



Encasement as a morphogenetic mechanism: The case of bending[☆]



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ABSTRACT

We study how the encasement of a growing elastic bulk within a possibly differently growing elastic coat may induce mechanical instabilities in the equilibrium shape of the combined body. The inhomogeneities induced in an incompressible bulk during growth are also discussed. These effects are illustrated through a simple example in which a growing elastic cylinder may undergo a shape transition towards a bent configuration.

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1. Introduction

Shape is one of the most prominent features of cells, plants, organs, and of living beings in general. Specific shapes may play a crucial role in enabling the achievement of specialized biological goals, which might allow for an organism's survival and thriving in its environment. Morphogenesis has been linked to mechanical origins in a natural way because mechanics offers innumerable examples of systems whose equilibrium configurations depend on external parameters, with bifurcations among equilibria which may imply very different shapes and structures for a body. Perhaps the most studied and exploited example of such morphogenetic bifurcation phenomena is given by Euler's elastica. In more recent times we mention the studies by Biot [5] who understood how three-dimensional rubbers under compression may develop surface instabilities, as have also later been found in soft, strain-hardening materials [7,16].

A mechanical approach in the creation of form for bodies undergoing growth was envisaged already at the beginning of last century by Thompson [39]. Interesting studies along these lines were later performed, such as for instance [9], where shell theory was used to estimate the surface stresses that can be induced in a growing surface, showing how they may related to splitting and cracking in vegetables. These methods give very fertile ground for

the mechanical investigation of bio-morphogenesis, greatly expanding the scope of continuum mechanics well into the boundaries of biophysics and biology in general. A growing body indeed evolves in a natural way under the effect of a number of external parameters which vary with time inducing morphogenetic effects with lesser need for genetic encoding of information. This offers attractive avenues for the explanation of form [31], within a background of natural hypotheses of genetic parsimony.

Understanding in terms of mechanical instabilities has since been proposed for numerous observed shapes of growing bodies, using a wide variety of approaches, and sometimes exhibiting remarkable agreement with experimental observations. To name but a few examples, buckling under external stress has been related to morphogenesis for instance in growing spheroidal shells [41], or in the growth of other constrained systems [12,17]. More complex shapes, observed in plant organs such as long leaves [26], or in blooming flowers [11,27], have also been modeled by adapting the theory of elastic shells to a growing surface [13]. See [24] for a review of the mechanics of buckling-related morphogenesis. Further recent studies have further analyzed the growth of vegetable matter, as in growing pumpkins [22] or in the ripening of kiwi fruit [19], see also the review [29]. In the biomedical sciences, the investigation of mechanical instabilities has helped investigate the role of external stress in tumor growth [2,3], and mechanics has since provided fruitful soil for cancer modeling [30]. Recent work has also related mechanical instabilities to morphogenetic development during the growth of animal organs [34,37], and in brain formation [8,21,38].

In most cases, the basic trigger for morphogenetic instabilities derives from the presence of differential growth and distinct mechanical properties in different neighboring parts of a growing body. Thus,

[☆]Dedicated to Martine Ben Amar whose research illuminates the interplay between Mechanics and Biology.

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adjacent layers or domains sharing open two-dimensional [28,23] or one-dimensional [34] adhesion boundaries have been examined. Confinement of a growing body within a closed regular two-dimensional boundary not undergoing growth has also been considered [25,32]. Less explored appear to be the morphogenetic possibilities for *encased* growing bodies, wherein a growing bulk is surrounded/protected by a closed regular growing surface layer (as with the skin or rind of fruits, or in bacterial membrane [15]), whose mechanical and growth properties will in general differ from those in the bulk.

The aim of the present study is thus to highlight how encasement may generate interesting morphogenetic instabilities in growing bodies. We treat growth by following the approach introduced in [14,33], and extensively adopted in theoretical studies of growing systems, as in [4,10] among many examples. A peculiarity in our approach is that two multiplicative decompositions for the deformation gradient must be introduced to correctly account for the possibly independent growth of the bulk and the coat. In the bulk, growth is described by the factor \mathbf{F}_g in the decomposition $\mathbf{F} = \mathbf{F}_e \mathbf{F}_g$ of the three-dimensional deformation gradient \mathbf{F} . Simultaneously, a similar decomposition $\mathbf{A} = \mathbf{A}_e \mathbf{A}_g$ is introduced for the surface deformation gradient \mathbf{A} . The strain energy then depends only on the elastic factors \mathbf{F}_e and \mathbf{A}_e . By following [18,36] in our treatment of elastic continua surrounded by elastic surfaces, we consider an incompressible neo-Hookean material for the bulk, and Föppl–Van Kármán elastic coat, undergoing finite strains.

The growth components $\mathbf{F}_g, \mathbf{A}_g$ are at least partially determined by external processes, typically of biochemical origin. Furthermore, material remodeling may possibly influence such processes [1], and at least partially relieve the residual stresses which may have been originated by incompatible growth. The choice of including or not such an evolution for the growth components determines whether we are considering morphogenesis at stress-free conditions vs. in the presence of residual stresses. This might for instance depend on the relative time scales of growth and relaxation (see [6] for an example of how a soft material may exhibit purely elastic or apparently plastic behavior, depending on the deformation and relaxation times). We keep our study as simple as possible here, and do not consider any remodeling, so that in general the deformed shapes we characterize possess residual stresses (as, for instance, the systems considered by [26]).

Our analysis is based on the combination of two effects. The first is the role that non-homogeneous growth may play in giving incompressible bodies the possibility of undergoing apparently non-isochoric deformations. The second factor is showing how encasement, i.e. the coexistence of a growing bulk inside a possibly differently growing skin, may affect the equilibrium configurations of the body even in the absence of instabilities of the bulk or the boundary separately.

Here we illustrate these effects by means of a simplest example, that is, a bending instability for an isotropically growing straight cylinder encased within a cylindrical boundary which is in turn growing at possibly different rates in the longitudinal and transverse directions. Such growth anisotropy may occur, for instance, when parallel fibers are present in the skin, which may also possess anisotropic elastic moduli. We show how encasement induces, in a range of growth and elastic parameters, instabilities which lead to new equilibria with a bent shape for the cylinder. Depending on the material properties, other instabilities, which we do not explore here, may occur in encased growing cylinders, such as bulging, twisting, or others (see for instance the deformations considered in [20]). Our analysis shows that for a growing body the constraint of encasement is different from simple confinement as in [25,32], as the growth of the external coat along with the growth of the bulk creates instabilities which might not be present when the coat is (deformable but) incapable of growth.

This paper is organized as follows. In Section 2 we show how inhomogeneous growth may provide new degrees of freedom for the distortion of incompressible growing bodies. In Section 3 we analyze the effects of encasement on growth, showing how mechanical instabilities may arise when a growing body is surrounded by a differently growing coat. In Section 4 we evidence a bending instability generated by encasement. An Appendix contains some of the computations leading to the results presented in the main text.

2. Growth in incompressible materials

In this section we analyze how inhomogeneous growth may enlarge the class of deformations available to incompressible materials. Let χ be the map transforming the reference configuration into the present placement, and $\mathbf{F} = \nabla \chi$. We model growth by assuming [14,33] that \mathbf{F} may be decomposed as the product of an elastic and a growth component:

$$\mathbf{F} = \mathbf{F}_e \mathbf{F}_g. \quad (1)$$

The growth tensor \mathbf{F}_g describes how growth would locally shape body volume elements, where they allowed to grow stress-free, that is, in the absence of the surrounding elements. The balance equations driving \mathbf{F}_g may not entirely be included in the biomechanical model. When this is the case, some or all of its entries may be explicitly specified, and therefore treated as external parameters. We remark that \mathbf{F}_g need not be the gradient of any ‘growth deformation’, as growth is a local phenomenon which may induce a lack of compatibility whenever $\text{curl } \mathbf{F}_g \neq \mathbf{0}$. Moreover, since mass is not conserved during growth, no isochoricity condition must be a priori enforced on $\det \mathbf{F}_g$.

The elastic distortion \mathbf{F}_e is defined by the decomposition (1): $\mathbf{F}_e = \mathbf{F} \mathbf{F}_g^{-1}$. The assumption that \mathbf{F}_g identifies the current stress-free configuration implies that the strain-energy density must be a function of the elastic strain

$$\mathbf{C}_e = \mathbf{F}_e^T \mathbf{F}_e = \mathbf{F}_g^{-T} \mathbf{F}^T \mathbf{F} \mathbf{F}_g^{-1} = \mathbf{F}_g^{-T} \mathbf{C} \mathbf{F}_g^{-1}, \quad (2)$$

where $\mathbf{C} = \mathbf{F}^T \mathbf{F}$ is the standard Lagrangian strain tensor. As \mathbf{C}_e is itself a function of \mathbf{C} , any strain-energy density depending on \mathbf{C}_e automatically complies with frame-invariance requirements.

The incompressibility constraint establishes an isochoricity condition on the elastic distortion \mathbf{F}_e , so that

$$\det \mathbf{F} = \det \mathbf{F}_g. \quad (3)$$

If the point-wise mass supply is assigned, the map $\det \mathbf{F}_g$ must be treated as an external parameter, and incompressibility limits as usual the class of deformations available to the growing body. If, on the contrary, the system deforms sufficiently slowly, apparently non-isochoric deformations become possible, in which growth accommodate local volume variations by concentrating mass production at sites undergoing greater expansion $\det \mathbf{F}_g$. When this is the case, the incompressibility constraint applies only globally, and the determinant of \mathbf{F} may neither be 1 nor even uniform. Much more general deformations thus become available to a slowly growing body, the map $\det \mathbf{F}$ giving the explicit details on the local mass production.

3. Encasement

We now study how the independent growth of an elastic bulk and of a closed, regular elastic surface surrounding it, may induce morphological instabilities. We consider the simplest geometry and constitutive assumptions on the material to better evidence the origin of such instabilities. The bulk of the body is given by a capped, isotropically growing cylinder made of simple

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