


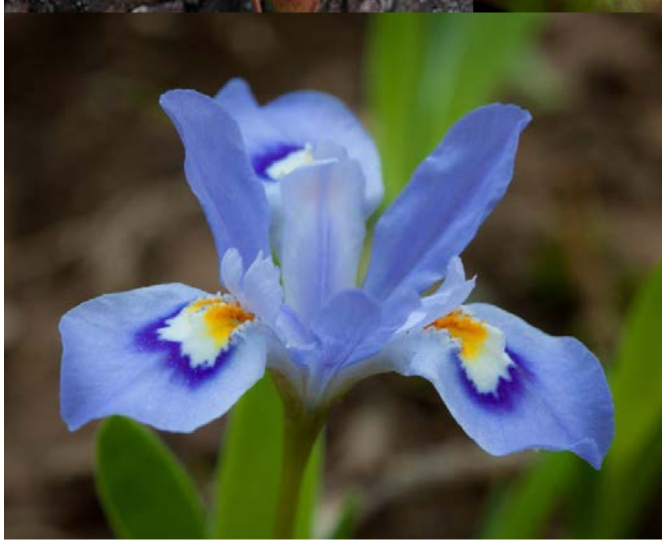
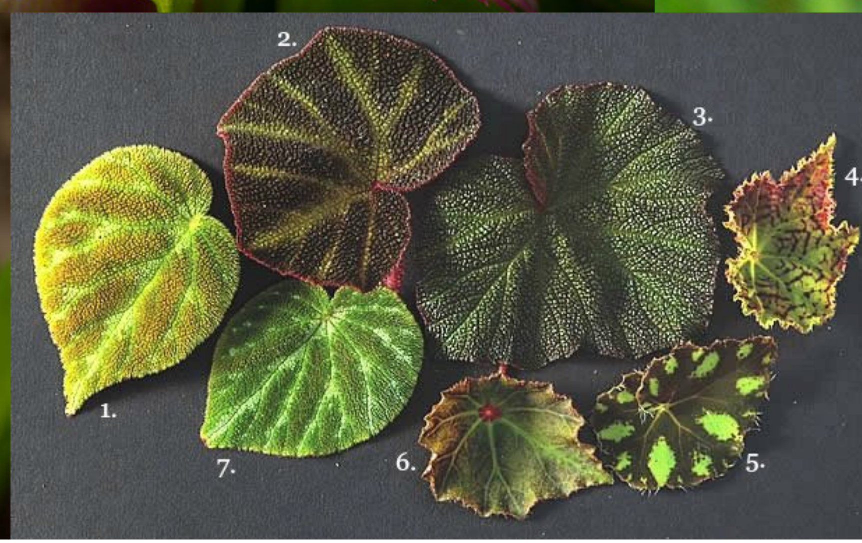
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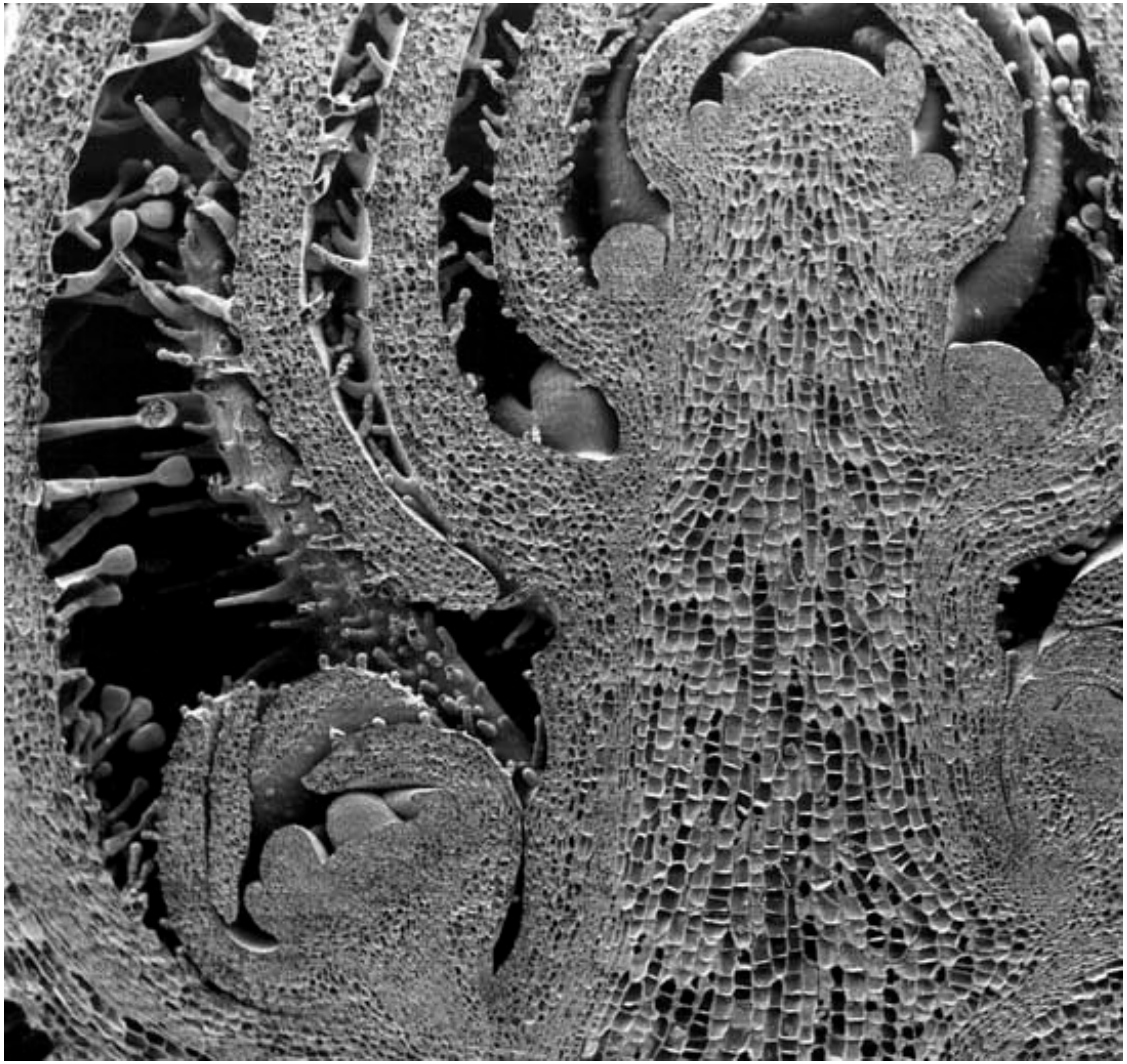
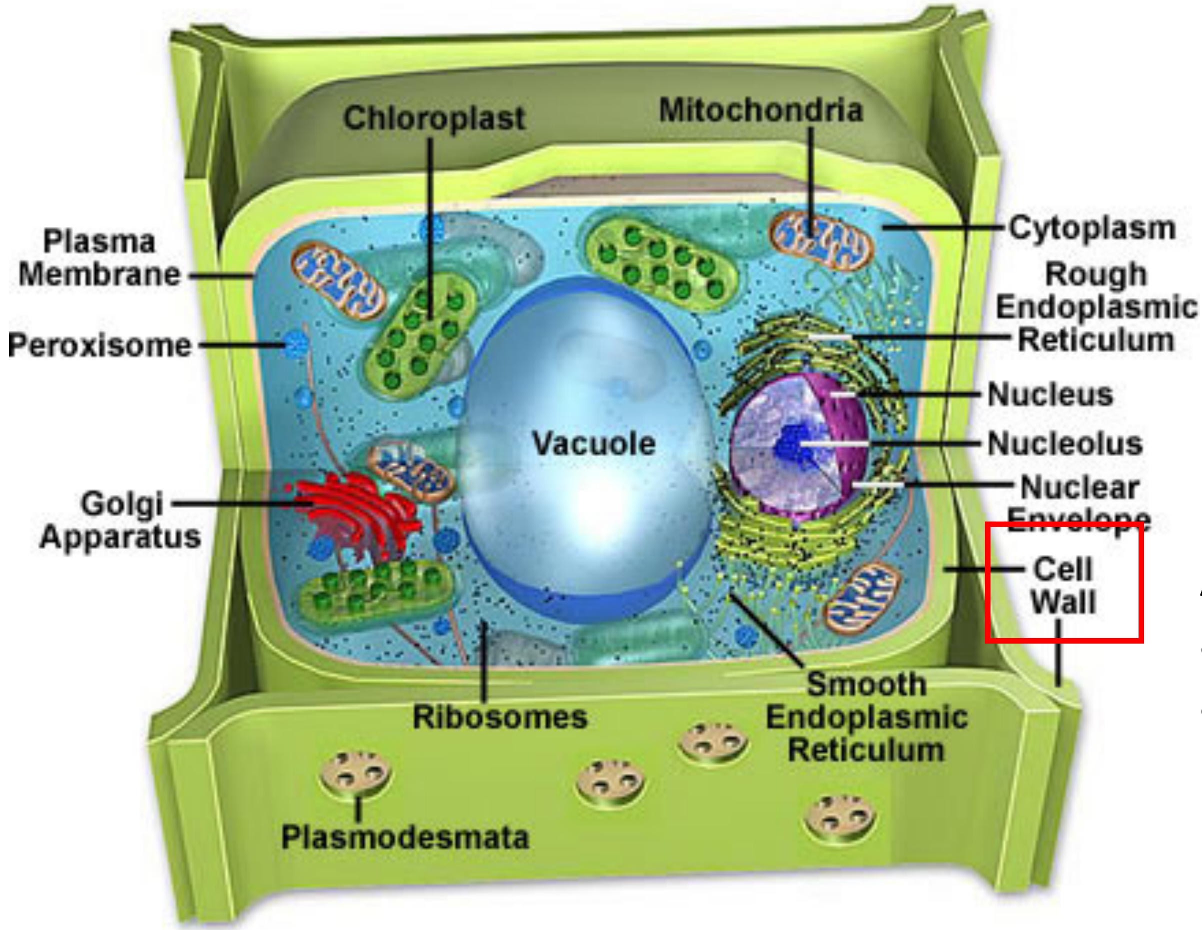


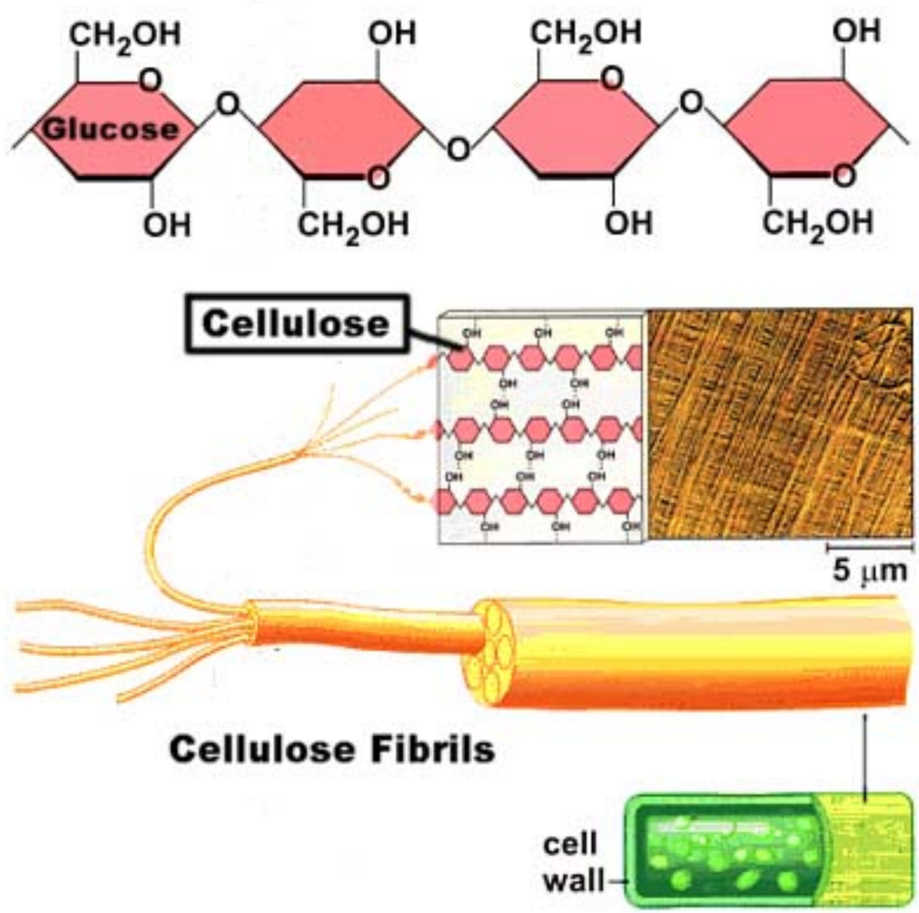
How do plants generate complex forms?

How do the fundamental properties of plant cells and tissues influence these processes?

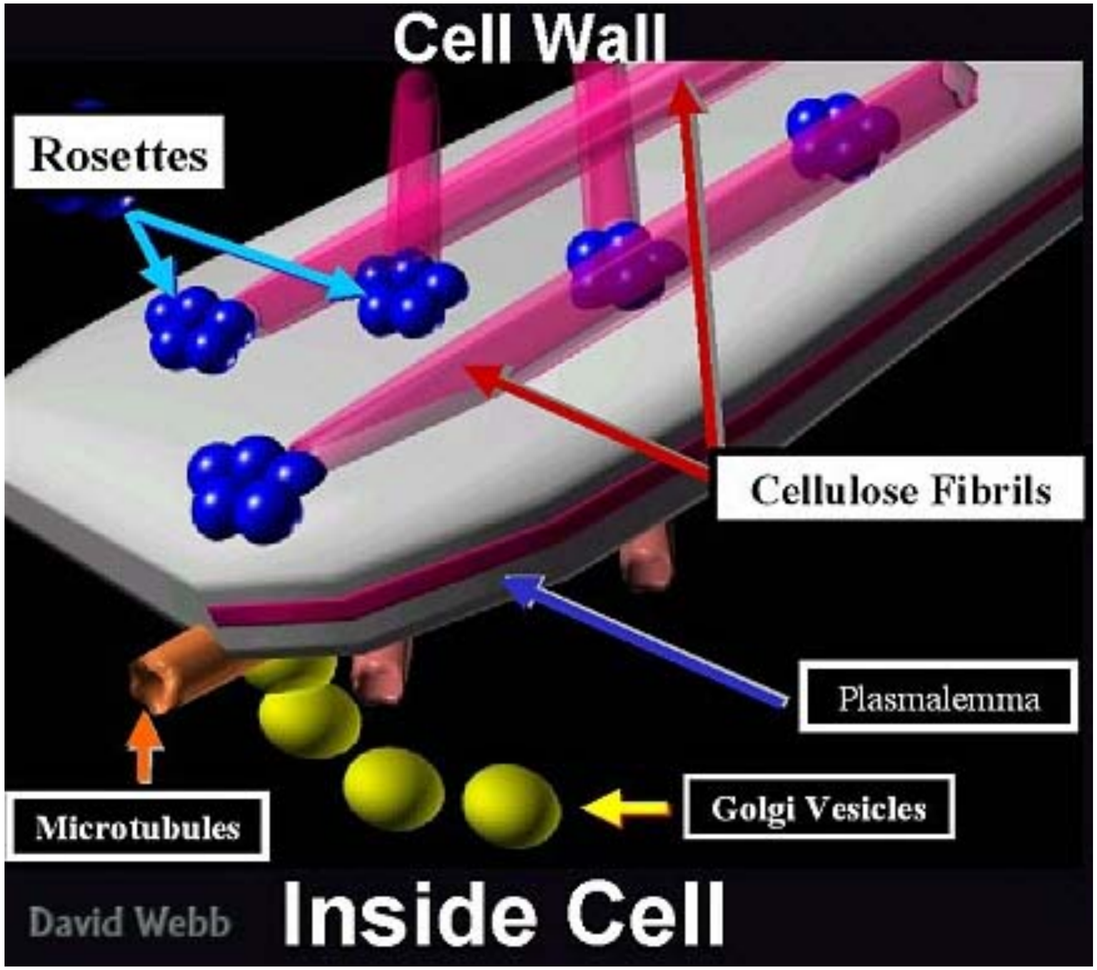


All plant cells are bounded by a cell wall

Cell walls are primarily composed of cellulose, a polymer of glucose

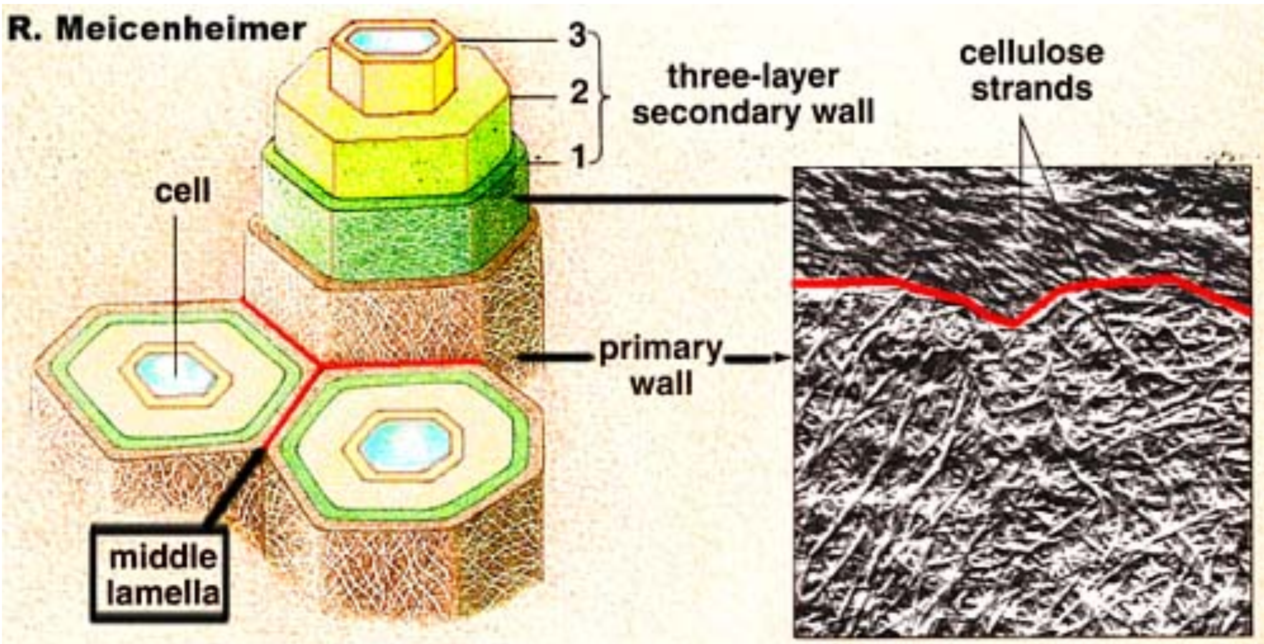


Specialized enzymes are embedded in the plant cell's plasma membrane, here labelled as "rosettes." These enzymes synthesize cellulose, spinning the fibers (or "fibrils") into the space outside the plasma membrane, thereby building the cell wall.

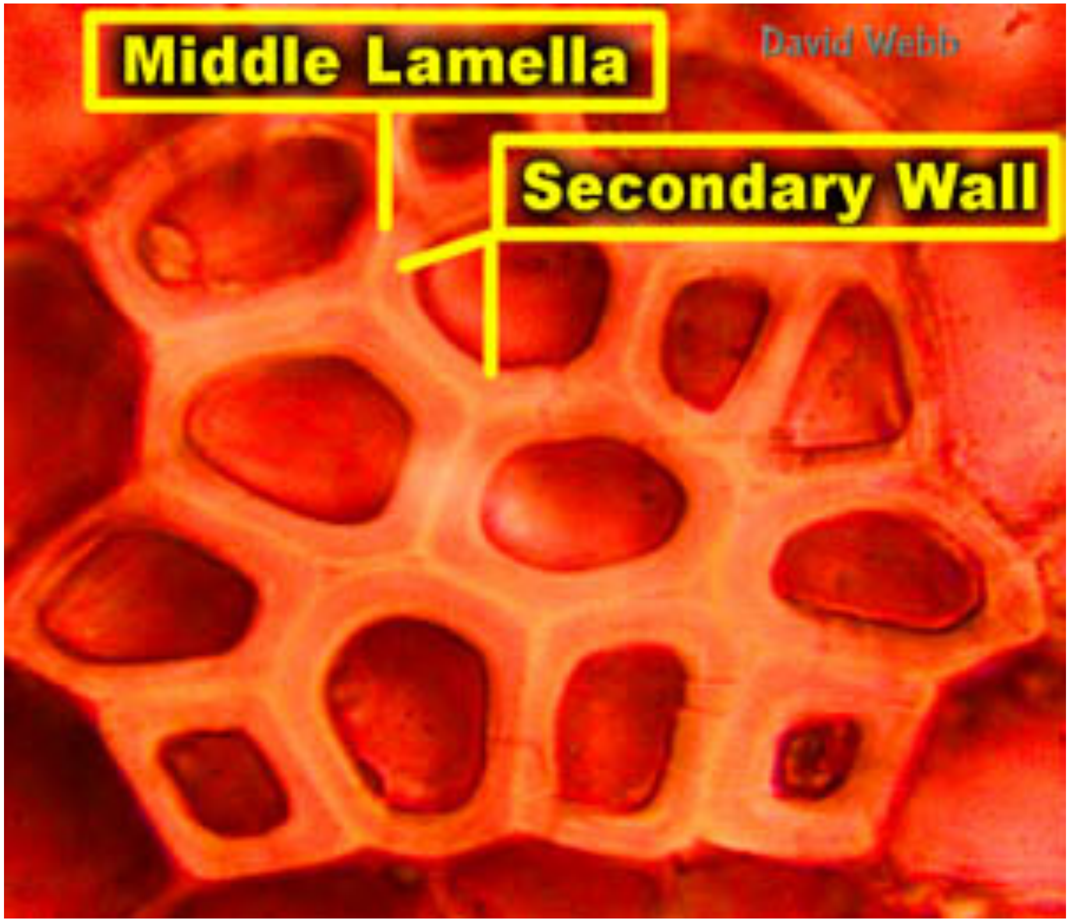


The enzymes are mobile within the plasma membrane and are moved around the cell by the action of protein motors attached to the cytoskeleton (microtubules) that are inside the cell.

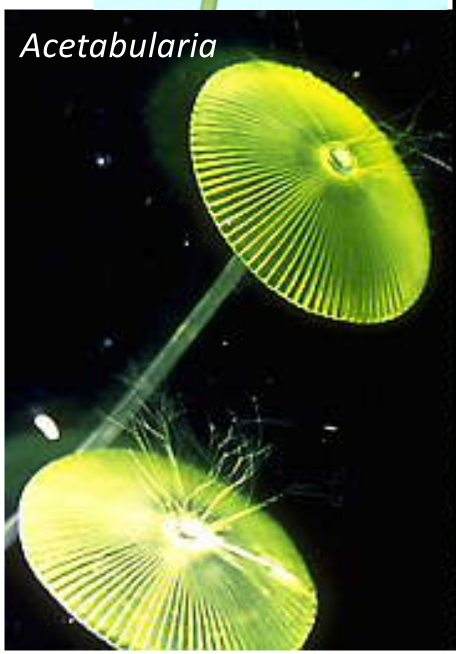
Plant cell walls have several layers. Because they are constructed from the outside in, the oldest wall is always on the inside.

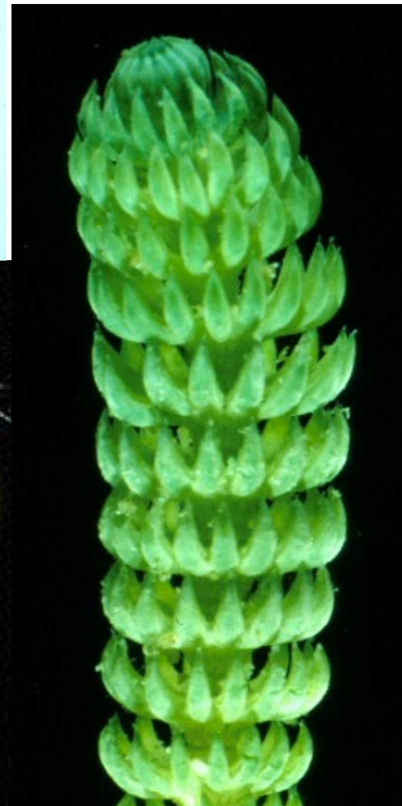


Cells are adhered to one another by a secreted glue called the middle lamella.



Plant cells can achieve complex shapes. These algae are single cells!





The presence of the cell wall has a cascading series of effects on the ways plants build their bodies and go about their lives.

autotrophy

sessile

cell wall

No cell migration

No germ line

Many totipotent cells

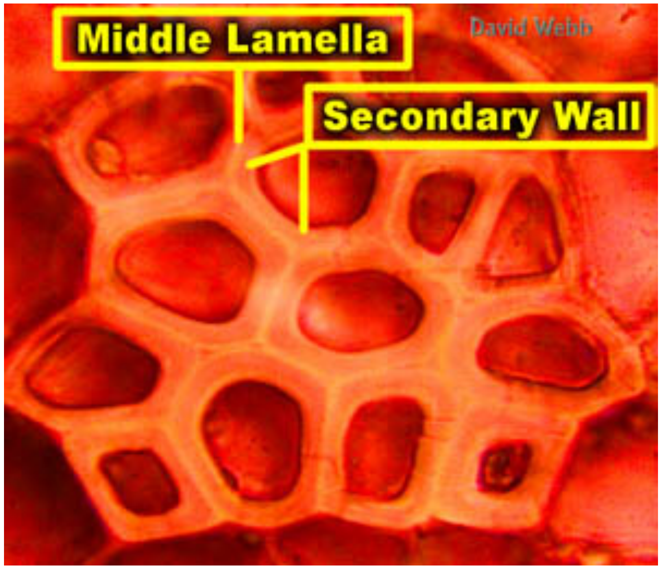
Alternation of generations

Continual organogenesis

Extreme modularity

Plastic development

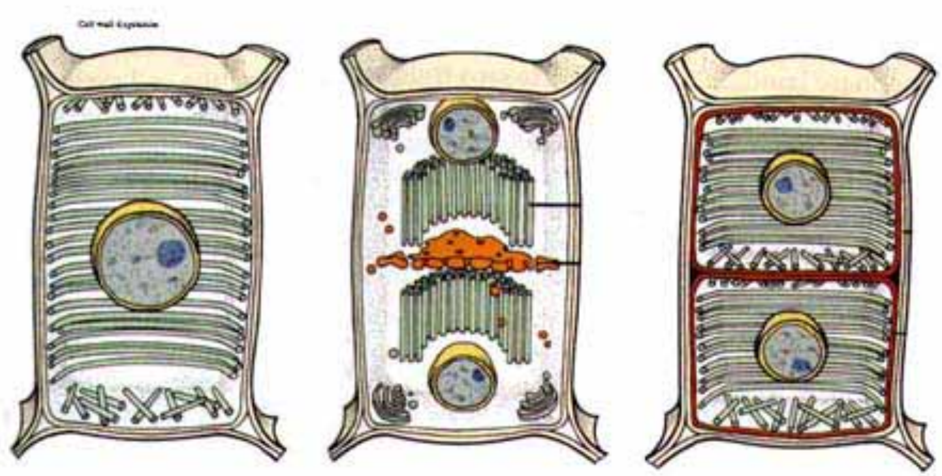
Due to the fact that plant cells are bound together by their cell walls, the behavior of individual cells is critical to the control of plant growth and development.



Critical processes related to cell division:

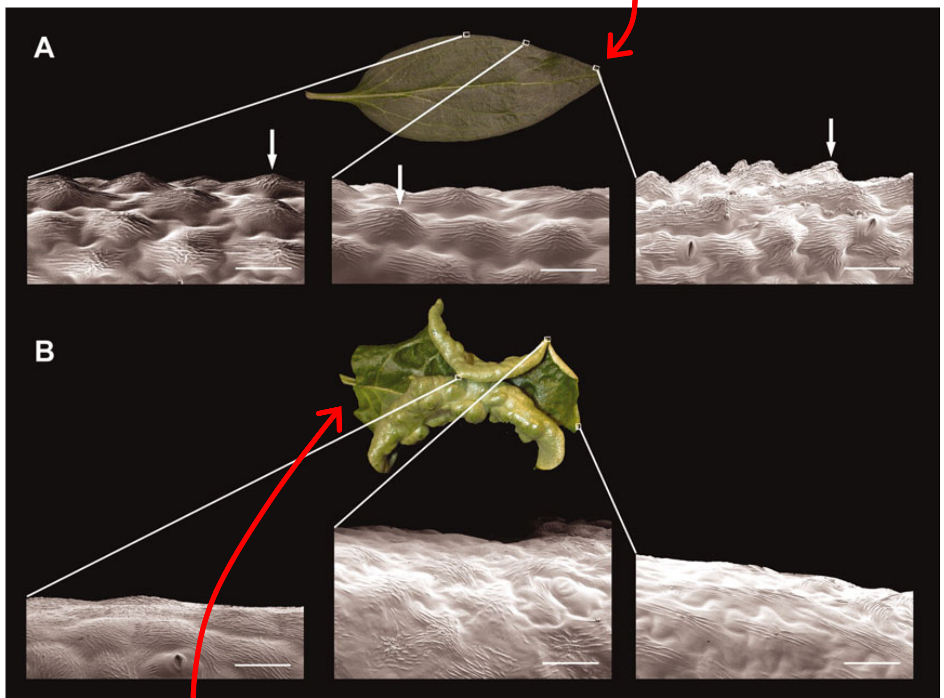
→ - timing and rate of cell division

- orientation of cell wall formation
  - periclinal vs. anticlinal
- symmetry of cell division



Deposition of new cell walls during plant cell division.

A normal, flat snapdragon leaf



A leaf where the relative rates of cell division are uncoordinated.

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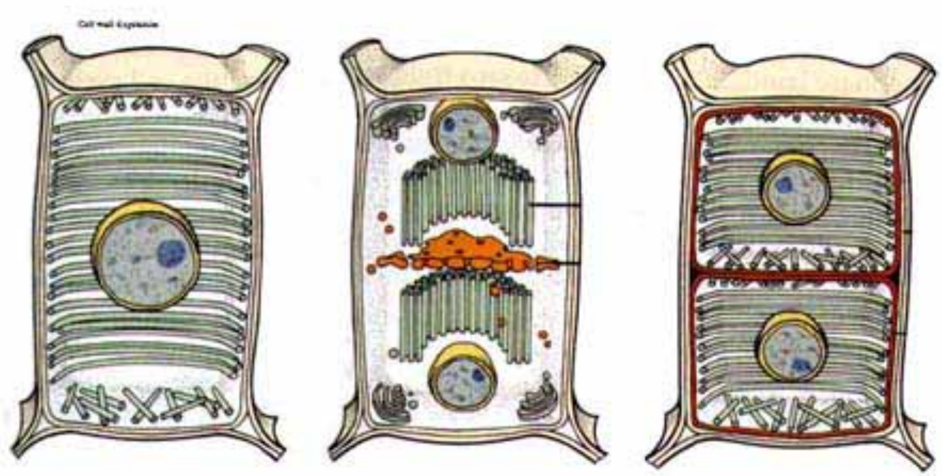

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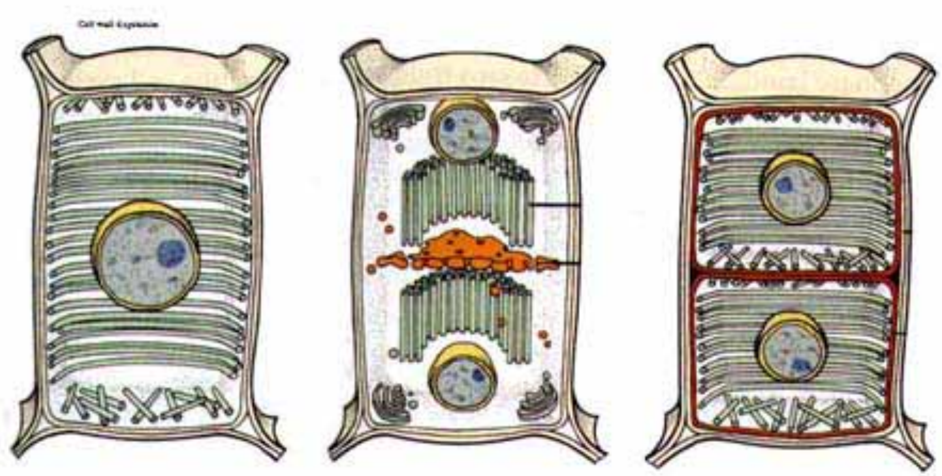
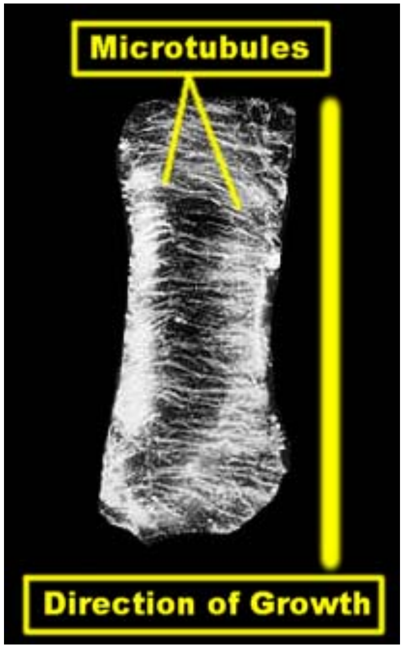
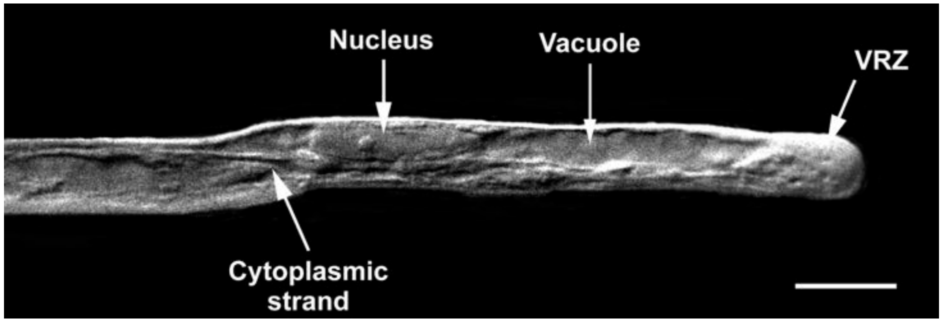


Deposition of new cell walls during plant cell division.

Plants tend to segregate the processes of cell division and expansion – first they divide, then they expand.

The rate and direction of cell expansion is controlled by cooperative interactions between the cytoskeleton, vacuole and cell wall.

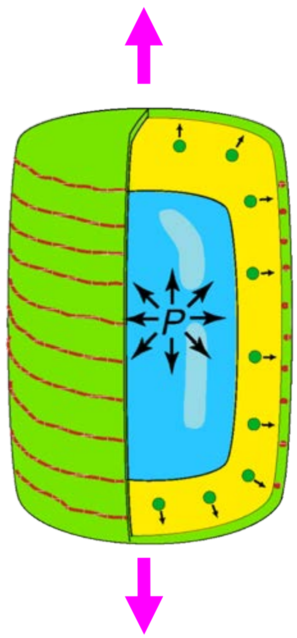




Two Modes of Cell Growth

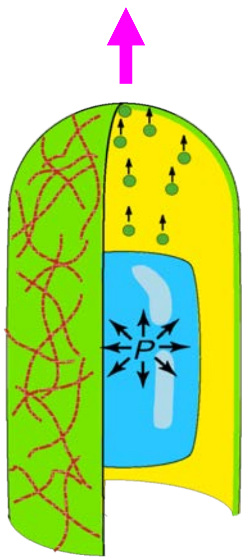
Diffuse Growth

Wall expansion is distributed over the whole cell surface



Tip Growth

Wall expansion is localized to one end of the cell



The Drawbacks of Turgor-Driven Cell Growth

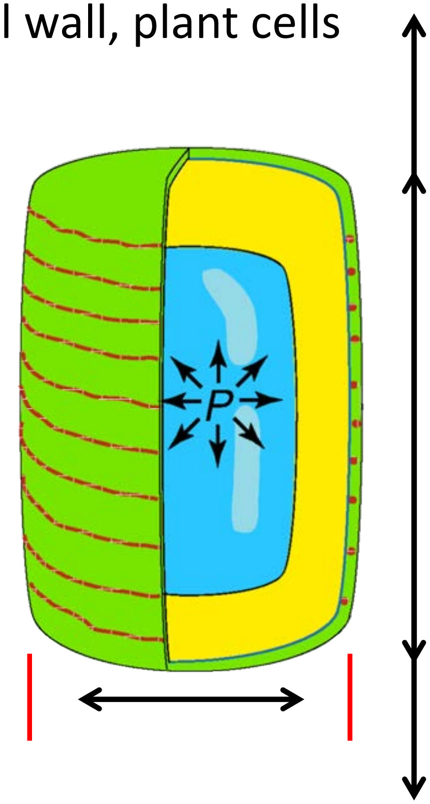
Pressure-driven growth has the unfortunate consequence of turning most objects into spheres.

Walled cells using pressure to drive growth must also control when and where the wall can expand, or else be spherical

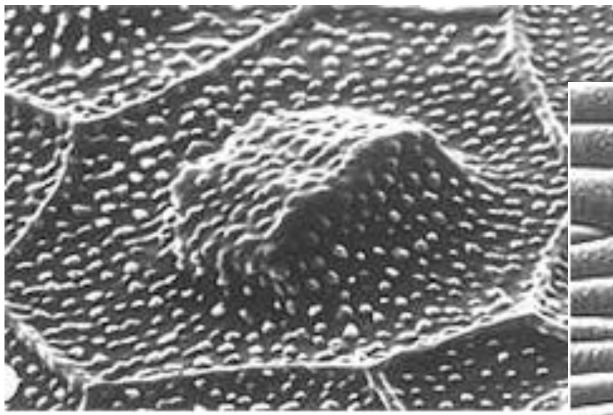
So how do plant cells make shapes other than spheres?

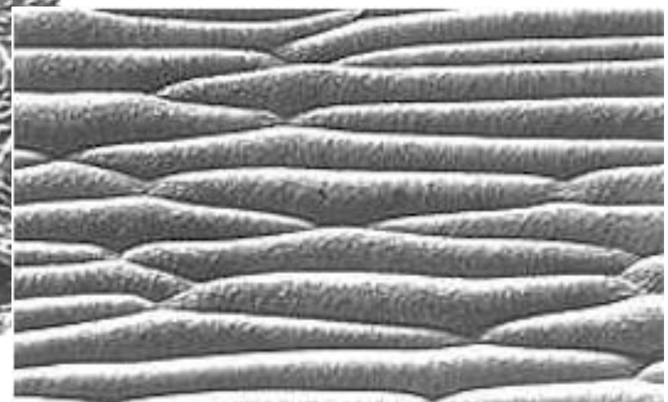
The secret is in the cytoskeleton and cell wall. By controlling the orientation of the cytoskeleton and the cellulose microfibrils in the cell wall, plant cells can sculpt complex cell shapes, even when the force generating cell expansion is diffuse.

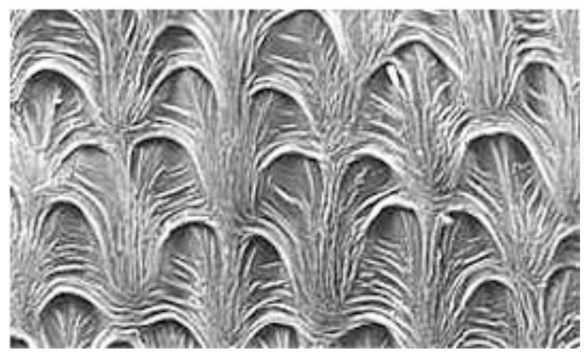
In this example, the cellulose strands in the cell wall are strongly oriented in one direction. They act like the hoops in a barrel – constraining expansion in one orientation but allowing it in another.



Plant cells can achieve lots of different shapes.

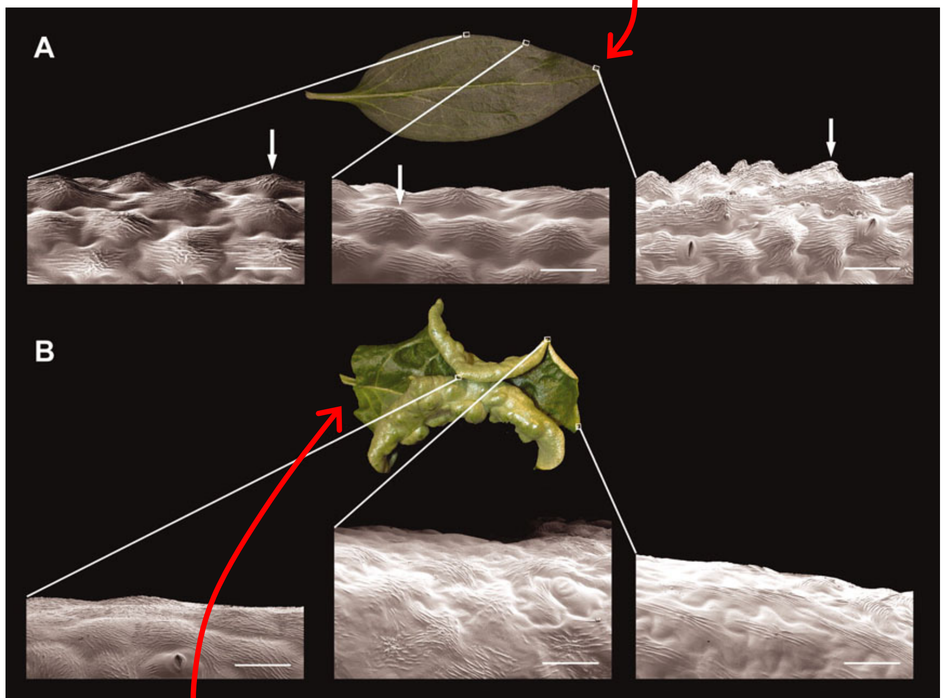






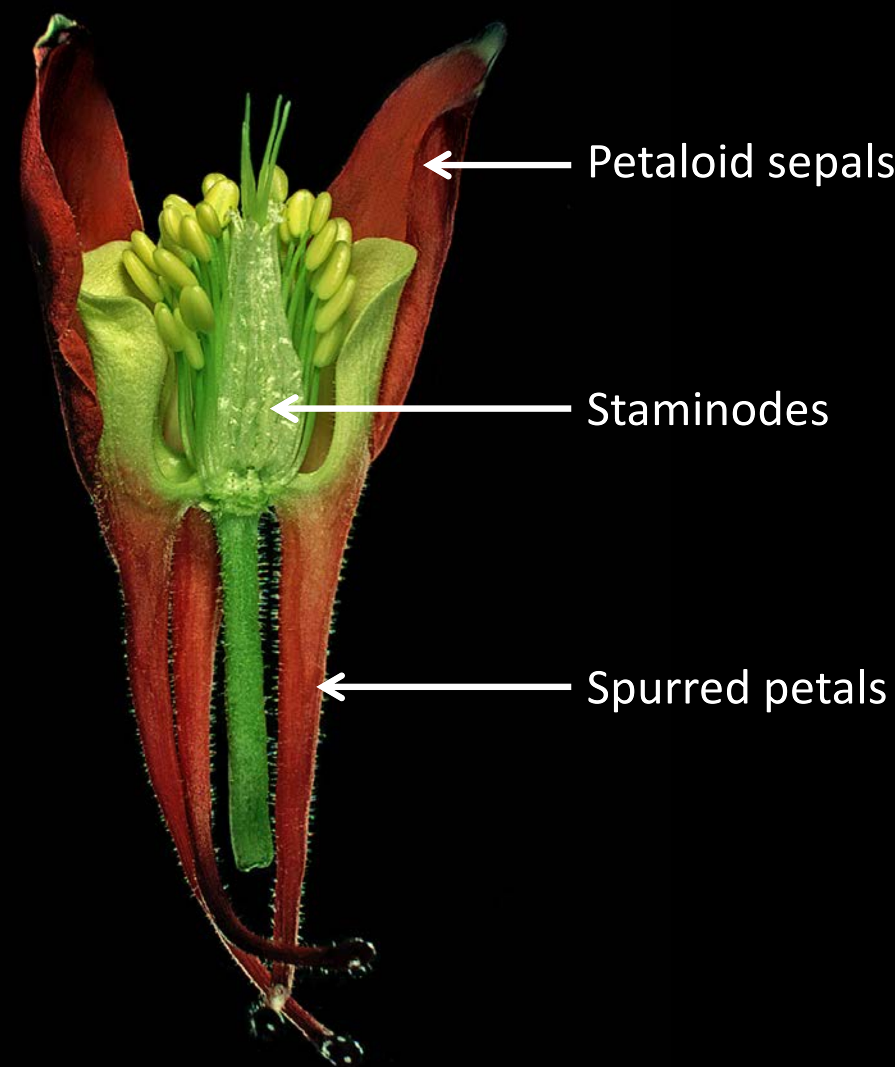
A normal, flat snapdragon leaf

How does the control of cell division and expansion contribute to the shapes of lateral organs (e.g., leaves, petals)?



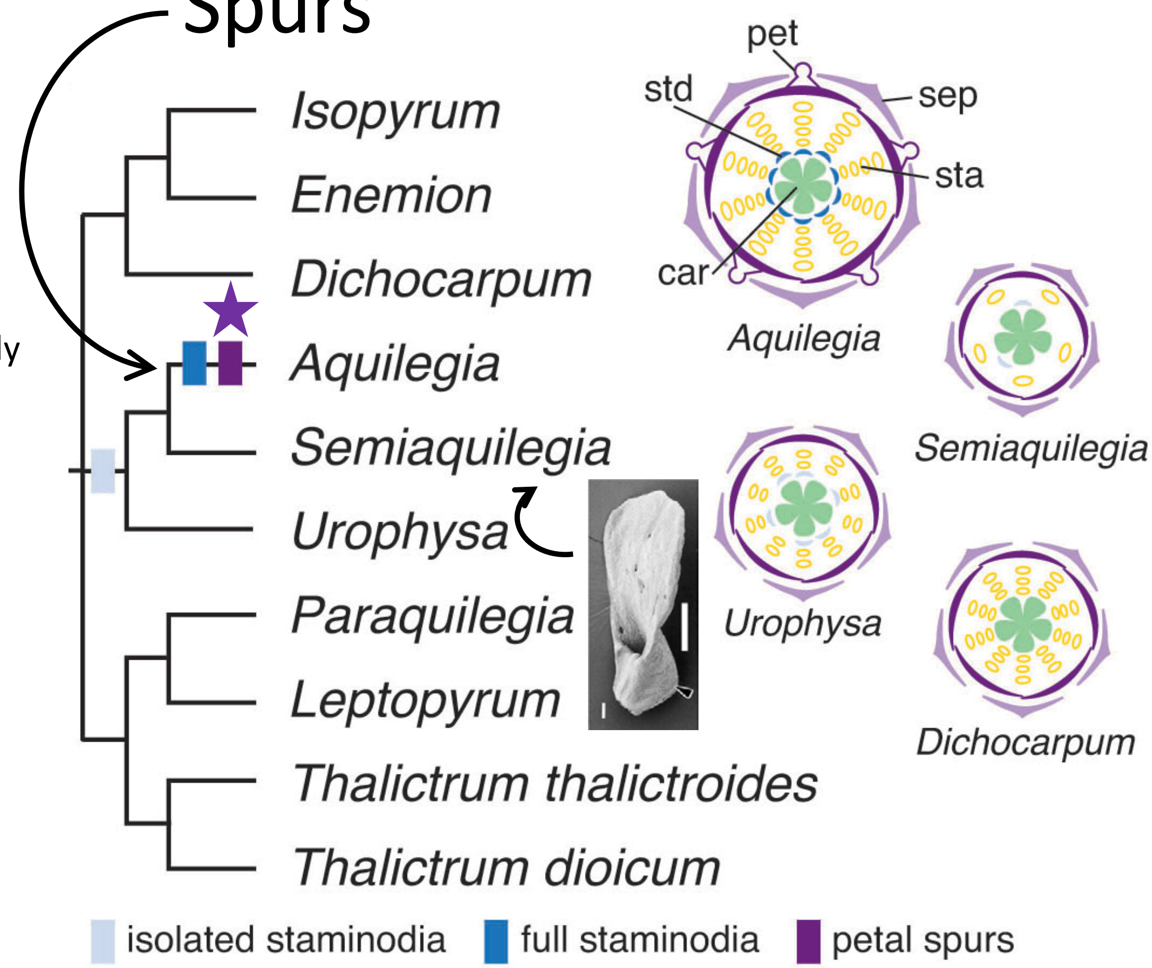
A leaf where the relative rates of cell division are uncoordinated.

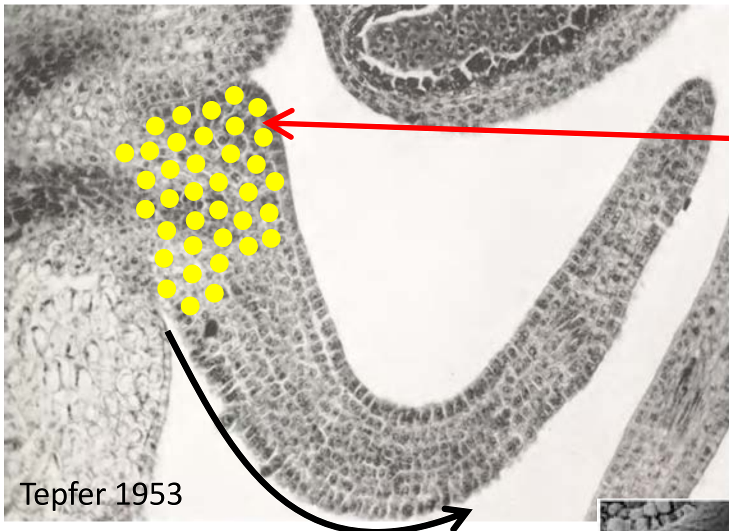
Aquilegia (columbine) is a great model for studying complex organ shape, especially the spurred petals.

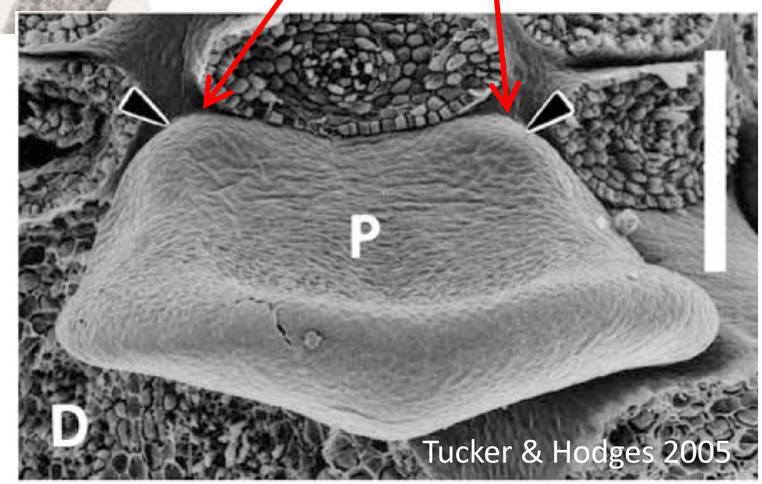


Spurs

Spurs are recently evolved.

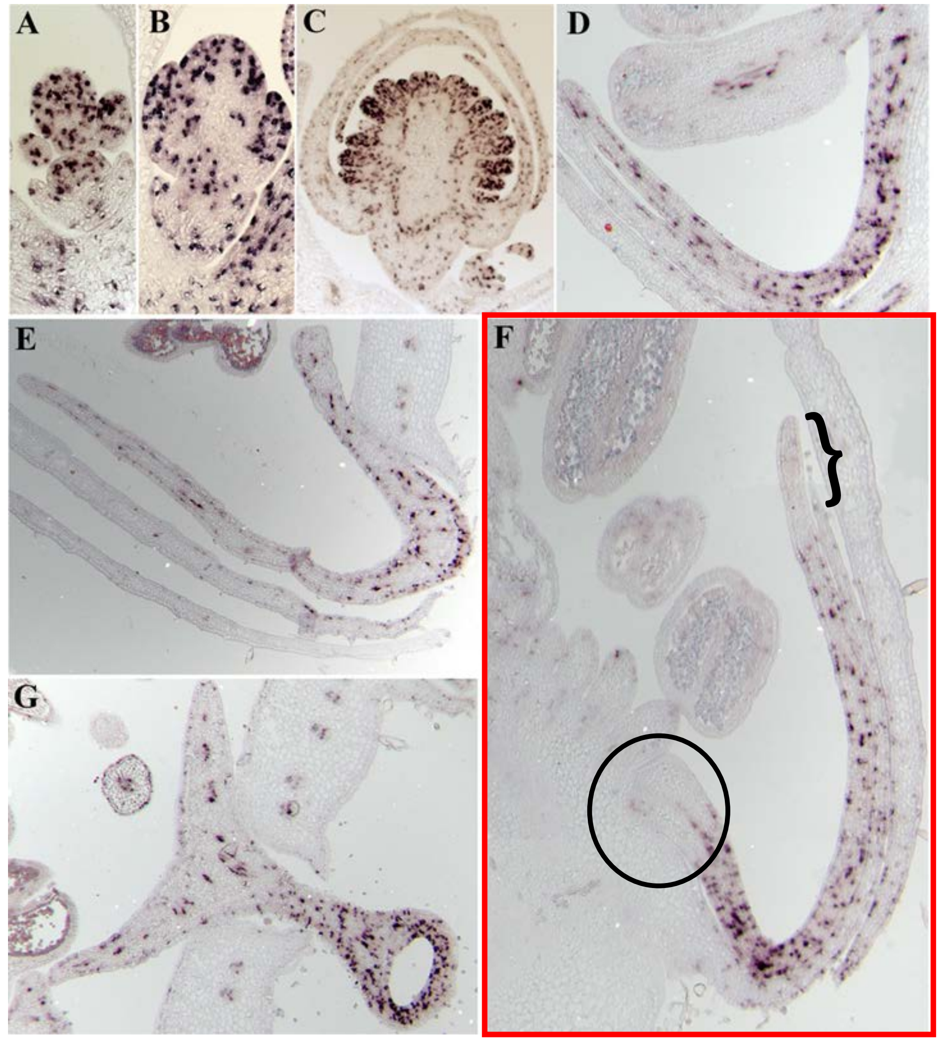






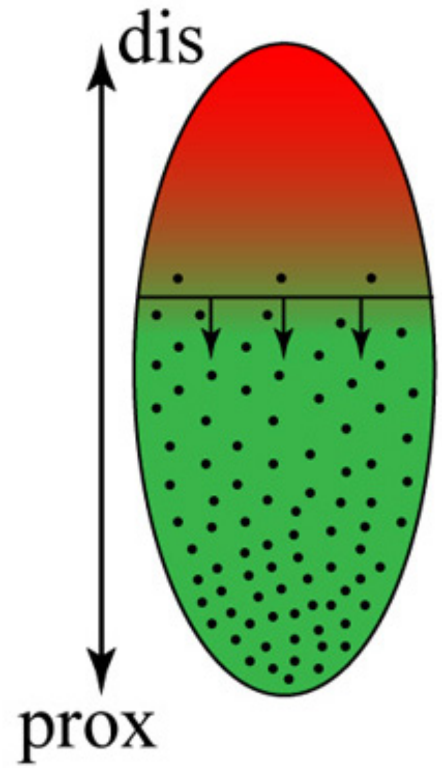
This is the original theory about how spurs develop – localized cell divisions at the attachment point of the petal.

HISTONE H4
A genetic marker for cell division



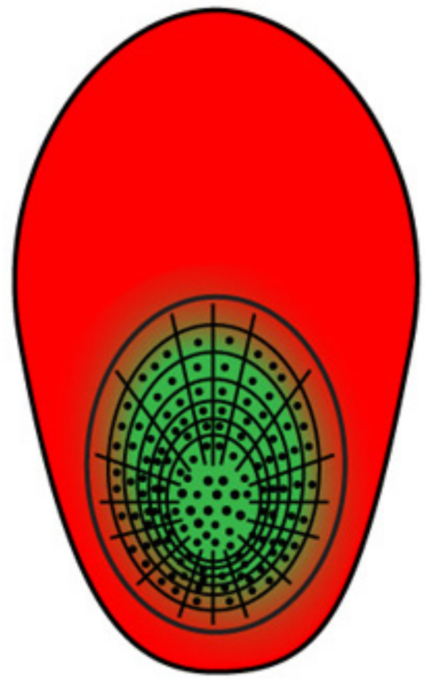
That's wrong. There are no cell divisions in that area. Instead, cell divisions are focused in the area of the spur itself.

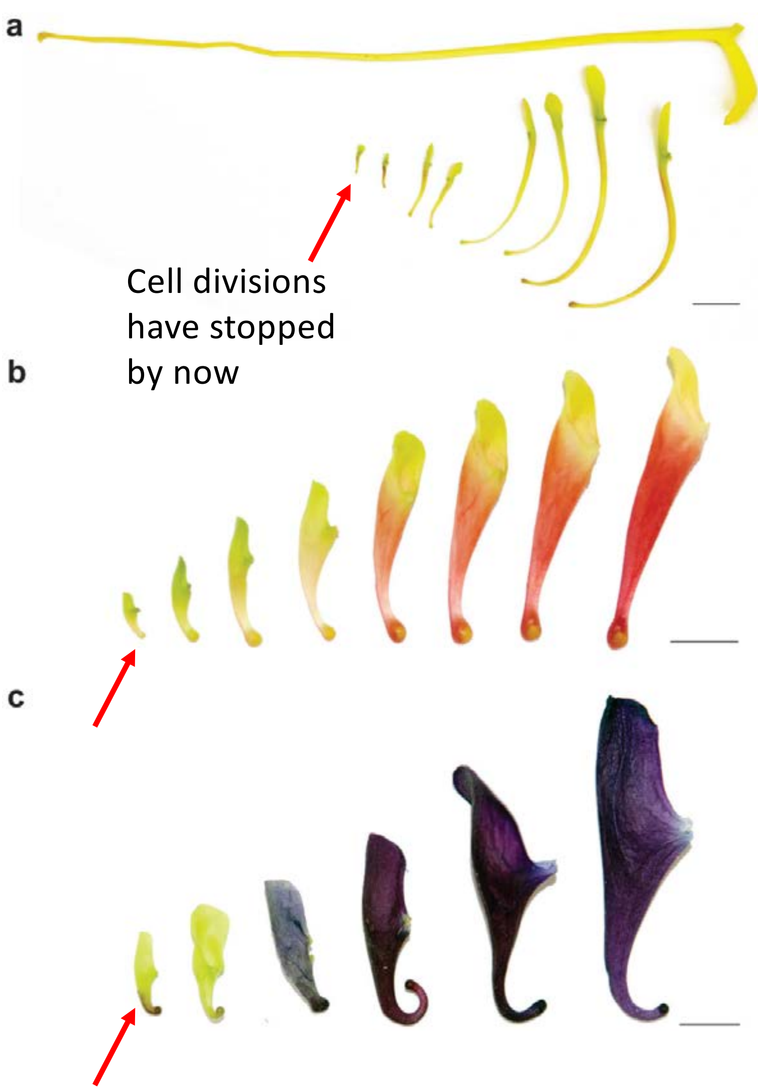
Silvio Collani



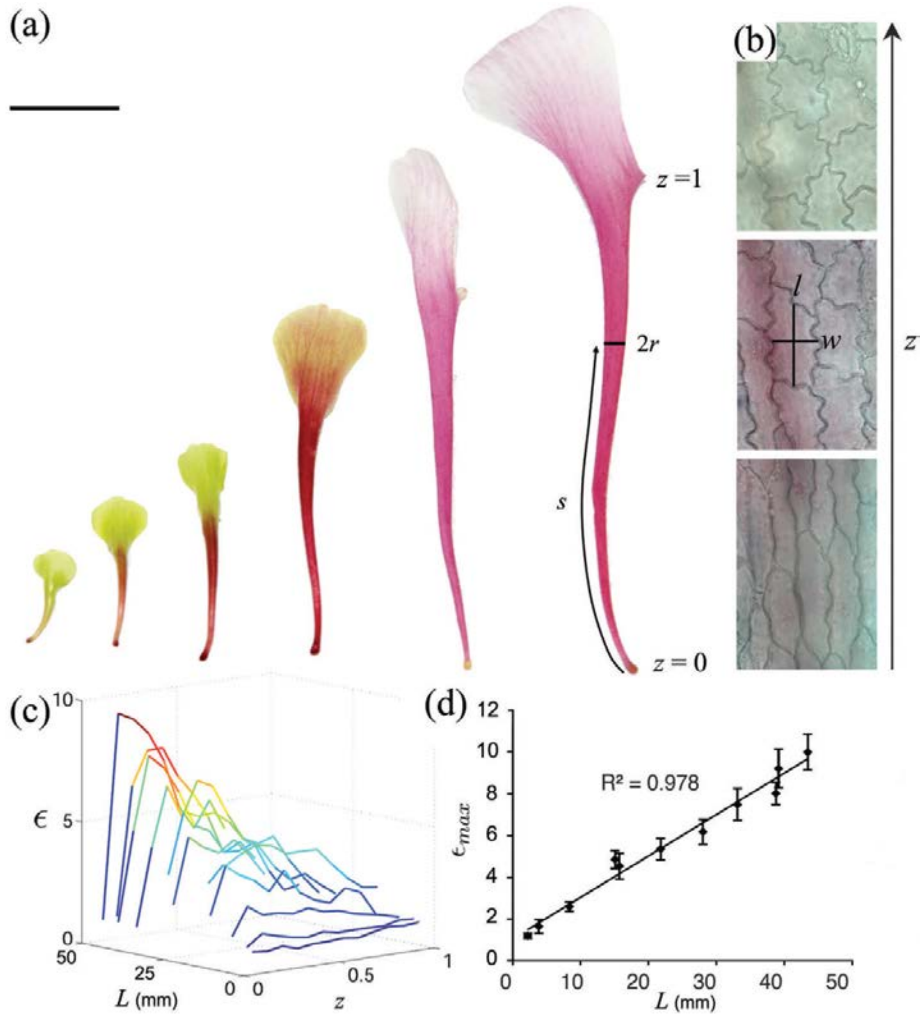
In leaves, cell division typically ceases in a wave that progresses from the distal tip to the proximal attachment point.

In *Aquilegia* petals, cell divisions cease in a wave that collapses down towards the nectary from all sides. The divisions in the nascent spur are tangentially oriented around the nectary.





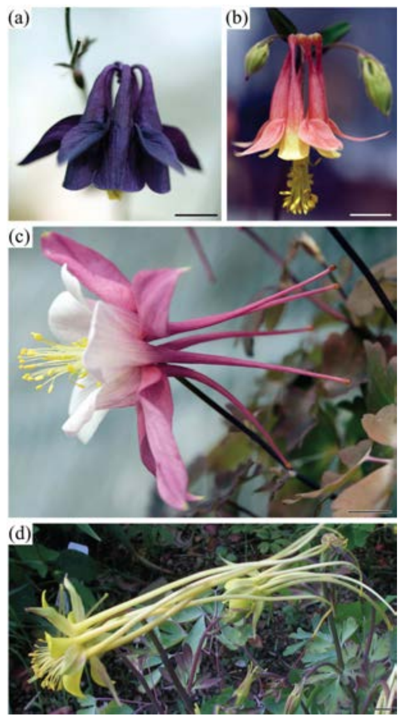
Cell divisions do appear to be important for creating the initial out-pocketing of the petal but explain only a very small component of spur growth.

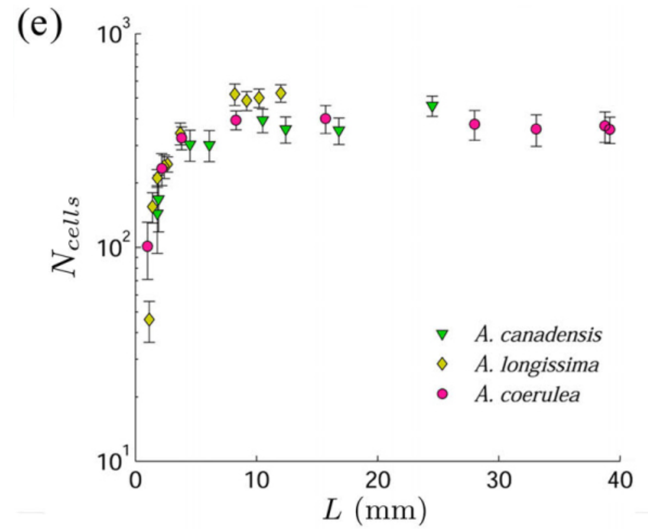


Overall increase in cell area is consistent across the developing petal but the spur is marked by dramatic differences in cell shape due to highly anisotropic expansion.

Puzey et al. 2011

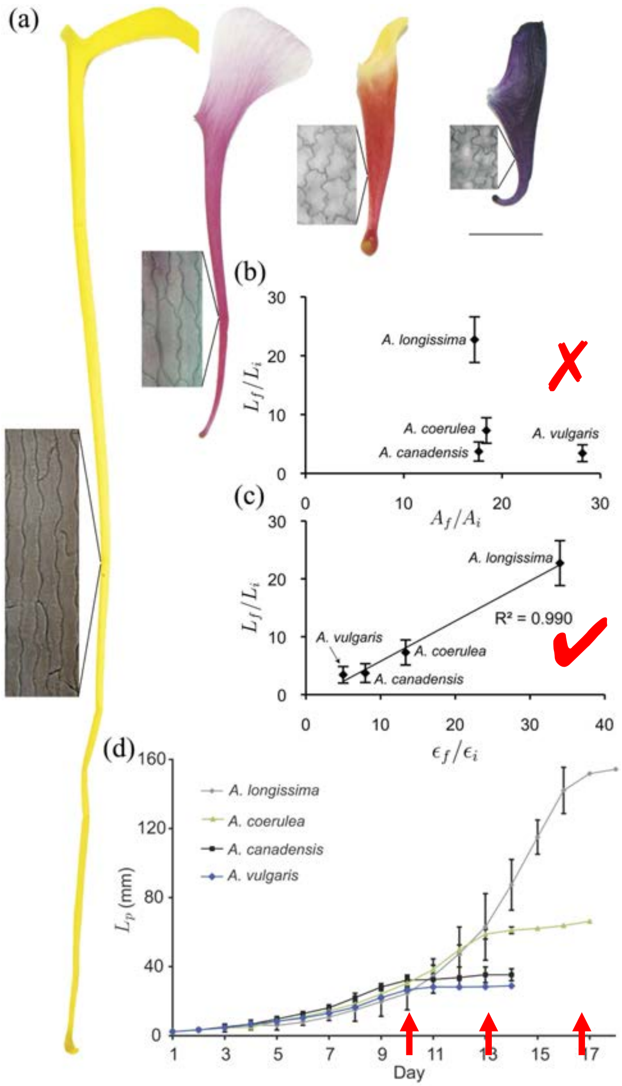
OK, so cell divisions appear to end early in petal development and the vast majority of spur elongation is driven by highly oriented cell elongation. What about spur diversity? Is variation in spur length mostly driven by cell division, cell expansion or both?





Cell number does not vary significantly between diverse species

Puzey et al. 2011



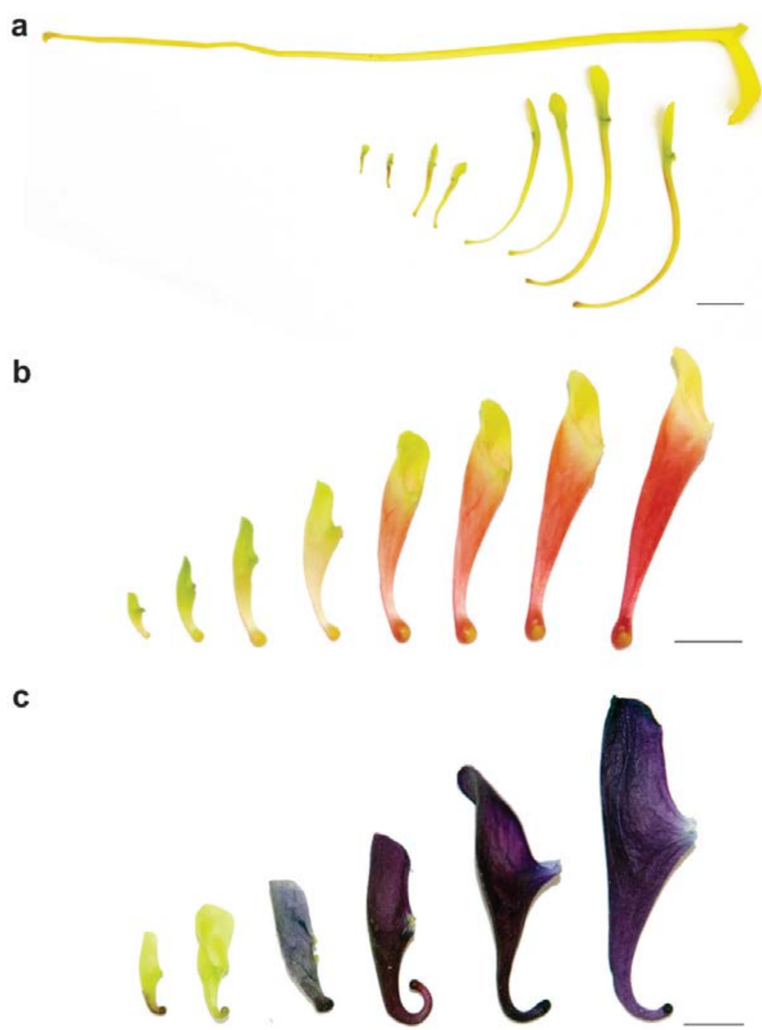
Across species, cell area shows no relationship with spur length.

In contrast, cell anisotropy is highly correlated with spur length with a R^2=0.990.

Comparison of spur growth dynamics indicates that longer spurs develop at the same rate as others but over a longer period.

**Variation in spur length from 3-12 cm can be produced by modulation of a single cell growth parameter.

Puzey et al. 2011



Spur development occurs in two phases Phase I involves localized cell divisions that create a spur cup. In Phase II, oriented cell elongation drives spur growth and final elaboration. Variation in Phase II appears to largely underlie variation in spur length.

We can manipulate spur development by turning off the expression of specific genes. In these treated spurs, we see dramatic outgrowths that are not ectopic spurs but, rather, appear to be due to buckling caused by uncontrolled proliferation in specific areas.

Yant et al. 2015

Yant et al. 2015

Aquilegia is also a great model because of diversity among species

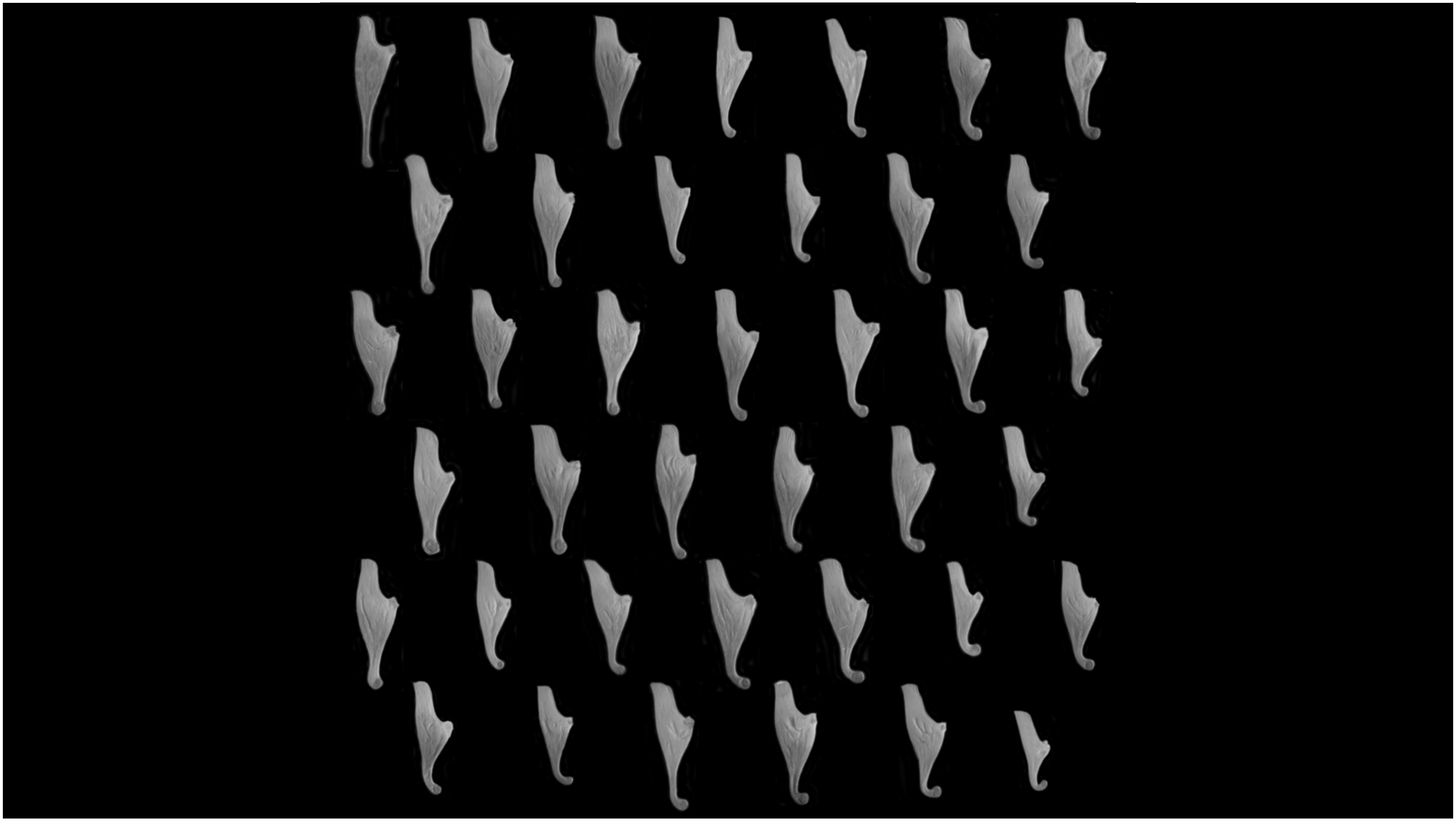
Photos: Hodges & Puzey

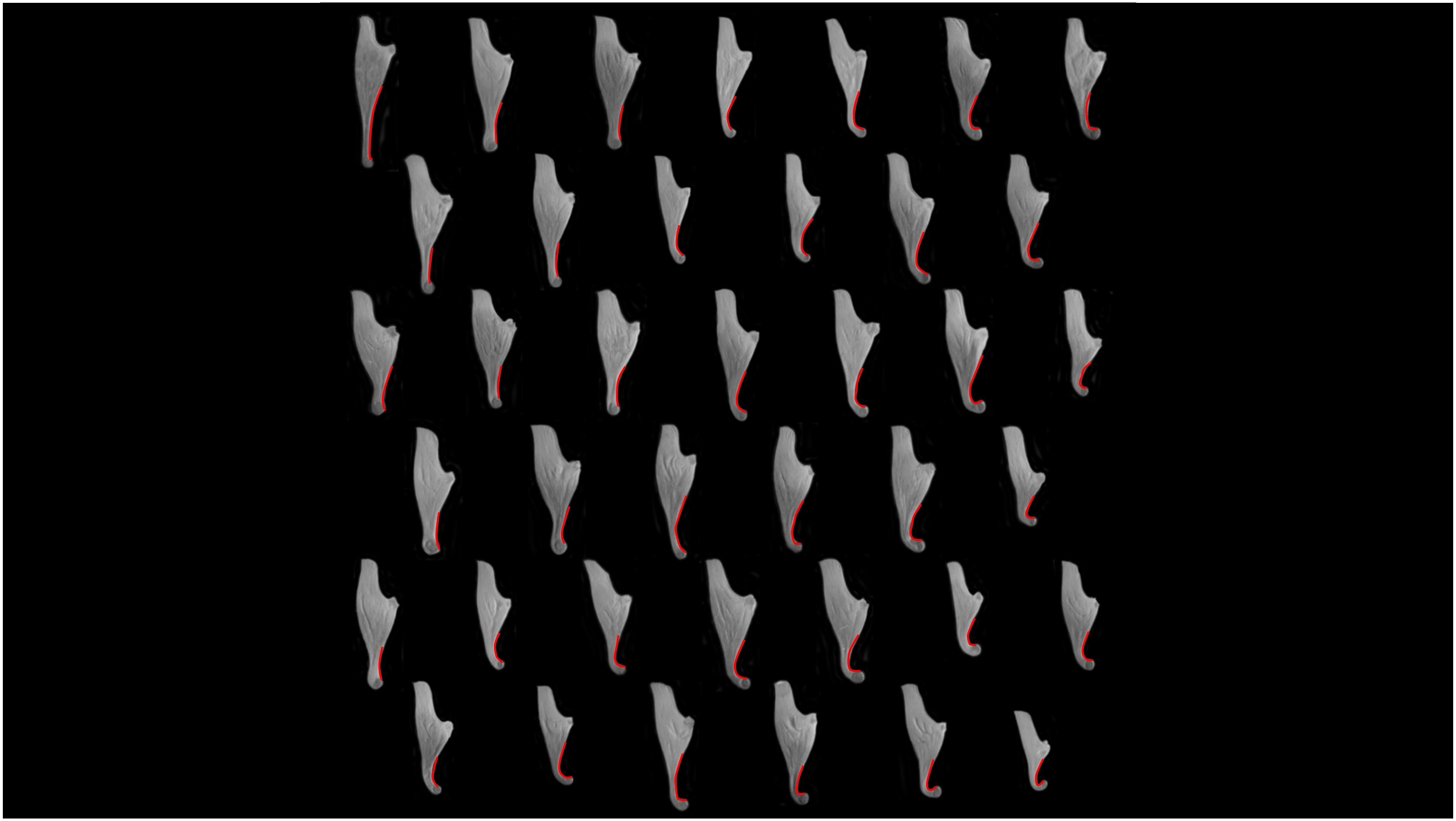
Quantitative Trait Locus Mapping Project

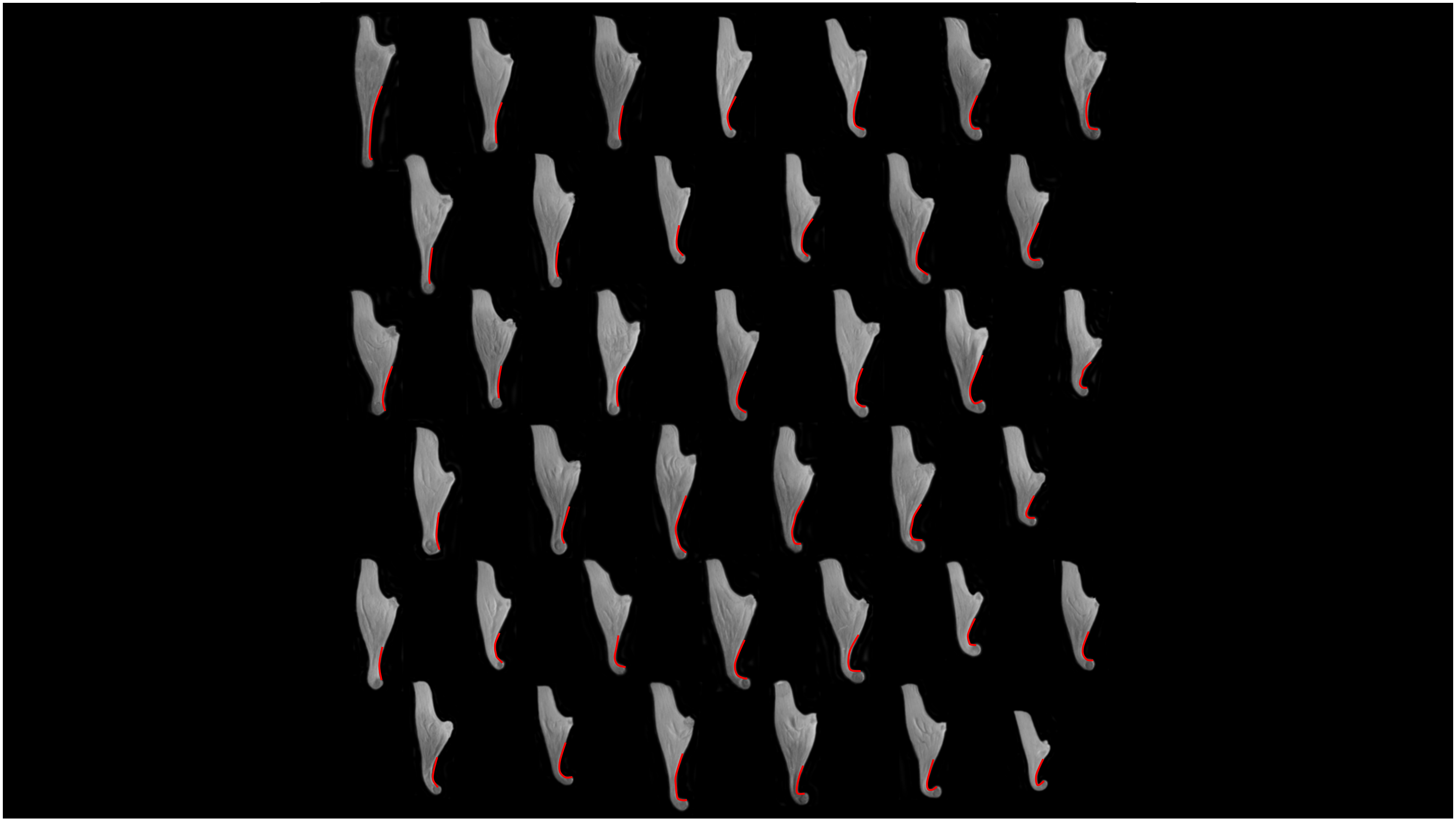
Quantitative Trait Locus Mapping Project

First generation hybrid of
A. brevistyla x A. canadensis

Second Generation of Hybrids







How do plants generate complex forms?

Plants need to carefully control the rate, orientation and localization of both cell division and cell expansion because all their cells are bound together by their cell walls.

How do the fundamental properties of plant cells and tissues influence these processes?

Plants can modulate the behavior of cell expansion by controlling the patterns in which cellulose is deposited in their cell walls and by altering the rigidity of the cell wall itself, which can flow like a liquid or be incredibly rigid.