Volvox Inversion Mechanics

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Outline

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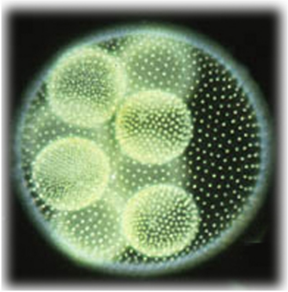
What is *Volvox carteri?*

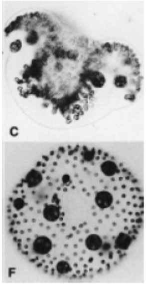
- Chlorophycaean family
- Fresh water globular algae and algal community comprised of 2000+ cells
- Biflagellate individuals cells held together by cytoplasmic bridges and extracellular matrix (ECM)



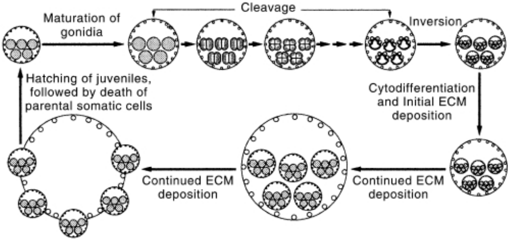
Posterior < ——– > Anterior

WHY STUDY *Volvox carteri?*

- Model system for studying multicellular tissues and epithelial sheet movements, which occur in processes such as gastrulation and notochord formation in vertebrates, such as humans.
- Rich quantitative literature with genetic, developmental, and evolutionary data
- Several developmental mutants and techniques are available for experiment

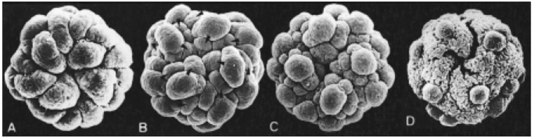


Development



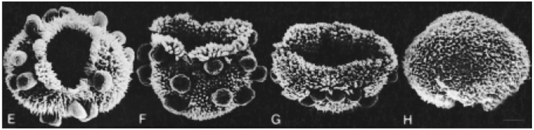
- Single celled individuals (gonidia) hatch from adult and are motile
- Several (11-12) rounds of volume increase and division (cleavage)
- Both somatic (body) and gametic (reproductive) cell types are differentiated during this process
- A single anterior-posterior axis over the entire colony develops

Pre-inversion



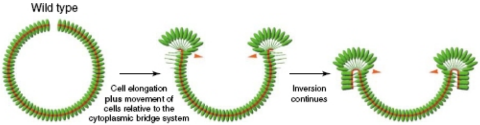
- After 5th cleavage cycle (=32 cells), half of the anterior 16 cells differentiate into gonidia precursors.
- The gonidia precursors undergo 3 more rounds of division, resulting in (8,16,32)=64 gonidia pre-inversion
- The somatic cells divide 6-7 more times, depending on environmental conditions, resulting in (24,48,96,192,384,768,1536)=3072 maximum cells pre-inversion
- Somatic cells are $\frac{1}{10}th$ of the volume of the gonidia, and are connected via 25000 cytoplasmic bridges, forming a continious epithelial sheet
- Gonidia are on the outside before inversion

Inversion



- Actually, it's an eversion...
- Between the 3rd and 4th round of cleavage, a swastika-shaped opening develops in the anterior side of the epithelial sheet.
- Somatic cell geometry changes from ellipsoidal to flask-shaped, causing negative curvature
- Geometry change passes as wave from anterior to posterior, resulting in a curling epithelium
- Once the curl passes over the anterior/posterior (A/P) midline, the posterior half contracts, and "pops" through the opening
- The epithelium reconnects to itself, completing the inversion

Geometry Changes in Somatic Cells



- Transverse section of inversion process, with anterior on top.
- Somatic cells change from ellipsoidal to flask shaped, extending inward.
- Due to the decrease in circumference and conservation of volume, the sheet bends outward
- Cells change back from flask-shaped to ellipsoidal after a few minutes
- Wave of geometry change stops at A/P midline
- Entire process takes about 45 minutes

Questions

- Does the geometry change of the anterior somatic cells account for the entire inversion?
- Does the posterior actomyosin contraction account for the inversion?
- What role does geometry play in this process?
- What role do protein kinetics play in this process?

Outline

Assumptions

- Treat epithelial sheet as continuous media. This is justified due to cytoplasmic bridges and high cell count.
- Treat epithelial sheet as **linear elastic**, accounting for **large deformations**. There is currently no data on the viscous response of the epithelial sheet.
- Although the organism is completely surrounded by, and filled with water, fluid effects on the inversion process are considered to be minimal. I.e. I consider the dynamics of the solid epithelial sheet in a vacuum.

Equations and Parameters

Momentum Balance: $$\frac{\partial \sigma_{ij}}{\partial x_j} + b_j = \rho \frac{\partial^2 u_i}{\partial t^2}$$

Strain-Displacement: $$\varepsilon_{ij} = \frac{1}{2}\left(\frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i}\right)$$

Hooke's Law: $$\varepsilon_{ij} = \frac{1+\nu}{E}\sigma_{ij} - \frac{\nu}{E}\sigma_{kk}\delta_{ij} + \alpha \Delta T$$

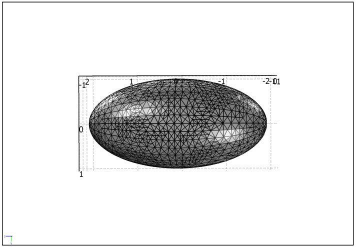
Reaction-Diffusion: $$\frac{\partial c}{\partial t} = D\nabla^2 c + f_R(c, \mathbf{x})$$

Young's Modulus (E): $10^5 Pa$

Poisson Ratio (ν): 0.49

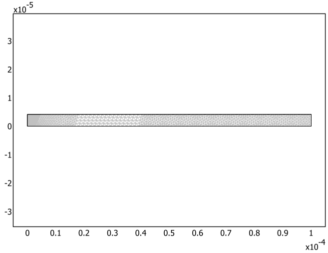
Note: Although spherical coordinates should be the obvious choice for solving this problem, recti-linear coordinates are used due to the FEM package used.

Single Cell Shape Change Geometry



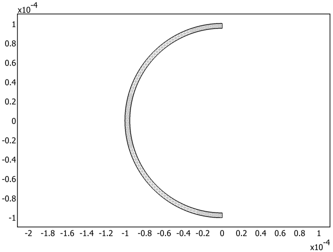
- A single cell experiences a contraction on one side, and an expansion on the other, resulting in the flask shaped change we observe.

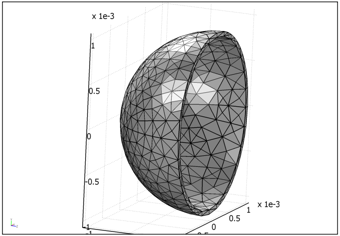
LINE / ARC OF CELLS GEOMETRY



- A single straight line of cells (in series) is used to model the ellipsoid-flask-ellipsoid travelling wave observed experimentally
- The travelling wave was modeled using a volume increase equivalent to thermal expansion. The equation used to represent this is

2D/3D Posterior Geometry

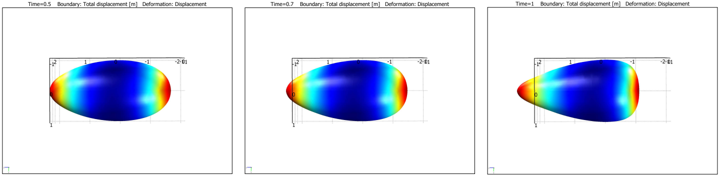




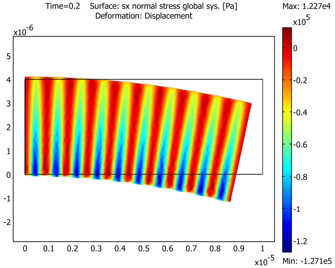
- Surgical mutant removes anterior half, and inversion still occurs
- Posterior inversion is controlled by actomyosin contraction
- Combined with anterior half, the contraction + the geometry change can explain the entire inversion.

Outline

Single Cell Shape Change

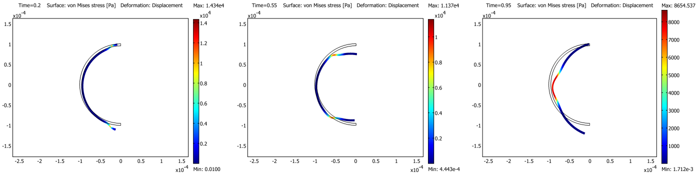


Line / Arc of Cells



Fixed Line of Cells Travelling Elongation Wave `file:///F:/SolidsES240/project/lineCellsElongationWave.avi`

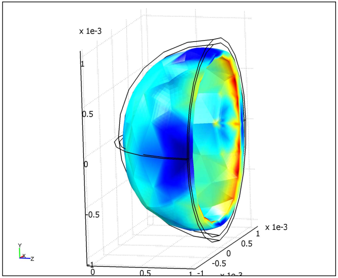
Posterior Inversion - 2D



- Plain strain approximation is used, and doesn't reflect actual geometry properly
- Change in geometry due to contraction begins properly
- Failure due at larger deformation requires further investigation

Posterior Inversion - 3D

Time=0 Subdomain: von Mises stress [Pa] Deformation: Displacement



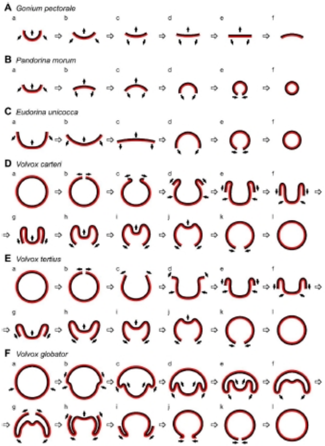
- This plot is the von Mises stress after contraction

Outline

Open questions

- Compare stress and pressure results to see if they are of the right magnitude.
- Viscoelastic tissue model may help account for the maintainence of curvature ofter cell shape change
- 2D model helps to understand cell geometry change, but doesn't account for the pop-through event of the posterior.
- Singularities develop in plastic and FEM models of full inversion at the A/P midline. How does the organism overcome this? Discreteness of cells and bridge rearrangement may account for this.
- Studies of curved sheets may be helpful here.
- Comparison with discrete truss model may be useful, and would account for cytoplasmic bridges more accurately.
- Rheological study of the cell sheet may be useful

Generalize to other Volvocacean inversions



- Other species of Volvox exhibit inversion as well
- Gastrulation in *Xenopus laevis* is model for vertebrate gastrulation; a process that is essential in many "higher" organisms

Thin 2D Shells vs. Thin 3D Shells

- Thin shell theory has been used to describe cell walls, epithelial layers, and other thin biological membranes
- Thin shell theory is implemented as a 2D sheet that interacts with 3D structures as a boundary
- These thin shells can also be modeled as 3D sheets, with a single layer of elements in the thickness.
- Are these equivalent? Which is more accurate for large, nonlinear deformations?
- Snapping Membrane
  `file:///F:/SolidsES240/project/snapMembrane.avi`

The End