

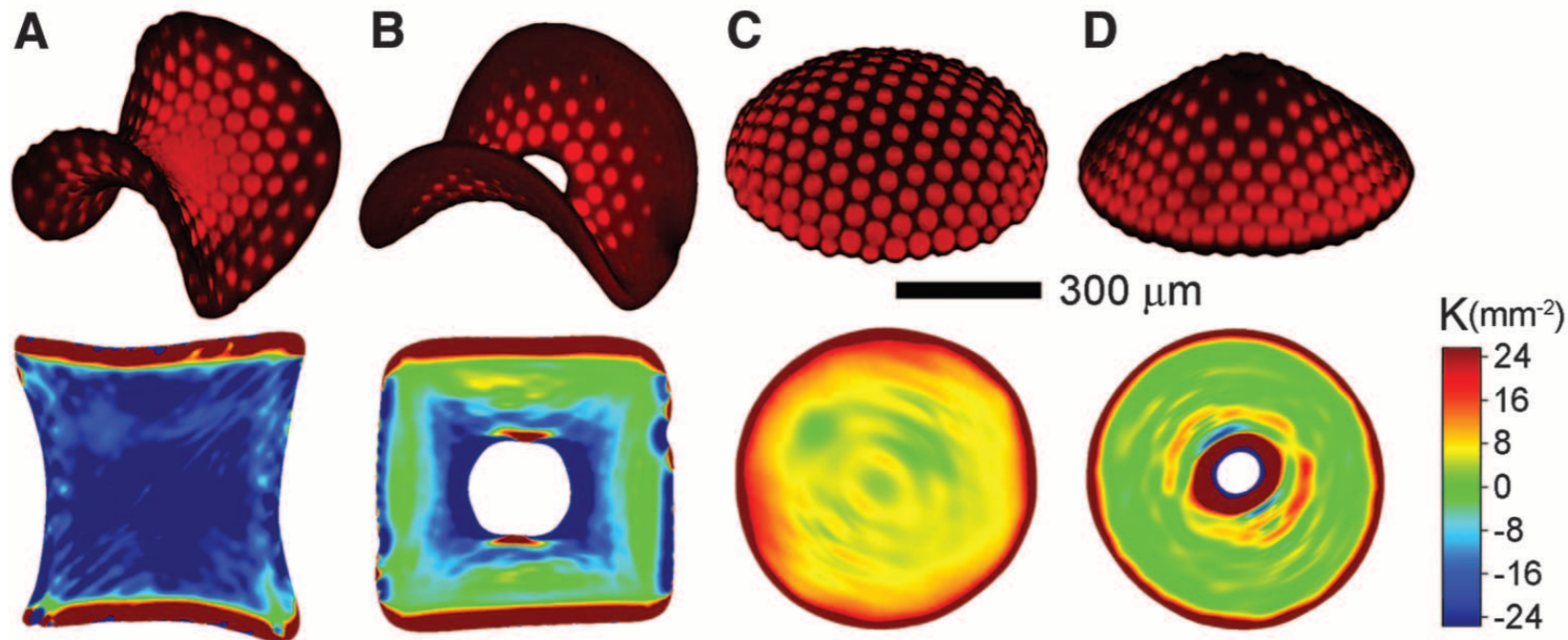
MAE 545: Lecture 21 (12/8)

Helices, spirals and phyllotaxis

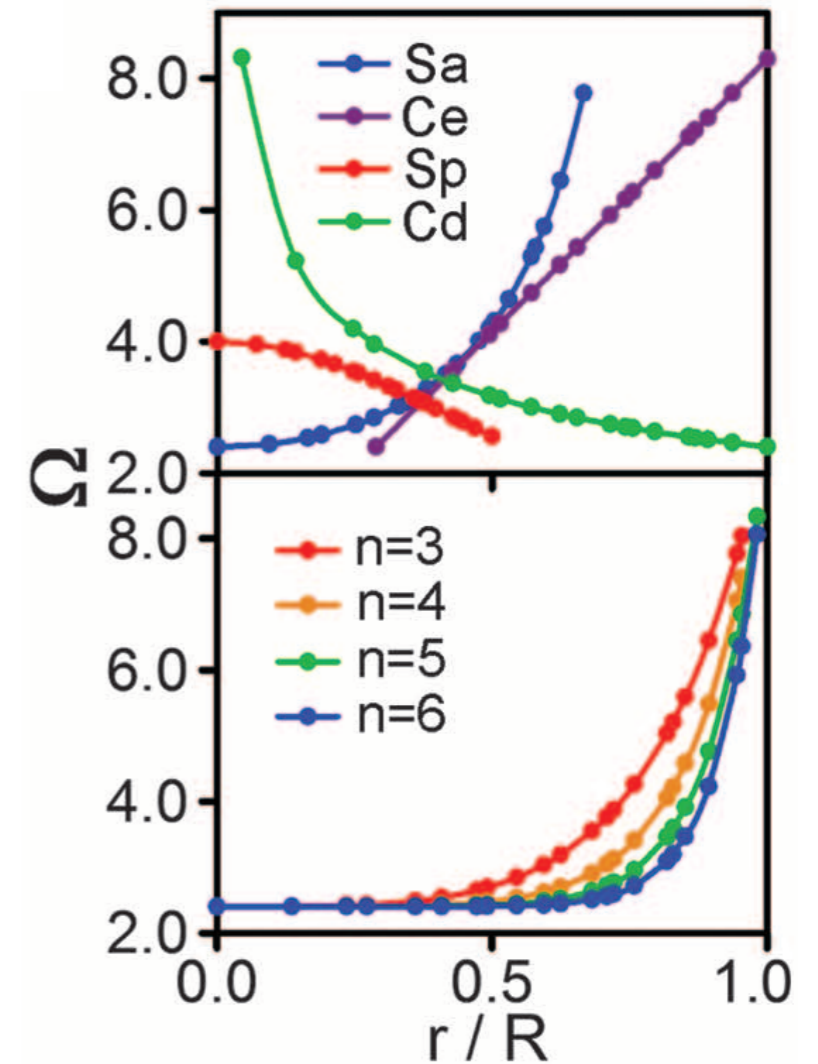


Shaping of gel membrane properties by halftone lithography

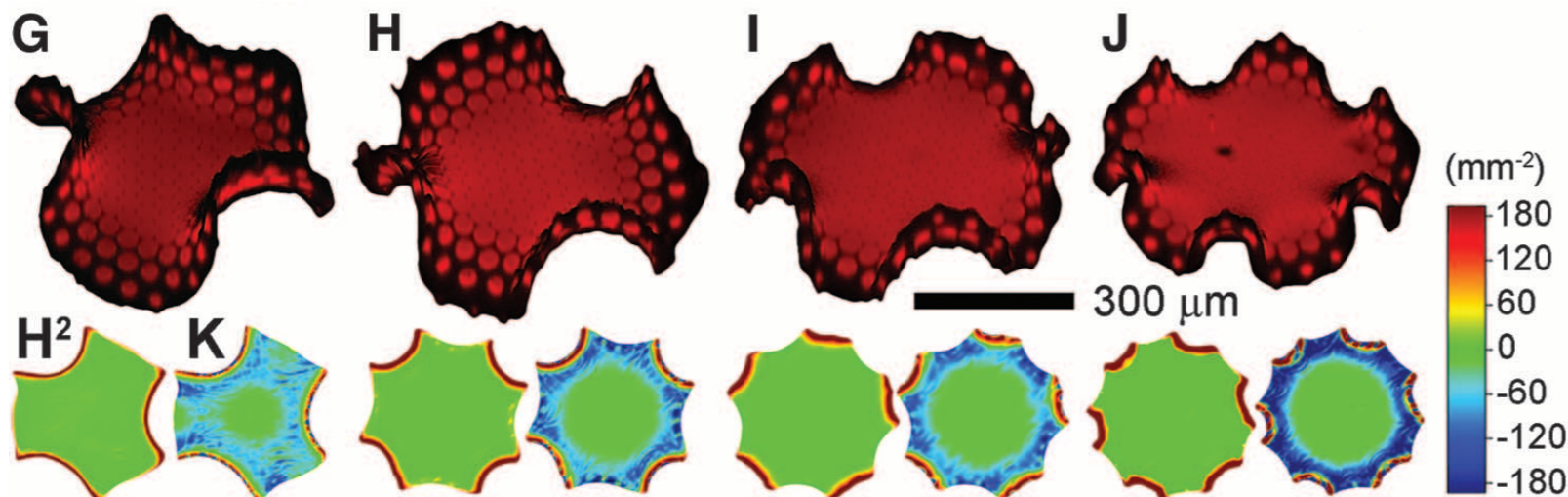
saddle (Sa) cone with excess angle (Ce) spherical cap (Sp) cone with deficit angle (Cd)



swelling profiles



Enneper's minimal surfaces ($H=0$)



H - mean curvature

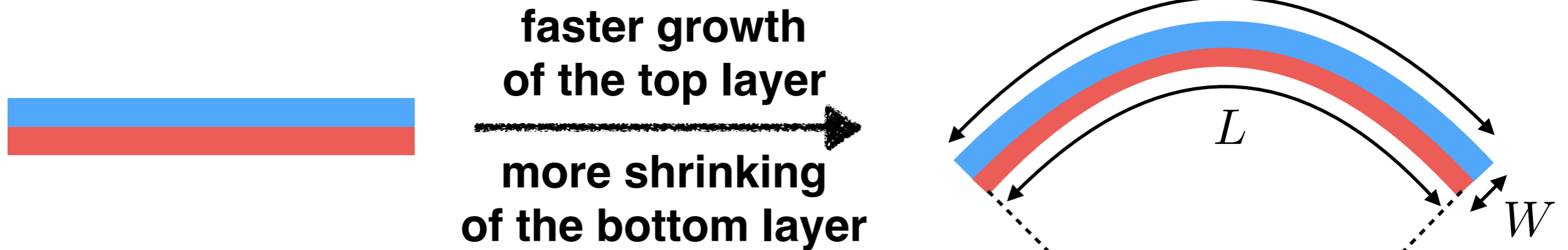
K - Gauss curvature

Helices in plants



How are helices formed?

Differential growth or differential shrinking produces spontaneous curvature



Differential growth (shrinking) of the two layers produces spontaneous curvature

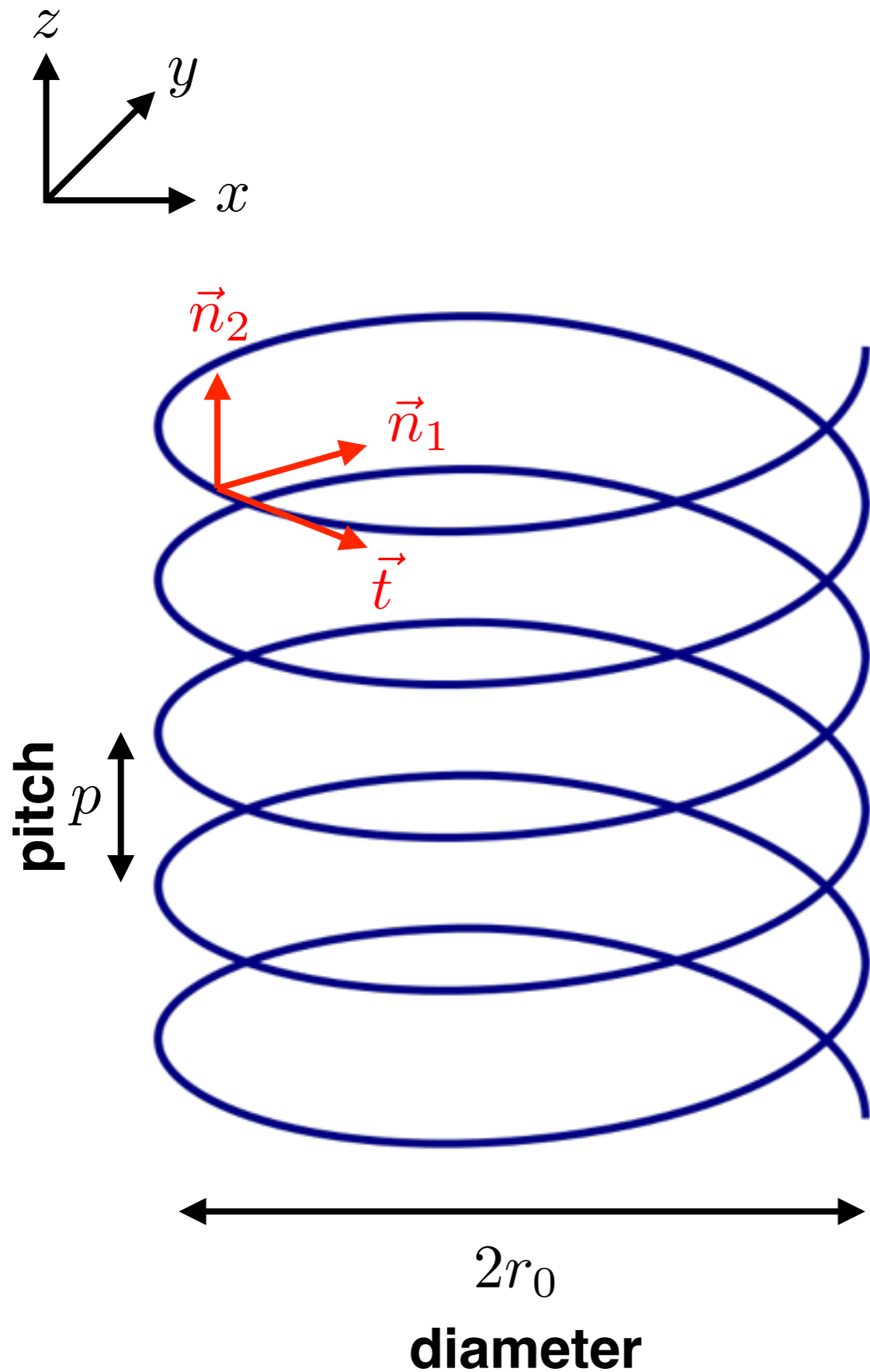
$$K = \frac{1}{R} = \frac{\epsilon}{W}$$

$$\frac{L(1 + \epsilon)}{L} = \frac{R + W}{R}$$

Filaments that are longer than $L > 2\pi R$ form helices to avoid steric interactions.



Helix



Mathematical description

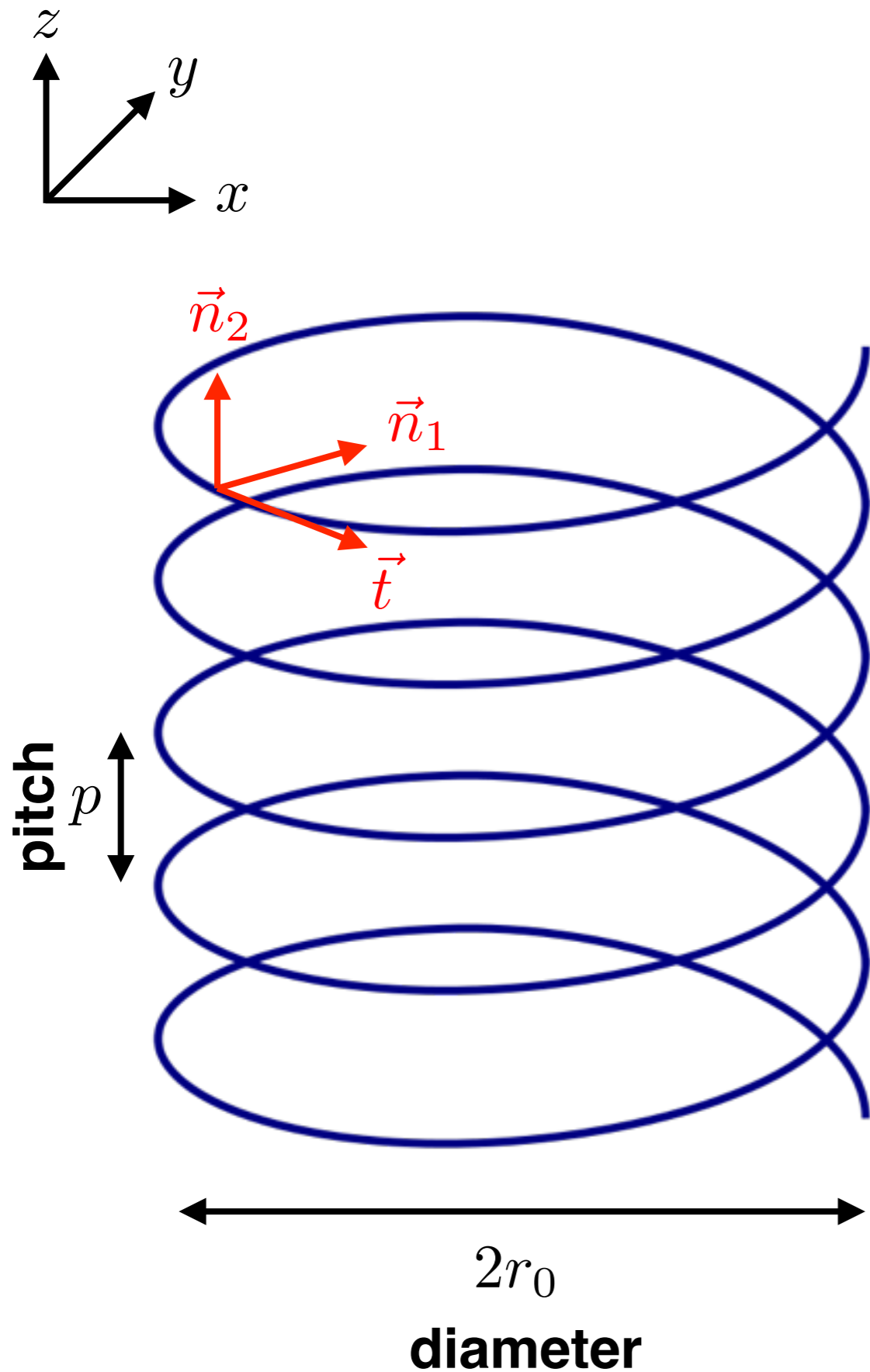
$$\vec{r}(s) = \left(r_0 \cos(s/\lambda), r_0 \sin(s/\lambda), \frac{p}{2\pi\lambda} s \right)$$

Set λ to fix the metric

$$\vec{t}(s) = \frac{d\vec{r}}{ds} = \left(-\frac{r_0}{\lambda} \sin(s/\lambda), \frac{r_0}{\lambda} \cos(s/\lambda), \frac{p}{2\pi\lambda} \right)$$
$$g = \vec{t} \cdot \vec{t} = \frac{r_0^2}{\lambda^2} + \frac{p^2}{4\pi^2\lambda^2} = 1$$

$$\lambda = \sqrt{r_0^2 + (p/2\pi)^2}$$

Helix



Mathematical description

$$\vec{r}(s) = \left(r_0 \cos(s/\lambda), r_0 \sin(s/\lambda), \frac{p}{2\pi\lambda} s \right)$$

$$\lambda = \sqrt{r_0^2 + (p/2\pi)^2}$$

Tangent and normal vectors

$$\vec{t}(s) = \frac{d\vec{r}}{ds} = \left(-\frac{r_0}{\lambda} \sin(s/\lambda), \frac{r_0}{\lambda} \cos(s/\lambda), \frac{p}{2\pi\lambda} \right)$$

$$\vec{n}_1(s) = \left(-\cos(s/\lambda), -\sin(s/\lambda), 0 \right)$$

$$\vec{n}_2(s) = \left(\frac{p}{2\pi\lambda} \sin(s/\lambda), -\frac{p}{2\pi\lambda} \cos(s/\lambda), \frac{r_0}{\lambda} \right)$$

Helix curvatures

$$\vec{n}_1 \cdot \frac{d^2\vec{r}}{ds^2} = \frac{r_0}{\lambda^2} = \frac{r_0}{r_0^2 + (p/2\pi)^2} = K$$

$$\vec{n}_2 \cdot \frac{d^2\vec{r}}{ds^2} = 0$$

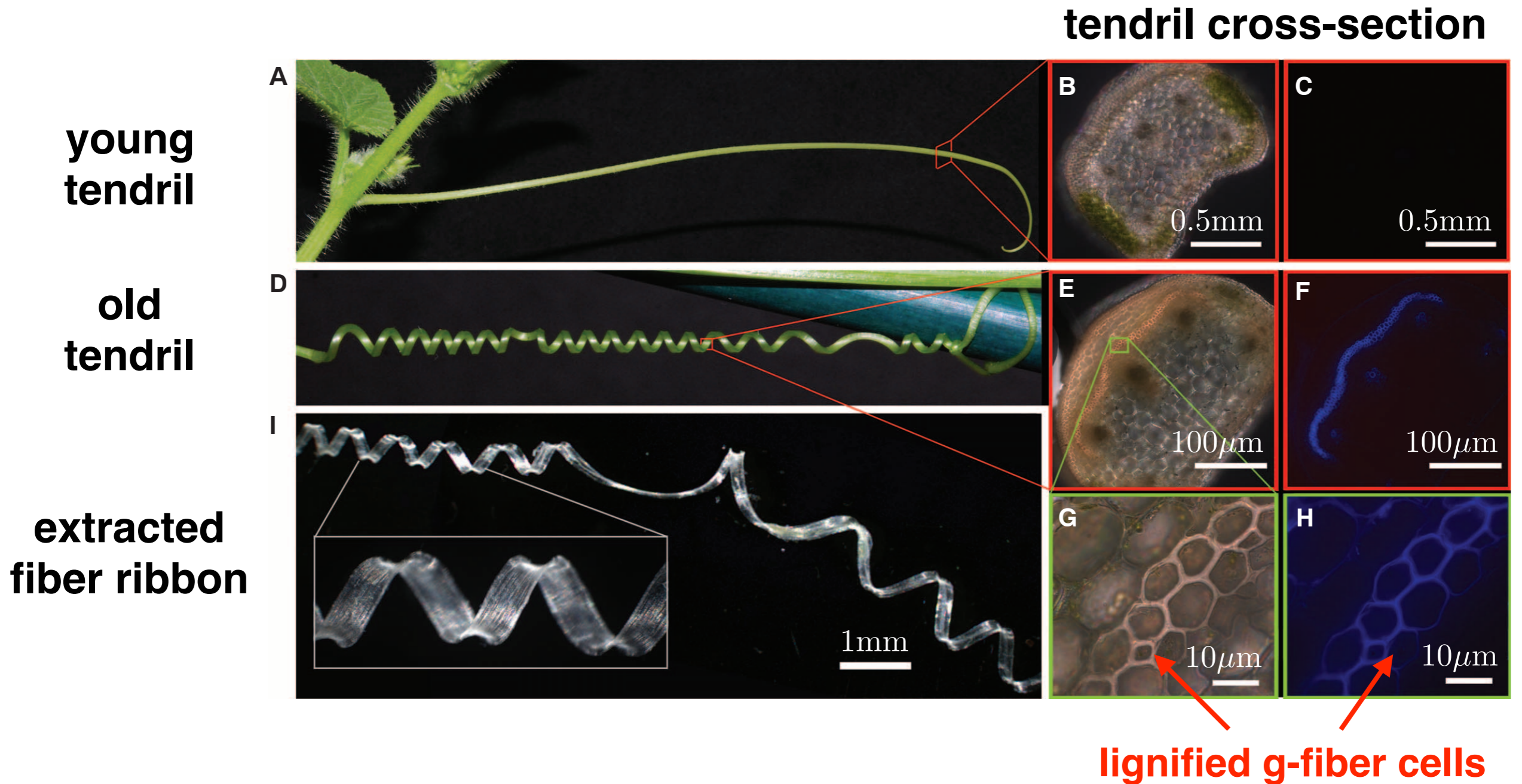
Cucumber tendril climbing via helical coiling



**Cucumber tendrils
want to pull
themselves up above
other plants in order
to get more sunlight.**

S. J. Gerbode et al., Science 337, 1087 (2012)

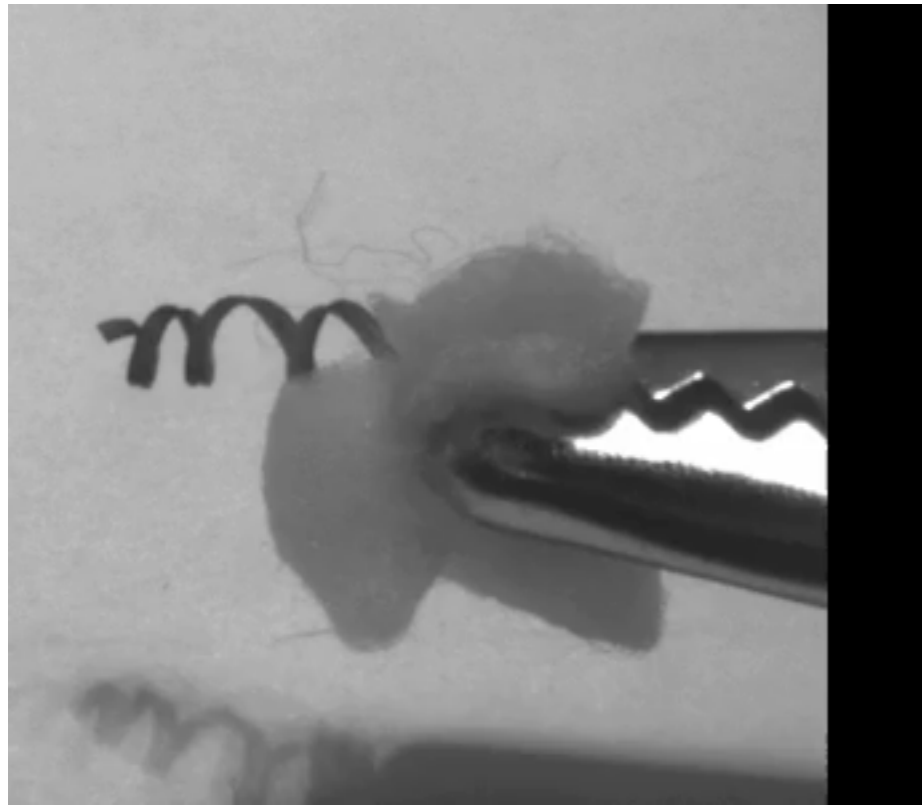
Helical coiling of cucumber tendril



Coiling in older tendrils is due to a thin layer of stiff, lignified gelatinous fiber cells, which are also found in wood.

Helical coiling of cucumber tendril

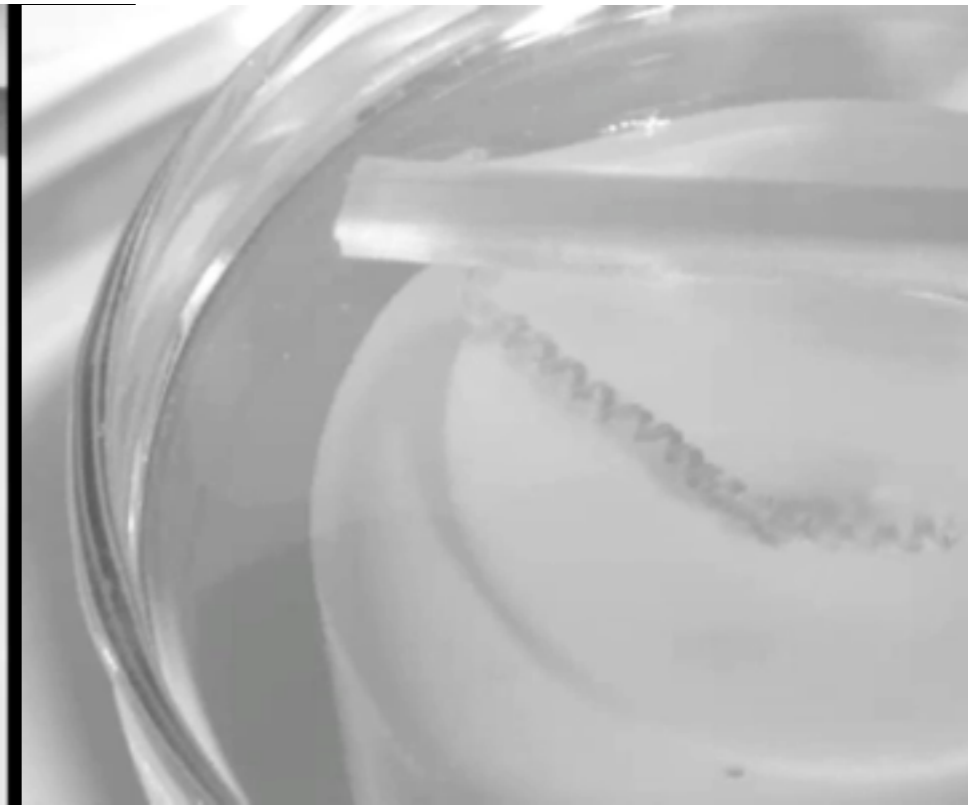
Drying of fiber ribbon increases coiling



Drying of tendril increases coiling

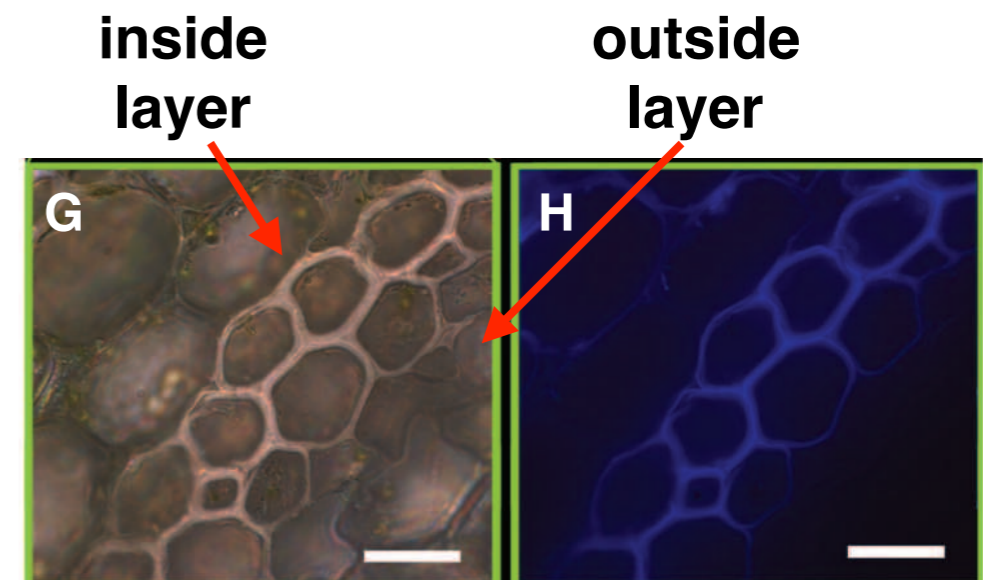


Rehydrating of tendril increases coiling

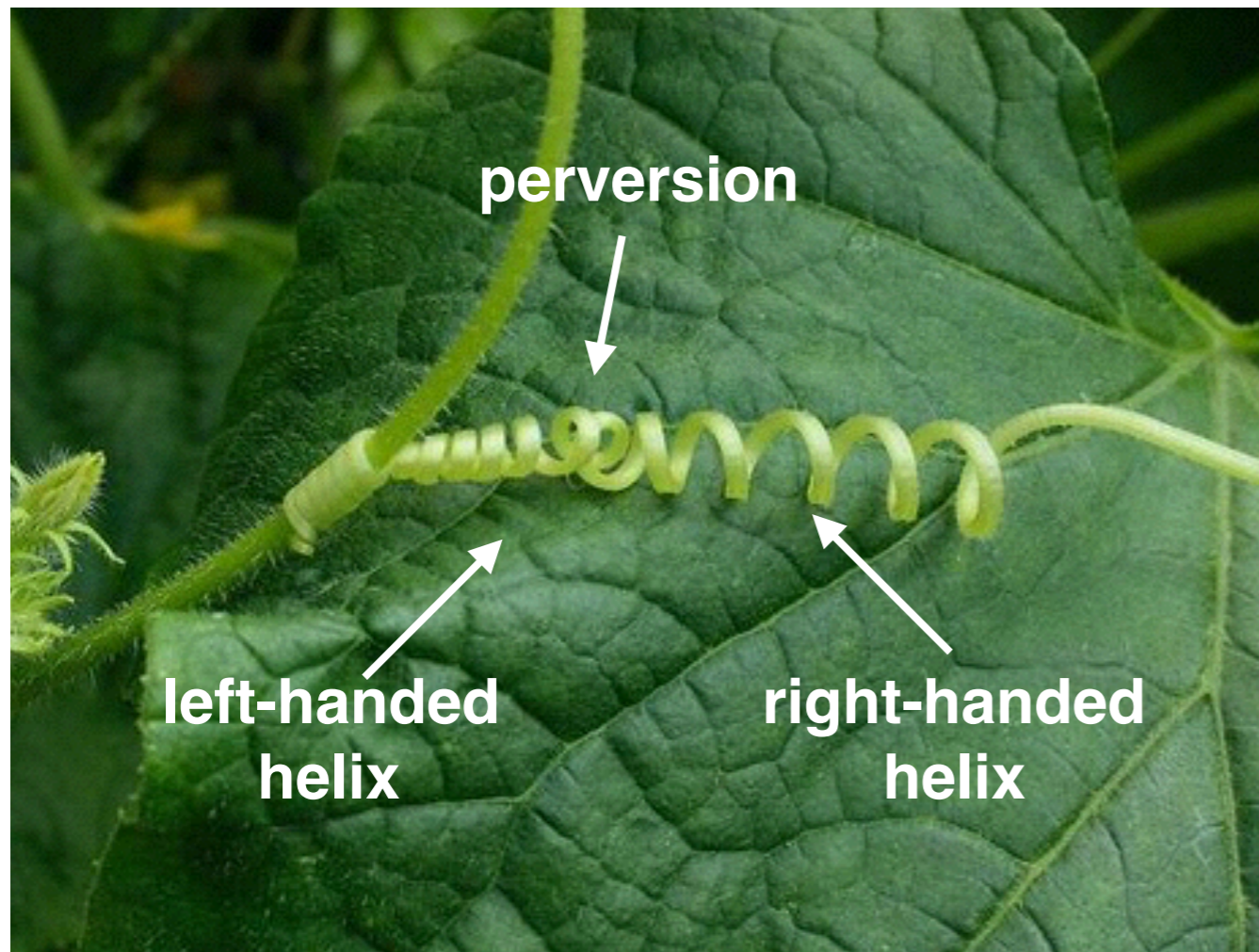


During the lignification of g-fiber cells water is expelled, which causes shrinking.

The inside layer is more lignified and therefore shrinks more and is also stiffer than the outside layer.



Coiling of tendrils in opposite directions



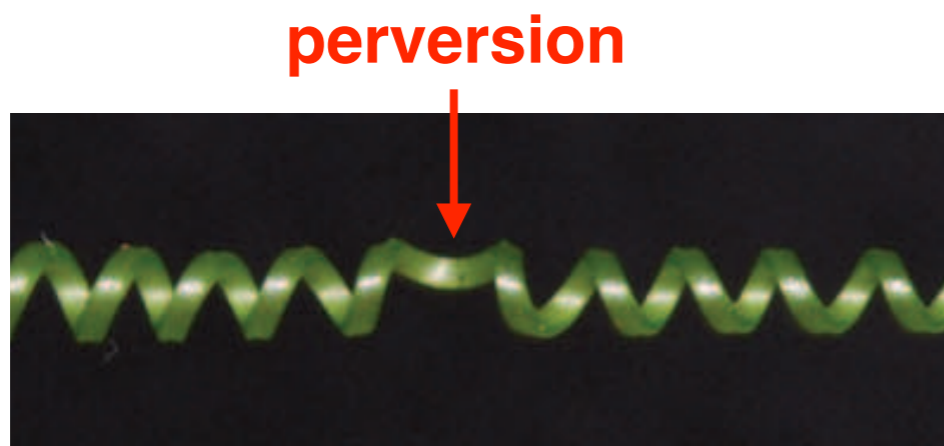
Ends of the tendril are fixed and cannot rotate. This constraints the linking number.

$$\text{Link} = \text{Twist} + \text{Writhe}$$

Coiling in the same direction increases Writhe, which needs to be compensated by the twist.

In order to minimize the twisting energy tendrils combine two helical coils of opposite handedness (=opposite Writhe).

Note: there is no bending energy when the curvature of two helices correspond to the spontaneous curvature due to the differential shrinking of fiber.



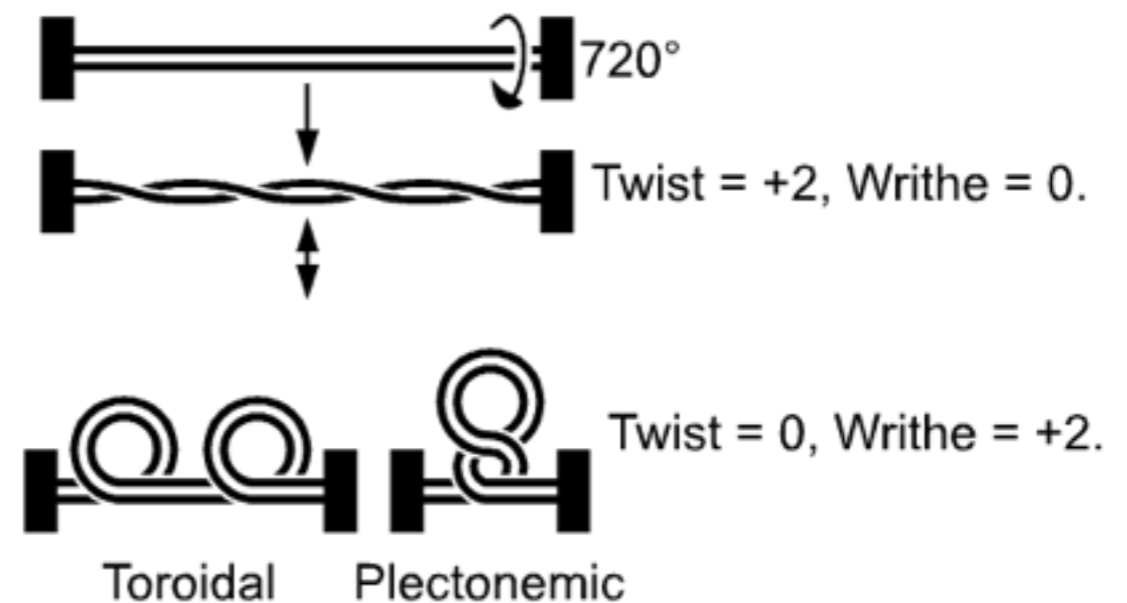
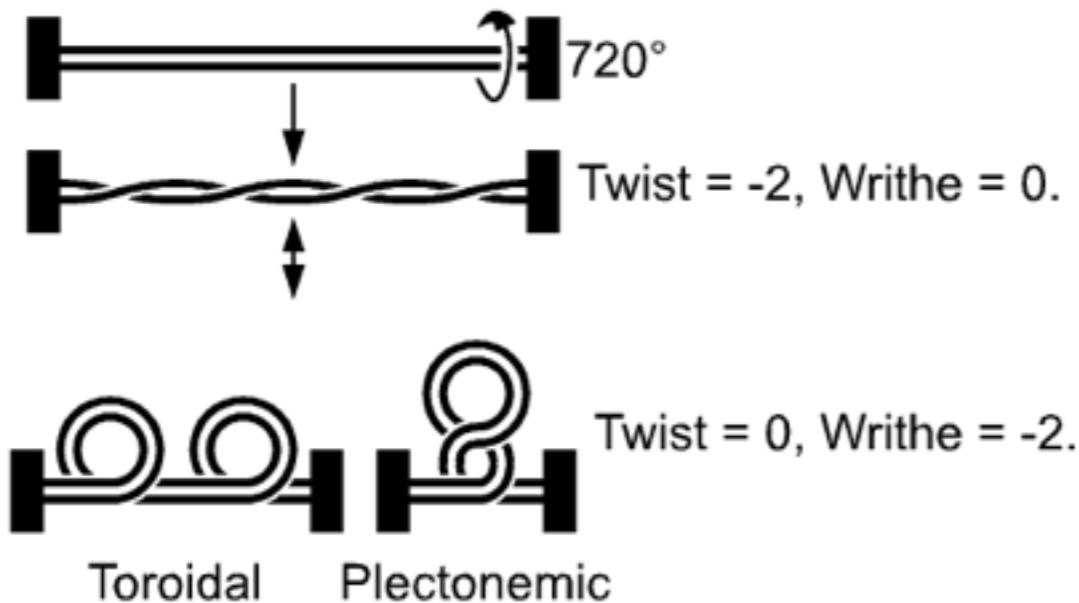
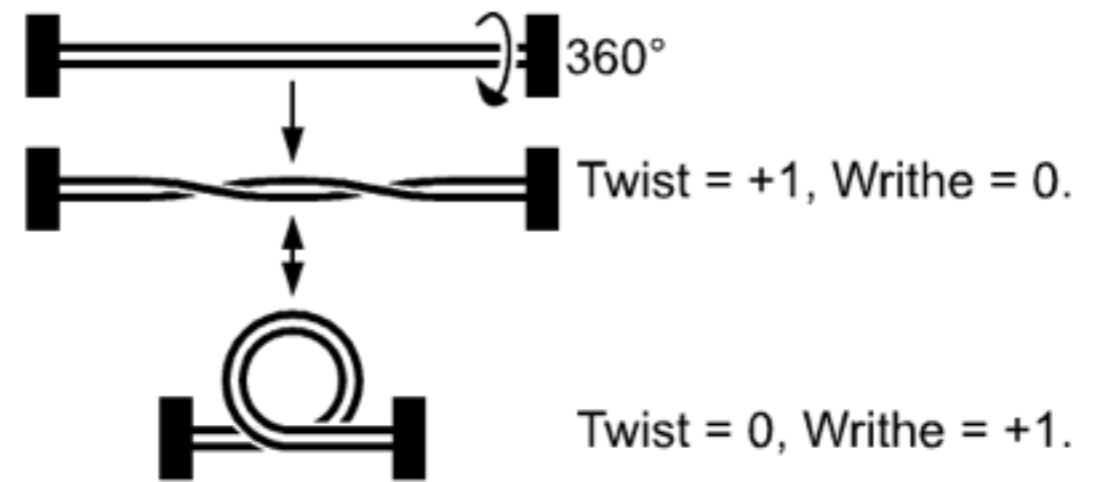
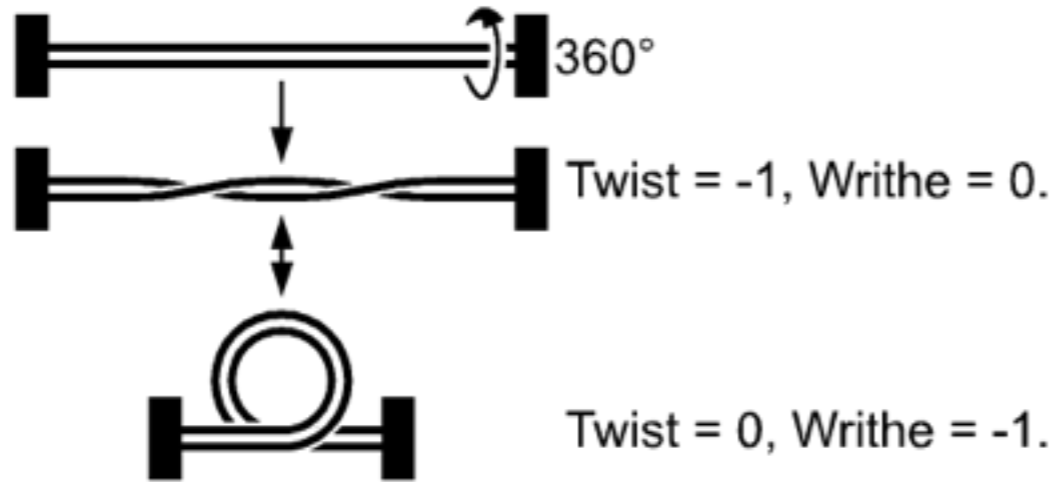
Twist, Writhe and Linking numbers

$L_n = Tw + Wr$

linking number: total number of turns of a particular end

Tw twist: number of turns due to twisting the beam

Wr writhe: number of crossings when curve is projected on a plane



Overwinding of tendril coils

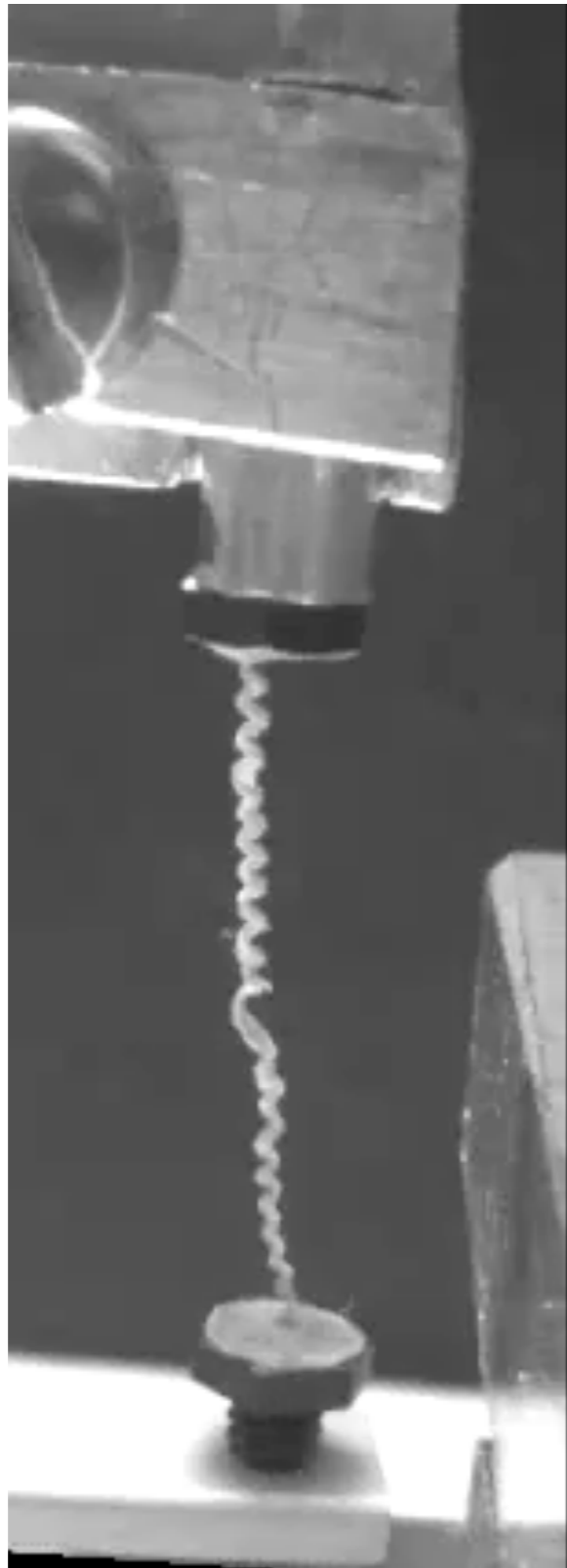
Old tendrils overwind when stretched.

Rubber model unwinds when stretched.

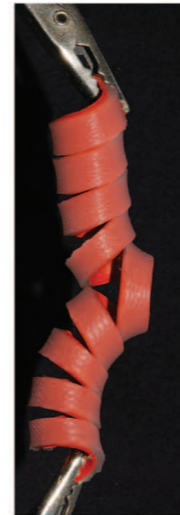
relaxed



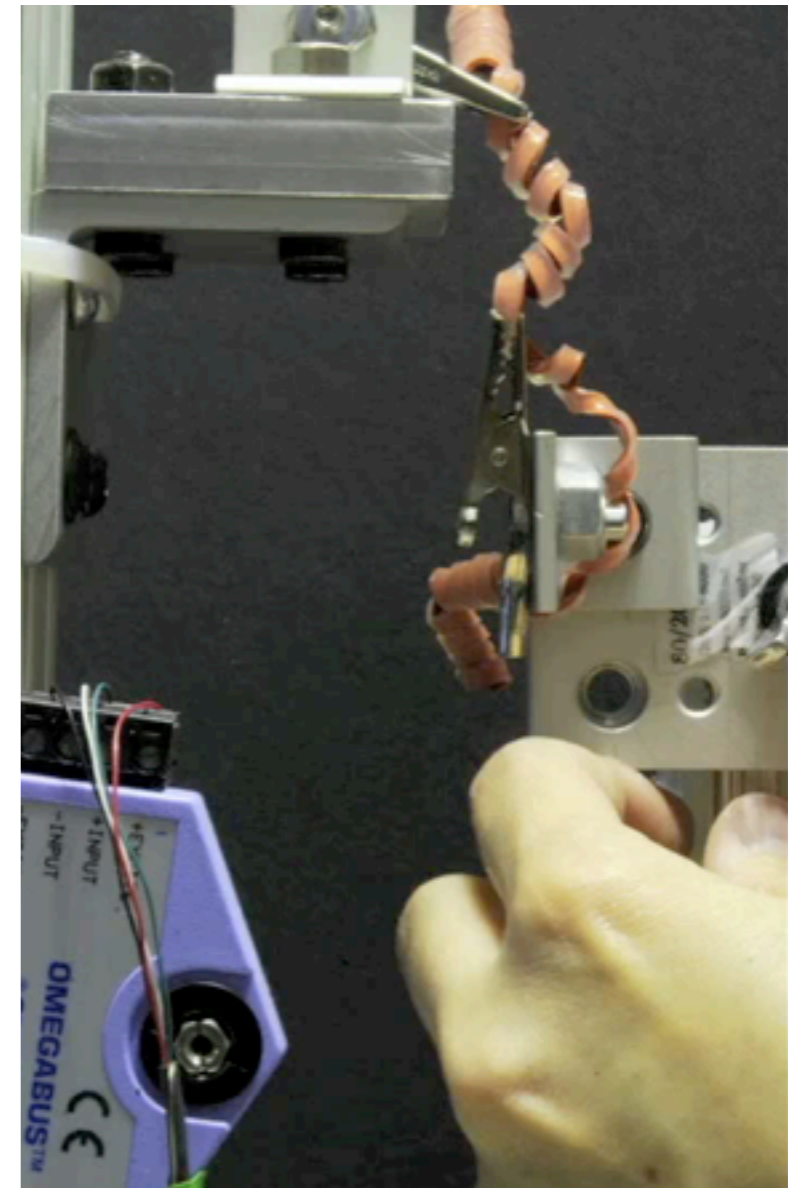
stretched



relaxed

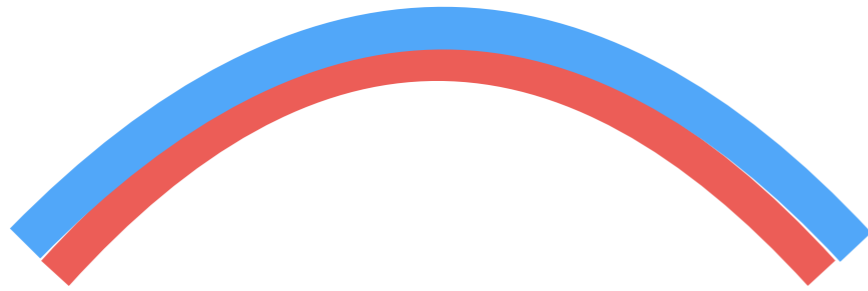


stretched



Overwinding of tendril coils

Preferred curved state



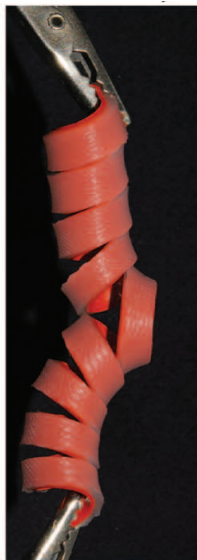
Flattened state



In tendrils the red inner layer is much stiffer than the outside blue layer.

High bending energy cost associated with stretching of the stiff inner layer!

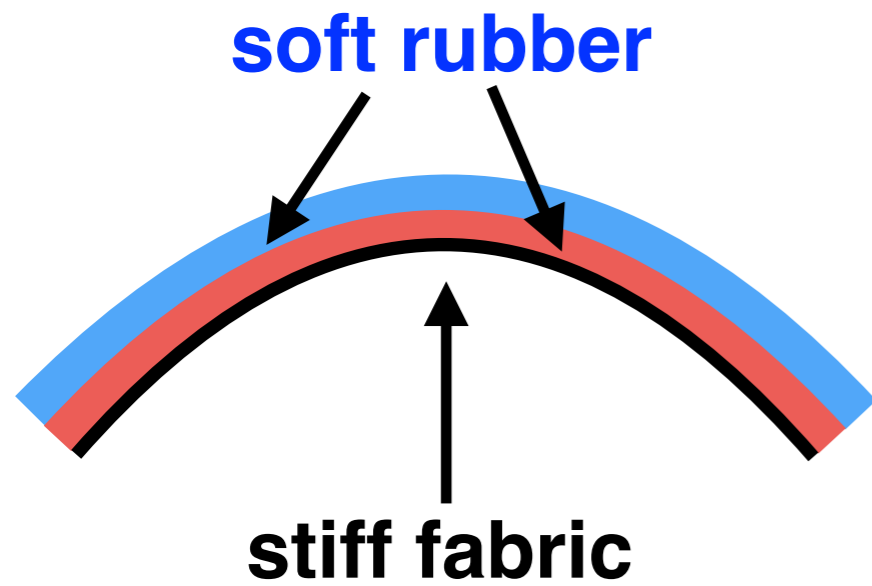
Tendrils try to keep the preferred curvature when stretched!



In rubber models both layers have similar stiffness.

Small bending energy.

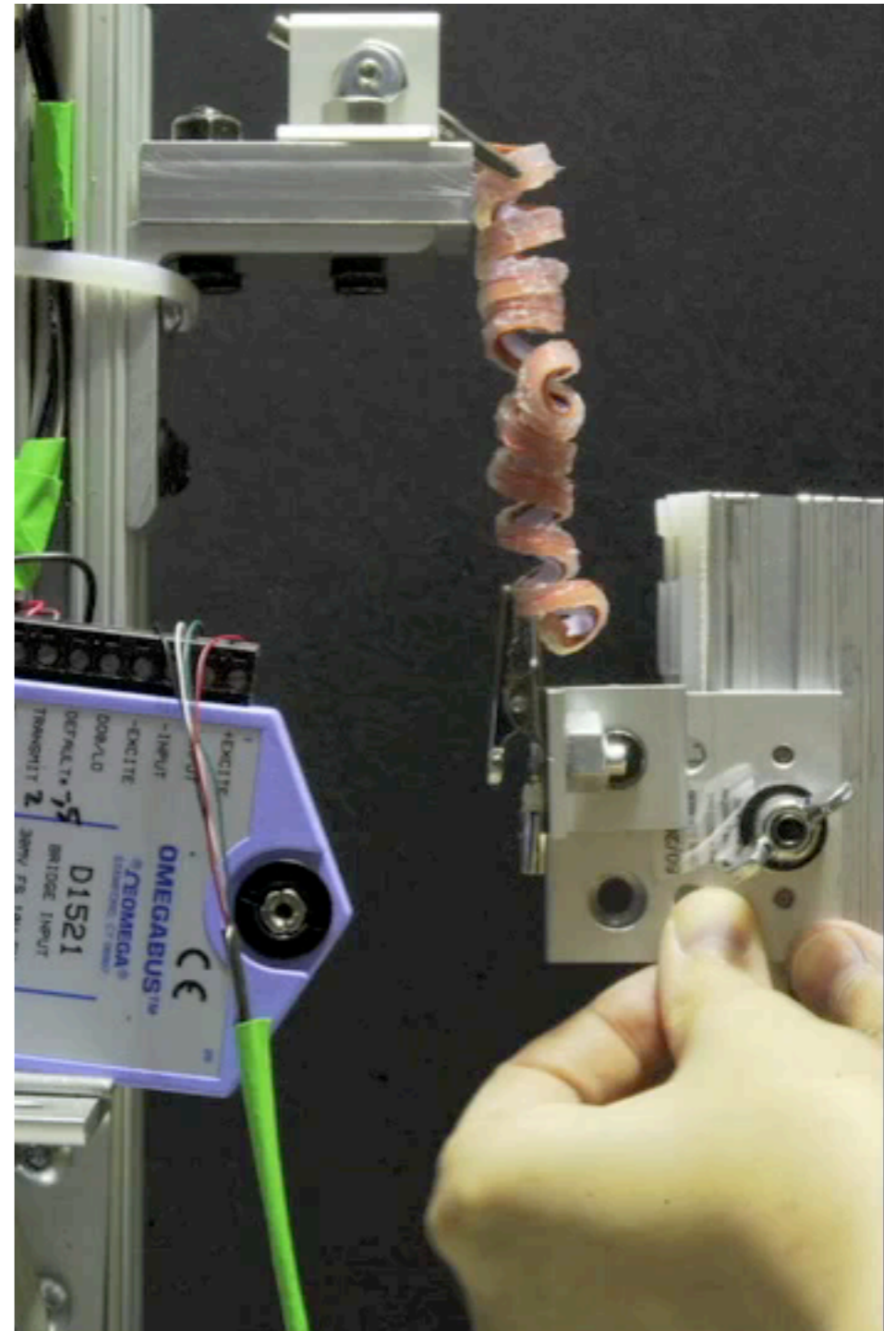
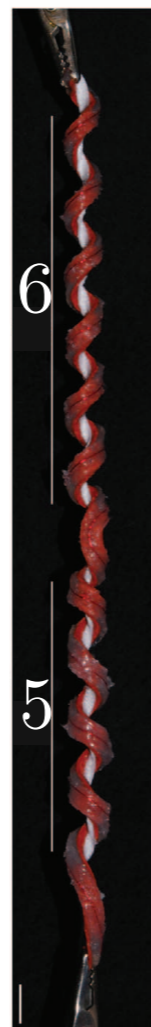
Overwinding of rubber models with an additional stiff fabric on the inside layers



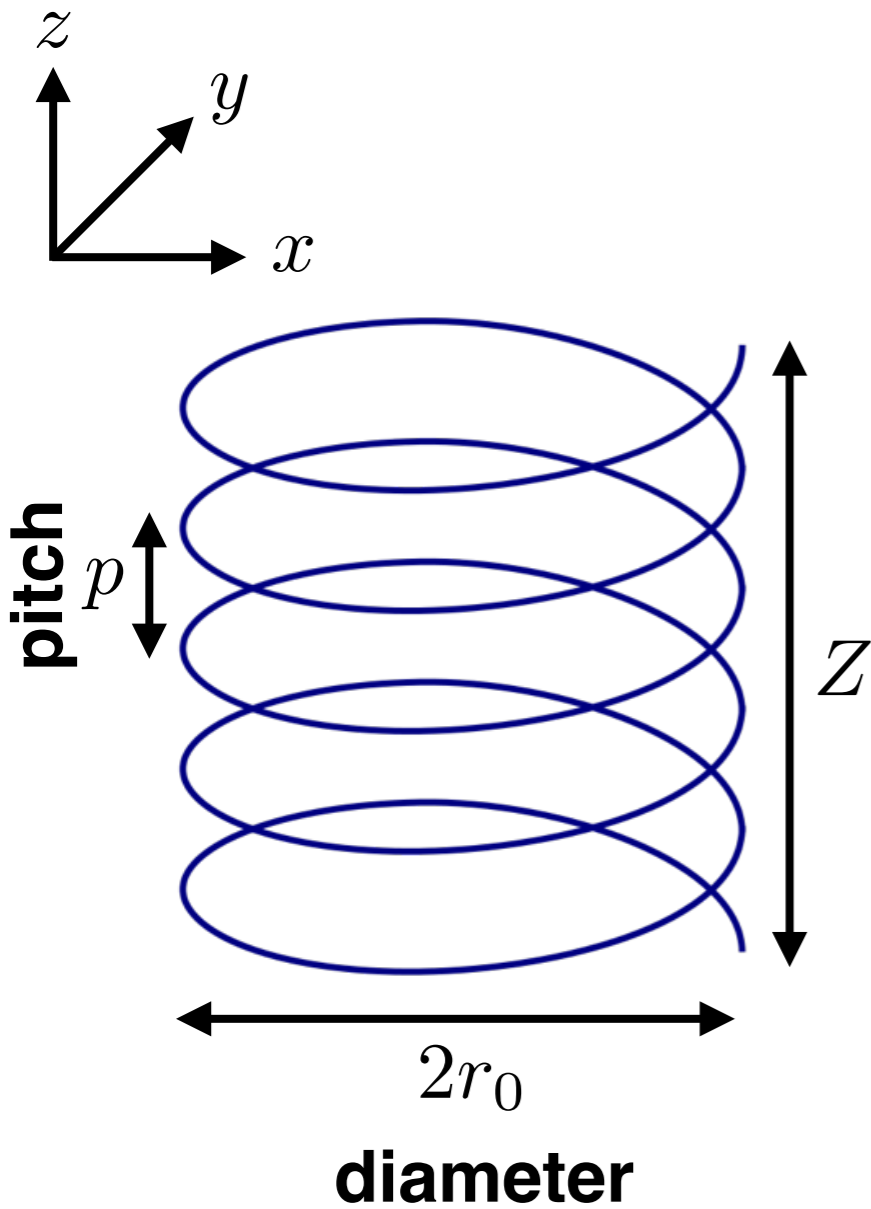
relaxed



stretched



Overwinding of helix with infinite bending modulus



Mathematical description

$$\vec{r}(s) = \left(r_0 \cos(s/\lambda), r_0 \sin(s/\lambda), \frac{p}{2\pi\lambda} s \right)$$

$$\lambda = \sqrt{r_0^2 + (p/2\pi)^2} \quad Z = pN = p(L/2\pi\lambda)$$

Infinite bending modulus fixes the helix curvature during stretching

$$K = \frac{r_0}{r_0^2 + (p/2\pi)^2}$$

Helix pitch and radius

$$r_0 = \frac{1}{K} \left(1 - \frac{Z^2}{L^2} \right)$$

$$p = \frac{2\pi Z}{KL} \sqrt{1 - \frac{Z^2}{L^2}}$$

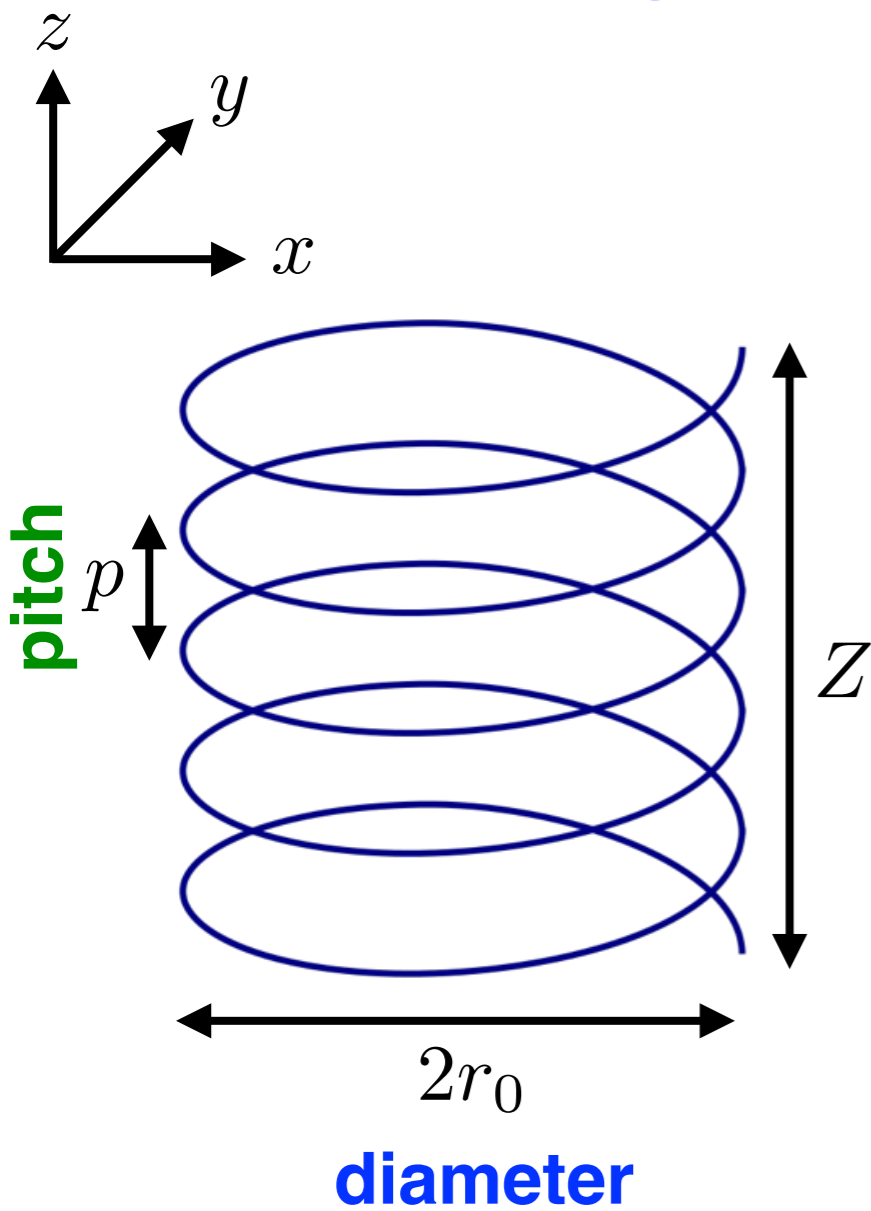
Number of loops

$$N = \frac{Z}{p} = \frac{KL}{2\pi \sqrt{1 - (Z/L)^2}}$$

L length of the helix backbone

$N = \frac{Z}{p}$ number of loops

Overwinding of helix with infinite bending modulus



Helix pitch and radius

$$r_0 = \frac{1}{K} \left(1 - \frac{Z^2}{L^2} \right)$$

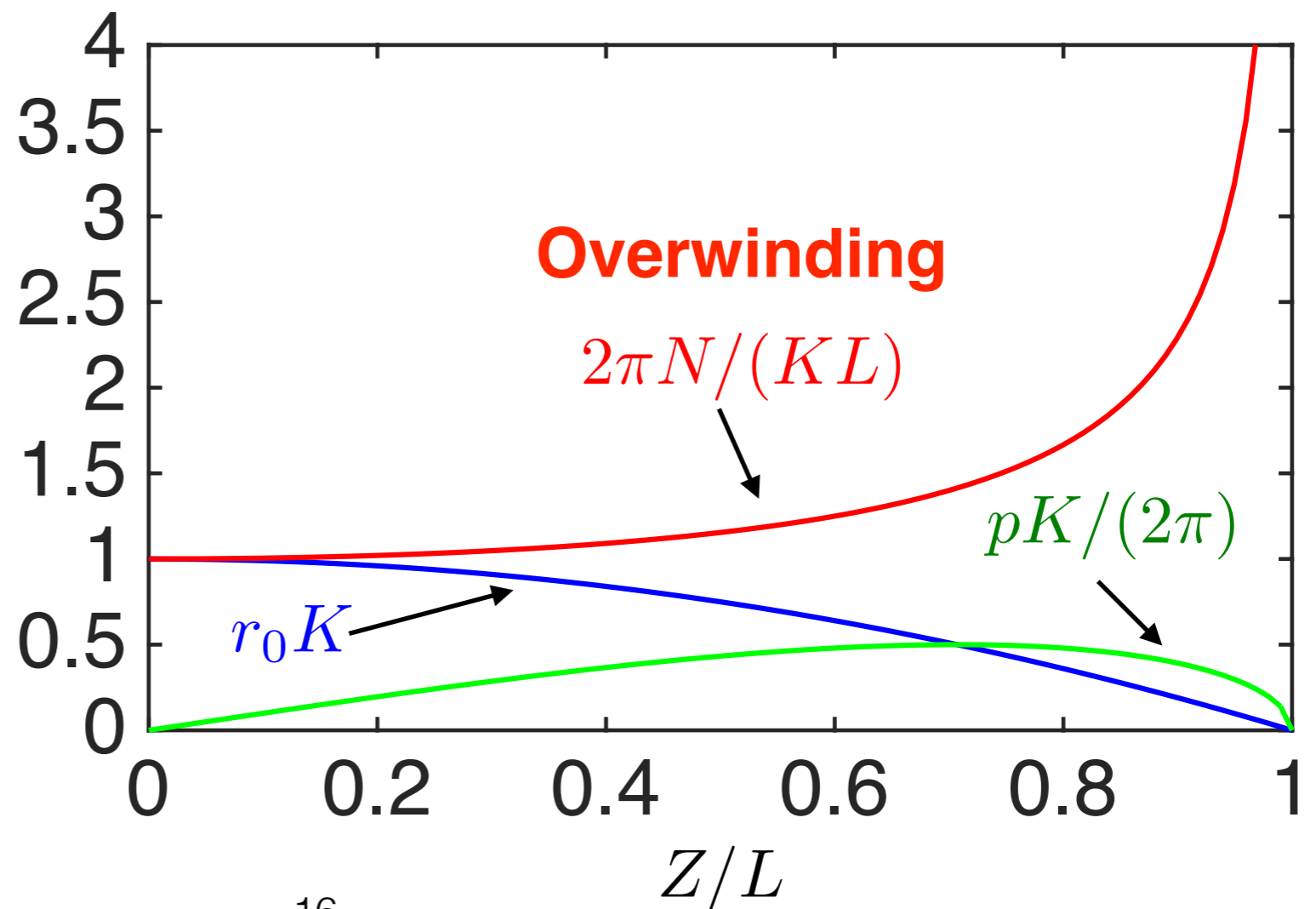
$$p = \frac{2\pi Z}{KL} \sqrt{1 - \frac{Z^2}{L^2}}$$

Number of loops

$$N = \frac{Z}{p} = \frac{KL}{2\pi \sqrt{1 - (Z/L)^2}}$$

L length of the helix backbone

$N = \frac{Z}{p}$ number of loops



Spirals in nature

shells



beaks



claws



horns



teeth



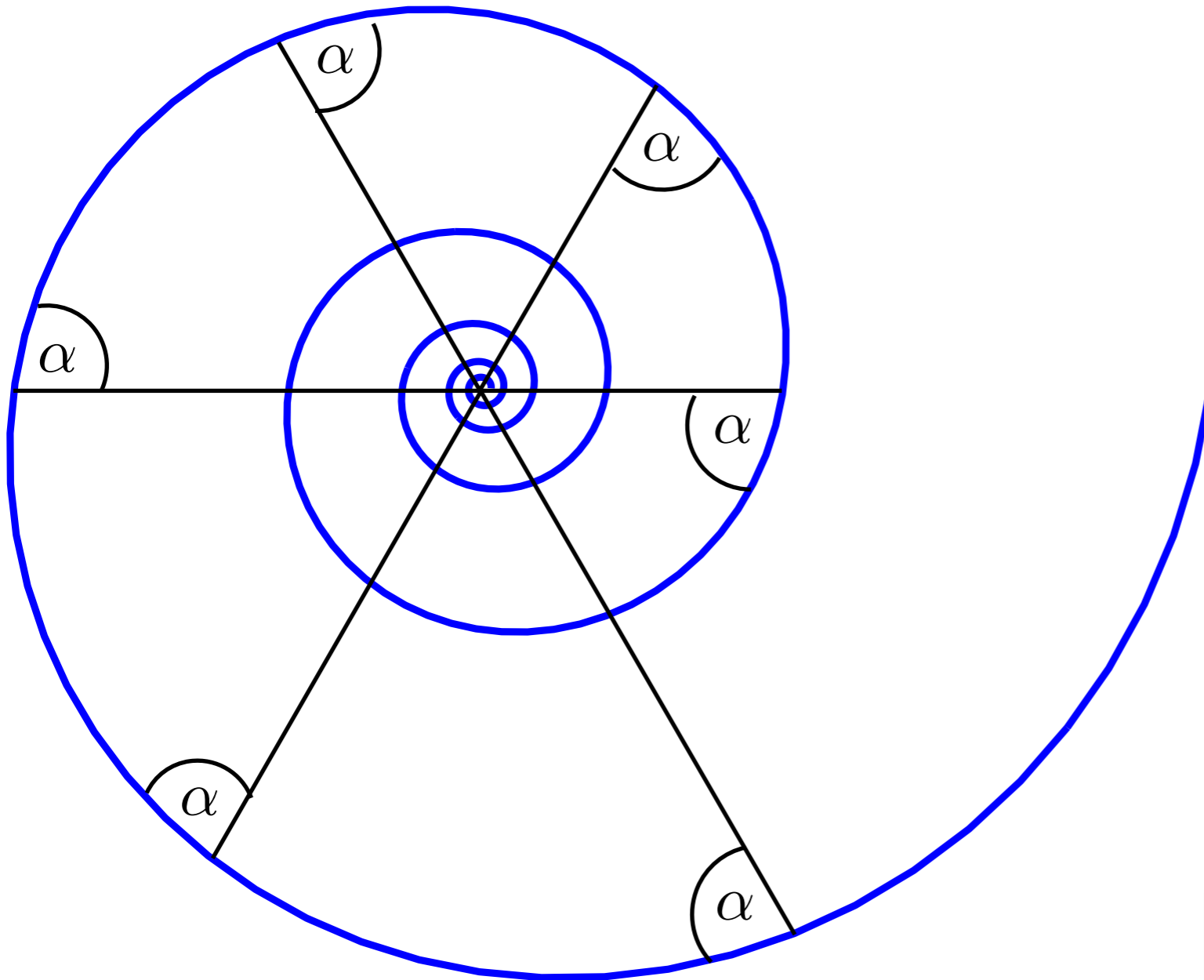
tusks



What simple mechanism could produce spirals?

Equiangular (logarithmic) spiral

$$\alpha = 82^\circ$$



in polar coordinates radius grows exponentially

$$r(\theta) = a^\theta = \exp(\theta \cot \alpha)$$

$$\cot \alpha = \ln a$$

name logarithmic spiral:

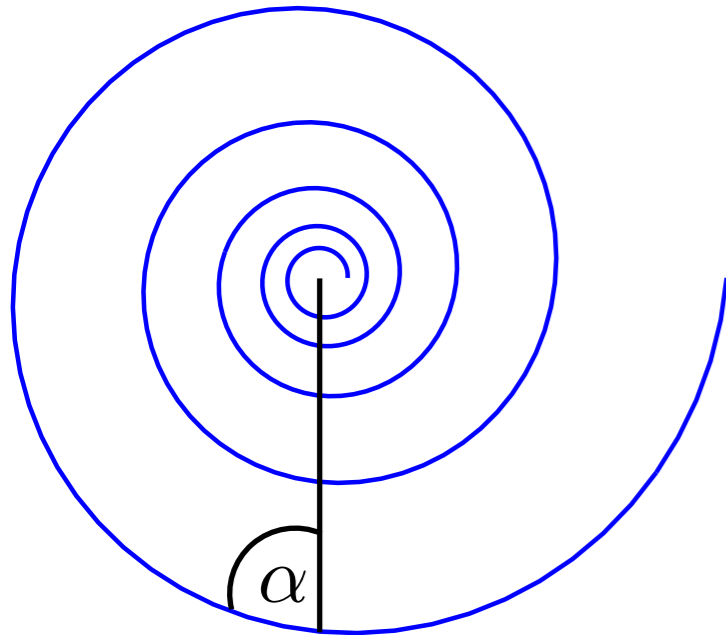
$$\theta = \frac{\ln r}{\ln a}$$

Ratio between growth velocities in the radial and azimuthal directions is constant!

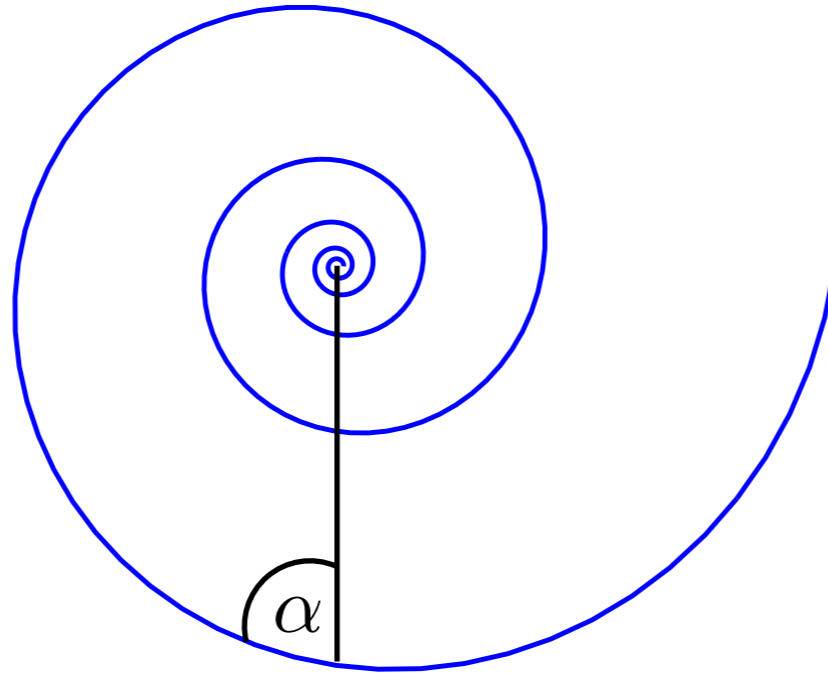
$$\cot \alpha = \frac{dr}{r d\theta} = \frac{dr/dt}{r d\theta/dt} = \frac{v_r}{v_\theta}$$

Equiangular (logarithmic) spiral

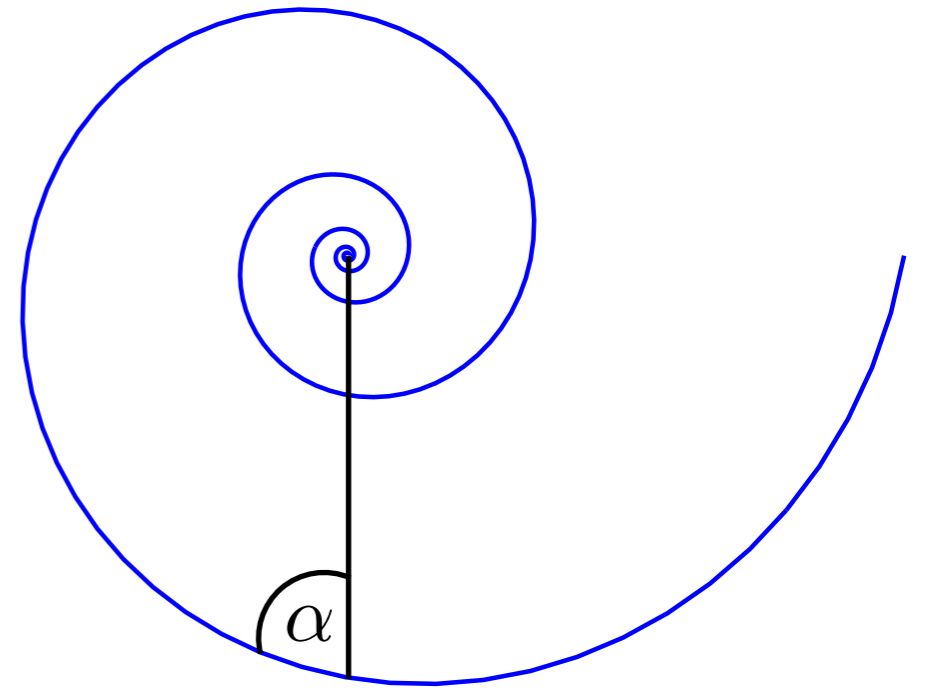
$$\alpha = 85^\circ$$



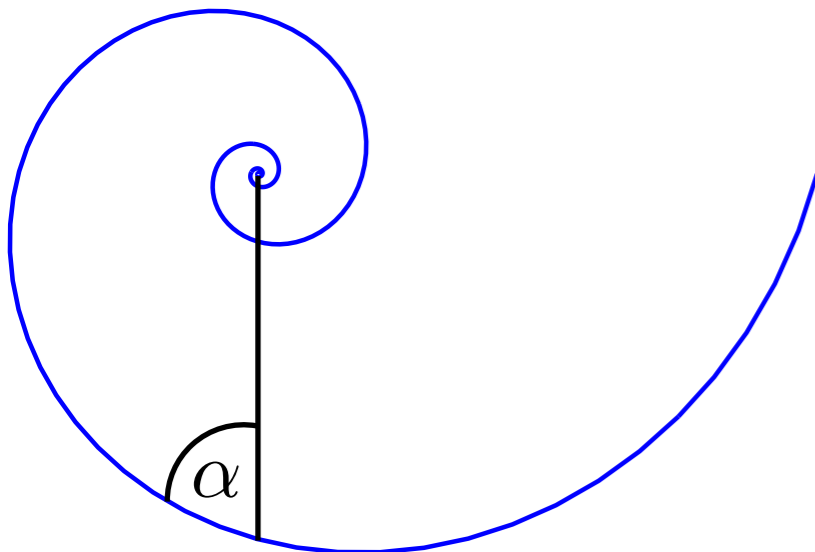
$$\alpha = 82^\circ$$



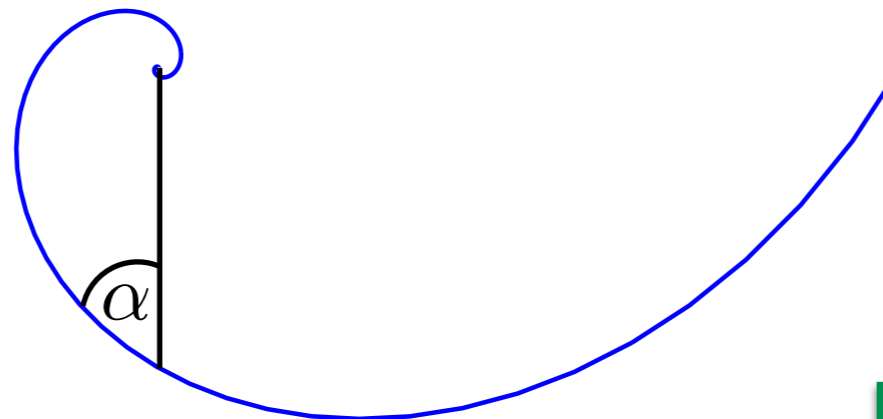
$$\alpha = 80^\circ$$



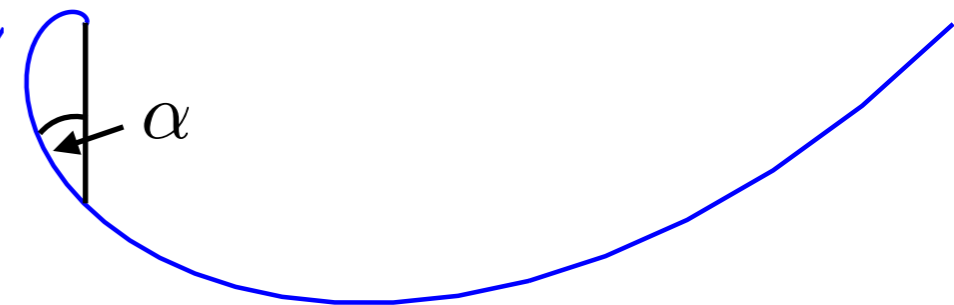
$$\alpha = 75^\circ$$



$$\alpha = 60^\circ$$

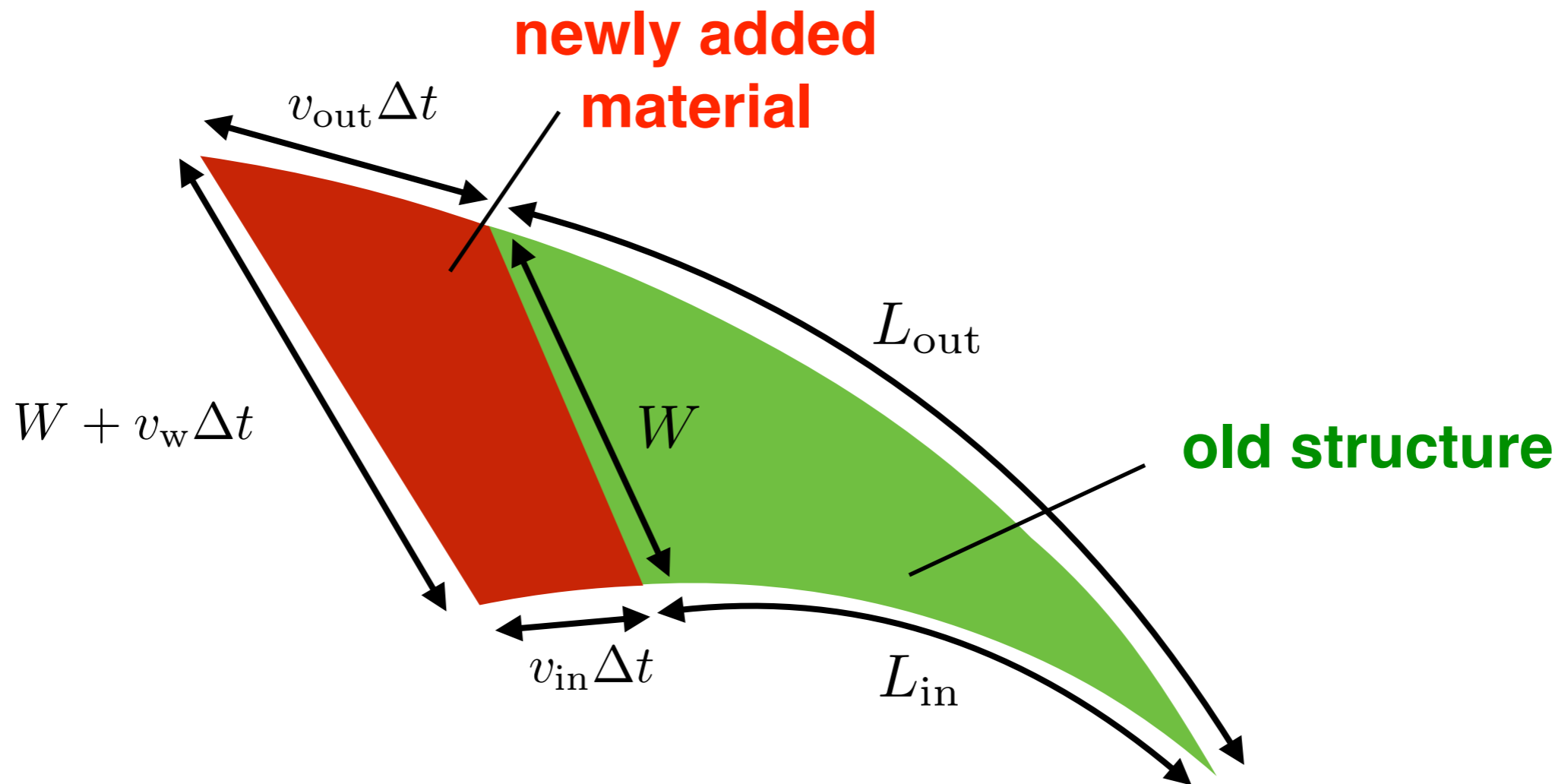


$$\alpha = 45^\circ$$



$$r(\theta) = a^\theta = \exp(\theta \cot \alpha)$$

Growth of spiral structures



New material is added at a constant ratio of growth velocities, which produces spiral structure with side lengths and the width in the same proportions.

$$v_{out} : v_{in} : v_W = L_{out} : L_{in} : W$$

Note: growth with constant width ($v_w=0$) produces helices

Growth of spiral structures

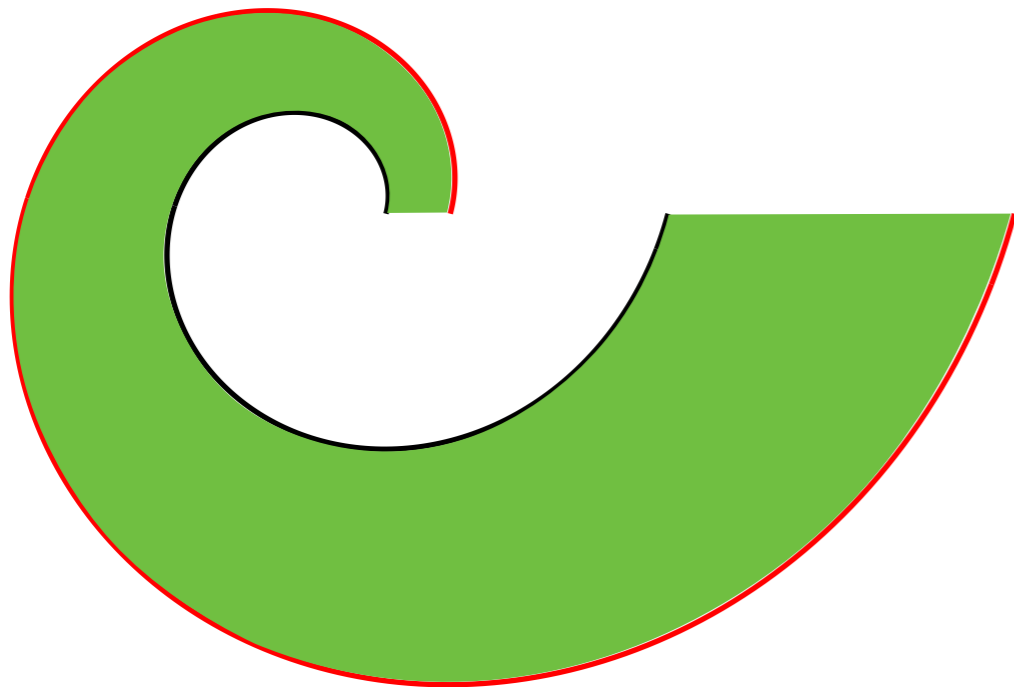
Assume the following spiral profiles of the outer and inner layers:

$$r_{\text{out}}(\theta) = e^{\theta \cot \alpha}$$

$$r_{\text{in}}(\theta) = \lambda e^{\theta \cot \alpha}$$

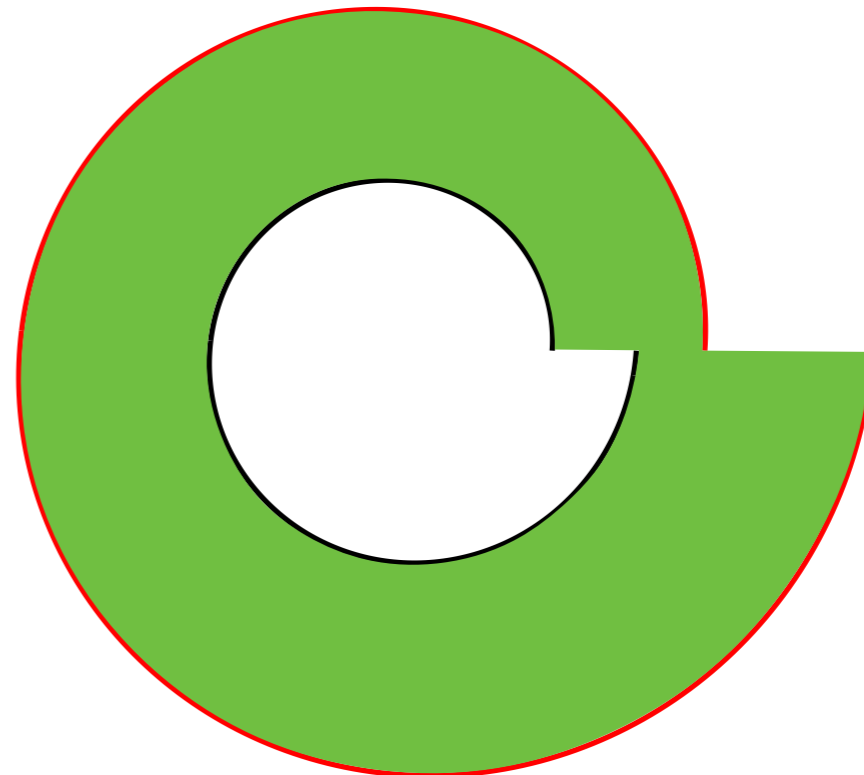
$$\lambda e^{2\pi \cot \alpha} > 1$$

$$\lambda = 0.5, \alpha = 75^\circ$$



$$\lambda e^{2\pi \cot \alpha} < 1$$

$$\lambda = 0.5, \alpha = 86^\circ$$

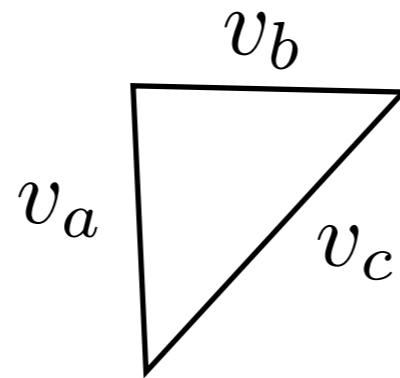


In some shells the inner layer does not grow at all

3D spirals



3D spiral of ram's horns is due to the triangular cross-section of the horn, where each side grows with a different velocity.



Shells of mollusks are often conical

Phyllotaxis

Phyllotaxis is classification of leaves on a plant stem

maize



**distichous
pattern**

leaves alternating
every 180°

Coleus sp.



**decussate
pattern**

pairs of
leaves at 90°

Veronicastrum
virginicum



**whorled
pattern**

3 or more leaves
originating from the
same node (180°)

sunflower

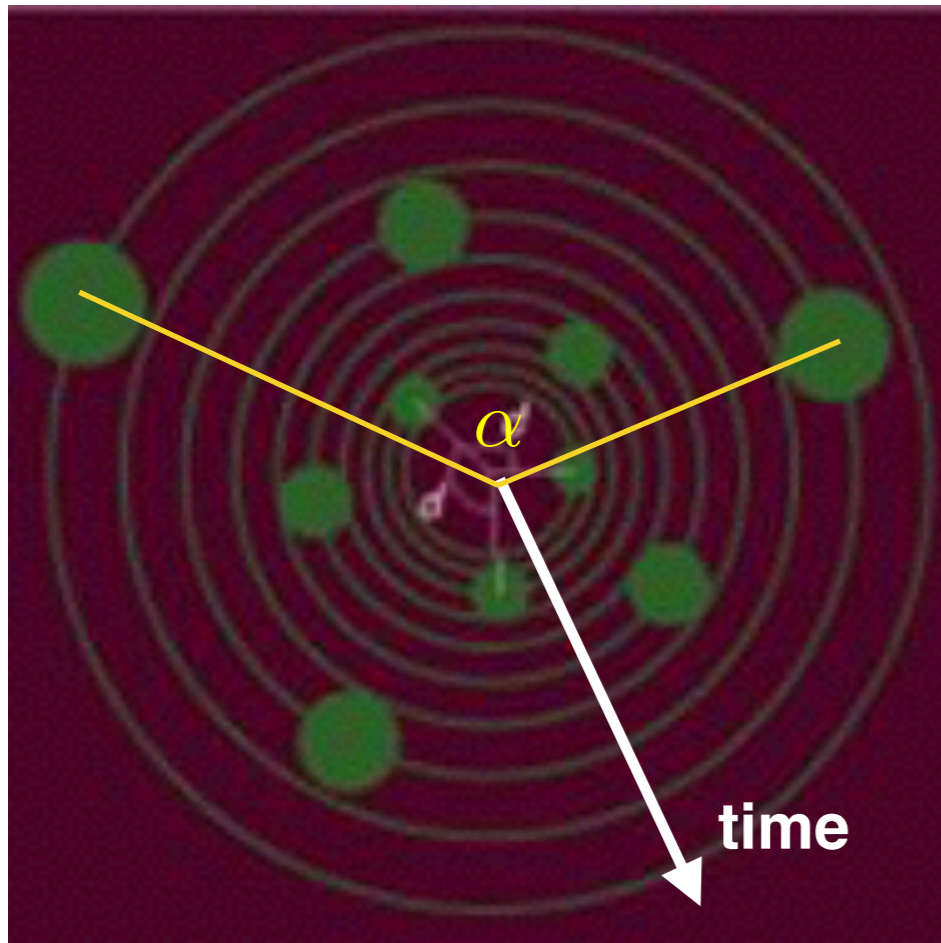


**alternate
(spiral)
pattern**

successive
leaves at 137.5°

Spiral phyllotaxis

schematic description
of leaves arrangement



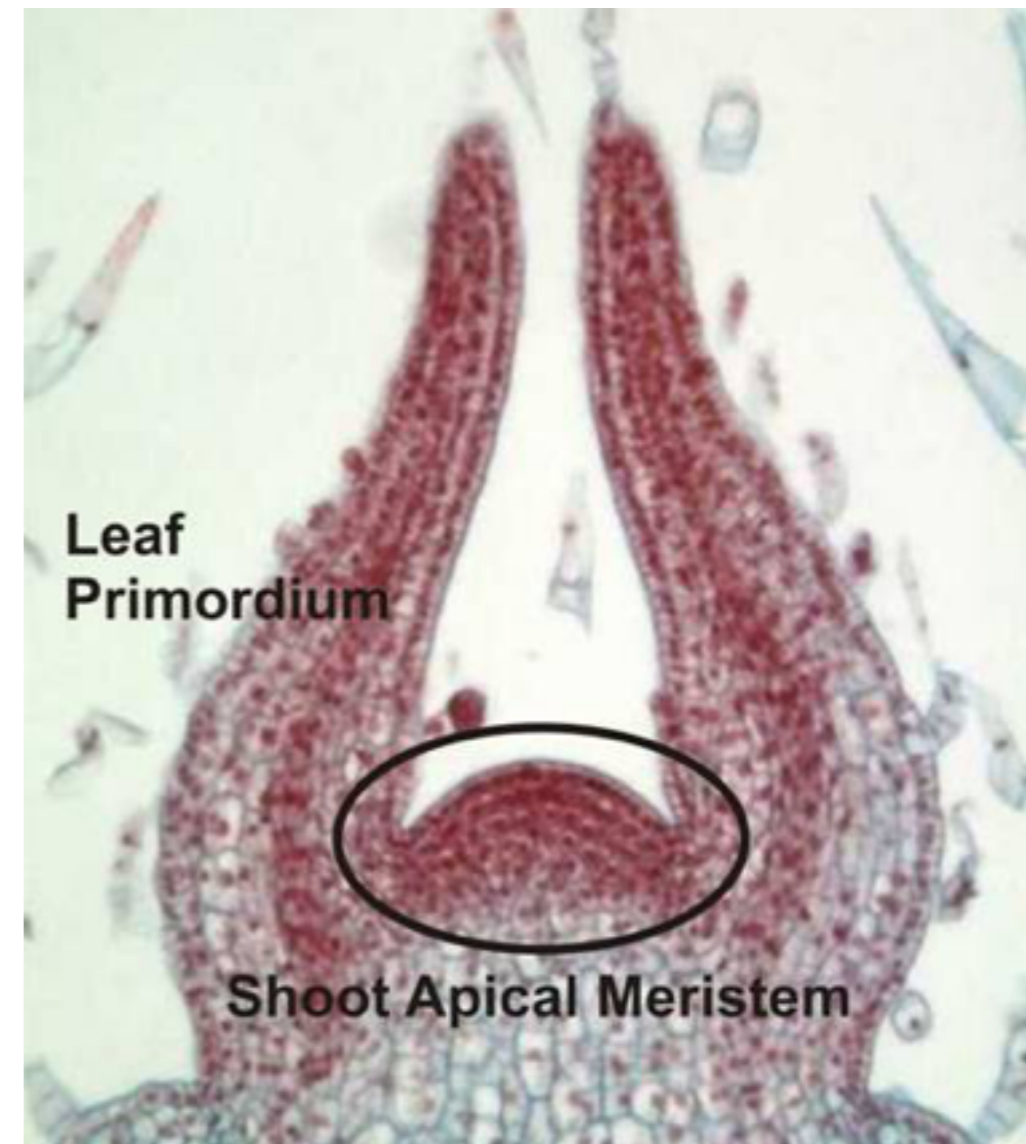
$$\alpha \approx 137.5^\circ$$

florets
(petals) floral
primordia



leaves

leaves grow from the
apical meristem, which
also gives rise to
petals, sepals, etc.



Parastichy numbers



21 left-handed spirals

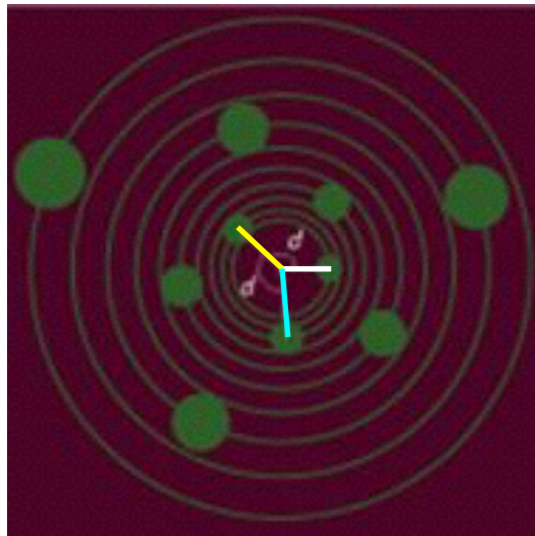
34 right-handed spirals



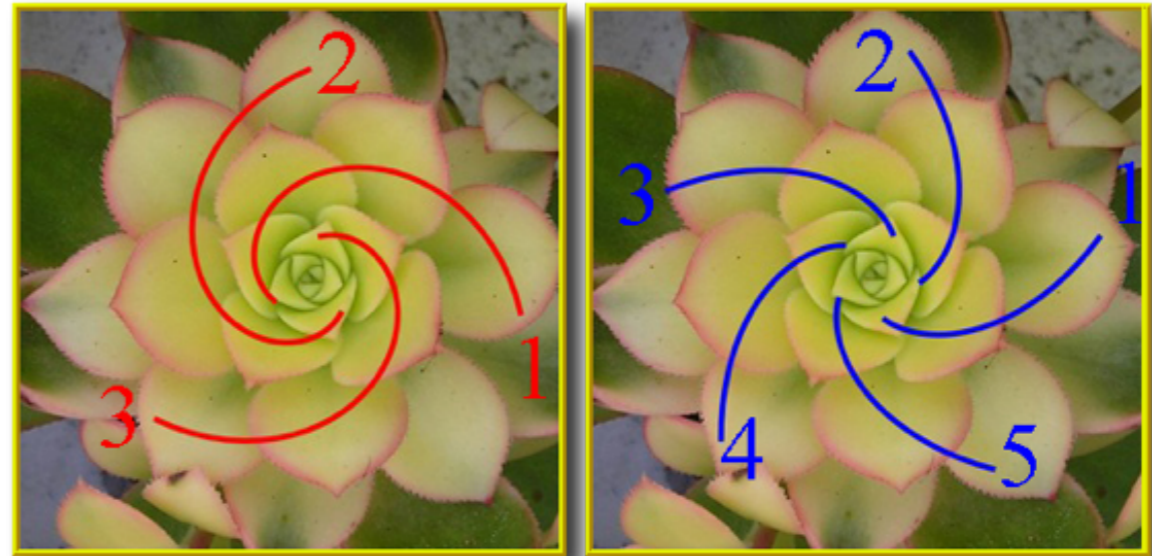
Parastichy numbers (21,34)

Parastichy numbers

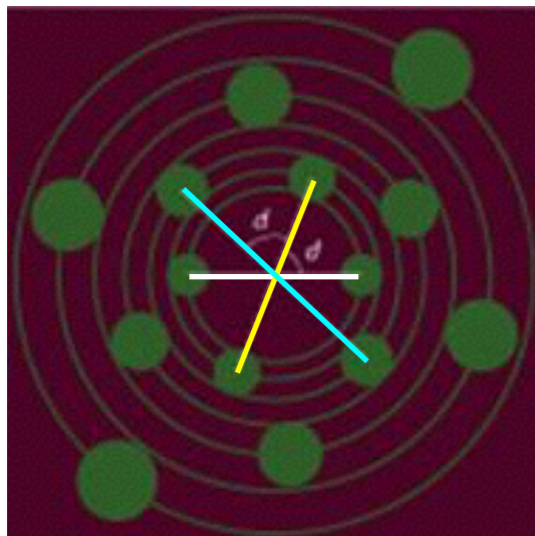
spiral
phyllotaxis



succulent plant (3,5)

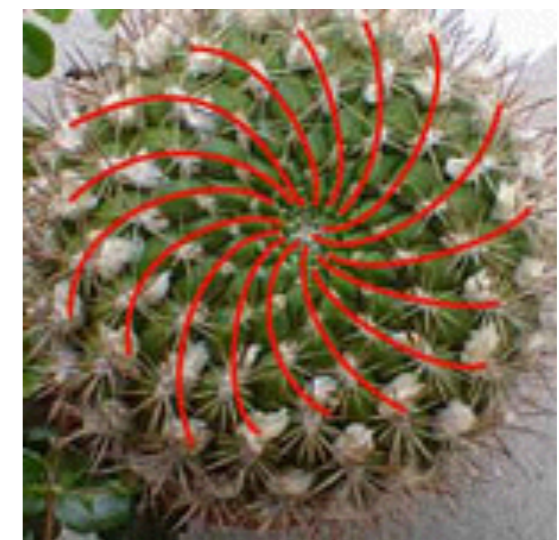


multijugate
phyllotaxis



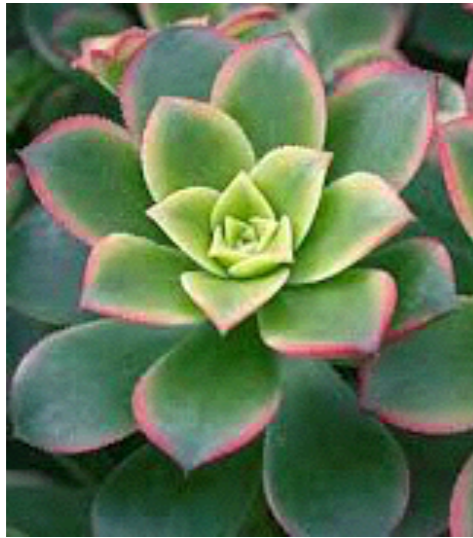
(e.g. 2 new leaves are added at the same time)

Gymnocalycium (10,16)=2(5,8)



Parastichy numbers

aonium (2,3)



succulent plant (3,5)



aloe (5,8)



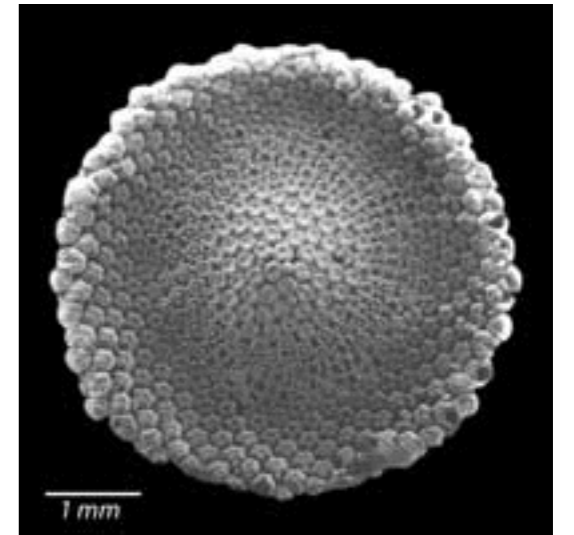
pine cone (8,13)



sunflower (21,34)



artichoke (34,55)



Parastichy numbers very often correspond to successive Fibonacci numbers!

Fibonacci numbers



$$F_1 = 1$$

$$F_2 = 1$$

$$F_n = F_{n-1} + F_{n-2}$$

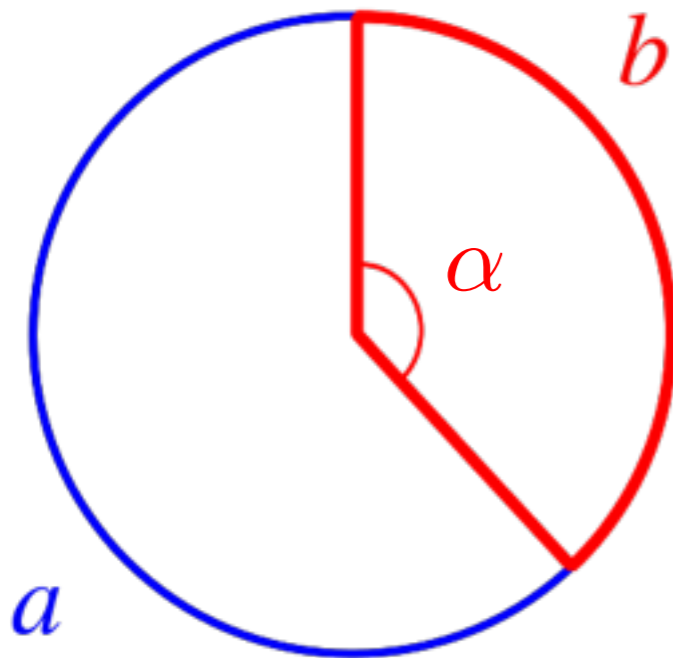
Golden ratio $\varphi = \frac{1 + \sqrt{5}}{2}$

$$F_n = \frac{1}{\sqrt{5}} [\varphi^n - (1 - \varphi)^n]$$

Sequence of Fibonacci numbers

1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, ...

Golden angle



**divide perimeter
in golden ratio**

$$\frac{a + b}{a} = \frac{a}{b} \longrightarrow \frac{a}{b} = \varphi$$

$$\alpha = 360^\circ \frac{b}{(a + b)} = \frac{360^\circ}{\varphi^2} \approx 137.5^\circ$$

**In spiral phyllotaxis successive leaves
grow at approximately Golden angle!**

Non-Fibonacci parastichy numbers



Statistics for pine trees in Norway

95% Fibonacci numbers

4% Lucas numbers

1% not properly formed

Lucas numbers

$$L_1 = 1$$

$$L_2 = 3$$

$$L_n = L_{n-1} + L_{n-2}$$

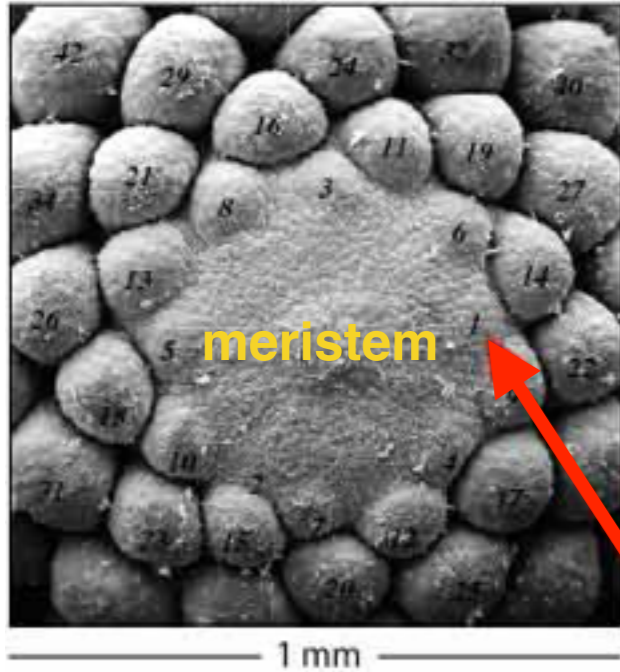
Sequence of Lucas numbers

1, 3, 4, 7, 11, 18, 29, 47, 76



Spiral phyllotaxis

Norway spruce

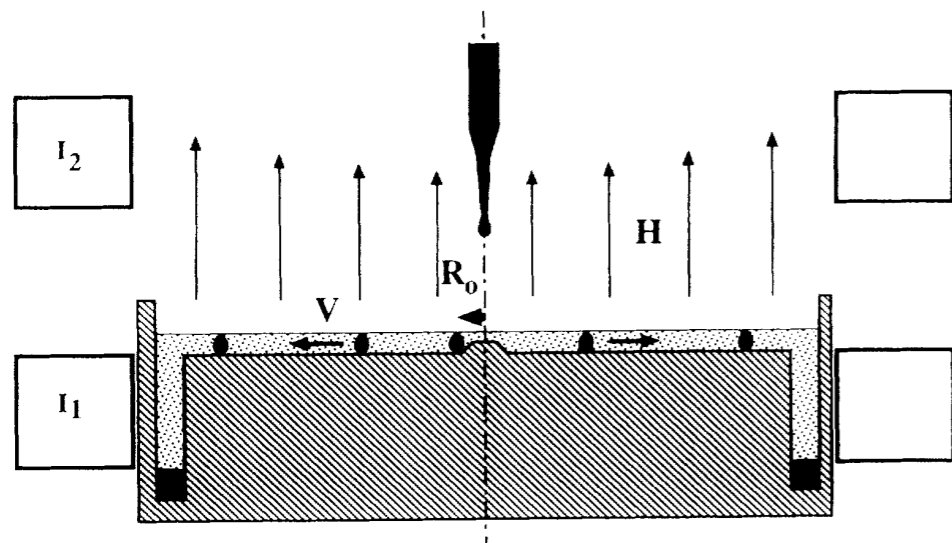


New primordia start growing at the site where plant hormone auxin is depleted.

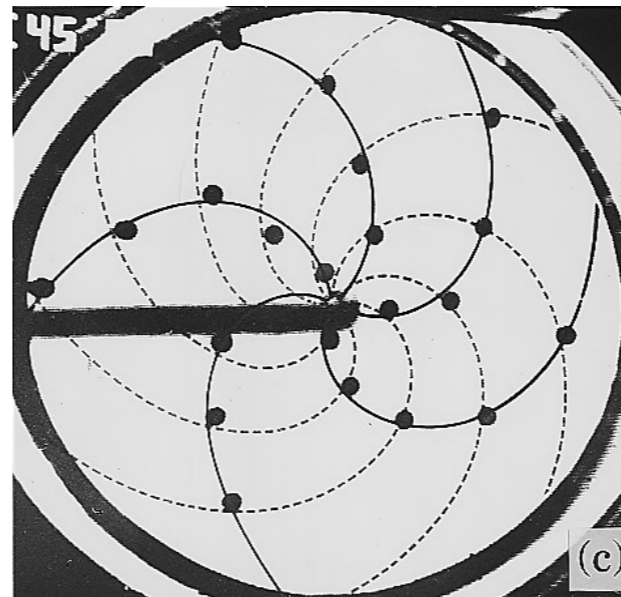
Auxin hormones are released by growing primordia. New primordium wants to be as far apart as possible from the existing primordia.

new primordial

Mechanical analog with magnetic repelling particles



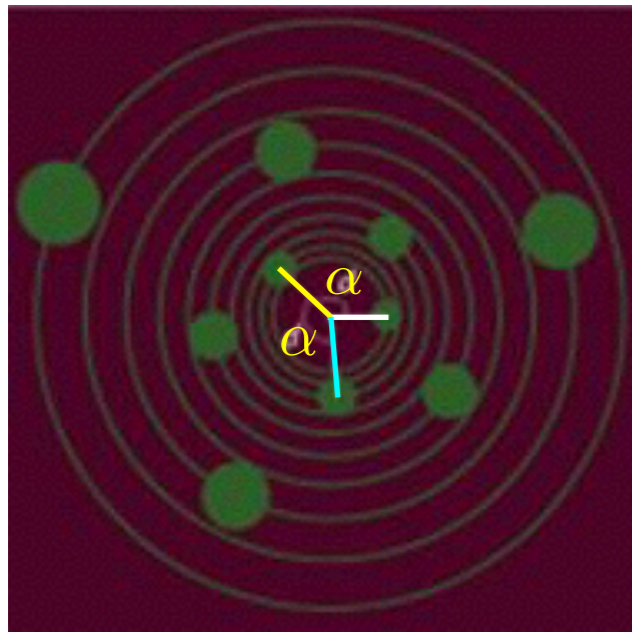
magnetic field drives particles away from the center



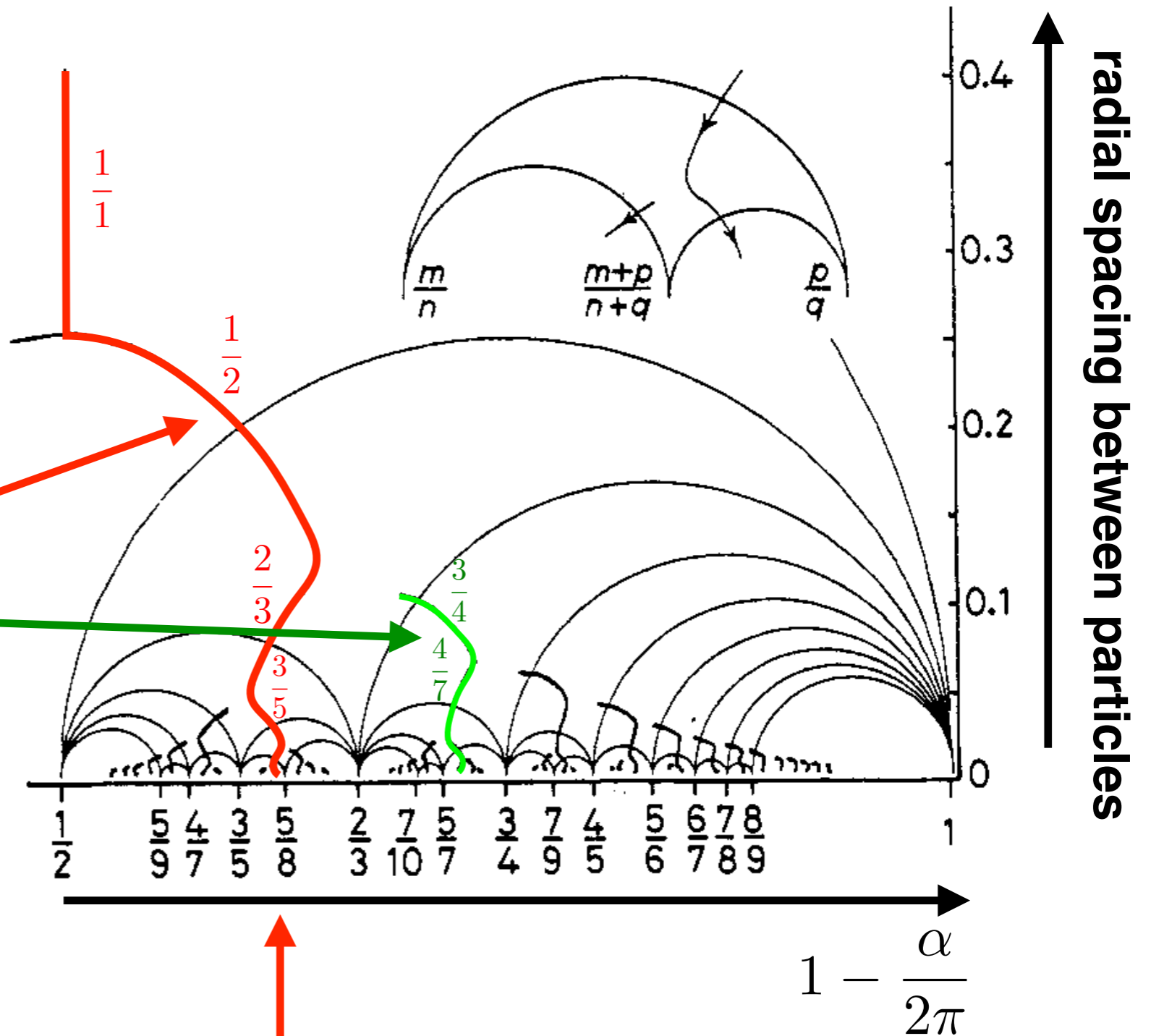
Parastichy numbers (5,8)

particles repel via magnetic dipole interactions

Energy minimization between repelling particles



Local energy minima for repelling particles



Fibonacci numbers

Lucas numbers

As the plant is growing it is gradually reducing the time delay between formation of new primordia. The spiral patterns then go sequentially through all the Fibonacci parastichies.

Occasional excursions to the neighbor local minima produce Lucas parastichy numbers.

golden angle

L. Levitov, PRL 66, 224 (1991)

L. Levitov, EPL 14, 533 (1991)

Further reading

