Morphomechanics and developmental constraints in the evolution of ammonites shell form

ALEXANDER ERLICH[1], DEREK E. MOULTON[1], ALAIN GORIELY[1] and REGIS CHIRAT[2*]

[1] Mathematical Institute, University of Oxford, Oxford, UK

[2] Université Lyon 1, ENS de Lyon, CNRS, UMR 5276 LGL-TPE, France

Total number of figures: 10

Abbreviated title: Morphomechanics and constraints in ammonites

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* Correspondence to: Régis Chirat, Université Lyon 1, CNRS, UMR 5276 LGL-TPE, 27–43 Boulevard du 11 Novembre 1918, F-69622 Villeurbanne Cedex, France. Tel. +33 (0)4 72 44 85 59/Fax. +33 (0)4 72 44 85 93. regis.chirat@univ-lyon1.fr

ABSTRACT

The idea that physical processes involved in biological development underlie morphogenetic rules and channel morphological evolution has been central to the rise of Evolutionary Developmental Biology (Evo-Devo). Here we explore this idea in the context of seashell morphogenesis. We show that a morphomechanical model can predict the effects of variations in shell shape on the ornamental pattern in ammonites, a now extinct group of cephalopods with external chambered shell. Our model shows that several seemingly unrelated characteristics of synchronous, ontogenetic, intraspecific and evolutionary variations in ornamental patterns among various ammonite species may all be understood from the fact that the mechanical forces underlying the oscillatory behaviour of the shell secreting system scale with the cross-sectional curvature of the shell aperture. This simple morphogenetic rule, emerging from biophysical interactions during shell formation, introduced a non-random component in the production of phenotypic variation and influenced the morphological evolution of ammonites over millions of years. As such, it provides a paradigm for the concept of “developmental constraints”.

For the second half of the 20th century, the neo-Darwinian synthesis established the mainstream of evolutionary biology. According to this view, evolution is the result of cumulative effects of natural selection (a non-random reproductive bias) on intraspecific random (unbiased) heritable variations in populations that spread across generations according to the advantage they confer over less fit. An important consequence of considering variation as random, isotropic, unbiasing the evolution trajectories (e.g. Wright, ’67; Dobzhansky et al., ’77), has been that selection came to be considered as the only source of non-randomness and the “Modern Synthesis” defined as ‘‘*the theory that selection is the only direction-giving factor in evolution*’’ (Mayr, ’80 p. 117). Challenging this basic tenet of neo-Darwinism, the realization that development biases both the generation of phenotypic variation and the direction of morphological evolution (Alberch, ’80, ’82) spurred the rise of Evolutionary Developmental Biology, or Evo-Devo, in the 1980’s (see Reiss et al., 2008). The concept of developmental constraints (or bias), despite a confusion in terminology in subsequent literature (Antonovics and van Tienderen, ’91), has been clearly summarized in an early work of Pere Alberch: “*epigenetic interactions drastically constrain the universe of possible morphological novelties and impose directionality in morphological transformations through phylogeny*”, so that “*in evolution, selection may decide the winner of a given game but development non-randomly defines the players*” (Alberch, ’80, p. 654, 665).

Although Evo-Devo is now often perceived as synonymous with comparative developmental genetics (Diogo, 2016), the exploration of the relationships between the processes of individual development and phenotypic changes during evolution actually involves a more diversified set of conceptual and methodological approaches, including theoretical modelling of developmental processes and the study of generic physical and self-organizing properties of developmental systems (Müller and Newman 2005; Müller 2007). It is worth noting that Alberch drew his inspiration, in part, from the complex behaviour of dynamical systems, and was also interested in the mechanics of morphogenesis (e.g. Oster et al., ’80; Odell et al., ’81; Oster and Alberch, ’82), which he saw as key in addressing the central issue of the genotype-phenotype relationships and in uncovering the rules that channel morphological evolution. Central to this perspective was the idea that “*each level of organization is characterized by its own dynamics*” and that “*the dynamics inherent in the process of development itself imposes constraints and biases on morphological evolution that cannot be comprehended from a genetic or a population perspective alone*” (Oster and Alberch, ’82, p. 454), a view at odds with the gene-centred neo-Darwinian synthesis from which developmental biology was absent.

The relevance of this framework is illustrated here by considering ammonites as a model system. The ammonites are an iconic group of mollusc cephalopods that populated the seas for 335 million years and became extinct 65 million years ago. The form of the ammonites’ external chambered shell evolved over millions of years, but also emerged in each individual through a development spanning a few years, the result of a growth process synchronously occurring around the shell aperture on the timescale of a few days (a growth increment itself may have been formed on a daily cycle). While the evolution of ammonites involved a range of mechanisms not reducible to the development of their shell, the purpose of the present paper is to explore whether common morphogenetic rules, emerging from biophysical interactions of the shell formation process, governed the generation of variations across such vastly different time scales (Figure 1).

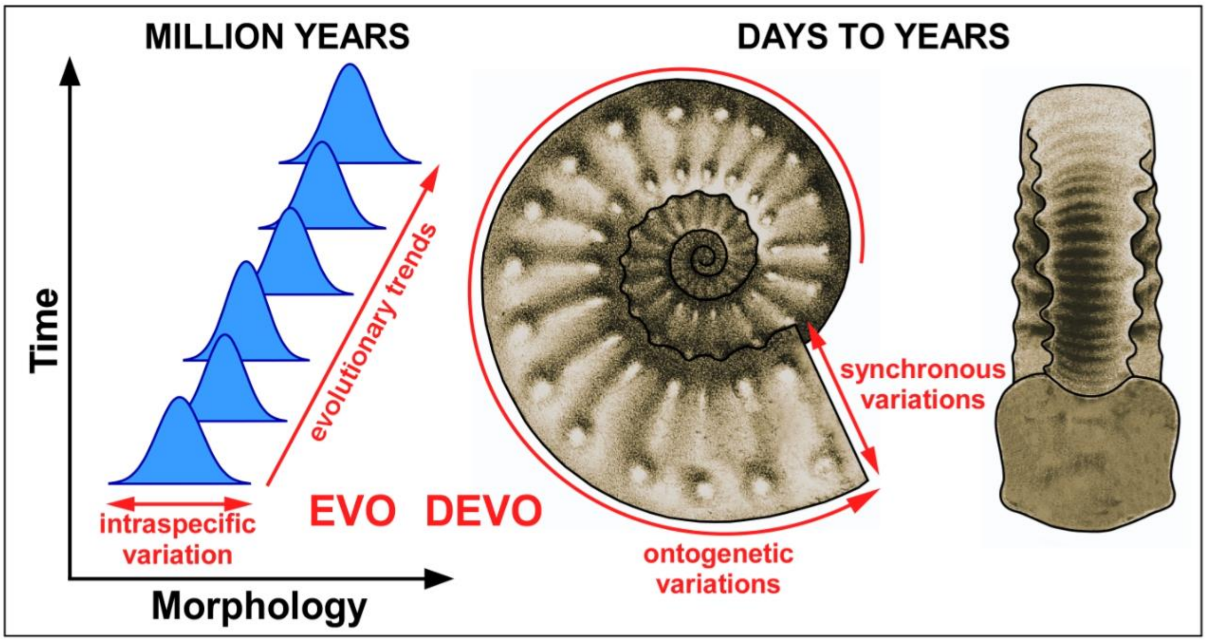

Figure 1. Evo-Devo of ammonites shell: investigating whether common morphogenetic rules governed the generation of synchronous, ontogenetic, intraspecific and evolutionary variations of form.

AMMONITES' SHELLS AS "MECHANICAL OSCILLATORS"

The mechanical forces that shape developing organisms have been the subject of renewed interest during the last decade (e.g. Eiraku et al., 2011; Budday et al., 2015; Takigawa-Imamura et al., 2015; Varner et al., 2015; Hofhuis et al., 2016). In a mechanical perspective, all processes that affect morphogenesis do so by influencing (either directly or indirectly) the forces exerted within the developing organism and/or the mechanical properties of the tissues in which these forces act. Our work has been partly motivated by the desire to provide a biophysical description of the shell secreting system and the mechanical forces that affect its behaviour and ultimately the form of the shell. Most notably, in order to uncover the mechanism behind the emergence of commarginal ornamentation of ammonite shells, we developed in Moulton et al. (2015) a morphomechanical model of commarginal ornamentations based on the physical interactions underlying mollusc shell secretion. We have extended the original idea of Hammer (2000) of stress-regulated oscillations through several key extensions. In particular, by formalizing explicitly this notion within the framework of continuum mechanics, we showed how these stresses could emerge during growth. Given the structure of the shell secreting system (assumed to be similar to *Nautilus* and other molluscs), our morphomechanical model was developed through detailed consideration of the mechanical interactions between the soft secreting tissue (the mantle) and the stiffer outer organic layer of the shell (the periostracum), both constrained by the calcified shell to which they adhere. Furthermore, by connecting the mechanically-induced oscillations to the shell expansion rate, our model could be validated against shell measurements and used to derive new morphogenetic rules governing ammonite evolution.

However, a limitation of our first model is that the growth process was modelled within a fixed circular geometry of the growing shell edge. And while the shell cross-section is well approximated as circular in many species, it may also display a fairly wide range of shapes with more or less acute shoulders around the aperture. This leaves open the question of how variations in the shell aperture shape affect the ornamental pattern both during development and evolution. To explore this issue and maintain a tractable approach, we extend the model to the situation of an elliptical geometry. Our objective here is to explore the effects of curvature variation in a system still amenable to mathematical analysis, and to interpret in greater depth the relevance of this model system in the context of Evo-Devo.

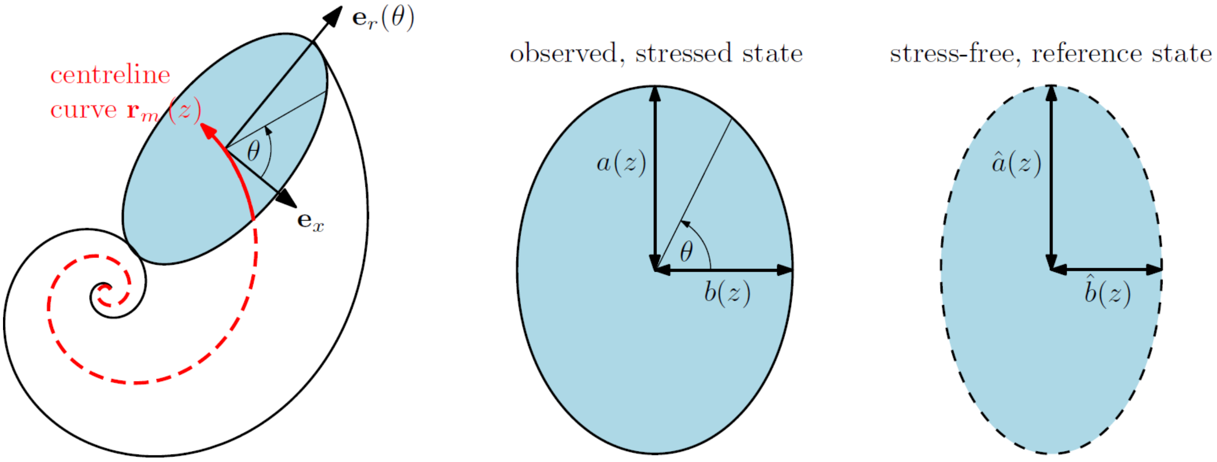

Figure 2. Schematic of the model. The mantle and shell aperture are assumed to have an elliptical shape, described by (semi-)major axis a and (semi-)minor axis b and eccentricity $e = \sqrt{1 - b^2/a^2}$, all functions of arc length z. The stress-free reference state (dashed ellipse) is the shape the mantle would take if it did not interact with the shell, and is described by $\hat{a}$, $\hat{b}$ and $\hat{e} = \sqrt{1 - \hat{b}^2/\hat{a}^2}$, again functions of z.

MORPHOMECHANICAL MODEL

The basic physical premise for the model (illustrated in Figure 2) is described in Moulton et al. (2015). The shape of the shell at any given point emerges as a balance between the elastic forces within the shell secreting mantle/periostracum (hereafter referred to as simply the mantle) and a generating zone force, akin to a torque spring, that describes the resistance of the generative zone to change orientation from the portion of the calcified shell to which it is continuously attached. The change to an elliptical geometry means that the stresses within the soft tissue are not constant but rather vary with position along the mantle edge. This added complexity renders a force-balance description, such as presented in Moulton et al. (2015), impractical. Rather, our approach is to use a Lagrangian energy-based description, which can be formulated in terms of two independent functions: the semi-minor axis $b(z)$ and the semi-major axis $a(z)$, both written as functions of shell arc-length z (details are provided in Section A of the supplementary material). In order to capture the stresses within the mantle, we also require as an input to the model the reference shape of the mantle, i.e. the shape that it would take in the absence of any interaction with the shell. In our formulation, this is accomplished by positing two functions, $\hat{b}(z)$ and $\hat{a}(z)$, such that the mantle is stress-free if and only if $b = \hat{b}$ and $a = \hat{a}$. The functions $\hat{b}(z)$ and $\hat{a}(z)$ characterize both the expansion of the growing mantle and allometric variation.

To better characterize allometric variation, we also track the eccentricity $e(z)$ of the ellipse, which is a measure of how much it deviates from being circular and is defined as

$$e^2 = 1 - \frac{a^2}{b^2} \tag{1}$$

A similar equation holds for the reference hatted variables. We remark that in our formulation, with $b(z)$ and $a(z)$ independent functions, there is no *a priori* assumption on the magnitude of ribbing on the higher curvature side compared to the lower curvature side of the shell. While it has previously been suggested (Hammer and Bucher, 2005a) that differences in ribbing amplitude is simply a matter of size and scale, an objective in this paper is to examine whether such scaling correlations emerge naturally through energy minimization during the growth process.

In order to simplify the study and obtain a clearer picture, it is also useful to consider a reduced model, in which we make a simplifying restriction on the Lagrangian: we consider the case $e \equiv \hat{e}(z)$; i.e. the eccentricity is prescribed as a given function of the arc length z. This assumption allows us to remove the effect of bending energy while preserving the elliptical geometry, enabling us to isolate the role of eccentricity in the pattern and thus facilitating a direct comparison of the results with Moulton et al. (2015). This approach also lends itself to analytical treatment as the resulting system may be solved exactly (see Appendix B.1.1). The simulated shells presented in the main text were produced under this simplifying assumption. However, we note that in the reduced model, $b(z)$ and $a(z)$ are no longer independent functions; hence when examining the difference in ribbing between the ventral and lateral sides in the Section Synchronous Variations below, we will use the full model. Further, for completeness, this restriction is relaxed in Section B.2 of the supplementary material, where we show that the full model displays the same general trends as shown below, justifying *a posteriori* the use of the reduced model.

In our framework, the ammonites' shell ornamental pattern is governed by the mantle expansion rate, a mechanical parameter k characterising the stretching stiffness of the mantle, and the eccentricity $\hat{e}(z)$. Note that with $e \equiv \hat{e}(z)$, the minor and major axes are related via

$$a(z) = b(z)/\sqrt{1-\hat{e}(z)^2}. \tag{2}$$

Without loss of generality we can assume $a > b$. The basic modelling approach is to input a reference shape (i.e. the functions with an overhat) and solve the resulting Euler-Lagrange equations to analyse the effect of expansion rates and non-uniform mantle curvature on the ribbing pattern.

As a starting point, we suppose that the mantle grows isometrically, i.e. without changing its reference eccentricity ($e = \hat{e} =$ constant), and with a linear expansion $\hat{b} = \hat{b}_0 + \gamma_b z$. In this case, the system supports the exact solution (see Section B.1 of the supplementary material)

$$b(z) = \hat{b}(z) + \delta b\, A\sqrt{\frac{\hat{b}(z)}{\hat{b}_0}}\cos\left(\omega \log\frac{\hat{b}(z)}{\hat{b}_0} - \nu\right). \tag{3}$$

where $b(0) = \hat{b}_0 + \delta b$ and δb is the initial perturbation from the relaxed position at $z = 0$. The parameters ω, A and ν are given by

$$\omega = \frac{\sqrt{4\,f\,k-\gamma_b^2}}{2\,\gamma_b},\ \ A = \frac{\sqrt{4\omega^2+1}}{2\omega},\quad \nu = -\arctan\left(\frac{1}{2\omega}\right),\ \text{and}\ f = \frac{2-2\hat{e}_0^2}{2-\hat{e}_0^2}\,. \tag{4}$$

As expected, the system produces an oscillatory pattern. The effect of eccentricity and growth rate will be discussed further below. It is worth noting that in the case $\hat{e} = 0$, which corresponds to a circular aperture (and which implies $f = 1$), we recover the results of Moulton et al. (2015).

VARIATIONS AT DIFFERENT TIME SCALES

Synchronous variations

We begin our analysis of the ribbing pattern at the level of variation along the shell margin. To investigate how variations in curvature along the shell margin affect the ribbing pattern, we must turn to the full model, in which no implicit assumptions are made regarding the relative amplitudes of the major and minor axes. In Figure 3, we plot the relative ribbing amplitude as a function of the reference eccentricity for oscillations around the fixed stress-free states $\hat{b}$ and $\hat{a}$. For each eccentricity, we provide the same initial displacement δ for both $\hat{b}$ and $\hat{a}$ and observe that the higher curvature side $a(z)$ automatically assumes a higher oscillation amplitude than the lower curvature side $b(z)$. Thus, the model predicts that *in shells with a noncircular cross section, the amplitude of ornamentation around the shell aperture is positively correlated with the local cross-sectional curvature,* a prediction consistent with empirical observations made in many non-related species. Indeed, in addition to commarginal ribs, many ammonites display more or less rounded or longitudinally elongated protuberances called tubercles or *clavi* respectively, and much of the morphological diversity of ammonite shells results from the combination of these basic ornamental features.

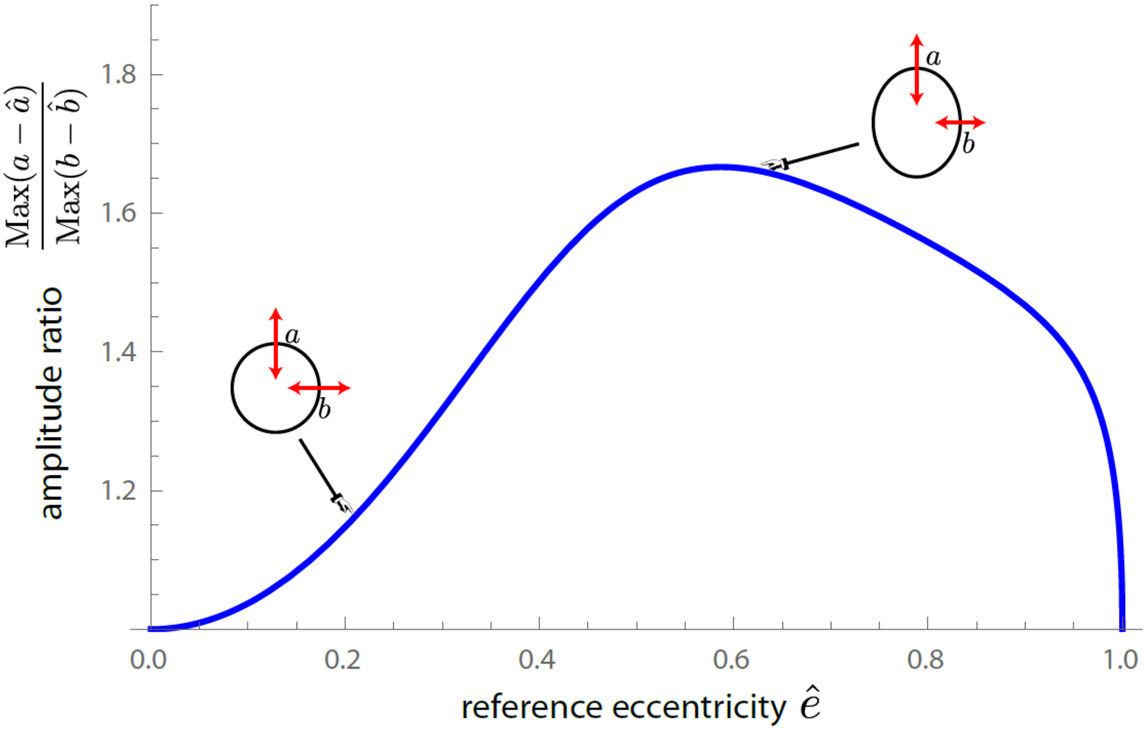

Figure 3. Synchronous variation. Relative ribbing amplitude between the high curvature side $a(z)$ and low curvature side $b(z)$ as a function of reference eccentricity. Plot produced through simulations using the full model and with equal initial displacement for a and b.

These protuberances correspond to a local increase in the amplitude of oscillations at the level of high curvature zones of the shell cross section, while oscillations tend to damp out at the level of less curved zones (Figure 4a) (see e.g. Wright et al., '96; Schlegelmilch '94, 2014ab). Interestingly, the model predicts a non-monotonic relation between the amplitude ratio and the eccentricity. While this nonlinear effect merits further investigation, it is worthwhile to note that simple explanations of ribbing amplitude based on scaling and proportionality (e.g. Hammer and Bucher 2005a) cannot capture such non-monotonicity.

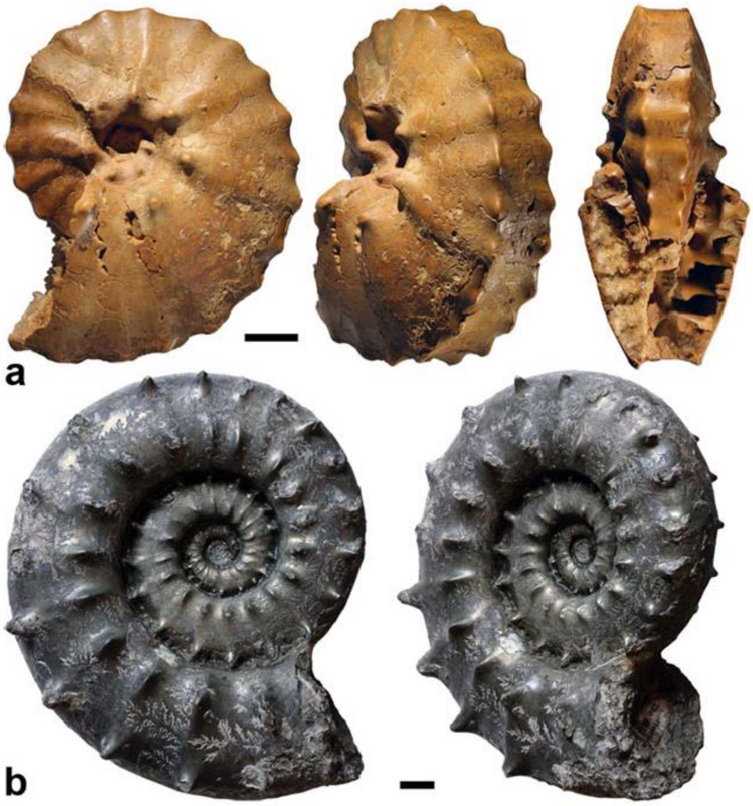

Figure 4. (a) *Knemiceras uhligi* (Albian, Egypt). Damped oscillations on the less curved flanks (laterally), emerge synchronously with higher amplitude oscillations at the level of high curvature zones of the shell cross section, in the form of rounded tubercles on the dorsal side and elongated clavi on the ventral side. (b) *Euaspidoceras douvillei* (Oxfordian, France). Spines emerge at the level of high curvature zones of the shell cross section. Scale bar 10mm.

Although the classical terminology used to describe the ornamentation of ammonites differentiates commarginal ribs, tubercles or *clavi*, our approach suggests that these ornamental features, which are synchronously secreted along the shell edge of some species, are morphogenetically identical. In some genera (e.g. *Aspidoceras*, *Collignoniceras*….), tubercles or *clavi* may also transform into spines during development (Figure 4b), suggesting that tubercles, *clavi,* and spines are themselves morphogenetically related, a conclusion supported by a morphomechanical model showing that spines emerge as a consequence of a mechanical instability of the growing front (Chirat et al., 2013).

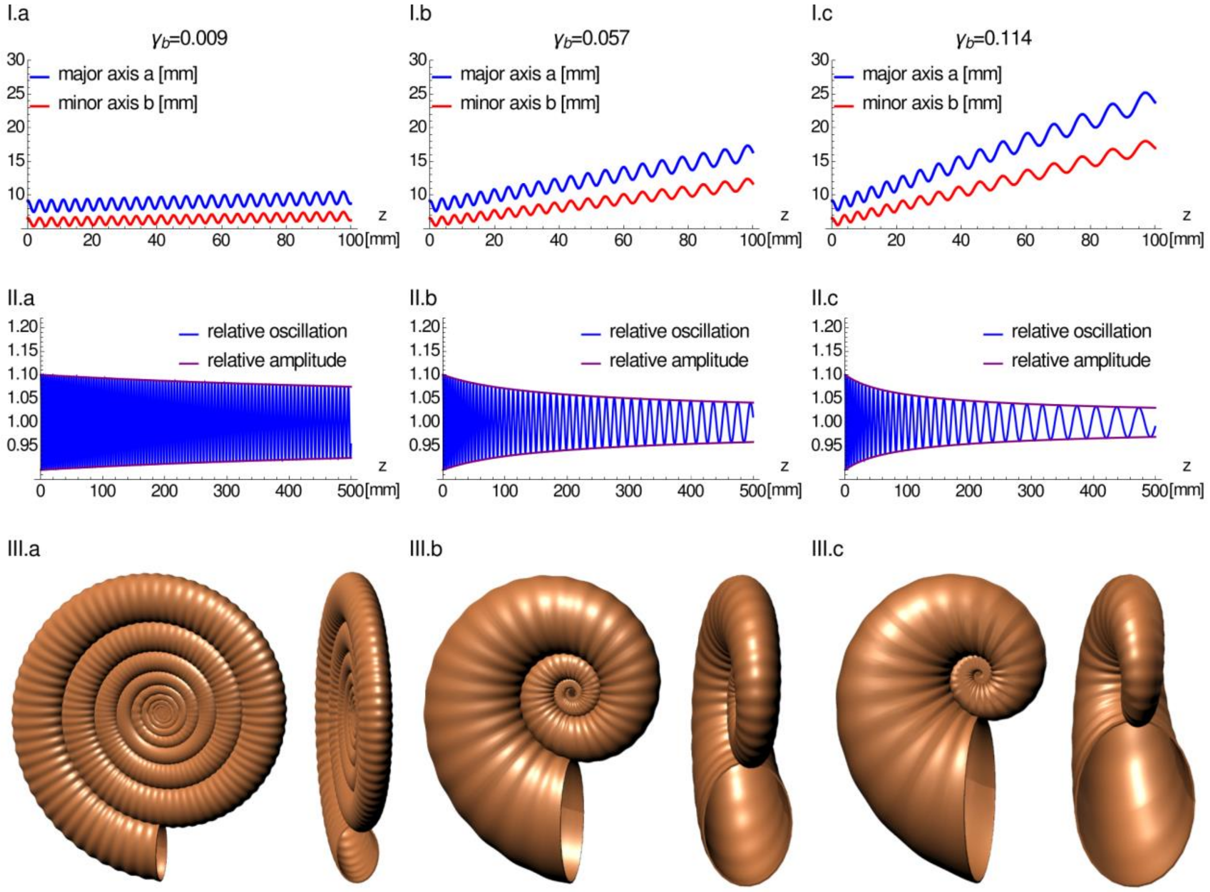

Figure 5. Effect of expansion rate γ_b on the ribbing pattern at constant eccentricity. In all three cases, the material properties are identical so that the variation in ornamental pattern is purely a manifestation of the growth mechanics and the difference in geometry, that is, the expansion rate. **I.a - I.c**: Oscillations of major and minor axes. A higher expansion rate causes a faster increase in wavelength (see Section B.1 of the supplementary material). **II.a - II.c**: Relative oscillation $b/\hat{b}$ (which coincides with $a/\hat{a}$), as well as relative amplitudes, which are the enveloping curves. The larger the expansion rate γ_b, the faster is the decrease in relative amplitude and increase in wavelength, leading to an increasingly smooth shell (see Section B.1 of the supplementary material). **III.a - III.c**: Rendering of coiled seashell surface, in which the coiling properties result from the expansion rate (see Section C of the supplementary material). All simulation parameters can be found in Section D of the supplementary material.

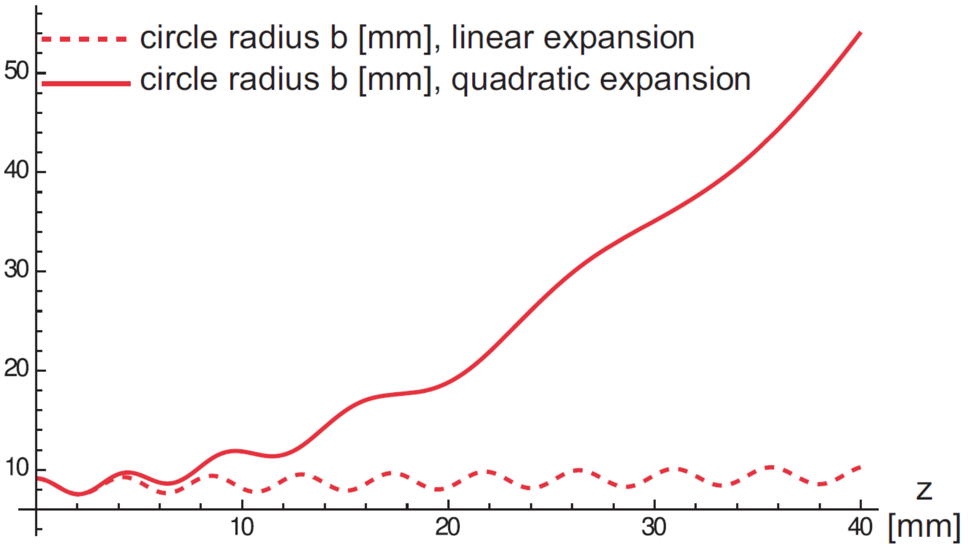

Figure 6. How various types of expansion influence the ribbing pattern. Comparison between linear expansion ($\hat{b} = \hat{b}_0 + \gamma_b z$) and quadratic expansion ($\hat{b} = \hat{b}_0 + \gamma_b z^2$) for a circle ($\hat{e} = 0$). All simulation parameters can be found in Section D of the supplementary material.

Ontogenetic variations

We next examine variation through the development of an individual. The wavelength of oscillations in our mechanical model increases during development, which is evident from Equation (3) by the log term inside the cosine (which implies that the effective wavelength of oscillation increases logarithmically with arc length). Here again, the logic behind this morphogenetic rule is rooted in fundamental principles of physics, which can be understood by considering a simple experiment. If an elastic ring of radius R is stretched to radius $R + \delta$, the material experiences a stretch of $\frac{R+\delta}{R} - 1 = \frac{\delta}{R}$. If the restoring force is proportional to the stretch, as is typical of elastic materials, it is thus inversely proportional to the radius. Thus, in a curved piece of elastic material, the restoring force due to stretching scales with the local curvature. This simple principle means that as the shell develops and the cross-sectional curvature decreases, the restoring force that generates the oscillatory pattern reduces and thus the ribbing wavelength increases. It is important to note here that the key control parameter of increase in wavelength is geometric, the expansion rate of the shell tube during development (and thus the rate at which the shell cross-sectional curvature decreases), and is independent of the growth rate of the shell (length of shell secreted per unit of time). These variations are illustrated in Figure 5, in which three shells are simulated, each with equivalent initial and material parameters, and constant eccentricity, but with different rates of expansion. This relationship may be further explored by considering a non-linear expansion, e.g. $\hat{b}(z) = \hat{b}_0 + \gamma_b z^2$. Figure 6 compares the ribbing pattern of the quadratic expansion to the linearly expanding case, showing that the increase in wavelength for quadratic expansion is considerably larger compared to a linear expansion.

We extract from Figures 5 and 6 the trend that an increased expansion leads to a diminished ribbing pattern. These results show that oscillations tend to damp out more quickly (decrease in relative amplitude), when expansion rate increases. Following on the simple analogy of stretched elastic rings, a faster ring expansion leads to faster reduction of the restoring force (driving oscillations in this system). Our results from Figures 5 and 6 therefore predict *that rapidly expanding shells that are ornamented in the juvenile stages will tend to become smoother during development while slowly expanding shells will tend to remain more strongly ornamented at later stages of development.* This prediction matches empirical observations in countless unrelated ammonite genera for rapidly (e.g. Amaltheidae, Hammatoceratidae, Cardioceratidae…) or slowly expanding shells (e.g. Arietitidae, Eoderoceratidae, Perisphinctidae…) (Figure 7) (see e.g. Wright et al., ’96; Schlegelmilch ’94, 2014ab). We also note that the non-linear decrease in the relative amplitude of oscillations during development does not support a simple explanation of ribbing amplitude based on isometric scaling (Hammer and Bucher 2005a). We will see below that these ontogenetic trends may be further explored in the case of an allometric increase of eccentricity during development.

Figure 7. (a) *Cardioceras* sp. (Oxfordian, France) and (b) *Aegoceras* sp. (Carixian, France).The rapidly expanding shell ornamented in the juvenile stages tends to become smoother during development (a) while the slowly expanding shell tends to remain more strongly ornamented at later stages of development (b). Scale bar 10mm.

Our morphomechanical model thus suggests that the synchronous variations of the ornamental patterns around the shell aperture and their variations over ontogeny are both governed by the same morphogenetic rule, rooted in generic physical principles. These individual variations all relate to the fact that curvature of the shell cross-section is a parametric modulator of the mechanical forces underlying the oscillatory behaviour of the shell secreting system.

Intraspecific variations

Ever since Darwin, variation has been a central concept in biology, the neo-Darwinian theory stating that individuals in populations exhibit heritable phenotypic variations that fuel natural selection and spread across generations depending on the reproductive success they confer on their bearers. But despite the fact that natural selection presupposes variation, the study of variability or the propensity to vary has received less attention in the study of the mechanisms of evolutionary change (Hallgrimsson and Hall, 2005). A basic reasoning of Alberch in his quest to integrate development and evolution was that if developmental processes bias morphological evolution (interspecific level), then one must expect to find the fingerprint of this bias in trends of intraspecific variation (Alberch, ’85). Unfortunately, the genetic basis of variations will never be accessible in ammonites. However, our approach suggests that *the oscillations of the shell margin emerge spontaneously from dynamical interactions taking place at the macroscopic level of the shell secreting system*. This observation implies that the rules governing the behaviour of the shell-secreting generative zone are at least as determinative of morphological variations as the gene products that, in this context, can act only as parametric modulators of a self-organized system.

Our morphomechanical model allows us to explore this aspect of intraspecific variation. Taking the basic assumption that the elastic stiffness of the mantle is constant across different specimens within a species, the model predicts that *quantitative variations of the ribbing pattern depend only on the expansion rate in circular cross-section, that is the rate at which the cross sectional curvature decreases during development*. To test this prediction we performed (Moulton et al., 2015) a detailed study of a species, *Peltoceras schroederi,* with a sub-circular cross-section and exhibiting an important intraspecific variation in both expansion rate and rib number over a given shell segment. Although the actual elastic stiffness of a 160 million-year-old species cannot be experimentally measured, we determined a single value of relative stiffness for which the model predictions of rib count on both ventral and dorsal sides fit the empirical data across 19 specimens, as a function only of shell expansion rate. The computed value was further validated through a direct comparison of the ribbing pattern overlaid on an image of a shell, showing a remarkable agreement. This quantitative comparison provides a clear example in which the variability of a pattern within a species is primarily determined by a single developmental parameter, here the expansion rate. The present study further confirms that *the rate of curvature decrease is a key control parameter for both individual variation and intraspecific variability*.

The relationship between magnitude of ribbing and curvature of the shell cross section is well documented in literature. However, the importance of this last parameter has remained hidden by the terminology used to describe shell shape. Buckman (1892, p. 313) was indeed the first to note (in the Jurassic genus *Sonninia)*, that "*roughly speaking inclusion and compression of whorls correlate with the amount of ornament – the most ornate species being the most evolute, and having almost circular whorls*". Buckman made the same observation in a not-closely-related Jurassic genus, *Amaltheus*. Westermann ('66, p. 289) has shown that the specimens in which Buckman described this correlation belong to a single species and that this intraspecific variability reveals a covariation between general shell geometry and magnitude of ribbing, "*from subcircular, highly ornate to compressed smooth whorls*", that he called the "Buckman's law of covariation". This phenomenological law has been documented in several not closely related Palaeozoic and Mesozoic ammonoid species (e.g. Kennedy and Cobban, '76; Swan and Saunders, '87; Dagys and Weitschat, '93; Dagys et al., '99; Hammer and Bucher, 2006; Weitschat, 2008). A new example is given in Figure 8.

Figure 8. A series of 6 *Sonninia propinquans* (Lower Bajocian, France) showing the typical gradation of the Buckman law of covariation. This species, notably the specimens of the bottom row, shows also the ontogenetic variations commonly observed in not closely related species: shell ornamented in the juvenile stages tend to become smoother during development correlatively with an allometric decrease in curvature of the cross section. Scale bar 10mm.

In spite of an enormous range of temporal scales separating these not-closely-related species (more than 100 million years), they display a similar covariation between ornamental pattern and shell geometry, a law-like variational trend which suggests that a generic, physical process may be involved. Previous theories for this trend have been proposed based on diffusion of morphogens (Guex et al., 2003) or simple isometric scaling (Hammer and Bucher, 2005a). However, understanding the developmental basis of Buckman's law of covariation will by necessity involve the morphogenetic process underlying commarginal ribs, and this is what our mechanical model can help elucidate. Indeed, within our framework, the Buckman's law, "*from subcircular, highly ornate to compressed smooth whorls*" can be formalized as *the magnitude of ribbing is positively correlated with the shell cross-sectional curvature*, or in other words that *the oscillations of the growing shell edge will tend to damp out as the curvature decreases*.

Our circular model already suggested that Buckman's law emerges as the predictable manifestation of the scaling of mechanical forces with curvature. We can now further explore its developmental basis within the elliptical framework. Despite the morphological differences between species following the Buckman's law, the differences in adult forms among individuals of the same species may be seen in all cases as differences in the rate at which eccentricity of the cross-section increases during development, starting from an early juvenile shell with sub-circular cross section (ammonites hatched with a nearly circular cross-section), to a still rounded, or on the contrary to a compressed adult shell when eccentricity increases more rapidly. This characteristic is illustrated in the transverse sections of shells of different morphotypes of species displaying the Buckman's law (e.g. Dagys and Weitschat, '93, fig. 9; Weitschat, 2008, fig. 1).

In Figure 9 we explore how the ribbing pattern is affected by allometric variations in reference eccentricity of the cross-section during development. Three shells are simulated: in each case the initial cross section is circular and the material properties are identical, the only variation is in the rate at which eccentricity increases during development. The model predicts that a *rapid increase in eccentricity leads to rapidly damped oscillations* and *a smoother shell, while a shell with slow increase in eccentricity, i.e. that remains subcircular during development, remains strongly ornamented*. This oscillatory pattern is combined with a mathematical description of shell coiling to produce full 3D shells in Figure 9 IV; we see that the Buckman's law is well captured by the model and can thus be understood as emerging as a manifestation of growth mechanics and geometry.

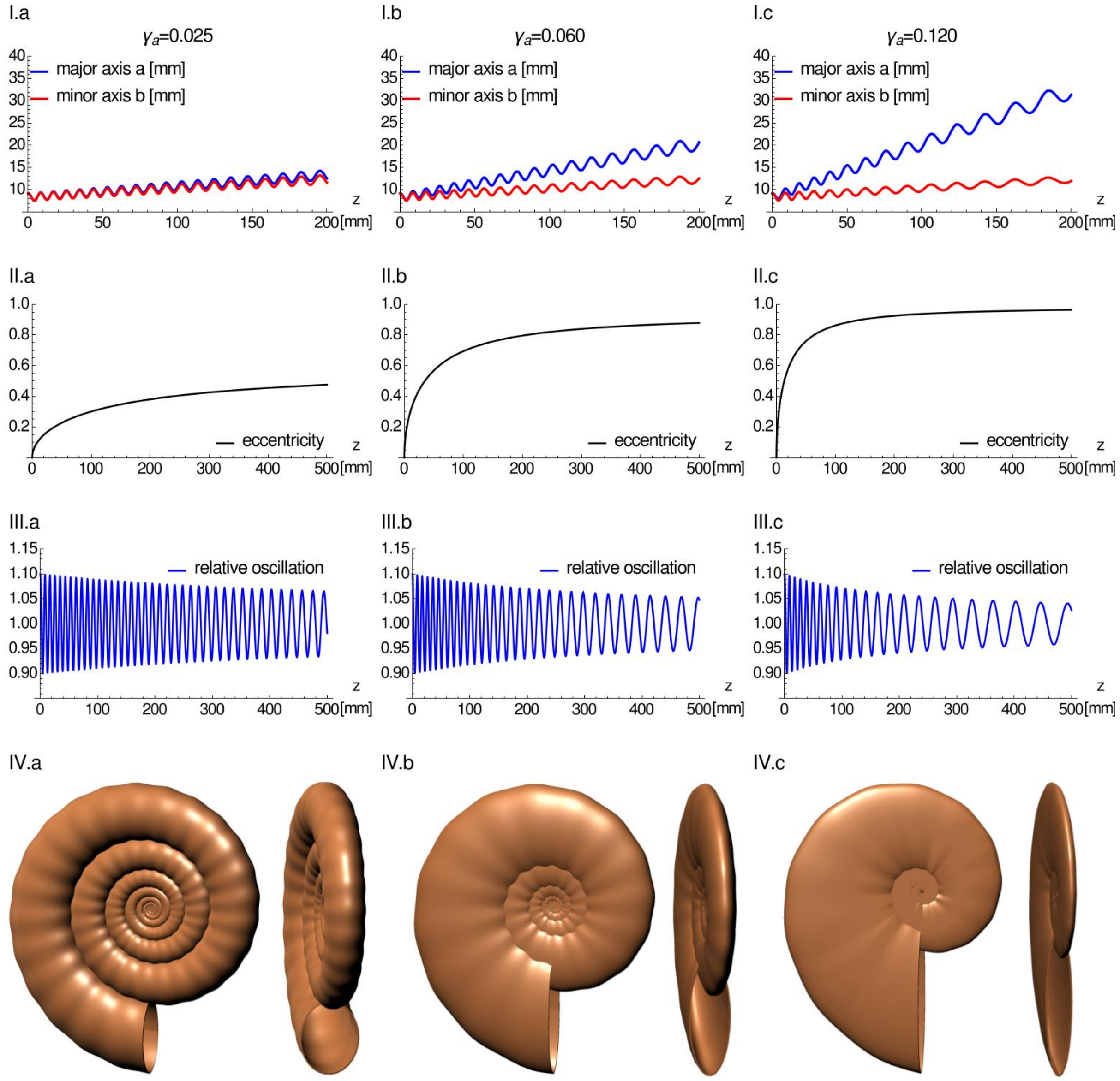

Figure 9. Effect of allometric increase of eccentricity $\hat{e}$ on ribbing pattern. Starting from a circular cross-section in all three cases, the reference lengths $\hat{a}$ and $\hat{b}$ increase at unequal linear rates, creating a nonlinear increase in eccentricity. The faster the eccentricity increases (see **II.a - II.c**), the faster is the increase in wavelength of the oscillations of the major and minor axis (**I.a - I.c**), the decrease in relative amplitude (**III.a - III.c**), and the stronger is the difference between high and low curvature points in the final shell cross-section (**IV.a - IV.c**). All simulation parameters can be found in Section D of the supplementary material.

Evolutionary trends

Several authors have shown that similar morphological evolutionary trends are observed in not-closely-related ammonite lineages, and the trend from more rounded ornamented to more compressed smooth shells, is the most commonly described one (e.g. Haas, ’42; Rieber, ’63; Bayer and McGhee, ’84; Dommergues, ’90; Monnet et al., 2016). Bayer and McGhee (’85) argued that the recurrence of these similar evolutionary trends may be interpreted as the consequence of environmental changes only and does not require “*mysterious ‘intrinsic’ or orthogenetic processes*” to be explained. This explanation runs counter to the interpretation of one leading advocate of the theory of “orthogenesis” (Schindewolf, ’50) that the recurrence of these evolutionary trends was imposed by some internal mechanisms. According to the “externalist” interpretation, directional evolution is thought to have been repeatedly generated during environmental changes by natural selection viewed as the only source of non-randomness. But if development is considered as a source of non-randomness in variation, this premise should be revisited. In particular, these recurring evolutionary trends taking place over millions of years, from more rounded ornamented shells to more compressed smooth shells, are similar to the pattern of intraspecific variation expressed by the Buckman’s law. In this last case, individuals of the same species contemporaneously living in the same environment display a similar covariation between ornamentation and shell geometry. Therefore, this covariation pattern could not have been generated by environmental changes.

The trend observed in Figure 9 – capturing the intraspecific variation of Buckman’s law – may be interpreted in an evolutionary perspective as well, by supposing that eccentricity of the cross-section increases during development at a higher rate in a descendant species than in an ancestor. This hypothetical evolutionary trend may be interpreted as an acceleration in terms of heterochrony (see Alberch et al., ’79). In an evolutionary perspective, the model predicts that *descendant species will become smooth at earlier growth stages if the rate at which eccentricity increases over development is accelerated during evolution*. This theoretical prediction precisely captures, not only the evolutionary trends described by Bayer and McGhee ('84), but also a 5 million years long trend described by Dommergues ('90, fig.7.1) in Jurassic species (Psiloceratacea), and interpreted by this author as resulting from an acceleration. According to our model, the trends observed by Dommergues can be fully understood in terms of variations in geometry. To test this, we have taken each shell image in the figure of Dommergues, and extracted three geometric parameters: the expansion rate, the eccentricity, and an overlap parameter characterising the degree of involution (details in the supplementary material)[2]. We have used the same fixed value of the elastic parameter in each case, taken within the reasonable physical range (see section D of the supplementary material), and simulated the ribbing predicted by the model[3]. The result appears in Figure 10, showing that the geometric differences between the shells, coupled with the morpho-mechanical model, are sufficient to capture the 5 million years long evolutionary trend. Hence, we have a mechanistic explanation for the observed covariation between shell geometry and ornamental pattern. Our model shows that this evolutionary trend commonly described in not-closely-related species, from more rounded ornamented to more compressed smooth shells, can be understood as the predictable outcome of modulation of the mechanical forces underlying the oscillatory behaviour of the shell secreting system by the curvature of the shell cross-section.

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[2] This is assuming, for simplicity, that both the expansion rate and the eccentricity are constant throughout development. This excludes the case of allometric variation, which we can not readily extract from the images.
[3] This shell simulating process is outlined in detail in the supplementary material, including a recipe for generating 3D printed shells and a web interface for shell simulation.

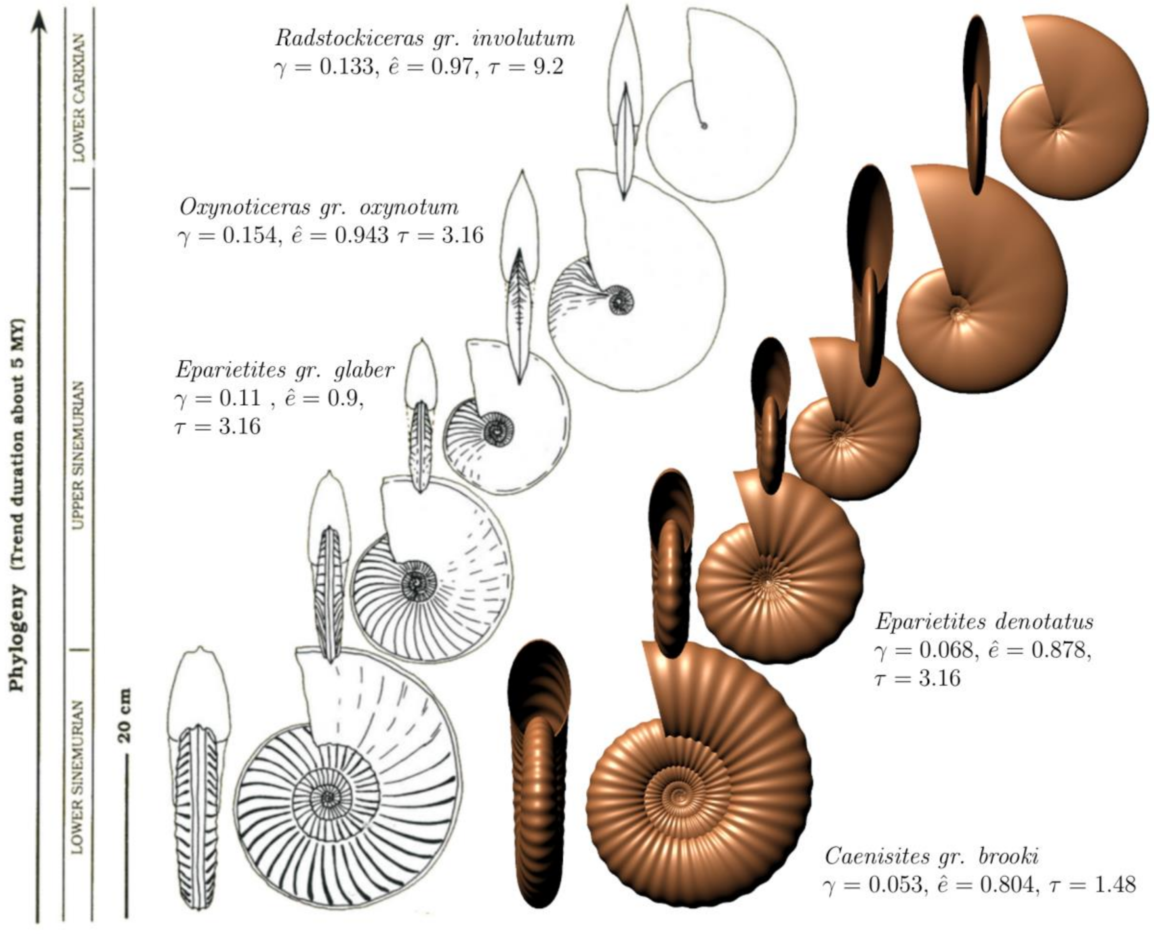

Figure 10. Simulations of the evolutionary trend described by Dommergues ('90, fig 7.1). For each shell, we have extracted from the image three geometric parameters and then simulated the ribbing from the model, taking the same elastic constant and initial conditions in each case.

Given the generic nature and ubiquity of this morphogenetic rule governing variations at different levels and time scales, one might wonder how morphological diversity of ammonite shells has been generated. There are a number of ways in which the expression of this morphogenetic rule may be itself modulated by combinatorial variations of parameters, which are in turn modulated by genetic and epigenetic interactions. These include not only the variations of expansion rate of the shell tube and the shape of its cross section, but also variations in material properties in the generative zone and its relative thickness (thickness of the generative zone relative to the radius of the shell cross section). Our model is based on the simplifying assumption that the thickness of the generative zone is constant all around the shell cross section. Despite this simplifying assumption, and despite the morphological diversity of shells allowed by the combinatorial variations of control parameters, *our model suggests that a common biomechanical rule introduced a non-random component in the production of phenotypic variation and channelled morphological evolution of different lineages along predictable paths, a bias constituting a "developmental constraint"*.

The example of the ammonites therefore shows that before attributing a feature only to natural selection sifting randomly generated variations, one must consider the possibility of the inherent predictability of that feature. If biological forms exhibit variational trends that are *a posteriori* predictable on the basis of models of morphogenesis, rooted in fundamental principles of physics but disconnected from considerations of function or environment, then natural selection would hardly be the only direction-giving factor in evolution. This interpretation does not of course deny the crucial role played by environmental changes and natural selection in morphological evolution. It provides however a complementary view by pointing out the inherent bias introduced by development on directions of morphological evolution likely to be followed, that is "*on the determination of the 'tracks' available for the railroad car to move on rather than on the forces that fuel the movement*" (Alberch, '89, p. 46).

DISCUSSION

In this paper we have extended our previous model of the mechanics of commarginal rib formation to an elliptical shell margin geometry, and we have shown that the results may be interpreted in light of a founding concept of Evo-Devo, i.e. "developmental constraints".

We have demonstrated that, within this modelling framework, there is a strong effect of curvature on the ribbing pattern, manifest both in the shell expansion rate and in variations in curvature along the shell margin. Surprisingly, the predictions of our model can be observed from the scale of individual variation up to evolutionary trends (i.e. from “Devo” to “Evo”), providing strong evidence that the mechanical forces underlying the morphogenetic process introduced a non-random component in the production of phenotypic variation and channelled the morphological evolution of ammonites over millions of years.

A natural question is then: why commarginal ribs are not more common in molluscs? We note that among coiled shells of molluscs with nearly circular or elliptical shell margin (for which our model might be expected to apply), ammonites have among the slowest expanding shell (see the famous Raup's cube; Raup, ’66). Therefore, our model predicts that commarginal ribs that are common in ammonites should be uncommon or absent in molluscs with faster expansion rate. This prediction is consistent with the general absence of commarginal ribs in nautilids (including the current genus *Nautilus*) that have been restricted to a rapidly expanding shell coiling morphology since at least the Early Jurassic (Moulton et al., 2015). Although a rigorous test of this prediction for gastropods and bivalves (about 60 000 and 10 000 current species respectively) is beyond the scope of this work, a consultation of comprehensive syntheses (e.g. Abbott and Dance, ’90) does support this prediction. On the one hand, commarginal ribs are indeed usually absent in gastropod shells with low curvature of the shell cross section (e.g. Naticidae, Conidae, Tonnidae, Olividae) while they are more generally present in species with more curved shell cross section (e.g. Fasciolariidae, Nassariidae). On the other hand, apart from other commarginal structures such as frills and beads, commarginal ribs similar to those seen in ammonites (oscillating shell edge) are absent in almost all bivalves species, that have a rapidly expanding shell (in most cases, these shells are smooth or display antimarginal structures).

Regarding the generality of the predicted pattern, though, it is important to bear in mind that any mathematical model is restricted by its simplifying assumptions and aimed at answering specific questions. In particular, there are obvious limitations of the current work. We have examined an isolated mechanism (the mechanical interaction between the stretched/compressed mantle and the shell margin to which it adheres) in an idealized system. In particular, as our primary interest is to investigate the effect of variations in cross-sectional curvature, we have had to constrict the class of allowable deformations of the mantle tissue (a fixed geometry of an elliptical cross-section). Such restriction becomes necessary to make mathematical progress. In reality, of course there is no such restriction, and the mantle tissue could deform in other ways, for instance by buckling, which would produce a different ornamentation. In actual shells, with no such restrictions, the pattern that is observed will come from a combination of competing effects, and may also involve biochemical processes, a component we have not included and cannot therefore be explored within the proposed model. However, the premise of our modelling is that the balance of mechanical forces of the deformable soft tissues must be maintained. Within this framework various generalizations can be included to test other hypotheses.

It is also important to compare our model with previous theories for commarginal ribs. Geometric descriptions and simulations of shell formation have been presented since the 60's, going back to the pioneering work of Raup (Raup, '66), and have seen increasing computational sophistication in recent decades (e.g. Rice, 1998; Urdy et al., 2010). While such models can provide valuable insight to shell geometry and growth relations, they do not explicitly link the geometry to a physical underpinning. Previous theories based on the underlying morphogenetic process can be categorized as mechanical or biochemical (Hammer and Bucher (2005b). This work (and our previous work, Moulton et al., 2015) builds on the stress regulating idea of Hammer (2000). An alternative mechanical hypothesis was formulated by Checa ('94), in which commarginal ribs form due to episodic muscular contraction of the mantle pulling backward a periostracal sheet extending far beyond the calcified shell edge and causing folds subsequently fixed by calcification. However, this mechanism has no known analogue in living species, and may not be compatible with the emergence of spines (Hammer and Bucher, '99). On the biochemical side, numerous reaction-diffusion based models have been proposed (e.g. Meinhardt and Klinger, '87; Fowler et al, '95; Hammer and Bucher, '99; Guex et. al, 2003; Meinhardt, 2009). In terms of colour patterns on shells, these models can be extremely convincing, capable of producing a large variety of patterns that are observed in not closely related groups of molluscs. While colour patterns (i.e. 2D patterns) are biochemical in nature (e.g. Hedegaard et al., 2006; Mann and Jackson, 2014), three-dimensional ornamentations (i.e. 3D forms) are foremost the result of the deformation of the soft mantle for which the role of biochemical processes is less clear. Clearly, biochemical processes are involved in molluscan shell development: they act as modulators of biophysical parameters and may create mechanical inhomogeneities that impact on the shell form (see e.g. Chirat et al., 2013). In turn, inhomogeneities of stress across the mantle could provide regulatory biochemical signals trough mechanotransduction pathways (see. Mammoto et al., 2013).

However, Howard et al. (2011) note that mechanical processes can both pattern and shape concurrently. Indeed, our model shows that the oscillatory behaviour of the shell margin is a property that emerges naturally from the dynamic balance of stresses intrinsic to the growing macroscopic mantle-periostracum/shell system. This behaviour does not require a molecular pre-pattern along the mantle edge. And far from being a passive recorder of biochemical processes, the shell is in fact involved in the mechanical deformations of the mantle underlying its own morphogenesis. Mechanical processes have also the advantage to act at long range in morphogenetic processes (Howard et al., 2011), unlike diffusion gradients, which do not scale with the size of the organism. In the case of ammonites, larger species (*Parapuzosia seppenradensis*) measure up to 2.5 meters in diameter (Kennedy and Kaplan, ’95) and display commarginal ribs, around a shell aperture reaching about 1.5 meters of perimeter. These synchronous oscillations constitute an exceptional long-range coordination, especially by comparison with model organisms in developmental biology. Since the stress generated by the global deformation of the mantle scales with the size of the organism, our mechanical hypothesis is consistent with the presence of commarginal ribs in both large and small species.

Molluscan shell development is an extremely complex process. The power of a mathematical formulation based on measurable quantities is that it can be used to distinguish between contrasting hypotheses. Yet, this approach is also challenging in palaeontology, particularly with a group that has been extinct for 65 million years. Nevertheless, geometric measurements are easily obtained, and lend the possibility for comparison with theory. In our approach, measurements of coiling can be taken as input with ribbing pattern predicted as a model output for a given shell (see Appendix), and in this regard the mechanical model performs well (see Figs 3, 6 of Moulton et al 2015, and Figure 10 of the present work).

While only geometric measurements are available on extinct species, much can be learned by studying shell development in living specimens. The modelling assumptions of the mechanical basis can be informed by biophysical experiments on living molluscs. For instance, it may be possible to characterize more accurately the “generative zone” force described here, though one can only speculate as to how any such details may have differed in extinct species.

From a modelling perspective, there are several useful directions for future work. By considering arbitrary aperture shape, we could explore the simultaneous formation of commarginal and antimarginal ornamentation. Other mechanical effects, such as including the full mantle tube, rather than just the secreting edge (note that a model aimed at studying the mechanics of the mantle tube has been proposed by Morita ('91), though without explicit accretion/solidification at a growing edge), as well as contact with the previous whorl, form interesting possible extensions, though any such added components will lead to high computational complexity and likely render mathematical analysis intractable. Finally integrating biochemical or biomechanical effects in a single framework would be an important step in bridging between the molecular levels and our tissue level mechanical approach. Ultimately, the goal in building mathematical models of the shell development is to understand various forms emerging as potential outcomes within a single framework. The form achieved in any given mollusc would then simply be due to the particular set of geometric and biophysical parameters for that species or individual, these parameters being themselves modulated by genetic and epigenetic interactions. Such a tool would be of great benefit in connecting shell form and the evolutionary path of any species to the physical process of morphogenesis.

In the context of Evo-Devo, trying to explain how biological forms come into being through theoretical models of morphogenesis is also to presume that these forms are, to some degree, *a posteriori* predictable despite the contingencies inherent to biological evolution. It is therefore natural that conclusions derived from theoretical models of morphogenesis have been central to the formulation of the concept of developmental constraints in the 80's (e.g. Oster and Alberch, '82; Oster et al., '88; Oster and Murray, '89). Indeed, in the neo-Darwinian framework, biological forms are retrospectively unpredictable outcomes of a particular history, incrementally "built" for function from random genetic variations through a series of contingent cumulative reproductive successes, i.e., are "built" by natural selection.

In contradiction, the concept of developmental constraints is rooted first in the idea that developmental processes, as real builders of forms, should take their rightful place in evolutionary theories, and secondly that "*a comprehensive knowledge of the epigenetic rules that govern the unfolding of biological form would allow us to predict what evolutionary transformations are more likely to occur"* (Alberch, '83, p. 862). It is interesting to put in perspective this early Evo-Devo agenda with the recent debate about whether Evo-Devo, and notably its molecular genetic approaches, will ever fulfil the gold standard of science in becoming a predictive theory (e.g. Carroll, 2008; Duboule, 2010; Jaeger et al., 2015; Kirschner, 2015). Although we cannot enter this multifaceted debate, we note that mechanical models of morphogenesis constitute a powerful predictive tool to uncover the rules that physical laws impose to the generation, variation, and evolution of form of the "players".

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