MAE 545: Lectures 7,8 (2/27)

Wrinkled surfaces

Shapes of growing sheets

How are villi formed in guts?

Villi increase internal surface area of intestine for faster absorption of digested nutrients.

Lumen patterns in chick embryo and an inner, luminal endo stearna in ahialz alichis fillus formation FI-40014Jyväskylä, Finland. ⁴ inhrvo Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA. ⁶ array of fingerlike projections termed intestinal villi **unich pattens i** ahial ambryo inner endormal tion of smooth muscle is a substantial of the smooth muscle in the substantial of the substantial substantial o mends in chick a sion of the gut segments of the grown in vehicle alone developed a layer of circular smooth muscle and formed luminal folds.

face of the guidant of the gut the gu To a convolution DAPI marks cell nuclei Morphogenesis and Differentiation of Constrained Azimuthal Growth of the

as in marked and birds, the angles of the state of the state and birds, the state of the sta \mathbb{R} abrus interved interved in the Miles aSMA marks smooth muscle actin Endoderm-Mesenchyme Composite th muscle actin

E…: age of chick embryo in days tissues can lead to epithelial buckling is classical mbryo in days **compared to example.** plain longitudinal ridge formation in healthy and

sity, Cambridge, MA 02138, USA. ⁷ Wyss Institute for Biologically It muscles arow slower us maconoo grom oromor an softer mesen *These authors contributed equally to this work. and endoderm layers Quantifying the constraint provided by the mus-**Stiff muscles grow slower** of the muscle layer in the control samples to the than softer mesenchyme

This individual compression due of the inner circumference of the inner circumferences striped wrinkles to differential growth

to 0.55 across the developmental stages from E8 to E12 (Fig. 2B). However, the separation of the separation **endoderm from the composite of mesenchyme**

3 A. Shyer et al., Soience 342, 212 (2013) $\frac{1}{\sqrt{2}}$ second longitudinal muscle layer forms, interior to the formation of villiant $\frac{1}{\sqrt{2}}$ Schematic illustration of villiant $\frac{1}{\sqrt{2}}$ compression and buckling. This suggests that suggests that \mathcal{L}

Lumen patterns in chick embryo (1, 2) although a variety of morphologies such as \blacksquare attarna in ahiak allerns in Ghick *These authors contributed equally to this work. \mathbf{m} hrv \mathbf{n} \mathbf{r} indiyo \mathbf{v} the Chick Midgut **LUNTURII PALLEI** University, Cambridge, MA 02138, USA. is in chick em †Corresponding author. E-mail: lm@seas.harvard.edu (L.M.); face of the gut transforms from a smooth surface **Lanch pattens in Giller** \blacksquare USA. ⁸ Kavli Institute for Nanobio Science and Technology, Harvard University, Cambridge, MA 02138, USA.

ferentiation of smooth muscle layers. (Left photos) Transverse sections of $\mathcal{M}(\mathcal{M})$ close-ups of left photos, showing muscle layers. (Right) Whole-mount

4

exterior to the circular layer (arrowhead) coincident with the formation of zigzags whose periodicity is maintained but with increasing amplitude and compactness over time. (D) A second longitudinal muscle layer forms, interior to the circular layer (arrowhead), coincident with the formation of villi. (E) Schematic illustrating the process A. Shyer et al., Science **342**, 212 (2013)

Lumen patterns in chick embryo Until embryonic day 7 (E7), the gut tube, with its inner endodermally derived epithelium and outer <u>tabina de l</u> axial compression that mimics the role of the arne in chick a za aristmenters (fundameters (fundameters (fundameters ϵ derm (supplementary materials, fig. S9, and movie mhryn initially, the endoderm and mesenchyme are the endoderm and mesenchyme are the endoderm and mesenchyme a assumed to have \mathbf{y}

Villi start forming at E16 because **Though and Lease and Lease and Lease Canada** of the faster growth in valleys across the mesenchyme and endoderm before villi **Propertion in Addition in Addition** VIIII start forming \sim f the fer Although additional compression from the inner

Zigzag Zigzag Twisting Bulges

images of corresponding gut lumen pattern; longitudinal axis runs top to bottom. Scale bars indicate 100 mm; time is in days past fertilization (e.g., E6). (A) Lumen is smooth before muscle layers form. A, anterior; P, posterior. (B) Longitudinal ridges for $\mathbf{v}_\mathbf{I}$ **in other organisms! The second of the set o The same mechanism for villi formation also works** Previous work in mouse has shown that, alwill formation also works arise, as villi form, proliferating cells are found

5 5 A. Shyer et al., **Science 342**, 212 (2013) patterns may be a displaced a displacement of the displacement of the displacement of the displacement of the σ

Why are guts shaped like that?

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RESEARCH ARTICLE **Guts in chick embryo** RESEARCH ARTICLE finite radius of the loop. To deform the gut into a loop of radius R, the in chick embryo exerted by the membrane with strain energy and a length α width with strain energy and a length R

Above to derive Surgically removed guts from chick embryo strip is the size of the size of the size of the size of the strip is the strip is the strip is the size of t $\mathbf{f}_{\mathbf{M}}$ \mathbf{y} uture to a thin, double-epithelial sheet with no observable left–

separation from **mesentery** Cells per mm2 \overline{a} 12 **Tube straightens after** attached, there is a differential strain,e, that compresses the tube axially

we faetor than Tube grows faster than were under the dorsal to cut the dorsal SMA in order to cut the document of the document of the during guide a mesentery sheet! \mathbf{A} comparison of the results of our predictions with \mathbf{A} and \mathbf{A} and \mathbf{A} and \mathbf{A} igntens after the measurement of the grows faster than

7

T. Savin et al., **Nature 476**, 57 (2011) **tio**, si (2011) \overline{z} $\overline{$ b, Prodition in the End of Andrew States (blue) and the End method is and mediant of the End method is and mes vin e

Synthetic analog of guts tion whereas the mesentery relaxes to an almost flat configuration implies that the tissues behave elastically, a fact that will allow us to **Synthetic a**

8

Rubber model of guts

Chick guts at E12

stretched uniformly along its length and then stitched to a straight, unstretched rubber tube (gut) along its boundary; the differential strain minics of the differential strain minics the differential strain minics the differential strain minics the differential strain minics of the differential strain differential growth of the two times. The system was then allowed to relax, free to relax, free to relax, free
, the system was the $F = \frac{F}{2}$ constructed wavelength of the rubber model of the rubber sheet (mesentery) was sheet (mesentery) was sheet (me
The rubber sheet (mesentery) was sheet (mesentery) was sheet (mesentery) was sheet (mesentery) was sheet (mese stretched uniformly along the composite rubber model to a straight, uniformly along the composite rubber model \mathbf{r}_i rubber tube (gut) along its boundary; the distribution of the $\frac{d}{dt}$ differential growth of the two times. The system was then allowed to relax, free allowed to relax, free allowed to relax, $\frac{d}{dt}$ **What is the wavelength of**

Compression of stiff tube on soft elastic mesentery sheet

$$
\begin{array}{c}\n 2h_0 \uparrow \\
\hline\n L\n \end{array}
$$

assumed profile $h(s) = h_0 \cos(2\pi s/\lambda)$

amplitude of wrinkles

$$
h_0 = \frac{\lambda}{\pi} \sqrt{\frac{\Delta}{L}} = \frac{\lambda \sqrt{\epsilon}}{\pi}
$$

deformation of the soft mesentery decays exponentially away from the surface

w

d

 $2r_0$ $2r_i$

y

 $h(s, y) \approx h_0 \cos(2\pi s/\lambda) e^{-2\pi y/\lambda}$

bending energy of stiff tube

$$
U_b \sim L \times \kappa_t \times \frac{1}{R^2} \sim L \times E_t I_t \times \frac{h_0^2}{\lambda^4} \sim \frac{LE_t I_t \epsilon}{\lambda^2}
$$

deformation energy of soft mesentery

$$
U_m \sim A \times E_m d \times \epsilon_m^2 \sim L\lambda \times E_m d \times \frac{h_0^2}{\lambda^2} \sim L E_m d\lambda \epsilon
$$

minimize total energy (U_b+U_m) **with respect to**

$$
\lambda \sim \left(\frac{E_t I_t}{E_m d}\right)^{1/3}
$$

bending stiffness of tube $\kappa_t = E_t I_t$ $\kappa_t \propto E_t (r_0^4 - r_i^4)$

Wavelength of oscillations in guts \mathbf{M}_{e} similar set of measurements the course of gut development in mouse with α birds, the geometrical and biophysical properties of the developing might be regulated by mechanical feedback. Discussion $T_{\rm tot}$ investigate the physical origins of the physical origins of the physical origins of the physical origins $T_{\rm tot}$ developed a simple simulacrum of the gut–mesentery composite \mathbf{u} silicone rubber tube (mimicking the guide the guide sheet) and a thin latex sheet shee

10

 \blacksquare

10 **chick quail finch mouse**

1/3 1/3

 q *uail*

chick

at Boston University. Fertile Japanese quail eggs were obtained from Strickland results are consistent with the scaling law in equation (1) across species. Black *E*m

Savin et al., Nature $476, 57$ (2011) T. Savin et al., <u>Nature</u> **476**, 57 (2011)

Compression of the soft existing and soft existing energy of soft exists and soft exists and

when soit elastic material is compressed by more than 55%
surface forms sharp creases. This is effect of nonlinear elasticity! When soft elastic material is compressed by more than 35%

Swelling of thin membranes on elastic substrates

12 12 T. Tallinen et al., **PNAS 111**, 12667 (2014) $F = \frac{1}{2}$ and subset to different subsets in a layered material subsets to different $\frac{1}{2}$

Cortical convolutions in brains

Migration of neurons to the cortex leads to "swelling" of gray matter!

Fetal/children brains 2.5 **Formation of cortical convolutions in developing brains a** Gwelet a Gwelet a

hrai **Magnetic resonance images (MRI) of fetal brains**

GW 22−23 GW 25−26 GW 28−29

GW 33−34 3D-printed Brain GW 36−37

h gestational week (GW): age of fetus in weeks

Numerical simulations of developing brain $\overline{}$ 19 **Diam 11** *t* developing broin

Initial condition: shape from MRI image of fetal brain at GW 22. GW 33−34 GW 36−37 3D-printed brain model Master moulds

Formation of cortical convolutions Example 10.103 Developing brains Nature Physics and **a** Gwelet a ition of cortical cor

Company imported (NIDI) of fatal busin **Magnetic resonance images (MRI) of fetal brains**

GW 33−34 GW 36−37 3D-printed brain model Master moulds

Tangential \blacktriangleright

expansion

GW 22-23

a Gwelet a Gwelet a

GW 22−23 GW 25−26 GW 28−29 GW 33−34 GW 36−37 3D-printed brain model Master moulds GW 33−34 GW 36−37 3D-printed brain model Master moulds *t* = *t*¹ *t* = *t*² *t* = *t t* = 0 ³ GW 28-29 $GW 33 - 34$ GW 36-37 GW 33−34 3D-printed Brain GW 36−37

IS IN WAAKS ARE ANDERED AT LOCAL ANDERS AND LOCAL ANDERS AND LOCAL ANDERS AND LOCAL AND LOCA **d** f fai gestational week (GW): age of fetus in weeks α accretional wook (CW): 200 of fotu SiltAtion is a control of $\overline{}$ **d**

MRI image at Io GW 29 $\frac{1}{2}$ *that*
that the *at doveloping brain* **Numerical simulations of developing brain**

 $\mathcal{L}_{\mathcal{A}}$

 $\sqrt{2}$

GW 22

Subplate 1984 White matter *y* 50 White matter zone *^y*

Cortical plate

 $\sqrt{1}$

Cortical plates of the cortical plates of

 Δ

Gw 29

(photographs from ref. 1, adapted with permission from Elsevier). **b**, A 3D-printed model of the brain is produced from a 3D MRI image of a smooth fetal **Figure 1 | Physical mimic and numerical simulation of tangential cortical expansion. a**, Gyrification of the human brain during the latter half of gestation

GW 40

 \sim

GW 26

adult

Adult

Adult

$\sum_{i=1}^n$ $\binom{n}{i}$ $\binom{n}{i}$ $\binom{n}{i}$ from a 3D-printed model is produced from a 3D-printed from a 3D-printed from a 3D MRI in produced from a 3D MRI in a smooth fetale f brain and the silicone moulds for casting. The constrained growth of the constraints for constraints for constr matter) is completed with a solvent (hexanes) over time $\sum_{i=1}^n x_i^2 + \sum_{i=1}^n x_i$ **del progressively pattern of substantial process. And gyri during the sweeps:** $\mathbf{d} \mathbf{w}$ and $\mathbf{d} \mathbf{w}$ substanting from a smooth fetal brain shows that $\mathbf{d} \mathbf{w}$ gyrification as a result of uniform tangential expansion of the cortical layer. The brain is modelled as a soft elastic solid and a relative tangential expansion is Simulation mesh from Fram $\bigcap \mathsf{M}$ $\bigcap \mathsf{A}$ a casting for case Fram **From GW 22 to adult stage:** The Second Stage of the Second St

matter) is coated with a thin layer of gel (cortex) that swells by absorbing a solvent (hexanes) over time *t* (*t*¹ ⇡4 min, *t*² ⇡9 min, *t*³ ⇡16 min). **c**, The layered gel progressively evolves into a complex pattern of sulci and gyri during the swelling process. **d**, A simulation starting from a smooth fetal brain shows gyrification as a result of the brain is modelled as a soft elastic solid and a relative tangential \mathcal{L} imposed on the cortical layer as shown at left, and the system allowed to relax to its elastic equilibrium. 20-fold increase in brain volume (approximately 60 ml to 1,200 ml), P is stingular stimess of the similar stiness of the cortex and subsets and subsets and sublayers implies \mathcal{P} volume increases 20-fold from 60 ml to 1.200 il area increases 30-fold fro), whereas the expanding correction is the expanding correction in σ \bullet similar stiness of the correction \bullet n 80 cm $^{\circ}$ to 2.400 cm $^{\circ}$ \ldots and a non-linear substantial installer substantial installer substantial installer substantial in $\frac{1}{2}$ $\frac{1}{2}$ GW 34 increases 20-f **Figure 1 | Physical mimic and numerical simulation of tangential cortical expansion. a**, Gyrification of the human brain during the latter half of gestation (photographs from ref. 1, adapted with permission from Elsevier). **b**, A 3D-printed model of the brain is produced from a 3D MRI image of a smooth fetal dll Adult **Figure 1 | Physical mimic and numerical simulation of tangential cortical expansion. a**, Gyrification of the human brain during the latter half of gestation (photographs from ref. 1, adapted with permission from Elsevier). **b**, A 3D-printed model of the brain is produced from a 3D MRI image of a smooth fetal **Figure 1 | Physical mimic and numerical simulation of tangential cortical expansion. a**, Gyrification of the human brain during the latter half of gestation brain and then used to create a pair of negative silicone moulds for casting. To mimic the constrained growth of the cortex, a replicated gel-brain (white **COFFICAL AFEA INCREASES 30-TOIG TRON** gel progressively evolves into a complex pattern of sulci and gyri during the swelling process. **d**, A simulation starting from a smooth fetal brain shows gyrification as a result of uniform tangential expansion of the cortical layer. The brain is modelled as a soft elastic solid and a relative tangential expansion is brain volume increases 20-fold from 60 ml to 1,200 ml cortical area increases 30-fold from 80 cm² to 2,400 cm² $\mathcal{L}_{\mathcal{A}}$ arises as a non-trivial combination of a smooth of a smooth of a smooth of a smooth

and a $30-4$ fold increase in correction in correction \mathcal{A} ¹⁵ T. Tallinen et al.. Nature Physics 12, 588 (2016) \mathcal{S} the physically simulated brains \mathcal{S} we the tangential expansion during the fetal stagential expansion during the fetal stagential expansion of the T. Tallinen et al., <u>Nature Physics</u> 12, 588 (2016) 15 15 T Tallinon at al Naturo Physics 12 588 (2016) $\frac{15}{15}$ $\frac{1}{15}$ $\frac{1}{15}$ $\frac{1}{15}$ $\frac{1}{15}$ $\frac{1}{15}$ $\frac{1}{2}$ $\frac{1}{2}$ 15 T. Tallinen et al., Nature Physics 12, 588 (2016) matter) is coated with a thin layer of gel (cortex) that swells by absorbing a solvent (hexanes) over time *t* (*t*¹ ⇡4 min, *t*² ⇡9 min, *t*³ ⇡16 min). **c**, The layered gel progressively evolves into a complex pattern of sulci and gyri during the swelling process. **d**, A simulation starting from a smooth fetal brain shows gyrification as a result of uniform tangential expansion of uniform tangential layer. The brain is modelled as gyrification as a result of uniform tangential expansion of the cortical layer. The cortical layer. The brain is modelled as a soft elastic solid and a relative tangential expansion is modelled and a relative tangential e \mathcal{L} , whereas the expanding cortical layer changes little, with \mathcal{L} shown in Fig. 2a, b exhibit a bulging of \mathcal{S}

Formation of cortical convolutions in developing brains a Gwelet a Gwelet a

Magnetic resonance images (MRI) of fetal brains

GW 22−23 GW 25−26 GW 28−29

GW 33−34 3D-printed Brain GW 36−37

gestational week (GW): age of fetus in weeks
Swelling of gol models of brain

t = *t*¹ *t* = *t*² *t* = *t t* = 0 ³ **Summal ween (GW). age of lettes in weeks**
Swelling of gel models of brain

thin coated layer swells Text + 1 **t** = $\frac{1}{2}$ *t* = $\frac{1}{2}$ *t* = $\frac{1}{2}$ = **In experiments only the by absorbing a liquid!** Γ ₃4 σ 3 σ 3 σ 3 σ 3 σ 3 σ 3 σ model $\frac{1}{2}$ $\frac{1}{2}$

¹⁶ T. Tallinen et al., Nature Physics **12**, 588 (2016) The Second State of the United States of the United States (2016)

 ~ 1 ¹ T. Tallinen et al Wature Physics 12, 588 (2016) we then take the tangential expansion during the fetal stage α $\sum_{i=1}^n \frac{1}{i}$ and $\sum_{i=1}^n \frac{1}{i}$ sections from MRI sections. 17 T Tallings of all Nature Dhysics 12, 588 (2016) 1–1.5 mm at GW 22) and decays rapidly in the subplate (Fig. 1d, ¹⁷ T. Tallinen et al., Nature Physics 12, 588 (2016) extends the cortical plate (which has a thickness of about the cortical plate (which has a thickness of about s of any <u>indicato tinyoloo</u> $s = 0$, ooo (2010)

<u>davalahing hraine davalang dari sebagai dan anak dalam ke</u> **b Formation of cortical convolutions in developing brains** 2.5 \boldsymbol{J} *^t* = 0 (GW 22) *^t* = *t*³ 1 cm **^a c**

Magnetic resonance images (MRI) of brains 40 $\overline{4}$ **10** I′ I iⁱ II Gyrification index

50 100 200 400

adult

Figure 2 | Sectional views of model brains during convolutional development. a, Planform and cross-sectional images of a physical gel-brain showing convolutional development development during the starts from an initial process that starts from an initial sta (right panels). **b**, The coronal sections of the simulated brain (top panels) with comparisons to corresponding MRI sections35,39. **c**, Gyrification index as a Brain volume (ml) **Numerical simulations of developing brain**

GW 22 GW 29 GW 34 GW 40 adult

GW 29 compressive stress in the primary substitution of α cortical growth in our model is relatively uniform in space, the spa S corrected corrections S modele of hrein **Swelling of gel models of brain** in turn is reflected in the dominant orientation or the dominant orientations of the frontal and the frontal and **GW 22 GW 29 GW 34 GW 40 adult**

 Ω_{M} compares to the largest compare of the largest co compressive stress in our model and compressive stress in G **(t=0)** (t=9 min) (t=1 \mathbf{f} first generations of such perpendicular to the maximum perpendicula some deviations from perfect bilateral symmetry. The hemispheres 34 $(t=0)$ $(t=9 \text{ min})$ $(t=16 \text{ min})$ preparation can cause the two hemispheres to dier more than in (right panels). **b**, The coronal sections of the simulated brain (top panels) with comparisons to corresponding MRI sections35,39. **c**, Gyrification index as a \mathbf{r} **GW 22 (t=0) GW 34**

18 T. Tallinen et al., Nature Physics 12, 588 (2016) correlation is particularly correlation in real brains. α and <u>nature infolde</u> is, soo (2010) only the outer layer sweeps the volume grows less than in real brains. The volume grows less than in real brains.

Brains for various organisms

g

 ${\mathsf C}$

brain parameters for a simulations of Fig. 2 A and B, respectively. A simulation of Fig. 2 A and B, respectively. The simulations of Fig. 2 A and B, respectively. The simulations of Fig. 2 A \sim 2 A and B and B and B **measurements of**

*R***: brain size**

T: **thickness of gray matter**

tangential expansion

area of convex hull

19 T. Tallinen et al., **PNAS 111**, 12667 (2014) Fig. 3. Known empirical scaling laws for gray-matter volume and thickness is gray-matter volume and thickness l., \overline{P}

20 deviations of the white matter volumes from the regression line are, respectively, 18% and 13% on a linear scale. *Sources of data*: If the same species appeared PNAS **97**, 5621 (2000)

Brain malformations

polymicrogyria lissencephaly pachygyria (small number of larger gyri) (large number of smaller gyri)

Reduced neuronal migration to cortex

Gray matter is thicker and it swells less!

Typically gray matter has only four rather than six layers in the affected areas.

whrange and state the state of the state **Compression of thin membranes on elastic substrates with finite adhesion Strong adhesion between membrane and substrate** where an university of the company of the

Weak adhesion between membrane and substrate

thin membrane delaminates/buckles!

The morphology of compressed structures can be obtained by minimizing the total energy

Compression of thin membranes on elastic substrates with finite adhesion

Experimental protocol

Compression of thin membranes on elastic substrates with finite adhesion

Computationally predicted phase diagram www.nature.com/scientific/

24 Q. Wang and X. Zhao, Sci. Rep. **5**, 8887 (2015) 24 Q. Wang and X. Zhao, <u>Sci. Rep.</u> 5, 8887 (20

Compression of thin membranes on elastic substrates with finite adhesion

Very strong adhesion ($\Gamma/(E_s d) \gg 1$)

25 Q. Wang and X. Zhao, Sci. Rep. **5**, 8887 (2015)

Compression of thin membranes on elastic substrates with finite adhesion Strong adhesion

30 Q. Wang and X. Zhao, Sci. Rep. **5**, 8887 (2015)

 Γ

= 3*.*99

Compression of thin membranes on elastic substrates with finite adhesion

Moderate adhesion

$$
\frac{\Gamma}{E_s d} = 0.81
$$

"Ridge" and "Period-double" phases disappear delamination/buckling of folds

$$
\frac{\Gamma}{E_s d} = 0.46
$$

"Ridge" and "Period-double" phases disappear

delamination/buckling of wrinkles

31 Q. Wang and X. Zhao, Sci. Rep. **5**, 8887 (2015)

Compression of thin membranes on elastic substrates with finite adhesion

Weak adhesion

$$
\frac{\Gamma}{E_s d} = 0.28
$$

"Ridge", "Period-double" and

"Fold" phases disappear

 Γ *Esd* = 0*.*13

nou-uoupie and the uclaimiane.
International completely tai **delaminatied/buckled phase almost completely takes over the other phases delamination/buckling of flat phase**

Shapes of growing/swelling sheets and coiling of rods

Shapes of flowers and leaves

saddles

wrinkled edges

helices

Wrinkled and straight blades in macroalgae Pachydictyon coraceum Haring and Carpenter (2007) Haring and Carpenter (2007) **Saccordization (1969)**

bull kelp (seaweed)

Slow water flow environment (v~0.5 m/s)

the blade is changed. For the same inhomogeneous growth profile, narrow blades respond by twisting globally into helicoidal and the second by twisting globally into h shapes (A) which because the broad blades respond by undulated by undulated by undulated by undulated by undulated vicinity of the lateral edges (B, C). It is easy to understand the lateral edges ($t_{\rm max}$, when the blade width wid P40.05).

Fast water flow Serious (v~0.5 m/s) environment (v~1.5 m/s)

transplanted (flat)

new growth after and a N. lueter beform a N. lueter substitute at SC. In the slow-flow-flow-flow-flow-flow-flow-The dotted indicates the blade position defined as the blade position in the position of the position of the p
The position in growth experiments (the position and position and position and position and position and the p blade first wide into a flat blade into a flat blade deltate de luette de luette de luette de luette de la ter **Fig. 2 (A) New growth after and analysis luminositis luminositis** T doet dotted as the blade position defined as the blade position T transplantation (wrinkled) bladens fransplanted (flat)

Hollenberg 1976) where they are exposed to the second t the other changes **and the sites at some sites morphology!** Tuenen lentetien of blade HITHITHATHIT 1988; Johnson and Koehl 1994; Johnson and Koehl 1994; Gaylord et al. 2003).
1994; Gaylord et al. 2003; Gaylord et al. 2003; Gaylord et al. 2003; Gaylord et al. 2003; Gaylord et al. 2003 **Transplantation of blade** from one environment to approximately 1/50 (only the ratio appears in the scaled energy).

to rapid current are flat, narrow, and strap-like are flat, narrow, and strap-like are flat, narrow, and strap **blades**

to rapid currents are flat, narrow, and strap-M. Koehl et al., Integ. Comp. Biol. 48, 834 (2008) 35 Riol \overline{A} proximal end of some blades of a N. luetkeana transplanted from

Wrinkled and straight blades in macroalgae Pachydictyon coraceum Haring and Carpenter (2007) Haring and Carpenter (2007) **Saccordization (1969)**

bull kelp (seaweed)

Slow water flow environment (v~0.5 m/s)

blades flap like flags

flapping prevents bundling of blades, which can thus receive more sunlight (photosynthesis) 1988; Johnson and Koehl 1994; Gaylord et al. 2003). 1988 and 1998 1998 1998 1998 **more sunlight (photosynthesis)**

Fast water flow environment (v~1.5 m/s)

Example 20 and Series and Series increased drag increased drag detachment from base (=death) blade first widens from a cylindrical string into a flat blade). (C) Nereocystis luetkeana bed at TR, the current-swept habitat.

minimal flapping

blades bundle together and e and the bottom some blades on the bottom receive less sunlight and B), whereas the blades of the blades of the blades sunlight to rapid currents are flat, narrow, and strap-like

 M K ooblat al late M. Koehl et al., Integ. Comp. Biol. 48, 834 (2008)

Wrinkled and straight blades in macroalgae

37

Slow water flow environment (v~0.5 m/s)

faster than the midline

Fig. 4 Transverse growth strain rates (M W \mathbf{f} function of the distance from the origin (Fig. 1C) of each \mathbf{f} $\frac{1}{2}$ at the start of the start of the experiment of the experiment of the experiment of the experiment on the experiment on $\frac{1}{2}$ **What is the effect of differential growth rate between the edge and the midline of the blade?**

Fast water flow environment (v~1.5 m/s)

edges of blades grow edges or blades grow at the **Example 19 Same speed as the midline faster than the midline edges of blades grow at the**

M. Koehl et al., Integ. Comp. Biol. 48, 834 (2008) Day 0, for wide, ruffled blades on N. luetkeana growing at the Ω oron tissues die 30–50 cm from the 30–50 cm from the 300 cm from the 300 cm from the 300 cm from the 300 cm from th
September evident. In the rapid proximal regions of \mathcal{B} ruffled blades, the edges of the blade grew more \overline{D} iel 40, 904/0 at the slow-flow SC site (A), and for strap-like flat blades on

Differential growth produces internal stress point to light the specific distance from the specific specific to the specific specific specific specific spec and vertical neighbors. If the sheet remains flat, adjacent hor-*y*

tical connecting springs more and more for longer and longer sheets. Something has to give the planet $\mathbf s$

faster growth of the **bottom edge in x direction**

If √*gxx* decreases in a convex fashion, its second derivative is positive in the Gaussian curvature must be negative. The α which means that at every point that at every point the surface resembles a sadtal springs in successive rows are increased, but vertical **Differential growth produces internal stresses,** springs are under tension and are not at their equilibrium which can be partially released via bending! high energy, so the structure will buckle.

Sheets can form fascinating patterns even when they are flat almost everywhere. Original provides one set of the set of α \mathbf{B} and \mathbf{B} are a fundamental sin-**Next: Short detour to differential geometry.** taking an elastic plate and applying forces to its boundary.5

Metric for measuring distances along curves

metric for measuring lengths

$$
d\ell^2 = d\vec{r}^2 = \vec{t}^2 (dx^1)^2 = g (dx^1)^2
$$

$$
g = \vec{t}^2
$$

$$
d\ell = \sqrt{g} dx^1
$$

Natural parametrization corresponds to $g \equiv 1$, where x^1 **measures distance along the beam.**

Metric for measuring distances along curves

Strain and energy of beam deformations

$$
k=EA
$$

- *E* **3D Young's modulus**
- *A* **beam cross-section area**

strain measures the difference

of metric g' for deformed beam

from the preferred metric g!

Metric tensor for measuring distances on surfaces

metric tensor for measuring lengths

$$
d\ell^2 = d\vec{r}^2 = \sum_{i,j} \vec{t}_i \cdot \vec{t}_j dx^i dx^j = \sum_{i,j} g_{ij} dx^i dx^j
$$

$$
g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} \vec{t}_1 \cdot \vec{t}_1, & \vec{t}_1 \cdot \vec{t}_2 \\ \vec{t}_2 \cdot \vec{t}_1 & \vec{t}_2 \cdot \vec{t}_2 \end{pmatrix}
$$

$$
g = \det(g_{ij}) = |\vec{t}_1 \times \vec{t}_2|^2
$$

area element

$$
dA = |\vec{t_1}||\vec{t_2}| \sin \alpha dx^1 dx^2
$$

$$
dA = \sqrt{g} \, dx^1 dx^2
$$

Examples

Strain tensor and energy of shell deformations

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$$
g_{ij} = \frac{\partial \vec{r}}{\partial x^i} \cdot \frac{\partial \vec{r}}{\partial x^j}
$$

$$
d\ell^2 = \sum_{i,j} g_{ij} dx^i dx^j
$$

strain tensor

$$
u_{ij} = \frac{1}{2} \sum_{k} (g^{-1})_{ik} (g'_{kj} - g_{kj})
$$

inverse metric tensor

$$
\sum_{k} (g^{-1})_{ik} g_{kj} = \sum_{k} g_{ik} (g^{-1})_{kj} = \delta_{ij}
$$

 $(1 - \nu^2)$

Strain tensor for deformation of flat plates

undeformed plate deformed plate

$$
\frac{\partial \vec{r}}{\partial i} = \vec{e}_i \qquad \qquad \vec{t'}_i = \partial_i \vec{r'} = \vec{e}_i + \sum_k
$$

metric tensor

 $\vec{t}_i = \partial_i \vec{r} \equiv$

$$
g_{ij} = \vec{t}_i \cdot \vec{t}_j = \delta_{ij} \equiv \begin{pmatrix} 1, & 0 \\ 0, & 1 \end{pmatrix}
$$

$$
\text{strain tensor}
$$
\n
$$
u_{ij} = \frac{1}{2} \left(g'_{ij} - \delta_{ij} \right)
$$
\n
$$
2u_{ij} = \left(\partial_i u_j + \partial_j u_i \right) + \sum_k \partial_i u_k \partial_j u_k + \partial_i h \partial_j h
$$

 $(\partial_i u_k) \vec{e}_k + (\partial_i h) \vec{e}_z$

Curvature of curves

Curvature tensor for surfaces

metric tensor for $g_{ij} = \vec{t}_i \cdot \vec{t}_j$ measuring lengths

curvature tensor for surfaces

$$
K_{ij} = \sum_{k} (g^{-1})_{ik} \left(\vec{n} \cdot \frac{\partial^2 \vec{r}}{\partial x^k \partial x^j} \right)
$$

principal curvatures correspond to the eigenvalues of curvature tensor

mean curvature

$$
\frac{1}{2}\left(\frac{1}{R_1} + \frac{1}{R_2}\right) = \frac{1}{2}\sum_i K_{ii} = \frac{1}{2}\text{tr}(K_{ij})
$$

Gaussian curvature

$$
\frac{1}{R_1 R_2} = \det(K_{ij})
$$

Surfaces of various principal curvatures

Examples for Gaussian curvature

$Examples$

 $\frac{\partial}{\partial x}$ = (1,0,0)

 $\frac{\partial}{\partial y}$ = (0, 1, 0)

 $\vec{r}(x, y) = (x, y, 0)$

 $\partial \bar r$

 $\partial \bar r$

 $\vec{t}_x =$

 $\vec{t}_y =$

$$
K_{ij} = \sum_{k} (g^{-1})_{ik} \left(\vec{n} \cdot \frac{\partial^2 \vec{r}}{\partial x^k \partial x^j} \right)
$$

$$
g_{ij} = \vec{t}_i \cdot \vec{t}_j = \begin{pmatrix} 1, & 0 \\ 0, & 1 \end{pmatrix}
$$

$$
K_{ij} = \begin{pmatrix} 0, & 0 \\ 0, & 0 \end{pmatrix}
$$

$$
\frac{1}{\sqrt{\frac{1}{\pi^{2}}}}
$$

 \vec{t}_{θ}

 $\not\equiv$ *tx*

 $\bar{\mathcal{t}}$ *ty*

 \vec{n}

$$
\vec{n} = \frac{\vec{t}_x \times \vec{t}_y}{|\vec{t}_x \times \vec{t}_y|} = (0, 0, 1)
$$
\n
$$
\vec{r}(\phi, z) = (R \cos \phi, R \sin \phi, z)
$$
\n
$$
\vec{t}_\phi = \frac{\partial \vec{r}}{\partial \phi} = R(- \sin \phi, \cos \phi, 0)
$$
\n
$$
\vec{t}_z = \frac{\partial \vec{r}}{\partial z} = (0, 0, 1)
$$
\n
$$
\vec{n} = \frac{\vec{t}_\phi \times \vec{t}_z}{|\vec{t}_\phi \times \vec{t}_z|} = (\cos \phi, \sin \phi, 0)
$$
\n
$$
K_{ij} = \begin{pmatrix} -\frac{1}{R}, & 0\\ 0, & 0 \end{pmatrix}
$$

$$
\vec{r}(\theta,\phi) = R(\sin\theta\cos\phi,\sin\theta\sin\phi,\cos\theta) \n\vec{t}_{\phi} \quad \vec{t}_{\theta} = \frac{\partial\vec{r}}{\partial\theta} = R(\cos\theta\cos\phi,\cos\theta\sin\phi,-\sin\theta) \n\vec{n} \quad \vec{t}_{\phi} = \frac{\partial\vec{r}}{\partial\phi} = R\sin\theta(-\sin\phi,\cos\phi,0) \n\vec{n} = \frac{\vec{t}_{\theta}\times\vec{t}_{\phi}}{|\vec{t}_{\theta}\times\vec{t}_{\phi}|} = (\sin\theta\cos\phi,\sin\theta\sin\phi,\cos\theta) \n\vec{n} = \frac{\vec{t}_{\theta}\times\vec{t}_{\phi}}{|\vec{t}_{\theta}\times\vec{t}_{\phi}|} = (\sin\theta\cos\phi,\sin\theta\sin\phi,\cos\theta)
$$

Bending energy for deformation of shells

undeformed shell deformed shell

sheet thickness
$$
d
$$

\n**Young's modulus** E

\n**Poisson's ratio** ν

 $\vec{r}^{\,\prime}$

◆

$$
K'_{ij} = \sum_{k} \left(g'^{-1} \right)_{ik} \left(\vec{n}' \cdot \frac{\partial^2 \vec{r}'}{\partial x^k \partial x^j} \right)
$$

bending strain tensor

 $ik \n\left($

 $\vec{n} \cdot \frac{\partial^2 \vec{r}}{\partial x^k \partial x^k}$

 $\partial x^k\partial x^j$

◆

$$
b_{ij}=K_{ij}^{\prime}-K_{ij}
$$

 (g^{-1})

 $K_{ij} = \sum$

k

(local measure of deviation from preferred curvature)

Energy cost of bending

$$
U = \int \left(\sqrt{g} dx^1 dx^2\right) \left[\frac{1}{2} \kappa \left(\text{tr}(b_{ij})\right)^2 + \kappa_G \text{det}(b_{ij})\right]
$$

$$
\kappa = \frac{Ed^3}{12(1-\nu^2)} \quad \kappa_G = -\frac{Ed^3}{12(1+\nu)}
$$

Bending strain for deformation of flat plates

undeformed plate deformed plate

local normal

$$
\vec{n} = \frac{\vec{t}_x \times \vec{t}_y}{|\vec{t}_x \times \vec{t}_y|} = \vec{e}_z
$$

$$
K_{ij} = \vec{n} \cdot \partial_i \partial_j \vec{r} = 0
$$

local normal (neglecting in-plane deformations)

$$
\vec{n'} \approx \frac{\vec{e_z} - (\partial_x h) \vec{e_x} - (\partial_y h) \vec{e_y}}{\sqrt{1 + (\partial_x h)^2 + (\partial_y h)^2}}
$$

reference curvature tensor bending strain tensor

$$
\vec{r} = 0 \qquad \qquad \boxed{b_{ij} = K'_{ij} \approx \partial_i \partial_j h + \cdots}
$$

Mechanics of growing sheets

Growth defines preferred metric tensor g_{ij} , and preferred curvature tensor K_{ij} .

The equilibrium membrane shape $\vec{r}^{\,\prime}(x^1,x^2)$ **corresponds to the minimum of elastic energy:**

$$
U = \int \left(\sqrt{g} dx^1 dx^2\right) \left[\frac{1}{2}\lambda \left(\sum_i u_{ii}\right)^2 + \mu \sum_{i,j} u_{ij} u_{ji} + \frac{1}{2}\kappa \left(\text{tr}(b_{ij})\right)^2 + \kappa_G \text{det}(b_{ij})\right]
$$

Growth can independently tune the metric tensor g_{ij} and the curvature tensor K_{ij} , which may not be compatible with any **surface shape that would produce zero energy cost!**

Zero energy shape exists only when preferred metric tensor g_{ij} **and** preferred curvature tensor K_{ij} satisfy Gauss-Codazzi-Mainardi relations!

Mechanics of growing sheets

One of the Gauss-Codazzi-Mainardi equations (Gauss's Theorema Egregium) relates the Gauss curvature to metric tensor

$$
\det(K_{ij}') = \mathcal{F}(g_{ij}')\Big|
$$

The equilibrium membrane shape $\vec{r}^{\,\prime}(x^1,x^2)$ **corresponds to the minimum of elastic energy:**

$$
U = \int \left(\sqrt{g} dx^1 dx^2\right) \left[\frac{1}{2}\lambda \left(\sum_i u_{ii}\right)^2 + \mu \sum_{i,j} u_{ij} u_{ji} + \frac{1}{2}\kappa \left(\text{tr}(b_{ij})\right)^2 + \kappa_G \text{det}(b_{ij})\right]
$$

scaling with membrane thickness d

 $\kappa, \kappa_G \sim E d^3$

 $\lambda, \mu \sim E d$

For very thin membranes the equilibrium shape matches the preferred metric tensor to avoid stretching, compressing and shearing. This also specifies the Gauss curvature!

$$
g'_{ij} = g_{ij}
$$

$$
\det(K'_{ij}) = \mathcal{F}(g_{ij})
$$