

A morphogenetic explanation of Buckman's law of covariation

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Key words. – Ammonoids variability, Covariation, Pathology, Morphogenesis

Abstract. – In this paper, we demonstrate that Buckman's law of covariation, describing the cases of extreme variability observed in ammonoids, can be explained in a simple way by analysing the internal shell geometry. This geometry can be characterized by the amount of lateral and ventral curvature of the shell which controls the thickness of the mantle and the concentration of morphogens present in the shell-secreting epithelium. The most salient ornamentation is present where the whorls are most curved, shells with slight angular bulges often being spinose or carinate and flat ones being almost smooth. These observations agree with a morphogenetic model based on Meinhardt's reaction – diffusion mechanisms [Meinhardt 1995].

Une explication morphogénétique de la loi de covariation de Buckman

Mots clés. – Variabilité morphologique, Ammonoidés, Covariation, Pathologie, Morphogénèse

Résumé. – Nous montrons ici que les cas d'extrême variabilité découverts au 19^e siècle et décrits chez les ammonites comme résultant de la loi de covariation de Buckman [1887] dépendent essentiellement de la géométrie interne des coquilles de ces organismes. Cette géométrie peut être caractérisée en termes de degré de courbure ventrale et latérale et ces paramètres contrôlent la concentration de morphogènes présents dans l'épithélium qui sécrète la coquille. Les ornements les plus saillants sont présents là où les tours sont les plus incurvés et les régions plates de la coquille sont presque lisses. Ces observations sont testées ici dans le cadre des modèles de réaction-diffusion développés par Meinhardt (1995).

INTRODUCTION

Reaction-diffusion numerical models simulating morphogenesis of different animal ornamental patterns were first created by Alan Turing [1952] and later completed by Meinhardt and Klingler [1988] and Meinhardt [1995]. Meinhardt (loc. cit.) in particular demonstrated that such models allowed to generate all the different kinds of pigmentation patterns observed on molluscan shells. Several authors have recently realized that Meinhardt's equations can also be used to simulate the morphogenesis of ornamental patterns such as ribs and striation of ammonite shells [Savazzi, 1990 ; Bucher *et al.*, 1996 and Hammer and Bucher 1998]. This idea was based on the fact that certain complex morphological pigmentation patterns, illustrated by Meinhardt [1995], are indeed quasi identical to some of the most complex ornamentations observed in ammonites (see fig 1a and b).

The goal of the present paper is to discuss a very old morphogenetical problem in the light of these recent results.

One of the most important open problems in understanding morphological evolution of ammonites is known as *covariation*. First observed by Buckman [1887] in *Sonninia* and *Amaltheus* (fig. 2) and rediscussed later by Westermann [1966], covariation was originally described as follows : "Roughly speaking, inclusion and compression of the

whorls correlate with the amount of ornament – the most ornate species being the more evolute (i.e. loosely coiled) and having almost circular whorls..."

In 1999, Guex proposed the hypothesis that covariation depends on internal shell geometry [see also Guex, 2001]. Internal shell geometry being defined by the lateral and ventral curvature of the shell which controls the thickness of the mantle and the concentration of morphogens present in that shell-secreting epithelium. The most salient ornamentation is present where the whorls are the most curved, shells with slight angular bulges often being spinose or carinate and flat ones being almost smooth. As a general rule, juvenile ammonites belonging to peramorphic lineages are more evolute and have a greater lateral curvature of the whorl than adult ones.

These observations have recently been tested by one of us (A. K. : see below) within the conceptual framework of Meinhardt's reaction – diffusion (RD) models [Meinhardt, 1995]. It should be noted that our RD model is an abstraction. The chemical nature of morphogens is not known. They could be transmembranar proteins or even free intercellular ions.

To show the molecular plausibility of these ideas, we constructed a numerical reaction-diffusion (activator – in-

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hibitor) model in order to simulate intensity of ribbing and spination on ammonite shells. A summary of this simulation is given in the Appendix. Our aim was to check that variations of the shell patterns can be induced either by small changes of mantle curvature, or by slight modifications of the parameters governing the rate of the involved chemical reactions – in particular the mantle’s local thickness or the variations of the mantle’s thickness.

Following Meinhardt [1995], we assume that the patterning process takes place in the mantle of the ammonite, along the growing edge of its shell. Ribs and spines are generated by cells belonging to the animal’s mantle. The intensity of the shell’s corrugations is likely to be proportional to the concentration of some morphogen in the cells of the mantle : only those cells presenting a high concentration of certain morphogens take an active part in generating shell ornaments (i.e. ribs and/or spines).

Thus, the cells located in a thin and elongated domain at the front of the mantle are supposed to contribute to the positioning of ribs and spines on the shell. According to our numerical simulations, the average number of neighbours of the mantle cells appears, in the active region, to be important for pattern formation ; this is linked with diffusion of certain chemicals. In the formal model described below, we have fixed the border conditions as follows : the shell behaves as a barrier to the diffusion of the activator and the in-

ternal part of the mantle allows its internal diffusion; the inhibitor itself is restricted to the mantle.

As a consequence, cells located in the vicinity of the shell will tend to accumulate the activator, whereas those on the inner side of the mantle can expel it. In addition, cells near the region of the mantle, which are characterized by a strong curvature, have less space for diffusion, and this will increase the considered effect. In other words the geometry

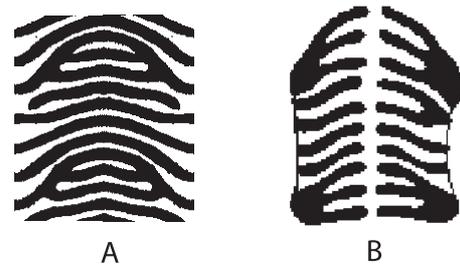


FIG. 1. – Comparison between pigmentation pattern generated by Meinhardt equations [A : redrawn from Meinhardt, 1995 fig. 4.8] and the ventral ribbing of a *Collina* [B : redrawn from Guex 1973].
 FIG. 1. – Comparaison entre les motifs de pigmentation générés par les équations de Meinhardt et la costulation ventrale d’une *Collina*.

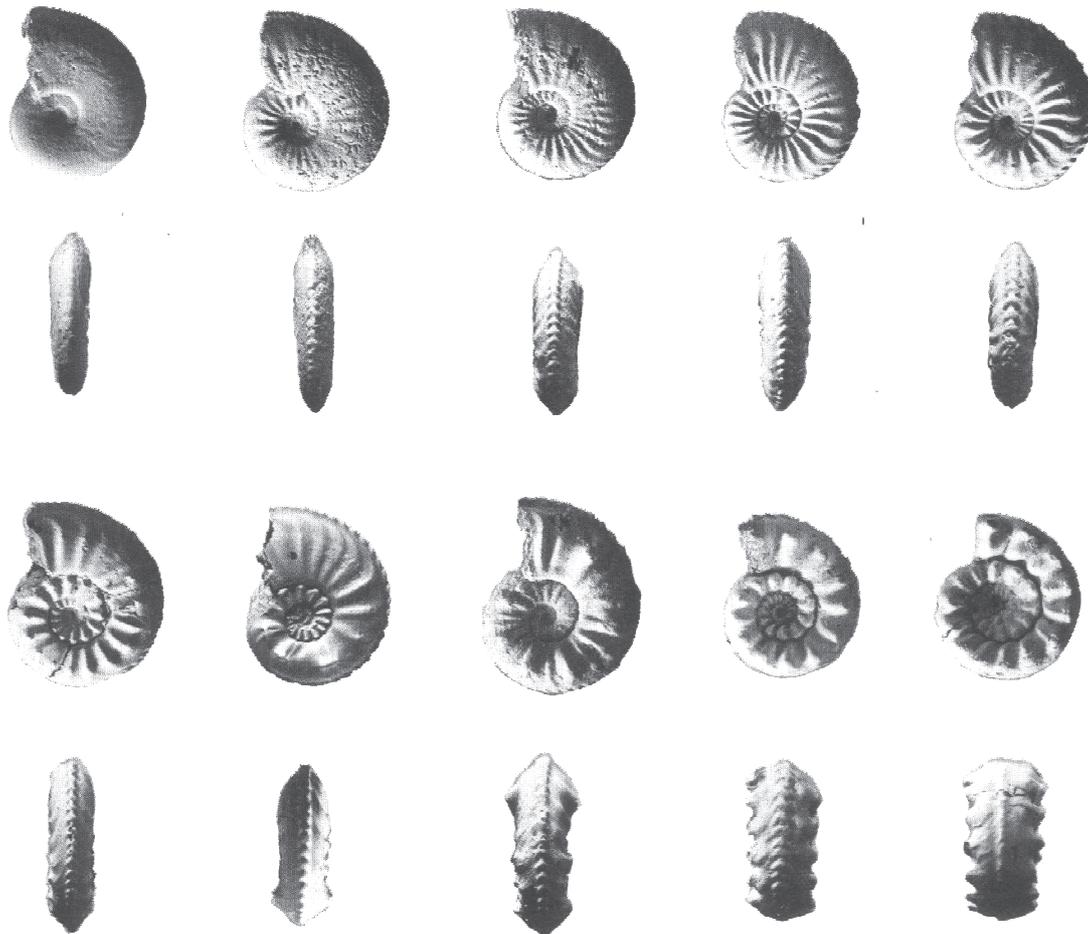


FIG. 2. – Example of covariation in the genus *Amaltheus* [reinterpreted, from Mattei, 1985].
 FIG. 2. – Exemple de covariation chez les *Amaltheus*.



FIG. 3.— In our simulation, the domain of the mantle responsible for the shell corrugations is assumed to be conical. The diagram is a frontal view and its position can be either lateral or ventral. The concentration of activator (left) and inhibitor (right) morphogens interacting according to the Gierer-Meinhardt model are plotted. Dark grey corresponds to high concentrations while light grey is assigned to low ones. The maximal concentrations of both morphogens are observed at the apex of the ogival domain.

FIG. 3. — Dans notre simulation, la partie du manteau responsable des reliefs coquilliers est considéré comme conique. Le diagramme est une vue frontale qui peut être soit latérale, soit ventrale ; il représente la concentration en morphogènes activateur (à gauche) et inhibiteur (à droite) interagissant selon le modèle de Gierer-Meinhardt. Les tons foncés correspondent à de fortes concentrations, les tons clairs à de faibles concentrations. Les concentrations maximales des deux morphogènes s'observent à l'apex du domaine ogival.

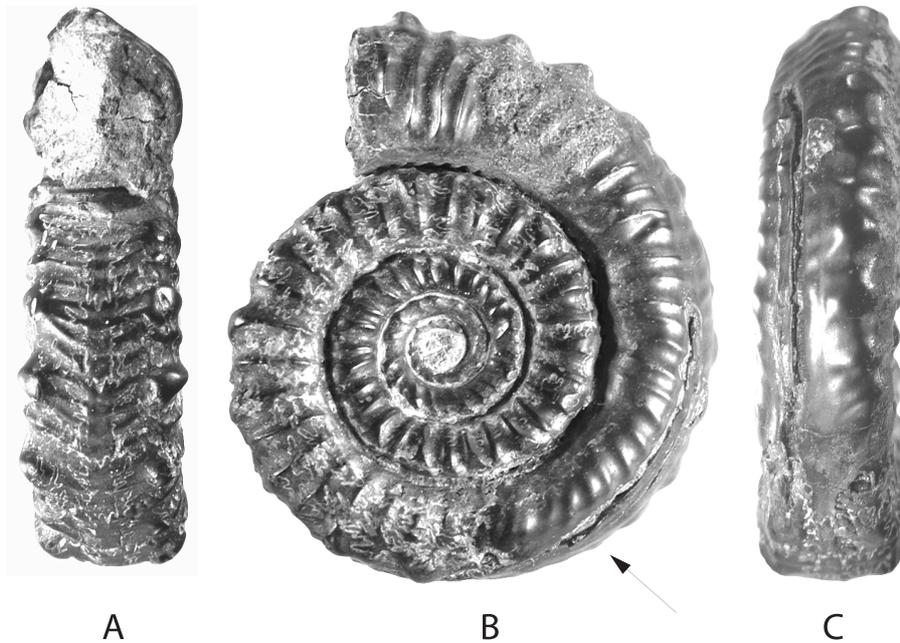


FIG. 4.— Ammonite belonging to a genus normally characterized by two rows of spines. At a given stage of its life, this animal was injured as shown by arrow. In the subsequent portion of the animal, one observes only one row of spines; this loss of ornamentation is fully in agreement with our model.

FIG. 4. — Ammonite appartenant à un genre normalement caractérisé par deux rangées d'épines. Cet animal a été blessé au cours de sa vie (flèche). Par la suite, une seule des rangées d'épines persiste ; cette perte ornementale est parfaitement en accord avec notre modèle.

of the mantle has a strong influence on the concentration of diffusing morphogens. Figure 3 illustrates this effect in the case of a Gierer-Meinhardt couple of activator-inhibitor substances (see Appendix). We observe that the highest concentration of morphogens appears at the position of maximal curvature (which is correlated with the maximum thickness of the mantle). If the simulated shell has two such highly curved regions, one would observe a concentration peak at each bending point. Note that the shape of the ribs can be simulated by slightly modifying the geometry by considering the domain having the shape of a lunule.

Pattern modifications on injured animals support these views. Figure 4a shows an ammonite the genus of which

normally presents two parallel rows of spines. The usual pattern is visible on the earlier parts of the animal's shell, located in the vicinity of the umbilicus. Part of the shell was damaged during a growing phase (arrow in fig. 4a). Interestingly enough, the recovered animal exhibits only one row of spines, which moreover has been displaced in the symmetry plane of the animal's shell [from Guex, 1967].

When an injury is located in the animal's plane of symmetry, we observe an atrophy of median ornamentation and its replacement by lateral ornaments. This phenomenon is called ornamental compensation [Guex, 1967].

This general rule of recovery not only accords fully with our model, but can also be easily reproduced in laboratory by artificially injuring living molluscs. It is not yet known if the grafting of healthy tissue collected at the same location of the injured part can regenerate the original lost ornamentation.

CONCLUSIONS

Our model explains that the intensity of ornamentation (ribbing and/or spination) depends on the geometry of the mantle (more or less strong curvature), thus providing a simple explanation of Buckman's law of covariation.

It also explains one major phenomenon which is common in ammonite evolutionary history, i.e. the frequent trend where evolute ancestral spinose or coarsely ornate forms give rise to involute smooth or weakly ornamented descendants. To take just two examples, we can cite the *Arietitidae* giving rise to the smooth oxycone *Oxynoticeratidae*, and the evolute strongly ribbed *Tauromeniceras* giving rise to the smooth *Oxyparoniceras* [see other examples in Guex, 2001].

Our present model also provides a simple explanation of ornamental compensation, that is to say disappearance of the ornament generated by an injured and destroyed part of the mantle and its replacement by the adjacent ornament.

Appendix (by A.K.)

Numerical solution of the Gierer-Meinhardt equations for a cross-section through an ammonite shell, orthogonal to the growth axis

We present a numerical solution of the following reaction-diffusion equations of Gierer-Meinhardt in a bidimensional domain :

$$\partial_t a = D_a \Delta a + \rho_a a^2 / h - \mu_a a + \sigma_a$$

$$\partial_t h = D_h \Delta h + \rho_h a^2 - \mu_h h$$

with $\Delta \equiv \partial^2 / \partial x^2 + \partial^2 / \partial y^2$; $a(x,t)$ and $h(x,t)$ corresponding to the activator and inhibitor morphogens, respectively. In the numerical simulation, the constants have the following values :

$$D_a = 0.012 \quad \rho_a = 1.0 \quad \mu_a = 0.001 \quad \sigma_a = 0.002$$

$$D_h = 0.4 \quad \rho_h = 1.0 \quad \mu_h = 0.001$$

The units of distance, time and concentration are arbitrary ! The domain of computation corresponds to the union of the two following areas :

1) area delimited by two arcs of circles $\{(-33.5120, -12.1072), 50.00\}$ and $\{(-24.5332, -11.5931), 40.00\}$, and contained in the region $x \geq 0$ and $y \geq -0.052$;

2) area delimited by two arcs of circles $\{(33.5120, -12.1072), 50.00\}$ and $\{(24.5332, -11.5931), 40.00\}$, and contained in the region $x \leq 0$ and $y \geq -0.052$.

The boundaries of the domains are supposed to be impervious to the inhibitor. The outer boundary (arc of circle of radius 50.00) is impervious to the activator whereas the other boundaries are pervious. The choice of these boundary conditions is motivated by the following arguments : The activator is supposed to diffuse

freely outside the mantle's cells into the environment (intercellular medium and sea water). However, the mantle being in close contact with the shell of the ammonite, the molecules of the activator cannot transit through the shell. Therefore the regions of the mantle in contact with the shell are considered to be impervious to the activator.

The reaction-diffusion equations are solved numerically on a hexagonal mesh containing 1500 nodes corresponding to a hexagon radius of 0.23 units. The concentrations $a(x,t)$ and $h(x,t)$ are determined at each node of the mesh. The initial values of the concentrations at $t=0$ correspond approximatively to the values taken from the (unstable !) homogeneous stationary solution. We add small random deviations $\varepsilon(x,0)$ to the concentrations of the activator to allow the system to leave the initially homogeneous state. The initial values are thus given by :

$$a(x,0) = 1.0 [1. + \varepsilon(x,0)] \quad \text{with } -0.05 < \varepsilon(x,0) < +0.05$$

$$h(x,0) = 100.0.$$

The stationary inhomogeneous solution is found using a standard iterative procedure.

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