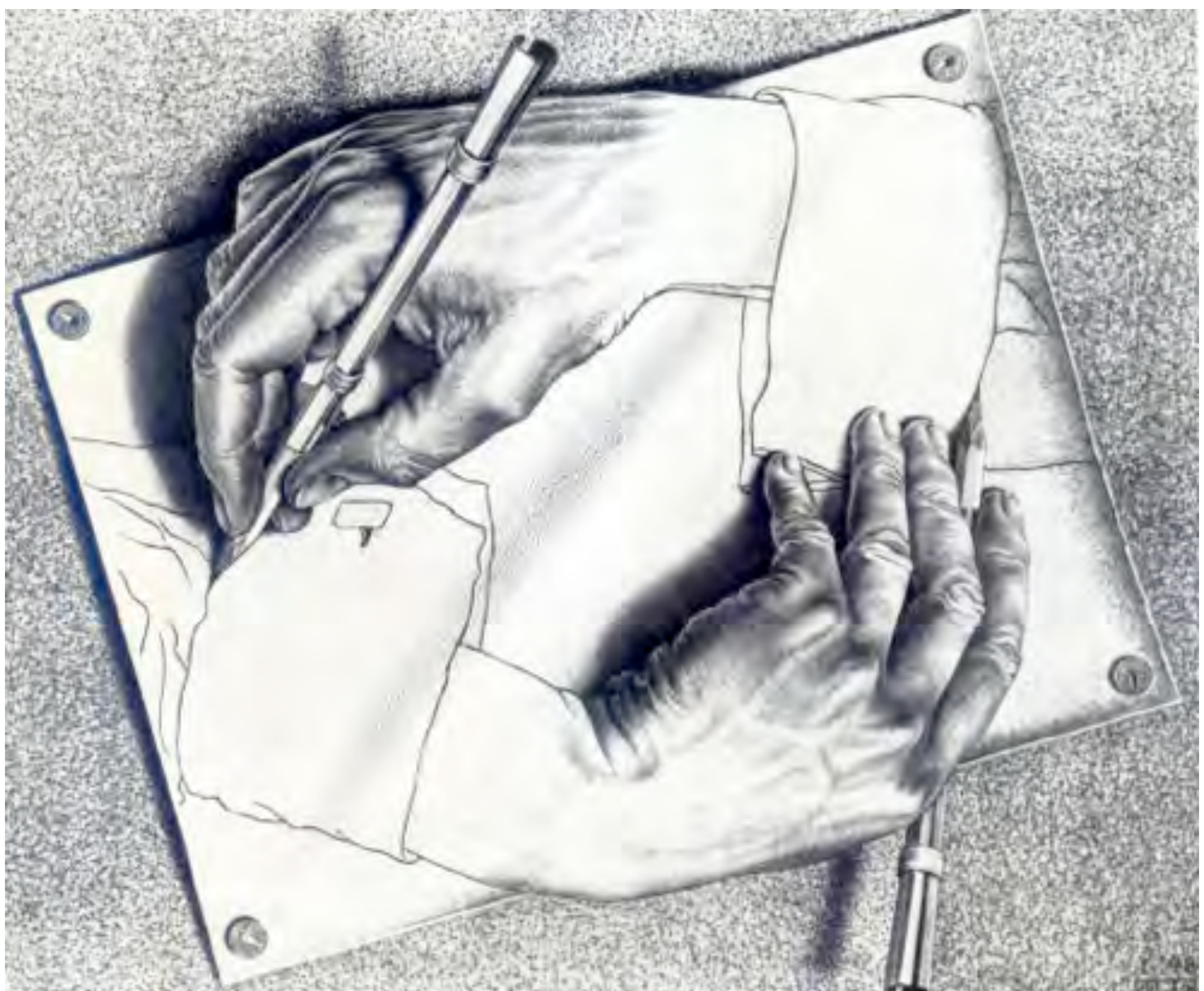
OCCAM

Oxford Centre for Collaborative Applied Mathematics

Inversion, Rotation, and Perversion in Mechanical Biology: From Microscopic Anisotropy to Macroscopic Chirality



M.C. Escher, *Drawing hands*,1948

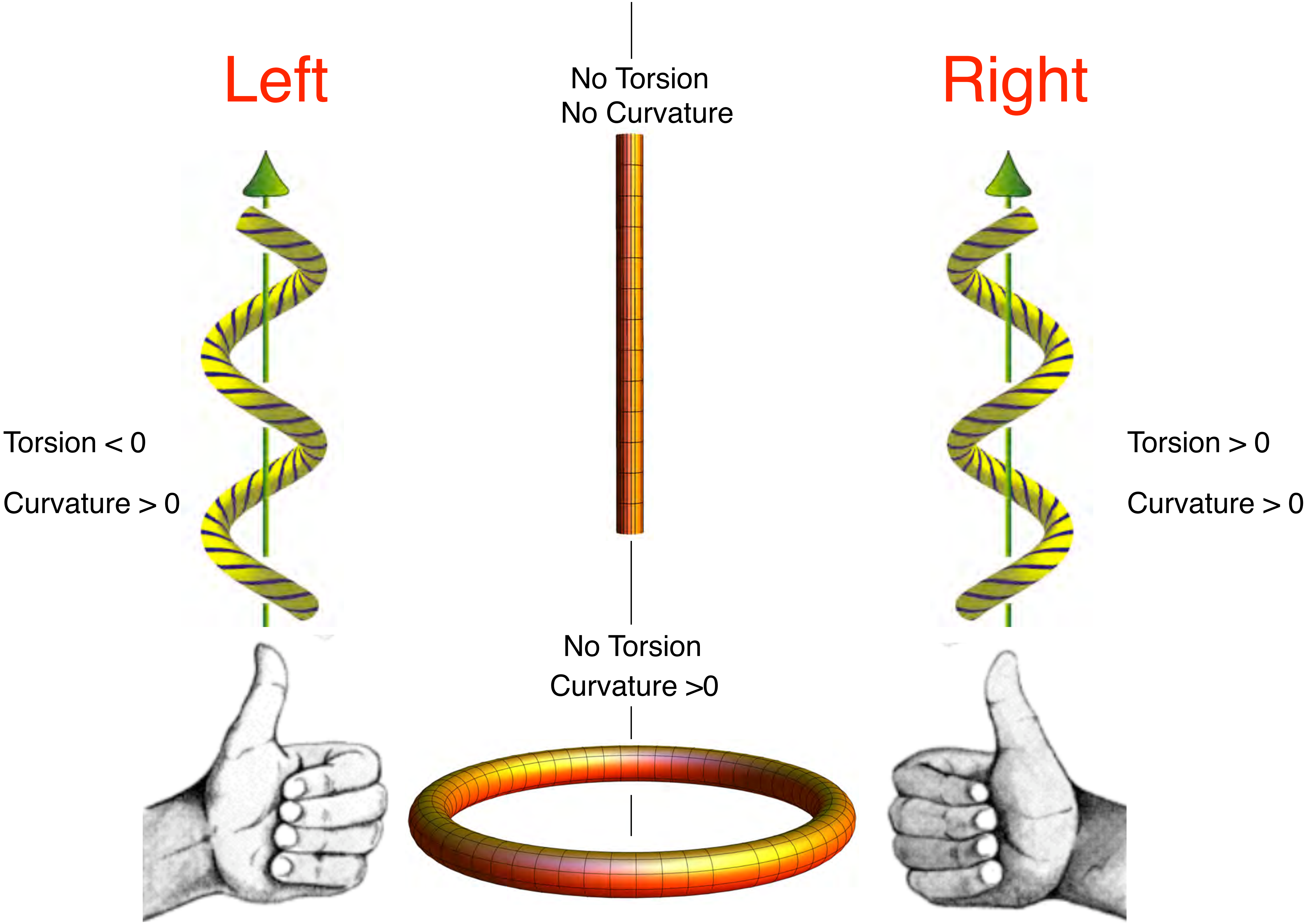
Alain Goriely

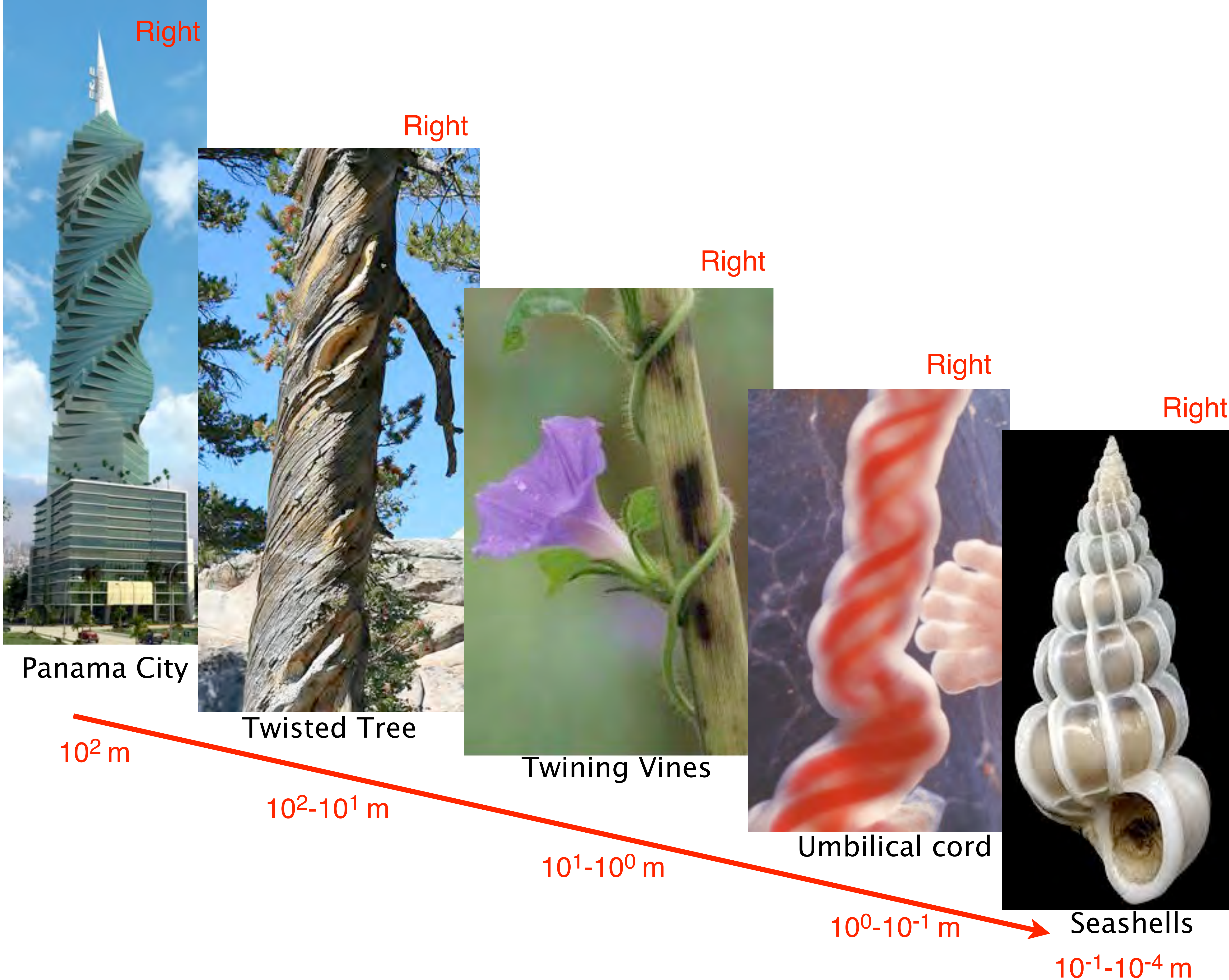
Mathematical Institute

University of Oxford

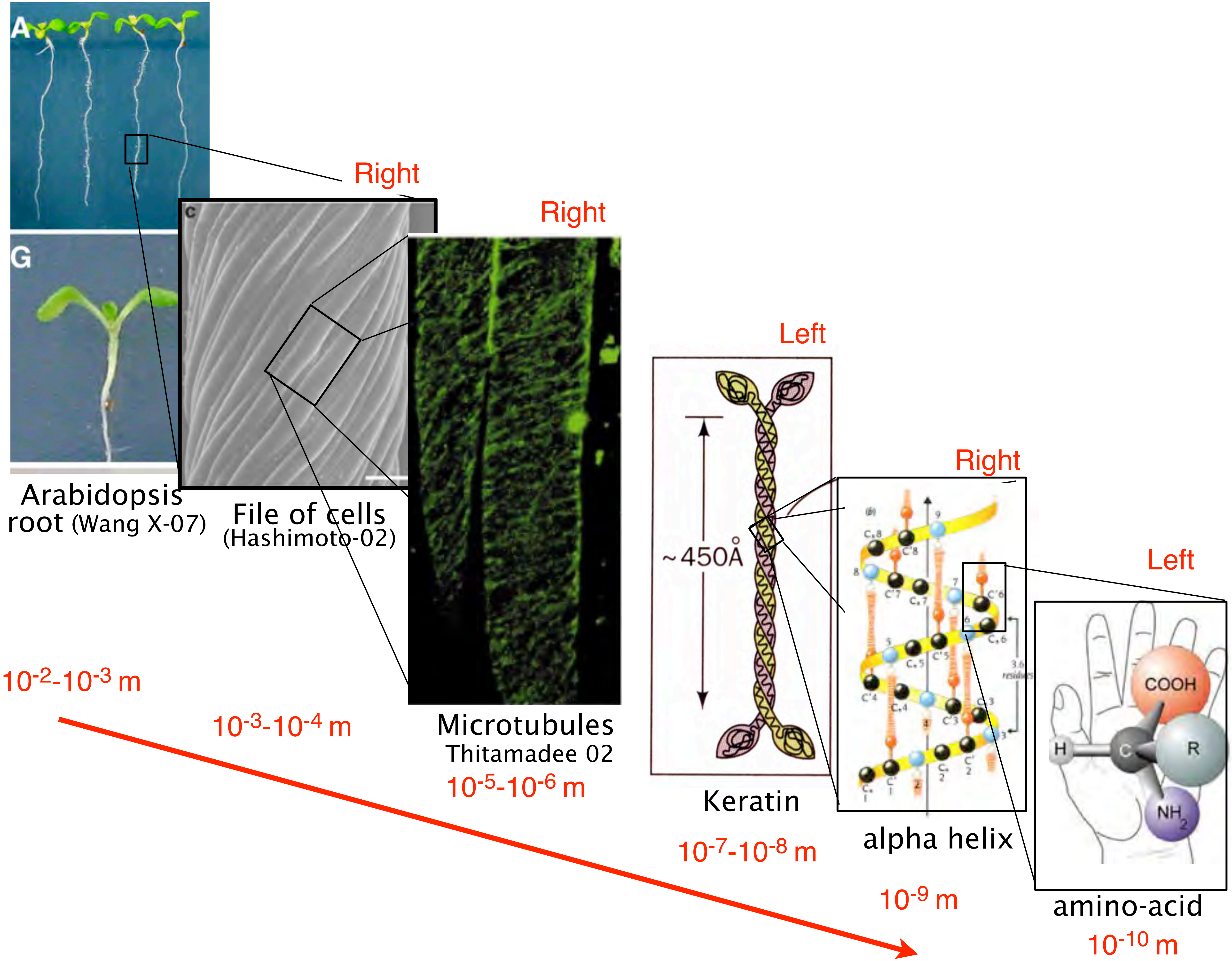
SIAM-Day Cardiff,
January 2013

Research supported in part by the NSF, EPSRC, the Royal Society, and the KAUST-GRP initiative


Left
No Torsion
No Curvature
Right
Torsion < 0
Curvature > 0
Torsion > 0
Curvature > 0
No Torsion
Curvature >0



Right
Right
Right
Right
Right
Panama City
Twisted Tree
Twining Vines
Umbilical cord
Seashells
10^2 m
10^2-10^1 m
10^1-10^0 m
10^0-10^{-1} m
10^{-1}-10^{-4} m


Right
Right
Left
Right
Left
Arabidopsis root (Wang X-07)
File of cells (Hashimoto-02)
Microtubules Thitamadee 02
Keratin
alpha helix
amino-acid
~450Å
COOH
H
C
R
NH2
10-2-10-3 m
10-3-10-4 m
10-5-10-6 m
10-7-10-8 m
10-9 m
10-10 m

GRAND QUESTIONS

- Absolute or relative notion of space (Immanuel Kant)

  "What can more resemble my hand or my ear, and be more equal in all points, than its image in the mirror? And yet I cannot put such a hand as is seen in the mirror in the place of its original ..."(1783)

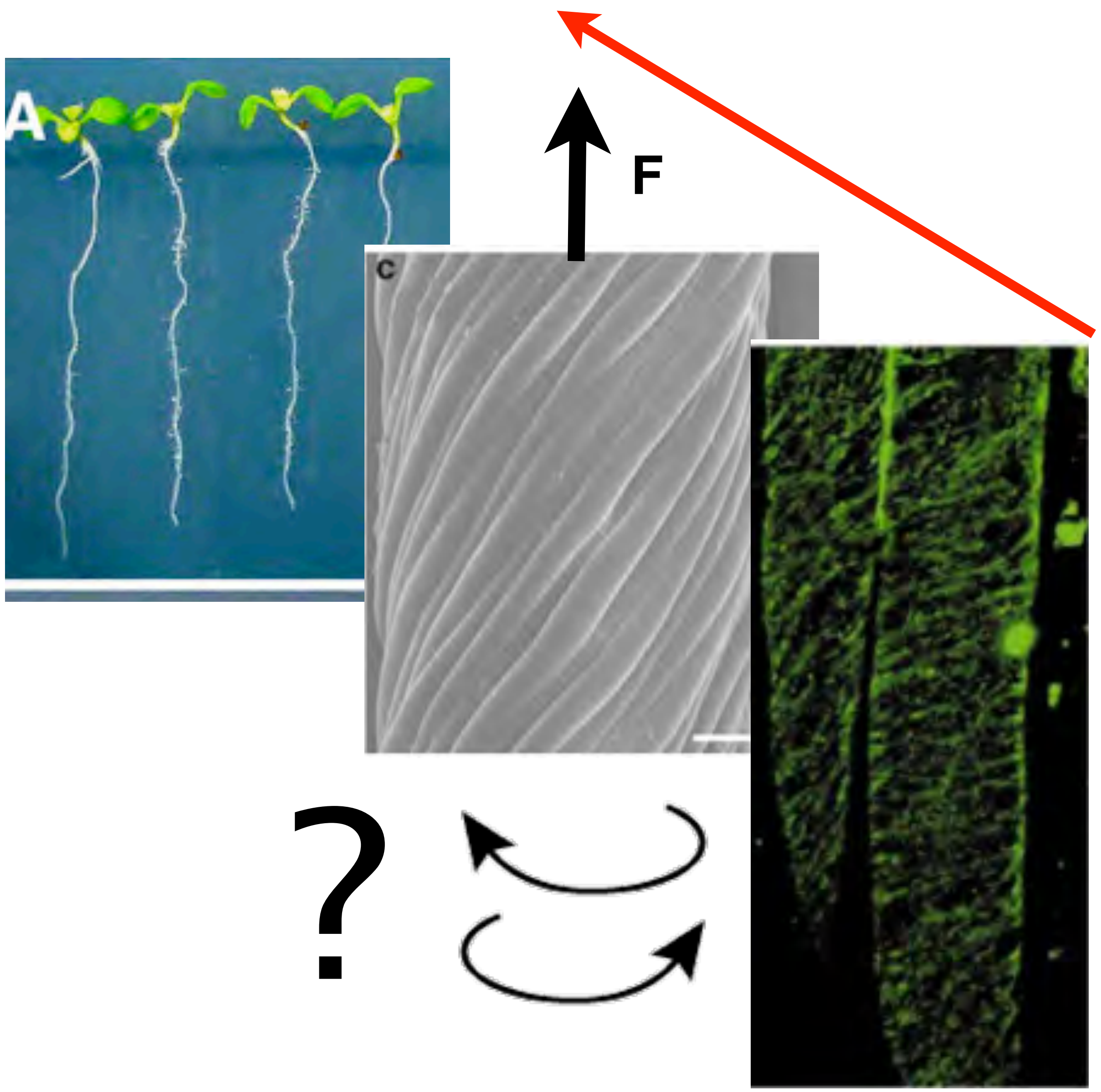
- Parity and symmetry breaking in physics (R. Feynman)

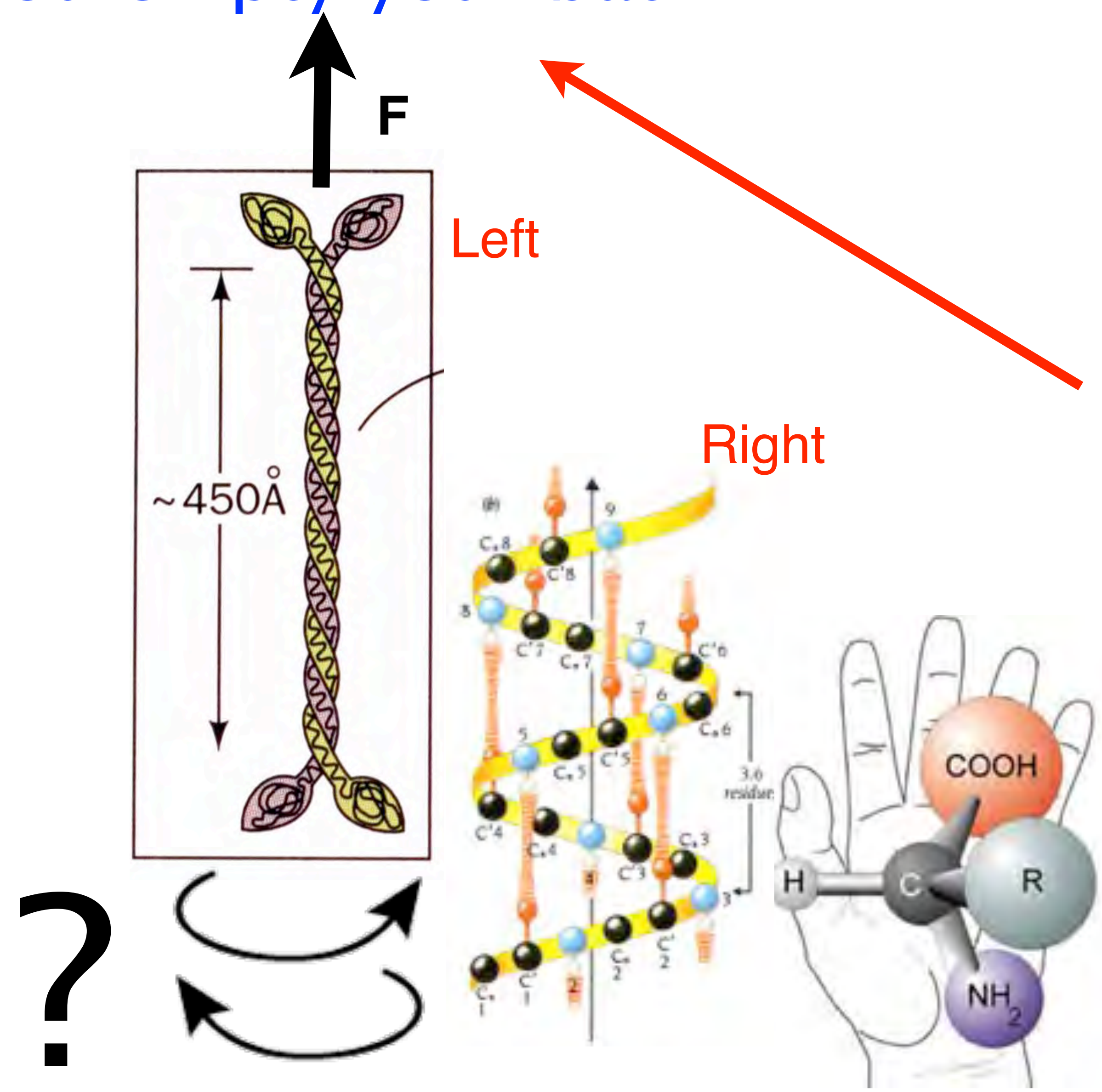
  "The rule is that the particles which carry spin, like the electron, neutrino and so on, come out (in weak decays) with a spin mostly to the left. Now that is the rule, but today we do not really understand the whys and wherefores of it. Why is this the right rule, what is the fundamental reason for it, and how is it connected to anything else?" (1964)

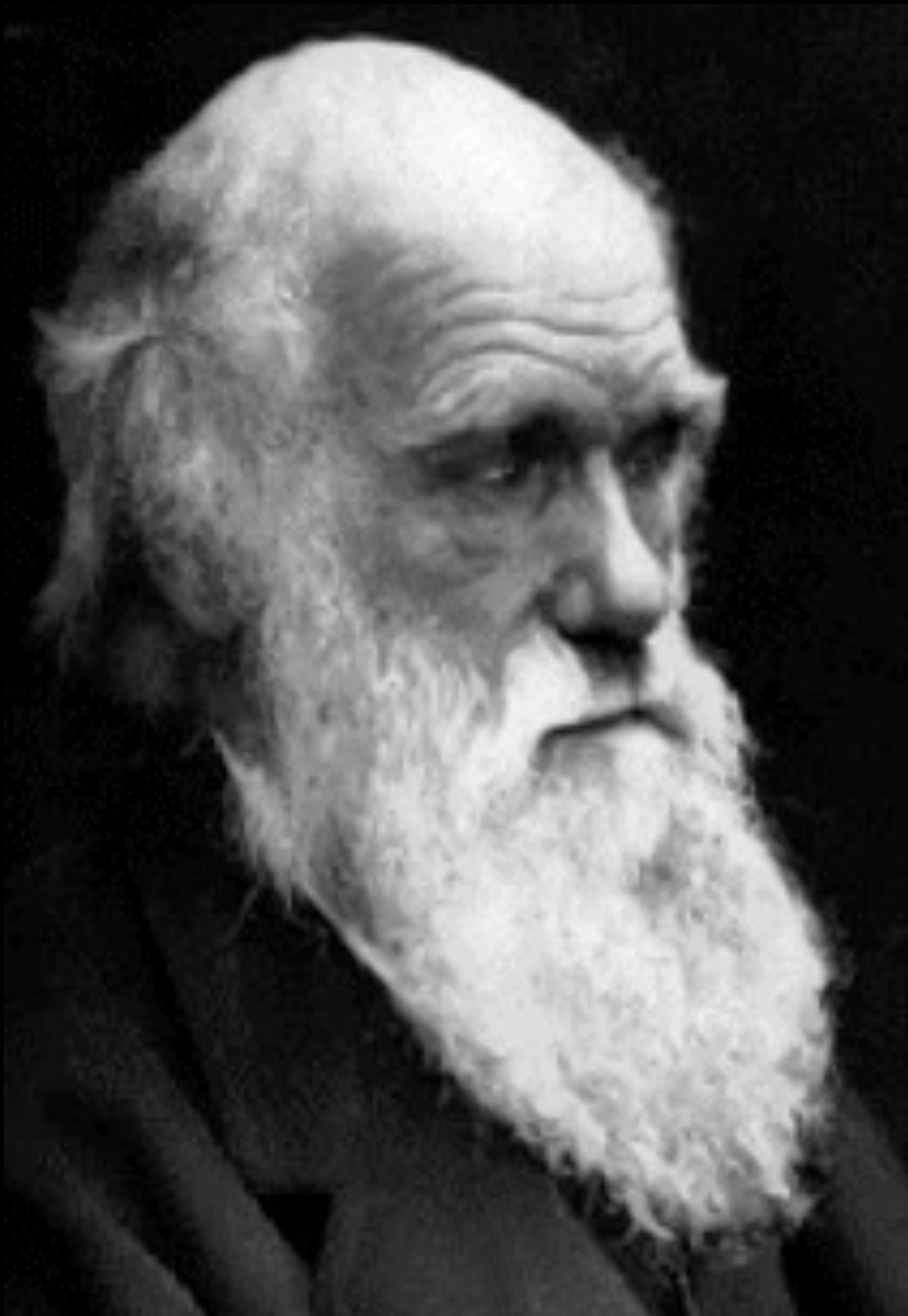
- Ultimate origin of chirality in nature
- Functions of laterality in biology, neurosciences
- Selection of handedness in genetics

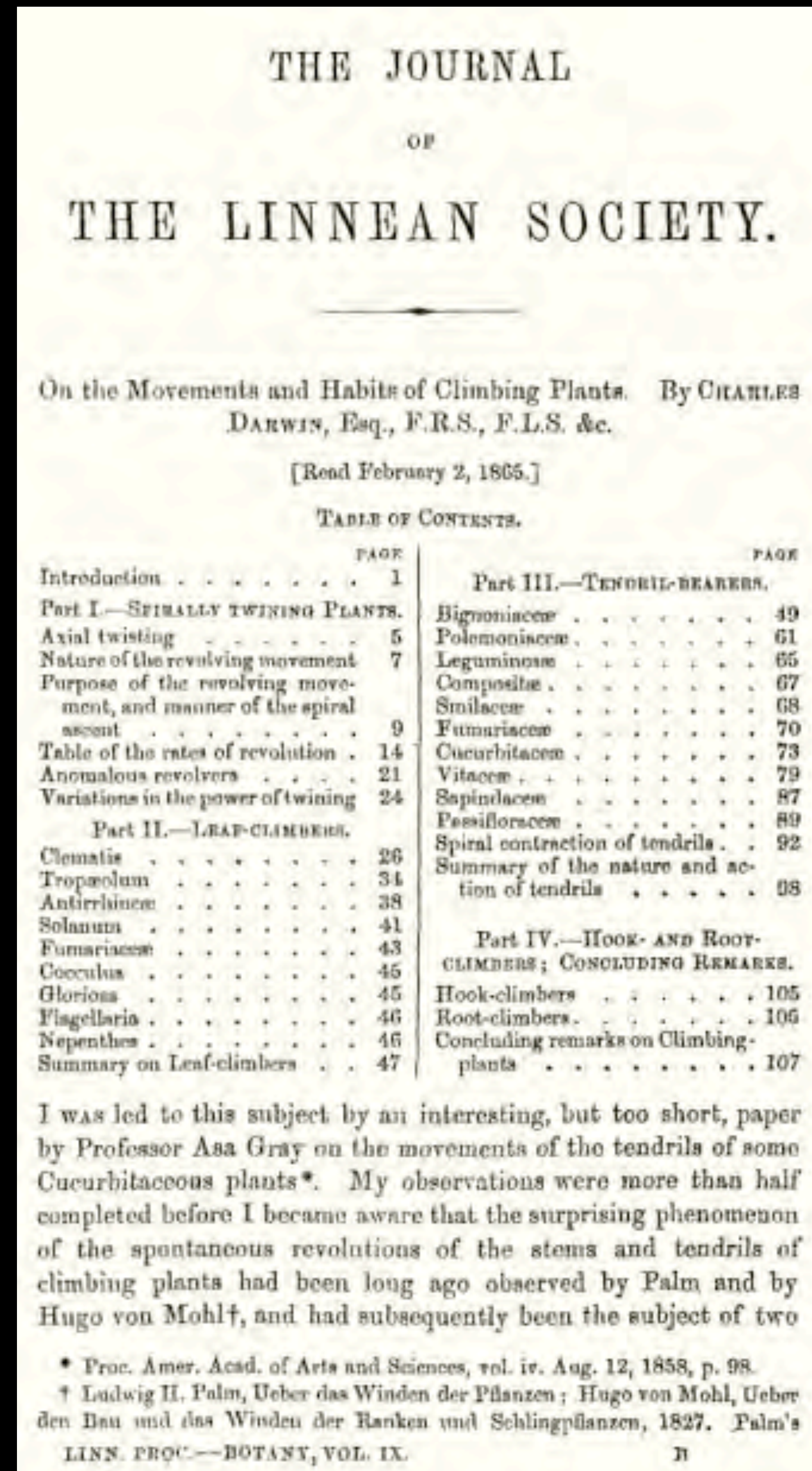
petite questions

- Mechanics: chirality transfer from scale to scale
- Response of a chiral structure: winding or unwinding?
- Explaining inversion (and perversion)
- and what really happens when you empty your bath?









THE JOURNAL

OF

THE LINNEAN SOCIETY.

On the Movements and Habits of Climbing Plants. By CHARLES DARWIN, Esq., F.R.S., F.L.S. &c.

[Read February 2, 1865.]

TABLE OF CONTENTS.

I WAS led to this subject by an interesting, but too short, paper by Professor Asa Gray on the movements of the tendrils of some Cucurbitaceous plants*. My observations were more than half completed before I became aware that the surprising phenomenon of the spontaneous revolutions of the stems and tendrils of climbing plants had been long ago observed by Palm and by Hugo von Mohl†, and had subsequently been the subject of two

* Proc. Amer. Acad. of Arts and Sciences, vol. iv. Aug. 12, 1858, p. 98.

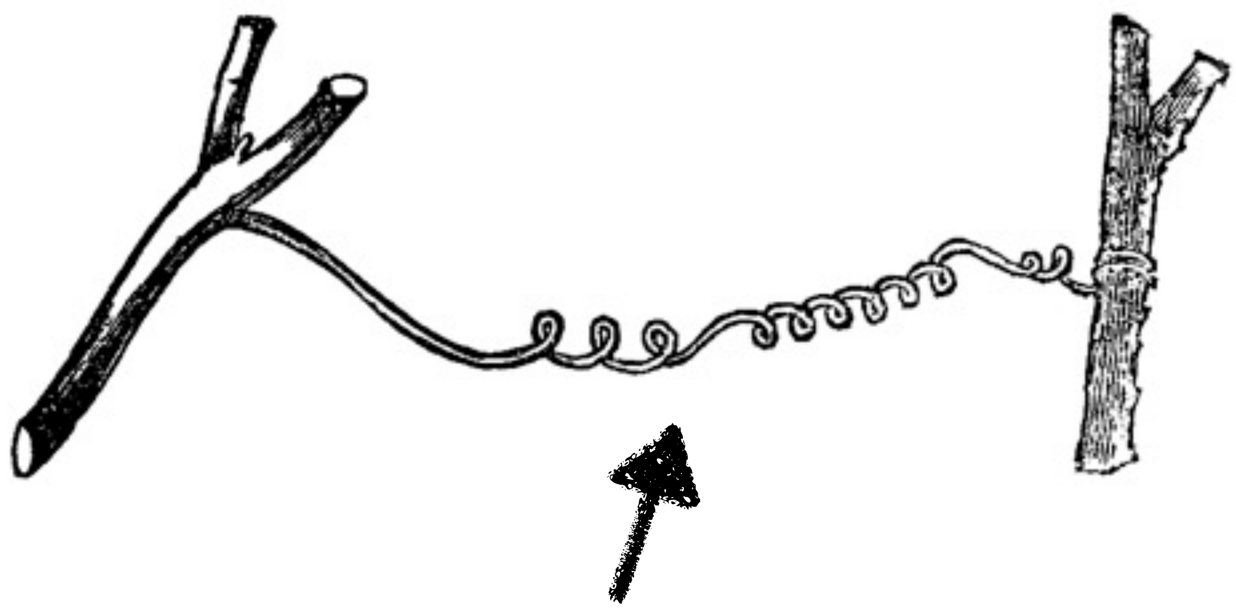
† Ludwig H. Palm, Ueber das Winden der Pflanzen; Hugo von Mohl, Ueber den Bau und das Winden der Ranken und Schlingpflanzen, 1827. Palm's

Tendril Perversion

BBC documentary EARTH (Plants) narrated by D. Attenborough (2009)

A tendril invariably becomes twisted in one part in one direction, and in another part in the opposite direction... This curious and symmetrical structure has been noticed by several botanists, but has not been sufficiently explained.

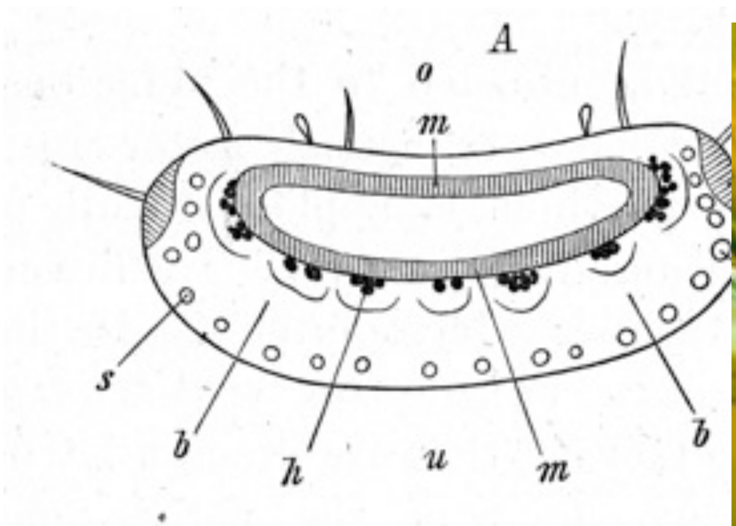
Darwin *The movements and habits of climbing plants*



Tendril perversion

1865	1858	1844	1827	1790	1760
Darwin	Léon	Dutrochet	de Candolle	Goethe	**Ampère**

A mechanism

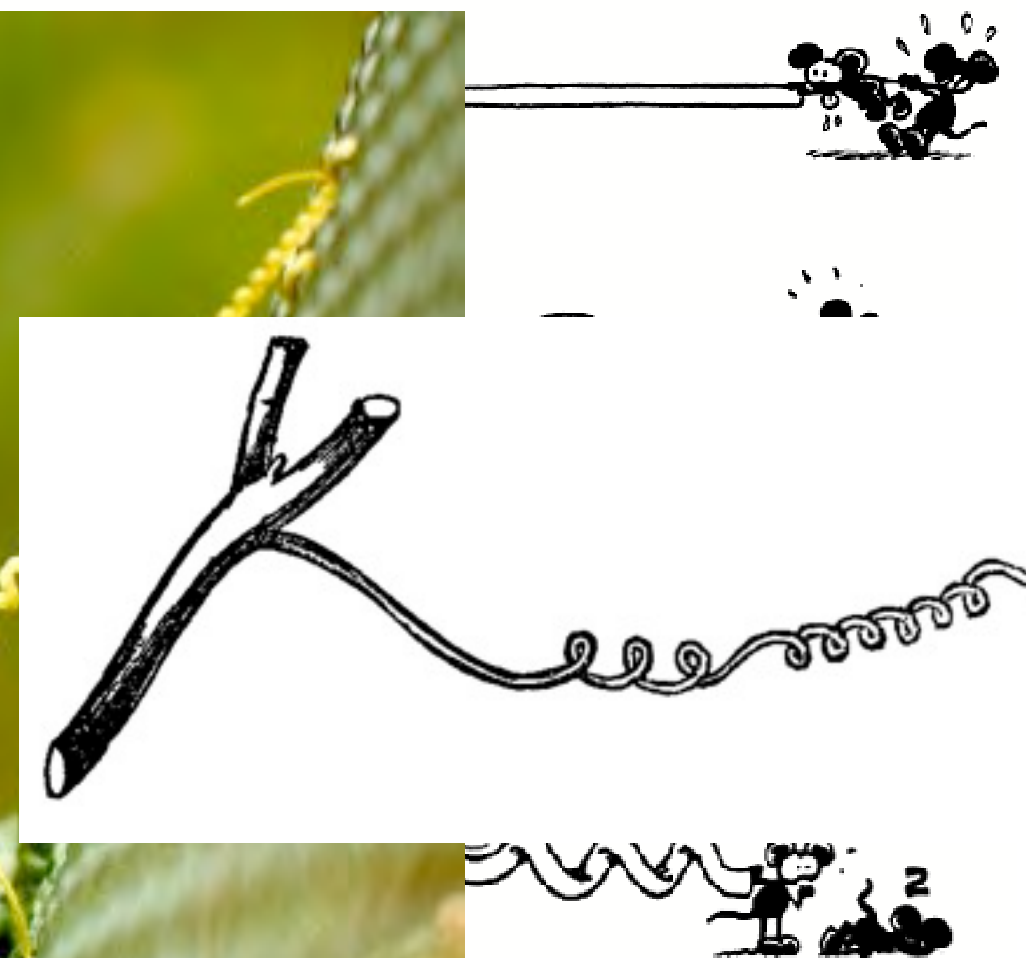


Transverse section through a te
H. de Vries (1877)

GROWTH INDUCED CUR

TENSION

NO NET ROTATIO

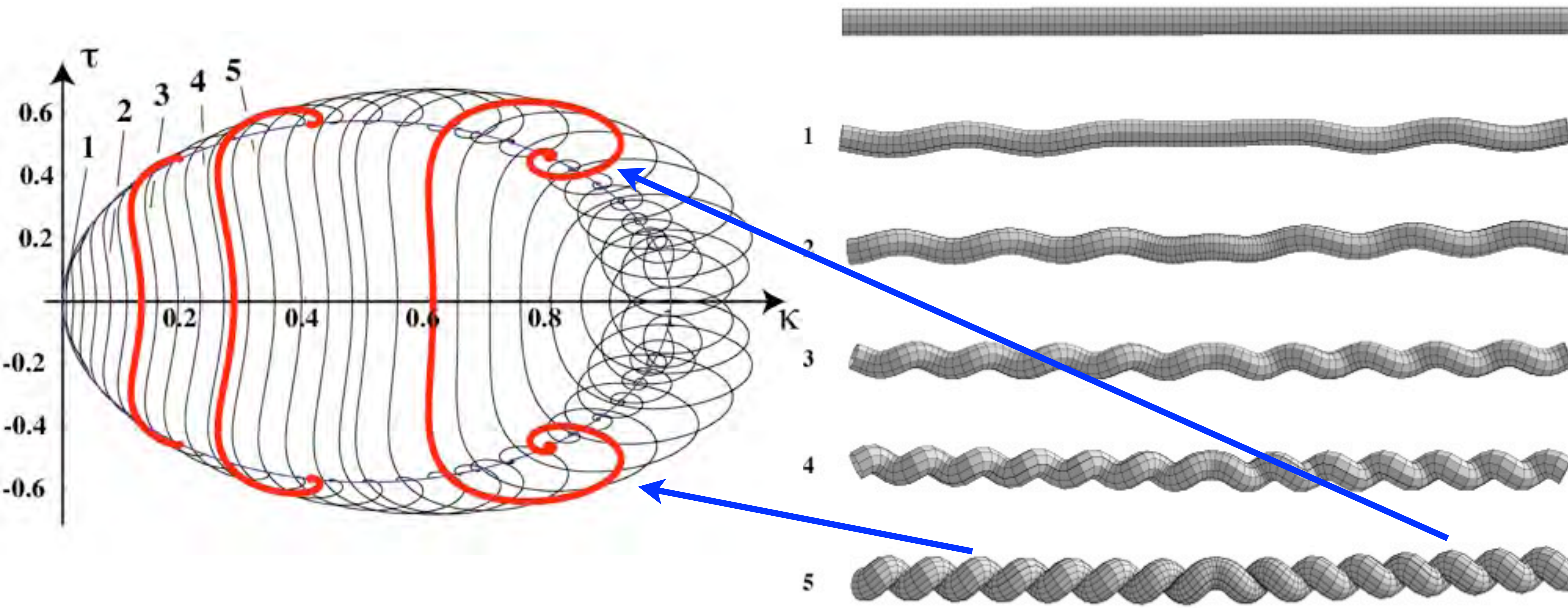


Mechanically, a tendril is an elastic filament with intrinsic curvature under tension whose ends are prevented from rotating

→

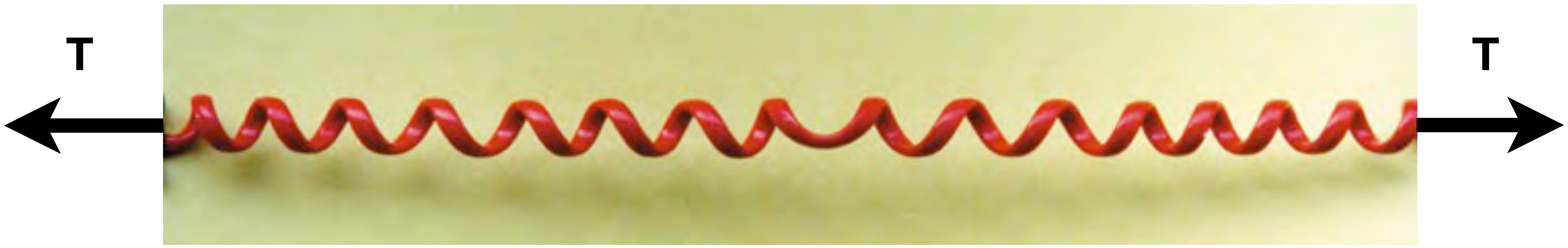
Increasing curvature or reducing tension creates an instability

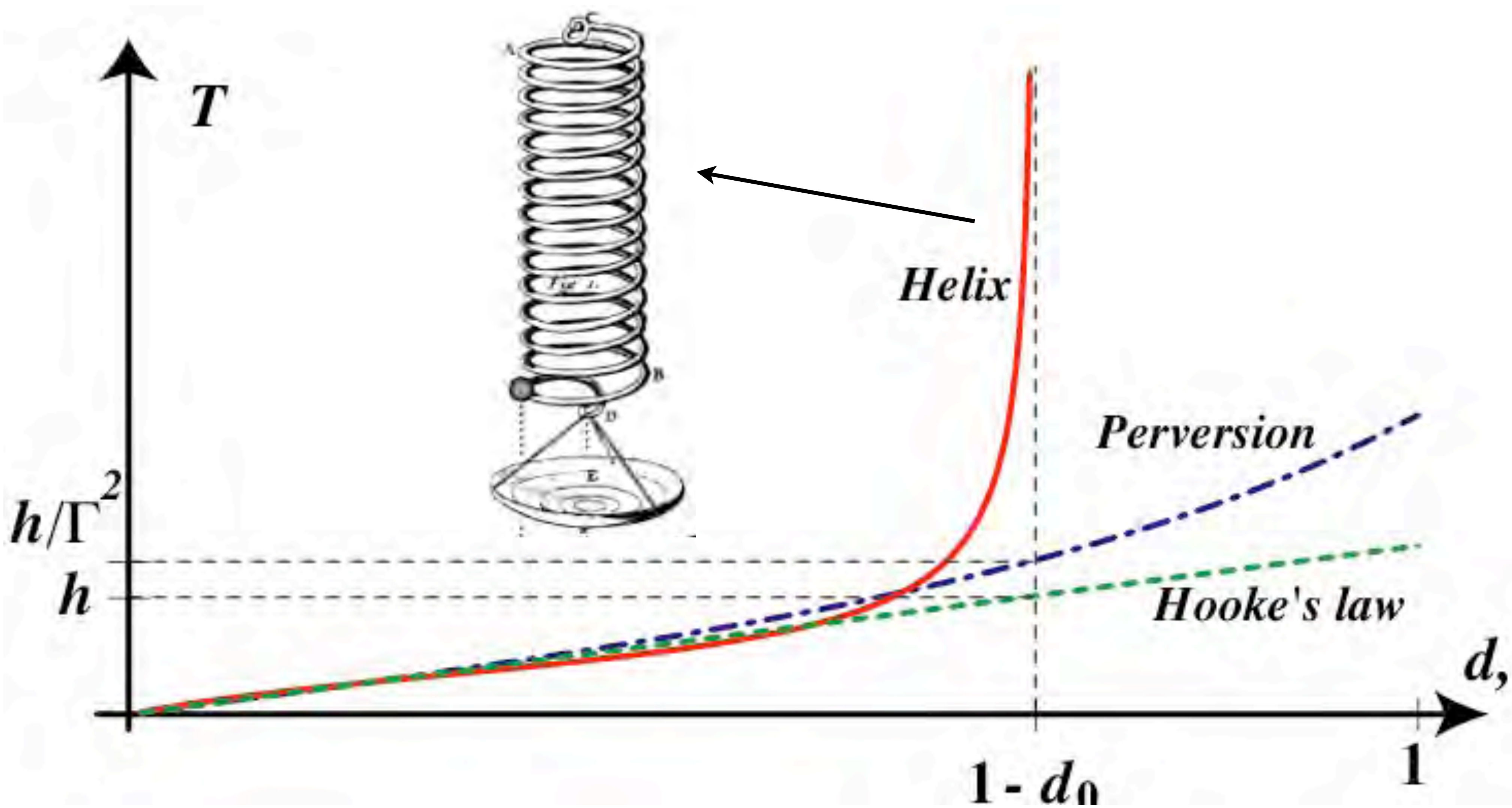
A mathematical model



AG, McMillen, 02

A better spring?





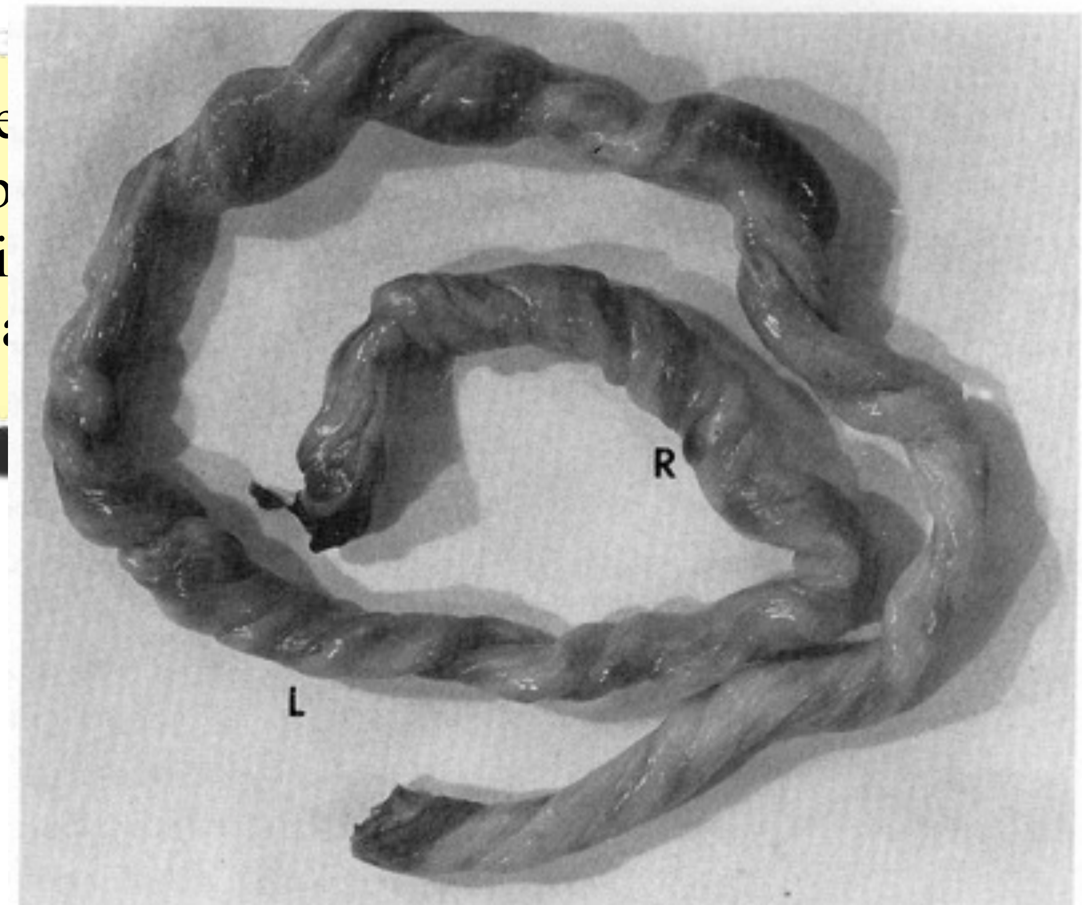
Tendrils are better springs than helical springs

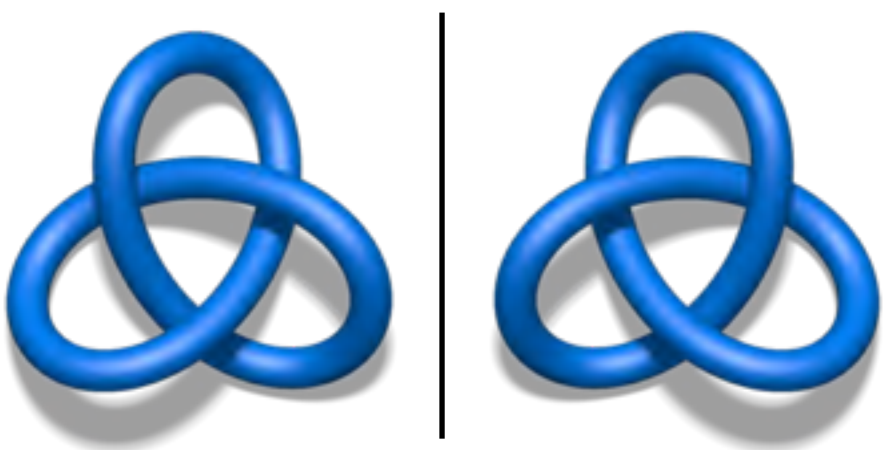
AG, McMillen, 02

Perversion?

J. C. Maxwell (1831-1879)

The ope… …ner is
called b… …ct in a
mirror i…
J. C. Ma… …, 1892





Tait's example of perversion
The trefoil knot

Digression: a convention

London Mathematical Society, 1871

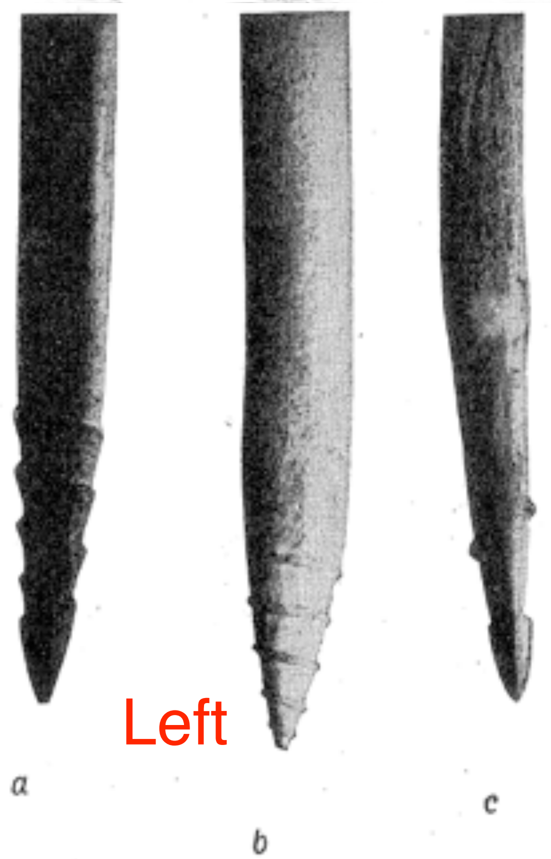
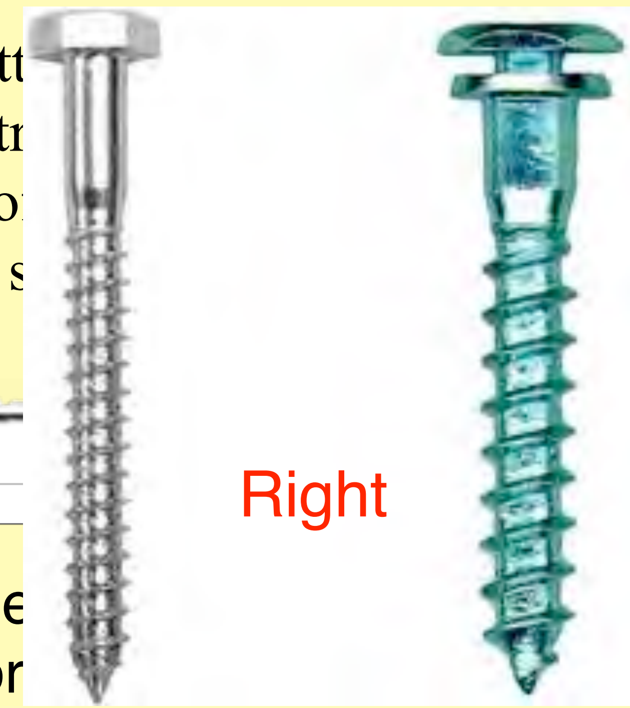


FIG. 2.—Types of Eskimo screws. a, The simplest type. b, A more elaborate type. c, The most elaborate type. (Exact size.)

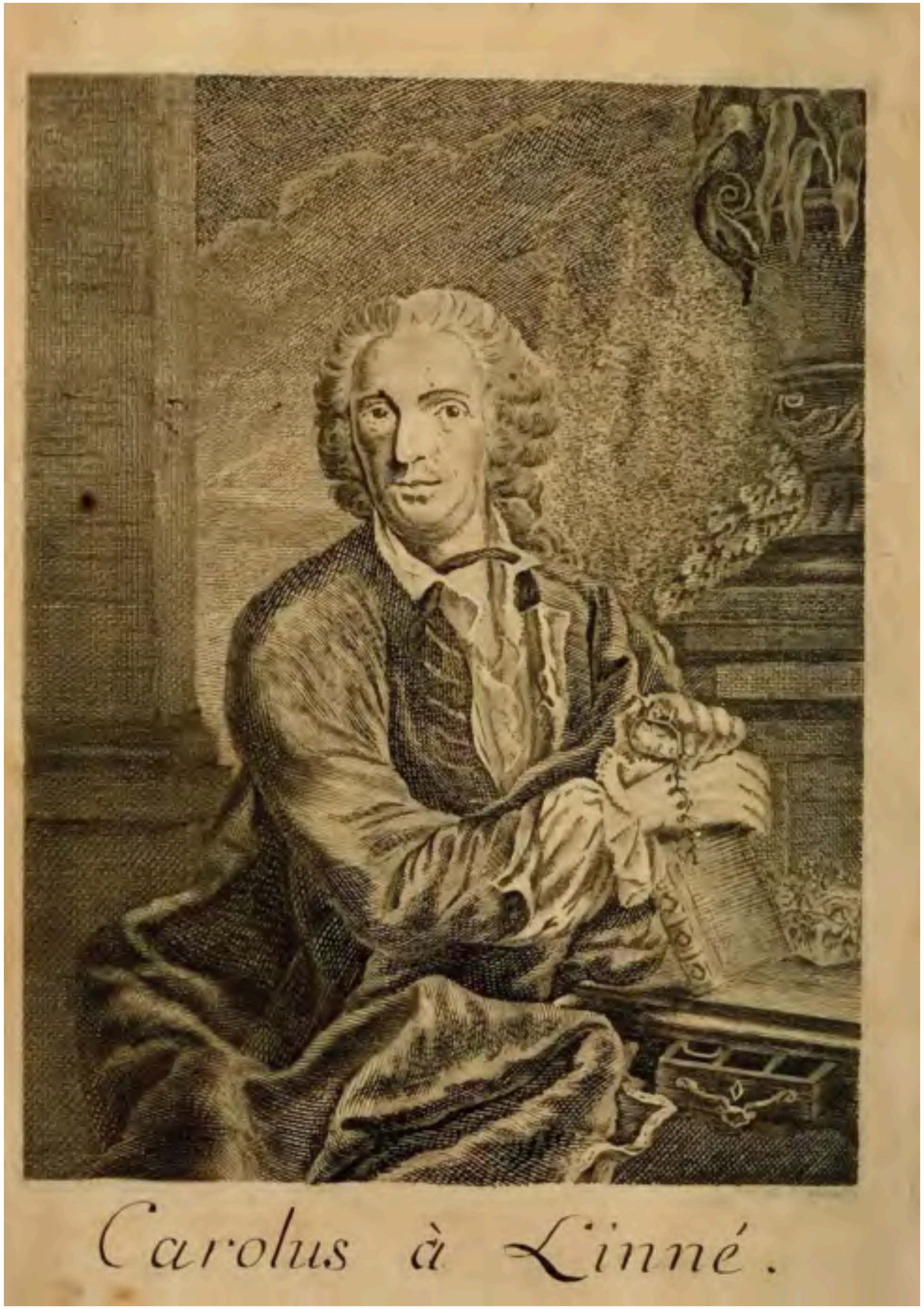
, litt … om the want
astr … and all
is o … hat one or
be s …

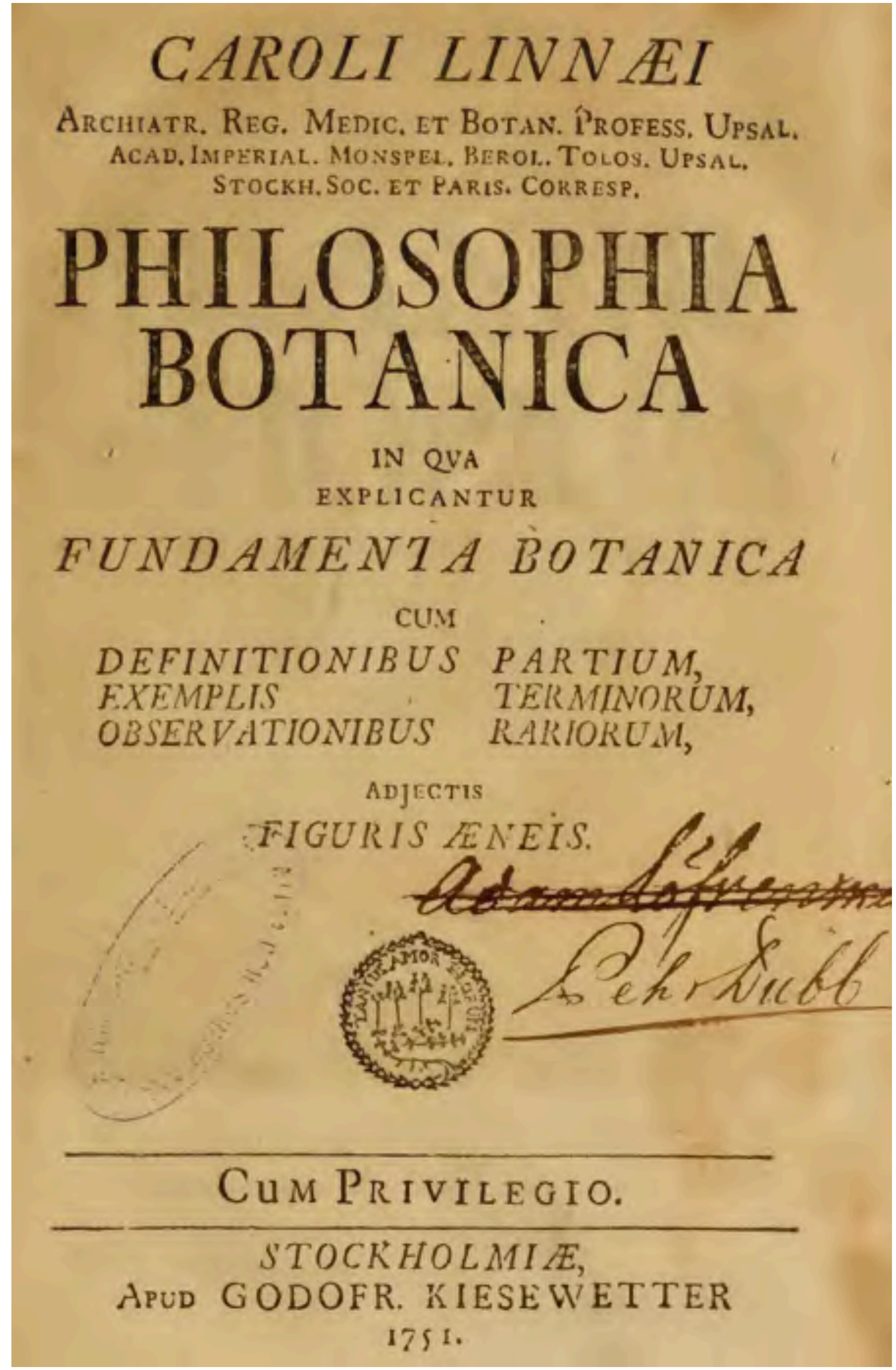


the …
cor … the vine
the Society (Nature, May 1871)

Professor Miller has suggested to me that as the tendrils of the vine are right-handed screws and those of the hop left-handed, the two systems might be called those of the vine and the hop respectively. The system of the vine, which we adopt, is that of Linnaeus, and of screw-makers in all civilized countries except Japan.

J. C. Maxwell, *A Treatise of Electricity and Magnetism,* 1892




CAROLI LINNÆI
ARCHIATR. REG. MEDIC. ET BOTAN. PROFESS. UPSAL.
ACAD. IMPERIAL. MONSPEL. BEROL. TOLOS. UPSAL.
STOCKH. SOC. ET PARIS. CORRESP.

PHILOSOPHIA
BOTANICA

IN QVA
EXPLICANTUR
FUNDAMENTA BOTANICA
CUM
DEFINITIONIBUS PARTIUM,
EXEMPLIS TERMINORUM,
OBSERVATIONIBUS RARIORUM,
ADJECTIS
FIGURIS ÆNEIS.

CUM PRIVILEGIO.

STOCKHOLMIÆ,
APUD GODOFR. KIESEWETTER
1751.

Carl Linnaeus (1707-1778)

8) Folia & Fructificationem pro-
s ſunt VI. *Caulis*, *Culmus*, *Sca-*
Petiolus, *Frons*, *Stipes*; at *Ramus*

proprius herbæ, elevat Folia Fructifica-

ta ſerie verſus apicem extenditur.
mpliciſſimus, ramis vix ullis.
s deſtitutus: *Euphorbia*, *Cactus*, *Stape-*
, *Cuſcuta*.
is inſtructus eſt.
undum articulos horſum vorſum flexus:

. IV. f. 115. ſpiraliter adſcendens per
num.

Siniſtrorſum ☾ ſecundum ſolem vulgo: *Humulus*, *Helxine*, *Lonicera*, *Tamus*.

Dextrorſum ☽ contra motum ſolis vulgi: *Convolvulus*, *Baſella*, *Phaſeolus*, *Cynanche*, *Euphorbia*, *Eupatorium*.

6. *Reclinatus*, arcuatim verſus terram: *Ficus*.

p. 39

IV. INTORSIO eſt flexio partium verſus alterum latus.

CAULIS volubilis ſiniſtrorſum ☾:

Tamus, *Dioſcorea*, *Rajania*, *Meniſpermum* *Ciſſampelos*, *Hippocratea*.
Lonicera
Humulus
Helxine.

dextrorſum ☽:

Phaſeolus, *Dolichos*, *Clitoria*, *Glycine*, *Securidaca*.
Convolvulus, *Ipomœa*,
Cynanche, *Periploca*, *Ceropegia*,
Euphorbia, *Tragia*.
Baſella,
Eupatorium,
Tournefortia.

CIRRHUS volubilis dextrorſum retrorſumque.

Leguminoſæ pleræque ejusmodi cirrhos gerunt.
Smilax petiolos cirrhiferos profert; idem ferme *Piper*

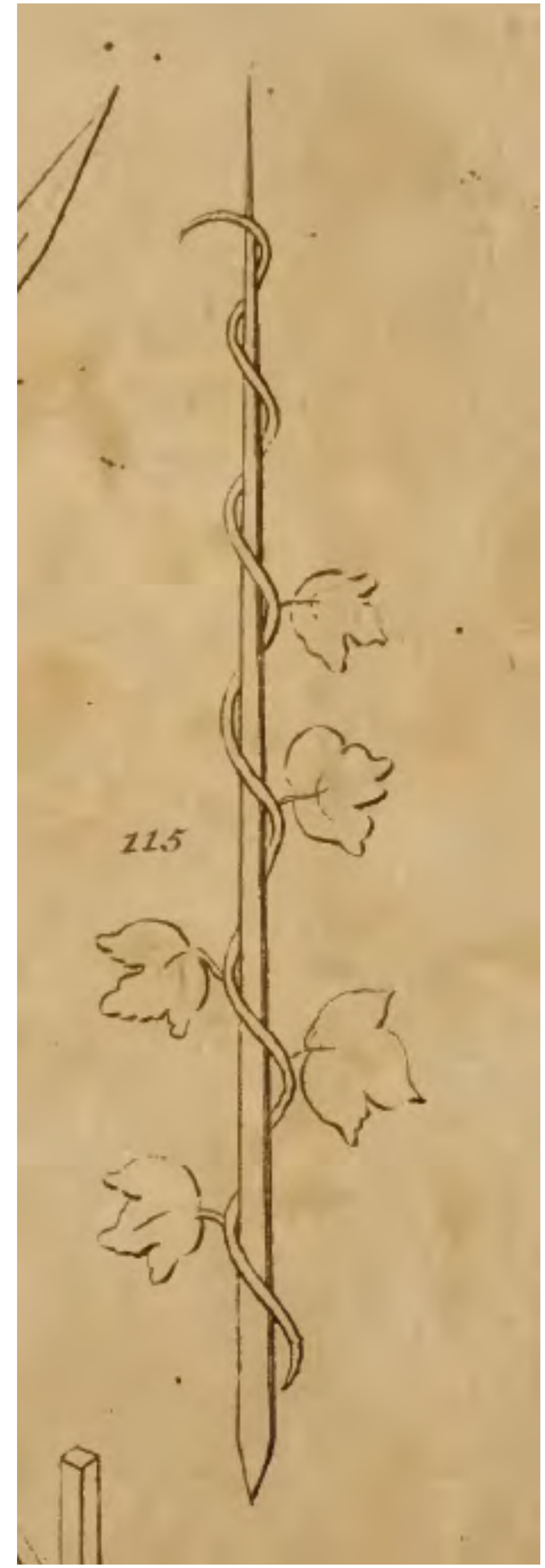
COROLLA ſiniſtrorſum (*):

Aſclepias, *Nerium*, *Vinca*, *Rauwolfia*, *Periploca*, *Stapelia*.

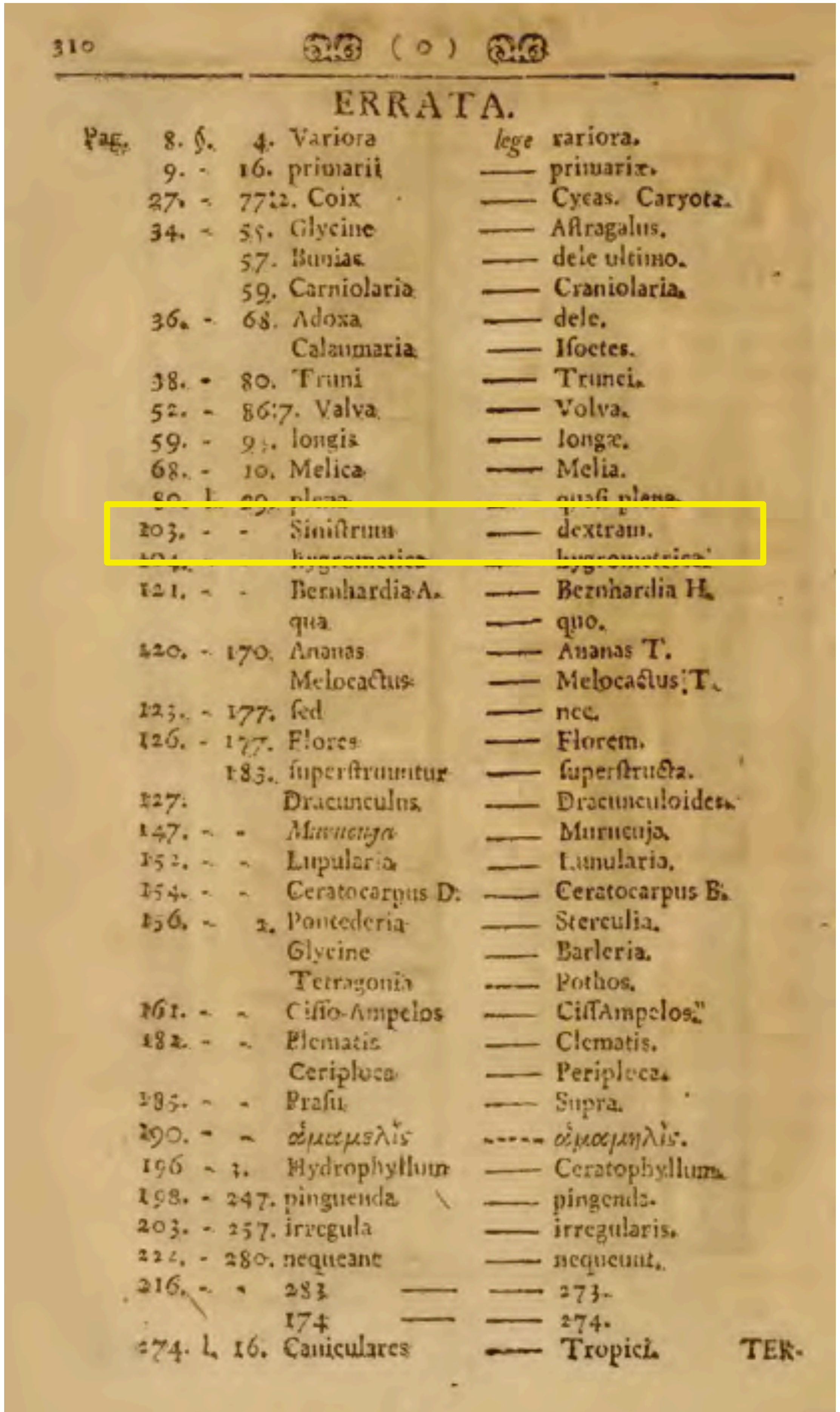
dextrorſum: *Pedicularis* *Fl. ſu.* 505. 507. 508.

 Trien-

(*) *Siniſtrorſum* hoc eſt, quod reſpicit dextram, ſi ponas Te ipſum, in centro conſtitutum, meridiem adſpicere; *Dextrorſum* itaque contrarium.



p. 103



310 (o)

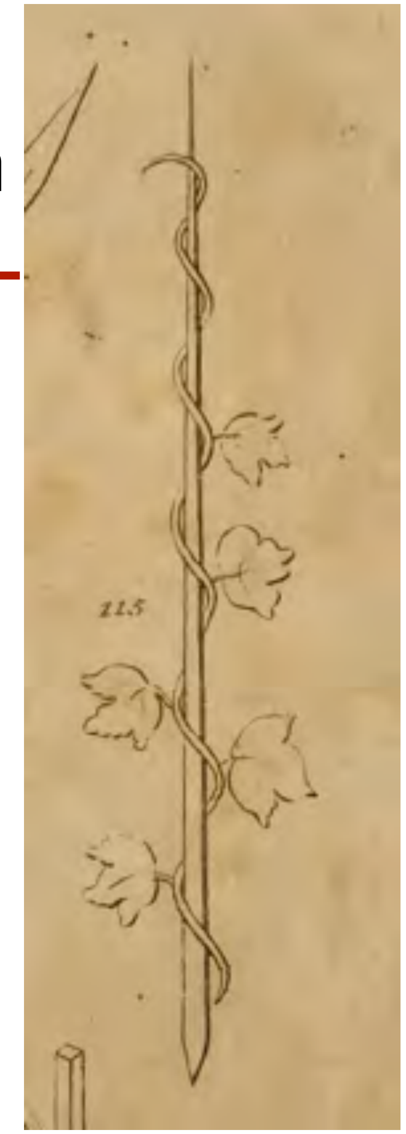
ERRATA.

Pag. 8. §.	4.	Variora	*lege*	variora.
9. -	16.	primarii	——	primariæ.
27. -	77:2.	Coix	——	Cycas. Caryota.
34. -	55.	Glycine	——	Aſtragalus.
	57.	Bunias	——	dele ultimo.
	59.	Carniolaria	——	Craniolaria.
36. -	68.	Adoxa	——	dele.
		Calaumaria	——	Iſoetes.
38. -	80.	Truni	——	Trunci.
52. -	86:7.	Valva	——	Volva.
59. -	95.	longis	——	longæ.
68. -	10.	Melica	——	Melia.
80. l.	29.	plena	——	quaſi plena.
103. -	-	Siniſtrum	——	dextram.
104. -	-	hygrometica	——	hygrometrica.
121. -	-	Bernhardia A.	——	Bernhardia H.
		qua	——	quo.
120. -	170.	Ananas	——	Ananas T.
		Melocactus	——	Melocactus T.
123. -	177.	ſed	——	nec.
126. -	177.	Flores	——	Florem.
	183.	ſuperſtruuntur	——	ſuperſtructa.
127.		Dracunculus	——	Dracunculoides.
147. -	-	*Mumeuja*	——	Murucuja.
152. -	-	Lupularia	——	Lunularia.
154. -	-	Ceratocarpus D.	——	Ceratocarpus B.
156. -	2.	Pontederia	——	Sterculia.
		Glycine	——	Barleria.
		Tetragonia	——	Pothos.
161. -	-	Ciſſo-Ampelos	——	CiſſAmpelos.
182. -	-	Blematis	——	Clematis.
		Ceriploca	——	Periploca.
185. -	-	Praſu	——	Supra.
190. -	-	*ἀμαμελὶς*	----	*ἀμαμηλὶς.*
196 -	3.	Hydrophyllum	——	Ceratophyllum.
198. -	247.	pinguenda	——	pingenda.
203. -	257.	irregula	——	irregularis.
212. -	280.	nequeant	——	nequeunt.
216. -	-	283 ——	——	273.
		174 ——	——	274.
274. l.	16.	Caniculares	——	Tropici.

TER-

Left Sinistrorsum

Linnaeus
Gray
Eichler
Duchartre
Darwin
...



Right Dextrorsum

Linnaeus
de Candolle
von Mohl
Bischoff
Sachs
...

Sinistrorsum externe visus

==

Dextrorsum e centro visus

==

Following the course of the sun

==

Like the hand of a watch

==

Left handed !

ELEMENTS

OF

QUATERNIONS.

BY THE LATE

SIR WILLIAM ROWAN HAMILTON, LL. D., M. R. I. A.,

1866

W. R. Hamilton (1805-1865)

110. Again in estimating this *angle*, for the purpose of *distinguishing* one quotient of vectors from another, we must consider not only its *magnitude* (or *quantity*), but also its PLANE: since otherwise, in violation of the principle stated in Art. 104, we should have OB′ : OA = OB : OA, if OB and OB′ were *two distinct rays* or sides of a *cone* of revolution, with OA for its *axis*; in which case (by 2) they would necessarily be *unequal vectors*. For a similar reason, we must attend also to the *contrast* between two *opposite angles*, of equal magnitudes, and in one *common plane*. In short, for the purpose of knowing *fully* the *relative direction* of two co-initial lines OA, OB in *space*, we ought to know not only *how many degrees*, or other *parts* of some *angular unit*, the *angle* AOB contains; but also (comp. Fig. 33) the *direction of the rotation* from OA to OB: including a knowledge of the *plane*, *in which* the rotation is performed; and of the *hand* (as *right* or *left*, when *viewed* from a known *side* of the plane), *towards which* the rotation is *directed*.

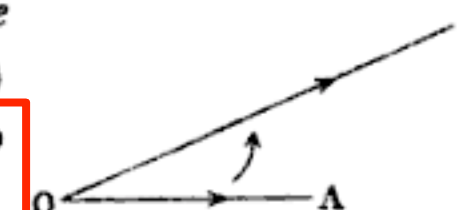


Fig. 33.

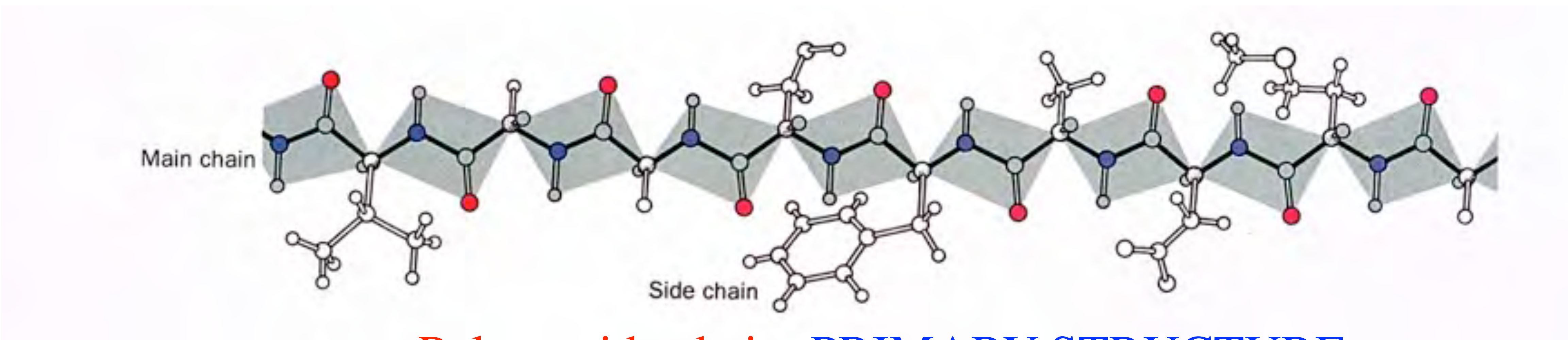
111. Or, if we agree to *select* some *one fixed hand* (suppose the *right*† hand), and to call all *rotations positive* when they

* This *number*, which we shall presently call the *tensor* of the quotient, may be *whole* or *fractional*, or even *incommensurable* with unity; but it may always be *equated*, in calculation, to a *positive scalar*: although it might perhaps more *properly* be said to be a *signless number*, as being derived solely from comparison of *lengths*, without any reference to *directions*.

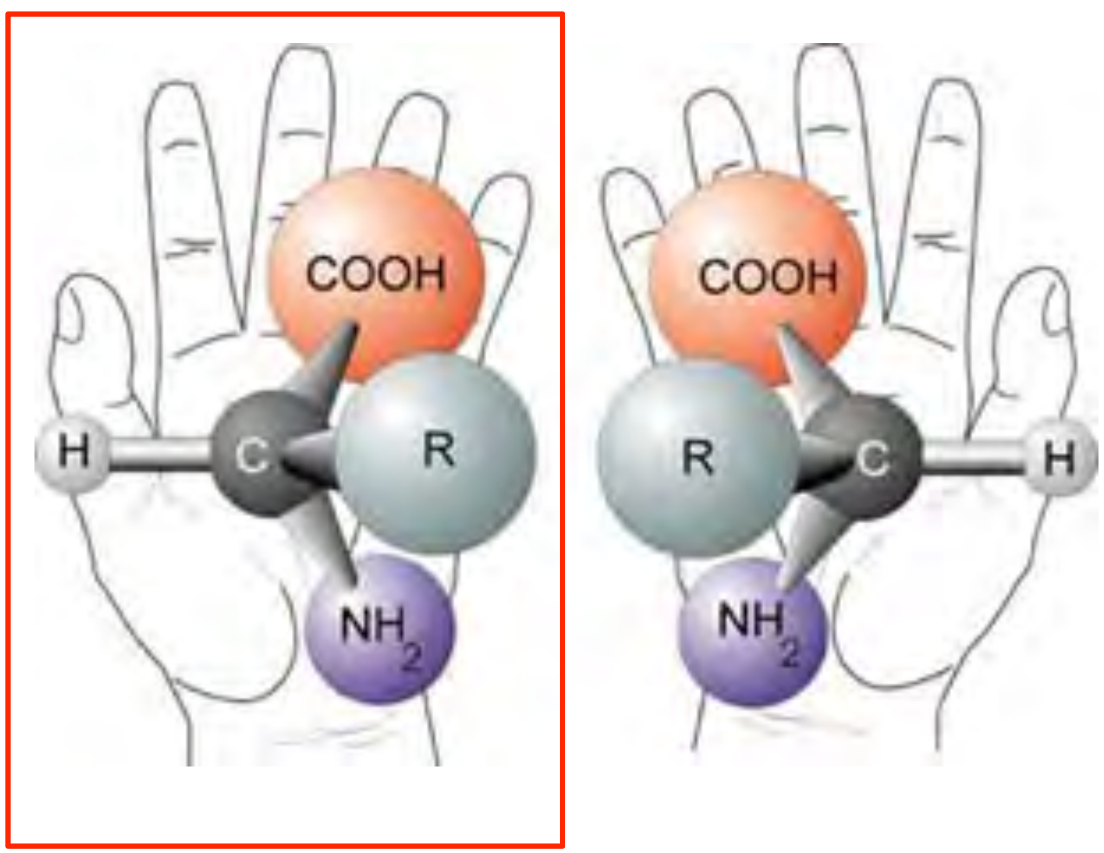
† If *right-handed rotation* be thus considered as *positive*, then the *positive axis* of the rotation AOB, in Fig. 33, must be conceived to be directed *downward*, or *below* the plane of the paper.

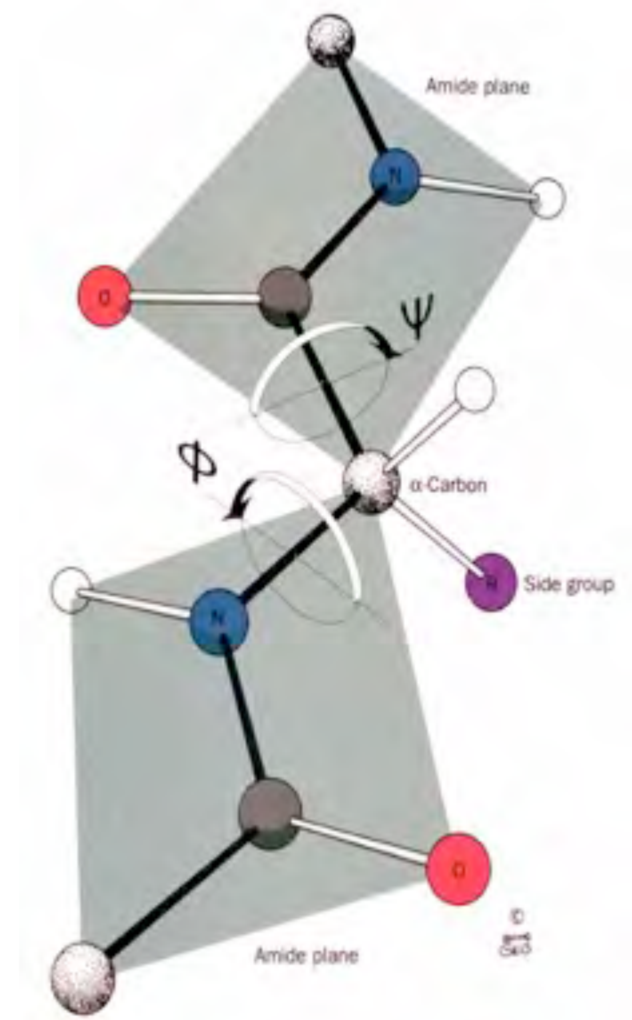
Sunday, January 27, 13

Handedness in proteins

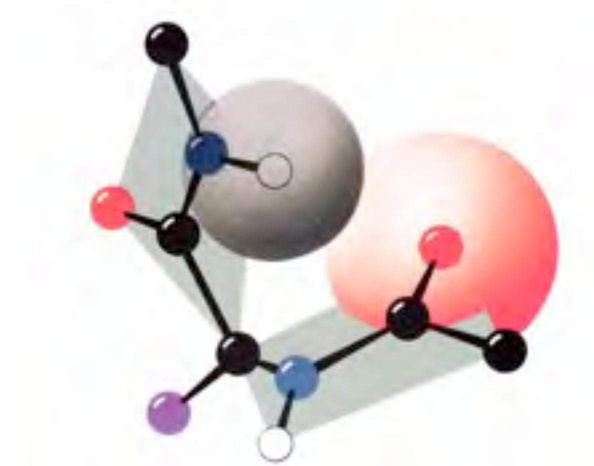


Polypeptide chain: PRIMARY STRUCTURE



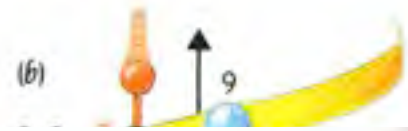


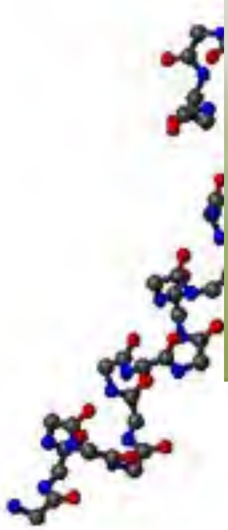
Steric hindrance

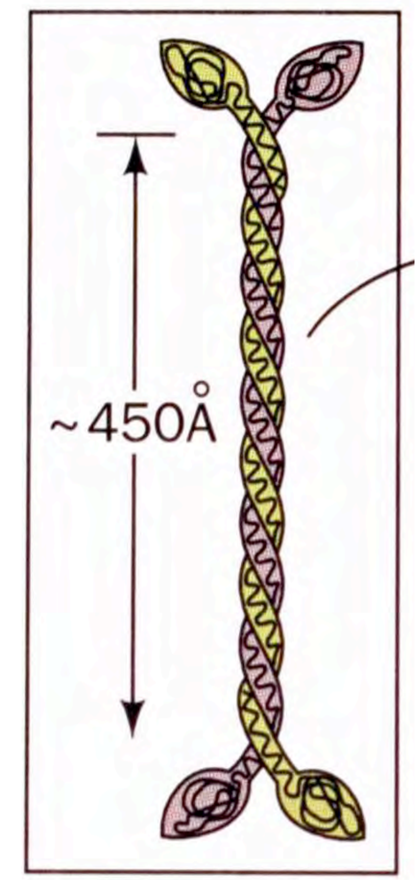


Handedness in proteins

alpha-helix





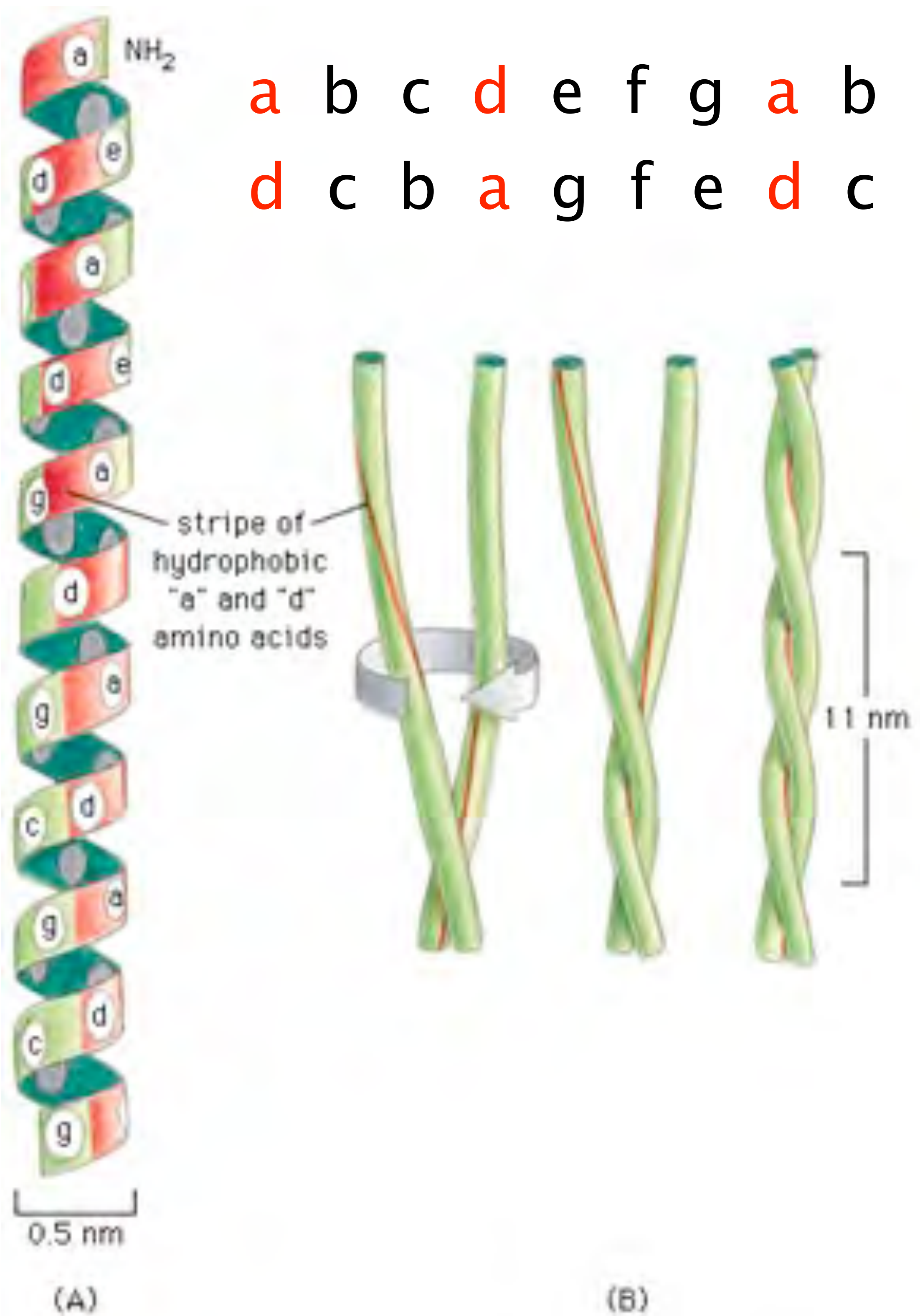


Secondary structure **Tertiary structure**

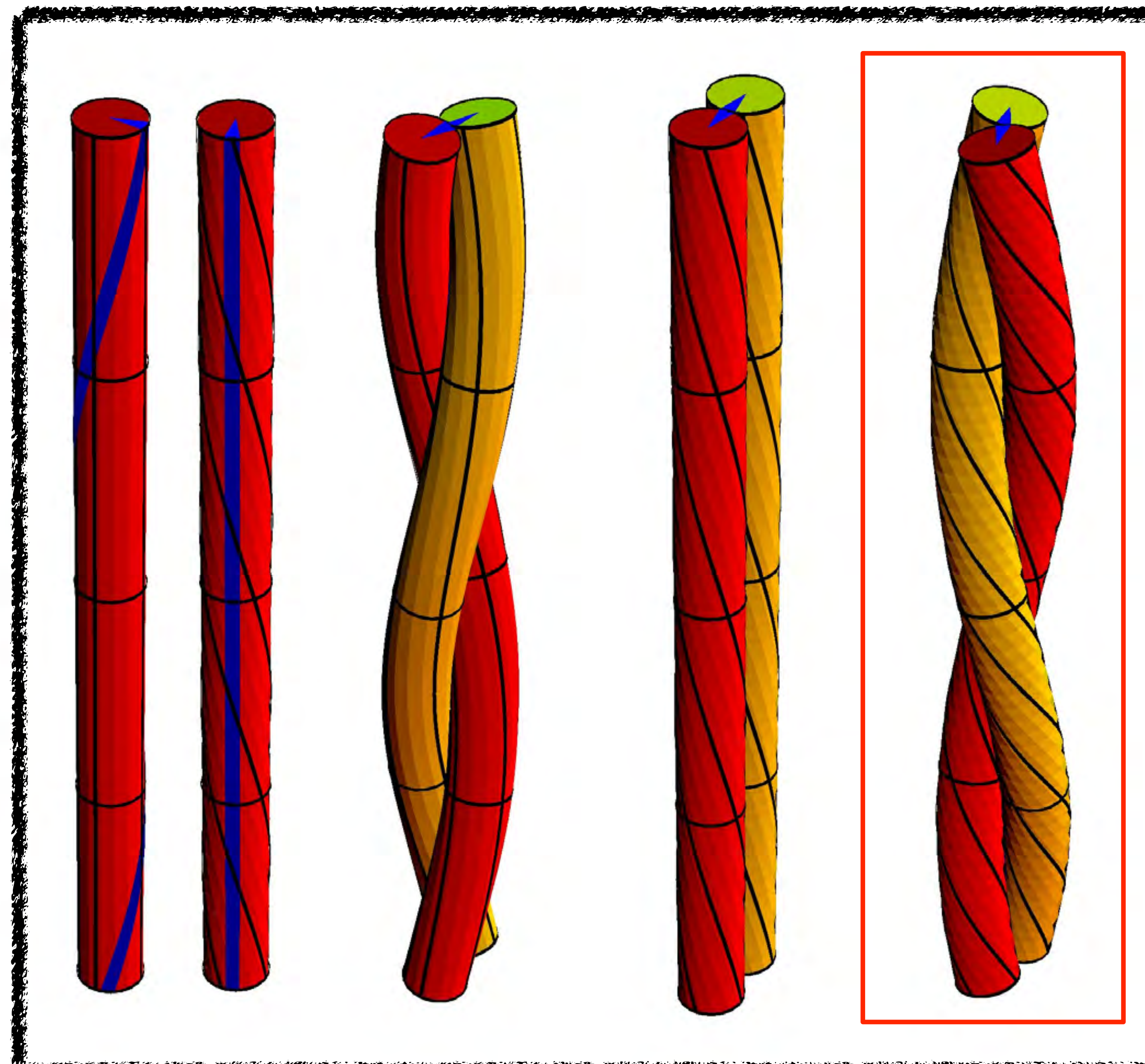
Coiled-coils, the heptad repeat

a b c d e f g a b c d e f g

d c b a g f e d c b a g f e



A mechanical model



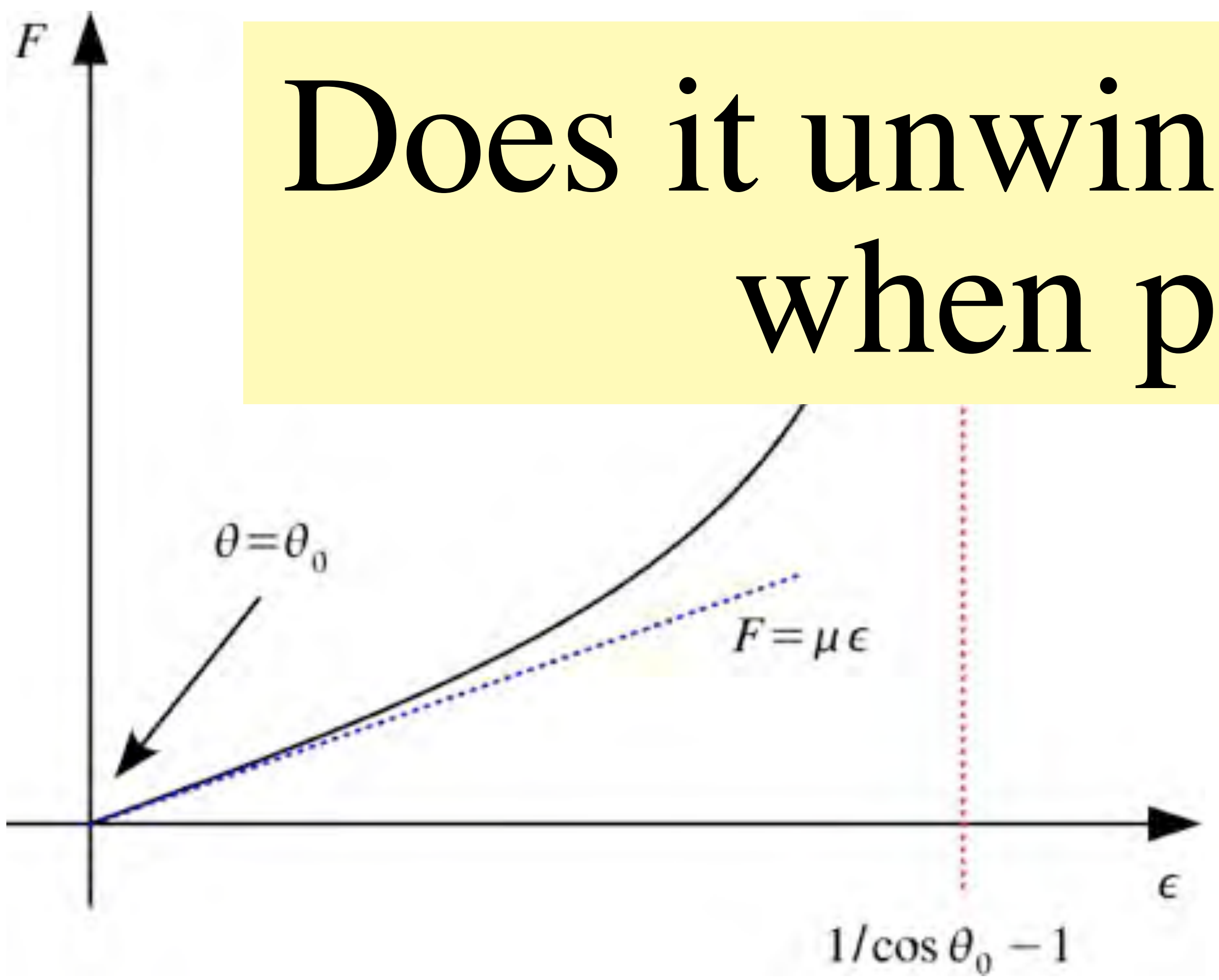
(C)

S. Neukirch & AG, '06

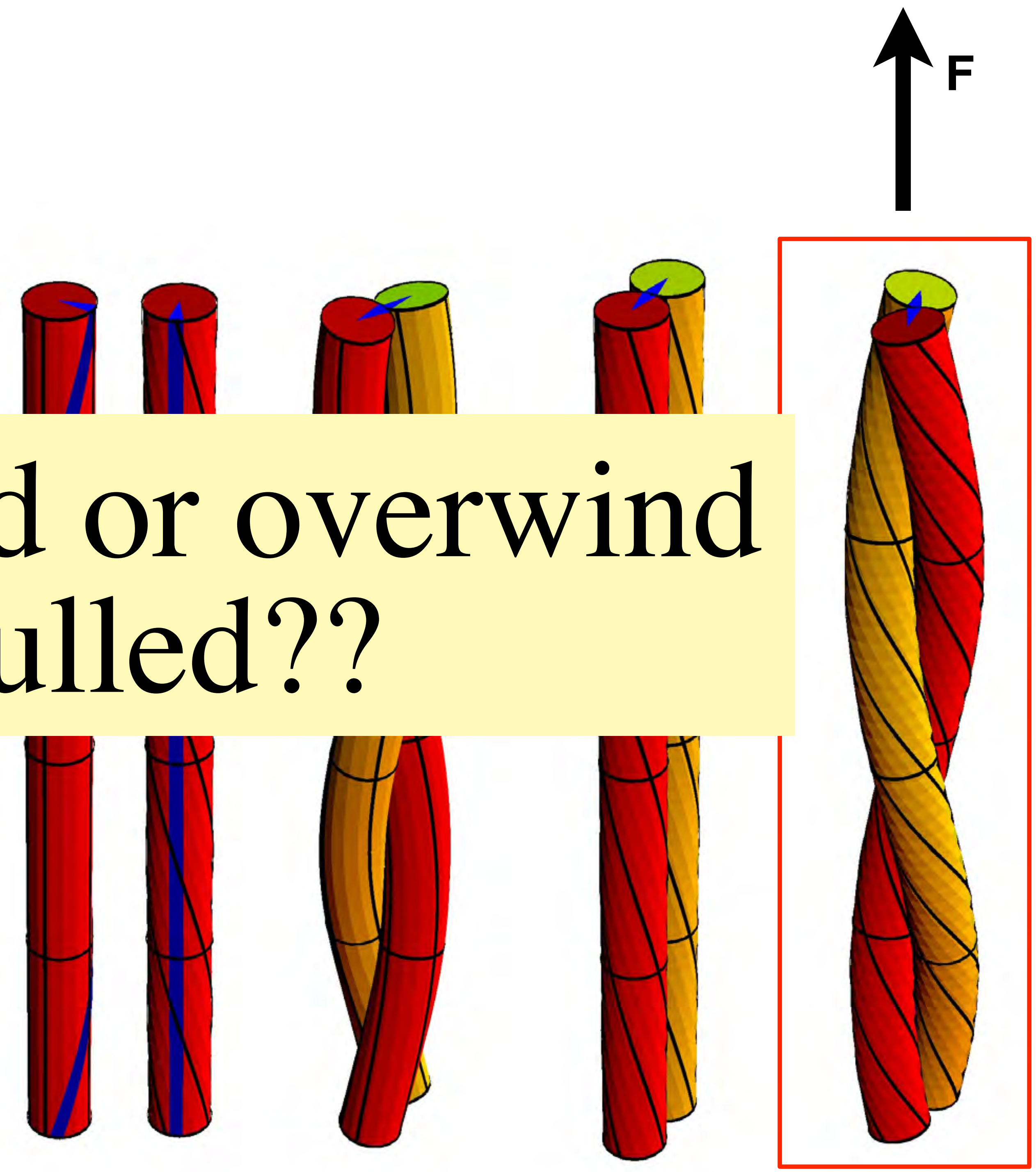
Pulling on coiled-coils

Comparison with crystal data

GCN4	super-helix 2θ	model $\hat{\tau}$	model 2θ
dimer	$-23.4°$	-0.039	$-22°$
trimer	$-26.8°$	-0.033	$-25°$
tetramer	$-26.0°$	-0.030	$-26°$

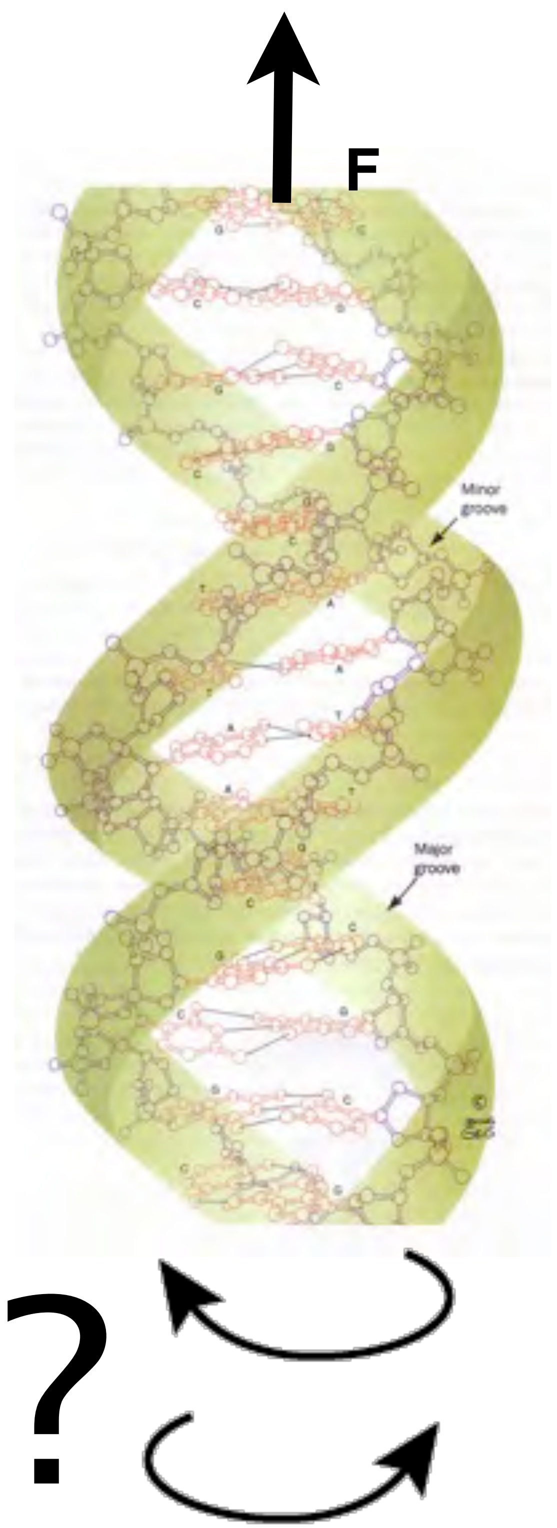


Does it unwind or overwind when pulled??

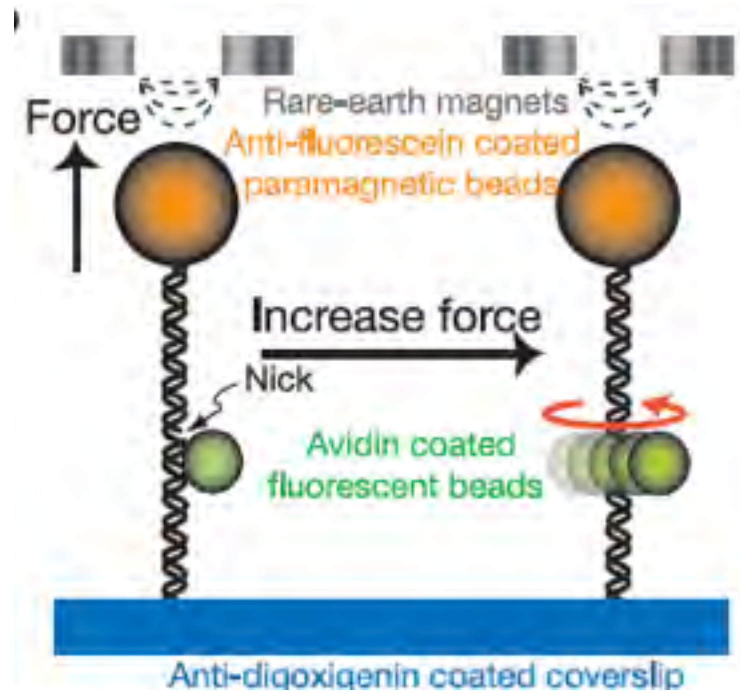


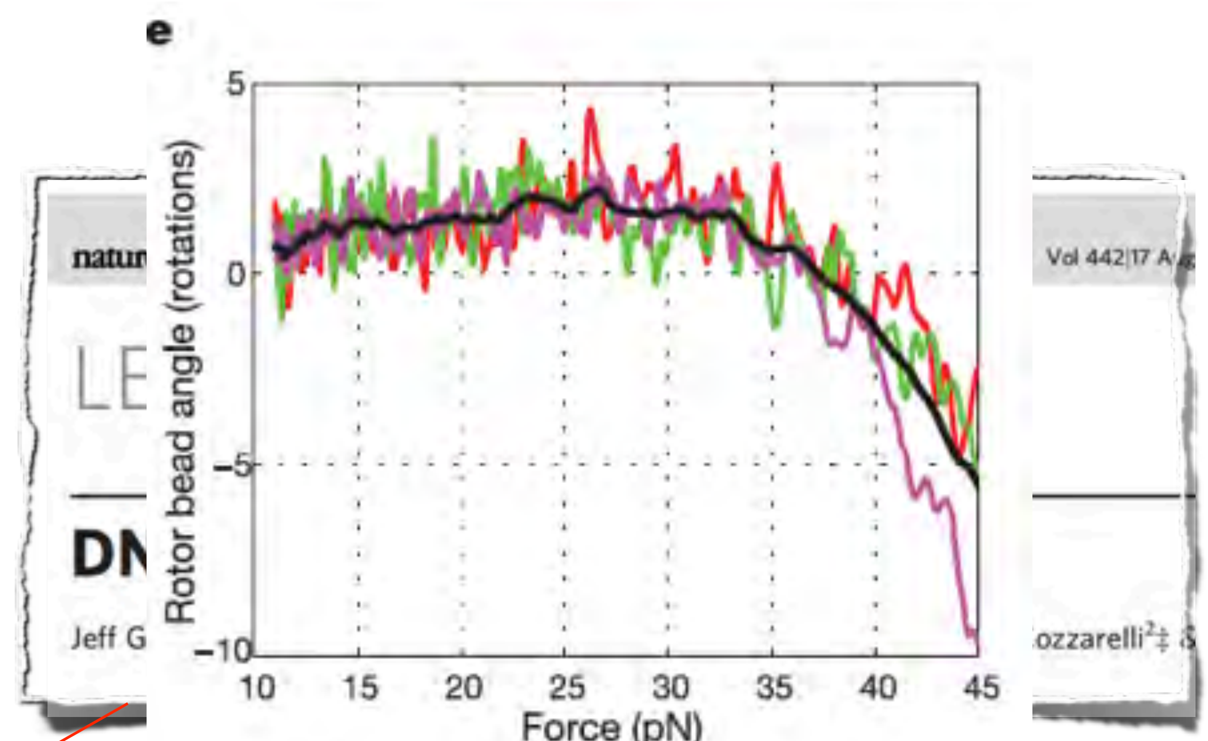
S. Neukirch & AG, '06

Winding or unwinding?



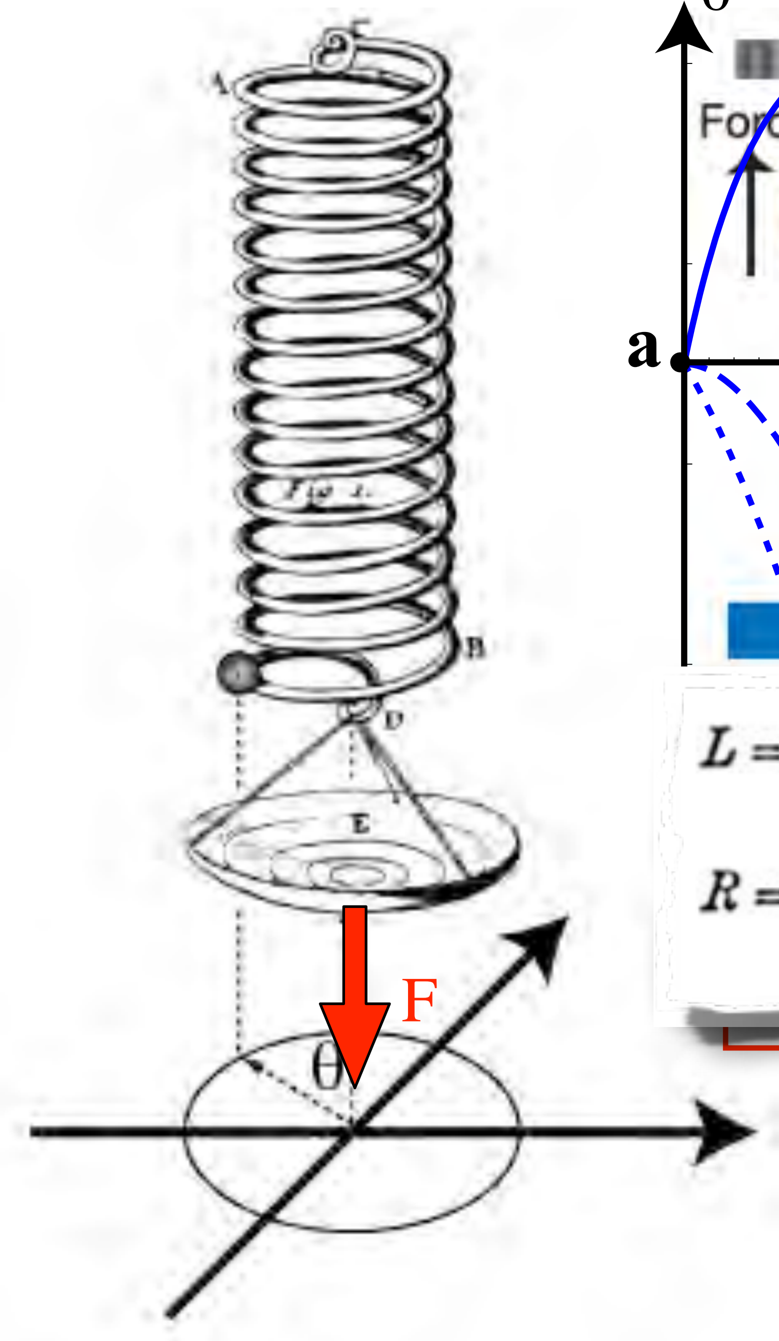
double stranded DNA helix,
B-form (right-handed)

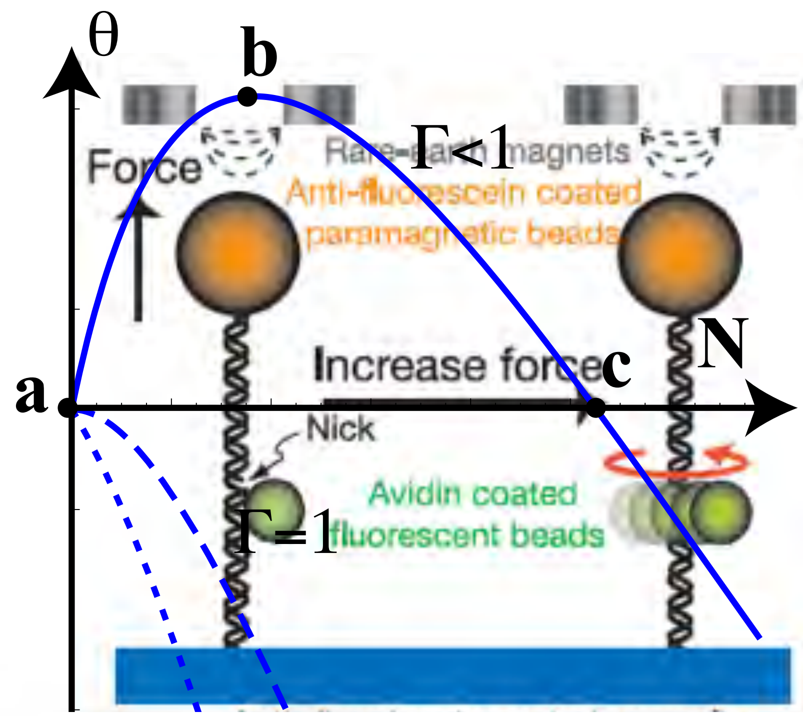


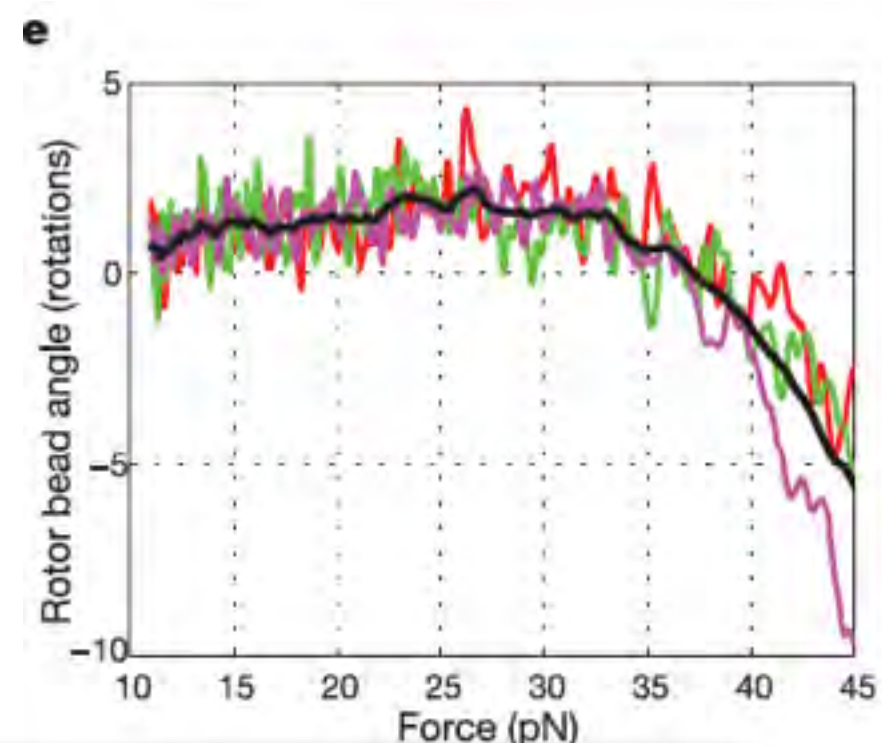


Simple physical intuition predicts that DNA should unwind under tension, ... Here we show that for small distortions, contrary to intuition, DNA overwinds under tension

Winding or unwinding?







$$\left.\begin{aligned} L &= \frac{B}{l^3}\{\sqrt{(l^2-x^2)}\,\phi - \sqrt{(l^2-x_0^2)}\,\phi_0\}\sqrt{(l^2-x^2)} + \frac{A}{l^3}(x\phi - x_0\phi_0)\,x \\ R &= -\frac{B}{l^3}\{\sqrt{(l^2-x^2)}\,\phi - \sqrt{(l^2-x_0^2)}\,\phi_0\}\frac{x\phi}{\sqrt{(l^2-x^2)}} + \frac{A}{l^3}(x\phi - x_0\phi_0)\,\phi \end{aligned}\right\} \quad (9).$$

Tait and Thomson *Treatise on natural Philosophy 1867*

All uniform helical springs in tension
first wind then unwind!

Spring (Drawing by Hooke)

AG & Maddocks 2013

Unwinding in plant cells

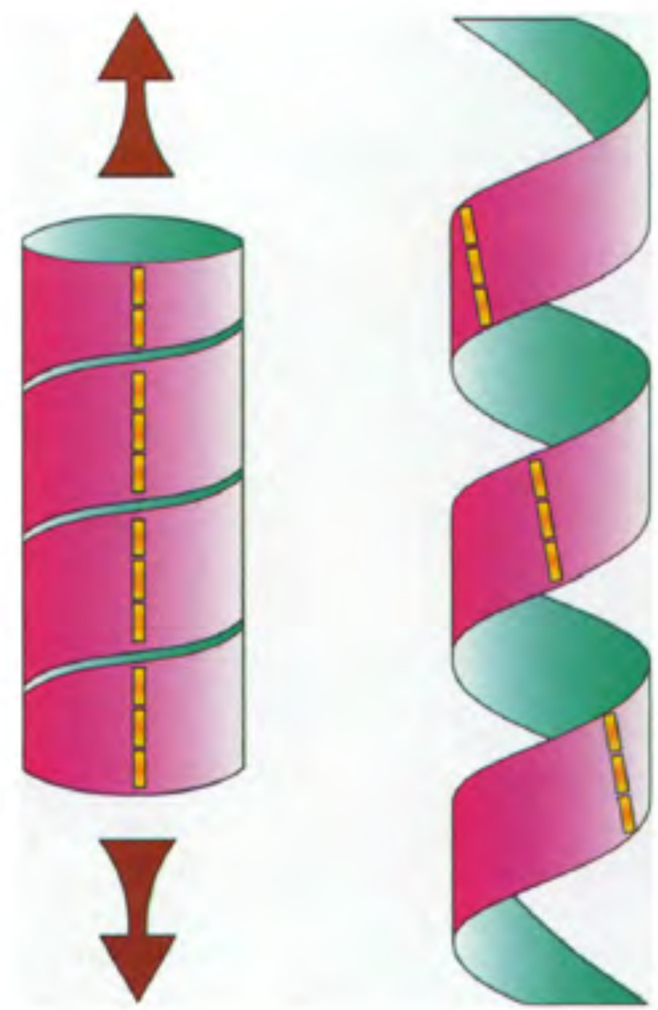


Figure 2. Helices Unwind When They Are Stretched.

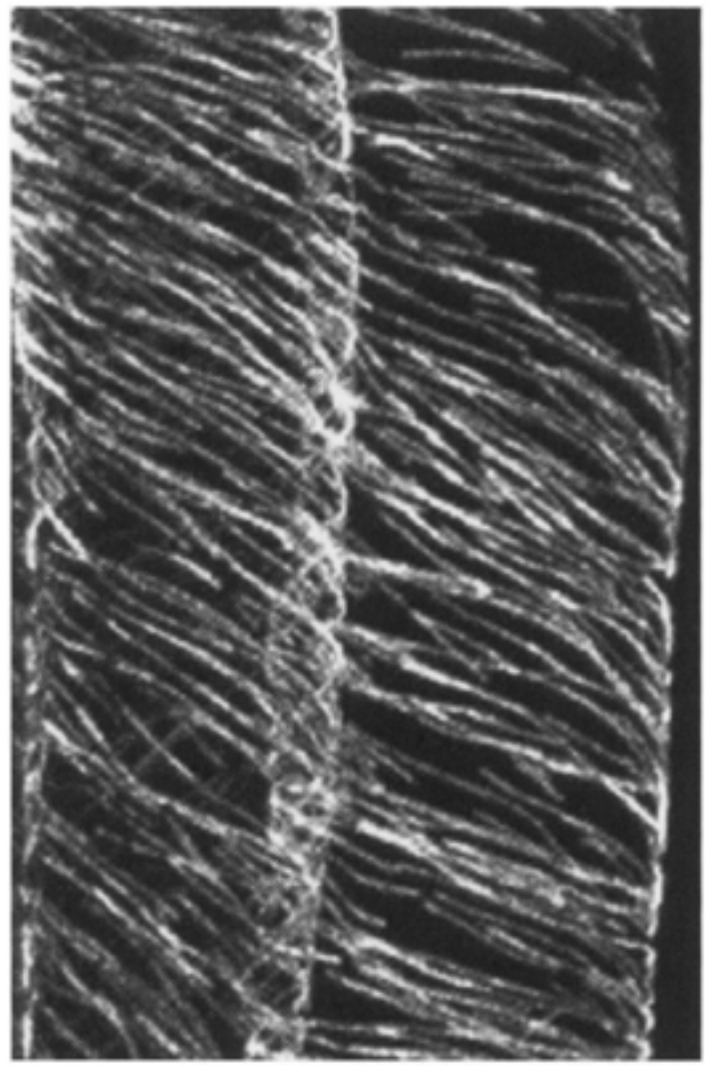


Figure 1. Microtubules in the *spiral* Mutant.

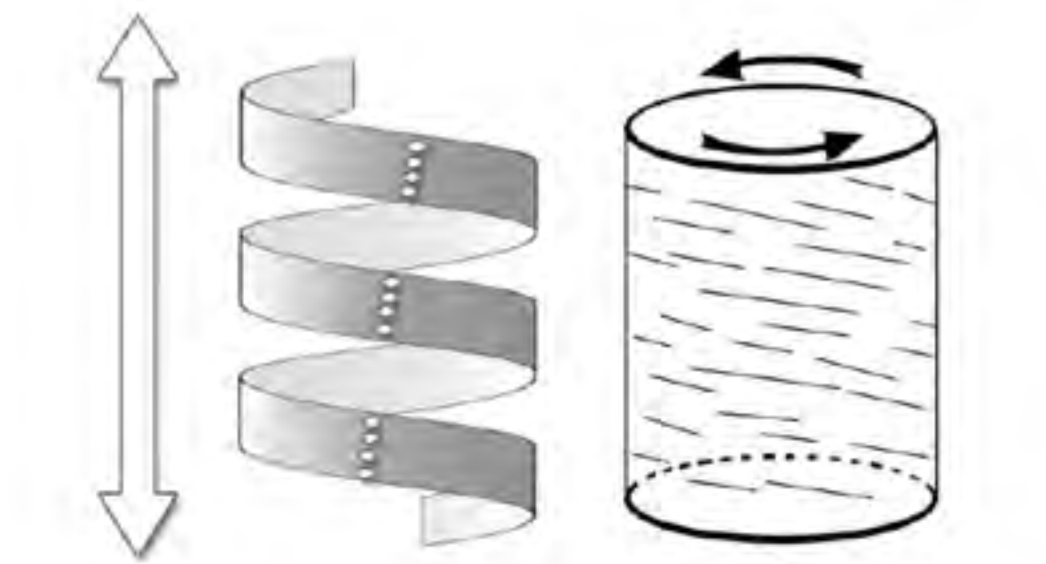
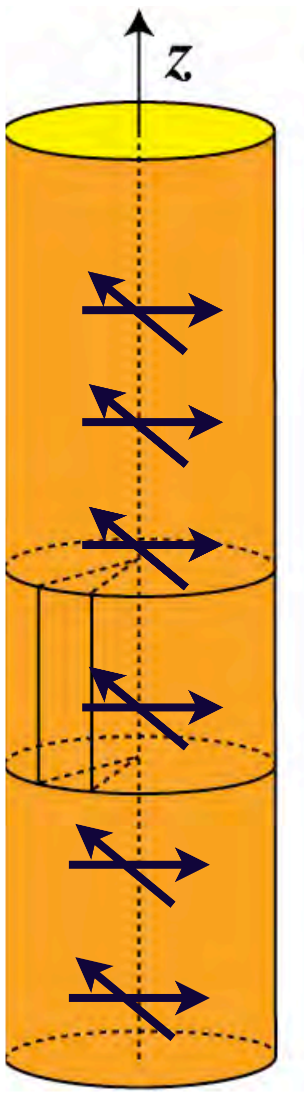


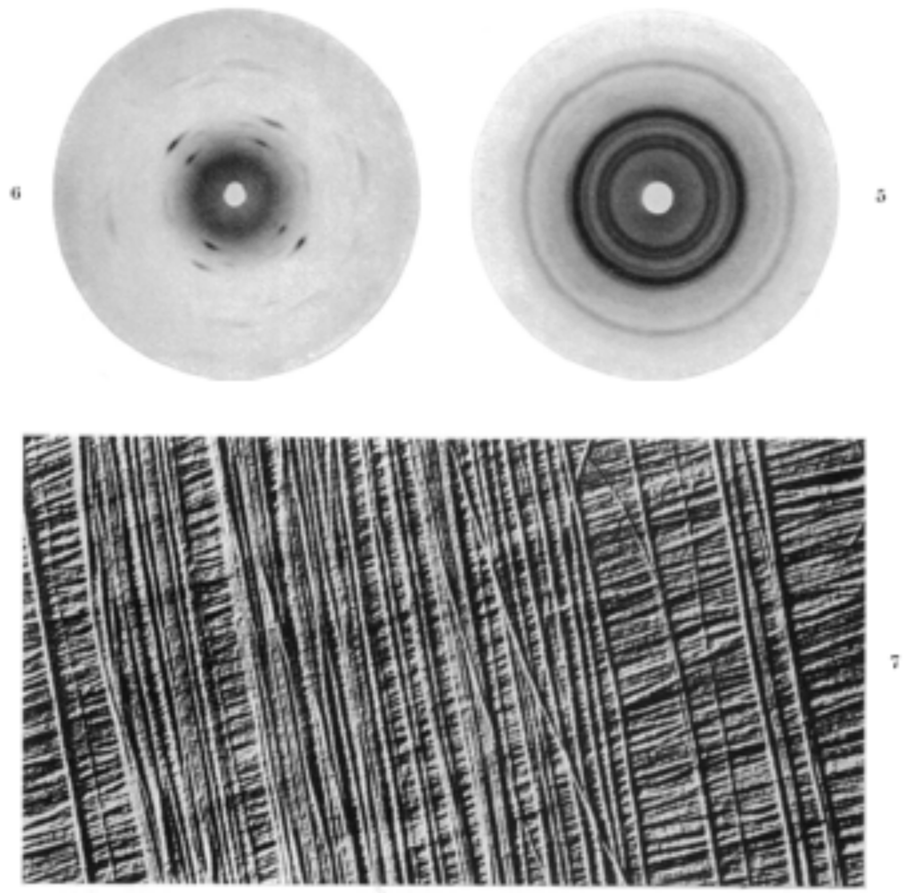
Figure 9. Simple Models Can Explain Helical Growth of Cells Growing in Isolation.

LLoyd and Chan 2002.
The Plant Cell

Buschmann et al 2009.
The Plant Cell

Left or right?





Frei-Preston (1961)
Green Algae

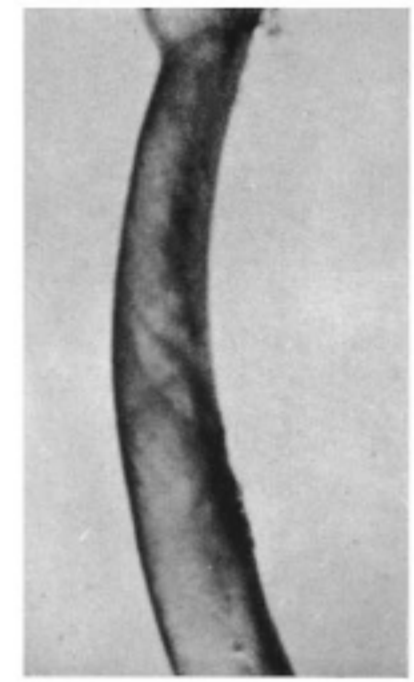
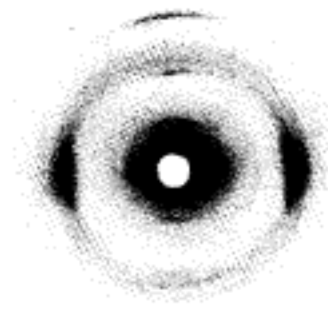


Fig. 18. Growth zone region of a Stage 4 sporangiophore, showing spirals in the cytoplasm.



Middlebrook-Preston (1952)
Phycomyces

Freeze one fibre, rotate the other one

Left or right?
Is there a critical angle?
How does it depend on stiffness?

Exact Anisotropic Elasticity I

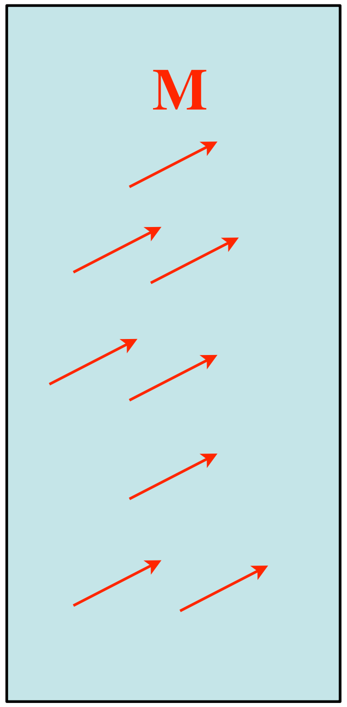
Incompressible anisotropic hyperelasticity, e.g. fibre reinforcement of an elastic cylinder.

Introduce new invariants into free energy

$$W = W(I_1, I_2, I_4, I_5)$$

$$I_4 = M.(CM), \quad I_5 = M.(C^2 M)$$

$$C = F^T F$$



M = fibre orientation in reference configuration, e.g. fibres parallel or transverse to a cylinder axis

m = F.M = fibre orientation in current configuration

I_4 = m.m = measure of fibre extension

See Pence, Horgan & Murphy, Ogden & Merodio,.

Exact Anisotropic Elasticity II

Incompre
e.g. fib
W

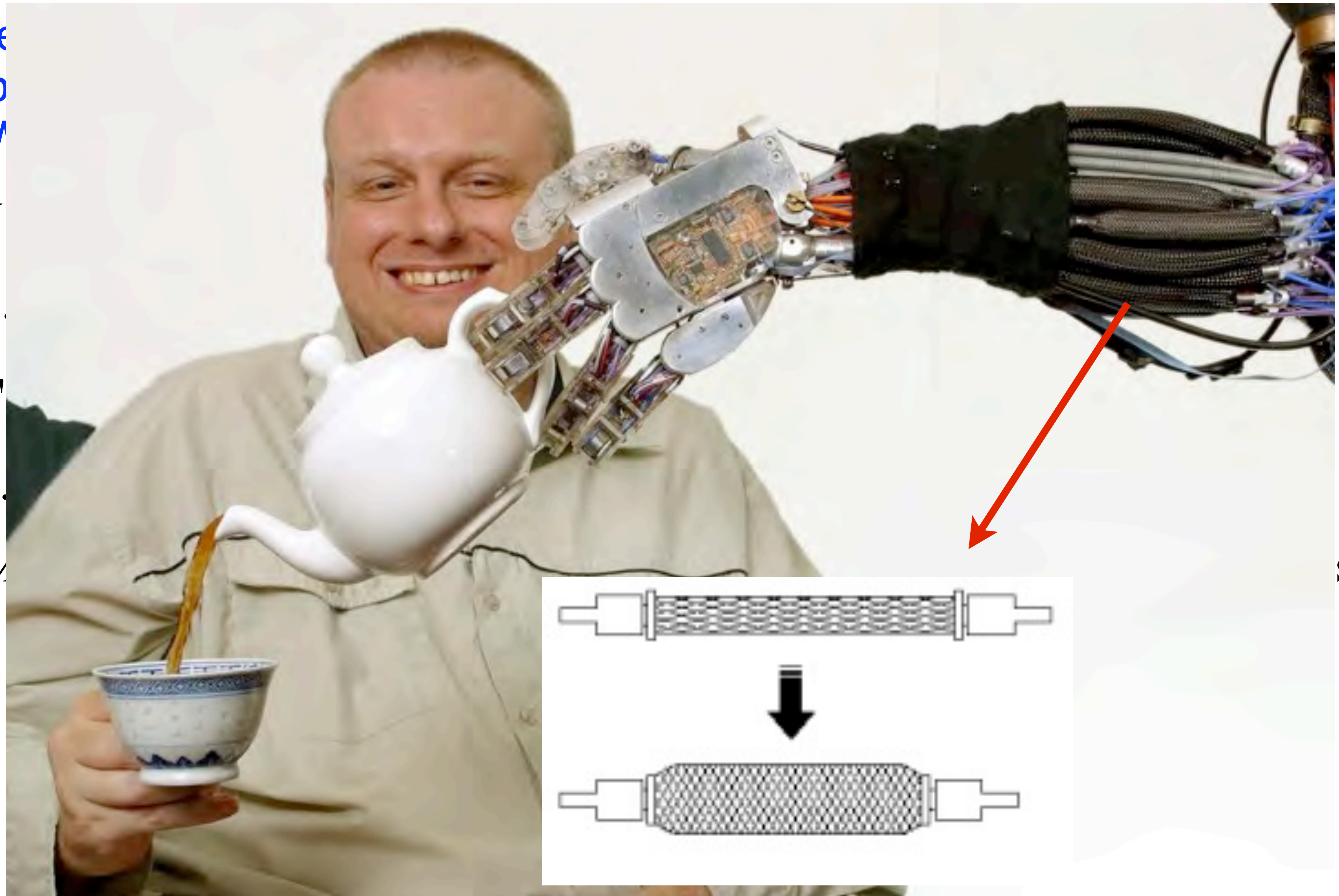
$$W = W$$

$$I_4 = M$$

$$I_6 = M'$$

$$I_8 = M$$

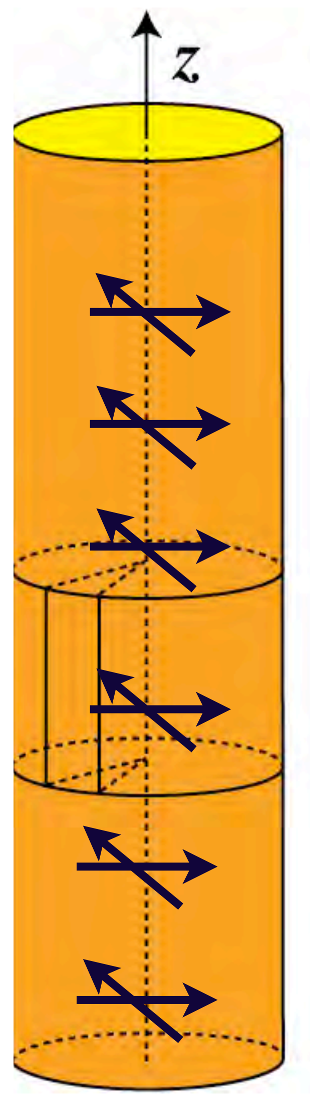
$$M = \left(M \quad \sin\Phi'\right),$$



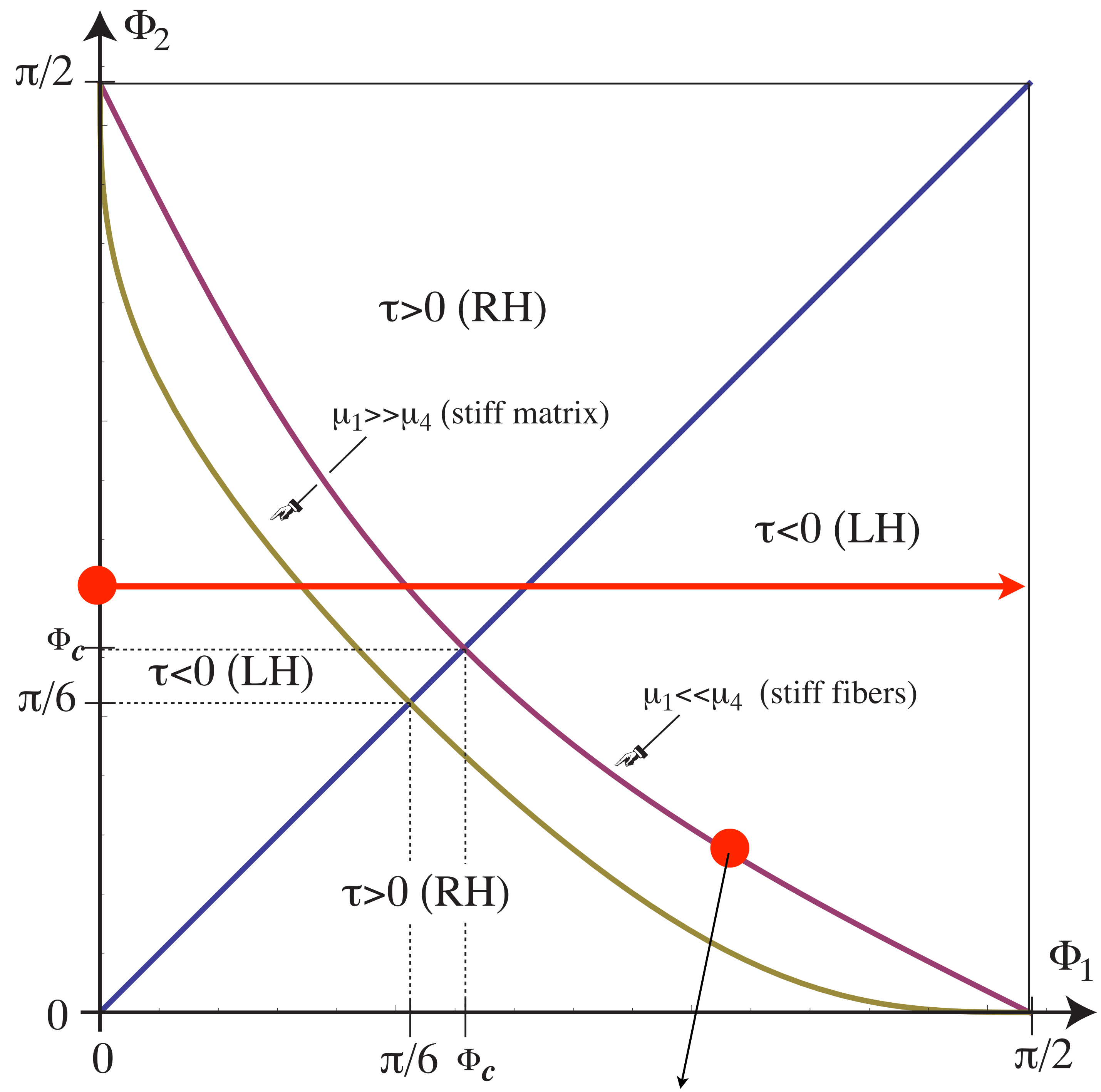
If M and M’ equal and opposite no net torque on cylinder

Unequal fibres

Fix one fibre, rotate the other one. Will it turn CW (left) or CCW (right)?

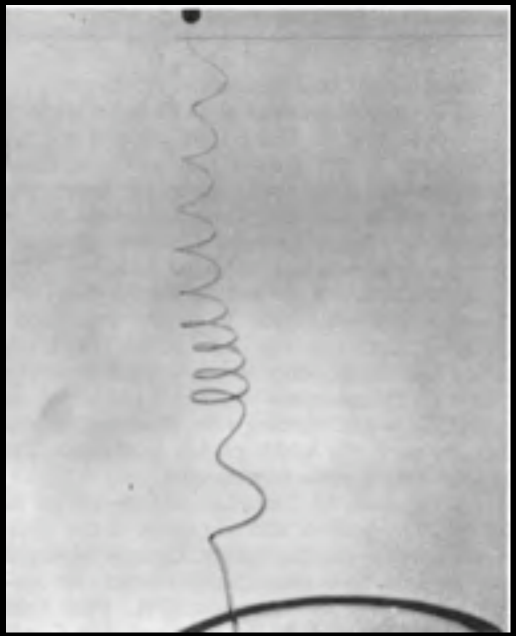


$$\Phi_c = \sqrt{\arcsin(1/3)} \sim 33.4^{\circ}$$



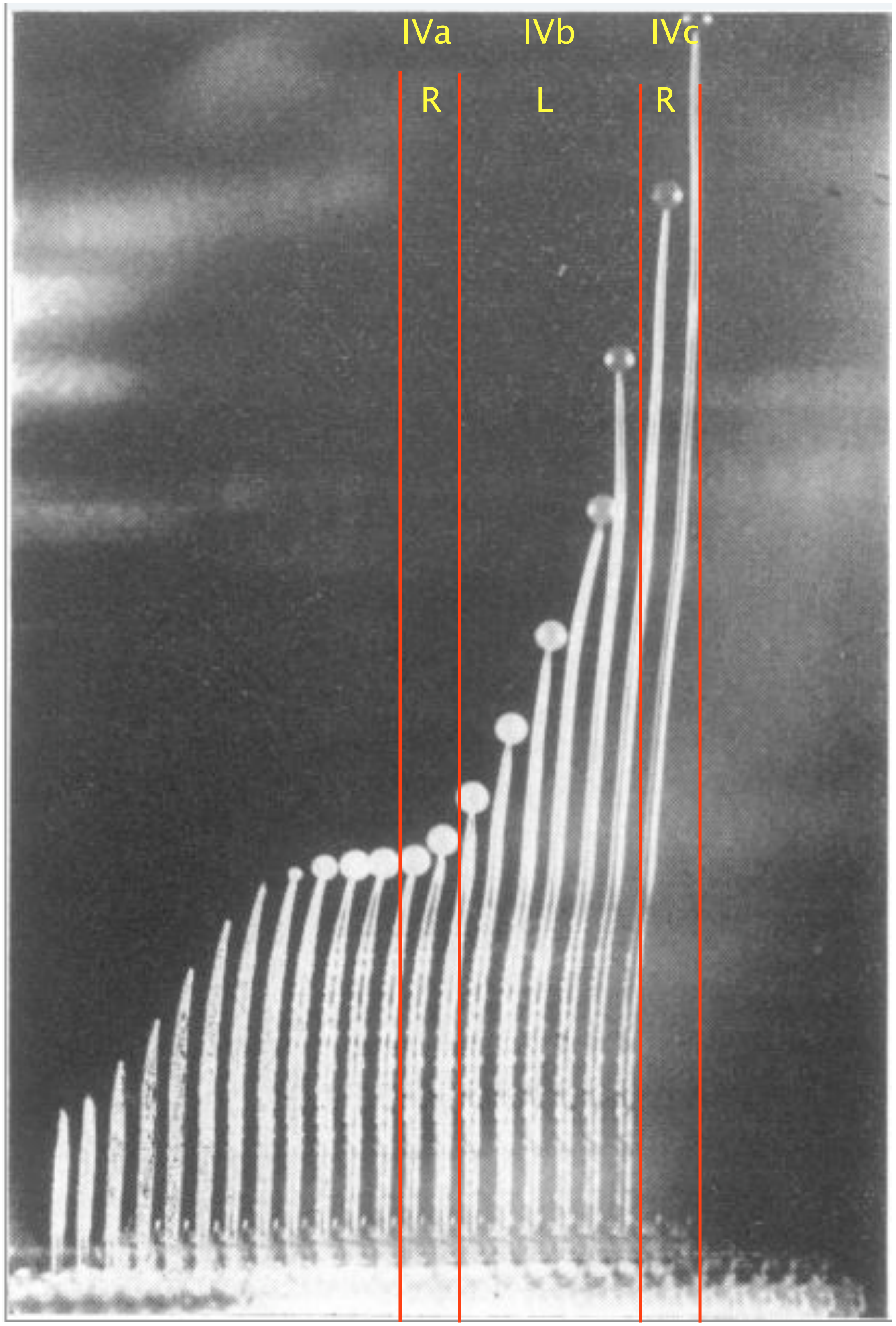
Unequal fibres but no rotation!

Phycomyces



M. Tabor & AG ('11)

Phycomyces: left AND right!

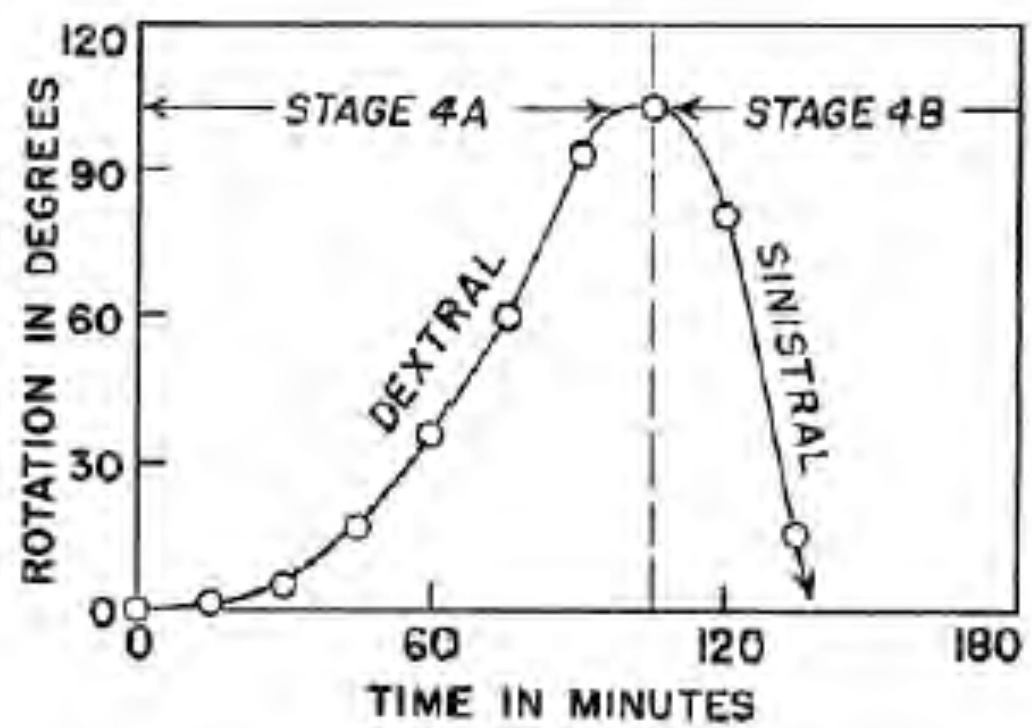


■ Rotation

IVa: Counter-clockwise rotation (1-2h)

IVb: Clockwise rotation (24-48h).

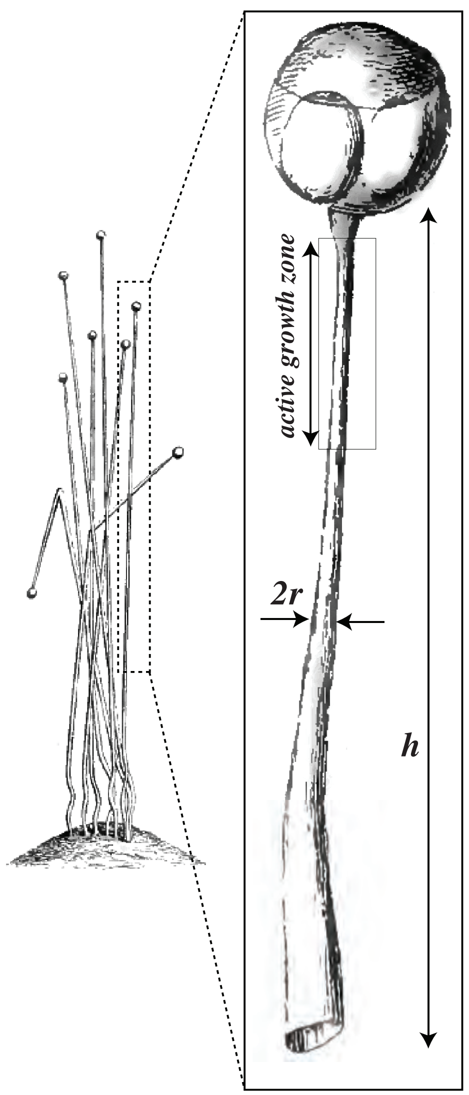
IVc: Counter-clockwise rotation in (1-2h)

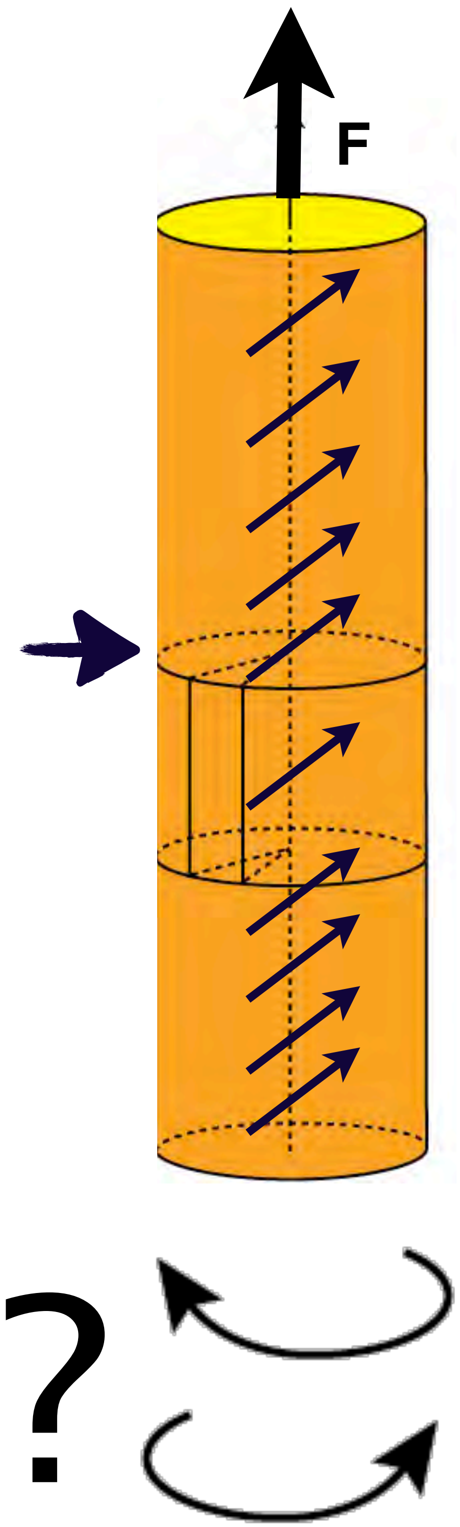


Helical growth:1915 (Burgeff)

1940's - 1950's: Castle, Roelofsen, Preston,

A model for Phycomyces



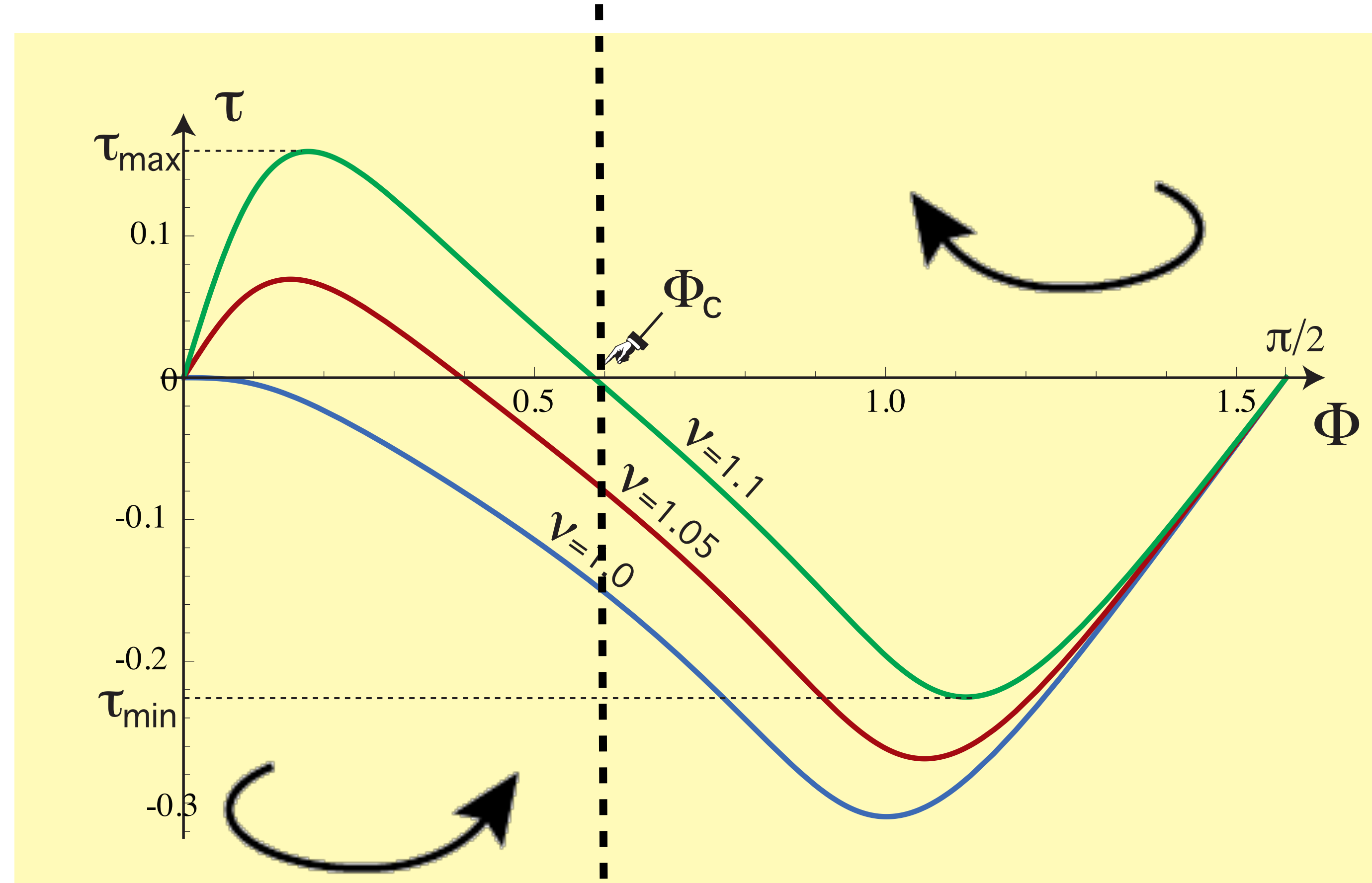


ASSUMPTIONS

(1) Elastic thin tube with reinforced fibres

(2) Right handed helical fibres

(3) As the tube grows, new fibres are laid down continuously, stress free, and aligned with previous fibres

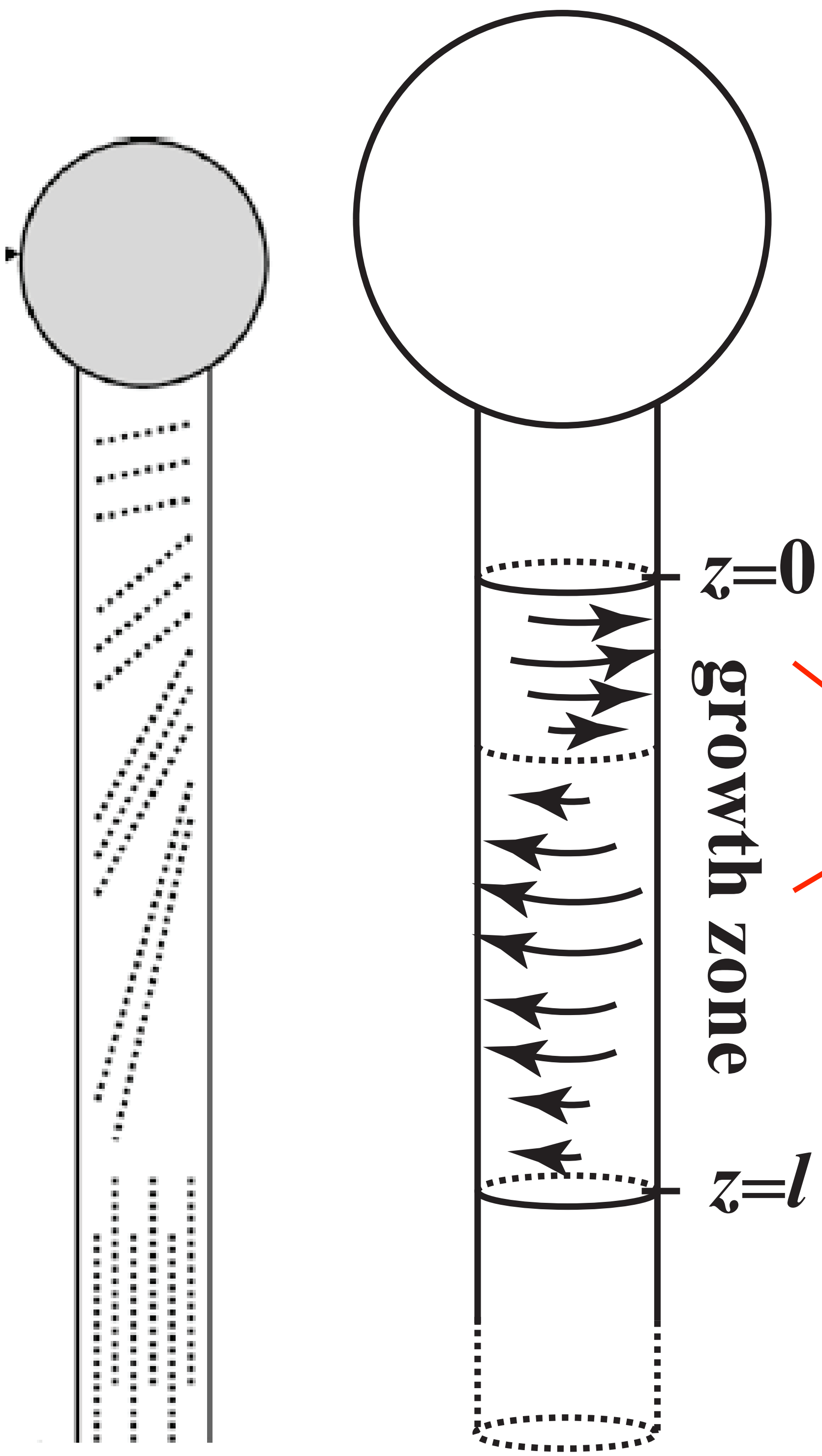


Low angle fibres rotate CCW

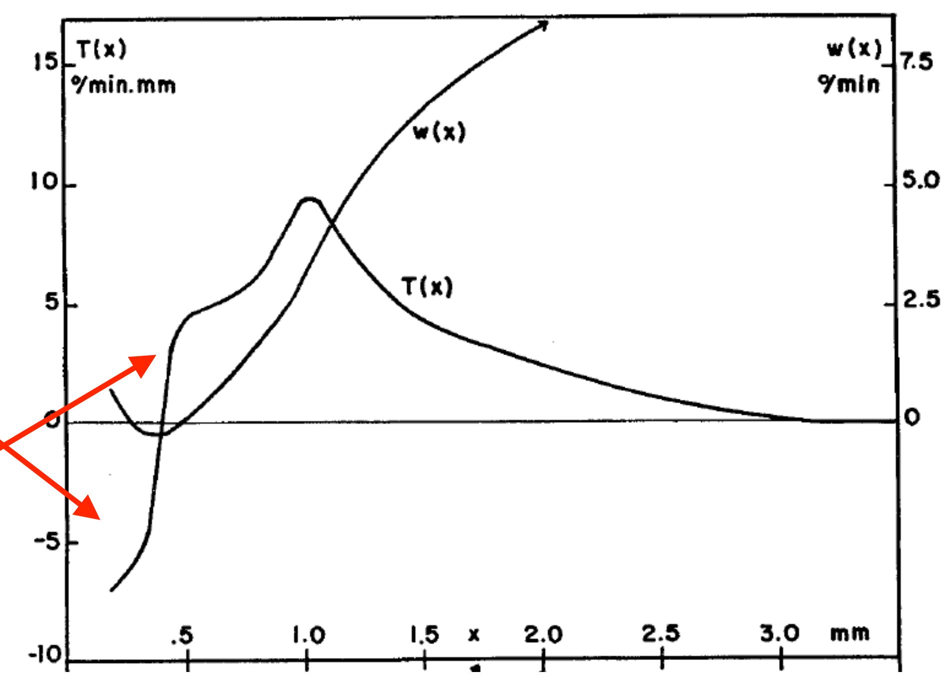
High angle fibres rotate CW

Contradictory rotation

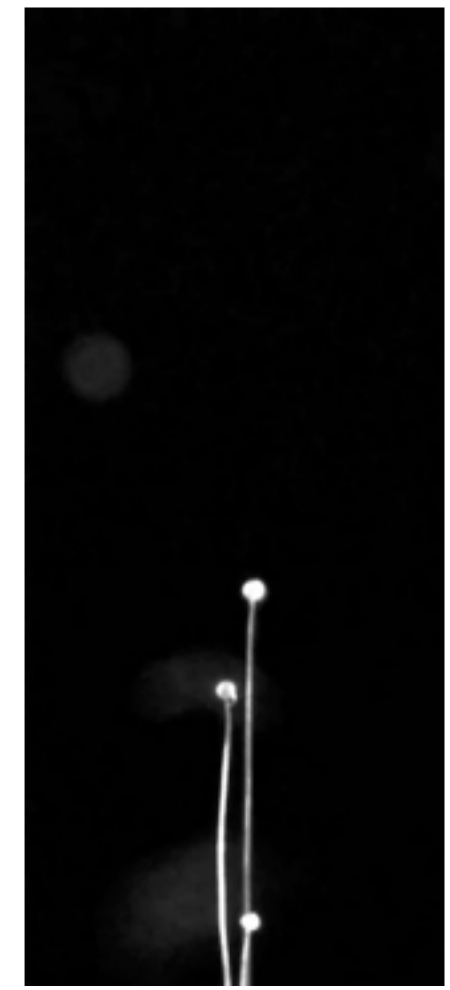
According to our model, points in the upper part of the growth zone turn counter-clockwise where points below turn clockwise

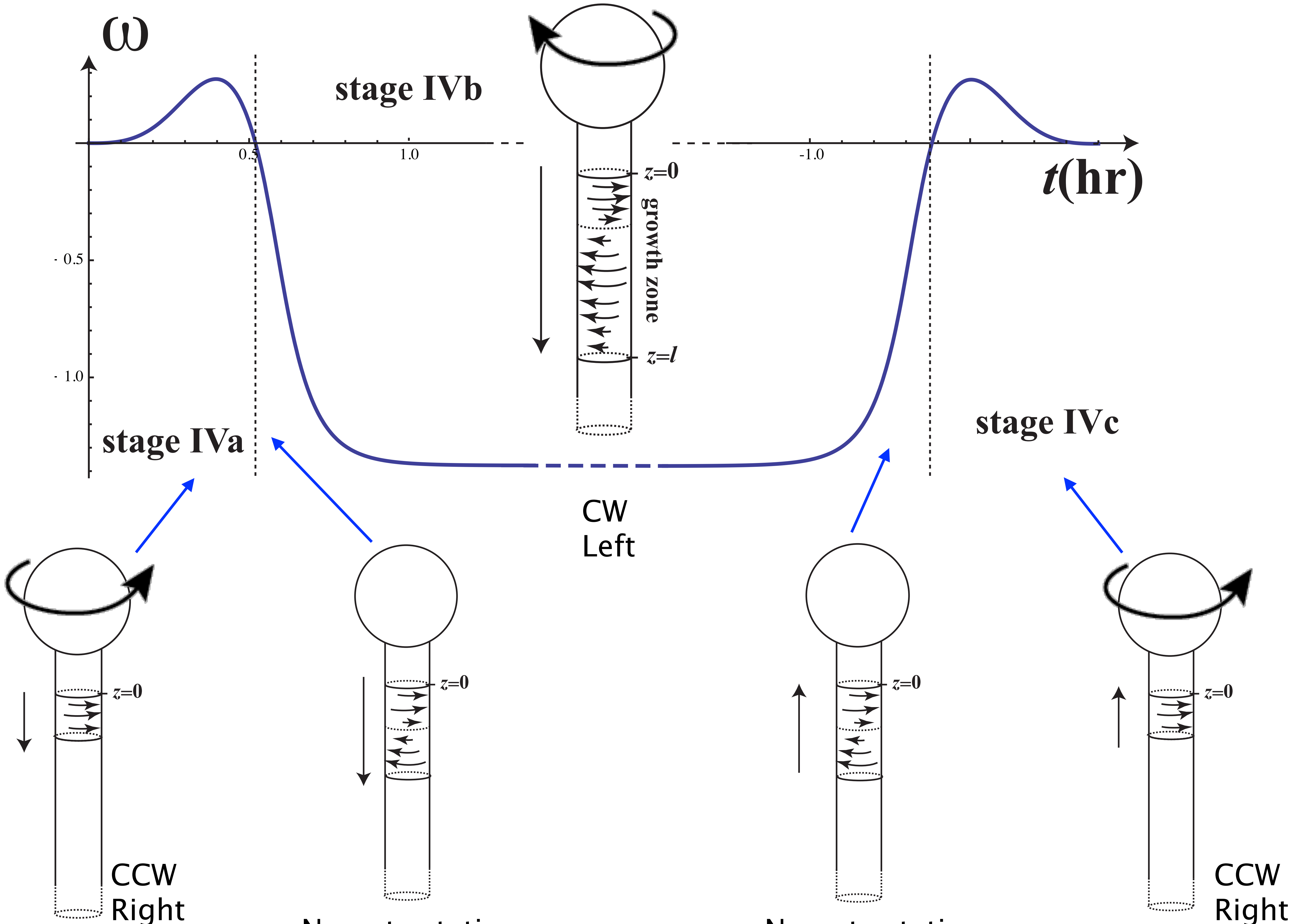


Ortega-Gamow 1992



Cohen & Delbrück (1958)
"Distribution of
stretch and twist along the growing zone..."

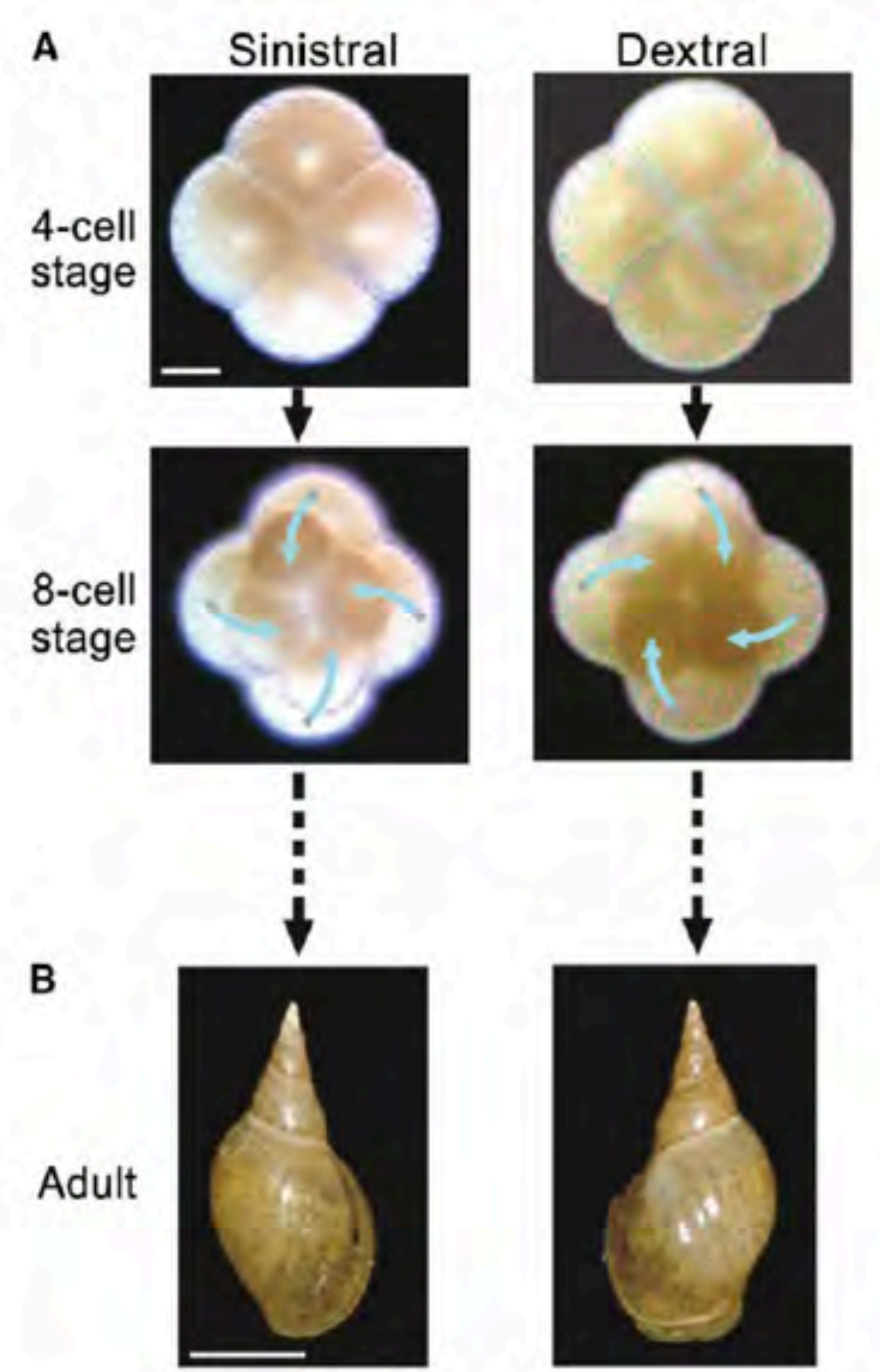




AG &Tabor (2011)

Conclusions

- Response of a chiral structure:
  Combination of geometry, material properties, large deformations, nonlinear response
- Inversion/perversion
  Non-monotonous response
- Other inversion (AG&Tabor,'13)
  Poynting effect
  Shell inflation
  Inversion of axial strain in arteries
  ....
- Chirality
  Measure of chirality?
  Helicity/Writhe
  Gyrality



Kuroda et al. 2009