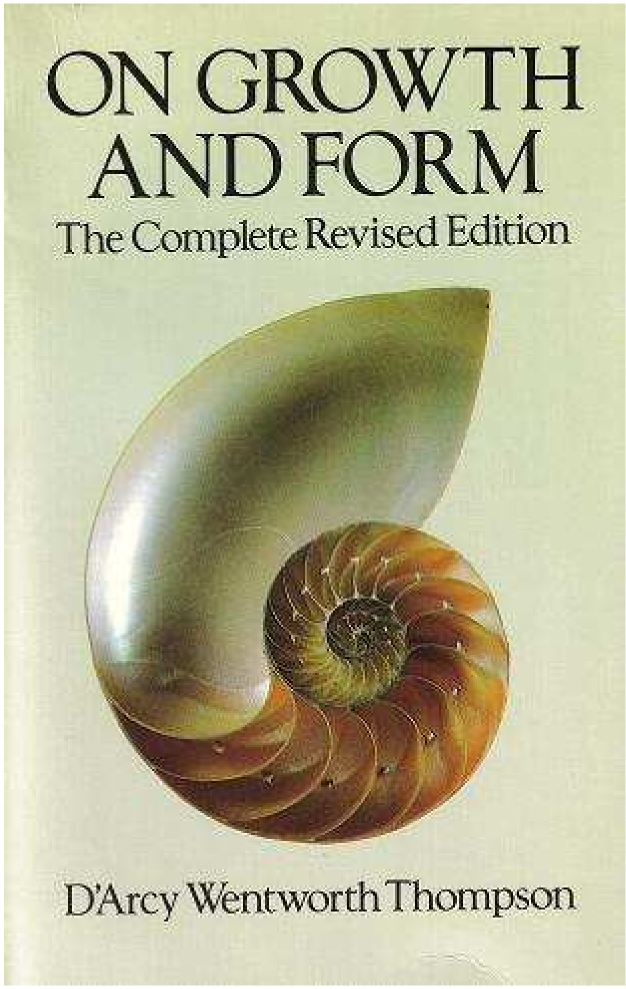


1860-1948

Mathematician, Naturalist, Greek scholar

How far even then mathematics will suffice to describe, and physics to explain, the fabric of the body, no man can foresee.....

Cell and tissue, shell and bone, leaf and flower, are so many portions of matter, and it is in obedience to the laws of physics that their particles have been moved, moulded and conformed. They are no exceptions to the rule that God always geometrizes. Their problems of form are in the first instance mathematical problems, their problems of growth are essentially physical problems, and the morphologist is, *ipso facto*, a student of physical science.

Simple aspects of growth and form (morphogenesis)

L. Mahadevan

Harvard University

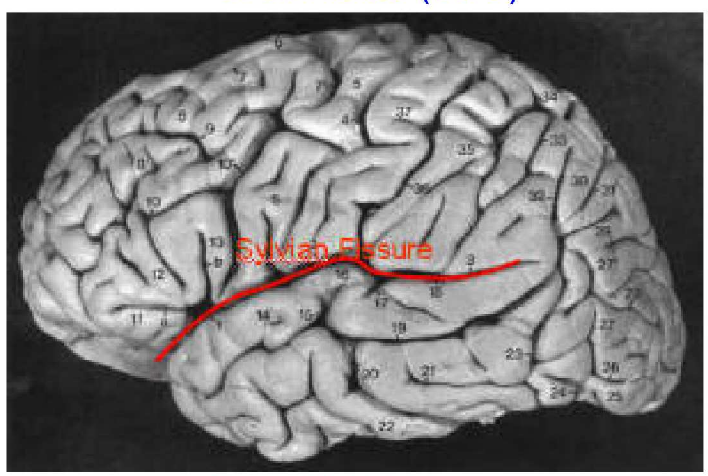
Pollen tube growth

Otger Campas

Leaf and ribbon form

Haiyi Liang

Brain folds (sulci)

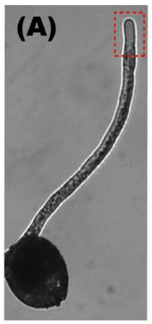


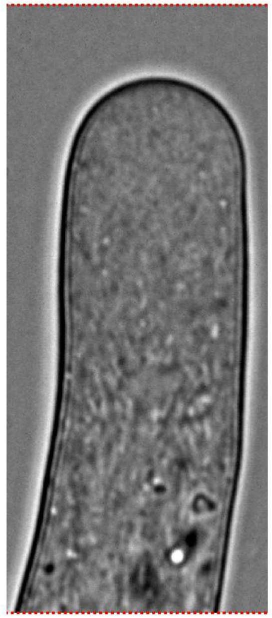
Evan Hohlfeld

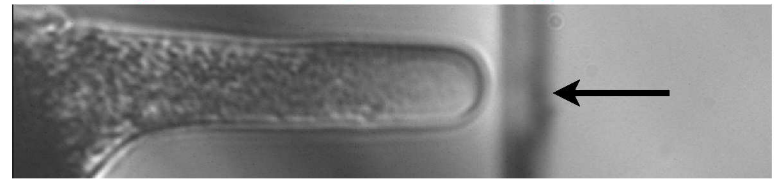
Campas, LM (2008)

Pollen tubes: growth, movement and form

turgor driven hydraulic engine



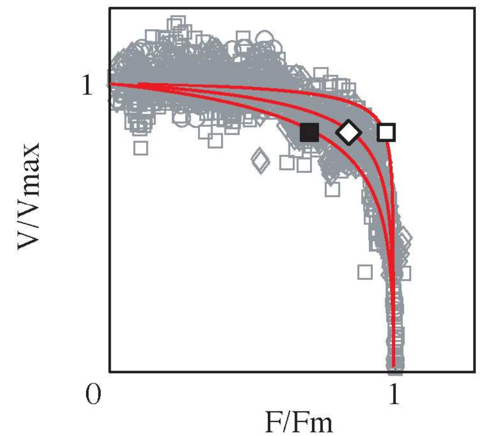




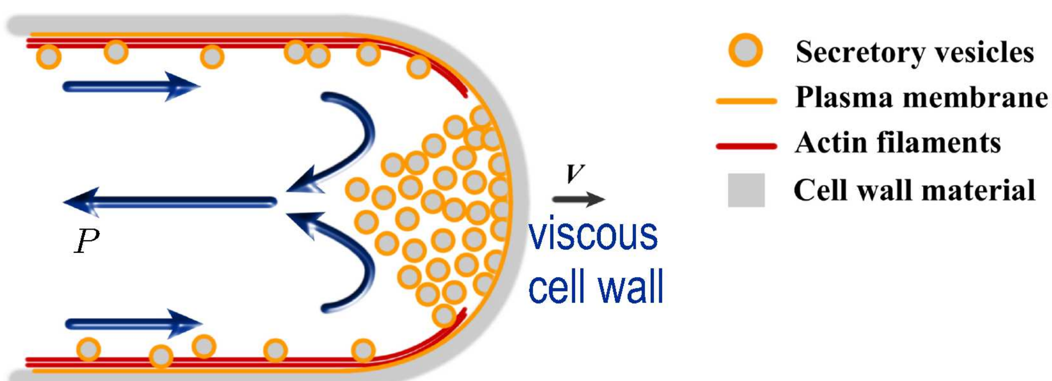
$l_s \sim 100\mu m - 1mm$

load plate

Force-velocity curve



Tip growth



- Geometry (tubular)
- Transport (growth)
- Mechanics (+ chemistry)

new uncrosslinked (fluidized) material at tip ---- flow due to internal turgor ---- ---- gelation transition ---- rigidifies and leaves tube behind ---tip moves forward.

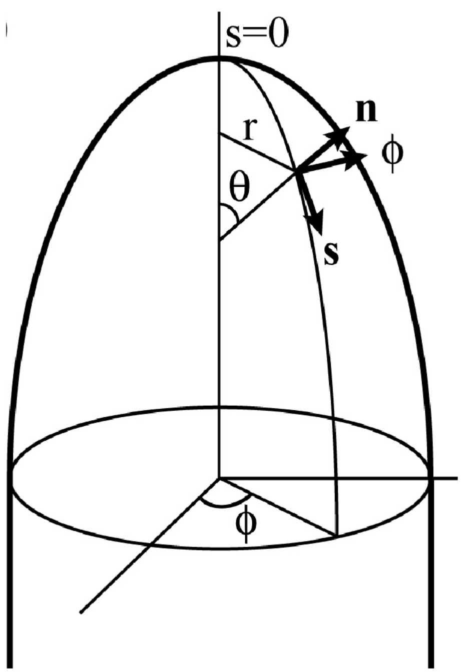
Questions:

- Shape ? $R, \quad H \quad ?$
- Speed ? $V\ ?$
- ~~Stability ?~~

Dependence on:

- internal turgor $P?$
- rheology, flux $\mu(s), \quad J(s)\ ?$
- ~~external load~~ $F\ ?$

Theory



$$\kappa_s = \frac{\partial \theta}{\partial s} \qquad \kappa_\phi = \frac{\sin\theta}{r}$$

geometry

$$\kappa_s \sigma_{ss} + \kappa_\phi \sigma_{\phi\phi} = P$$
$$\kappa_\phi \sigma_{ss} = \frac{P}{2}$$

force balance

$$\sigma_{ss} = 4\mu h \left[\frac{\partial u}{\partial s} + \nu \frac{d \log r}{dt} \right]$$
$$\sigma_{\phi\phi} = 4\mu h \left[\nu \frac{\partial u}{\partial s} + \frac{d \log r}{dt} \right]$$

incompressibility $\nu = 1/2$

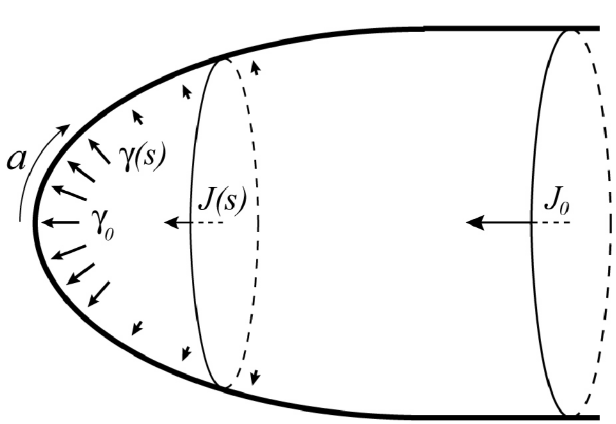
constitutive law - simple viscous fluid ...

$\boxed{u(s,t), \ r(s,t), \ h(s,t)\ ?}$

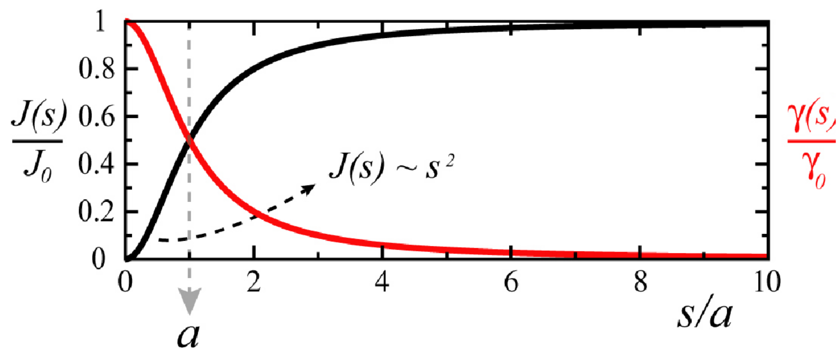
$$2\pi r \gamma(s,t) = \frac{\partial J(s,t)}{\partial s} \qquad \frac{\partial (rh\,\rho_w)}{\partial t} + \frac{\partial (urh\,\rho_w)}{\partial s} = r\,\gamma$$

mass balance

$\boxed{\mu(s), \quad J(s)\ ?}$



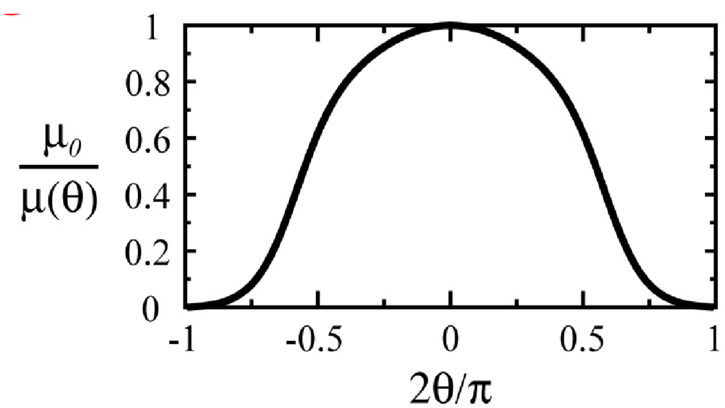
$$J(r) \sim r^2, \text{ as } s \sim r \text{ for } \theta \to 0$$



$$J(r) \sim J_0 \text{ as } \theta \to \pi/2$$

$$2\pi r \gamma(s,t) = \frac{\partial J(s,t)}{\partial s}$$

a transport length scale



$$\mu(s) \sim \mu_0, \ \theta \to 0$$

$$\mu(s) \sim (\pi/2 - \theta(s))^{-1}$$

other details of functional form do not matter !

Steady state:

$$\begin{aligned} u(s) &= \frac{(2-\nu)\,\kappa_\phi - \kappa_s}{8\mu h\,(1-\nu^2)\,\kappa_\phi{}^2}\,\frac{\tan\theta}{\kappa_\phi}\,P \\ \frac{du}{ds} &= \frac{(1-2\nu)\kappa_\phi + \nu\kappa_s}{8\mu h\,(1-\nu^2)\,\kappa_\phi{}^2}\,P\,, \\ \frac{d(urh)}{ds} &= \frac{r\gamma}{\rho_w}\,, \end{aligned}$$

Scaling ?

Force balance $PR^2 \sim \mu V h$

Mass balance $\rho_w V R h \sim J \sim \gamma_0 a^2$

$R \sim (\mu_0 J_0 / P \rho_w)^{1/3}$ characteristic tube radius

Asymptotics near the tip:

$R_0 \sim \frac{\mu_0 \gamma_0}{P \rho_w}$ = tip radius (balancing turgor-driven flow with material transport)

$u_0 \sim \frac{\gamma_0 r}{h_0 \rho_w}$ = velocity near tip (mass balance)

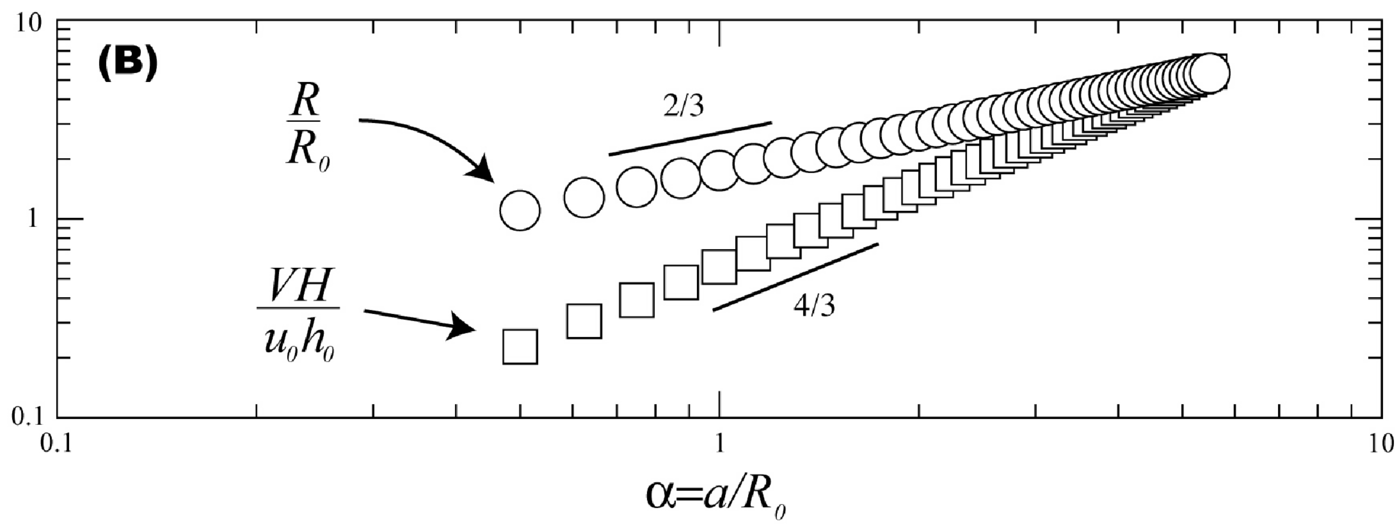
Dimensionless parameter: $\alpha = a/R_0$

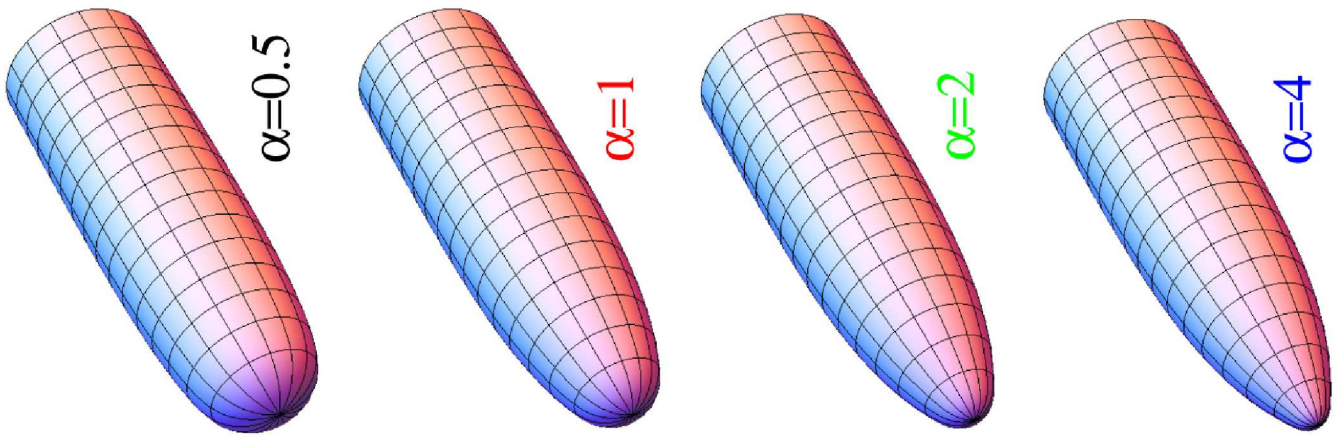
h_0 = thickness at tip (microscopic mechanism)

Scaling laws

$$R/R_0 \sim \alpha^{2/3} \qquad VH/u_0 h_0 \sim \alpha^{4/3}$$

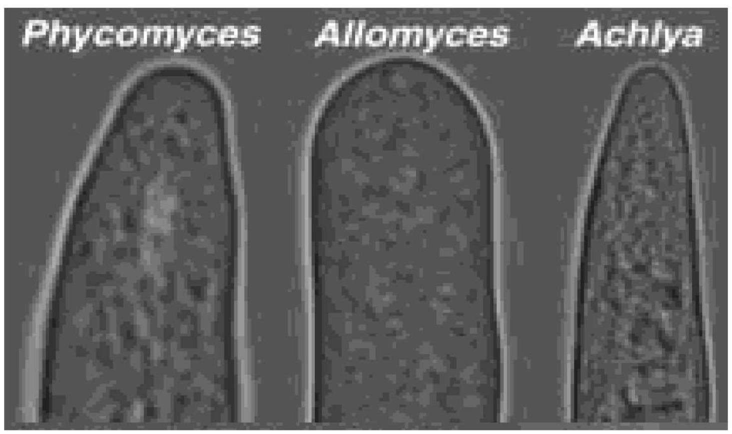
Numerical solution ....

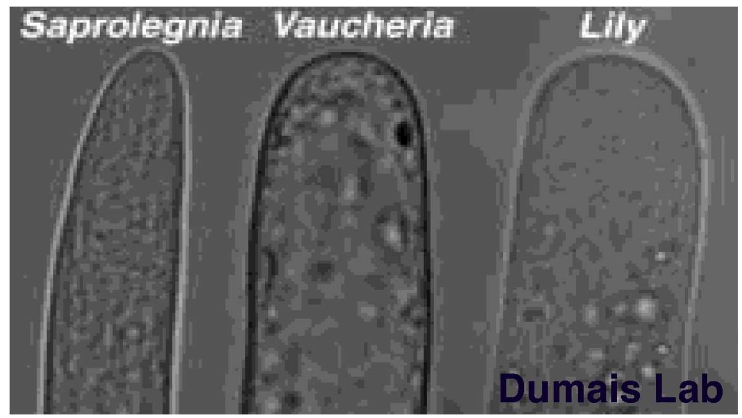


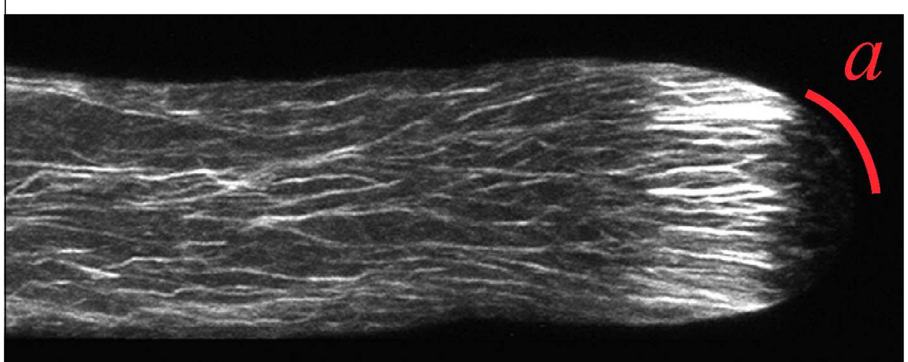


One parameter family
of solutions ....

Reinhardt rule
- relating shape to speed ?







Hepler Lab

Comparative morphology ? $\alpha = aP\rho_w/\mu_0\gamma_0$

Tip thickness h_0 ?

Stability ? w.r.t. transport, pressure,... ?

Kelp, leaf and ribbon morphology

Koehl, Silk, Liang, LM (2008)

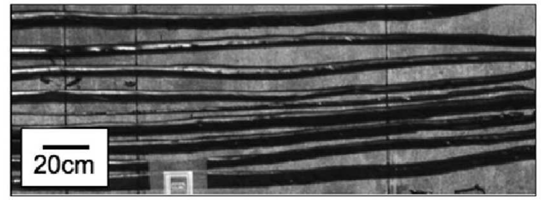
- phenotypic plasticity in *Nereocystis leutkeana*

slow flow - wide ruffled blades

high photosynthetic efficiency
- flapping, no shade

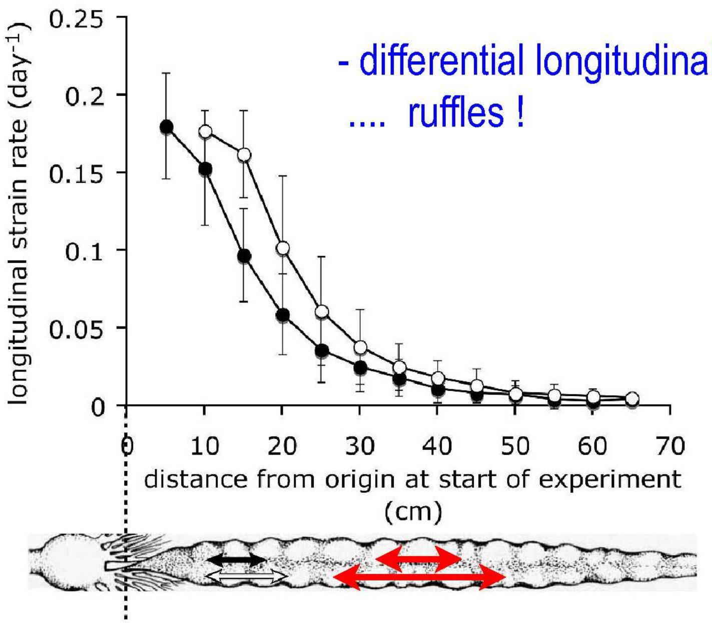
How ?

rapid flow - narrow straight blades

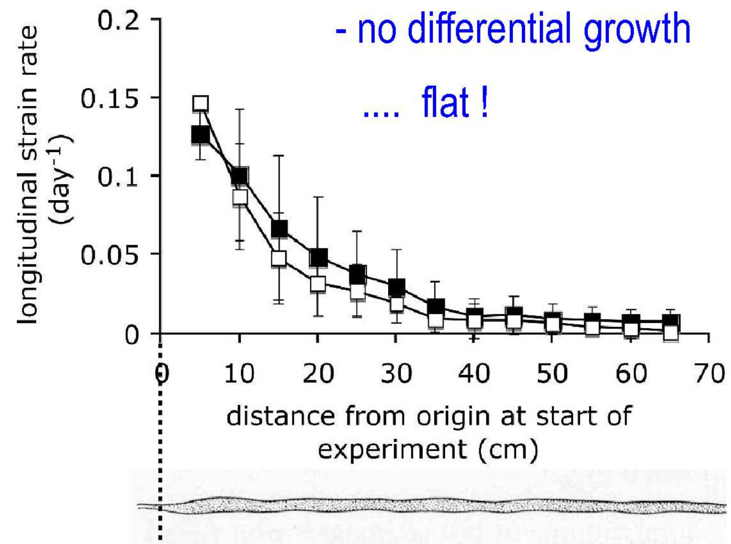


flapping + low drag!

- differential longitudinal growth
.... ruffles !



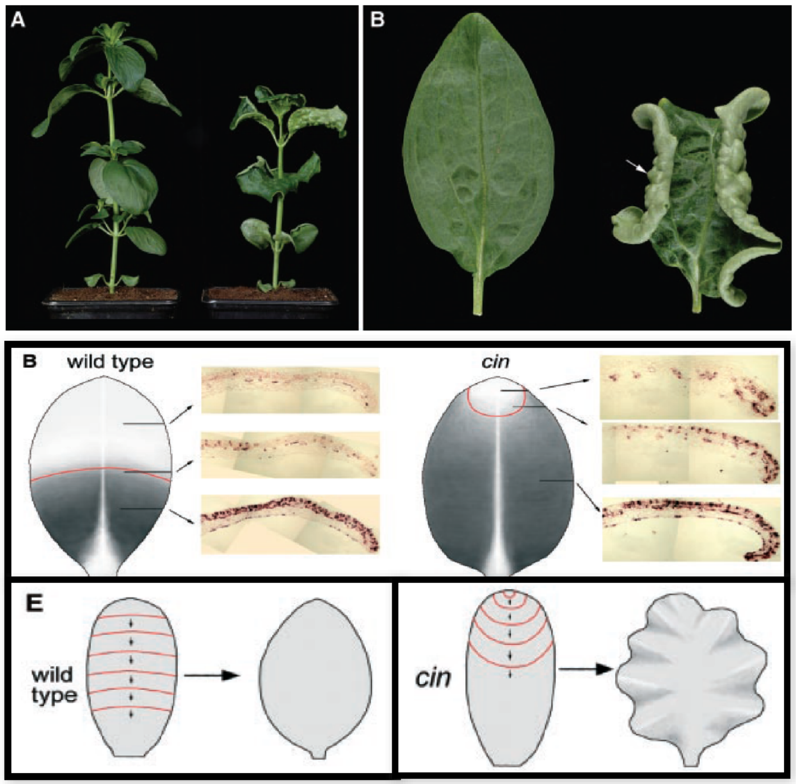
- no differential growth
.... flat !

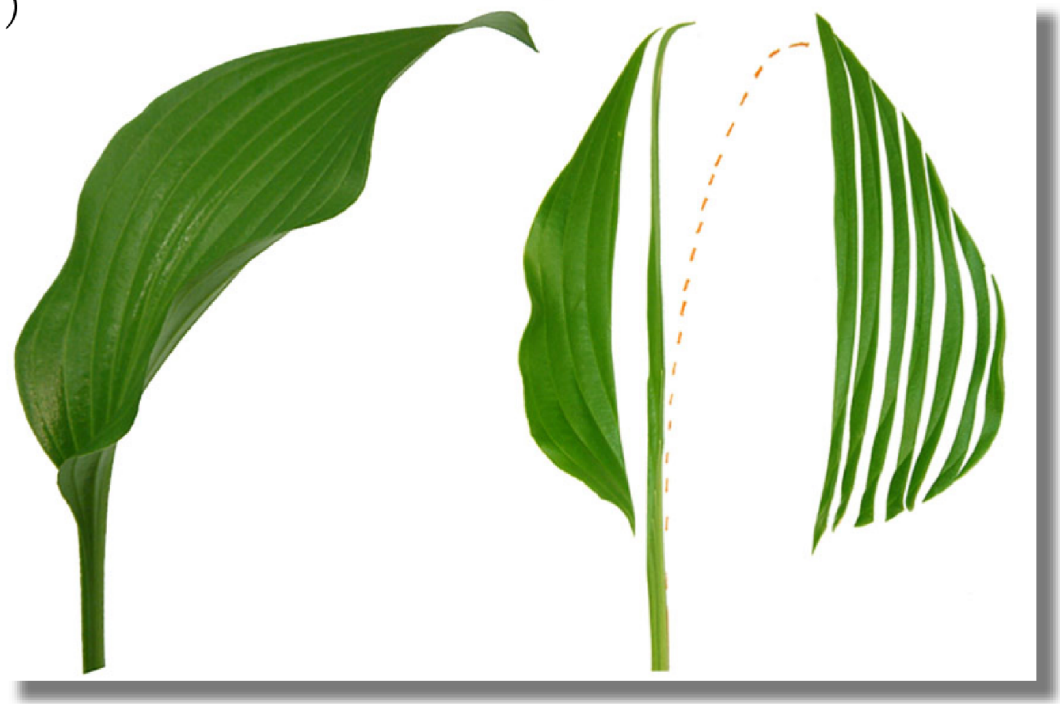


- Genetic control of surface curvature in *Antirhinium*

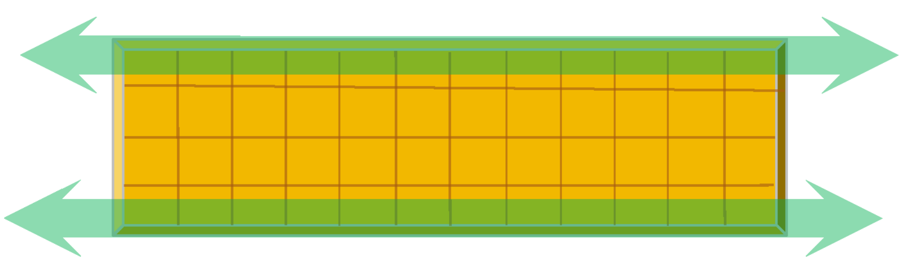
Surgery -- relaxation of internal strains !

Nath et al (2003); Science

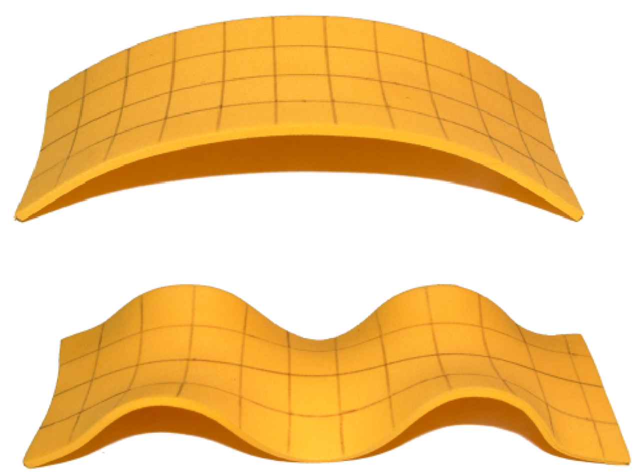




Morphology = growth-induced differential strains
+ elastic energy minimization....



?



Saddle

Ripple

Sharon et al,
Marder et al, Boudaoud et al,

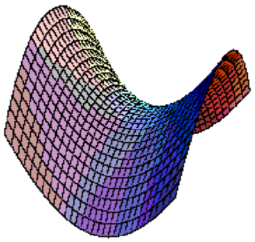
Phase diagram ?

Geometry

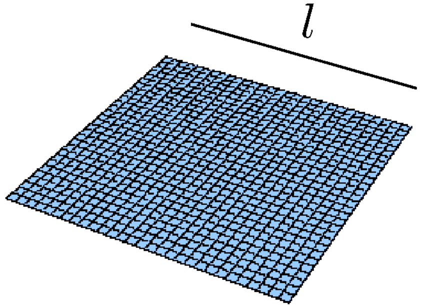
κ_1, κ_2 principal curvatures

Mean curvature $\kappa_M = \frac{1}{2}(\kappa_1 + \kappa_2)$

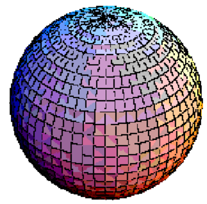
Gauss curvature $\kappa_G = \kappa_1 \kappa_2$



$\kappa_G < 0$



$\kappa_G = 0$



$\kappa_G > 0$

κ_G intrinsic - isometric invariant

Physics

thickness h

$h/l \ll 1$

$h\kappa \ll 1$

long wavelength deformations

Stretching (tangential) mode

strain $\gamma \sim \frac{\Delta l}{l}$

energy/area $U_s \sim Eh\gamma^2$

Expensive

Bending (transverse) mode

curvature $\kappa \sim \frac{\Delta \theta}{l}$ strain $h\kappa$

energy/area $U_b \sim Eh(h\kappa)^2 \sim Eh^3\kappa^2$

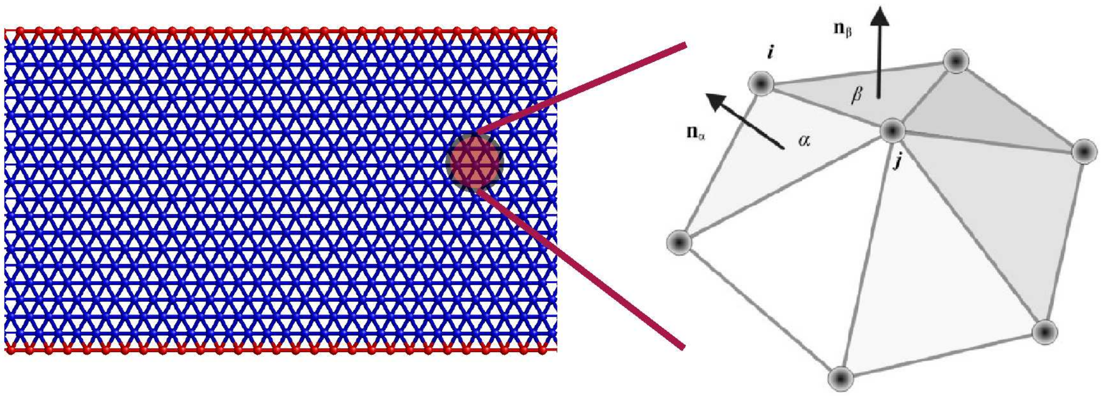
Cheap

E - modulus

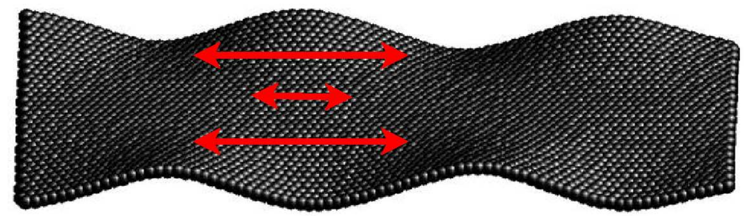
- Coupling of stretching to bending ? - via geometry $\kappa_G \neq 0$

Liang, LM (2008)

Energy minimization ?



e.g. ribbon crinkling and wrinkling ...



$$U_{disc} = \frac{S}{2}\Sigma_{a,b}(|\mathbf{r_a} - \mathbf{r_b}| - \underline{l_{ab}})^2 + \frac{B}{2}\Sigma_{i,j}|\mathbf{n_i} - \mathbf{n_j}|^2$$

stretching energy

bending energy

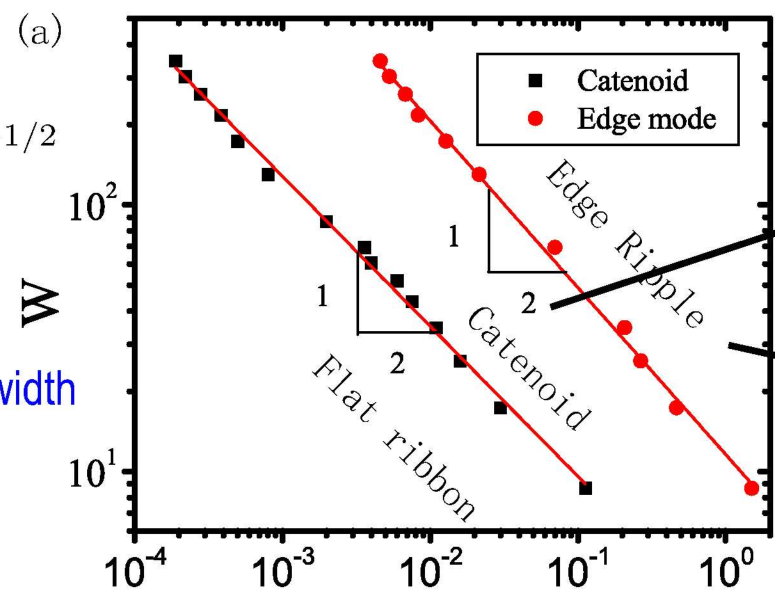
rest length

$$S \sim Eh, \quad B \sim Eh^3$$

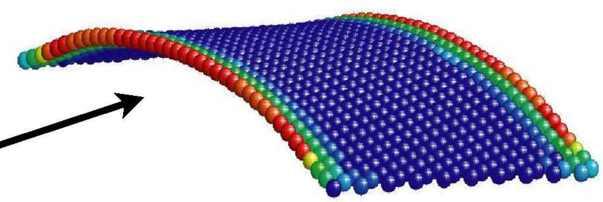
S. Seung , D. Nelson (1988)

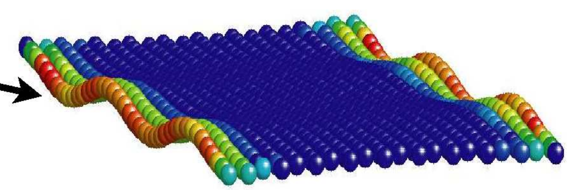
$W/h \sim \beta^{-1/2}$

scaled width



edge “eigen”-strain





Scaling ?

$\epsilon_{gmax} = \beta$

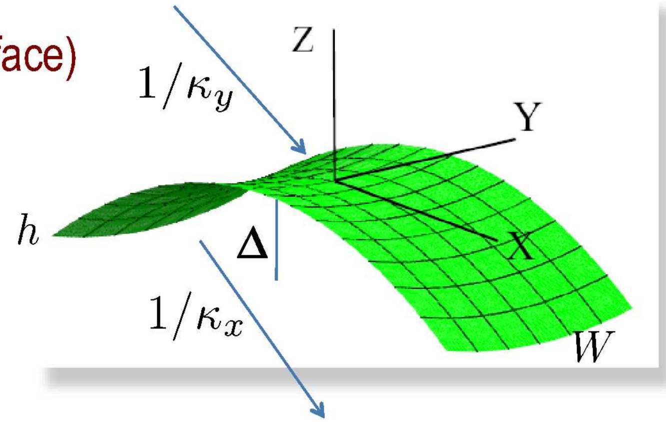
onset of buckling

stretching bending

$$S\beta^{*2} \sim B\kappa^2 \sim B\Delta^2/W^4, \quad \Delta \sim h$$

$$\beta^* \sim h^2/W^2$$

I - Saddle (surface)



$$\beta \sim -\Delta\kappa_x \qquad \kappa_y \sim \Delta/W^2$$

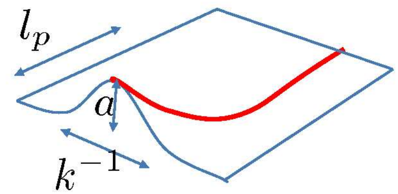
$$\kappa_x\kappa_y \sim -\beta/W^2$$

$$\kappa_x + \kappa_y \sim -\beta/\Delta + \Delta\,/W^2$$

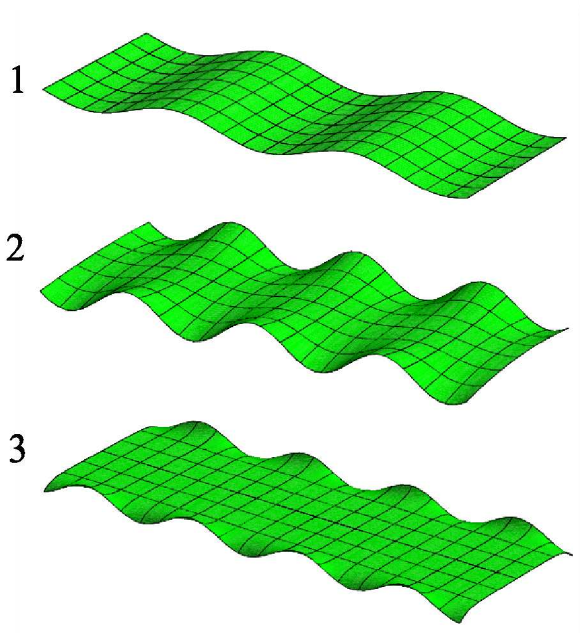
II - Periodic (edge)

persistence of a pinch ...

$$\underbrace{Eh^3(ak^2)^2 l_p/k}_{\text{bending}} \sim \underbrace{Eh(a^2/l_p^2)^2 l_p/k}_{\text{stretching}}$$



$$l_p \sim \left(\frac{a}{hk^2}\right)^{1/2}$$



1. Euler buckling

$$l_p \gg W: \;\; \beta^* \sim h^2k^2$$

2. bi-sinusoidal buckling

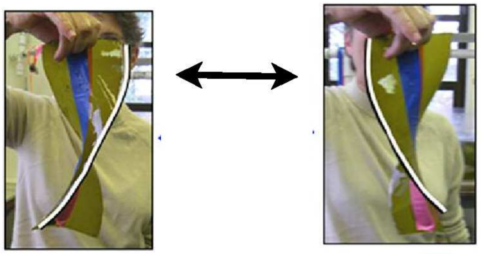
$$l_p \sim W: \;\; \beta^* \sim h^2/W^2$$

3. Edge rippling

$$l_p \ll W: \;\; \beta^* \sim h^2k^2$$

bell boundary layer ... Lamb (1891)

Multistability has been observed ... in algal blades



Koehl/Silk labs

Other examples of growing surfaces - Crochet

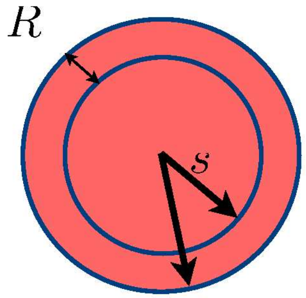
Optimal embedding of the hyperbolic plane H^2 in R^3 ?

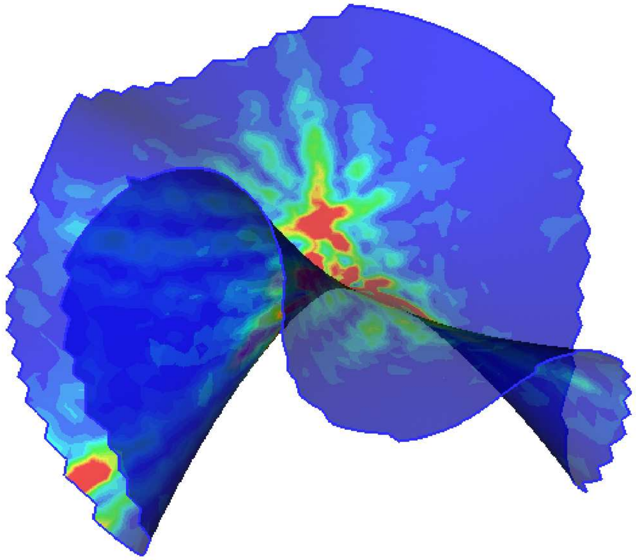
Theorem (Hilbert): There is no real analytic isometric embedding of H^2 in R^3.

Models ? - Poincare, Klein, Lorentz disk ..... but planar !

3-d visualization ? - Thurston/Taimina: Crochet disk with exponentially growing perimeter !

D. Taimina, S. Rowel (2000)





$$s = s_0 e^{R/\rho}$$

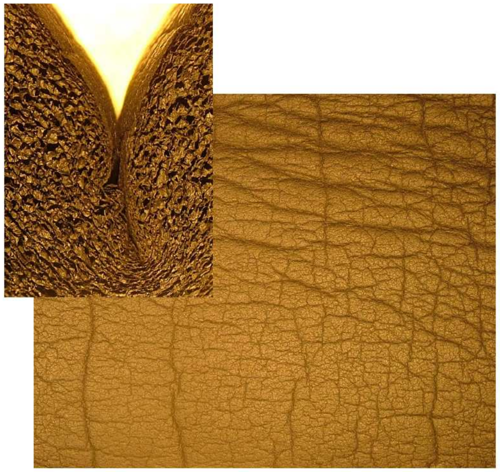
$\kappa_G = -1/\rho^2$

radius of pseudosphere

analytic theory ?

Creases and cusps, or how to lose (part of) a boundary ?

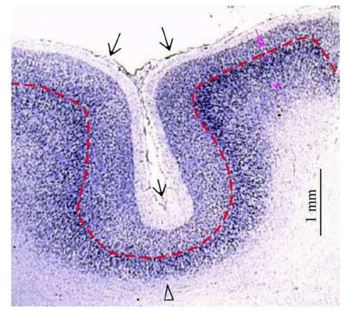
Hohlfeld, LM; 2008



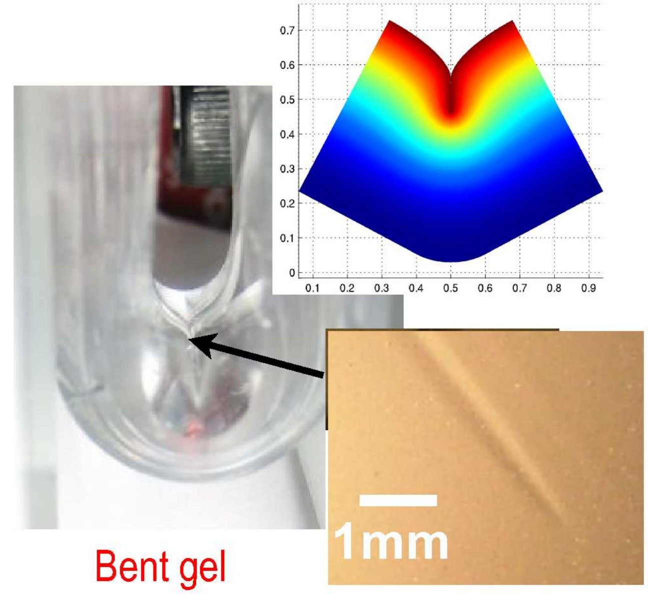
Cellular foam

Swollen gel

Barbas (2003)



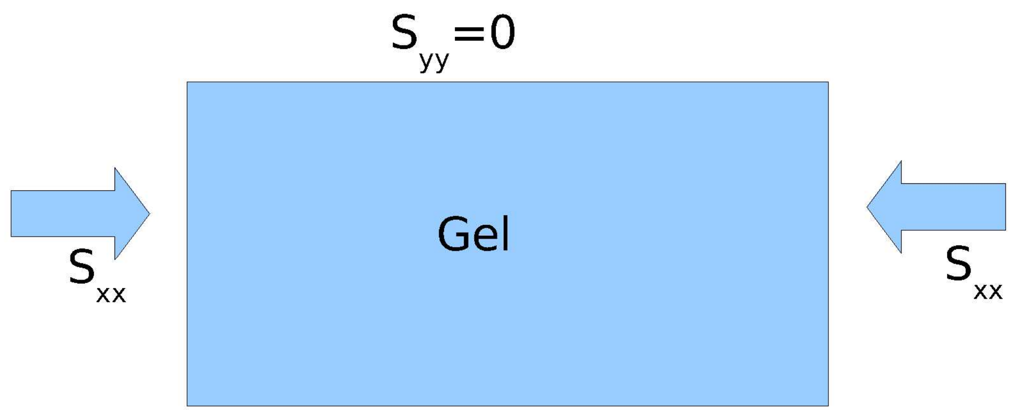
Folded cortex



Bent gel

- anti-crack ?
- topological instability ?
- length scale of crease/cusp ?

Compressing a half space of a gel (Biot; 1960s)



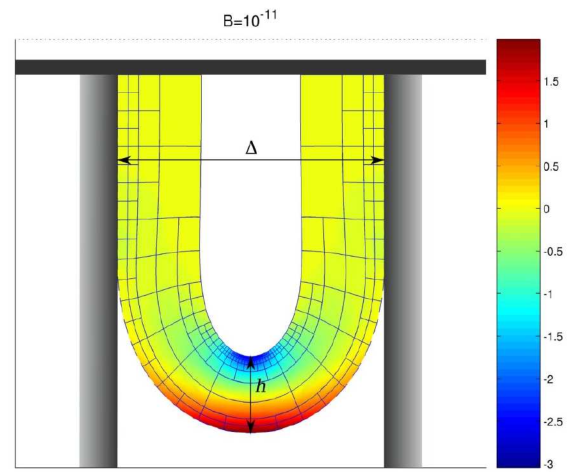
Classical elasticity is scale invariant ....

- infinite wave number instability ... i.e. translation invariance => creases at multiple locations !
- free surface supports surface (Rayleigh) waves .... become unstable when $\epsilon = \epsilon_c = S^c_{xx}/G$

Regularized problem + limiting process ?

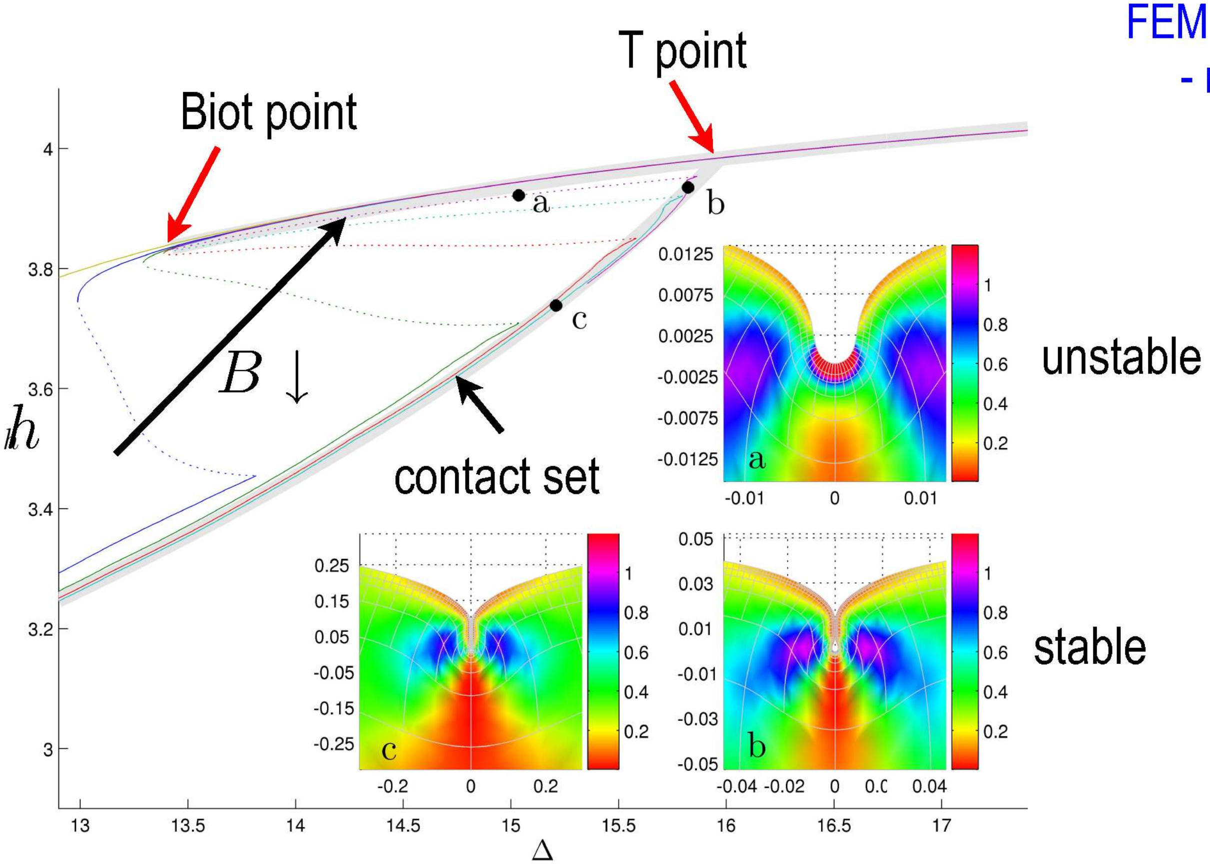
- break translation invariance symmetry

- introduce a skin of small but finite stiffness *B*

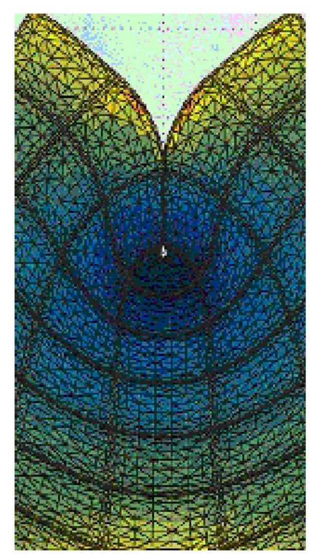


Bifurcation diagram ?
- convergence to a T : (power law as B => 0)

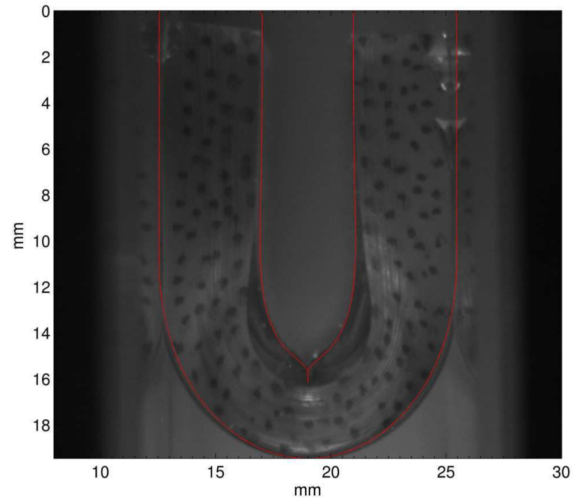
FEM with geometric grid + continuation + contact
- neo Hookean plane strain model



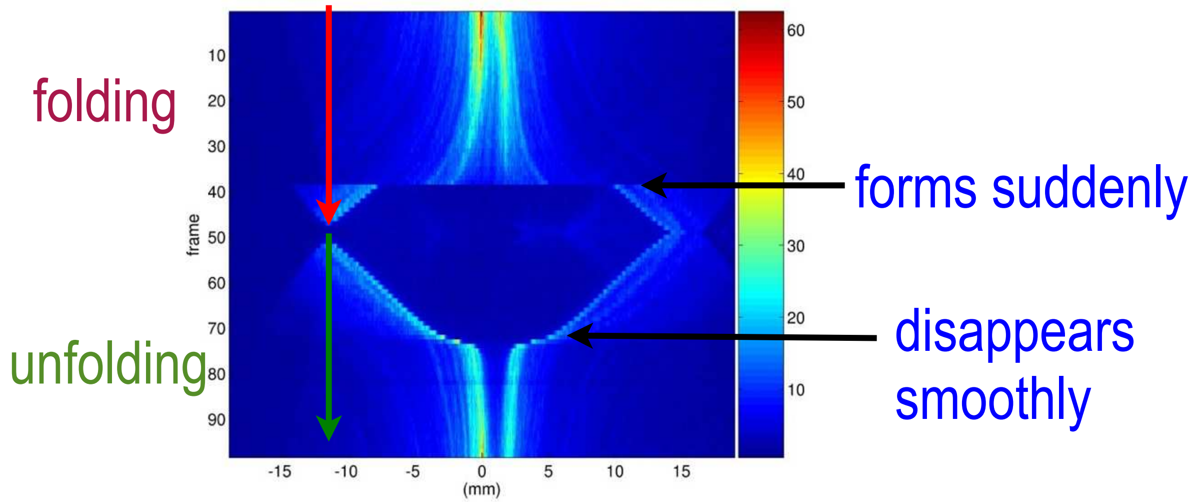
Lagrangian view of cusp



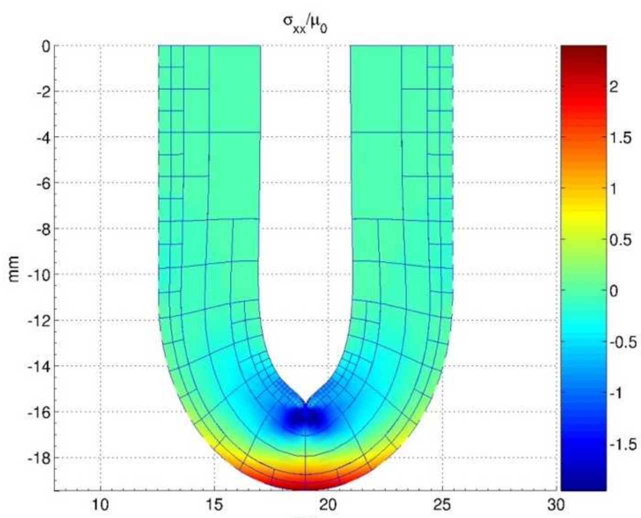
Experiment

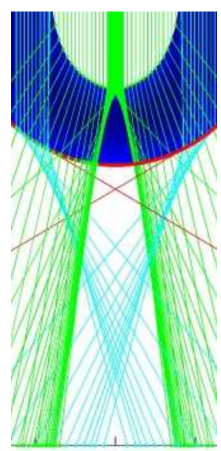


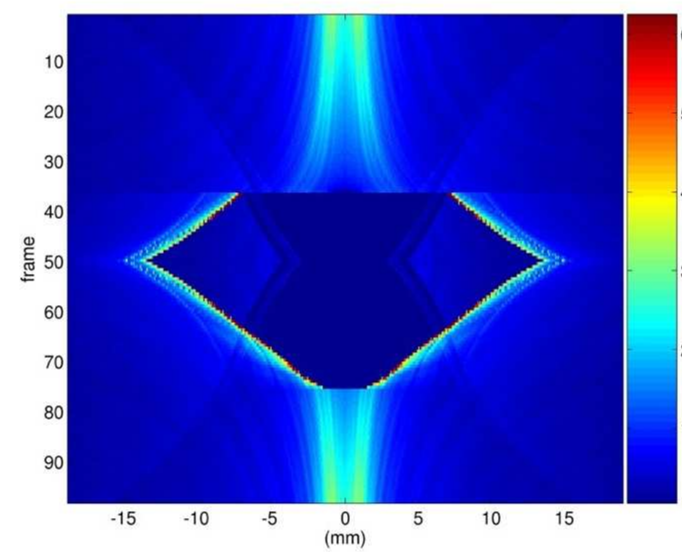
optical caustic signature



Numerical simulation



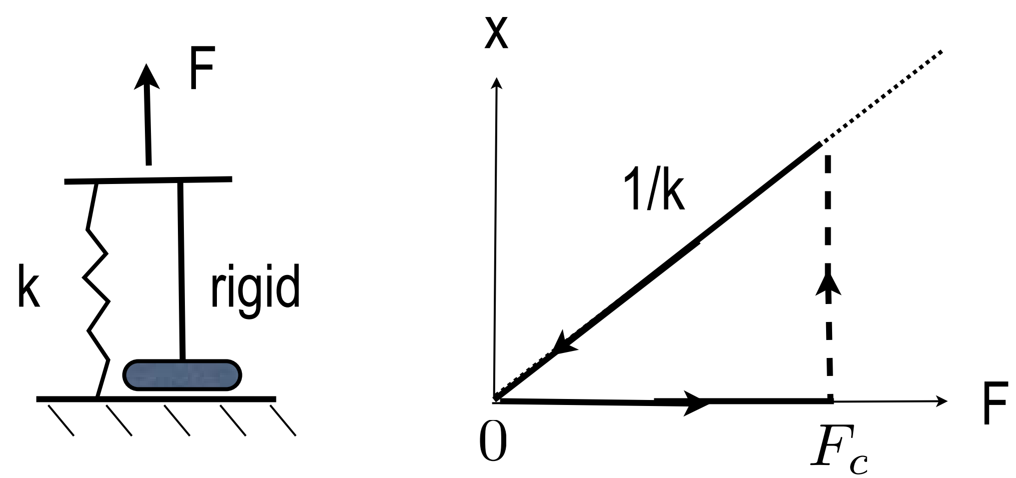




Point bifurcation - an unusual singularity / pattern-forming instability ?

- linear instability fails completely ..... essential singularity at infinite wave number ...
- regularization via contact (no length scale !)
- need to compute nonlinear solutions (stable/unstable).

- 2 critical stresses !
- “perfect” hysteresis



- loss of convexity at a boundary (surface wave speed vanishes)
- loss of boundary - anti-crack !

But the zoologist or morphologist has been slow, where the physiologist has long been eager, to invoke the aid of the physical or mathematical sciences; and the reasons for this difference lie deep, and are partly rooted in old tradition and partly in the diverse minds and temperaments of men.

... he is deeply reluctant to compare the living with the dead, or to explain by geometry or by mechanics the things which have their part in the mystery of life. ...

But of the construction and growth and working of the body, as of all else that is of the earth earthy, physical science is, in my humble opinion, our only teacher and guide.