EMBRYOGENESIS OF INTESTINAL TISSUES: ANISOTROPIC GROWTH AND SECONDARY BIFURCATIONS

Fei Jia[a,c], Pasquale Ciarletta[b], Martine Ben Amar[c*]
[a] *Institute of Biomechanics and Medical Engineering, Department of Engineering Mechanics, Tsinghua University, Beijing 100084, China*
[b] *CNRS and Institut Jean le Rond d'Alembert, UMR7190, Place Jussieu 4, Case 162, 75005 Paris, France*
[c] *Laboratoire de Physique Statistique, Ecole Normale Supérieure, UPMC Univ Paris 06, Université Paris Diderot, UMR CNRS 8550, 24 rue Lhomond, 75005 Paris, France*

Summary Experimental observations on chick embryos have shown that the mucosal layer in the duodenum initially folds into cylindrical stripes, while forming zigzag patterns in later stages. A three-dimensional model is adopted to investigate this pattern transition. First, we obtain the critical growth parameter and the amplitude of the primary buckling. Then, after perturbing this undulated morphology, zigzag patterns are obtained. This study represents a fundamental step to understand the complex microstructural patterns observed in intestinal embryogenesis.

INTRODUCTION

Growth instabilities in soft tissues are commonly observed in the human body, e.g. wrinkles on human skin, mucosal buckling in tubular organs, or convolutions in brain. Such instabilities are the final result of complex interactions between genetic, biochemical, and physical processes. In this work, we are interested in the mechanical description of volumetric growth and its ability to generate buckling instabilities in soft tissues. Much effort has been directed over the last years toward the investigation of the primary growth instabilities, such as the folding in tubular organs [1], or the contour undulations in skin tumors [2]. Due to technical complexity, only few works were concerned with post-buckling phenomena in pattern formation [3].

In this paper, we focus on the embryonic development of chick's duodenum [4]. In the early stage, about 11 days after chick's incubation, cylindrical stripes appear at the inner surface of the duodenum. In a later stage, the surface folding evolves toward a highly regular zigzag pattern. Our aim is to understand the pattern transition of the inner surface from the cylindrical to the zigzag undulations (see Fig.1), investigating if the growth anisotropy can drive such elastic instabilities. Previous studies have been only focused on the cylindrical buckling in isotropic growth [5]. In the following, we aim to derive the post-buckling amplitude equation in mechanical constrained growth problems. For this purpose, we perform a nonlinear analysis of the elastic growth problem, making further simplifications for deriving the threshold conditions for the occurrence of the zigzag pattern.

BIOMECHANICAL MODEL AND METHODS

Let us consider a soft body with thickness H (chosen as length unit) in the direction of the z-axis and lateral widths $L_x, L_y \gg H$. The volumetric growth model originally postulated for biological tissues [6] is adopted. We use the coordinate system $\mathbf{X}$=$\mathbf{X}(X,Y,Z)$ for initial configuration, whilst $\mathbf{X}_g$=$\mathbf{X}_g(g_xX, g_yY, g_zZ)$ refers to the grown state and $\mathbf{x}$=$\mathbf{x}(x,y,z)$ to the current configuration. The body is treated as an incompressible neo-Hookean material, with elastic strain energy density $W = \frac{1}{2}\mu_s(\lambda_1^2 + \lambda_2^2 + \lambda_3^3 - 3)$, where μ_s is the shear modulus and $\lambda_i (i = 1, 2, 3)$ represent the principal stretches. The body is fixed at the bottom, while its top surface is free.

According to the volumetric growth theory, the deformation gradient $\mathbf{F} = \partial\mathbf{x}/\partial\mathbf{X}$ can be multiplicatively decomposed as: $\mathbf{F} = \mathbf{F}_e \cdot \mathbf{G}$, where $\mathbf{F}_e$ denotes the elastic deformation tensor. $\mathbf{G}$ is the growth tensor, defined as $\mathbf{G}$ =diag(g_x, g_y, g_z), so that $J = det\mathbf{G} = g_xg_yg_z$. Assuming that $g_x \geq g_y$, we get the primary cylindrical buckling (i.e. stripes) along the x-axis, as studied by Ben Amar and Ciarletta [5]. Above a secondary growth threshold, these stripes collectively deform towards zigzag pattern modes, which can be observed only if they possess less elastic energy. With the aim to study the formation of complex three-dimensional instability patterns, we choose the variational formulation proposed in [7] for simplifying a generic hyperelastic boundary value problem.

PATTERN TRANSITION FROM THE PRIMARY TO THE SECONDARY BUCKLING

For the primary buckling analysis, we introduce an intermediate state in the mixed coordinates (x, y, Z). Let us consider a multiplicative decomposition applied to the elastic deformation tensor, so that $\mathbf{F}_e = \mathbf{F}_{e1} \cdot \mathbf{F}_{e2}$, as depicted in Figure 2. After imposing the incompressibility condition, the unknown material coordinates can be expressed as:

$$X = \phi_{,Z}/J, \quad Y = y, \quad z = \phi_{,x} \tag{1}$$

We derive the stationary energy as a function of ϕ, where, $\phi = JxZ + \epsilon_1 h(Z)\sin(k_xx)$. Minimization with respect to ϕ gives the critical growth condition as $g_x\sqrt{g_y} = g^* \approx 1.839$. The nonlinear analysis gives the instability amplitude, as

* Corresponding author. E-mail: benamar@lps.ens.fr

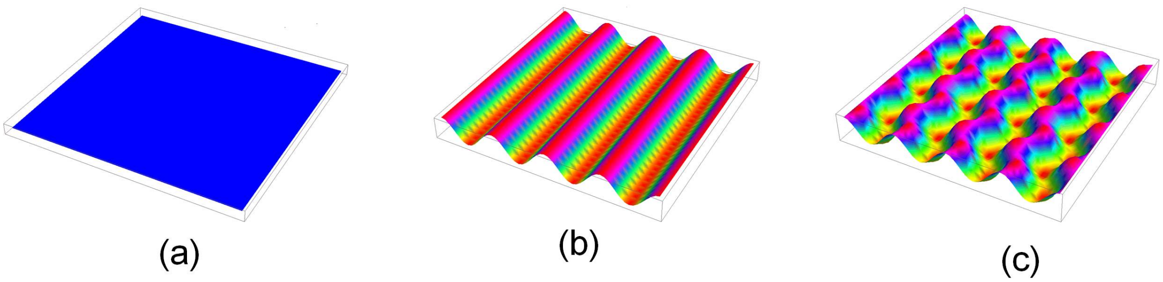

Figure 1. Transition from the stripe buckling to the zigzag pattern: (a) initial flat state, (b) cylindrical stripes, (c) zigzag pattern

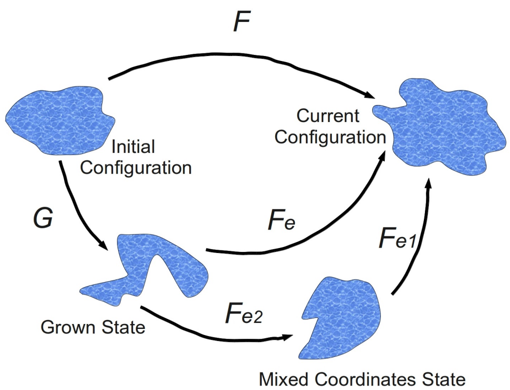

Figure 2. Schematic of the volumetric growth configurations

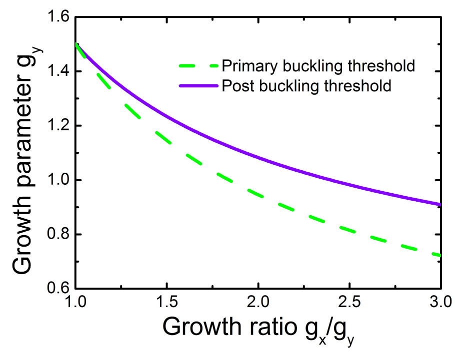

Figure 3. Growth threshold g_y versus the anisotropy ratio g_x/g_y. The dashed and solid lines represent the cylindrical and zigzag stripe patterns, respectively.

$\epsilon_1 \sim \frac{e^{-g_y k_x/g_x}}{k_x^2}(g_x\sqrt{g_y} - g^*)^{1/2}$.

For the analysis of secondary bifurcations, we impose a perturbation on the primary pattern as:

$$X = \phi_{,Z}/J + \epsilon_2\varphi_{,yZ}, \quad Y = y + \epsilon_2\varphi_{,xZ}, \quad z = \phi_{,x} + 2\epsilon_2\varphi_{,xy} \tag{2}$$

where, φ is expressed as $\varphi = f(Z)\cos(k_x x)cos(k_y y)$, resulting in a zigzag pattern at the free surface.

After imposing the incompressibility condition and minimizing the total elastic energy, we obtain the critical condition for the secondary bifurcation (zigzag pattern), which is slightly above the primary threshold (see Fig.3). Comparing the energy of the cylindrical and zigzag pattern, we find that the latter is smaller, meaning that the zigzag pattern is the natural choice of the growing body. Referring to the case of isotropic growth with $g_x = g_y$, the same threshold is found for both cylindrical and biaxial buckling, so that a square checkerboard pattern emerges for energetic reasons.

CONCLUSIONS

We have proposed a biomechanical model to study the emergence of secondary patterns during the embryonic growth of chick's duodenum. Both the threshold conditions and the elastic energy of the primary and secondary patterns are given. The results indicate that growth anisotropy can drive a shape transition from cylindrical to zigzag stripes, as experimentally observed in chick embryos [4].

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