



Chapter 3: The Shape of Shells

She Sells Self-Similar Spiral

Seashells Shore-Side

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You are walking on a beach when a glint of sun catches your eye; you look down and you see a seashell, a beautiful object that you can't resist picking up and turn in your hand. Most of us have enjoyed this experience and wondered about the secrets it hides. Hold on to that shell and ask yourself: How does it come to look the way it does? What is the history of the shell? How did it achieve such a mesmerizing beauty? If you are mathematically inclined, your head is already spinning with infinite geometric possibilities.

Shells have permeated our culture for millennia. They are used as art forms, jewelry, currency, musical instruments, and even bathroom sinks. But shells are also incredibly valuable scientific objects, their apparent simplicity and extensive fossil record making them ideal model systems for questions of development, pattern formation, and evolutionary processes. They are also of great interest in different domains of earth and life sciences and bioengineering as the paradigm for biomineralization, the production of minerals by living organisms.

Each shell is the vacant remnants of a house built incrementally by a humble soft-bodied creature, a mollusk. It is a house with surprising mathematical regularity and beauty, a house of uncommon strength and durability, a house with delightful variations and patterns. From sharp spines to fractal protrusions to very regular ribs, the mollusk is a fabulous architect and house builder. Each shell tells the story of the mollusk that lived in and built it day after day, weeks after weeks until maturation. And all the shells over the world, taken together, tell a 540 million year long story, the story of the evolution of mollusks, the second most diverse phylum of the animal kingdom. The shells also tell the mathematical story of an organism achieving near spiral perfection with infinite pattern variations that we seek to unravel.

3.1 A marvelous spiral

The first pattern you notice as you look down at the tip of the shell in your hand is a spiral (see [Figure 3.1](#)). This is a very regular planar curve that can be approximated, in most shells, with exquisite accuracy by a logarithmic spiral. Denoted *spira mirabilis*, "marvelous spiral", by the famous 17th century mathematician Jacob Bernoulli, the logarithmic spiral is also found in the

shape of some galaxies and horns. A logarithmic spiral has many particular properties. For instance, as it winds outward any point on the curve keeps the same angle between the curve and the line drawn from the centre, no matter how far it extends; this constant angle is why it is sometimes called the *equiangular spiral*. More strikingly, as the spiral grows, its shape never changes, only its size, so zooming in or out reveals the same curve again and again, a property known as *self-similarity*. This means that scaling the spiral up or down is equivalent to rotating it, which explains why logarithmic spirals appear so often in natural growth processes, where form is preserved while size increases.

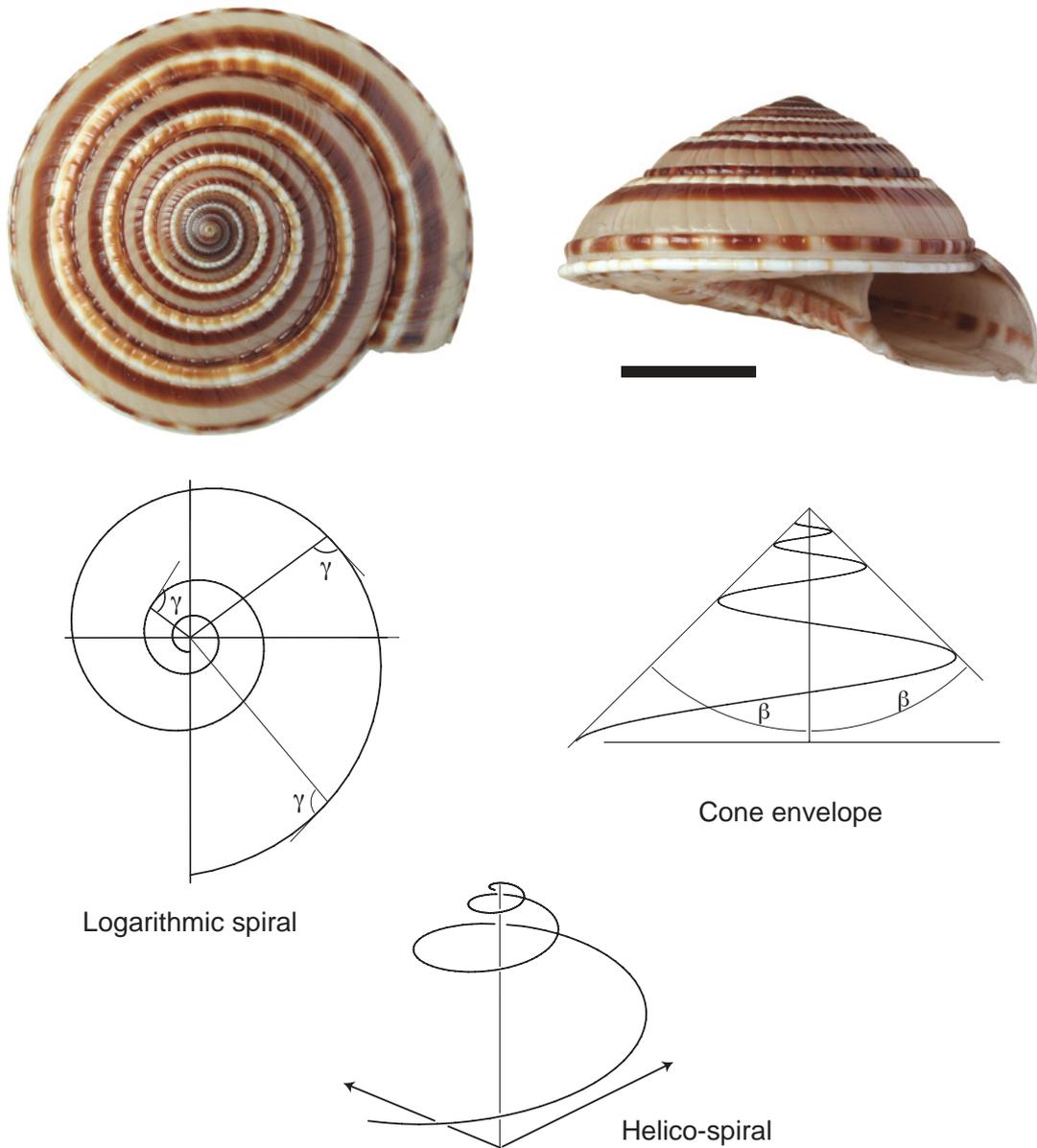


Figure 3.1: *Architectonica* Viewed from the top, the logarithmic spiral underlying seashell shapes appears clearly. Viewed from the side, the seashell appears as cone. Together, the cone and spiral extend in three dimensions to form a helico-spiral (scale bar is 10 mm).]

Another remarkable feature of the logarithmic spiral is that many geometric constructions derived from it remain logarithmic spirals themselves. Much like the exponential function it is derived from, the logarithmic spiral remains the same after transformation. For instance, if one

traces the involute by unwinding a taut string from the curve, or the evolute by following the centres of curvature, the resulting curves are again logarithmic spirals with the same centre. The same is true for the pedal curve formed by dropping perpendiculars from a fixed point, and for the radial trajectory that follows the direction of growth. This geometric stability means the logarithmic spiral is closed under many natural transformations, reinforcing why it is such a robust and recurrent shape in both mathematics and nature.

Its three-dimensional version, the *logarithmic helico-spiral*, is nearly ubiquitous in shells, a fact that has been quantified as early as 1838 [7] by Reverend Moseley. The way Moseley defined it is by taking a logarithmic spiral in the plane and allowing it to grow at constant pace in the vertical direction as it rotates, so that each turn of the spiral is lifted by a fixed amount along an axis. In simple terms, the curve keeps the equiangular, self-similar expansion of the logarithmic spiral when viewed from above, but adds a helical rise in height, much like a spiral staircase that widens as it ascends. Mathematically, the radial distance still increases exponentially with angle, while the height increases linearly with the same angle, coupling planar growth with axial translation.

3.2 The humble architect

But a mollusk knows very little of our logarithms and exponentials and nothing about spirals or self-similarity, so how does the mollusk generate this pattern with such great regularity? The growth of a shell is handled by a part of the mollusk's anatomy called the *mantle*, a thin soft organ that incrementally secretes new shell material at the shell opening, termed the aperture. The mantle sits permanently against the shell opening and slowly adds new material to the edge and inner surface, much like a living 3D printer systematically adding new layers. The mantle releases calcium and carbonate taken from seawater, together with a thin organic framework, and these components crystallise as calcium carbonate forms exactly where the animal controls them, so the shell lengthens at the rim and thickens from inside. Although this secretion happens almost continually, growth only becomes visible when the rate of addition exceeds wear and dissolution, which is why shells show growth lines that record pauses, day, night rhythms, or seasonal changes rather than separate construction events. Over time, the repetition of this simple process produces the familiar hard, layered, and always beautiful patterned shells seen on the shore. Importantly, since it all happens at the margin, the mollusk can only follow *local rules* for this accretion, the direction and amount of material accreted at each point around the aperture.

Surprisingly, the intricate and mathematically regular shape of shells does not require a complex algorithm, but rather emerges through simple local rules, which can be uncovered using the tools of differential geometry. In this mathematical description, accretion at each point around the aperture is decomposed into local orthogonal coordinates – for example the directions perpendicular and tangent to the aperture. There are *three basic rules* that the mollusk follows. First, *expansion*: by uniformly depositing more material, the mollusk creates a slightly larger opening at each iteration. This process generates a cone from an initial circle. Second, a *rotation*: by depositing slightly more material on one side of the aperture, a global rotation of the aperture is achieved [8]. By itself, this operation builds a torus from an initial circle. Third, *twist*: rotating the point of maximal deposition while expanding at each iteration leads to a twist of the aperture. Together these three operations create a non-planar, helico-spiral shell seen in [Figure 3.2](#).

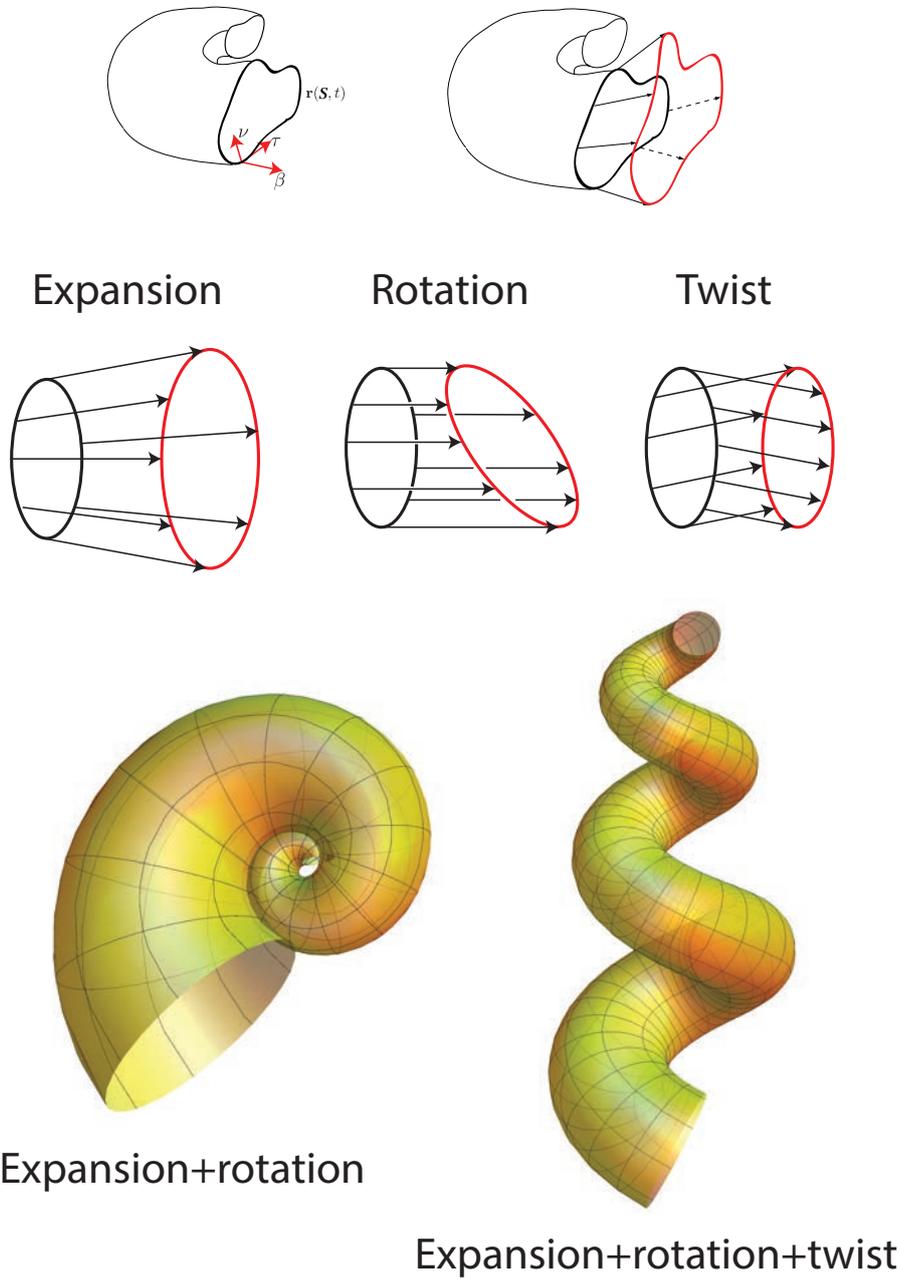


Figure 3.2: Local rules. Seashells are generated by the local accretion of new calcified material at the aperture. Mathematically, the evolution of the aperture can be described by three elementary transformations.

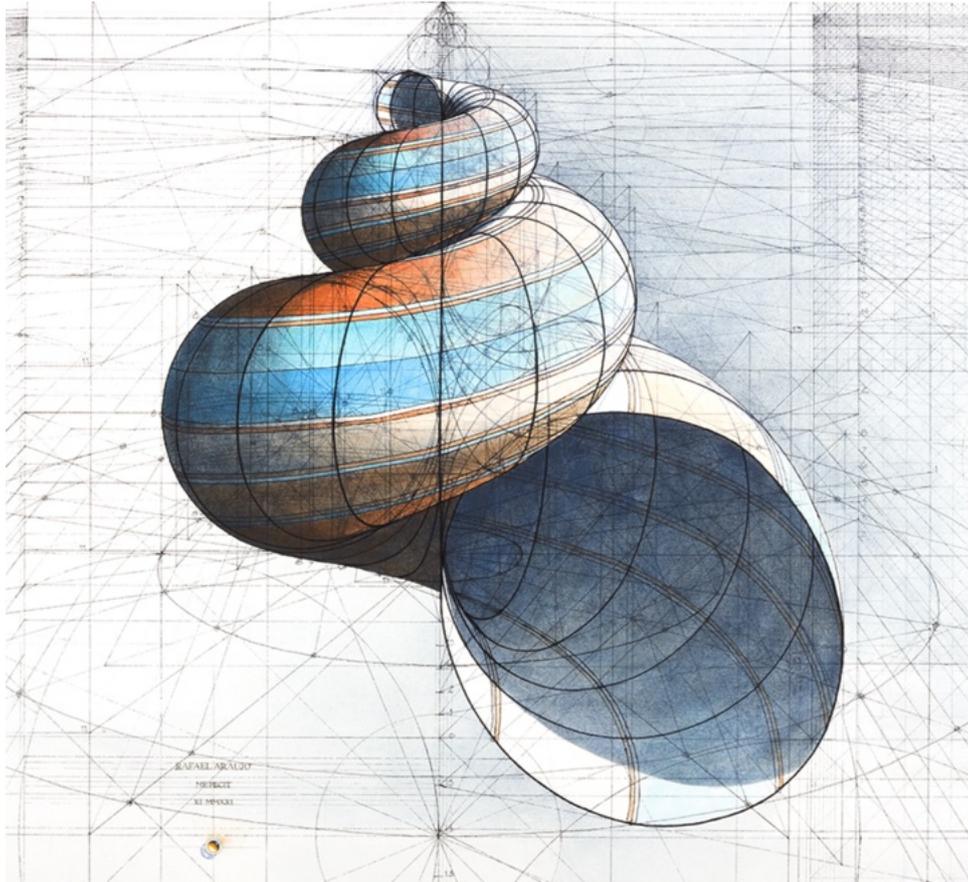


Figure 3.3: Artist rendering of a logarithmic helico-spiral seashell Courtesy of Rafael Araujo (see acknowledgements).

3.3 Morphological patterns

A closer look at the shell in your hand reveals that on top of the basic spiral pattern, the shell has secondary patterns in the form of wrinkles, ridges, spines, spikes, or other morphological ornamentation. The shells that turn up most commonly on a beach form only a very small subset of the some 100,000 extant species of shell producing mollusks. A view of the more exquisite shell shapes requires diving or a trip to a museum. In the depths of the ocean, a dazzling array of shell ornamentations are found, from razor sharp spines and saw-like teeth to very regular ribs or even fractal structures. Each of these patterns exists on top of the basic shell shape, always following the helico-spiral. In all cases, the process of shell formation is as described above, with new shell material accreted at the aperture by the mantle.

There is no evidence to suggest, for instance, that *Murex pecten*, with its sharp spines, is building its shell in a different way from the fractal producing *Hexaplex cichoreum* (see [Figure 3.4](#)). So how do such different ornamentations appear? To understand the emergence of these shapes, we must examine the forces produced during shell growth.

3.4 A mismatch made in heaven

Considering more closely the shell secretion process, an interesting mechanical system becomes apparent. As discussed, the mantle is a thin and soft elastic organ that adheres to the rigid shell opening, such that mantle and shell form a continuum via the generative zone, a region of secreted but not-yet-calcified material. It is in that interaction that the potential for

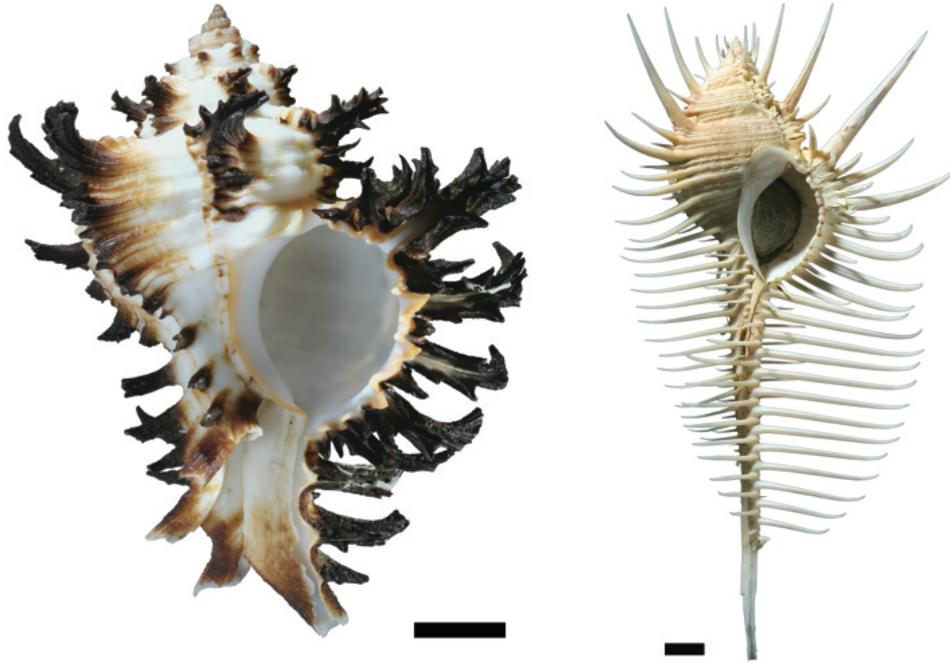


Figure 3.4: Seashell ornamentation. On top of the primary helicon-spiral shape, secondary patterns can be observed such as spines on *Murex pecten* and fractal-like structures on *Hexaplex cichoreum*.

pattern formation appears. If there is a mismatch between mantle and aperture, stresses will develop in the mantle tissue. If the mantle is too small for the opening, it will have to stretch in order to attach to it. If the mantle is too large it will have to be compressed to fit. But when an elastic material is sufficiently compressed, it will buckle. And if the generative zone is deformed due to these stresses, the new material it secretes at that increment will assume the deformed shape and be permanently solidified in the shell, only to further influence the mantle at the next growth step. Essentially, as the mollusk builds its own house, if the house does not grow at the exact same rate as the growing mollusk, the house building will naturally adapt. By studying the mechanics of that response, we can begin to uncover the array of patterns that appear as ornamentations on the house.

3.5 Spiny shells

Consider for instance spiny shells. Spines constitute the most prominent ornamentation, often protruding at a right angle to the shell aperture and often extending centimetres beyond the shell surface. Of particular interest for the evolutionary biologist is the fact that spines have evolved independently in not-closely-related bivalve, gastropod and cephalopod species, a phenomenon termed *convergent evolution*.

From a functional standpoint, the repeated evolution of spines might not seem surprising; indeed spiny shells have been classically interpreted as having convergently evolved as a functional response against predators. However, their potential role as a defense mechanism gives no information as to how the shape actually emerged, i.e. a physically realisable process of forming in the first place. In the case of spines, the answer comes from the potential for *elastic instability*.

Spines form at regular periods during which the mantle undergoes a growth spurt. The growth spurt means that the mantle develops so quickly that it has an excess of length and cannot

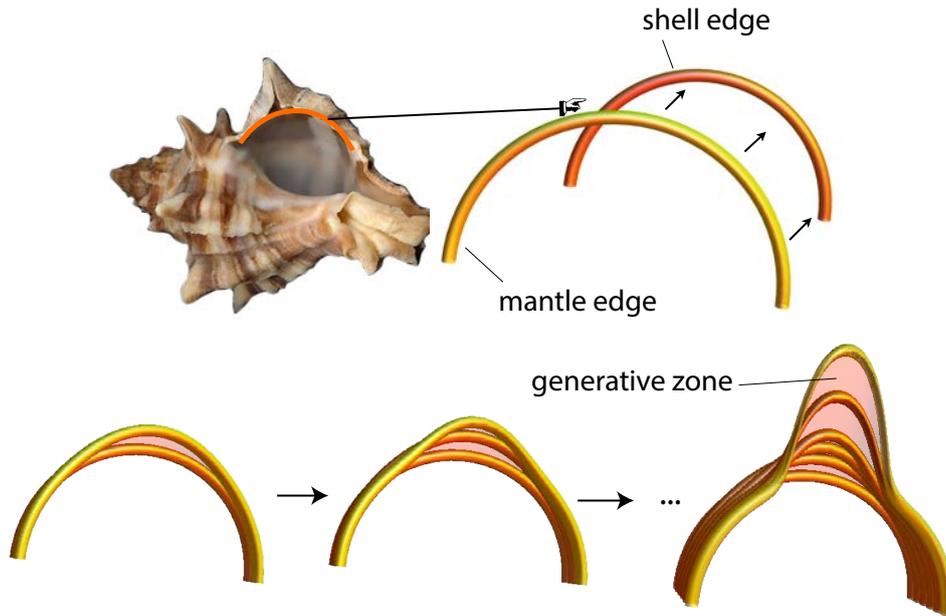


Figure 3.5: Spine formation. When the soft mantle grows faster than the accreted hard material, it deforms and provides a template for newly accreted material.

align with the aperture. This causes the mantle to buckle slightly, and the deposited material assumes the buckled shape. By the next increment the mantle has grown further and again has excess compared to the aperture, so the buckled pattern amplifies. Through this repeated process of growth and mechanical interaction, a row of spines is produced, the precise pattern primarily determined by the rate and duration of the growth spurt. To test this idea, we can run the same process in a mathematical model of a mantle growing on a foundation that evolves at each iteration [1]. By varying typical growth and material properties in the model, a wide variety of spine patterns emerges, similar to the forms observed in real shells (see [Figure 3.6](#)). In this perspective, the high reproducibility of spines can thus be understood as *naturally occurring by the laws of mechanics* in a growing tissue, a statement that is completely separate from any functional value of the shape itself. The mathematical model explains *how* the house was built, not *why* it is built in a particular way.

3.6 Wrinkly whorls

Enthused by your early discoveries of seashells on the beach, you yearn to discover more. There are certain places in the world that will provide you a special window to the past. For instance, a trip to the Jurassic coast in southern England is almost certain to reward the patient beachcomber with an ammonite fossil. Given their abundance on these beaches, it is hard to believe that ammonites have been extinct for 65 million years, but this group of cephalopods had tremendous success during a 335 million year run. Their abundance, high evolution rate, and great diversity make them one of the most studied groups of fossil invertebrates.

Looking at an ammonite shell, the most striking characteristic beyond its regular planar logarithmic spiral is the very regular ribs that form parallel to the shell edge (see [Figure 3.7](#)). This ornamentation most likely occurred as a result of the same mechanical conflict that produces spines, yet it is a completely different pattern. The key to understand this discrepancy is to realise that while the form of the conflicting forces is the same, their magnitude and the geometry on which they operate is not. The same system of forces operates but on a completely different regime.

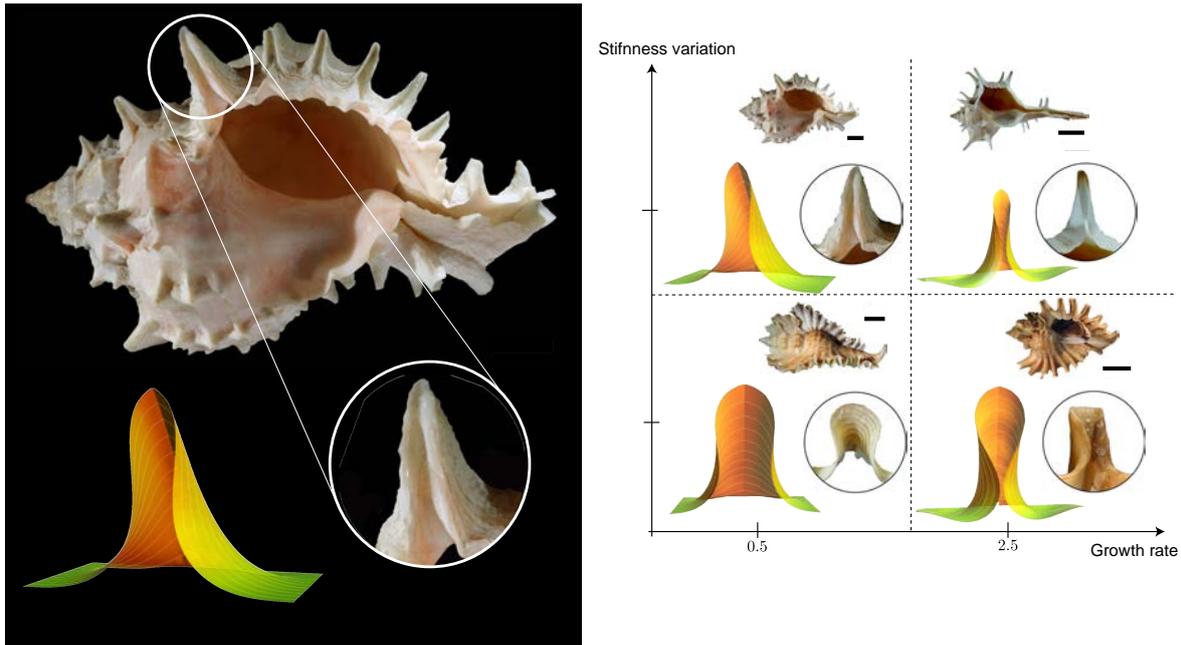


Figure 3.6: Spine morphogenesis. A variety of spine shapes can be created by varying the system's parameters as observed in actual seashells.

The ammonite aperture is very close to being circular or elliptical. Take the aperture to be a circle for simplicity of argument. If the mantle radius is larger than the current aperture radius, the mantle will be in compression, but not enough to cause a spine producing elastic instability. Rather, the compressed mantle pushes outward, and the shell radius at the next increment is larger. However, this outward motion is opposed by the calcifying generative zone, which acts as a torque spring trying to maintain the current shell orientation. The effect of these two opposing forces is an *oscillatory system* that can be described mathematically: the shell radius increases, reducing compression, but overshoots to a state of tension; the 'stretched' mantle then pulls inward to decrease its tensile force, again overshooting to a state of compression [9, 4]. This process is easily implemented in a mathematical model and our "*morphomechanical oscillator*" predicts the formation of very regular ribs, with a wavelength and amplitude that increase during the growth and development of the mollusk [3, 11]. These predictions are in excellent agreement with the known morphology of ammonites as shown in [Figure 3.6](#).

3.7 Unwrapping the mystery of a living fossil

An understanding of the mechanical system enables us to connect the ribbing pattern to the geometric factors in the growing mollusk that impact the pattern. This means, in particular, that evolutionary trends that have been observed in the fossil record of ammonites can be understood from changes in the expansion rate of the growing mollusk: roughly speaking, the model demonstrates that the higher the expansion rate (the faster the radius expands), the less pronounced the ribs ([Figure 3.8](#)). This observation also provides a simple mechanical and geometric explanation for a longstanding puzzle: nautilid shells have remained essentially smooth since at least the Jurassic period (200 million years ago), a lack of distinctive character and a conservative morphology wrongly suggesting that nautilids have not evolved and that has led to the unfair qualifier "living fossil" to be attributed to current *Nautilus*. However, in light of the biophysical growth model, the smoothness of nautilid shells can be understood as a simple and direct mechanical consequence of its rapid aperture expansion.



Figure 3.7: . Ammonites ribbing. Left: By extracting the central logarithmic spiral from an ammonite (red curve), the mathematical model predicts the ribbing pattern (blue curve). Middle: *Promicroceras planicosta* (scale bar is 10mm). Right: The corresponding three-dimensional model

As is illustrated by spiny mollusks and ammonite ribs, the shell in your hand, aside from being the remnants of an individual house, can also teach us about evolution. The form of shells is not arbitrary but constrained by mechanics, induced by the relative growth of the animal and its shell. These examples illustrate a more general principle: the form of living matter is governed by physical laws, which can be used to understand certain aspects of shape evolution both through the development of an individual organism and across the vast time scales over which evolution operates.

This basic concept can be traced back 100 years to the pioneering work of D’Arcy Thompson. In his classic 1917 tome *On Growth and Form*, Thompson argued that biological shapes and patterns are not fundamentally different from non-biological. Since cells, tissues, and organs must satisfy the same laws of physics as any other matter, their behaviour can be understood using the same tools, for example by analysing differential equations that emerge through a balance of forces. In non-biological soft matter, it is well appreciated that patterns emerge via conflict. Just as with mantle tissue, a sheet of rubber remains flat if untouched, then buckles when compressed at the edges. As d’Arcy Thompson writes: “*The form of any portion of matter, whether it be living or dead, and the changes of form which are apparent in its movements and in its growth, may in all cases, alike be described as due to the action of force. In short, the form of an object is a diagram of forces.*” That some of the same principles could apply to biological matter may seem obvious, but for most of the 20th century such ideas and approaches took a backseat in biology to the goal of uncovering the genetic code and tracing the functional path of biological patterns.

It is only in recent decades that physics based mathematical modelling has begun to be applied to biology. Such work has shown that while the information stored in genes is historically contingent, the evolution of form is to some extent constrained. This conclusion illustrates the concept of “*developmental constraint*”, a founding concept of *Evolutionary Developmental Biology* (a.k.a Evo-Devo), which carries the idea that development, and not natural selection alone, partly determines the direction of morphological evolution.

3.8 Epilogue

The story of mollusks is one that continues to unfold, a story for which numerous mysteries remain. A short stroll among any good shell collection reveals a number of patterns still mys-

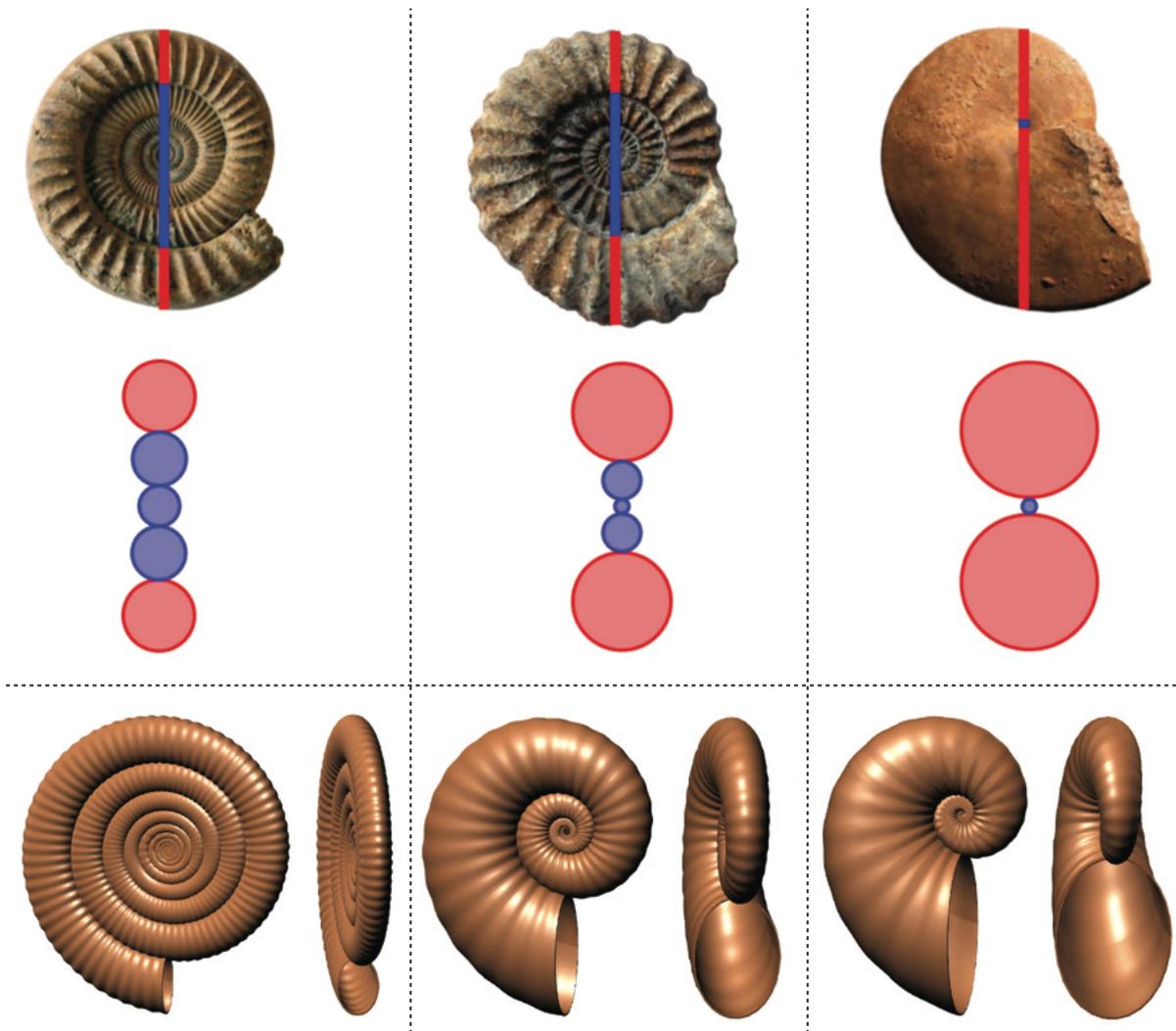


Figure 3.8: The ribbing pattern in ammonites depends on the rate of aperture expansion. Slow expansion (left) leads to fine ribbing while rapid expansion (right) leads to smooth shells. Bottom: corresponding simulation from the mathematical model.

terious to scientists. The handedness of shell coiling – e.g. over 90% of gastropods are ‘right handed’ – is one of the more striking examples of symmetry breaking for which developmental biology has yet to find a genetic explanation. Yet, some of our simple mechanical models establish the origin of these differences [2]. Other types of exquisite ornamentations include the mysterious fractal-like spine pattern found in a number of species in the Muricidae family, for instance *Hexaplex cichoreum*. We have recently shown that these patterns also arise through mechanical interactions [10]. Also, though we know that shell growth rate is influenced by environmental factors, the impact of environment on shell form is less clear: Can we learn about the oceans of the past by studying the shells that formed in them?

Developing mathematical frameworks to study shell form is one step in piecing together answers to these puzzles. A full understanding is inherently an interdisciplinary endeavour, in particular combining mathematics and biology. With so many mysteries surrounding such a simple, beautiful, and abundant object, it is undoubtedly true that shells will continue to intrigue mathematicians, biologists, and the beachcomber alike.

As you end your stroll on the beach, against your compulsion, do leave your seashell for the next visitor to enjoy and bring home with you the mathematical beauty that nature offers to the

attentive mind.

Acknowledgements

It is my great pleasure to thank Rafael Araujo who very generously shared his wonderful art work with me. You can find more about his work on his web page:

<https://www.rafael-araujo.com>.

3.9 Further Reading and Exploration

- National Geographic wrote an article on our work in 2024 with an interactive website where you can design your own seashell. Give it a try: <https://www.nationalgeographic.com/science/graphics/design-your-own-shell>.
- A classic book that explores patterns on seashells is *The Algorithmic Beauty of Sea Shells* by Hans Meinhardt (1995) [6].
- A detailed mathematical description of the construction of seashells is explained in my book: *The Mathematics and Mechanics of Biological Growth* [5].
- *Spirals in Time: The Secret Life and Curious Afterlife of Seashells* by Helen Scales (2015) is an interesting book on seashells from a natural history and science perspective [12].

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