

# Plant Development: Genes, Mechanics, Cells

Meyerowitz Laboratory: SCAM  
(Soft Condensed Active Matter)

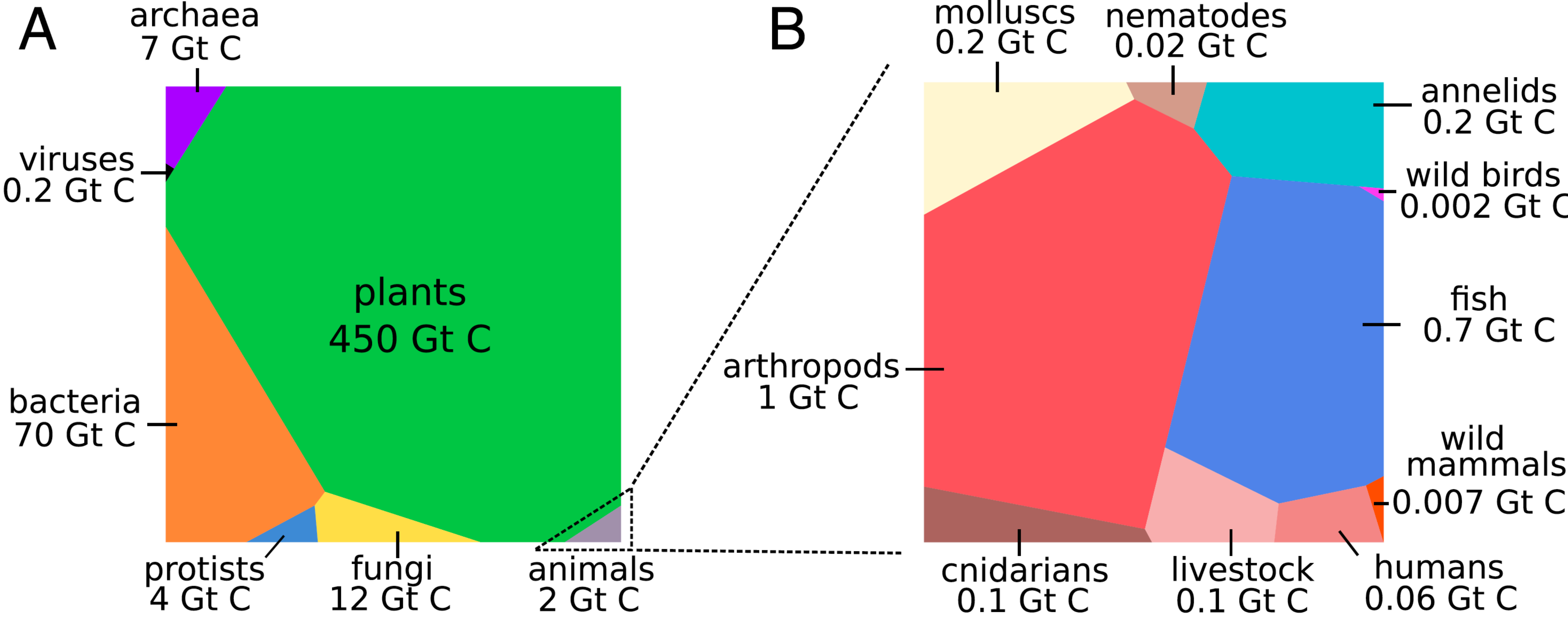


Caltech

hhmi

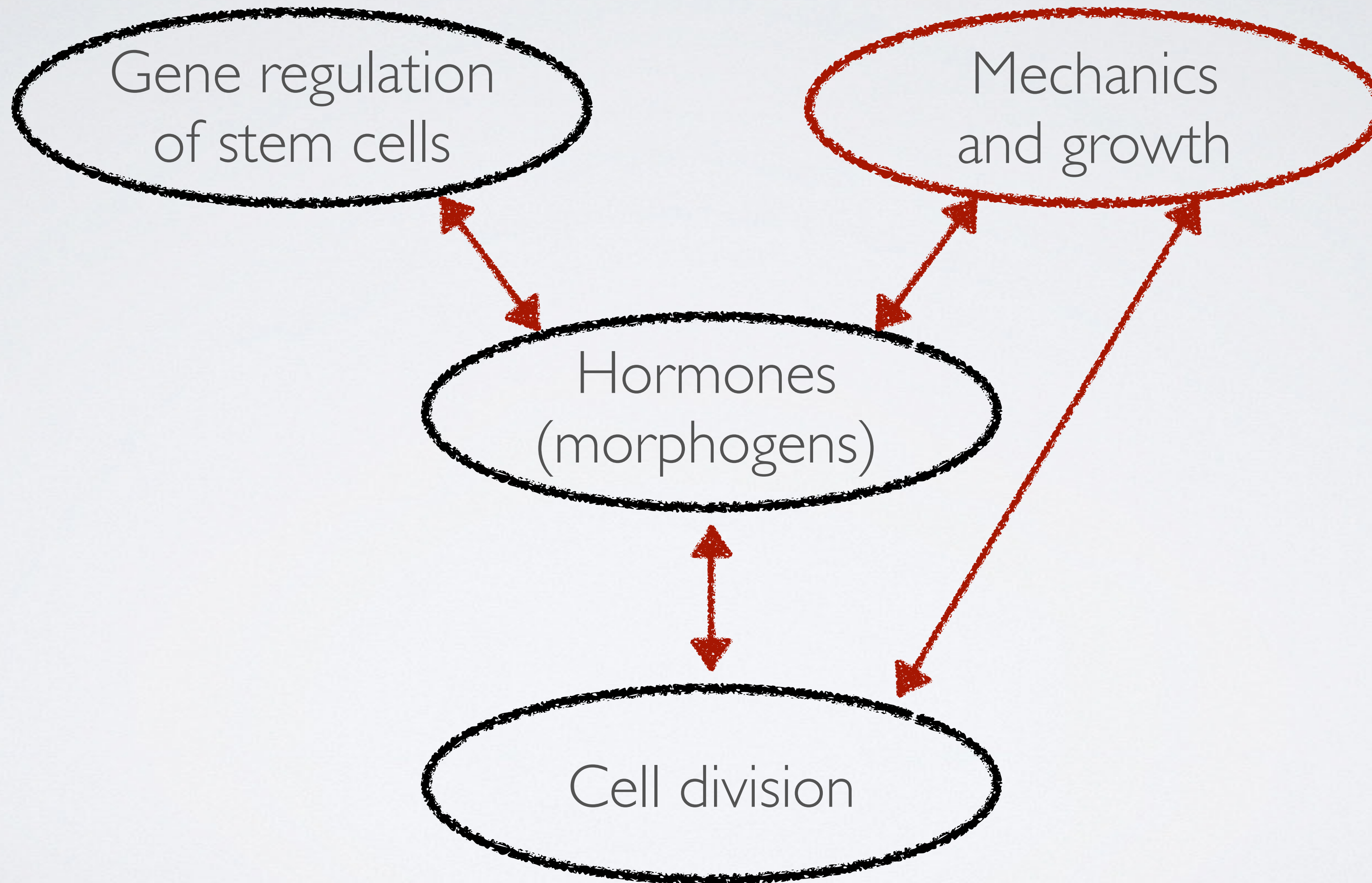


The sum of the biomass across all taxa on Earth is  $\approx 550$  Gt C, of which  $\approx 80\%$  ( $\approx 450$  Gt C) are plants, dominated by land plants (embryophytes). The second major component is bacteria ( $\approx 70$  Gt C), constituting  $\approx 15\%$  of the global biomass. Other groups, in descending order, are fungi, archaea, protists, animals, and viruses, which together account for the remaining  $< 10\%$ .



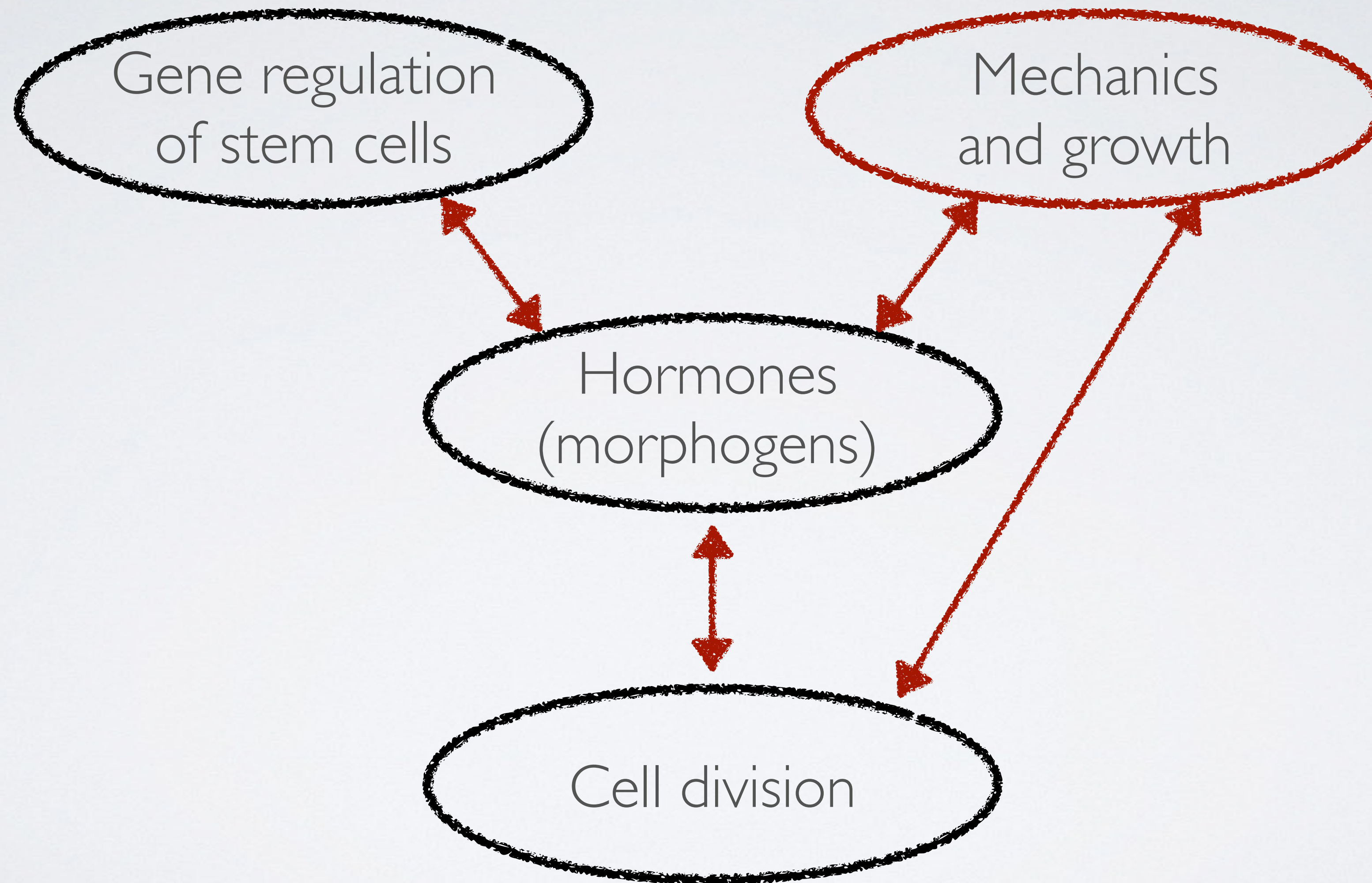


# How to generate shape





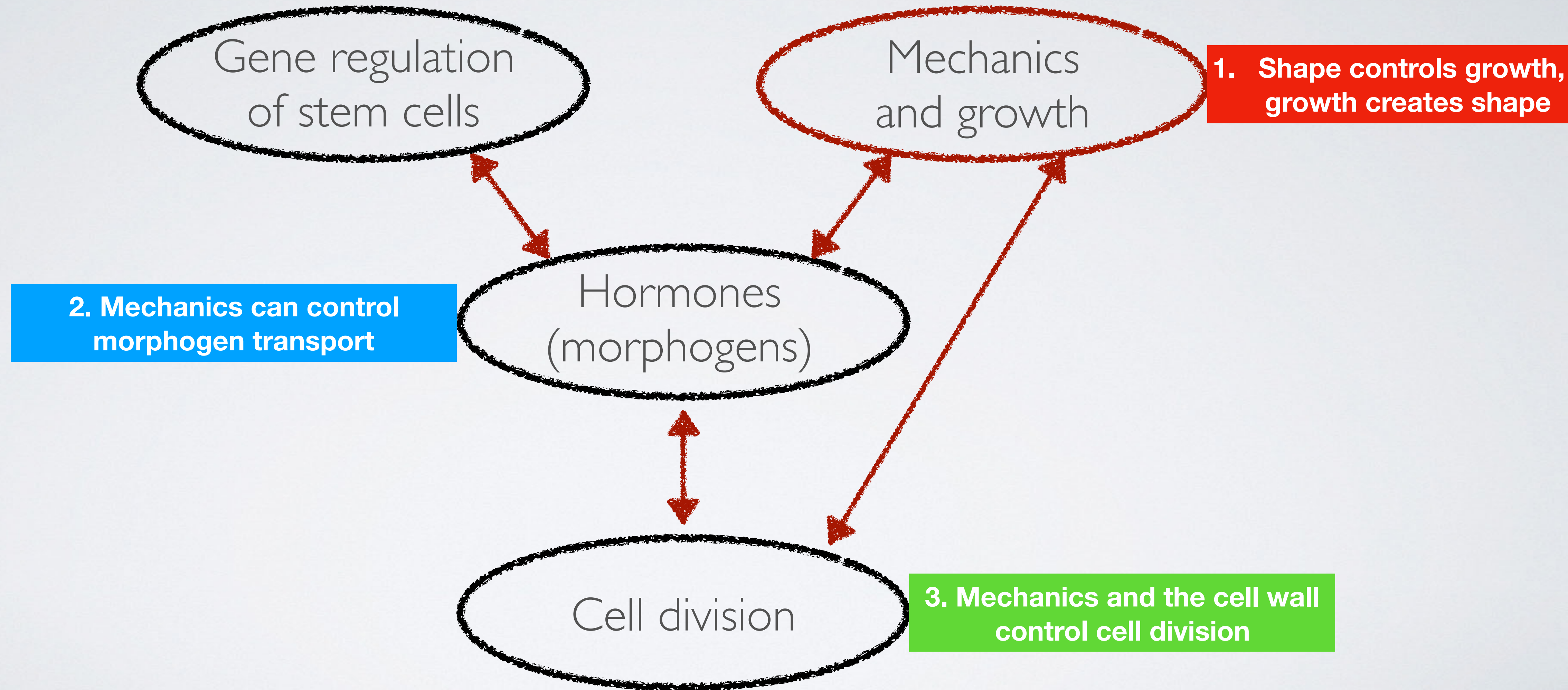
# COMPUTATIONAL MORPHODYNAMICS





# COMPUTATIONAL MORPHODYNAMICS

0. Introduction to plant growth (brief)





*Arabidopsis thaliana*





Fig. 35-2

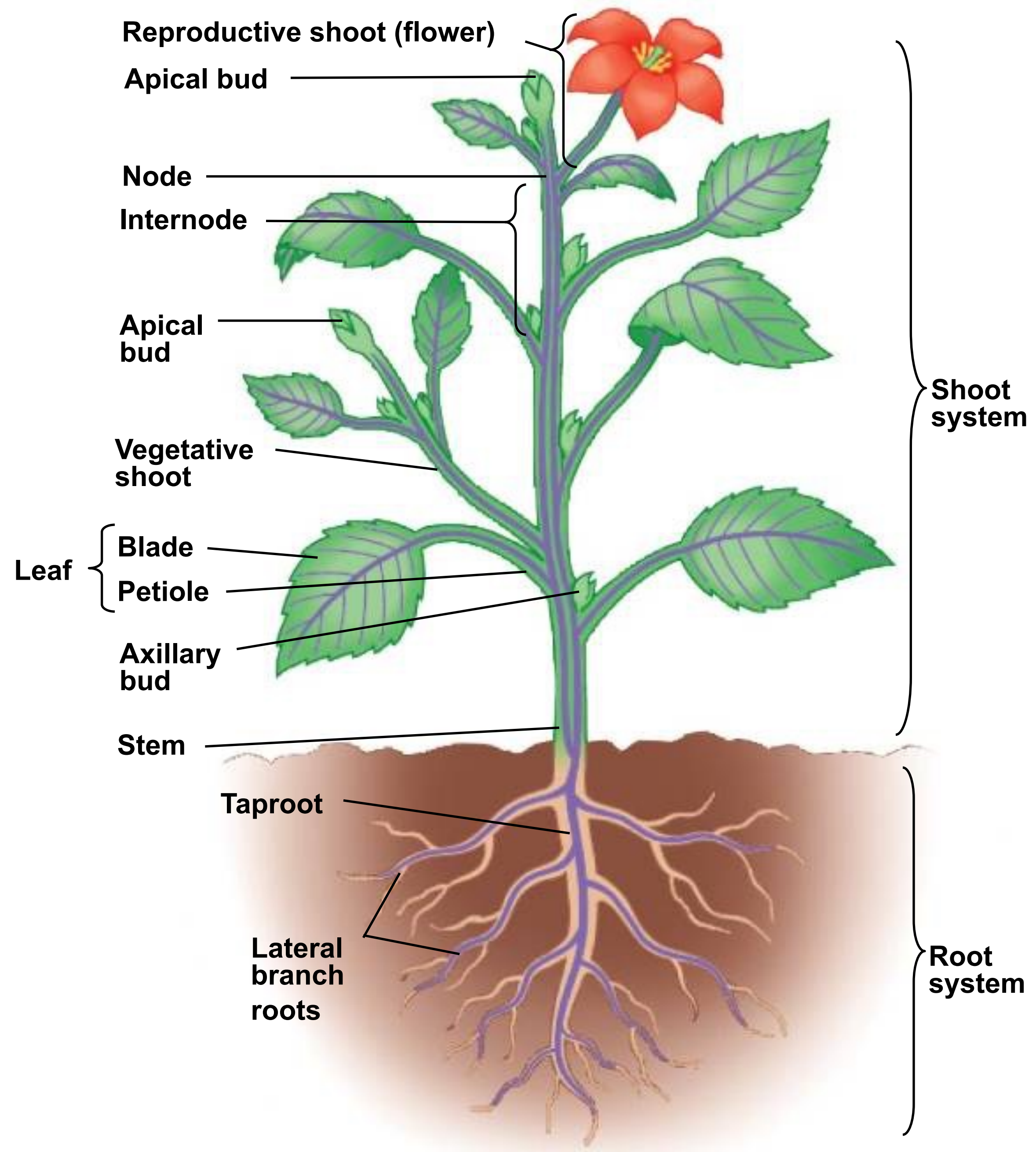


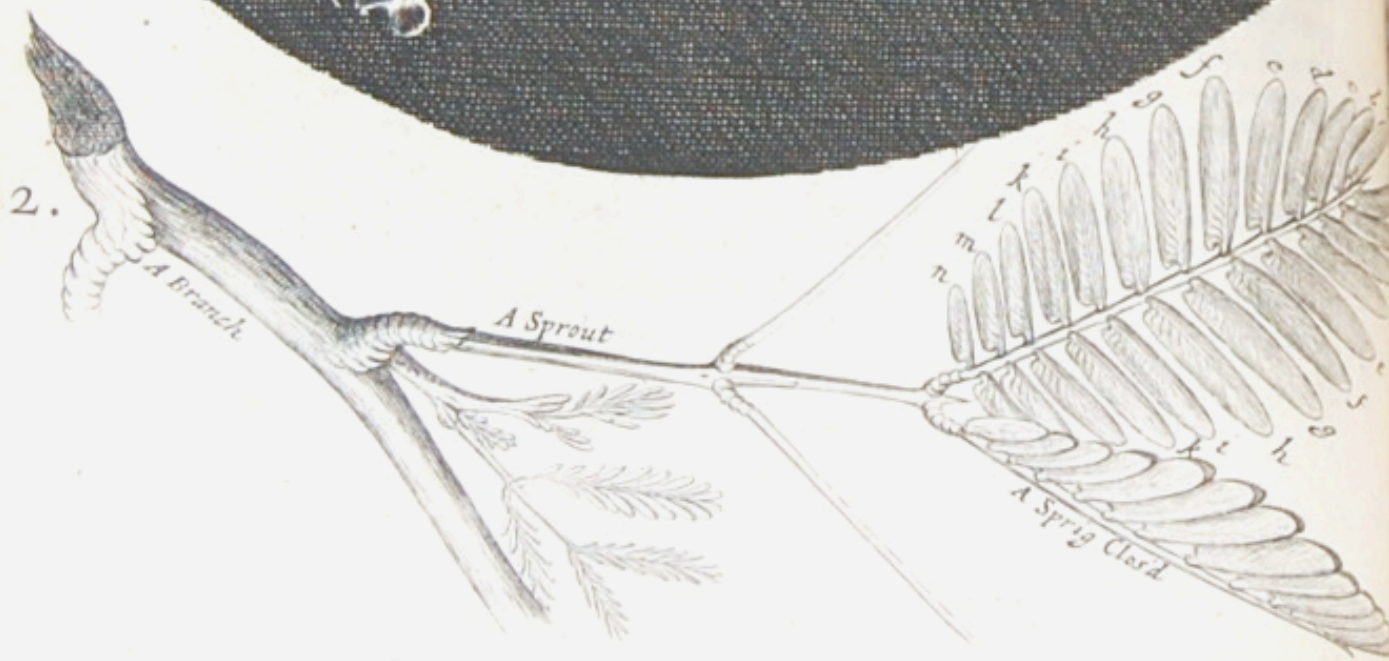


Fig: 1.

Schematiz



Fig: 2.



of other Vegetables to do to their bulk. But of these pores I have said more elsewhere.

To proceed then; Cork seems to be by the transverse constitution of the pores; a kind of *Fungus* or *Mushrome*, for the pores lie like so many Rays tending from the center, or pith of the tree, outwards; so that if you cut off a piece from a board of Cork transversly, to the flat of it; you will, as it were, split the pores, and they will appear just as they are expres'd in the Figure B of the XI. *Scheme*. But if you shave off a very thin piece from this board, parallel to the plain of it, you will cut all the pores transversly, and they will appear almost as they are expres'd in the Figure A, save onely the solid *Interstitia* will not appear so thick as they are there represented.

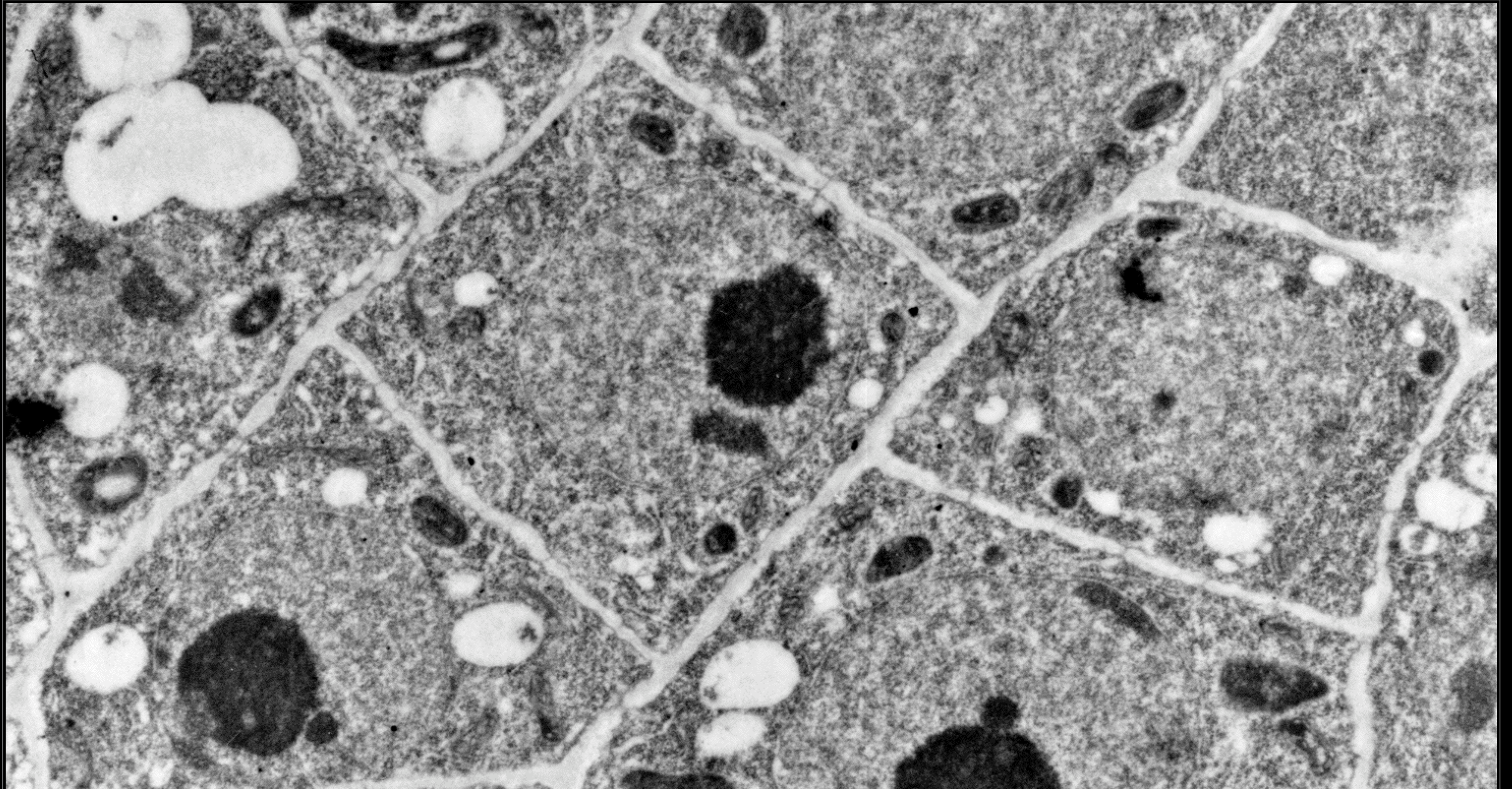
So that Cork seems to suck its nourishment from the subjacent bark of the Tree immediately, and to be a kind of excrescence, or a substance distinct from the substances of the entire Tree, something *analogus* to the *Mushrome*, or *Moss* on other Trees, or to the hairs on Animals. And having enquir'd into the History of Cork, I find it reckoned as an excrescency of the bark of a certain Tree, which is distinct from the two barks that lie within it, which are common also to other trees; That 'tis some time before the Cork that covers the young and tender sprouts comes to be discernable; That it cracks, flaws, and cleaves into many great chaps, the bark underneath remaining entire; That it may be separated and remov'd from the Tree, and yet the two under-barks (such as are also common to that with other Trees) not at all injur'd, but rather helped and freed from an external injury. Thus *Jonstonus* in *Dendrologia*; speaking *de Subere*, says, *Arbor est procerâ, Lignum est robustum, crascescens cortice in aquis non sinitat, Cortice in orbem detracto juvatur, crascescens enim prastringit & strangulat, intra triennium iterum repletur: Caudex ubi adolescit crassus, cortex superior densus carnosus, duos digitos crassus, scaber, rimosus, & qui nisi detrahatur debiscit, alioque subnascente expellitur, interior qui subest novellus ita rubet ut arbor minio picta videatur.* Which Histories, if well consider'd, and the tree, substance, and manner of growing, if well examin'd, would, I am very apt to believe, much confirm this my conjecture about the origination of Cork.

Nor is this kind of Texture peculiar to Cork onely; for upon examination with my *Microscope*, I have found that the pith of an Elder, or almost any other Tree, the inner pulp or pith of the Cane hollow stalks of several other Vegetables: as of Fennel, Carrets, Daucus, Bur-docks, Teasels, Fearn, some kinds of Reeds, &c. have much such a kind of *Schematizine*, as I have lately shewn that of Cork, save onely that here the pores are rang'd the long-ways, or the same ways with the length of the Cane, whereas in Cork they are transvers.

The pith also that fills that part of the stalk of a Feather that is above the Quil, has much such a kind of texture, save onely that which way soever I set this light substance, the pores seem'd to be cut transversly; so that I ghes this pith which fills the Feather, not to consist of abundance of long pores separated with *Diaphragms*, as Cork does, but to be a kind

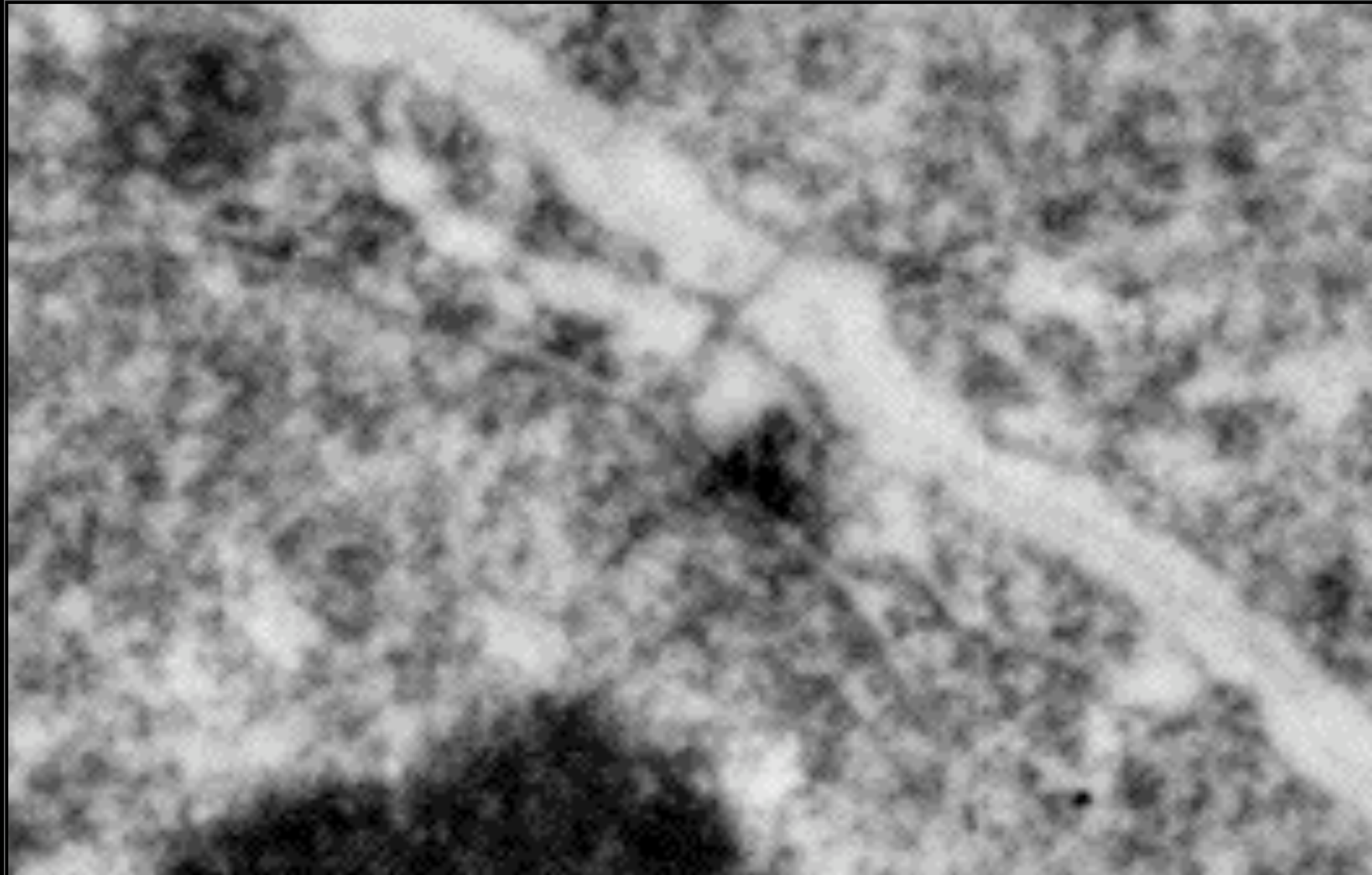


# Cell Walls, Turgor Pressure, Absence of Movement





# Cells are Connected





# Anatomy of the Plant Cell

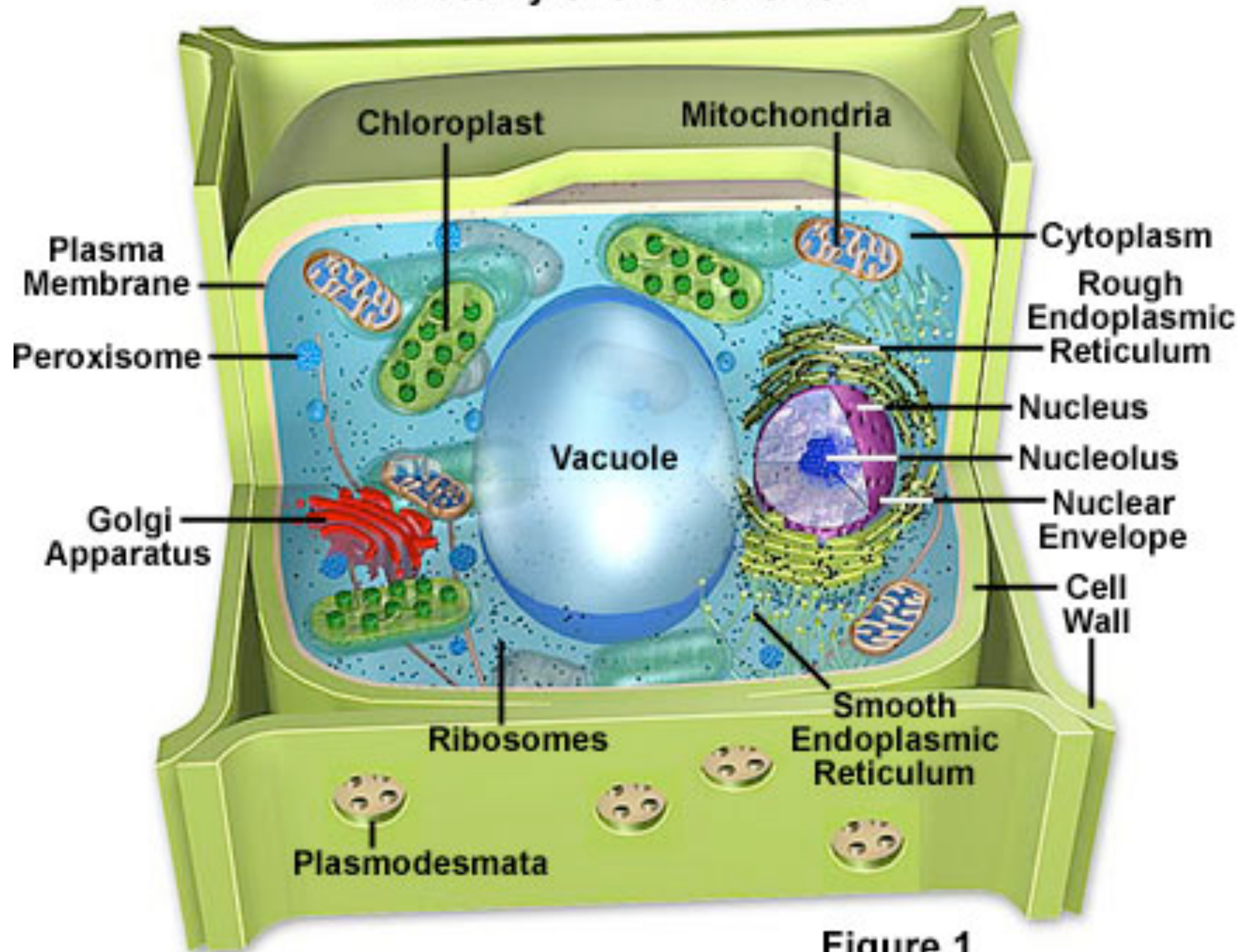
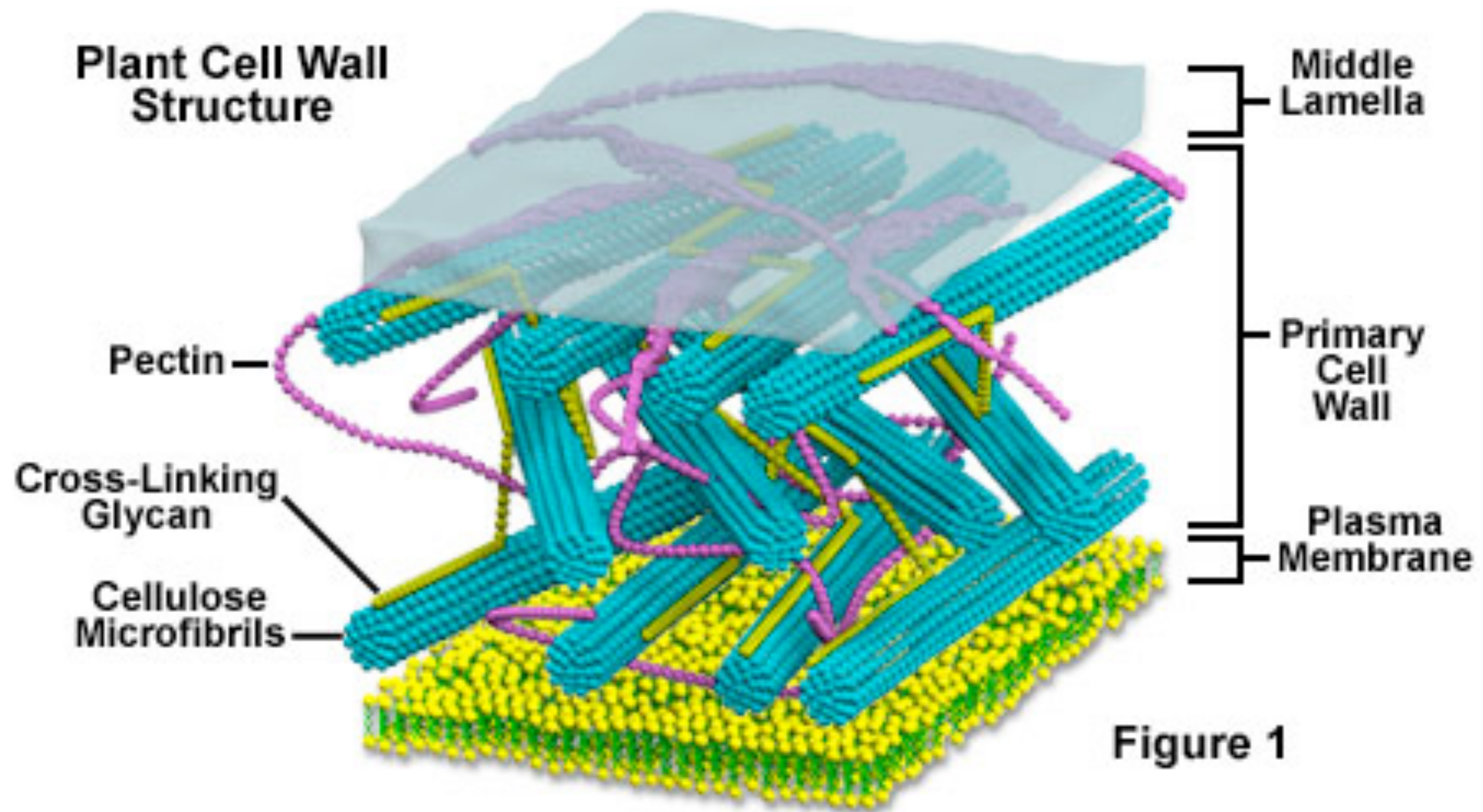


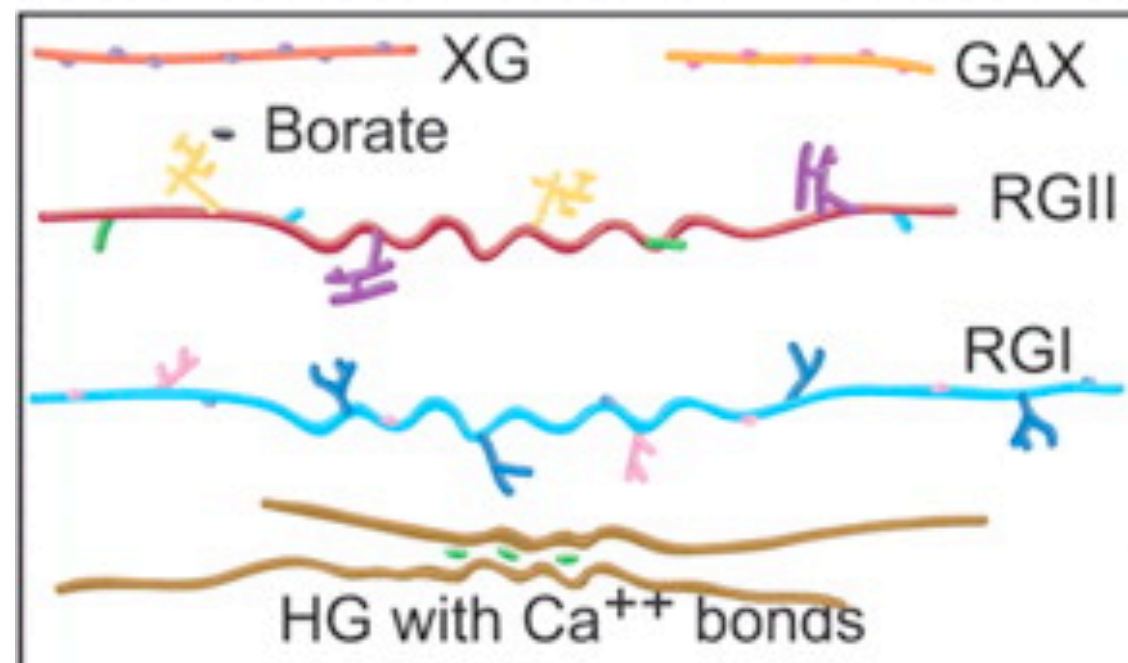
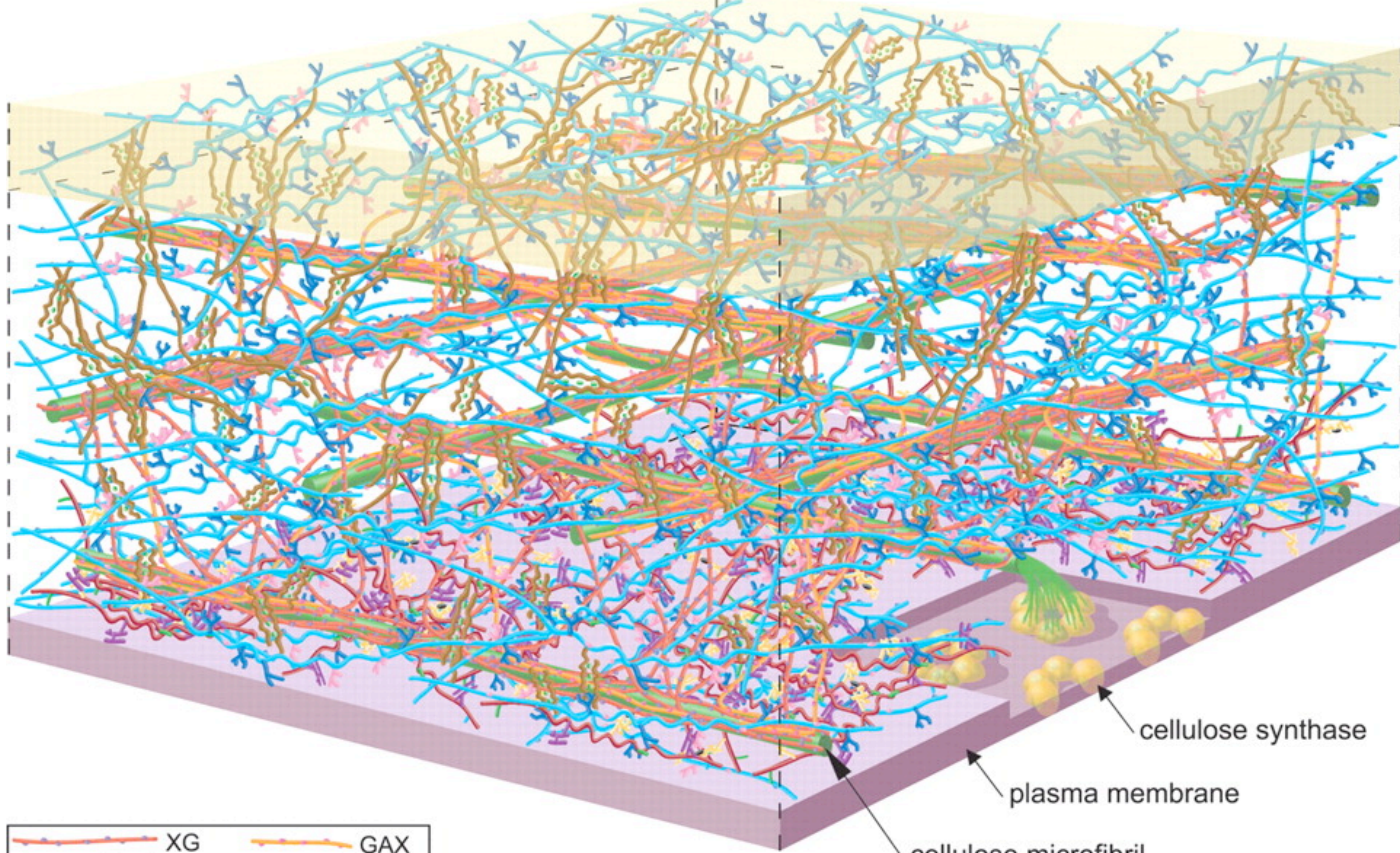
Figure 1





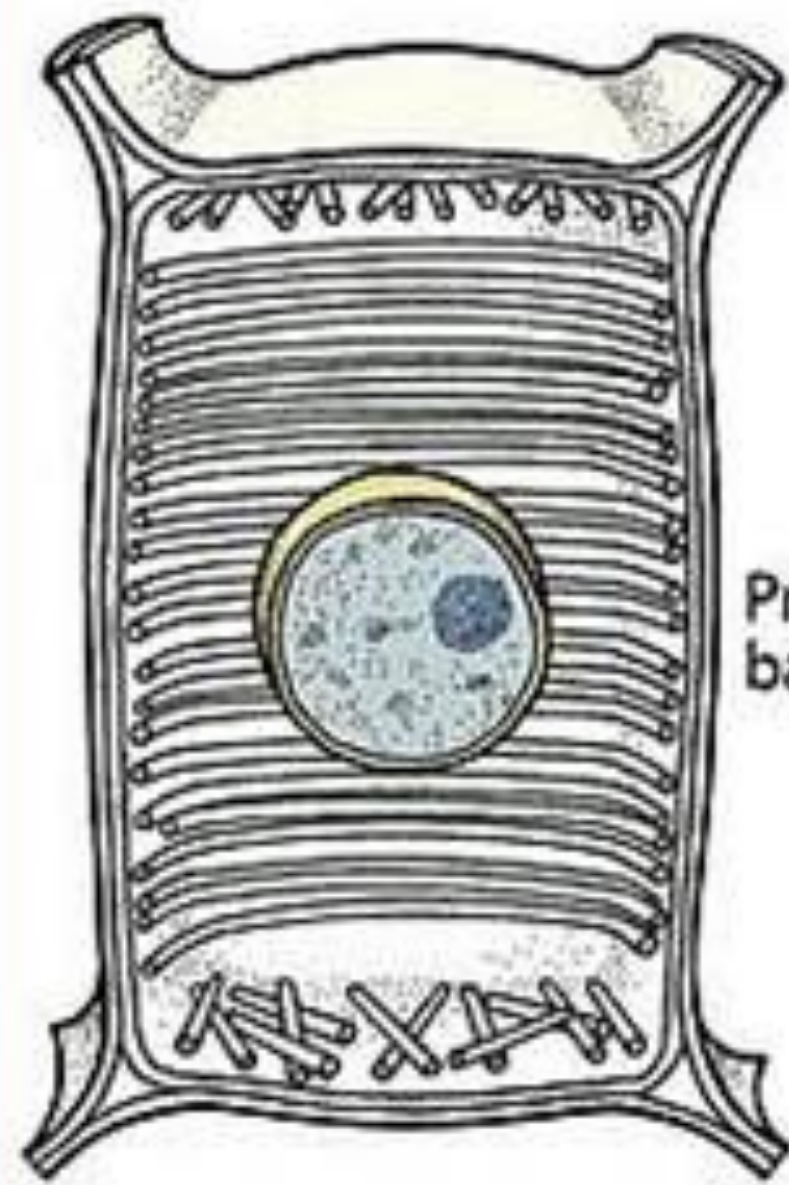
**Figure 1**





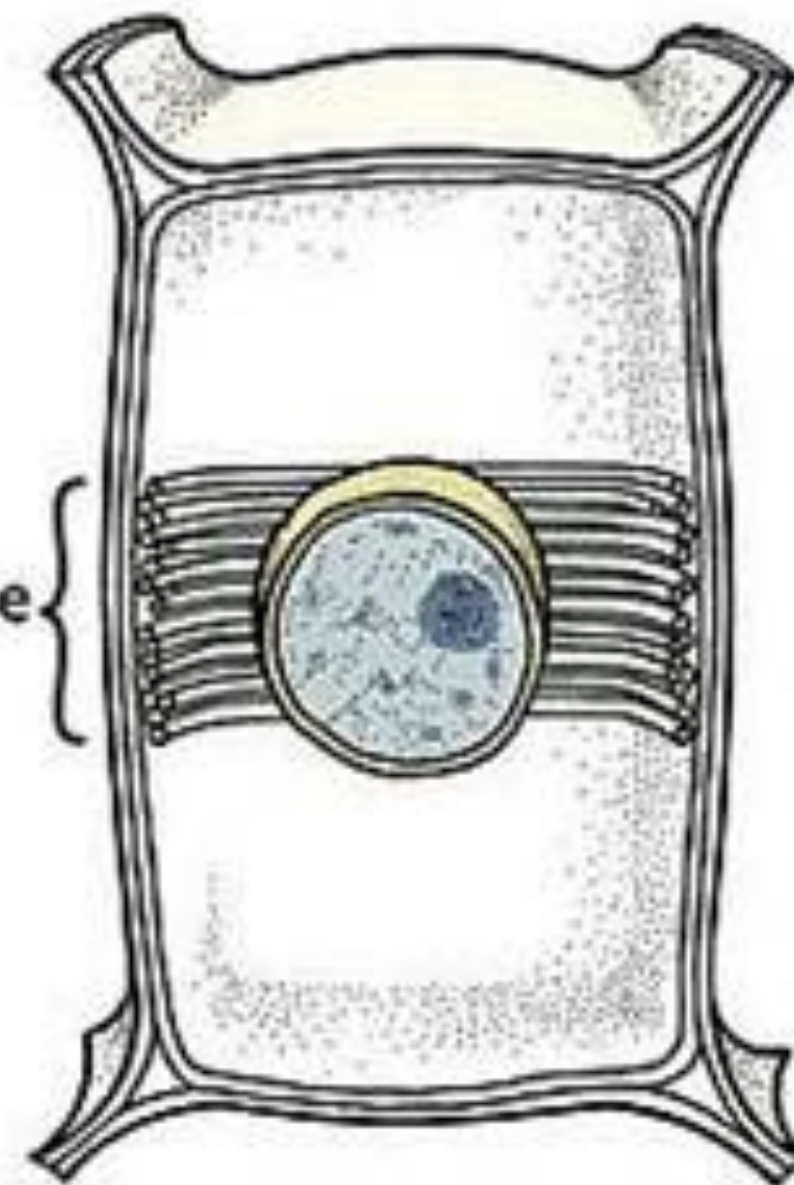
Somerville C, Bauer S, Brininstool G, Facette M, Hamann T, Milne J, Osborne E, Paredes A, Persson S, Raab T, Vorwerk S, Youngs H: Toward a systems approach to understanding plant cell walls. Science 2004, 306:2206-2211.



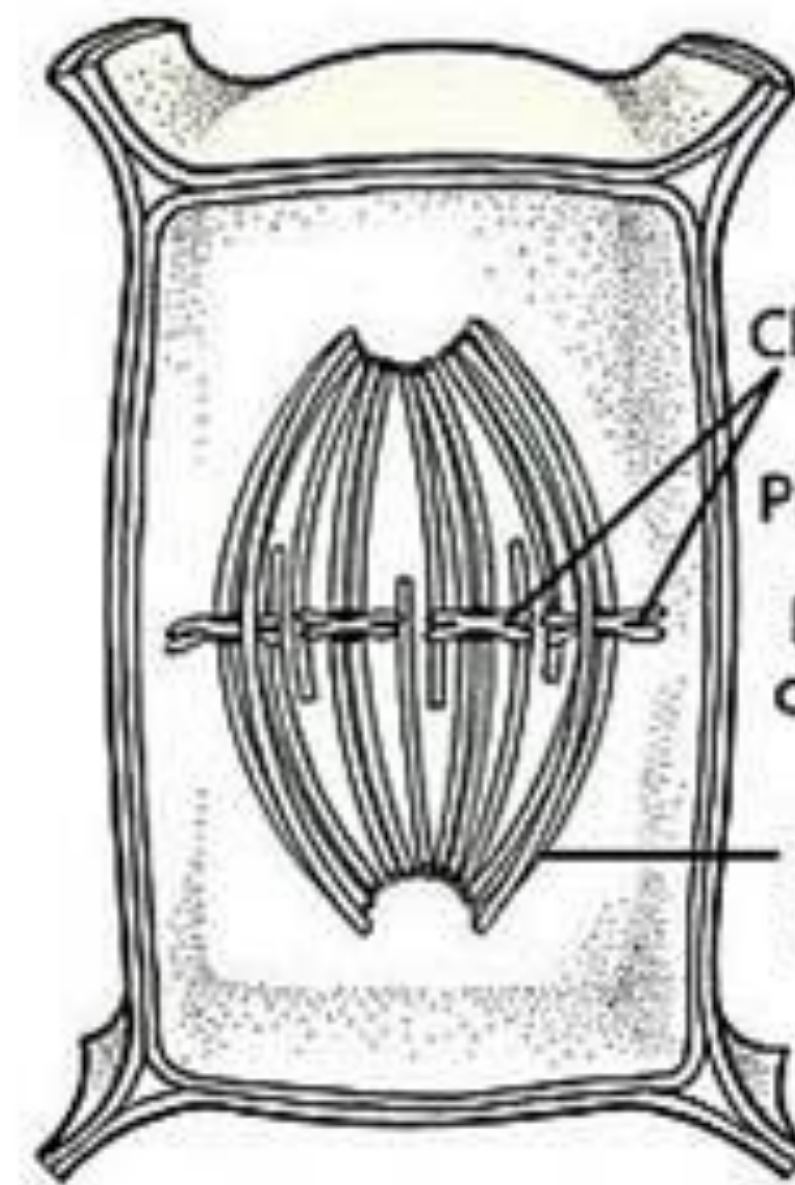


(a) Interphase

Preprophase band

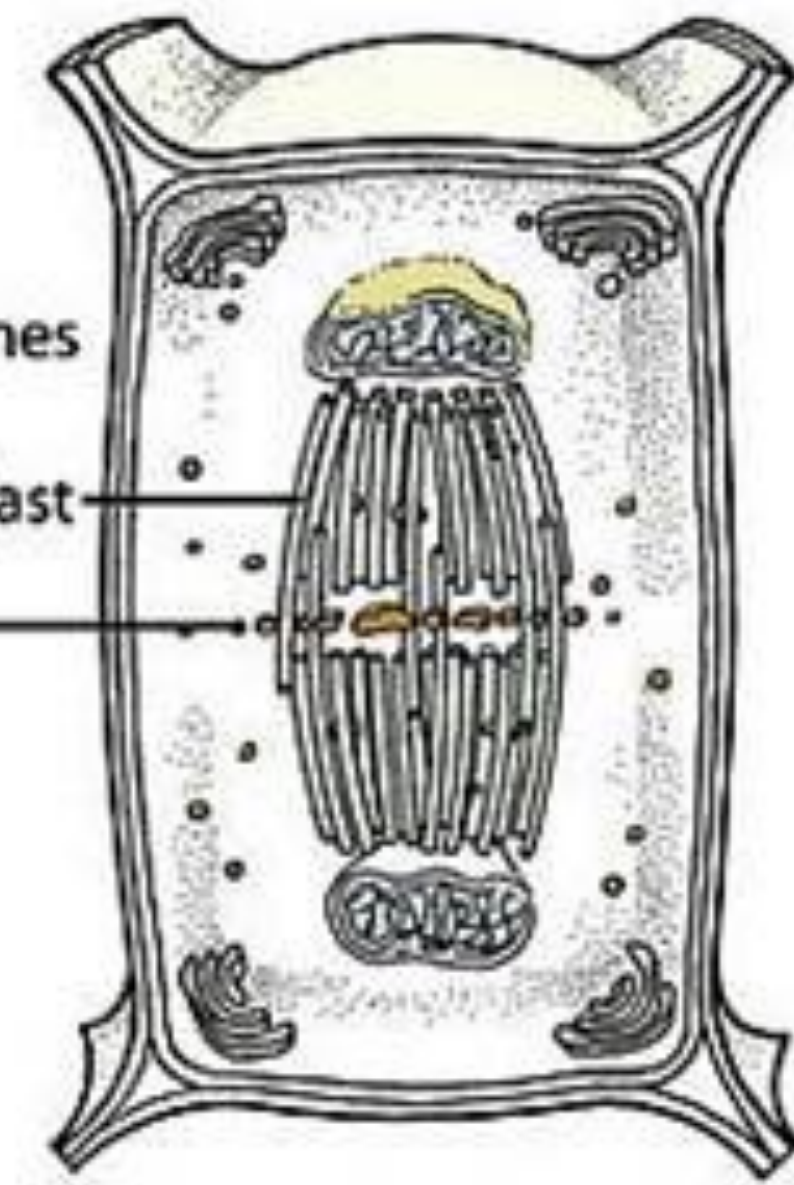


(b) Preprophase

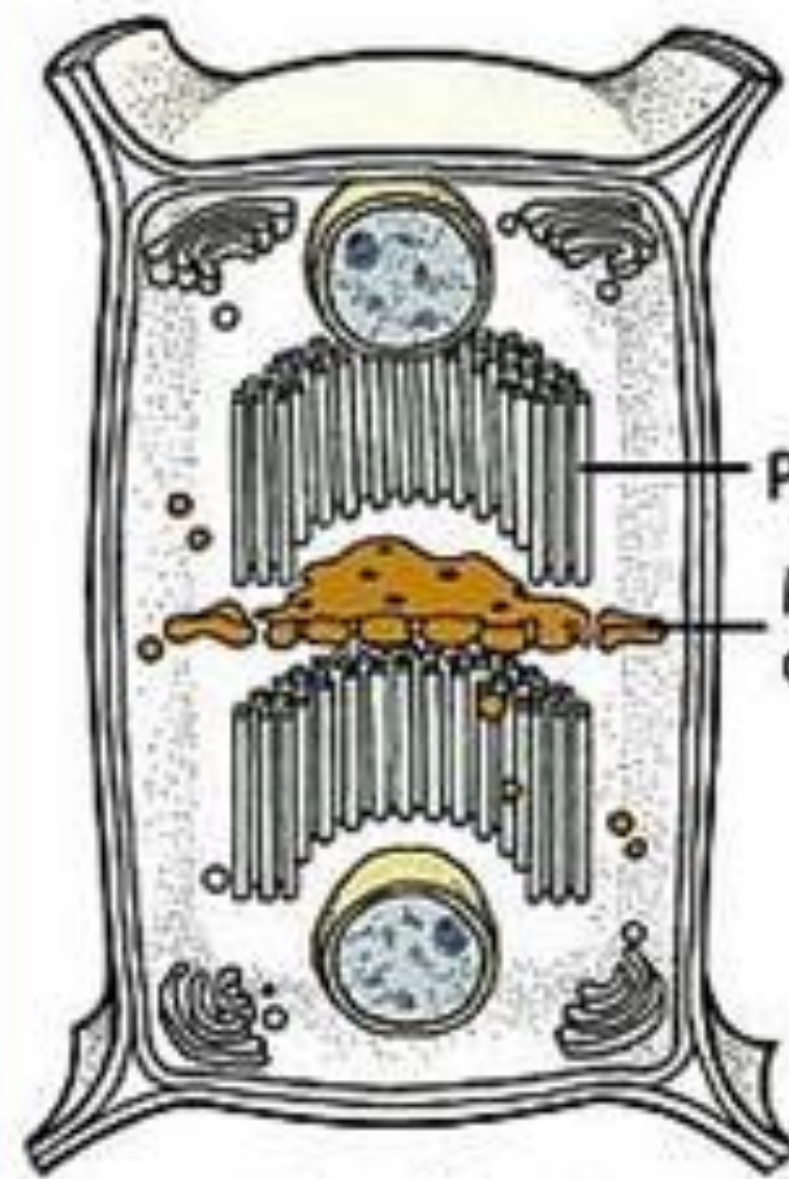


(c) Metaphase

Chromosomes  
Phragmoplast  
Forming cell plate  
Mitotic spindle

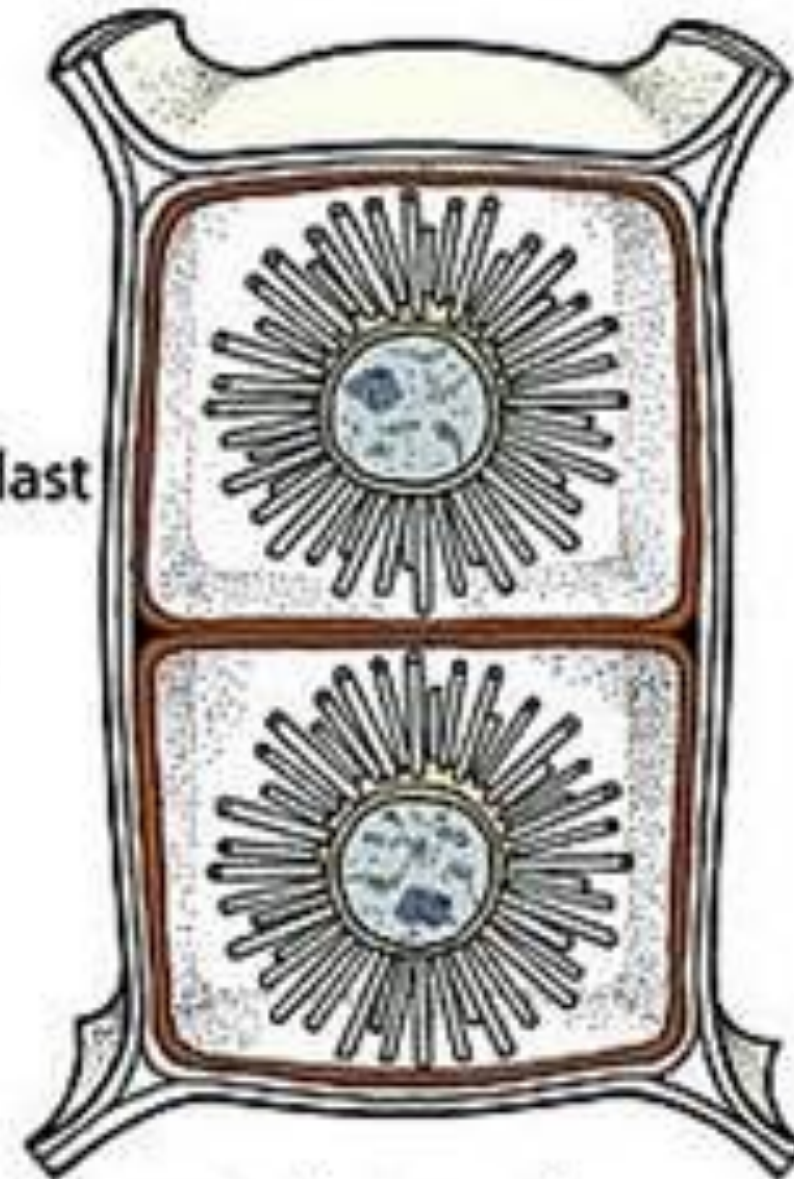


(d) Telophase and cytokinesis

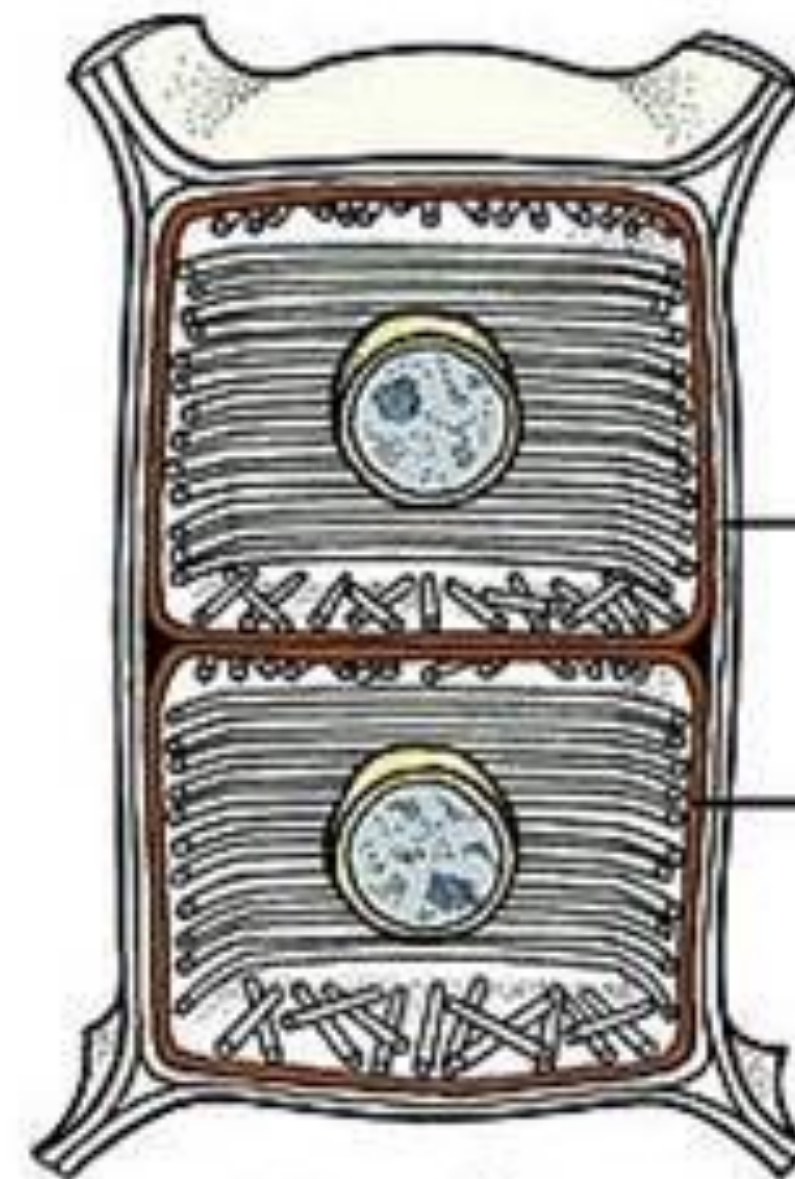


(e) Cytokinesis

Phragmoplast  
Maturing cell plate

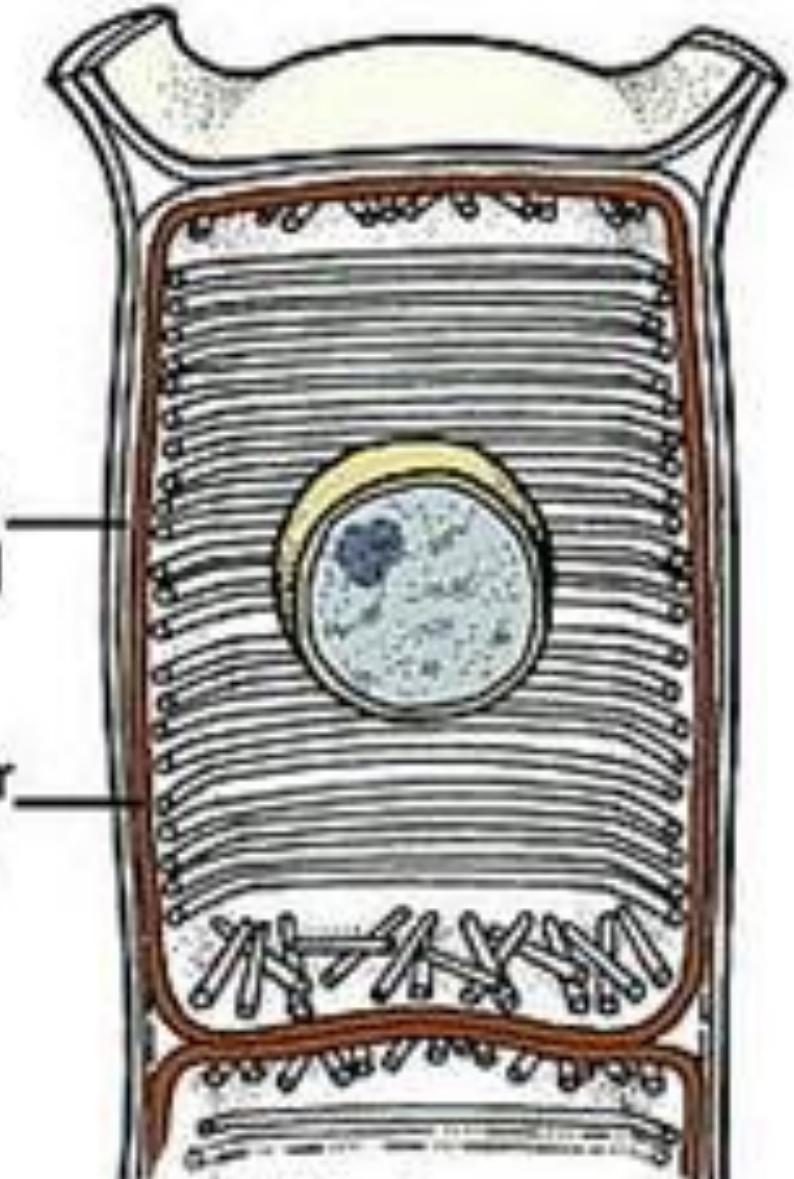


(f) Early interphase



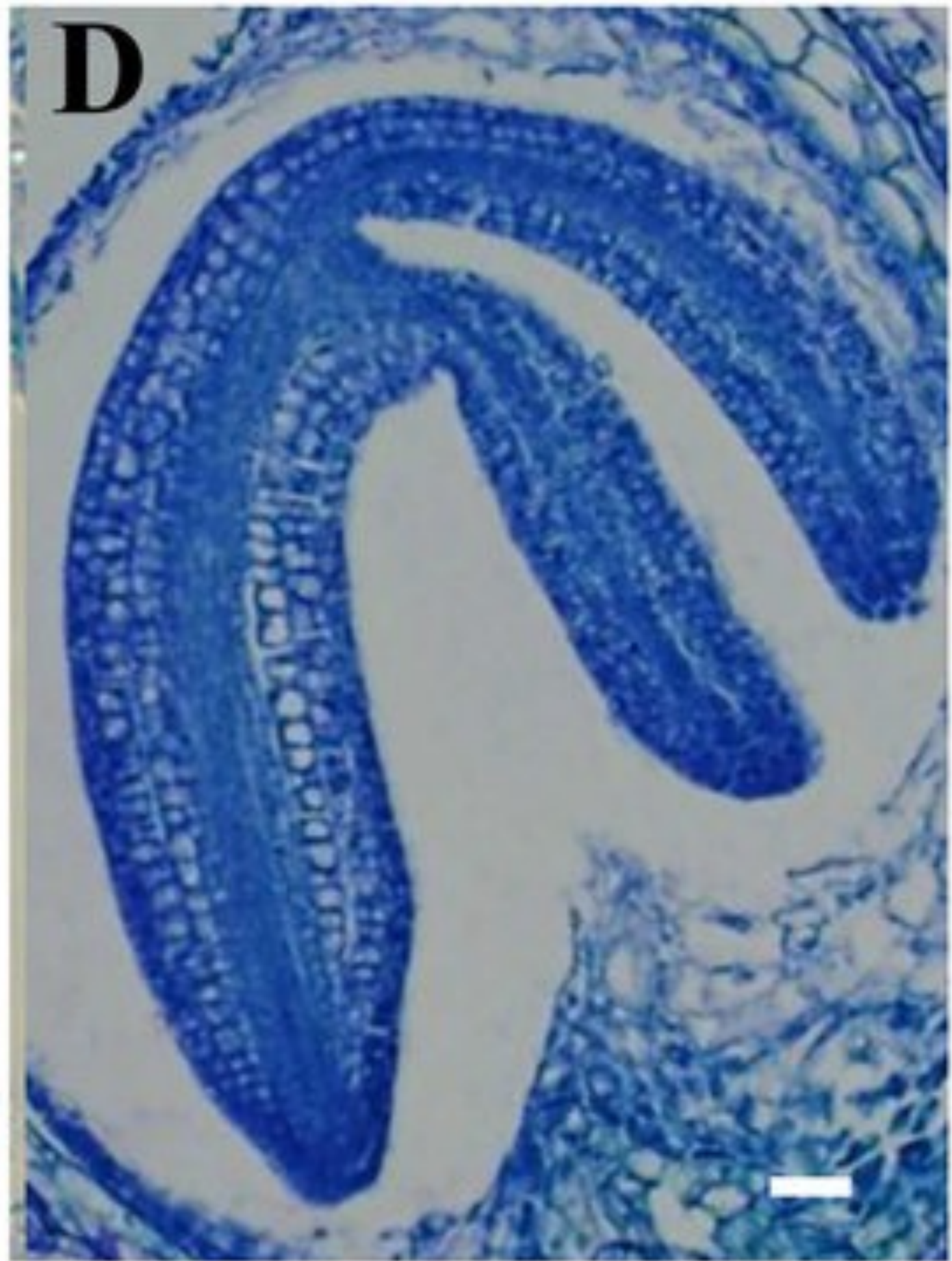
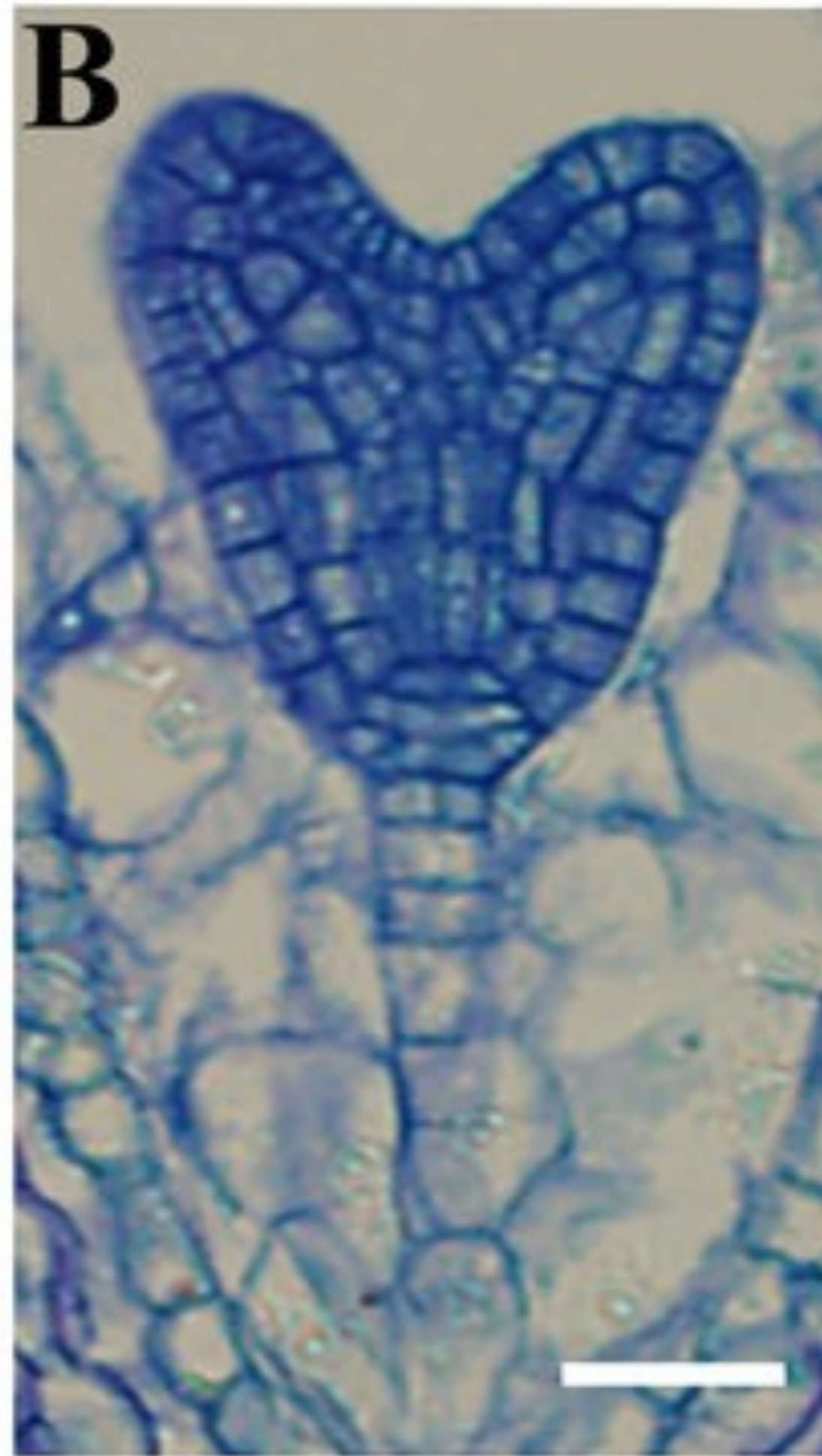
(g) Interphase

Mother cell wall  
Daughter cell wall

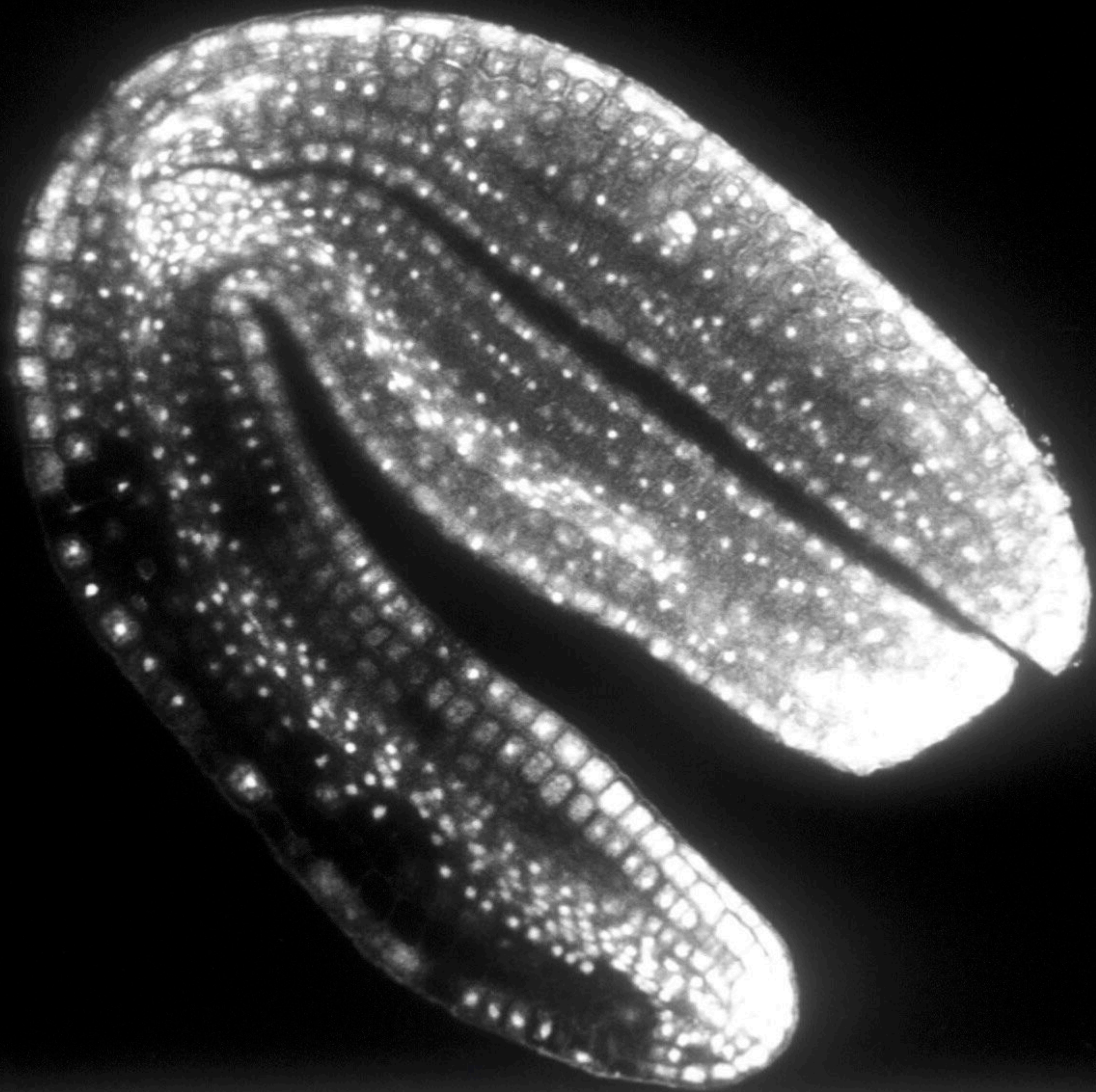


(h) Cell enlargement



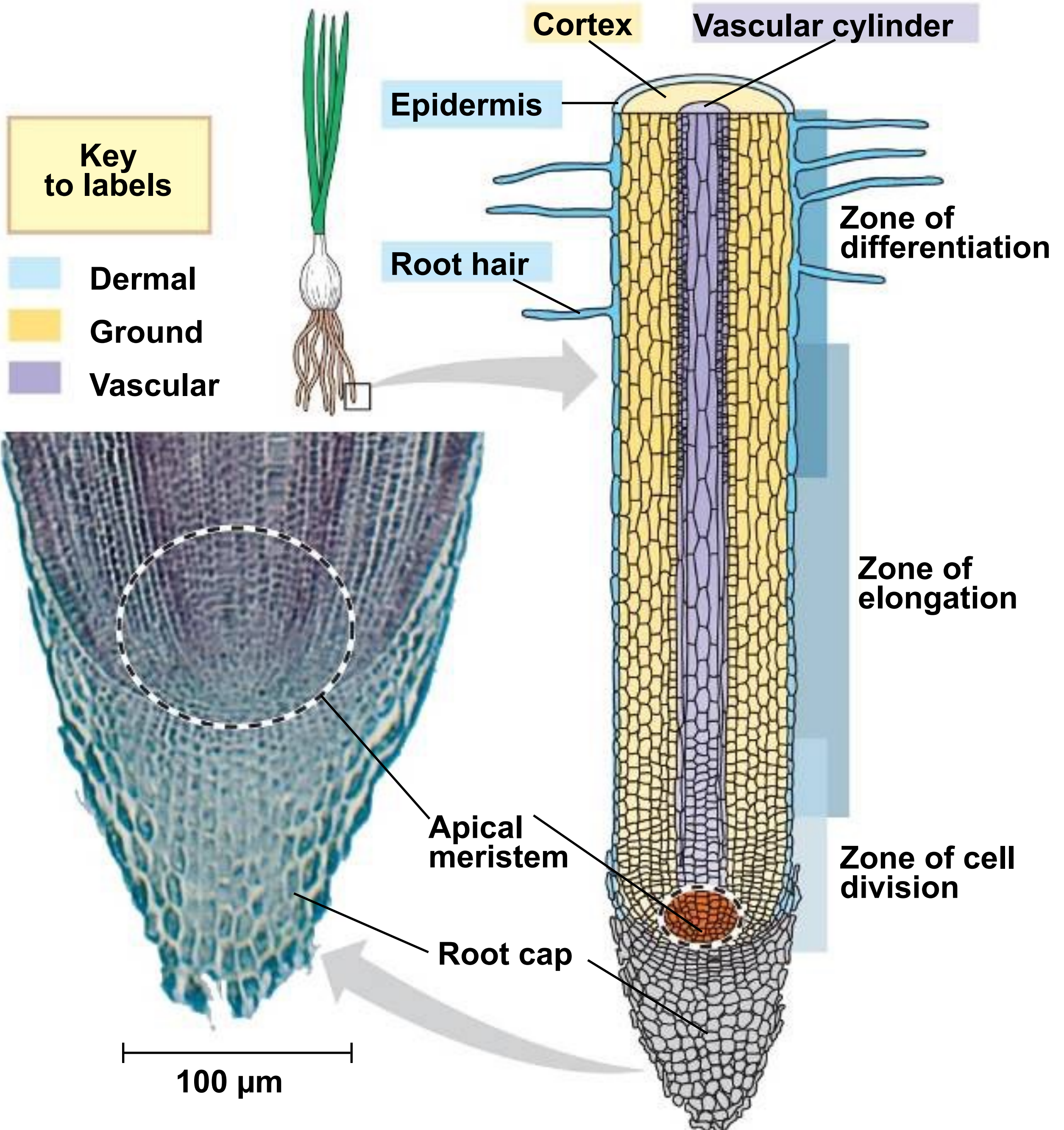








# ROOT APICAL MERISTEM





# CAMBIUM (VASCULAR SYSTEM STEM CELLS)

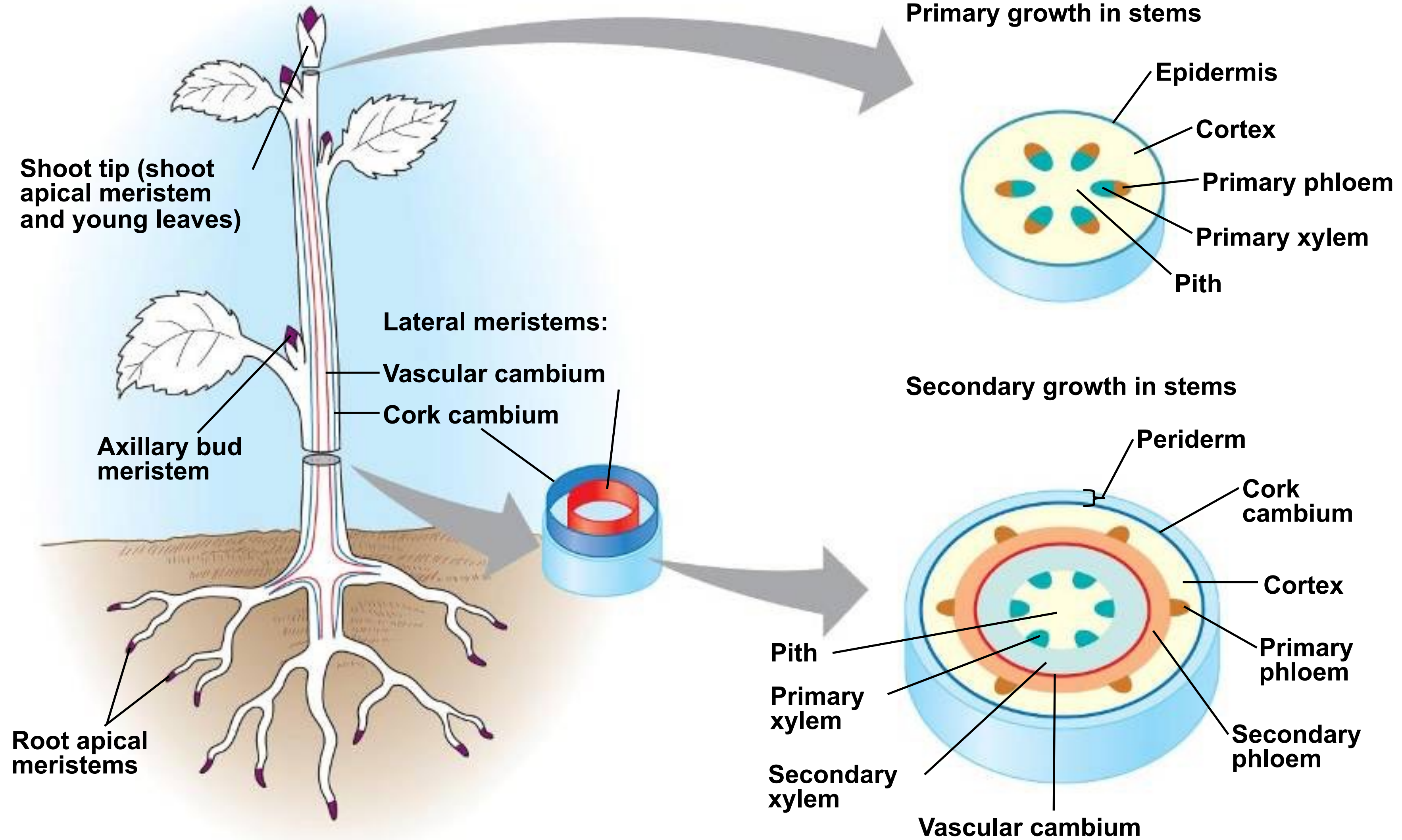
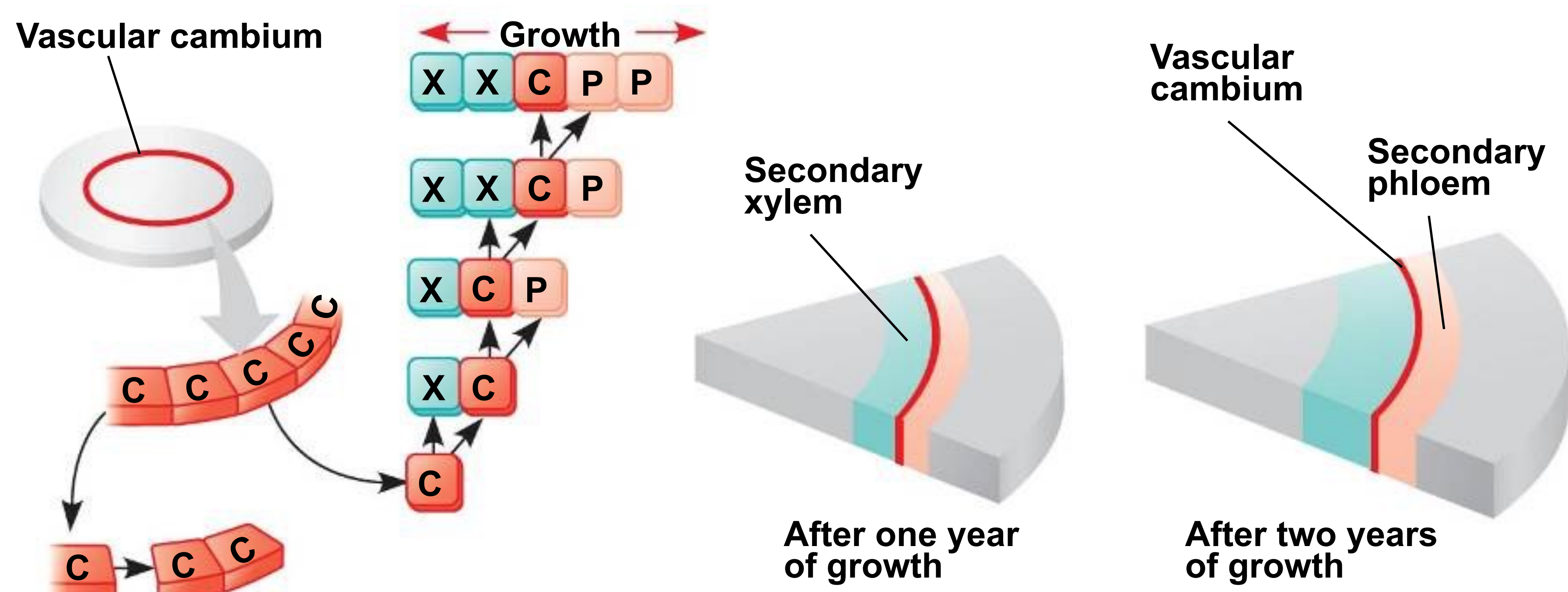




Fig. 35-20



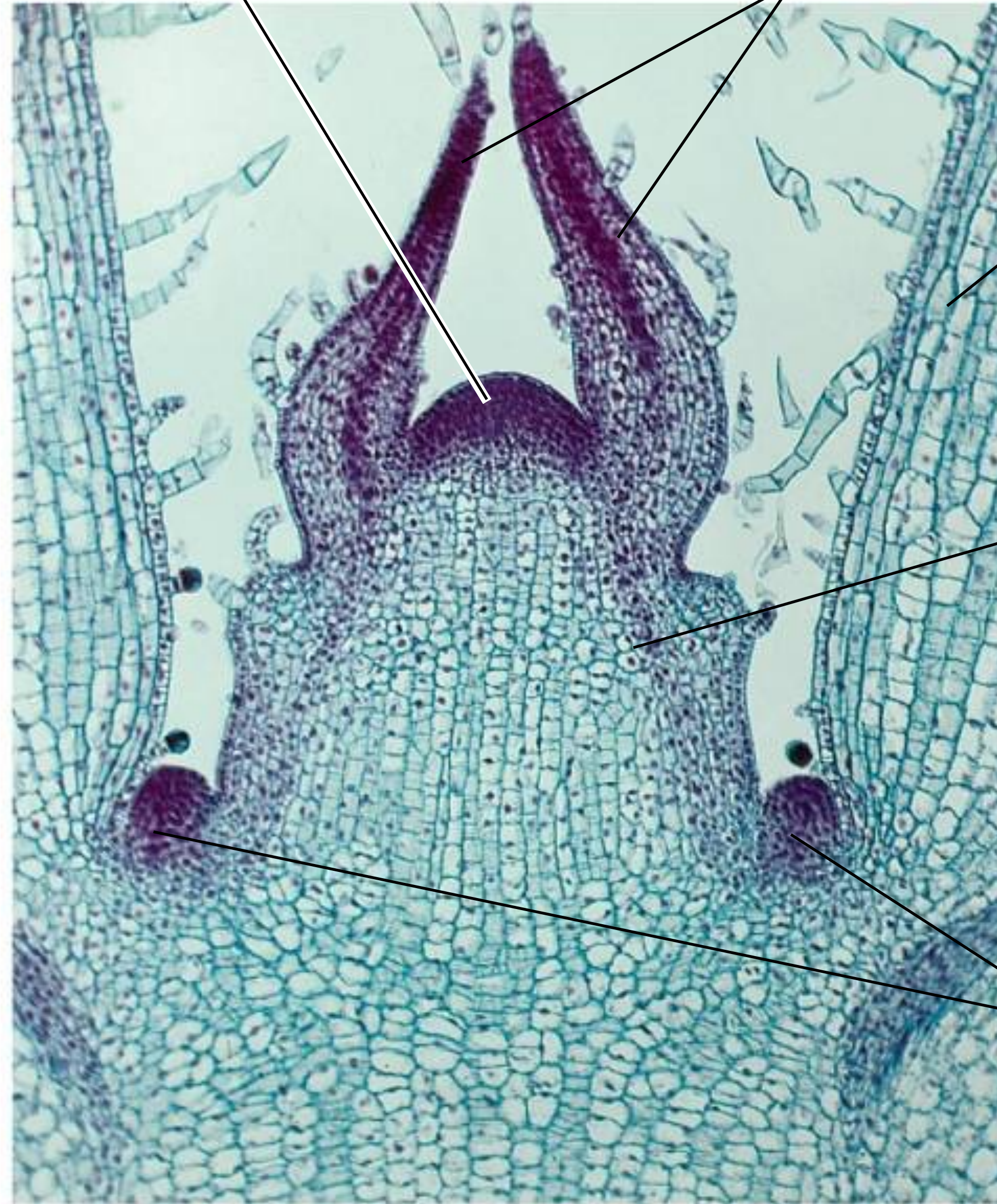
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# SHOOT APICAL MERISTEM

Shoot apical meristem

Leaf primordia



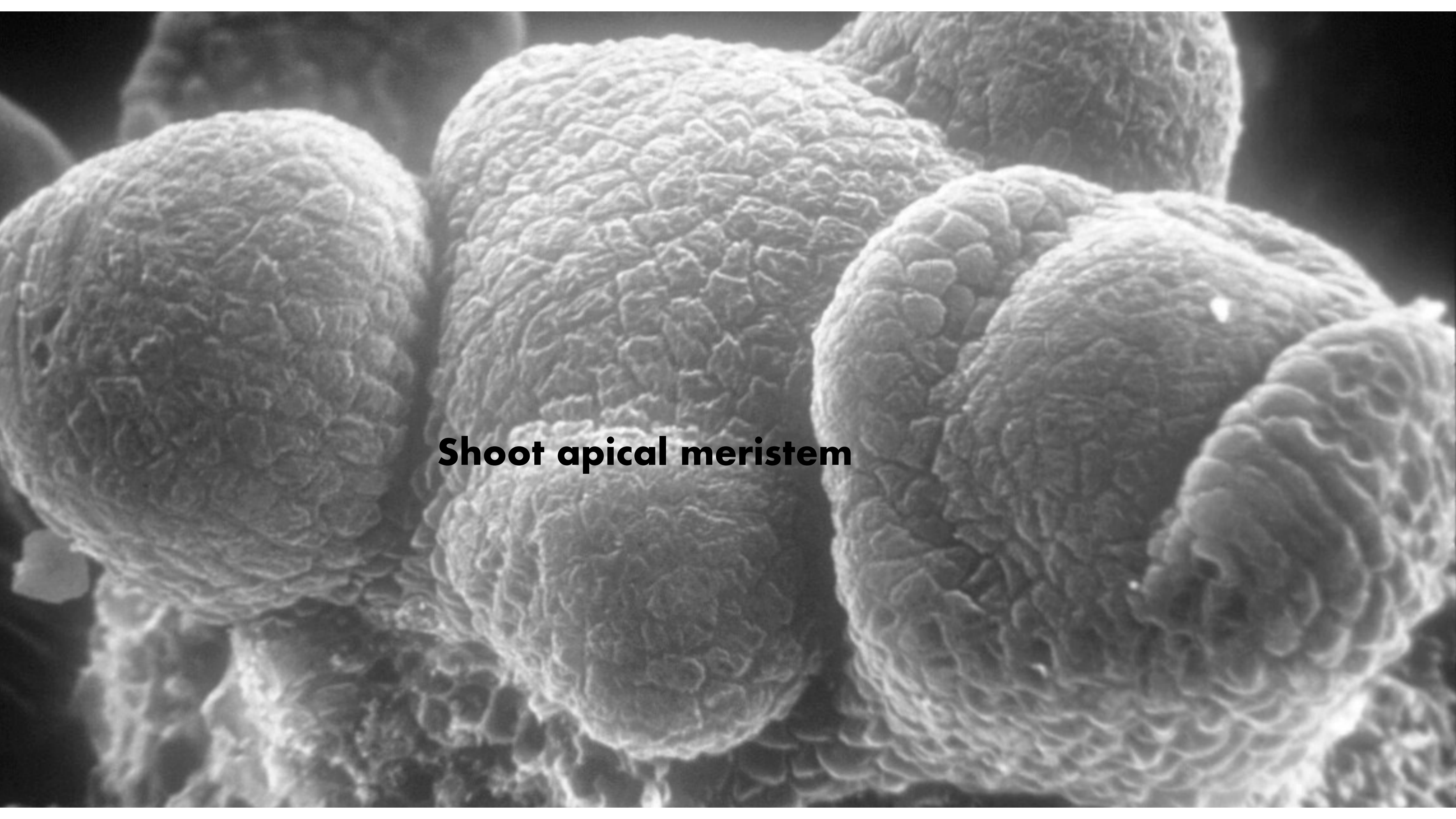
Young leaf

Developing vascular strand

Axillary bud meristems

0.25 mm



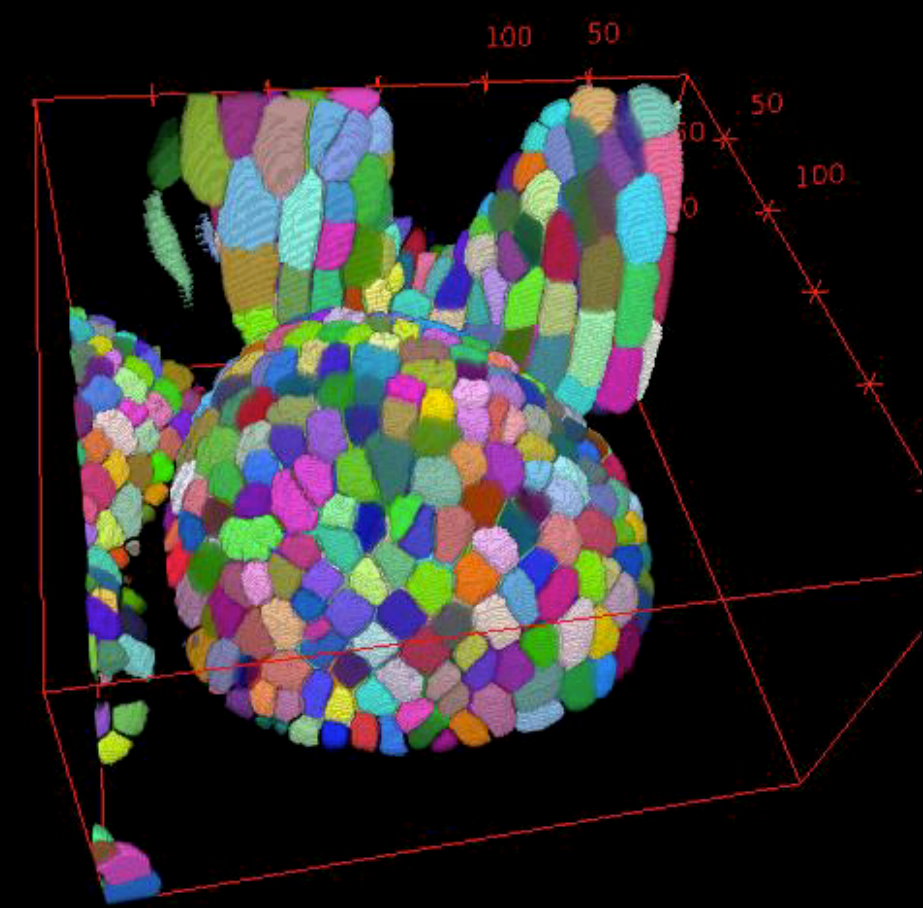
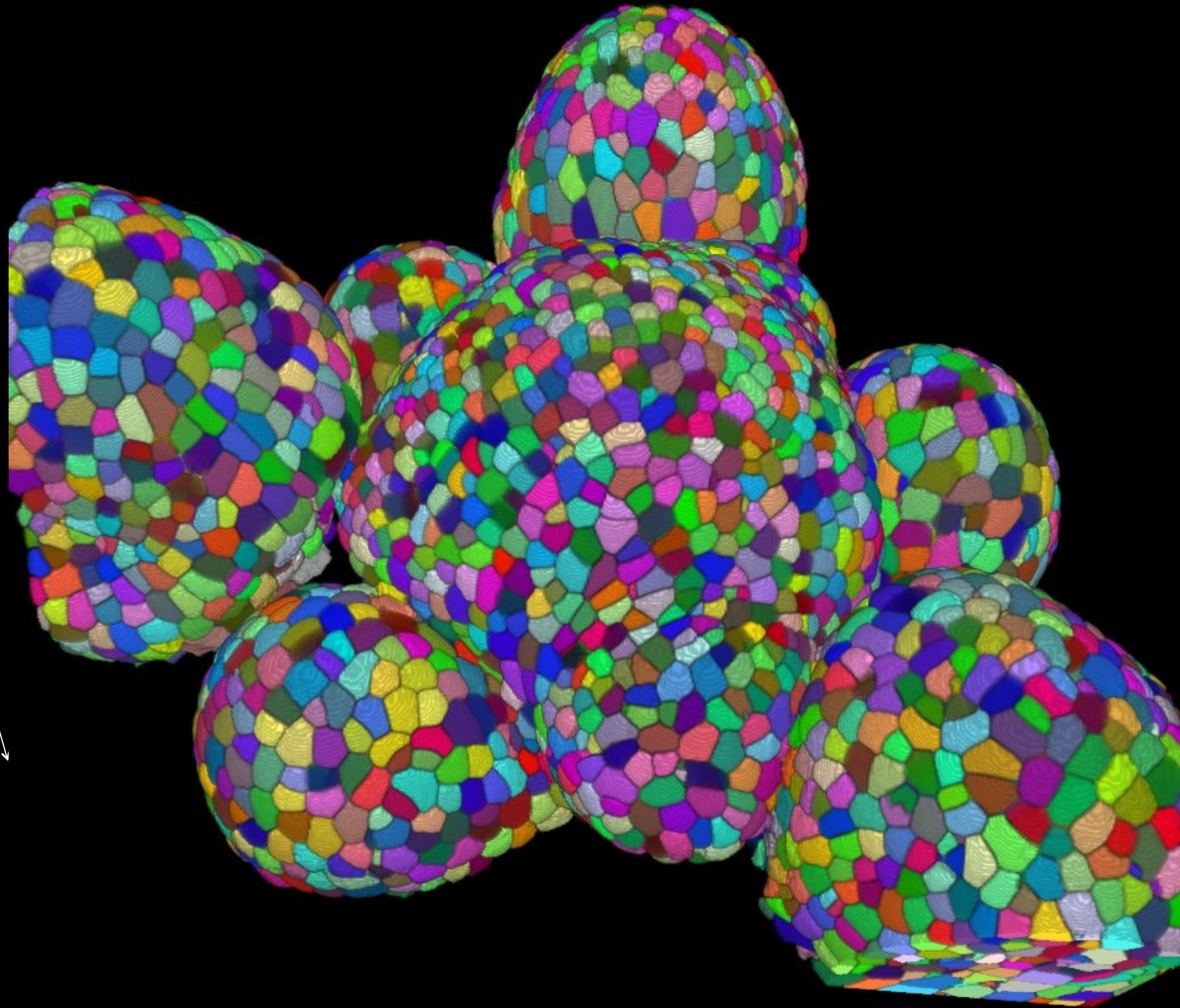


**Shoot apical meristem**

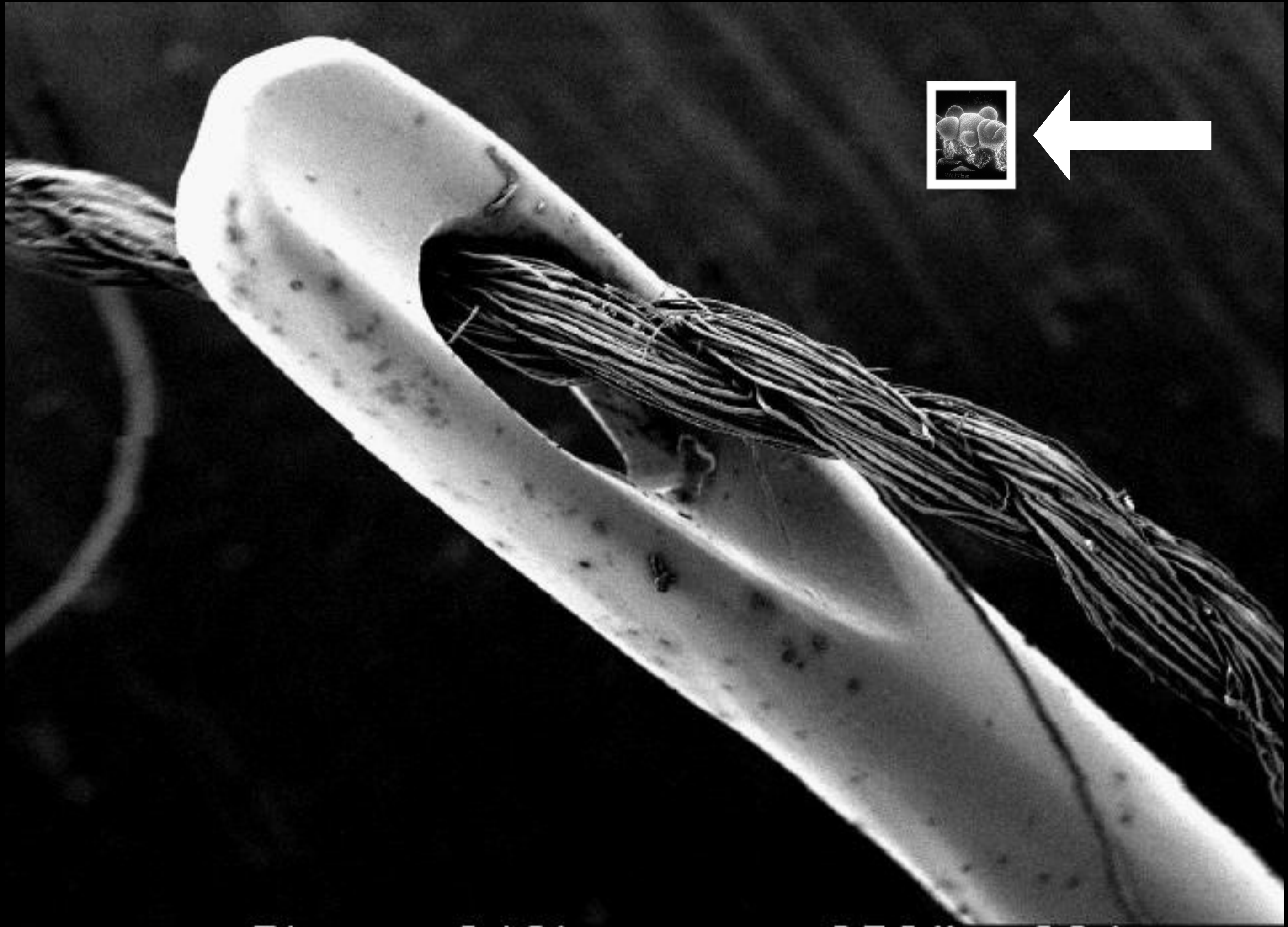


# Shoot Apical Meristem and Flowers

Arabidopsis





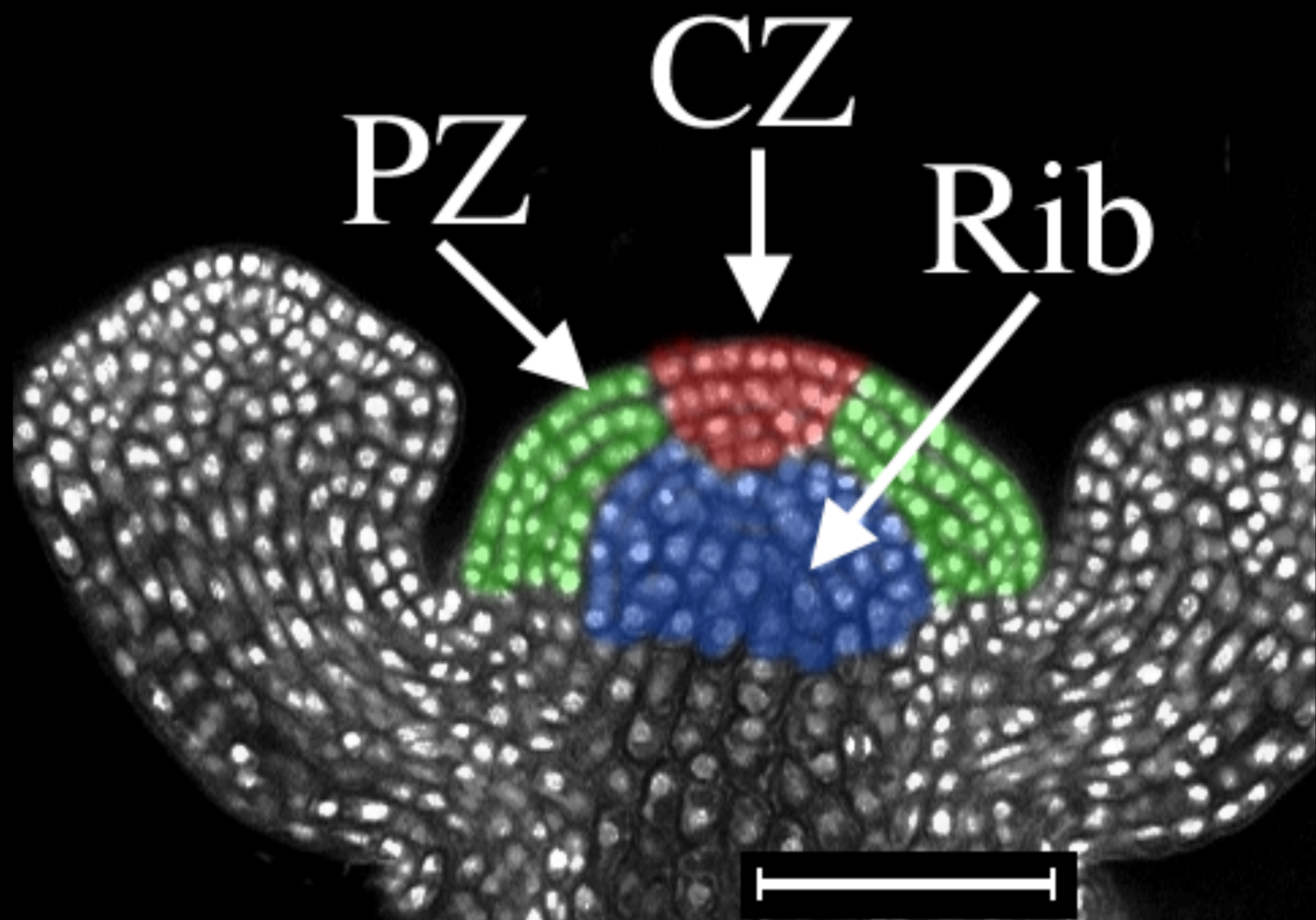


5kV .040kx

250µ 004







PZ

CZ

Rib

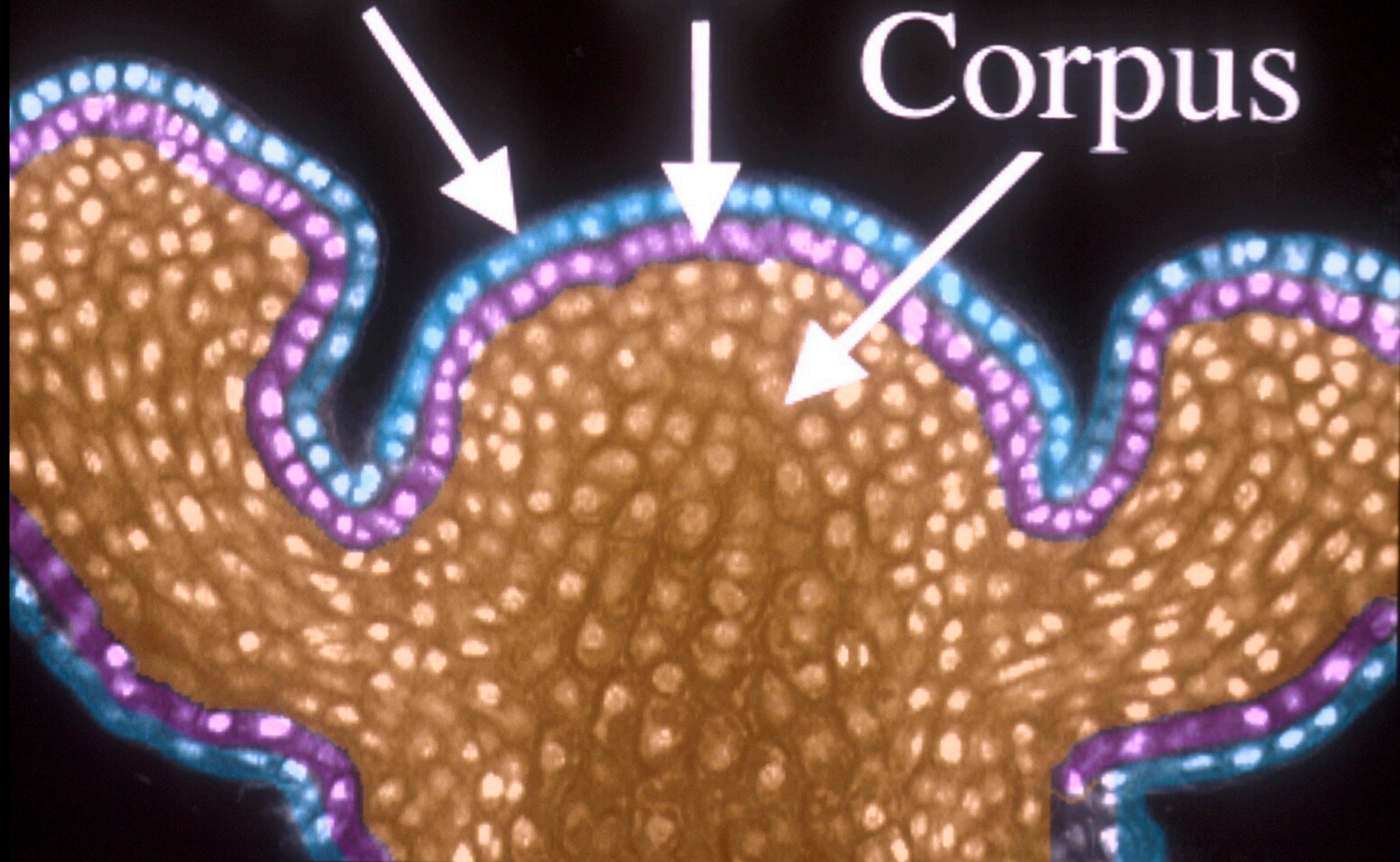




L1

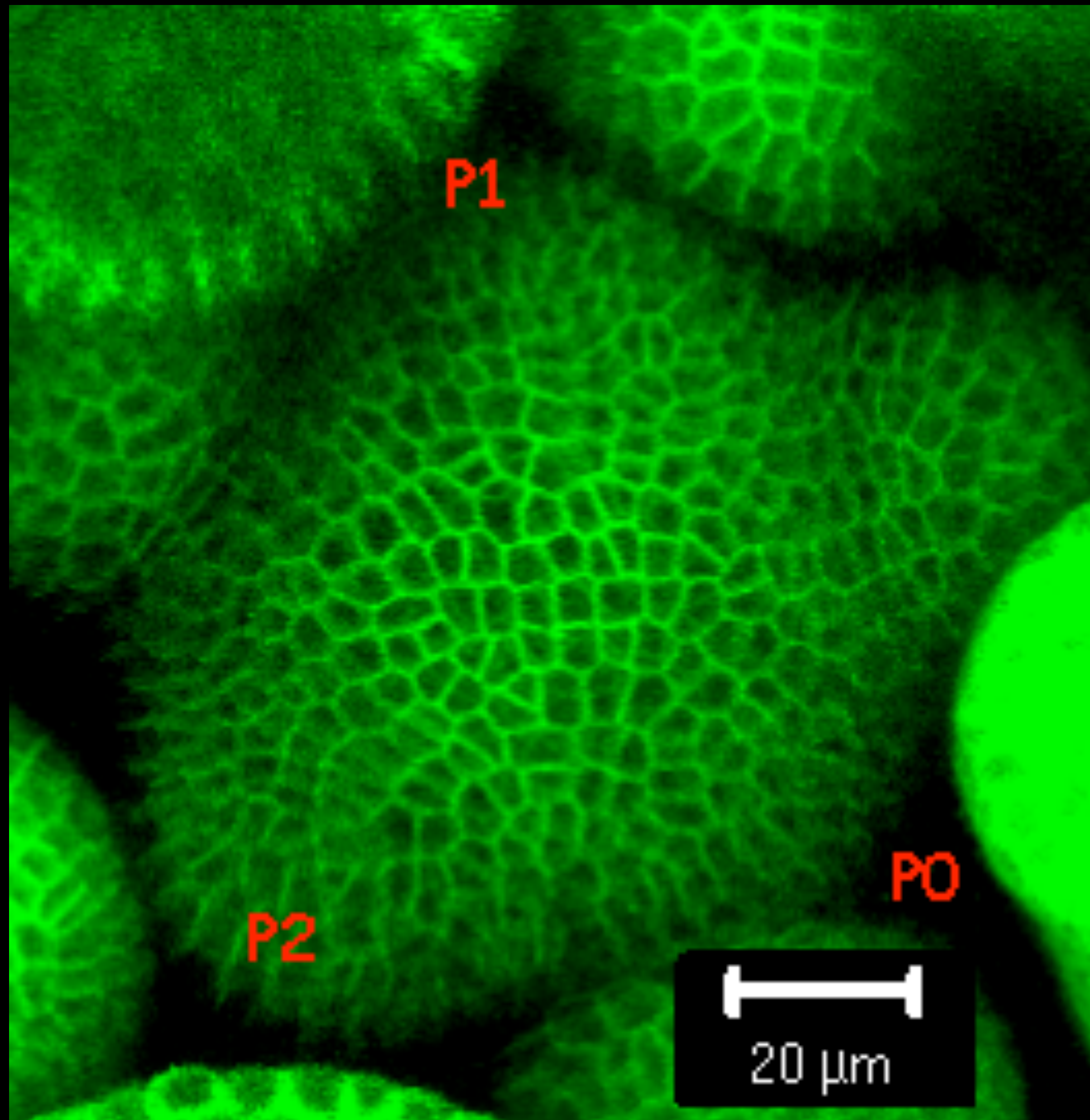
L2

Corpus

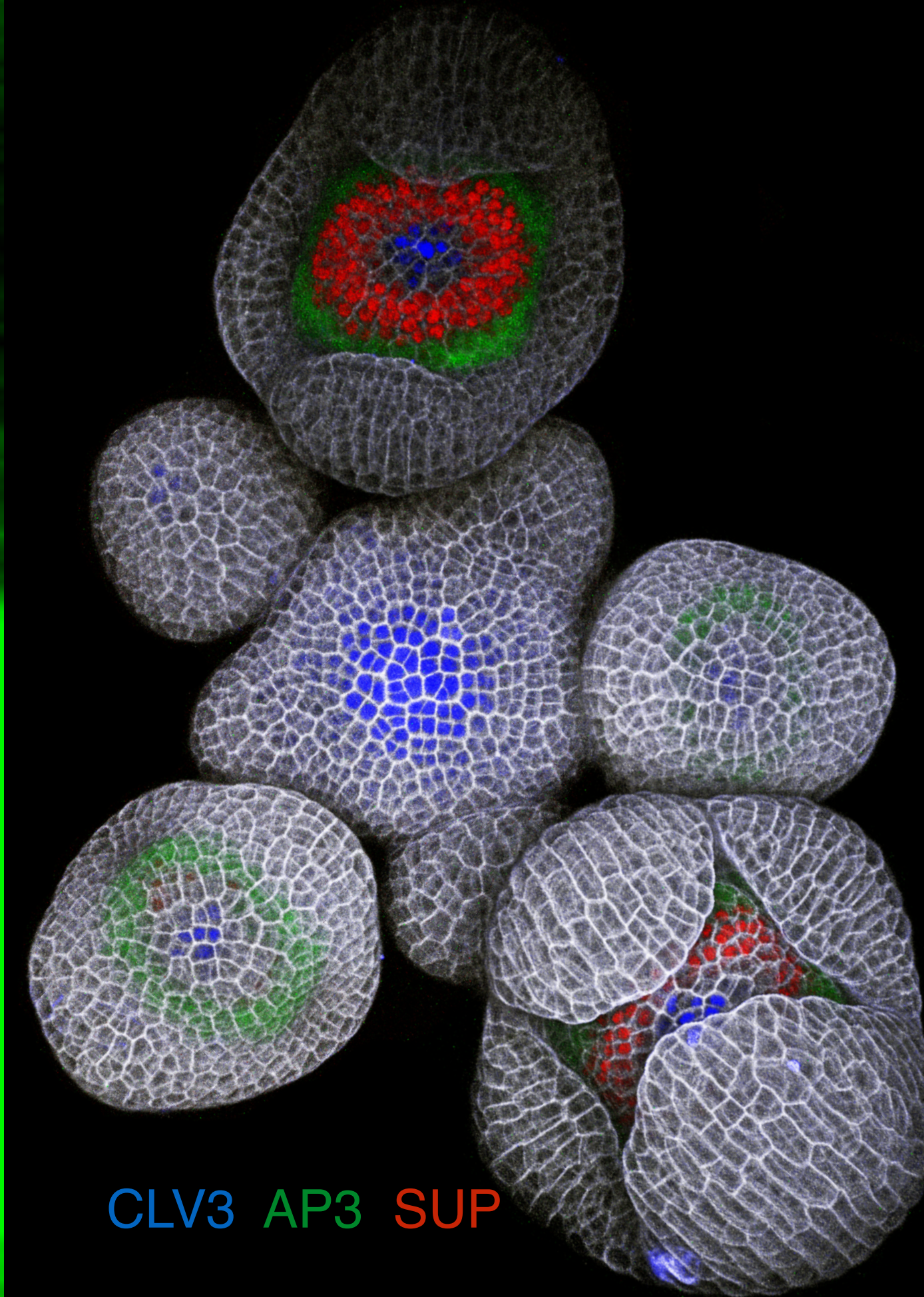




# Shoot Apical Meristem



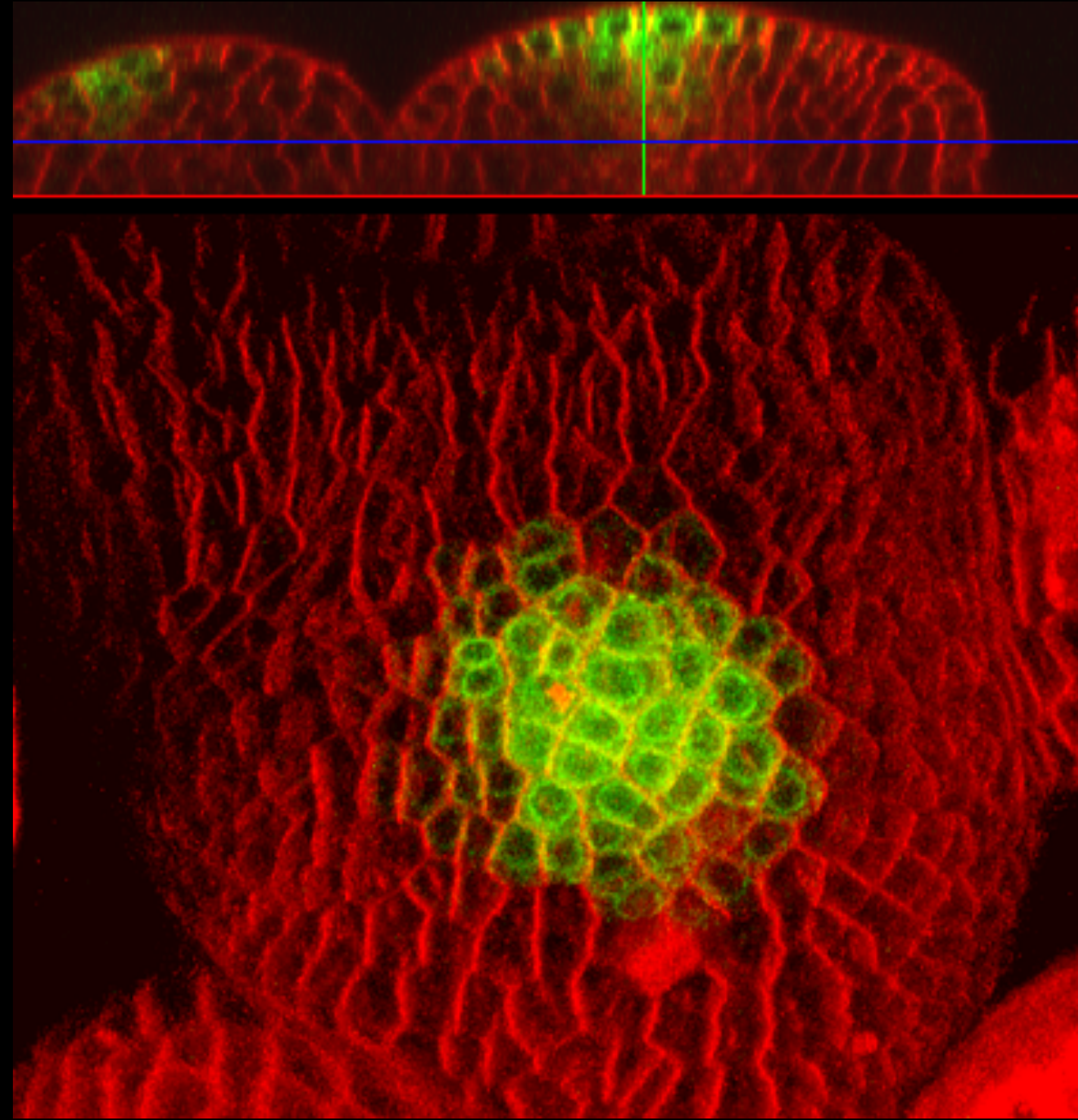
Venugopala Reddy



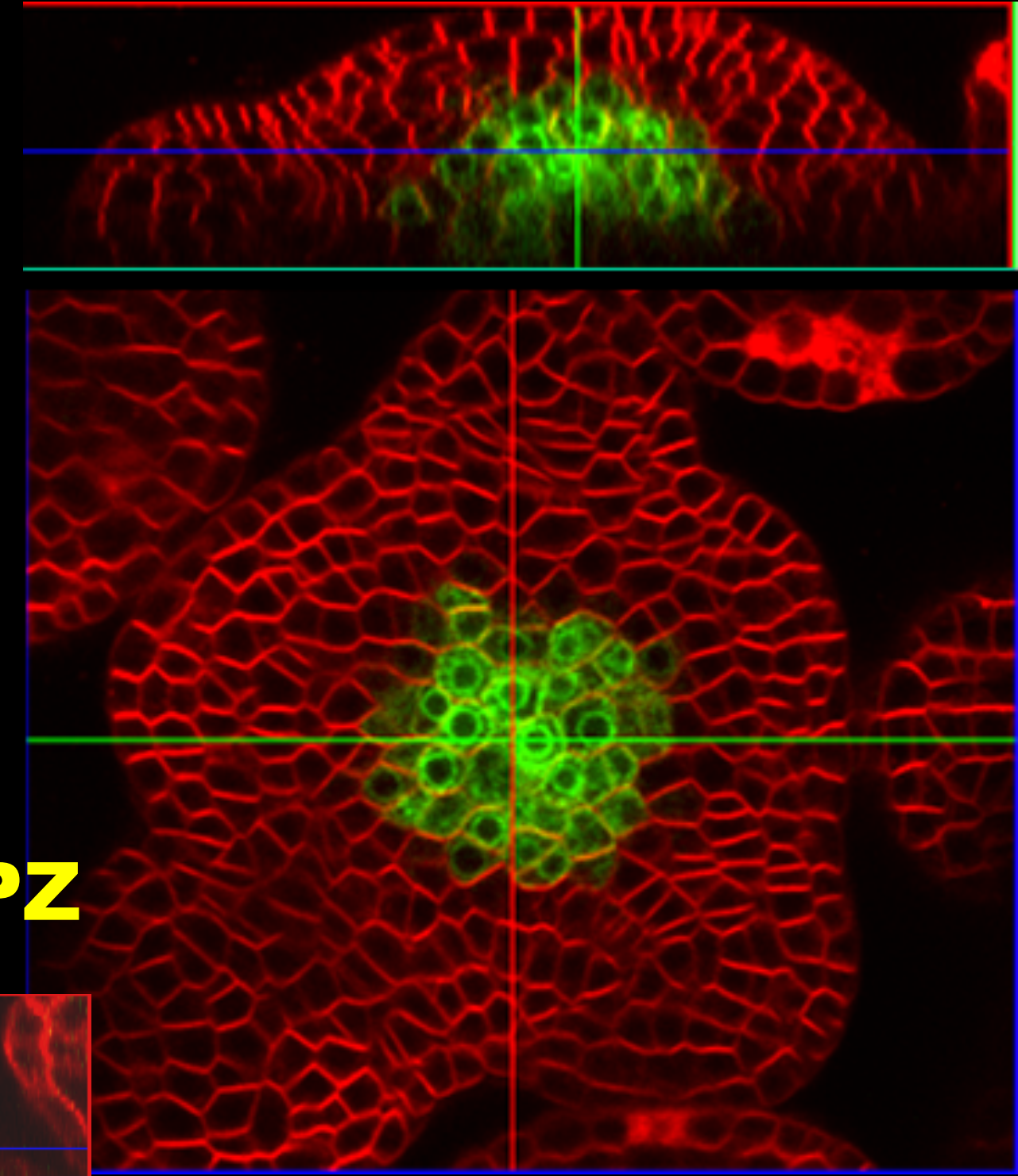
Nathanaël Prunet



**CLV3 FM4-64**



**WUS FM4-64**



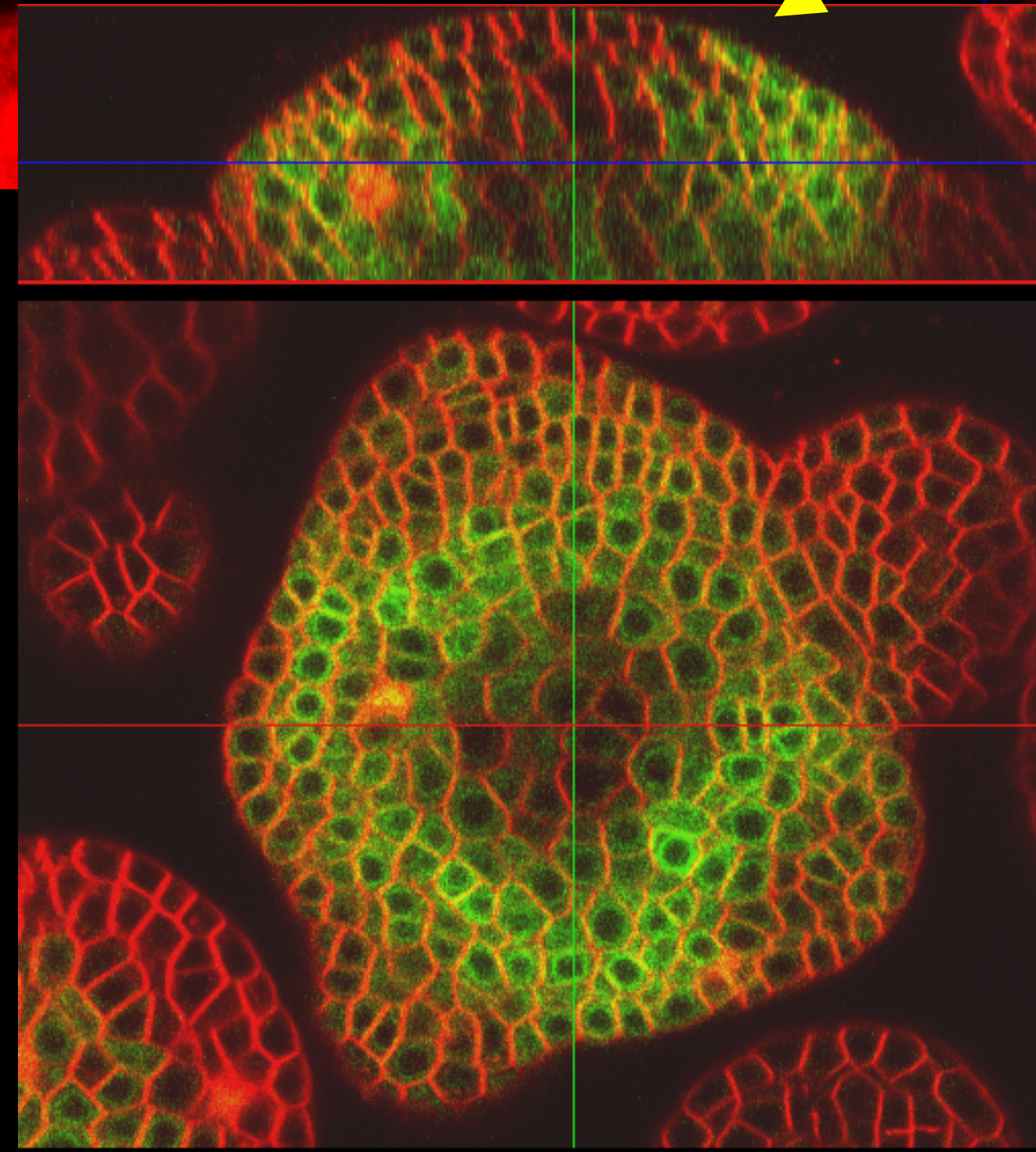
**CZ**



**PZ**

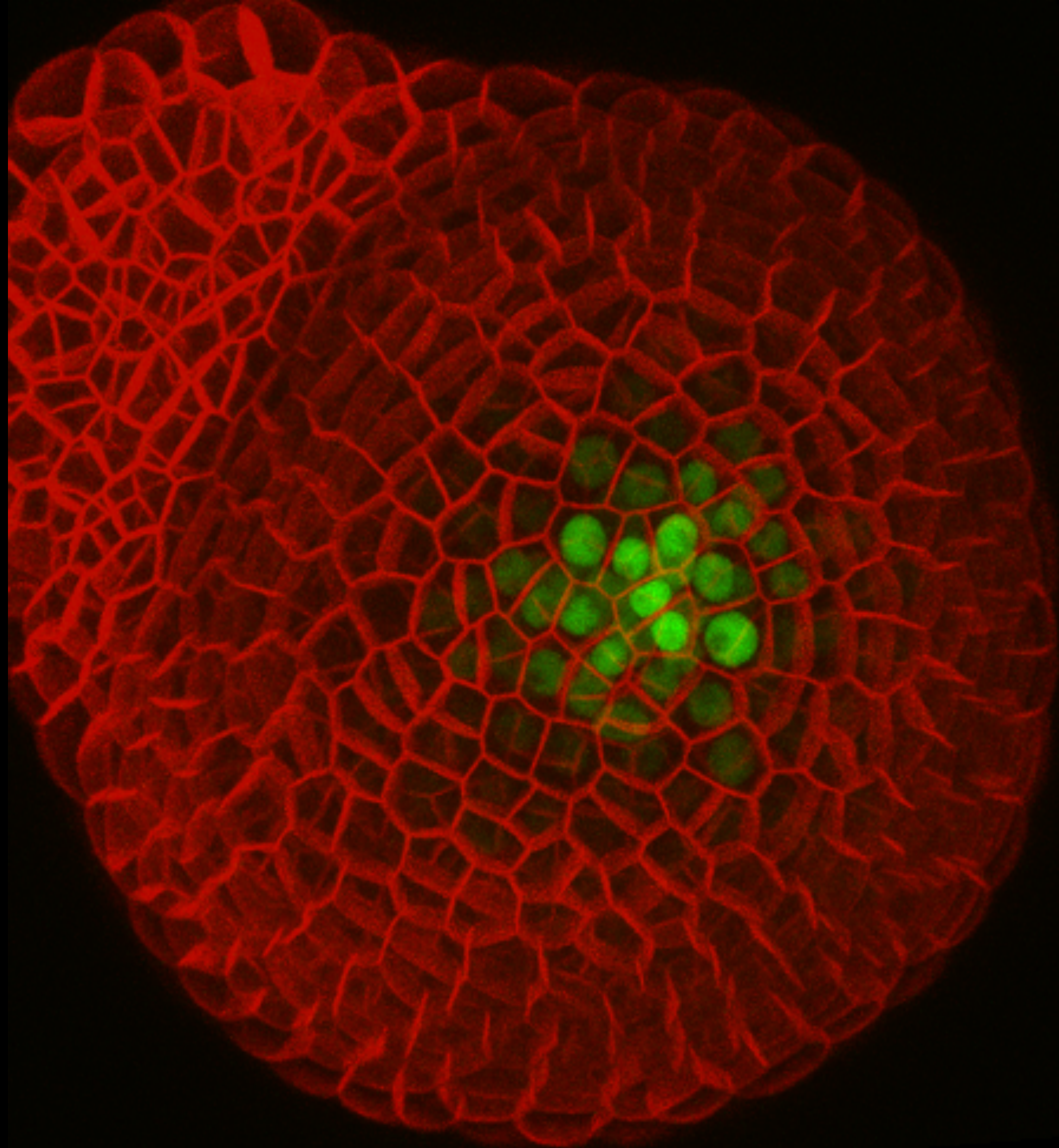


**UFO FM4-64**



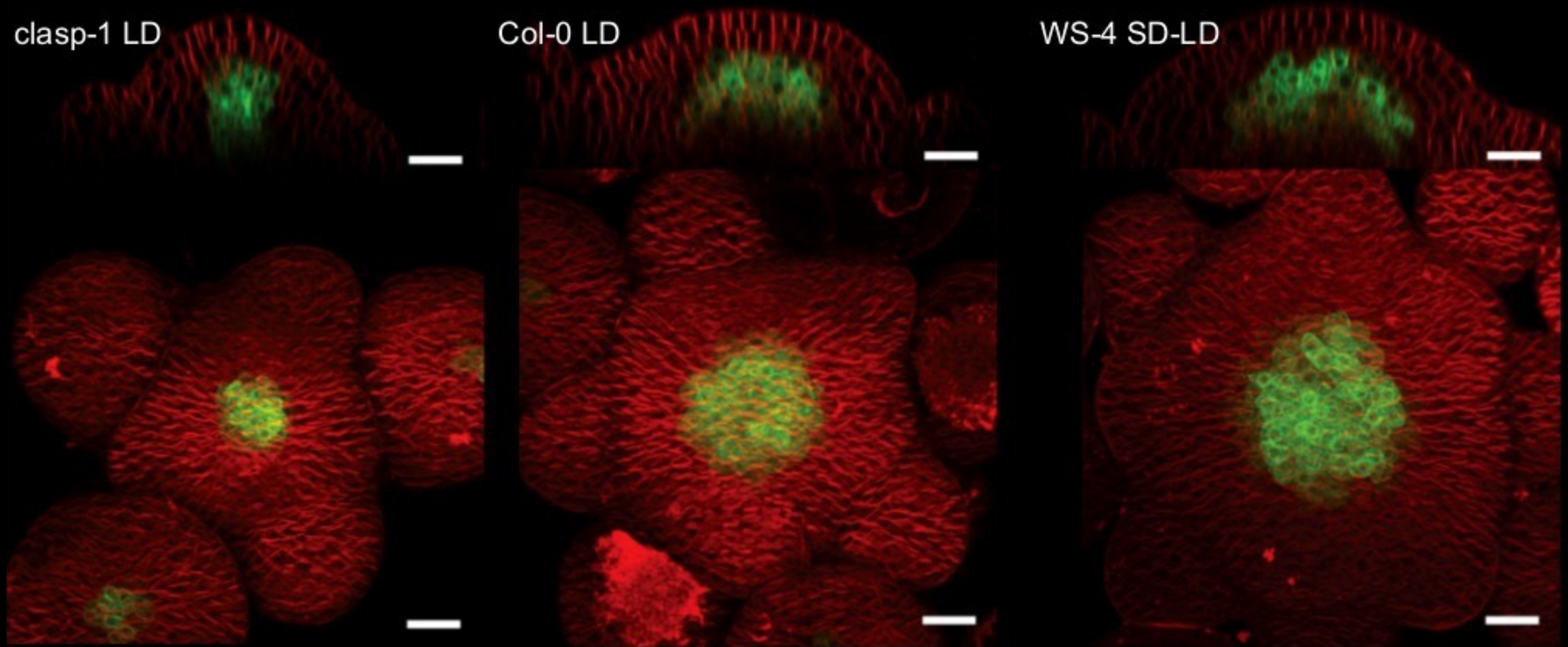


# Constant gene expression in a changing substrate



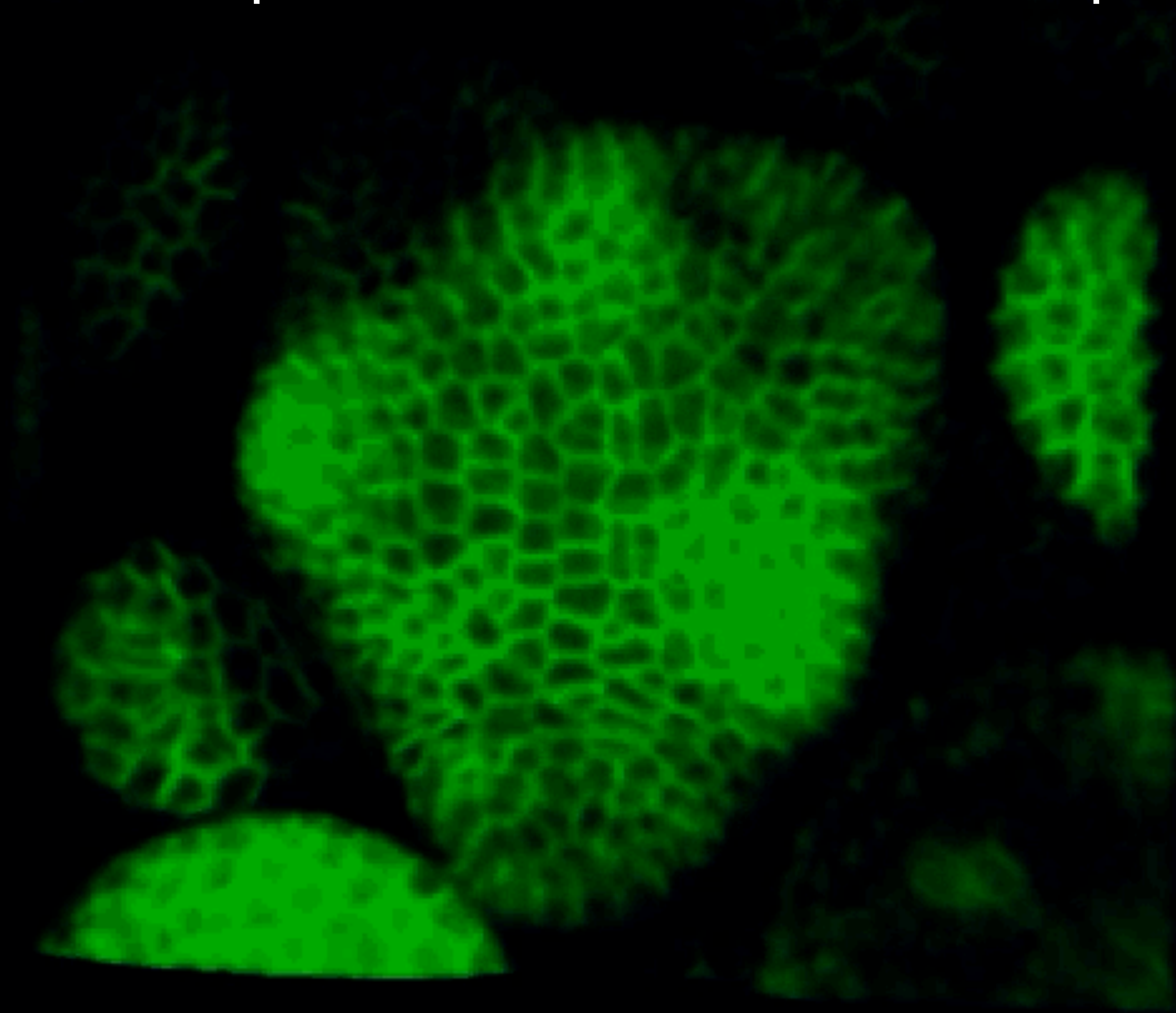


# size influences expression regions





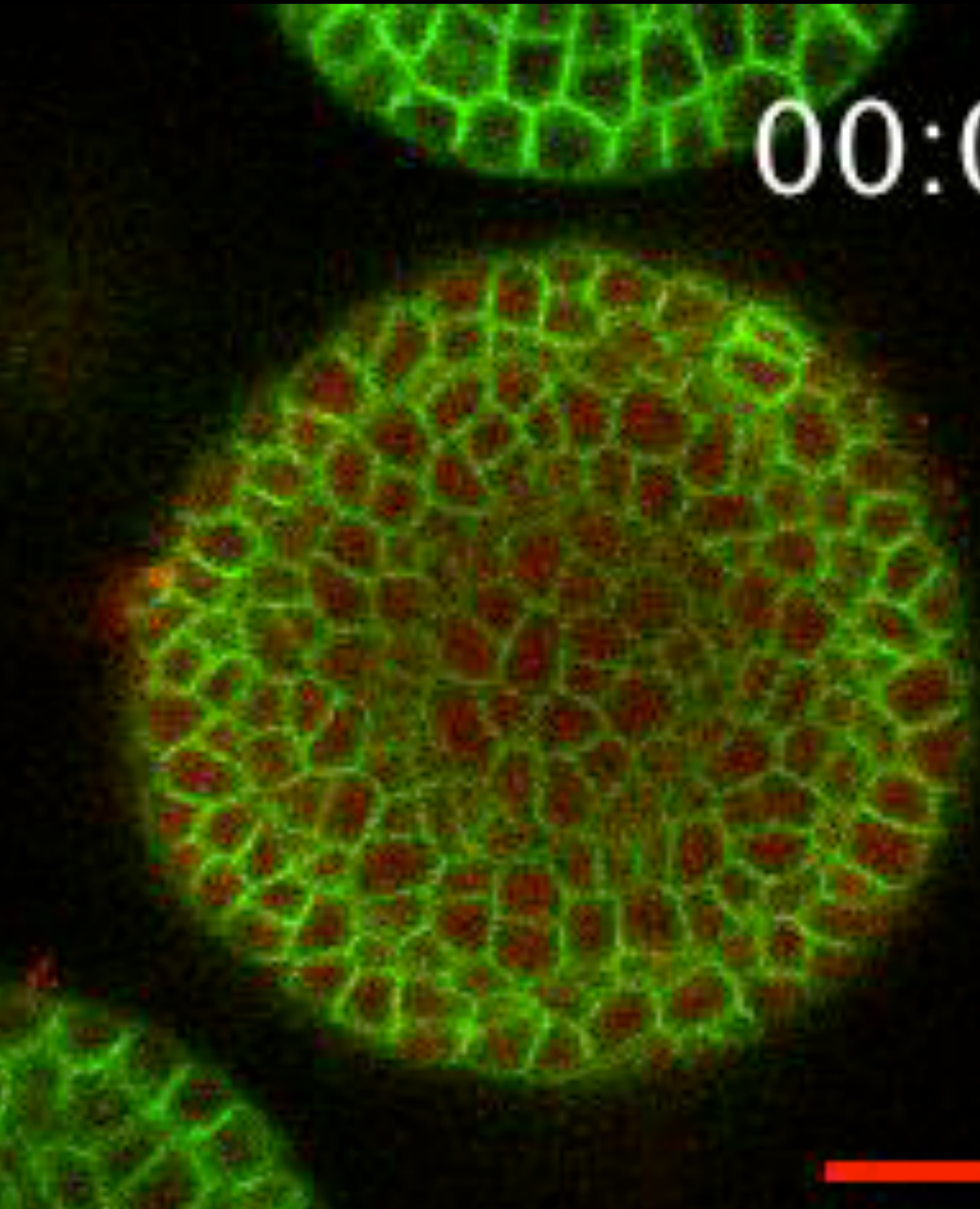
# PIN1 GFP is expressed relative to new floral primordial





Gene Expression Isn't Everything:  
The Meristem Responds to  
Mechanical Force

00:00



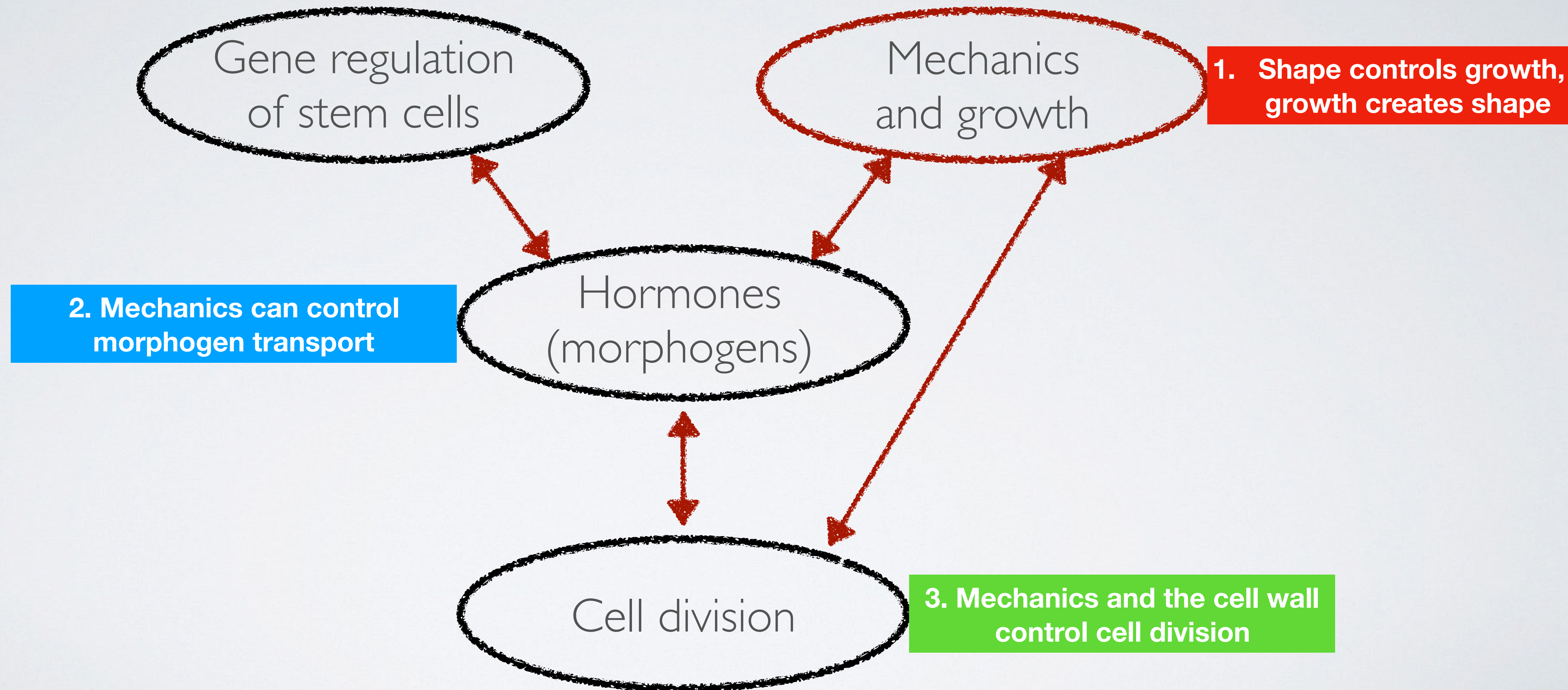
 = Increased Calcium ion level in cell cytoplasm

*Ting Li*



# COMPUTATIONAL MORPHODYNAMICS

0. Introduction to plant growth (brief)



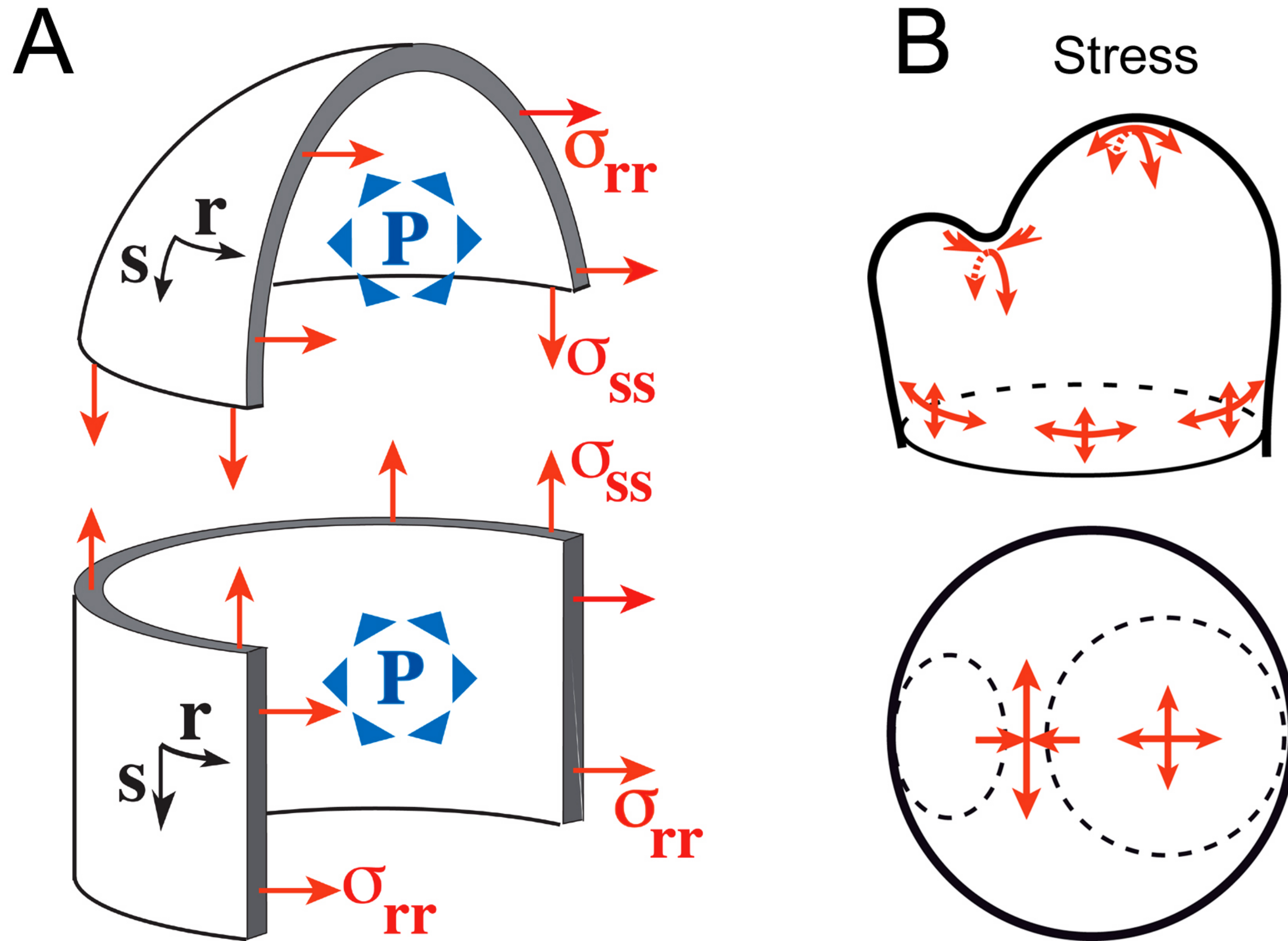


**Hofmeister 1859, 1863; Sachs, 1865**



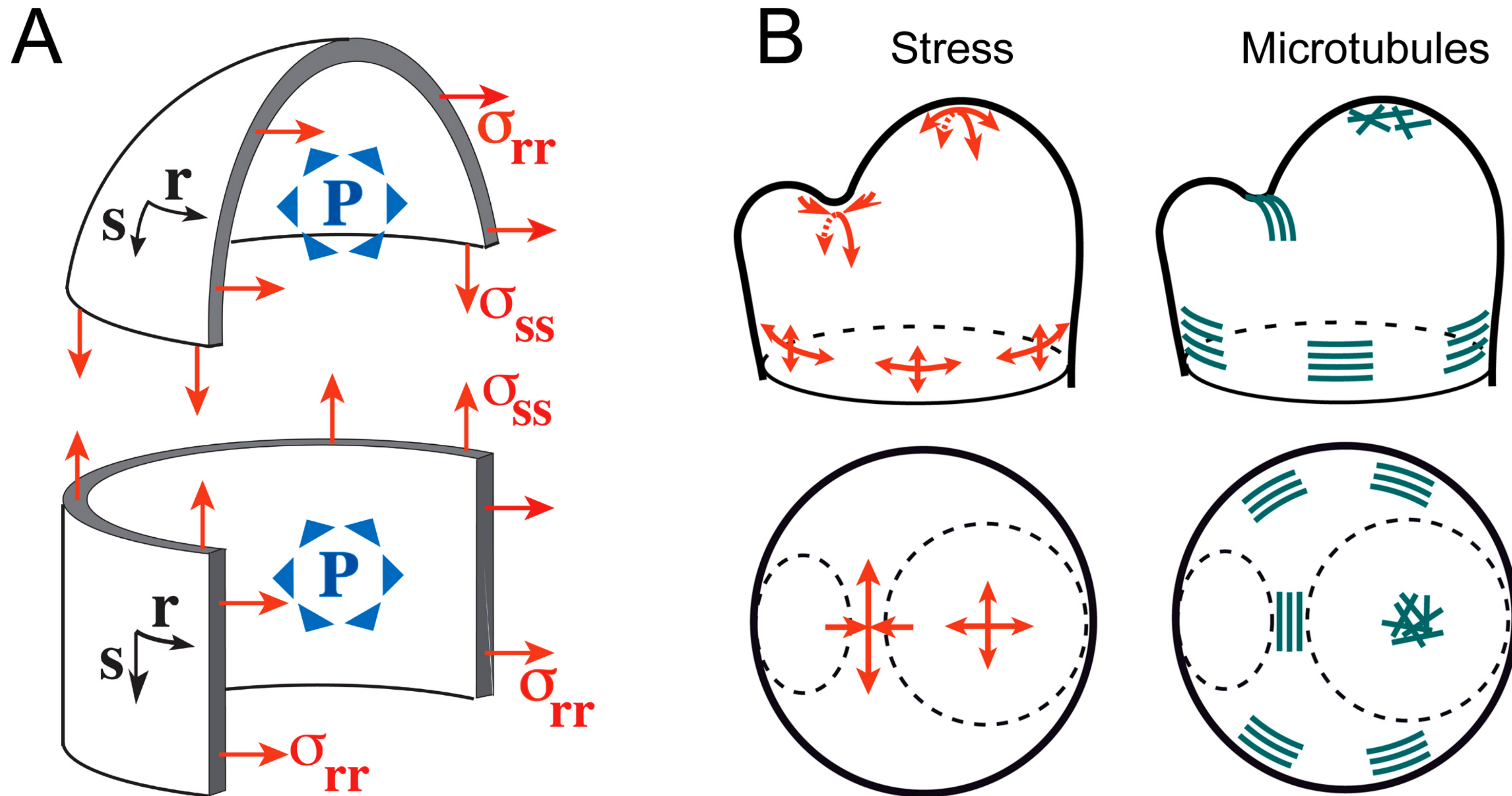


# Stress Pattern in SAM Epidermis



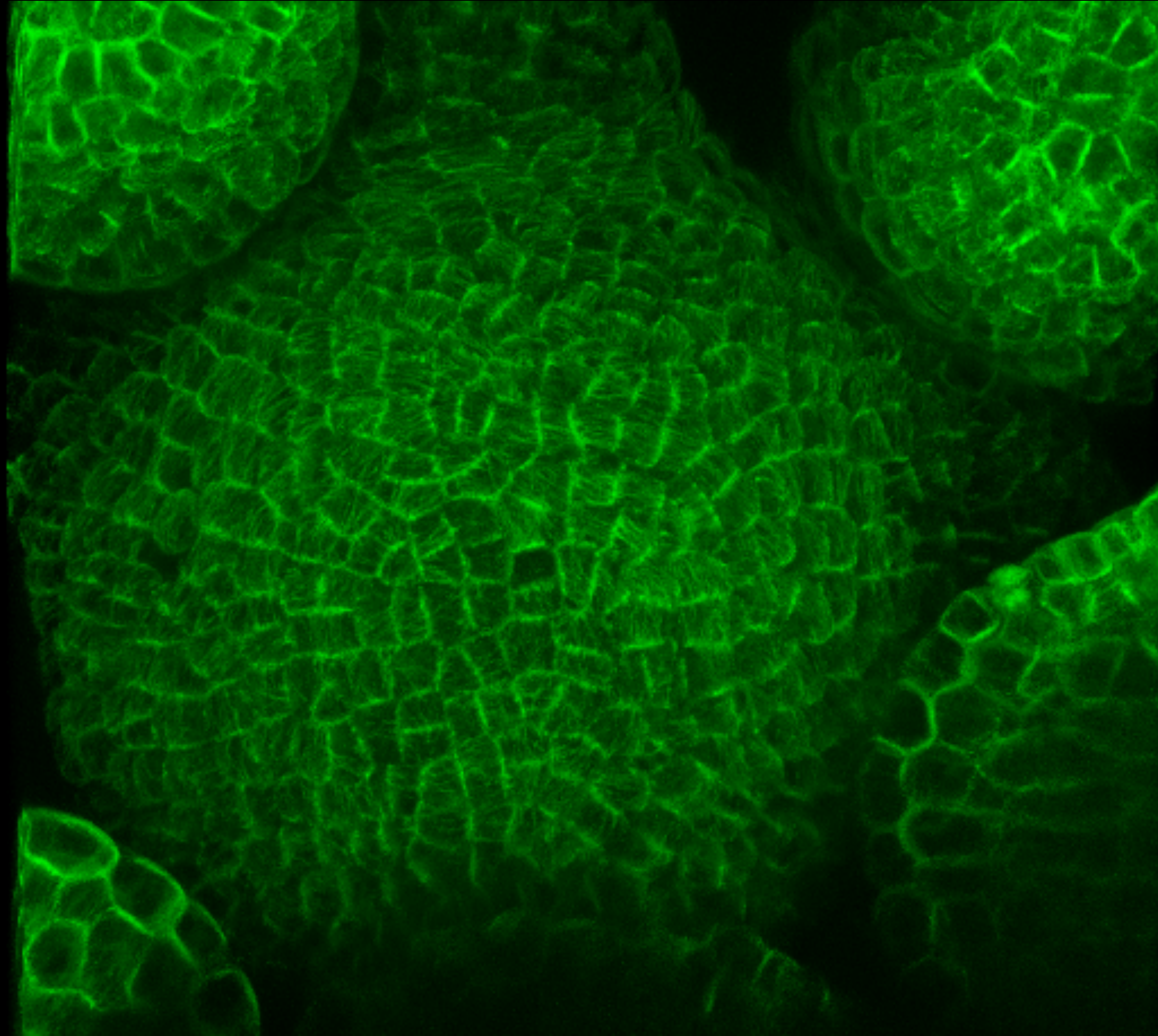


# Stress Pattern in SAM Epidermis



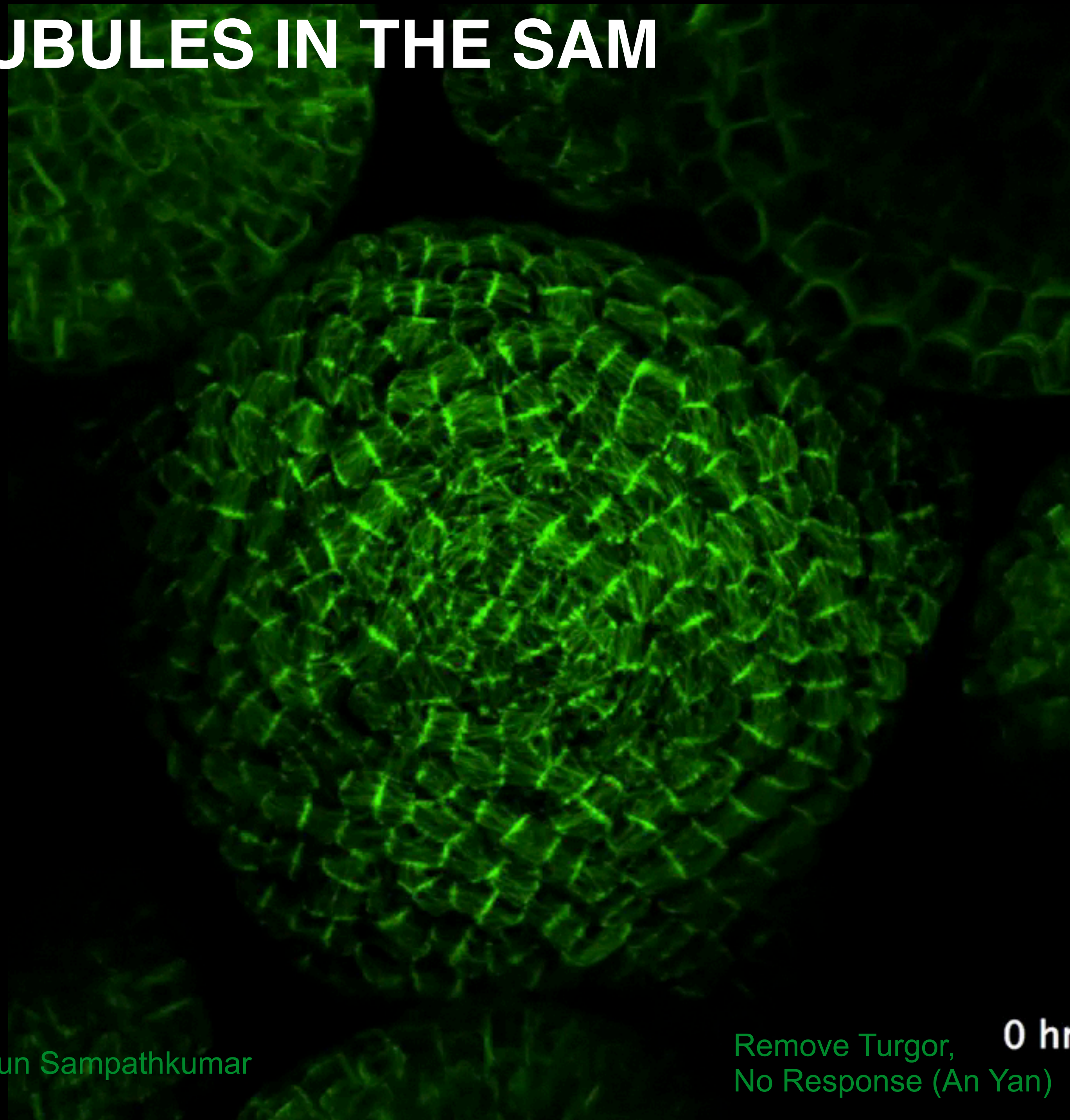
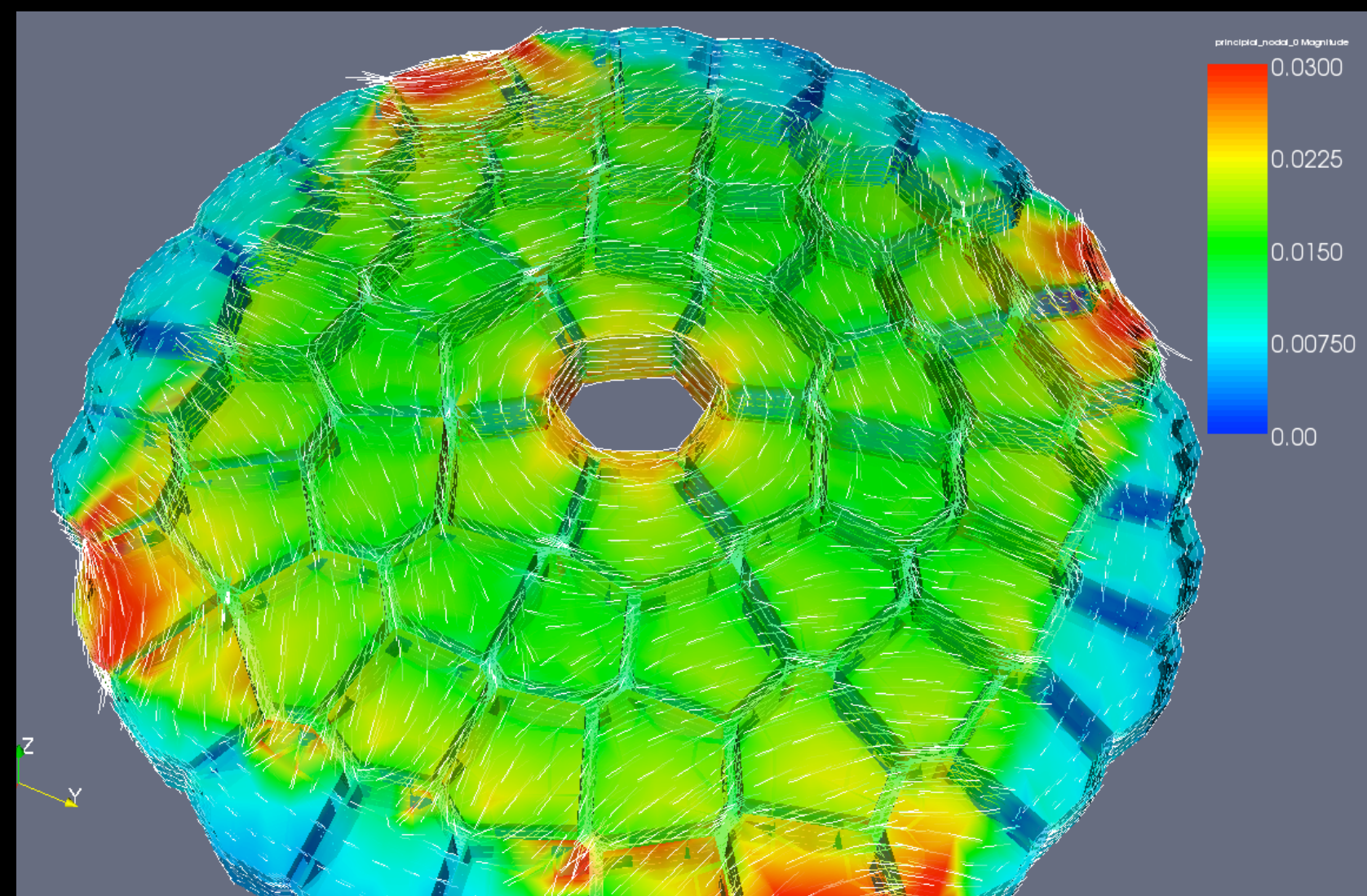
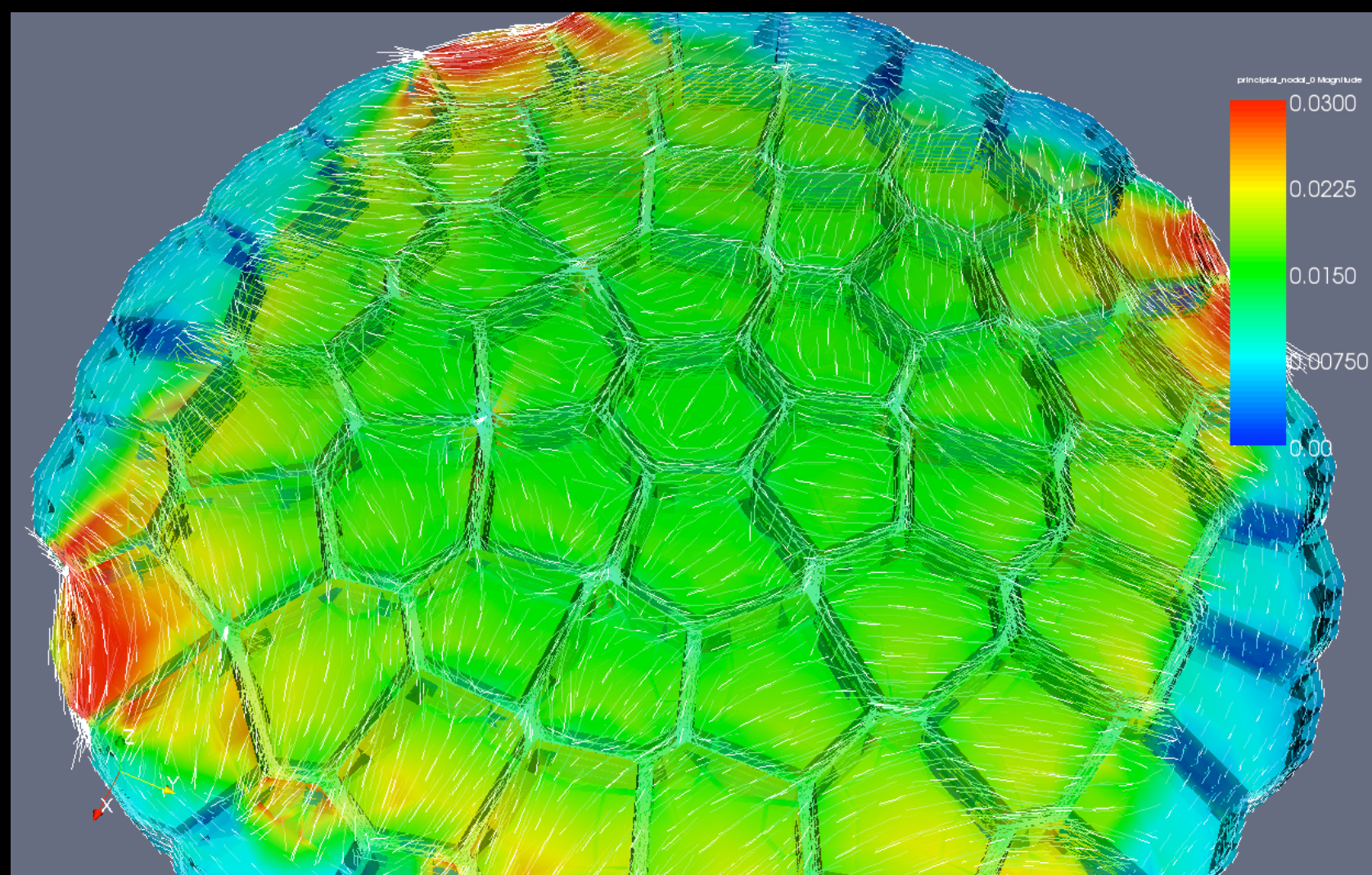


# MICROTUBULES IN THE SAM





# MICROTUBULES IN THE SAM

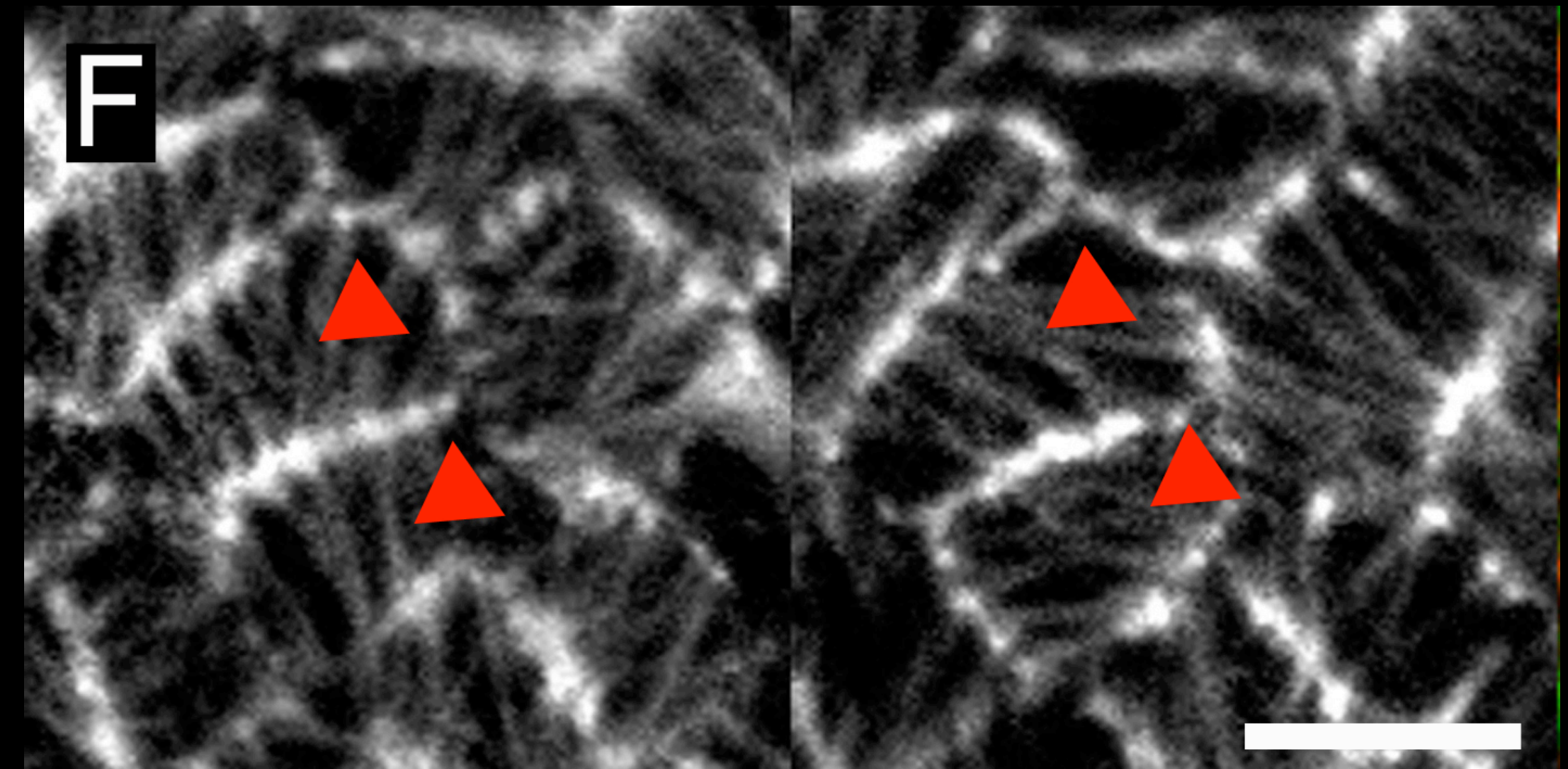
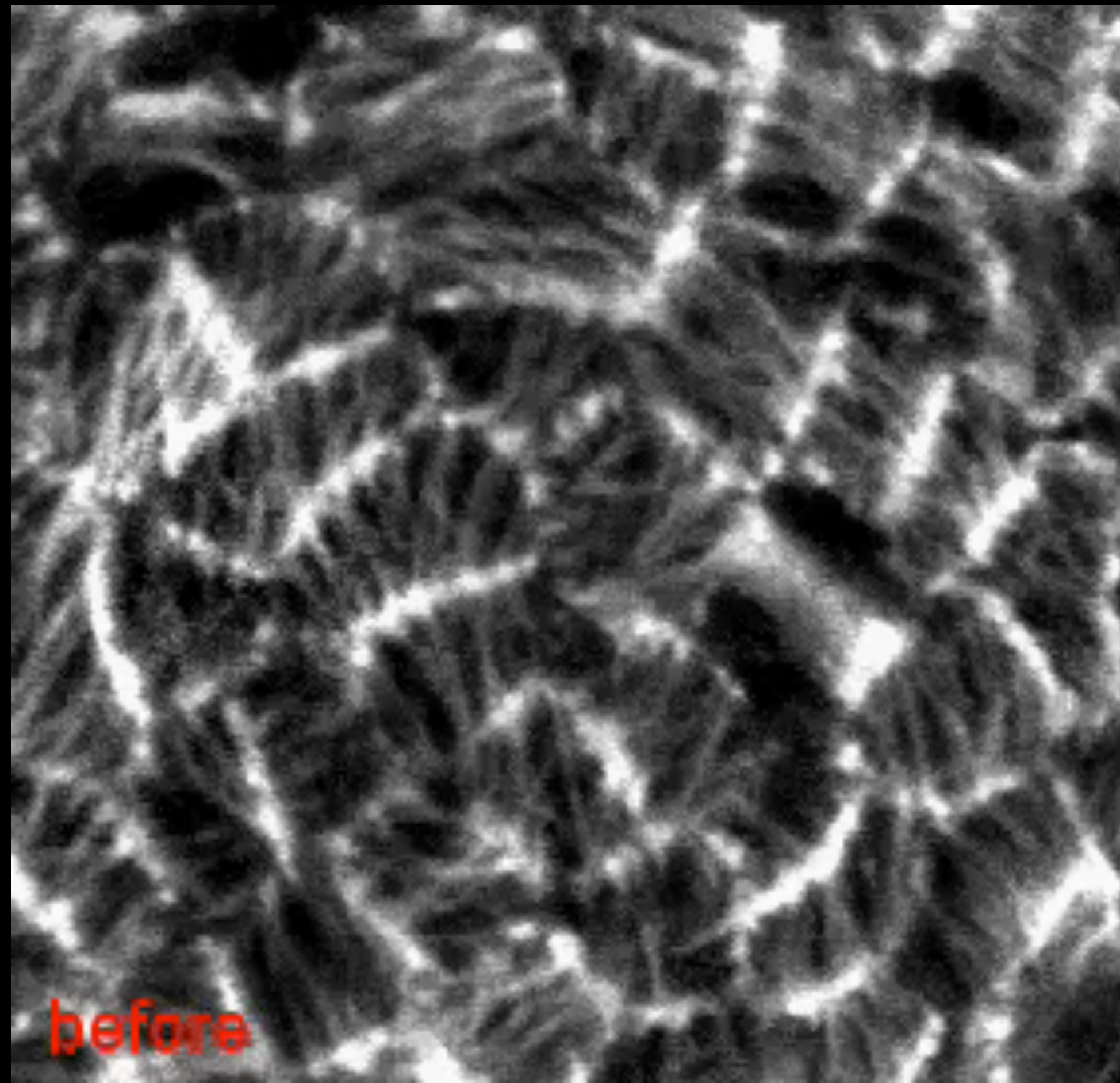
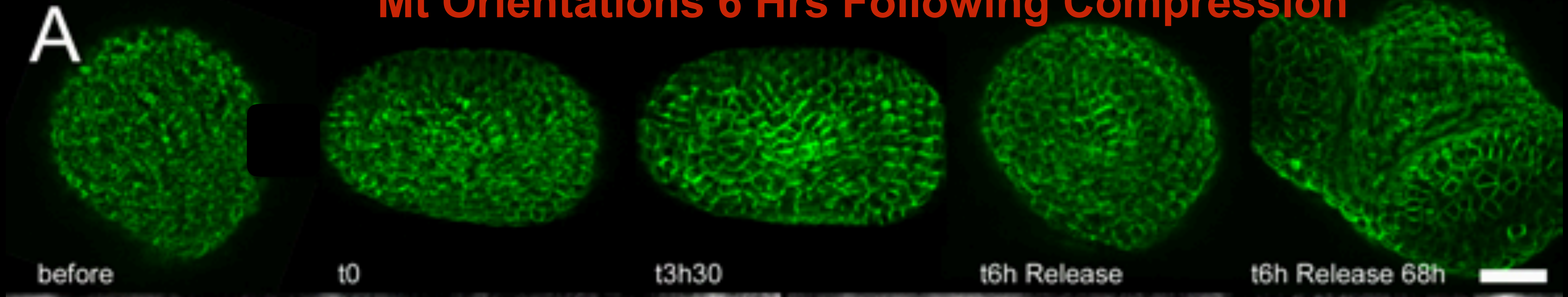


Arun Sampathkumar

Remove Turgor, 0 hr  
No Response (An Yan)



# Mt Orientations 6 Hrs Following Compression

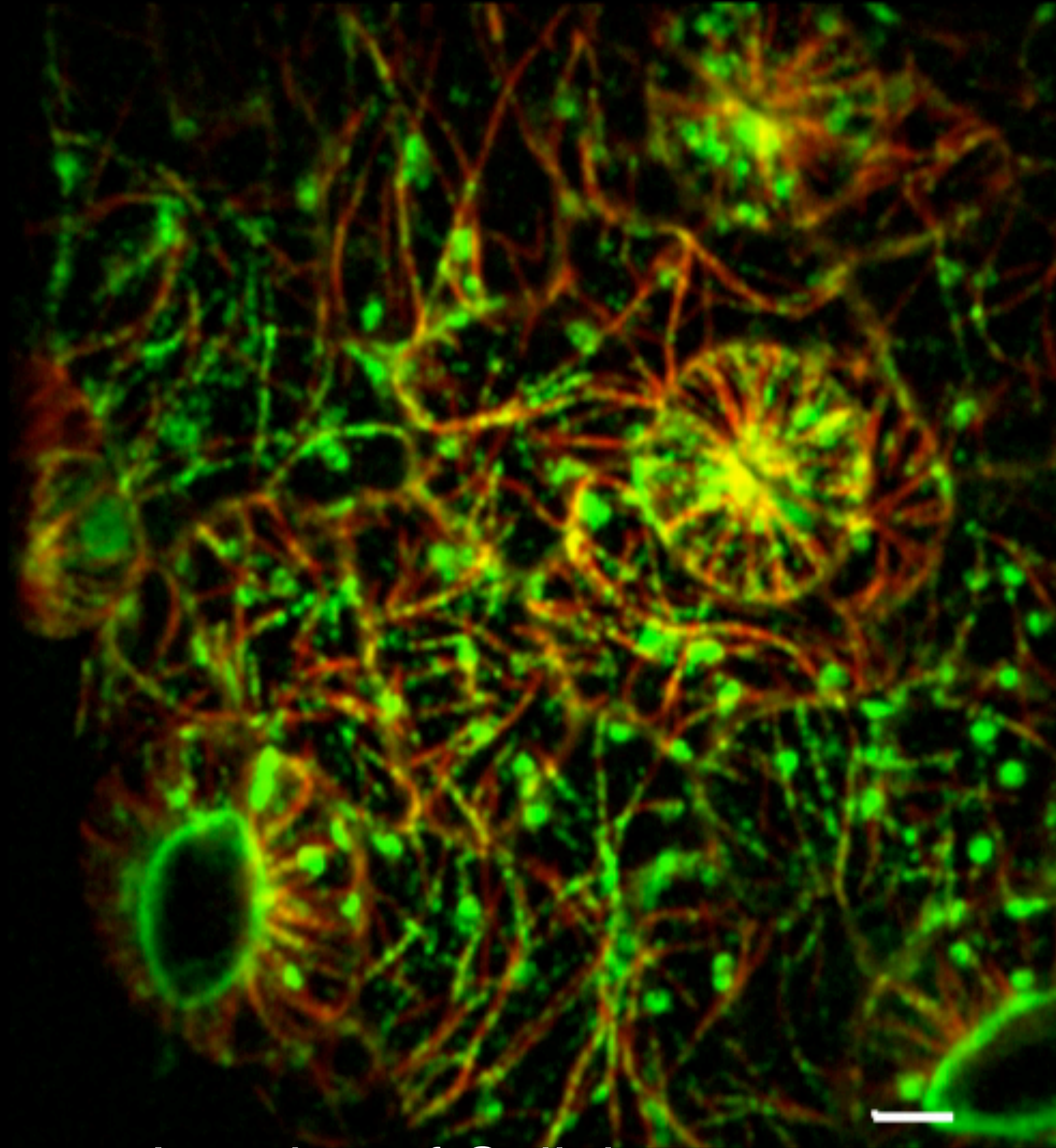


Hamant et al. 2008

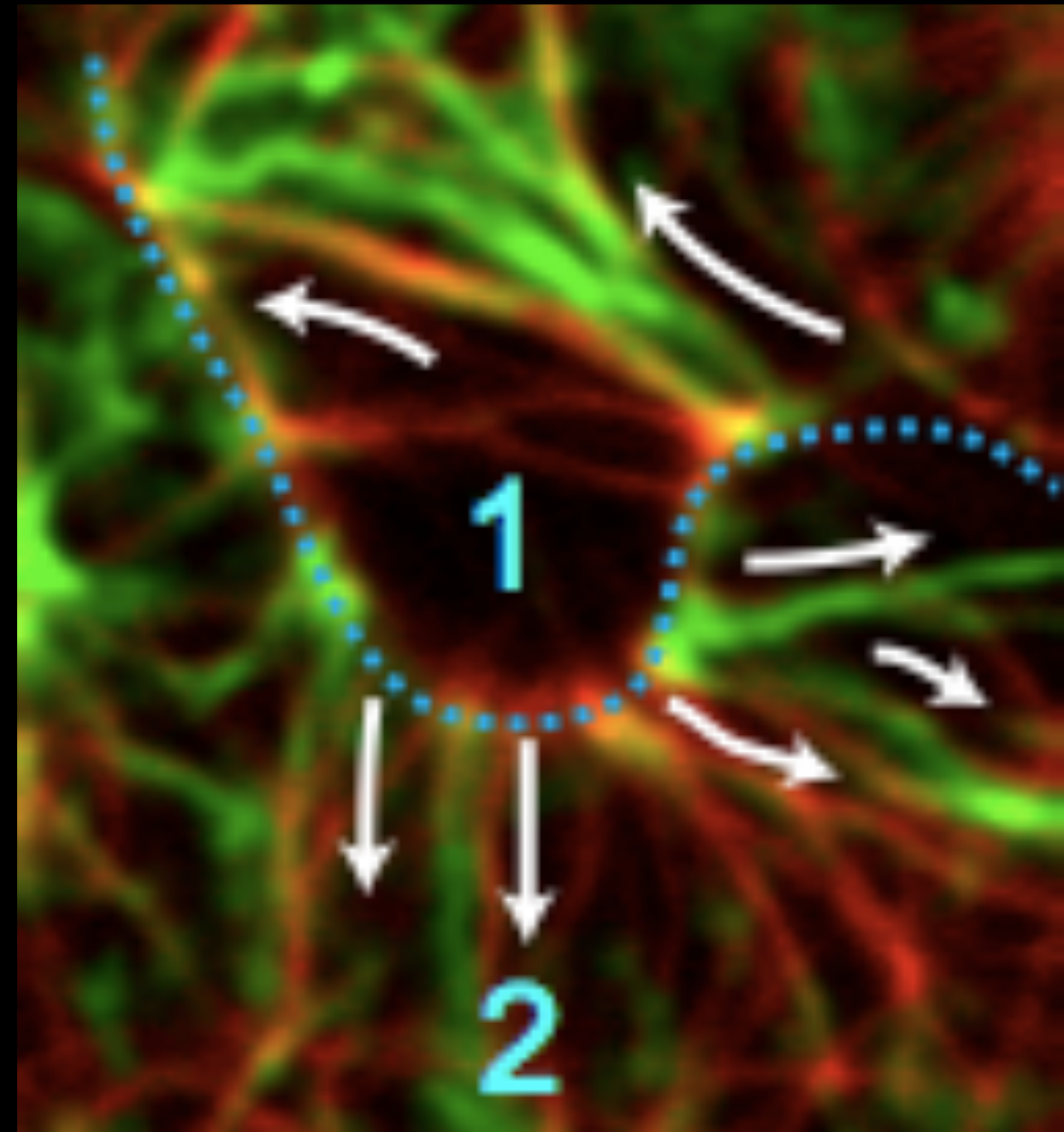


# Cellulose Synthesis Follows Microtubules

mCherry::TUA5 CESA3::GFP



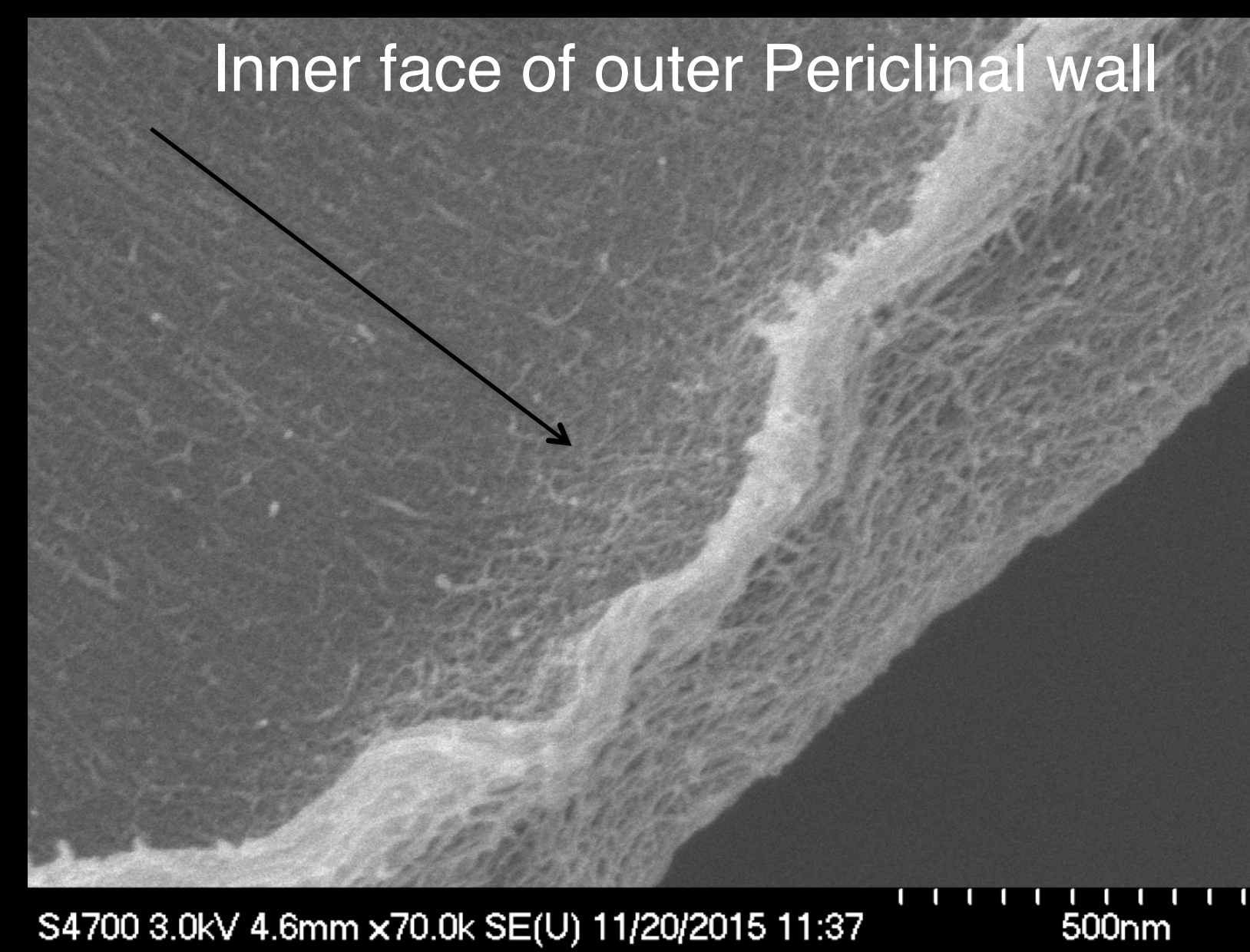
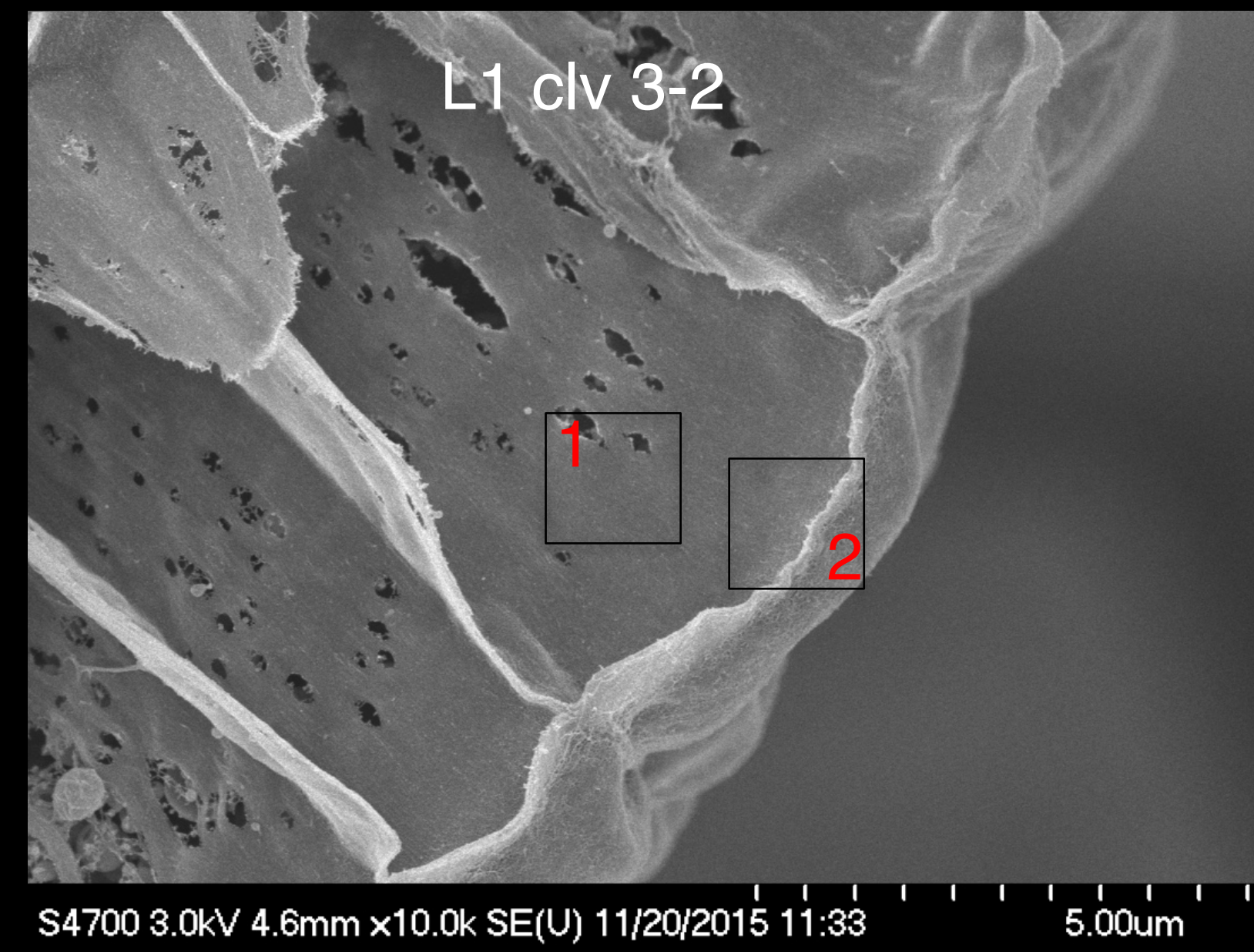
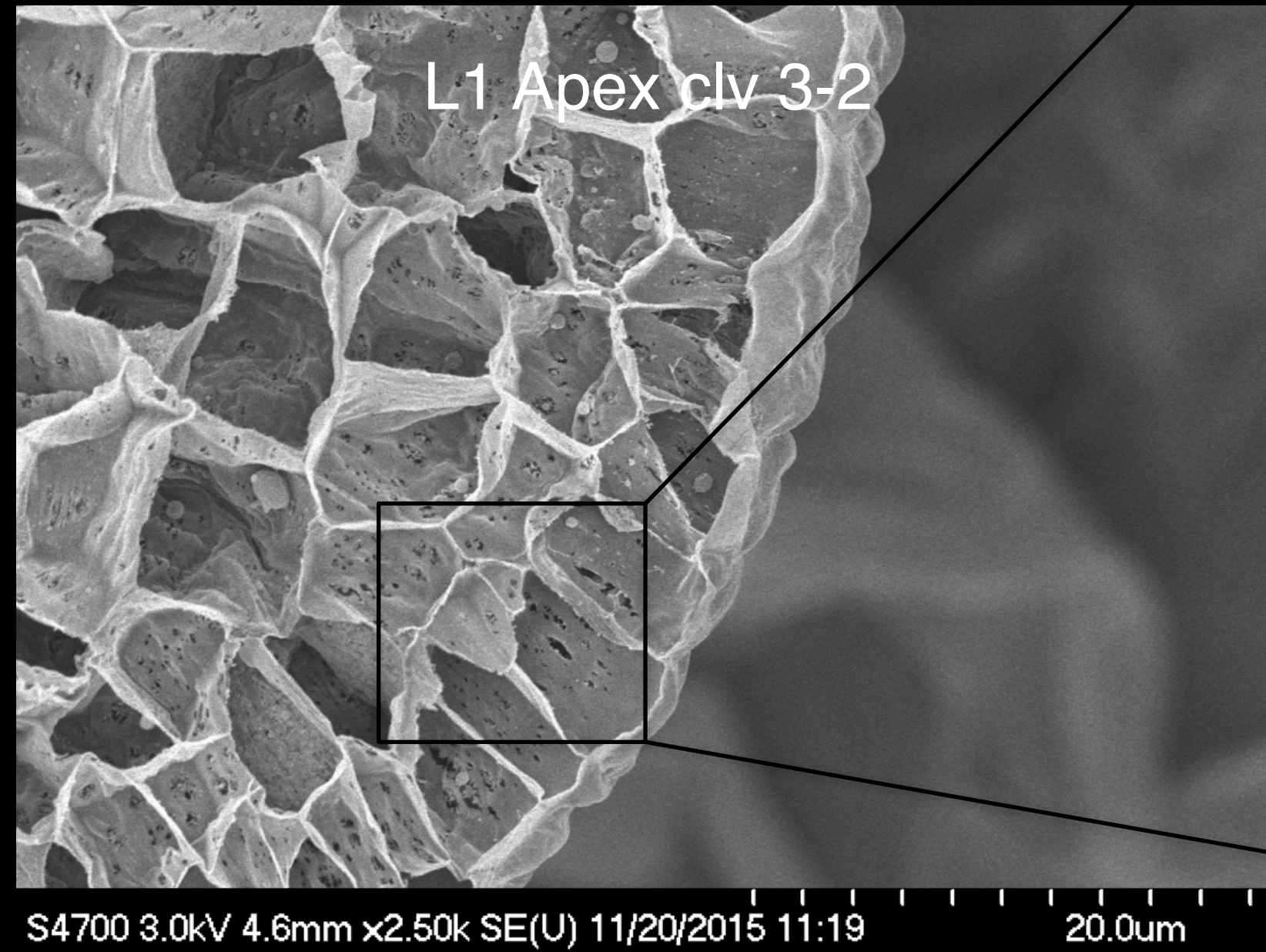
Imaging of Cellulose synthesizing complexes in pavement cells and shoot apical meristem



Arun Sampathkumar with David Ehrhardt (SLCU/Caltech) (Carnegie/Stanford)



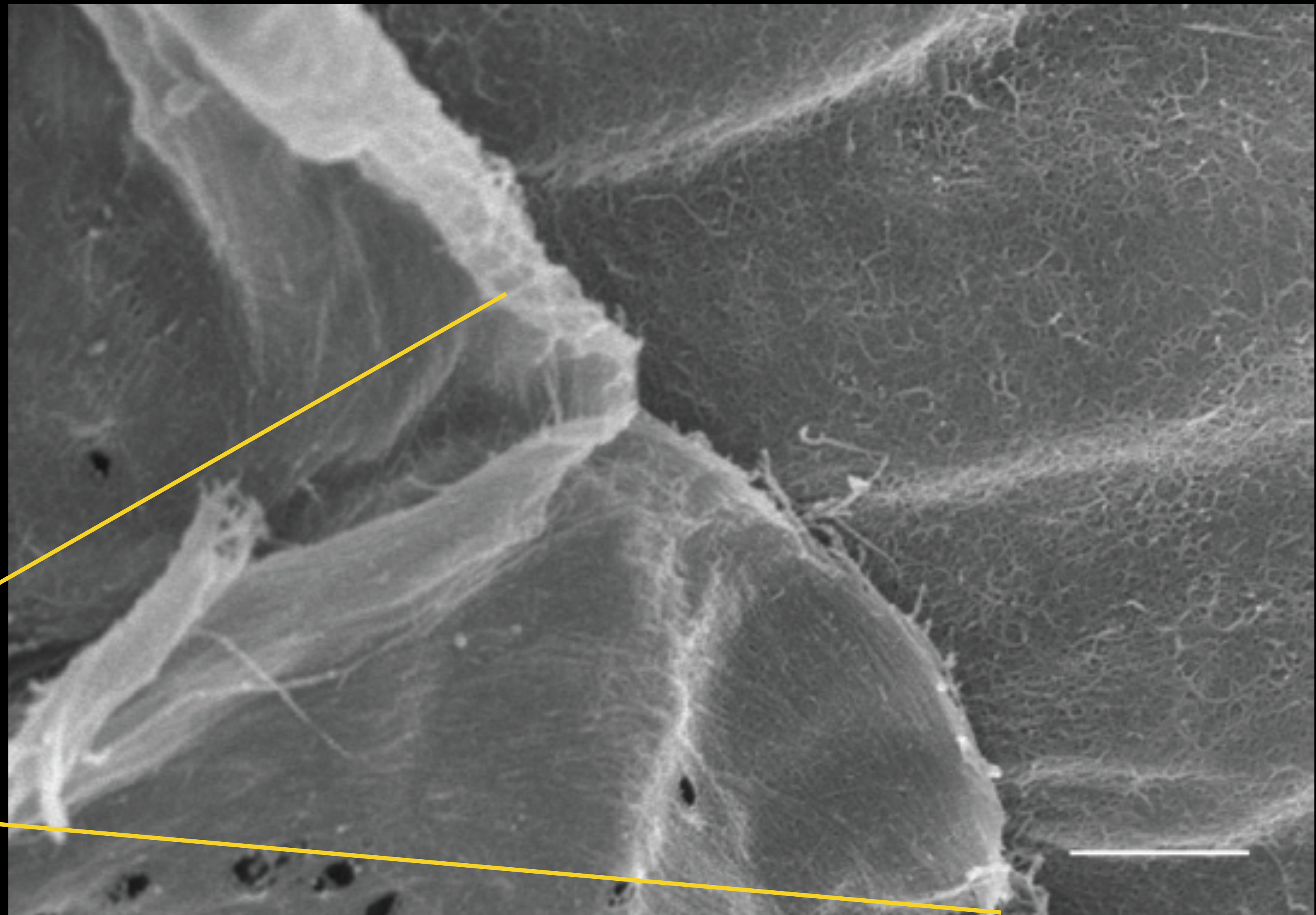
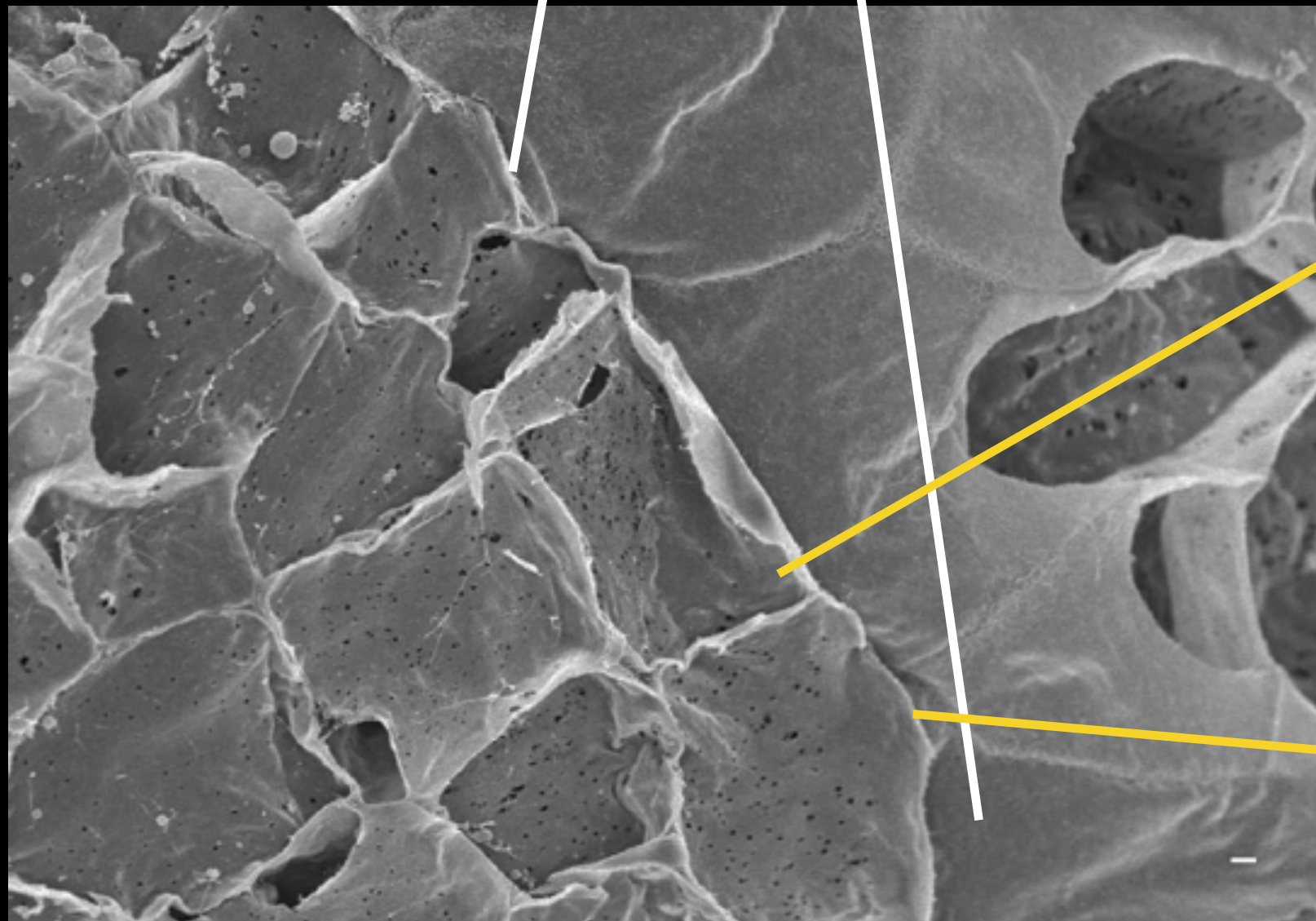
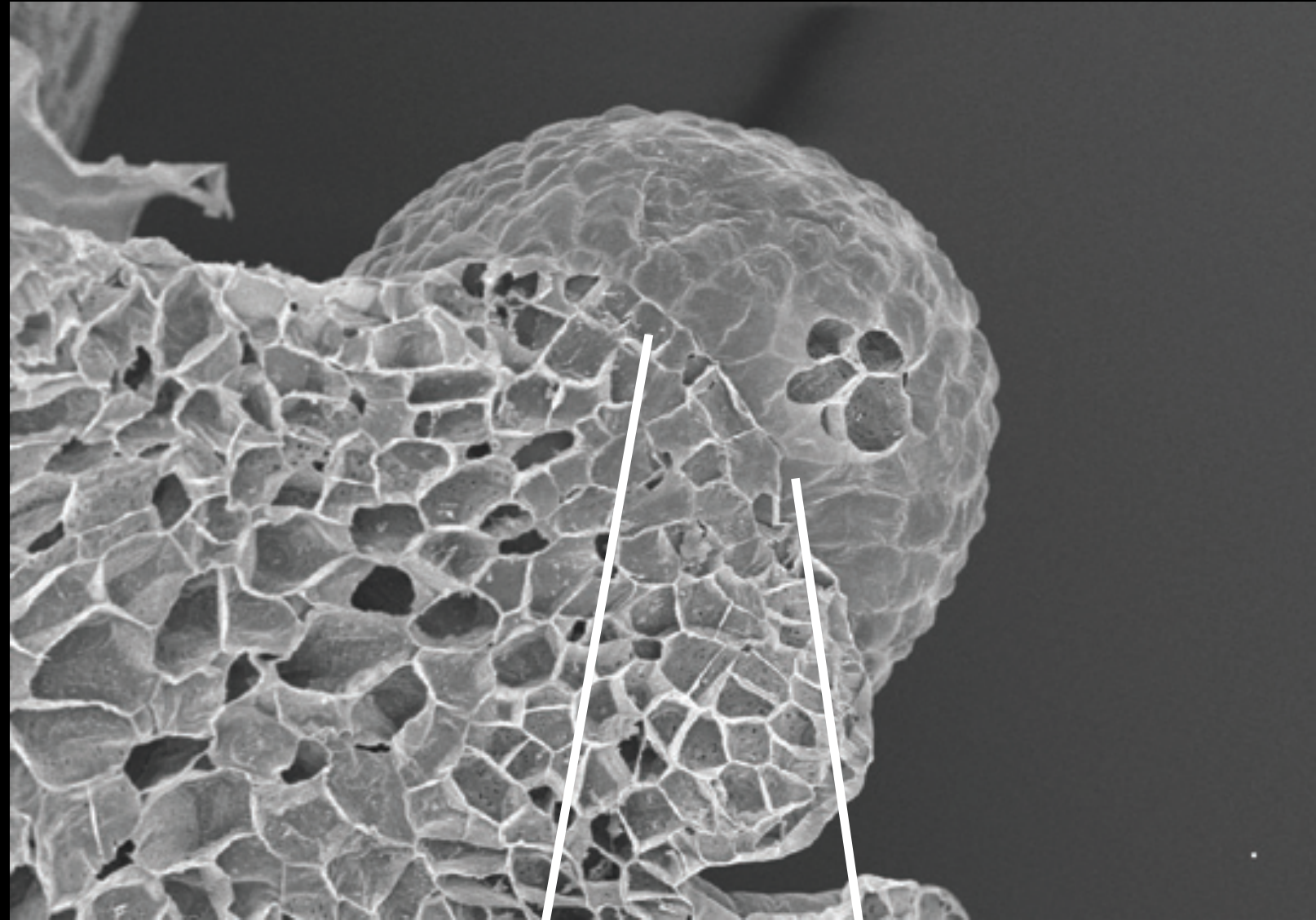
# Field Emission Scanning Electron Microscopy of Cellulose



Hitachi S4700 FESEM



# Field Emission Scanning Electron Microscopy of Cellulose

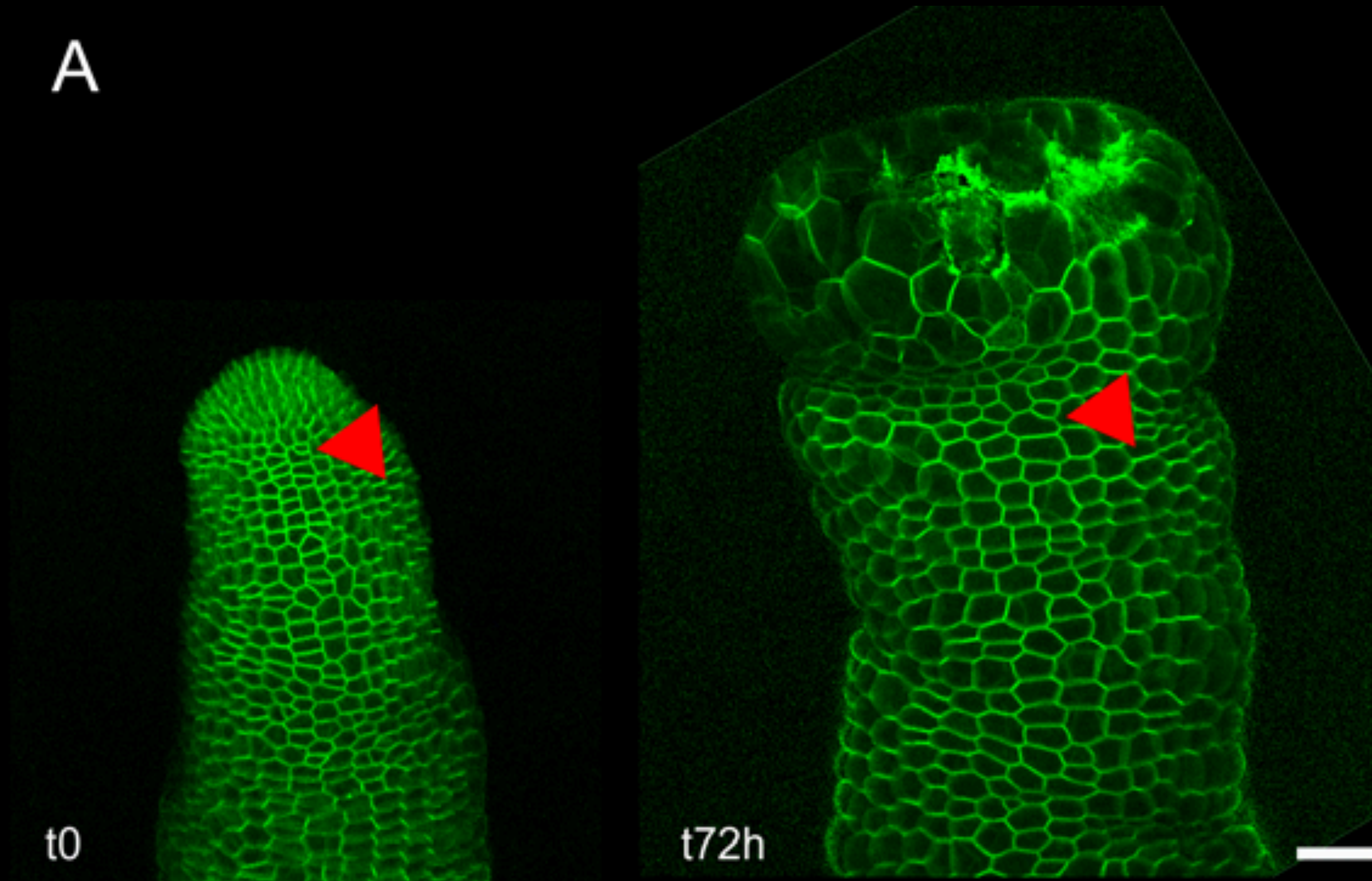




# Depolymerize Microtubules, Shape is Lost

Hamant et al. (2008) Science 322, 1650

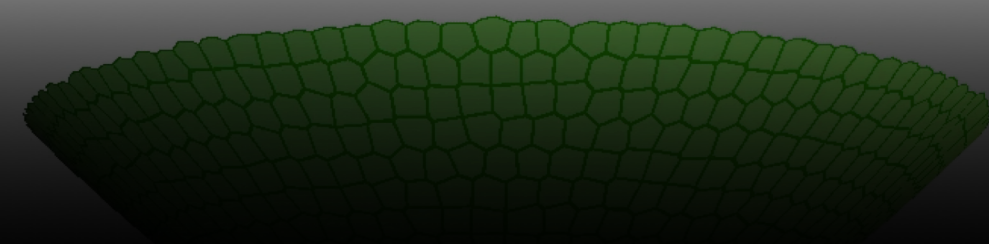
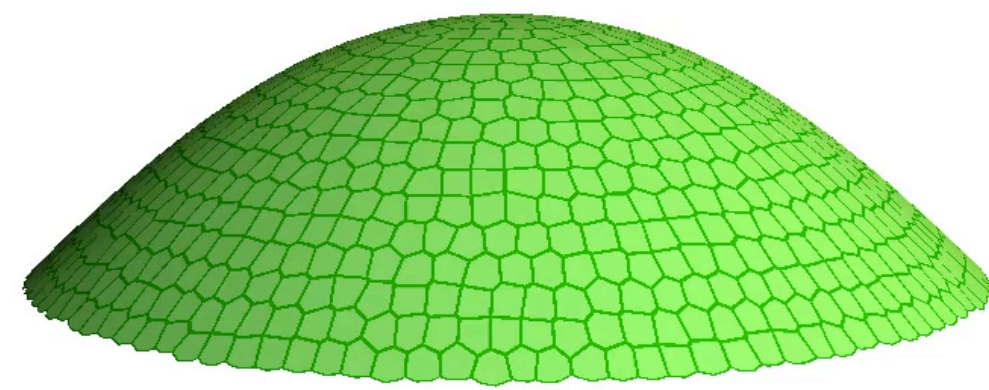
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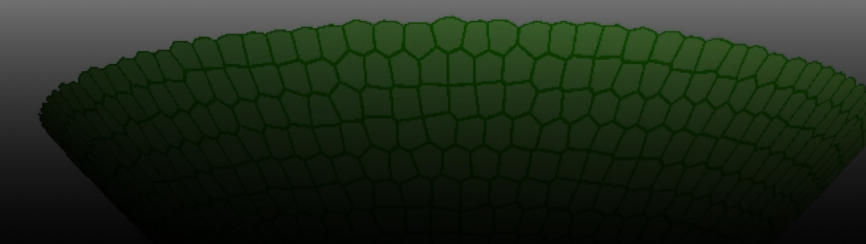
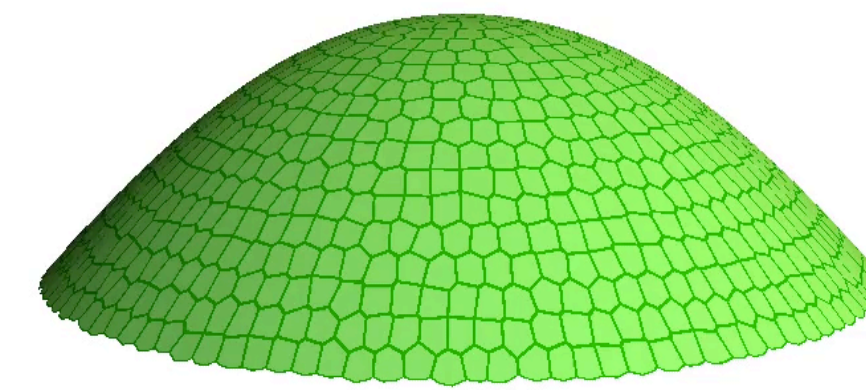




# Development of finite element based model of growth and morphogenesis

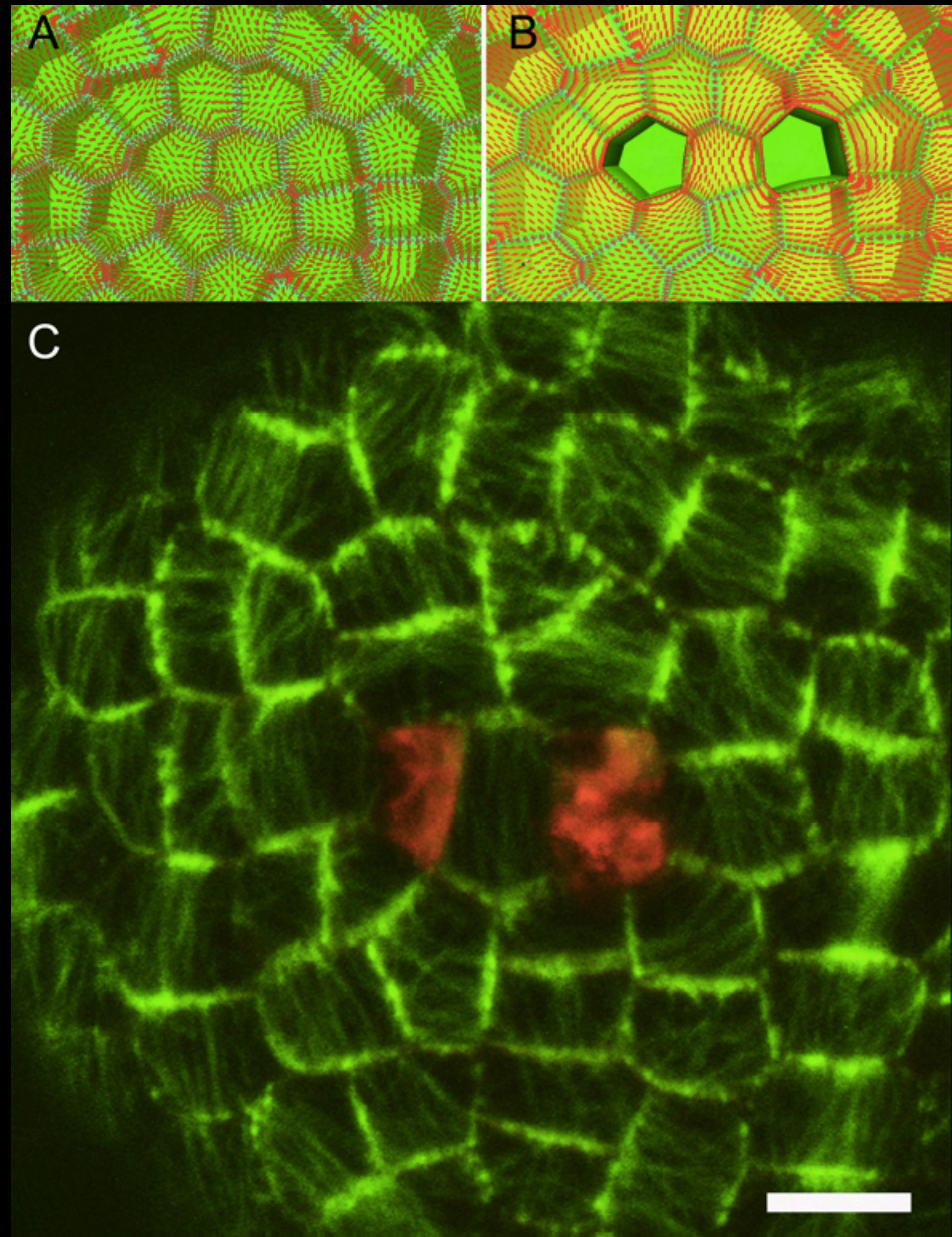


Henrik Jönsson



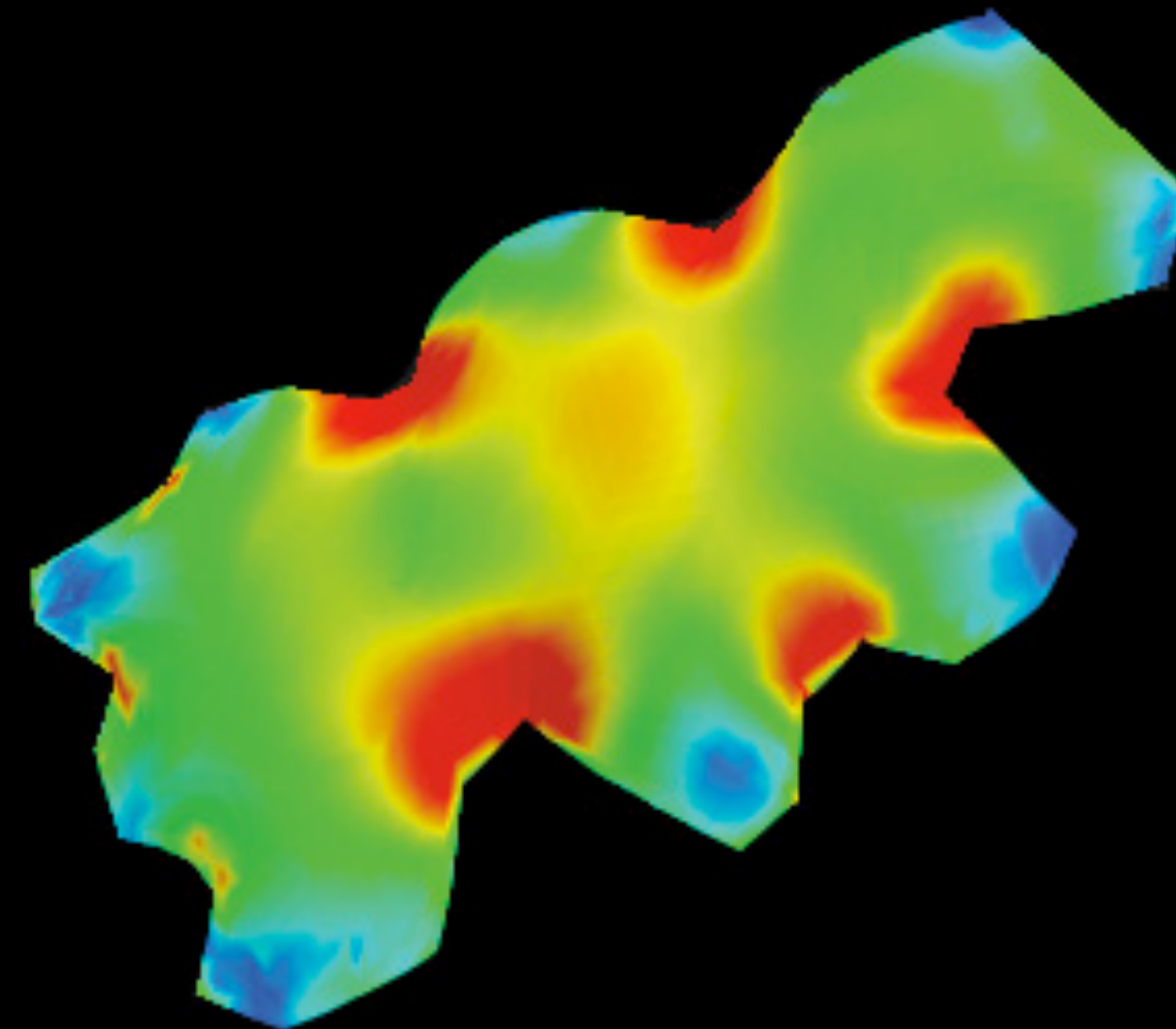
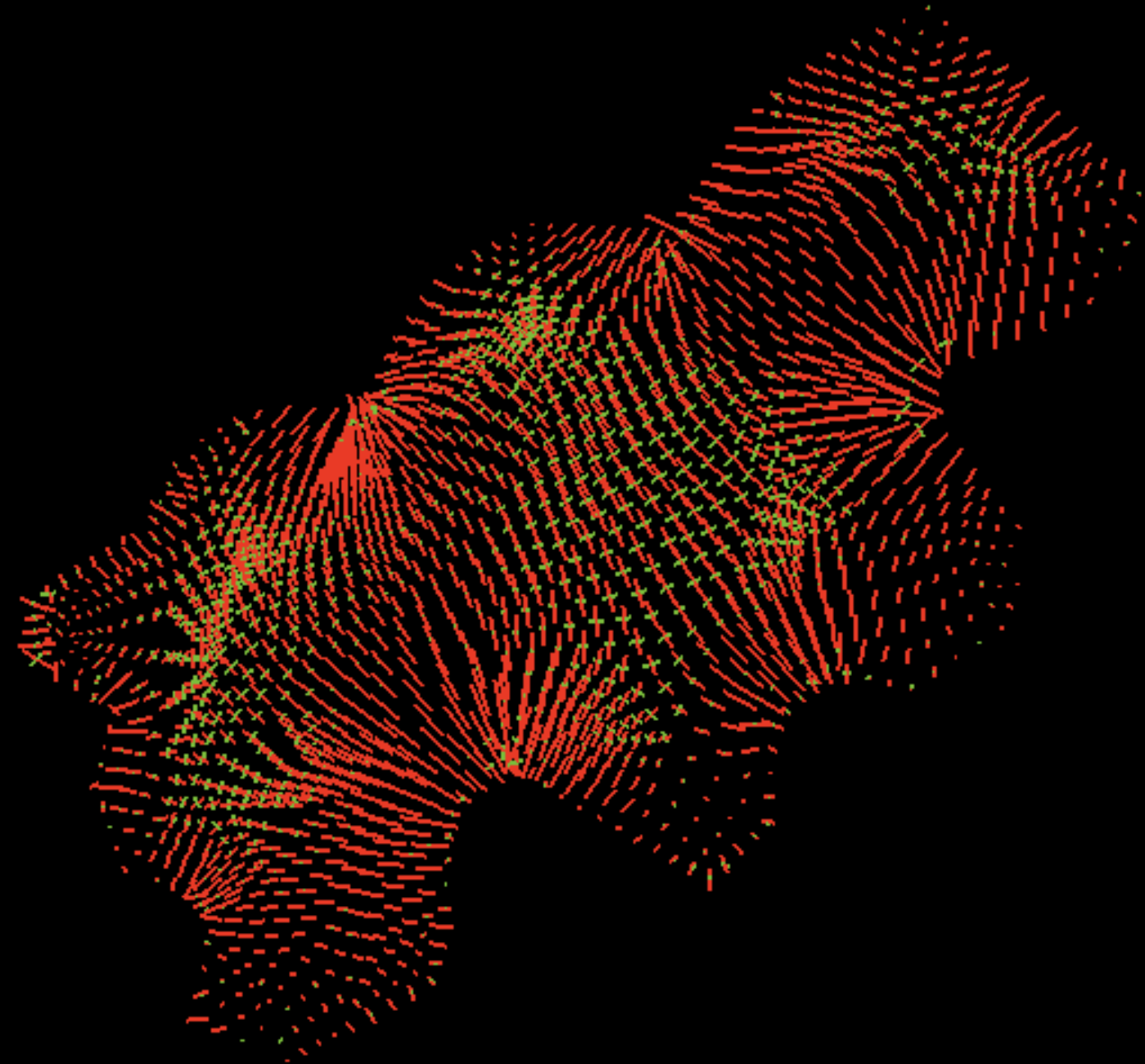
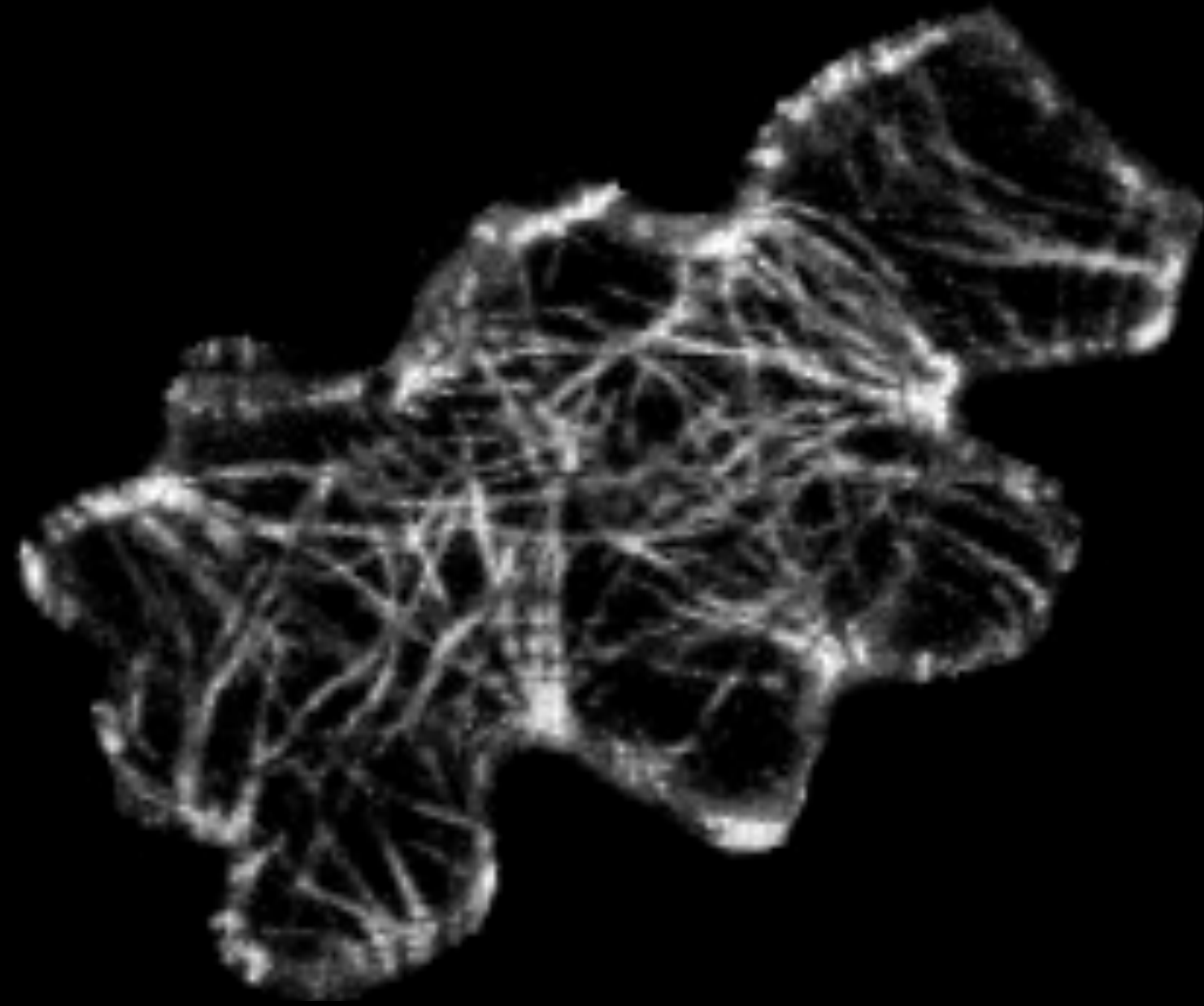


- Stress is generated by tissue shape and an epidermis in tension
- This mechanical stress controls the cytoskeleton, and thus cellulose direction in the walls
- Cellulose controls subsequent cell expansion, which in turn changes the stress pattern
- TISSUE SHAPE IS SENSED LOCALLY BY CELLS, LEADING TO FUTURE CHANGES IN



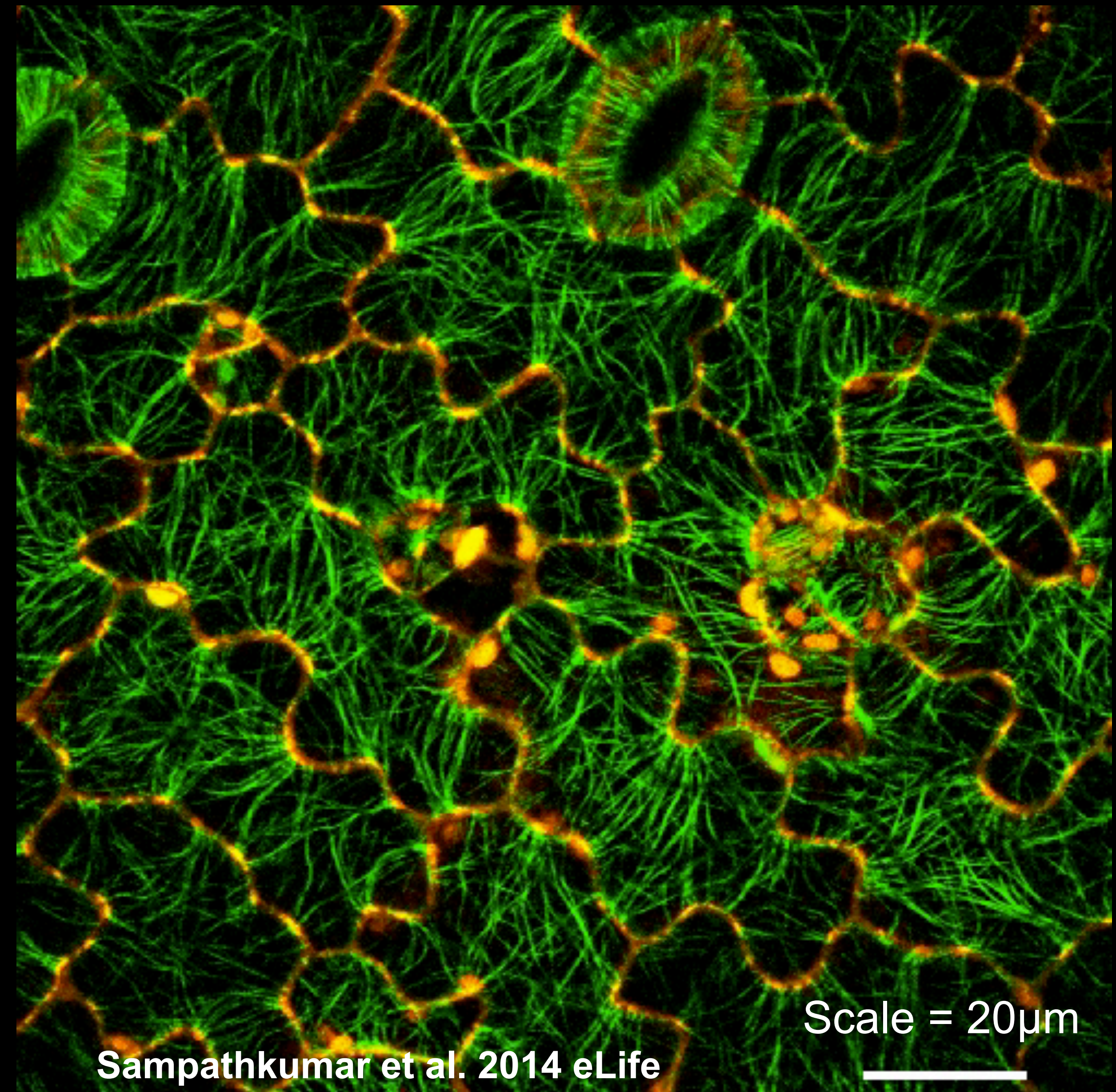
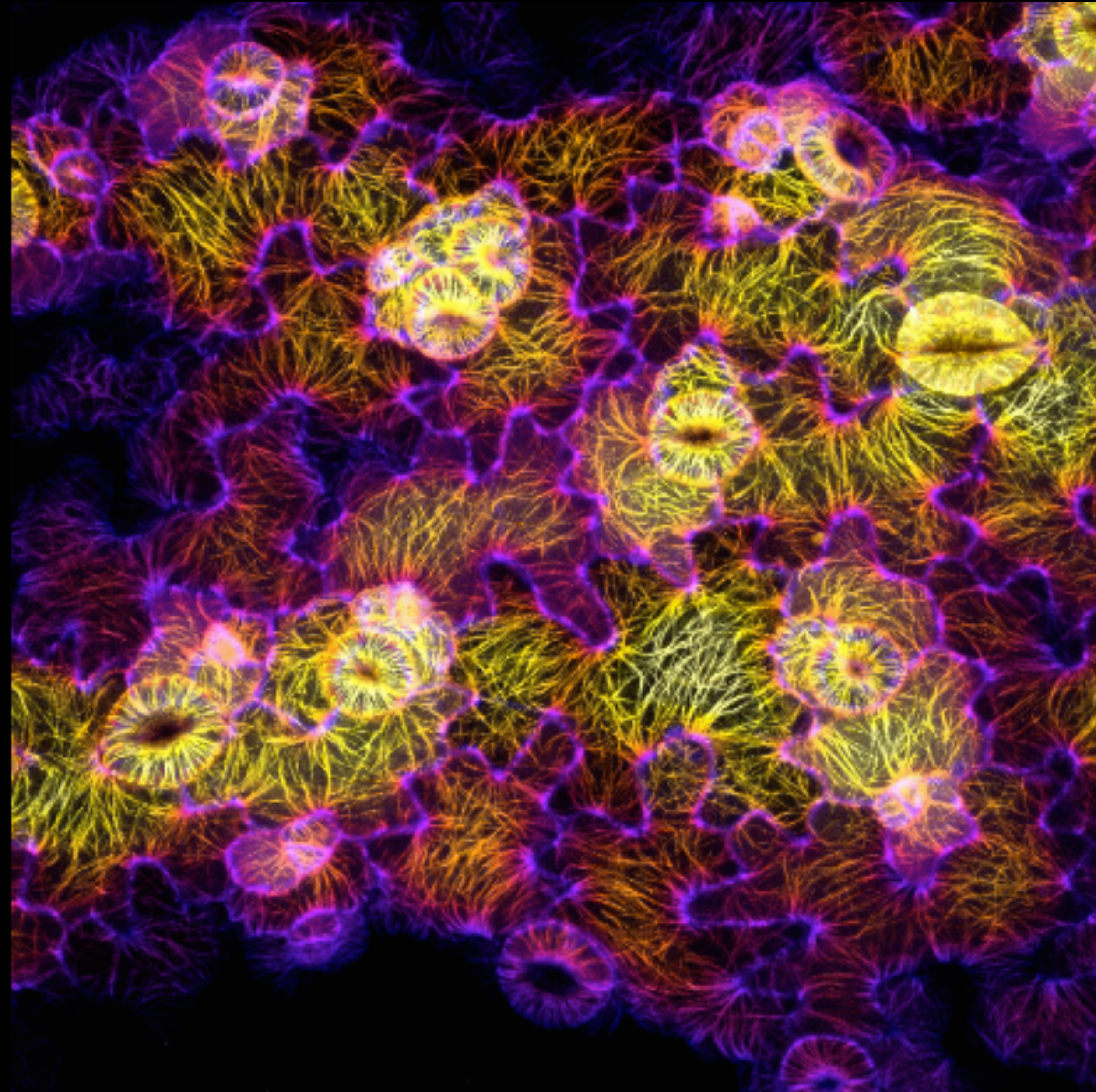


MICROTUBULE PATTERNS  
CORRESPOND TO PHYSICAL  
STRESS PATTERNS - EVEN  
SUBCELLULAR



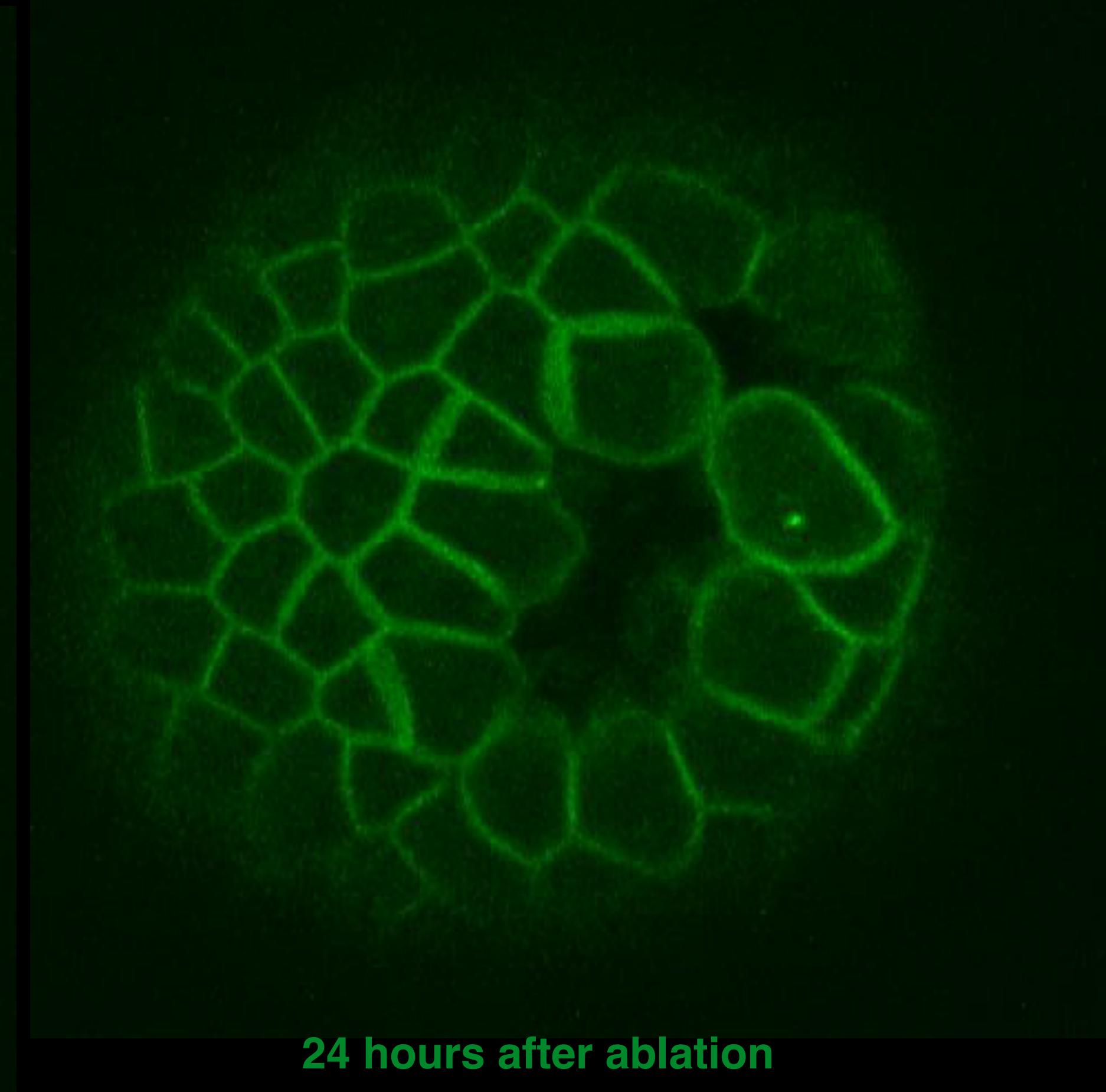
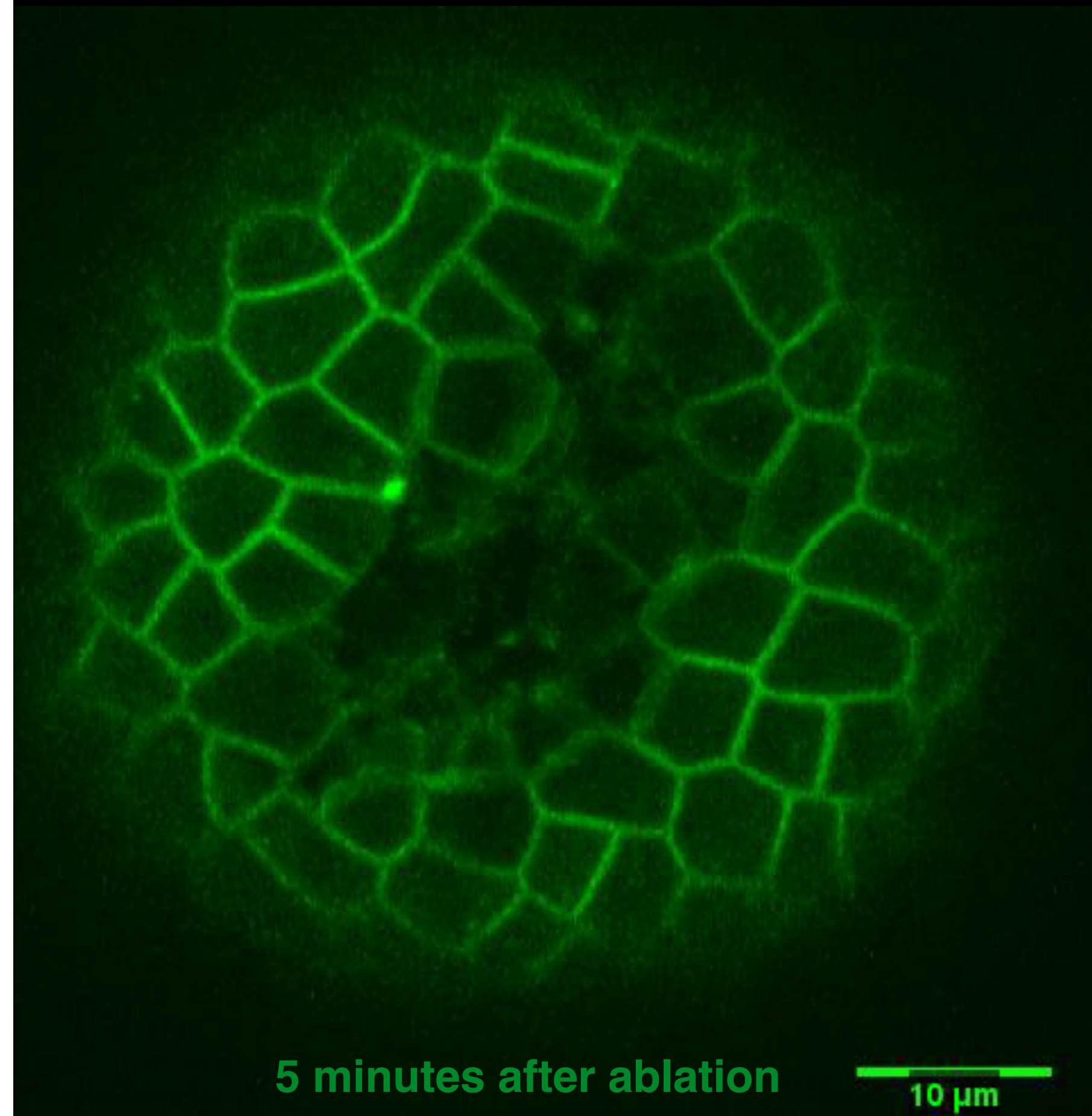
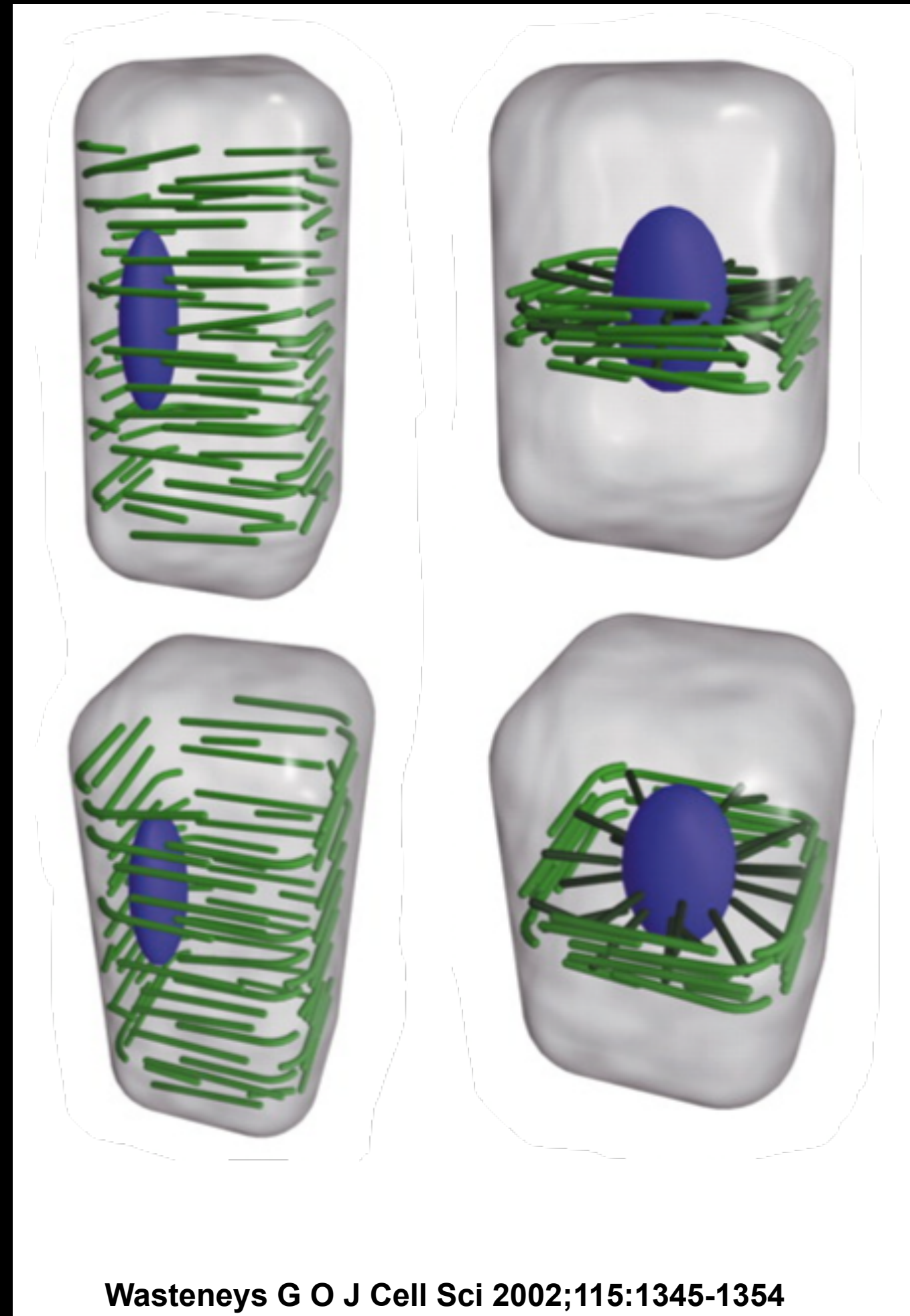


# Re-Orientation of Cortical Microtubules in the Presence of Mechanical Stress - Laser Ablation





# Microtubules and therefore tissue shape determine cell division





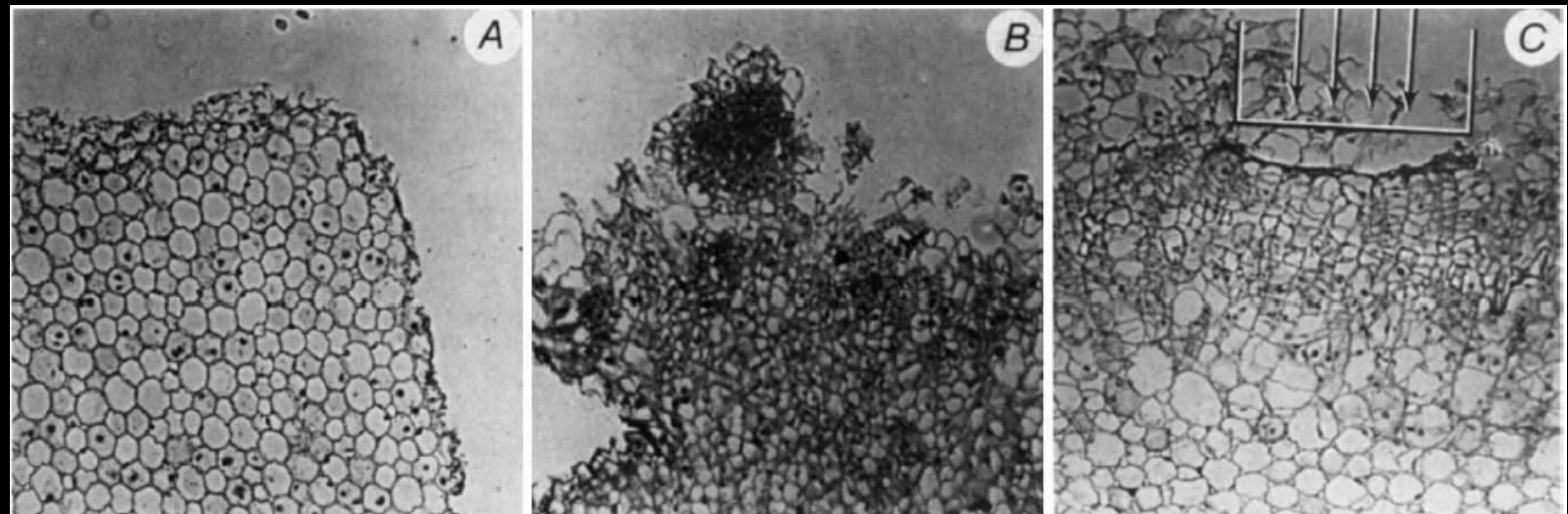
# THAT PHYSICAL STRESS IN PLANT TISSUES CONTROLS CELL DIVISION WAS SHOWN

Kny (1896) Ber. d. bot. Gess. 398 (*Equisetum* spores)  
(1901) Jahrb. f. wiss. Bot. 37, 55 (*Impatiens* pith)



**Stress-induced alignment of division plane in plant tissues grown *in vitro***

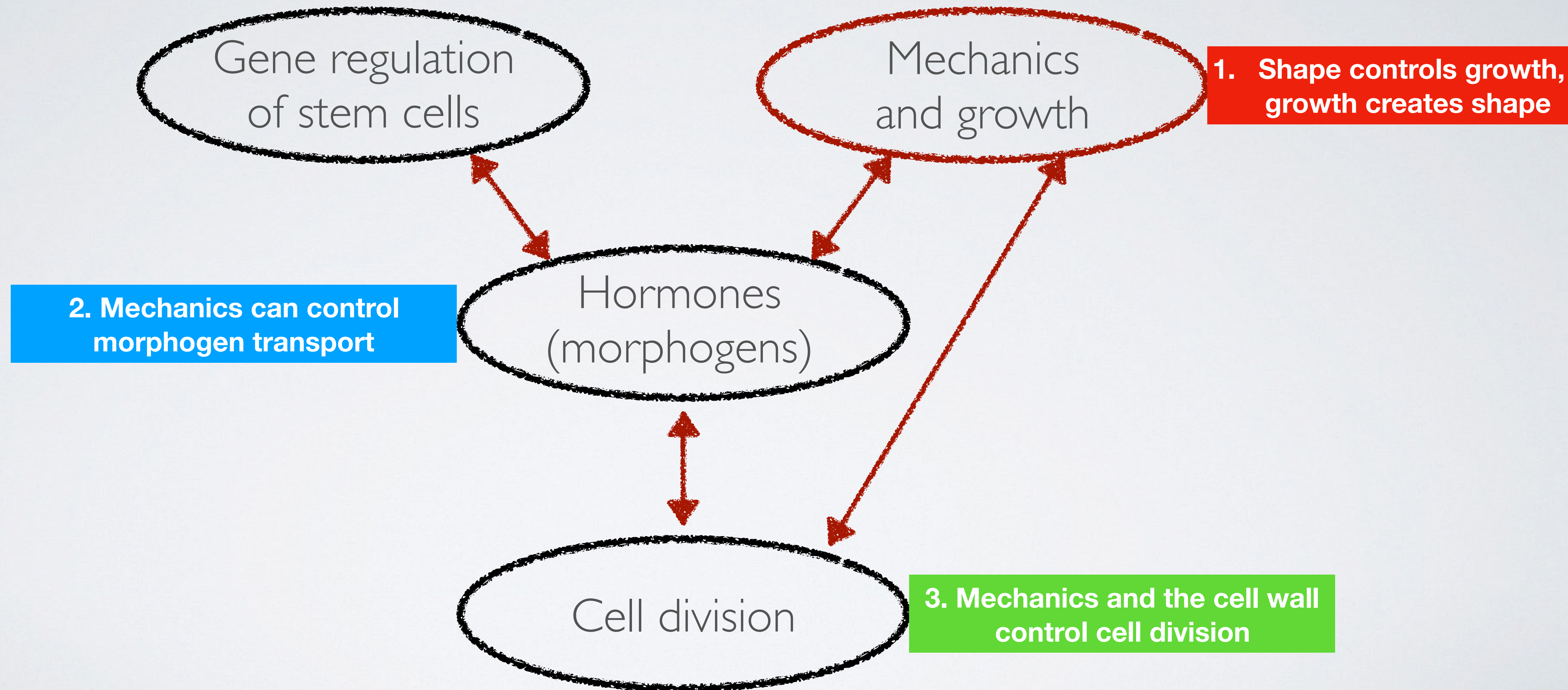
Philip M. Lintilhac & Thompson B. Vesecky (1984) Nature 307, 363:





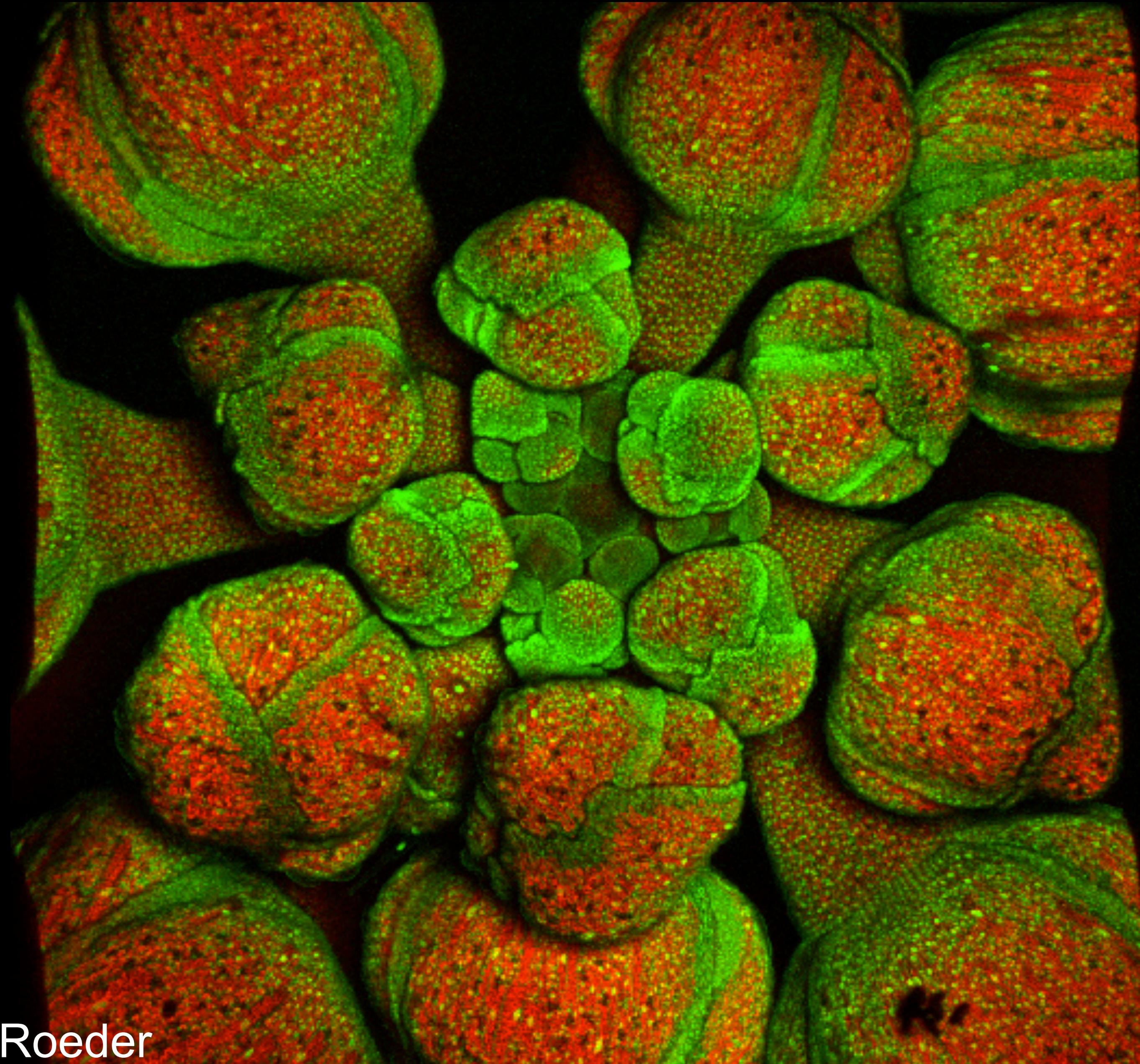
# COMPUTATIONAL MORPHODYNAMICS

0. Introduction to plant growth (brief)



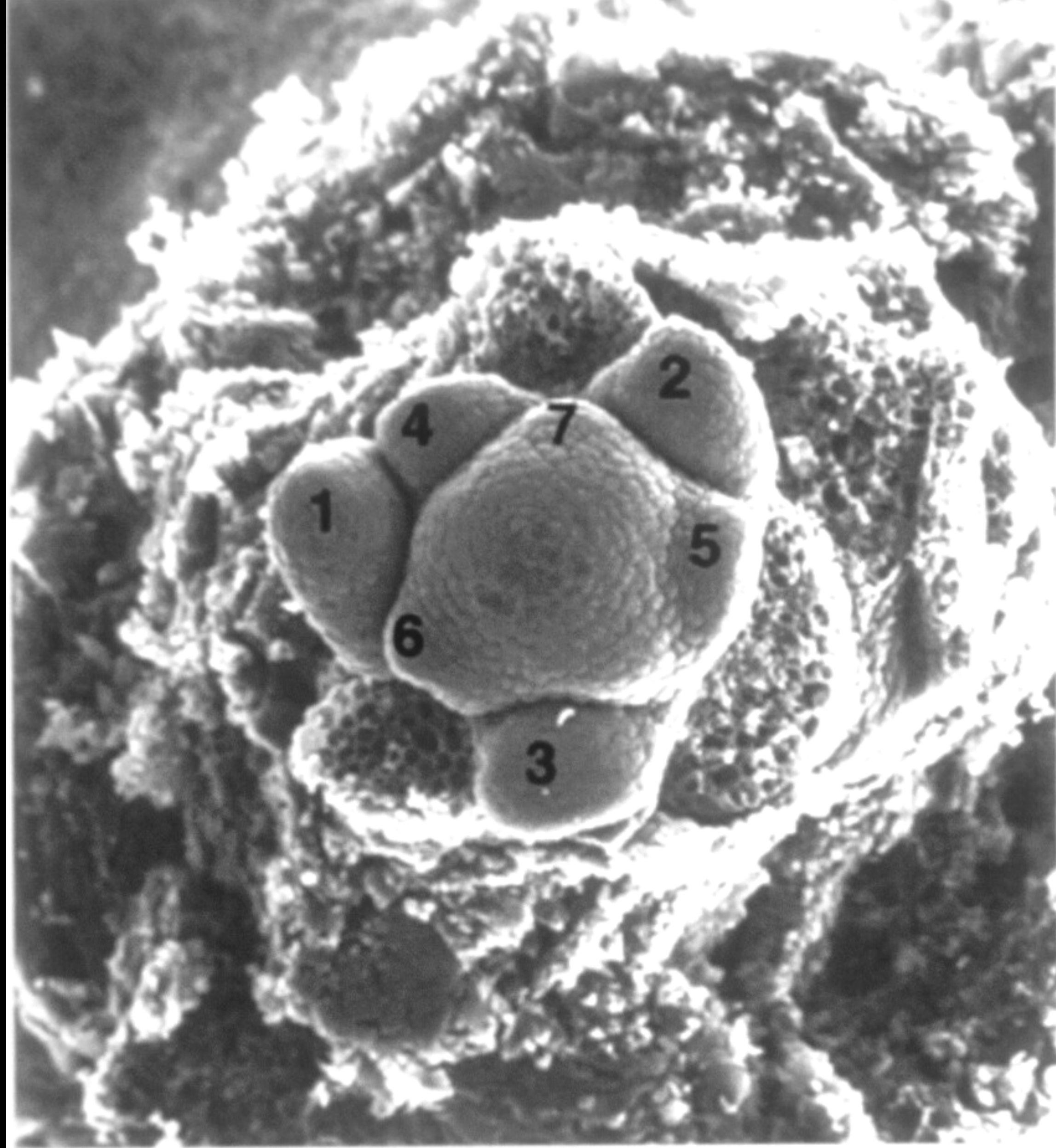


# Arabidopsis Phyllotaxis

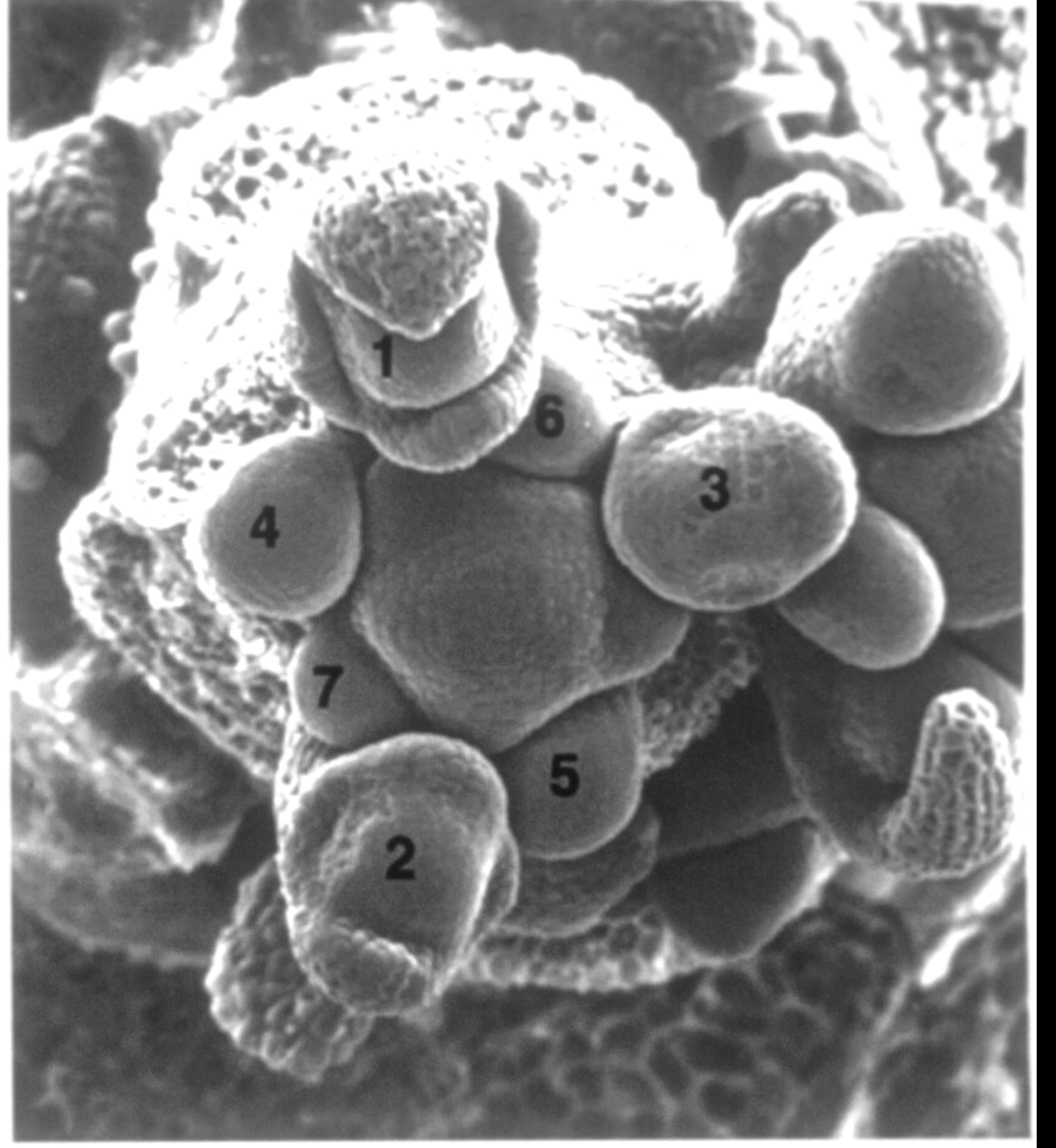


Adrienne Roeder





Vegetative SAM



Inflorescence SAM



# SPIRAL PHYLLOTAXIS

Hofmeister, W.(1868) Handbuch der physiologischen Botanik; Band 1, Abteilung 2, Allgemeine Morphologie der Gewächse (W. Engelmann, Leipzig), pp 405–664

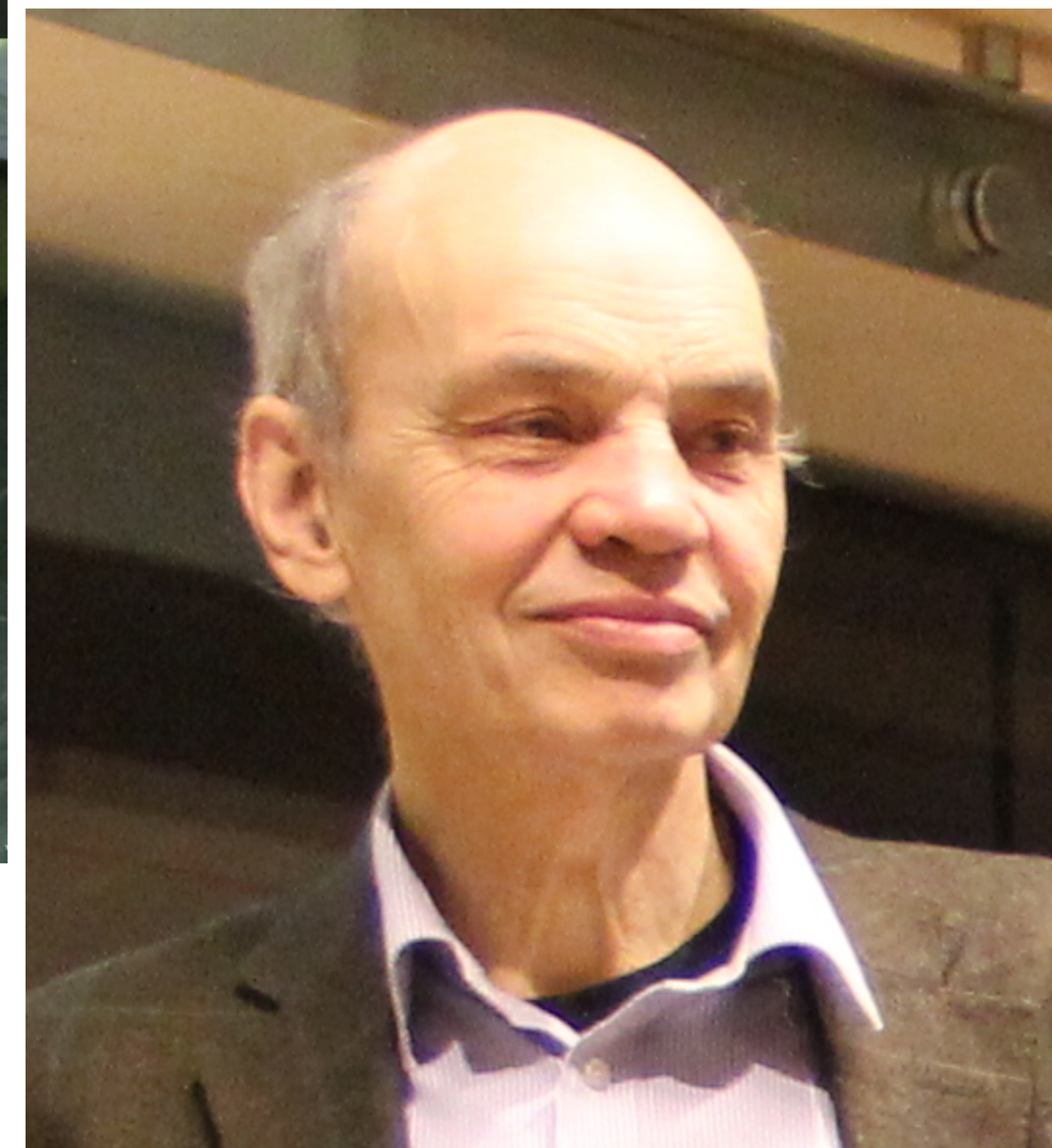


Turing, 1952 The Chemical Basis of Morphogenesis, Phil. Trans. Roy. Soc. B 237, 37-72





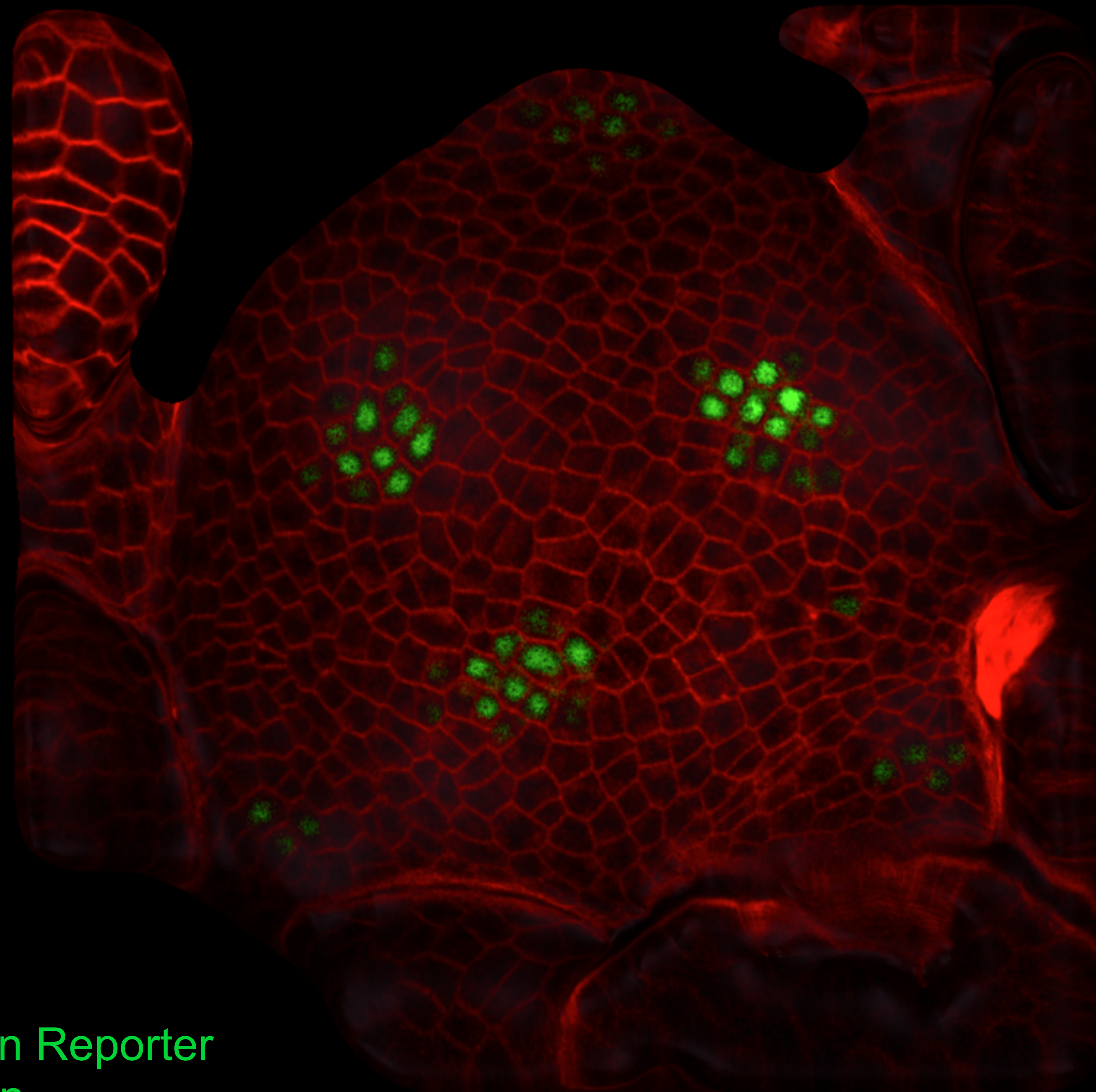
# SPIRAL PHYLLOTAXIS



Douady and Couder (1992) *Physical Review Letters* **68**, 2098  
Douady and Couder (1998) *J. Theor. Biol.* **178**, 255

Mitchison G.J. 1977 *Phyllotaxis and the Fibonacci series. Science*, **196**, 270





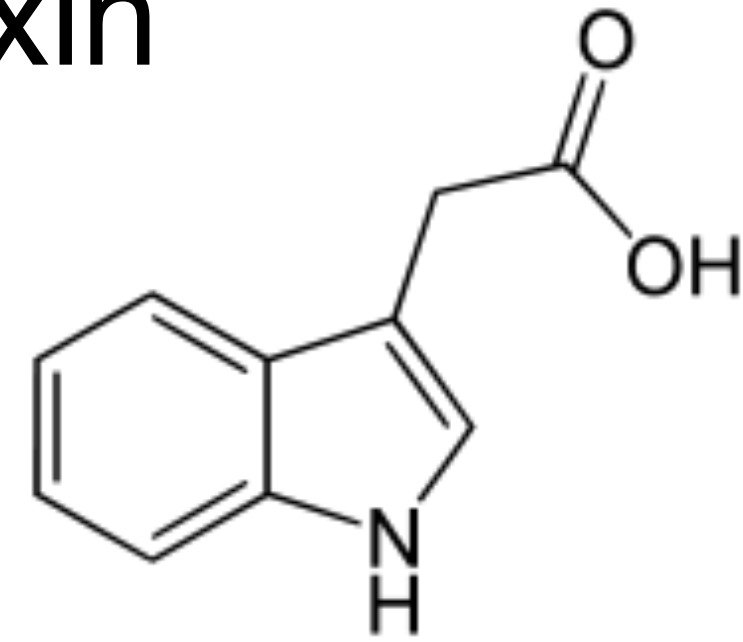
DR5 Auxin Reporter  
Cory Tobin

20  $\mu$ m





# Auxin



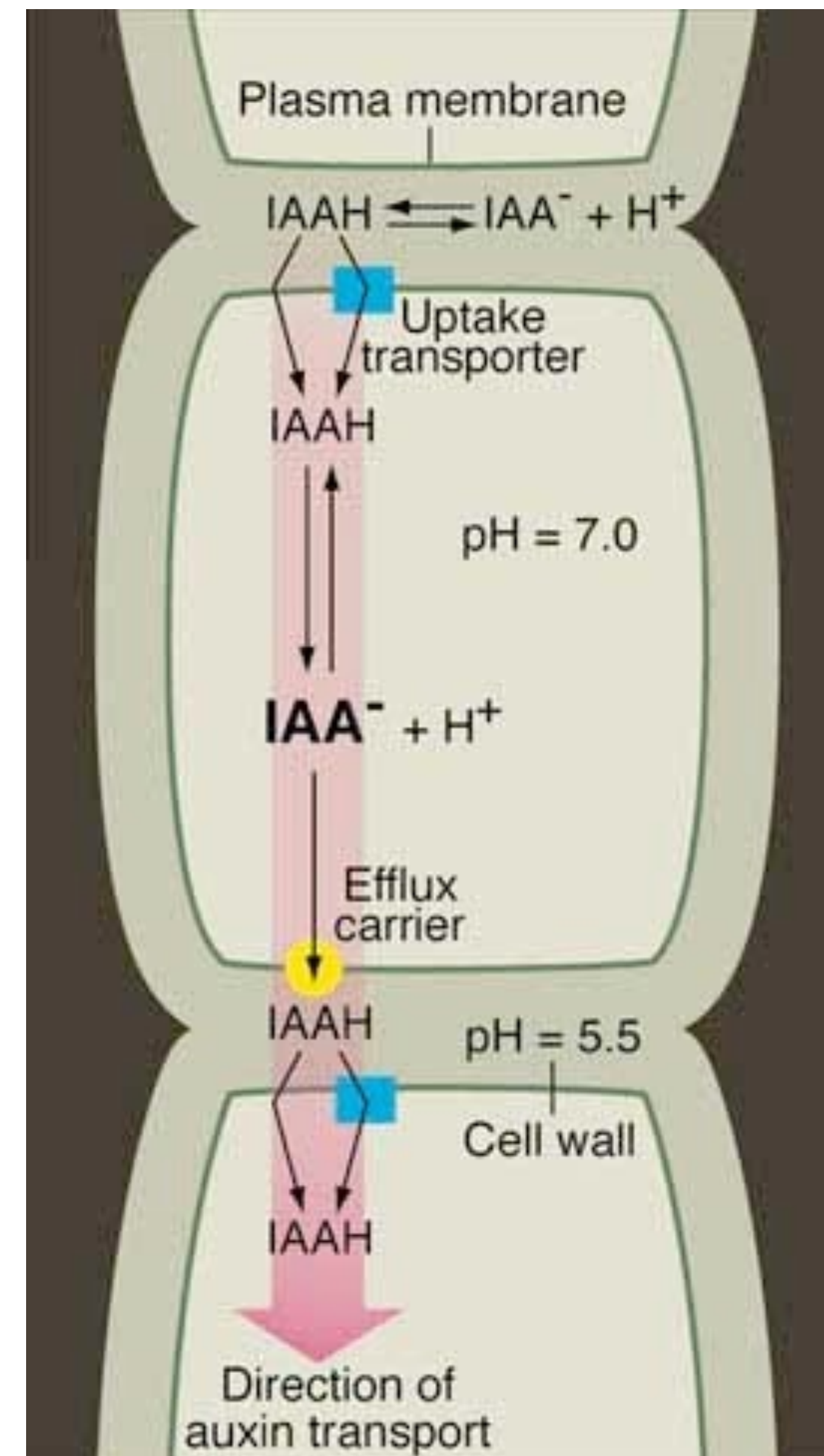
Induces new leaves and flowers

Causes shoot cell expansion

Causes changes in gene activity

Has private circulatory system

Gets out of cells through a specific efflux carrier, PIN

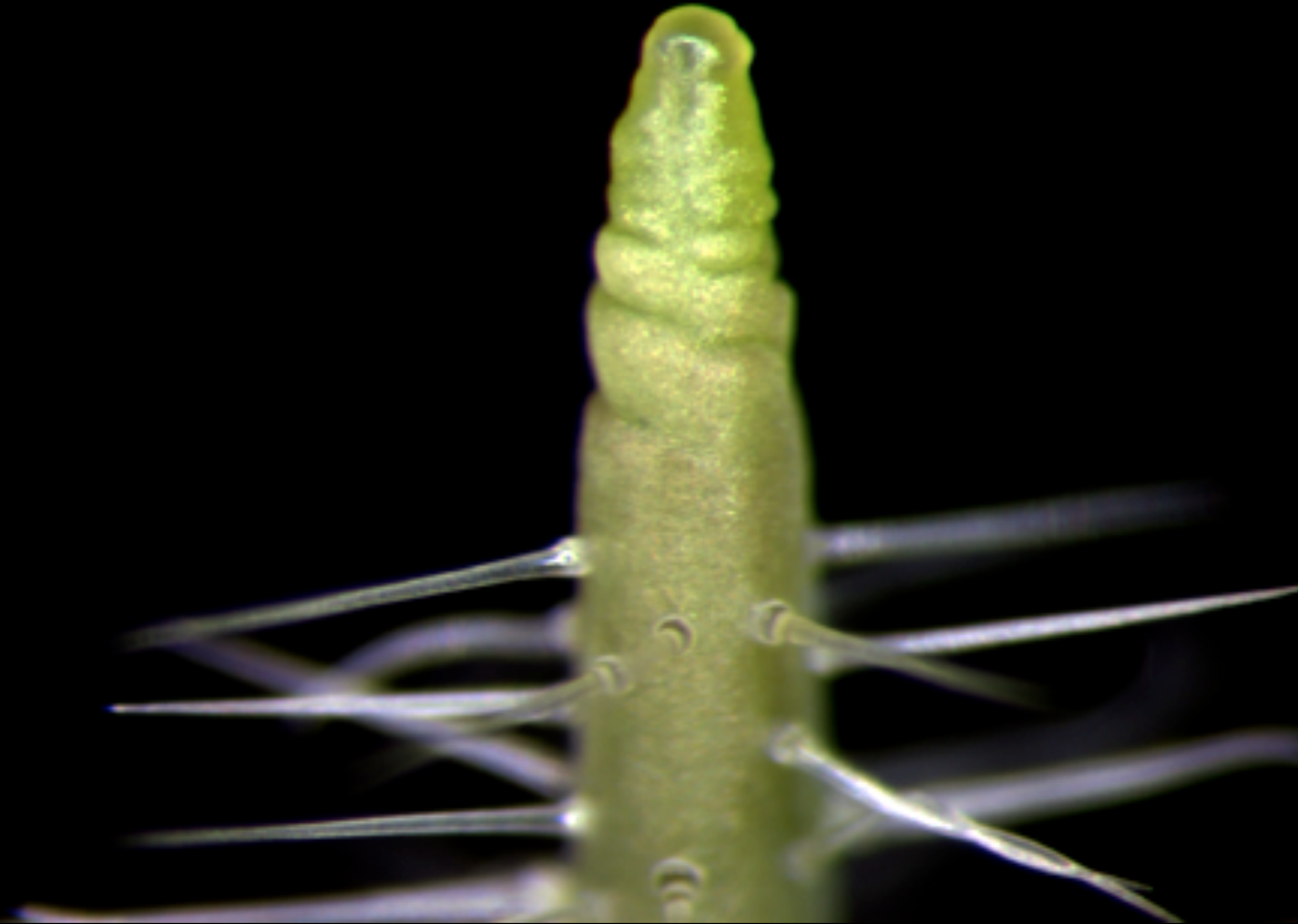


Jones, A.M.

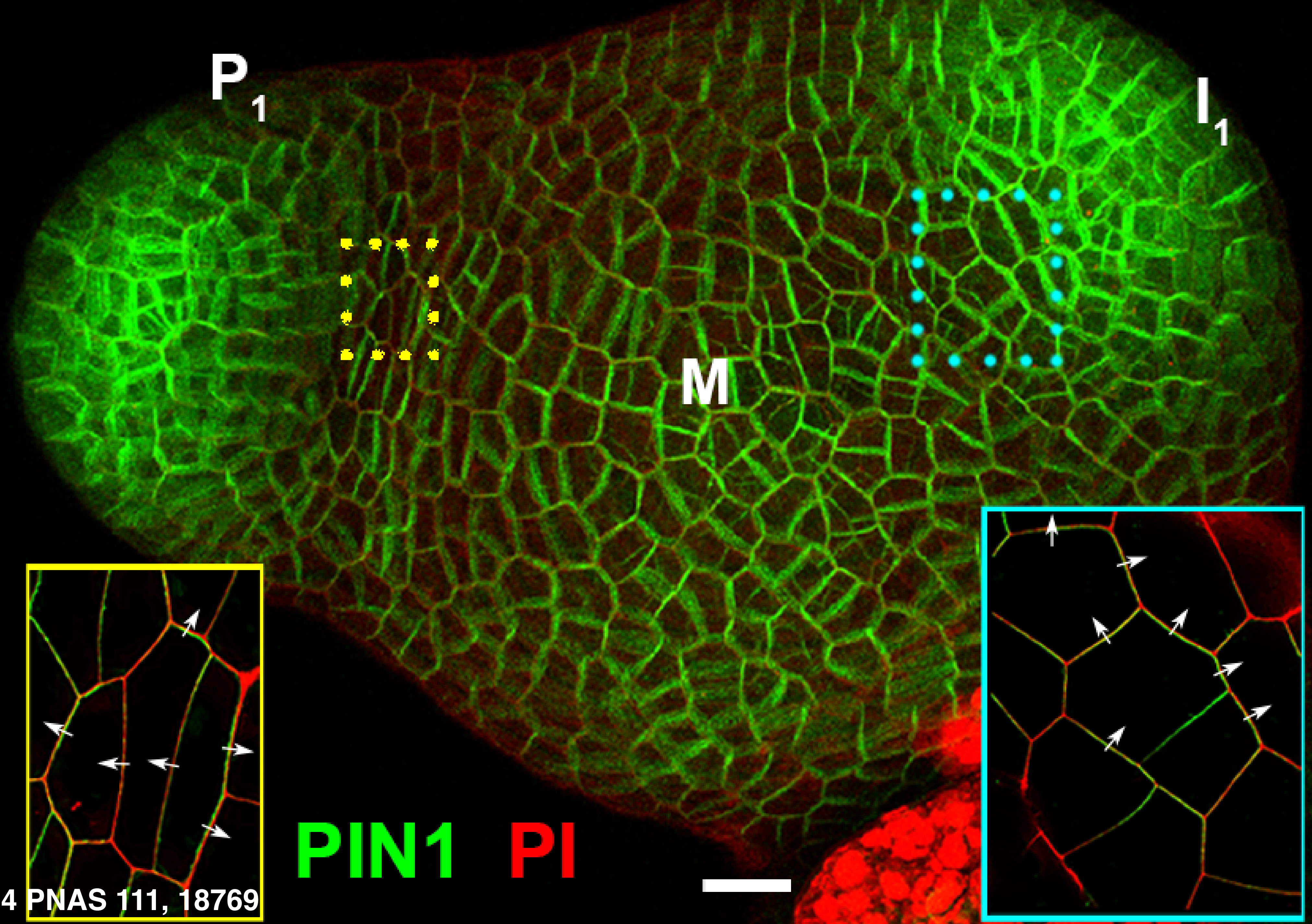
Science (1998) 282, 2201



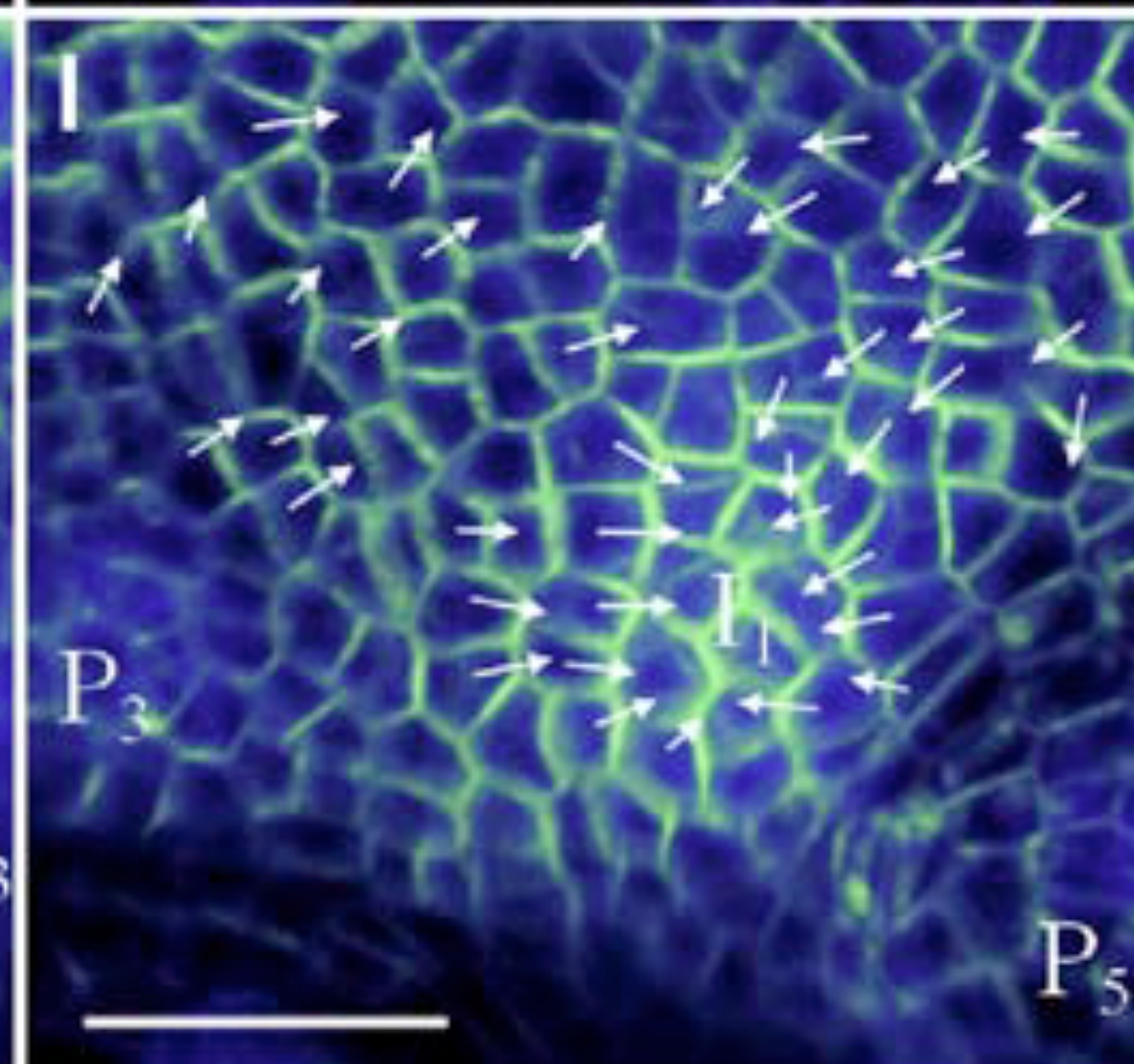
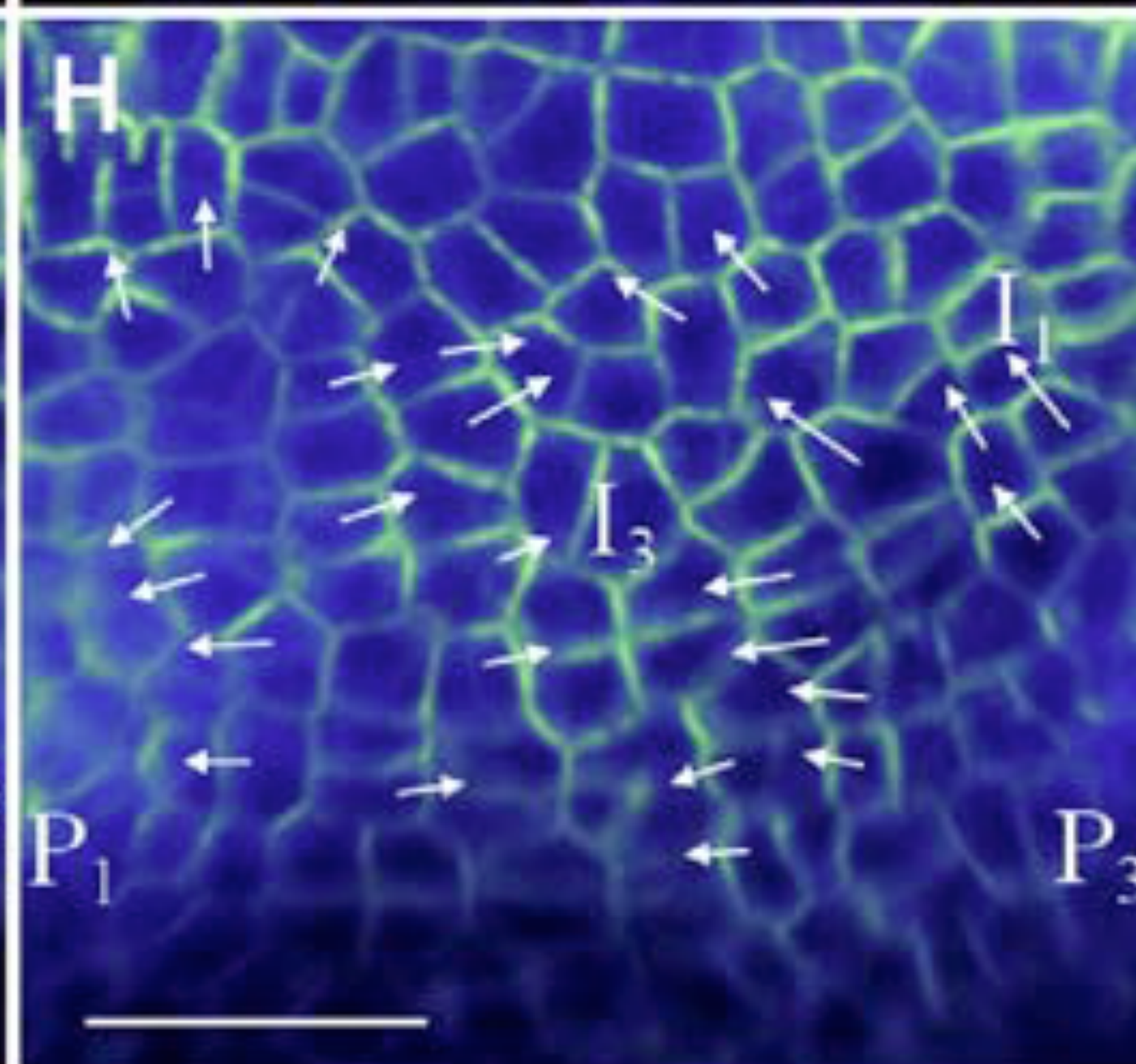
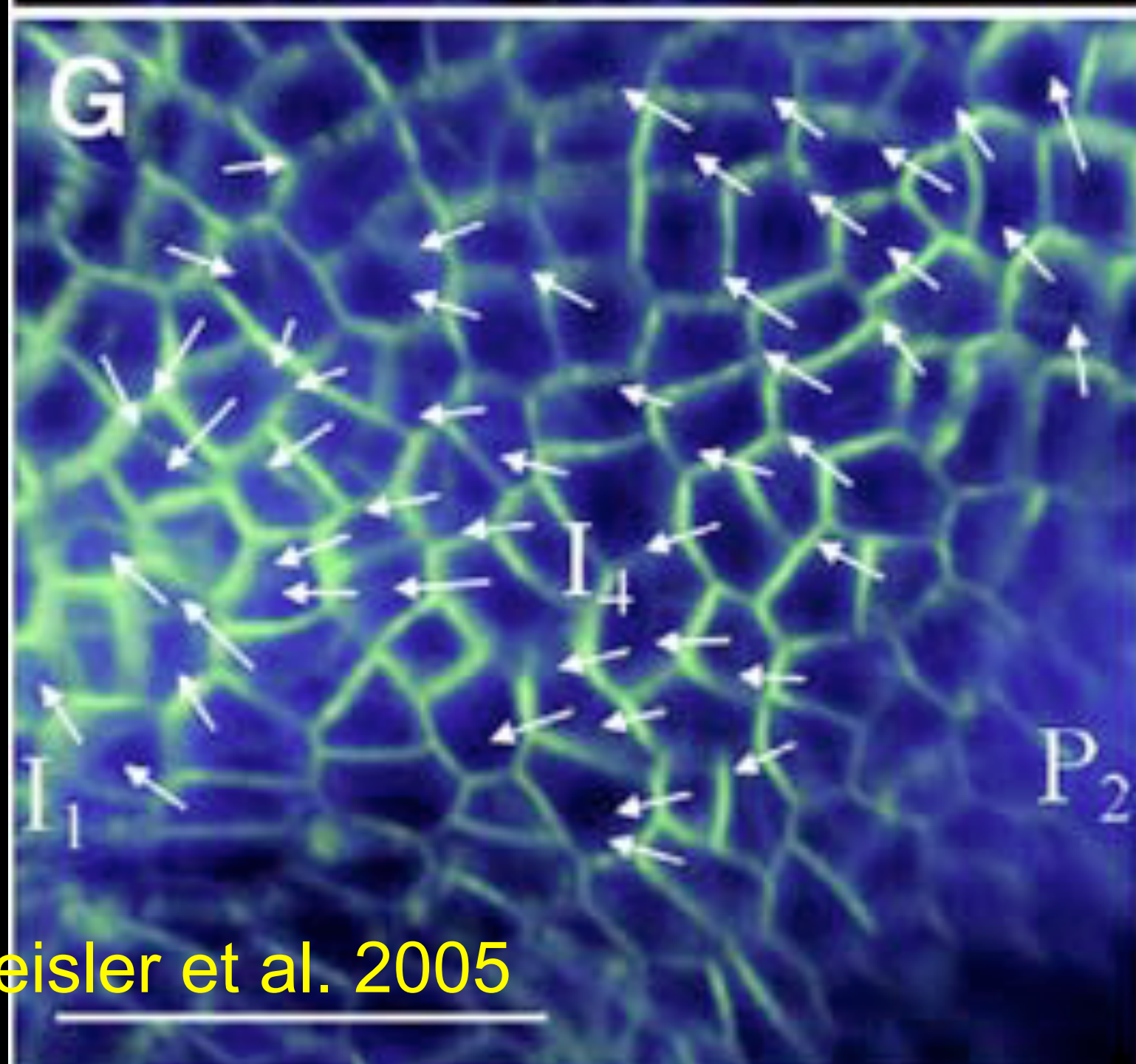
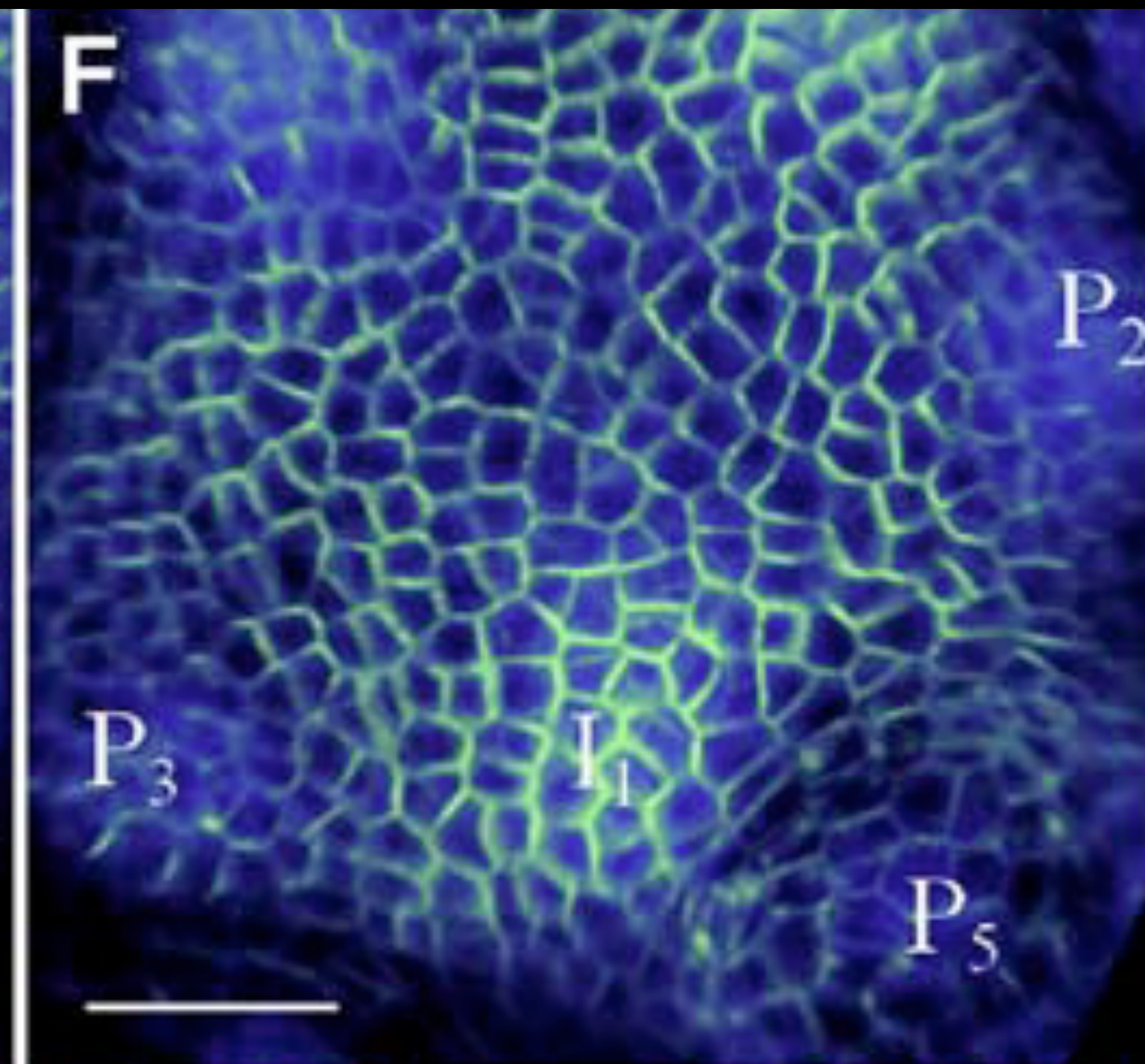
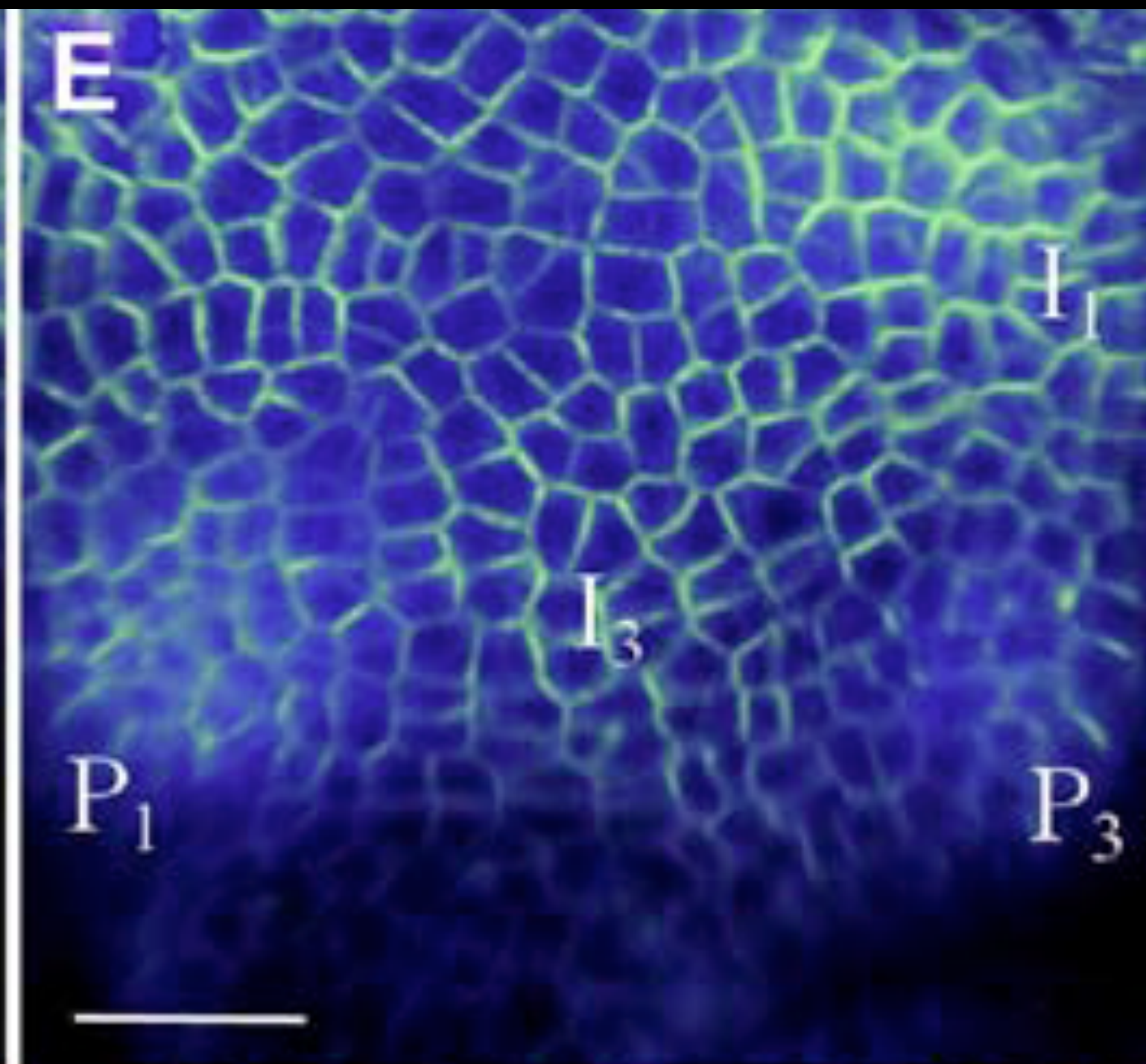
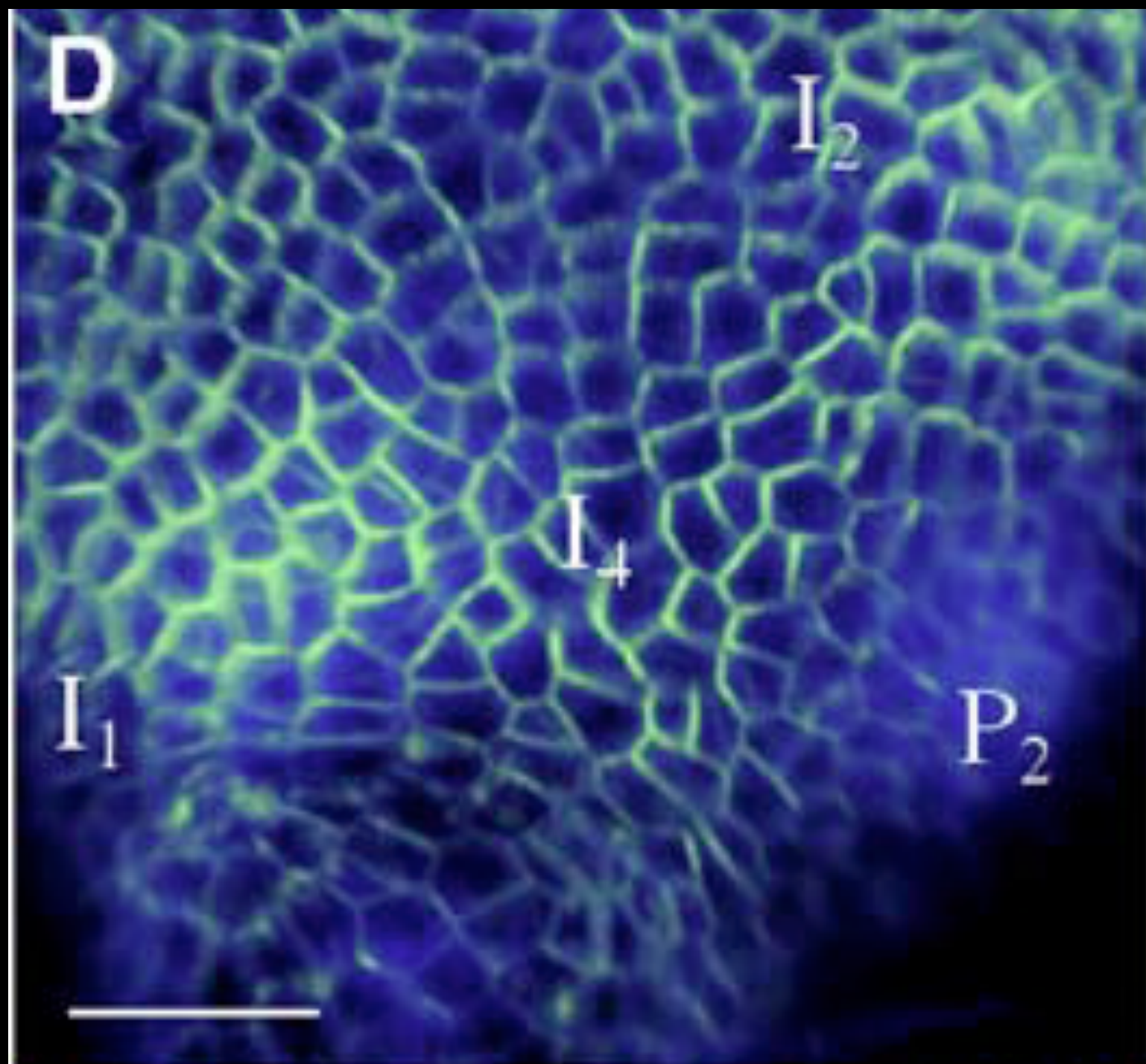
pin1 Mutant (Okada, 1991);  
PIN1 is the efflux carrier (Luschnig et al. 1998; Chen et













# MODEL

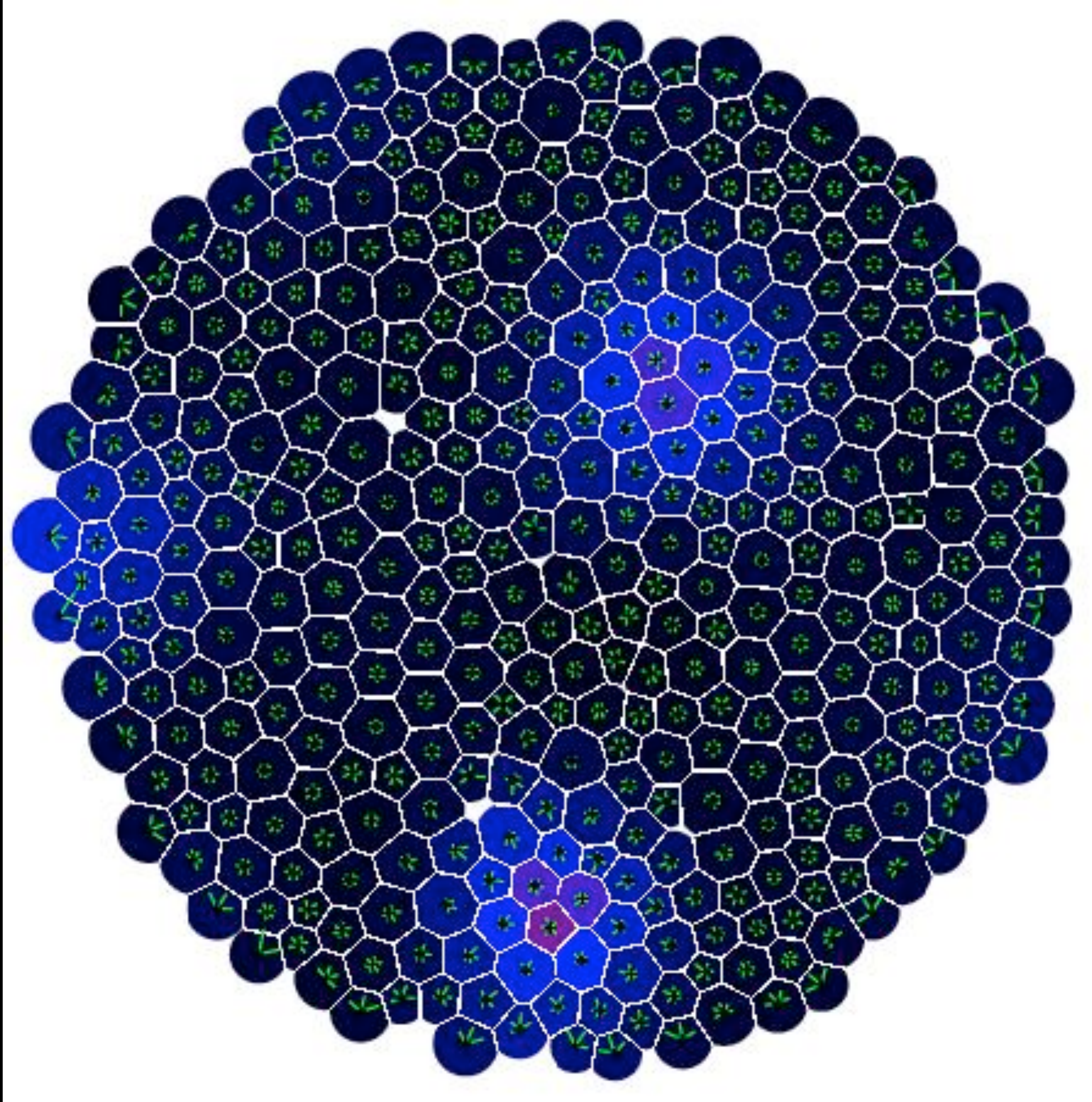
- 1) Local high auxin concentration causes new primordia, and it gets high locally by transport and diffusion
- 2) Auxin efflux carrier moves auxin, and its gene is auxin-induced - so rate of transport from a cell depends on the auxin level in the cell
- 3) Auxin efflux carrier is polarized in cells, and points toward neighboring cells with the highest auxin concentration



$$\begin{aligned}
\frac{dA_i}{dt} &= c_A - d_A A_i + \frac{1}{V_i} \left[ p_{AH} \sum_{k \in \mathcal{N}_i} a_{ik} (f_{AH}^{\text{wall}} A_{ik} - f_{AH}^{\text{cell}} A_i) \right. \\
&+ \left. p_{A^-} \sum_{k \in \mathcal{N}_i} a_{ik} P_{ik} \left( f_{A^-}^{\text{wall}} N_{\text{influx}} \frac{A_{ik}}{K_A + A_{ik}} - f_{A^-}^{\text{cell}} N_{\text{efflux}} \frac{A_i}{K_a + A_i} \right) \right], \\
\frac{dA_{ij}}{dt} &= -d_A A_{ij} + \frac{1}{V_{ij}} \left[ a_{ij} \left\{ p_{AH} (f_{AH}^{\text{cell}} A_i - f_{AH}^{\text{wall}} A_{ij}) \right. \right. \\
&+ \left. \left. p_{A^-} P_{ij} \left( f_{A^-}^{\text{cell}} N_{\text{efflux}} \frac{A_i}{K_a + A_i} - f_{A^-}^{\text{wall}} N_{\text{influx}} \frac{A_{ij}}{K_A + A_{ij}} \right) \right\} \right. \\
&+ \left. D_A \left\{ \frac{a_{ijijl}}{d_{ijijl}} (A_{ijl} - A_{ij}) + \frac{a_{ijijr}}{d_{ijijr}} (A_{ijr} - A_{ij}) + \frac{a_{ijji}}{d_{ijji}} (A_{ji} - A_{ij}) \right\} \right], \\
\frac{dP_i}{dt} &= \frac{1}{V_i} \sum_k^{N_i} a_{ik} \left( k_2 P_{ik} - P_i \frac{k_1 A_k^n}{K^n + A_k^n} \right), \\
\frac{dP_{ij}}{dt} &= P_i \frac{k_1 A_j^n}{K^n + A_j^n} - k_2 P_{ij}.
\end{aligned}$$



# The auxin concentration model



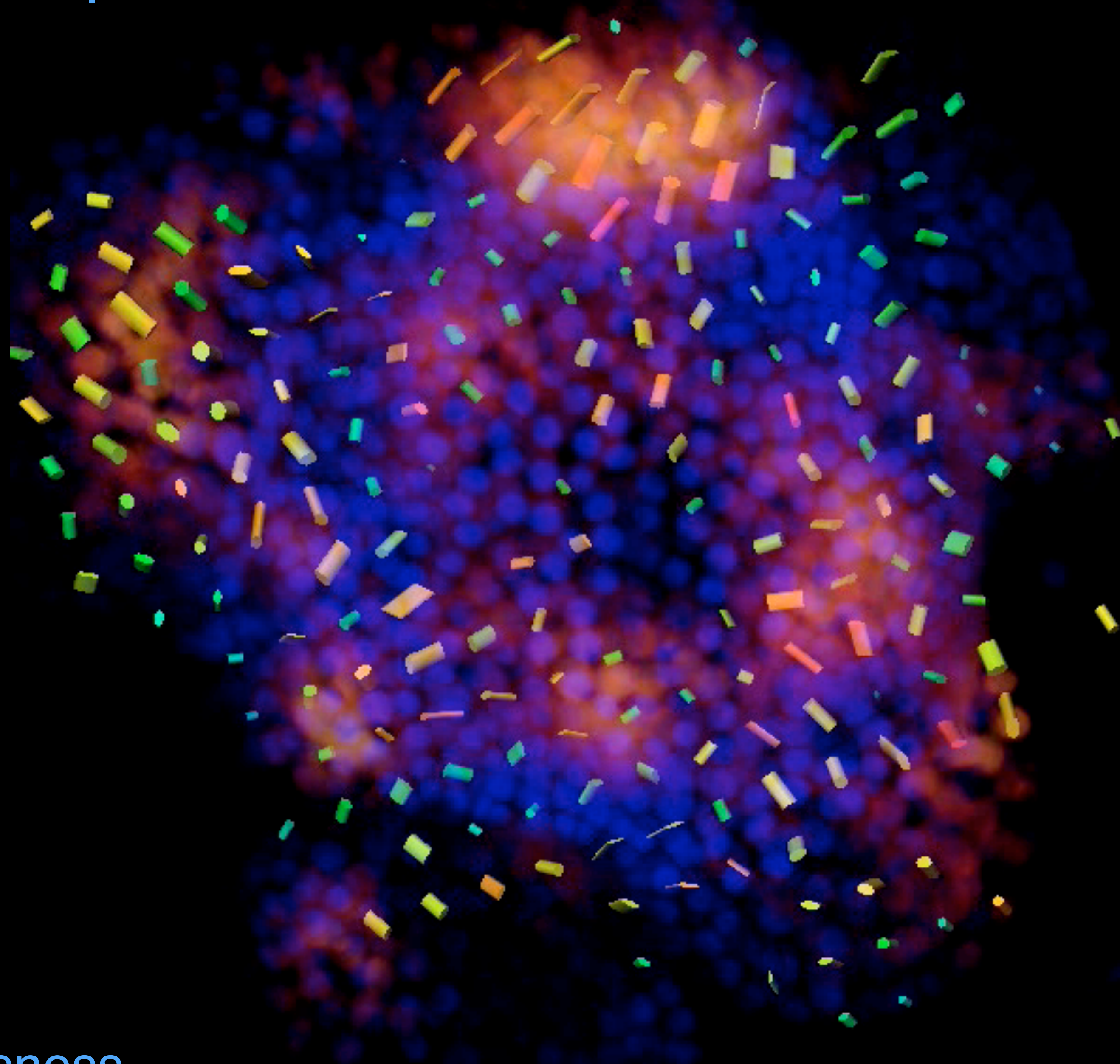
Local high auxin concentration causes new primordia, and it gets high locally by transport and diffusion

Auxin efflux carrier moves auxin, and its gene is auxin-induced - so rate of transport from a cell depends on the auxin level in the cell

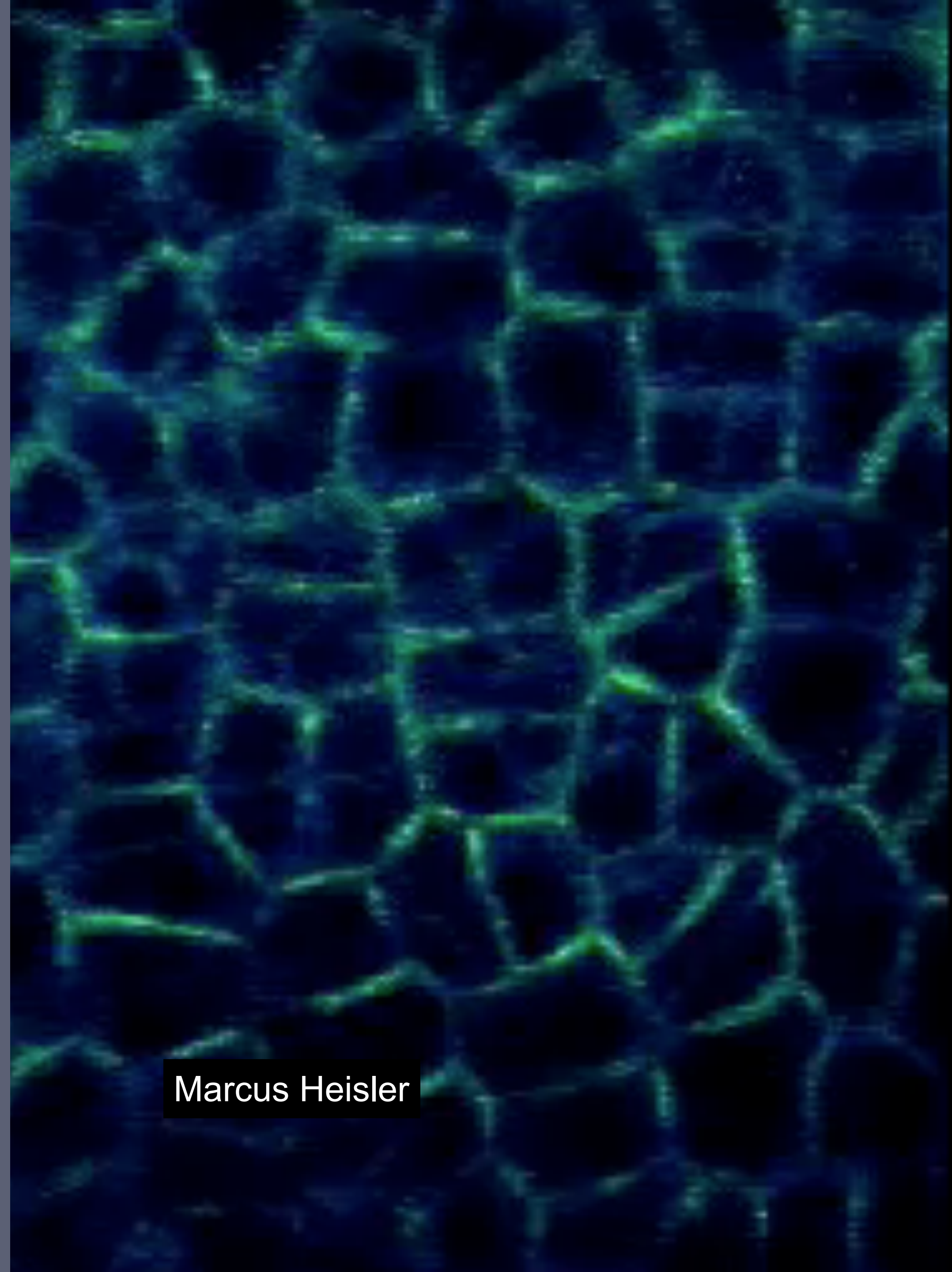
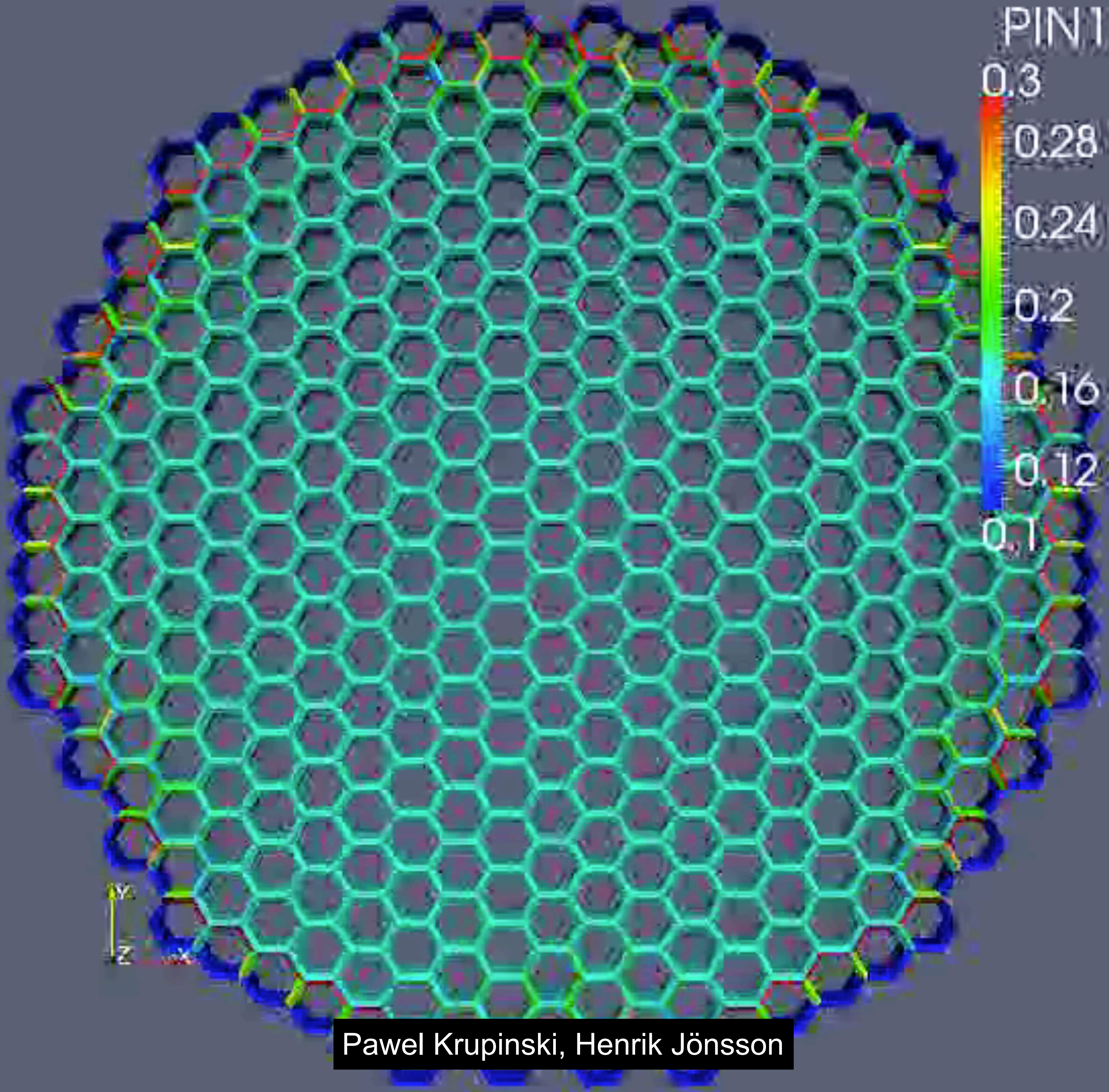
**Auxin efflux carrier is polarized in cells, and points toward neighboring cells with the highest auxin concentration**



# Local Cell Expansion in Meristem Matches Auxin Concentration

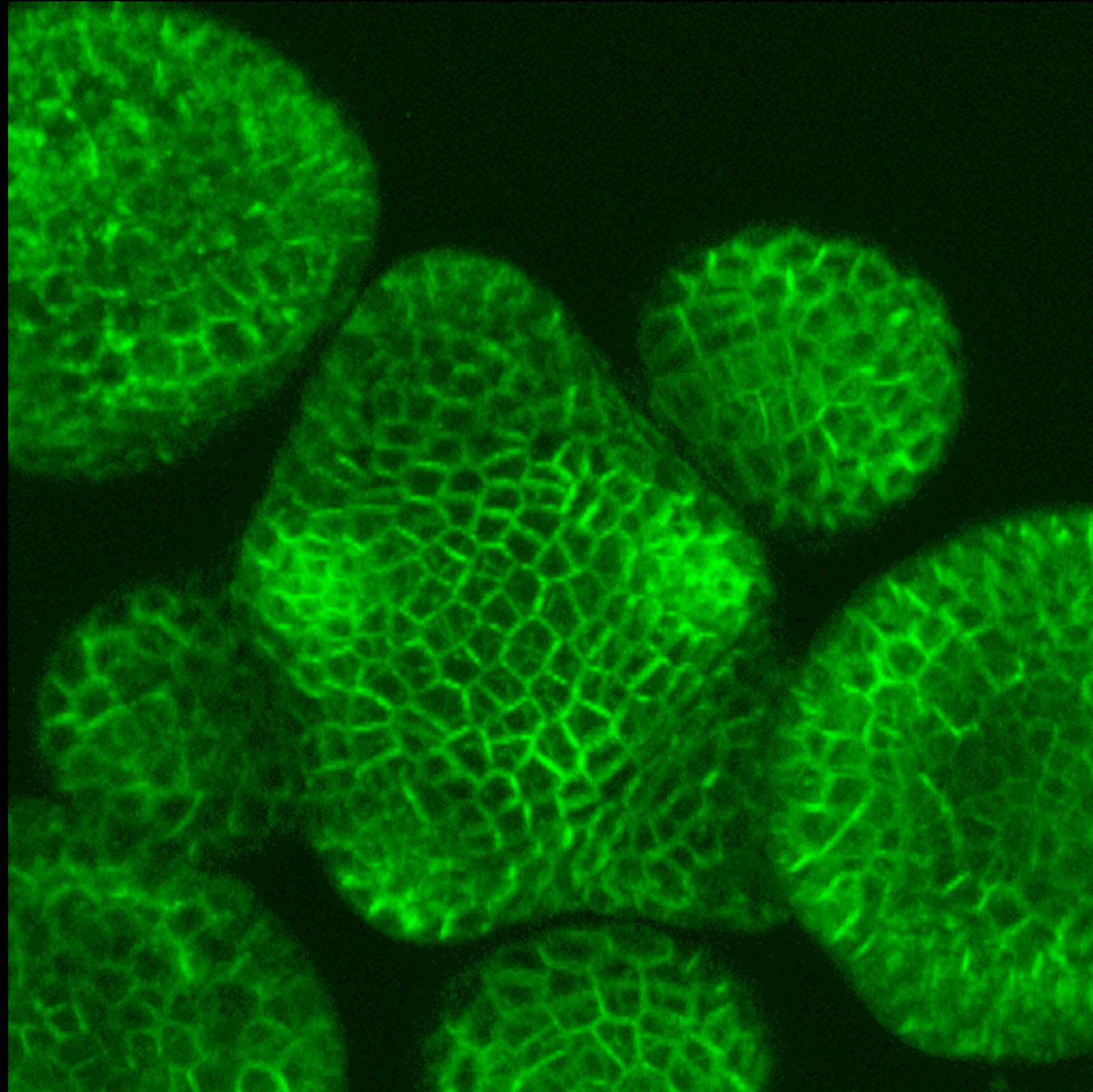




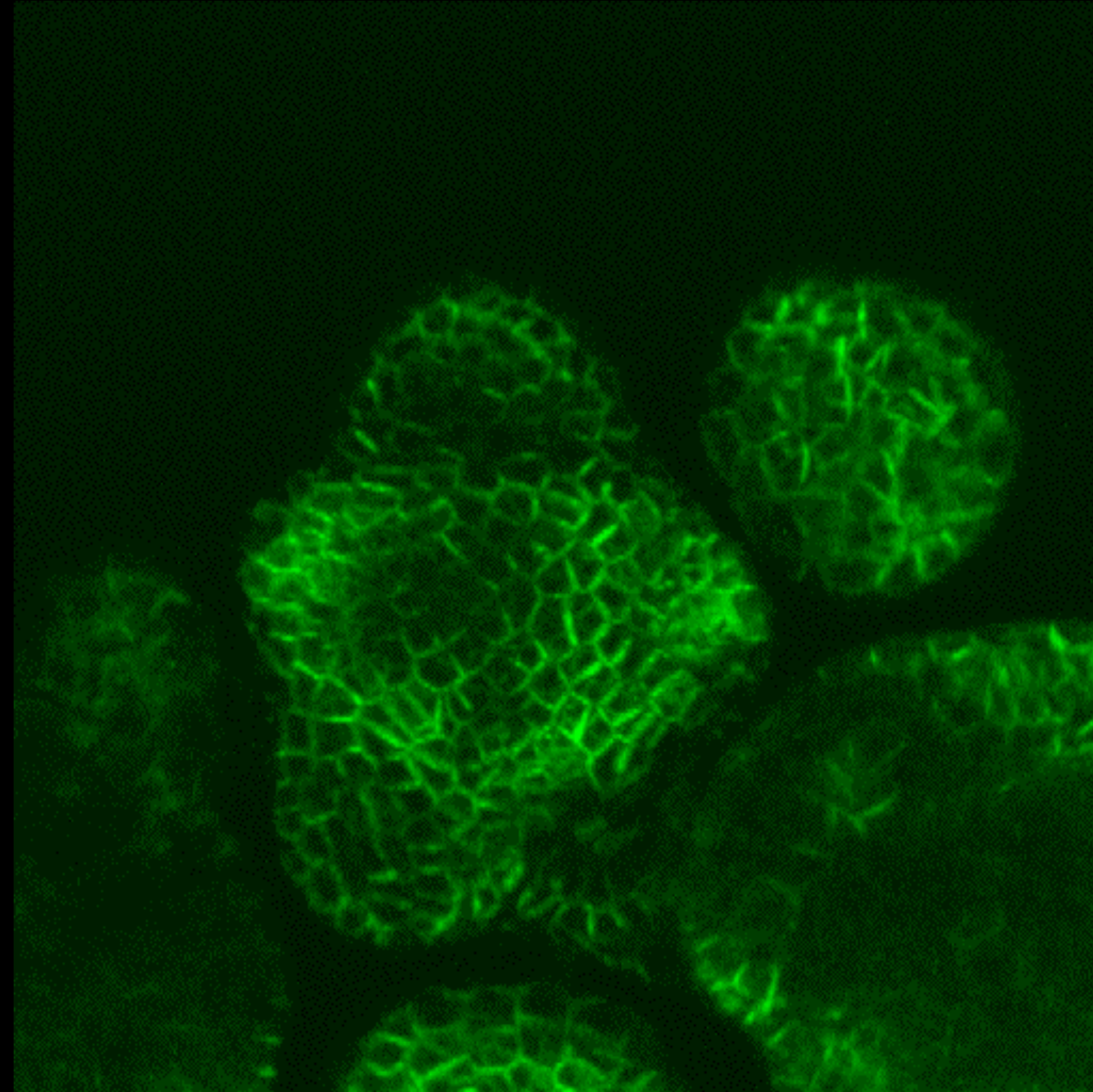




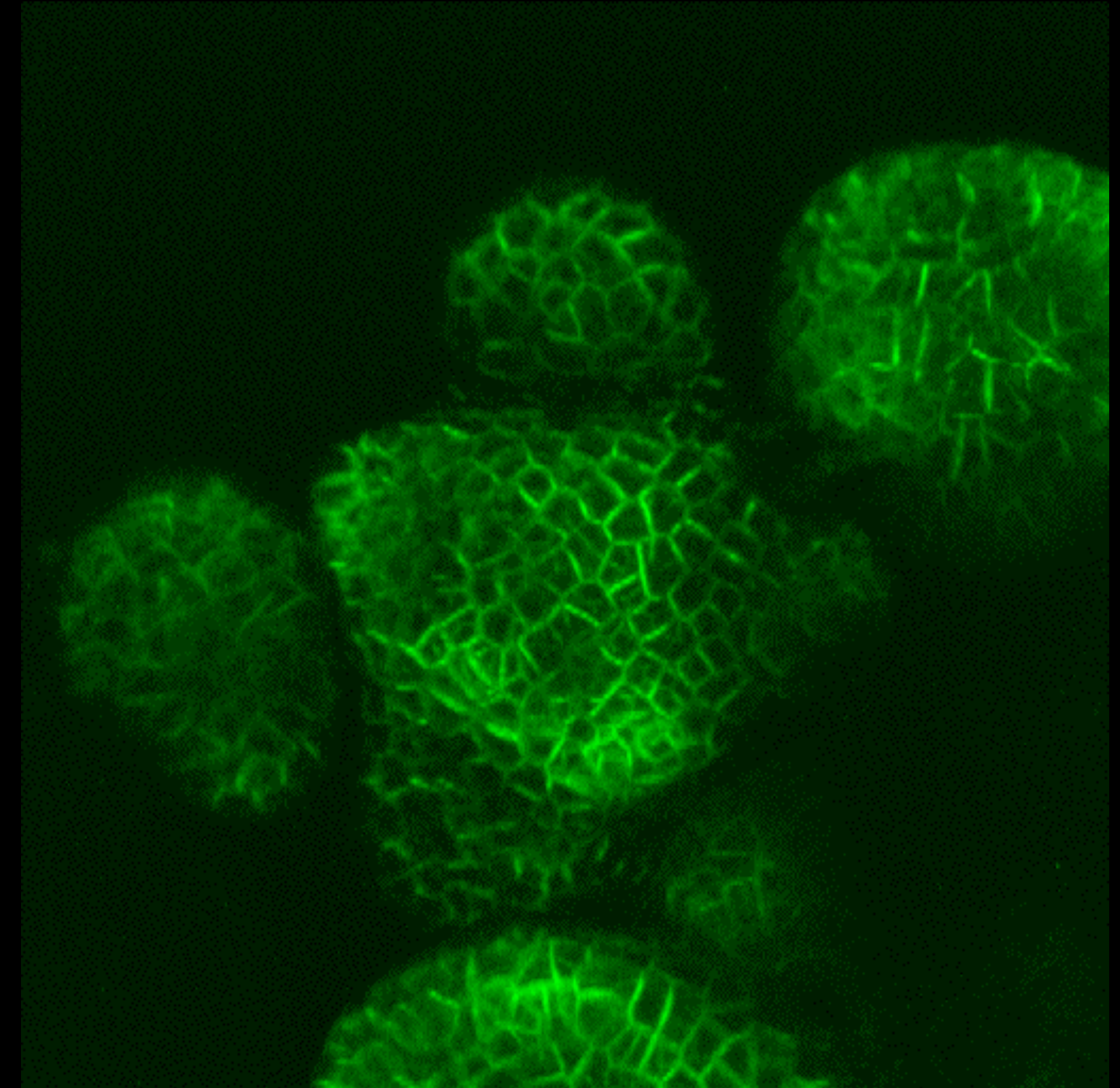
# Effects of Cell Wall



Prior to treatment



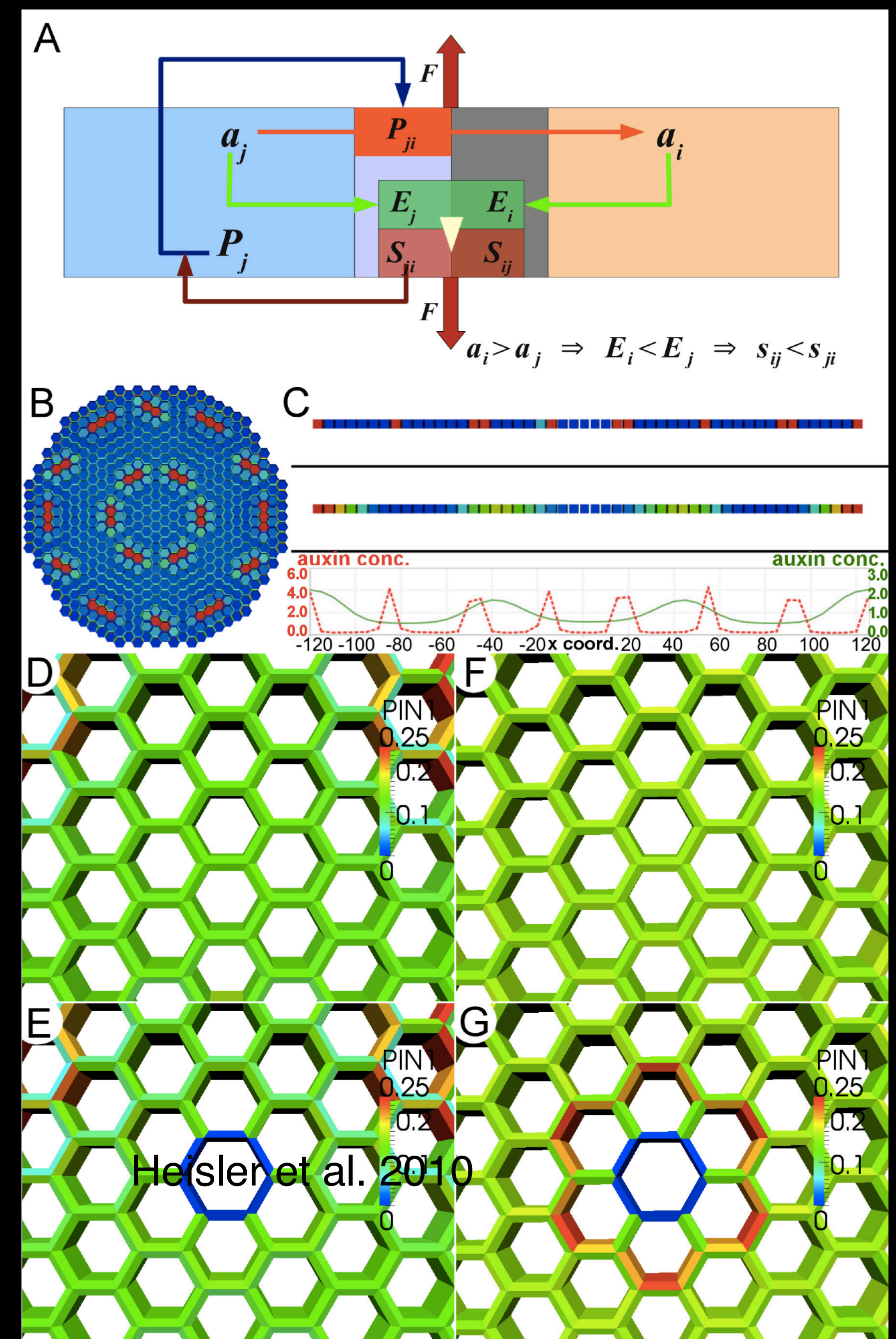
Cellulase Bead 18h



24h Recovery

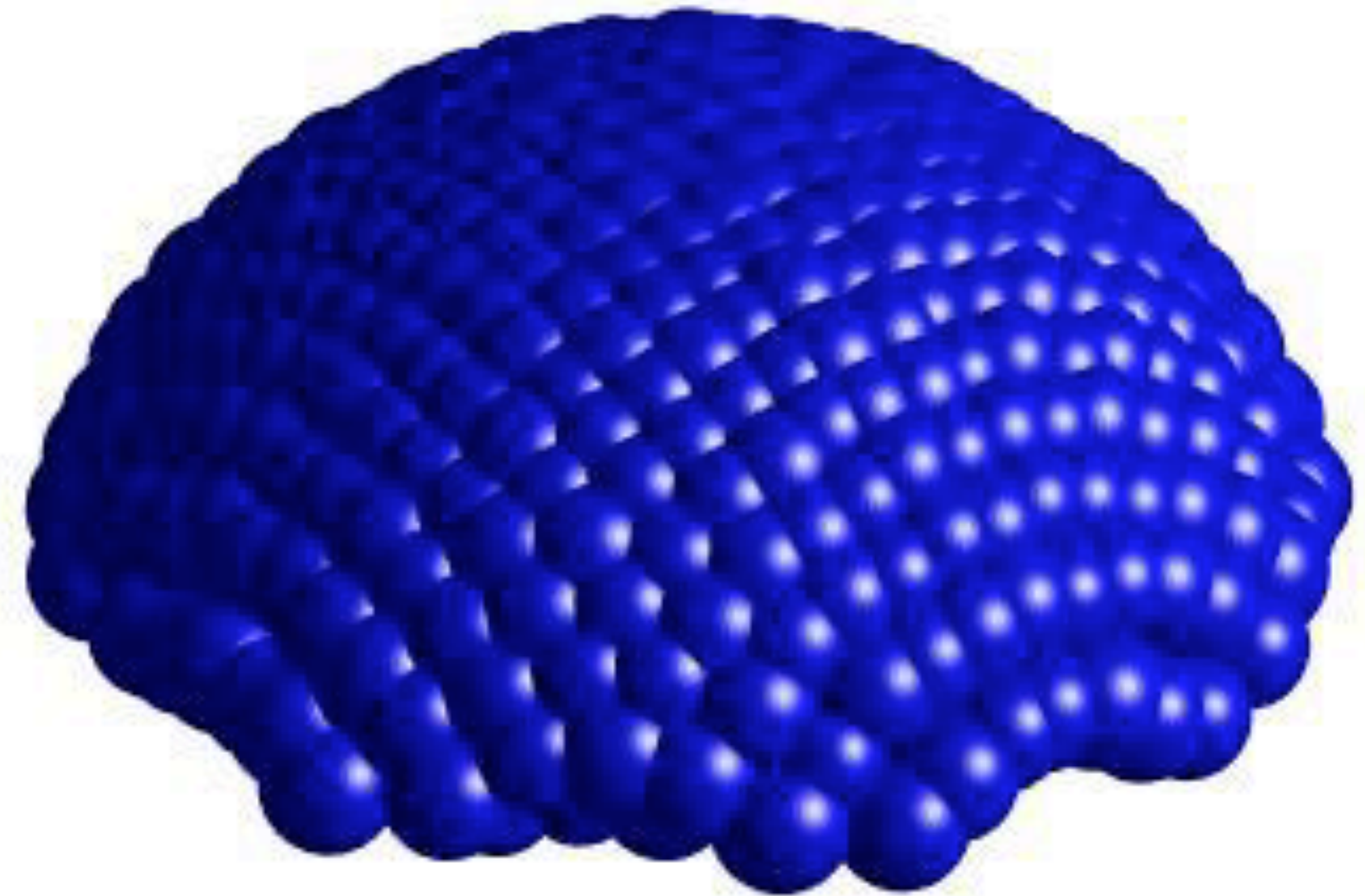
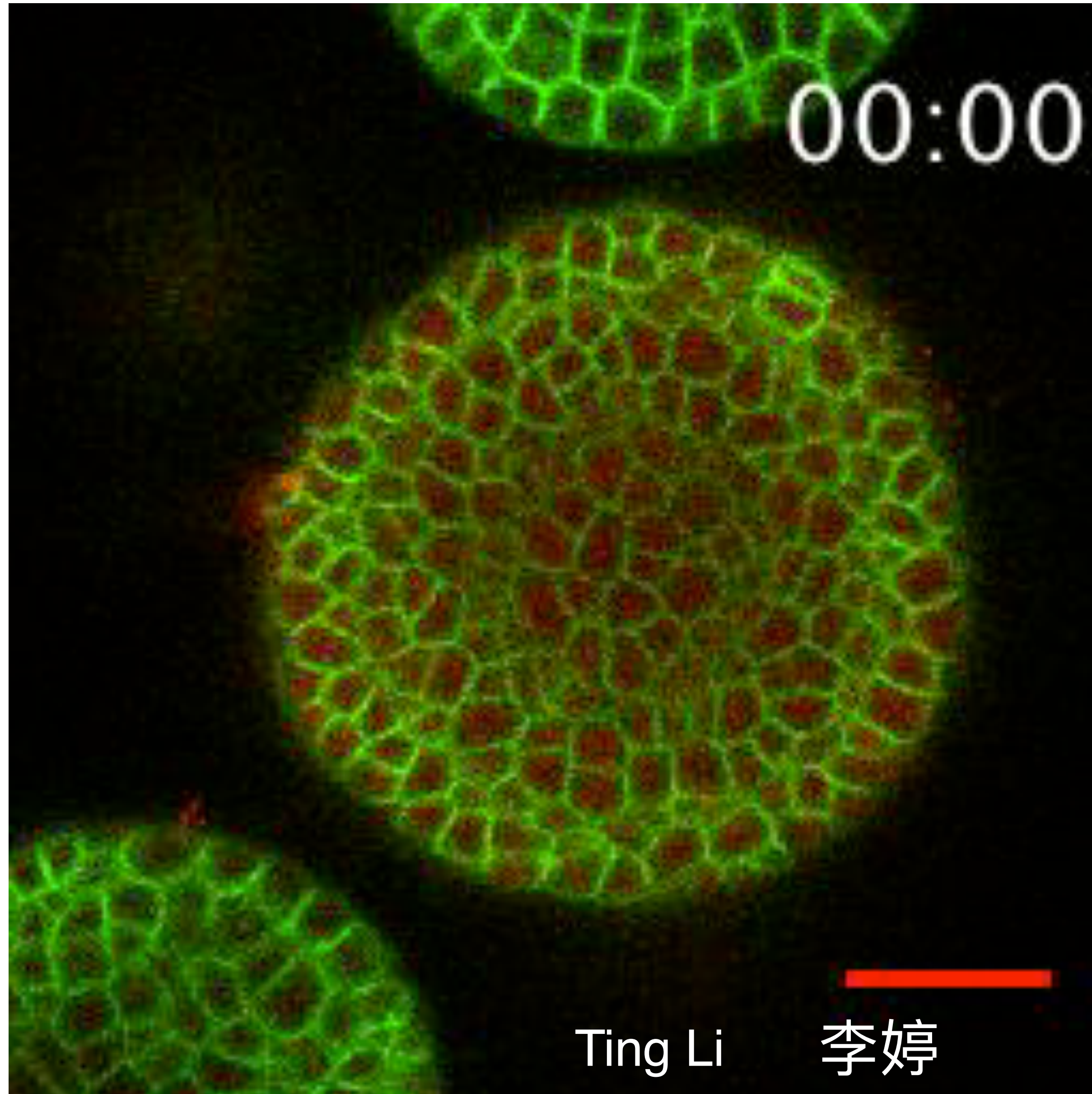


- Auxin causes cell expansion
- Resulting mechanical stress controls auxin transport from neighbors
- New auxin peaks changes which cells are expanding
- Thereby changing auxin flow again
- NOVEL DEVELOPMENTAL MECHANISM: REGULATED TRANSPORT OF A





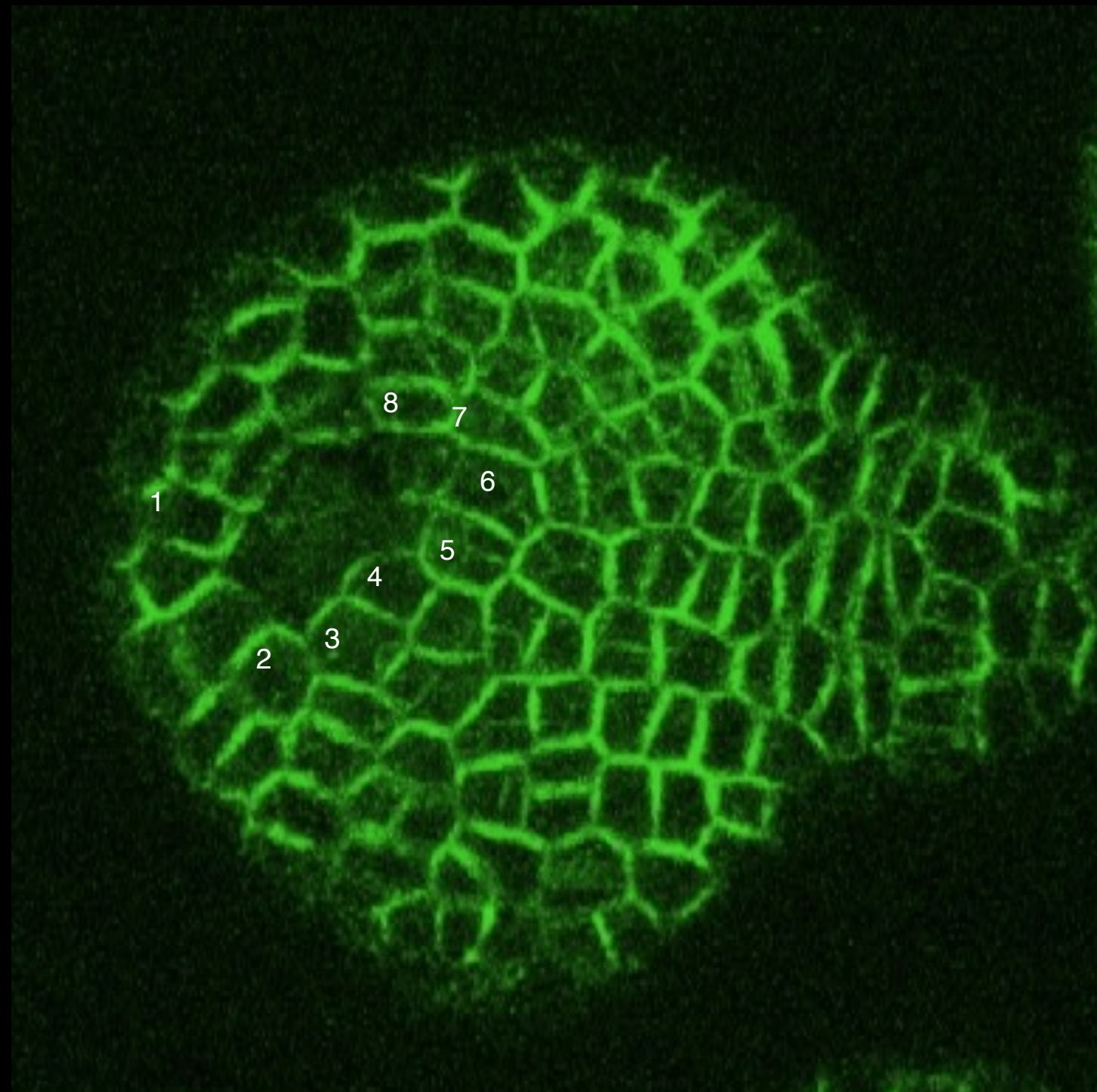
# Calcium Waves in SAM





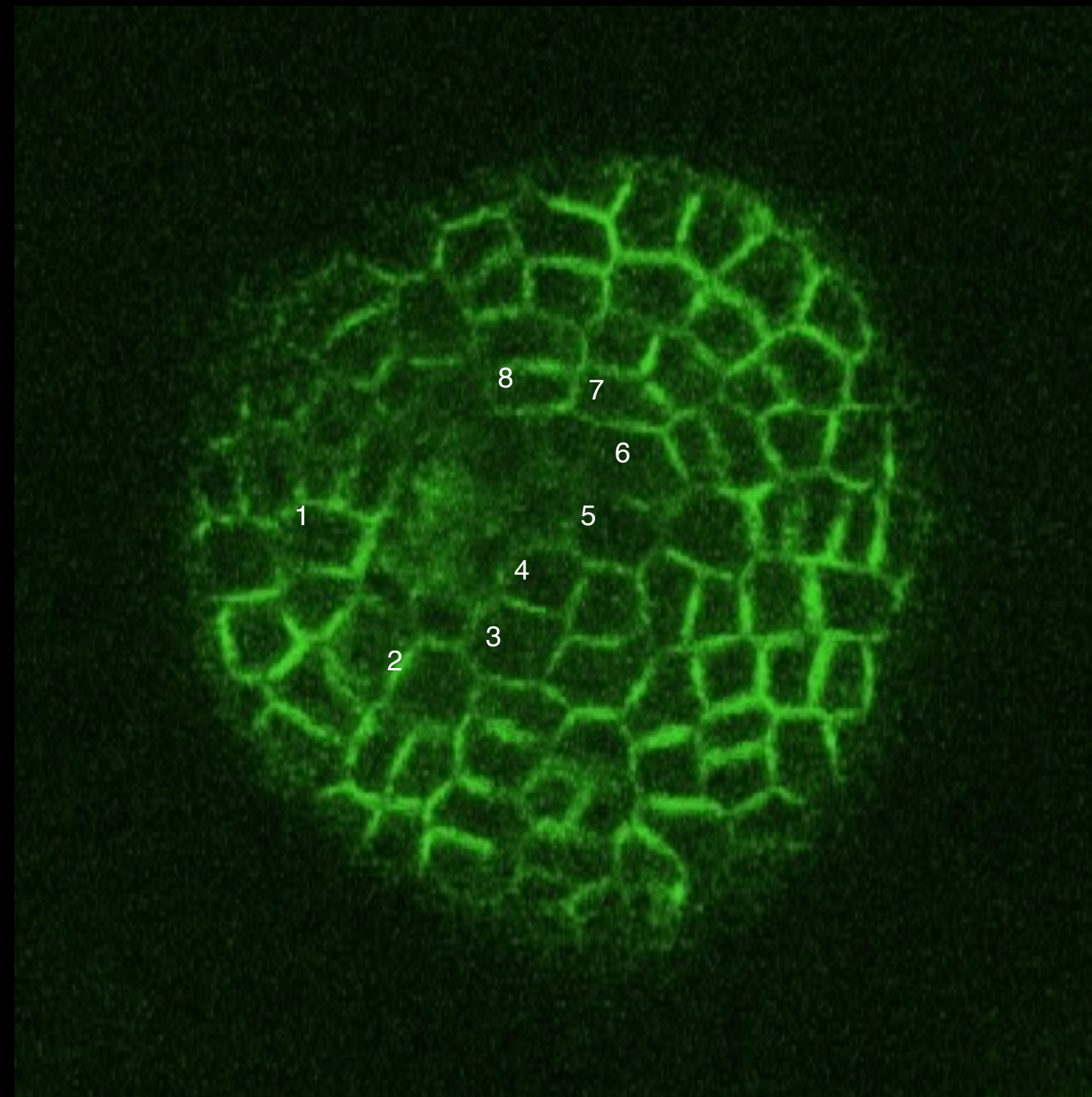
# Calcium Response Is Necessary for Later PIN1 Mechanical Response

- Pretreat 5mM LaCl<sub>3</sub> 0h, 3h, recover 3h

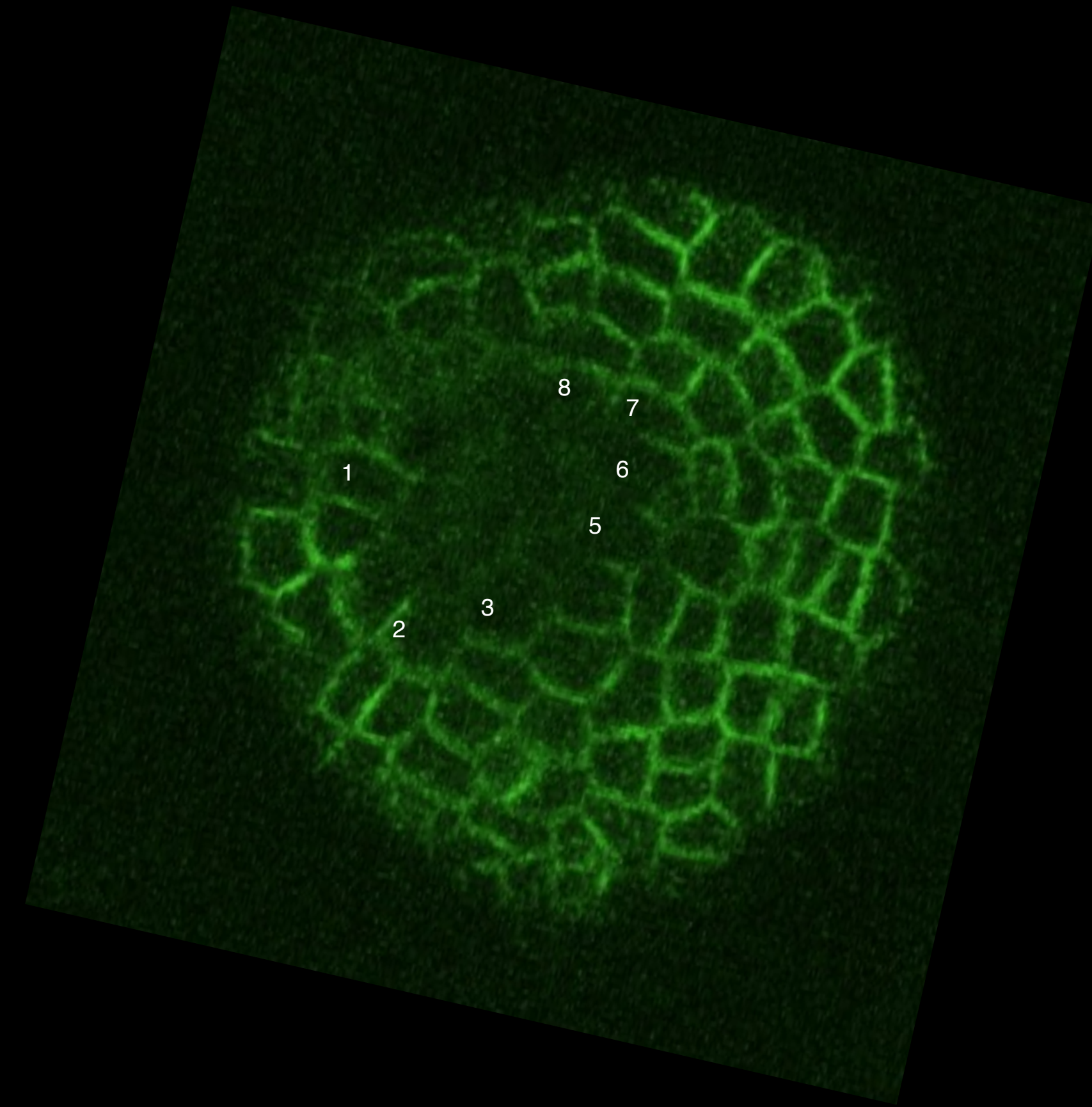


0h

N=4



3h



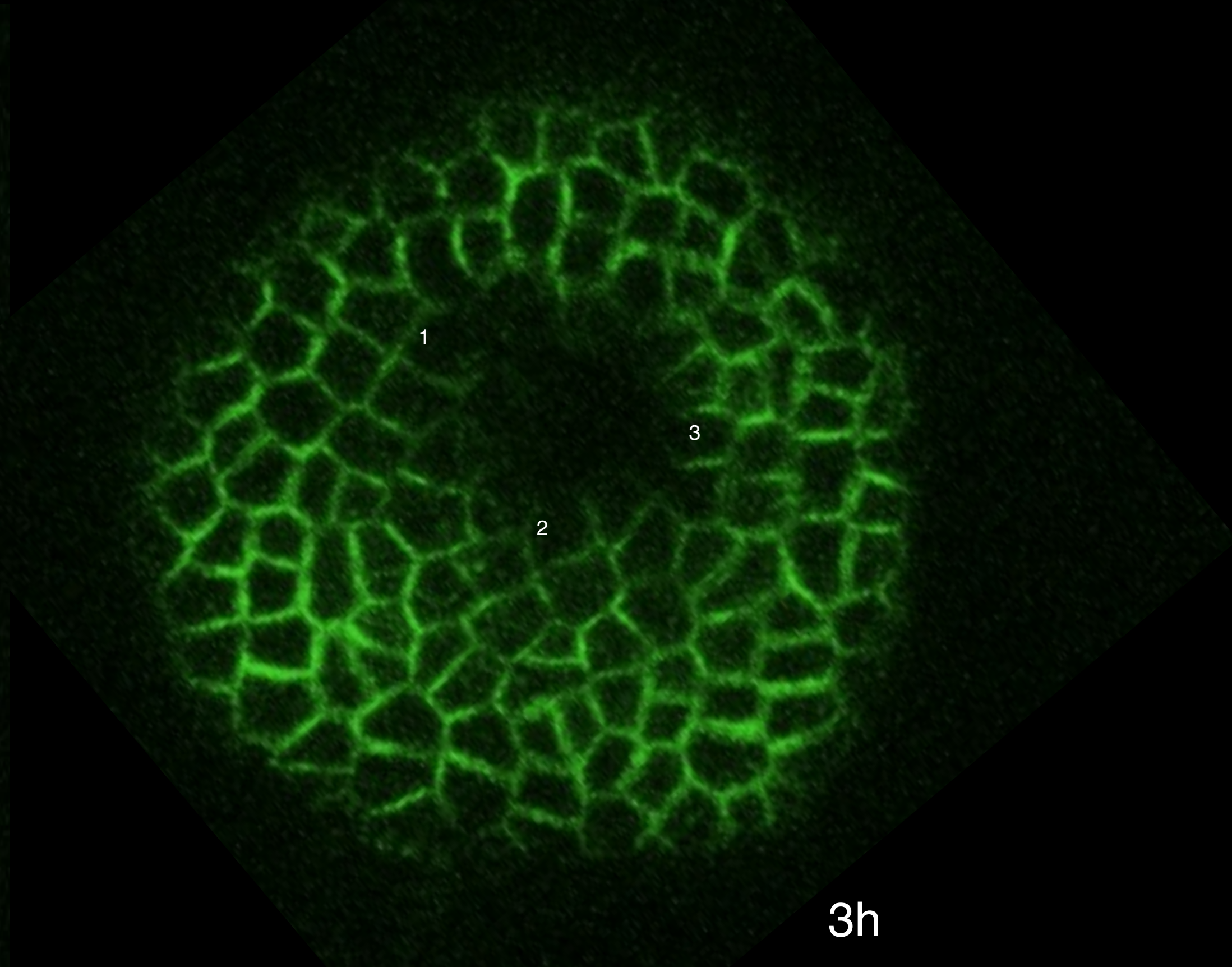
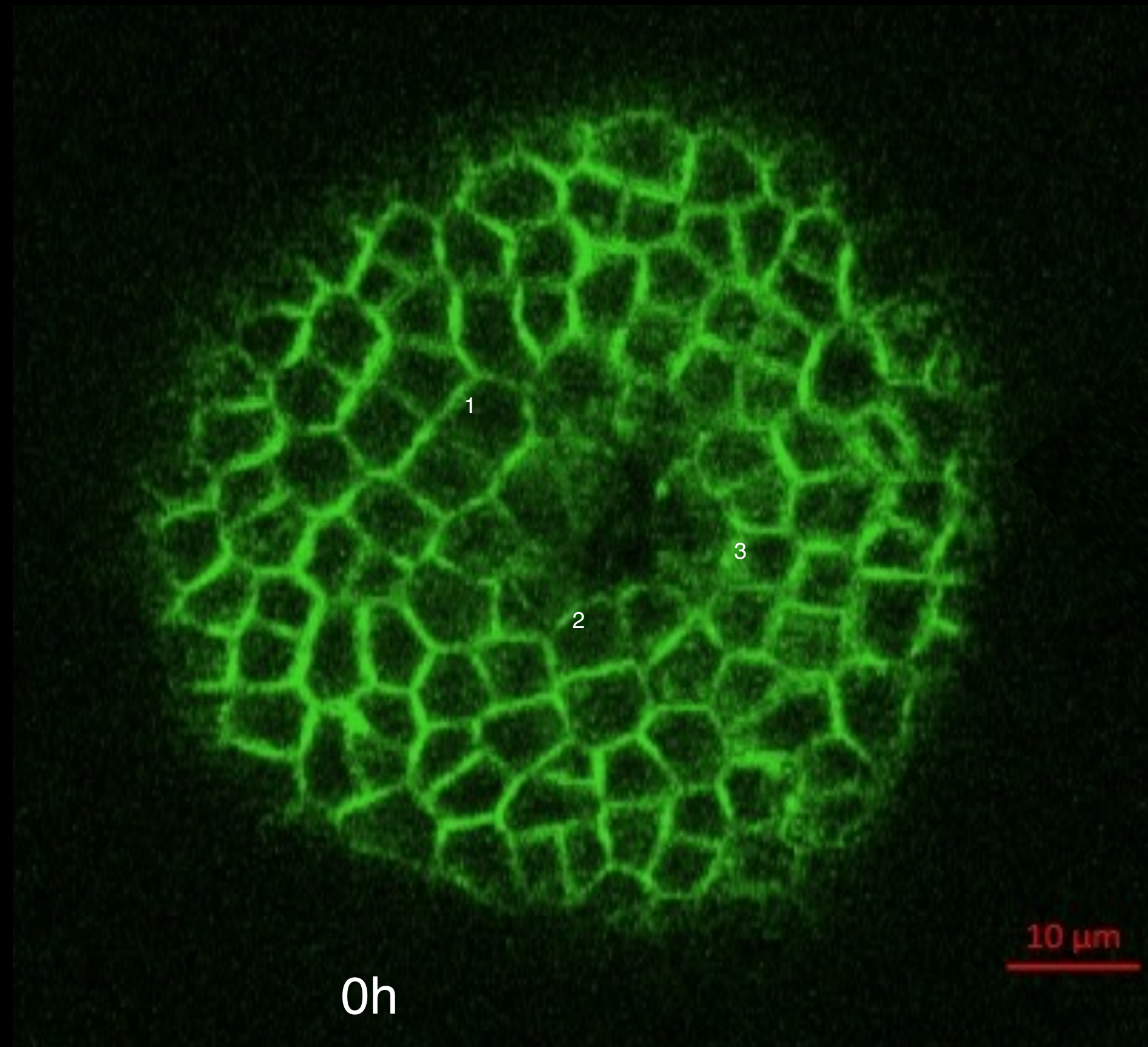
recover3h

An Yan



# Calcium Wave Only Needed for Initial Response

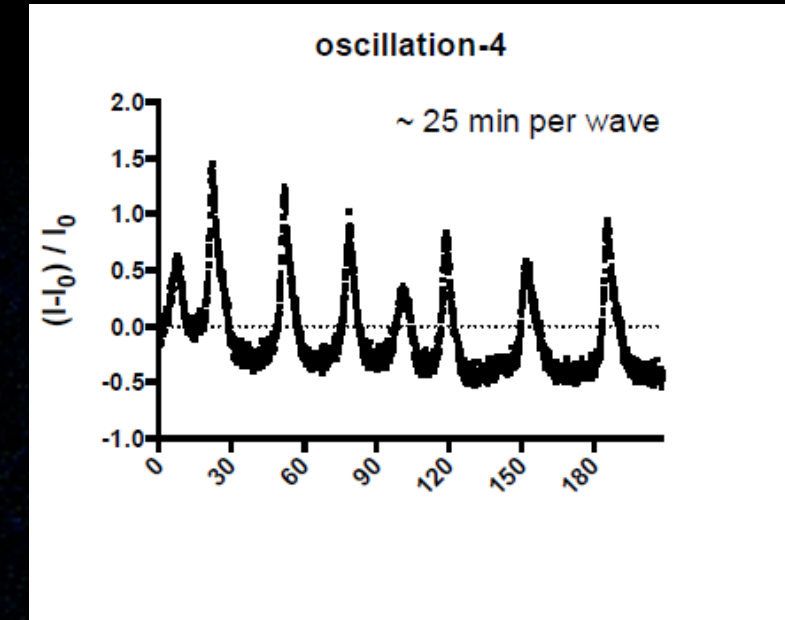
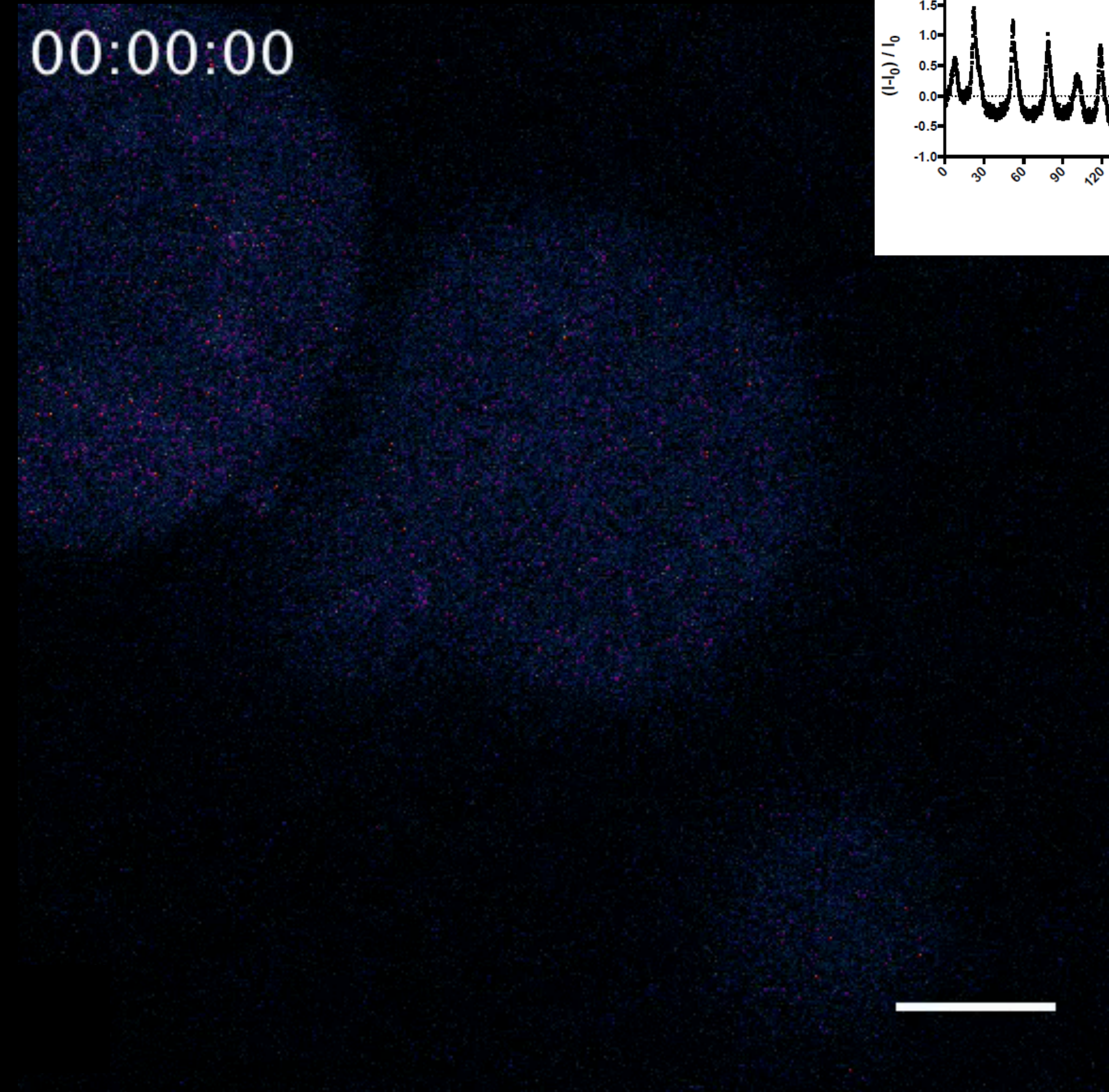
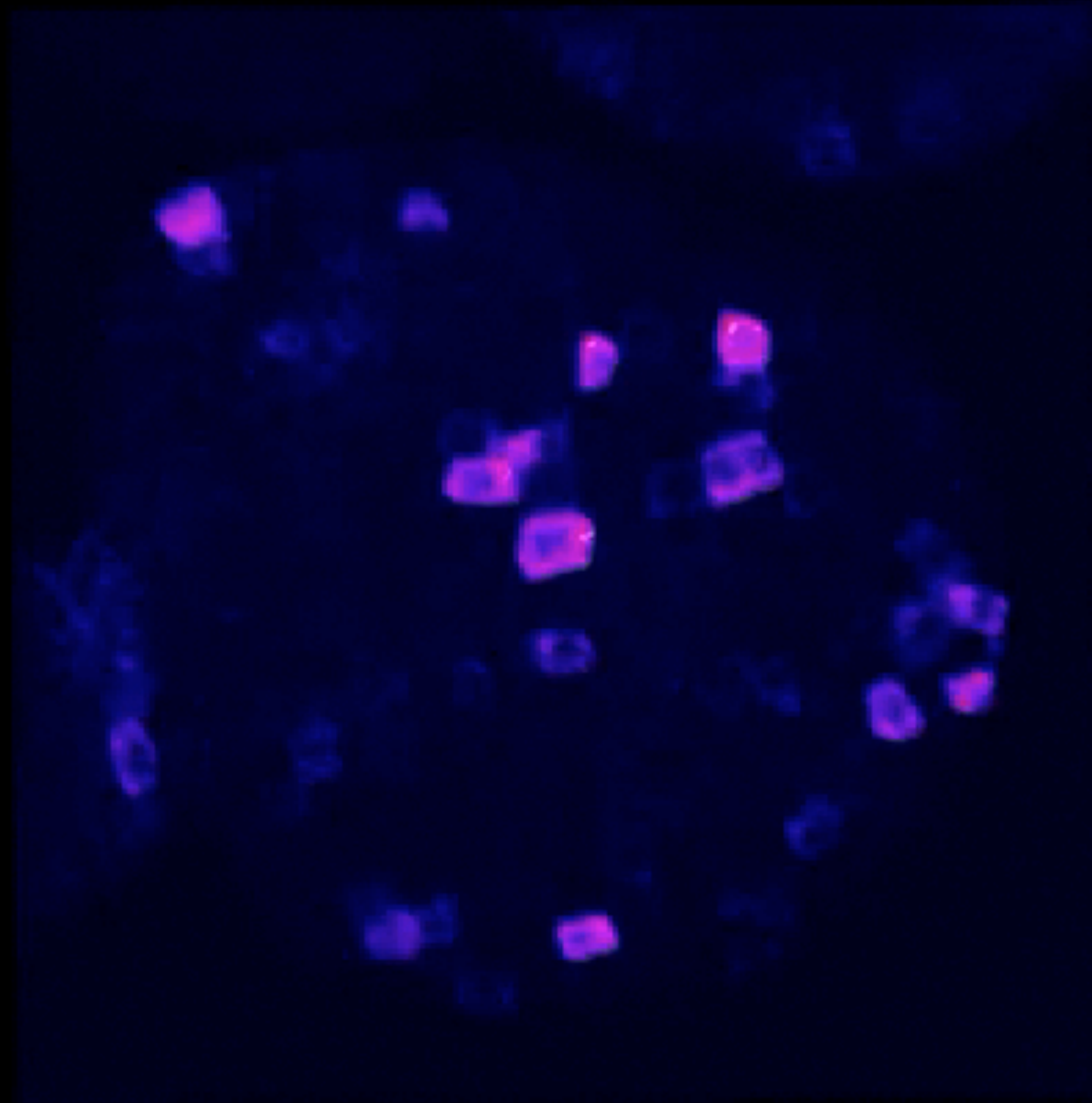
- Post-treat 5mM (15 minutes) LaCl<sub>3</sub> 0h, 3h





# Spontaneous Single-Cell Calcium Activation and Oscillations

Each frame 3.8 sec. 13 z per stack, 33 stacks, 2.1 min



20  $\mu$ m

Time  
0.00.00.000

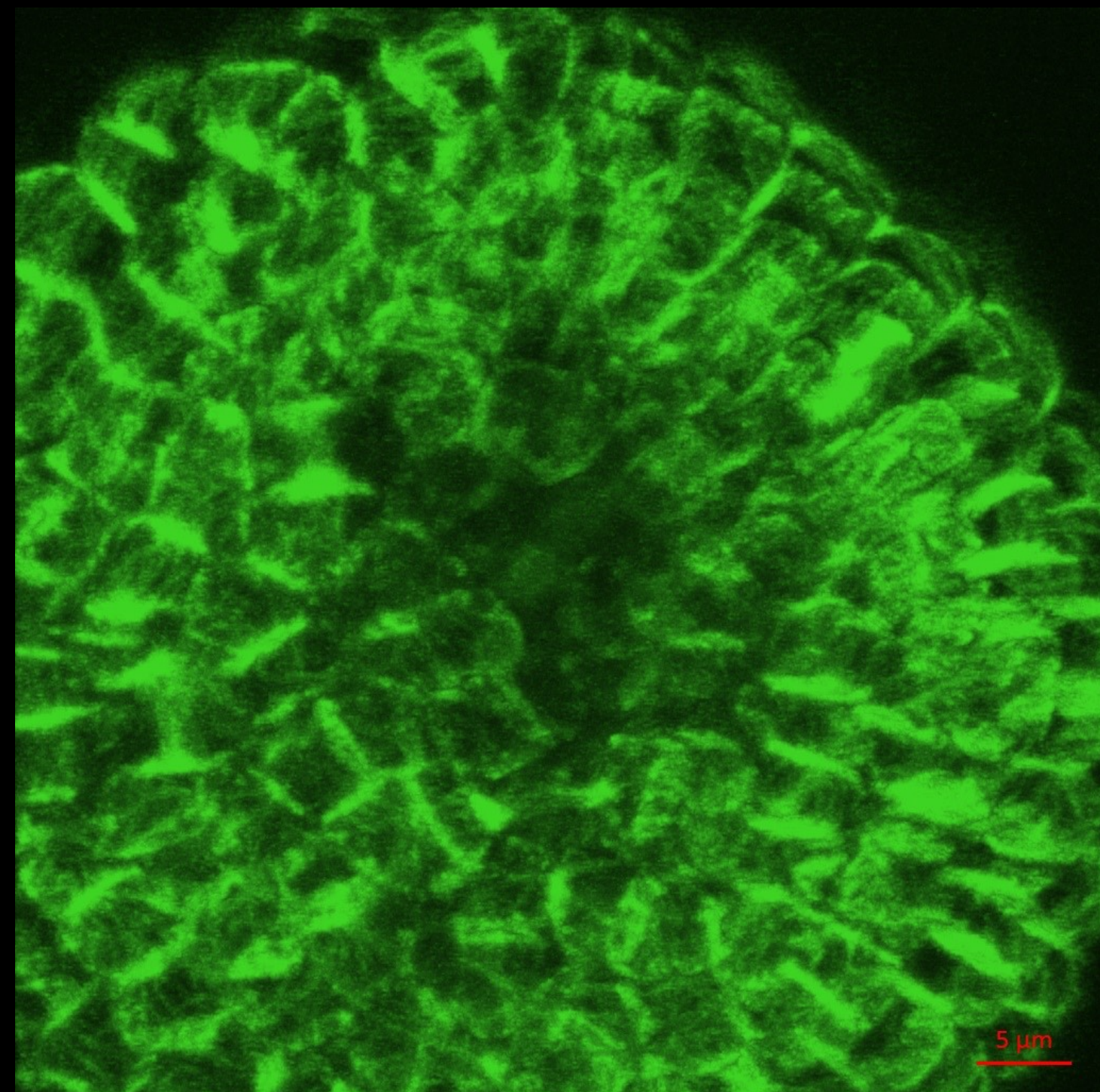
Ting Li, Neha Bhatia, Marcus Heisler

Ting Li

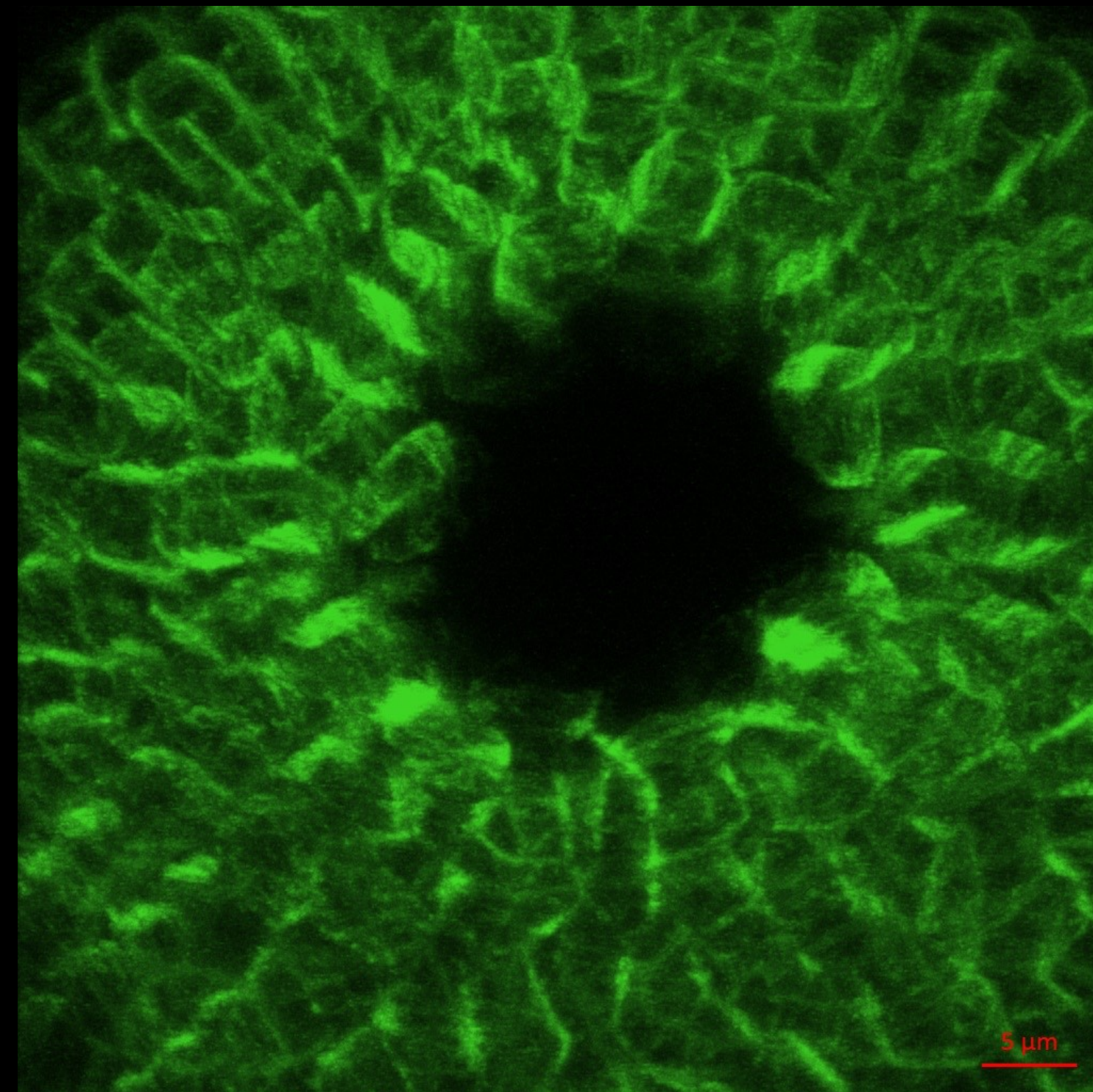


# Calcium Wave Is Not Precursor To MT Mechanical Response

- 2mM BAPTA 6h



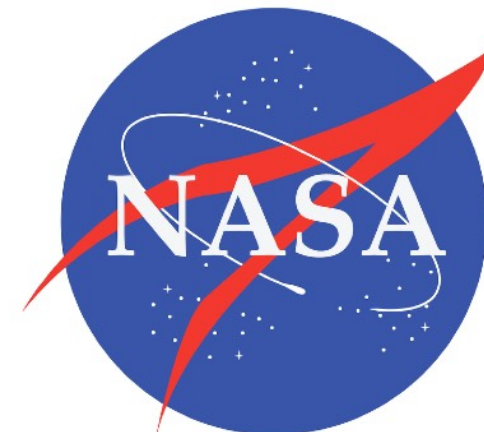
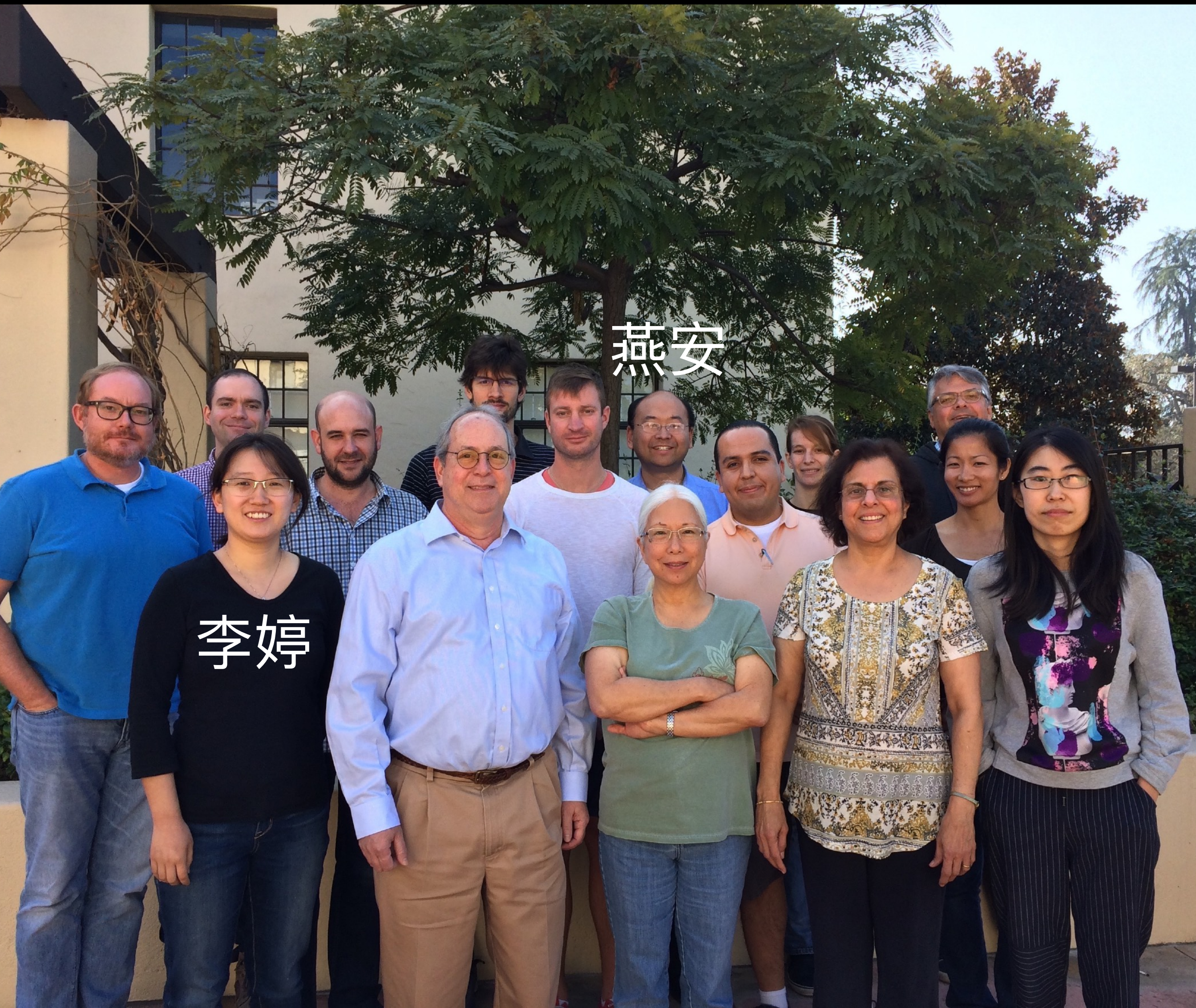
2mM\_BAPTA\_MTKill\_0h



2mM\_BAPTA\_MTKill\_6h

N=6









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Cambridge University



Alexis Peaucelle  
INRA Versailles



Olivier Hamant  
INRA Lyon



Arun Sampathkumar  
MPI for Plant  
Physiology



Jan Traas  
INRA Lyon



Arezki Boudouad  
INRA Lyon



Marcus Heisler  
Univ. Sydney



Eric Mjolsness  
U.C. Irvine

