

Mechanical basis of morphogenesis and convergent evolution of spiny seashells

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Convergent evolution is a phenomenon whereby similar traits evolved independently in not closely related species, and is often interpreted in functional terms. Spines in mollusk seashells are classically interpreted as having repeatedly evolved as a defense in response to shell-crushing predators. Here we consider the morphogenetic process that shapes these structures and underlies their repeated emergence. We develop a mathematical model for spine morphogenesis based on the mechanical interaction between the secreting mantle edge and the calcified shell edge to which the mantle adheres during shell growth. It is demonstrated that a large diversity of spine structures can be accounted for through small variations in control parameters of this natural mechanical process. This physical mechanism suggests that convergent evolution of spines can be understood through a generic morphogenetic process, and provides unique perspectives in understanding the phenotypic evolution of this second largest phylum in the animal kingdom.

Homoplasy, the appearance of similar traits in separate evolutionary lineages as a result of convergence, parallelism, or evolutionary reversals, is a major concern in phylogenetic analysis for which it is viewed as noise. However, over the past two decades, homoplasy has also become a subject of increasing interest, stimulated by the rise of evolutionary developmental biology (evo devo) and the wish to uncover the developmental basis of this phenomenon (1–3). Spines constitute the most prominent ornamentation of mollusk shells and have evolved in many distantly related fossil and current mollusk species (at least 55 genera and 21 families of current gastropods; 10 genera and 8 families of current bivalves; 11 genera and 8 families of ammonoids; and 6 fossil nautiloid genera; see Fig. 1 for examples). Convergent evolution of spines in mollusks has been addressed in functional terms, these structures being interpreted as having evolved as a defense in response to shell-crushing predators (4–6). This hypothesis is itself the basis of the widely cited “escalation hypothesis,” according to which long-term trends in the fossil record were caused by the evolutionary response of prey to predation pressure (7). The idea that convergent evolution of similar mollusk ornamentations might be fully explained in functional terms is based on the premise that similar characters, perceived as well designed for a presumed function, cannot conceivably have independently evolved fortuitously. Therefore, natural selection is thought to have repeatedly shaped similar functional traits out of random variations.

Over the past two decades, there has been an increasing awareness that selectionist hypotheses on their own have partial explanatory value for understanding the evolution of biological form, because they do not address the origin of traits thought to increase reproductive success (8–10). In other words, even if spines act in some species as protection against predators, to hypothesize that this feature has spread among populations through differential reproductive success of their bearer does not explain how it came into being in the first place. At the fundamental level, the question of function is best suited to address the repeated selective retention of the trait, but leaves unanswered its repeated emergence in distantly related lineages. Thus, complementary is the mechanistic approach addressing morphogenesis of the trait;

that is, we must ask whether the morphogenetic processes that actually shape these structures make them likely to reappear. In this study, we focus on the mechanistic approach and the natural mechanical process that shapes spines in mollusk shells and underlies their repeated emergence.

Spines, like other ornamentations found in seashells, are incrementally secreted and represent the spatiotemporal record of the shape modifications of the shell edge during growth. Spines first emerge as a bulge of the shell edge that curves both longitudinally and transversely as growth proceeds, resulting in a fold that eventually closes in on itself as the lateral edges converge toward the fold axis.

A mollusk's shell is composed of an outer organic layer, called periostracum, and underlying calcified layers, all being secreted by a thin membranous elastic organ called the mantle (11). During growth, the mantle moves forward slightly beyond the calcified shell edge while secreting the periostracum, which isolates from the external environment the extrapallial fluid from which the calcified shell is precipitated. The periostracum is secreted in the periostracal groove, between the outer and middle mantle lobes, and subsequently reaches its external position where it becomes fixed on the outer shell surface when calcification occurs. The periostracum surrounds the outer mantle lobe, is attached at both extremities along the calcified shell edge and inside the periostracal groove, and thus establishes a close physical elastic link between the calcified shell and the mantle edge. The shape of the generative zone—the periostracum surrounding the outer mantle lobe—is therefore incrementally recorded and fixed in the calcified shell during growth. In turn, the calcified shell edge acts as a template for the new growth increment, and partly determines the shape of the generative zone. Spines emerge during phases of excess in growth rate. In this way, the formation of spines can be understood in terms of the changing morphology of the shell edge, driven by the growth and elastic response of the mantle. A primary focus for the present study is to model molluscan shell morphogenesis based on this mechanical interaction.

Mechanical Model

Several papers have reproduced pigmentation patterns in shells using either reaction-diffusion (12) or neural-based models (13). However, the development of mechanistic models for 3D ornamentations is still in its infancy. We propose a model on the premise that biological morphogenesis is proximately a mechanical process (14, 15). Such an idea has been proposed empirically and theoretically for the genesis of ornamentation by different authors (16–19). Explicit models can be found in two previous works that address shell formation from a mechanical perspective.

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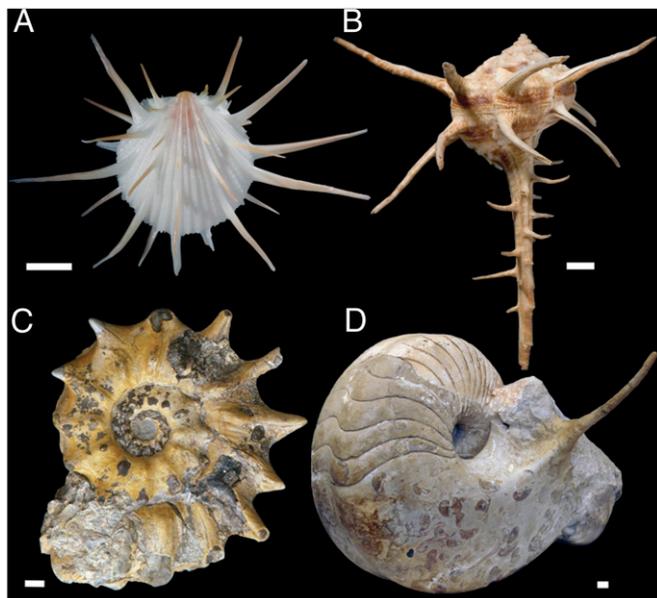


Fig. 1. Spiny shells in mollusks. (A) Bivalve (*Spondylus imperialis*, recent, Philippines), (B) gastropod (*Bolinus cornutus*, recent, Senegal), (C) ammonoid (*Collignonicerus praecox*, Middle Turonian, United States), and (D) nautiloid (*Paracenoceras spinatum*, Middle Oxfordian, France). (Scale bars, 10 mm.)

First, in Morita (20), an elastic, double-membrane tube model is proposed to explain some features of morphology; however, it did not include accretionary growth. Second, in Moulton et al. (21), we presented a model for the time evolution* of the shell edge based on the mechanical deformation of the secreting mantle. The model was able to explain and reproduce antimarginal ornamentations, such as those found in giant clams. However, more complex ornamentations, such as spines, were not considered. Here, following the general framework of Moulton et al. (21), we develop a model to explain the formation of spines through simple mechanical considerations. Our approach is to focus on the level of a single spine, and to ask the questions: Can the spontaneous mechanical behavior of the growing mantle-shell system provide a mechanism to account for spine morphogenesis? Can the variety of spine structures emerge through the same basic and natural mechanism? To answer these questions, we develop a mechanical model based on the theory of one-dimensional elastic structures, and explore the patterns that emerge through the process of growth and adhesion.

A schematic for our model is given in Fig. 2. The basic idea is to predict the form incrementally generated by the edge of the thin elastic mantle displaying an excess of length relative to the previously formed and fixed configuration. The mantle edge is modeled as an inextensible elastic rod, and is assumed to grow at a fixed rate. At each growth increment, the mantle adheres to the current shell edge through the elastic periostracum. Because the mantle has grown since the last secretion, it is longer than the shell edge and deforms upon adhering. The shape of the deformed mantle is the configuration that minimizes the total mechanical energy. This energy minimizer is determined by solving the equations of mechanical equilibrium (details in *Appendix*). The mechanical equilibrium represents a balance of two components: bending of the mantle dependent upon the geometric curvature of the mantle edge, and an attachment force that relates the adhering

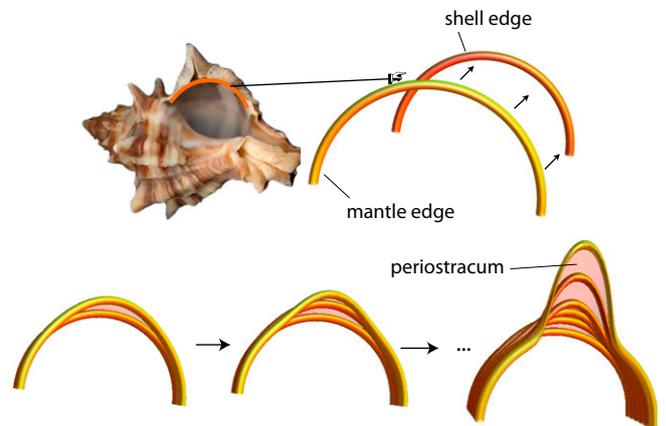


Fig. 2. Setup for modeling spine formation. The elastic mantle edge, showing an excess of length compared with the previous and fixed shell edge, deforms, then secretes new material in the deformed shape.

strength between the mantle and the shell edge (the template that serves as a mechanical rigid foundation).

The development of the shell proceeds by incrementally increasing the length of the mantle edge, determining the mantle shape by solving the equations of mechanical equilibrium, and then updating the shell edge as the shape of the deformed mantle. The emergent form is governed by the length dimensions and elastic properties of the mantle edge, the strength of adhesion, and the marginal growth rate, i.e., the excess of length compared with the previous growth increment. Here we demonstrate how variations in these parameters can account for a diversity of spine structures. Geometric and elastic properties of the mantle edge can be estimated from the literature (*SI Text*). To isolate the pattern formation in the emergence of a single spine, we implemented clamped-clamped boundary conditions and an initially flat shell edge, and chose the strength of the adhesion (or equivalently the length of the mantle under consideration) to be consistent with the initial formation of a single spine (which corresponds to a mode 3 instability in the initial buckling of the elastic rod).

Results

As an initial model, we assume uniform growth and a homogeneous mantle edge. Then the main governing parameter is the growth rate, i.e., how much excess of length is present at each growth increment; this is governed by the parameter g , the rate of increase of length of the elastic structure (details in *Appendix*). Fig. 3 depicts the time evolution as the growth rate g is varied. A larger growth rate produces a more highly curved and shorter structure. Decreasing the growth rate leads to a taller structure before the spine folds and closes on itself; note, however, that if the growth rate is further decreased from the leftmost time evolution in Fig. 3, a noticeable increase in height is not attained.

Variable Bending Stiffness. As evidenced in Fig. 3, varying the growth rate changes the height and appearance of the spine, but cannot account for the long, straight spines seen in, for instance, *Bolinus cornutus* (Fig. 1B). Mechanically, the reason is that in such spines, the curvature, and thus the bending energy, is quite large at the tip, and so it is not mechanically favorable for a uniform elastic rod to form such a structure. In this section we propose a simple variation on the model to investigate whether longer and/or sharper spines also emerge naturally through the mechanical mantle deformation process.

In order for a spine with high curvature at the tip to be mechanically favorable, the bending stiffness at this point must be lower. This inhomogeneity can have two origins. First, there

*Note that in *Mechanical Model* and *Results*, we use "time evolution" to refer to evolution of the varying morphology of the shell edge during development of a single specimen, as opposed to the concept of Darwinian evolution that forms the focus of the *Introduction* and *Discussion*.

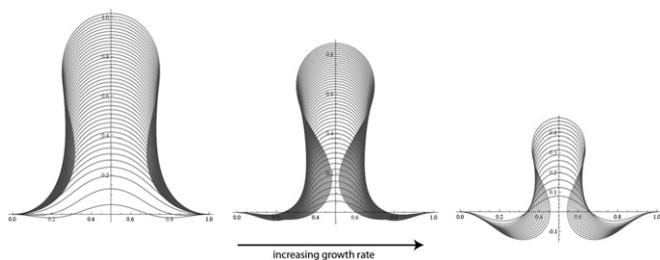


Fig. 3. Simulation of spine formation with uniform growth and thickness, for growth rates $g = 1, 4, 8$ (left to right). Other parameters are provided in *SI Text*.

may be a difference in the material stiffness of the mantle at the location of the spines, i.e., a decreased Young's modulus. For instance, it has been found that there exist discrete specialized zones of the mantle where changes in secreted proteins are linked to shell fabrication and patterning (22). These specialized zones were found to correlate with shell pigmentation and ridge patterns. In light of this evidence of mantle heterogeneity, we suggest the possibility of a varying Young's modulus.

Second, a decreased bending stiffness can emerge from a decreased thickness. In spine-producing mollusks, the shell edge is several times longer at the location of the spines than away from it. In order for the mantle edge to secrete the shell material, the mantle must itself extend greatly in length. Such an increase in length, which can also be empirically inferred from the sharp dilation of spiral ridge patterns, should be accounted for by an accompanying decrease in thickness, to conserve the overall mantle volume. The idea, then, is that the mantle becomes thinner in regions of high curvature, thus reducing the bending energy.

Both of these scenarios result in a heterogeneous bending stiffness, an idea we now incorporate into the model; that is, we take the bending stiffness of the elastic mantle to be a function of position. For simplicity, we take the bending stiffness to have the form of an upside-down Gaussian (Fig. 4). Letting $E_b(s_0)$ be the bending stiffness at material point s_0 , such that $E_b = 1$ is the baseline stiffness and $s_0 \in [0, 1]$ is the scaled reference material variable (see *Appendix*), we assume

$$E_b(s_0) = 1 - b_1 e^{-\left(\frac{s_0 - 0.5}{b_2}\right)^2} \quad [1]$$

The parameter b_2 controls the width of the Gaussian and thus the size of the region of decreased stiffness, whereas $b_1 \in [0, 1)$ controls the amount of decreased stiffness. We choose b_2 so that the Gaussian is approximately the same width as the spine in the initial buckled state, we then update b_2 so that width of the region of decreased stiffness remains the same at all times (in the current configuration of the mantle; details in *Appendix*).

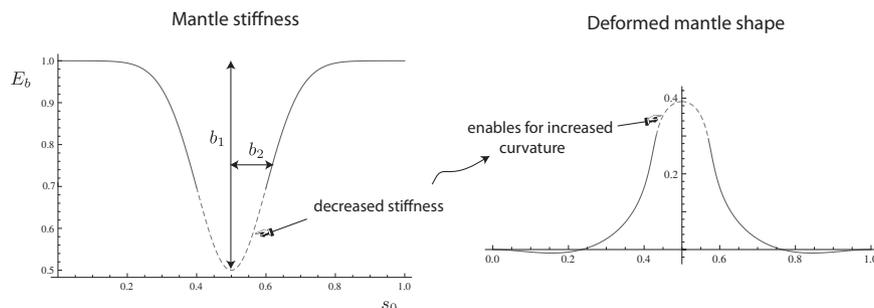


Fig. 4. Form of bending stiffness. A decreased stiffness allows for higher curvature at the tip of the spine.

There are now two main parameters that govern the form of the evolving spine: the growth rate g and the decrease of stiffness at the location of the spine, i.e., the value of b_1 in Eq. 1. Fig. 5 gives a phase diagram showing the morphospace (23, 24) as we vary these two parameters. Here we have extended the curves in the growth direction at each increment so as to give a 3D representation of the shape predicted by the model. As in Fig. 3, a decrease in growth rate leads to a taller structure before folding in on itself. Increasing the degree of stiffness variation (i.e., increasing b_1) leads to a narrower structure and thus a decreased aspect ratio of width to height of the spine. Also included in Fig. 5 are four shells from the family Muricidae. These shells show a range of spine morphology, the basic forms of which are well captured in the two parameter morphology space. Note that we have assumed that the mantle edge remains planar; though this is generally a reasonable approximation, inspection of certain spines, e.g., *Ceratostoma bumetti* (Fig. 5D), demonstrates that the tip of the spine curls back into the third dimension. This curling back gives the spine the appearance, when viewed head-on, of being flat-ended, though in fact the tip does maintain the rounded structure predicted by our model.

Self-Contact. Note that the curves shown in this paper correspond to the centerline of the mantle edge. The basic time evolution can be summarized as follows. (i) An initial bulge forms. (ii) The bulge grows, reaching a point where the sides of the spine are nearly parallel and the tip of the spine is highly curved. (iii) The middle section pinches, causing the spine to fold on itself. If self-contact of the mantle edge is included, step (iii) can be altered. That is, if the radius of curvature of the tip is the same as the thickness, the middle section cannot pinch, and any further growth would lead to an extension of the height. This idea is illustrated schematically in Fig. 6. Fig. 6A shows the spine development via our model. In Fig. 6B, self-contact is included. Self-contact constrains the middle of the spine from pinching, thus allowing for a longer spine with parallel sides.

Note that this self-contact will only be a contributing factor in the case of very narrow spines, such as those seen in *Bolinus comutus* (Fig. 1B). Such spines correspond to large stiffness variation and high marginal growth in the phase diagram Fig. 5. Indeed, in wider spines, such as *Pterynotus phyllopterus* (Fig. 5C) pinching of the middle section is evident.

Discussion

The theoretical model that we have presented suggests that the morphogenesis of mollusk spines can be accounted for by the spontaneous mechanical behavior of the thin elastic mantle that, constrained in its growth by the previous fixed configuration onto which it adheres, incrementally deforms to a shape of mechanical equilibrium and accretes new shell material. In other words, our model demonstrates that natural mechanical forces can explain how mollusks grow their spiny shells.

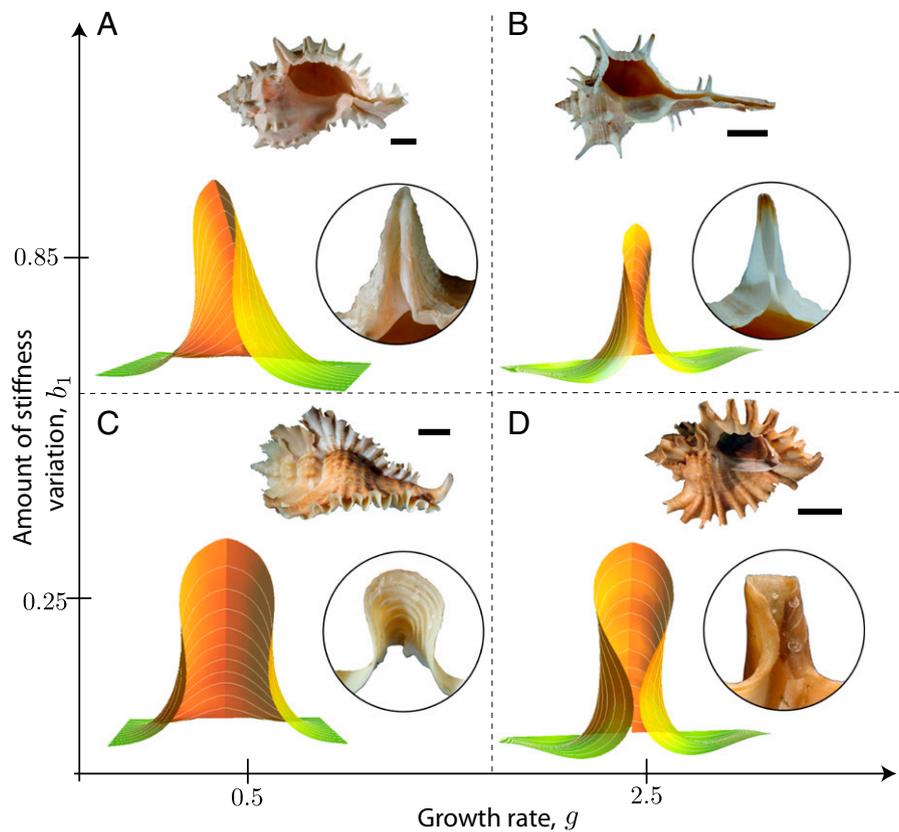


Fig. 5. Phase diagram showing the effect of the growth rate and the degree of stiffness variation on the evolving spine. Variations in spine morphology among species of the same family (Muricidae) are shown for comparison: (A) *Hexaplex erythrostomus*, (B) *Bolinus brandaris*, (C) *Pterynotus phyllopterus*, and (D) *Ceratostoma burnetti*. Other parameters are provided in [SI Text](#). (Scale bar, 10 mm.)

We showed that the growth process in its simplest form leads to very rounded spine structures with a large aspect ratio of width to height. By incorporating a natural heterogeneity to the bending stiffness, we then demonstrated that a variety of spines emerge in the two parameter morphospace of marginal growth rate and degree of heterogeneity. The notion of a heterogeneous bending stiffness is empirically supported by the necessary change in length (and thus thickness) of the mantle edge during spine production, as well as the variation in mantle properties at the level of protein encoding. Mechanically, these two processes lead to a similar heterogeneous structure that is modeled here by a prescribed Gaussian form for the bending stiffness. To produce a detailed model that takes into account cellular properties, it would be necessary to distinguish the form and cause of this heterogeneity, and whether it varies during the growth of the spine. Measuring the mechanical properties of the mantle at different locations would be a challenging yet useful experimental direction. Likewise, it would be of great benefit to capture visual recordings of a spine as it is being secreted by a mollusk over long periods of time.

Biomechanics lies at the core of connecting the genetic and molecular basis of cell activities to the macroscopic tissue deformations that shape developing organisms (25). Aside from the heterogeneity, our model suggests that a key parameter governing the shell form is the marginal growth rate. Recent efforts to identify growth-related genes in gastropods (26) might offer a new avenue of investigation of the biomechanics of mollusk shells morphogenesis in an integrative developmental perspective. In turn, these approaches could provide new insights into the developmental bases of environmentally induced phenotypic plasticity of some spiny gastropod species (27).

From an evolutionary perspective, our model suggests that the incremental natural deformation of the growing elastic mantle constitutes a generic morphogenetic process that contributes to the reproducibility of spines across generations and provides also a simple explanation for how these structures have repeatedly emerged in distantly related mollusk species. The shape of spines corresponds to a configuration that emerges by an accretion process in which at each growth increment the mechanical energy of the system is minimized, suggesting that these structures are configurations toward which the growing system may naturally tend. This hypothesis implies that other biological systems displaying an accretionary growing structure secreted by an elastic membrane may be expected to generate similar mechanically preferred configurations. And indeed, similar hollow spines have

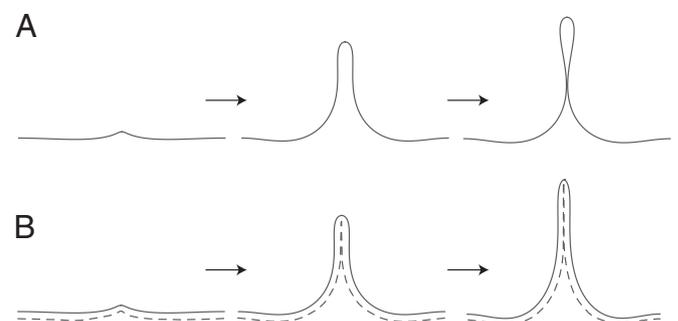


Fig. 6. (A) Time evolution of the shell edge via our model. (B) Proposed evolution when including self-contact of the mantle edge (dashed lines). Self-contact prohibits the middle section from pinching.

emerged in brachiopods (28), a phylum whose shell, incrementally secreted by a thin elastic mantle, follows the same basic rules for growth.

The neo-Darwinian framework emphasizes the role of contingencies and history-dependent variations in determining the course of evolution. In this perspective, a biological form is incrementally shaped for function through a contingent series of cumulative reproductive successes. The emergence of spines in mollusks is contingent in the sense that they require certain conditions to be formed—in particular, an excess in growth rate and perhaps heterogeneous mantle stiffness. However, once these conditions are met, the morphogenesis of spines reveals the operation of well-established physical principles that may shape both living and inanimate matter in a predictive way, as shown previously for fingerprints (29), phyllotaxis (30), or mucosal folding in airways (31), for example. Likewise, the mechanisms that underlie the morphogenesis of spines should not be approached from a purely functional perspective.

The idea that changes in development underpin evolutionary changes constitutes the most basic rationale behind the rise of evolutionary developmental biology in the 1980s. A primary evo devo guideline is that explanations of the evolution of form have to consider how form is generated (32). In this perspective, explanations of homoplasy (convergence and parallelism) must take into account not only the developmental and genetic mechanisms that are embedded in the evolutionary history of lineages (3), but also the physical mechanisms that are involved in development, and that explain why physical models of biological morphogenesis may to some extent keep their predictive power despite the contingencies inherent to biological evolution. Once the ahistorical generic bases of morphogenesis are analyzed, we are in a better position to understand the course followed by the evolutionary history of biological form. From this point of view, it should be noted that spines are prevalent in a number of mollusk species and may be associated with other kinds of 3D ornamentations on shells whose morphogenesis remains unknown, and it is natural to ask whether in fact each of these forms can be produced with different parameter regimes within a single mechanical model. Such a unifying theory would provide a new, far-reaching perspective of the phenotypic evolution of the shells of the second largest phylum in the animal kingdom.

Appendix

Model Formulation. To simulate spine formation, we model the mantle edge as a growing inextensible unsharable planar elastic rod, and the shell edge as a rigid foundation to which the mantle is elastically adhered via the periostracum. The center line of the mantle is parameterized by the curve $\mathbf{R}(S) = [X(S), Y(S)]$, where $S = S(t)$ is the mantle arc length in its current configuration; the foundation likewise has arc length parametrization $\mathbf{P}(\hat{S}) = [P_X(\hat{S}), P_Y(\hat{S})]$. Following the approach outlined in ref. 33, we define the growth of the mantle through a mapping from an initial configuration in which the mantle has arc length parameter S_0 . The attachment requires also a mapping between the variable \hat{S} and S , i.e., a map defining how the mantle adheres to the shell edge. Here we use a linear relation, implying a uniform attachment map.

In what follows, we adopt the convention of expressing the system in the pregrown variable S_0 ; this relates to the current variable through a growth parameter $\gamma := \frac{\partial S}{\partial S_0}$. Let the resultant force in the mantle edge be given by $\mathbf{N}(S_0) = [N_X(S_0), N_Y(S_0)]$. We define θ as the angle between the tangent to \mathbf{R} and the horizontal x axis. Letting primes denote derivatives with respect to S_0 , mechanical equilibrium requires

$$\begin{aligned} N'_X &= \gamma K_f (X - P_X) \\ N'_Y &= \gamma K_f (Y - P_Y) \\ M' &= N_X X' - N_Y Y'. \end{aligned} \quad [2]$$

Here, K_f , which has units of pressure, characterizes the strength of the adhesion between mantle and shell edge. Thus, the shell edge applies a linear spring force to the mantle. Also, M is the bending moment, which is related to θ by the standard constitutive equation $M = EI \frac{\partial \theta}{\partial S}$, where E is the Young's modulus and I the second moment of area of the mantle edge. Along with Eq. 2, we have the geometric relation

$$X' = \gamma \cos \theta, \quad Y' = \gamma \sin \theta. \quad [3]$$

Next, we nondimensionalize the system. We scale all lengths by L_0 , the initial pregrowth length of the mantle edge (more accurately, the section of the mantle under consideration, i.e., roughly the length between spines), the bending moment M by EI/L_0 , and N by EI/L_0^2 . Letting lowercase symbols define the dimensionless quantities and $' = \frac{d}{ds_0}$, the resulting system is

$$\begin{aligned} x' &= \gamma \cos \theta, & y' &= \gamma \sin \theta \\ n'_x &= \gamma k_f (x - p_x), & n'_y &= \gamma k_f (y - p_y) \\ \theta' &= \gamma m, & m' &= \gamma (n_x \sin \theta - n_y \cos \theta). \end{aligned} \quad [4]$$

Here, $k_f = K_f L_0^4 / EI$ characterizes the relative effects of bending and foundation attachment. Note also that primes denote differentiation with respect to $s_0 = S_0 / L_0$. For given growth γ and foundation $\mathbf{p} = [p_x, p_y]$, Eq. 4 forms a system of six first-order ordinary differential equations for the variables $\{x(s_0), y(s_0), \theta(s_0), m(s_0), n_x(s_0), n_y(s_0)\}$. We solve this system for clamped boundary conditions, which requires $x = y = \theta = 0$ at $s_0 = 0$ and $s_0 = 1$. To simulate the time evolution of the shell edge, we input $\gamma = \gamma(t)$, as well as a rule for updating the foundation. Because the growth time scale is much longer than the elastic time scale, we assume the system is always in mechanical equilibrium. Hence t may be thought of as the growth time. The simple case of uniform growth, considered here, corresponds to $\dot{\gamma} = g = \text{constant}$, where dots denote (growth) time derivatives. To update the foundation at each growth increment, we begin with the time continuous rule

$$\dot{\mathbf{p}} = \eta (\mathbf{r} - \mathbf{p}), \quad [5]$$

which states that the foundation relaxes to the current mantle shape with rate η , which may be thought of as corresponding to the rate of calcification of the newly secreted shell edge.

To compute the time evolution, time is discretized, and the equations of mechanical equilibrium (Eq. 4) are solved using a shooting method. In each simulation, we start with a flat foundation, and the initial parameters for the shooting variables are computed using a linear buckling analysis (33).

Heterogeneous Mantle Stiffness. Here we consider the case where the mantle stiffness is a function of material position. For simplicity, define the bending stiffness $\mathcal{E}_b = EI$. The formulation proceeds as above, but now we scale quantities by $\mathcal{E}_{b_0} := \mathcal{E}_b(0)$, the bending stiffness at the edge of the domain, and define $E_b(s_0) = \mathcal{E}_b(s_0) / \mathcal{E}_{b_0}$. The only change to the system (Eq. 4) is in the constitutive relation for m , which becomes $\theta' = \gamma E_b^{-1} m$. The homogeneous case is recovered if $E_b(s_0) \equiv 1$. The form of E_b used in this paper is

$$E_b = 1 - b_1 e^{-\left(\frac{s_0 - 0.5}{2b_2}\right)^2}. \quad [6]$$

That is, the bending stiffness decreases in the center of the domain with the shape of a Gaussian flipped upside down. The width of the Gaussian, and thus the length of the region of decreased stiffness, is controlled by b_2 . Note that in our approach, we always work in the initial, pregrown material variable s_0 , because this gives the computational convenience of a fixed domain $s_0 \in [0, 1]$. Note that if s is the arc length parameter in the current configuration, then $\gamma = \partial s / \partial s_0$. Thus, to keep the size of the Gaussian constant in the current configuration, we select an initial value, b_{2_0} , and then at each time step take $b_2 = b_{2_0} / \gamma$. In this way, the actual size of the region of the mantle with decreased stiffness is maintained throughout development.

To check the sensitivity of the form of heterogeneity, we computed the evolution using a (smoothed-out) step function, which would correspond to a discrete change in stiffness at the location of a varying cell type, and found no significant difference due to the particular choice of function as long as width and depth agree.

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