



Surface tension shapes the powerful water-conserving morphology of the trilayered rectal complex in insects

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ARTICLE INFO

Keywords:

Surface tension
Growth-induced instability
Insect rectal complex
Morphoelasticity
Elastocapillarity
Water-conserving morphology

ABSTRACT

Specialized water-conservation morphologies contribute to the broad evolutionary success of insects, especially in arid environments. At the core of these morphologies is the trilayered rectal complex, a functional organ whose intricate folds and papillae enable efficient water reabsorption. Although the physiological processes of this organ have been studied extensively, the fundamental morphoelastic principles governing its morphogenesis remain insufficiently understood. To address this gap, we propose a morphoelastic hypothesis in which efficient water-conserving structures emerge through a deterministic mechanical instability driven by the synergistic effects of differential growth across tissue layers and the contribution of luminal surface tension. To elucidate the mechanics of rectal-complex morphogenesis, we develop a nonlinear morphoelastic theoretical framework that models the organ as a multilayered, residually stressed, hyperelastic cylinder. The framework employs a triphasic decomposition of the deformation gradient, allowing prescribed initial residual stresses, volumetric growth, and purely elastic deformation to be characterized simultaneously. To capture the nonlinear response of soft biological tissues, we introduce a strain-stiffening Gent constitutive law and incorporate elastocapillary effects through the Young–Laplace equation applied at the luminal interface. By solving for axisymmetric base states and performing linear perturbation analysis, we derive an analytical expression for the incremental curvature. The surface impedance matrix method is then used to solve the incremental boundary-value problem, establishing quantitative criteria for mode selection and instability thresholds. Our results show that surface tension reorganizes the instability landscape during morphogenesis. Rather than acting as a uniformly stabilizing or destabilizing contribution, surface tension reshapes the critical growth-ratio spectrum, shifts the minimal critical growth ratio in a parameter-dependent manner, and switches the selected mode when competing instability families are close in threshold. We further construct instability phase diagrams that predict axial, circumferential, and coupled morphological modes under different surface-tension conditions and interlayer stiffness contrasts in the trilayered structure. These theoretical predictions

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<https://doi.org/10.1016/j.jmps.2026.106859>

Received 17 June 2026; Received in revised form 10 September 2026; Accepted 12 September 2026

Available online 15 September 2026

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are consistent with experimental observations across multiple insect species. This study identifies a mechanical basis for formation of water-conserving architectures driven by surface tension in insects, supports a role for surface tension in organogenesis, and provides principles for designing advanced water-management systems in biomimetic materials and soft robotics.

1. Introduction

Insects represent one of the most diverse animal groups on Earth, with an estimated global diversity of approximately 5.5 million species. More than one million insect species have been described, accounting for over half of all documented eukaryotes (Willmer et al., 2009; Eggleton, 2020). Their remarkable evolutionary success, particularly their adaptation to arid environments, is closely associated with highly specialized water-conservation mechanisms that evolved to meet the challenge of water regulation in terrestrial habitats (Noble-Nesbitt, 1970; Chown and Nicolson, 2011; Wang et al., 2023b). Cuticular structures and respiratory regulation reduce water loss, whereas the final and highly efficient stage of water recovery is performed by a specialized organ, the rectal complex. Across Coleoptera, the rectal complex occurs in multiple beetle lineages rather than being restricted to a single clade (Fig. 1(a)). A comparable phylogenetic distribution is found in Lepidoptera, spanning moth and caterpillar lineages over an evolutionary timescale of approximately 300 Myr (Fig. 1(b)). Together, these phylogenetic patterns suggest that rectal water recovery represents a recurrent evolutionary route for terrestrial water regulation (Zhang et al., 2022; Naseem et al., 2023; Beaven and Denholm, 2025).

The rectal complex can overcome large osmotic gradients to reclaim water and, in some species, even condense water from unsaturated media, producing extremely dry excreta (O'Donnell and Ruiz-Sanchez, 2015; Noble-Nesbitt, 1969; Beaven et al., 2023). This physiological capability arises from a hierarchical cryptonephridial system composed of the hindgut, Malpighian tubules, and perinephric membrane (Grimstone et al., 1968; Beaven and Denholm, 2025). The three layers establish an enclosed microenvironment regulated by active ion transport. Yet the water-reclaiming surface is also morphologically structured: the luminal wall develops folded topographies (Figs. 1(c)–(d)) (Magni and Riccobelli, 2025; Bai et al., 2025), linking transport physiology to a mechanical problem of surface-pattern generation and selection.

Although the physiological and biochemical pathways of ion transport and water movement in the rectal complex have been studied for decades (Phillips, 1980), the structure–function relationship underlying its exceptional water-conserving capacity remains incompletely understood. In particular, the morphoelastic mechanisms that generate and select its folded luminal architecture have not been fully resolved. Biological morphogenesis is a coupled physicochemical and biological process: it implements genetic programmes while remaining constrained by constitutive laws, thermodynamics, and force balance. Biological tissues therefore act as active materials whose mechanical states are regulated by local stress and strain fields (Wang et al., 2023a) as well as by geometric incompatibility (Erich and Zurlo, 2025). Final organ morphology emerges from a dynamic equilibrium between endogenous factors, including gene-regulated cell mechanics, tissue properties, and growth stresses, together with exogenous factors, especially mechanical interactions with the surrounding physical environment.

Morphoelasticity theory provides a central framework for analysing such processes (Rodriguez et al., 1994; Goriely, 2017). By treating biological growth as a source of local material addition, this theory extends classical continuum mechanics to growing living systems. Its core idea is the multiplicative decomposition of the total deformation into a growth tensor and a purely elastic tensor, with the latter restoring mechanical and geometric compatibility. Differential growth, a principal mechanical regulator of morphogenesis, introduces intrinsic deformation mismatch and geometric incompatibility. The resulting elastic accommodation preserves tissue continuity while generating residual stress fields. As development proceeds, these stress fields evolve spatially. When the mechanical constraint exceeds a stability threshold, a simple configuration may lose stability and form spatially periodic structures (Ben Amar and Goriely, 2005; Balbi et al., 2015; Wang et al., 2024), such as folds and grooves, through nonlinear deformation and symmetry breaking.

Morphological patterns generated by instability are widespread in both natural and artificial systems. They occur across scales, from wrinkling of polymer films at the microscale to circumferential folds in intestines and cortical folding in the brain at the macroscale. The underlying physics lies in the accumulation of internal stress caused by growth heterogeneity or thermodynamic gradients. Once this stress exceeds a critical level, an initial configuration may become unstable and evolve toward a new lower-energy morphology. The resulting macroscopic pattern reflects the interplay between intrinsic material response and environmental constraint, and the transition itself is a form of nonequilibrium self-organization. Related topological design strategies (Li et al., 2012; Ciarletta, 2014; Tallinen et al., 2016; Tan et al., 2020; Wang and Wang, 2022; Zhang et al., 2024, 2025, 2026) have been successfully applied to flexible electronics and soft robotics.

The insect rectal complex is an ideal biological system for studying growth-induced morphological instability and pattern selection during organogenesis (Naseem et al., 2023; Beaven and Denholm, 2025). Its tripartite structure, comprising the hindgut, Malpighian tubules, and perinephric membrane, exhibits marked differences in mechanical properties and growth behaviour. These differences include layer-dependent growth rates, progressive tissue remodelling, and heterogeneous distributions of matrix components. Such heterogeneity generates mechanical incompatibilities at interfaces (Du et al., 2018; Wang et al., 2023a), produces residual stress fields, and renders the multilayer structure sensitive to perturbations that can initiate morphological transitions. Differential growth is therefore essential, but it is not the only mechanical driver of rectal morphogenesis.

At the mesoscale, surface effects can also make a substantial contribution to biological mechanics. Classical continuum theories often treat interfacial phenomena as secondary, yet the forces generated at boundaries are central to cellular and subcellular self-organization. As system dimensions approach a critical length scale, surface-dominated effects become increasingly important. This

Nomenclature

B_r, B_g, B_c	Reference, virtual grown, and current configurations
$\mathbf{X}, \mathbf{x}$	Position vector of a material point in the reference and current states
χ	Nonlinear deformation mapping from B_r to B_c
$\Omega_{HG}, \Omega_{PT}, \Omega_{PM}$	Material domains for the hindgut (HG), perirectal tubule (PT), and perinephric membrane (PM) layers
$\mathbf{F}$	Total deformation gradient tensor
$\mathbf{F}_e, \mathbf{F}_g, \mathbf{F}_s$	Elastic, growth, and initial residual stress parts of the deformation gradient
J	Determinant of the total deformation gradient, $\det(\mathbf{F})$
J_e, J_g, J_s	Determinants of the elastic, growth, and initial residual stress parts of the deformation gradient
$\mathbf{C}, \mathbf{b}$	Right and left Cauchy-Green deformation tensors
$\mathbf{C}_e, \mathbf{b}_e$	Elastic right and left Cauchy-Green tensors
$\mathbf{C}_s, \mathbf{b}_s$	Right and left Cauchy-Green tensors associated with the initial residual stress state
$\mathbf{E}$	Green-Lagrange strain tensor
$\mathbf{L}_g$	Growth velocity tensor ($\dot{\mathbf{F}}_g \mathbf{F}_g^{-1}$)
$g_{[i]}$	Volumetric growth factor for layer i
$\dot{G}_{[i]}$	Prescribed linear growth rate for layer i
$\dot{G}_1, \dot{G}_2$	Ratios of the HG growth rate to the PT and PM growth rates
t	Parameter of the quasi-static prescribed-growth path; no physiological time scale is assigned
λ	Axial stretch ratio (l/L)
$\mathbf{T}, \mathbf{P}, \mathbf{S}$	The Cauchy, first Piola-Kirchhoff, and second Piola-Kirchhoff stress tensors
$\mathbf{t}$	Prescribed initial residual stress tensor
Ψ	Helmholtz free energy density function
$\mu, \bar{\mu}, \mu_{[i]}$	Generic, average, and layer-specific infinitesimal shear moduli
$J_m, J_m^{[i]}$	Generic and layer-specific strain-stiffening parameters in the Gent model
p, p_s	Pressure-like Lagrange multipliers for elastic and initial residual stress incompressibility
I_1^t, I_2^t, I_3^t	Principal invariants of the prescribed initial residual stress tensor $\mathbf{t}$
s	Dimensionless amplitude of the prescribed initial residual stress ansatz
$\mathbf{Y}$	Surface stress tensor
γ, α_γ	Dimensional and non-dimensional surface tension parameters
l_{cr}	Elastocapillary length scale
$\mathcal{K}, \mathcal{K}_1, \mathcal{K}_2$	Mean, first principal, and second principal curvatures of the inner surface
$\mathbf{N}, \mathbf{n}$	Unit normal vectors in the reference and current configurations
$\delta \mathbf{u}; u, v, w$	Incremental displacement vector and its radial, circumferential, and axial components
$U(r), V(r), W(r)$	Amplitude functions of the radial, circumferential, and axial displacement components
Γ	Gradient of the incremental displacement ($\text{grad}(\delta \mathbf{u})$)
$\delta \mathbb{P}$	Incremental nominal stress tensor pushed forward to the current state
$\delta p, \delta \mathcal{K}$	Incremental pressure field and incremental surface curvature
$\mathcal{L}$	The fourth-order instantaneous elastic modulus tensor
δ_{il}	Kronecker delta symbol
m, n	Circumferential and axial wavenumbers (mode numbers)
k	Scaled axial wavenumber ($n\pi/(\lambda L)$)
$\eta_{[i]}$	Six-dimensional displacement-traction state vector for layer i
$\mathbb{G}_{[i]}$	6×6 Stroh matrix for layer i
Z^L, Z^R	Inner and outer conditional surface impedance matrices
$\Delta \tilde{\mathcal{G}}$	Critical growth ratio (metric for onset of instability)
$\tilde{\mathcal{G}}_{\text{MCGR}}$	Minimal critical growth ratio (lowest instability threshold)
$\ \Delta \tilde{\mathcal{G}}\ _F$	Frobenius norm of the critical growth ratio matrix
R_a, R_b, R_c, R_d	Inner, HG/PT-interface, PT/PM-interface, and outer radii in the reference configuration
r_a, r_b, r_c, r_d	Inner, HG/PT-interface, PT/PM-interface, and outer radii in the current configuration
L, l	Initial and current axial lengths of the complex
Q_1, Q_2, Q	Lumen and outer-surface physical pressures, and signed pressure difference $Q = Q_1 - Q_2$
ξ	Normalised reference radial coordinate, $\xi = (R - R_a)/(R_d - R_a)$
μ_{ratio}	Ratio of shear moduli between adjacent layers

follows from scaling laws: volumetric forces scale with the cube of length, whereas surface forces scale with the square of length. The resulting increase in the ratio of surface area to volume makes surface energy minimization a major energetic constraint as equilibrium is approached (Roman and Bico, 2010; Taffetani and Ciarletta, 2015). The competition between surface tension and bulk elasticity is known as elastocapillarity. It describes the balance between the energetic cost of creating or deforming interfaces and the resistance of the material to elastic deformation.

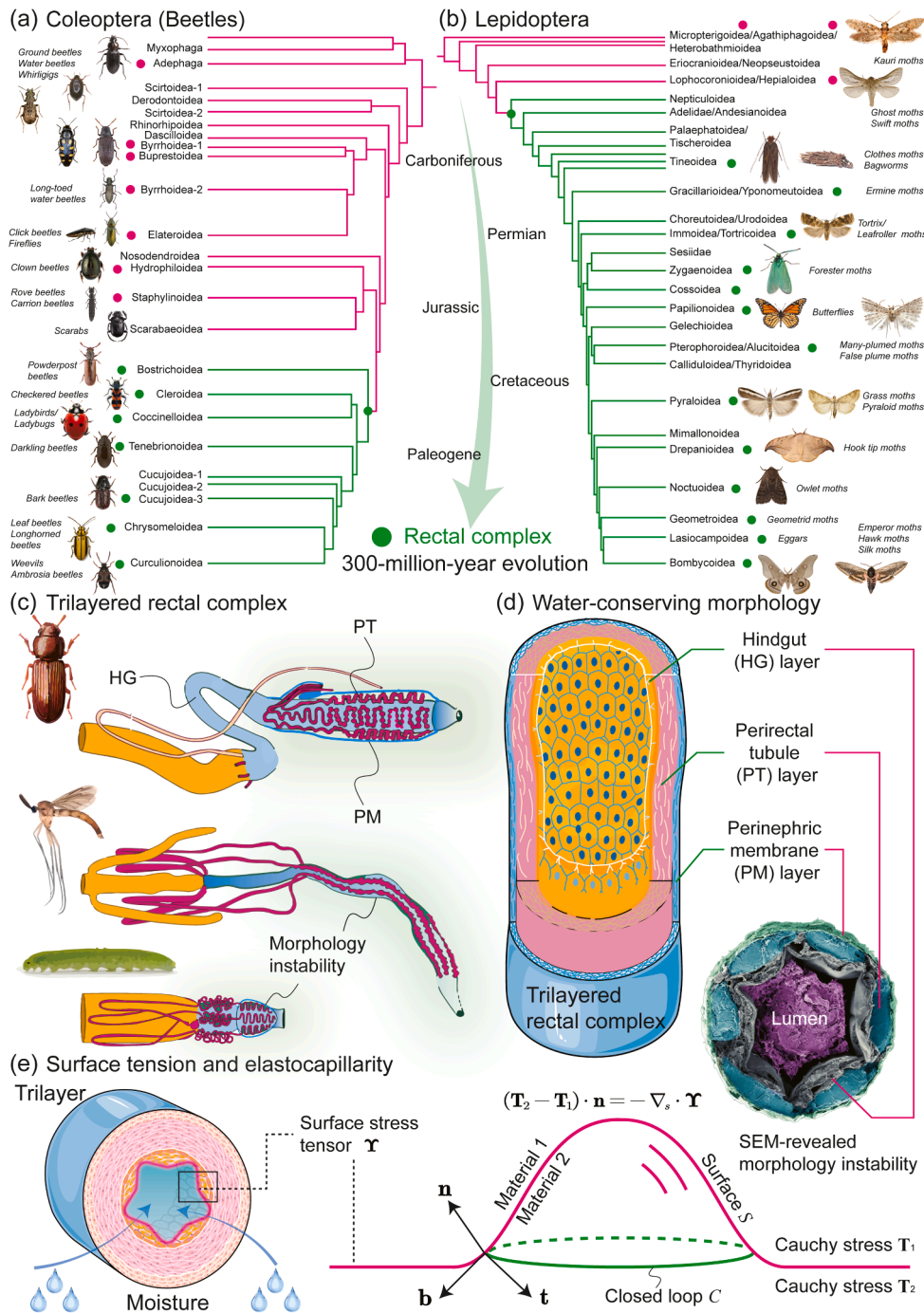


Fig. 1. Evolutionary distribution, trilayered architecture, and elastocapillary mechanics of the insect rectal complex. (a) Phylogenetic distribution of the rectal complex in Coleoptera, with green taxa indicating lineages that possess the complex and magenta taxa indicating lineages in which it is absent. (b) Phylogenetic distribution in Lepidoptera, highlighting a convergent origin of the rectal complex over an evolutionary timescale of approximately 300 Myr. (c) Representative rectal complexes from an adult beetle, adult moth, and caterpillar, showing distinct morphology-instability patterns within the trilayered organization. (d) Cross-sectional view of the water-reclaiming rectal complex, alongside scanning electron microscopy evidence of the undulated luminal morphology (Naseem et al., 2023). (e) Elastocapillary representation of the moist trilayer interface, where surface stress along a closed interfacial loop produces a traction jump between the adjacent Cauchy stress fields. In the right schematic, the magenta shaded surface represents the interfacial patch S , whereas the green closed loop represents its boundary $C = \partial S$; $\mathbf{b}$ is the outward co-normal to C within S .

Elastocapillary effects have been shown to govern tissue spheroid fusion, the Rayleigh–Plateau instability in elastic threads, edge rounding of elastic solids, and the encapsulation of droplets by elastic membranes (Style et al., 2017). Their characteristic length scale is given by the ratio of surface tension to elastic modulus. When the characteristic dimension of a soft body approaches this scale, surface and elastic energies become comparable, and the mechanical response can deviate from classical elasticity. Because soft biological materials often have micron-scale dimensions and low moduli, elastocapillary coupling can contribute strongly to morphological instability and pattern formation (Mora et al., 2010; Ang et al., 2020), thereby providing a physical route to self-organization.

Biological tissues also exhibit pronounced nonlinear mechanical behaviour owing to their internal fibrous microstructure. In the small-strain regime, network entropy dominates the response, giving high compliance and shear moduli on the order of kilopascals. When strain increases, fibre alignment and tension markedly increase stiffness, producing strain-stiffening behaviour. This nonlinearity and initial residual stress govern the mechanics of morphogenesis. From a morphomechanical perspective, strain-stiffening enables elastic energy storage, whereas initial residual stress can preload the system near an instability threshold. In insect rectal morphogenesis (Chen et al., 2022), the cooperation of these mechanical fields with surface tension from environmental liquid films (Huang et al., 2023; Wang et al., 2023a, 2024) may help overcome the energy barrier for folding and select characteristic wavelengths.

These adaptive mechanical features are important for the development and maintenance of functional biological structures, including fold formation in the insect rectum and mechanical adaptation of blood vessel walls (Nørgaard and Dacke, 2010; Liu et al., 2010; Lehnert et al., 2013; Zheng et al., 2024). Rectal morphogenesis therefore involves a tightly regulated system in which differential growth, material nonlinearity, initial residual stress, and surface tension interact. In this coupled system, strain-stiffening controls the capacity for elastic energy storage, initial residual stress sets the proximity to instability, and surface tension modifies the boundary tractions that can trigger and select unstable modes. Such multiphysics coupling supports biological self-organization by allowing high compliance at low strains for physiological adaptation while providing enhanced stiffness at high strains (Tan et al., 2025; Feng et al., 2026) to prevent damage.

Despite these advances, several theoretical gaps remain. A unified constitutive framework that simultaneously incorporates differential growth, material nonlinearity, initial residual stress, and elastocapillarity has not yet been established for the trilayered insect rectal complex. Moreover, the mechanistic interplay among surface tension, initial residual stress, and strain-stiffening remains insufficiently quantified, limiting the ability to predict biological morphogenesis in terms of instability thresholds and pattern selection. Addressing these mechanical challenges is essential for clarifying the physical basis of structural self-organization in systems such as the insect rectum.

The present study establishes an integrated theoretical framework to elucidate the synergistic roles of elastocapillary effects, nonlinear tissue mechanics, initial residual stress, and differential growth in shaping the insect rectal complex. Building on the central hypothesis that instability is jointly driven by surface tension and growth-induced residual stress, we develop a multilayer hyperelastic cylindrical model (Goriely, 2017; Naseem et al., 2023). The model adopts a triphasic decomposition of the deformation gradient (Du et al., 2018; Wang et al., 2023a), which distinguishes initial residual stress (Gower et al., 2015; Ciarletta et al., 2016; Fraldi and Carotenuto, 2018), volumetric growth, and elastic deformation within a continuum mechanics framework. We further incorporate a strain-stiffening constitutive law (Jin and Suo, 2015; Hang and Xu, 2022; Tian and Gong, 2025) and the generalized Young–Laplace equation to capture elastocapillary effects. Linear perturbation analysis is then used to determine the critical conditions for pattern formation, the evolution of curvature increments, and the selection of characteristic wavenumbers. To our knowledge, this study provides the first systematic mechanical explanation for the formation of this water-conserving structure and highlights the role of curvature increments in morphological evolution, offering a new insight into how volumetric growth, residual stress, and surface tension collectively drive complex morphogenesis in soft active materials.

The remainder of this paper is organized as follows. Section 2 introduces the fundamental concepts of elastocapillarity and uses scaling analysis to demonstrate its relevance to the morphogenesis of the insect rectal complex. Section 3 establishes the morphoelastic theoretical model, including the triphasic kinematic decomposition, nonlinear equilibrium equations, constitutive relations for multilayer structures with residual stress, and the construction of the base state. Section 4 establishes the incremental boundary-value problem and develops its solution through the Stroh formalism and surface impedance matrix techniques. Section 5 analyses how morphological selection depends on physical parameters, including surface tension, differential growth, and interlayer stiffness. Section 6 summarizes the principal findings and discusses potential applications of capillarity-driven instability in self-pumping wound dressings and biomimetic water-harvesting surfaces. Appendix B presents a bioinspired strategy for regulating interfacial water transport through surface morphology.

2. Elastocapillary water conservation in insects

The insect rectal complex reclaims water with remarkable efficiency through a cryptonephridial system that acts in concert with Malpighian tubules. Under severe aridity, this system can also capture environmental water vapour. Water molecules first nucleate as microdroplets on rectal walls and cellular surfaces. These droplets then coalesce into larger droplets and are transported back into the body along coupled mechanical and chemical gradients. During rectal-complex morphogenesis, the interaction between droplet surface tension and rectal-wall elasticity can induce capillarity-dominated deformations. These deformations reshape the local mechanical landscape, help maintain growth stability, and contribute to specialized topographies with hydrophilic crests and hydrophobic troughs that direct water transport. In this way, elastocapillary morphogenesis enhances water uptake, improves resilience in desiccating habitats, and supports the physiological performance of the rectal complex.

To quantify how elastocapillary effects contribute to the water-conserving architecture of the insect rectal complex, we first derive the boundary conditions that couple bulk stresses in the tissue to interfacial stresses on the luminal wall. We introduce the *surface stress tensor* $\mathbf{Y}$, which is the two-dimensional analogue of the three-dimensional Cauchy stress tensor $\mathbf{T}$. For a differential line element on the interface with unit co-normal $\mathbf{b}$, the traction per unit length is $\mathbf{Y} \cdot \mathbf{b}$. This traction can be decomposed into a line-normal component $\mathbf{b} \cdot \mathbf{Y} \cdot \mathbf{b}$ and a tangential component $\mathbf{t} \cdot \mathbf{Y} \cdot \mathbf{b}$, where $\mathbf{t}$ denotes the unit tangent vector.

As illustrated in Fig. 1(e), the static equilibrium of an interfacial patch S with boundary $C = \partial S$ requires

$$\int_S \mathbf{T}_2 \cdot \mathbf{n} \, dS - \int_S \mathbf{T}_1 \cdot \mathbf{n} \, dS + \oint_C \mathbf{Y} \cdot \mathbf{b} \, dl = 0, \quad (1)$$

where $\mathbf{T}_1$ and $\mathbf{T}_2$ are the Cauchy stress tensors in the lumen and the surrounding tissue, respectively, and $\mathbf{n}$ is the unit normal directed from medium 2 toward medium 1.

The surface divergence theorem gives

$$\oint_C \mathbf{Y} \cdot \mathbf{b} \, dl = \int_S \nabla_s \cdot \mathbf{Y} \, dS, \quad (2)$$

so the contour integral in Eq. (1) can be converted into a surface integral and the local traction balance can be written as

$$(\mathbf{T}_2 - \mathbf{T}_1) \cdot \mathbf{n} = -\nabla_s \cdot \mathbf{Y}. \quad (3)$$

This expression is the generalized Young–Laplace equation for a curved, elastically deformable interface. Here, ∇_s denotes the surface divergence operator acting in the tangent plane of S .

We next write this balance in a form suitable for a curved luminal surface. Consider a curved surface S described by the orthonormal triad $\{\mathbf{b}, \mathbf{t}, \mathbf{n}\}$, where $\mathbf{b}$ and $\mathbf{t}$ are unit basis vectors in the tangent plane and $\mathbf{n}$ is the unit normal. The generalized Young–Laplace equation in Eq. (3) can then be expressed as

$$\begin{aligned} (\mathbf{T}_2 - \mathbf{T}_1) \cdot \mathbf{n} = & -(\mathcal{K}_1 \gamma_{11} + \mathcal{K}_2 \gamma_{22}) \mathbf{n} \\ & - \frac{1}{h_1 h_2} \left[\frac{\partial(h_2 \gamma_{11})}{\partial \alpha_1} + \frac{\partial(h_1 \gamma_{21})}{\partial \alpha_2} + \frac{\partial h_1}{\partial \alpha_2} \gamma_{12} - \frac{\partial h_2}{\partial \alpha_1} \gamma_{22} \right] \mathbf{b} \\ & - \frac{1}{h_1 h_2} \left[\frac{\partial h_1}{\partial \alpha_2} \gamma_{11} + \frac{\partial(h_2 \gamma_{12})}{\partial \alpha_1} + \frac{\partial h_2}{\partial \alpha_1} \gamma_{21} + \frac{\partial(h_1 \gamma_{22})}{\partial \alpha_2} \right] \mathbf{t}, \end{aligned} \quad (4)$$

where two mutually orthogonal parametric curves on S generate the metric coefficients h_1 and h_2 . The quantities α_1 and α_2 are the associated surface coordinates. The principal curvatures are $\mathcal{K}_1$ and $\mathcal{K}_2$, and the surface-stress tensor $\mathbf{Y}$ has components $\gamma_{11}, \gamma_{22}, \gamma_{12}, \gamma_{21}$.

When the surface-stress tensor $\mathbf{Y} = \gamma \mathbf{I}_{2D}$ is uniform and isotropic, the tangential contributions in Eq. (4) vanish, where γ is a scalar surface tension. The traction balance then reduces to

$$(\mathbf{T}_2 - \mathbf{T}_1) \cdot \mathbf{n} = -\gamma(\mathcal{K}_1 + \mathcal{K}_2) \mathbf{n}, \quad (5)$$

where $\mathcal{K}_1$ and $\mathcal{K}_2$ are the two principal curvatures.

To estimate the importance of surface tension relative to bulk elasticity, we consider an unloaded and ungrown tubular rectal complex occupying the domain Ω and containing fluid. Let $\mathbf{T}$ denote the Cauchy stress in the tissue. If body forces, residual stresses, and external potentials are neglected, the generalized Young–Laplace equation reduces to Style et al. (2015b,a)

$$\mathbf{T} \cdot \mathbf{n} = -Q_1 \mathbf{n} + \gamma \mathcal{K}_1 \mathbf{n}. \quad (6)$$

Here, Q_1 is the fluid pressure.

Treating the rectal complex as an incompressible hyperelastic solid gives $\nabla \cdot \mathbf{T} = \mathbf{0}$ and $\mathbf{T} = -p \mathbf{I}$, where p is the Lagrange multiplier enforcing incompressibility. Applying the elastocapillary boundary condition at the inner surface $R = R_a$ yields

$$\Delta p = \gamma \mathcal{K}_1 \implies \gamma = \Delta p R_a, \quad (7)$$

the classical Young–Laplace relation with Δp the Laplace pressure.

The competition between surface tension and bulk elasticity is characterized by the scaling relation $\gamma \mathcal{K} \sim \mu \epsilon$, where μ is the shear modulus and ϵ is the strain. Large deformations ($\epsilon \sim 1$) are expected when $1/\mathcal{K} \sim \gamma/\mu$. This balance defines the capillary length

$$l_{cr} = \frac{\gamma}{\mu}. \quad (8)$$

Bodies much larger than l_{cr} are only weakly affected by surface tension, whereas bodies with dimensions comparable to or smaller than l_{cr} can exhibit pronounced elastocapillary responses.

Experimental observations (Naseem et al., 2023) indicate that the beetle rectal complex has a cross-sectional dimension of roughly 100 μm . Assuming a Laplace pressure difference of 1000 Pa (Lee et al., 2019), Eq. (7) gives a surface tension of approximately $\gamma \approx 0.1 \text{ N/m}$. Taking the shear modulus of the inner rectal wall tissue as $\mu \sim 1000 \text{ Pa}$ (Akhtar et al., 2011), Eq. (8) gives a capillary length on the order of 100 μm . This value is comparable to the geometric scale of the rectal complex, indicating that elastocapillary effects should be mechanically relevant in this system.

This estimate provides a useful consistency check for the elastocapillary interpretation. Although a comprehensive experimental characterization of surface tension and elastocapillary properties in rectal tissue is not yet available, the model-predicted range $\gamma = 0.01\text{--}0.1 \text{ N/m}$ is physically plausible. It is comparable to surface tensions of 0.01–0.05 N/m reported for developmental tissues

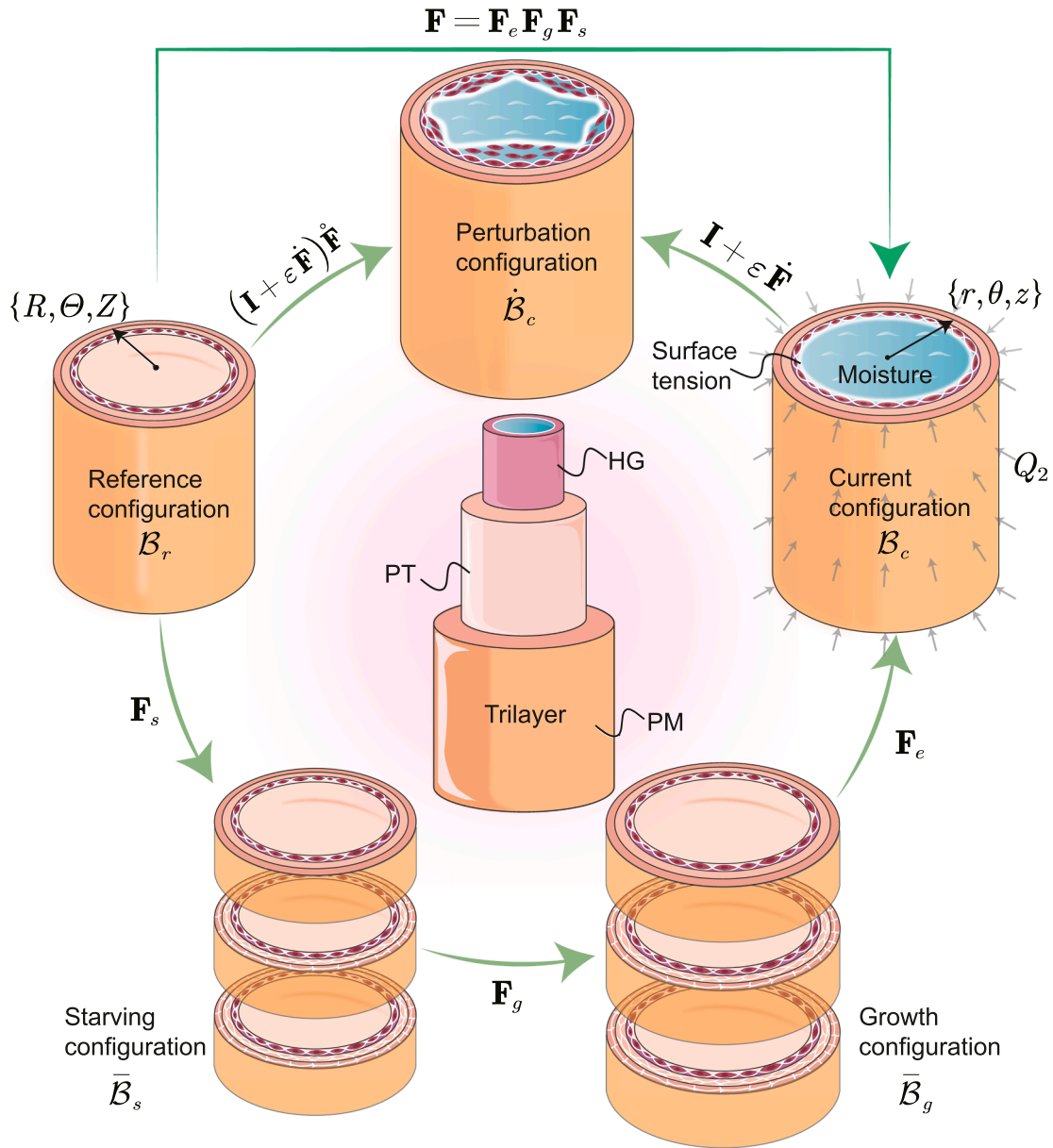


Fig. 2. Triphasic kinematics of growth and elastocapillary perturbation in the insect rectal complex. The rectal complex is modeled as a trilayered cylindrical structure consisting of the hindgut (HG), perirectal tubule (PT), and perinephric membrane (PM). The reference configuration B_r is first mapped to the configuration with prescribed initial residual stress $\bar{B}_s$ by F_s , then to the virtual grown configuration $\bar{B}_g$ by F_g , and finally to the current configuration B_c by the elastic deformation F_e , giving the multiplicative split $F = F_e F_g F_s$. Surface tension generated by the moist luminal interface, combined with the external load Q_2 , drives the superimposed perturbation used in the subsequent instability analysis. Green arrows indicate the sequence of transformations between configurations.

such as zebrafish embryos (Riccobelli and Bevilacqua, 2020). This agreement supports the order of magnitude estimate used here and is consistent with general biophysical principles governing tissue surface tension (Foty and Steinberg, 2005; Heisenberg and Bellaïche, 2013).

Only the luminal contribution is retained in the subsequent stability analysis. In principle, the total potential energy may also include interfacial tensions γ_b , γ_c , and γ_d at $R = R_b$, $R = R_c$, and $R = R_d$, in addition to the inner-wall tension γ_a at $R = R_a$. The corresponding energy contribution can be written as $\int_{\Omega} (\gamma_b + \gamma_c + \gamma_d) dV$, which reduces to $|\Omega|(\gamma_b + \gamma_c + \gamma_d) \det F$. For purely elastic deformation without growth or remodelling, living tissues are commonly treated as incompressible, so that $\det F = 1$ (Holzapfel, 2000). Under this isochoric constraint, the additional surface-energy term is deformation invariant and therefore does not contribute to the variational force balance or stability criterion. These interfacial terms are consequently excluded from the morphoelastic instability analysis (Goriely, 2017).

3. Morphoelasticity model of the rectal complex

3.1. Kinematics of triphasic growth

As illustrated in Fig. 2, the rectal complex is represented as a nonlinear, strain-sensitive solid subjected to a pre-existing field of prescribed initial residual stress and externally applied loads. Let $\mathcal{B}_r$ denote the reference configuration, parameterized by the material coordinate $\mathbf{X}$, and let $\mathcal{B}_c$ denote the current configuration, parameterized by the spatial coordinate $\mathbf{x}$. The motion is described by the diffeomorphic mapping $\mathbf{x} = \chi(\mathbf{X}, t)$, with $\chi : \mathcal{B}_r \times \mathbb{R}_{\geq 0} \rightarrow \mathcal{B}_c$. The associated deformation gradient is

$$\mathbf{F} = \nabla_{\mathbf{X}} \chi, \quad (9)$$

with Jacobian $J = \det \mathbf{F} > 0$, which ensures local injectivity and preservation of orientation.

To separate the effects of prescribed initial residual stress, biological growth, and elastic accommodation, we introduce the multiplicative *triphasic* decomposition as (Fraldi and Carotenuto, 2018; Wang et al., 2023a)

$$\mathbf{F} = \mathbf{F}_e \mathbf{F}_g \mathbf{F}_s. \quad (10)$$

In this split, $\mathbf{F}_s$ represents the deformation associated with prescribed initial residual stress and introduces the intermediate stress-free configuration $\bar{\mathcal{B}}_s$. The growth tensor $\mathbf{F}_g$ then maps $\bar{\mathcal{B}}_s$ to the virtual grown configuration $\bar{\mathcal{B}}_g$, whereas the elastic tensor $\mathbf{F}_e$ restores compatibility and carries the body to the current configuration $\mathcal{B}_c$. The corresponding Jacobians are $J_s = \det \mathbf{F}_s$, $J_g = \det \mathbf{F}_g$, and $J_e = \det \mathbf{F}_e$. Under the incompressibility assumptions used for initial residual stress and elastic response, $J_s = 1$ and $J_e = 1$, so that the total volume change reduces to $J = J_g$. These kinematic definitions provide the basis for analyzing how initial stress, growth kinetics, and elastic compatibility jointly govern morphological instability.

This triphasic decomposition extends the classical biphasic Kröner–Lee split widely used in morphoelasticity (Rodriguez et al., 1994; Goriely, 2017). In its standard form, $\mathbf{F} = \mathbf{F}_e \mathbf{F}_g$, the framework separates elastic deformation from growth or remodelling, but treats the grown configuration generated by $\mathbf{F}_g$ as a single coherent stress-free state. This assumption is restrictive for biological tissues, which often contain residual stresses even in unloaded configurations (Holzapfel, 2000; Fung, 2013; Gower et al., 2015). Such intrinsic stresses can influence subsequent growth and instability and therefore need to be represented explicitly. We therefore introduce the additional intermediate state $\bar{\mathcal{B}}_s$ and the associated deformation gradient for the initial residual stress $\mathbf{F}_s$, yielding the more complete decomposition $\mathbf{F} = \mathbf{F}_e \mathbf{F}_g \mathbf{F}_s$ (Ciarletta et al., 2016; Du et al., 2018; Wang et al., 2023a).

3.2. Balance of mass and momentum

The slow-growth hypothesis in morphoelasticity assumes a clear separation between the time scale of tissue growth and that of elastic relaxation. Growth evolves over long biological times, from hours to years, whereas elastic equilibration occurs over much shorter mechanical times, typically seconds, through elastic wave propagation. Within this approximation, mass is added by volumetric sources during the transition from the virtual stress-free configuration $\bar{\mathcal{B}}_s$ to the virtual grown configuration $\bar{\mathcal{B}}_g$. The subsequent elastic deformation from $\bar{\mathcal{B}}_g$ to the current configuration $\mathcal{B}_c$ is taken to be mass preserving.

In the reference configuration, the density ρ_r changes at the rate $\dot{\rho}_r$. For an open system such as a growing biological tissue, the local balance of mass must account for both the mass flux $\mathbf{R}$ and the volumetric source term $\mathcal{R}_0$ (Kuhl and Steinmann, 2004), giving

$$\dot{\rho}_r = \nabla_{\mathbf{X}} \cdot \mathbf{R} + \mathcal{R}_0. \quad (11)$$

To link this balance to growth kinematics, we relate the density in the grown configuration to that in the reference configuration through $\rho_g = J_g^{-1} \rho_r = j_g \rho_r$. Differentiating this relation with respect to time yields $j_g \dot{\rho}_r + \dot{j}_g \rho_r = 0$. If mass flux is neglected, which is a common approximation for soft tissue growth, the source term can be written in terms of the growth tensor and its rate as

$$\mathcal{R}_0 = \dot{\rho}_r = -\rho_r J_g \dot{j}_g = -\rho_r J_g \dot{j}_g \operatorname{tr}(\mathbf{F}_g^{-1} \dot{\mathbf{F}}_g) = \rho_r \operatorname{tr}(\mathbf{L}_g), \quad (12)$$

where $\mathbf{L}_g = \dot{\mathbf{F}}_g \mathbf{F}_g^{-1}$ is the growth rate tensor. This expression makes the source term $\mathcal{R}_0$ directly dependent on the local rate of growth.

The corresponding balance of linear momentum is written in the Lagrangian framework for an open system in which the reference density may vary (Ambrosi and Guillou, 2007):

$$\dot{\rho}_r \mathbf{v} + \rho_r \dot{\mathbf{v}} = \nabla_{\mathbf{X}} \cdot \mathbf{P} + \rho_r \mathbf{f}, \quad (13)$$

where $\mathbf{v}$ is the material velocity, $\mathbf{P}$ is the first Piola–Kirchhoff stress, and $\mathbf{f}$ is the body force per unit mass. Under quasi-static conditions, density-rate and inertial terms are neglected, so that $\dot{\rho}_r = 0$ and $\dot{\mathbf{v}} = 0$. The balance then reduces to $\nabla_{\mathbf{X}} \cdot \mathbf{P} + \rho_0 \mathbf{f} = \mathbf{0}$. If body forces are further neglected ($\mathbf{f} = \mathbf{0}$), the governing equation becomes

$$\nabla_{\mathbf{X}} \cdot \mathbf{P} = \mathbf{0}. \quad (14)$$

Finally, angular momentum balance imposes the symmetry condition

$$\mathbf{F} \mathbf{P}^T = \mathbf{P} \mathbf{F}^T \implies \mathbf{P} = \mathbf{F} \mathbf{P}^T \mathbf{F}^{-T}. \quad (15)$$

Here, $\mathbf{P}^T$ denotes the nominal, or engineering, stress tensor.

3.3. Dissipation inequality

The constitutive formulation is constrained by the Clausius–Duhem inequality (Lamm et al., 2022), which enforces consistency with entropy balance. For the present open-system description, the dissipation inequality D is written as

$$D = \frac{1}{\rho_r} \mathbf{S} : \dot{\mathbf{E}} - \dot{\Psi} - TS_0 \geq 0, \quad (16)$$

where $\mathbf{S}$ is the second Piola–Kirchhoff stress and $\mathbf{E} = (\mathbf{C} - \mathbf{I})/2$ is the Green–Lagrange strain tensor, with $\mathbf{C} = \mathbf{F}^T \mathbf{F}$ denoting the right Cauchy–Green deformation tensor. The quantity $\Psi(\mathbf{F}_e) = \rho_r \psi(\mathbf{F}_e)$ is the volume-specific Helmholtz free energy density. When an internal constraint is imposed for the hyperelastic material, the free energy is replaced by the constrained potential $\Psi(\mathbf{F}_e) - pC(\mathbf{F}_e)$, where $C(\mathbf{F}_e)$ is a smooth scalar constraint function. The absolute temperature is denoted by T , and S_0 represents the external entropy source.

For the prescribed fields $\mathbf{F}_s$ and $\mathbf{F}_g$ considered here, the elastic response is specified directly as incompressible and hyperelastic. The constrained potential is $\Psi(\mathbf{F}_e) - pC(\mathbf{F}_e)$, with $C(\mathbf{F}_e) = \det(\mathbf{F}_e) - 1$. Accordingly, the second Piola–Kirchhoff stress is obtained by differentiating this constrained potential with respect to the Green–Lagrange strain:

$$\mathbf{S} = \frac{\partial[\Psi(\mathbf{F}_e) - pC(\mathbf{F}_e)]}{\partial \mathbf{E}} = 2 \frac{\partial[\Psi(\mathbf{F}_e) - pC(\mathbf{F}_e)]}{\partial \mathbf{C}}. \quad (17)$$

Combining $\mathbf{P} = J\mathbf{F}\mathbf{S}$ with the chain-rule relation between derivatives with respect to $\mathbf{C}$ and $\mathbf{F}$, the first Piola–Kirchhoff stress tensor is obtained as

$$\mathbf{P} = 2J\mathbf{F} \frac{\partial[\Psi(\mathbf{F}_e) - pC(\mathbf{F}_e)]}{\partial \mathbf{C}} = J\mathbf{F} \frac{\partial[\Psi(\mathbf{F}_e) - pC(\mathbf{F}_e)]}{\partial \mathbf{F}} \mathbf{F}^{-T}. \quad (18)$$

To express this stress in terms of the elastic part of the triphasic decomposition, we combine Eqs. (15) with (18) and use the identities

$$\mathbf{F}_e = \mathbf{F}\mathbf{F}_s^{-1}\mathbf{F}_g^{-1}, \quad \frac{\partial \Psi(\mathbf{F}_e)}{\partial \mathbf{F}} = \mathbf{F}_s^{-1}\mathbf{F}_g^{-1} \frac{\partial \Psi(\mathbf{F}_e)}{\partial \mathbf{F}_e}, \quad \frac{\partial \det(\mathbf{F}_e)}{\partial \mathbf{F}_e} = \det(\mathbf{F}_e) \mathbf{F}_e^{-1}, \quad (19)$$

which gives the nominal stress tensor as

$$\mathbf{P}^T = J \frac{\partial \Psi(\mathbf{F}_e)}{\partial \mathbf{F}} - pJ \frac{\partial [\det(\mathbf{F}_e) - 1]}{\partial \mathbf{F}} = J\mathbf{F}_s^{-1}\mathbf{F}_g^{-1} \frac{\partial \Psi(\mathbf{F}_e)}{\partial \mathbf{F}_e} - pJ \det(\mathbf{F}_e) \mathbf{F}^{-1}. \quad (20)$$

Finally, imposing elastic incompressibility, $\det(\mathbf{F}_e) = 1$, and using $\mathbf{T} = J^{-1}\mathbf{F}\mathbf{P}^T$ lead to the Cauchy stress tensor

$$\mathbf{T} = \mathbf{F}\mathbf{F}_s^{-1}\mathbf{F}_g^{-1} \frac{\partial \Psi(\mathbf{F}_e)}{\partial \mathbf{F}_e} - p\mathbf{I} = \mathbf{F}_e \frac{\partial \Psi(\mathbf{F}_e)}{\partial \mathbf{F}_e} - p\mathbf{I}. \quad (21)$$

3.4. Initial residual stress and deformation fields

The deformation of the insect rectal complex is described using a Gent-type constitutive model, which is well suited to soft biological tissues that exhibit volume preservation and strain stiffening. The corresponding strain-energy density reads

$$\Psi = -\frac{\mu J_m}{2} \ln \left[1 - \frac{\text{tr}(\mathbf{F}_e^T \mathbf{F}_e) - 3}{J_m} \right]. \quad (22)$$

Here, μ is the infinitesimal shear modulus and J_m is the structural parameter controlling the degree of strain stiffening. In the limit $J_m \rightarrow \infty$, the Gent model reduces to the neoHookean form, $\Psi = \mu [\text{tr}(\mathbf{F}_e^T \mathbf{F}_e) - 3]/2$.

Substitution of Eq. (22) into the stress relations in Eqs. (20) and (21) yields the following nominal and Cauchy stress tensors:

$$\mathbf{P}^T = \frac{\mu J J_m}{J_m - [\text{tr}(\mathbf{F}_e^T \mathbf{F}_e) - 3]} \mathbf{F}_s^{-1}\mathbf{F}_g^{-1}\mathbf{F}_e - pJ\mathbf{F}^{-1}, \quad (23)$$

$$\mathbf{T} = \frac{\mu J_m}{J_m - [\text{tr}(\mathbf{F}_e^T \mathbf{F}_e) - 3]} \mathbf{F}_e^T \mathbf{F}_e - p\mathbf{I}. \quad (24)$$

For axisymmetric growth, the growth tensor $\mathbf{F}_g$ and the relevant gradient tensors are taken to be diagonal, so that their products commute. The prescribed initial residual stress state is obtained by setting $\mathbf{F}_g = \mathbf{I}$ and $\mathbf{F} = \mathbf{I}$ (Gower et al., 2015; Wang et al., 2023a), which relates the initial residual stress $\mathbf{t}$ to the deformation measure $\mathbf{C}_s^{-1} = \mathbf{F}_s^{-T}\mathbf{F}_s^{-1}$:

$$\mathbf{t} = \frac{\mu J_m}{J_m - [\text{tr}(\mathbf{C}_s^{-1}) - 3]} \mathbf{C}_s^{-1} - p_s \mathbf{I}, \quad (25)$$

$$\mathbf{C}_s^{-1} = \frac{J_m - [\text{tr}(\mathbf{C}_s^{-1}) - 3]}{\mu J_m} (\mathbf{t} + p_s \mathbf{I}). \quad (26)$$

Taking the trace of Eq. (25) and enforcing the incompressibility condition $\det(\mathbf{C}_s^{-1}) = 1$ yields

$$\text{tr}(\mathbf{C}_s^{-1}) = \frac{(3 + J_m)[3p_s + \text{tr}(\mathbf{t})]}{\mu J_m + 3p_s + \text{tr}(\mathbf{t})} \implies \left[\frac{3 + J_m}{\mu J_m + 3p_s + \text{tr}(\mathbf{t})} \right]^3 \det(p_s \mathbf{I} + \mathbf{t}) = 1. \quad (27)$$

Consequently, the Lagrange multiplier p_s associated with the initial residual-stress deformation satisfies the cubic relation

$$p_s^3 + p_s^2 I_1^t + p_s I_2^t + I_3^t = \frac{(\mu J_m + 3p_s + I_1^t)^3}{(3 + J_m)^3}. \quad (28)$$

where I_1^t , I_2^t , and I_3^t are the principal invariants of $\mathbf{t}$.

3.5. Residual stress of trilayered morphology

In the reference configuration shown in Fig. 2, the rectal complex is represented by three concentric layers. From the lumen outward, these are the hindgut (HG), perirectal tubule (PT), and perinephric membrane (PM). Their radial domains are

$$R_a \leq R \leq R_b, \quad R_b \leq R \leq R_c, \quad R_c \leq R \leq R_d, \quad (29)$$

with the axial coordinate spanning $0 \leq Z \leq L$.

To examine the mechanical consequences of a pre-existing residual stress without attributing a measured distribution to starvation, we prescribe an axisymmetric initial residual-stress field across the trilayer wall. Following the stress-potential construction for residually stressed tubular tissues (Ciarletta et al., 2016), the field is generated by the cubic potential

$$f(R) = \frac{s\bar{\mu}}{3R_a^2} R(R - R_a)(R - R_d). \quad (30)$$

where $\bar{\mu}$ is the average shear modulus and s is a dimensionless amplitude parameter. This field is a mechanically admissible ansatz used for sensitivity analysis, rather than a stress profile inferred from direct measurements in a starved insect rectal complex. The associated initial residual stress is

$$\mathbf{t} = \text{diag}\left(\frac{f(R)}{R}, \frac{df(R)}{dR}, 0\right) = \text{diag}\left(\frac{s\bar{\mu}(R - R_a)(R - R_d)}{3R_a^2}, \frac{s\bar{\mu}[3R^2 + R_a R_d - 2R(R_a + R_d)]}{3R_a^2}, 0\right). \quad (31)$$

In cylindrical coordinates, the total deformation gradient and the isotropic growth tensor in each layer $[i] \in \{\text{HG}, \text{PT}, \text{PM}\}$ are defined as

$$\mathbf{F} = \text{diag}\left(\frac{dr(R)}{dR}, \frac{r(R)}{R}, \lambda\right), \quad \mathbf{F}_g^{[i]} = g_{[i]} \mathbf{I}. \quad (32)$$

where $\lambda = l/L$ is the axial stretch and $g_{[i]}$ is the volumetric growth factor of layer i .

Combining the stress expressions in Eqs. (24)–(26) with the layer-wise growth tensor in Eq. (32) and using $\mathbf{C}_e = g^{-2} \mathbf{C}_s^{-1} \mathbf{C}$ gives the Cauchy stress tensor with the prescribed initial residual stress contribution $\mathbf{t}$:

$$\mathbf{T} = \frac{\mu g^{-2} J_m \mathbf{C}_s^{-1} \mathbf{C}}{J_m - [\text{tr}(\mathbf{C}_e) - 3]} - p \mathbf{I} = \frac{\mu g^{-2} J_m (3 + J_m) (p_s \mathbf{I} + \mathbf{t}) \mathbf{C}}{(J_m - \text{tr}(\mathbf{C}_e) + 3) [\mu J_m + 3p_s + \text{tr}(\mathbf{t})]} - p \mathbf{I}. \quad (33)$$

In the absence of body forces, the balance of linear momentum reduces to

$$\nabla_{\mathbf{x}} \cdot \mathbf{T} = \mathbf{0} \quad \text{in } \Omega_{HG}, \Omega_{PT}, \Omega_{PM}. \quad (34)$$

On the inner luminal boundary, a constant surface tension γ imposes the elastocapillary traction condition

$$\mathbf{T} \mathbf{n} = -Q_1 \mathbf{n} + \gamma \mathcal{K} \mathbf{n}, \quad (35)$$

$$\mathbf{P}^T \mathbf{N} = -J Q_1 \mathbf{F}^{-T} \mathbf{N} + J \gamma \mathcal{K} \mathbf{F}^{-T} \mathbf{N}, \quad (36)$$

where $\mathbf{n}$ and $\mathbf{N}$ are the outward unit normals in the current and reference configurations, respectively.

At the HG–PT and PT–PM interfaces, traction continuity requires

$$\langle \mathbf{T} \rangle \mathbf{n} = \mathbf{0}, \quad \langle \mathbf{P}^T \rangle \mathbf{N} = \mathbf{0}, \quad (37)$$

where $\langle \bullet \rangle$ denotes the jump of a field across the corresponding interface.

The stress expression in Eq. (33) requires elastic and initial residual stress kinematics to remain distinct. The invariants of the elastic right Cauchy–Green tensor $\mathbf{C}_e$ and those of the structural tensor $\mathbf{C}_s$ are therefore treated as independent, so that $\text{tr}(\mathbf{C}_s^{-1}) \neq \text{tr}(\mathbf{C}_e)$. If one instead imposes $\text{tr}(\mathbf{C}_s^{-1}) = \text{tr}(\mathbf{C}_e)$ for algebraic convenience, the resulting simplified stress, $\mathbf{T} = J_g^{-2/3} (\mathbf{F} \mathbf{F}^T + p_s \mathbf{F} \mathbf{F}^T) - p \mathbf{I}$, has no clear physical basis, because initial residual stress remodelling and recoverable elastic distortion arise from different mechanisms and occur on different time scales. Conflating these kinematic measures compromises stress evaluation and propagates errors to the tangent moduli used in stability and bifurcation analysis. Preserving their independence is therefore essential for nonlinear simulations of morphoelastic materials.

3.6. Fundamental solution of trilayered morphology

To obtain the radially symmetric fundamental solution of the trilayered morphology, we first impose elastic incompressibility, $J_e = \det(\mathbf{F}_e) = 1$. This constraint gives the geometric relation

$$\det(\mathbf{F}_e) = \det(\mathbf{F}\mathbf{F}_s^{-1}\mathbf{F}_g^{-1}) = 1 \implies r \, dr = \lambda^{-1} g^3 R \, dR. \quad (38)$$

Integrating Eq. (38) and enforcing radial continuity across the interfaces give the layer-wise mappings

$$r_{HG}^2 = r_a^2 + \lambda^{-1} g_{HG}^3 (R^2 - R_a^2), \quad (39)$$

$$r_{PT}^2 = r_a^2 + \lambda^{-1} g_{HG}^3 (R_b^2 - R_a^2) + \lambda^{-1} g_{PT}^3 (R^2 - R_b^2), \quad (40)$$

$$r_{PM}^2 = r_a^2 + \lambda^{-1} g_{HG}^3 (R_b^2 - R_a^2) + \lambda^{-1} g_{PT}^3 (R_c^2 - R_b^2) + \lambda^{-1} g_{PM}^3 (R^2 - R_c^2). \quad (41)$$

Let Q_1 and Q_2 denote the physical lumen and outer-surface pressures, respectively. The physical radial stresses at the two boundaries are $T_{rr}^{\text{phys}}(r_a) = \gamma/r_a - Q_1$ and $T_{rr}^{\text{phys}}(r_d) = -Q_2$. Since Q_1 is spatially uniform, we introduce a gauge referenced to the lumen pressure:

$$\hat{\mathbf{T}} = \mathbf{T}^{\text{phys}} + Q_1 \mathbf{I}, \quad \hat{T}_{rr}^{PM} \Big|_{r_d} = Q \equiv Q_1 - Q_2. \quad (42)$$

The inner boundary condition then becomes

$$\hat{T}_{rr}^{HG} \Big|_{r_a} = \gamma r_a^{-1}. \quad (43)$$

The gauge stress is written with its hat throughout Eqs. (44)–(55); the physical stress is recovered from $\mathbf{T}^{\text{phys}} = \hat{\mathbf{T}} - Q_1 \mathbf{I}$.

Under axisymmetric deformation, the first Cauchy equilibrium equation in each layer $[i] \in \{HG, PT, PM\}$ is

$$\frac{d\hat{T}_{rr}^{[i]}}{dr_{[i]}} + \frac{\hat{T}_{rr}^{[i]} - \hat{T}_{\theta\theta}^{[i]}}{r_{[i]}} = 0 \implies \frac{d\hat{T}_{rr}^{[i]}}{dR} + \frac{g_{[i]}^3 \lambda^{-1} R (\hat{T}_{rr}^{[i]} - \hat{T}_{\theta\theta}^{[i]})}{r_{[i]}^2} = 0. \quad (44)$$

Combining this relation with Eq. (33) and $dr_{[i]}/dR = g_{[i]}^3 R/(r_{[i]} \lambda)$ yields the following layer-wise gauge Cauchy stress components:

$$\hat{T}_{rr}^{[i]} = \frac{\mu_{[i]} J_m^{[i]} (3 + J_m^{[i]}) (p_s^{[i]} + t_{RR}^{[i]}) (R g_{[i]}^2 / (r_{[i]} \lambda))^2}{(J_m^{[i]} - \text{tr} \mathbf{C}_e^{[i]} + 3) (\mu_{[i]} J_m^{[i]} + 3 p_s^{[i]} + t_{RR}^{[i]} + t_{\theta\theta}^{[i]} + t_{ZZ}^{[i]})} - p^{[i]}, \quad (45)$$

$$\hat{T}_{\theta\theta}^{[i]} = \frac{\mu_{[i]} J_m^{[i]} (3 + J_m^{[i]}) (p_s^{[i]} + t_{\theta\theta}^{[i]}) (r_{[i]} / (R g_{[i]}))^2}{(J_m^{[i]} - \text{tr} \mathbf{C}_e^{[i]} + 3) (\mu_{[i]} J_m^{[i]} + 3 p_s^{[i]} + t_{RR}^{[i]} + t_{\theta\theta}^{[i]} + t_{ZZ}^{[i]})} - p^{[i]}, \quad (46)$$

$$\hat{T}_{zz}^{[i]} = \frac{\mu_{[i]} J_m^{[i]} (3 + J_m^{[i]}) (p_s^{[i]} + t_{ZZ}^{[i]}) (\lambda / g_{[i]})^2}{(J_m^{[i]} - \text{tr} \mathbf{C}_e^{[i]} + 3) (\mu_{[i]} J_m^{[i]} + 3 p_s^{[i]} + t_{RR}^{[i]} + t_{\theta\theta}^{[i]} + t_{ZZ}^{[i]})} - p^{[i]}, \quad (47)$$

where the elastic invariant entering the Gent denominator is

$$\text{tr} \mathbf{C}_e^{[i]} = \frac{g_{[i]}^{-2} (3 + J_m^{[i]}) \left[(t_{RR}^{[i]} + p_s^{[i]}) (R g_{[i]}^3 / (r_{[i]} \lambda))^2 + (t_{\theta\theta}^{[i]} + p_s^{[i]}) (r_{[i]} / R)^2 + (t_{ZZ}^{[i]} + p_s^{[i]}) \lambda^2 \right]}{\mu_{[i]} J_m^{[i]} + 3 p_s^{[i]} + t_{RR}^{[i]} + t_{\theta\theta}^{[i]} + t_{ZZ}^{[i]}}. \quad (48)$$

Here, μ_{HG} , μ_{PT} , and μ_{PM} denote the shear moduli of the HG, PT, and PM layers, respectively.

Integrating Eq. (44) from the inner boundary through the three layers gives the radial gauge Cauchy stresses

$$\hat{T}_{rr}^{HG}(R) = \frac{\gamma}{r_a} - \int_{R_a}^R \frac{g_{HG}^3}{\lambda} \frac{R}{r_{HG}^2(R)} \Phi_{HG}(R) \, dR, \quad (49)$$

$$\hat{T}_{rr}^{PT}(R) = \hat{T}_{rr}^{HG}(r_b) - \int_{R_b}^R \frac{g_{PT}^3}{\lambda} \frac{R}{r_{PT}^2(R)} \Phi_{PT}(R) \, dR, \quad (50)$$

$$\hat{T}_{rr}^{PM}(R) = \hat{T}_{rr}^{PT}(r_c) - \int_{R_c}^R \frac{g_{PM}^3}{\lambda} \frac{R}{r_{PM}^2(R)} \Phi_{PM}(R) \, dR. \quad (51)$$

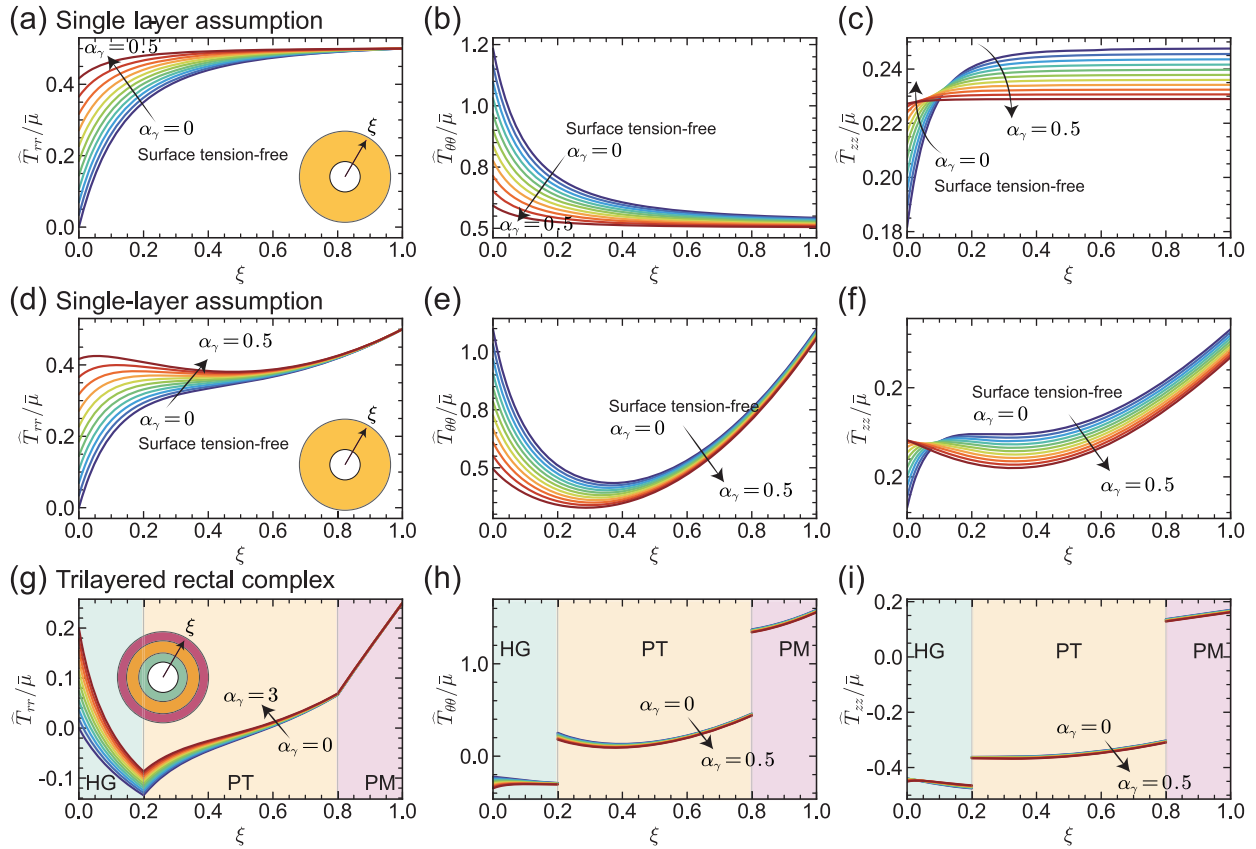


Fig. 3. Surface tension redistributes gauge Cauchy stress in single-layer and trilayer cylindrical models. Stresses are normalised by the average shear modulus $\bar{\mu}$ and plotted as radial profiles of $\hat{T}_{rr}/\bar{\mu}$, $\hat{T}_{\theta\theta}/\bar{\mu}$, and $\hat{T}_{zz}/\bar{\mu}$. The displayed gauge stress is $\hat{\mathbf{T}} = \mathbf{T}^{\text{phys}} + Q_1 \mathbf{I}$, and the physical Cauchy stress is recovered as $\mathbf{T}^{\text{phys}} = \hat{\mathbf{T}} - Q_1 \mathbf{I}$. (a)–(c) Single-layer model without initial residual stress under varying surface-tension levels. (d)–(f) Single-layer model with prescribed initial residual stress. (g)–(i) Trilayer rectal complex with layer-specific material parameters and growth functions. The horizontal coordinate is the normalised reference radius $\xi = (R - R_a)/(R_d - R_a)$; the background bands identify the HG, PT, and PM layers. The HG–PT–PM thickness ratio is 1:3:1.

where the common stress-difference integrand is collected in the auxiliary function

$$\Phi_{[i]}(R) = \frac{\mu_{[i]} J_m^{[i]} \left(3 + J_m^{[i]} \right) \left[\left(p_s^{[i]} + t_{RR}^{[i]} \right) \left(R g_{[i]}^2 / (r_{[i]} \lambda) \right)^2 - \left(p_s^{[i]} + t_{\theta\theta}^{[i]} \right) \left(r_{[i]} / (R g_{[i]}) \right)^2 \right]}{\left(J_m^{[i]} - \text{tr } \mathbf{C}_e^{[i]} + 3 \right) \left(\mu_{[i]} J_m^{[i]} + 3 p_s^{[i]} + t_{RR}^{[i]} + t_{\theta\theta}^{[i]} + t_{ZZ}^{[i]} \right)}. \quad (52)$$

The outer boundary condition $\hat{T}_{rr}^{PM} = Q = Q_1 - Q_2$ at $r = r_d$ then gives

$$Q = \hat{T}_{rr}^{PT}(r_c) - \int_{R_c}^{R_d} \frac{g_{PM}^3}{\lambda} \frac{R}{r_{PM}^2(R)} \Phi_{PM}(R) dR, \quad (53)$$

which determines the inner radius r_a through an explicit Newton iteration. Once r_a is known, the circumferential $\hat{T}_{\theta\theta}^{[i]}$ and axial $\hat{T}_{zz}^{[i]}$ gauge stress components in each layer are evaluated from Eqs. (46) and (47). If the rectal complex is also subjected to an external axial load F , global axial equilibrium requires

$$F = \pi \sum_{[i]=\text{HG,PT,PM}} \int_{R_{[i]}^-}^{R_{[i]}^+} \Xi_{[i]}(R) R dR, \quad (54)$$

where the auxiliary integrand is

$$\Xi_{[i]}(R) = \lambda^{-1} g_{[i]}^3 \left[2 \hat{T}_{zz}^{[i]}(R) - \hat{T}_{rr}^{[i]}(R) - \hat{T}_{\theta\theta}^{[i]}(R) \right], \quad (55)$$

and the inner and outer radii of the layers are $(R_{HG}^-, R_{HG}^+) = (R_a, R_b)$, $(R_{PT}^-, R_{PT}^+) = (R_b, R_c)$, and $(R_{PM}^-, R_{PM}^+) = (R_c, R_d)$.

3.7. Effects of surface tension on the ground state

For the radial profiles in Figs. 3 and 4, we use the normalised reference coordinate $\xi = (R - R_a)/(R_d - R_a) \in [0, 1]$. For the 1:3:1 trilayer geometry with $R_b/R_a = 2$, $R_c/R_a = 5$, and $R_d/R_a = 6$, the HG, PT, and PM layers occupy $\xi \in [0, 0.2]$, $[0.2, 0.8]$, and $[0.8, 1]$, respectively; the background bands in the trilayer panels mark these intervals.

Fig. 3 first examines how luminal surface tension redistributes the ground-state Cauchy stresses in simplified and trilayered cylindrical descriptions of the insect rectal complex. For the single-layer cases in Fig. 3(a)–(f), we set $R_a = 1$, $R_d = 6$, $\lambda = 1$, $Q = 0.5$, $\mu = 1$, $J_m = 100$, and $g = 1.1$. The eleven curves use equally spaced values of α_γ from 0 to 0.5; $s = 0$ in (a)–(c) and $s = 0.05$ in (d)–(f). In the single-layer model without initial residual stress (Fig. 3(a)–(c)), increasing the non-dimensional surface-tension parameter α_γ from 0 to 0.5 raises the radial stress $\hat{T}_{rr}/\bar{\mu}$ throughout the wall, with the largest change near the lumen. Over the same range, the hoop stress $\hat{T}_{\theta\theta}/\bar{\mu}$ decreases, indicating that capillary loading partially relieves circumferential tension. The axial stress $\hat{T}_{zz}/\bar{\mu}$ responds in a nonmonotonic manner: increasing α_γ elevates the axial stress for $\xi \lesssim 0.1$, but reduces it for $\xi \gtrsim 0.1$. This inversion reflects the way in which capillary traction is transmitted into the axial direction through elastic coupling among the radial, circumferential, and axial deformation modes.

Introducing a small prescribed initial residual stress, $s = 0.05$, changes the stress profiles from smooth monotonic curves to non-convex distributions (Fig. 3(d)–(f)). The radial stress develops a minimum at intermediate radii, and increasing α_γ amplifies the separation among the curves while leaving the radial position of this minimum nearly unchanged. The hoop and axial stresses form U-shaped profiles whose curvature and amplitude are modified by surface tension. Thus, in the single-layer setting, capillarity primarily modulates stress magnitude and profile contrast, whereas the radial locations of the extrema remain controlled by the underlying geometry and prescribed pre-stress.

The full trilayer model preserves this capillary modulation but adds the layer-resolved stress heterogeneity that is absent from the single-layer approximation (Fig. 3(g)–(i)). These panels use $(R_a, R_b, R_c, R_d) = (1, 2, 5, 6)$, $\lambda = 1$, $s = 0.05$, and $Q = 0.5$. The layer-specific values are $(\mu_{HG}, \mu_{PT}, \mu_{PM}) = (1, 2, 3)$, $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (100, 200, 300)$, and $(g_{HG}, g_{PT}, g_{PM}) = (1.3, 1.2, 1.1)$, with the same eleven α_γ values. With distinct material and growth parameters in the hindgut (HG), perirectal tubule (PT), and perinephric membrane (PM), compression concentrates near the HG–PT interface and extends into the inner PT layer, whereas the stress recovers and becomes tensile toward the outer wall. Varying α_γ shifts the absolute stress levels but does not move the radius of maximum compression. Similar robustness appears in the circumferential and axial stress components. These trends indicate that luminal surface tension tunes the intensity of the ground-state stress field, while the multilayer morphoelastic architecture fixes the main spatial organisation of compression and tension.

Fig. 4 then examines how this ground state is regulated by strain stiffening, initial residual stress, and surface tension in the trilayered rectal complex. The profile calculations in Fig. 4(a)–(f) use $(R_a, R_b, R_c, R_d) = (1, 2, 5, 6)$, $(\mu_{HG}, \mu_{PT}, \mu_{PM}) = (1, 2, 3)$, $\lambda = 1$, and $Q = 0.5$. With $s = -0.1$, $\alpha_\gamma = 0.1$, $g_{HG} = g_{PT} = g_{PM} = 1.3$, and $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (J_m, 2J_m, 3J_m)$ evaluated at eleven equally spaced J_m values, increasing the strain-stiffening parameter from $J_m = 2$ to $J_m = 50$ slightly reduces the radial-stress peak in the PT layer, with the corresponding curves converging near the PT–PM interface (Fig. 4(a)). The circumferential stress shows a stronger layer dependence: a larger J_m raises hoop stress close to the inner HG boundary, but lowers it over much of the remaining HG and PT regions (Fig. 4(b)). The axial stress increases across the HG, PT, and PM layers, but retains sharp changes across layer interfaces (Fig. 4(c)). These results suggest that strain stiffening adjusts local stress magnitude and interfacial contrast without eliminating the multilayer stress topology.

The prescribed initial residual stress provides a second route for reshaping the base state. For Fig. 4(d)–(f), $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (100, 200, 300)$, $\alpha_\gamma = 0.1$, and $g_{HG} = g_{PT} = g_{PM} = 1.3$ are fixed. Increasing s from -0.1 to 0.1 in eleven equally spaced values lowers the radial stress across all three layers (Fig. 4(d)). The circumferential stress decreases through the HG and inner PT regions, then increases after a crossover near $\xi \approx 0.6$ (Fig. 4(e)). The axial stress shows a pronounced nonmonotonic response and changes sharply near the PT–PM interface (Fig. 4(f)). The initial residual stress therefore tunes both the amplitude and the radial gradient of the ground-state stress components.

Finally, the inner-boundary relation between $\hat{T}_{rr}(r_a)$ and r_a/R_a links the ground state to limit-point instability (Fig. 4(g)–(i)). These continuation calculations retain the geometry and shear moduli used in Figs. 4(a)–(f), but use $(g_{HG}, g_{PT}, g_{PM}) = (1.4, 1.15, 1.2)$ and $Q = 0.1$; λ is solved at each r_a/R_a from $\hat{T}_{rr}^{PM}(r_d) = 0.1$. The local maximum of $\hat{T}_{rr}(r_a)$ marks the onset of the limit point. Varying α_γ over eleven equally spaced values from 0 to 2, with $s = 0.4$ and $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (5, 5, 5)$, changes the height and position of this local maximum while preserving the limit-point character of the response (Fig. 4(g)). For Fig. 4(h), $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (J_m, J_m, J_m)$ spans eleven equally spaced values from 5 to 15, while $s = 0.4$ and $\alpha_\gamma = 0.02$ are fixed. A lower strain-stiffening level, $J_m = 5$, produces a clear instability peak, whereas a higher level, $J_m = 15$, flattens and removes this peak, consistent with the stabilising effect of nonlinear stiffening (Fig. 4(h)). Increasing the initial residual stress amplitude from $s = 0$ to $s = 0.4$ at $\alpha_\gamma = 0.02$ and $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (5, 5, 5)$ transforms the response from a monotonic branch without a limit point to a branch with a pronounced instability peak (Fig. 4(i)). These trends indicate that morphological bifurcation in the trilayered rectal complex is governed by the coupled effects of capillary loading, nonlinear material stiffening, and initial residual stress.

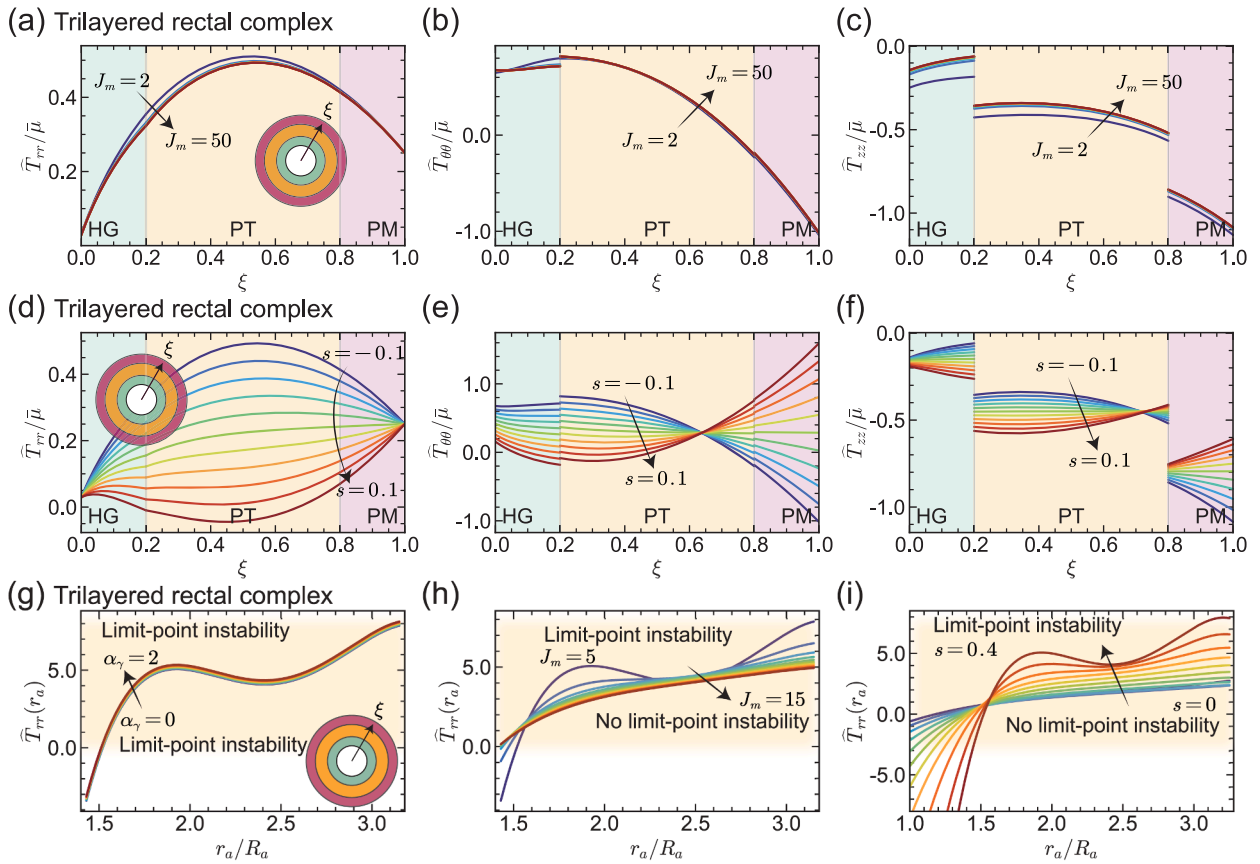


Fig. 4. Strain stiffening, initial residual stress, and surface tension shape gauge base-state stresses and limit-point instability in the trilayered insect rectal complex. (a)–(c) Radial profiles of $\hat{T}_{rr}/\bar{\mu}$, $\hat{T}_{\theta\theta}/\bar{\mu}$, and $\hat{T}_{zz}/\bar{\mu}$ as J_m increases from 2 to 50, showing how strain stiffening modifies stresses across the HG (cyan), PT (orange), and PM (red) layers as the non-dimensional radius ξ varies. Here $\xi = (R - R_a)/(R_d - R_a)$, the background bands identify the layers, and $\hat{\mathbf{T}} = \mathbf{T}^{\text{phys}} + Q_1 \mathbf{I}$. (d)–(f) Stress profiles under prescribed initial residual stress $s \in [-0.1, 0.1]$ with fixed, layer-specific J_m values. (g)–(i) Inner-boundary radial gauge stress $\hat{T}_{rr}(r_a)$ as a function of r_a/R_a , identifying limit-point instability thresholds controlled by the surface-tension parameter α_r , strain-stiffening parameter J_m , and initial residual stress amplitude s . The HG:PT:PM thickness ratio is 1:3:1.

4. Generation of the water-conserving morphology in the insect rectal complex

4.1. Kinematics of superimposed incremental deformation

We assume that the growth tensor $\mathbf{F}_g$ and the deformation tensor $\mathbf{F}_s$ associated with initial residual stress are prescribed fields that remain fixed during the incremental process. Neglecting body forces, taking the strain-energy density as $\Psi = \Psi(\mathbf{F}_e)$, and imposing the single kinematic constraint $C(\mathbf{F}_e) = 0$, we linearize the motion about the base-state mapping $\hat{\chi}(\mathbf{X})$.

Under a small perturbation $\varepsilon \ll 1$, the perturbed motion is written as

$$\chi(\mathbf{X}) = \hat{\chi}(\mathbf{X}) + \varepsilon \dot{\chi}(\mathbf{x}). \quad (56)$$

The corresponding total deformation gradient is

$$\mathbf{F} = \nabla_{\mathbf{X}} \chi = (\mathbf{I} + \varepsilon \dot{\mathbf{F}}) \hat{\mathbf{F}}, \quad (57)$$

where $\dot{\mathbf{F}} = \nabla_{\mathbf{x}} \dot{\chi}$.

In this formulation, growth and the deformation associated with the initial residual stress act as control processes: they reshape the geometry and prescribe the residual stress, but they do not respond to the incremental perturbation. The purely elastic deformation gradient is therefore expressed as

$$\mathbf{F}_e = (\mathbf{I} + \varepsilon \dot{\mathbf{F}}_e) \hat{\mathbf{F}}_e. \quad (58)$$

Expanding the kinematic constraint $C(\mathbf{F}_e) = 0$ to first order gives

$$C(\mathbf{F}_e) = C(\hat{\mathbf{F}}_e) + \varepsilon \text{tr} \left[\det(\hat{\mathbf{F}}_e) \hat{\mathbf{F}}_e^{-1} \dot{\mathbf{F}}_e \hat{\mathbf{F}}_e \right] + \mathcal{O}(\varepsilon^2) = 0, \quad (59)$$

Using the base-state constraint $C(\hat{\mathbf{F}}_e) = 0$, the $O(\varepsilon)$ term should vanish, which gives

$$\text{tr}(\hat{\mathbf{F}}_e) = 0. \quad (60)$$

4.2. Derivation of the linearized constitutive equations

Because the bifurcation analysis is performed in the current configuration, we first expand the nominal stress tensor $\mathbf{P}^\top$ to first order in the perturbation amplitude ε and then push the incremental stress forward to the current configuration:

$$\mathbf{P}^\top = \hat{\mathbf{P}}^\top + \varepsilon \dot{\mathbf{P}}^\top + \mathcal{O}(\varepsilon^2). \quad (61)$$

The base-state nominal stress is

$$\hat{\mathbf{P}}^\top = J \mathbf{F}_s^{-1} \mathbf{F}_g^{-1} \frac{\partial \Psi}{\partial \hat{\mathbf{F}}_e} - \hat{p} J \hat{\mathbf{F}}_e^{-1}, \quad (62)$$

and the corresponding incremental contribution is

$$\dot{\mathbf{P}}^\top = J \mathbf{F}_s^{-1} \mathbf{F}_g^{-1} \left[\frac{\partial^2 \Psi}{\partial \hat{\mathbf{F}}_e \partial \hat{\mathbf{F}}_e} : \left(\Gamma \hat{\mathbf{F}}_e \right) + \hat{p} \hat{\mathbf{F}}_e^{-1} \left(\Gamma \hat{\mathbf{F}}_e \right) \hat{\mathbf{F}}_e^{-1} - \delta p \mathbf{F}_e^{-1} \right], \quad (63)$$

where $\delta p = \dot{p}$, $\Gamma = \dot{\mathbf{F}}_e = \nabla_{\mathbf{x}} \delta \mathbf{u}$, and $\delta \mathbf{u}$ denotes the incremental displacement.

We then define the pushed-forward stress increment by $\delta \mathbb{P} = \dot{\mathbf{P}}_0^\top$, with $\dot{\mathbf{P}}_0^\top = J^{-1} \hat{\mathbf{F}} \dot{\mathbf{P}}^\top$. This gives

$$\delta \mathbb{P} = \hat{\mathbf{F}}_e \frac{\partial^2 \Psi}{\partial \hat{\mathbf{F}}_e \partial \hat{\mathbf{F}}_e} : \left(\Gamma \hat{\mathbf{F}}_e \right) + \hat{p} \Gamma - \delta p \mathbf{I} = \mathcal{L} : \Gamma + p \Gamma - \delta p \mathbf{I}, \quad (64)$$

where $p = \hat{p}$ and $\mathcal{L}$ denotes the fourth-order instantaneous elastic modulus.

For the Gent-type material used here, $\mathcal{L}$ incorporates the strain-stiffening response through the components (Wang et al., 2023a)

$$\mathcal{L}_{jkl} = \frac{\mu J_m}{J_m - [\text{tr}(\mathbf{F}_e^\top \mathbf{F}_e) - 3]} \delta_{il} (\mathbf{B}_e)_{jk} + \frac{2\mu J_m (\mathbf{B}_e)_{ij} (\mathbf{B}_e)_{kl}}{[J_m - (\text{tr}(\mathbf{F}_e^\top \mathbf{F}_e) - 3)]^2}. \quad (65)$$

where $\mathbf{B}_e = \mathbf{F}_e \mathbf{F}_e^\top$ is the elastic left Cauchy–Green tensor and δ_{il} is the Kronecker delta.

4.3. Formation of the boundary-value problem

With body forces neglected and incompressibility enforced, the governing incremental equations read

$$\nabla_{\mathbf{x}} \cdot (\delta \mathbb{P}) = \mathbf{0} \quad \text{in } \Omega_{HG}, \Omega_{PT}, \Omega_{PM}. \quad (66)$$

$$\text{tr}(\Gamma) = 0 \quad \text{in } \Omega_{HG}, \Omega_{PT}, \Omega_{PM}. \quad (67)$$

On the outer boundary $r = r_d$, the gauge formulation uses the signed pressure difference $Q = Q_1 - Q_2$. The corresponding incremental traction condition is

$$(\delta \mathbb{P})^\top \mathbf{n} = Q \Gamma^\top \mathbf{n}. \quad (68)$$

Across the internal interfaces $r = r_b$ and $r = r_c$, continuity of displacement and traction requires

$$\langle \delta \mathbf{u} \rangle = 0 \quad \text{and} \quad \langle (\delta \mathbb{P})^\top \rangle \mathbf{n} = 0. \quad (69)$$

At the innermost wall $r = r_a$, surface tension γ imposes the incremental boundary condition (Riccobelli and Bevilacqua, 2020)

$$(\delta \mathbb{P})^\top \mathbf{n} = \gamma \delta \mathcal{K} \mathbf{n} - \gamma \mathcal{K} \Gamma^\top \mathbf{n}. \quad (70)$$

Here $\delta \mathcal{K}$ is the increment of the total curvature $\mathcal{K} = \kappa_\theta + \kappa_z$. At this inner material boundary, the outward unit normal is $\mathbf{n} = -\mathbf{e}_r$; we use $\mathcal{K} = -\text{div}_r \mathbf{n}$, which gives $\mathcal{K}_0 = r_a^{-1}$ in the base state.

Eqs. (66)–(70) define the full incremental boundary-value problem. The existence of nontrivial solutions indicates a bifurcation instability. We next recast this system into the Stroh formulation, which reduces the coupled PDEs to a more tractable set of ODEs (Stroh, 1962).

4.4. Incremental field for the insect rectal complex

Let $[i] \in \{HG, PT, PM\}$ denote the layer index. In cylindrical coordinates, the incremental equilibrium equations in Eq. (66) become

$$\frac{\partial \delta \mathbb{P}_{rr}^{[i]}}{\partial r} + \frac{1}{r} \frac{\partial \delta \mathbb{P}_{\theta r}^{[i]}}{\partial \theta} + \frac{\delta \mathbb{P}_{rr}^{[i]} - \delta \mathbb{P}_{\theta \theta}^{[i]}}{r} + \frac{\partial \delta \mathbb{P}_{zr}^{[i]}}{\partial z} = 0, \quad (71)$$

$$\frac{\partial \delta \mathbb{P}_{r\theta}^{[i]}}{\partial r} + \frac{1}{r} \frac{\partial \delta \mathbb{P}_{\theta\theta}^{[i]}}{\partial \theta} + \frac{\delta \mathbb{P}_{r\theta}^{[i]} + \delta \mathbb{P}_{\theta r}^{[i]}}{r} + \frac{\partial \delta \mathbb{P}_{z\theta}^{[i]}}{\partial z} = 0, \quad (72)$$

$$\frac{\partial \delta \mathbb{P}_{rz}^{[i]}}{\partial r} + \frac{1}{r} \frac{\partial \delta \mathbb{P}_{\theta z}^{[i]}}{\partial \theta} + \frac{\delta \mathbb{P}_{rz}^{[i]}}{r} + \frac{\partial \delta \mathbb{P}_{zz}^{[i]}}{\partial z} = 0. \quad (73)$$

In layer $[i]$, the incremental displacement is denoted by $\delta \mathbf{u}_{[i]} = (u_{[i]}, v_{[i]}, w_{[i]})^\top$. The corresponding cylindrical-coordinate gradient reads

$$\Gamma_{[i]} = \begin{bmatrix} \frac{\partial u_{[i]}}{\partial r} & \frac{1}{r} \left(\frac{\partial u_{[i]}}{\partial \theta} - v_{[i]} \right) & \frac{\partial u_{[i]}}{\partial z} \\ \frac{\partial v_{[i]}}{\partial r} & \frac{1}{r} \left(\frac{\partial v_{[i]}}{\partial \theta} + u_{[i]} \right) & \frac{\partial v_{[i]}}{\partial z} \\ \frac{\partial w_{[i]}}{\partial r} & \frac{1}{r} \frac{\partial w_{[i]}}{\partial \theta} & \frac{\partial w_{[i]}}{\partial z} \end{bmatrix}. \quad (74)$$

The linearized incompressibility condition in Eq. (67) requires

$$\frac{\partial u_{[i]}}{\partial r} + \frac{1}{r} \left(\frac{\partial v_{[i]}}{\partial \theta} + u_{[i]} \right) + \frac{\partial w_{[i]}}{\partial z} = 0. \quad (75)$$

To transform the PDE system into ODEs, we use separable modal representations for the incremental displacement $\delta \mathbf{u}$, incremental stress $\delta \mathbb{P}$, and incremental pressure δp :

$$(u_{[i]}, \delta P_{rr}^{[i]}, \delta p_{[i]}) = (U_{[i]}(r), P_{rr}^{[i]}(r), \phi_{[i]}(r)) \cos(m\theta) \cos(kz), \quad (76)$$

$$(v_{[i]}, \delta P_{r\theta}^{[i]}) = (V_{[i]}(r), P_{r\theta}^{[i]}(r)) \sin(m\theta) \cos(kz), \quad (77)$$

$$(w_{[i]}, \delta P_{rz}^{[i]}) = (W_{[i]}(r), P_{rz}^{[i]}(r)) \cos(m\theta) \sin(kz). \quad (78)$$

where $k = n\pi/(\lambda L)$ and $m \in \mathbb{Z}$.

Substituting Eqs. (76)–(78) into Eqs. (71)–(73) and (75) and using the Stroh formalism (Stroh, 1962) give the layer-wise incremental boundary-value problem in the unified form

$$\frac{d\boldsymbol{\eta}_{[i]}}{dr} = \frac{1}{r} \mathbb{G}_{[i]} \boldsymbol{\eta}_{[i]}, \quad (79)$$

where the displacement-traction vector is

$$\boldsymbol{\eta}_{[i]} = [U_{[i]}, V_{[i]}, W_{[i]}, r P_{rr}^{[i]}, r P_{r\theta}^{[i]}, r P_{rz}^{[i]}]^\top, \quad (80)$$

and the Stroh matrix $\mathbb{G}_{[i]}$ is partitioned as

$$\mathbb{G}_{[i]} = \begin{bmatrix} \mathbf{G}_1^{[i]} & \mathbf{G}_2^{[i]} \\ \mathbf{G}_3^{[i]} & \mathbf{G}_4^{[i]} \end{bmatrix}. \quad (81)$$

The explicit forms of the submatrices $\mathbf{G}_k^{[i]}$ ($k = 1, \dots, 4$) for each layer are listed in Appendix A.

4.5. Solution procedure for the trilayered morphology

The trilayered architecture of the rectal complex and luminal surface tension lead to a coupled stability problem. To solve the governing equations in a numerically stable form, we use the impedance matrix method. For each layer $[i] \in \{\text{HG}, \text{PT}, \text{PM}\}$, we introduce the inner conditional impedance matrix $Z_{[i]}^L(r, r_a)$ as

$$r \boldsymbol{\Pi}_{[i]} = Z_{[i]}^L(r, r_a) \mathbf{D}_{[i]}, \quad (82)$$

where $\mathbf{D}_{[i]} = [U_{[i]}, V_{[i]}, W_{[i]}]^\top$ is the displacement vector and $\boldsymbol{\Pi}_{[i]} = [P_{rr}^{[i]}, P_{r\theta}^{[i]}, P_{rz}^{[i]}]^\top$ is the traction vector.

Substituting Eqs. (82) into (79) yields

$$\frac{dZ_{[i]}^L}{dr} \mathbf{D}_{[i]} = \frac{1}{r} \left(\mathbf{G}_3^{[i]} \mathbf{D}_{[i]} + \mathbf{G}_4^{[i]} Z_{[i]}^L \mathbf{D}_{[i]} \right) - \frac{d\mathbf{D}_{[i]}}{dr} Z_{[i]}^L, \quad (83)$$

$$\frac{d\mathbf{D}_{[i]}}{dr} = \frac{1}{r} \left(\mathbf{G}_1^{[i]} \mathbf{D}_{[i]} + \mathbf{G}_2^{[i]} Z_{[i]}^L \mathbf{D}_{[i]} \right). \quad (84)$$

Eliminating $d\mathbf{D}_{[i]}/dr$ between Eqs. (83) and (84) gives the Riccati-type equation governing the inner conditional impedance matrix:

$$\frac{dZ_{[i]}^L}{dr} = \frac{1}{r} \left(\mathbf{G}_3^{[i]} + \mathbf{G}_4^{[i]} Z_{[i]}^L - Z_{[i]}^L \mathbf{G}_1^{[i]} - Z_{[i]}^L \mathbf{G}_2^{[i]} Z_{[i]}^L \right). \quad (85)$$

To determine the impedance boundary value $Z_{HG}^L(r_a, r_a)$, we use the incremental surface-tension boundary condition in Eq. (70), written as

$$(\delta \mathbb{P}^{HG})^\top \mathbf{n} = \left(\gamma \delta \mathcal{K} - \frac{\gamma}{r_a} \Gamma_{HG}^\top \right) \mathbf{n}, \quad (86)$$

where $\mathbf{n}$ is the outward unit normal to the HG surface and γ is the constant surface tension.

The perturbed inner HG surface is parameterised by

$$\mathbf{r}(\theta, z) = \left[(r_a + u_{HG}) \cos(\theta + v_{HG}/r_a), (r_a + u_{HG}) \sin(\theta + v_{HG}/r_a), z + w_{HG} \right] \Big|_{r=r_a}. \quad (87)$$

Here x and y denote the first two components of $\mathbf{r}$, while u_{HG} , v_{HG} , and w_{HG} are respectively the radial, circumferential, and axial incremental displacements evaluated at $r = r_a$.

At fixed z , the signed circumferential curvature follows from the plane-curve relation, while the total curvature is the sum of the circumferential and axial curvatures, $\mathcal{K} = \kappa_\theta + \kappa_z$:

$$\kappa_\theta = \left(\frac{dx}{d\theta} \frac{d^2y}{d\theta^2} - \frac{dy}{d\theta} \frac{d^2x}{d\theta^2} \right) \left[\left(\frac{dx}{d\theta} \right)^2 + \left(\frac{dy}{d\theta} \right)^2 \right]^{-3/2}. \quad (88)$$

Linearising the total curvature about the cylindrical base state gives

$$\delta \mathcal{K}(r_a, \theta, z) = -\frac{u_{HG} + \frac{\partial^2 u_{HG}}{\partial \theta^2}}{r_a^2} - \frac{\partial^2 u_{HG}}{\partial z^2}. \quad (89)$$

Combining Eqs. (75)–(78), (86), and (89) gives the traction-displacement relations at the inner boundary:

$$r_a P_{rr}^{[i]} = \frac{\gamma}{r_a} \left[(m^2 + (kr_a)^2) U_{HG} + m V_{HG} + kr_a W_{HG} \right], \quad (90)$$

$$r_a P_{r\theta}^{[i]} = \frac{\gamma}{r_a} (m U_{HG} + V_{HG}), \quad (91)$$

$$r_a P_{rz}^{[i]} = \gamma k U_{HG}. \quad (92)$$

These relations define the inner conditional impedance matrix associated with the incremental surface-tension boundary condition:

$$Z_{HG}^L(r_a, r_a) = \frac{\gamma}{r_a} \begin{bmatrix} m^2 + (kr_a)^2 & m & kr_a \\ m & 1 & 0 \\ kr_a & 0 & 0 \end{bmatrix}. \quad (93)$$

Integrating the Riccati-type equation in Eq. (85) successively through the PT and PM layers, from $Z_{HG}^L(r, r_a)$ to $Z_{PT}^L(r, r_a)$ and then to $Z_{PM}^L(r, r_a)$, yields the global impedance at the outer radius $r = r_d$. A growth mode driven by surface tension exists when

$$\det \left[Z_{PM}^L(r_d, r_a) + Q \begin{bmatrix} 1 & m & kr_d \\ m & 1 & 0 \\ kr_d & 0 & 0 \end{bmatrix} \right] = 0, \quad (94)$$

where $Q = Q_1 - Q_2$ enters through the outer incremental traction condition $(\delta \mathbb{P})^\top \mathbf{n} = Q \Gamma^\top \mathbf{n}$. Eq. (94) is therefore the solvability criterion that defines the critical growth parameters of the rectal complex in the presence of surface tension.

4.6. Through-thickness incremental displacement

Once the global solution satisfies the convergence criterion in Eq. (94), the incremental deformation pattern of the rectal complex is fully determined. According to Eq. (82), the inner conditional impedance matrix of the PM layer at $r = r_d$ satisfies

$$r_d \begin{bmatrix} P_{rr}^{PM}(r_d) \\ P_{r\theta}^{PM}(r_d) \\ P_{rz}^{PM}(r_d) \end{bmatrix} = -Q \begin{bmatrix} 1 & m & kr_d \\ m & 1 & 0 \\ kr_d & 0 & 0 \end{bmatrix} \begin{bmatrix} U_{PM}(r_d) \\ V_{PM}(r_d) \\ W_{PM}(r_d) \end{bmatrix} = Z_{PM}^L(r_d, r_a) \begin{bmatrix} U_{PM}(r_d) \\ V_{PM}(r_d) \\ W_{PM}(r_d) \end{bmatrix}, \quad (95)$$

where $Z_{PM}^L(r_d, r_a) = (Z_{PM}^{Lij}(r_d, r_a))_{3 \times 3}$.

Defining the incremental displacement ratio $K_{UV} = U_{PM}(r_d)/V_{PM}(r_d)$, we obtain

$$K_{UV}(r_d, r_a) = \frac{-Z_{PM}^{L23} Z_{PM}^{L32} + (Q + Z_{PM}^{L22}) Z_{PM}^{L33}}{k Q r_d Z_{PM}^{L23} + Z_{PM}^{L23} Z_{PM}^{L31} - (m Q + Z_{PM}^{L21}) Z_{PM}^{L33}}, \quad (96)$$

with all Z_{PM}^{Lij} evaluated at (r_d, r_a) for brevity.

To derive the through-thickness incremental displacement field for each layer $i \in \{\text{HG}, \text{PT}, \text{PM}\}$, we introduce an outer conditional impedance matrix $Z_{[i]}^R(r, r_d)$. This matrix suppresses the numerical singularities that can arise in impedance-based formulations (Biryukov, 1985) and satisfies the coupled first-order system

$$\frac{dZ_{[i]}^R(r, r_d)}{dr} = \frac{1}{r} \left[\mathbf{G}_3^{[i]} + \mathbf{G}_4^{[i]} Z_{[i]}^R - Z_{[i]}^R \mathbf{G}_1^{[i]} - Z_{[i]}^R \mathbf{G}_2^{[i]} Z_{[i]}^R \right]. \quad (97)$$

$$\frac{d\mathbf{D}_{[i]}}{dr} = \frac{1}{r} \left[\mathbf{G}_1^{[i]} \mathbf{D}_{[i]} + \mathbf{G}_2^{[i]} Z_{[i]}^R \mathbf{D}_{[i]} \right], \quad (98)$$

where all quantities are evaluated at the current radius r .

Once the displacement ratio K_{UV} has been evaluated from Eq. (96), the outer-impedance scheme is initialised at the matching radius $r = r_d$. For compactness, we introduce the auxiliary scalars

$$\Delta(r_d) = k Q r_d U_{PM}(r_d) + U_{PM}(r_d) Z_{PM}^{L31}(r_d, r_a) + \frac{U_{PM}(r_d)}{K_{UV}} Z_{PM}^{L32}(r_d, r_a), \quad \Lambda(r_d) = Z_{PM}^{L33}(r_d, r_a). \quad (99)$$

With these abbreviations, the boundary data required by the outer-impedance formulation are

$$Z_{PM}^R(r_d, r_d) = -Q \begin{bmatrix} 1 & m & k r_d \\ m & 1 & 0 \\ k r_d & 0 & 0 \end{bmatrix}, \quad (100)$$

$$\mathbf{D}_{PM}(r_d) = \begin{bmatrix} U_{PM}(r_d), & \frac{U_{PM}(r_d)}{K_{UV}}, & -\frac{\Delta(r_d)}{\Lambda(r_d)} \end{bmatrix}^T. \quad (101)$$

Integrating Eqs. (97)–(98) with the boundary data in Eqs. (100)–(101) and then propagating the solution from the outermost layer to the innermost layer give the complete through-thickness incremental displacement field. The impedance and displacement fields are transferred successively from Z_{PM}^R to Z_{PT}^R and Z_{HG}^R , and from $\mathbf{D}_{PM}$ to $\mathbf{D}_{PT}$ and $\mathbf{D}_{HG}$. The successive transfer in the surface-impedance technique suppresses round-off error accumulation and avoids numerical instability, providing a stable computational framework for multilayer analyses.

5. Results for morphogenesis in the trilayered rectal complex

We next use the nonlinear morphoelastic model and the incremental stability framework to analyse how the insect rectal complex generates its water-conserving morphology. The results focus on three linked questions. First, how does the developmental growth hierarchy of the HG, PT and PM layers establish a mechanically unstable trilayer? Second, how does luminal surface tension modify the critical growth ratio and the selected mode (m, n) ? Third, how do initial residual stress, strain stiffening, wall thickness, interlayer stiffness contrast, external loading and growth kinetics reshape this instability landscape? Throughout this section, the surface-impedance solution is used to enumerate admissible circumferential and axial modes, and the smallest growth threshold is taken as the onset of morphogenesis.

5.1. Developmental description of the rectal trilayer

Fig. 5 provides the biological and geometric basis for the growth model. Motivated by developmental observations of the cryptonephridial–rectal complex (Beaven and Denholm, 2025), the schematic reduces the assembly process to four mechanically relevant stages. The hindgut (HG) first forms the central epithelial tube (Fig. 5(a)). Posterior mesoderm is then recruited around the HG, giving rise to the nascent perirectal tubule (PT) layer (Fig. 5(b)). Continued PT deformation produces folded papilla-like structures around the HG core (Fig. 5(c)). Finally, the perinephric membrane (PM) encloses the HG–PT core and completes the trilayered HG–PT–PM architecture (Fig. 5(d)). This sequence preserves the developmental meaning of the earlier description, but the present analysis uses it primarily as a mechanical template for graded growth.

Across this process, each layer is assumed to grow isotropically but with a distinct volume-growth factor. The prescribed hierarchy is

$$g_{\text{HG}} > g_{\text{PT}} > g_{\text{PM}}. \quad (102)$$

This differential growth generates residual stress, which is further modulated by the luminal surface tension γ (Chown and Nicolson, 2011; Beaven et al., 2023). In the model, elastocapillary traction acts on the compliant HG wall while the surrounding PT and PM layers expand more slowly. The resulting mechanical mismatch promotes a wrinkling and coiling response in which the PT layer folds and the PM layer forms a compact outer constraint. In this way, the prestressed HG–PT–PM complex becomes a radial counter-current exchanger that supports efficient water and ion recovery in arid environments (Noble-Nesbitt, 1970; Zhang et al., 2022; Wang et al., 2023b).

To formulate this process, we recall from Eq. (12) that the mass-accretion rate determines the evolution of the growth tensor $\mathbf{F}_g^{[i]}$ in each layer $[i] \in \{\text{HG}, \text{PT}, \text{PM}\}$. Growth can be described either as a mechanically coupled process or as a prescribed field. In mechanically coupled formulations, growth is activated by local stress (Himpel et al., 2005) or strain (Tepole et al., 2011), often with

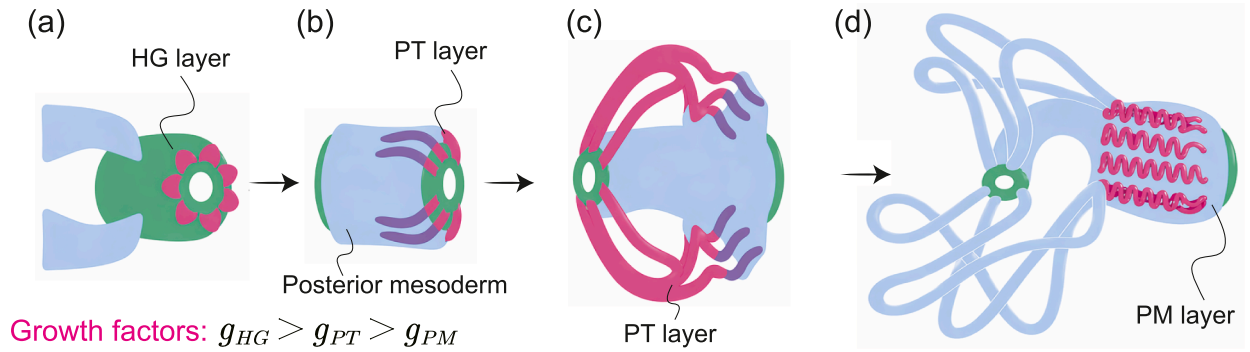


Fig. 5. Sequential assembly of the trilayered insect rectal complex under graded growth. (a) The hindgut (HG) forms the central epithelial tube. (b) Posterior mesoderm is recruited around the HG and establishes the nascent perirectal tubule (PT) layer. (c) Continued deformation of the PT layer generates folded papilla-like structures around the HG core. (d) The perinephric membrane (PM) encloses the HG-PT core, completing the folded trilayered architecture. The prescribed growth hierarchy $g_{HG} > g_{PT} > g_{PM}$ provides the geometric and mechanical basis for the subsequent morphoelastic model.

saturation functions that limit unbounded accumulation (Lee et al., 2020). Here, we adopt a nonmechanical growth law in which the growth rate is prescribed a priori, spatially partitioned by layer, and independent of the instantaneous stress state (Tepole, 2017). This choice allows the effects of differential accretion and luminal surface tension on the instability threshold, selected wavelength and resulting morphology to be evaluated independently of stress-regulated growth. The retained growth law is therefore

$$g_{[i]} = 1 + \dot{G}_{[i]}t. \quad (103)$$

where $\dot{G}_{[i]}$ is the growth rate assigned to layer $[i]$. Here $t \geq 0$ parametrises a quasi-static prescribed-growth path; it is not assigned a physiological time scale. The subsequent stability calculations are expressed in terms of the instantaneous growth factors, so t is eliminated from the growth-ratio relations below. Indeed, the HG-layer relation gives $t = (g_{HG} - 1)/\dot{G}_{HG}$.

To remain consistent with Eq. (102), we use the HG growth factor g_{HG} as the independent control variable. Substituting this choice into Eq. (103) gives the PT and PM growth factors:

$$g_{PT} = \frac{1}{\dot{G}_1} (g_{HG} + \dot{G}_1 - 1), \quad (104)$$

$$g_{PM} = \frac{1}{\dot{G}_2} (g_{HG} + \dot{G}_2 - 1). \quad (105)$$

Here, $\dot{G}_1 = \dot{G}_{HG}/\dot{G}_{PT}$ and $\dot{G}_2 = \dot{G}_{HG}/\dot{G}_{PM}$ denote the ratios between the HG growth rate and the growth rates of the PT and PM layers. To satisfy Eq. (102), these ratios are non-negative and ordered such that $\dot{G}_1 < \dot{G}_2$. Unless otherwise specified, the baseline values are $\dot{G}_1 = 100$ and $\dot{G}_2 = 200$.

The numerical analysis begins by calculating the critical differential-growth ratios g_{HG}/g_{PT} and g_{HG}/g_{PM} . To combine these two ratios into a single instability metric, we define the deviation of their arithmetic mean from unity:

$$\Delta\tilde{G} = \left| \frac{1}{2} \left[\frac{g_{HG}}{g_{PT}} \right]_{cr} + \frac{g_{HG}}{g_{PM}} \right|_{cr} - 1, \quad (106)$$

and use it as the control parameter in the incremental stability calculations. At each prescribed nondimensional surface-tension level

$$\alpha_\gamma = \frac{\gamma}{\mu_{HG} R_a}, \quad (107)$$

all admissible pairs of circumferential and axial wavenumbers are enumerated, the associated incremental boundary-value problems are solved, and the minimum value of $\Delta\tilde{G}$ is retained. The trivial uniform mode, the rigid-body mode, and modes for which no admissible critical threshold is obtained are excluded from this minimisation. The smallest threshold obtained over the parameter space is defined as the *minimal critical growth ratio* (MCGR),

$$\tilde{G}_{MCGR} = \min(\Delta\tilde{G}). \quad (108)$$

5.2. Synergistic growth instability and pattern formation

Fig. 6 first tests how luminal surface tension couples to prescribed initial residual stress. The calculations use $Q = -0.05$, $\dot{G}_1 = 100$, and $\dot{G}_2 = 200$. The HG, PT and PM layers have identical shear moduli, a thickness ratio of 1:3:1, and layer-wise strain-stiffening levels in the ratio 4:2:1. Fig. 6(a)–(c) compare the full CGR spectra $\Delta\tilde{G}(m, n)$ for compressive ($s = -0.01$), stress-free ($s = 0$), and tensile ($s = 0.01$) initial residual stress states. In each case, adding surface tension redistributes the spectrum rather than producing a uniform shift of all modes.

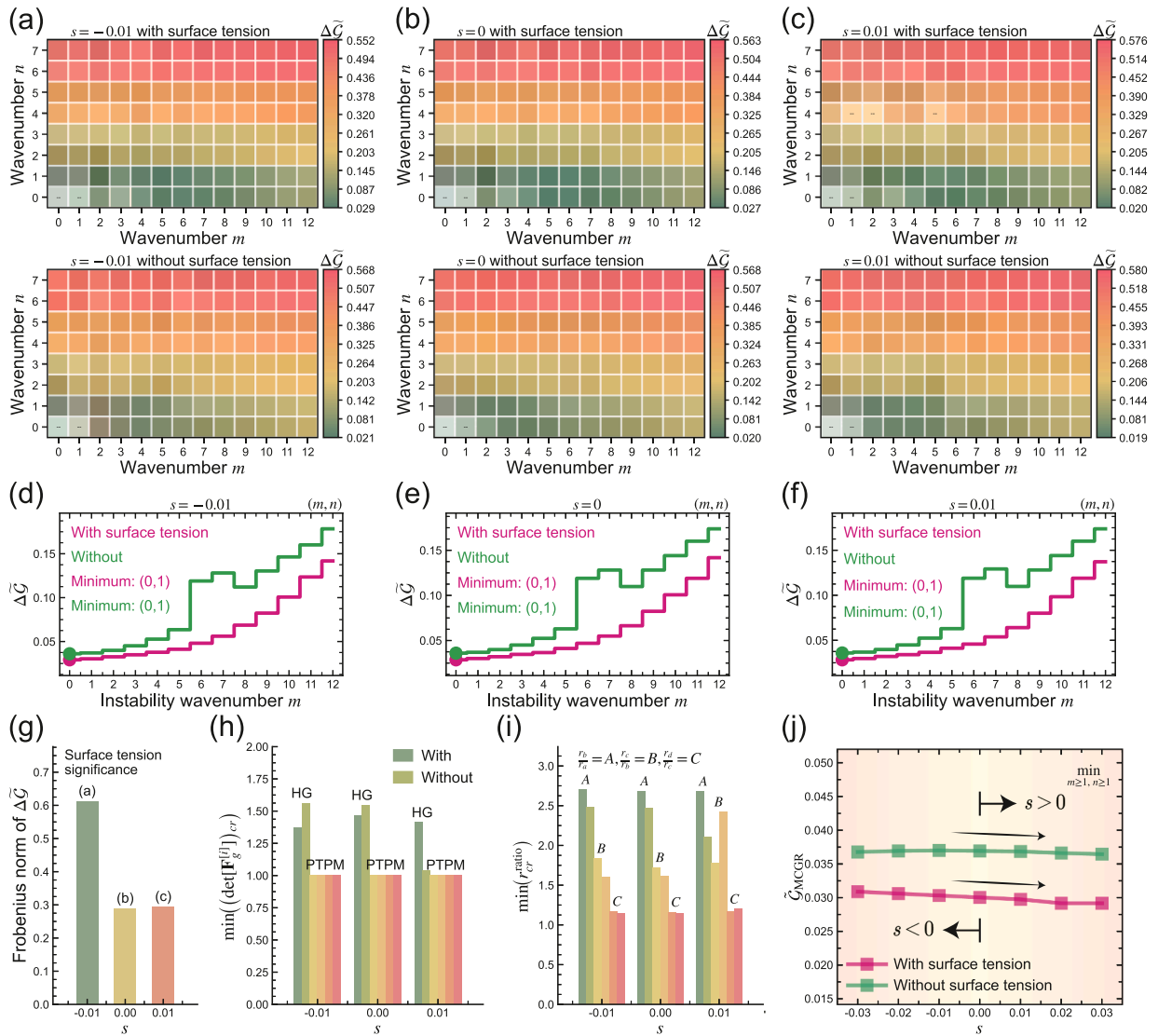


Fig. 6. Prescribed initial residual stress and luminal surface tension jointly set the growth threshold for instability. All calculations use $Q = -0.05$, $G_1 = 100$, and $G_2 = 200$. (a)–(c) Critical growth ratio spectra $\Delta\tilde{G}(m, n)$ for $s = -0.01$, $s = 0$, and $s = 0.01$, with the upper and lower rows showing the cases with and without surface tension. Grey cells in (a)–(c) denote modes excluded from the minimisation: the trivial uniform and rigid-body modes, and modes for which no admissible critical threshold was obtained within the prescribed search interval and tolerances. (d)–(f) Reduced spectra for the $n = 1$ modal family as functions of m , with markers identifying the minimum within this family. (g) Frobenius norm $\|\Delta\tilde{G}\|_F$ of the full modal spectrum as a function of s . (h), (i) Layer-resolved critical thresholds in the growth determinant and normalized radial change. (j) Dependence of $\tilde{G}_{\text{MCGR}}$ on the initial residual stress amplitude, comparing surfaces with and without luminal tension.

The reduced spectra in Fig. 6(d)–(f) focus on the $n = 1$ modal family. Within this family, the minimum remains $(m, n) = (0, 1)$ for all three initial residual stress states, both with and without surface tension. Under this parameter set, the branch including surface tension lies below the tension-free branch, so capillarity lowers the minimum within the $n = 1$ family while preserving the selected low-order mode. To quantify the global spectral change, we use the Frobenius norm of the CGR matrix:

$$\|\Delta\tilde{G}\|_F = \sqrt{\sum_m \sum_n \left(\Delta\tilde{G}_{mn}\right)^2}. \quad (109)$$

Fig. 6(g) shows that this norm is largest under compressive initial residual stress, lowest for $s = 0$, and slightly higher again under tensile initial residual stress. The layer-resolved indicators in Figs. 6(h) and 6(i) retain the ordering expected from Eq. (102): the HG layer generally reaches the largest critical values, followed by the PT and PM layers. Fig. 6(j) further shows that $\tilde{G}_{\text{MCGR}}$ varies only weakly with s over the sampled range, whereas the branch with surface tension remains lower than the tension-free branch. Thus, initial residual stress tunes the instability landscape, while surface tension supplies a persistent capillary bias in the threshold.

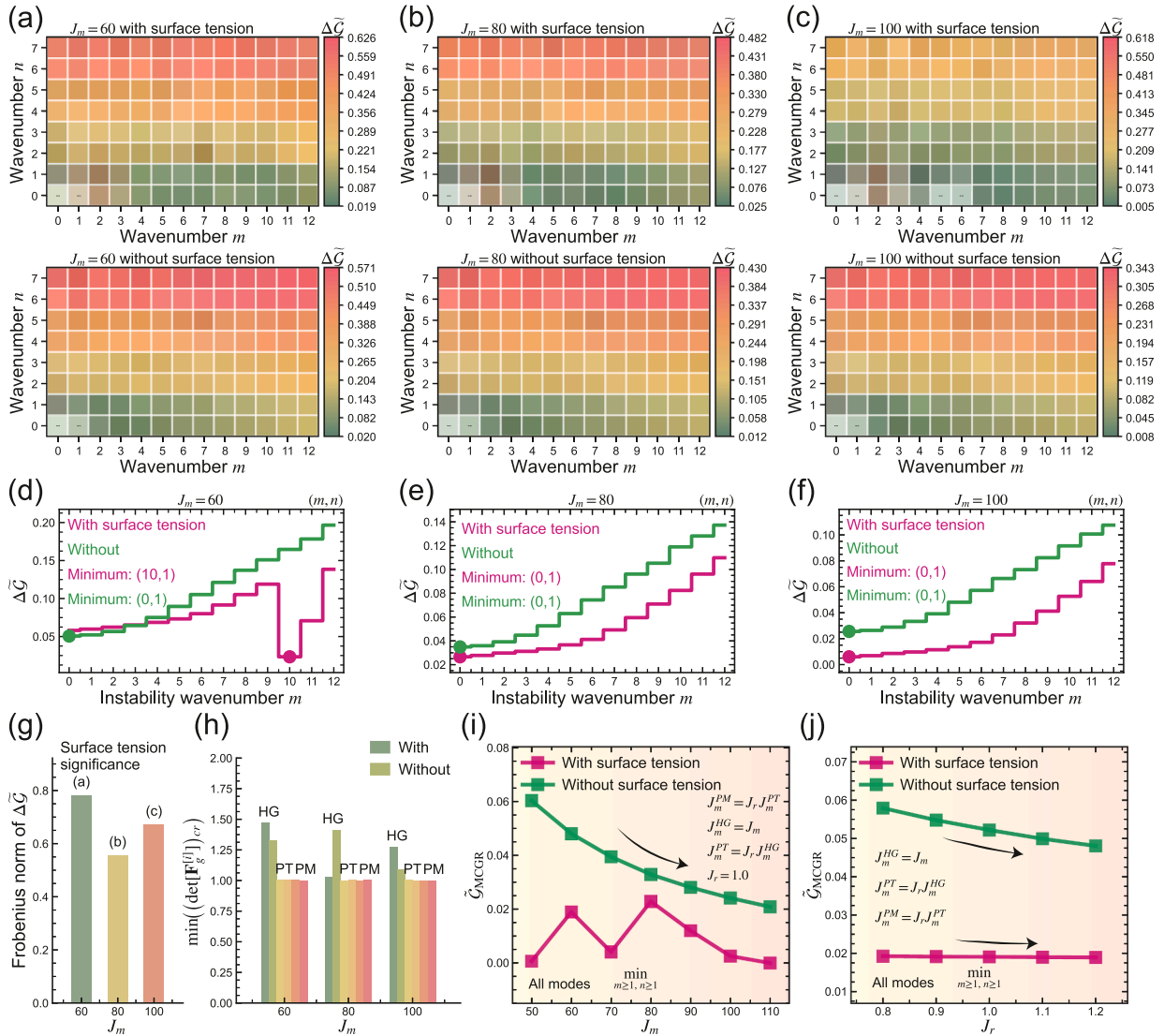


Fig. 7. Strain stiffening modulates the instability spectrum in the presence of surface tension. The prescribed initial residual stress amplitude is fixed at $s = -0.01$. (a)–(c) Critical growth ratio spectra $\Delta\tilde{G}(m, n)$ for $J_m = 60, 80$, and 100 , with upper and lower rows comparing calculations with and without surface tension. Grey cells in (a)–(c) denote modes excluded from the minimisation: the trivial uniform and rigid-body modes, and modes for which no admissible critical threshold was obtained within the prescribed search interval and tolerances. (d)–(f) Reduced spectra for the $n = 1$ modal family as functions of m , where the markers denote the minimum within this family. (g) Frobenius norm $\|\Delta\tilde{G}\|_F$ for the three strain-stiffening levels. (h) Layer-specific critical threshold $\min((\det \mathbf{F}_g^{(l)})_{cr})$ in the HG, PT, and PM layers. (i) Minimal critical growth ratio as a function of J_m at $J_r = 1$, for which $J_m^{HG} : J_m^{PT} : J_m^{PM} = 1 : 1 : 1$. (j) Minimal critical growth ratio as a function of the stiffening-ratio factor J_r , at fixed $J_m^{HG} = 60$, comparing calculations with and without surface tension.

Fig. 7 then examines the role of strain stiffening at $s = -0.01$, with the other parameters kept consistent with Fig. 6. The CGR spectra for $J_m = 60, 80$, and 100 (Fig. 7(a)–(c)) show that surface tension changes the distribution of admissible thresholds across the full (m, n) space. The reduced curves in Fig. 7(d)–(f) focus on the $n = 1$ modal family. Within this family, surface tension shifts the minimum from $(0, 1)$ to $(10, 1)$ at $J_m = 60$, whereas the minimum remains $(0, 1)$ at $J_m = 80$ and $J_m = 100$. Surface tension can therefore reorganize individual modal families when the nonlinear stiffening level places competing modes close in threshold.

The Frobenius norm in Fig. 7(g) is larger for the spectra including surface tension than for the tension-free spectra, with the strongest contribution among the sampled cases occurring at $J_m = 60$. Fig. 7(h) again shows a layer hierarchy in the minimum critical determinant of the growth tensor, with the HG layer exceeding the PT and PM layers. In Fig. 7(i), $J_r = 1$, so that $J_m^{HG} = J_m^{PT} = J_m^{PM} = J_m$. The tension-free MCGR decreases as this common J_m increases, whereas the branch including surface tension is lower overall but nonmonotonic. Fig. 7(j) is a separate scan of the stiffening-ratio factor J_r at fixed $J_m^{HG} = 60$, with $J_m^{PT} = J_r J_m^{HG}$ and $J_m^{PM} = J_r J_m^{PT}$.

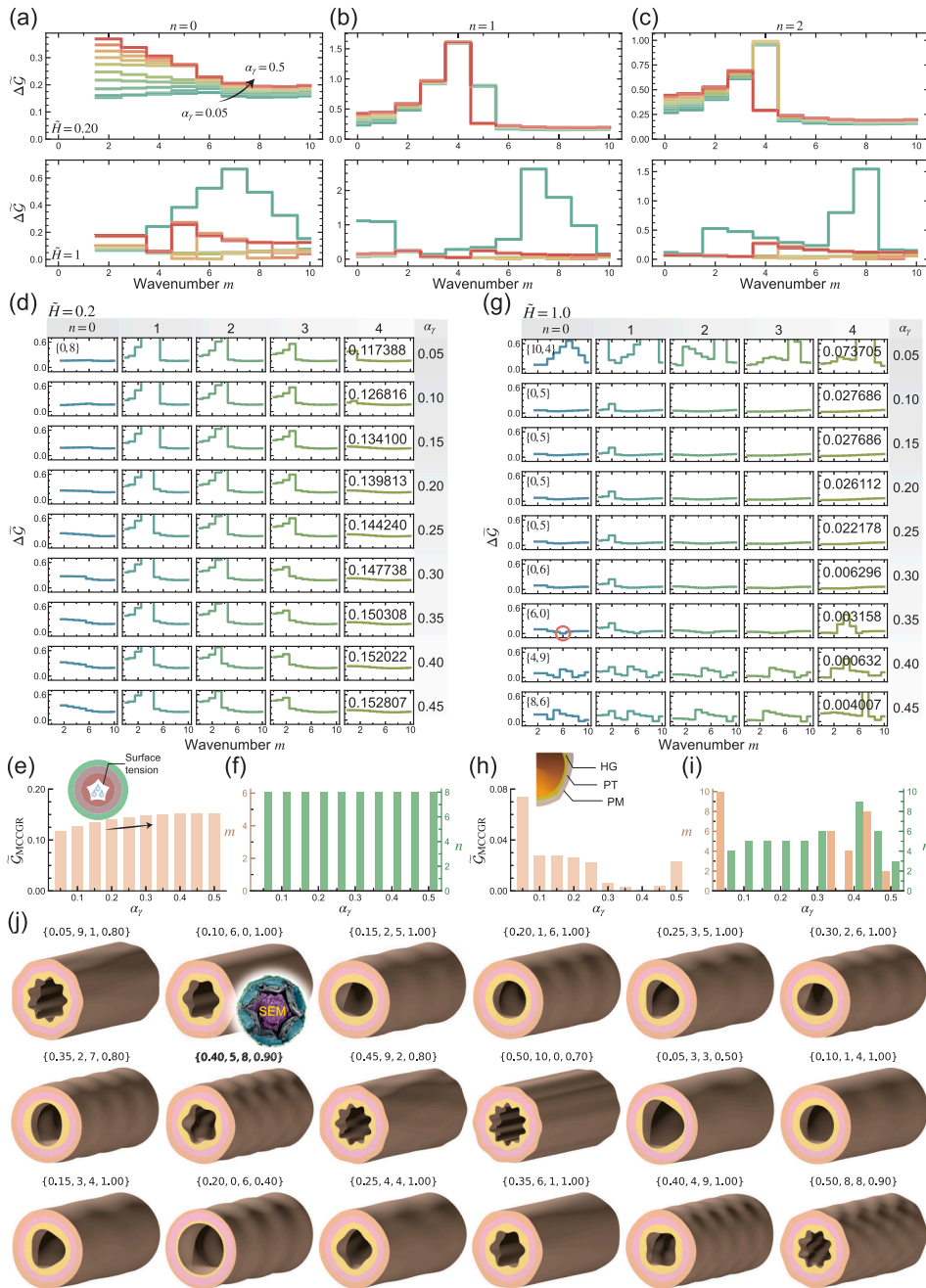


Fig. 8. Surface tension and wall thickness regulate the instability threshold and modal wavelength in trilayered walls. Here $\tilde{H} = H_{HG}/H_{PT} = H_{PM}/H_{PT}$, so that the layer-thickness ratio is $\tilde{H} : 1 : \tilde{H}$. (a)–(c) Critical growth spectra $\Delta\tilde{G}$ plotted against m for axial wavenumbers $n = 0, 1$, and 2 , comparing the thinner configuration $\tilde{H} = 0.20$ with the thicker configuration $\tilde{H} = 1$ over $\alpha_r = 0.05-0.50$. (d) Modal spectra for $\tilde{H} = 0.2$, displayed over $0 \leq m \leq 10$ and $0 \leq n \leq 4$ for increasing α_r , with each annotation reporting the minimum obtained from the complete scan $0 \leq m, n \leq 12$. (e),(f) Minimal critical growth ratio $\tilde{G}_{MCGR}$ and corresponding critical modes for $\tilde{H} = 0.2$. (g) Modal spectra for $\tilde{H} = 1.0$ under the same display and scan ranges and surface-tension sweep. (h),(i) Minimal critical growth ratio and corresponding critical modes for $\tilde{H} = 1.0$. (j) Representative instability morphologies for selected $\{\alpha_r, m, n, \tilde{G}\}$ combinations, including comparison with scanning electron microscopy of beetle rectal morphologies (Naseem et al., 2023).

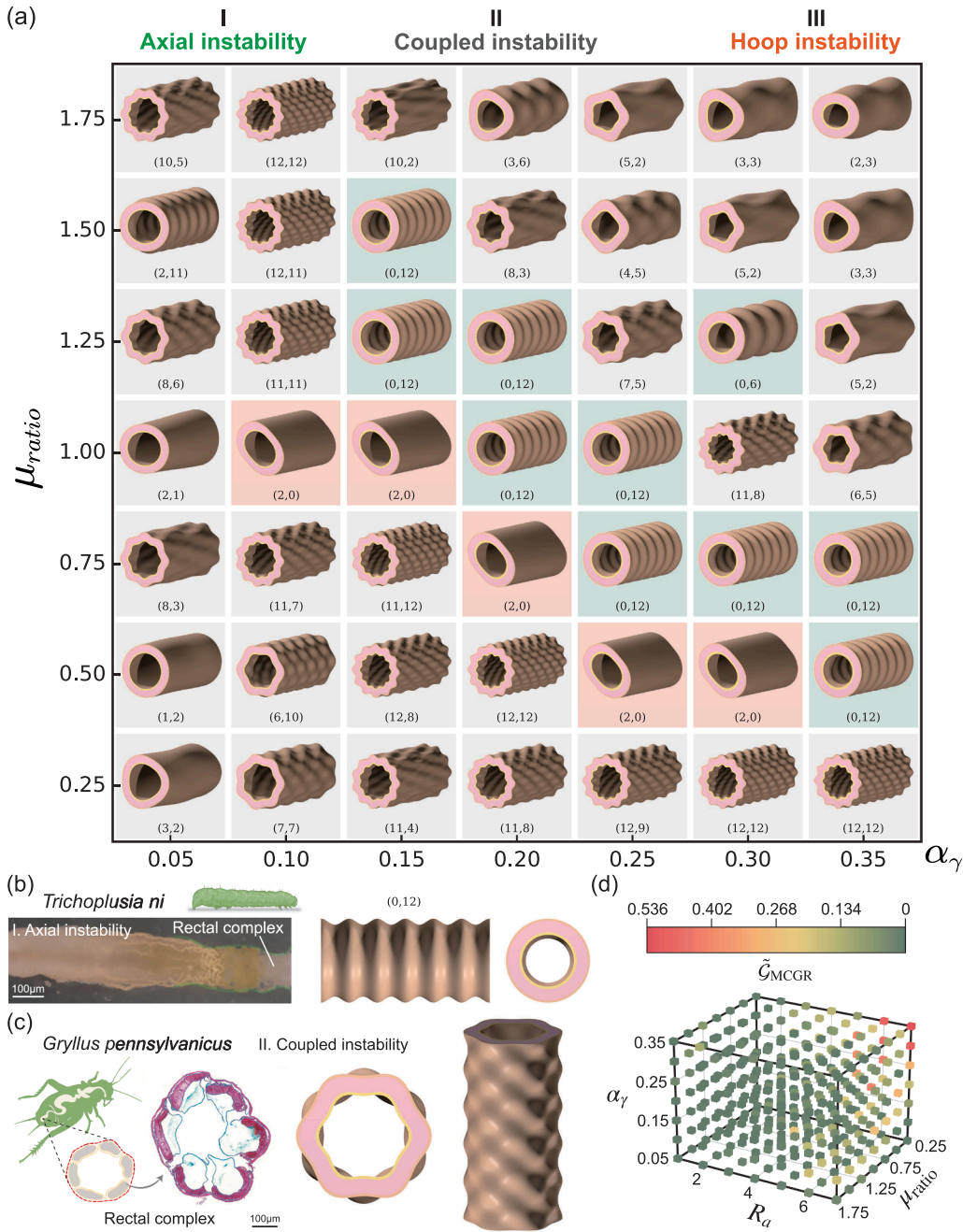


Fig. 9. Instability regimes are organized by surface tension and shear-modulus contrast. (a) Phase diagram in the α_γ - μ_{ratio} plane for a trilayer model with $\bar{H} = 0.2$, thickness ratio $\bar{H} : 1 : \bar{H}$, $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (200, 100, 50)$, $R_d = 3$, $s = 0.04$, $Q = -0.04$, and $L/R_d = 3$. Each cell shows a predicted morphology and its critical mode (m, n) , separating axial instability (I), coupled instability (II), and hoop instability (III). (b) Optical micrograph of the *Trichoplusia ni* rectal complex and the corresponding axial-instability prediction (O'Donnell, 2023); scale bar, 100 μm . (c) Masson-stained section of the *Gryllus pennsylvanicus* rectal complex and the corresponding coupled-instability prediction (Des Marteaux et al., 2018); scale bar, 100 μm . (d) Landscape of $\tilde{G}_{\text{MCGR}}$ over the extended parameter space spanned by R_d , μ_{ratio} , and α_γ .

These results preserve the earlier interpretation: heterogeneous strain stiffening and luminal surface tension jointly determine both the instability threshold and the selected mode.

Figs. 6 and 7 demonstrate that the capillary contribution depends on initial residual stress and strain stiffening. Fig. 8 next fixes $s = 0.10$, $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (200, 100, 50)$, $Q = 0.10$, $\mu_{HG}/\mu_{PT} = \mu_{PM}/\mu_{PT} = 0.20$, and $L/R_d = 3$ to examine the combined effects of surface tension and wall thickness. Fig. 8(a)–(c) plot $\Delta\tilde{G}$ against m for $n = 0, 1$, and 2, comparing the thinner wall $\bar{H} = 0.20$ with the

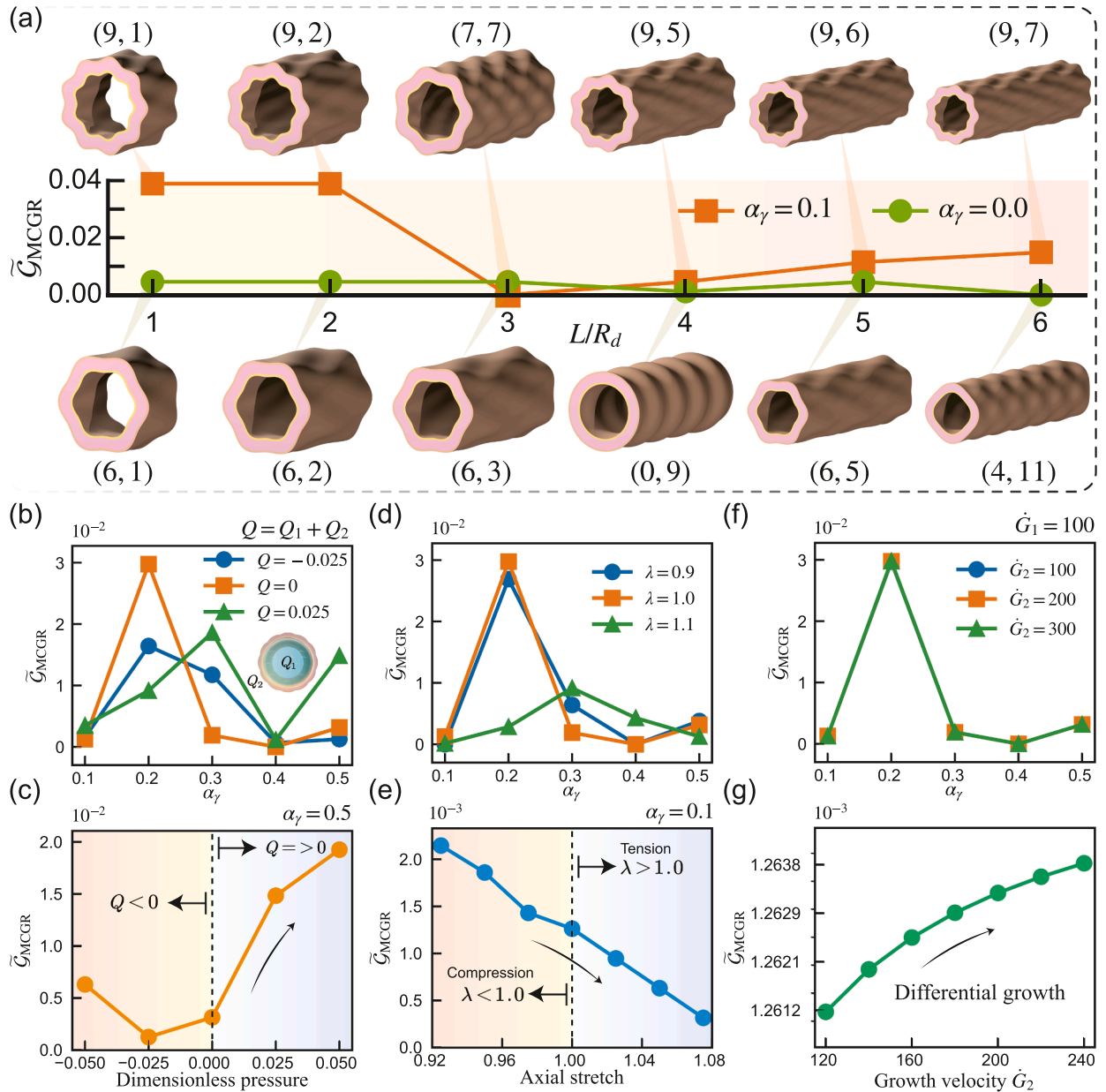


Fig. 10. Geometry, loading and growth kinetics regulate the minimal critical growth ratio. Panel (a) uses $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (200, 100, 50)$, $s = 0.04$, $Q = -0.04$, and $\bar{H} = 0.2$. Panels (b)–(g) use the same layerwise J_m values together with $s = -0.01$, $\bar{H} = 1/3$, $\mu_{HG} = \mu_{PT} = \mu_{PM}$, $R_a = 1$, and $L/R_d = 1$, unless otherwise stated. (a) Dependence of ζ_{MCGR} on the axial aspect ratio L/R_d , with representative instability patterns and critical modes shown for $\alpha_\gamma = 0.1$ and $\alpha_\gamma = 0.0$. (b) Variation of ζ_{MCGR} with surface tension for signed pressure differences $Q = -0.025$, 0 , and 0.025 . (c) Response to the signed pressure difference Q at fixed $\alpha_\gamma = 0.5$; $Q < 0$ corresponds to exterior-dominated compression, whereas $Q > 0$ corresponds to lumen-dominated loading. (d) Surface-tension response under axial stretches $\lambda = 0.9$, 1.0 , and 1.1 . (e) Axial-stretch dependence at fixed $\alpha_\gamma = 0.1$, distinguishing compression from tension. (f,g) Surface-tension response for $\dot{G}_1 = 100$ and $\dot{G}_2 = 100, 200$, and 300 , showing the weak variation of ζ_{MCGR} across the prescribed-growth sweep.

thicker wall $\bar{H} = 1.0$ as α_γ varies from 0.05 to 0.50 . The two thicknesses show different spectral organization, indicating that the same capillary loading can favor different modal families depending on wall geometry.

For $\bar{H} = 0.2$, the modal spectra displayed over $0 \leq n \leq 4$ show a gradual increase in the minimum threshold as α_γ increases (Fig. 8(d)). The annotated modes and the MCGR are obtained from the complete scan $0 \leq m, n \leq 12$. The MCGR rises from 0.117388 to 0.152807 over the sampled range (Fig. 8(e)), while the corresponding critical modes are summarized in Fig. 8(f). For $\bar{H} = 1.0$, the response is more complex: the spectra in Fig. 8(g) and the thresholds in Fig. 8(h) show a nonmonotonic dependence on α_γ , accompanied by changes in the selected modes (Fig. 8(i)). Representative morphologies in Fig. 8(j) show axial, circumferential, and coupled patterns, including a comparison with scanning electron microscopy of beetle rectal morphologies (Naseem et al., 2023).

Thus, surface tension does not act as a single stabilizing or destabilizing parameter; its effect depends strongly on wall thickness and modal competition.

The three modal classes are further examined through the finite-element calculations described in Appendix D. Fig. D.1(a) shows an axially uniform circumferential mode with $(m, n) = (6, 0)$, Fig. D.1(b) shows a coupled circumferential–axial mode with $(m, n) = (5, 8)$, and Fig. D.1(c) shows an axisymmetric axial mode with $(m, n) = (0, 6)$. For all three branches, the finite-element critical growth factors agree with the corresponding surface-impedance predictions to within 1%.

In addition to heterogeneity in initial residual stress and strain stiffening, the HG, PT, and PM layers can differ in shear modulus. Fig. 9 maps the resulting instability regimes in the α_γ – μ_{ratio} plane, where $\mu_{ratio} = \mu_{HG}/\mu_{PT}$ and $\mu_{PM} = \mu_{HG}$. The model uses $\tilde{H} = 0.2$, an interlayer thickness ratio $\tilde{H} : 1 : \tilde{H}$, $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (200, 100, 50)$, $s = 0.04$, $Q = -0.04$, and $L/R_d = 3$. The phase diagram in Fig. 9(a) is evaluated at $R_d = 3$. Three regimes emerge: axial instability (I), coupled instability (II), and hoop instability (III). The predicted morphologies and critical modes vary across the diagram, showing that surface tension and elastic contrast jointly organize mode transitions.

The biological comparisons in Fig. 9(b) and (c) support the interpretation of these regimes. An axial-instability prediction is compared with an optical image of the *Trichoplusia ni* rectal complex (O'Donnell, 2023), whereas a coupled-instability prediction is compared with a Masson-stained section of the *Gryllus pennsylvanicus* rectal complex (Des Marteaux et al., 2018). Fig. 9(d) then extends the threshold map over R_d , μ_{ratio} , and α_γ , providing a complementary view of how geometry, stiffness contrast, and capillarity regulate the MCGR.

Fig. 10 examines the robustness of these trends under changes in aspect ratio, pressure, axial stretch, and growth kinetics. Under the baseline conditions $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (200, 100, 50)$, $s = 0.04$, $Q = -0.04$, and $\tilde{H} = 0.2$, the MCGR varies nonmonotonically with the axial aspect ratio L/R_d (Fig. 10(a)). The accompanying mode labels show that changes in aspect ratio can alter both the threshold and the selected morphology. Fig. 10(b)–(g) use $(J_m^{HG}, J_m^{PT}, J_m^{PM}) = (200, 100, 50)$, $s = -0.01$, $\tilde{H} = 1/3$, $\mu_{HG} = \mu_{PT} = \mu_{PM}$, $R_d = 1$, and $L/R_d = 1$, with $Q = 0$, $\lambda = 1$, $\dot{G}_1 = 100$, and $\dot{G}_2 = 200$ unless the corresponding parameter is varied. Pressure further modifies the surface-tension response (Fig. 10(b)). At fixed $\alpha_\gamma = 0.5$, the threshold is lowest under weak compression and rises as the loading shifts toward positive pressure (Fig. 10(c)). Axial stretch produces another clear control route: at $\alpha_\gamma = 0.1$, $\tilde{G}_{MCGR}$ decreases as the deformation moves from compression to tension (Fig. 10(d)–(e)). Finally, within this large growth-rate-ratio regime, changing $\dot{G}_2$ while keeping $\dot{G}_1 = 100$ has only a weak effect on the threshold, with a slight increase across the sampled range (Fig. 10(f)–(g)). Additional full modal scans for comparable layerwise growth rates, with $\dot{G}_1 = 2$ and $\dot{G}_2 = 2.5, 3$, and 4, show that increasing $\dot{G}_2$ from 2.5 to 4 raises the MCGR by approximately 28.0%–28.2% over $\alpha_\gamma = 0.1$ –0.5. These results show that the capillary-growth instability is robust, but its quantitative threshold remains sensitive to geometry and loading.

Across these parameter sweeps, luminal surface tension is not merely an additional boundary load. It reshapes the CGR spectrum, changes the MCGR, and can switch the selected mode when several instability families compete. Its effect is mediated by initial residual stress, strain stiffening, wall thickness, shear-modulus contrast, aspect ratio, pressure, and axial stretch. The agreement between predicted morphologies and representative biological observations supports a capillary–elastic mechanism for the emergence of water-conserving rectal architectures.

5.3. Key limitations

Several idealizations should be addressed in future work. First, the HG, PT, and PM layers are treated as isotropic hyperelastic materials. This assumption highlights the elastocapillary instability, but real rectal tissues may be anisotropic because of oriented muscle fibers and extracellular matrix. Introducing anisotropic constitutive laws would help determine how preferential material directions influence wavelength selection and instability patterns. Second, growth is prescribed rather than coupled to the mechanical state. Many biological tissues adapt their growth to local stress and strain through mechanobiological feedback, so a coupled growth law would provide a more complete description of developmental adaptation. Third, the initial residual stress field is a mechanically admissible ansatz and has not been inferred from direct measurements in the insect rectal complex. Its amplitude s is therefore a sensitivity parameter rather than a quantitative measure of starvation; dedicated measurements are needed to identify its physiological origin and spatial distribution. Fourth, the luminal environment is simplified as a static system with constant surface tension and uniform pressure. A more realistic model should allow surface tension to vary with surface strain through the Shuttleworth effect (Andreotti and Snoeijer, 2016; Henkel et al., 2022) and should couple the deforming wall to luminal fluid transport. These extensions would refine the quantitative thresholds while preserving the central conclusion that surface tension can shape the water-conserving morphology of the trilayered insect rectal complex.

6. Discussion and conclusions

This study develops a morphoelastic framework for understanding how the trilayered insect rectal complex acquires its water-conserving morphology. The central result is that the folded HG–PT–PM architecture can be interpreted as the outcome of a deterministic mechanical instability controlled by differential growth, prescribed initial residual stress, nonlinear tissue stiffening, and luminal surface tension. The calculations show that surface tension is not simply an auxiliary boundary load. It reorganizes the instability spectrum, changes the minimal critical growth ratio, and can redirect mode selection when competing axial, circumferential, and coupled modes have comparable thresholds. This provides a mechanical explanation for how organ-scale surface effects can participate in biological pattern selection.

First, the analysis establishes why elastocapillarity is relevant to the rectal complex. Scaling arguments show that the geometric scale of the rectal complex is close to the characteristic capillary length, placing surface tension within the range where it can influence deformation. The derivation of the surface stress tensor and the generalized Young–Laplace equation then provides the boundary condition used throughout the model. The deformation gradient is decomposed into elastic, growth-induced, and initial residual stress components, so the formulation retains a prescribed initial residual stress while extending the conventional growth-elastic decomposition. Combined with the Gent strain-stiffening law, this framework gives explicit stress fields and clarifies how surface tension modifies the base state in both single-layer and trilayered geometries.

Second, the incremental formulation converts this base-state problem into a stability problem. The push-forward form of the incremental stress, the instantaneous Gent modulus, and the incompressibility constraint lead to a Stroh-type system for the trilayered wall. Recasting this system through the surface impedance matrix and Riccati equation provides a stable route for computing critical growth thresholds and displacement fields. The curvature variation induced by surface stress links the elastocapillary boundary condition directly to the bifurcation problem, allowing the model to predict not only when the axisymmetric state loses stability, but also which circumferential and axial wavenumbers are selected.

Third, the mode-selection process is strongly parameter dependent. The prescribed growth hierarchy $g_{\text{HG}} > g_{\text{PT}} > g_{\text{PM}}$ generates the residual mismatch needed for instability, while luminal surface tension reshapes the critical growth-ratio landscape rather than shifting it uniformly. Under changes in initial residual stress, surface tension alters the local MCGR and modifies the stability landscape. Under changes in strain stiffening, it can switch the selected mode when the material response brings competing modes close together. Wall thickness, shear-modulus contrast, aspect ratio, pressure, axial stretch, and growth kinetics further modulate the threshold, producing axial, coupled, and hoop instability regimes. These results revise the simpler interpretation that surface tension only raises the instability threshold or only favours long-wavelength patterns. Its role is more general: it redistributes stability across the full (m, n) -mode space and thereby controls both threshold and morphology.

Appendix B (Fig. B.1) presents an illustrative translational example of geometry–capillarity coupling and its potential to inform bioinspired liquid-management concepts.

The model uses idealized material, growth, and luminal-fluid descriptions to focus on the elastocapillary mechanism. Incorporating tissue anisotropy, mechanobiological feedback, and dynamic fluid–structure coupling would further refine the quantitative thresholds and broaden the applicability of the framework.

In conclusion, the present work provides a mechanics-based account of water-conserving morphogenesis in the insect rectal complex. By combining triphasic growth kinematics, residual stress, strain stiffening, elastocapillary boundary conditions, and incremental stability analysis, the study shows how differential growth and luminal surface tension can transform a trilayered cylindrical organ into a structured exchanger with axial, circumferential, or coupled folds. The broader implication is that surface tension can act as an active regulator of biological form at organ-relevant scales, and that the same capillary–elastic principle can inform the design of bioinspired materials for controlled liquid transport.

CRediT authorship contribution statement

Yafei Wang: Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization; **Chang Wang:** Validation, Software, Formal analysis, Data curation; **Lingfeng Yuan:** Software, Investigation, Data curation; **Fucheng Wang:** Visualization, Investigation, Data curation; **Yifan Yang:** Software, Data curation; **Yao Zhang:** Investigation, Data curation; **Chengxuan Zhai:** Software, Investigation; **Lizichen Chen:** Writing – original draft, Investigation; **Yangkun Du:** Writing – original draft, Visualization, Validation, Formal analysis; **Changguo Wang:** Methodology, Investigation; **Michel Destrade:** Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis; **Ji Liu:** Supervision, Methodology, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work is supported by the [National Natural Science Foundation of China](#) (Grant Nos. [12672131](#), [12602263](#), [52373139](#), [U2436202](#), and [12572074](#)), the National Key R&D Program of China (Grant No. 2024YFA0920100), the Shenzhen Basic Research Program (Grant No. JCYJ20240813094159001), and the Shenzhou Young Scholars Fund of Harbin Institute of Technology. The authors gratefully acknowledge Yunting Lan for her assistance with ethics-related procedures.

Data availability

Data will be made available on request.

Appendix A. Submatrices of the Stroh matrix

For each layer $[i] \in \{\text{HG}, \text{PT}, \text{PM}\}$, all moduli and pressure terms are evaluated in the corresponding base state. The partitioned matrix in Eq. (81) is written directly as

$$\mathbf{G}_{[i]} = \begin{bmatrix} -1 & -m & -kr & 0 & 0 & 0 \\ m \frac{\mathcal{L}_{r\theta\theta r}^{[i]} + p}{\mathcal{L}_{r\theta r\theta}^{[i]}} & \frac{\mathcal{L}_{r\theta\theta r}^{[i]} + p}{\mathcal{L}_{r\theta r\theta}^{[i]}} & 0 & 0 & \frac{1}{\mathcal{L}_{r\theta r\theta}^{[i]}} & 0 \\ kr \frac{\mathcal{L}_{rzrz}^{[i]} + p}{\mathcal{L}_{rzrz}^{[i]}} & 0 & 0 & 0 & 0 & \frac{1}{\mathcal{L}_{rzrz}^{[i]}} \\ g_{11}^{[i]} & g_{12}^{[i]} & g_{13}^{[i]} & 1 & -m \frac{\mathcal{L}_{r\theta\theta r}^{[i]} + p}{\mathcal{L}_{r\theta r\theta}^{[i]}} & -kr \frac{\mathcal{L}_{rzrz}^{[i]} + p}{\mathcal{L}_{rzrz}^{[i]}} \\ g_{21}^{[i]} & g_{22}^{[i]} & g_{23}^{[i]} & m & -\frac{\mathcal{L}_{r\theta\theta r}^{[i]} + p}{\mathcal{L}_{r\theta r\theta}^{[i]}} & 0 \\ g_{31}^{[i]} & g_{32}^{[i]} & g_{33}^{[i]} & kr & 0 & 0 \end{bmatrix}. \quad (\text{A.1})$$

Here, $g_{ab}^{[i]} = (\mathbf{G}_3^{[i]})_{ab}$. The independent entries of $\mathbf{G}_3^{[i]}$ read

$$g_{11}^{[i]} = \mathcal{L}_{rrrr}^{[i]} - \mathcal{L}_{rr\theta\theta}^{[i]} - \mathcal{L}_{\theta\theta rr}^{[i]} + \mathcal{L}_{\theta\theta\theta\theta}^{[i]} + 2p + m^2 \mathcal{L}_{\theta r\theta r}^{[i]} + k^2 r^2 \mathcal{L}_{zrzr}^{[i]} - \frac{m^2}{\mathcal{L}_{r\theta r\theta}^{[i]}} \left(\mathcal{L}_{r\theta\theta r}^{[i]} + p \right) \left(\mathcal{L}_{\theta r\theta r}^{[i]} + p \right) - \frac{k^2 r^2}{\mathcal{L}_{rzrz}^{[i]}} \left(\mathcal{L}_{rzrz}^{[i]} + p \right) \left(\mathcal{L}_{zrzr}^{[i]} + p \right), \quad (\text{A.2})$$

$$g_{12}^{[i]} = m \left[\mathcal{L}_{rrrr}^{[i]} - \mathcal{L}_{rr\theta\theta}^{[i]} + \mathcal{L}_{\theta r\theta r}^{[i]} - \mathcal{L}_{\theta\theta rr}^{[i]} + \mathcal{L}_{\theta\theta\theta\theta}^{[i]} + 2p \right] - \frac{m}{\mathcal{L}_{r\theta r\theta}^{[i]}} \left(\mathcal{L}_{r\theta\theta r}^{[i]} + p \right) \left(\mathcal{L}_{\theta r\theta r}^{[i]} + p \right), \quad (\text{A.3})$$

$$g_{13}^{[i]} = kr \left[\mathcal{L}_{rrrr}^{[i]} - \mathcal{L}_{rrzz}^{[i]} - \mathcal{L}_{\theta\theta rr}^{[i]} + \mathcal{L}_{\theta\theta zz}^{[i]} + p \right], \quad (\text{A.4})$$

$$g_{22}^{[i]} = m^2 \left[\mathcal{L}_{rrrr}^{[i]} - \mathcal{L}_{rr\theta\theta}^{[i]} - \mathcal{L}_{\theta\theta rr}^{[i]} + \mathcal{L}_{\theta\theta\theta\theta}^{[i]} + 2p \right] + \mathcal{L}_{r\theta r\theta}^{[i]} - \frac{1}{\mathcal{L}_{r\theta r\theta}^{[i]}} \left(\mathcal{L}_{r\theta\theta r}^{[i]} + p \right) \left(\mathcal{L}_{\theta r\theta r}^{[i]} + p \right) + k^2 r^2 \mathcal{L}_{z\theta z\theta}^{[i]}, \quad (\text{A.5})$$

$$g_{23}^{[i]} = kmr \left[\mathcal{L}_{rrrr}^{[i]} - \mathcal{L}_{rrzz}^{[i]} + \mathcal{L}_{z\theta\theta z}^{[i]} - \mathcal{L}_{\theta\theta rr}^{[i]} + \mathcal{L}_{\theta\theta zz}^{[i]} + 2p \right], \quad (\text{A.6})$$

$$g_{33}^{[i]} = m^2 \mathcal{L}_{\theta z\theta z}^{[i]} + k^2 r^2 \left[\mathcal{L}_{rrrr}^{[i]} - \mathcal{L}_{rrzz}^{[i]} - \mathcal{L}_{zzrr}^{[i]} + \mathcal{L}_{zzzz}^{[i]} + 2p \right]. \quad (\text{A.7})$$

The remaining entries follow from symmetry,

$$g_{21}^{[i]} = g_{12}^{[i]}, \quad g_{31}^{[i]} = g_{13}^{[i]}, \quad g_{32}^{[i]} = g_{23}^{[i]}. \quad (\text{A.8})$$

Appendix B. Illustrative bioinspired micro-architectures for liquid manipulation

This appendix illustrates how general geometry–capillarity coupling can inform liquid-management concepts. The prescribed microarchitectures provide a qualitative design perspective that complements the main mechanics results.

The desert beetle (Fig. B.1(a)) exemplifies mastery of water harvesting through hierarchical surface morphologies. The rectal complex functions as an internal water reclamation system in which Malpighian tubules (PT) and the perinephric membrane (PM) interact with the lumen to extract water from the haemolymph through active KCl transport mediated by Lp cells, ultimately delivering ultraconcentrated excreta to the anus while recovering water droplets. Externally, the elytra present patterned bump morphologies (Fig. B.1(b)) that promote fog droplet nucleation and coalescence. These bumps establish a geometric gradient (Figs. B.1(c)–(d)) that extends from the rectal complex through the anal canal and creates a physical pathway for directional liquid transport driven purely by differences in surface energy.

Inspired by this architecture, we fabricated bioinspired surfaces with engineered geometric gradients (Figs. B.1(e)–(g)). A series of micropillar arrays with systematically varied heights generates a wettability gradient that drives spontaneous droplet motion. Phase-field two-phase flow simulations performed in COMSOL Multiphysics (Fig. B.1(e), I–V) show that droplets transition between superhydrophobic and hydrophilic states across five configurations. The underlying mechanism mirrors manipulation of interfacial energy by geometric curvature in the rectal complex. Droplets preferentially spread toward regions with larger local curvature, which reduces total interfacial free energy. This passive and energy-efficient control of surface wettability is promising for microfluidic systems that operate without external pumping.

Mechanistically, the engineered gradient converts spatial variations in pillar height, curvature, and solid–liquid contact fraction into a gradient in interfacial free energy. A droplet moving over the array samples different apparent wettabilities and capillary

pressures, so the resulting surface-energy imbalance produces a net lateral driving force toward lower-energy configurations. Thus, the artificial surface is not a direct copy of the rectal complex; it translates the same geometry–capillarity coupling identified in the biological system into a controllable route for passive transport.

Water management principles embodied by the rectal complex also guide advanced electrode design for physiological monitoring. The ECG experiments involving human participants shown in Fig. B.1(j) were conducted at the Southern University of Science and Technology under a protocol approved by its institutional review board (IRB Protocol 2024PES303). Three male participants took part in the study, and Fig. B.1(j) presents representative ECG recordings from one participant. The experiment involved non-invasive, passive ECG acquisition using commercial and bioinspired electrodes under dry and perspiration-wet interface conditions. Conventional dry electrodes often make poor contact with skin, which yields ECG signals with substantial noise (Fig. B.1(f), left). Our bioinspired electrode uses a micropatterned surface featuring hierarchical bumps and geometric gradients that emulate the rectal morphology (Figs. B.1(g)–(i)). Top-view and side-view scanning electron microscopy reveal a periodic array of micropillars with a spacing of approximately $200\text{ }\mu\text{m}$ that enhances sweat wicking and maintains stable hydration at the electrode–skin interface. Performance tests (Fig. B.1(j)) indicate that under dry conditions commercial electrodes provide stable yet low-amplitude signals, while our electrode achieves comparable stability. Under perspiration-wet interface conditions, commercial electrodes display pronounced signal degradation and noise due to uncontrolled sweat accumulation. In contrast, our micropatterned electrode maintains stable, high-fidelity ECG traces by directing sweat away from critical sensing regions via lateral transport driven by capillary forces along the geometric gradient. Time-resolved optical imaging (Fig. B.1(i), bottom row, t from 0.23 to 4.16 s) shows progressive sweat spreading and directional drainage that prevents interfacial flooding. This morphology-mediated fluidic control translates the water-sorting strategy of the rectal complex into a robust bioelectronic platform and enables reliable long-term monitoring in ambulatory settings.

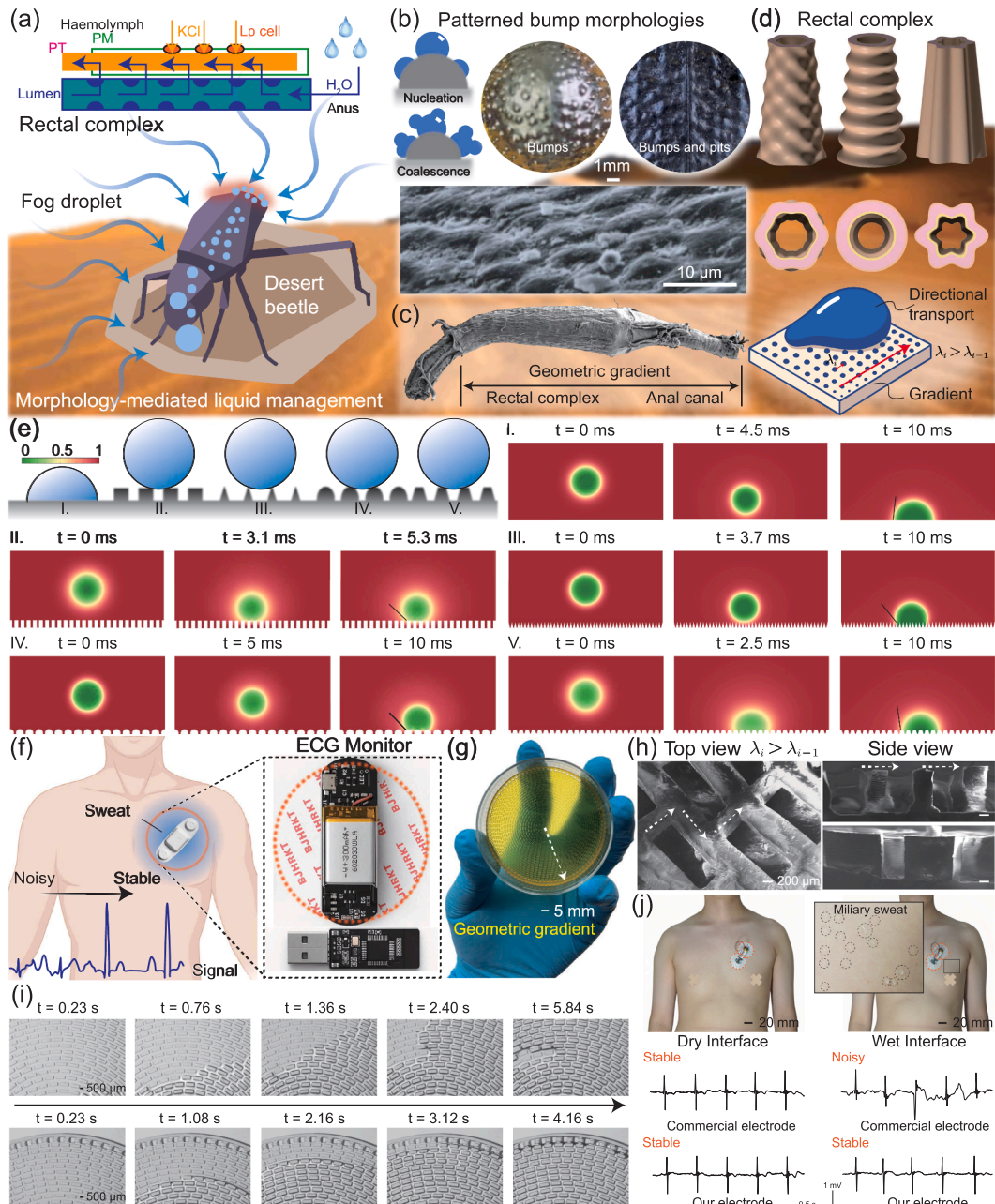


Fig. B.1. Illustrative bioinspired concepts for passive liquid management and bioelectronic sensing inspired by geometry–capillarity coupling. (a) Conceptual link between the desert beetle water-harvesting system and the rectal complex, where the HG–PT–PM architecture, Lp cells, and KCl-mediated transport support water recovery from haemolymph while fog droplets are collected externally. (b) Patterned bump morphologies on beetle elytra promote droplet nucleation and coalescence, with optical and scanning electron microscopy views of bumps and bumps with pits (Parker and Lawrence, 2001); scale bars, 1 mm and 10 μm . (c) Geometric gradient along the rectal complex and anal canal (Naseem et al., 2023). (d) Bioinspired gradient surface designed to drive directional droplet transport through spatially varying surface geometry. (e) COMSOL Multiphysics phase-field two-phase flow simulations showing wettability transitions and droplet motion on five micropillar arrays with distinct geometric gradients. (f) Schematic of wearable ECG monitoring under perspiration, highlighting the need for sweat-tolerant electrode interfaces. (g) Prototype bioinspired electrode with a radial geometric gradient. (h) Top-view and side-view SEM images of the hierarchical micropillar array, with a characteristic spacing of approximately 200 μm . (i) Time-resolved optical images showing sweat spreading and directional drainage on the electrode surface; scale bar, 500 μm . (j) ECG measurements under dry and miliary-sweat interfaces, comparing commercial electrodes with the bioinspired electrode; scale bars, 20 mm, 0.5 s, and 1 mV. The human-participant protocol for the ECG measurements in (j) was approved by the Institutional Review Board of the Southern University of Science and Technology (IRB Protocol 2024PES303; $n = 3$, all male); representative recordings from one participant are shown.

Appendix C. Sources of model parameters

The values of the principal model parameters used in the calculations and their corresponding sources are summarised in Table C.1.

Table C.1

Sources of model parameters.

Symbol	Values used	Source
D	$\sim 100 \mu\text{m}$	Cross-sectional dimension of the beetle rectal complex (Naseem et al., 2023)
Δp	10^3 Pa	Representative pressure scale in soft biological tissues (Lee et al., 2019; Style et al., 2017; Riccobelli and Bevilacqua, 2020)
μ	$\sim 10^3 \text{ Pa}$	Representative shear modulus of soft tissues (Akhtar et al., 2011; Holzapfel, 2000; Fung, 2013)
γ	$\sim 0.1 \text{ N m}^{-1}$	Eq. (7), using the values of D and Δp above (Style et al., 2017; Riccobelli and Bevilacqua, 2020)
L	$L/R_d = 1\text{--}6$	Geometric range examined in Fig. 10(a)
λ	$0.9\text{--}1.1$	Axial stretches examined in Figs. 10(d),(e)
$\tilde{H}$	$0.20, 1.00$	Wall thicknesses examined in Fig. 8
α_γ	$0\text{--}2$	Eq. (107); ranges examined in Figs. 3, 4, and 6–10 (Style et al., 2015b, 2017; Riccobelli and Bevilacqua, 2020)
s	$-0.10\text{--}0.40$	Initial stress potential; ranges examined in Figs. 3, 4, and 6–9 (Gower et al., 2015; Ciarletta et al., 2016; Wang et al., 2023a)
$\mu_{[i]}$	$\mu_{HG}/\mu_{PT} = 0.25\text{--}1.75$, with $\mu_{PM} = \mu_{HG}$ in Fig. 9	Layerwise modulus values in Figs. 3, 4, 6, and 9
$J_m^{[i]}$	$2\text{--}300$	Gent strain-stiffening model (Rubinstein and Colby, 2003; Wang et al., 2023a); values examined in Figs. 3, 4, and 6–9
J_r	$0.8\text{--}1.2$	Layerwise stiffening factors examined in Fig. 7(j)
$\dot{G}_1$	100	Growth rate ratio defined by Eq. (104) (Rodriguez et al., 1994; Goriely, 2017; Tepole, 2017)
$\dot{G}_2$	$100, 200, 300$	Growth rate ratio defined by Eq. (105); values examined in Figs. 10(f),(g) (Rodriguez et al., 1994; Goriely, 2017; Tepole, 2017)
Q	$-0.05\text{--}0.50$	Signed pressure difference defined in Eq. (42); values examined in Figs. 3, 4, 6, and 8–10 (Style et al., 2017; Riccobelli and Bevilacqua, 2020)

Appendix D. Finite-element validation

Finite-element calculations are performed to cross-check the three representative modal classes discussed in Fig. 8(j) and their critical growth factors obtained from the surface-impedance method. These three finite-element eigenmodes are shown individually in Fig. D.1: Fig. D.1(a) shows the axially uniform circumferential mode $(m, n) = (6, 0)$, Fig. D.1(b) shows the coupled circumferential–axial mode $(m, n) = (5, 8)$, and Fig. D.1(c) shows the axisymmetric axial mode $(m, n) = (0, 6)$. The finite-element formulation is implemented in Firedrake (Rathgeber et al., 2016). The reconstructed three-dimensional eigenmodes are visualised in ParaView (Ahrens et al., 2005). The model retains the Gent energy in Eq. (22), the prescribed initial distortion, isotropic growth, incompressibility, pressure loading, and luminal surface tension. For layer $[i] \in \{HG, PT, PM\}$, the constrained bulk potential is $\Pi_b = \sum_{[i]} \int_{\Omega_{[i]}^0} J_g^{[i]} \{ \Psi^{[i]}(\mathbf{F}_e^{[i]}) - p^{[i]} [J_e^{[i]} - 1] \} dV$, where $\Omega_{[i]}^0$ is the reference layer, $\mathbf{F} = \mathbf{I} + \text{Grad}_X \mathbf{u}$, $\mathbf{F}_e^{[i]} = \mathbf{F}(\mathbf{F}_s^{[i]})^{-1}(\mathbf{F}_g^{[i]})^{-1}$, $J_e^{[i]} = \det \mathbf{F}_e^{[i]}$, $J_g^{[i]} = \det \mathbf{F}_g^{[i]}$, and $p^{[i]}$ enforces $J_e^{[i]} = 1$. The luminal surface energy is $\Pi_\gamma = \gamma \int_{S_d^0} J_s dA$, with $J_s = \|\text{cof}(\mathbf{F})\mathbf{N}\|$. Here, S_d^0 is the reference luminal surface, γ is its uniform surface tension, $\mathbf{N}$ is its outward unit normal, and J_s is the surface-area stretch. The first variation of Π_γ gives the Young–Laplace traction in Eq. (35), and its linearisation gives the surface term in Eq. (70).

For every virtual displacement–pressure pair $(\hat{\mathbf{u}}, \hat{p})$, the mixed weak problem is written as

$$\mathcal{R}(\mathbf{u}, p; \hat{\mathbf{u}}, \hat{p}) = D_{(\mathbf{u}, p)}(\Pi_b + \Pi_\gamma)[\hat{\mathbf{u}}, \hat{p}] - Q \int_{S_d^0} [\text{cof}(\mathbf{F})\mathbf{N}] \cdot \hat{\mathbf{u}} dA = 0. \quad (\text{D.1})$$

Here, $D_{(\mathbf{u}, p)}$ is the directional derivative, $Q = Q_1 - Q_2$ is defined in Eq. (42), and S_d^0 is the outer reference surface. In the reported validation calculations, the displacement field is approximated by continuous piecewise-quadratic functions and the hydrostatic pressure by discontinuous piecewise-linear functions, so the displacement interpolation is one polynomial degree higher than the pressure interpolation. The complete-annulus $(6, 0)$ calculation uses structured quadrilateral cells with a $\text{CG}_2\text{--DQ}_1$ pair, whereas the $(5, 8)$ and $(0, 6)$ radial calculations use interval cells with a $\text{CG}_2\text{--DG}_1$ pair and retain the circumferential and axial Fourier factors analytically. The axisymmetric base fields follow from radial equilibrium. For $(6, 0)$, the circular base state is also solved on the complete annulus and m is identified from the eigenmode; for $(5, 8)$ and $(0, 6)$, the base fields are transferred to the radial discretisation. The calculations use the unperturbed geometry.

Linearisation of Eq. (D.1) about the axisymmetric base state gives the generalized eigenvalue problem

$$\mathbf{K}(g_{HG})\mathbf{q} = \kappa \mathbf{M}\mathbf{q}, \quad (\text{D.2})$$

where g_{HG} is the HG growth factor, $\mathbf{q}$ contains the displacement and pressure perturbation coefficients, $\mathbf{K}$ is the tangent matrix, and $\mathbf{M}$ is the displacement mass matrix with a zero pressure block. The auxiliary eigenvalue κ serves as the bifurcation indicator, with the critical point occurring when the eigenvalue of the tracked branch crosses zero.

The relative difference between the finite-element and surface-impedance predictions is defined as

$$\varepsilon_{\text{rel}} = \frac{|g_{\text{HG,cr}}^{\text{FE}} - g_{\text{HG,cr}}^{\text{IM}}|}{g_{\text{HG,cr}}^{\text{IM}}} \times 100\%. \quad (\text{D.3})$$

Here, ε_{rel} is the percentage relative difference; $g_{\text{HG,cr}}^{\text{FE}}$ and $g_{\text{HG,cr}}^{\text{IM}}$ are the critical HG growth factors from the finite-element (FE) and surface-impedance-matrix (IM) methods; and cr denotes the critical value. The relative differences are 0.3775%, $5.36 \times 10^{-4}\%$, and $7.26 \times 10^{-4}\%$ for (6, 0), (5, 8), and (0, 6), respectively, all below the stated 1% tolerance.

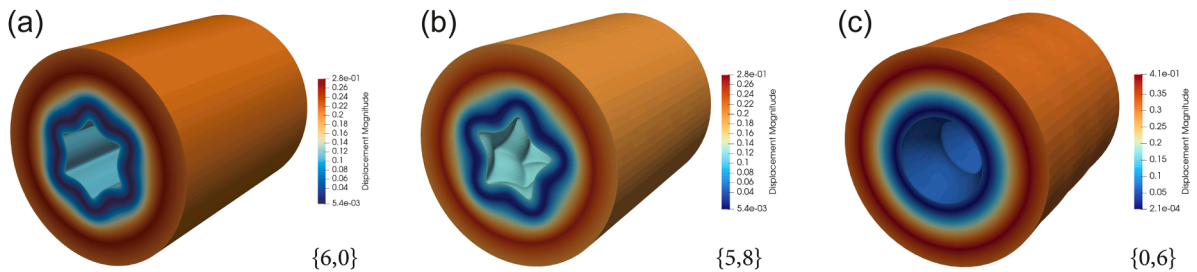


Fig. D.1. Finite-element linear eigenmodes corresponding to the three representative modal classes illustrated in Fig. 8(j) and used to cross-check the surface-impedance predictions. (a) Axially uniform circumferential mode (m, n) = (6, 0). (b) Coupled circumferential-axial mode (m, n) = (5, 8). (c) Axisymmetric axial mode (m, n) = (0, 6). The displacement amplitudes are scaled independently to display the linear eigenmode geometry.

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