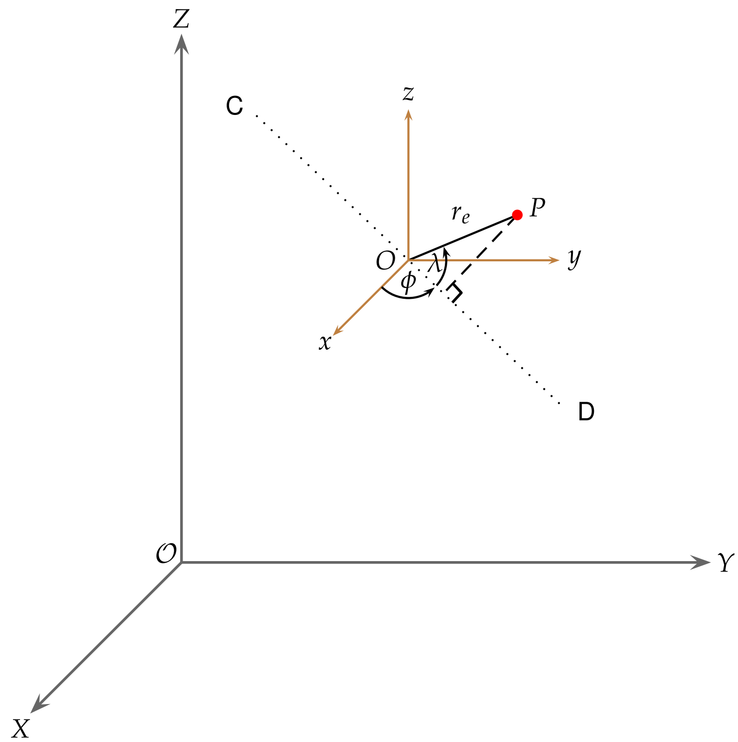

Figure 6: The local coordinate system $\{O, x, y, z\}$ placed at the center O of the ellipse. The x, y, and z axes of the local coordinate system are parallel to the corresponding X, Y, and Z axes of the global coordinate system. Given this orientation of the axes, the angle between the x-axis and the major axis CD of the ellipse is ϕ. Note that CD lies on the xy plane. | Drawing by AD.

A point P on the ellipse (which corresponds to a point on the surface of the shell) can then be described by $P = (r_e, \lambda)$ where r_e is the (local) radial distance OP and λ is the (local) counter-clockwise angle to P measured from the major axis CD of the ellipse (see Figure 5). Let the local planar coordinates of point P on the plane of the ellipse itself be $P = (x_e, y_e)$. In other words, when P is projected to the major and minor axes of the ellipse, x_e and y_e are the respective distances to these projections from its local coordinate origin O. Then, it is clear that $x_e = r_e \cos\lambda$ and $y_e = r_e \sin\lambda$. If the semi-major length and the semi-minor length of the ellipse are a and b, respectively, then, given that the ellipse can be described by the equation

$$\frac{x_e^2}{a^2} + \frac{y_e^2}{b^2} = 1$$

in local planar coordinates, it follows that,

$$r_e = \left[\left(\frac{\cos\lambda}{a} \right)^2 + \left(\frac{\sin\lambda}{b} \right)^2 \right]^{-1/2}; \quad a, b > 0, \quad 0 \leq |\lambda| \leq 2\pi. \tag{2}$$

We have thus expressed the radial distance to a point P on the non-growing ellipse in terms of two length parameters (a, b) and an angular variable (λ). A growth factor g can now be introduced to obtain the radial distance R_g to the point P from O when the ellipse is growing so that $R_g = g r_e$. (Here, and elsewhere in the essay, the subscript g signifies the generating curve.) Therefore, a point P in a growing ellipse (in this special orientation) has local coordinates $P = (x, y, z)$ such that,

$$\begin{aligned}
x &= R_g \cos\lambda \cos\phi = g r_e \cos\lambda \cos\phi, \\
y &= R_g \cos\lambda \sin\phi = g r_e \cos\lambda \sin\phi, \\
z &= R_g \sin\lambda = g r_e \sin\lambda.
\end{aligned}$$

This concludes our second step, which we summarize below:

Form of the Generating Curve of a Seashell: special orientation

Let the generating curve $\mathcal{G}$ be represented by an ellipse with center O on the structural curve $\mathcal{S}$. Let the polar coordinates of $O = (R_s, \theta, \phi)$. Then the global cartesian coordinates of O are

$$X_O = R_s \sin\theta \cos\phi, \tag{3}$$
$$Y_O = R_s \sin\theta \sin\phi, \tag{4}$$
$$Z_O = R_s \cos\theta, \tag{5}$$

where $R_s = A \exp(\phi \cot\psi)$; $A > 0$, $0 < \psi < \pi/2$, $\phi \geq 0$, $0 \leq \theta \leq 2\pi$.

Let the semi-major and semi-minor axes of the ellipse be a and b, respectively, and let the ellipse be oriented as in Figure 5. Let a point P on the non-growing ellipse have coordinates (r_e, λ) defined on the plane of the ellipse. Then, if the growth factor of the ellipse is g, the cartesian coordinates of $P = (x, y, z)$ relative to the local coordinate system defined as in Figure 6 are given by

$$x = g r_e \cos\lambda \cos\phi, \tag{6}$$
$$y = g r_e \cos\lambda \sin\phi, \tag{7}$$
$$z = g r_e \sin\lambda, \tag{8}$$

where

$$r_e = \left[\left(\frac{\cos\lambda}{a} \right)^2 + \left(\frac{\sin\lambda}{b} \right)^2 \right]^{-1/2}, \quad a, b > 0, \quad 0 \leq |\lambda| \leq 2\pi.$$

2.3 General Coordinates of a Point on a Smooth Seashell

Our goal now is to relax the special orientation of the elliptical generating curve and give it the freedom to rotate in space. For this purpose we introduce the Euler angles represented by α, β, γ. They induce Euler rotations of the ellipse in three-space as follows: Starting from the orientation of the ellipse shown in Figure 5, α is a counterclockwise rotation of the major axis (CD) of the ellipse about the Z- (equivalently, the z-) axis. Following the α rotation, β is a counterclockwise rotation of the ellipse about an axis that is perpendicular to the resulting plane of the ellipse. Following the β rotation, γ is a counterclockwise rotation of the ellipse about the resulting direction of the major axis (CD).

To track these rotations, let us assume that the local coordinate system $\{O, x, y, z\}$ attached to the ellipse rotates with the Euler rotations. The α and β rotations are depicted in Figures 7 and 8, respectively.

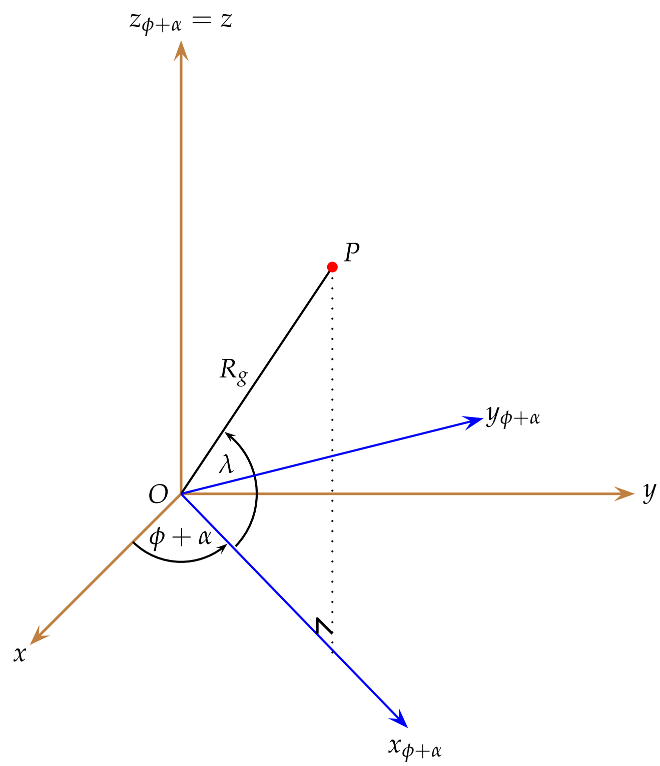

Figure 7: The ellipse has been rotated counterclockwise by an angle α about the z-axis from its orientation in Figure 5 (also see Figure 6). The resulting local coordinate system is now $\{O,\ x_{\phi+\alpha},\ y_{\phi+\alpha},\ z_{\phi+\alpha} = z\}$. The growth factor has now been included in measuring the distance to point P from the center of the ellipse O, and therefore, $OP = R_g = gr_e$. | Drawing by AD.

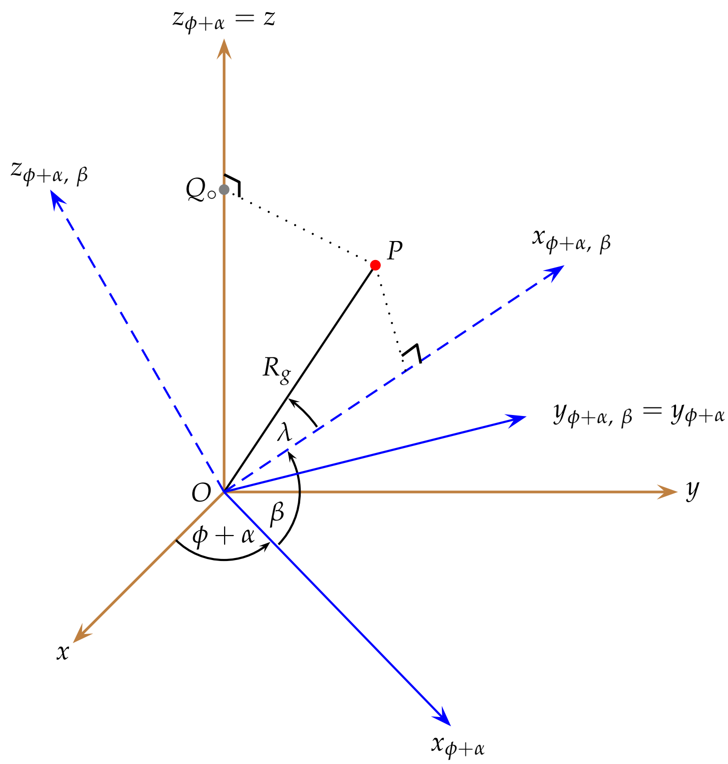

Figure 8: The ellipse has been rotated counterclockwise by an angle β about the normal to the ellipse resulting from the orientation in Figure 7. The resulting local coordinate system is now $\{O,\ x_{\phi+\alpha,\ \beta},\ y_{\phi+\alpha,\ \beta} = y_{\phi+\alpha},\ z_{\phi+\alpha,\ \beta}\}$. Note that the axis $x_{\phi+\alpha,\ \beta}$ lies on the same vertical plane as the axis $x_{\phi+\alpha}$. The projection of point P on the original z-axis is $Q_\circ$. Therefore, $OQ_\circ = R_g \sin(\lambda + \beta)$. | Drawing by AD.

Let us first deduce the local coordinates of point P on the ellipse when α and β rotations are implemented starting with the initial orientation depicted in Figure 5 (see also Figure 6). We note that per the initial orientation, ϕ and λ can be considered to have resulted from counterclockwise rotations about the Z-axis and about an axis that is perpendicular to the plane of the ellipse, respectively. As such, the effect of the α and β rotations on point P can be obtained by letting $\phi \to \phi + \alpha$ and $\lambda \to \lambda + \beta$ in (6)-(8). Thus, after implementing the α and β rotations, the local coordinates of P are:

$$x_{[\phi+\alpha,\ \lambda+\beta]} = gr_e \cos(\lambda+\beta)\cos(\phi+\alpha), \tag{9}$$

$$y_{[\phi+\alpha,\ \lambda+\beta]} = gr_e \cos(\lambda+\beta)\sin(\phi+\alpha), \tag{10}$$

$$z_{[\phi+\alpha,\ \lambda+\beta]} = gr_e \sin(\lambda+\beta). \tag{11}$$

At this point, then, the global cartesian coordinates of point P on the shell are:

$$X_{[\phi+\alpha,\ \lambda+\beta]} = X_O + x_{[\phi+\alpha,\ \lambda+\beta]}, \tag{12}$$

$$Y_{[\phi+\alpha,\ \lambda+\beta]} = Y_O + y_{[\phi+\alpha,\ \lambda+\beta]}, \tag{13}$$

$$Z_{[\phi+\alpha,\ \lambda+\beta]} = Z_O + z_{[\phi+\alpha,\ \lambda+\beta]}. \tag{14}$$

We are now left to consider the counterclockwise rotation by γ about the major axis CD of the ellipse. Since CD was originally on the xy plane, it lies on the $x_{\phi+\alpha,\ \beta}\ y_{\phi+\alpha,\ \beta}$ plane after the α and β rotations. Thus, a rotation about CD at this point is the same as a rotation about the axis $x_{\phi+\alpha,\ \beta}$ (see Figure 8). Since the axis $x_{\phi+\alpha,\ \beta}$ lies on the same vertical plane as the axis $x_{\phi+\alpha}$, the counterclockwise rotation by γ about $x_{\phi+\alpha,\ \beta}$ is equivalent to a counterclockwise rotation by γ about the axis $x_{\phi+\alpha}$, which is on the (original) xy plane. Therefore, a counterclockwise rotation by γ about the major axis CD of the ellipse is equivalent to a counterclockwise rotation by γ about the axis $x_{\phi+\alpha}$.

To proceed, let us first note (see Figure 8) that $OP = R_g$. Let the projection of P on the z-axis be $Q_\circ$. Since $\angle POQ_\circ = \pi/2 - (\lambda+\beta)$, $OQ_\circ = OP \cdot \cos[\pi/2 - (\lambda+\beta)] = R_g \sin(\lambda+\beta)$. Then, a counterclockwise rotation of OP (OP as shown in Figure 8) by an angle γ about $x_{\phi+\alpha}$ would make $OQ_\circ$ ($OQ_\circ$ as shown in Figure 8) rotate counterclockwise by an angle γ about $x_{\phi+\alpha}$. Figure 9 shows the new position of $Q_\circ$, which is $Q_\bullet$.

Now, $Q_\bullet$ projects a distance $OQ_\bullet \cdot \cos\gamma$ on the z-axis. Similarly, the respective projections of $Q_\bullet$ on the x- and the y-axes are $OQ_\bullet \cdot \sin\gamma\sin(\phi+\alpha)$ and $OQ_\bullet \cdot \sin\gamma\cos(\phi+\alpha)$ (see Figure 9). Since $OQ_\bullet = OQ_\circ = R_g\sin(\lambda+\beta) = gr_e\sin(\lambda+\beta)$, the resulting local coordinates of P are

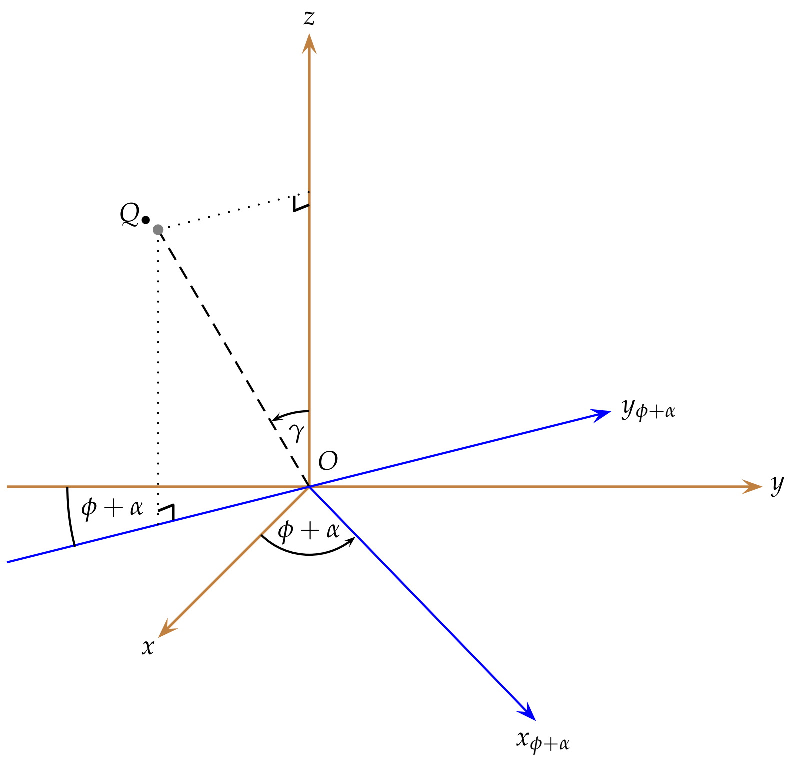

Figure 9: The ellipse has been rotated counterclockwise by an angle γ about its major axis (from the orientation in Figure 8) which is equivalent to a counterclockwise rotation by the same angle about the axis $x_{\phi+\alpha}$. The point $Q_\circ$, which is the projection of point P on the z-axis (see Figure 8) now moves to the new position $Q_\bullet$. But $OQ_\circ = OQ_\bullet$. Therefore, $OQ_\bullet = R_g \sin(\lambda + \beta)$. | Drawing by AD.

$$x_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]} = gr_e \sin(\lambda+\beta)\sin\gamma\sin(\phi+\alpha), \tag{15}$$
$$y_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]} = gr_e \sin(\lambda+\beta)\sin\gamma\cos(\phi+\alpha), \tag{16}$$
$$z_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]} = gr_e \sin(\lambda+\beta)\cos\gamma. \tag{17}$$

The above local coordinates of a point P on the shell fully account for a general orientation of the ellipse, and hence, the generating curve. To obtain the cartesian coordinates of a point P on the shell in terms of the global coordinates, which is what we actually need, we have to decide whether we need to add or subtract the local coordinates (15)-(17) from the global coordinates given in (12)-(14).

Since the center O of the ellipse is situated on the local xy plane, and the projection of point P on the z-axis stays above this plane (per Figure 9), we simply need to add $z_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]}$ to Z_O to obtain the global Z-coordinate of P. In other words, $z_{[\phi+\alpha,\ \lambda+\beta]}$ gets multiplied by the factor $\cos\gamma$ in obtaining $z_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]}$, which needs to be then added to Z_O.

The situation regarding the global X- and Y-coordinates is a little involved in the sense that we need to keep track of the projection of point P on the XY plane during the final rotation γ. Note that during the counterclockwise rotation γ about the $x_{\phi+\alpha}$-axis, the projection of point P traverses the path shown in Figure 10 on the XY plane.

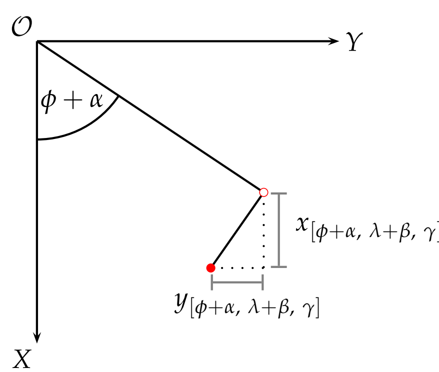

Figure 10: The projection of point P on the XY plane moves from point $\circ$ to point $\bullet$ when the Euler rotation γ is executed. Since $\circ = (X_{[\phi+\alpha,\ \lambda+\beta]}, Y_{[\phi+\alpha,\ \lambda+\beta]})$, the X-coordinate of $\circ$, $X_{[\phi+\alpha,\ \lambda+\beta]}$, increases by $x_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]}$ and the Y-coordinate of $\circ$, $Y_{[\phi+\alpha,\ \lambda+\beta]}$, decreases by $y_{[\phi+\alpha,\ \lambda+\beta,\ \gamma]}$. | Drawing by AD.

However, since the local coordinate axes were set up to be parallel to the global coordinate axes, the path traversed by the projection of P on the XY plane is the same as the path traversed by the projection of P on the xy plane. The corresponding changes in the x and y distances during the γ rotation are (15) and (16), respectively. But how would these changes affect the global coordinates of P determined after the α and β rotations as given in (12) and (13)? We note from Figure 10 that given the path of the projection of point P on the XY plane, the X-coordinate increases and the Y-coordinate decreases. Therefore, to obtain the final global X- and Y-coordinates of a point P on the shell we must add (15) to (12) and subtract (16) from (13).

Additionally, we note that the structural curve of the seashell may form a clockwise or a counterclockwise spiral as viewed from above (that is, looking toward the XY plane from the positive Z-direction). This means that the projection of the center O of the ellipse traverses clockwise or counterclockwise on the XY plane. The projection of O on the XY plane has coordinates: $X \sim \cos\phi$ and $Y \sim \sin\phi$. Since we take ϕ to be positive when measured counterclockwise (about the Z-axis) and negative when measured clockwise, when $\phi \to -\phi$, $X \to X$ and $Y \to -Y$. Thus, to account for the direction of coiling, we can multiply the Y-coordinate of a point P on the shell by the coiling factor c, which is $+1$ if counterclockwise and -1 if clockwise.

We are now only left to determine the form of the growth factor g of the elliptical generating curve. Given the essentially self-similar nature exhibited by the organism both longitudinally and cross-sectionally, and the fact that we have modeled the former by the structural curve, $R_s = A\exp(\phi\cot\psi)$, we posit to model the growth factor g by the same model having unit amplitude (that is, where $A = 1$). Thus, we represent the growth factor as $g = \exp(\phi\cot\psi)$. These steps then result in the most general global coordinates of a point P on a smooth shell, which we summarize as follows:

General Coordinates of a Point on a Smooth Seashell

Let the generating curve $\mathcal{G}$ of a seashell be represented by an ellipse with center $O = (R_s, \theta, \phi)$ on its structural curve $\mathcal{S}$ with coiling factor c, and let A be the amplitude of $\mathcal{S}$ when $\phi = 0$. Let the semi-major and semi-minor axes of the ellipse be a and b, respectively, and let a point P on the non-growing ellipse have coordinates (r_e, λ) defined on the plane of the ellipse. If the growth factor of the ellipse is g, and the orientation of the ellipse in three-space is given by the Euler angles (α, β, γ), then the global coordinates of point P on the smooth shell are given by

$$X_p = R_s \sin\theta \cos\phi + g r_e \cos(\lambda + \beta) \cos(\phi + \alpha) + g r_e \sin(\lambda + \beta) \sin\gamma \sin(\phi + \alpha), \quad (18)$$

$$Y_p = c \left[R_s \sin\theta \sin\phi + g r_e \cos(\lambda + \beta) \sin(\phi + \alpha) - g r_e \sin(\lambda + \beta) \sin\gamma \cos(\phi + \alpha) \right], \quad (19)$$

$$Z_p = R_s \cos\theta + g r_e \sin(\lambda + \beta) \cos\gamma, \quad (20)$$

where

$$\begin{aligned} R_s &= A \exp(\phi \cot\psi), \quad A > 0, \quad 0 < \psi < \pi/2, \quad \phi \geq 0, \\ g &= \exp(\phi \cot\psi), \\ r_e &= \left[\left(\frac{\cos\lambda}{a} \right)^2 + \left(\frac{\sin\lambda}{b} \right)^2 \right]^{-1/2}, \quad a, b > 0, \quad 0 \leq |\lambda| \leq 2\pi, \\ \alpha, \gamma &= [-\pi, \pi], \quad \beta = [0, \pi] \text{ or } [-\pi/2, \pi/2], \quad \theta = [0, 2\pi], \\ c &= +1 \text{ counterclockwise}, \quad -1 \text{ clockwise}. \end{aligned}$$

A smooth seashell can thus be modeled by the nine parameters
$\{\text{length}: \; A, a, b \mid \text{angular}: \; \psi, \theta, \alpha, \beta, \gamma \mid \text{dimensionless}: \; c\}$ and the two angular variables $\{\phi, \lambda\}$.

3 Some Models of Smooth Seashells

Using equations (18)-(20) we can now model smooth seashells where we ignore the nodules on their surface. (A lengthwise ridge can be considered a special type of nodule.) A sample of these shells are shown in the following figures where we can compare the models (drawn using Mathematica) against the basic structure of actual specimens. The equations seem to capture the basic characteristics of the seashells quite well.

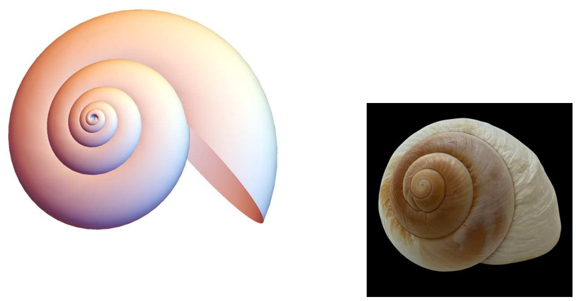

Figure 11: A Natalina shell model (left) and an actual speciman (right). $A = 30,\ \psi = 84°,\ \theta = 138°,\ a = 12,\ b = 20,\ c = -1,\ \alpha = 30°,\ \beta = 80°,\ \gamma = 15°,\ \phi = [0, 10 \times 180°],\ \lambda = [-270°, 90°]$. | Specimen image: author.

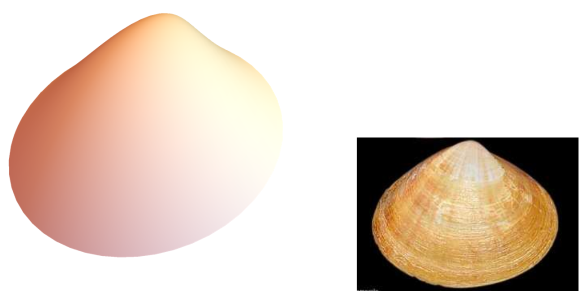

Figure 12: A Codakia shell model (left) and an actual specimen (right). $A = 10500,\ \psi = 37°,\ \theta = 90°,\ a = 10000,\ b = 10500,\ c = -1,\ \alpha = 1°,\ \beta = 0°,\ \gamma = 1°,\ \phi = [0, 2 \times 180°],\ \lambda = [0°, 360°]$. | Specimen image: online, author unknown.

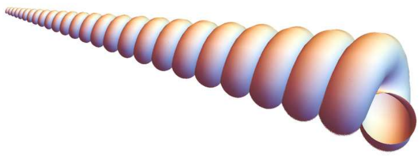 

Figure 13: A Turritella shell model (left) and an actual specimen (right). $A = 22$, $\psi = 89°$, $\theta = 176°$, $a = 1.3$, $b = 1.5$, $c = 1$, $\alpha = -2°$, $\beta = 55°$, $\gamma = 1°$, $\phi = [0, 50 \times 180°]$, $\lambda = [0°, 360°]$. | Specimen image in the public domain; black background added.

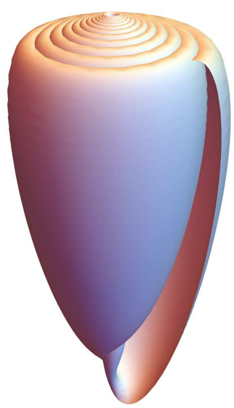 

Figure 14: A Conus shell model (left) and an actual specimen (right). $A = 7$, $\psi = 88°$, $\theta = 168°$, $a = 6$, $b = 1.5$, $c = -1$, $\alpha = 0°$, $\beta = 78°$, $\gamma = 0°$, $\phi = [0, 24 \times 180°]$, $\lambda = [0°, 360°]$. | Specimen image: Wikipedia, Shellnut, CC BY-SA 3.0.

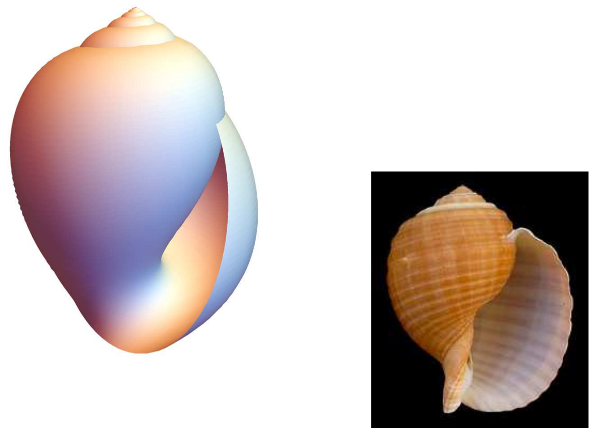

Figure 15: A Tonna shell model (left) and an actual specimen (right). $A = 50$, $\psi = 84°$, $\theta = 180°$, $a = 42$, $b = 33$, $c = -1$, $\alpha = 185°$, $\beta = -58°$, $\gamma = 15°$, $\phi = [0, 12 \times 180°]$, $\lambda = [0°, 360°]$. | Specimen image: Wikipedia, H. Zell, CC BY-SA 3.0.

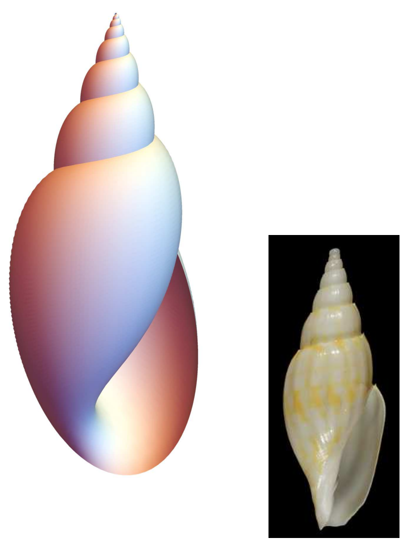

Figure 16: A Lyria shell model (left) and an actual specimen (right). $A = 67$, $\psi = 85°$, $\theta = 180°$, $a = 35$, $b = 20$, $c = -1$, $\alpha = 2°$, $\beta = 77°$, $\gamma = 2°$, $\phi = [0, 14 \times 180°]$, $\lambda = [0°, 360°]$. | Specimen image: Wikipedia, M. Caballer, Museum National d'Histoire Naturelle, CC BY 4.0.

4 Deriving the Mathematical Form of Noduled Seashells

As we know, most seashells show some form of structure on their surface, which we have not yet captured in the above treatment. Let us call these structures nodules, which can be narrow or broad in their extent. On closer inspection, these nodules may be approximated as a three-dimensional Gaussian distribution. In cartesian coordinates such a Gaussian distribution (see Figure 17) essentially has the form

$$\exp\left\{-\frac{(x-\mu_x)^2}{2\sigma_x^2}\right\} \cdot \exp\left\{-\frac{(y-\mu_y)^2}{2\sigma_y^2}\right\},$$

where corresponding μ and σ are the mean and the standard deviation in the respective directions. For the readers who wonder how the above form of the Gaussian distribution arises, a heuristic proof is given in the Appendix.

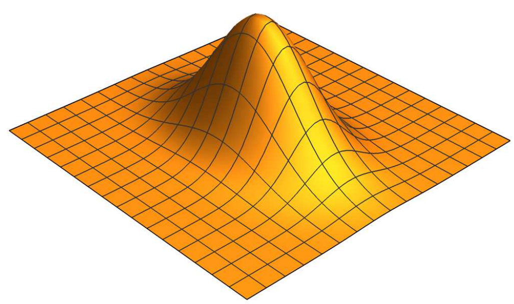

Figure 17: A three-dimensional Gaussian distribution which has the form stated in the text above. This distribution has been generated with the values: $\mu_x = 1$, $\sigma_x = 6$, $\mu_y = 2$, $\sigma_y = 10$ with $x, y = [-30, 30]$.

To add such Gaussian structures on a seashell, which we will call Gaussian nodules, let us situate them with respect to the structural and generating curves of the shell described earlier. Let us first consider situating a two-dimensional nodule (which we will also refer to as a Gaussian curve) on the generating curve $\mathcal{G}$ (see Figure 18).

If this Gaussian curve along the perimeter of the (elliptical) generating curve is situated such that its symmetric axis forms an angle μ_g with respect to the major axis, and its angular width is described by the standard deviation σ_g (where the corresponding angle is formed at the center of the ellipse), then the form of the two-dimensional nodule along $\mathcal{G}$ is $\exp\{-(\lambda-\mu_g)^2/(2\sigma_g^2)\}$. The angle λ has the same meaning as described earlier. Thus, the form of the two-dimensional nodule along the generating curve is:

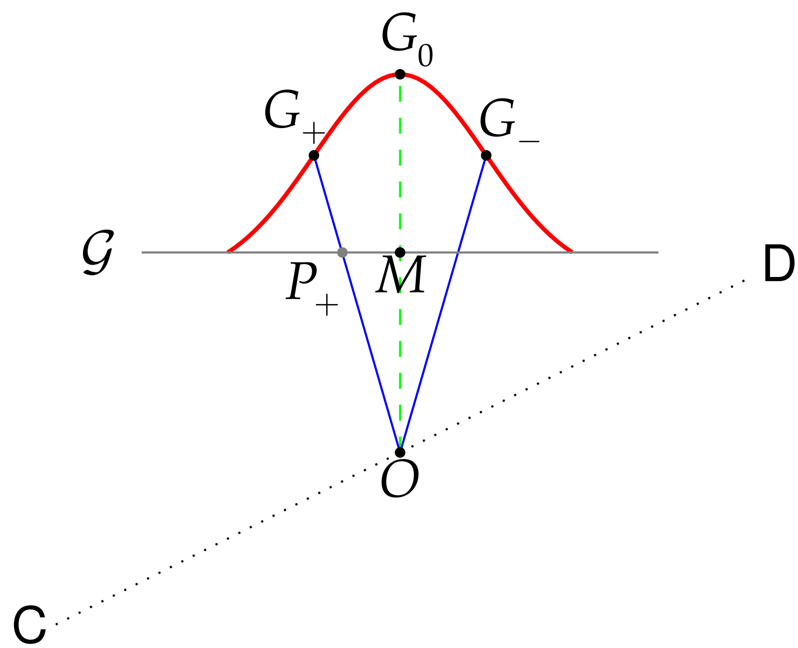

Figure 18: A cross section of a Gaussian nodule situated on the generating curve $\mathcal{G}$ of the shell. (Ideally, $\mathcal{G}$ is curved in space, of course, but here we show it as a horizontal line for illustrative purposes.) O is the center of the generating ellipse and CD is its major axis; alternatively, O is the origin of the local coordinates. The peak of the Gaussian nodule is G_0 which is situated at $\angle G_0 O\mathsf{D} = \mu_g$. $\angle G_+ O G_- = \sigma_g$ corresponds to the standard deviation of the Gaussian nodule and represents the width of the nodule along the cross section. The center of the nodule is located at M on the generating curve. The maximum height of the nodule is $MG_0 = H$. Let the gray circle on the generating curve marks the point P_+ and consider it as an arbitrary point where the radial from O to the Gaussian crosses $\mathcal{G}$. Then, $OP_+ = r_e$ and $P_+G_+ = r_n$; therefore, $OG_+ = r_e + r_n$. A similar cross section can be defined along the structural curve $\mathcal{S}$ where the corresponding standard deviation (width) σ_s is determined with respect to the origin $\mathcal{O}$ of the global coordinates.

$$\text{Form of the nodule along } \mathcal{G} \sim \exp\left\{-\frac{(\lambda-\mu_g)^2}{2\sigma_g^2}\right\}.$$

Note that the form of the nodule along $\mathcal{G}$ is, at present, two-dimensional. The three-dimensional form of the (Gaussian) nodule arises due to the movement of the center of the ellipse along the structural curve $\mathcal{S}$. This movement gives the two-dimensional nodule on $\mathcal{G}$ a depth on the surface of the shell, completing the additional three-dimensional structure of the shell. To factor this aspect of the Gaussian nodule, let there be N (integer) nodules in a 2π radians (360°) turn of $\mathcal{S}$. Then, for an arbitrary turn ϕ (where ϕ is defined as earlier), there will be $N\phi/(2\pi)$ nodules. But during such a ϕ turn we may land partially on a nodule, the fraction of which we have to account for. For this we have to subtract the integer part of $N\phi/(2\pi)$ – denoted by $\lfloor N\phi/(2\pi)\rfloor$ – from $N\phi/(2\pi)$ itself, which results in $n = N\phi/(2\pi) - \lfloor N\phi/(2\pi)\rfloor$ nodules. Note that the integer part acts as the mean for this Gaussian curve. Since N nodules cover an angle 2π radians, then, n nodules cover an angle $(2\pi/N)n$ or $(2\pi/N)\cdot(N\phi/(2\pi) - \lfloor N\phi/(2\pi)\rfloor)$ radians. This form, of course, does not have the Gaussian shape yet. If we now take the angular width of the Gaussian curve along the structural curve to be described by the standard deviation σ_s (where the corresponding angle is formed at the center $\mathcal{O}$ of the global coordinate system), then the form of the two-dimensional nodule along the structural curve is:

$$\text{Form of the nodule along } \mathcal{S} \sim \exp\left\{-\frac{[(2\pi/N)\cdot(N\phi/(2\pi) - \lfloor N\phi/(2\pi)\rfloor)]^2}{2\sigma_s^2}\right\}.$$

The three-dimensional Gaussian form of the nodule is then fundamentally given by the product of the above two cross-sectional forms of the nodule, which results in:

$$\text{Form of a nodule (unitless)} \sim \exp\left\{-\left(\frac{[(2\pi/N)\cdot(N\phi/(2\pi) - \lfloor N\phi/(2\pi)\rfloor)]^2}{2\sigma_s^2} + \frac{(\lambda-\mu_g)^2}{2\sigma_g^2}\right)\right\}.$$

The angular standard deviations σ_s and σ_g determine the narrowness or broadness of the Gaussian nodule in the respective directions. Note that the form of the nodule as it stands has no units. To complete the picture, we must track the height of the Gaussian nodule at any given point on the shell. Given the symmetry of the Gaussian nodule, a maximum height H can be defined to its peak from the surface of the shell. This then allows us to finally define the height r_n of any point of the nodule from the surface of the shell (here, the subscript n stands for nodule). Thus,

$$r_n = H\cdot\exp\left\{-\left(\frac{[(2\pi/N)\cdot(N\phi/(2\pi) - \lfloor N\phi/(2\pi)\rfloor)]^2}{2\sigma_s^2} + \frac{(\lambda-\mu_g)^2}{2\sigma_g^2}\right)\right\}.$$

If we consider the radial from the center of the ellipse (that generates $\mathcal{G}$) to the Gaussian curve outlining the nodule along the ellipse, then height r_n coincides with this radial and points from the edge of the ellipse to that outlining curve of the nodule (see Figure 18). Thus, additional structure on the shell can be added by letting $r_e \to r_e + r_n$ in (18)-(20). With this change, the form of the seashell takes the following final form:

General Coordinates of a Point on a Seashell

Let the generating curve $\mathcal{G}$ of a seashell be represented by an ellipse with center $O = (R_s, \theta, \phi)$ on its structural curve $\mathcal{S}$. Let $\mathcal{S}$ be an equiangular (logarithmic) spiral with angle ψ, amplitude A, and coiling factor c. Let the semi-major and semi-minor axes of the ellipse be a and b, respectively, and let a point P on the non-growing ellipse have coordinates (r_e, λ) defined on the plane of the ellipse. Let the growth factor of the ellipse be g and the orientation of the ellipse in three-space be given by the Euler angles (α, β, γ). Let μ_g be the angular position of the peak of the nodule along the ellipse measured counterclockwise relative to the major axis, N the number of nodules in a turn of 2π radians (360°) along $\mathcal{S}$, and let σ_g and σ_s be the angular standard deviations of the Gaussian nodule along $\mathcal{G}$ and $\mathcal{S}$ where the respective angles are formed at the center O of the ellipse and at the center $\mathcal{O}$ of the global coordinate system; and let H be the maximum height of the nodule from the surface of the shell along the corresponding radial from O. Then the global coordinates of a point P on the shell are given by

$$X_p = R_s \sin\theta \cos\phi + g(r_e + r_n)\cos(\lambda + \beta)\cos(\phi + \alpha) + g(r_e + r_n)\sin(\lambda + \beta)\sin\gamma\sin(\phi + \alpha), \tag{21}$$

$$Y_p = c\left[R_s \sin\theta \sin\phi + g(r_e + r_n)\cos(\lambda + \beta)\sin(\phi + \alpha) - g(r_e + r_n)\sin(\lambda + \beta)\sin\gamma\cos(\phi + \alpha)\right], \tag{22}$$

$$Z_p = R_s \cos\theta + g(r_e + r_n)\sin(\lambda + \beta)\cos\gamma, \tag{23}$$

where

$$\begin{aligned}
R_s &= A\exp(\phi\cot\psi), \quad A > 0, \quad 0 < \psi < \pi/2, \quad \phi \geq 0, \\
g &= \exp(\phi\cot\psi), \\
r_e &= \left[\left(\frac{\cos\lambda}{a}\right)^2 + \left(\frac{\sin\lambda}{b}\right)^2\right]^{-1/2}, \quad a, b > 0, \quad 0 \leq |\lambda| \leq 2\pi, \\
r_n &= H \cdot \exp\left\{-\left(\frac{[(2\pi/N)\cdot(N\phi/(2\pi) - \lfloor N\phi/(2\pi)\rfloor)]^2}{2\sigma_s^2} + \frac{(\lambda - \mu_g)^2}{2\sigma_g^2}\right)\right\}, \\
\alpha, \gamma &= [-\pi, \pi], \quad \beta = [0, \pi] \text{ or } [-\pi/2, \pi/2], \quad \theta = [0, 2\pi], \\
c &= +1 \text{ counterclockwise}, \quad -1 \text{ clockwise}.
\end{aligned}$$

A seashell can thus be modeled by the fourteen parameters
$\{\text{length}: A, a, b, H \mid \text{angular}: \psi, \theta, \alpha, \beta, \gamma, \mu_g, \sigma_g, \sigma_s \mid \text{dimensionless}: c, N\}$ and the two angular variables $\{\phi, \lambda\}$.

5 Some Models of Noduled Seashells

Several seashell models with nodules are shown below along with their natural specimen.

Figure 19: A Codakia Lila model (left) and an actual specimen (right). $A = 10500$, $\psi = 37°$, $\theta = 90°$, $a = 10000$, $b = 10500$, $c = -1$, $\alpha = 0°$, $\beta = 0°$, $\gamma = -10°$, $\mu_g = 0°$, $\sigma_g = 127°$, $\sigma_s = 3.5°$, $N = 30$, $H = 600$, $\phi = [0, 2 \times 180°]$, $\lambda = [-360°, 360°]$. | Specimen image: online, author unknown; black background added.

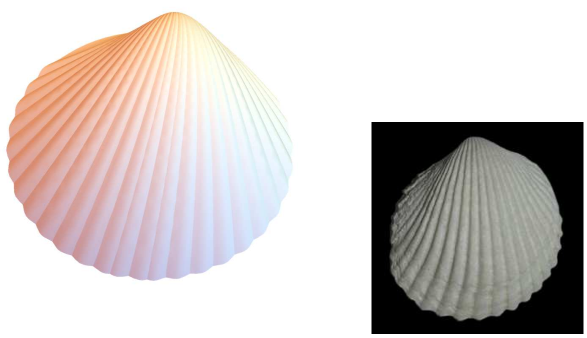

Figure 20: A Cockle model (left) and an actual specimen (right). $A = 10500$, $\psi = 37°$, $\theta = 90°$, $a = 10000$, $b = 10500$, $c = -1$, $\alpha = 0°$, $\beta = 0°$, $\gamma = -10°$, $\sigma_g = 3.5°$, $\sigma_s = 64°$, $N = 10$, $H = 400$, $\phi = [0, 2 \times 180°]$, $\lambda = [0°, 360°]$. This model has been generated by combining many images each with a specific μ_g where $\mu_g = [0°, 360°]$. (The reason for using μ_g as a variable than a parameter in this case is that, given the shell's large aperture, its generating curve does not wrap full circle around the structural curve to obtain multiple lengthwise ridges for a given μ_g.) | Specimen image: C. Obadage.

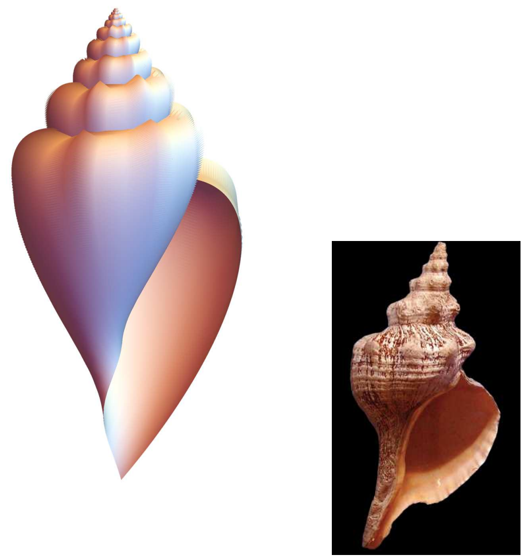

Figure 21: A Horse Conch model (left) and an actual specimen (right). $A = 50$, $\psi = 86^\circ$, $\theta = 200^\circ$, $a = 40$, $b = 14$, $c = -1$, $\alpha = -4^\circ$, $\beta = 45^\circ$, $\gamma = 1^\circ$, $\mu_g = 0^\circ$, $\sigma_g = 8.5^\circ$, $\sigma_s = 9.5^\circ$, $N = 8$, $H = 3$, $\phi = [0, 20 \times 180^\circ]$, $\lambda = [-50^\circ, 10^\circ]$. | Specimen image: Wikipedia, Hectonichus, CC BY-SA 3.0; background changed from blue to black.

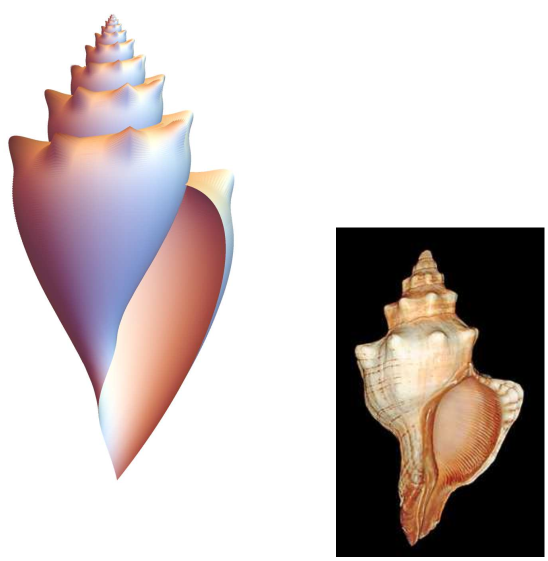

Figure 22: A Trapezium Horse Conch model (left) and an actual specimen (right). $A = 50$, $\psi = 86^\circ$, $\theta = 200^\circ$, $a = 40$, $b = 14$, $c = -1$, $\alpha = -4^\circ$, $\beta = 45^\circ$, $\gamma = 1^\circ$, $\mu_g = 0^\circ$, $\sigma_g = 2^\circ$, $\sigma_s = 9.5^\circ$, $N = 8$, $H = 4$, $\phi = [0, 20 \times 180^\circ]$, $\lambda = [-50^\circ, 10^\circ]$. | Specimen image: Wikipedia, H. Zell, CC BY-SA 3.0.

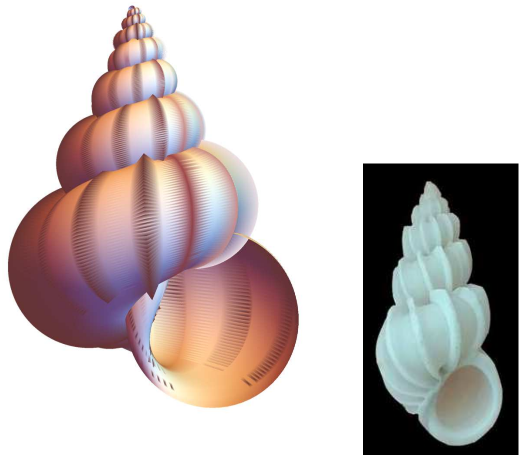

Figure 23: A Wentletrap model (left) and an actual specimen (right). $A = 80$, $\psi = 86°$, $\theta = 170°$, $a = 21$, $b = 21$, $c = -1$, $\alpha = 5°$, $\beta = -45°$, $\gamma = 0°$, $\mu_g = 20°$, $\sigma_g = 67°$, $\sigma_s = 0.15°$, $N = 180$, $H = 9$, $\phi = [0, 15 \times 180°]$, $\lambda = [-90°, 270°]$. | Specimen image (cropped) from the online article *Vanishing Beauty: New Jersey's Wentletrap*, S. Caruso.

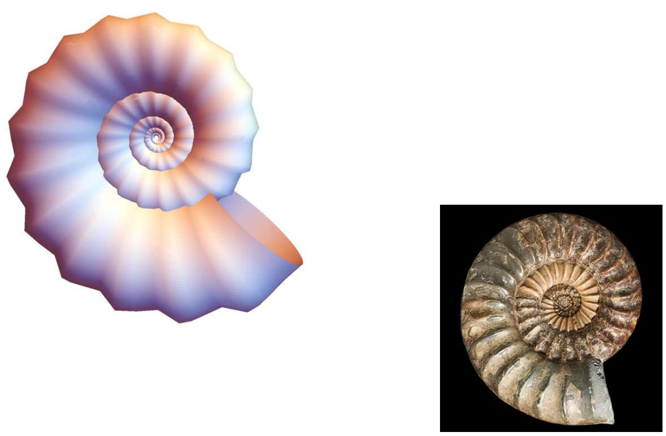

Figure 24: An Ammonite model (left) and an actual fossilized specimen (right). $A = 2$, $\psi = 83°$, $\theta = 90°$, $a = 1$, $b = 0.9$, $c = 1$, $\alpha = 1°$, $\beta = 40°$, $\gamma = 1°$, $\mu_g = 5°$, $\sigma_g = 53°$, $\sigma_s = 7°$, $N = 17$, $H = 0.25$, $\phi = [0, 10 \times 180°]$, $\lambda = [-180°, 180°]$. | Specimen image (rotated) from the article *Life in the Jurassic ocean* by K. Pavid, published online by the Natural History Museum, London, July 21, 2021.

We invite the reader to create their own favorite seashells by adjusting the parameters and variables in (21)-(23) until they produce corresponding reasonably approximate models. It is pleasantly surprising that the equations (21)-(23) seem to capture a wide variety of the beautiful forms of seashells.[7] In this sense, not only Nature is a mathematician, but also a mathematician with great attention to generality and aesthetics. The words attributed to Luca Pacioli, friend of Leonardo da Vinci, ring true: *Without mathematics there is no art*.

Appendix: Derivation of the Gaussian Curve

The Gaussian curve or the Gaussian distribution (also known as the normal distribution) arises in the theory of probability and statistics.[8] Our goal in this section is to derive the fundamental form of a nodule of a seashell, which we take to be a Gaussian distribution as shown in Figure 17. As stated earlier, this Gaussian distribution has the form

$$\exp\left\{-\frac{(x-\mu_x)^2}{2\sigma_x^2}\right\}\cdot\exp\left\{-\frac{(y-\mu_y)^2}{2\sigma_y^2}\right\},$$

up to a multiplicative constant. The following heuristic proof of the Gaussian distribution, constructed in the nineteenth century, is due to John Herschel.[9]

Consider a game where the goal is to throw darts at a target on a two-dimensional plane. Let us call this target O and let us set up a cartesian xy coordinate system centered at O. Since each throw will not be perfect, we can expect darts to randomly land outside of point O on the xy plane. It is reasonable to accept that (see Figure 25):

[7] It will be an interesting exercise to identify which sets of parameters correspond to existing seashell classes, subclasses, etc., and explore how sensitive the shapes are to changes in the parameters. It will also be a worthy exercise to ask whether there exist seashell models for which there are no corresponding living or fossilized specimens, and if so, the biological, evolutionary, and physical reasons that would explain such absences. Conversely, are there seashells that the model developed here cannot capture? If so, what new parameters must be introduced to the model?

[8] For example, the height of individuals is distributed according to the Gaussian curve. If people are to be sampled randomly, it is more likely that their height represent the average height of the population. The likelihood of finding an individual away from the average height decreases as we move away from that average and about 68% of the population would have heights within one standard deviation from the average. It is also observed that the weight of individuals is also distributed according to a Gaussian curve. Hence, if we are to model both the height and the weight of individuals, then the resulting Gaussian distribution will look like a Gaussian nodule, giving the likelihood of finding an individual with a particular height and a weight.

[9] See *The Art of Probability for Scientists and Engineers* by R. W. Hamming, Addison-Wesley Publishing Co., 1991, pp. 209-211.

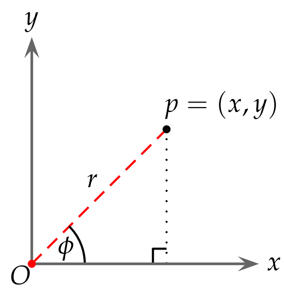

Figure 25: In throwing darts at the origin O of the xy plane, some will randomly land at a point $p = (x, y)$ a radial distance r away from O. | Drawing by AD.

1. The random errors that the player makes in throwing darts in perpendicular directions are independent or mutually exclusive.
   Thus, if the probability of hitting point x on the plane is $\mathfrak{p}(x)$ and that of hitting point y is $\mathfrak{p}(y)$, then the probability of hitting point $p = (x, y)$ is the product $\mathfrak{p}(x) \cdot \mathfrak{p}(y)$.

2. The random errors that the player makes in throwing darts are independent of the direction around the target.
   Thus, the probability that a dart will land at a point $p = (x, y)$ a radial distance r away from O (the target) does not depend on the angle ϕ and will only depend on r.

3. The probability of hitting a point closer to O (the target) is higher than the probability of hitting a point farther away from it.
   Thus, $\mathfrak{p}(x)$ and $\mathfrak{p}(y)$ decrease as $|x|$ and $|y|$ increase. Therefore, $\mathfrak{p}(r)$ decreases as r increases.

Given the above reasonable assumptions, our goal now is to find the form of, say, $\mathfrak{p}(x)$. (Since no direction is special, by symmetry, $\mathfrak{p}(y)$ will have the same form.) Toward this end, let us note that it follows from (1) and (2) that

$$\mathfrak{p}(r) = \mathfrak{p}(x) \cdot \mathfrak{p}(y).$$

Now, $x = r\cos\phi$ and $y = r\sin\phi$. Therefore, $\mathfrak{p}(x)$ and $\mathfrak{p}(y)$ depend on both r and ϕ whereas, per (2), $\mathfrak{p}(r)$ only depends on r. Taking the partial differential of the above expression with respect to ϕ, we obtain

$$\frac{\partial \mathfrak{p}(r)}{\partial \phi} = 0 = \frac{\partial \mathfrak{p}(x)}{\partial \phi} \cdot \mathfrak{p}(y) + \mathfrak{p}(x) \cdot \frac{\partial \mathfrak{p}(y)}{\partial \phi}.$$

Now,

$$\frac{\partial\mathfrak{p}(x)}{\partial\phi} = \frac{\partial\mathfrak{p}(x)}{\partial x}\cdot\frac{\partial x}{\partial\phi} = \frac{\partial\mathfrak{p}(x)}{\partial x}\cdot(-r\sin\phi) = \frac{\partial\mathfrak{p}(x)}{\partial x}\cdot(-y) = -y\cdot\frac{\partial\mathfrak{p}(x)}{\partial x} = -y\cdot\frac{d\mathfrak{p}(x)}{dx} = -y\mathfrak{p}'(x),$$

where $\mathfrak{p}'(x) = d\mathfrak{p}(x)/dx$. Similarly,

$$\frac{\partial\mathfrak{p}(y)}{\partial\phi} = \frac{\partial\mathfrak{p}(y)}{\partial y}\cdot\frac{\partial y}{\partial\phi} = \frac{\partial\mathfrak{p}(y)}{\partial y}\cdot(r\cos\phi) = \frac{\partial\mathfrak{p}(y)}{\partial y}\cdot(x) = x\cdot\frac{\partial\mathfrak{p}(y)}{\partial y} = x\cdot\frac{d\mathfrak{p}(y)}{dy} = x\mathfrak{p}'(y),$$

where $\mathfrak{p}'(y) = d\mathfrak{p}(y)/dy$. The last three expressions then yield

$$-y\mathfrak{p}(y)\mathfrak{p}'(x) + x\mathfrak{p}(x)\mathfrak{p}'(y) = 0,$$

which, after rearrangement, reads

$$\frac{\mathfrak{p}'(x)}{x\mathfrak{p}(x)} = \frac{\mathfrak{p}'(y)}{y\mathfrak{p}(y)}.$$

The left hand side of the above expression is dependent only on the variable x, and the right hand side is dependent only on the variable y. Since, according to (1), x and y are independent, the above equality can only hold if each corresponds to the same constant C. Thus,

$$\frac{\mathfrak{p}'(x)}{x\mathfrak{p}(x)} = \frac{\mathfrak{p}'(y)}{y\mathfrak{p}(y)} = C = \text{constant}.$$

Considering the expression for the x variable, then,

$$\frac{\mathfrak{p}'(x)}{x\mathfrak{p}(x)} = C,$$

which can be directly integrated. Thus,

$$\int\frac{d\mathfrak{p}(x)}{\mathfrak{p}(x)} = C\int x dx \implies \ln\mathfrak{p}(x) = \frac{1}{2}Cx^2 + K,$$

where K is the constant of integration. Solving for $\mathfrak{p}(x)$, the last expression becomes,

$$\mathfrak{p}(x) = \mathcal{A}\cdot\exp\{Cx^2/2\},\quad \mathcal{A} = \exp(K) = \text{constant}.$$

Invoking assumption (3), $\mathfrak{p}(x)$ must decrease as $|x|$ increases. Since x is quadratic in the expression, $x^2 \geq 0$, hence, condition (3) can only be accomplished if $C < 0$. Let us therefore write C as,

$$C = -\frac{1}{\sigma^2}, \quad \sigma = \text{constant} \neq 0.$$

Thus,

$$\mathfrak{p}(x) = \mathcal{A} \cdot \exp\left\{-\frac{x^2}{2\sigma^2}\right\}.$$

We have arrived at the fundamental form of the Gaussian (probability) distribution. Since our interest in this form is with regard to the shape of the seashell nodules, we will not carry on further to determine the constant $\mathcal{A}$, which can be found by integrating $\mathfrak{p}(x)$ along the entire x-axis and equating it to 1 since a dart must land somewhere between $-\infty$ and $+\infty$ along the x-axis. This evaluation yields $\mathcal{A} = 1/\sqrt{2\pi\sigma^2}$. The constant σ represents the spread of the distribution and is known as the standard deviation of the distribution, and its square, σ^2, the variance.

As far as a seashell nodule is concerned, then, its form along the x-direction can be modeled by a function of the form $G(x) \sim \exp\{-x^2/(2\sigma_x^2)\}$, where σ_x is a measure of the spread of the Gaussian curve in the x-direction. Given the above discussion, it is clear that a similar form results for the Gaussian curve along the y-direction, which can be written as $G(y) \sim \exp\{-y^2/(2\sigma_y^2)\}$, where σ_y is a measure of the spread of the Gaussian curve in the y-direction. Following the assumption (1), then, the full form of the Gaussian nodule results by taking the product of the two forms, which results in

$$G(x) \cdot G(y) \sim \exp\left\{-\frac{x^2}{2\sigma_x^2}\right\} \cdot \exp\left\{-\frac{y^2}{2\sigma_y^2}\right\}.$$

Note that this form assumes that the nodule is centered at the origin where $(x, y) = (0, 0)$. (Recall that we chose the target for the darts to be at the origin of the cartesian coordinate system.) Instead, if the nodule is centered at a point $P = (\mu_x, \mu_y)$, we will have to redefine the origin of the coordinate system there. This can be done by rescaling x and y above by $x - \mu_x$ and $y - \mu_y$, respectively, so that at $P = (x, y) = (\mu_x, \mu_y)$, $(x - \mu_x, y - \mu_y) = (0, 0)$. This rescaling then results in the following fundamental form for a Gaussian nodule:

$$G(x) \cdot G(y) \sim \exp\left\{-\frac{(x-\mu_x)^2}{2\sigma_x^2}\right\} \cdot \exp\left\{-\frac{(y-\mu_y)^2}{2\sigma_y^2}\right\},$$

which is the form with which we started to bring more structure onto the smooth seashells in the main text. Given the stochastic underpinnings of the above derivation of the form of a Gaussian distribution, it seems likely that there are stochastic elements at play in the processes that create nodules on seashells.

♣