Understanding Cambial Behaviour

The key to wood quality

- A brief history
- Terminology
- Dormancy and reactivation
- Growth of derivatives and wall formation
- Pitting and plasmodesmata

- A brief history

Nehemiah Grew (1641-1712)

Nehemiah Grew (1641-1712), engraved after the portrait by R. White, and reproduced in the *Cosmologia Sacra* in 1701


CHANGE
CAMBIO
CHANGE CHANGE
CHANGE
WC

THE

ANATOMY OF PLANTS.

WITH AN

IDEA

OF A

Philoſophical Hiſtory of Plants.

And ſeveral other

LECTURES,

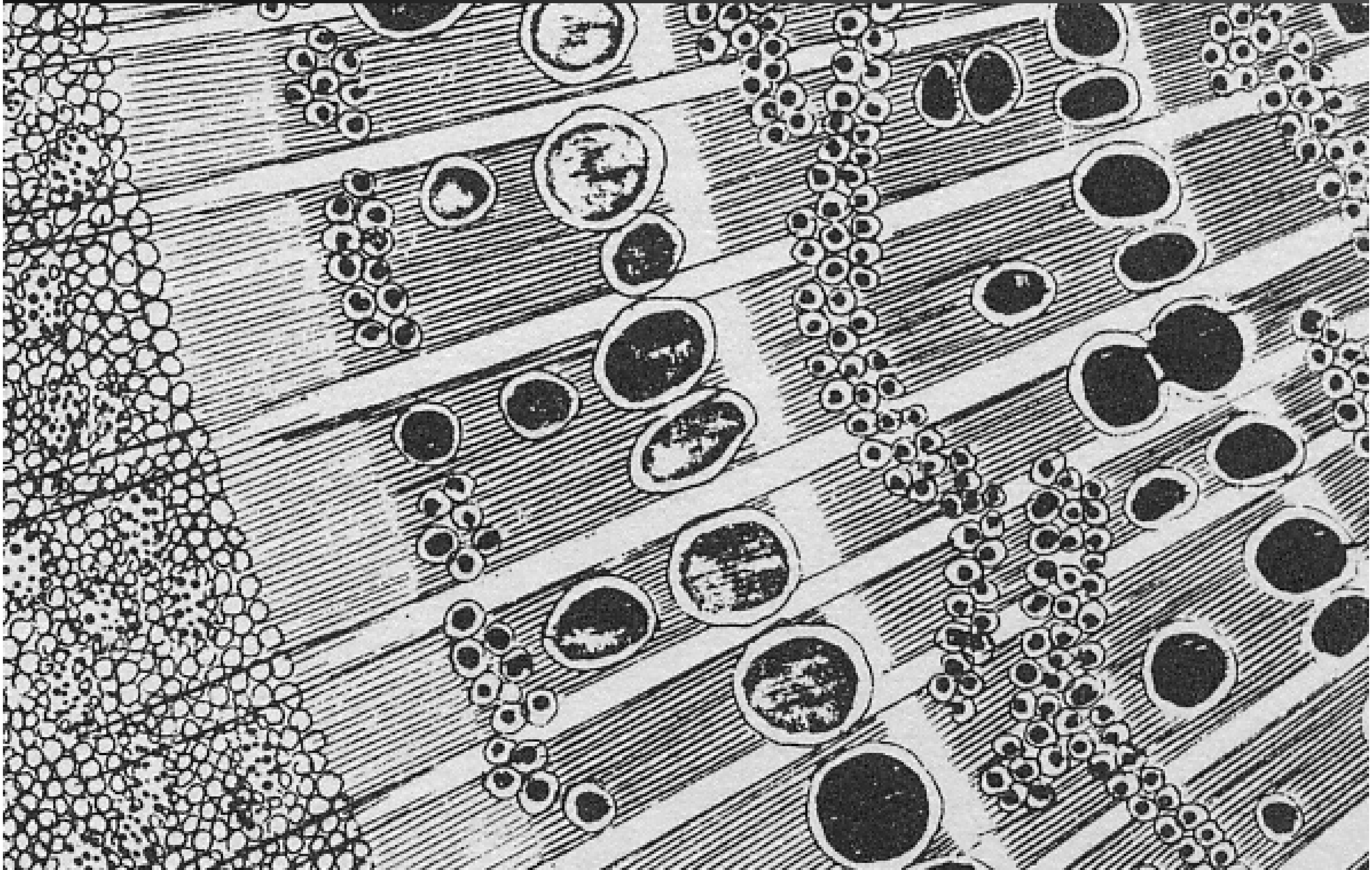
Read before the

ROYAL SOCIETY.

By *NEHEMJAH GREW* M.D. Fellow of the *ROYAL SOCIETY*, and of the *COLLEGE* of *PHYSICIANS*.

Printed by *W. Rawlins*, for the Author, 1682.

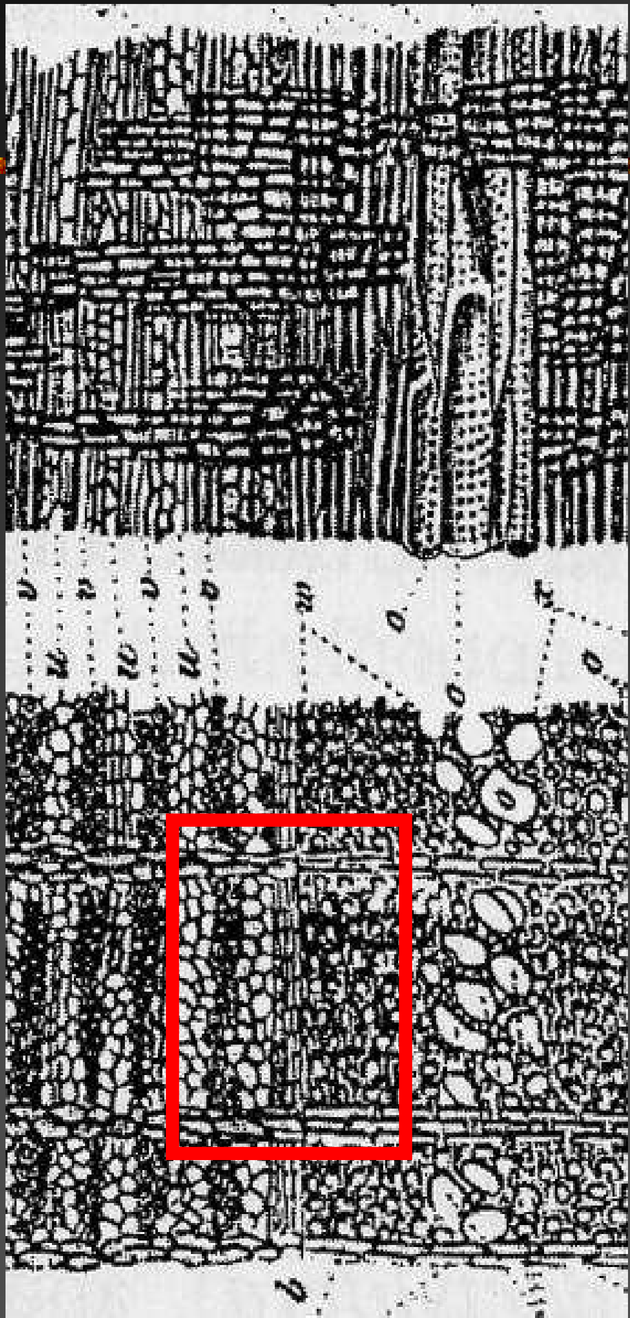
- Grew's drawing of elm (detail)



Charles Francois Brisseau-Mirbel

- Proposed that cambium was a tissue rather than a sap (1808)

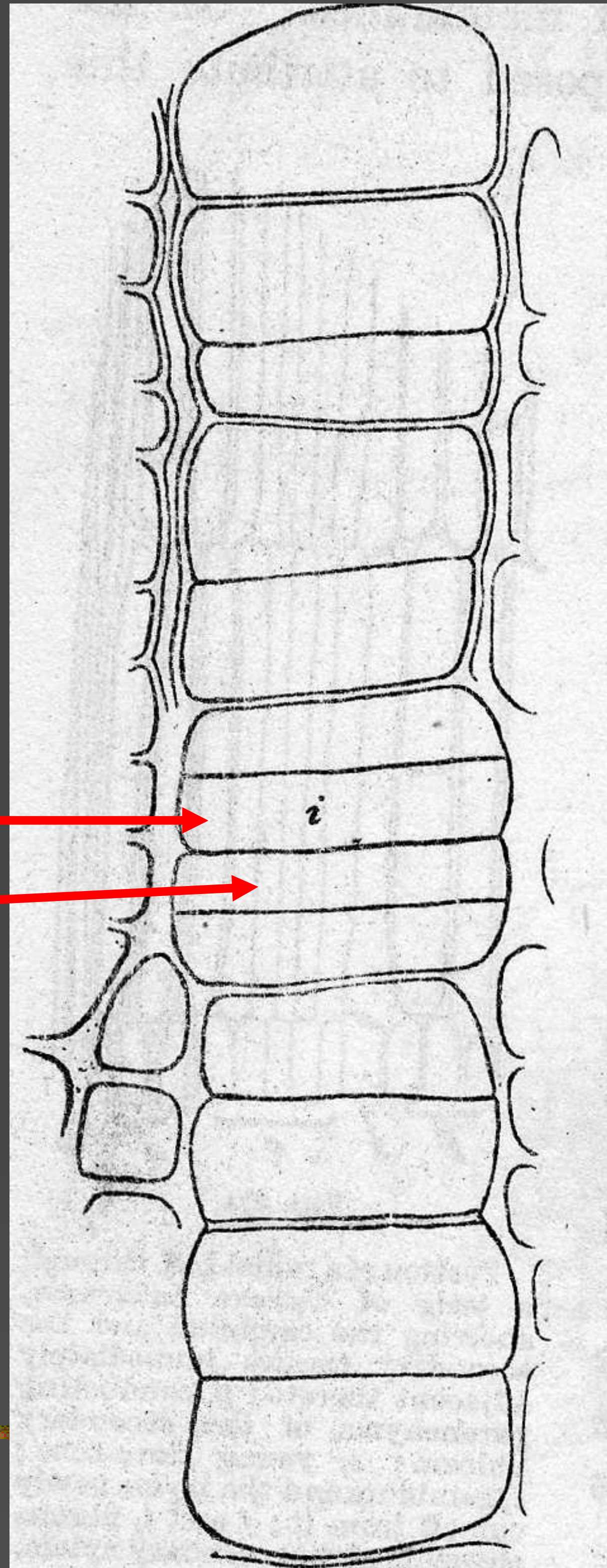
Mirbel's (1827) diagram of elm (from Larson, 1994)



Cambial cell theories

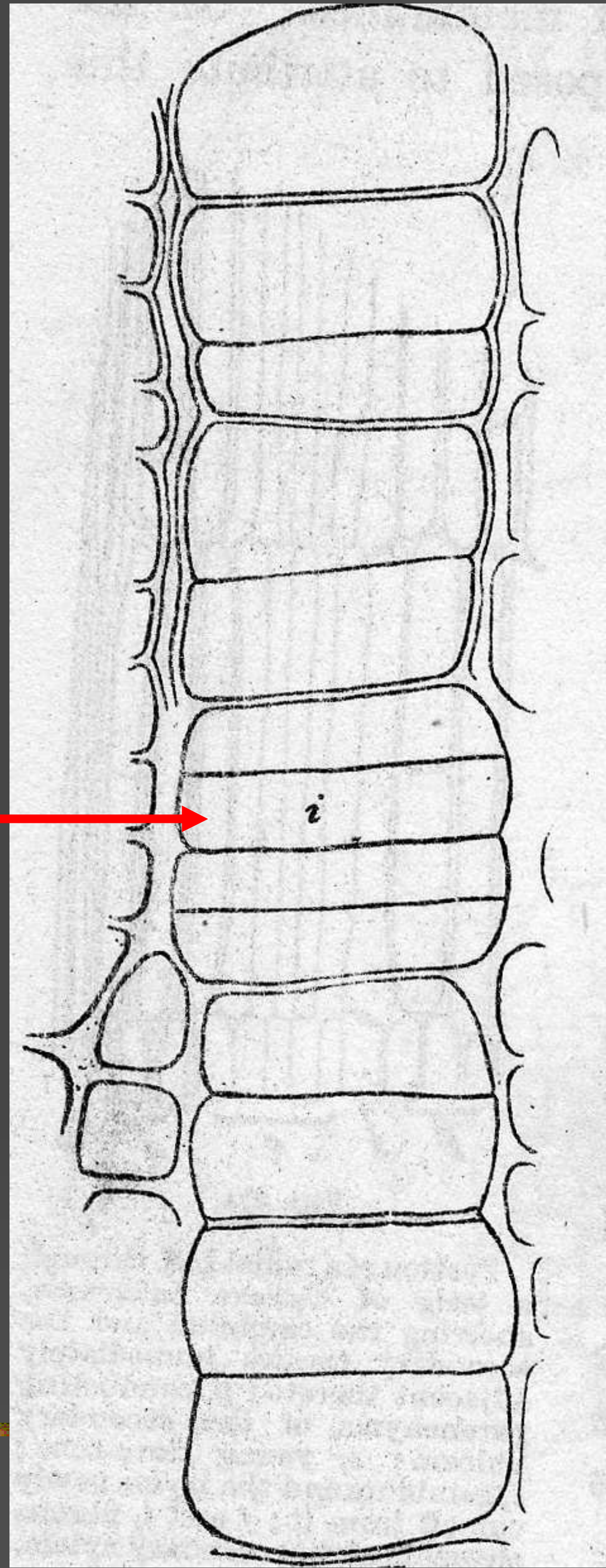
- Hartig (1853)- Back to back theory

- Phloem initial
- Xylem initial



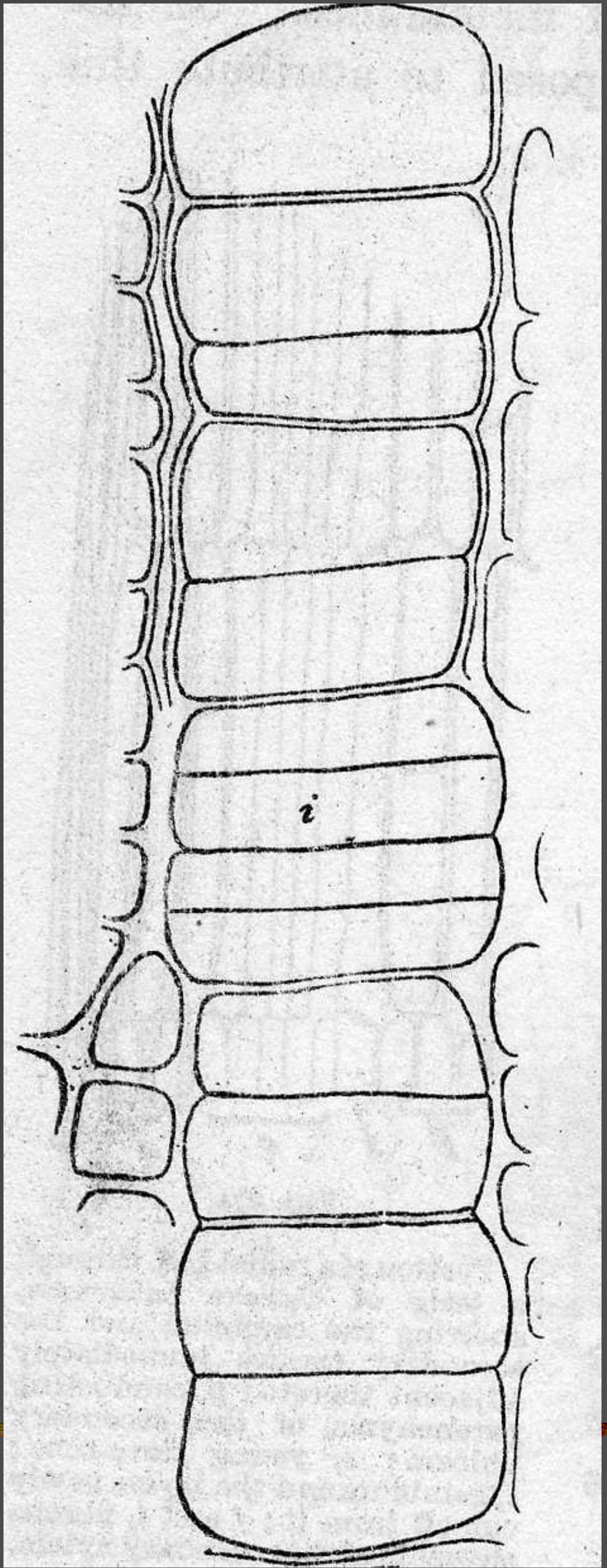
Cambial cell theories

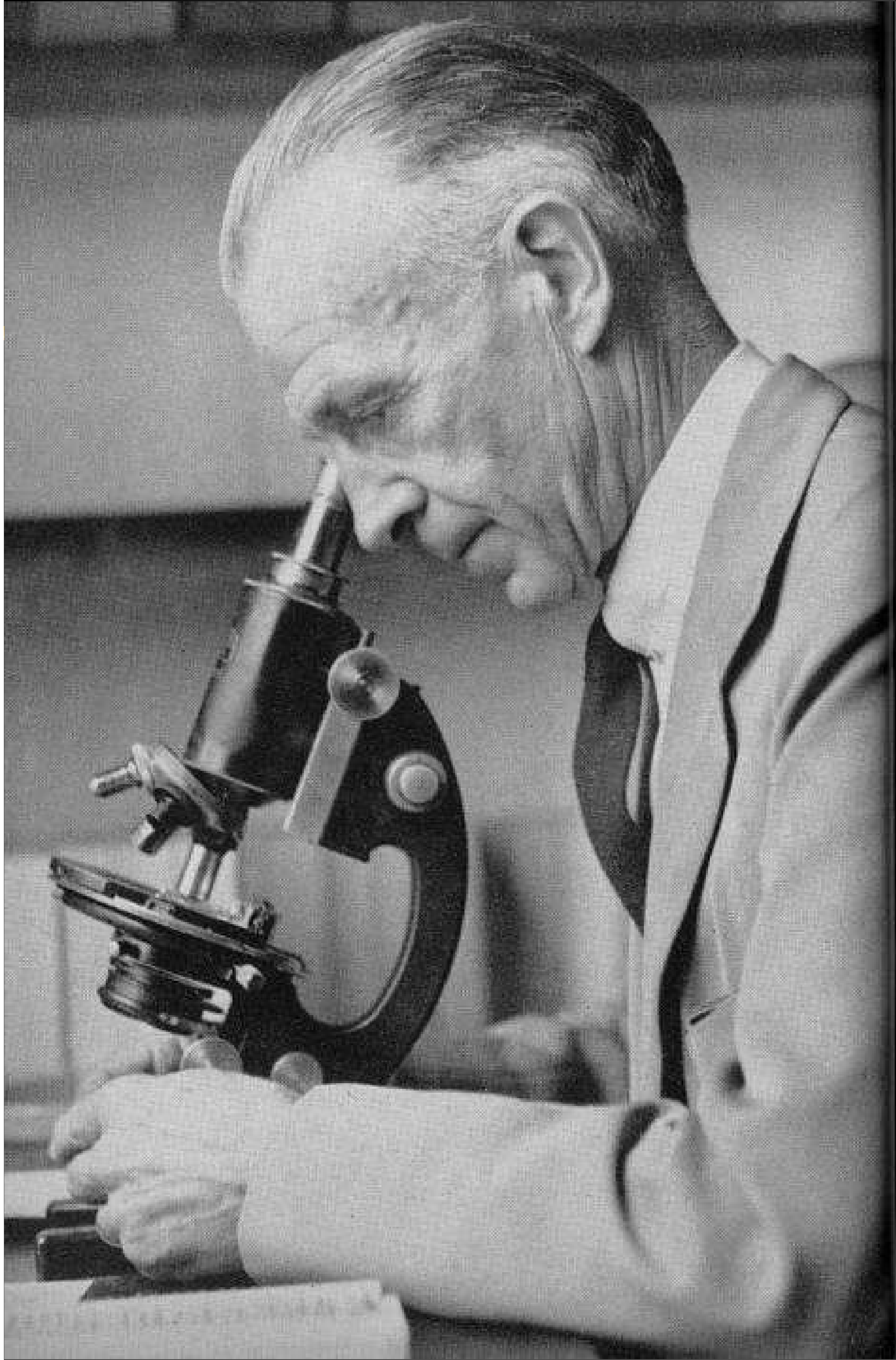
- Sanio (1863)- Single initial theory



Cambial cell theories

- Raatz/Mischke (1892) – Multiple initial theory





CONTRIBUTIONS
to
PLANT ANATOMY

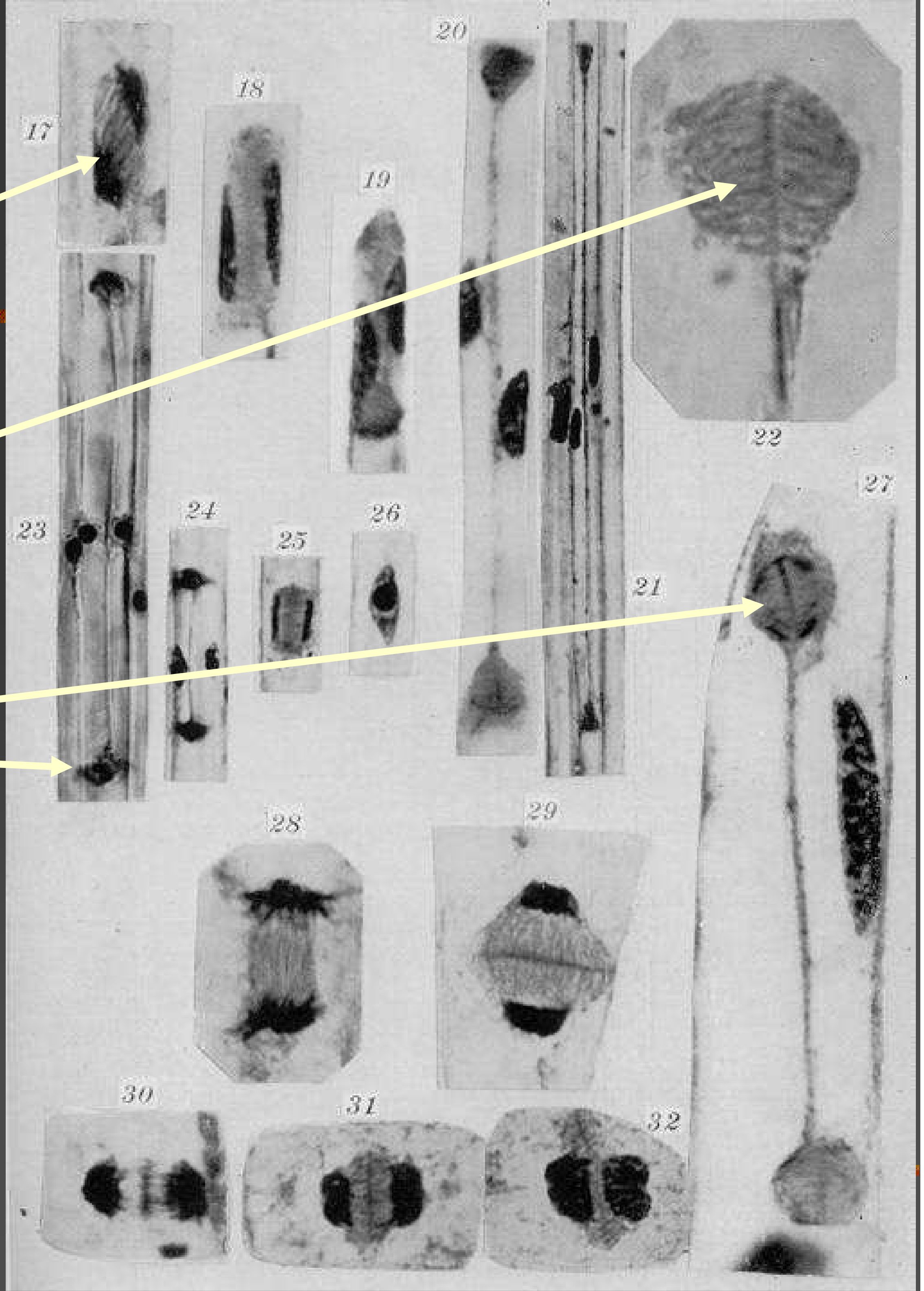
by IRVING W. BAILEY, Sc.D.
Professor of Plant Anatomy and Chairman of the Institute for Research in General Plant Morphology, Harvard University

1954

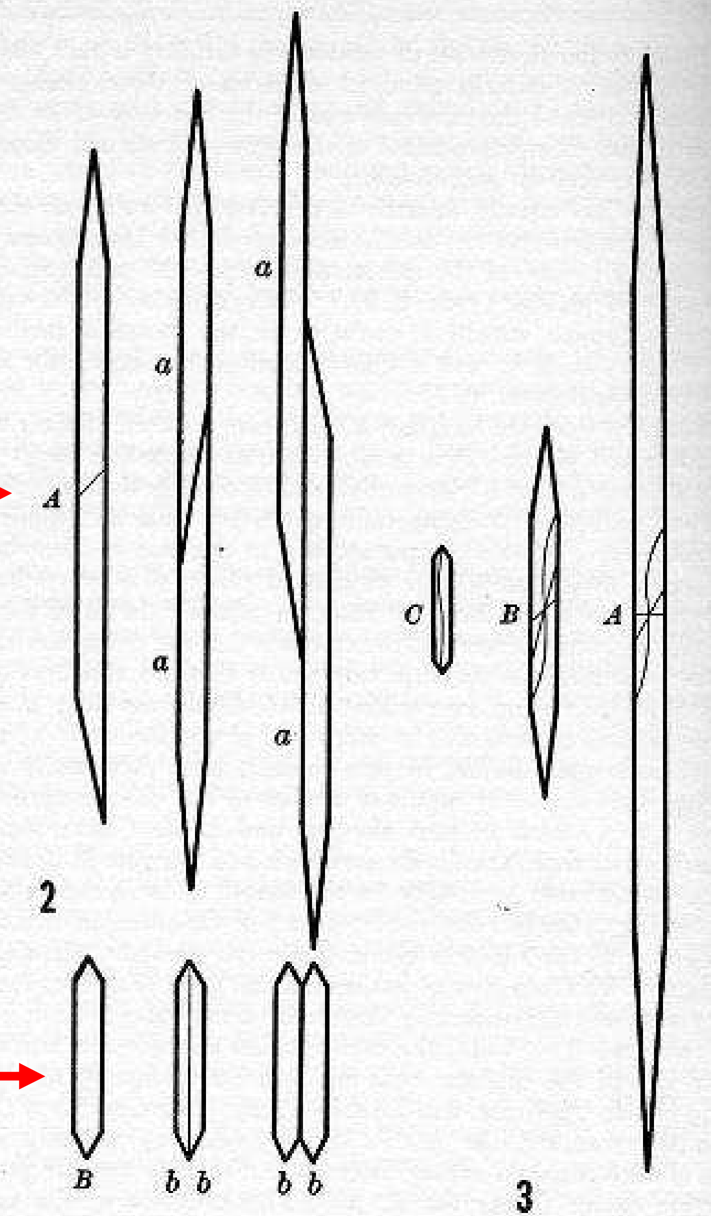
WALTHAM, MASS., U.S.A.

Published by the Chronica Botanica Company

- Oblique orientation of plane of division
- Kinoplasmic fibres (microtubules)
- Kinoplasmosomes (phragmoplast



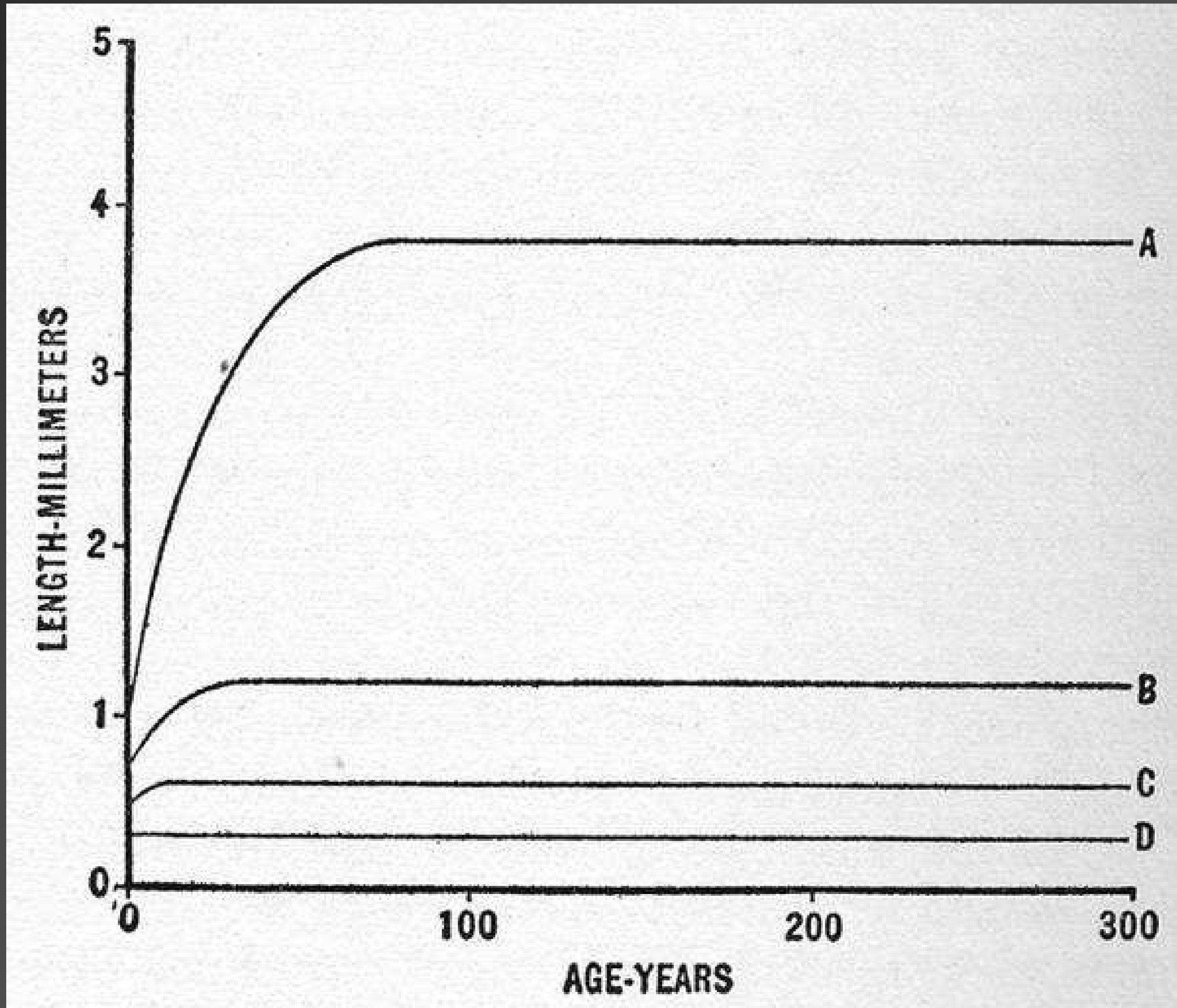
- From Bailey (1923)
  - Anticlinal pseudotransverse division
  - Transverse division



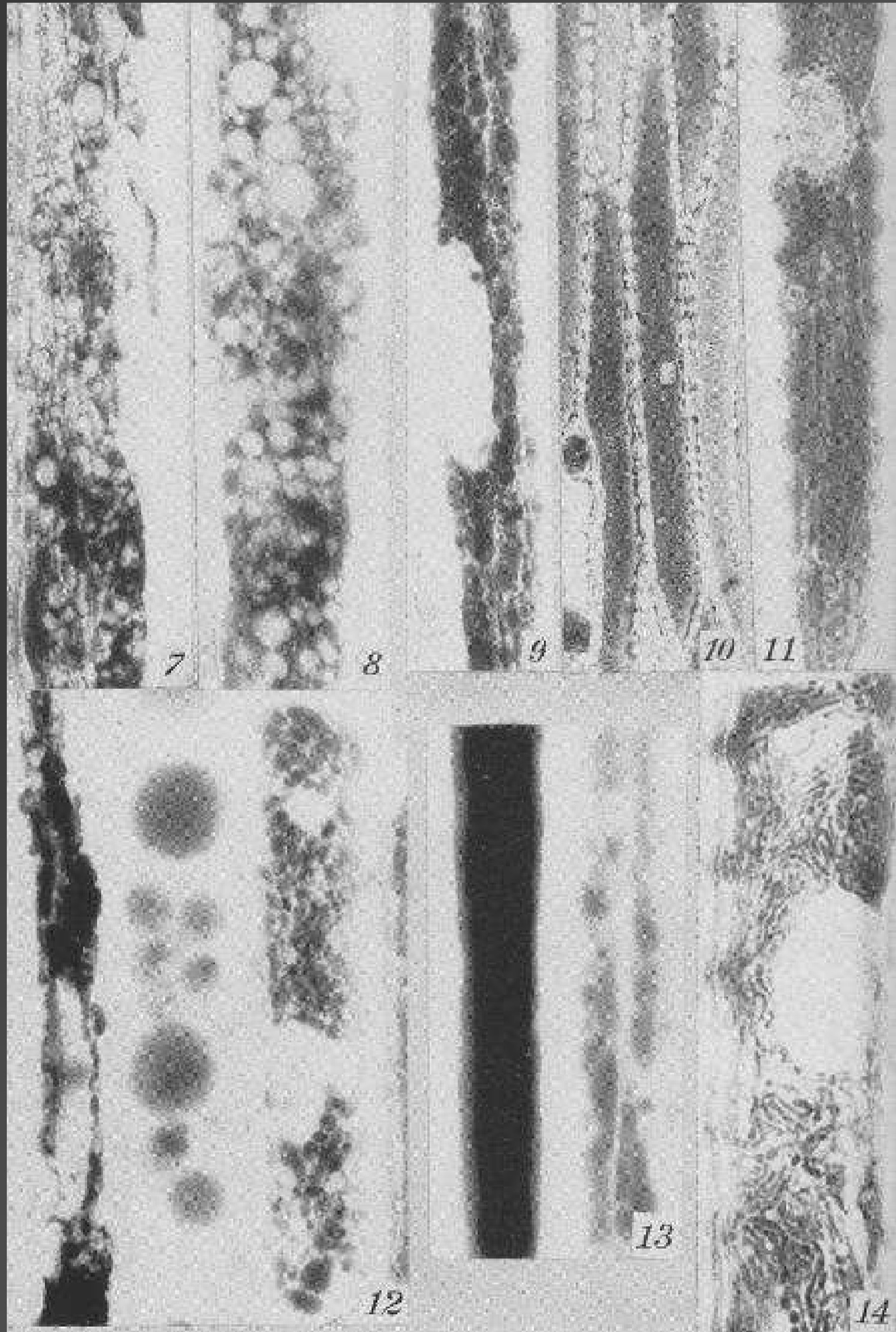
TEXT FIGURES 2-3.— FIG. 2: Diagrams illustrating *modus operandi* of the increase in girth of cambium in non-stratified and stratified lateral meristems. A, fusiform initial from non-stratified cambium, dividing pseudo-transversely; *a*, *a*, products of this division which elongate and slide by one another; *B*, fusiform initial from stratified cambium; *b*, *b*, products of the radio-longitudinal division of this initial, which expand laterally but not longitudinally. — FIG. 3: Types of anticlinal divisions in fusiform initials.—*A*, Typical fusiform initial of a conifer; B, fusiform initial of a dicotyledon, having non-stratified cambium; C, fusiform initial of a dicotyledon, having a stratified cambium.

Length of cambium/cambial age (from Bailey 1923)

- A: Conifer or vessel-less dicot. (12 species)
- B: Less specialised dicot. (10 species)
- C: Highly specialised dicot. (10 species)
- D: Dicot. with storeyed cambium (10 species)



Vacuolation in cambial cells (Bailey 1930)



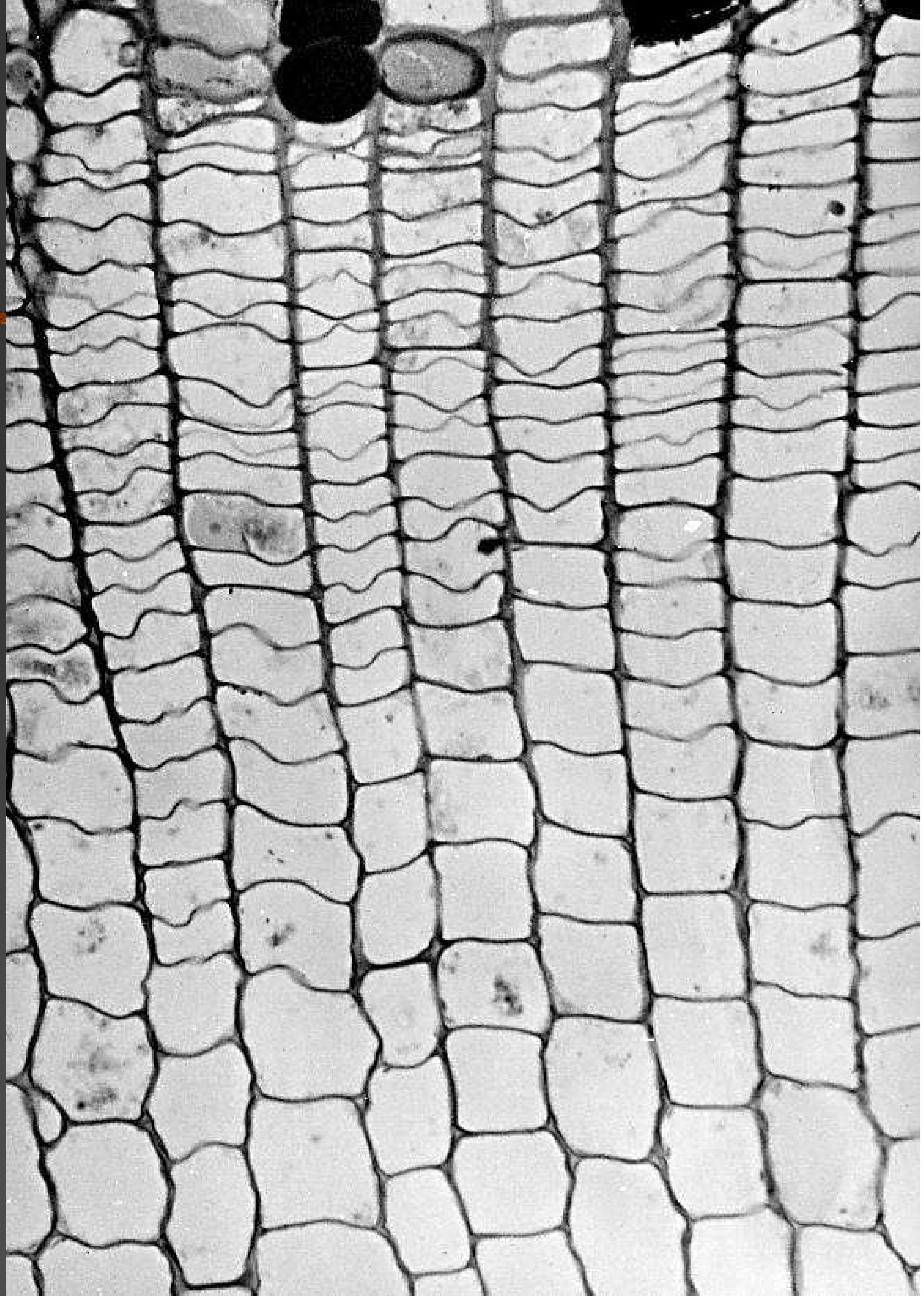
Pinus radiata

Active cambium

Nomenclature

Cambium?

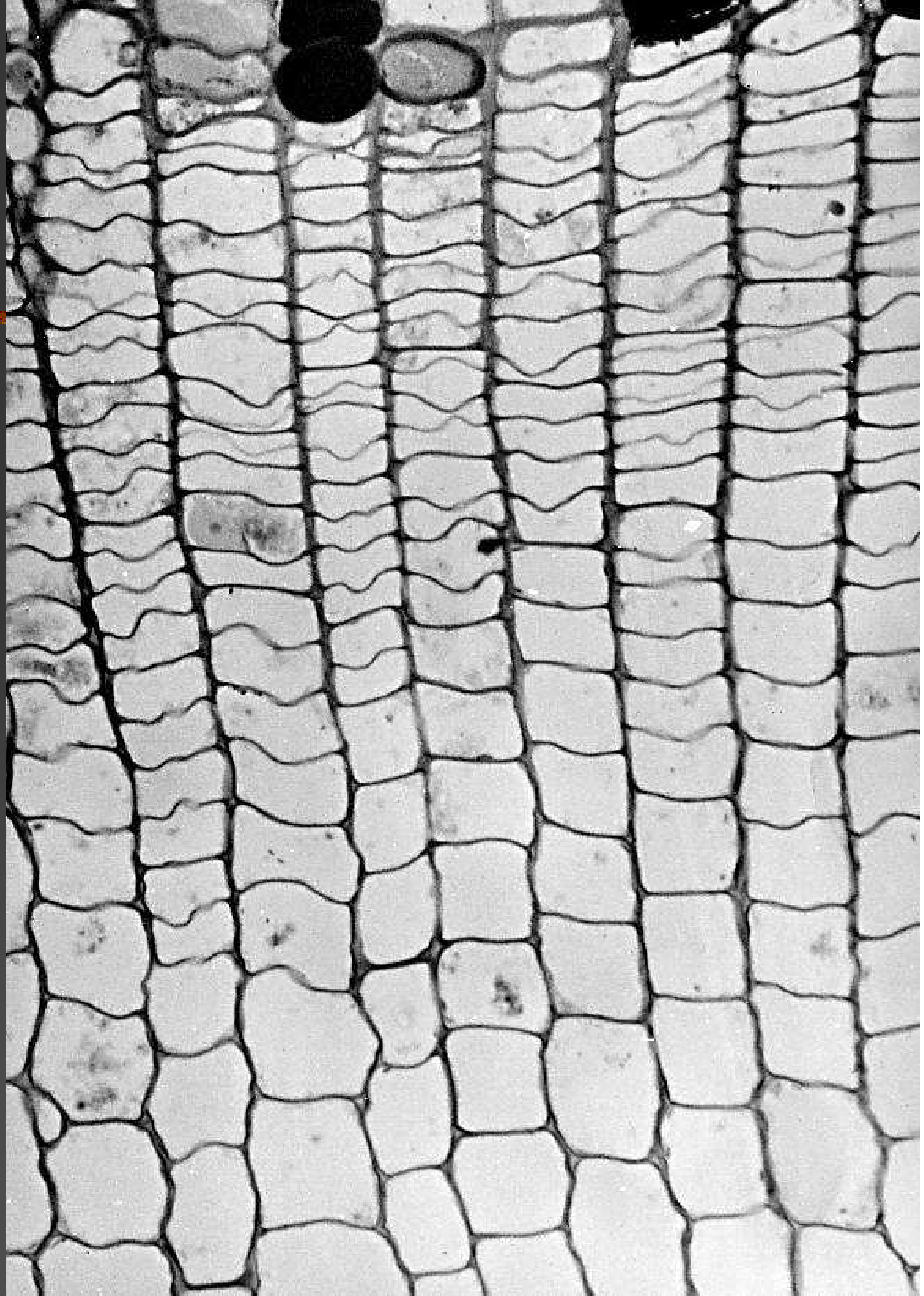
Cambial Zone?



Butterfield (1975) IAWA Bulletin 13 – 14

Cambium “a multiseriate zone of periclinally dividing cells lying between the differentiating secondary xylem and phloem, with a distinct initial capable of both periclinal and anticlinal divisions lying somewhere within each radial file of cells”

Cambium according to Butterfield



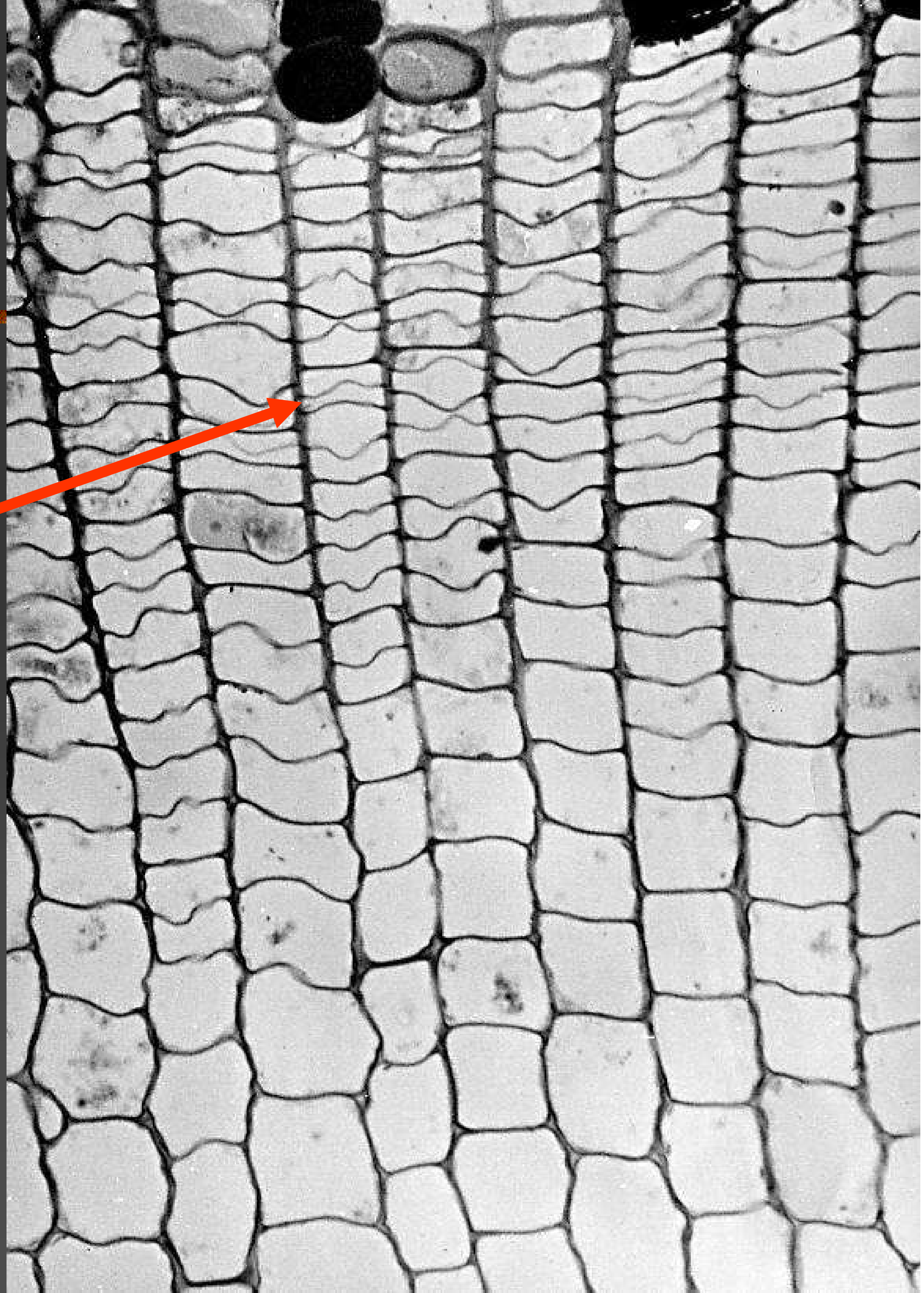
Schmid (1976) IAWA Bulletin 51-59

"Cambium" equivalent to the "initiating layer"

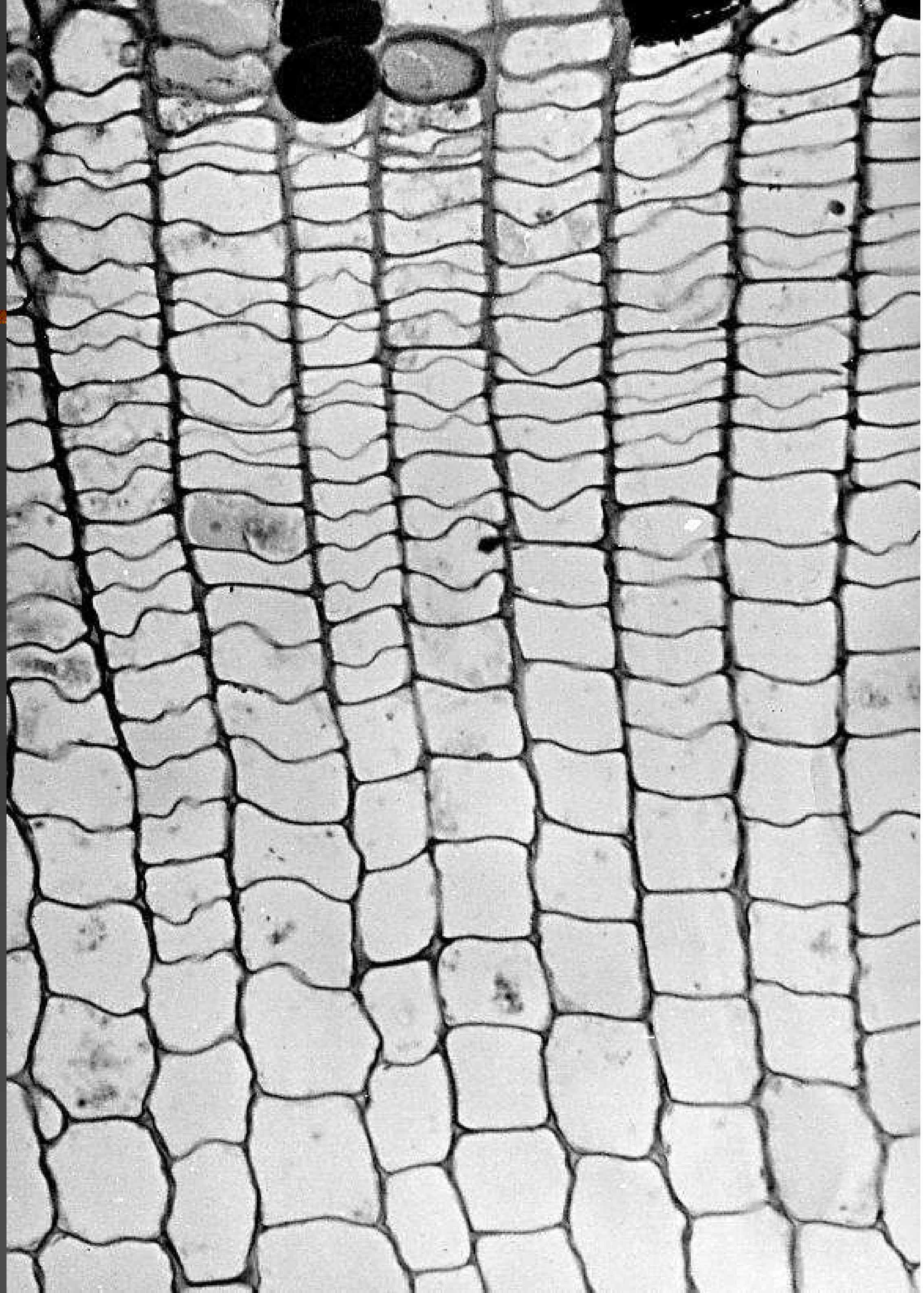
"Cambium" applied to the entire differentiating region might lead to the conception that the cambium is a multiseriate layer of initials"

Cambium according to Schmid

?



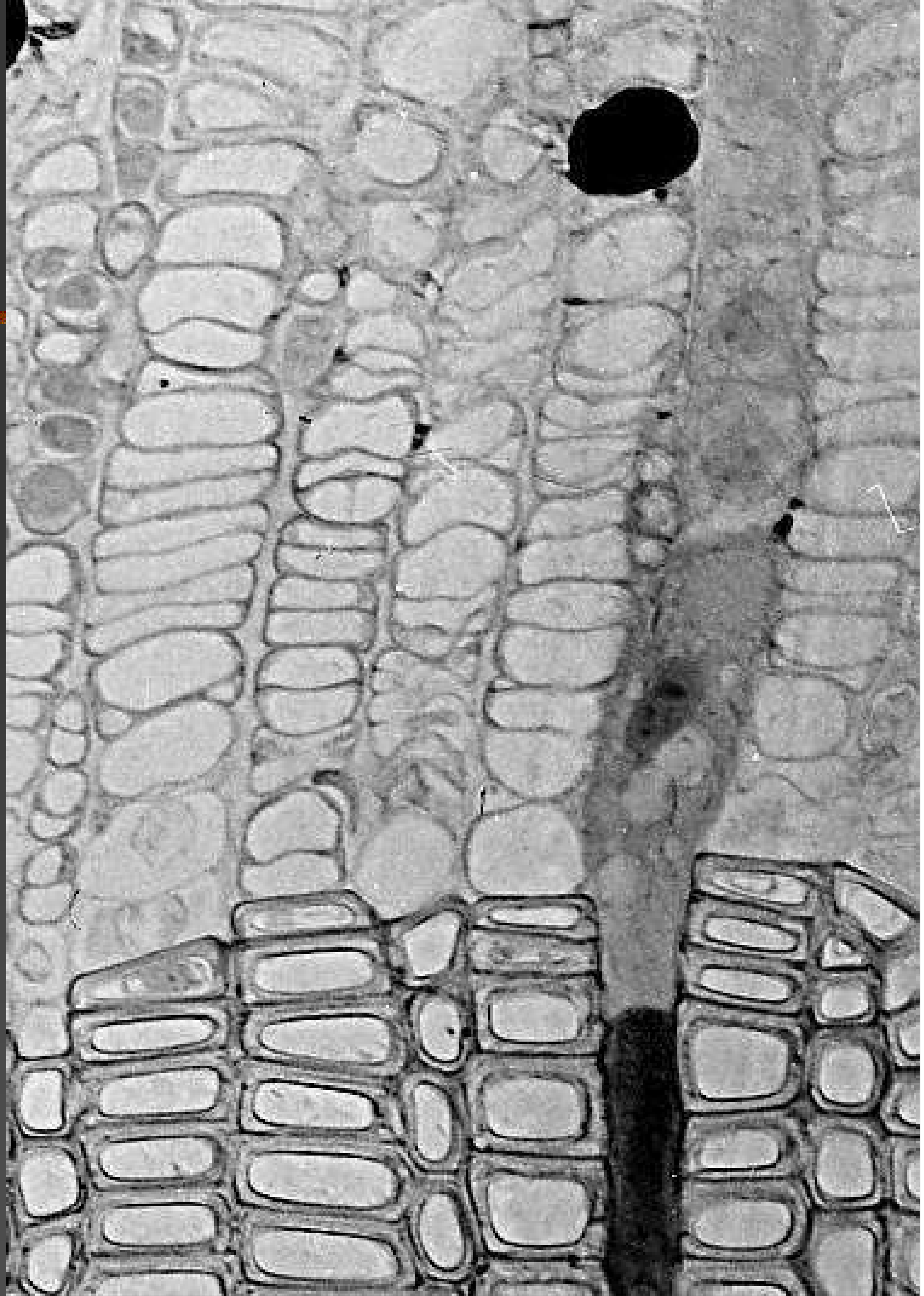
The difficulty of identifying the initial means the terms have been used interchangeably



Pinus radiata

Mid-winter

A slowly dividing meristem



Pinus radiata

Mid-winter

Cambium

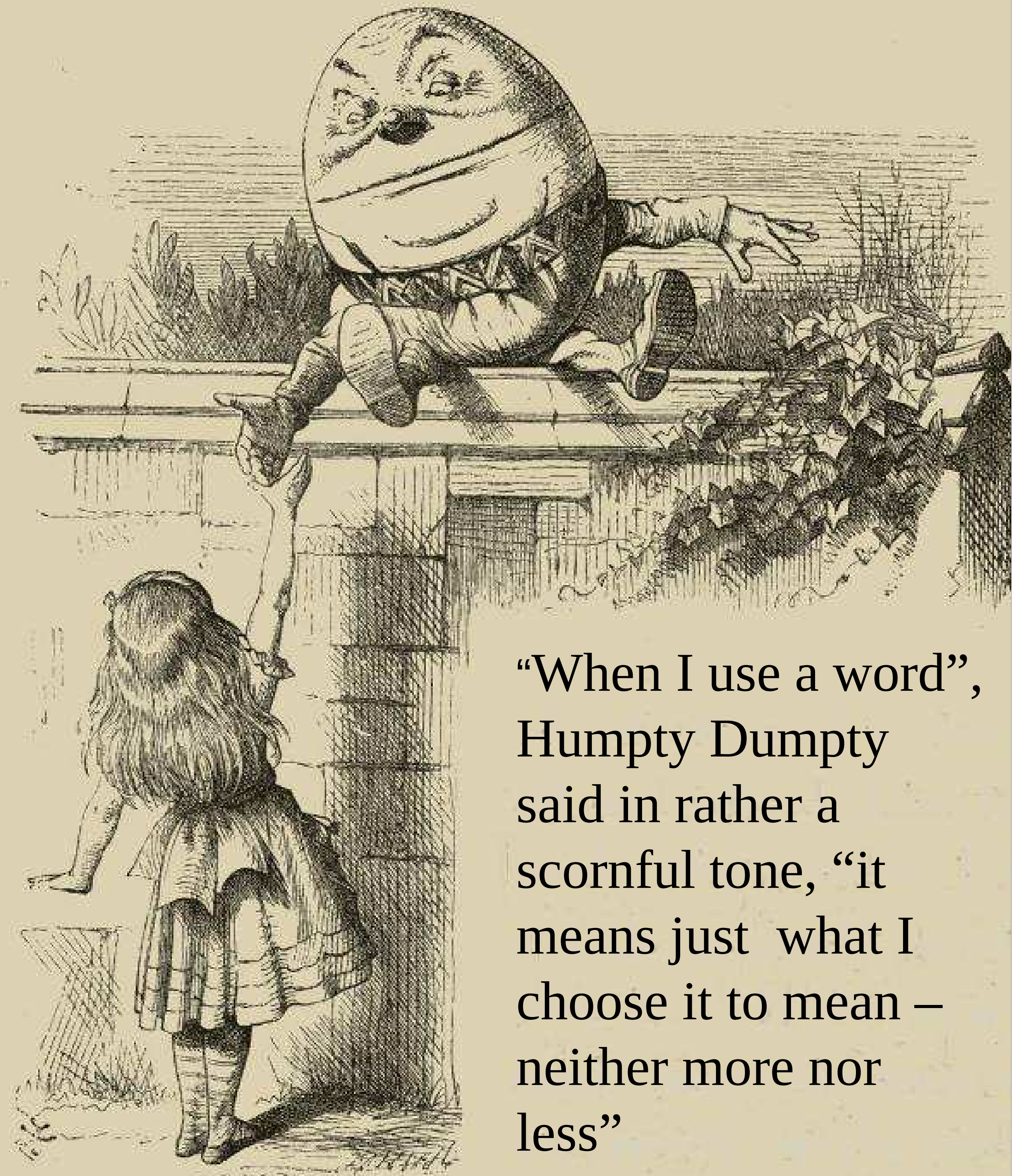
Butterfield

Schmid ?

Humpty Dumpty

From “Through the Looking Glass – and what Alice found there”

by Lewis Carroll

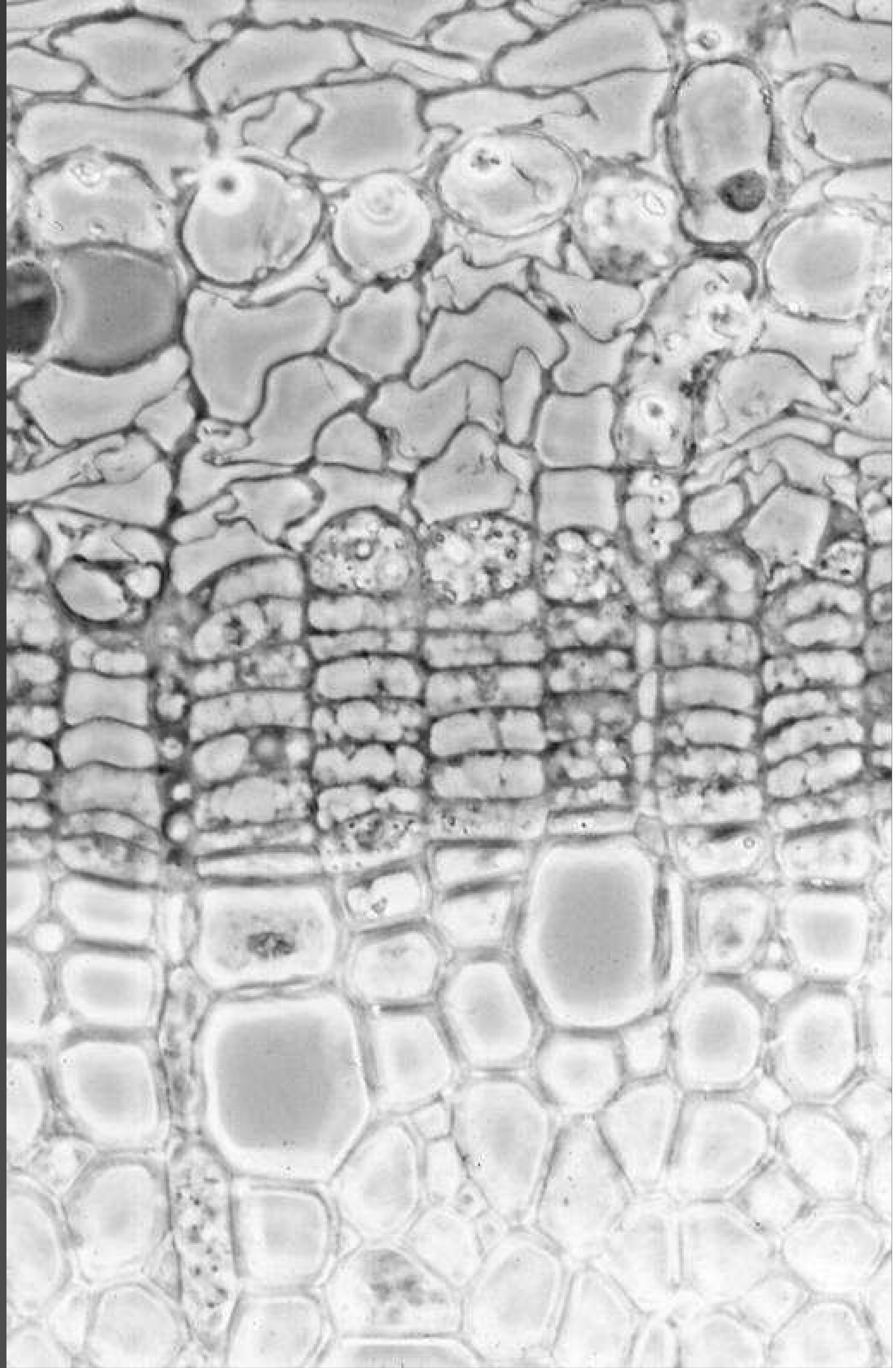


“When I use a word”, Humpty Dumpty said in rather a scornful tone, “it means just what I choose it to mean – neither more nor less”

- Can an initial ever be identified with certainty?

- *Aesculus hippocastanum*
- February

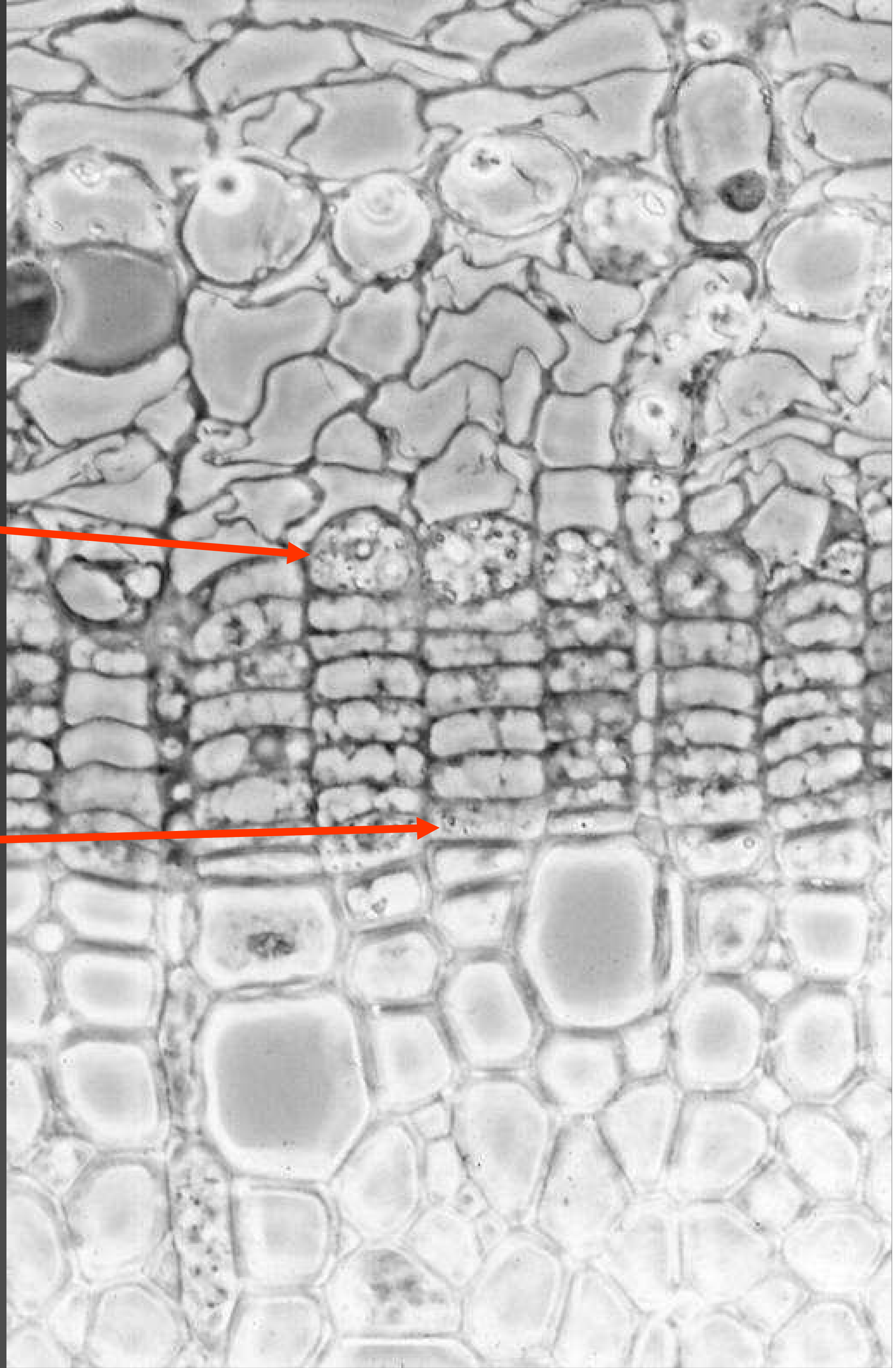
Cells appear similar across the cambium



Identifying an initial

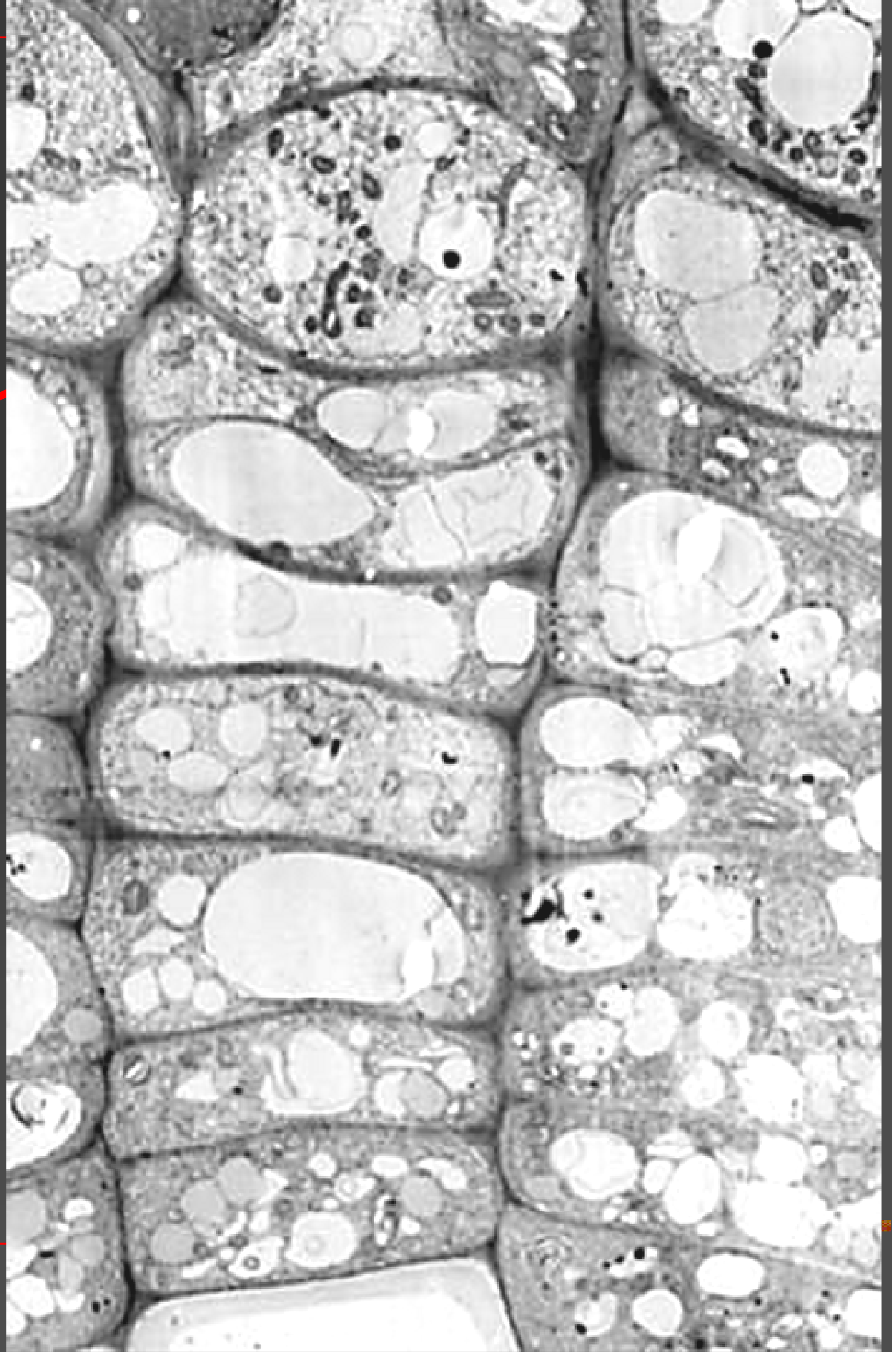
Boundary parenchyma phloem side

Boundary parenchyma xylem side



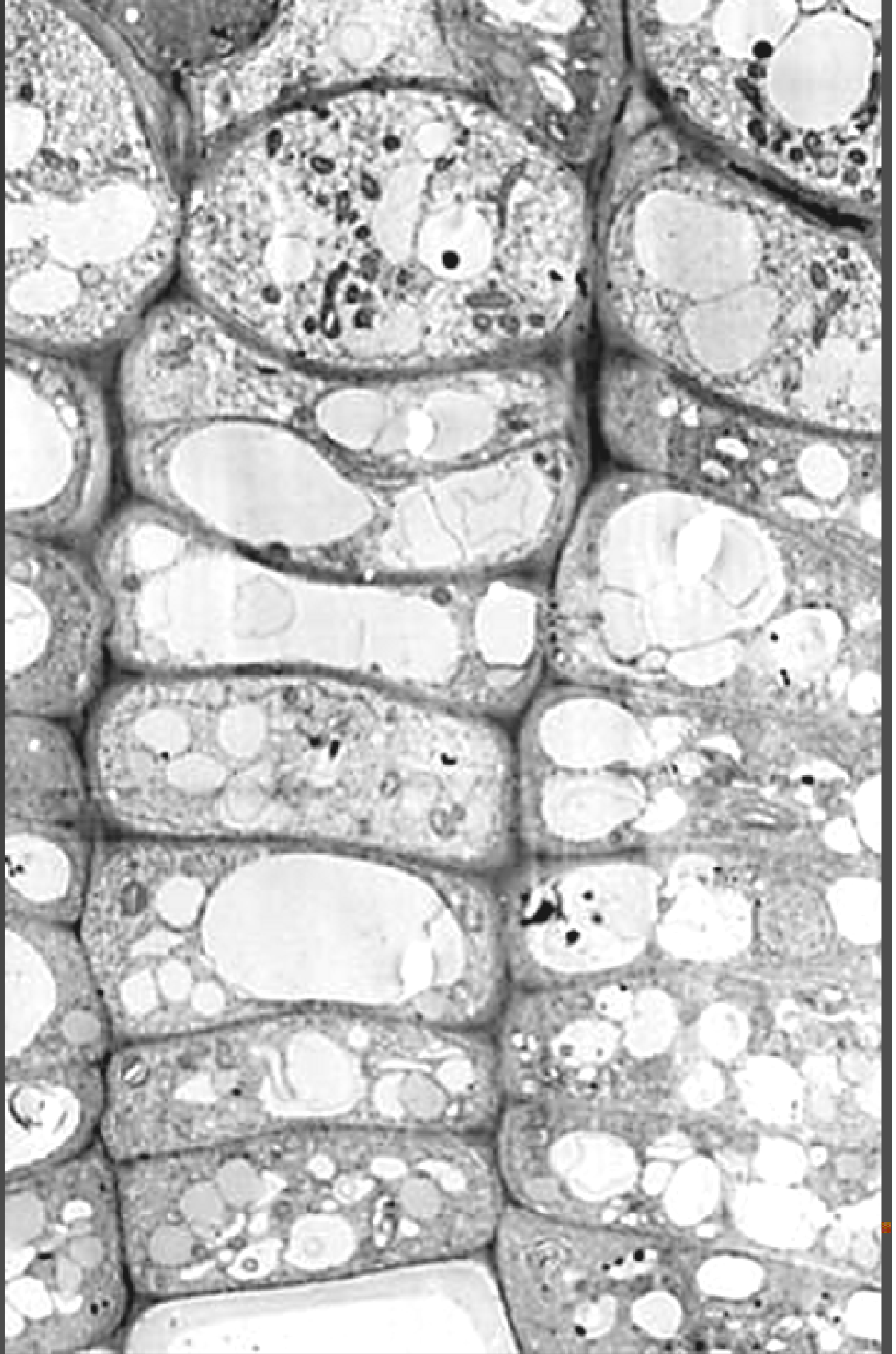
A. hippocastanum TEM

Boundary parenchyma
(phloem side)



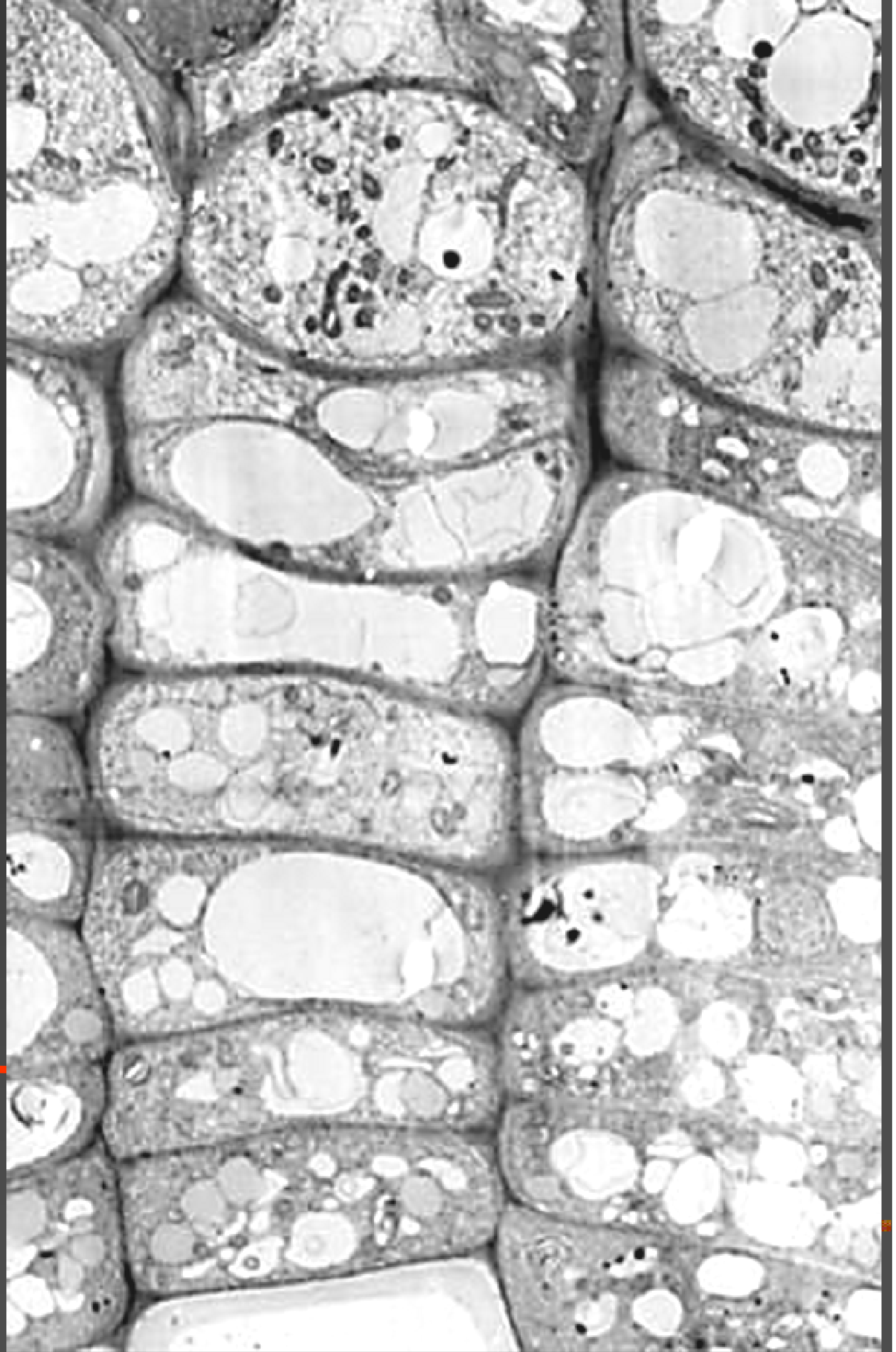
A. hippocastanum TEM

Phloem cells in suspended or slow development

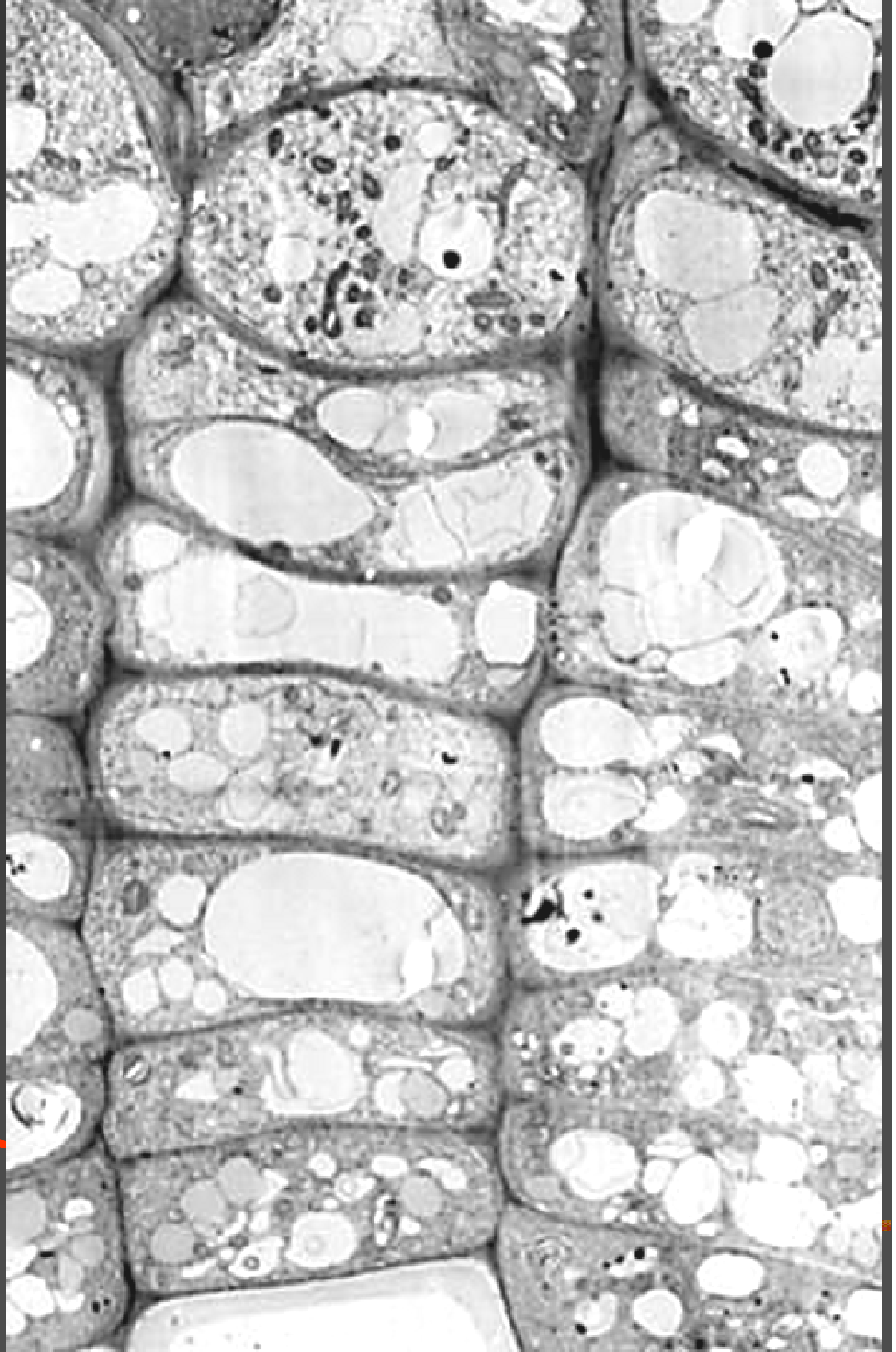


A. hippocastanum TEM

Fusiform Initial



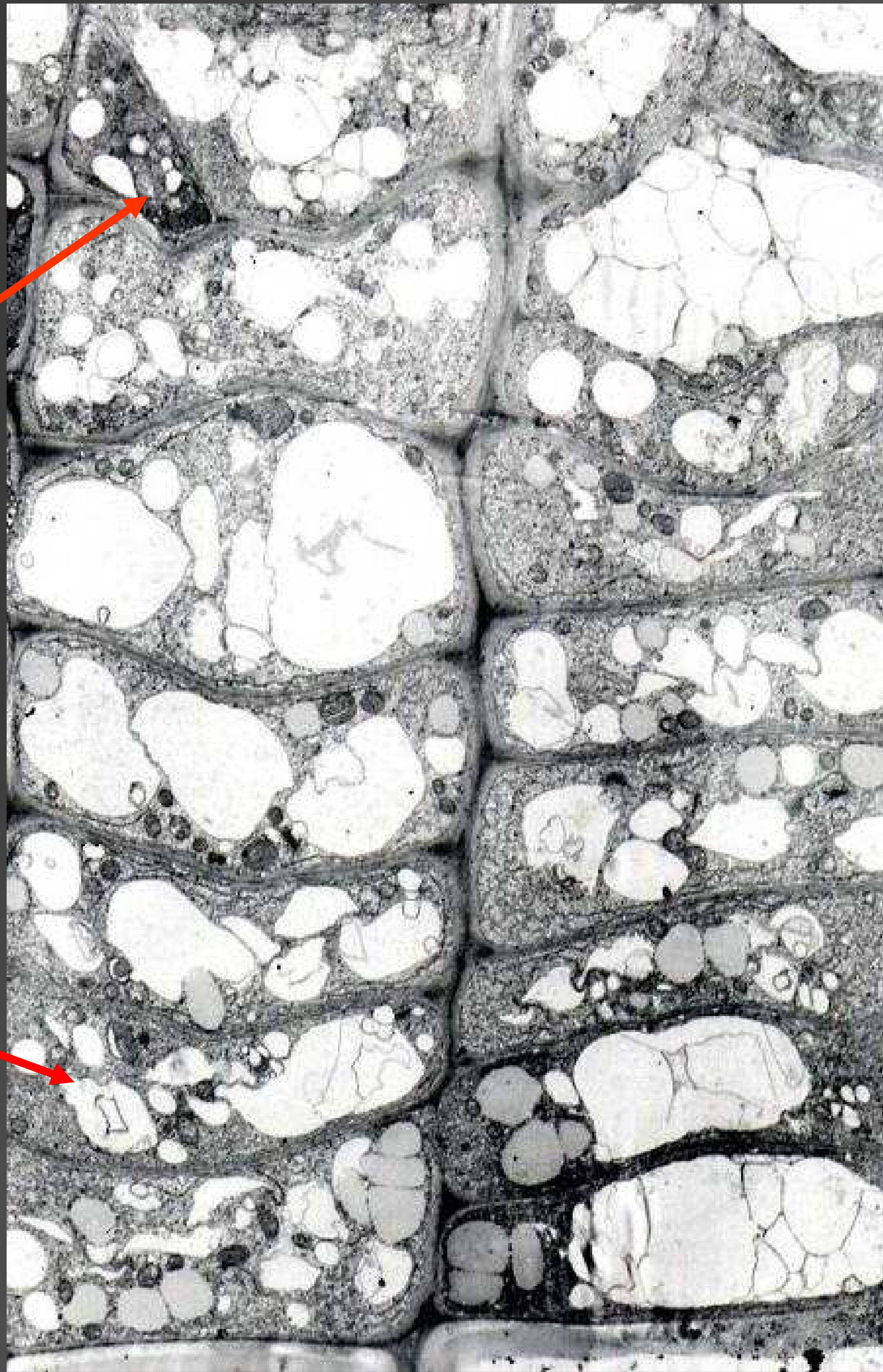
A. hippocastanum TEM



Boundary parenchyma
xylem side

Sieve element/companion cell pair in a state of arrested development

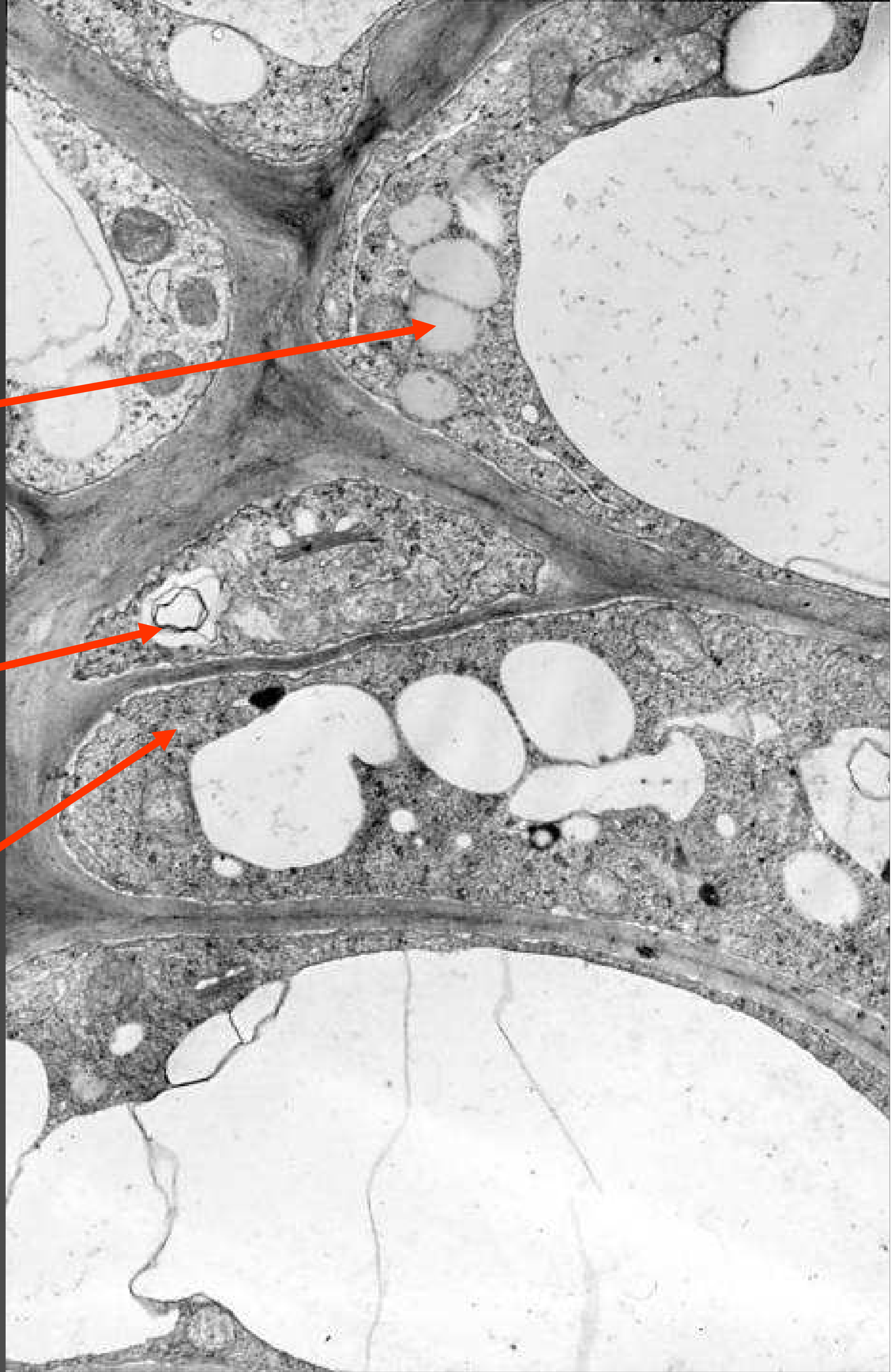
Initial



Boundary parenchyma

Companion cell precursor

Sieve/element precursor

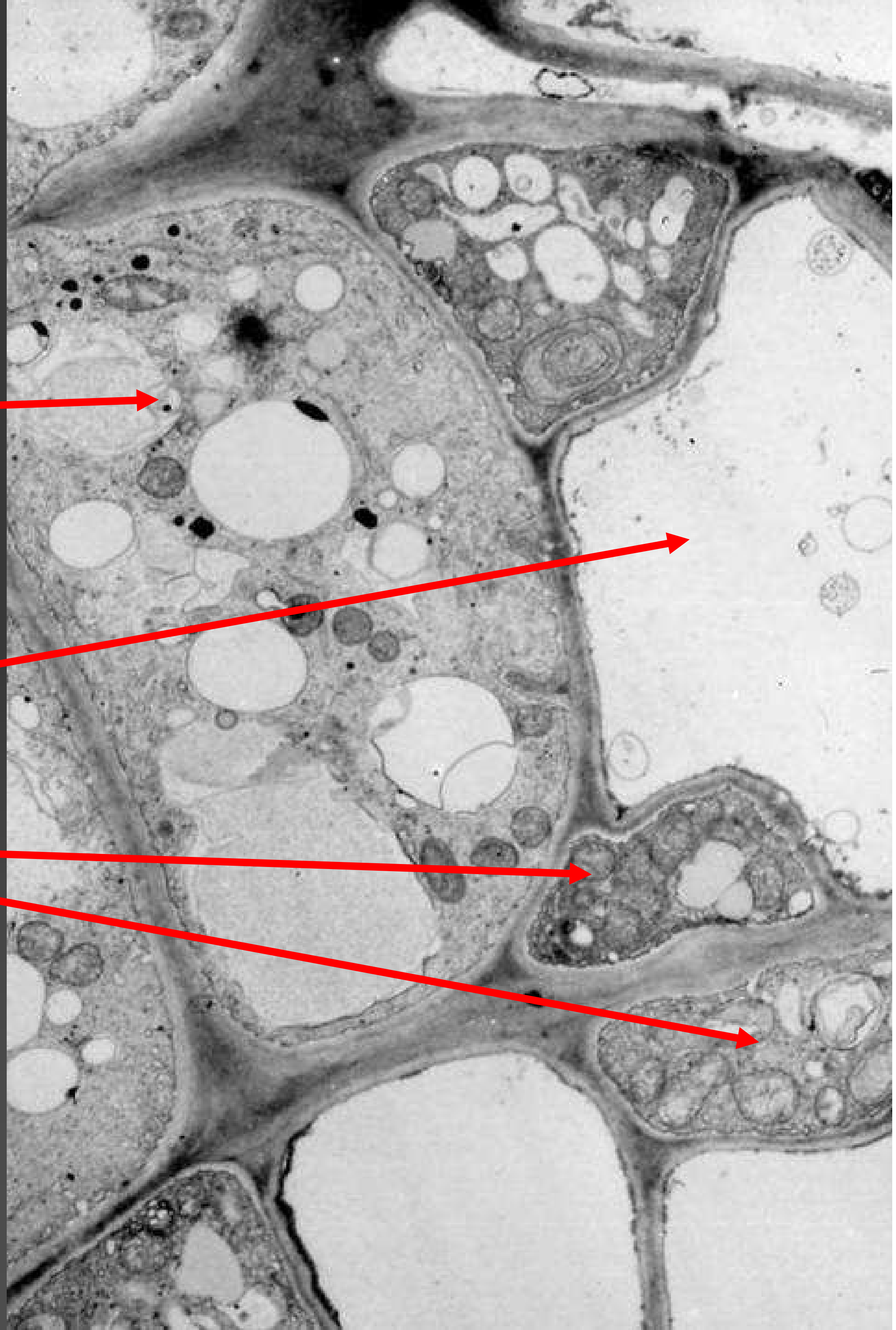


Phloem boundary cell

Previous season's phloem:

Sieve tube member

Companion cells

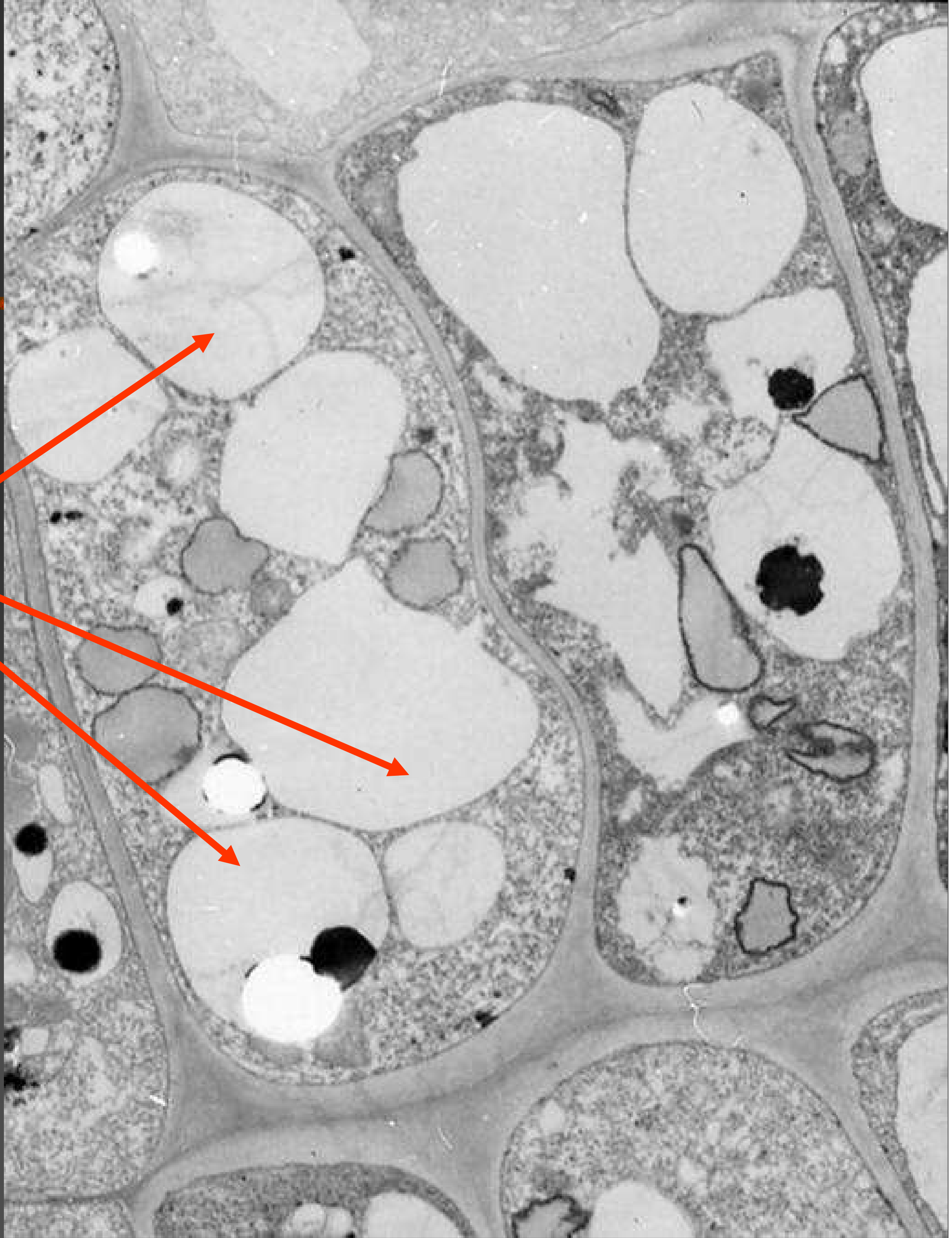


9 February

- Dormancy and reactivation

Dormant Cambium

Fragmented vacuome

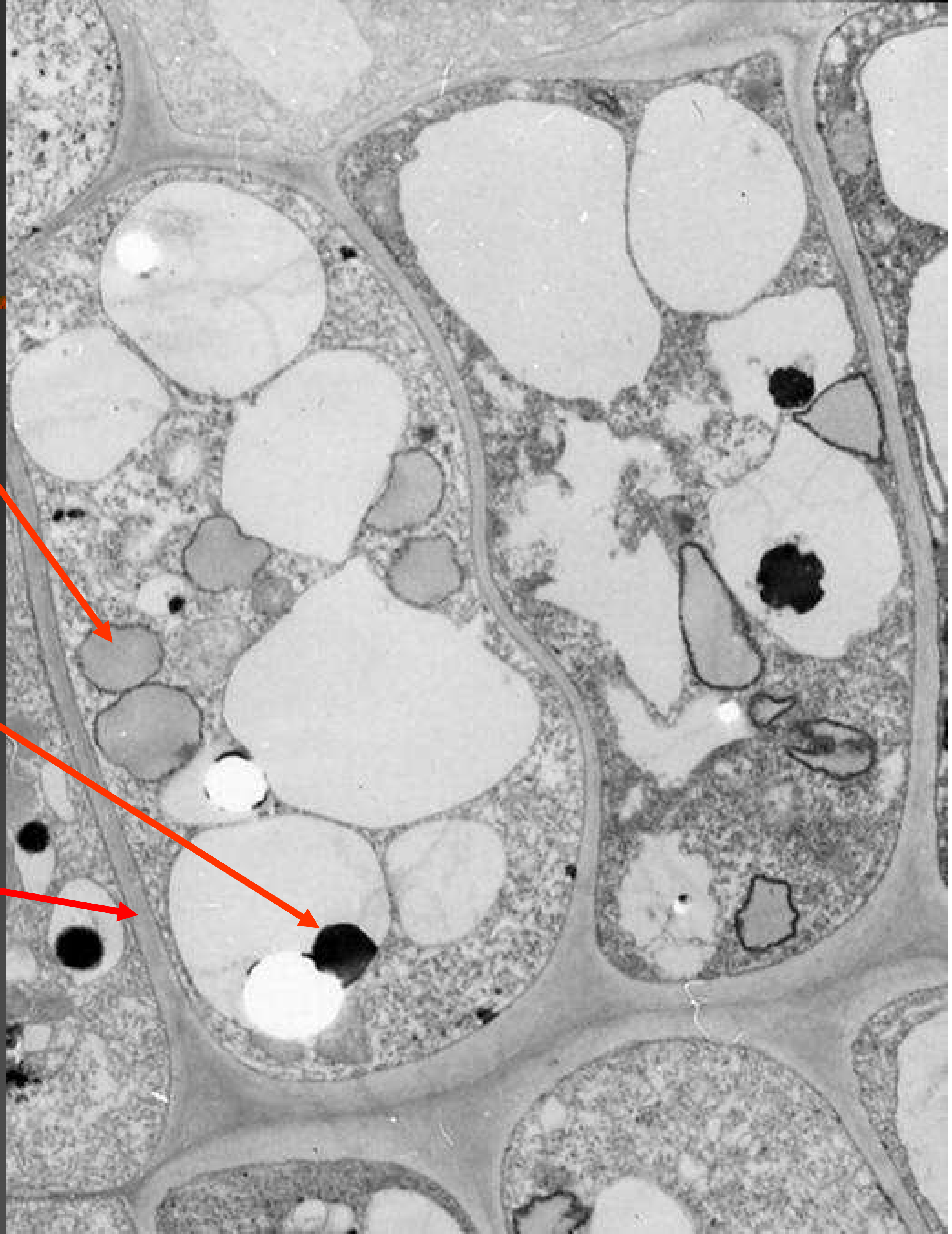


Storage materials in dormant fusiform cells

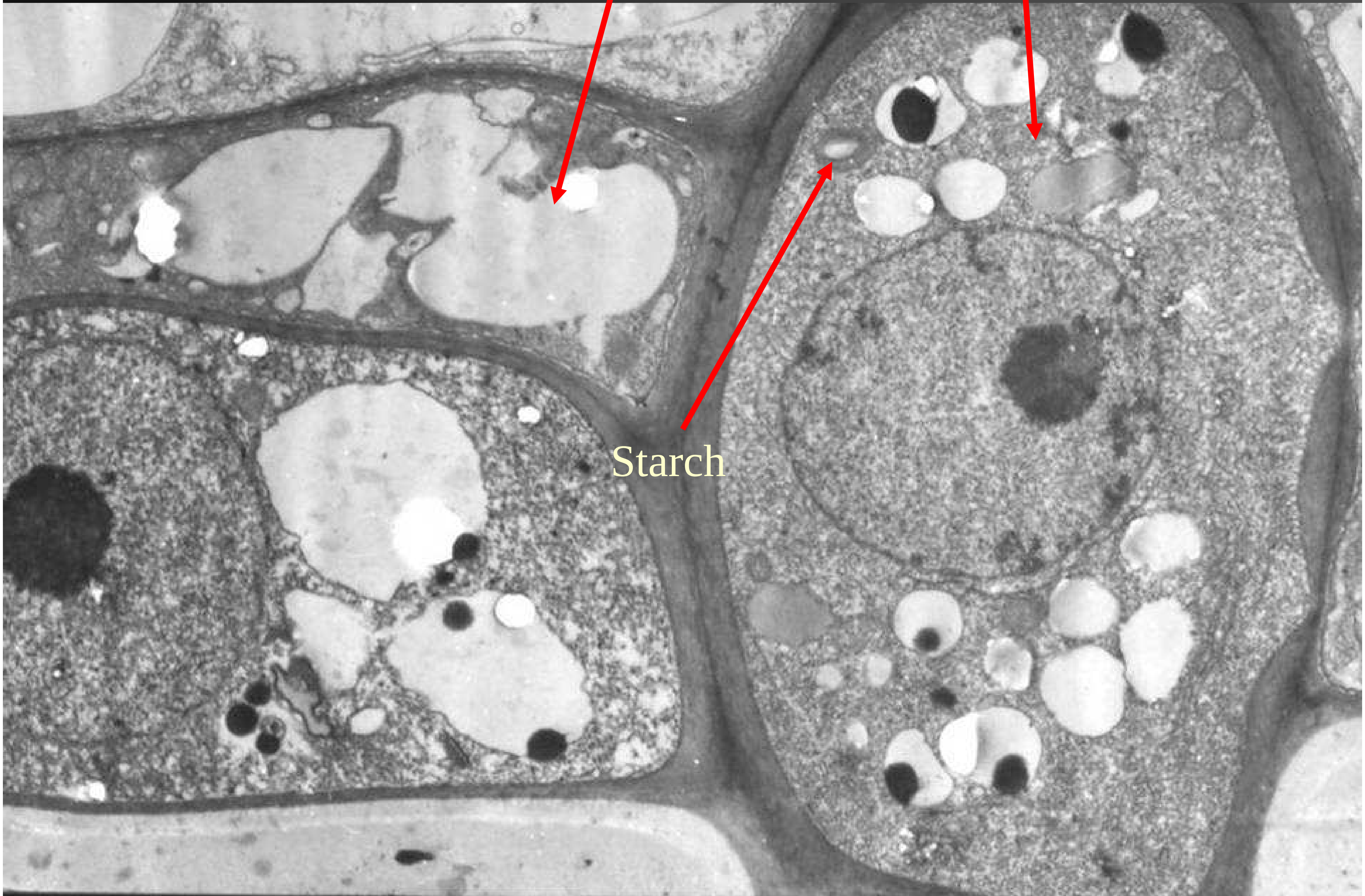
Spherosomes (lipids)

Protein bodies

“Thick” cell walls



9 February



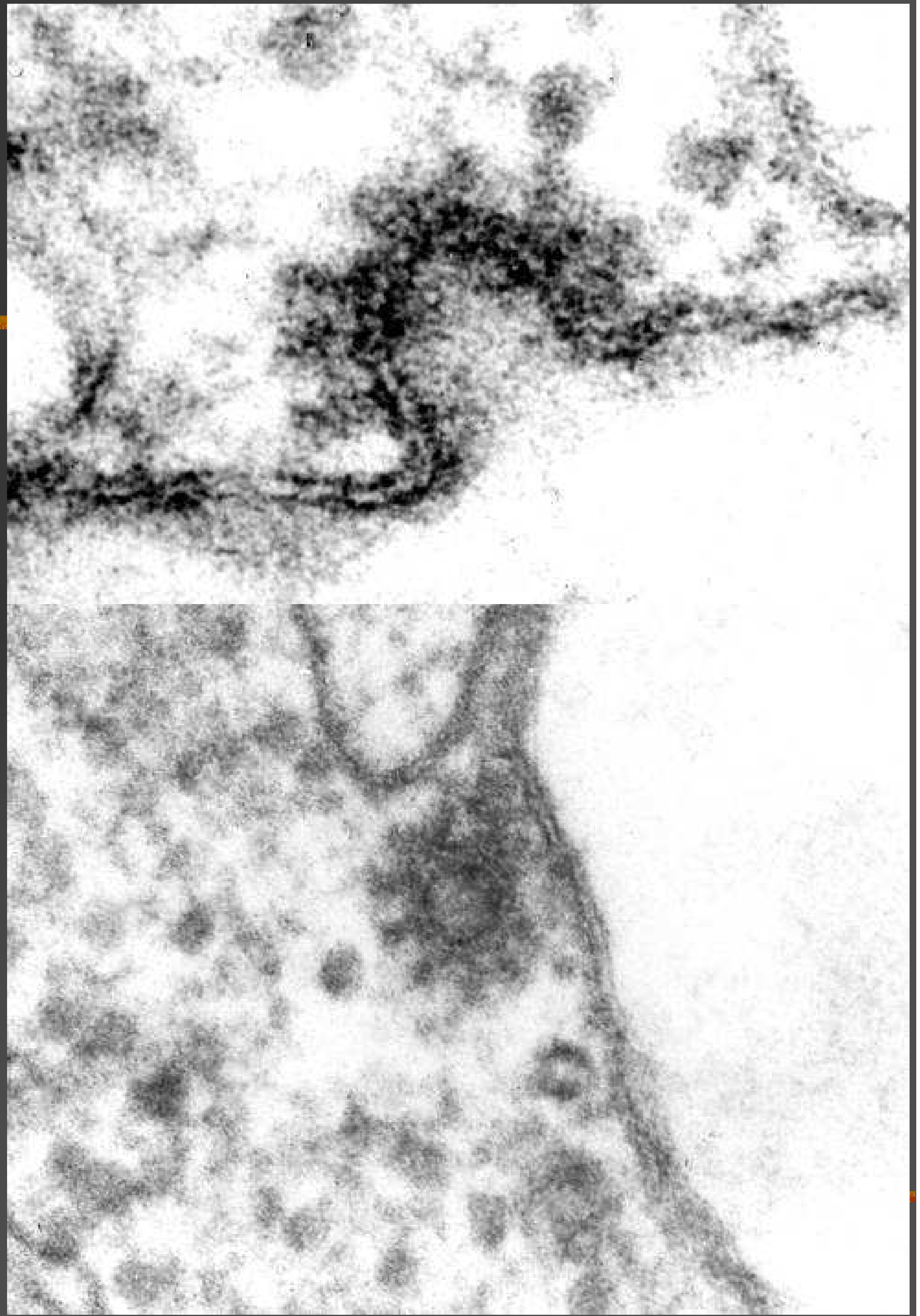
Cambial reactivation in *Aesculus*

- Activity can be detected in the cytoplasm of cambial zone cells long before any signs of activity are displayed by the tree.

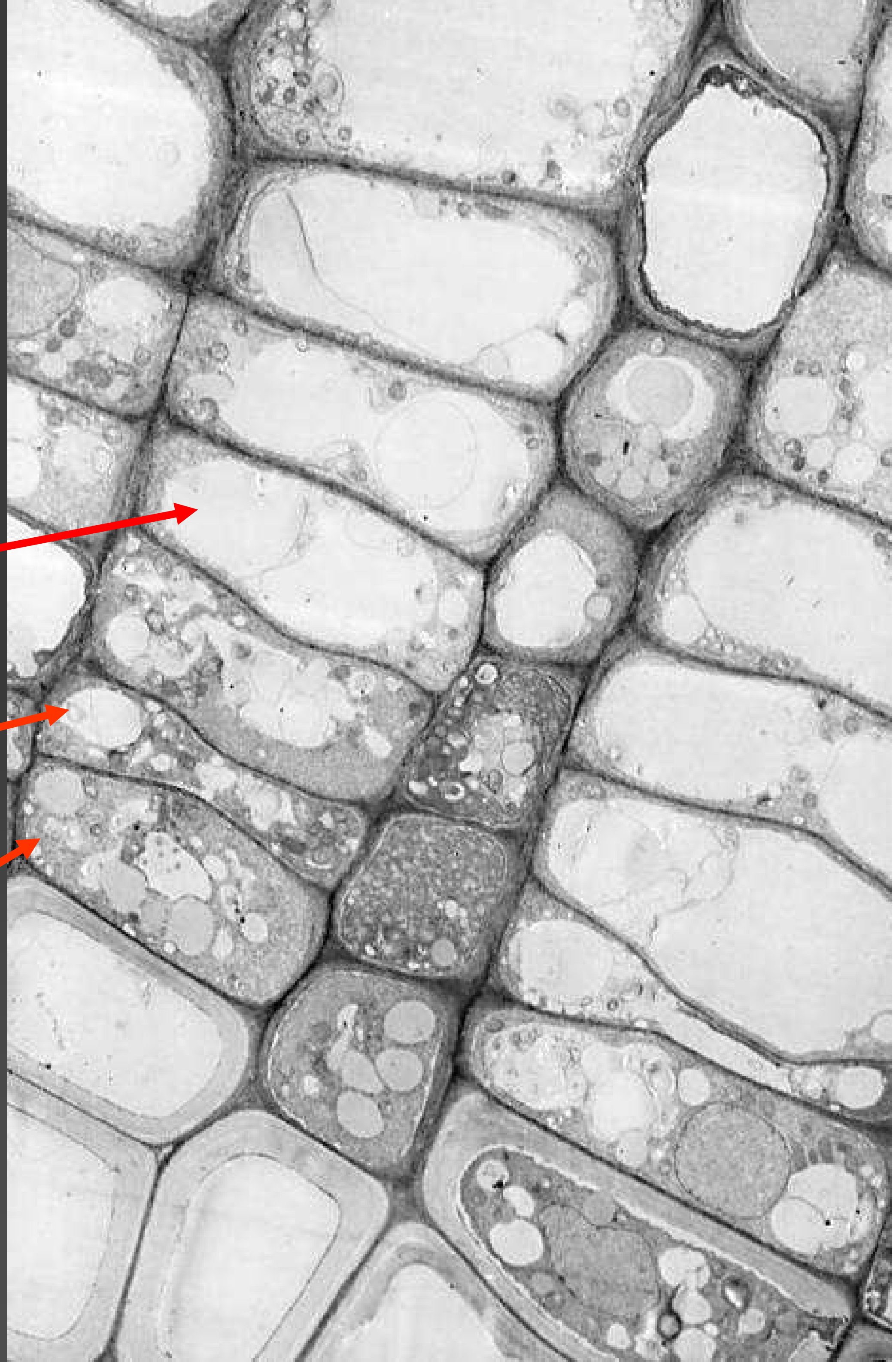
Active dictyosome in a boundary layer cell of dormant cambium

23 February

- Developing and mature coated vesicles
- 8 March



- Reactivation (16 March)



  - Expanding phloem precursors
  - Fusiform initial
  - Boundary parenchyma

Dividing phloem mother cell (16 March)

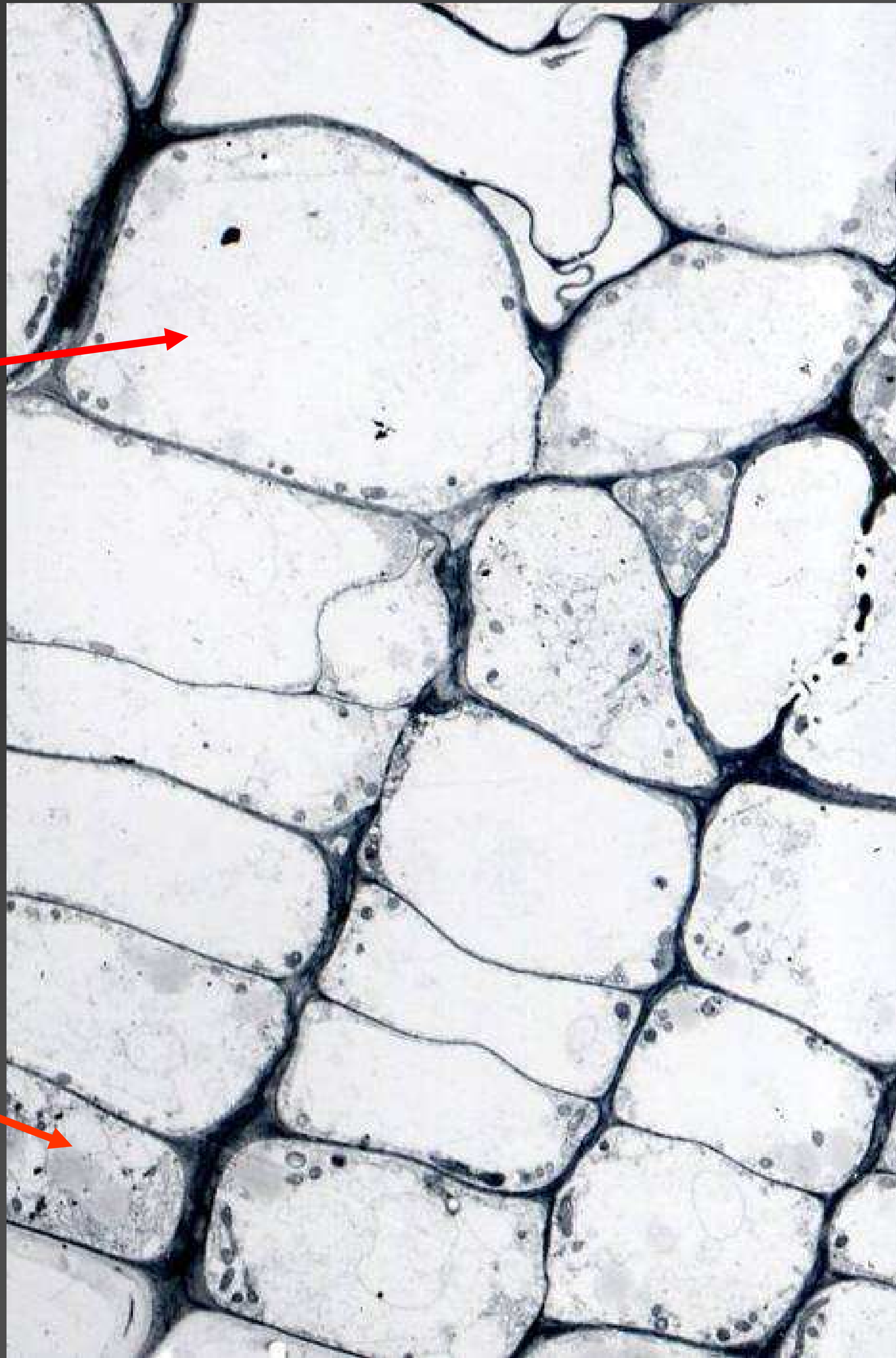
New tangential wall

- 13 April

- Boundary parenchyma

- Cytoplasm confined to a thin parietal layer

- Boundary parenchyma

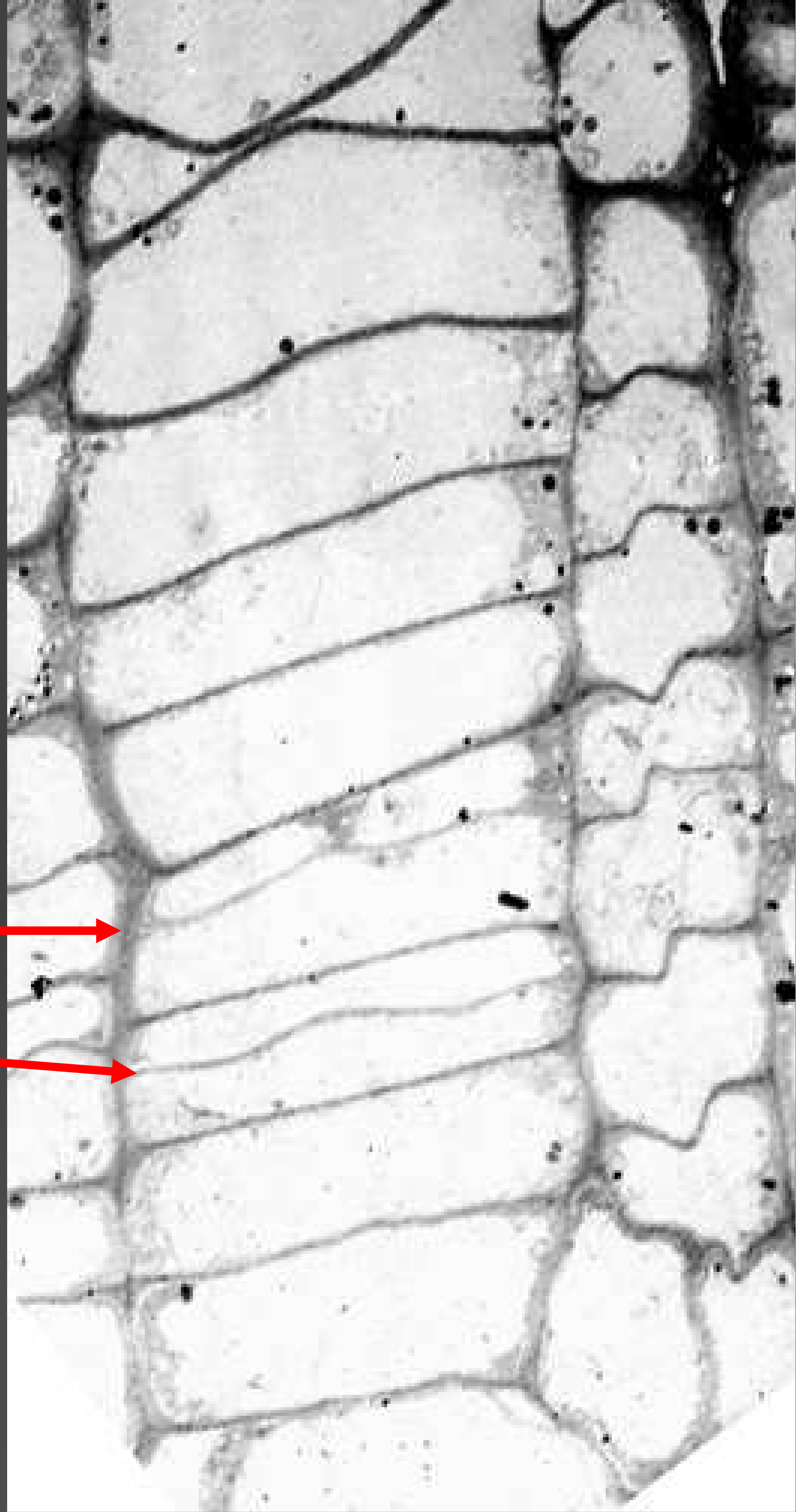


- 23 April

- Developing phloem cells

- Dividing initial
- Xylem mother cell

- New xylem elements



- Typically in the Reading area, *Aesculus* bud-break occurs in late March, with leaves fully emerged by late April

- Xylem formation appears to begin coincidentally with leaves beginning to export photosynthate

Reactivation sequence

- Larson (1994):
  - Xylem production first – 26 species
  - Phloem production first – 21 species
  - Simultaneous production – 10 species

Observations are inconsistent between authors

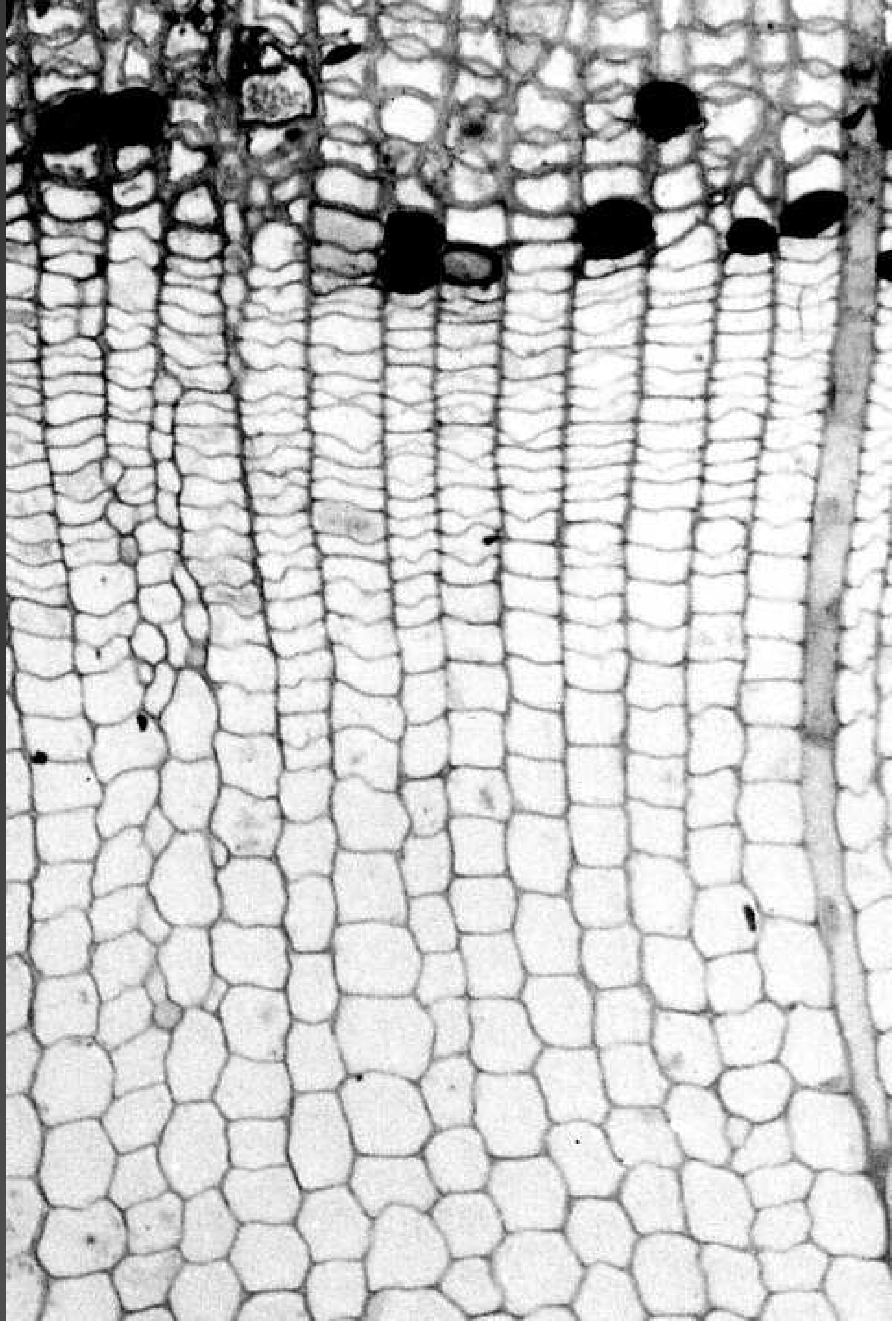
- *Acer pseudoplatanus, Quercus rubra , Pinus sylvestris and Vitis vinifera* appear in the list of xylem reactivators and phloem reactivators

- In the Pinaceae:
- *Pinus halepensis and rigida* are xylem reactivators
- *Pinus banksiana, resinosa, and strobus* (five authors) are phloem reactivators
- *Picea excelsa, rubens and rubra* are xylem reactivators,
- *Picea abies* is a phloem reactivator
- *Picea glauca* a simultaneous reactivator.

Phloem production in *Aesculus*

- Phloem annual growth rings marked by boundary parenchyma
- The number of phloem cells in each file is similar to the number of over-wintering precursors
- All the phloem for the season is produced at the beginning of the season

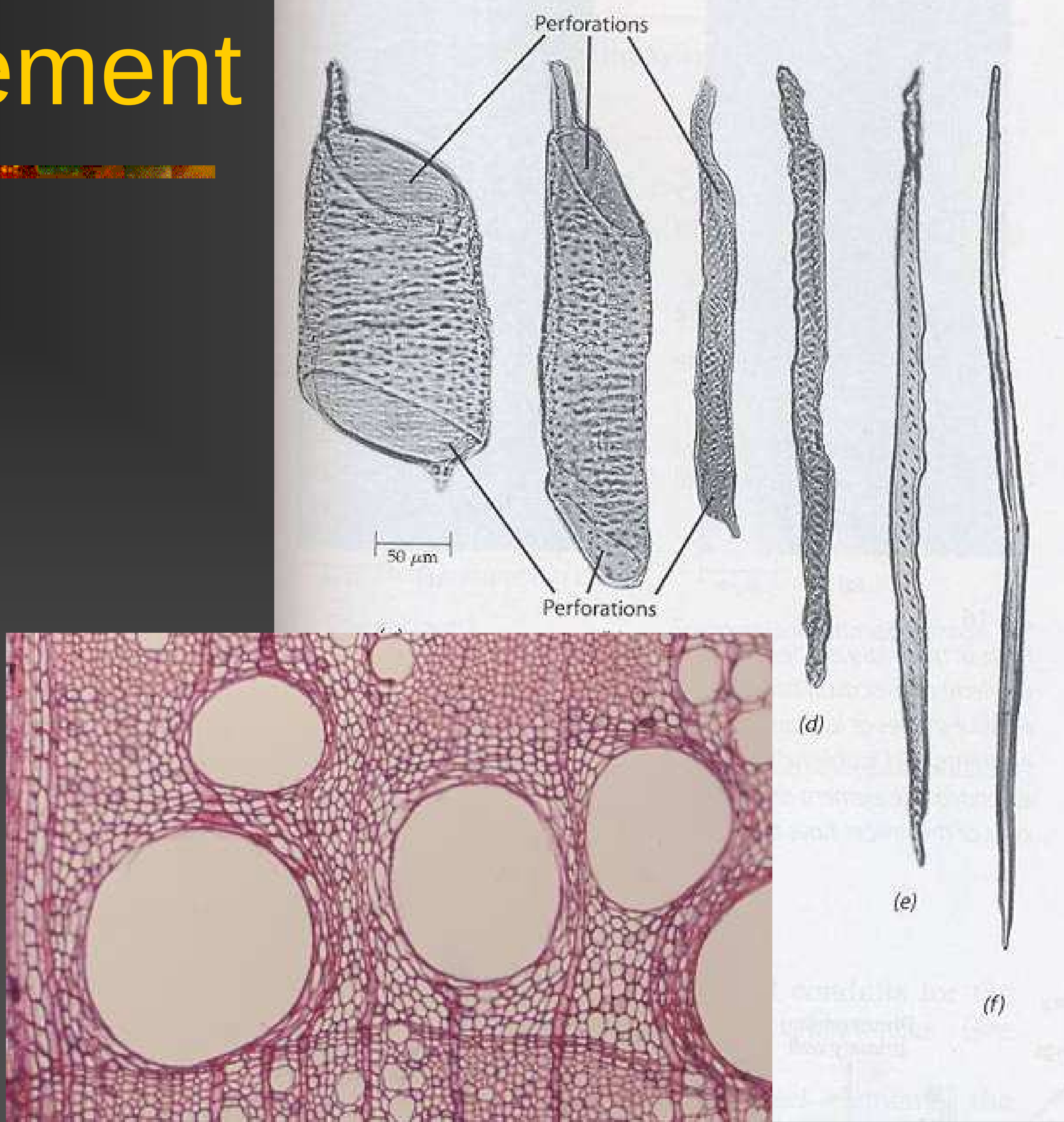
- *Pinus radiata*
- Active cambium producing both xylem and phloem throughout the season



- Growth of derivatives and wall formation

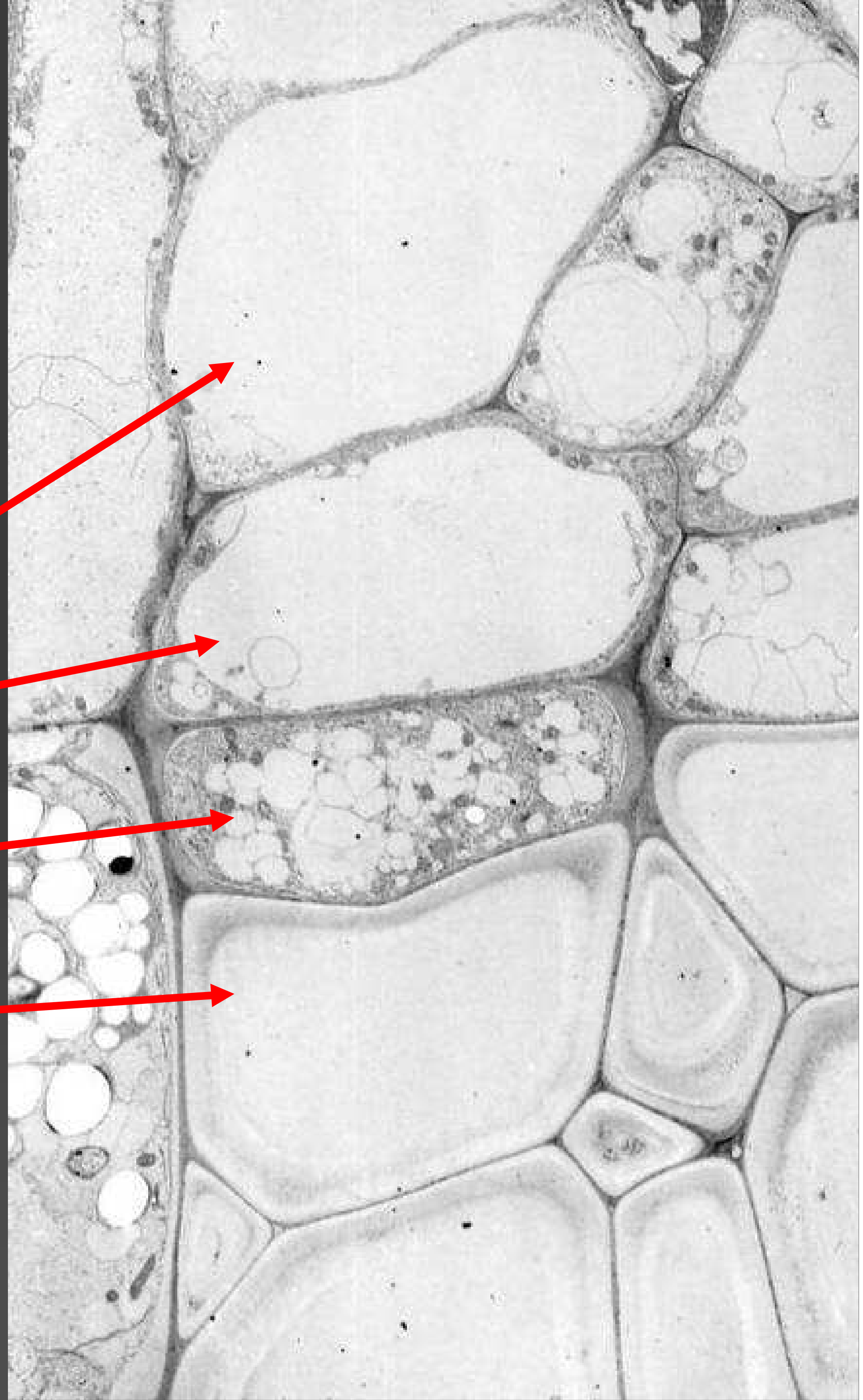
Cell enlargement

Quercus robur



- 20 April

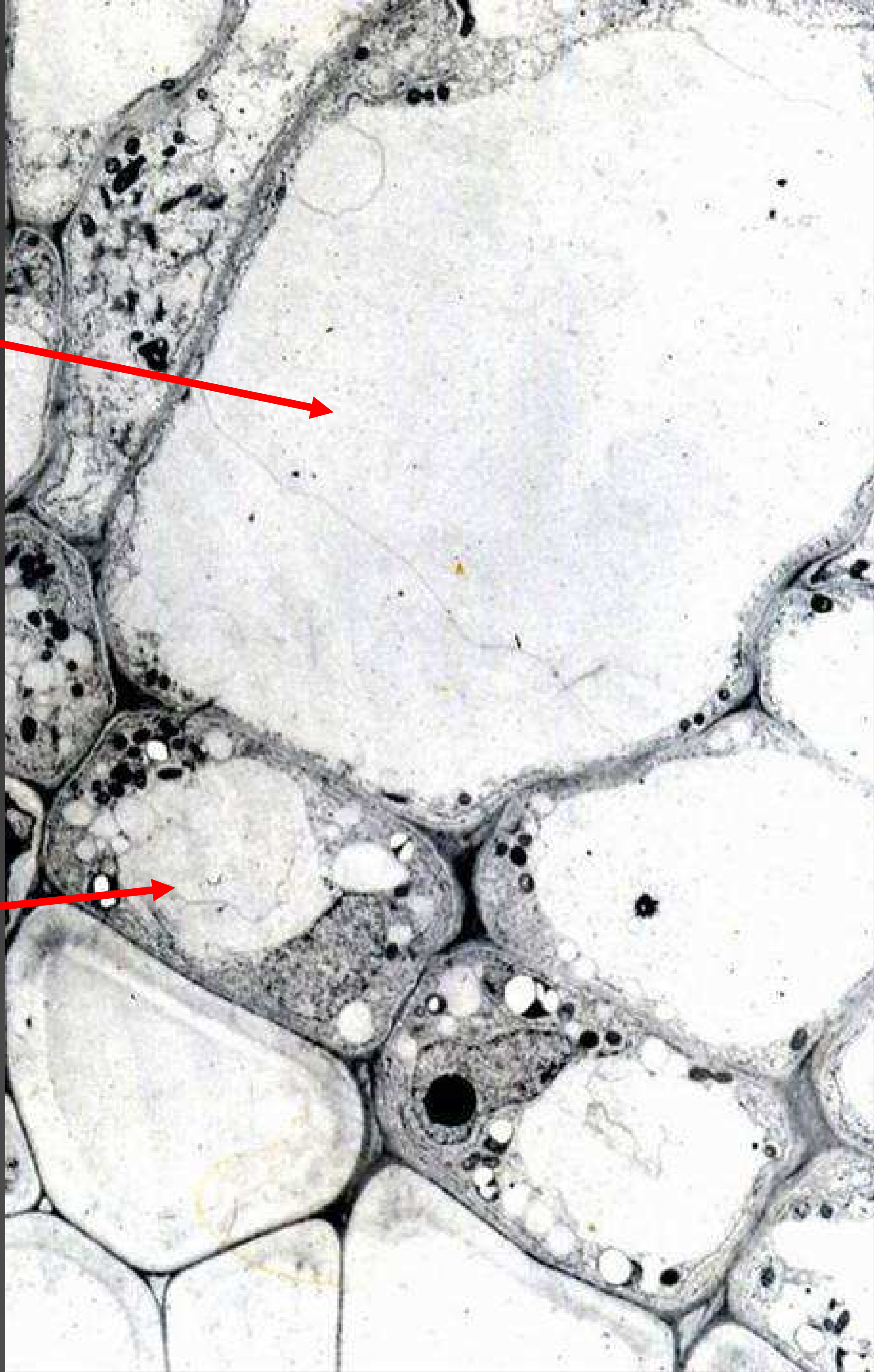
- Developing xylem cells
- Boundary parenchyma
- Previous year's latewood fibre



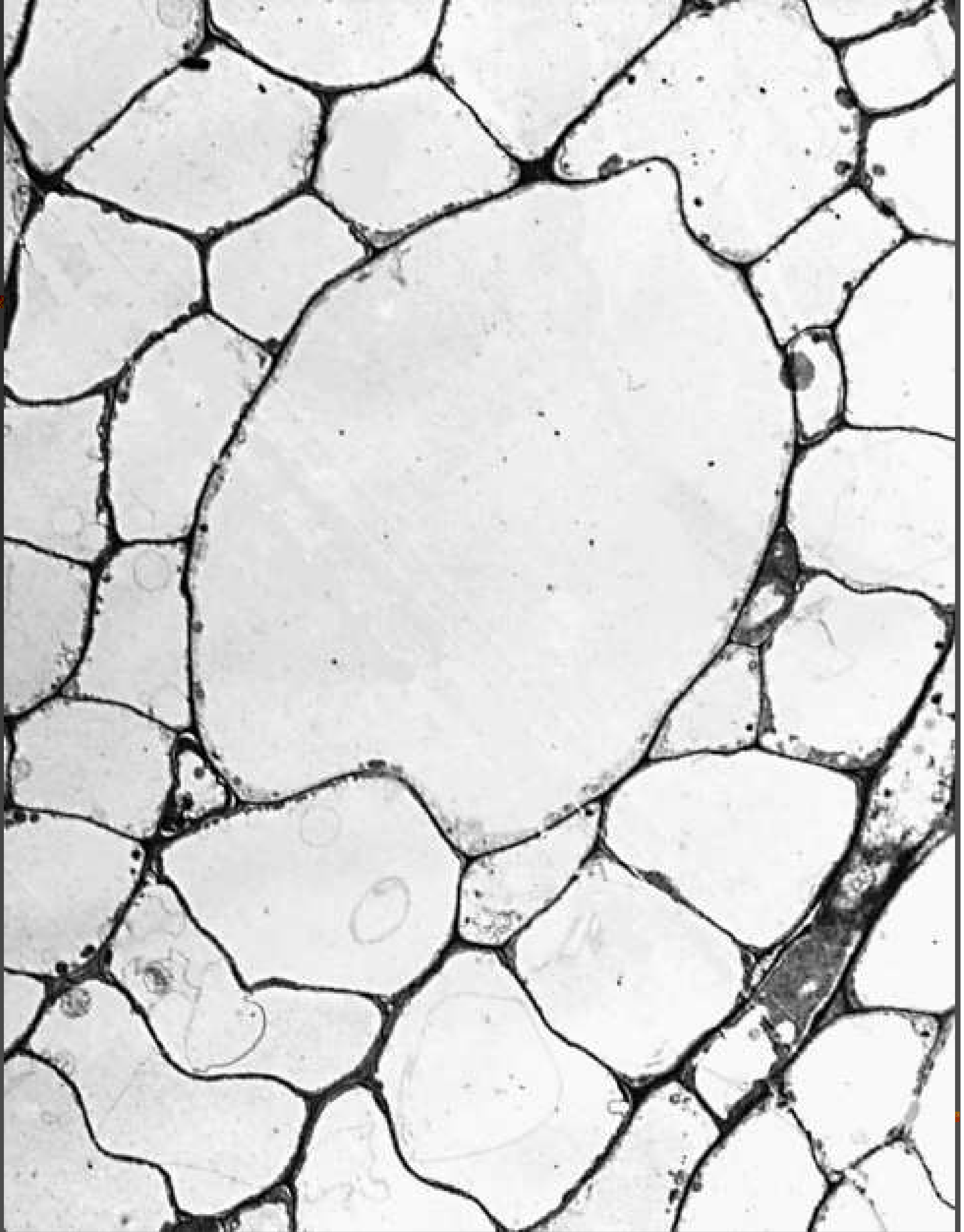
- Cell tip growing between fibres

Enlarging vessel element

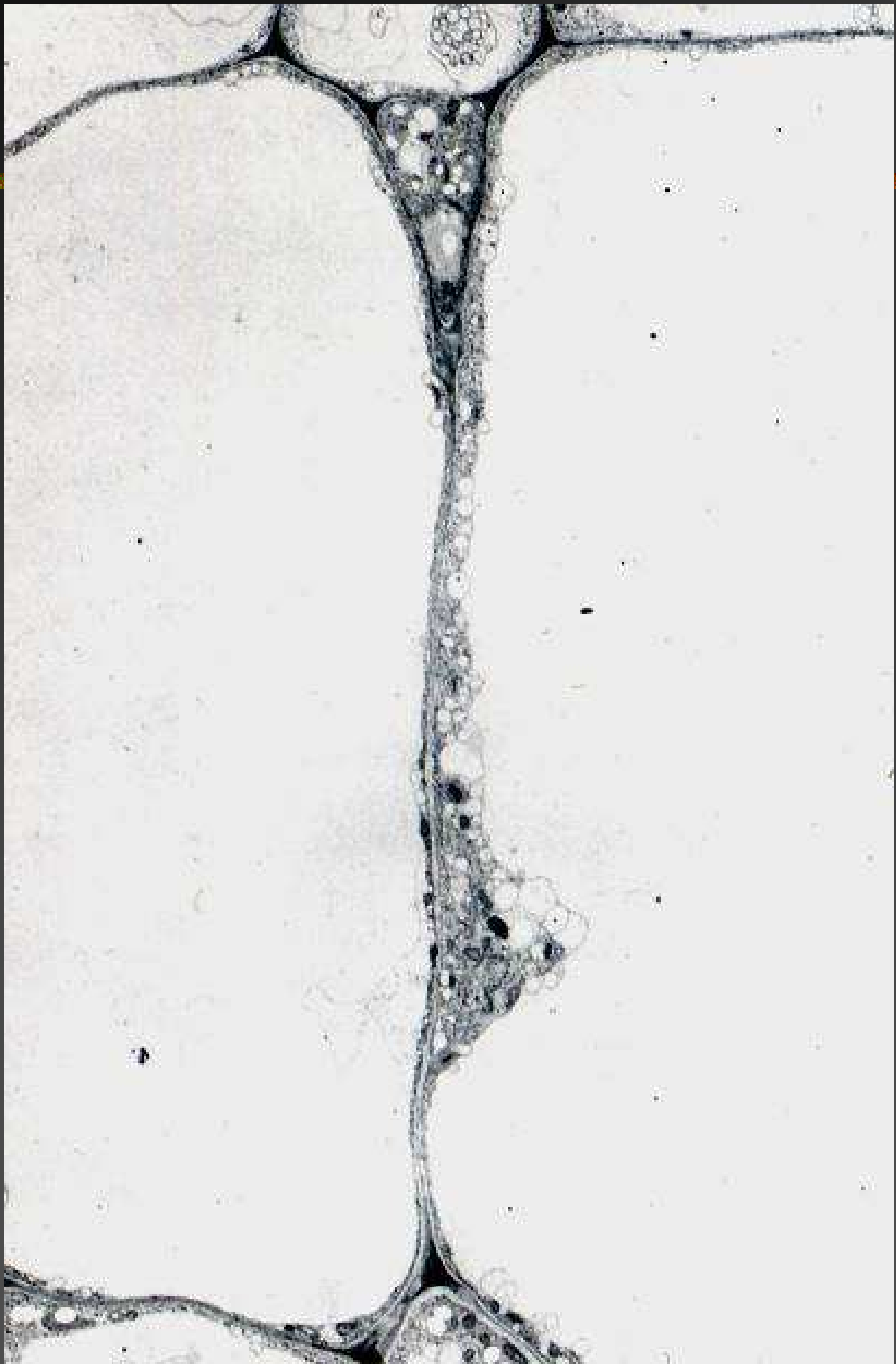
Boundary parenchyma

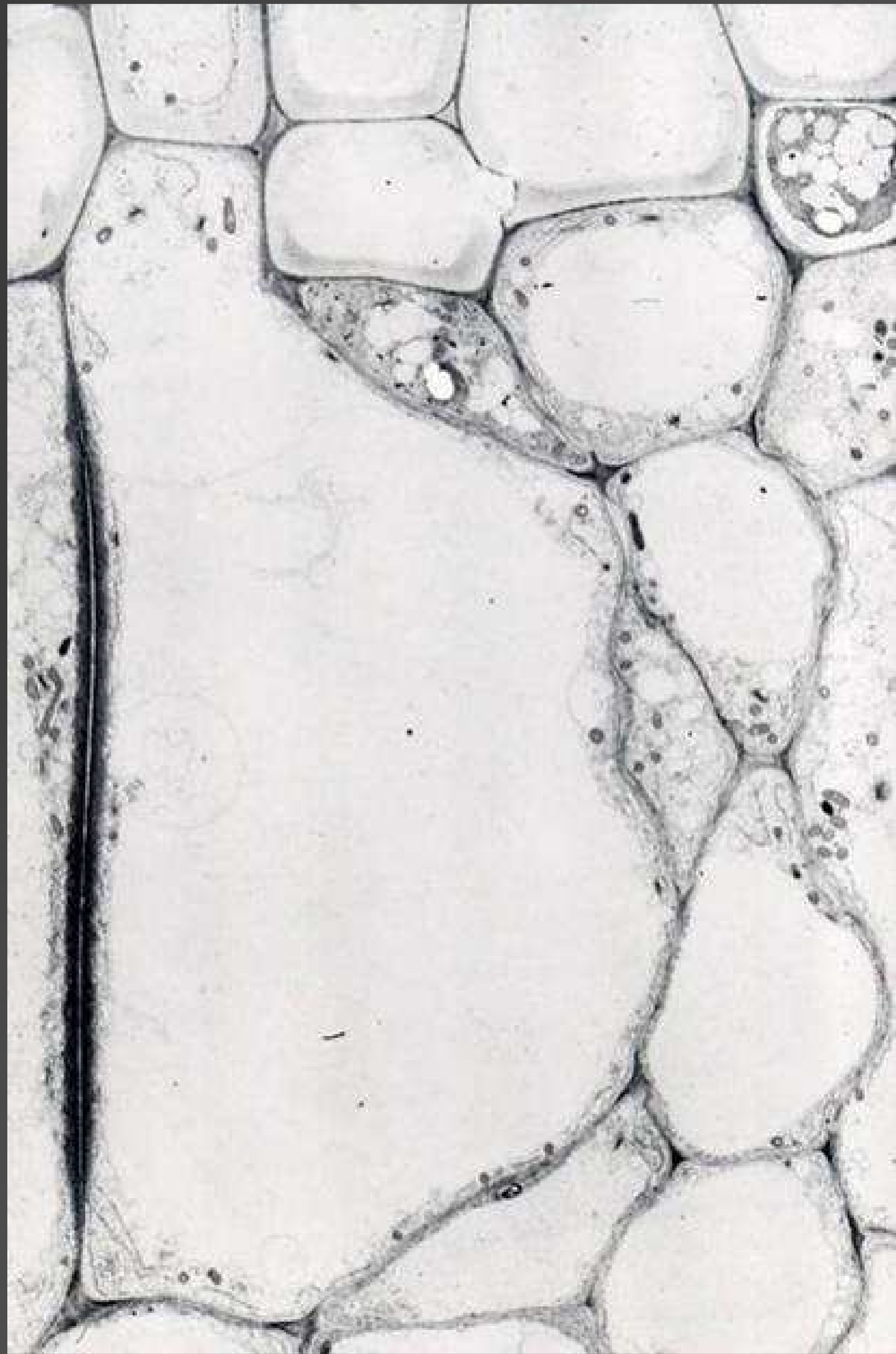


- Developing fibres are compressed and files of cells distorted by vessel enlargement



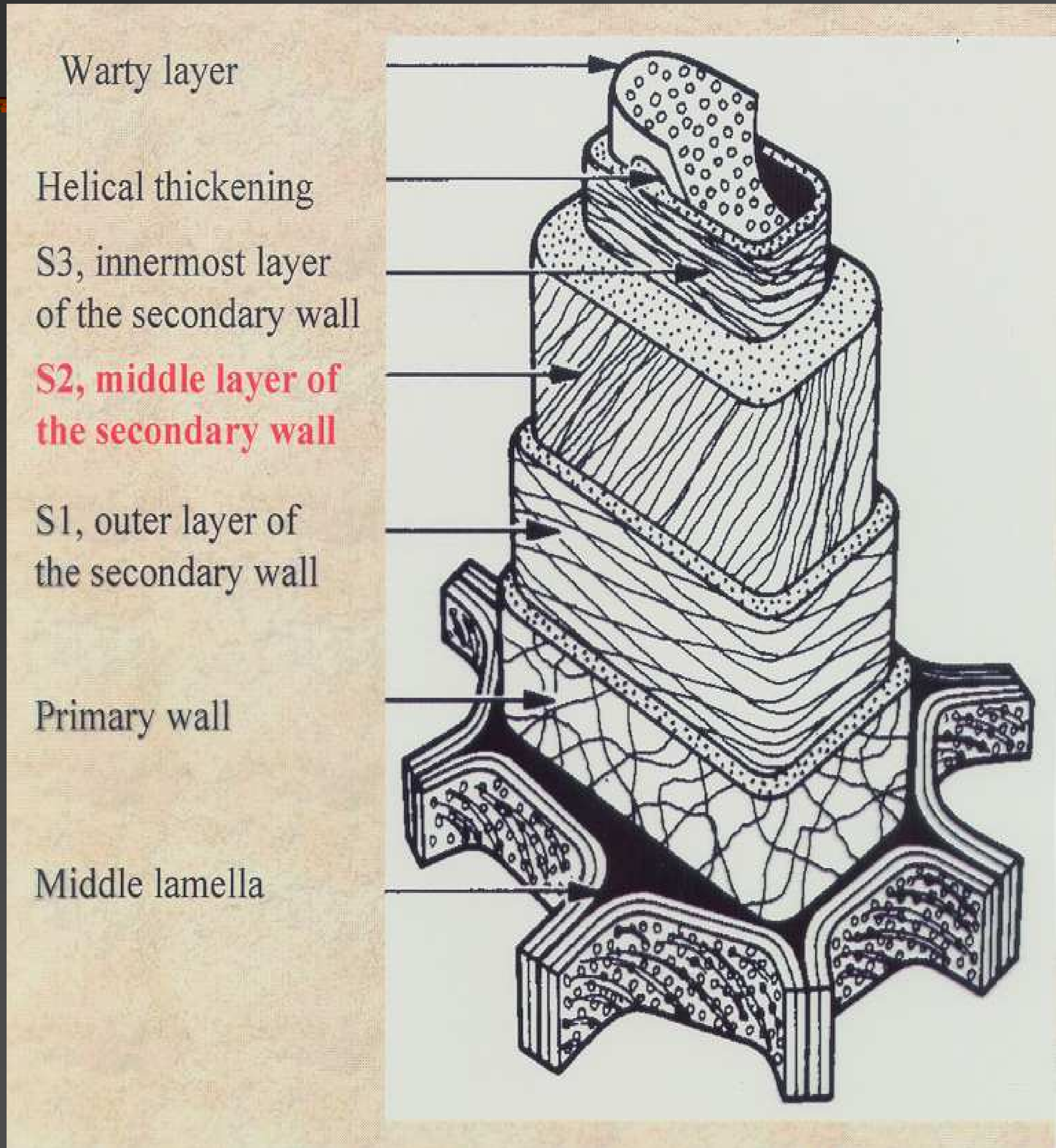
Perforation plates



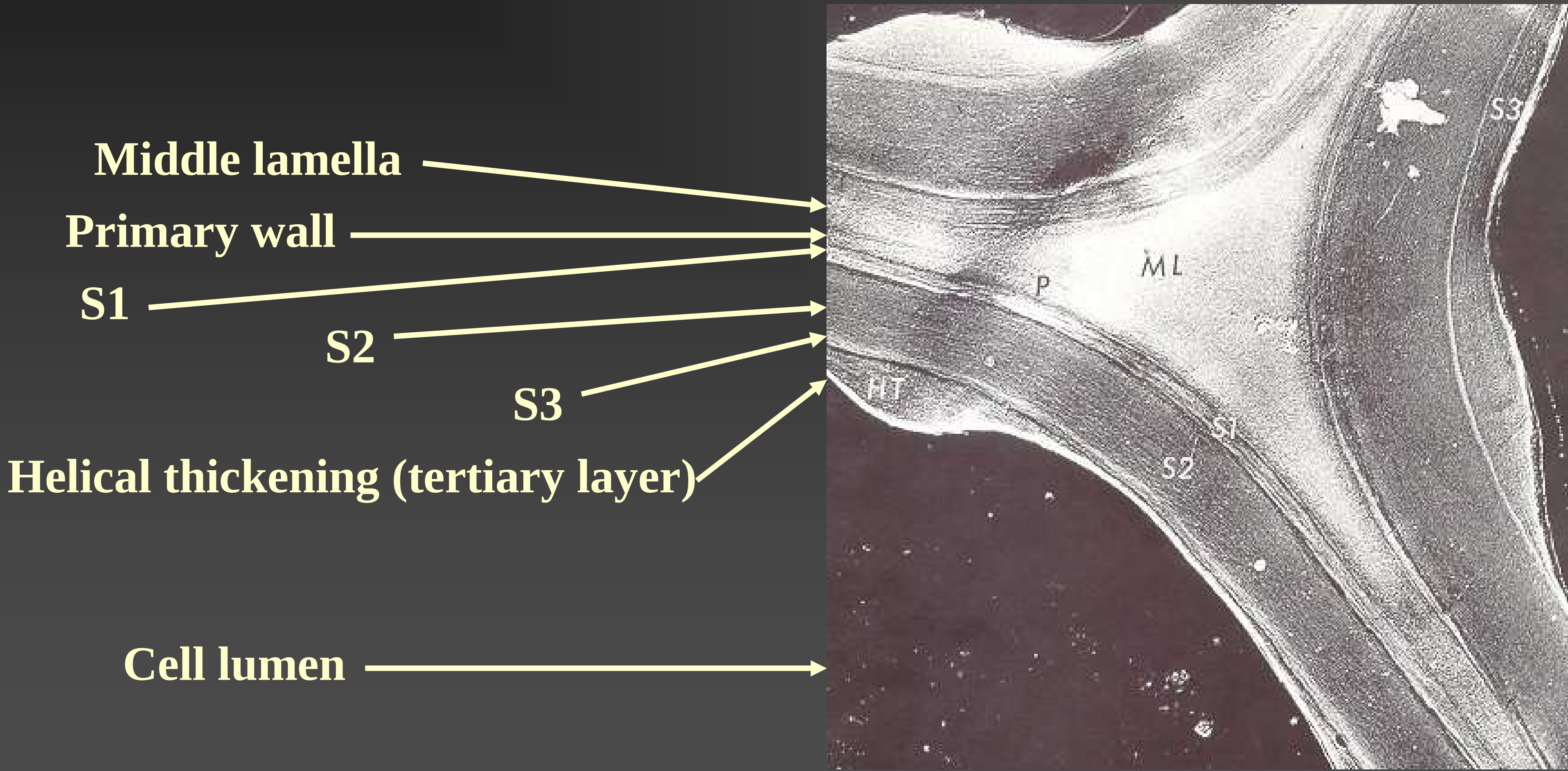


Secondary wall formation

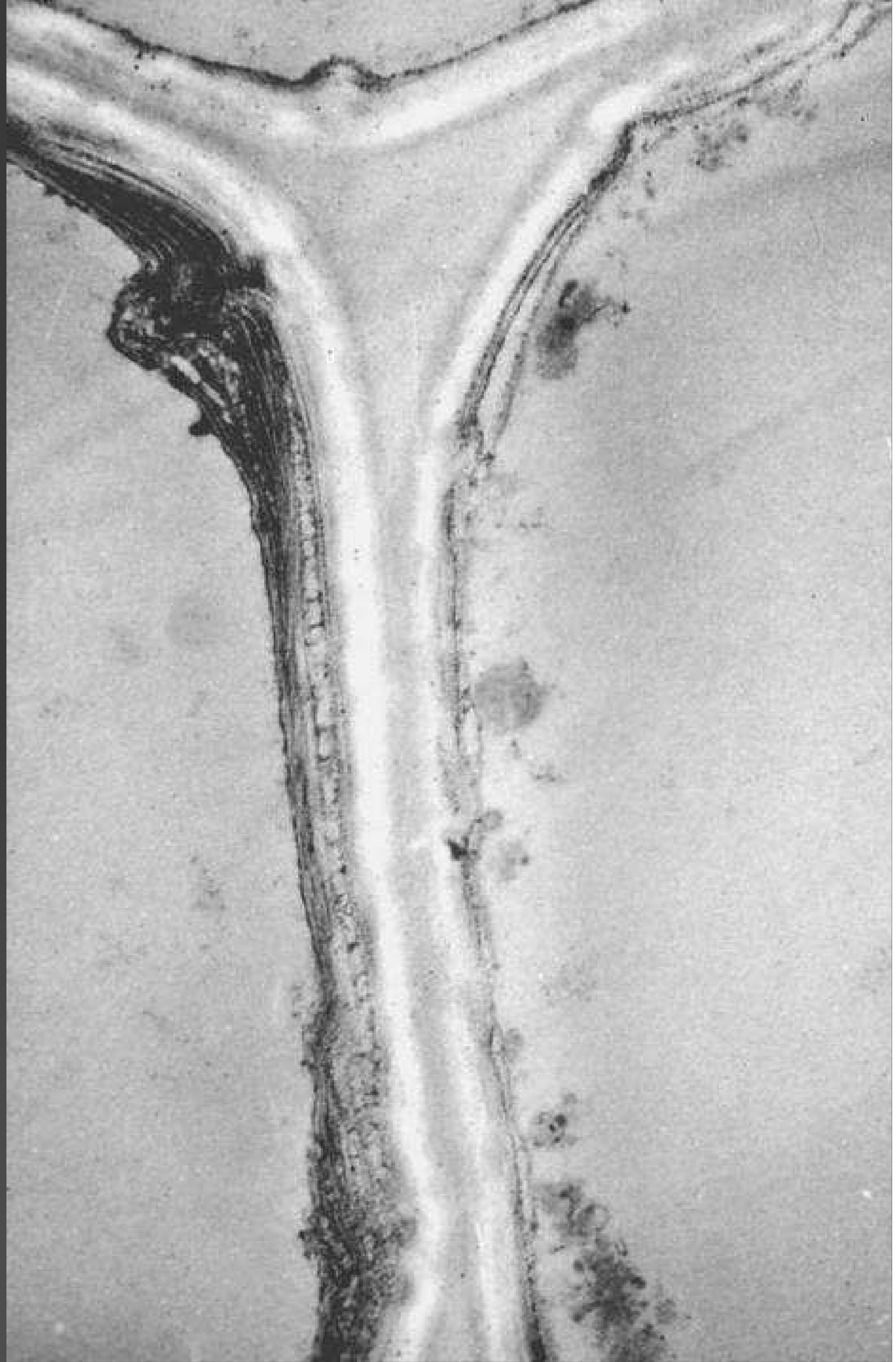
- This the classic representation of the wall of a cell that has all possible wall layers:
- the ML+P+S1+S2+S3 +HT+W wall zones



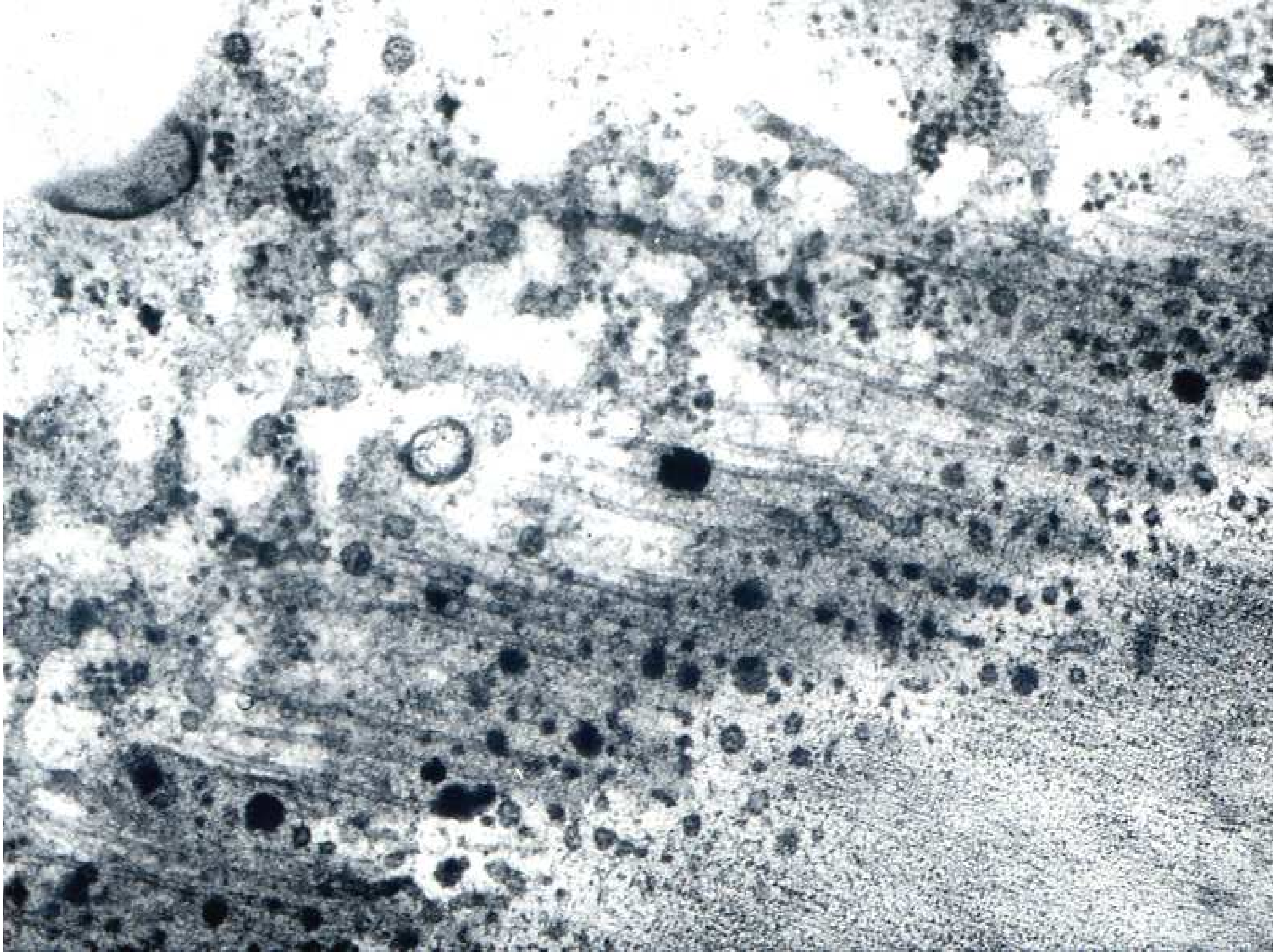
Cell wall Layers

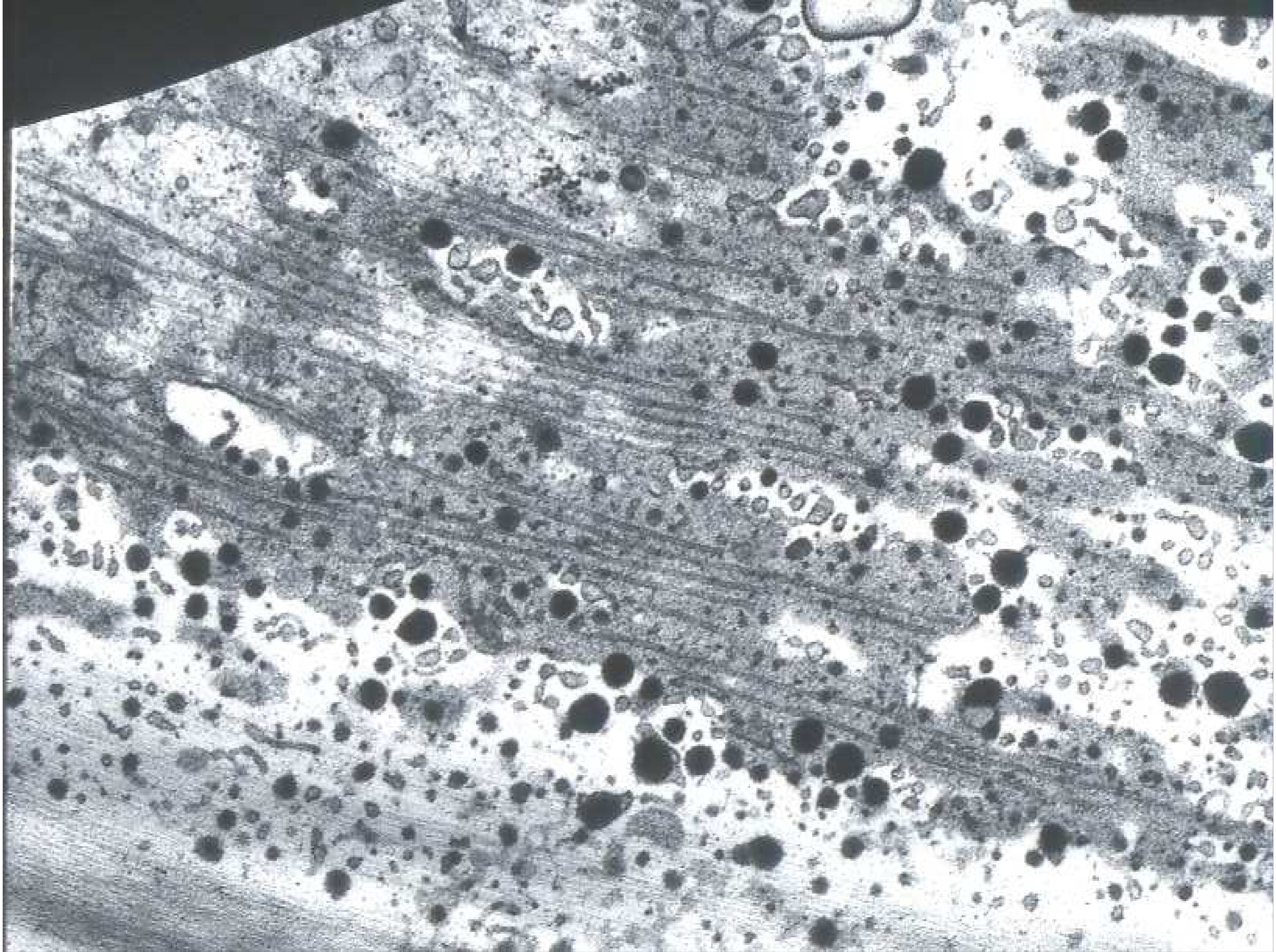


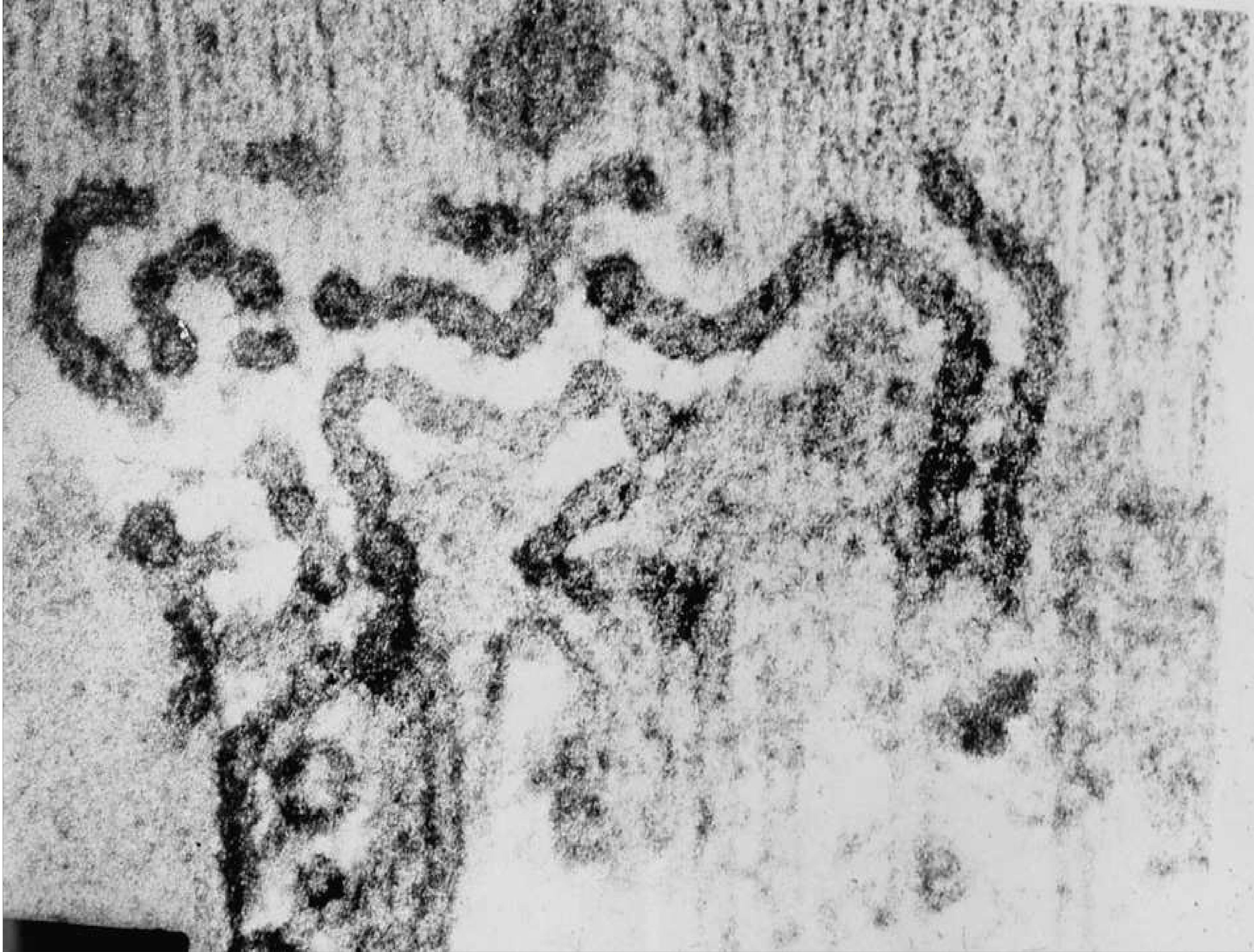
- Earliest stages of cellulose deposition forming the S1 layer



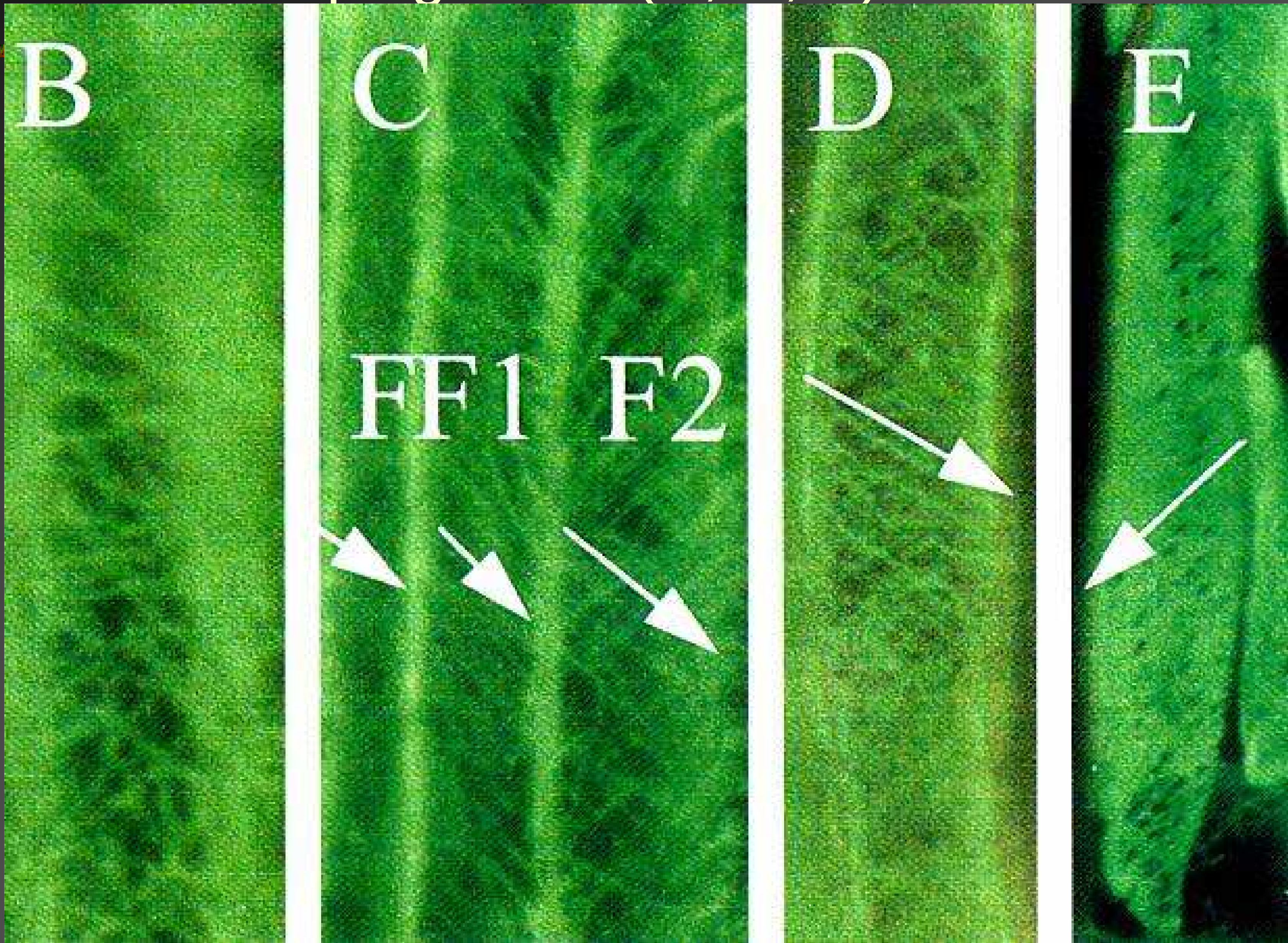
Microtubules and cellulose orientation



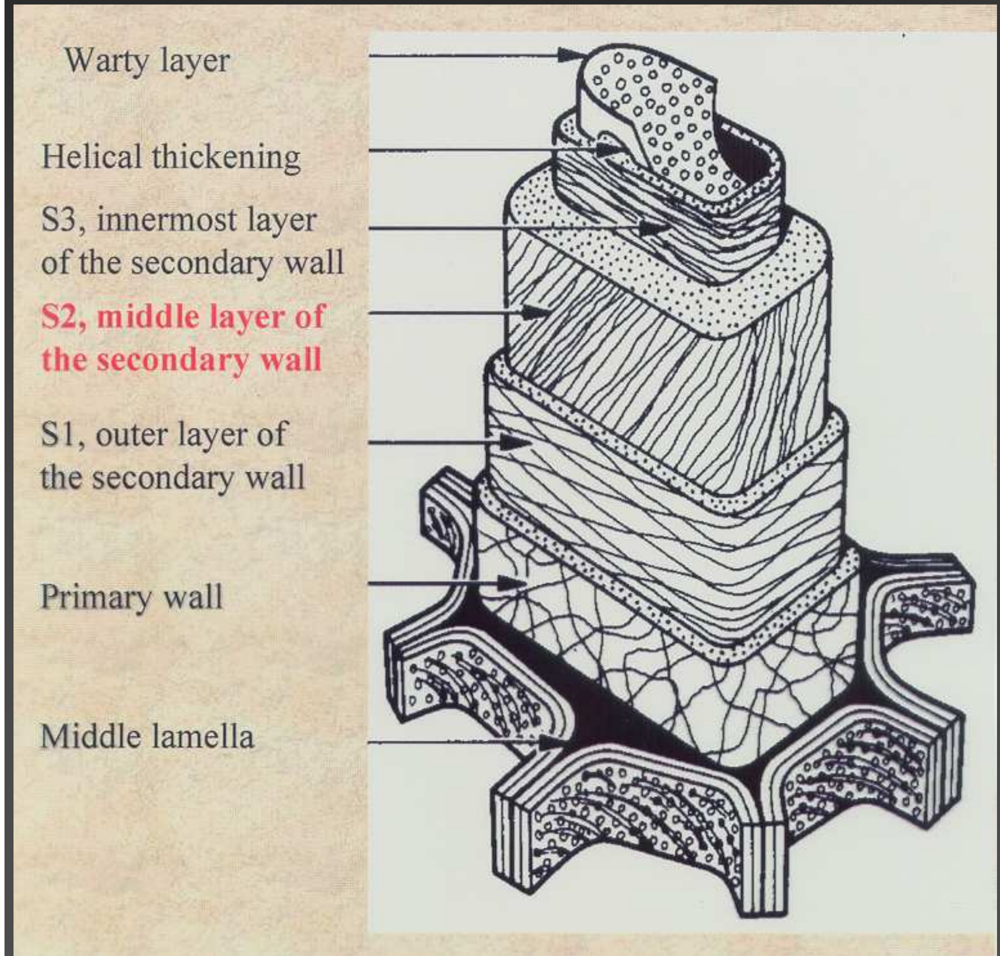


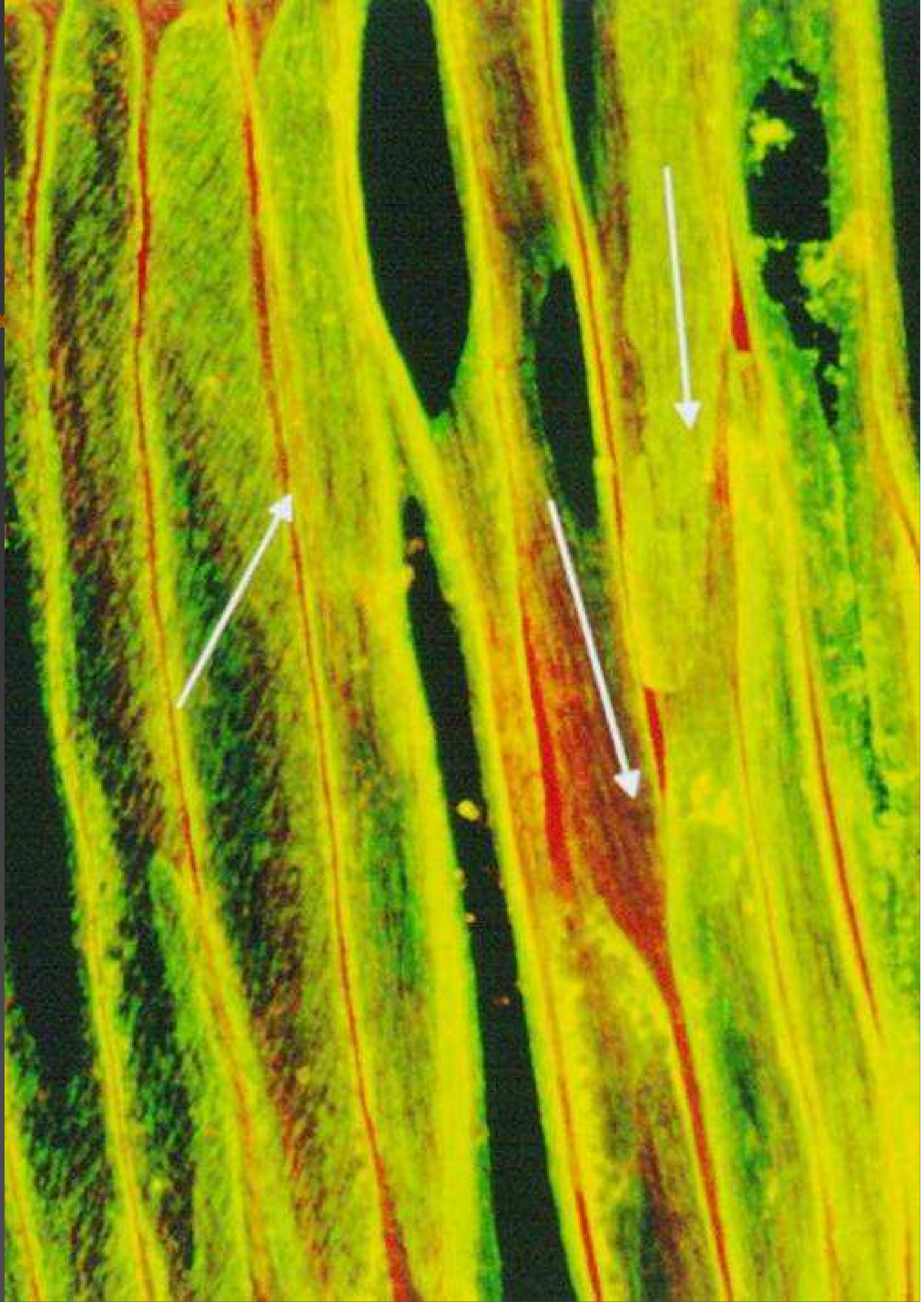


Tubulin in a fusiform cambial cell of *Aesculus* (B), and developing fibres (C, D, E)

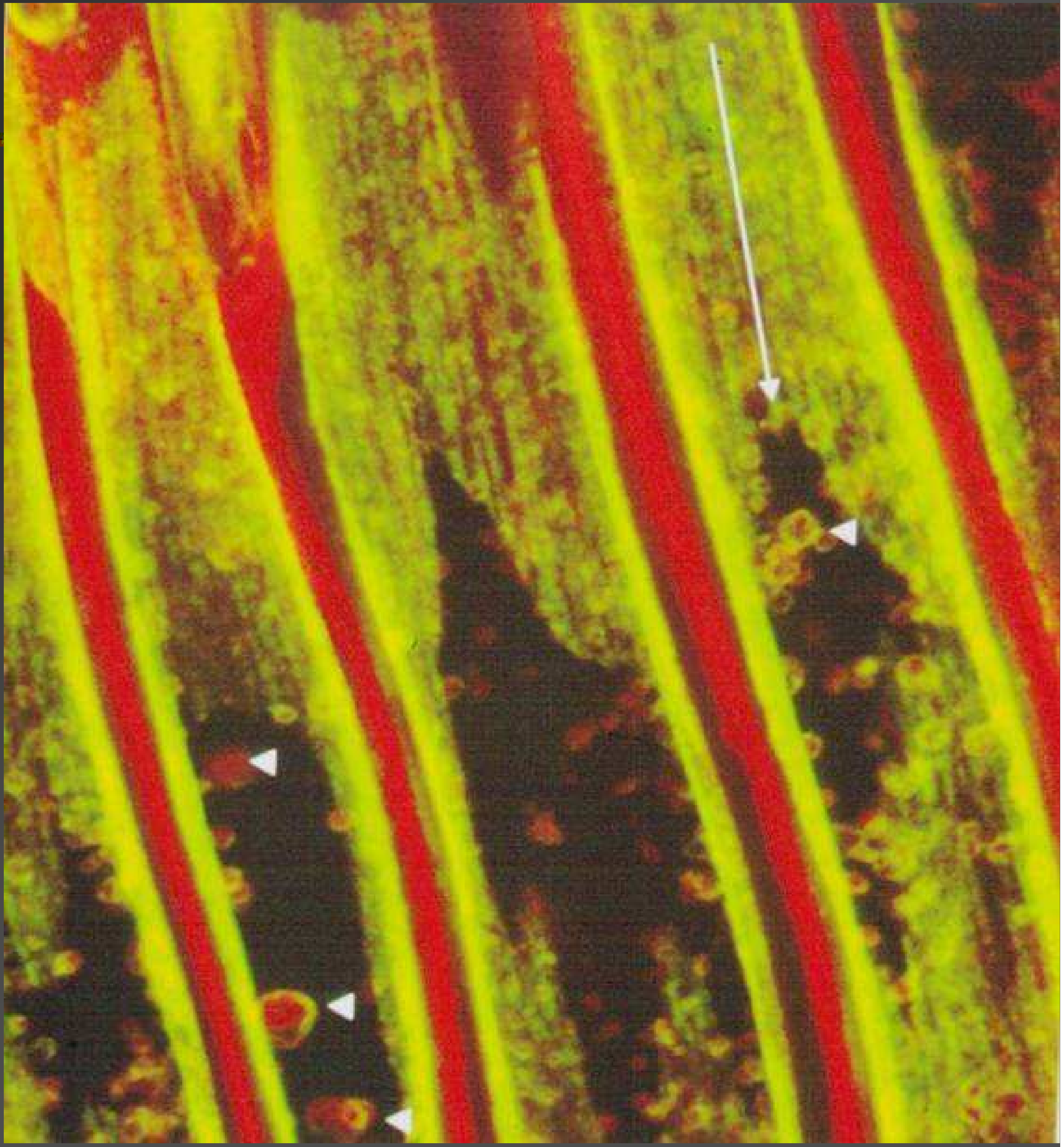


Tubulin in developing fibres in *Populus*



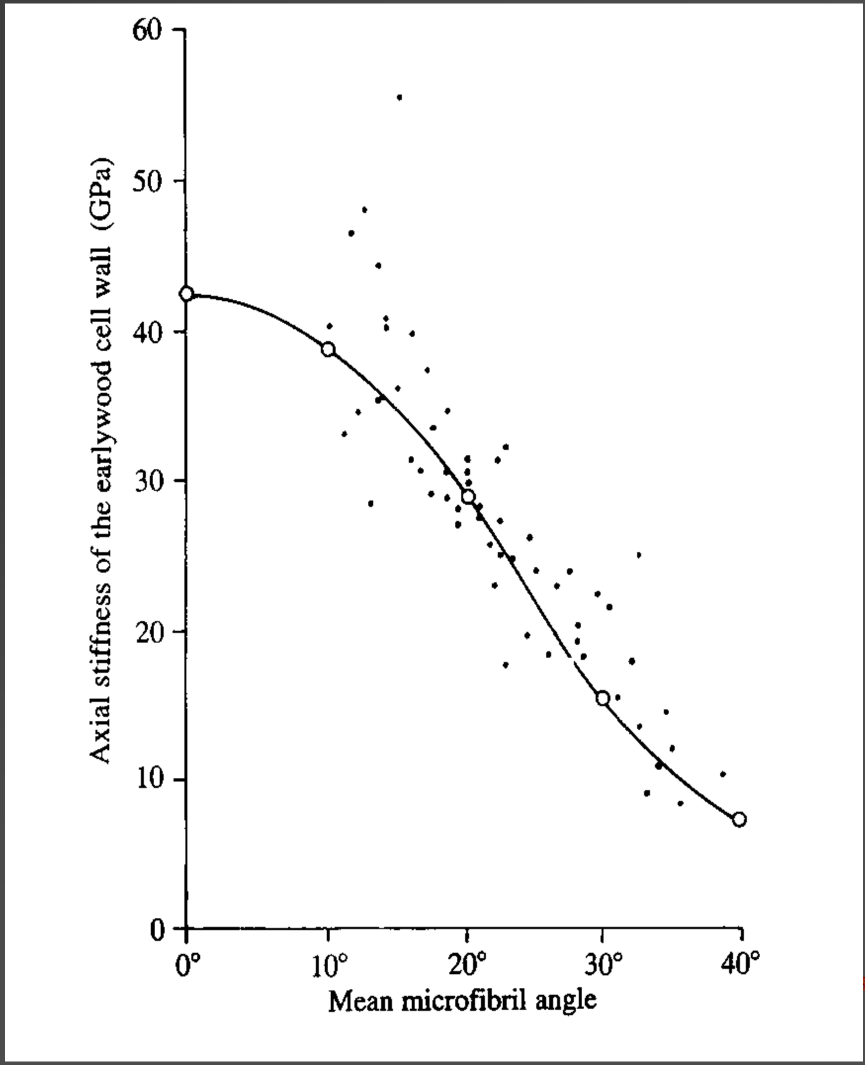


Tubulin in tension wood fibres of *Populus*



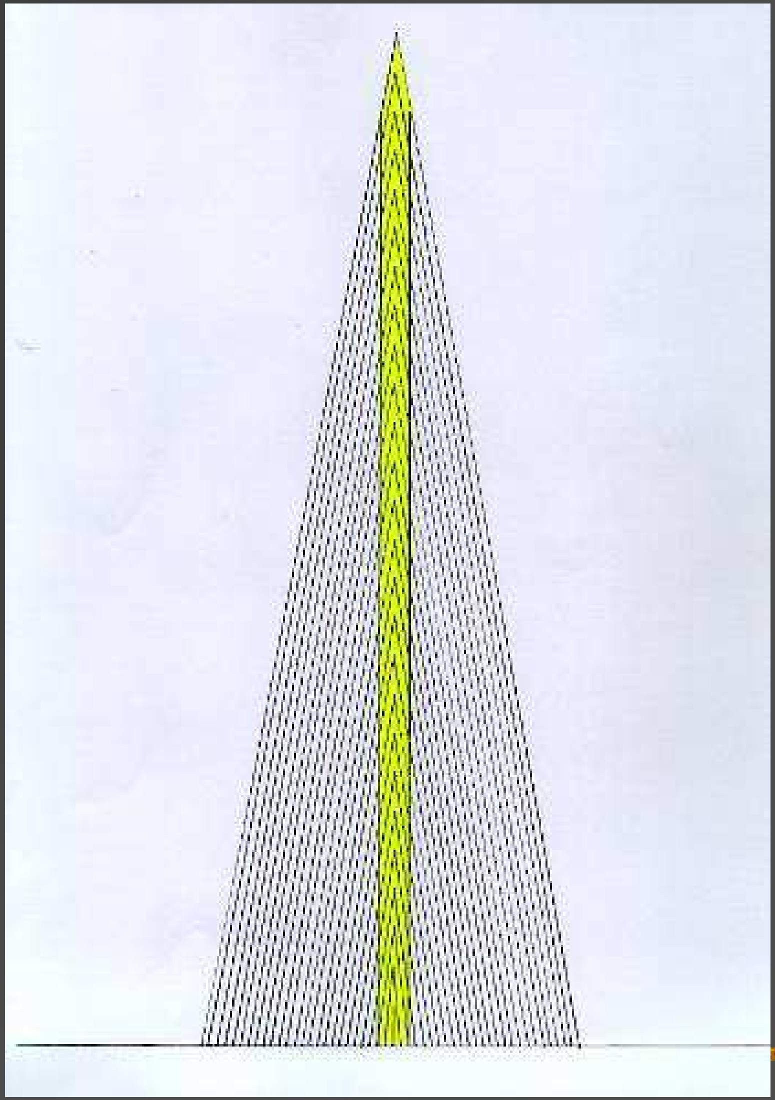
The significance of microfibril angle

- The relationship between MFA and axial stiffness according to Cave (1968)
- There is a 5 fold increase in stiffness when MFA shifts from 40 to 10 degrees



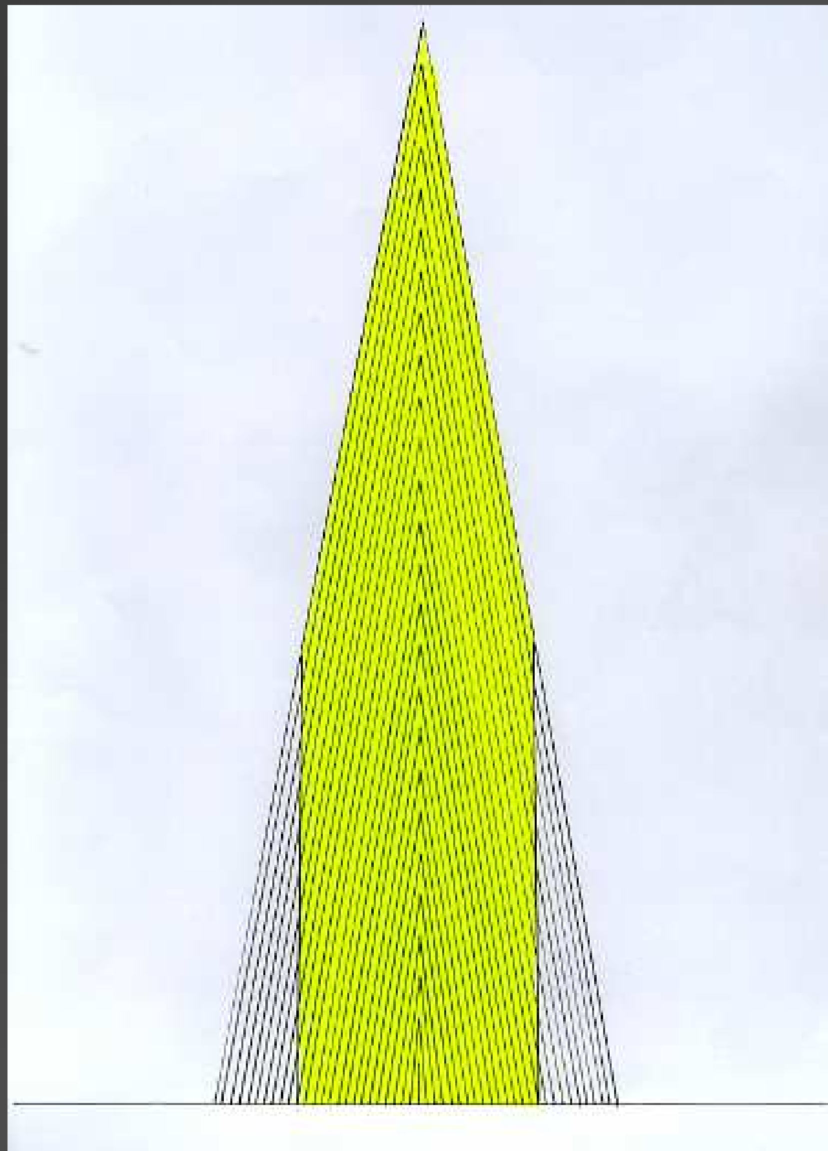
Corewood in a 125-year Old Tree

- Juvenile wood (large microfibril angle)
- Mature wood
- (small microfibril angle)



Corewood in a 25-year Old Tree

- Juvenile wood
- Mature wood



The Problem of High Microfibril Angle

- Corewood is too flexible to be used as high grade timber

- Any improvement that would reduce the amount of low grade timber would result in significant financial gain for the producer and result in more efficient use of forest land

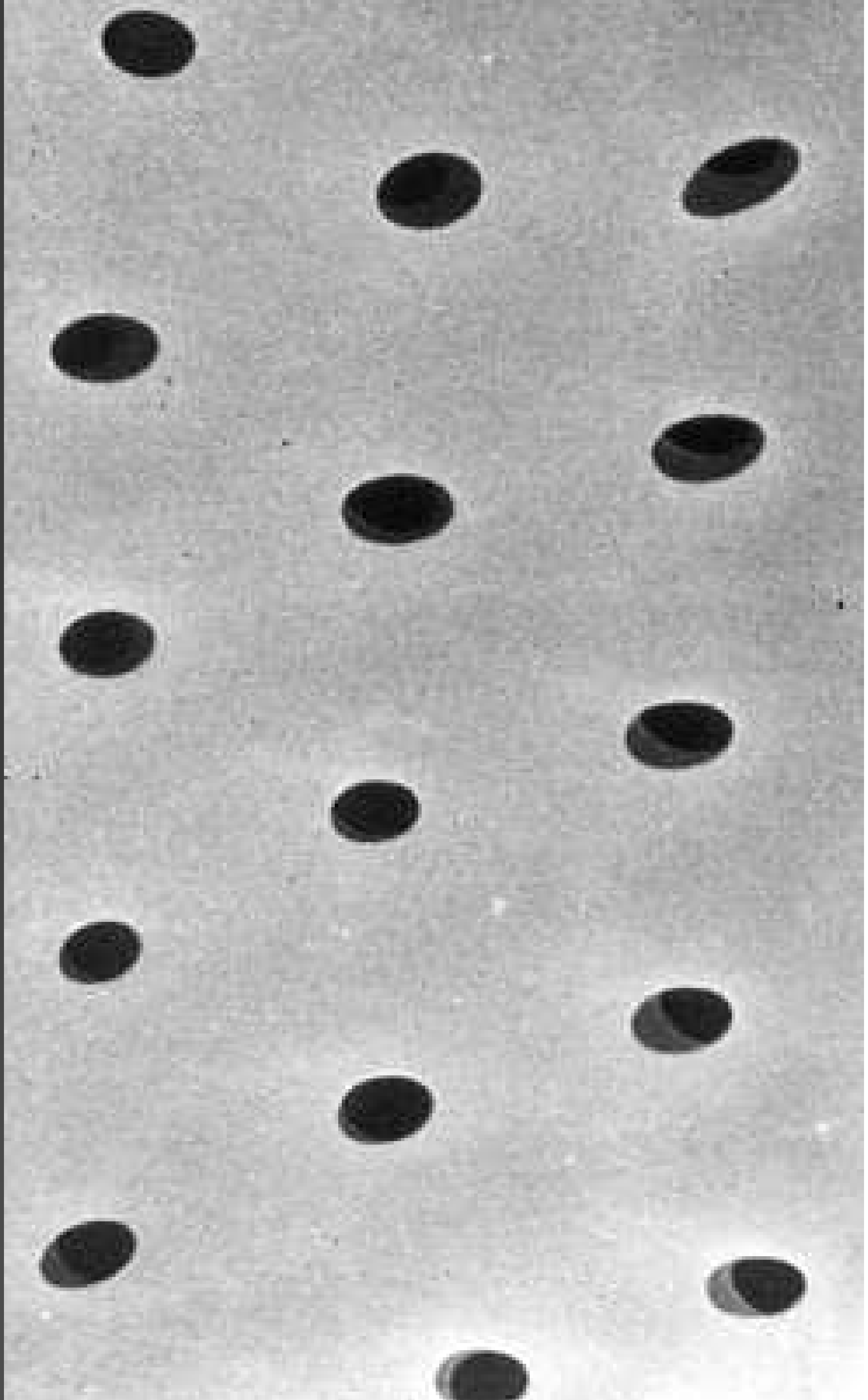
Consequences for the Tree

- High microfibril angle in corewood makes young trees flexible and able to withstand high winds
- Only small reductions in angle may be feasible without affecting survivability
- These may, however, still give significant increases in the quality of corewood

- Pitting and plasmodesmata

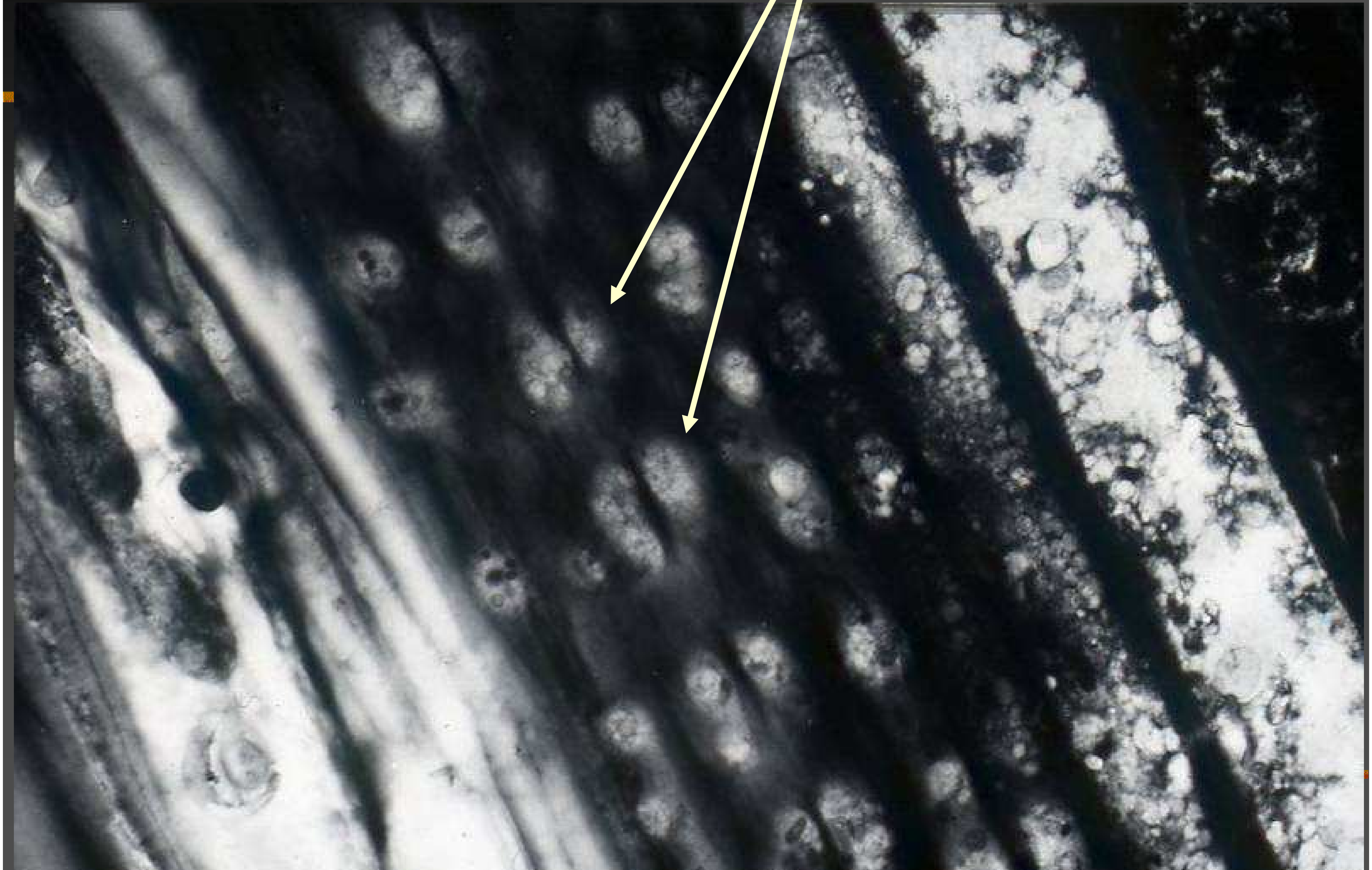
Formation of pits

Aesculus hippocastanum vessel wall

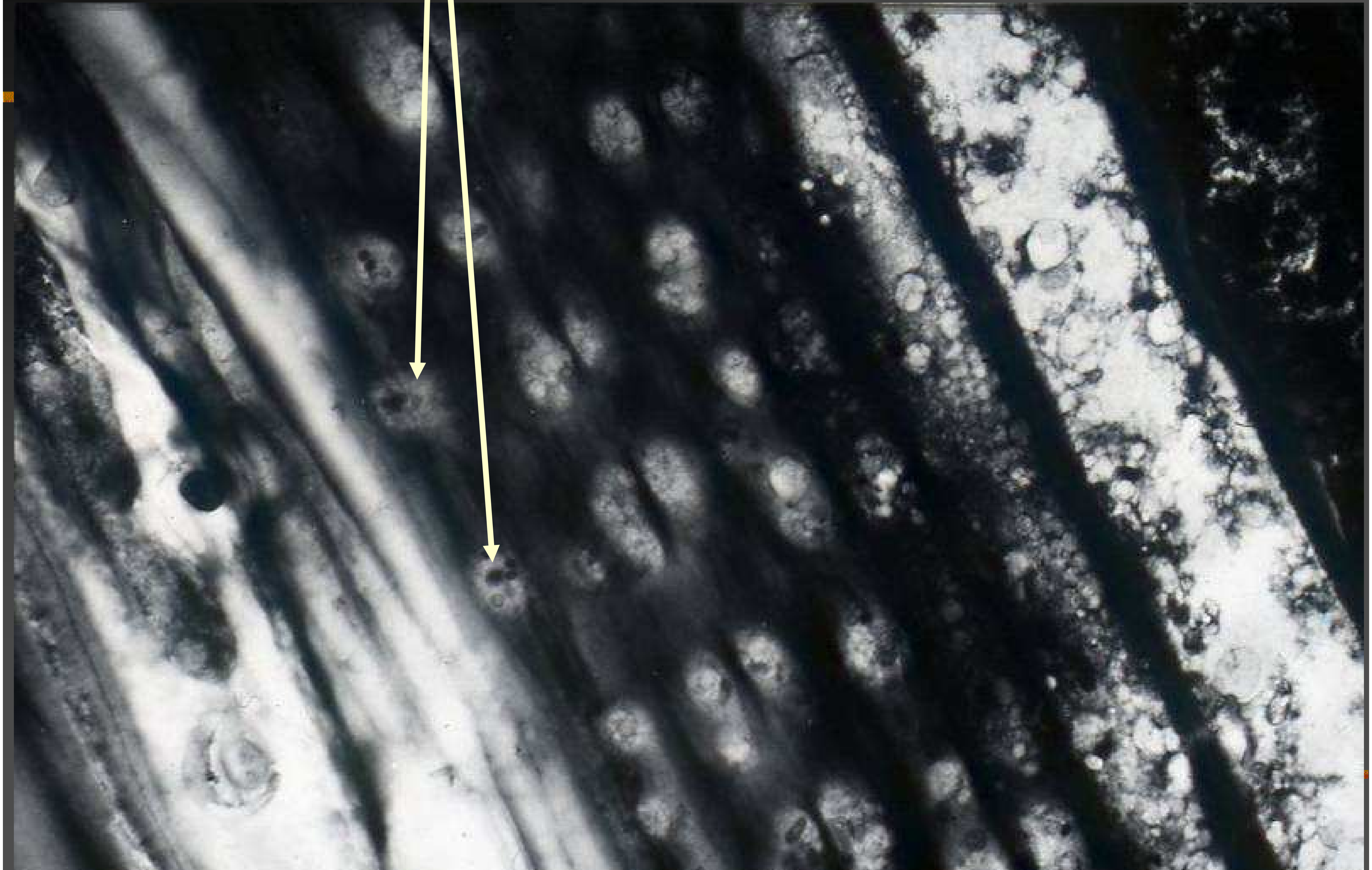


Sorbus aucuparia

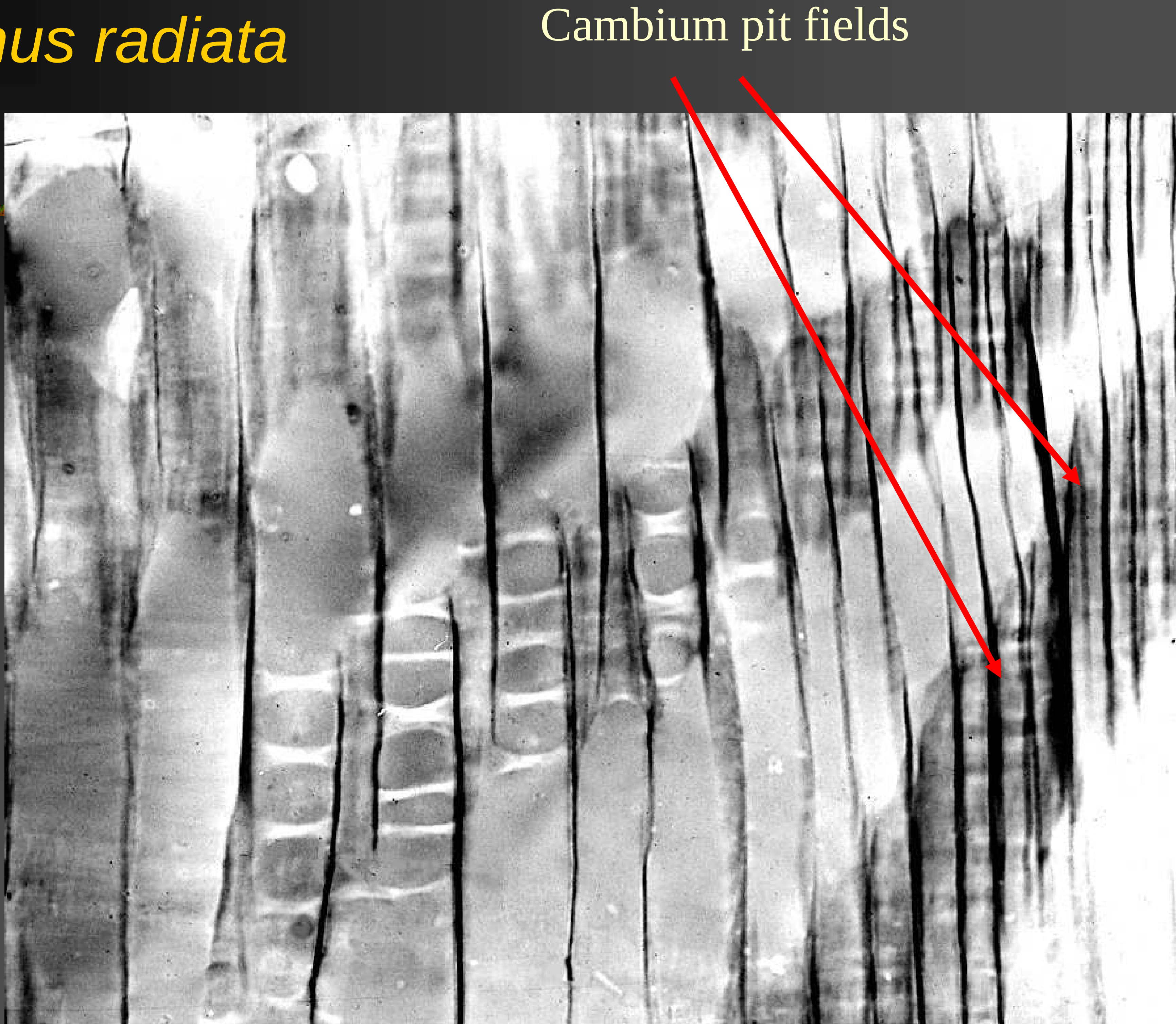
Cambium pit fields



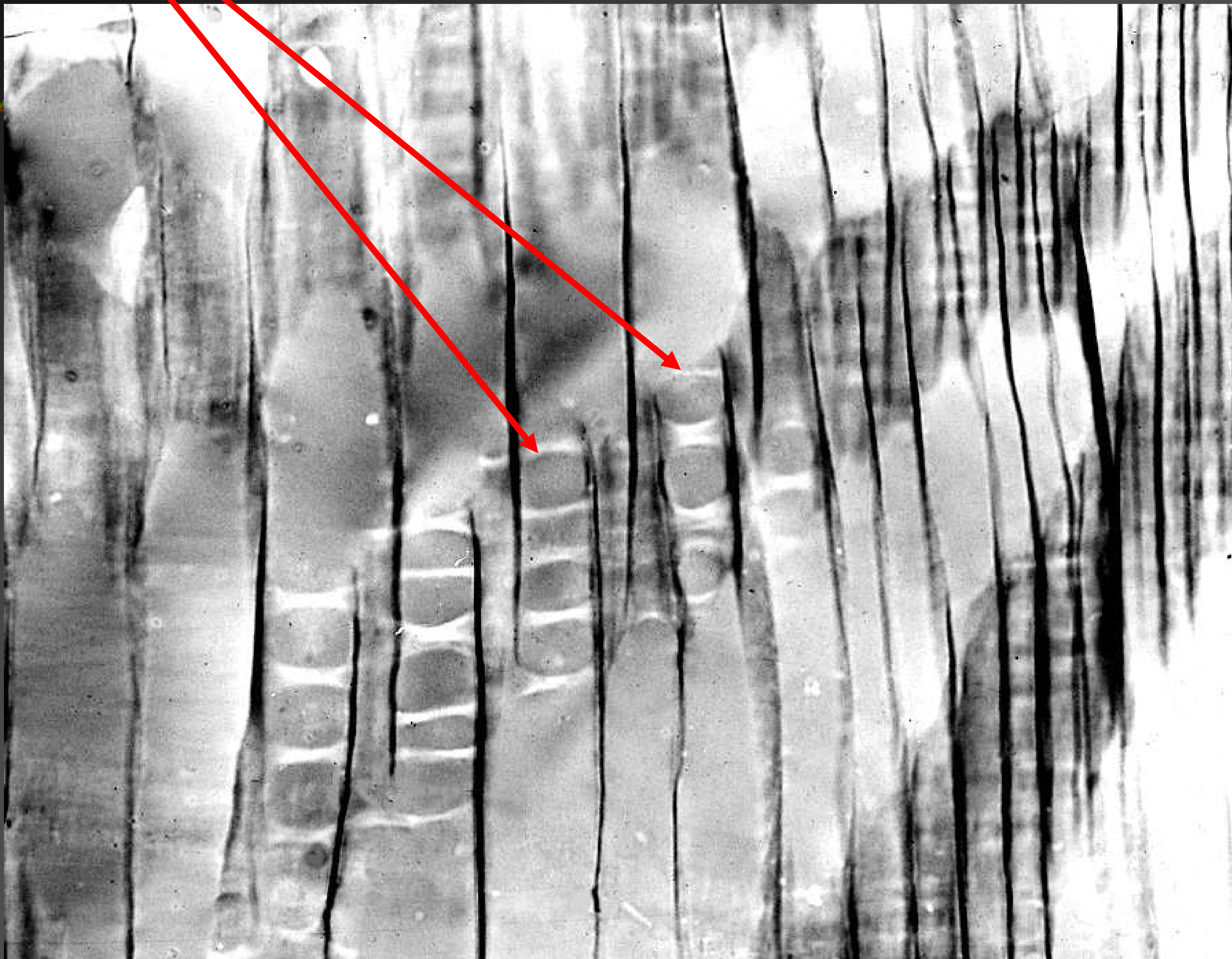
Pit fields in enlarging fibres



Pinus radiata



Pit fields in enlarging tracheids

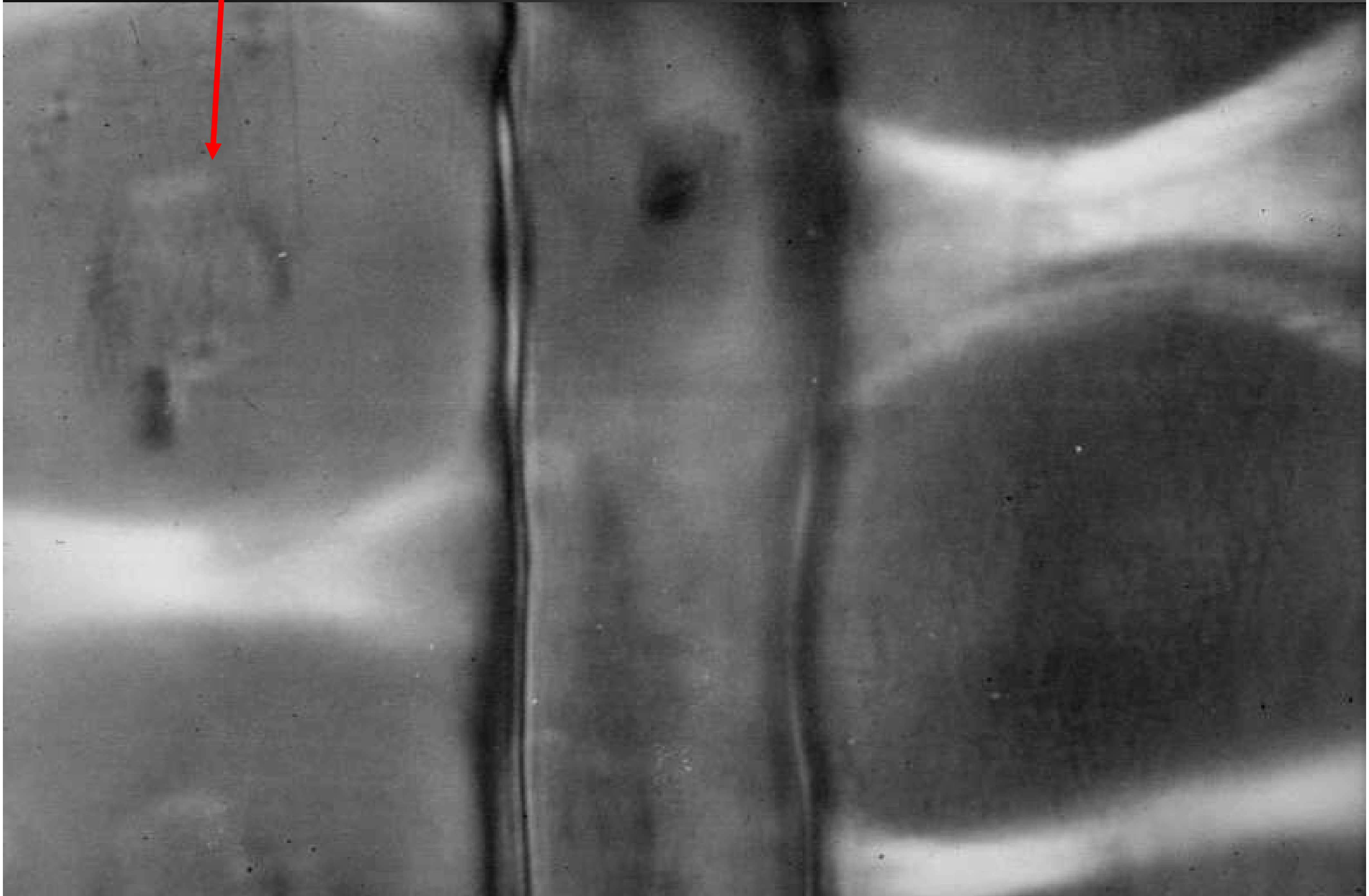


- Interference contract micrograph of a TLS through the radial wall of a tracheid of *Pinus radiata*

Pinus radiata

- Pit fields in radial walls of enlarging tracheids

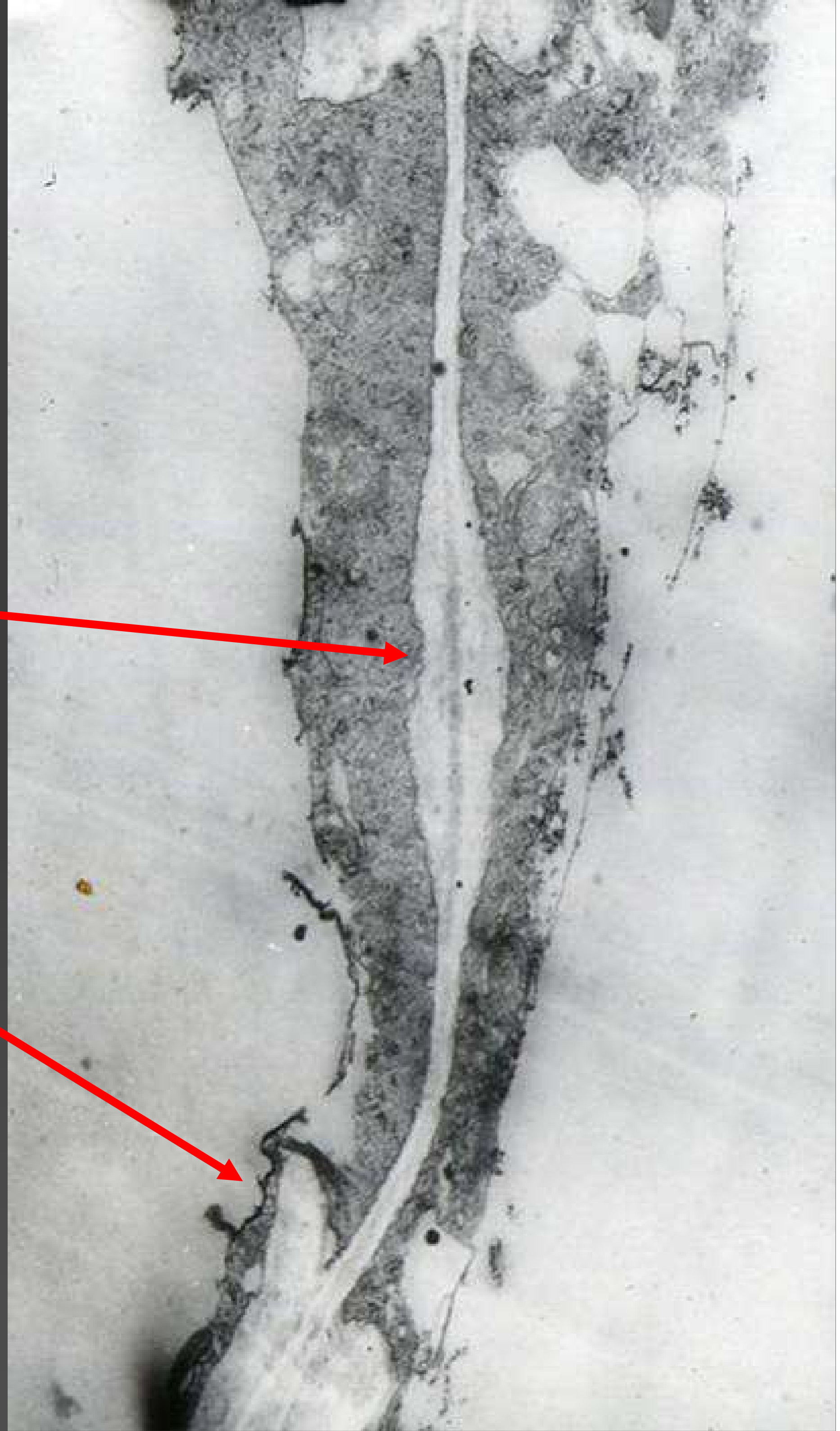
Developing torus



Pinus radiata

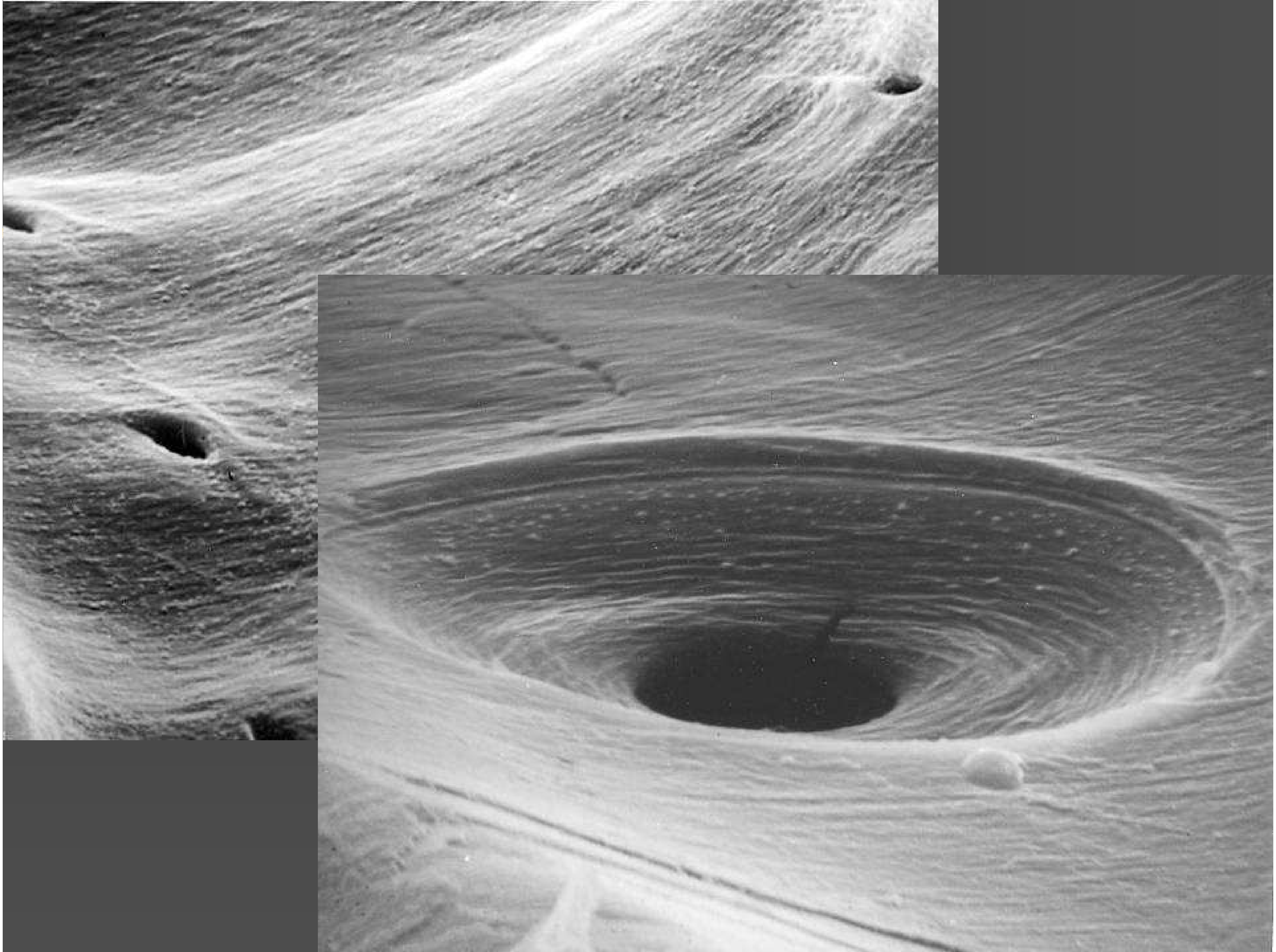
- Beginning of formation of the torus

  and pit border

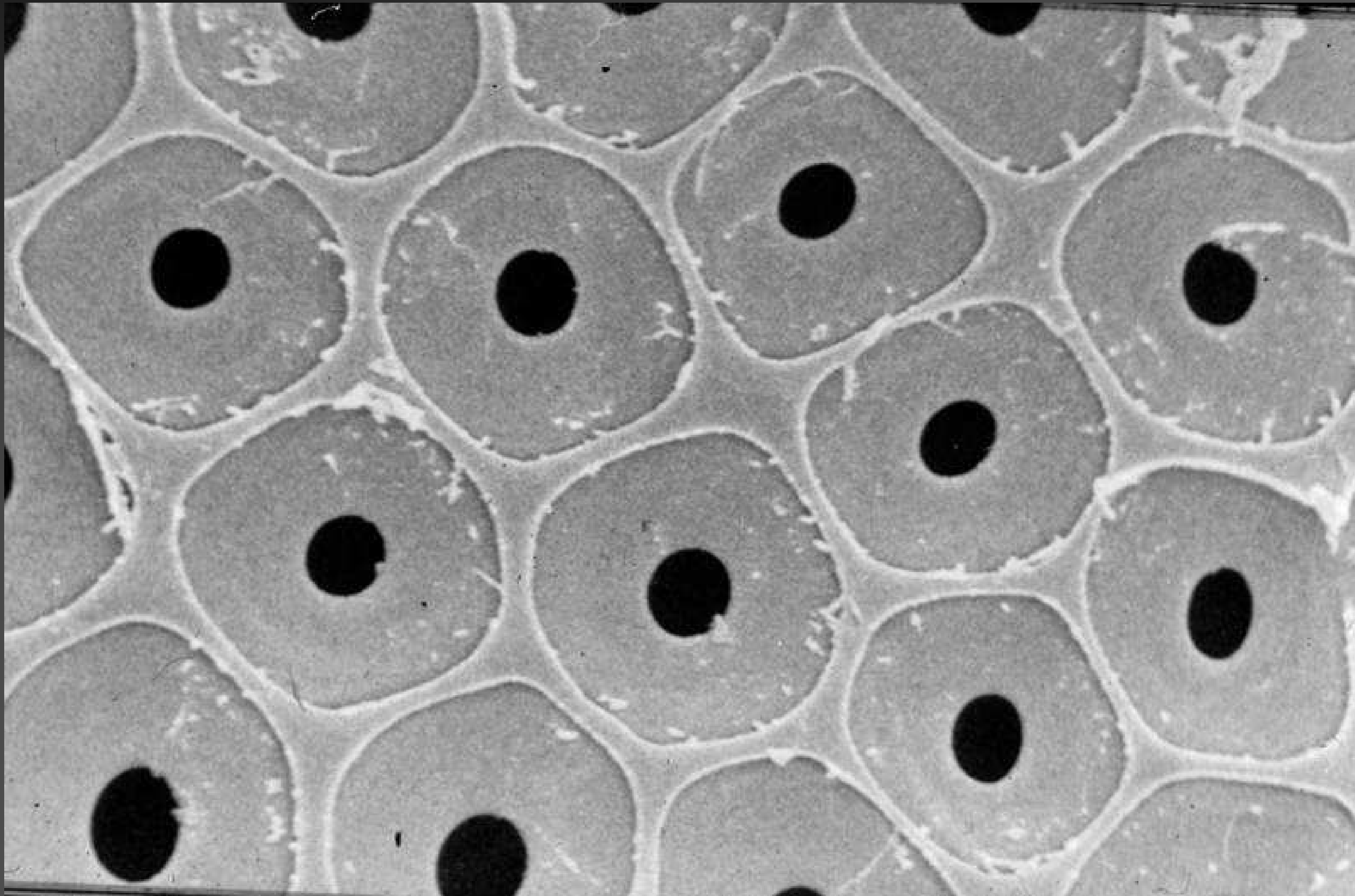


Functional and aspirated bordered pits

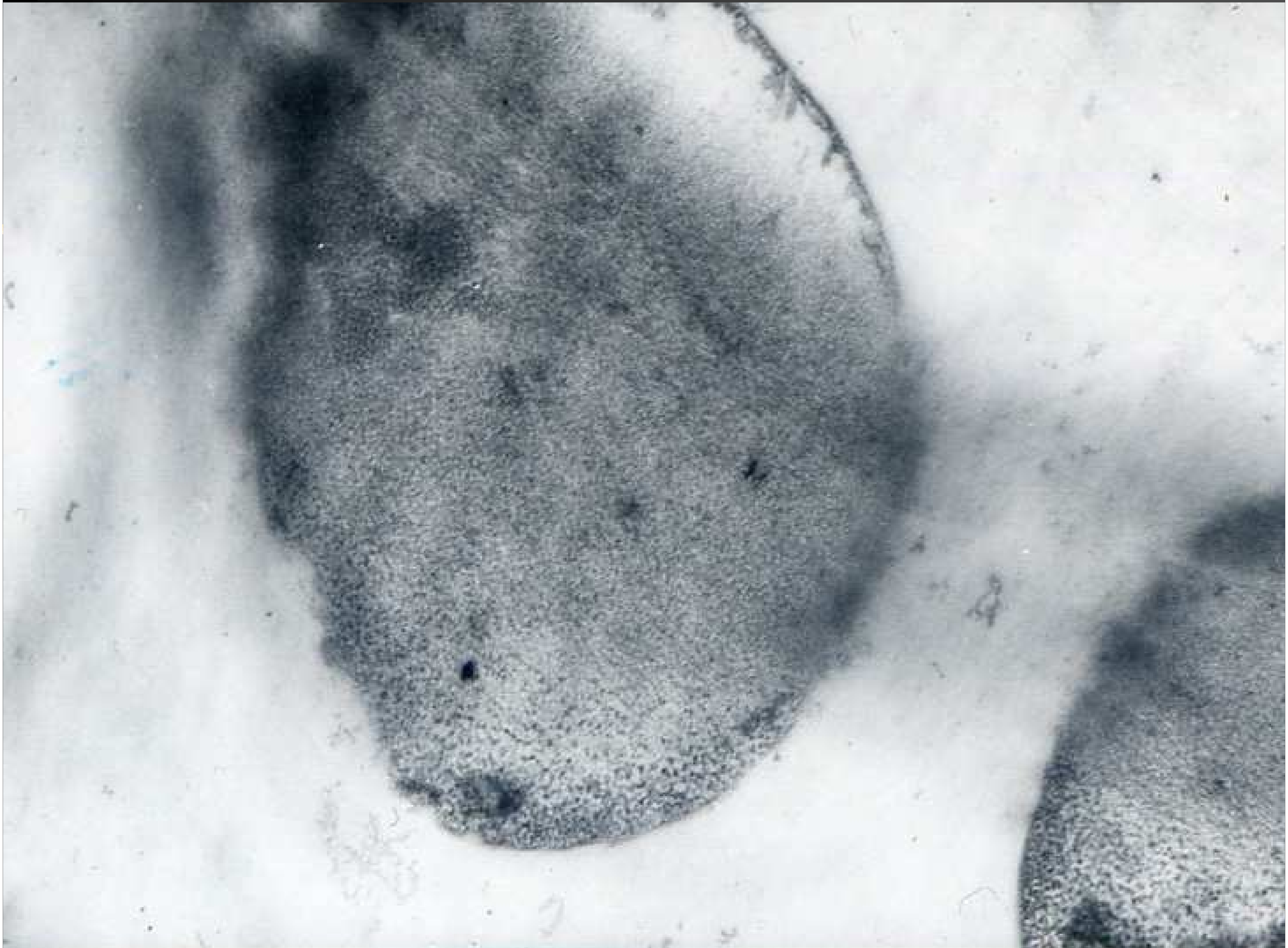
P. radiata

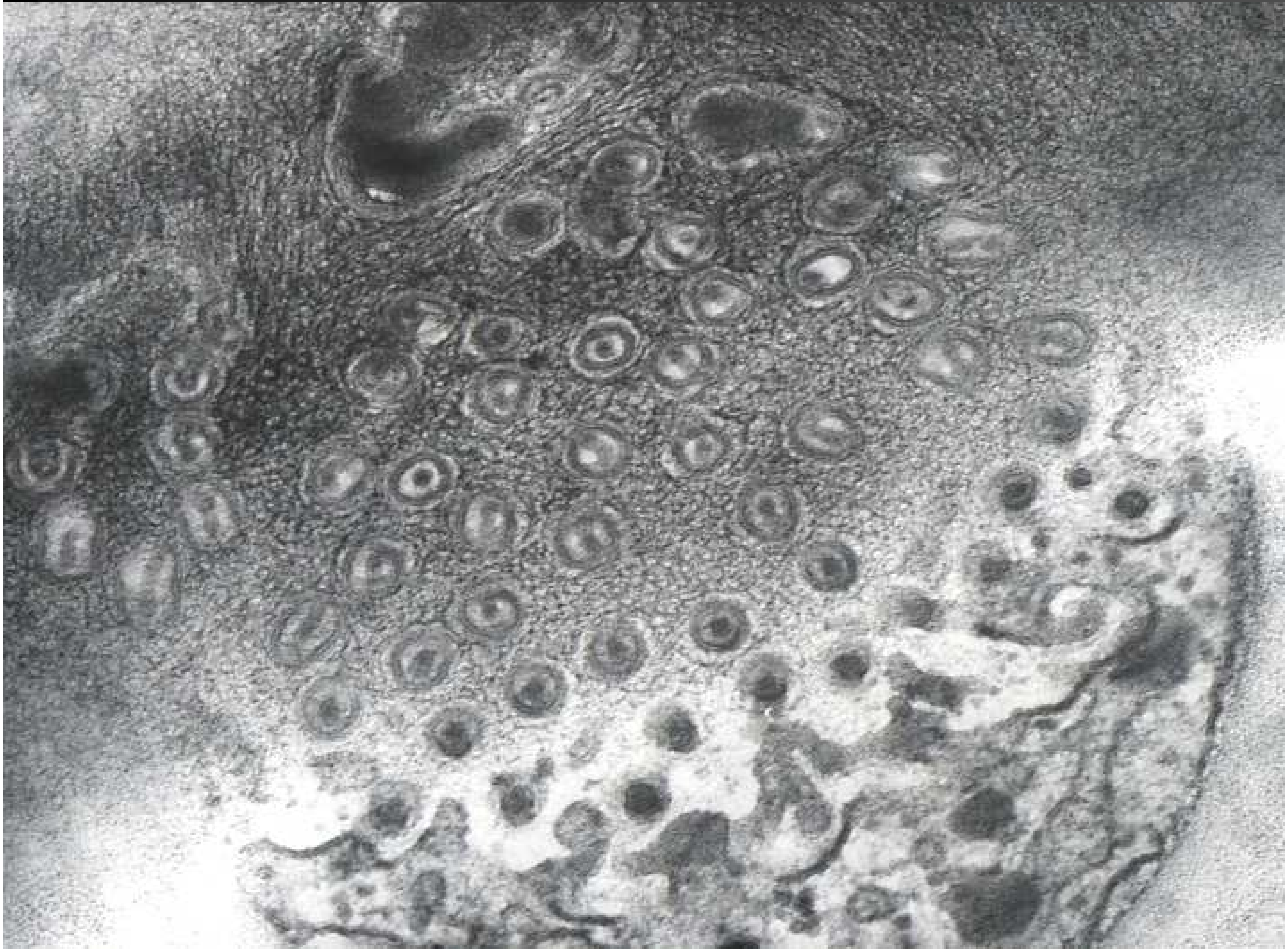


Vessel pitting seen from the middle lamella in *Aesculus*

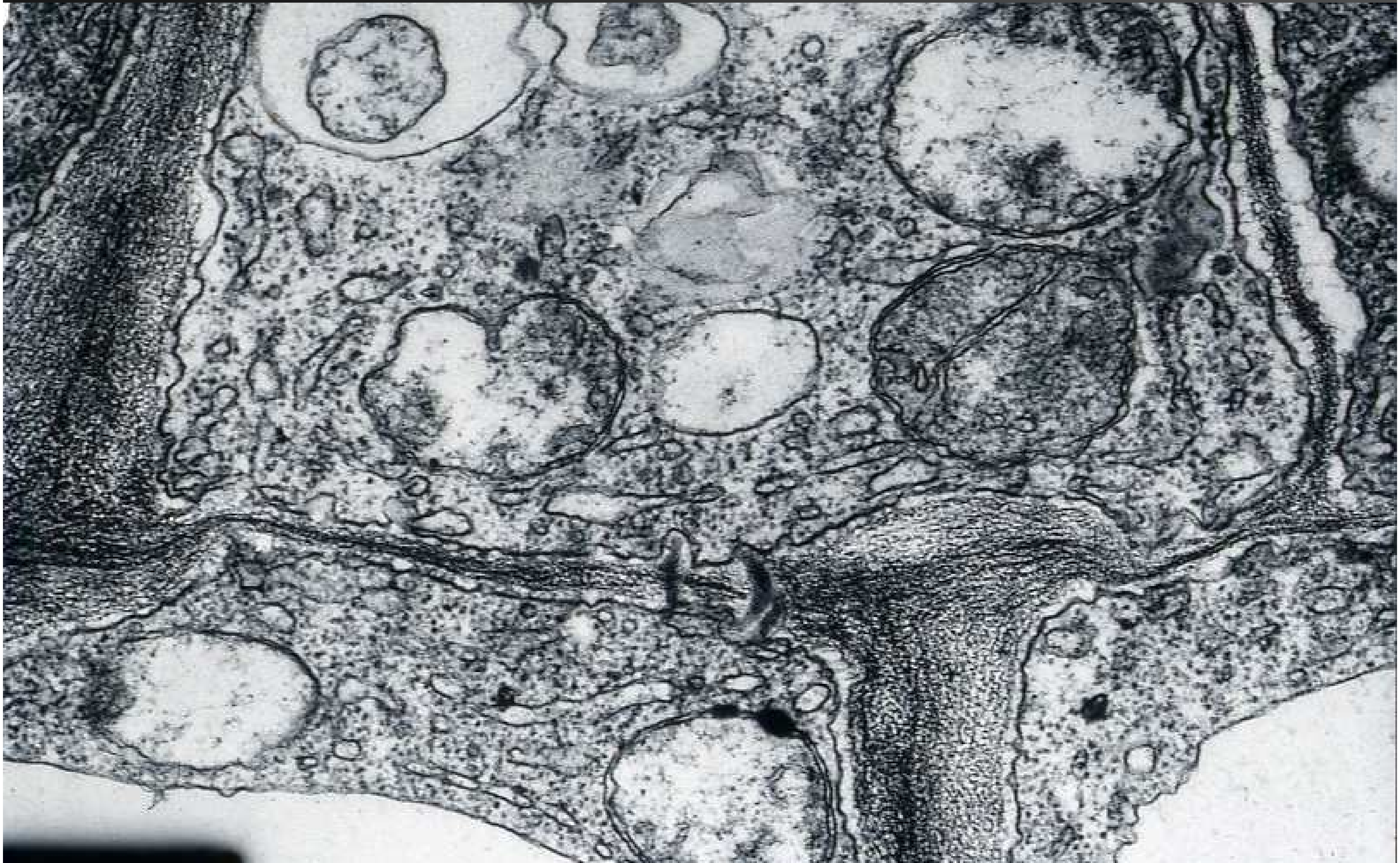


Vessel-vessel wall in *Aesculus hippocastanum*

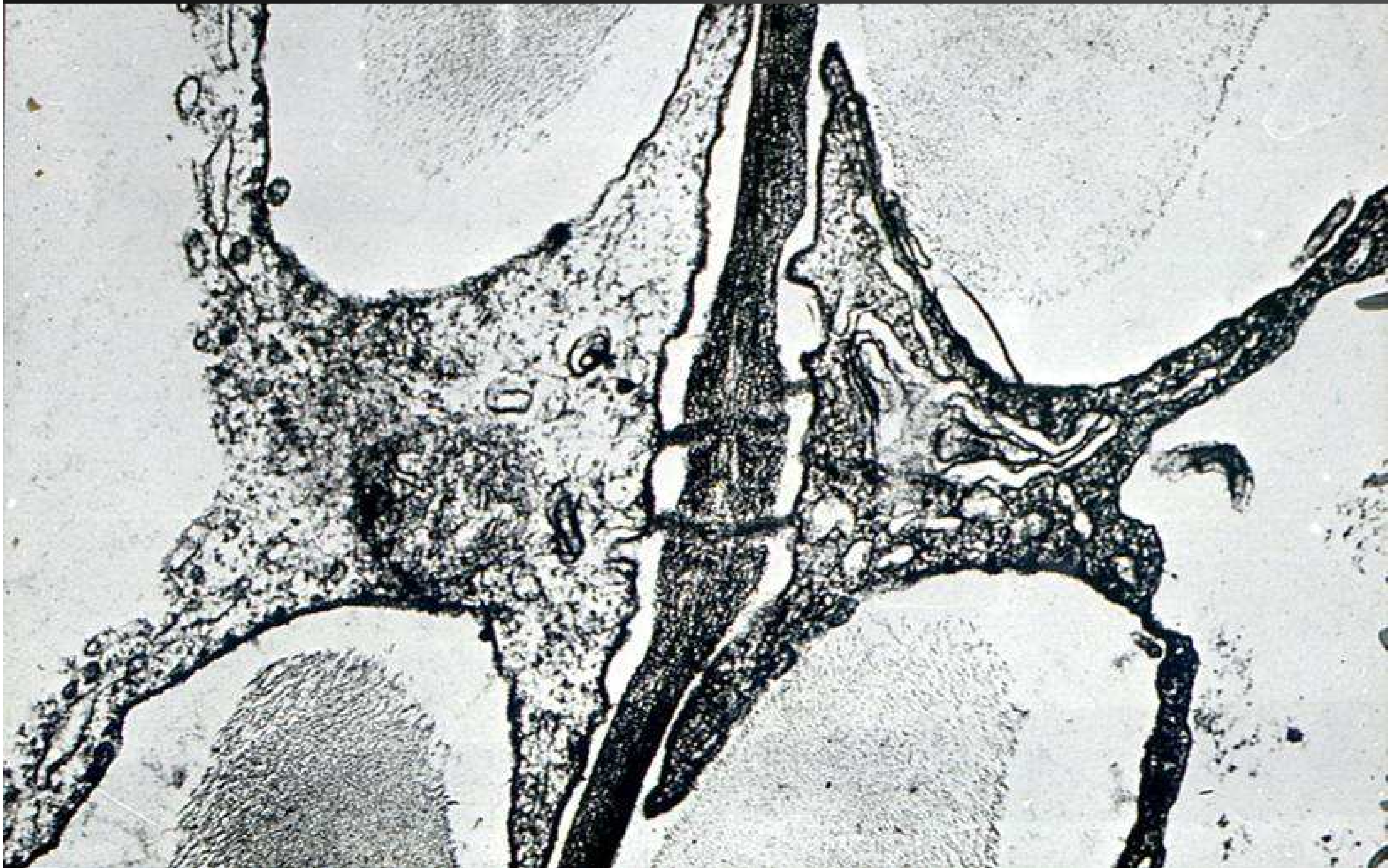




Plasmodesmata in radial wall of cambium in *Aesculus*



Fibre-fibre pit in *Aesculus*



Pits in a tangential wall between ray parenchyma

Plasmodesmata in pit fields

- Absent:

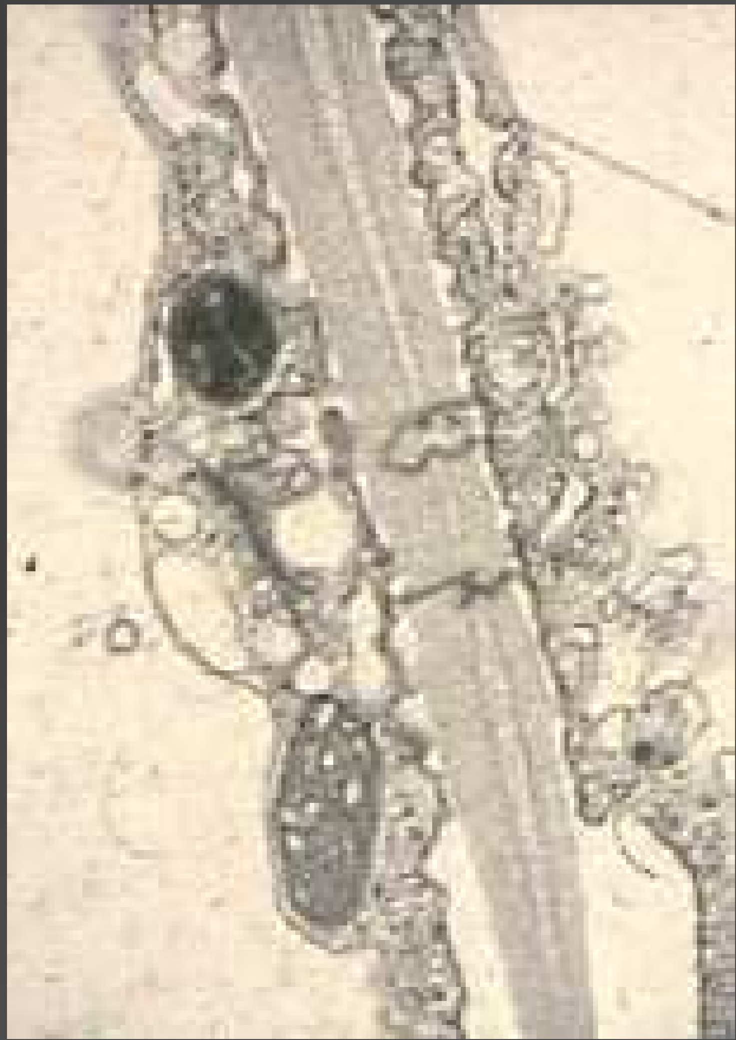
  Vessels and tracheids (conifer and angiosperm) to any other cell type

- Present:

  Fibres to fibres and parenchyma

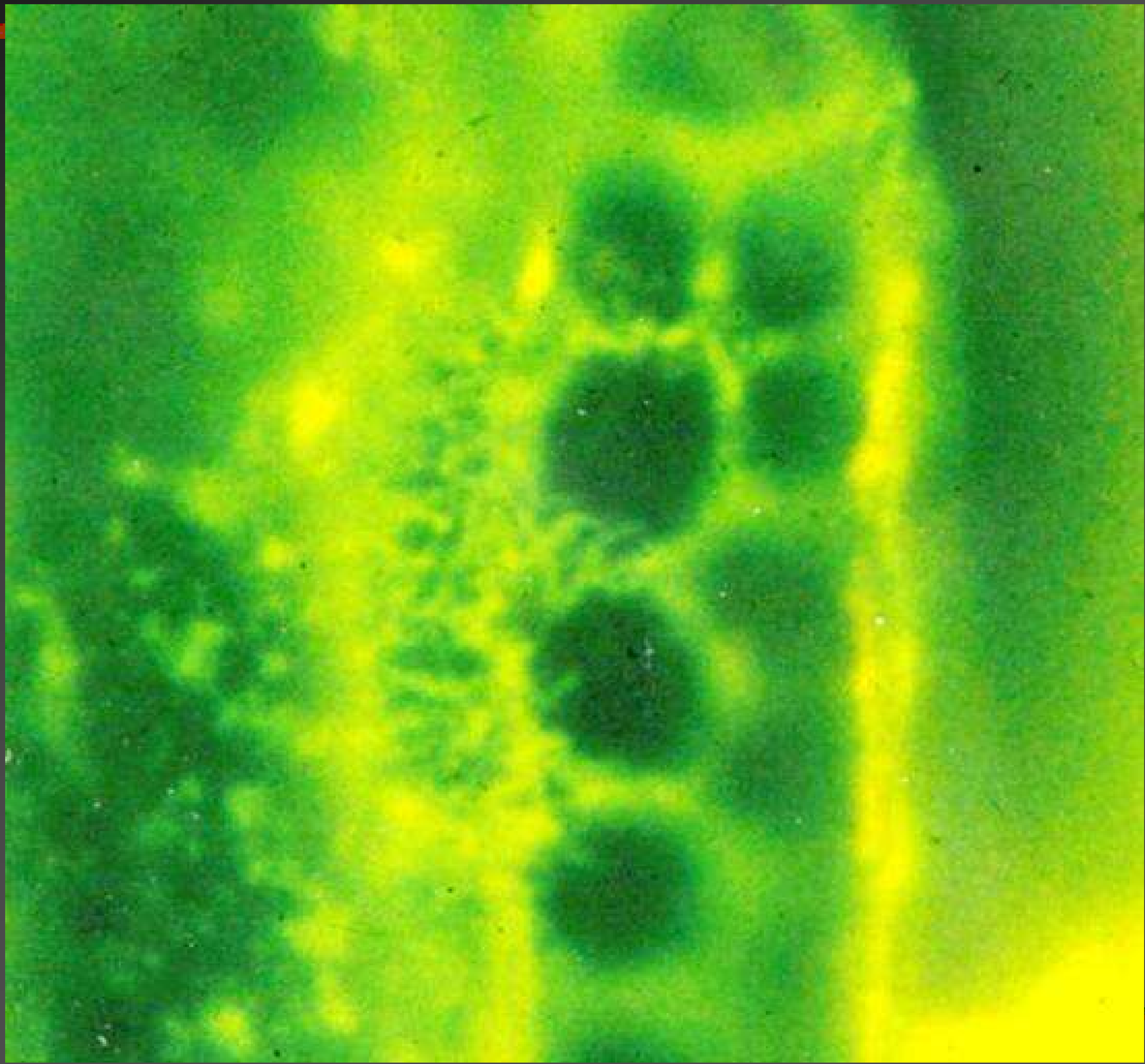
  Parenchyma to parenchyma and fibres

Plasmodesmata in developing vessel walls of hybrid aspen

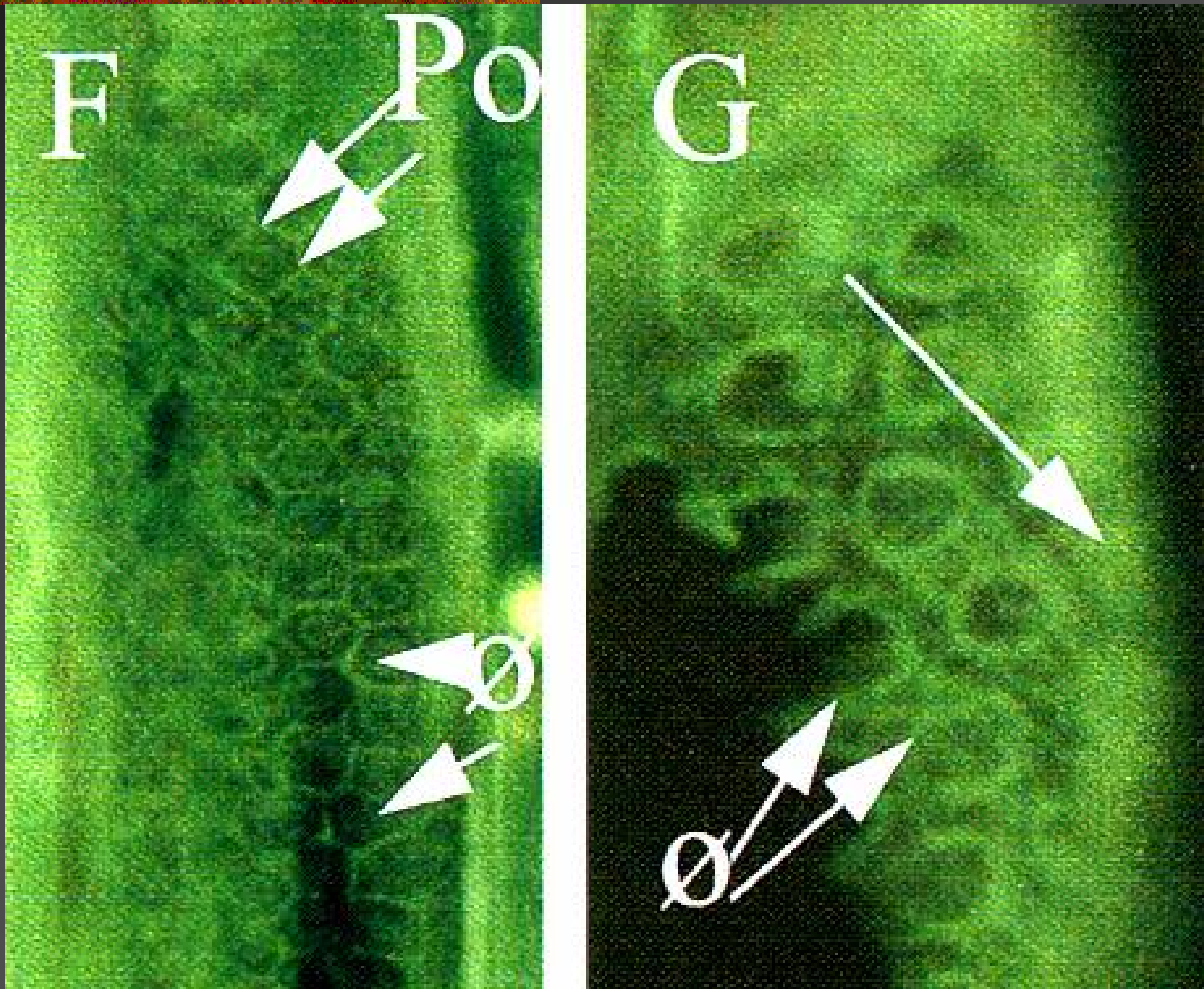


- Microtubules and pit formation

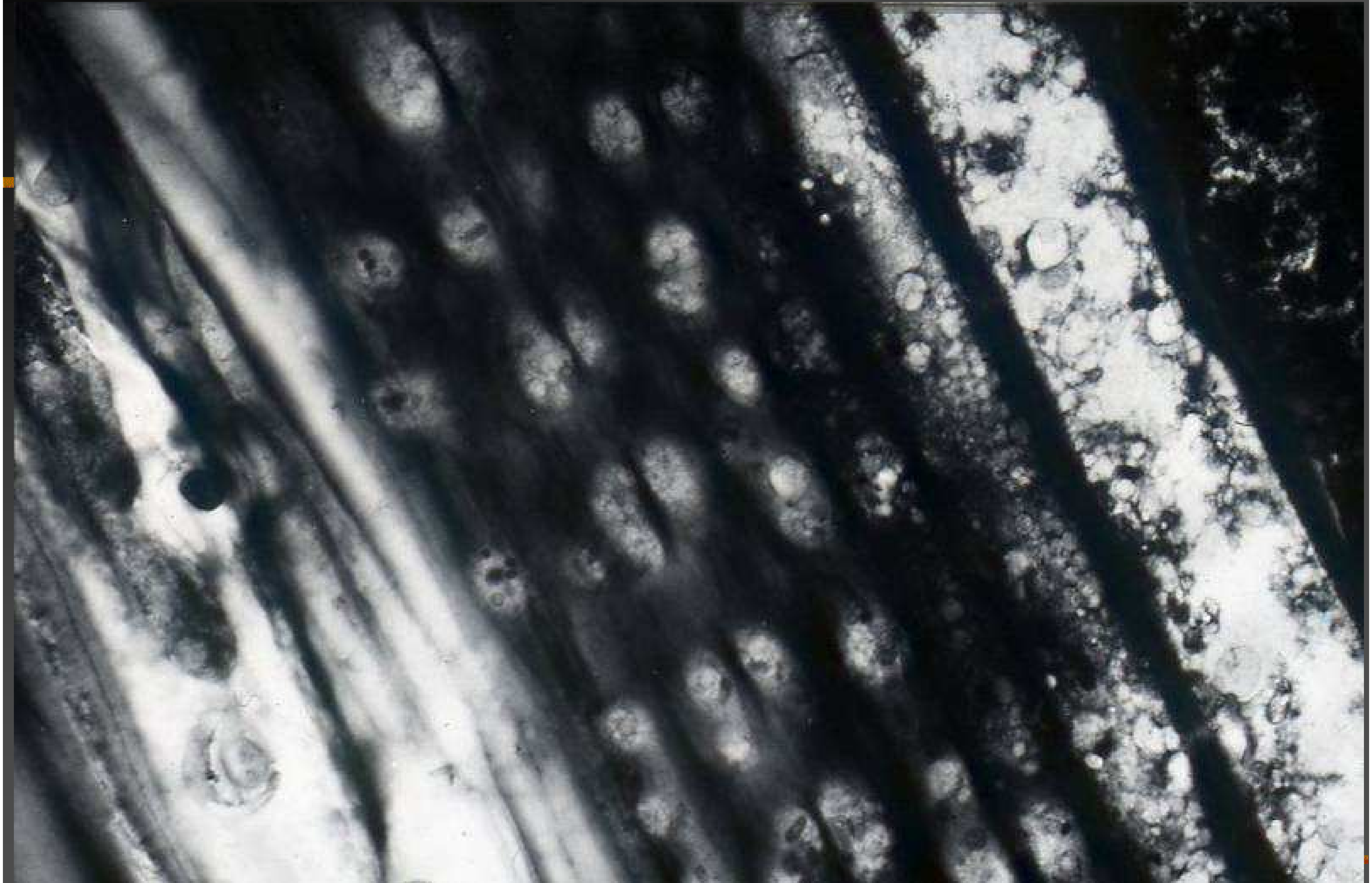
Tubulin in a developing *Aesculus* vessel



Tubulin in young vessel elements in *Aesculus*

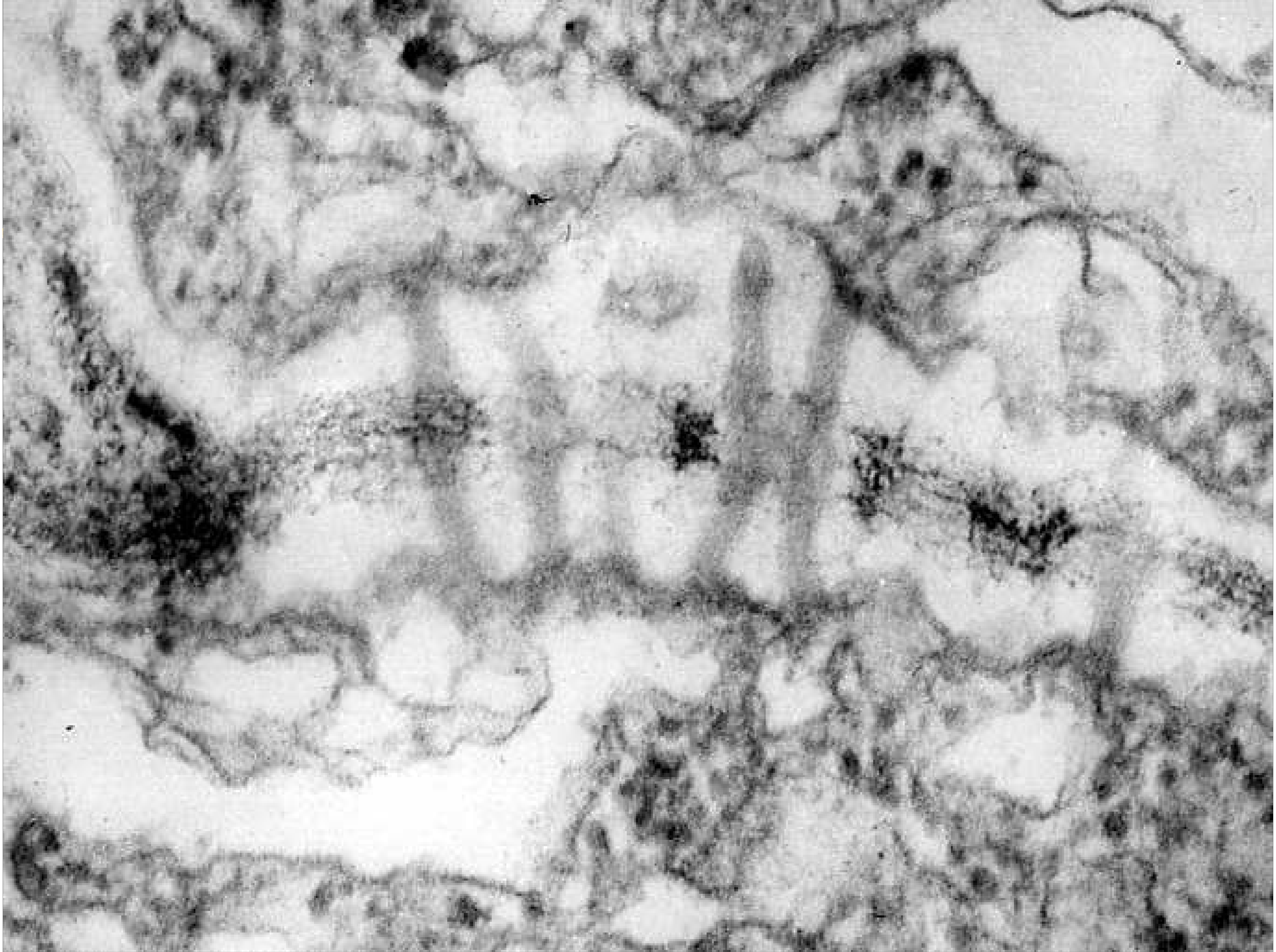


Plasmodesmata in pit membranes in some members of the Rosaceae

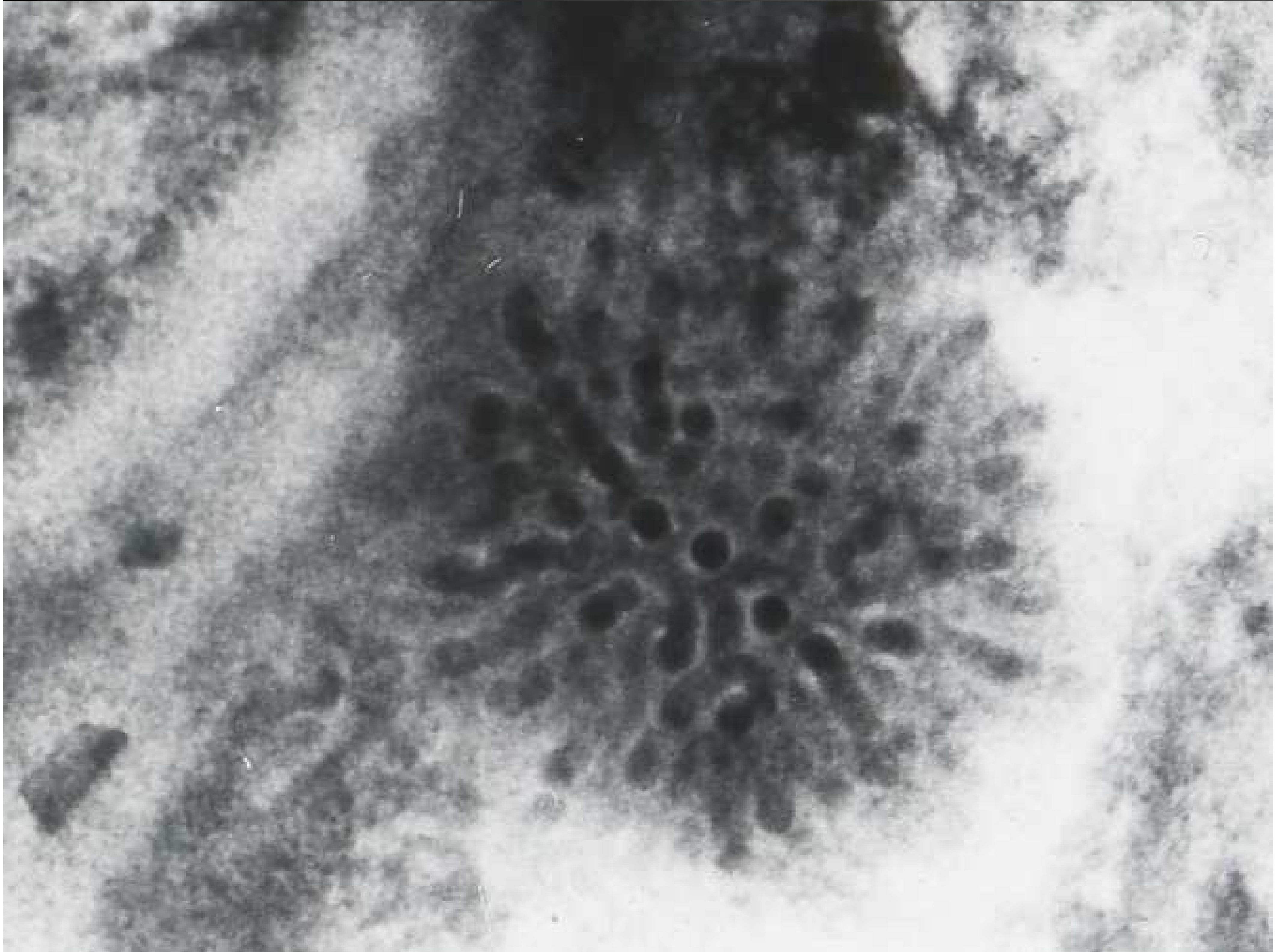


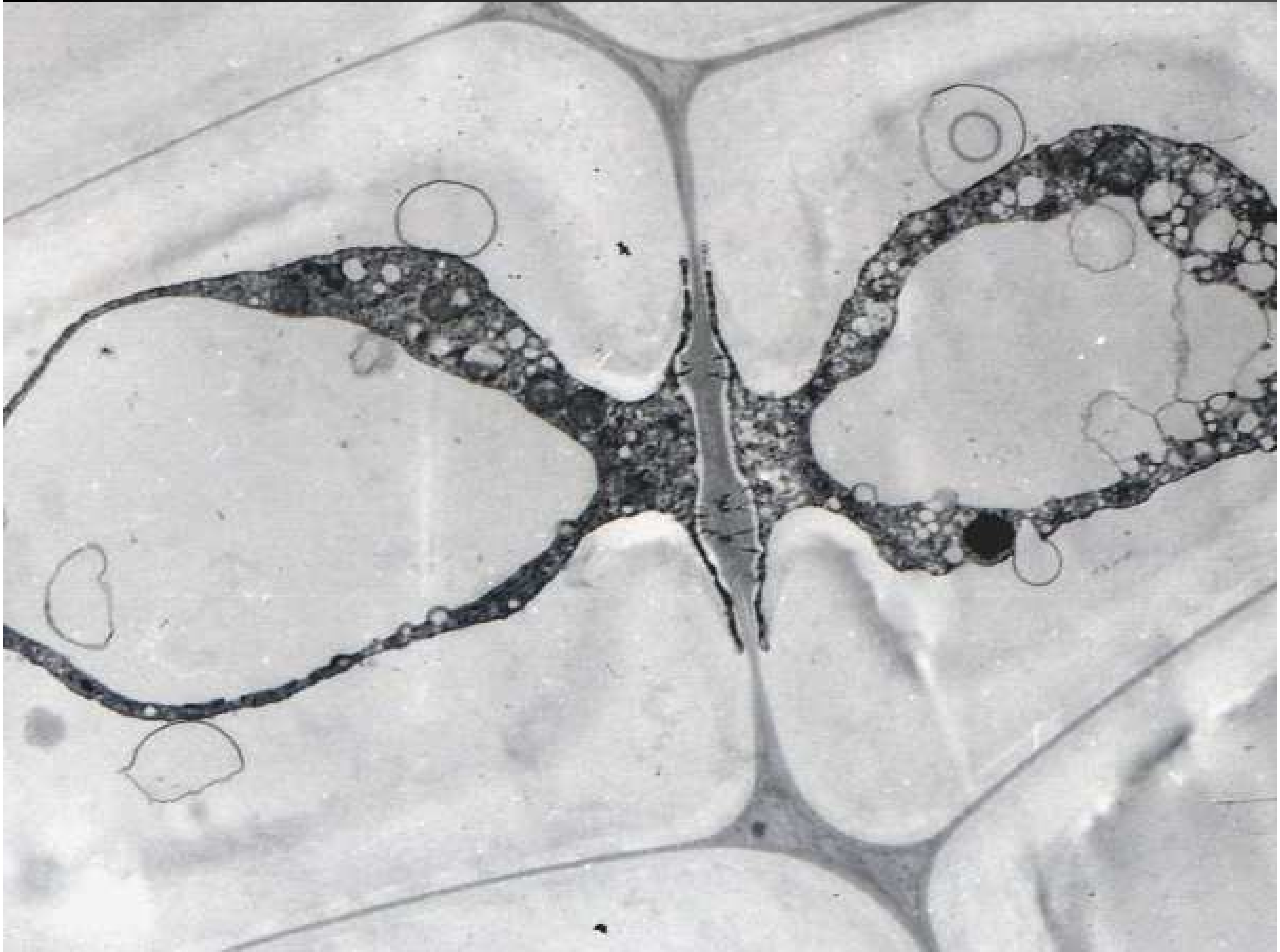
Sorbus aucuparia
RLS 2μm thick

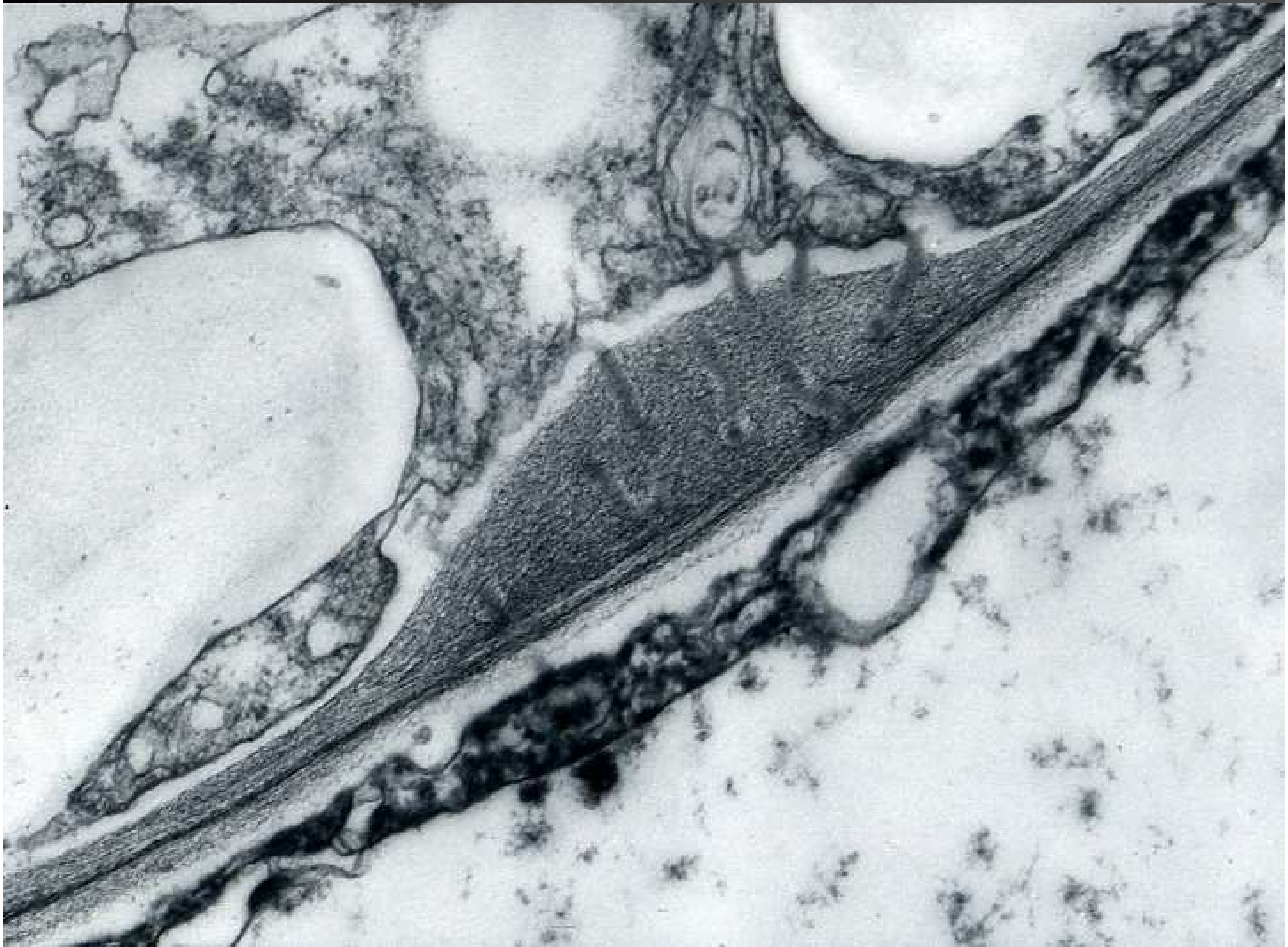
Plasmodesmata appear in section as black spots

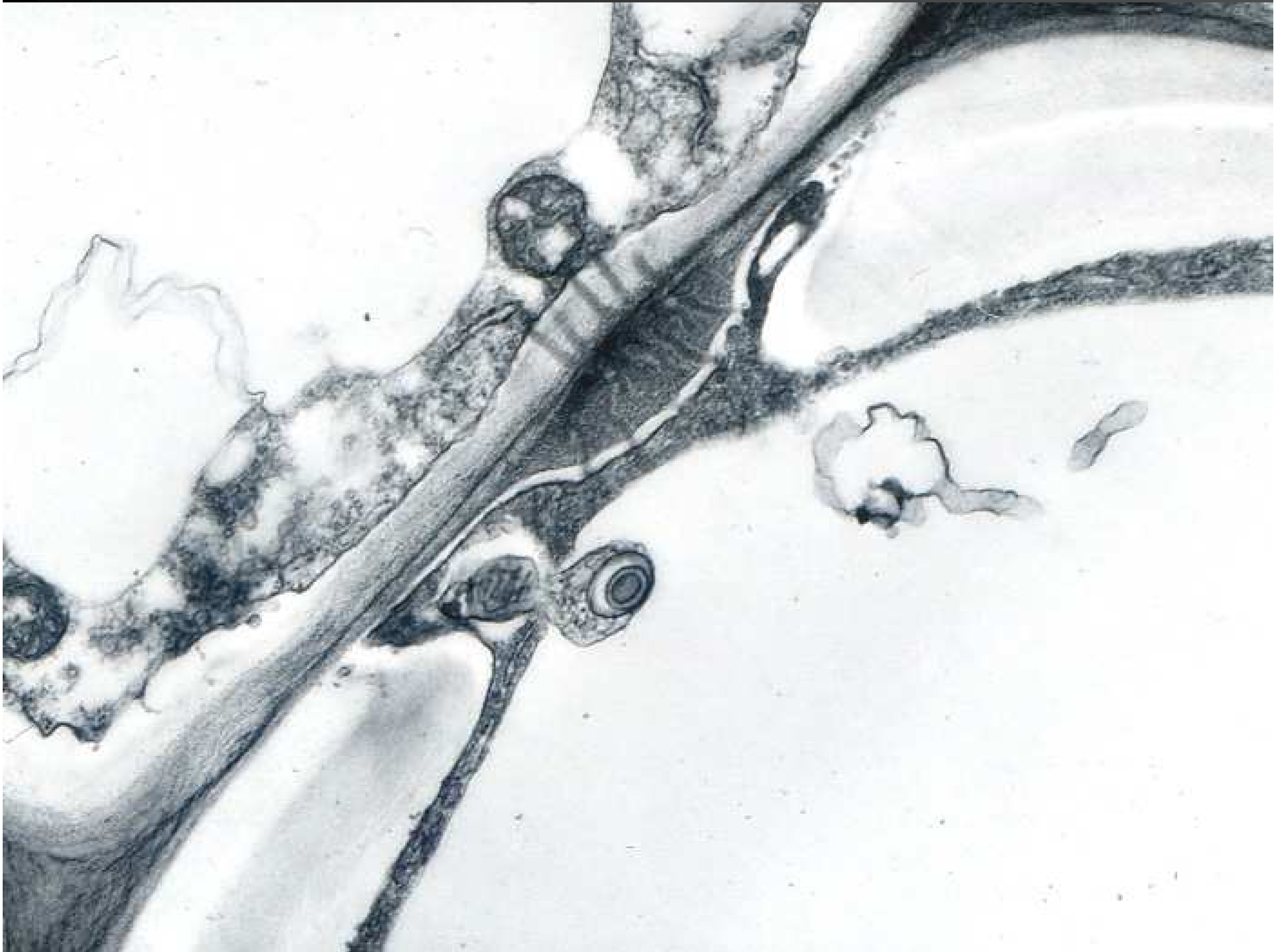


Pit fields in developing fibres of *Sorbus*









Conclusions

- Microscopy reveals that cambial behaviour varies between species
- A knowledge of ultrastructural changes during differentiation of xylem is essential to understanding wood formation processes
- The cytoskeleton and plasmodesmata are important factors in the control of xylem differentiation
- Cambial behaviour ultimately governs wood structure and quality


The End