

Alan Turing and the Patterns of Life

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Turing's most cited papers

On computable numbers, with an application to the Entscheidungsproblem	(1936)	5498
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The chemical basis of morphogenesis (1952) (Philosophical Transactions of the Royal Society of London Vol. 237 Nr. 641 pp. 37-72.)	6400

Q: How can biological patterns emerge from “nothing” ?

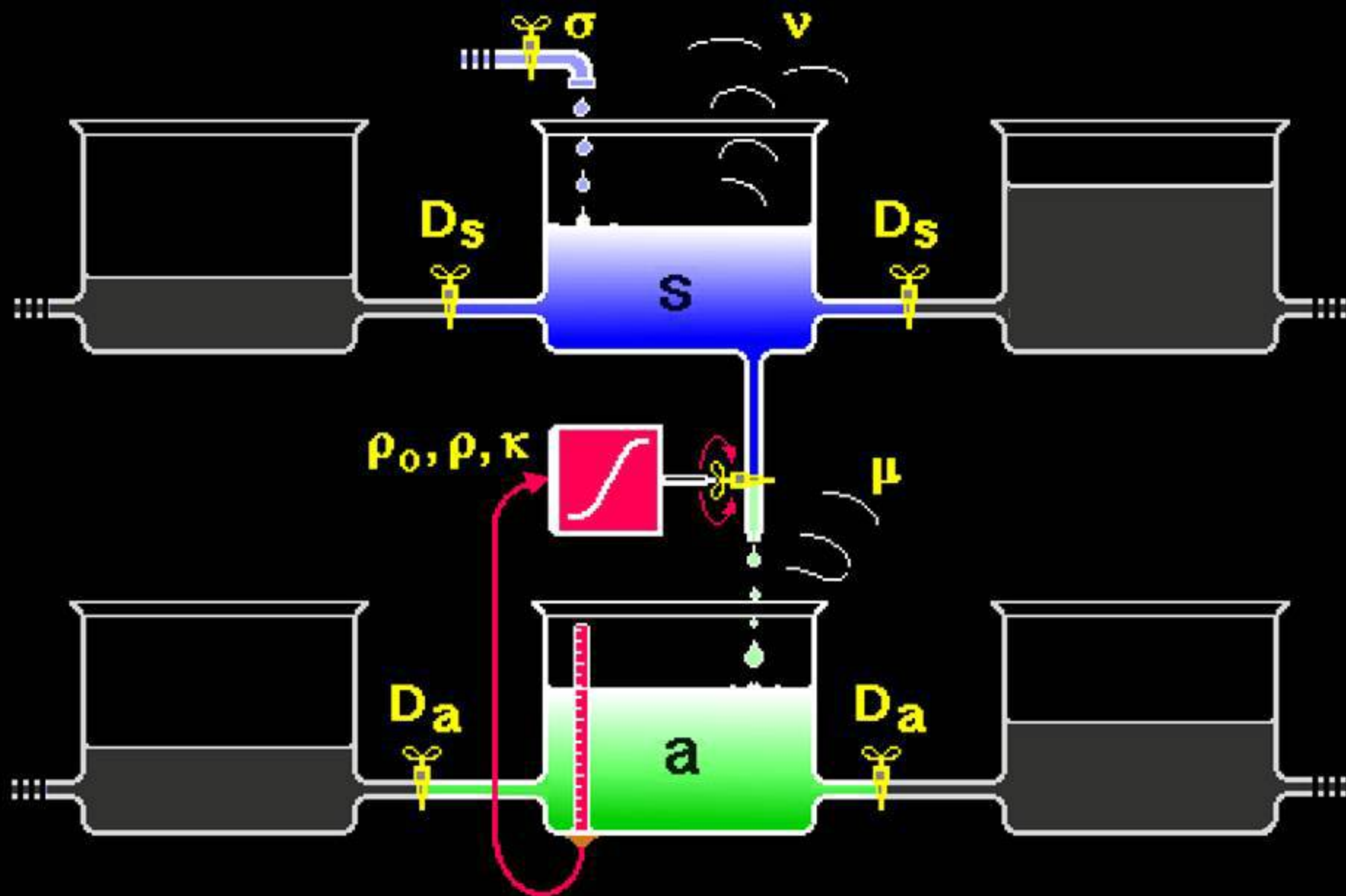
Basic idea: reaction-diffusion in 1D



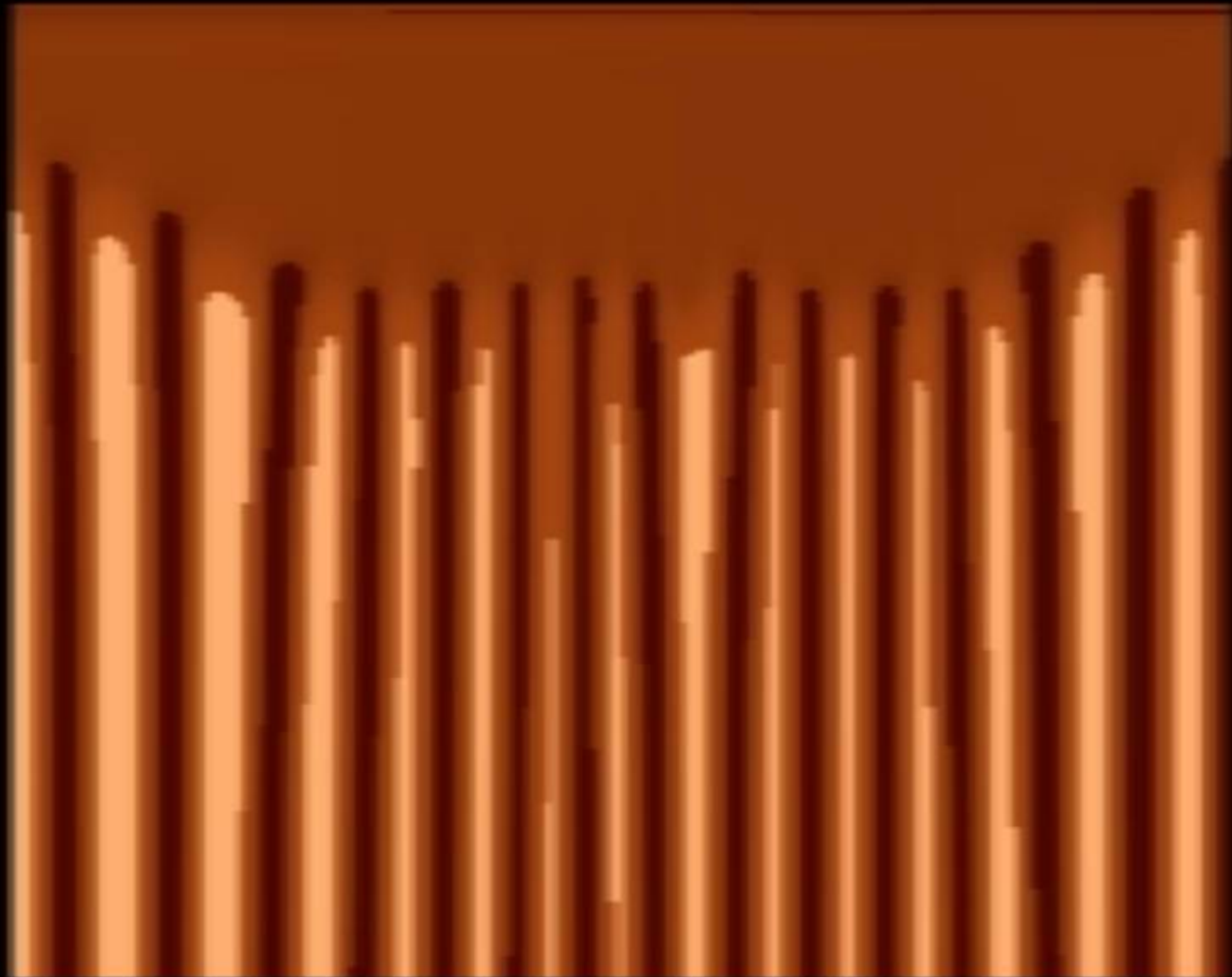
$$\frac{\partial a_i}{\partial t} = f(a_i, s_i) + D_a (a_{i-1} - 2a_i + a_{i+1})$$

$$\frac{\partial s_i}{\partial t} = g(a_i, s_i) + D_s (s_{i-1} - 2s_i + s_{i+1})$$

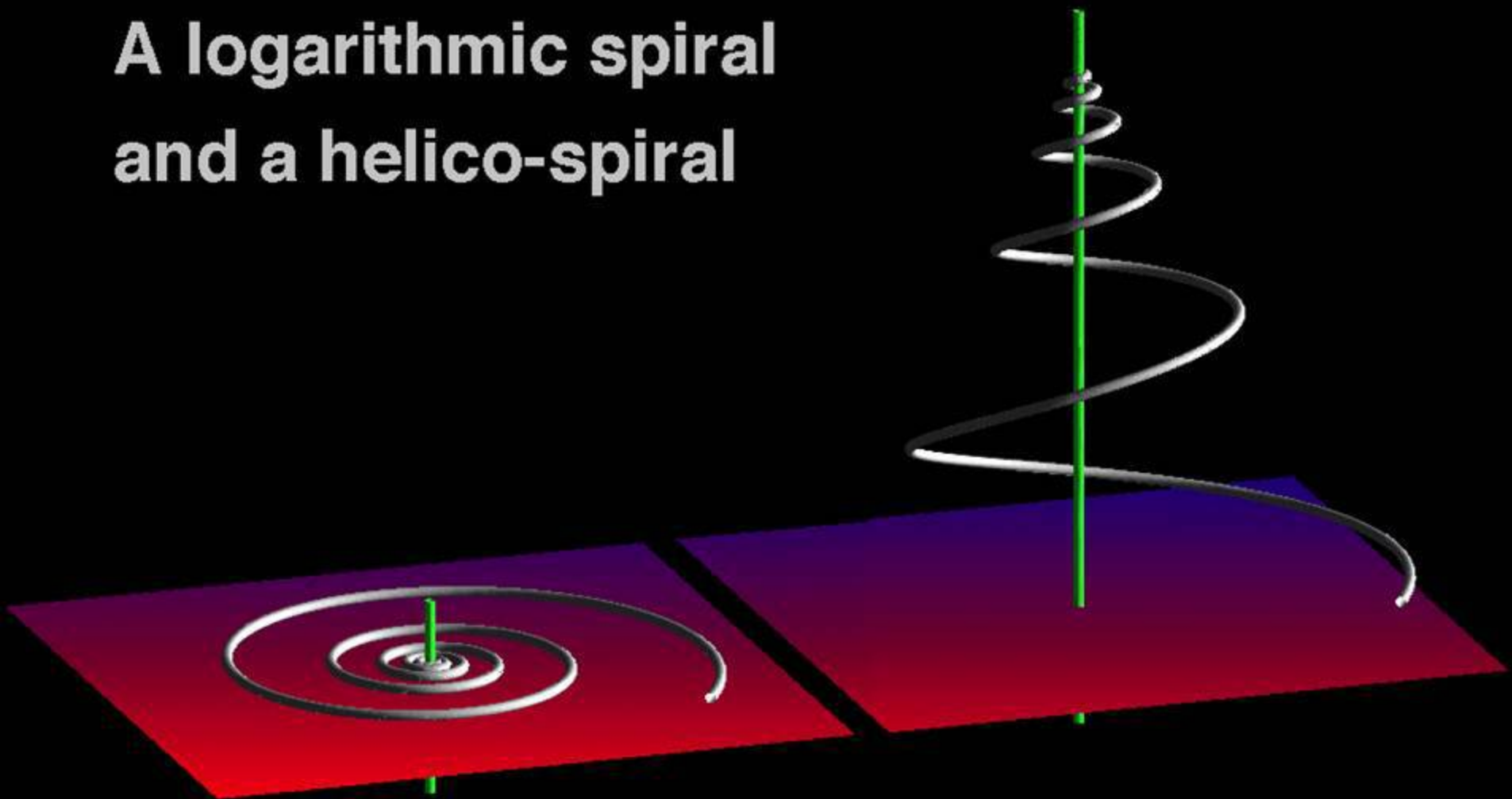
Intuition: the activator-substrate model

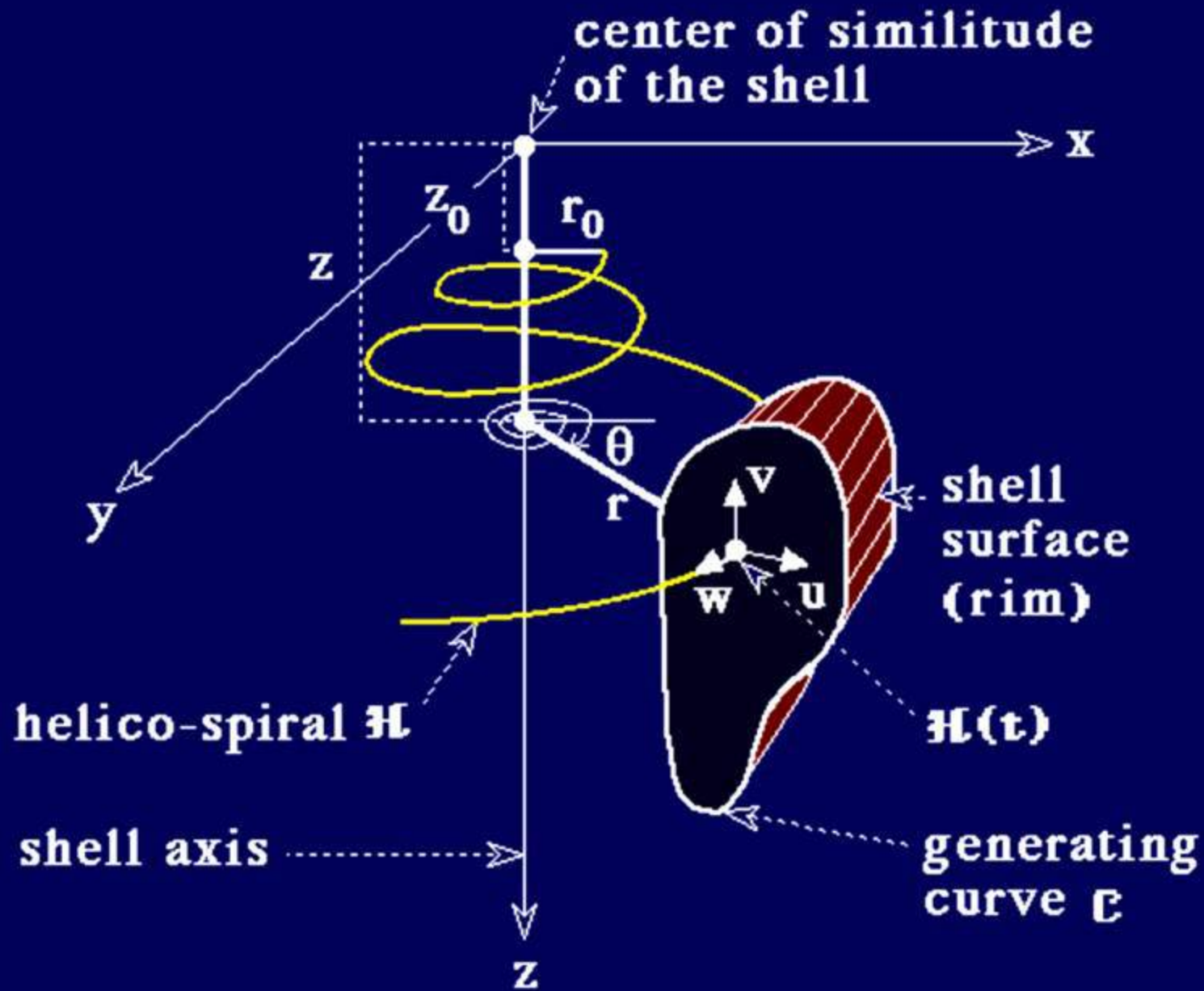


Emergence of a spatially periodic pattern



A logarithmic spiral and a helico-spiral



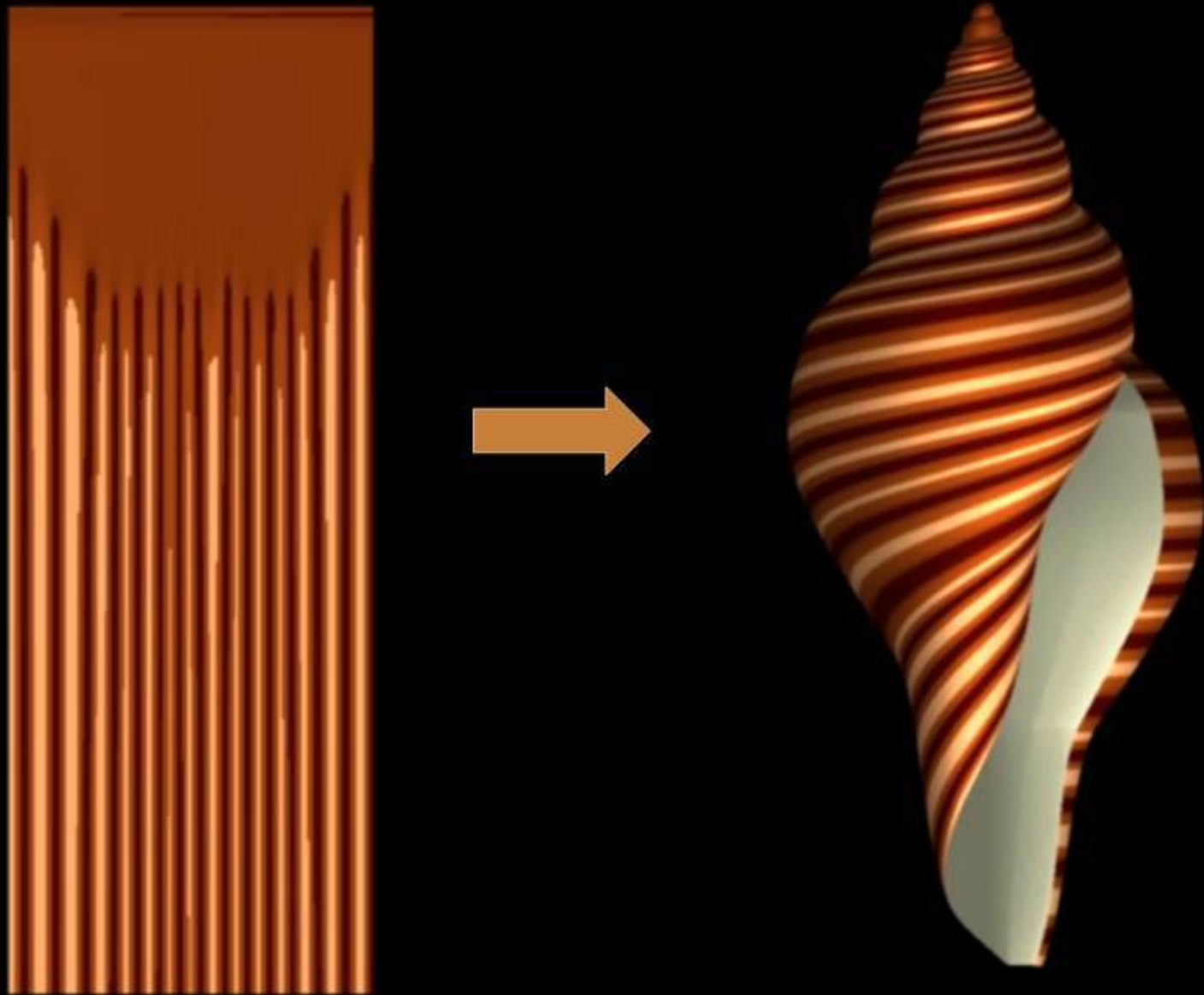


Construction of the shell surface

Geometry of a sea shell

Thatcheria mirabilis

A seashell with spatially periodic stripes

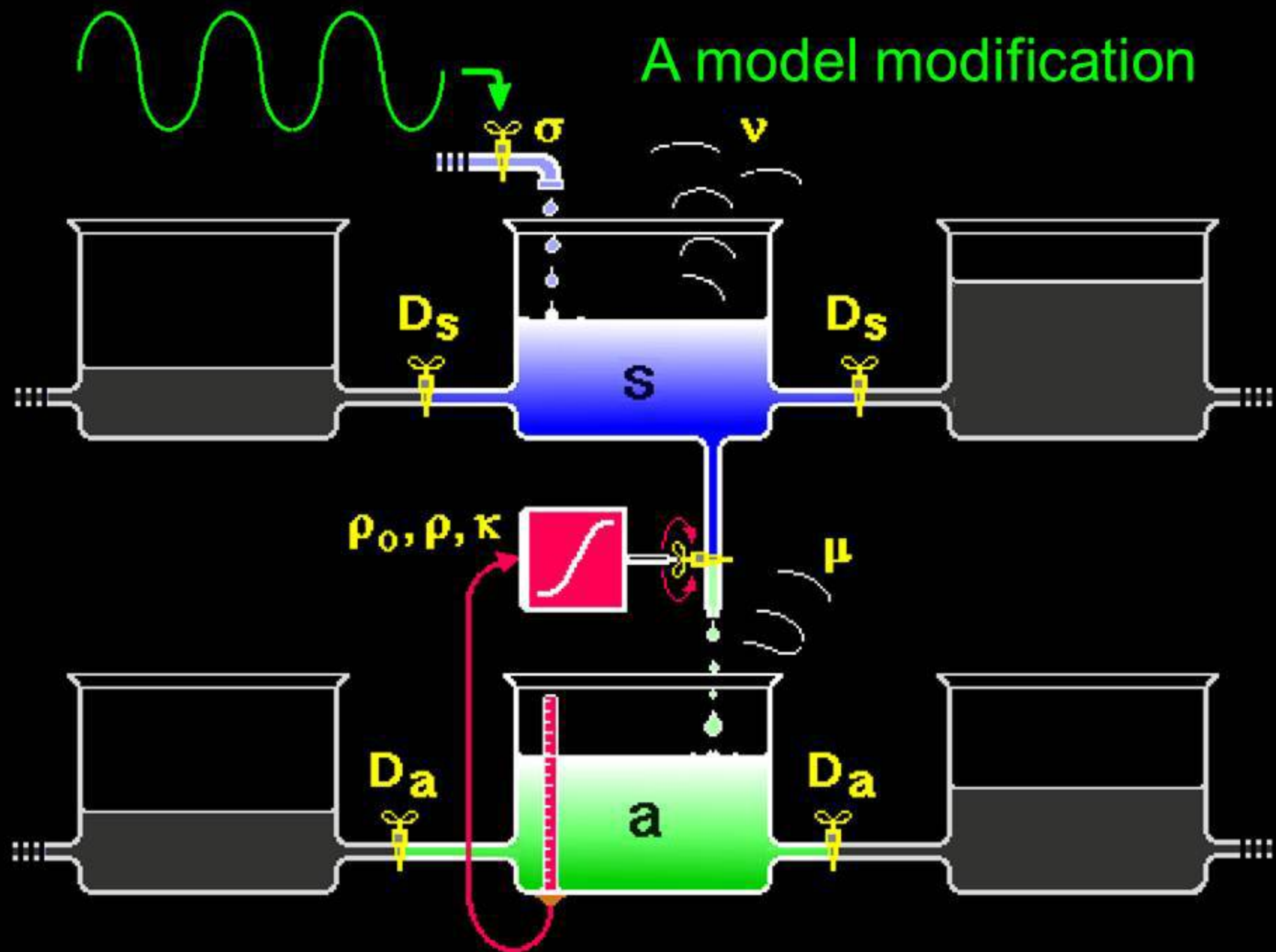


A seashell with temporarily periodic stripes

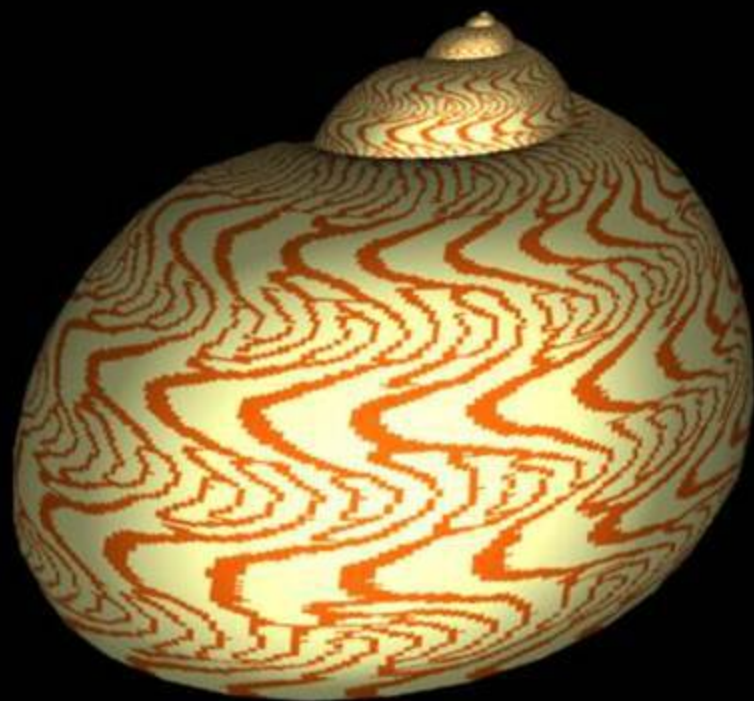


Amoria ellioti

A model modification



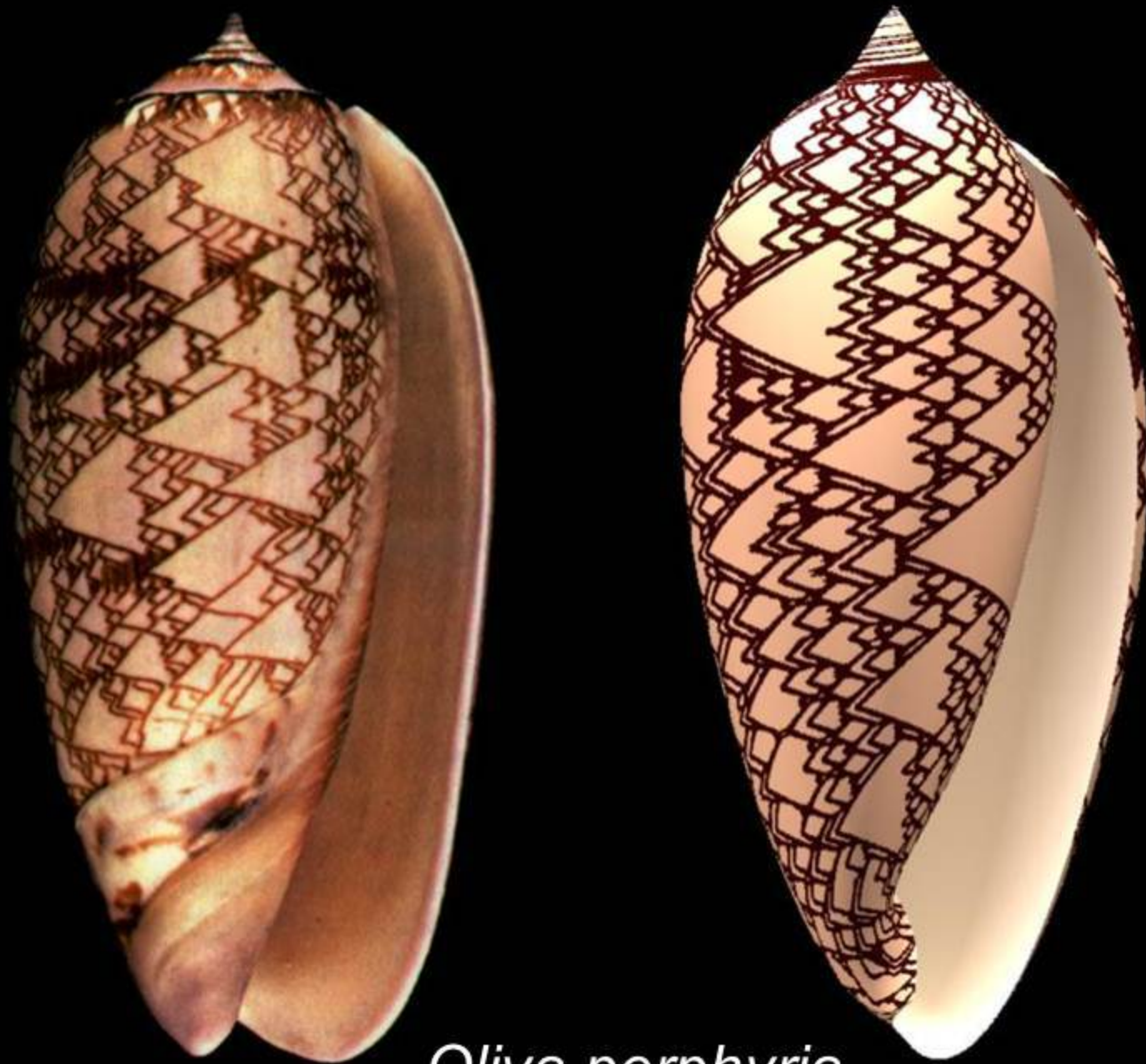
Natica euzona



Natica euzona



Volutoconus bednalli

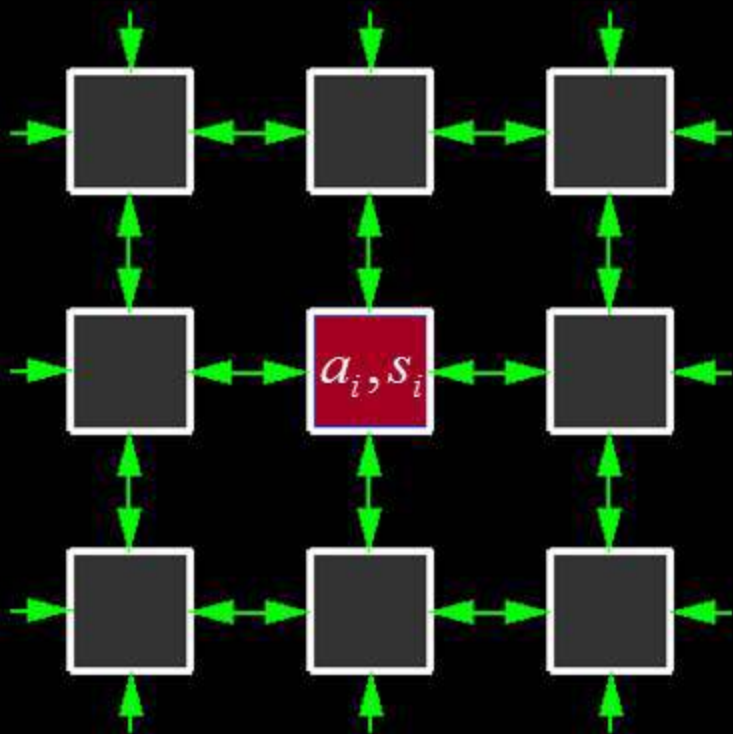


Oliva porphyria



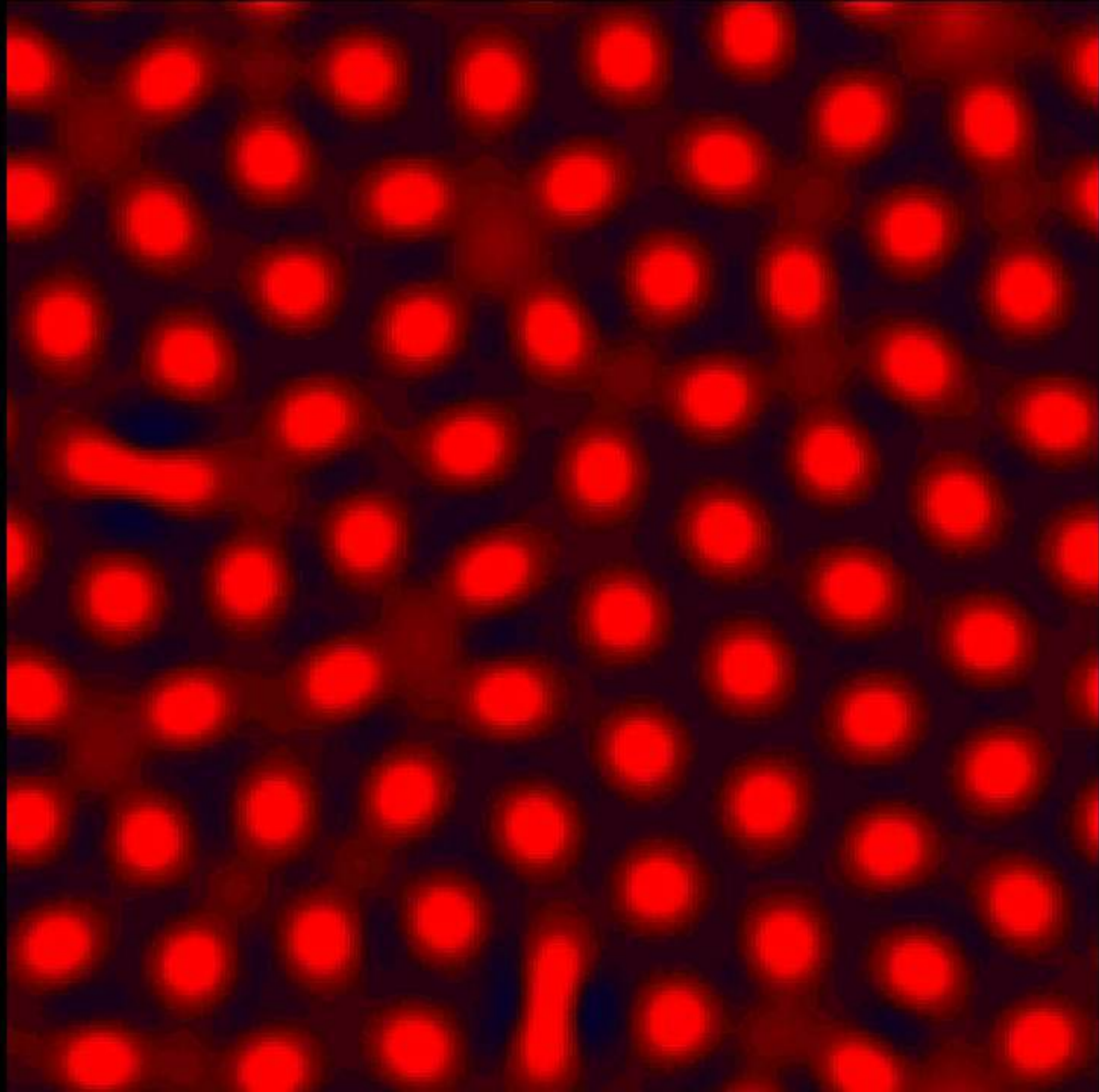
Conus marmoreus

Reaction-diffusion in 2D



$$\frac{\partial a_i}{\partial t} = f(a_i, s_i) + \text{diffusion}$$

$$\frac{\partial s_i}{\partial t} = g(a_i, s_i) + \text{diffusion}$$





Turing's manuscripts in biology

A diffusion reaction theory of morphogenesis in plants
(with C. W. Wardlaw)

Morphogen theory of phyllotaxis

Outline of the development of the daisy



Hockey
or

Watching the Daisies

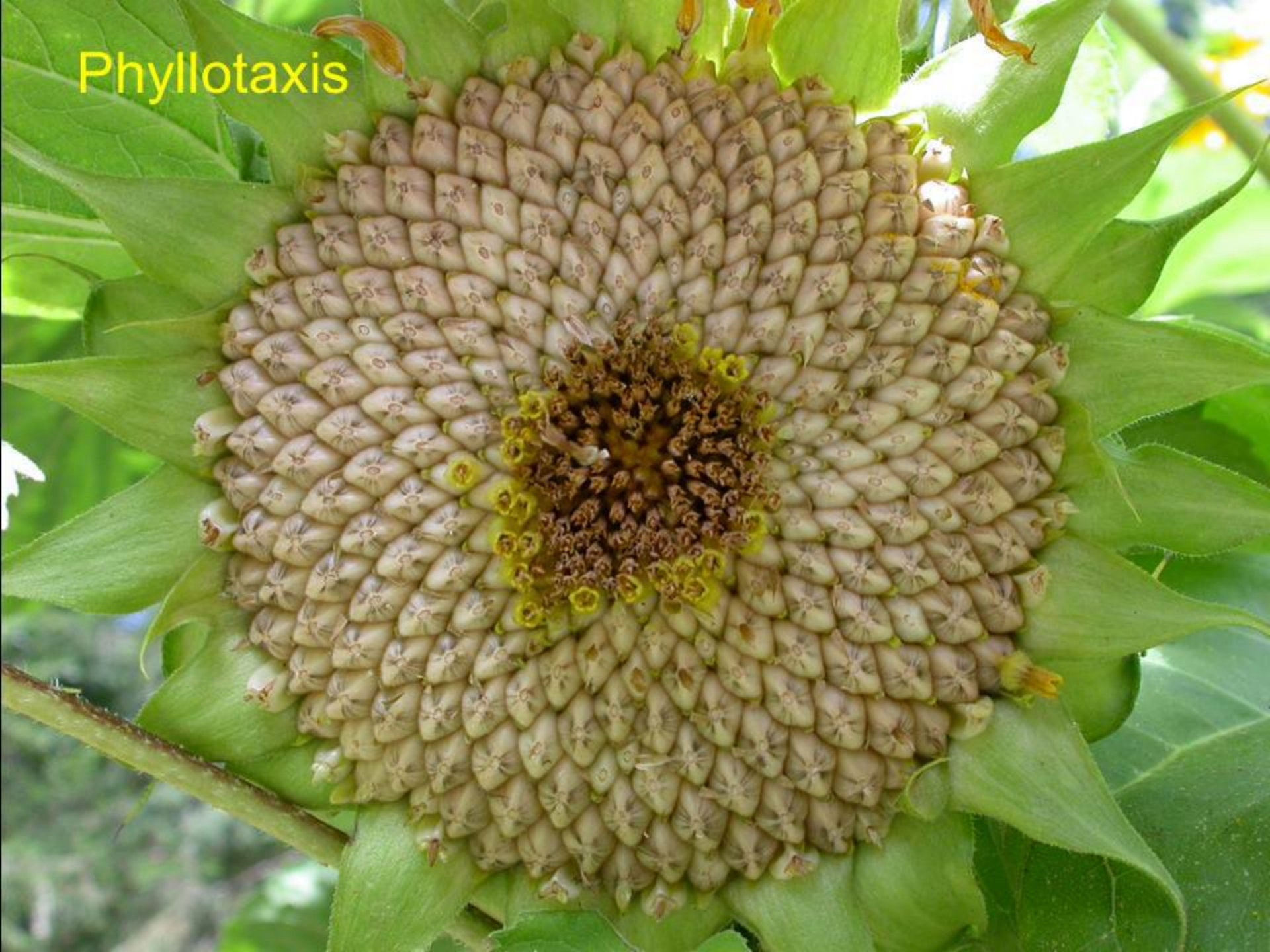
Crow

Turing at the age of 10 drawn by his mother

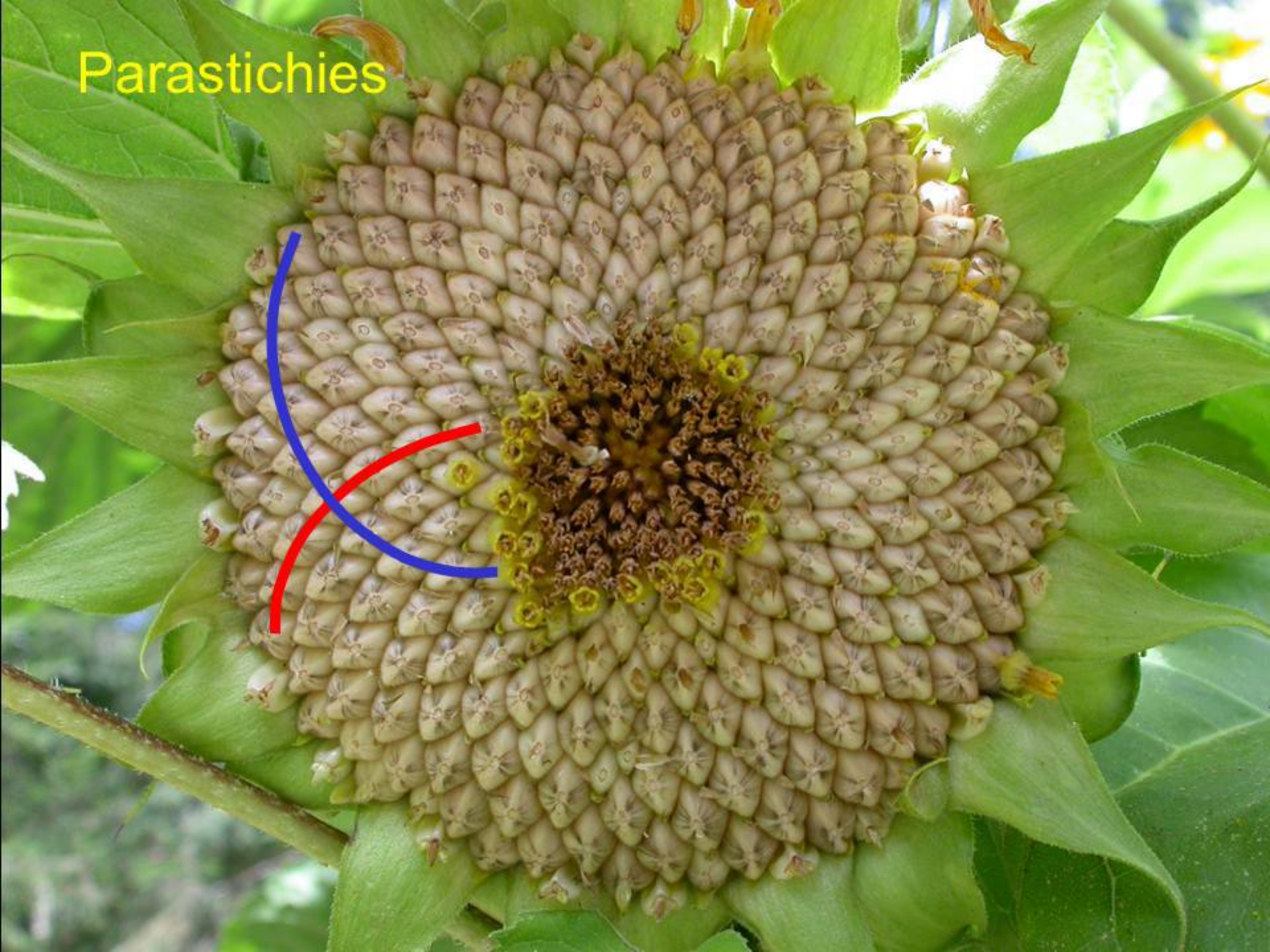




Phyllotaxis



Parastichies

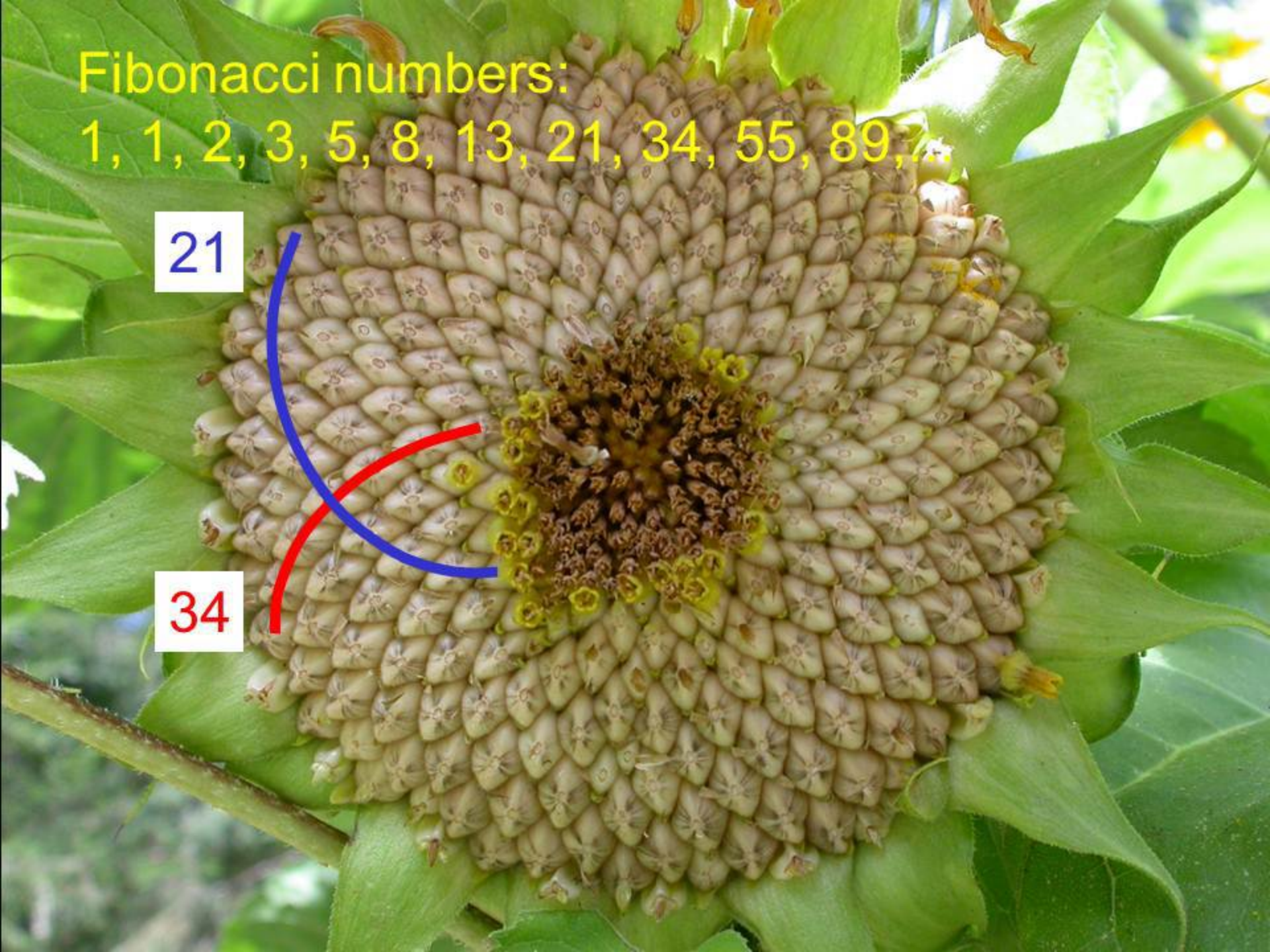


Fibonacci numbers:

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

21

34



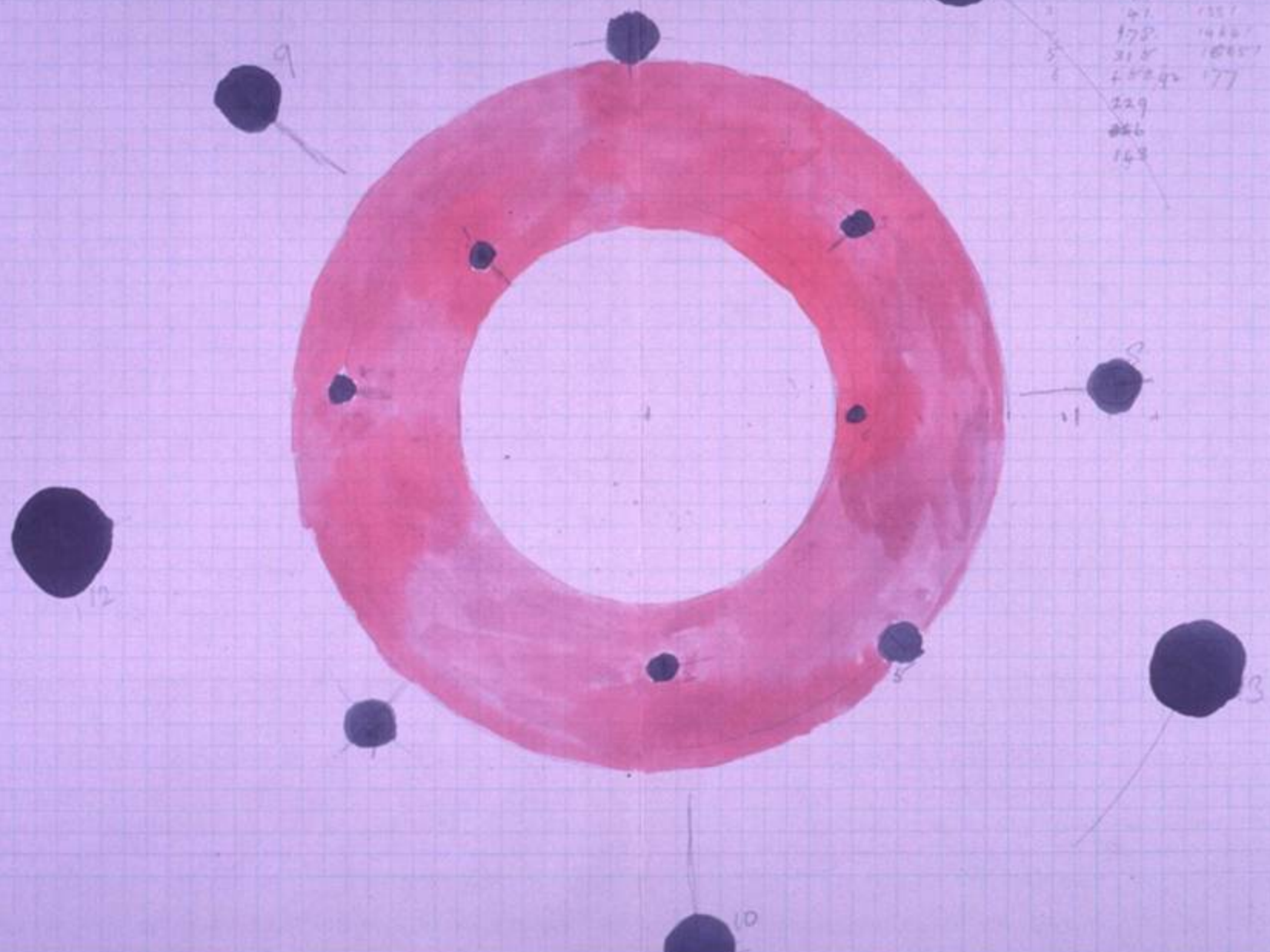
From Turing's archives...

1264
1265
1266
1267

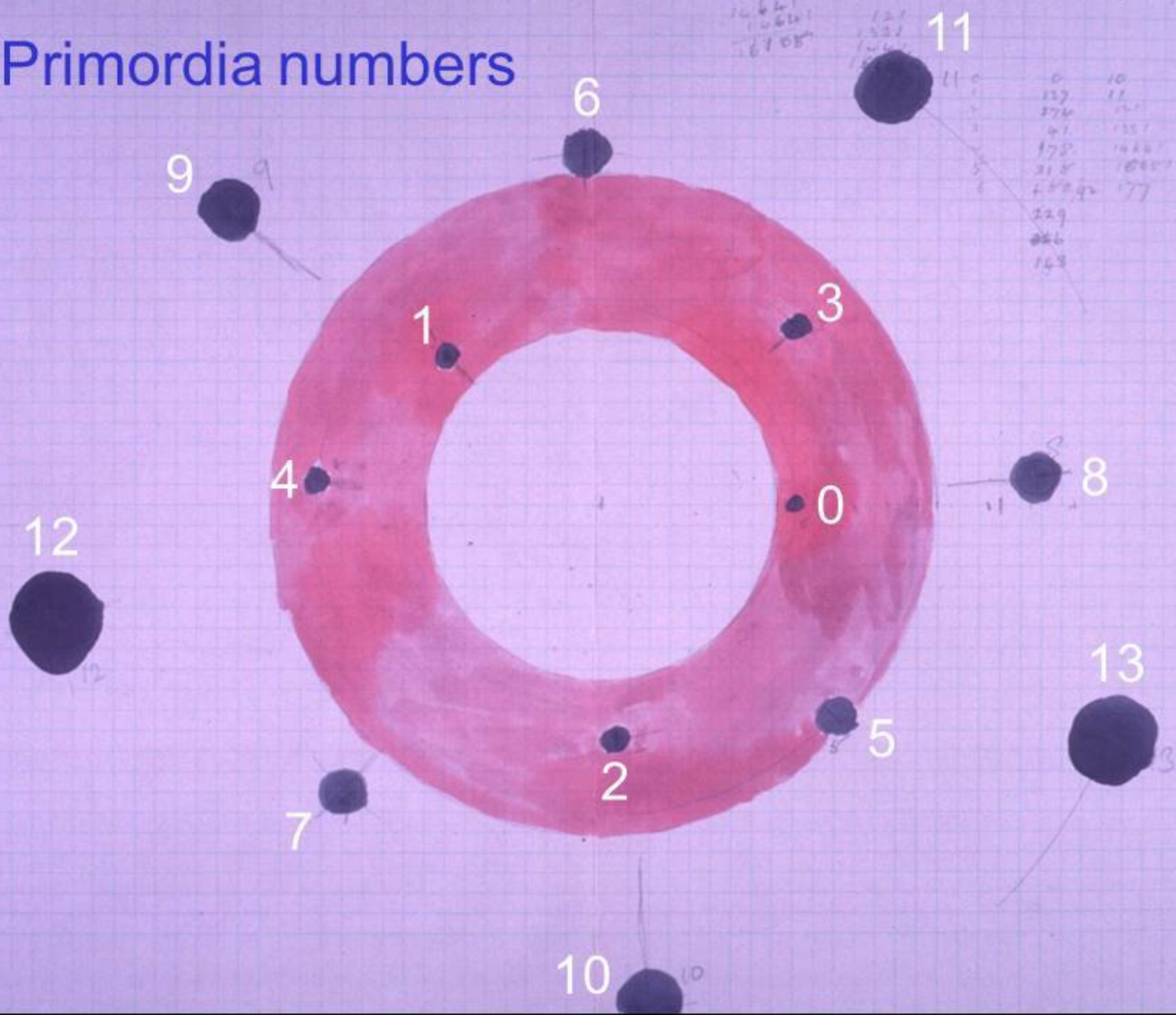
127
128
129

0

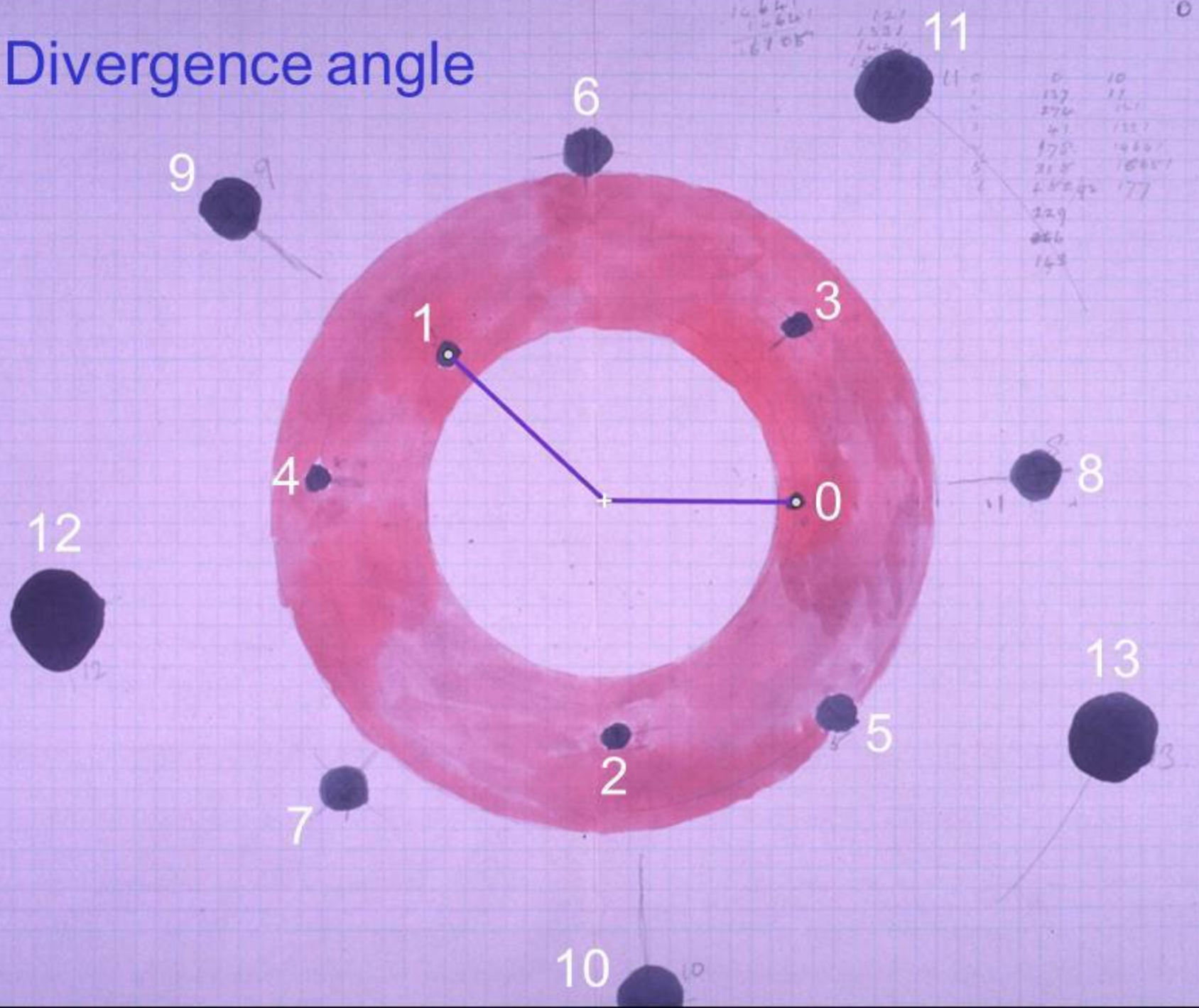
11	0	10
1	137	11
2	276	21
3	41	1337
4	172	1427
5	312	1007
6	452	177
7	229	
8	266	
9	153	



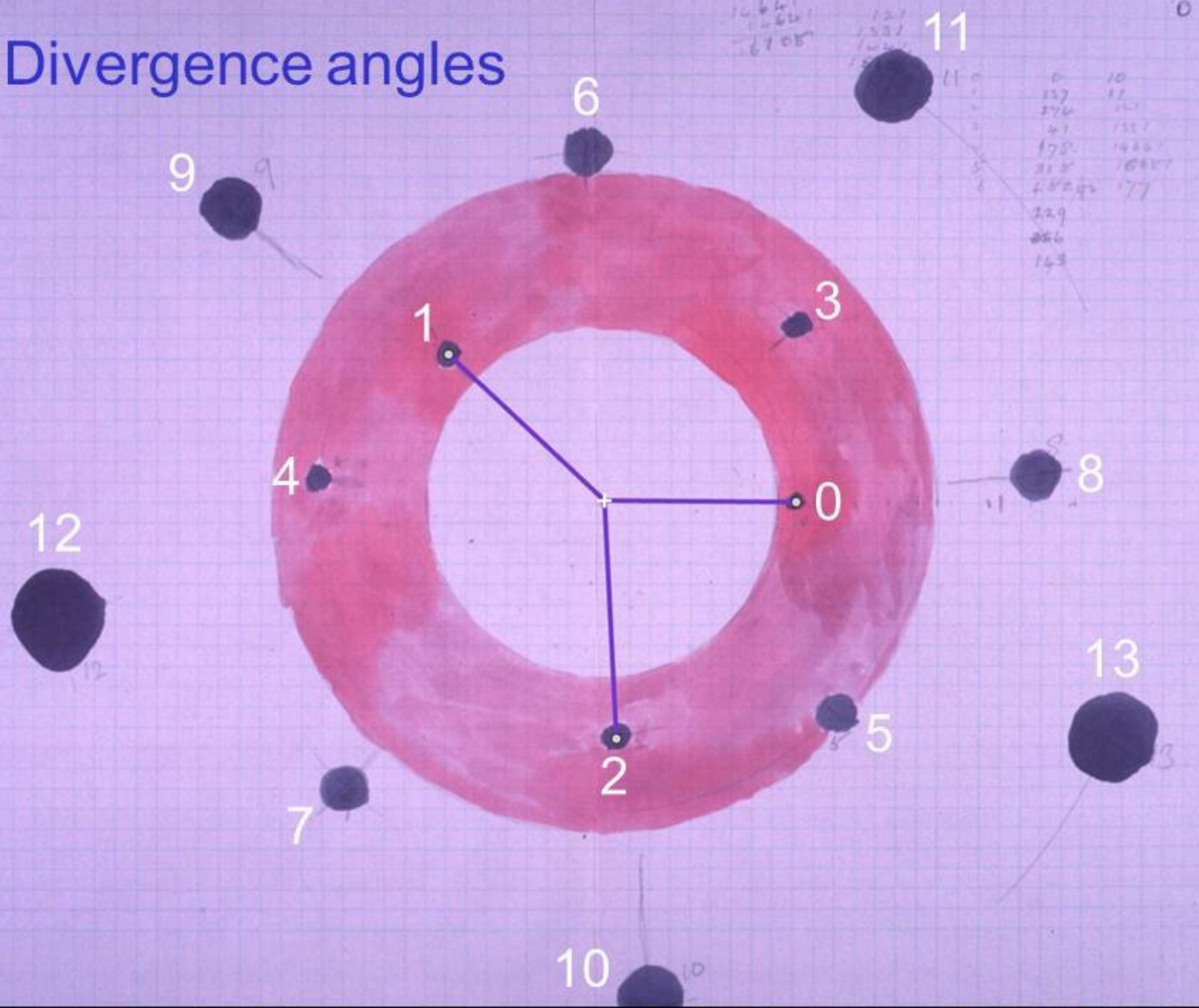
Primordia numbers



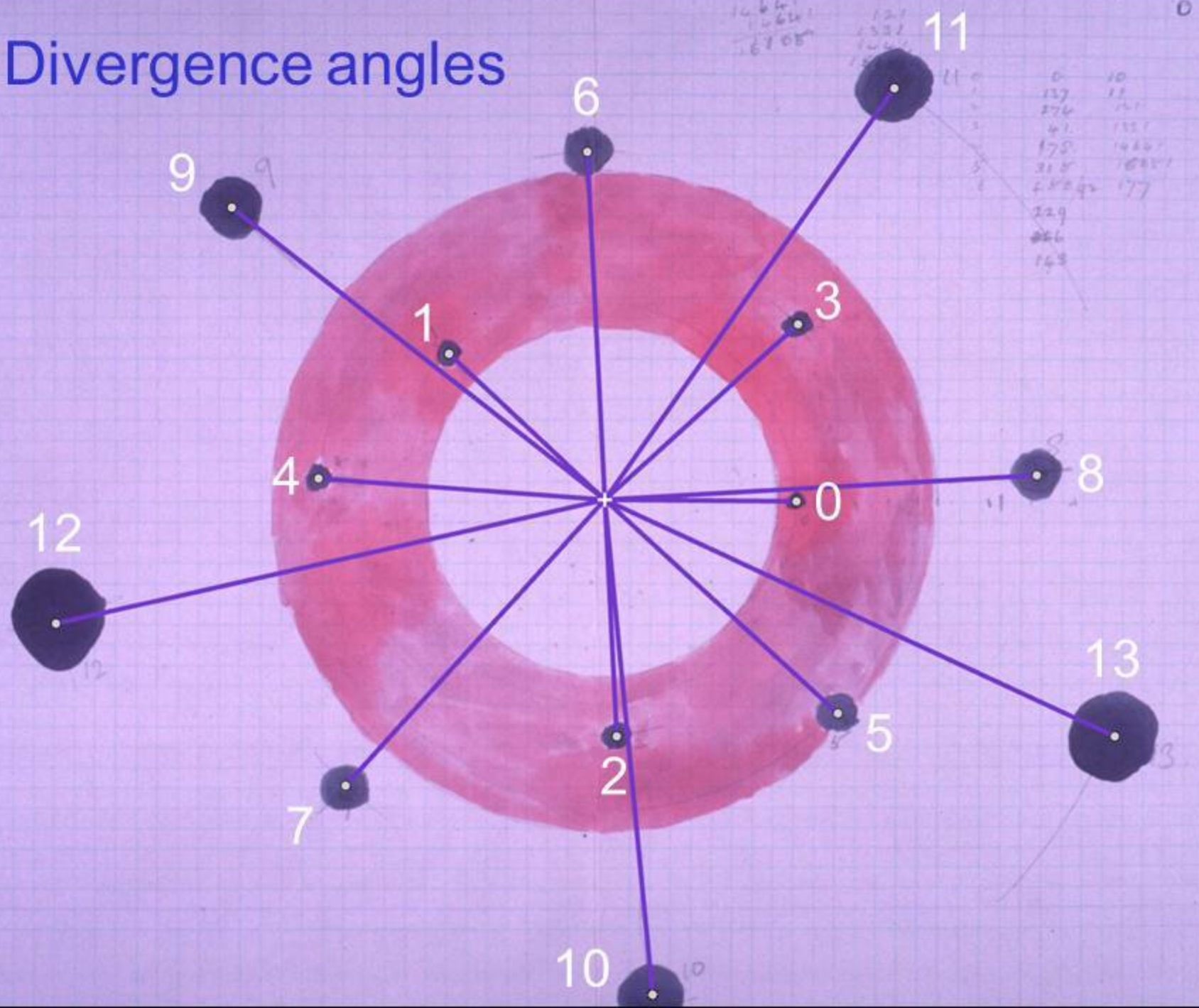
Divergence angle



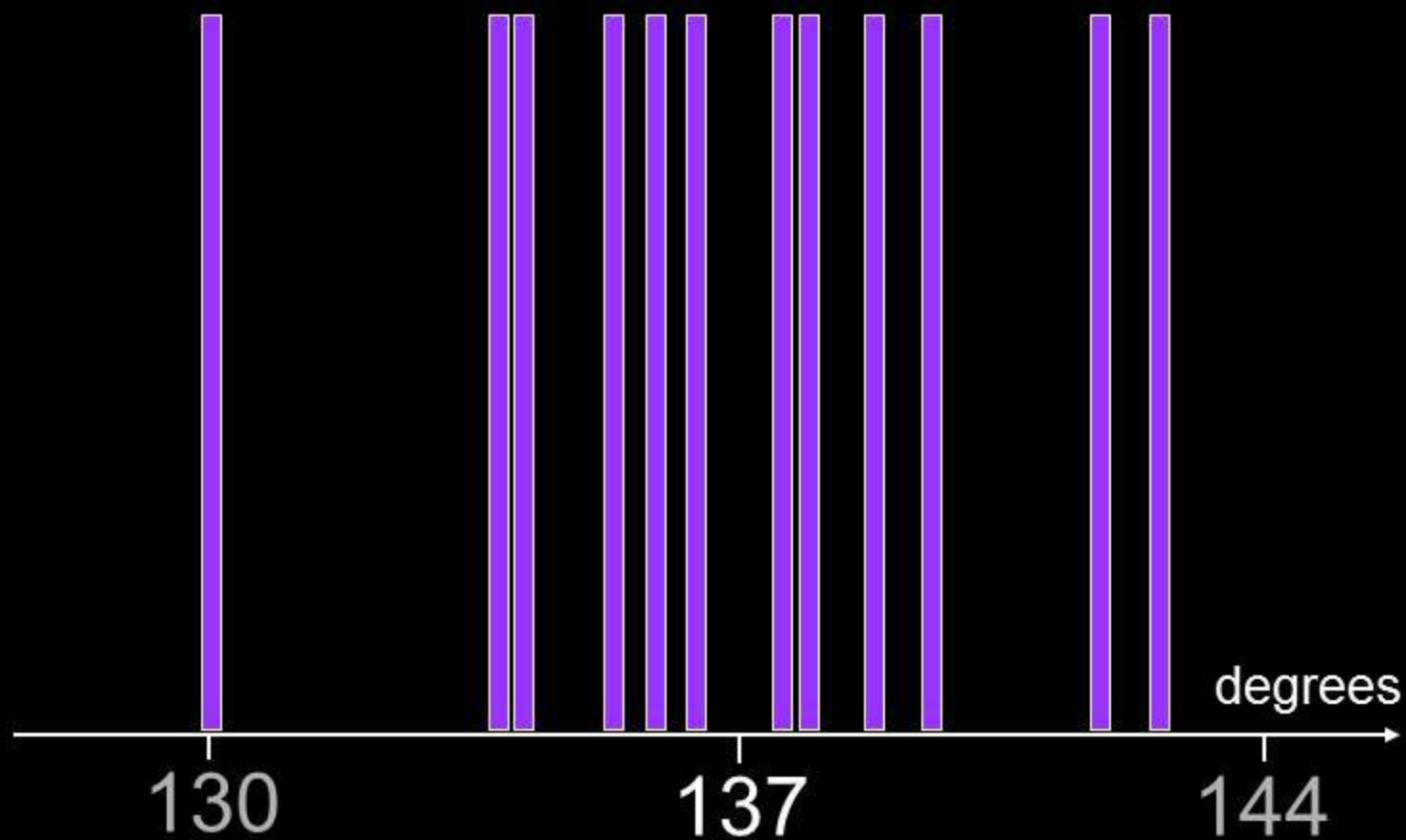
Divergence angles



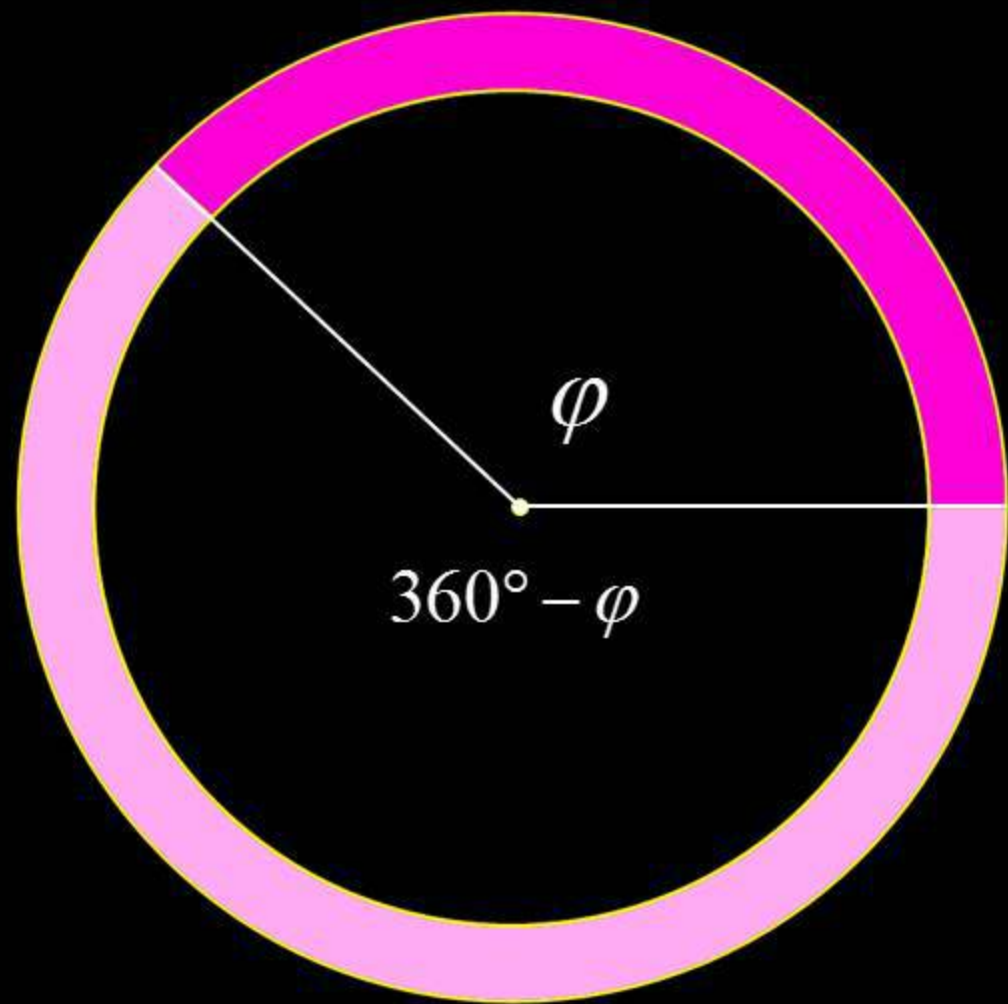
Divergence angles



Divergence angles



The golden angle



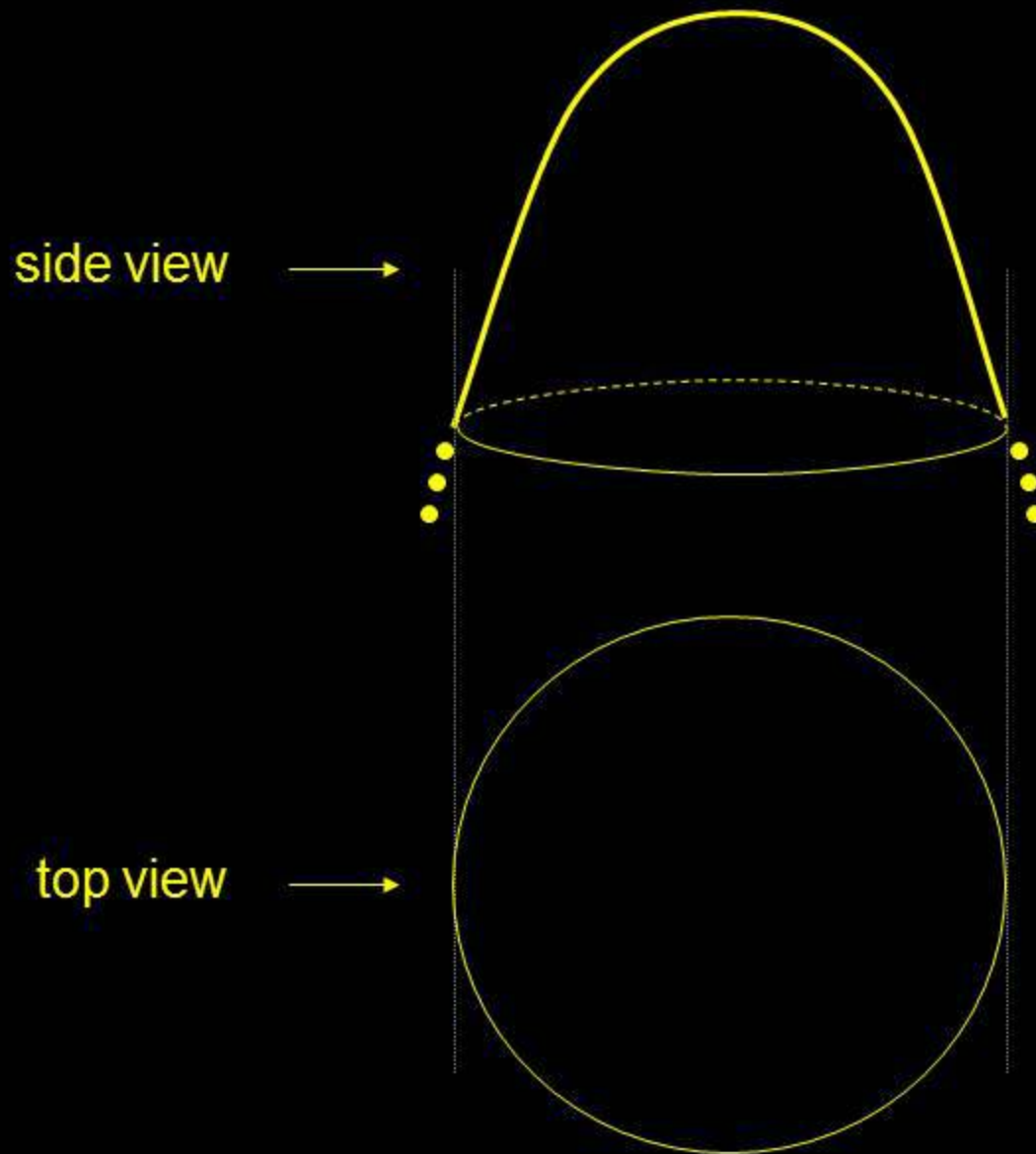
$$\frac{\varphi}{360^\circ - \varphi} = \frac{360^\circ - \varphi}{360^\circ}$$

$$\varphi \cong 137.5^\circ$$

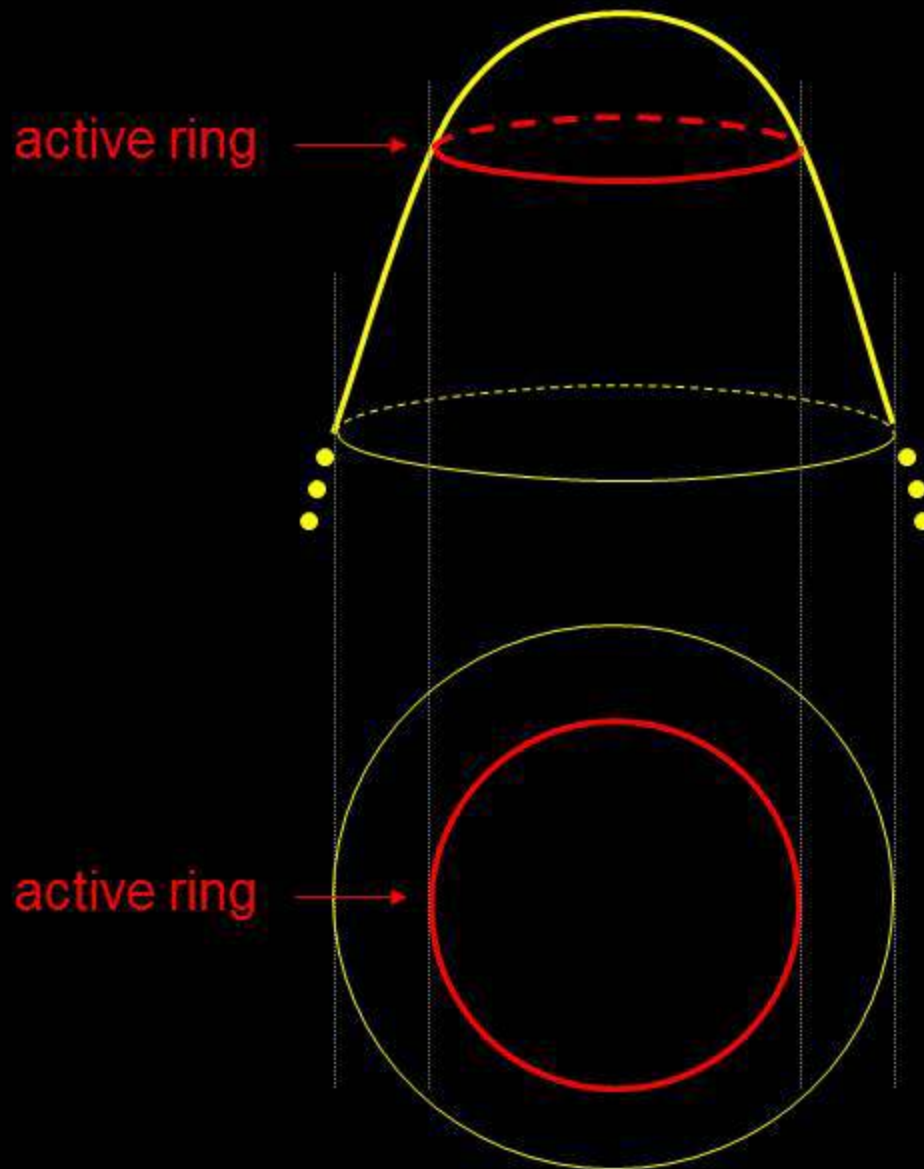
The golden angle and phyllotactic packing

Interactive model

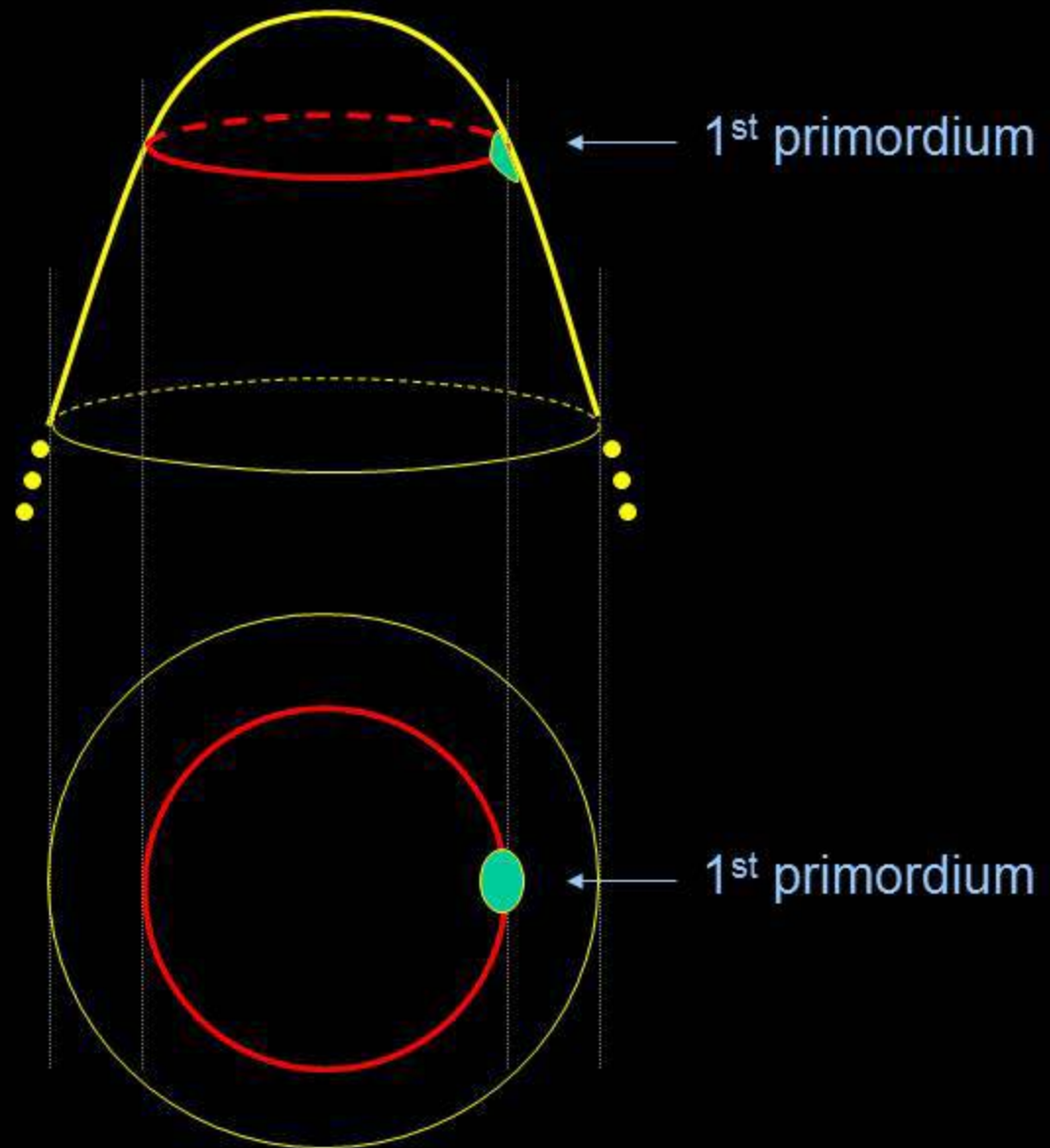
Inhibition field model (Hofmeister 1868)



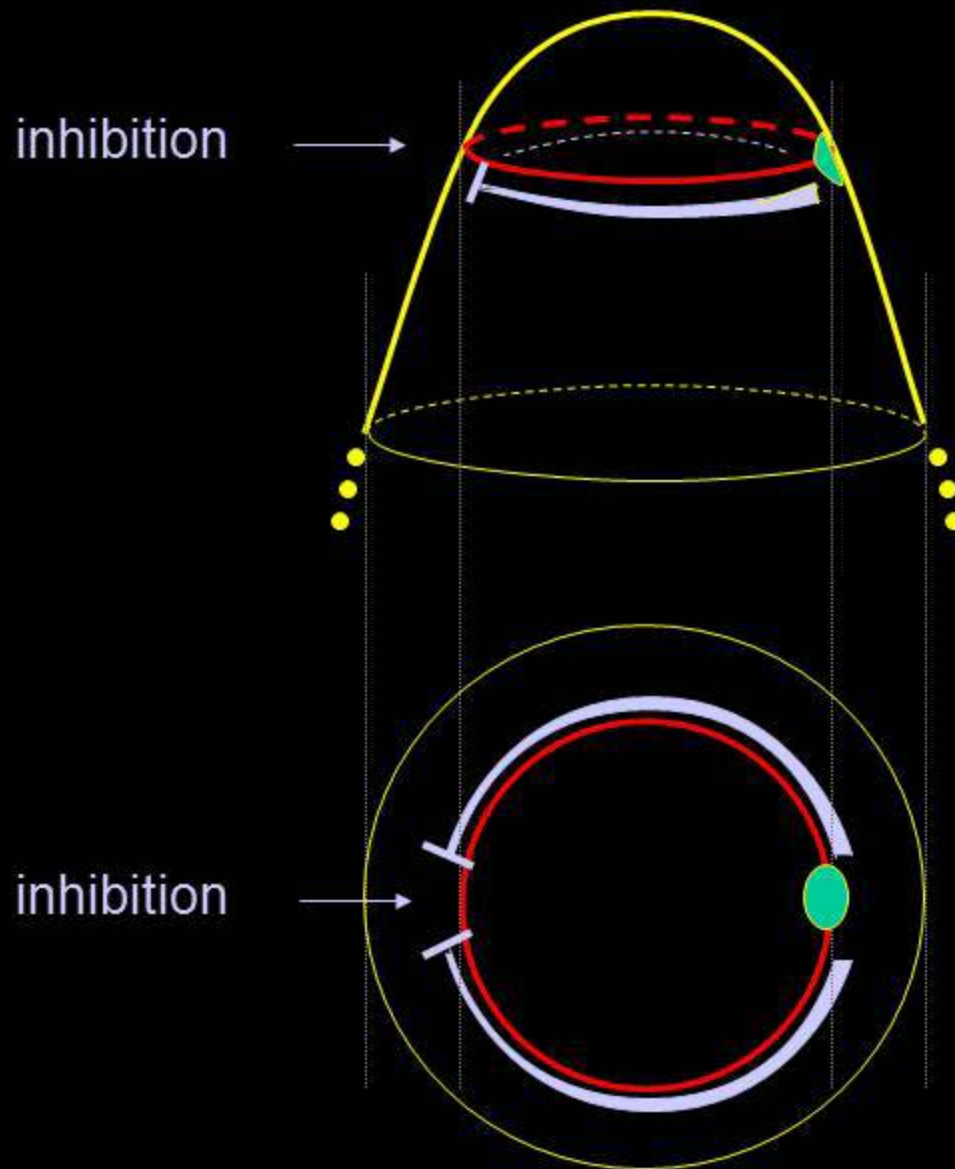
Inhibition field model



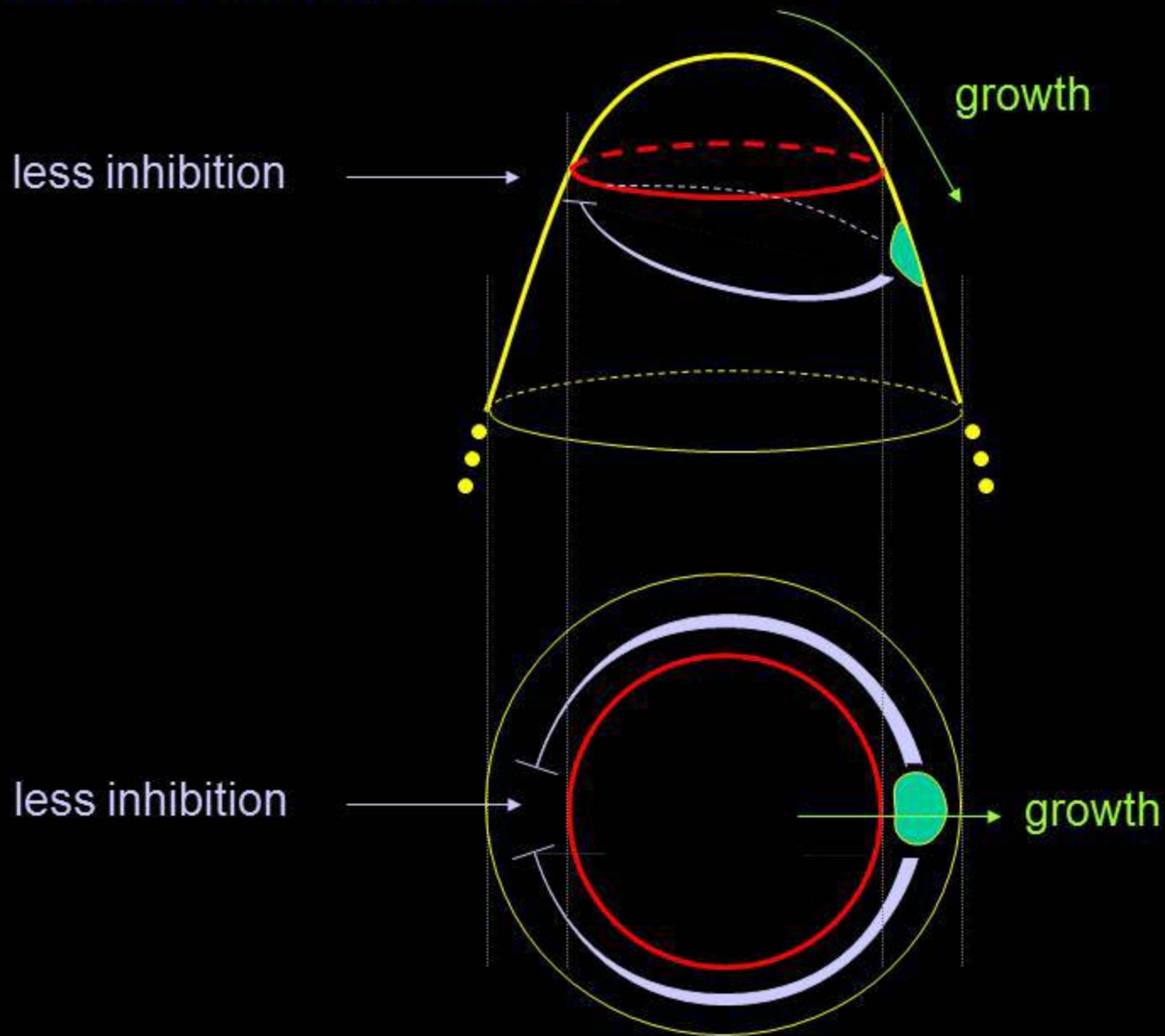
Inhibition field model



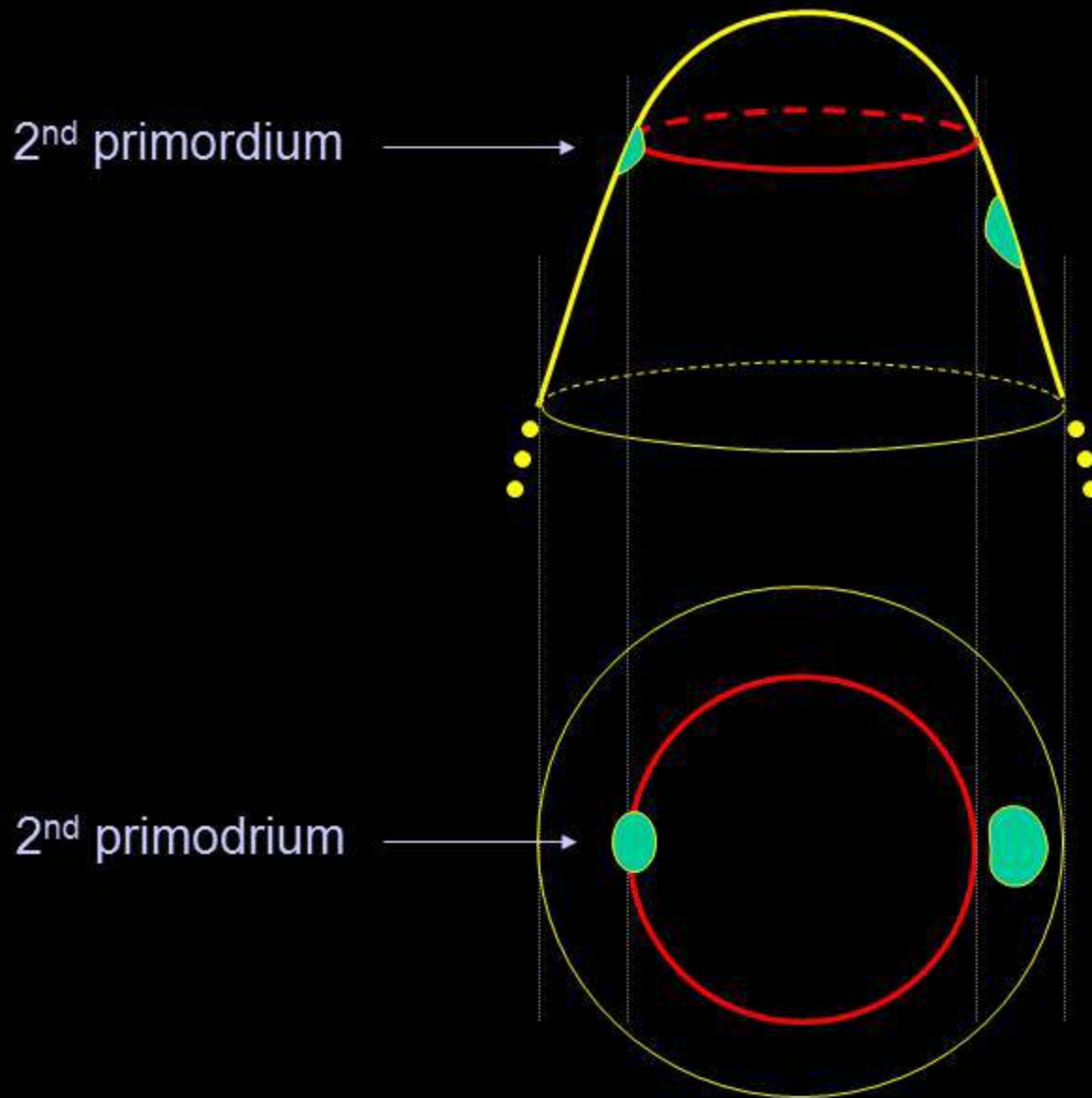
Inhibition field model



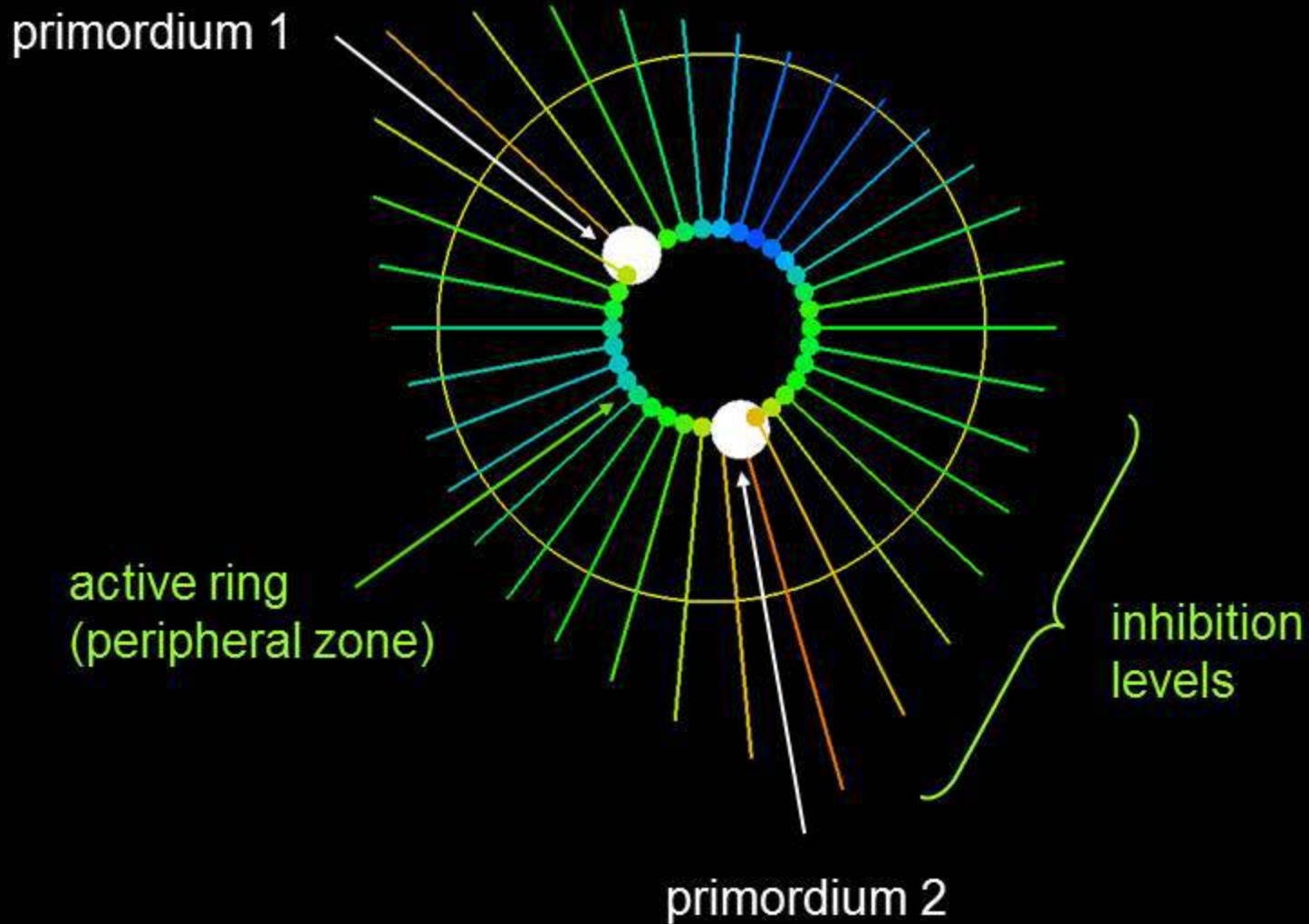
Inhibition field model



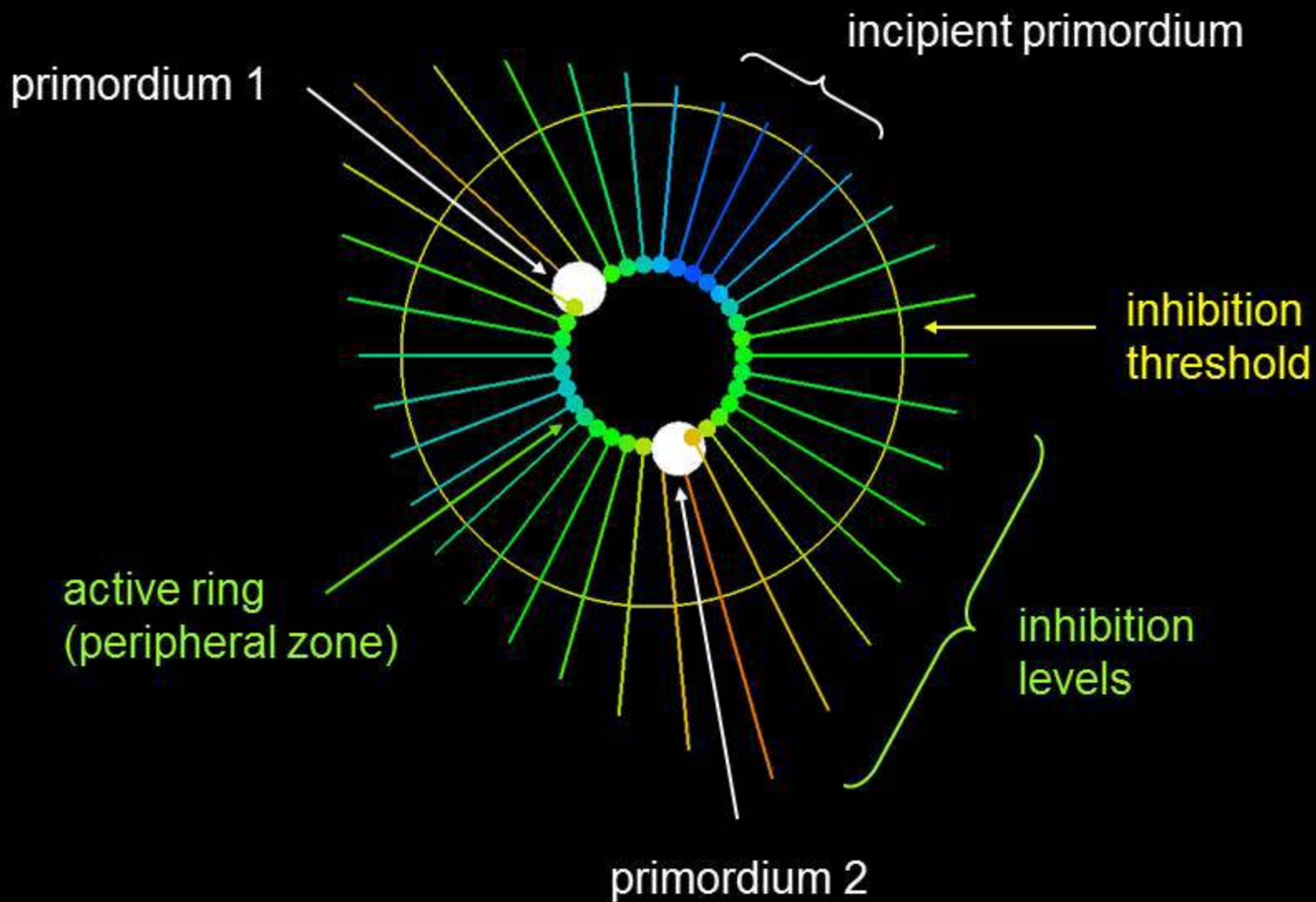
Inhibition field model



Towards reaction-diffusion



Towards reaction-diffusion



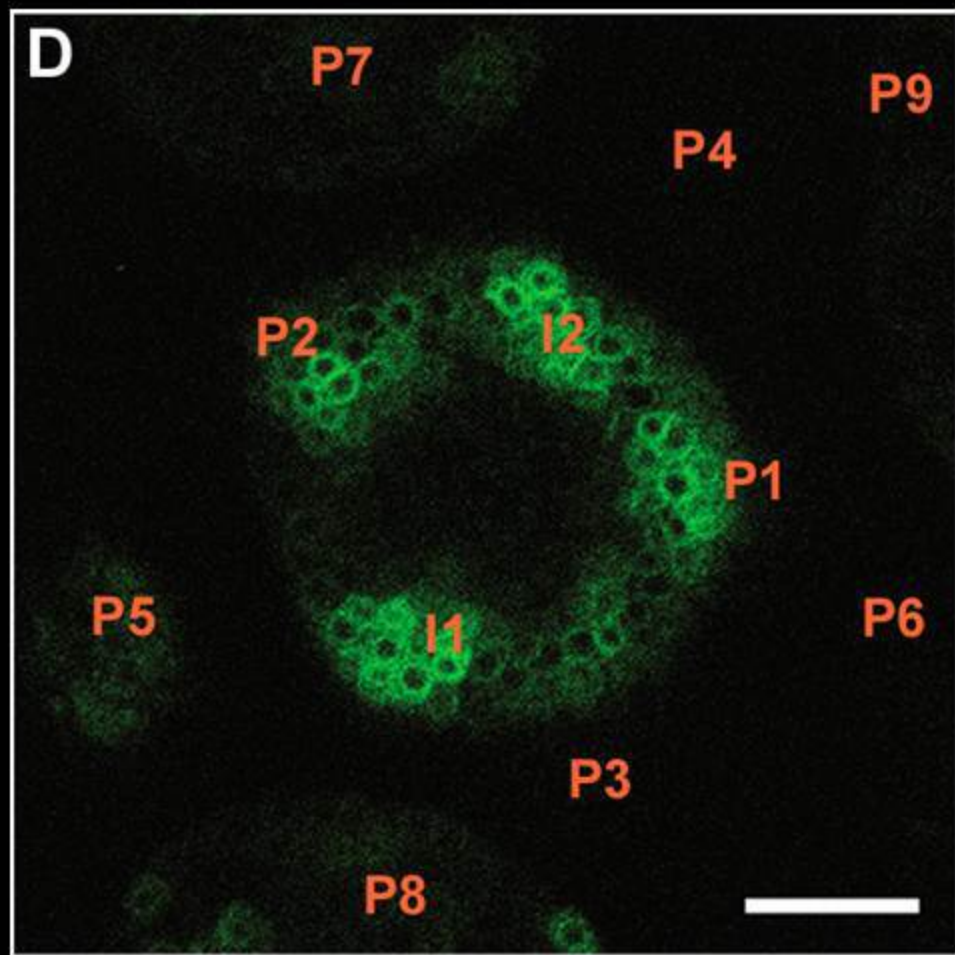
Computational models

Inhibitor

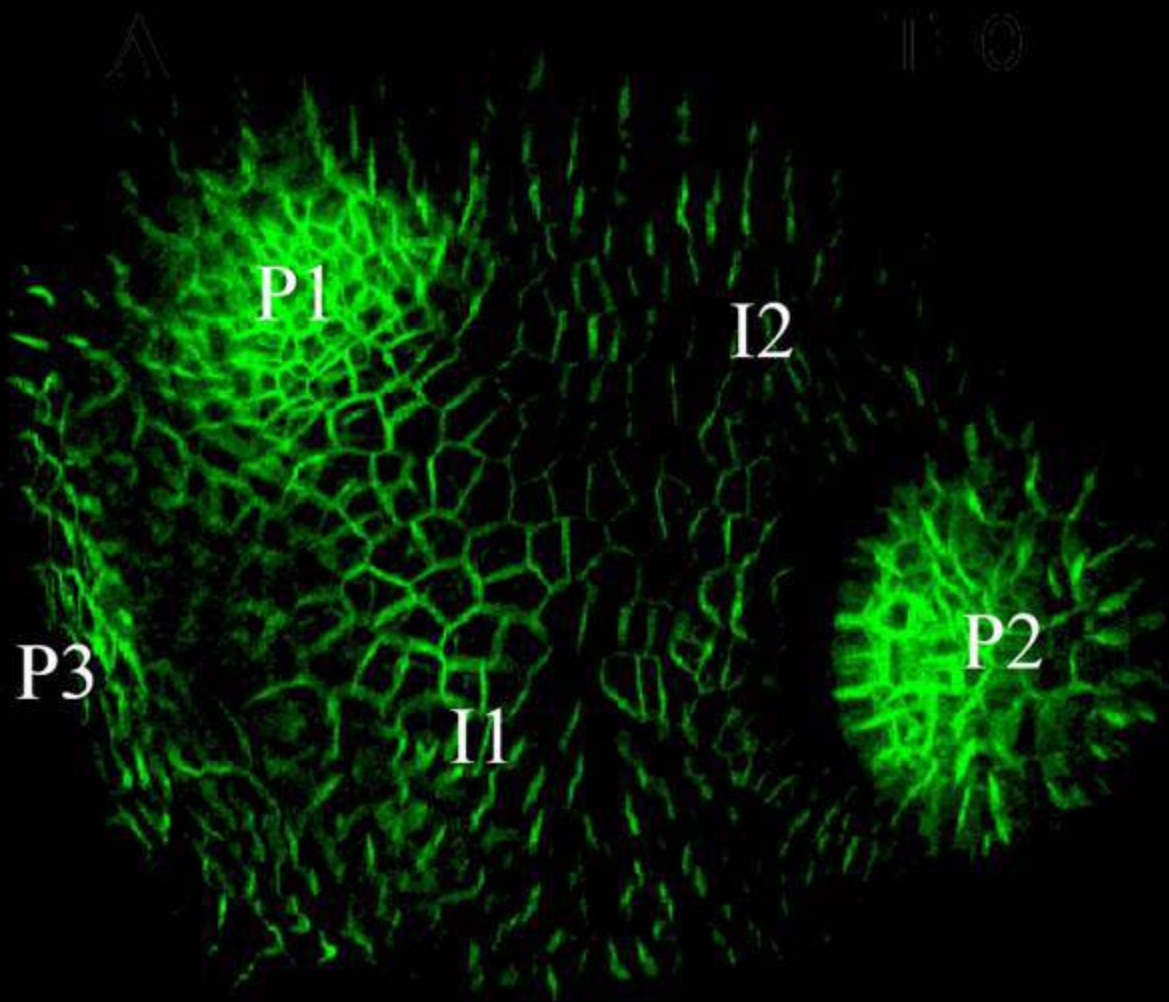
Activator

... but is it what Nature is doing?

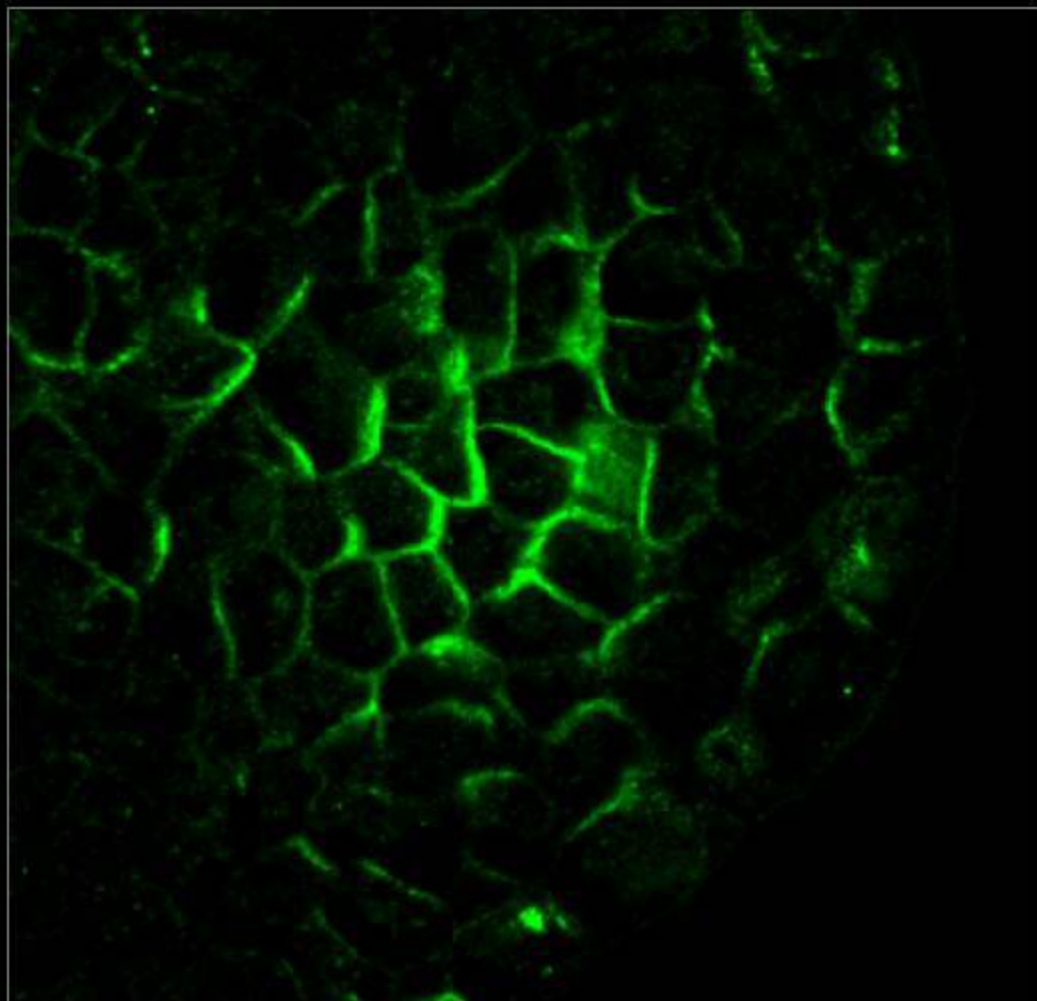
Auxin (reported using DR5::GFP) in the apex



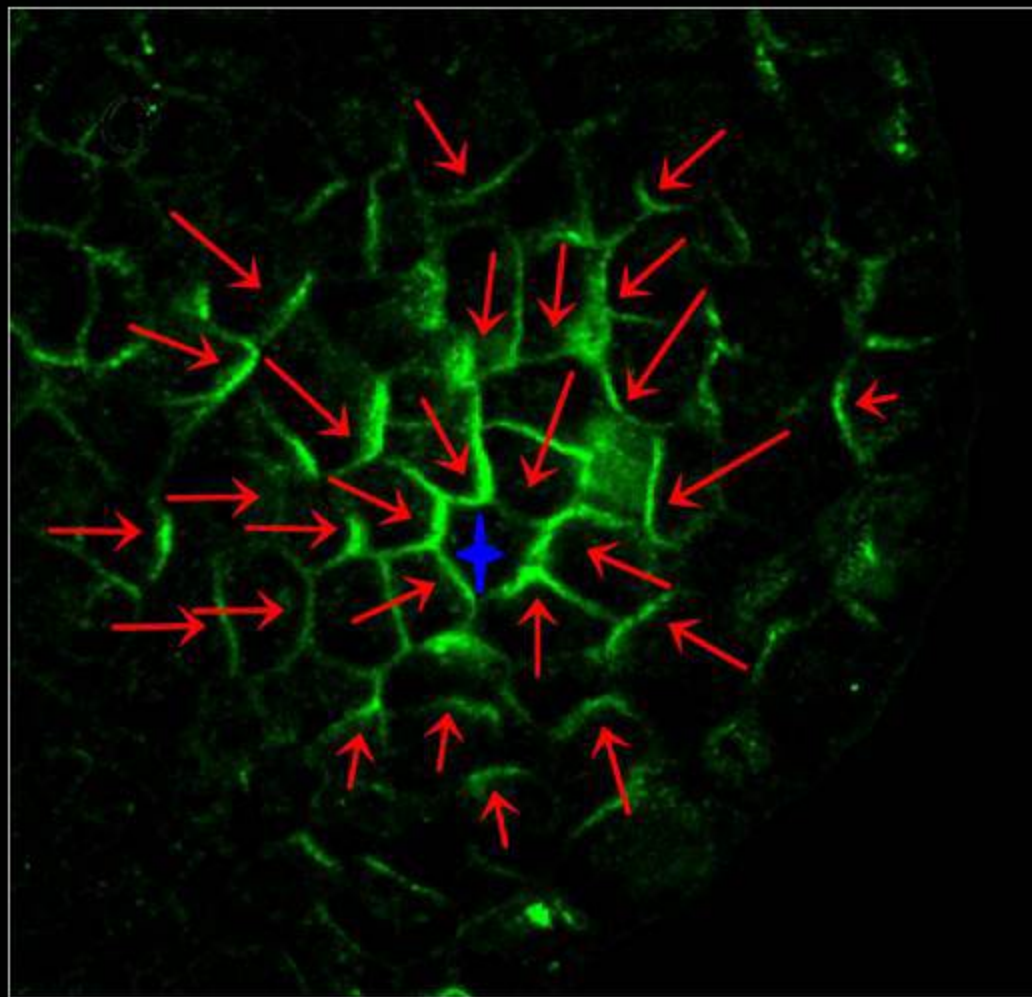
PIN::GFP localization in the apex



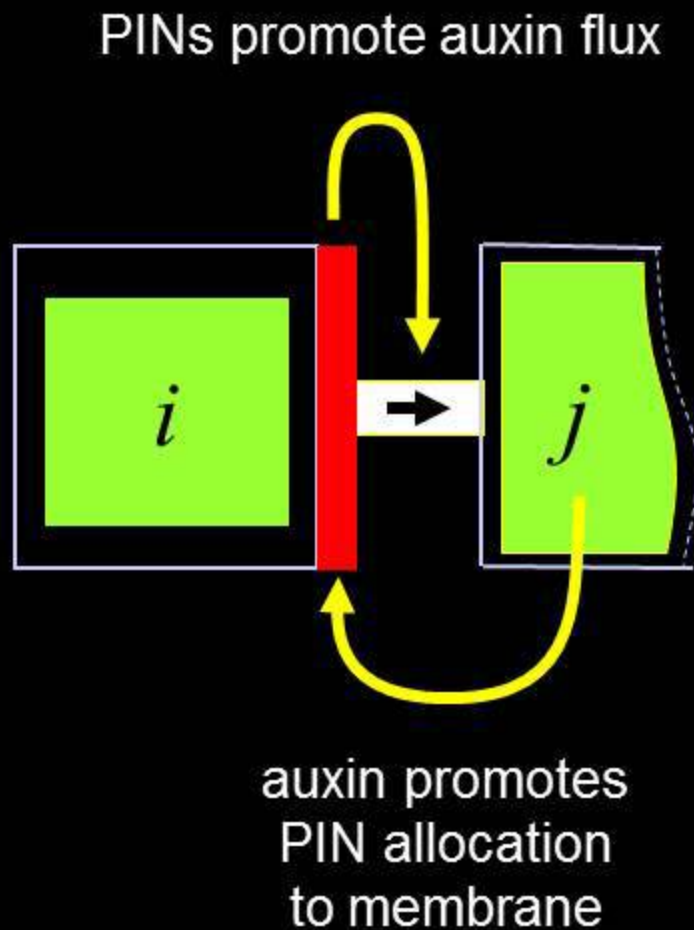
PIN::GFP localization near a primordium



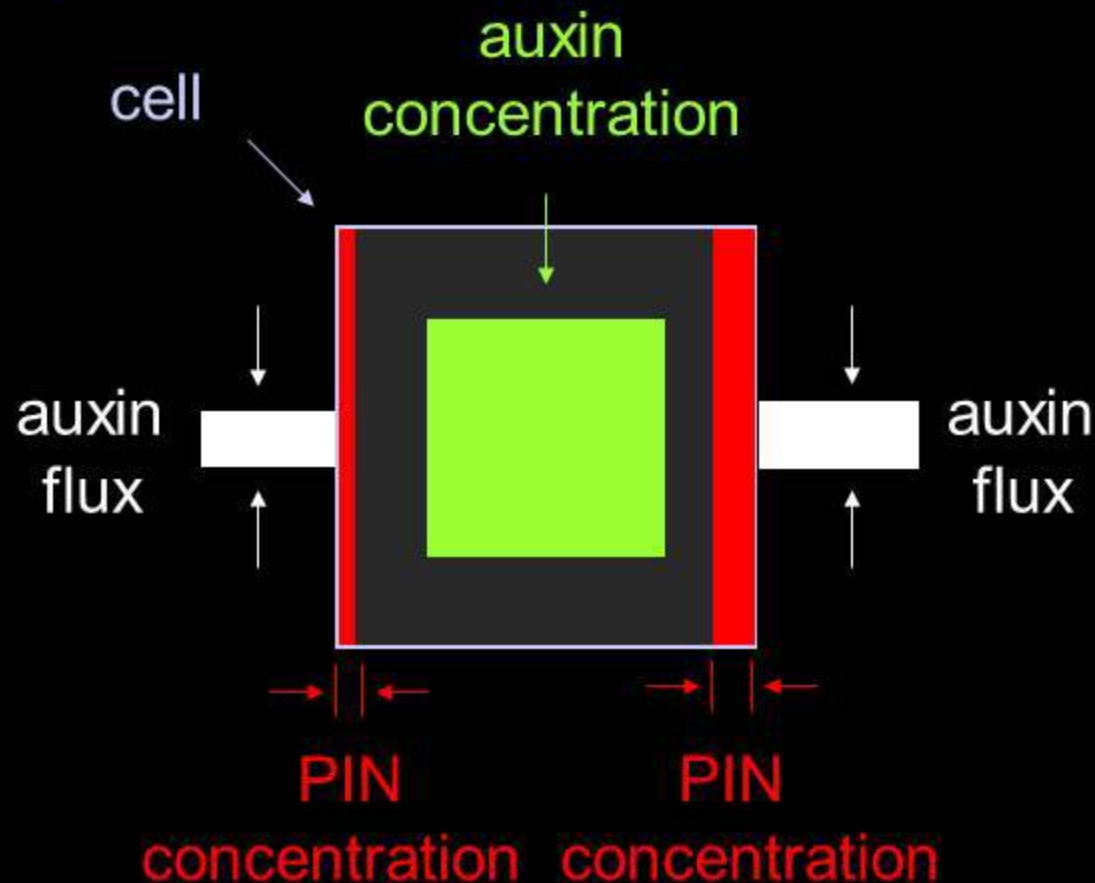
PIN::GFP localization near a primordium



Hypothesis: auxin controls its own transport

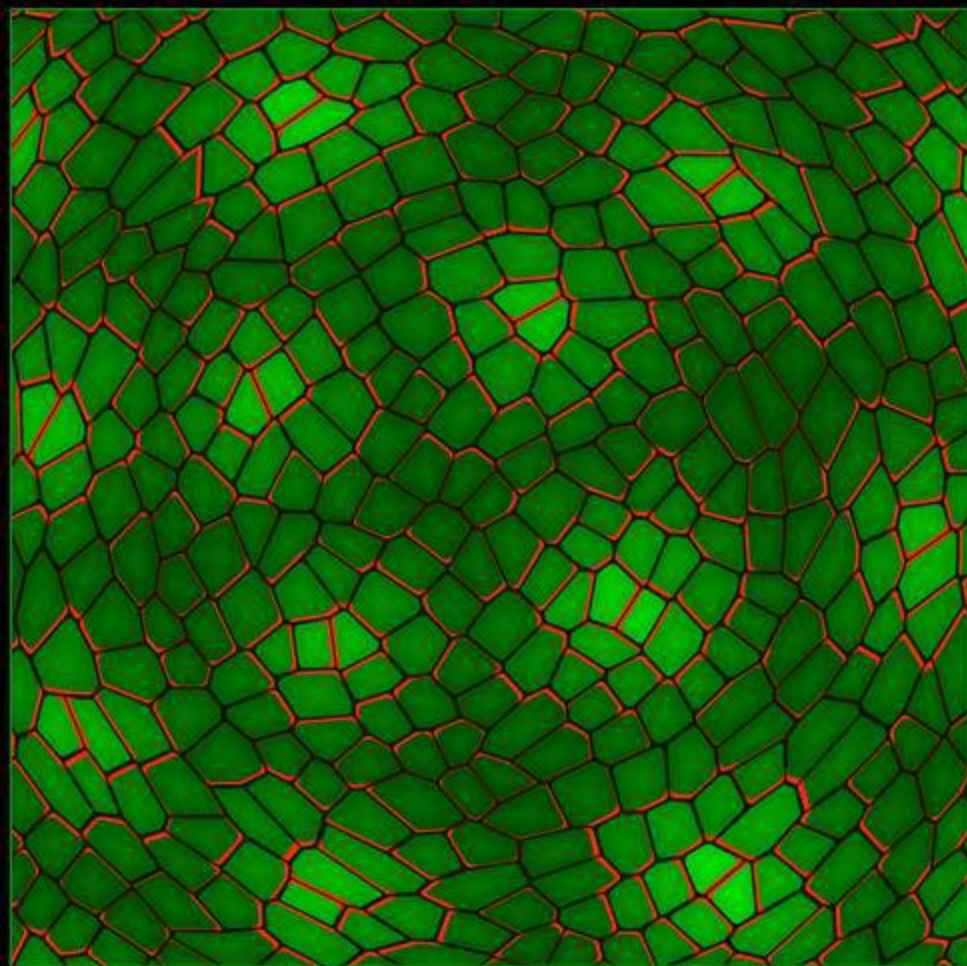


Pumping towards the highest concentration creates a pattern



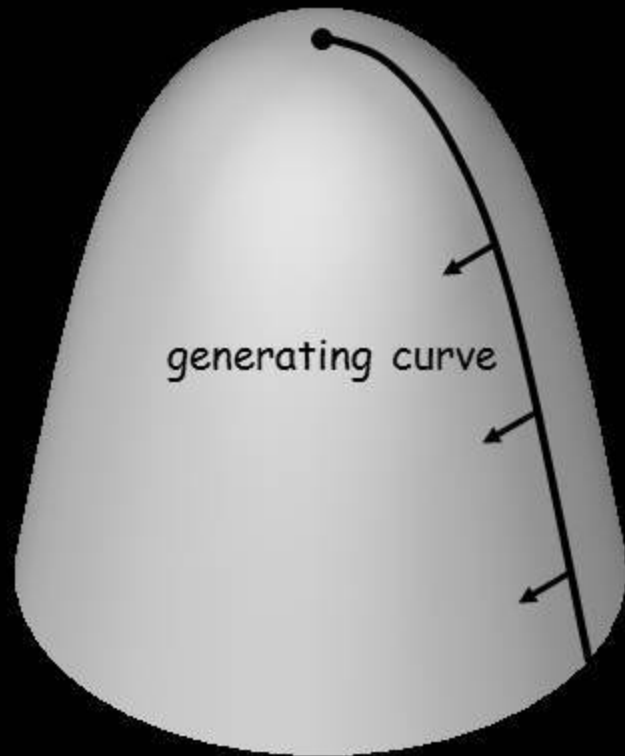
Simulation

Pumping towards the highest concentration creates a pattern



Auxin peaks on a plane of cells with **auxin** and **PIN** visualization

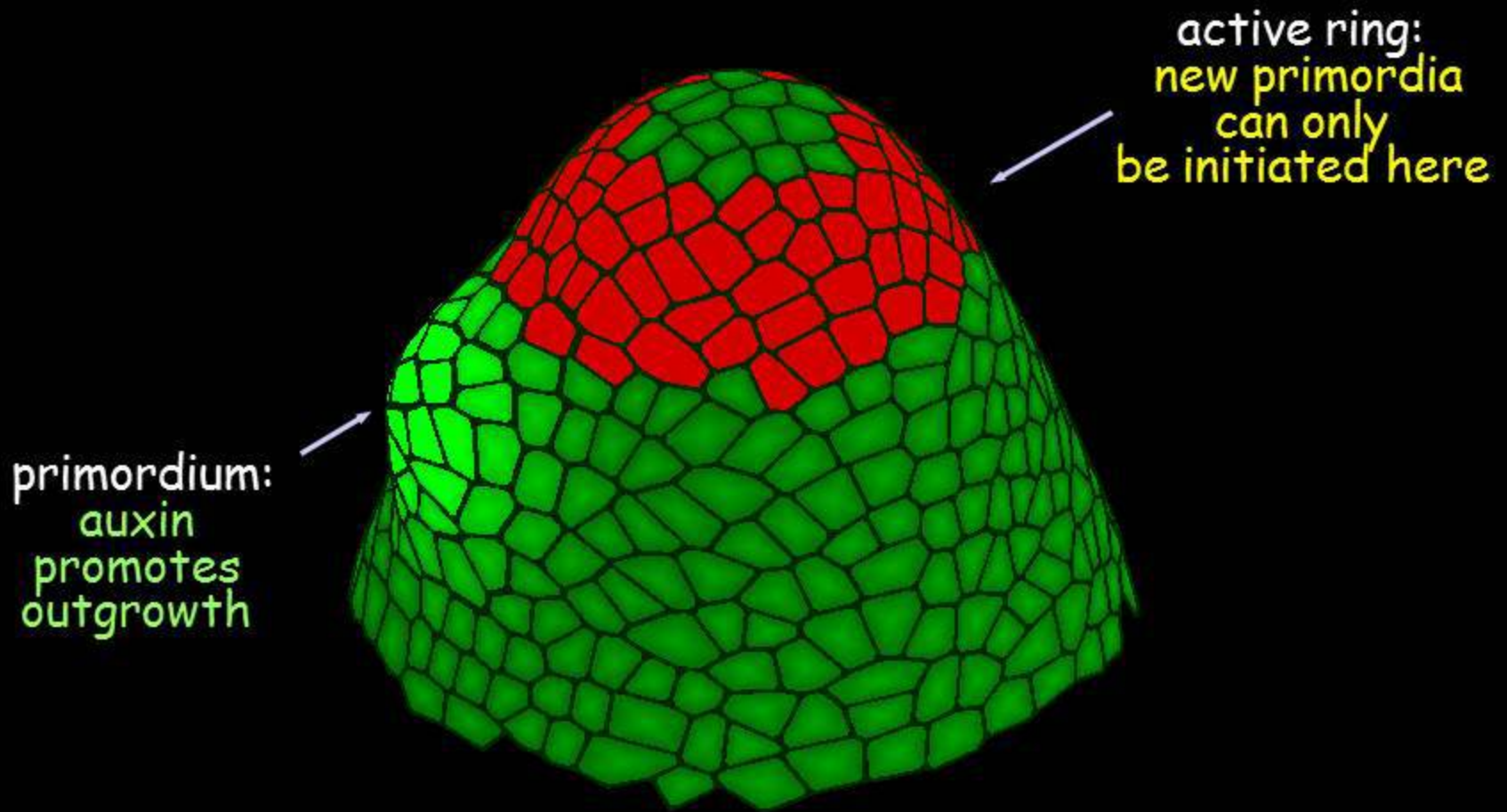
Modeling apex surface



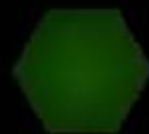
Simulation

- Surface of revolution made from a generating curve
- Apex shape can be changed by changing profile curve

The site of morphogenetic activities

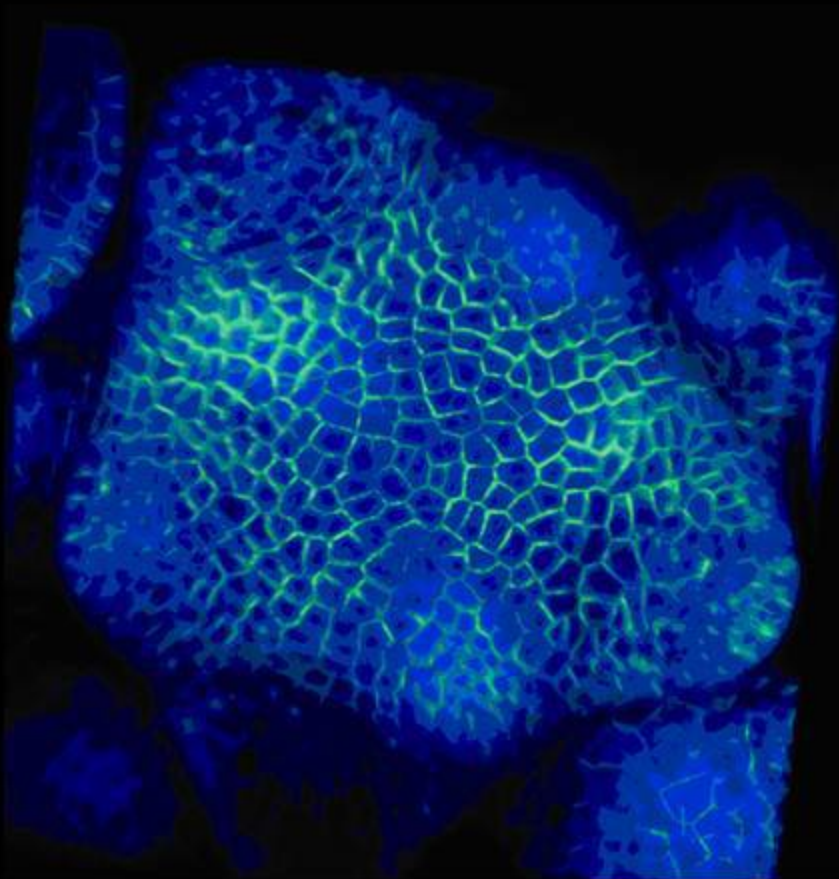


Simulation

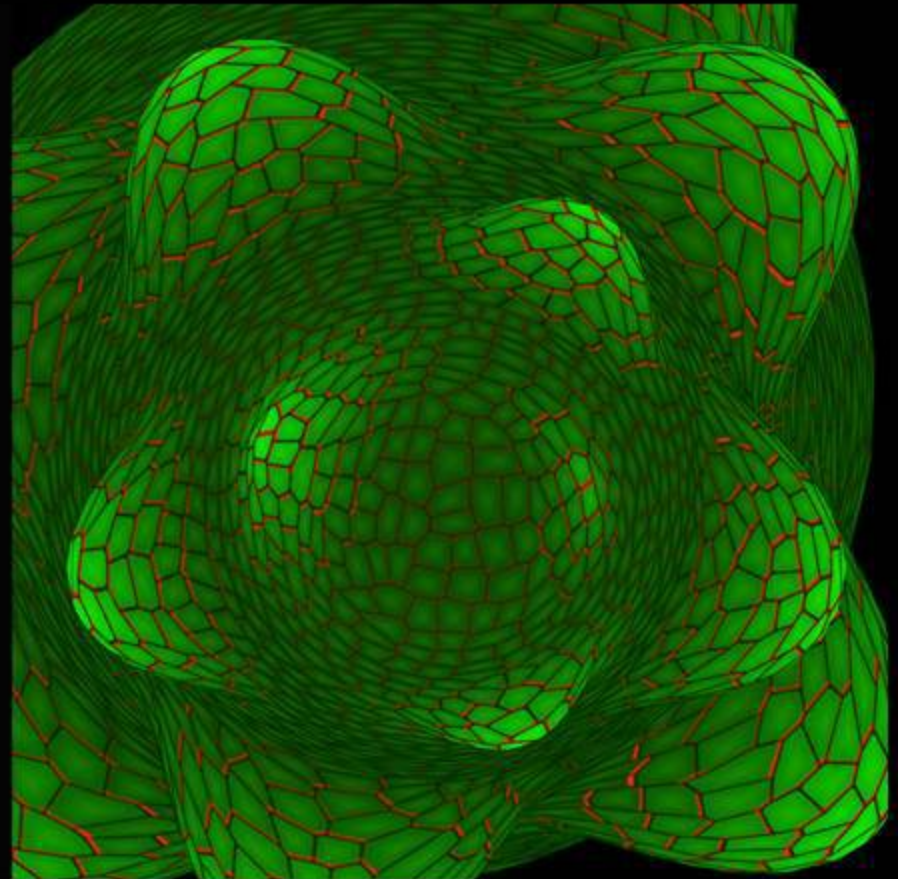


Model validation

Real and modeled apices look similar



Confocal microscopy image
courtesy of Marcus Heisler



Model

Real and modeled plants look similar, too



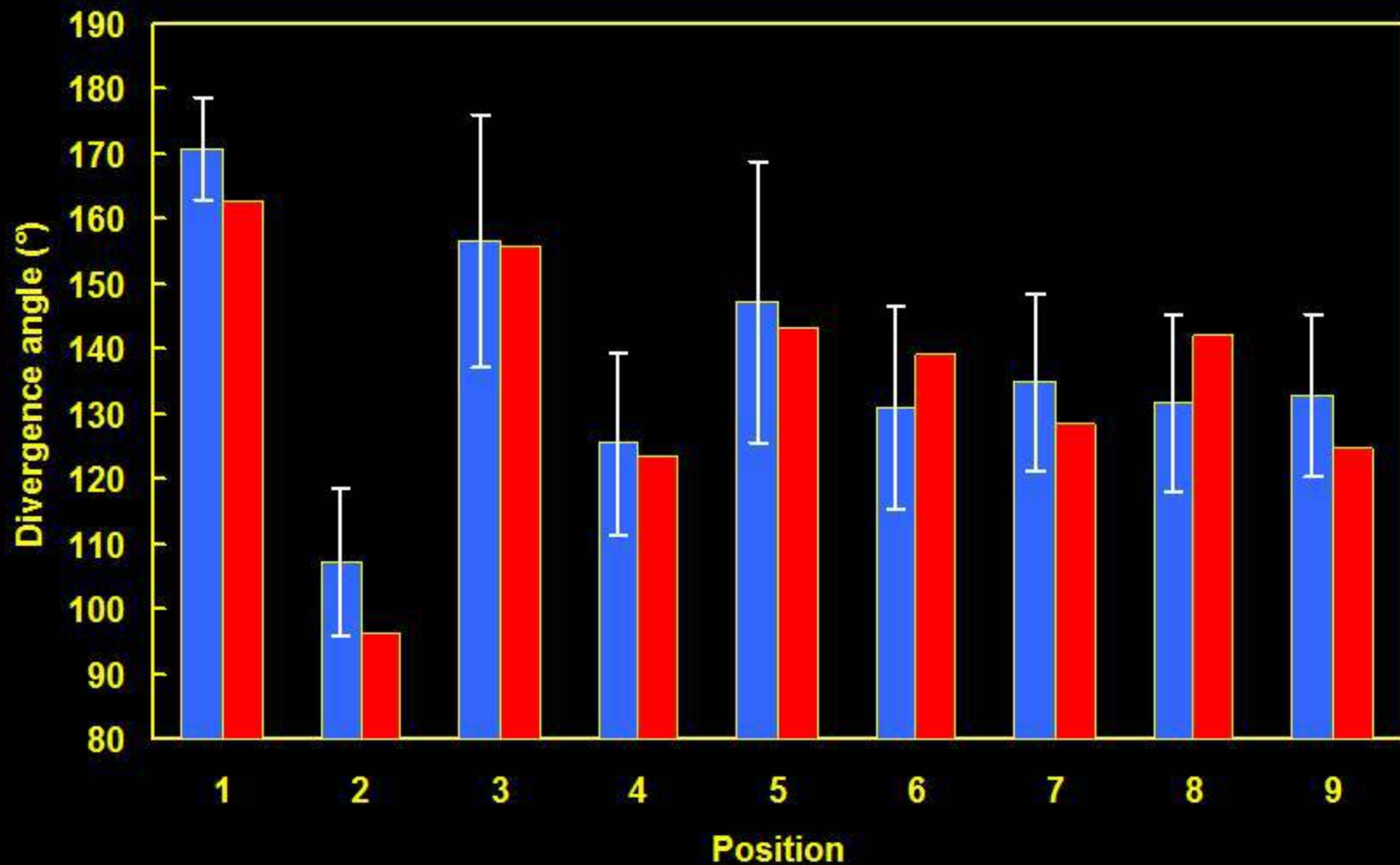
Real Arabidopsis



Model

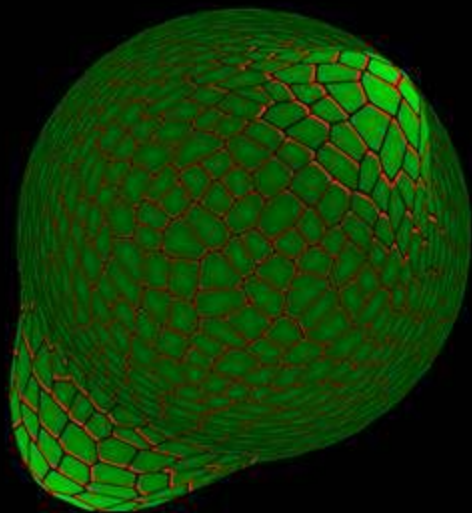
Model validation

Divergence angles are consistent with data

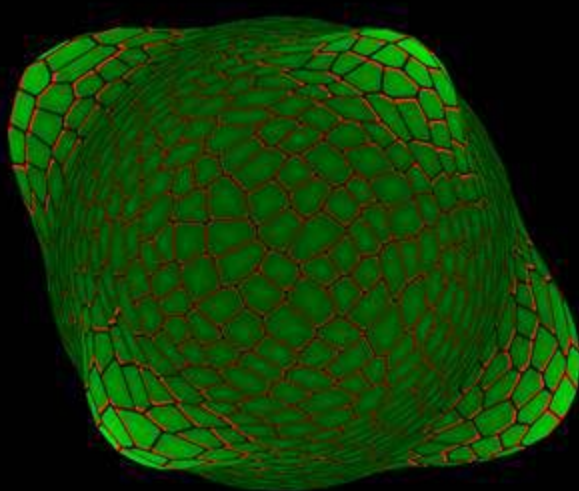


Model validation

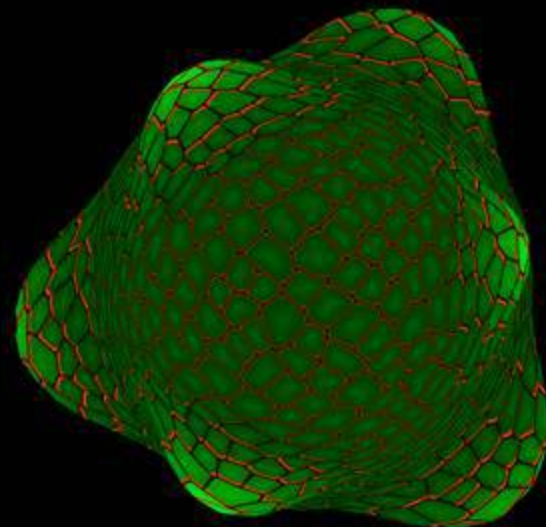
Alternative patterns can be generated



distichous

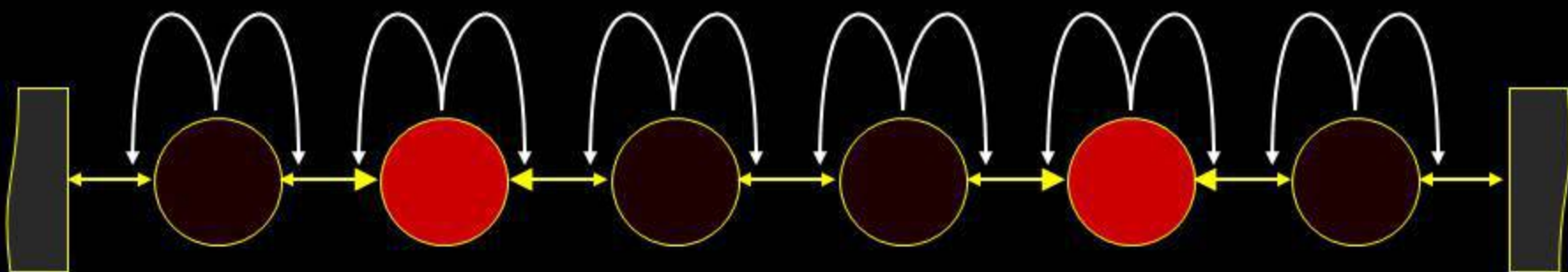


decussate



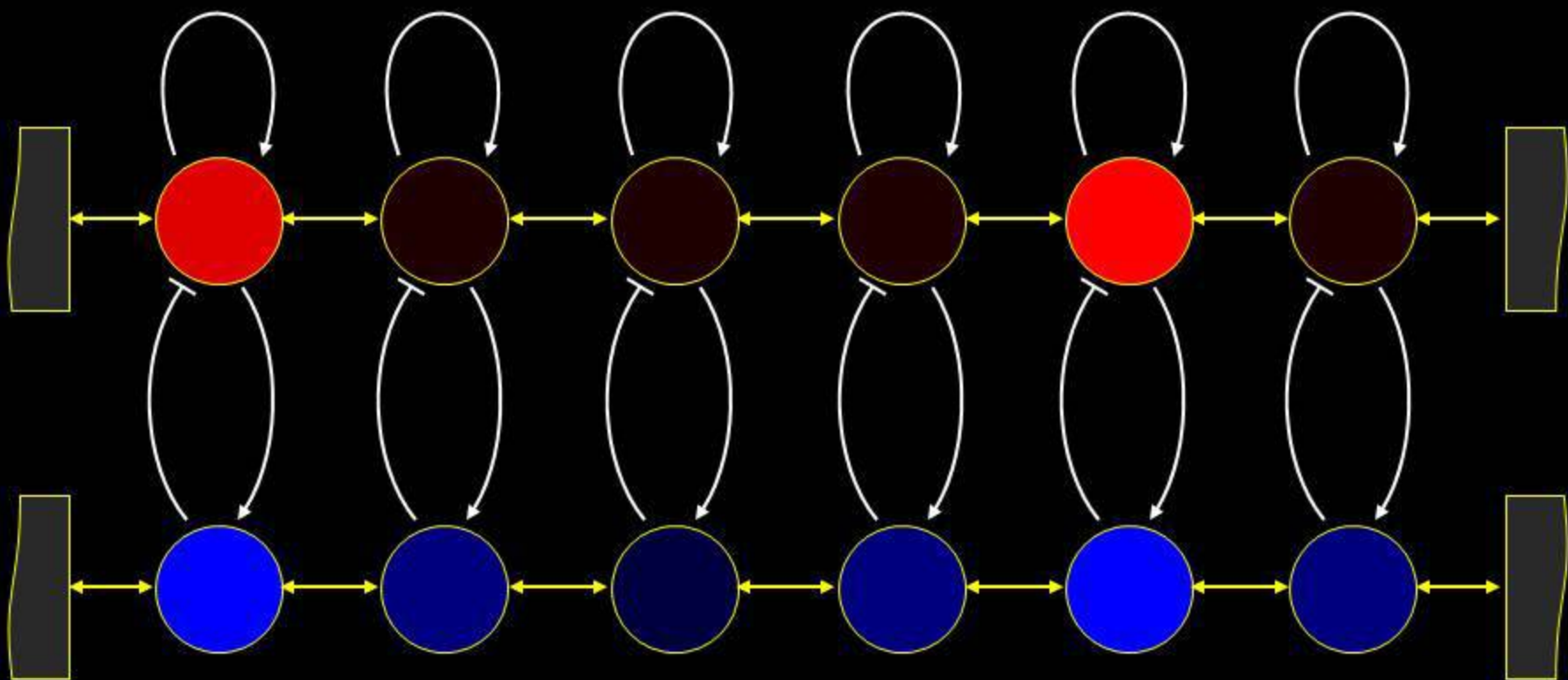
tricussate

But is this reaction-diffusion?



Is regulated transport a different paradigm of pattern formation, or a different implementation of reaction-diffusion?

“True” reaction-diffusion



Common paradigm: short-range activation and long-range inhibition?



Palubicki, Longay et al., ACM TOG 2009

Turing's legacy

- 1) Recognized that a fundamental problem in biology is to account for pattern and form.
- 2) Proposed reaction-diffusion as a fundamental pattern formation mechanism.
- 3) Recognized the role of self-organization in biological development.
- 4) Pioneered application of computational models.

"Most of an organism, most of the time, is developing from one pattern into another. One would like to be able to follow this process mathematically. The difficulties are, however, such that one cannot hope to have any very embracing theory of such processes, beyond the statement of equations. It might be possible, however, to treat particular cases in detail with the aid of digital computer".

Turing's impact

- Eclipsed by molecular genetics (Watson & Crick 1952)
- ~30 citations over the first 20 years.
- Considered irrelevant by mainstream biologists until 21st century.
- Current relevance: knowing genome is not enough
- Might Turing have been 50 years to soon?

Acknowledgments

Deborah Fowler	sea shell modeling
Hans Meinhardt,	(MPI, Tübingen)
Richard Smith	phyllotaxis modeling
Chris Kuhlemeier,	(University of Bern)
Brendan Lane	reaction-diffusion in 2D

The End