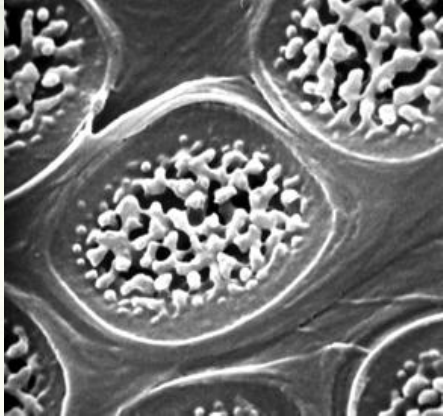
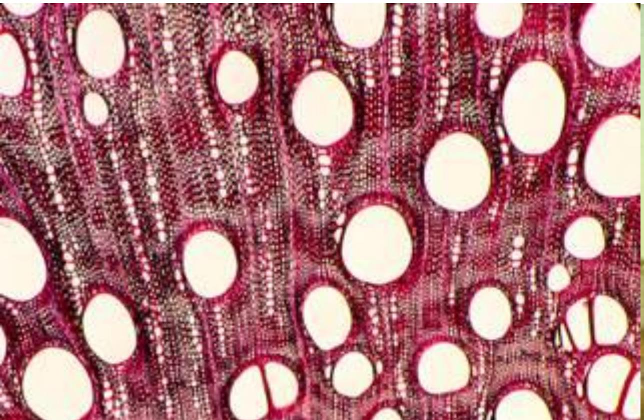


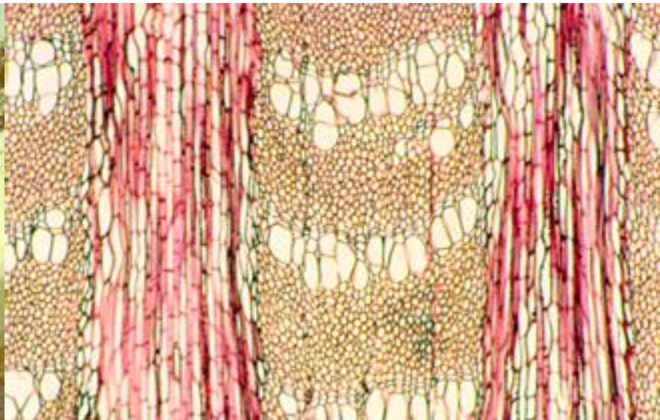




The Evolution of Wood Anatomical Diversity and its Significance

Pieter Baas

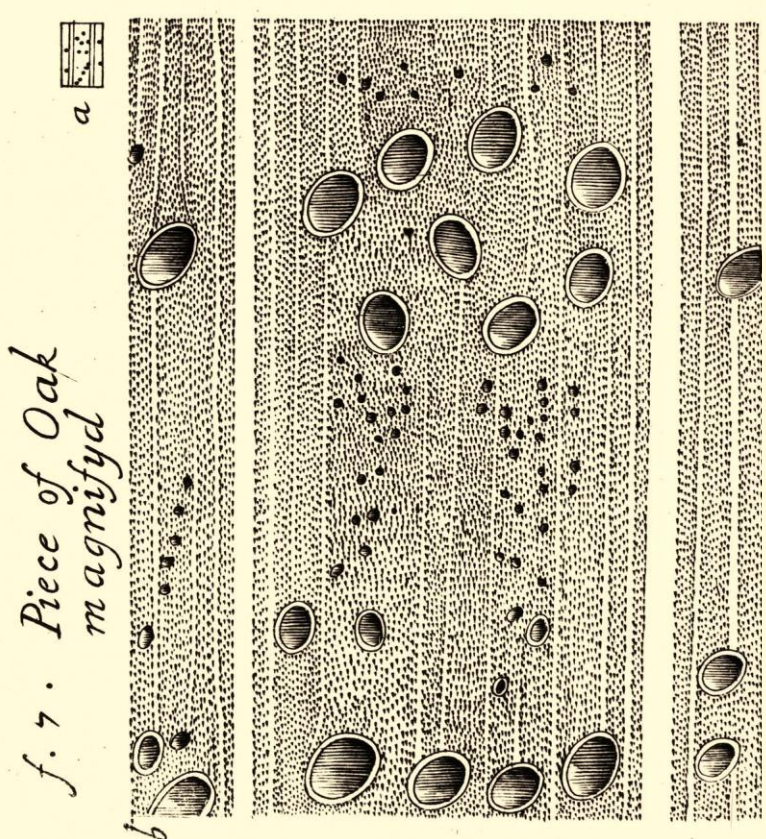


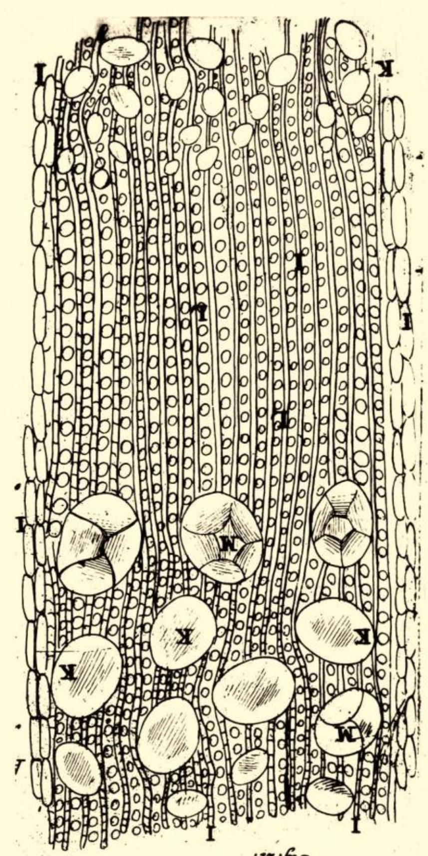


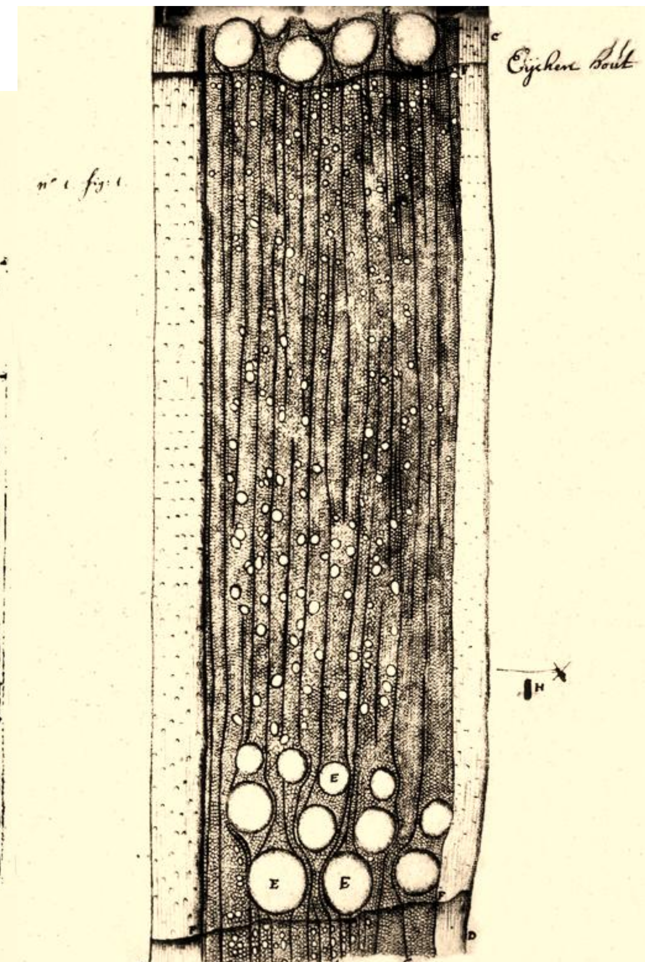
Contents

- A bit of history
- Wood in the living tree
- Wood diversity
- *Integration of phylogenetic and ecological approaches to the study of xylem evolution*
- Wood anatomy and climate change – proxies for mean annual temperature in wood structure
- Conclusions

Quercus wood as seen by Grew, Malpighi and Leeuwenhoek - three functional tree biologists!



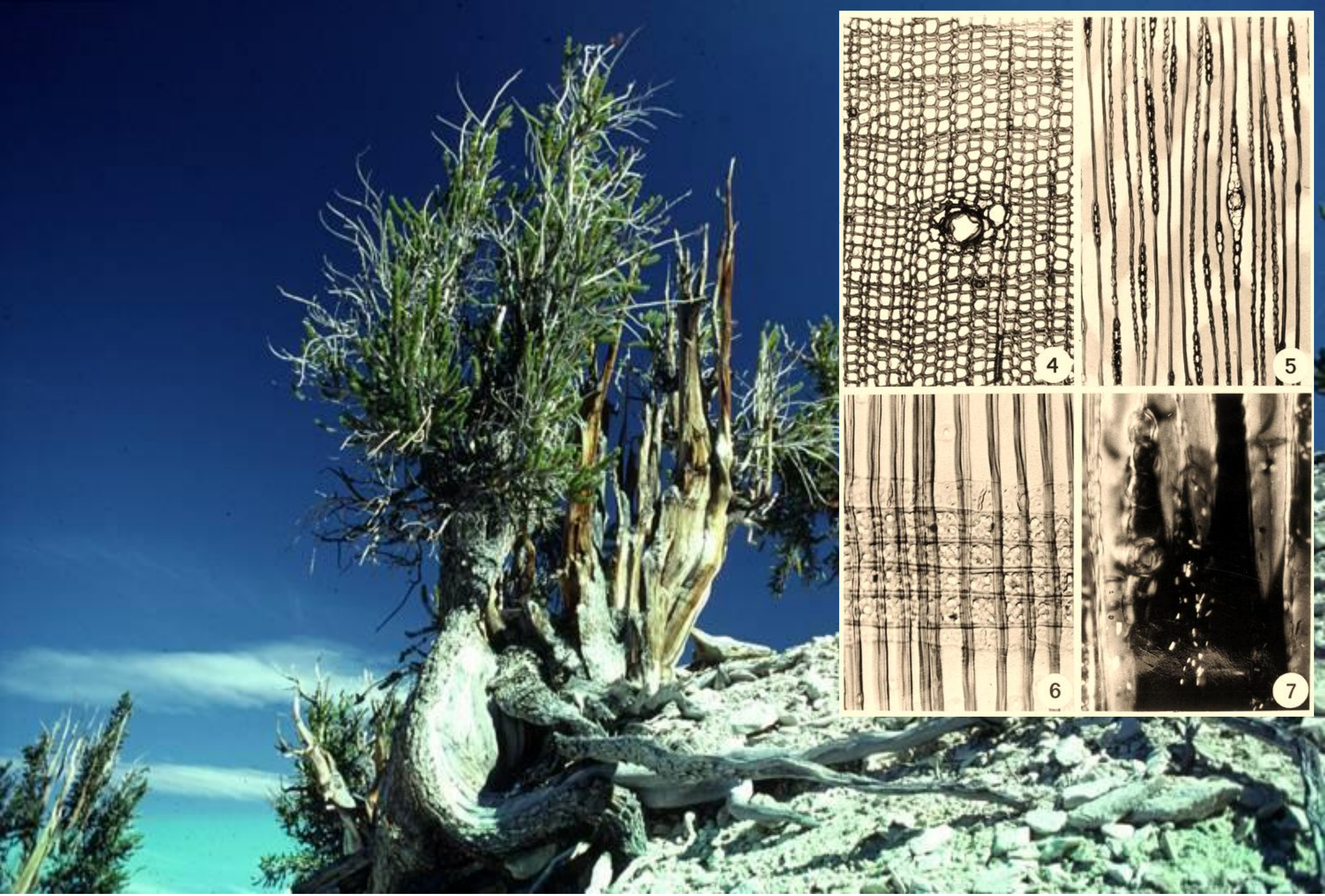




Ludwig Radlkofer (1829—1927)

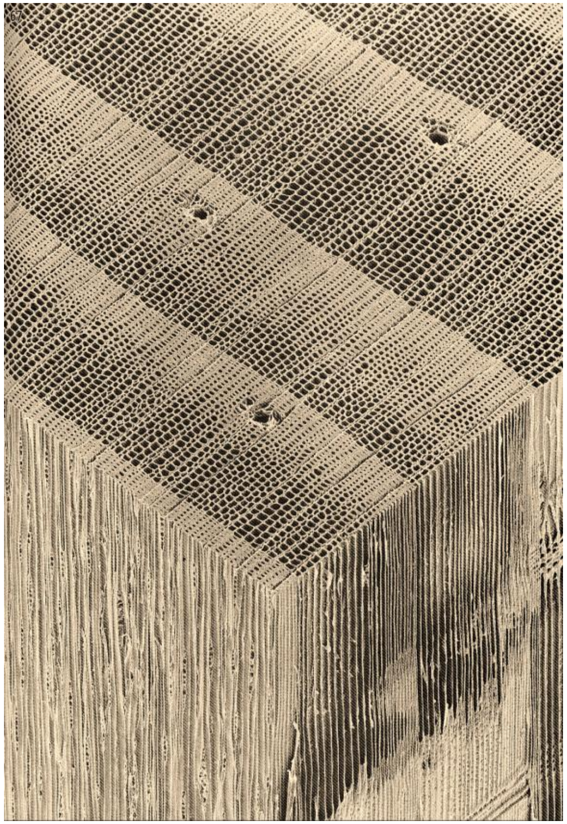
1883 in Munich: The next hundred years belong to the anatomical method

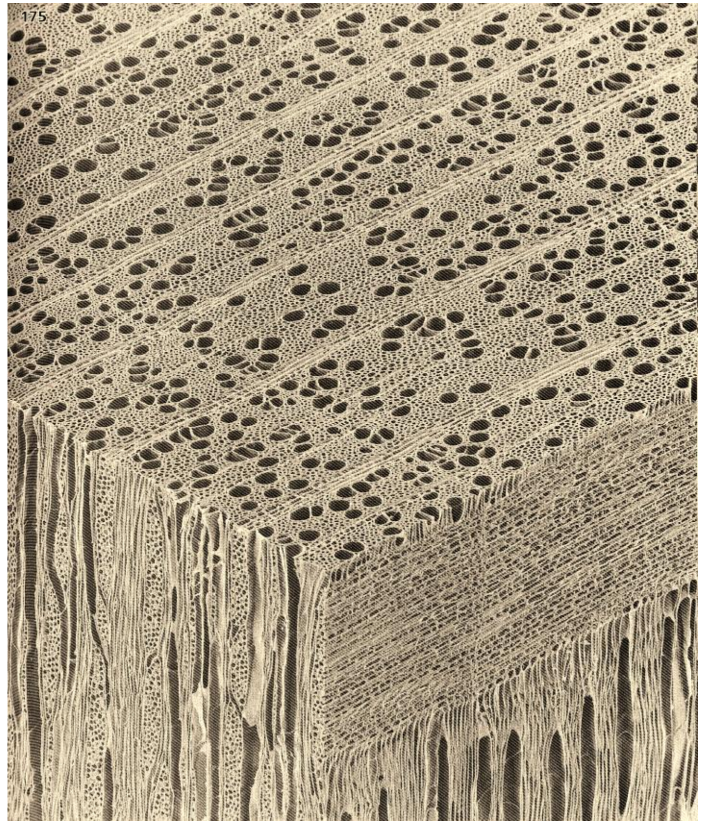
Sapindaceae taxonomy & morphology (including wood anatomy)

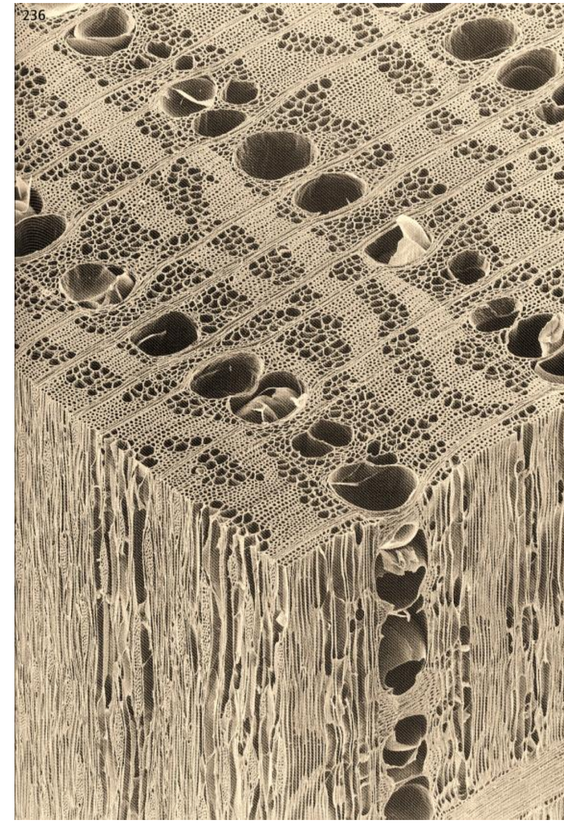


Pinus longaeva -bristlecone pine

Hydraulic architectural types





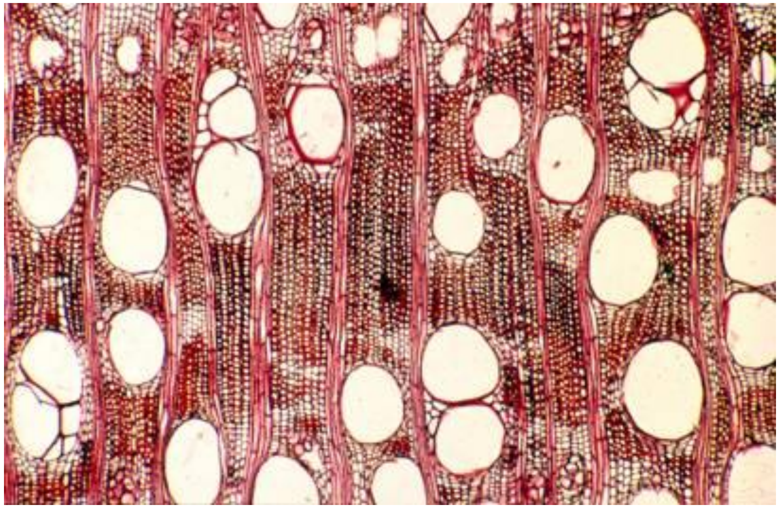


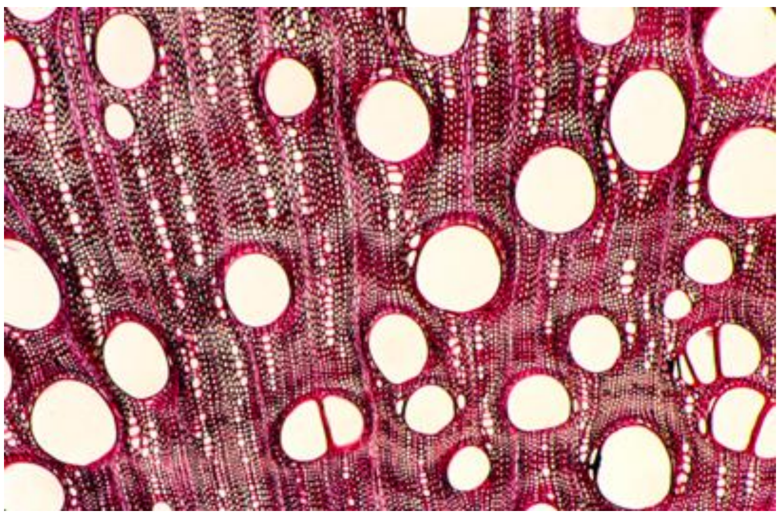
Softwood

Diffuse-porous hardwood

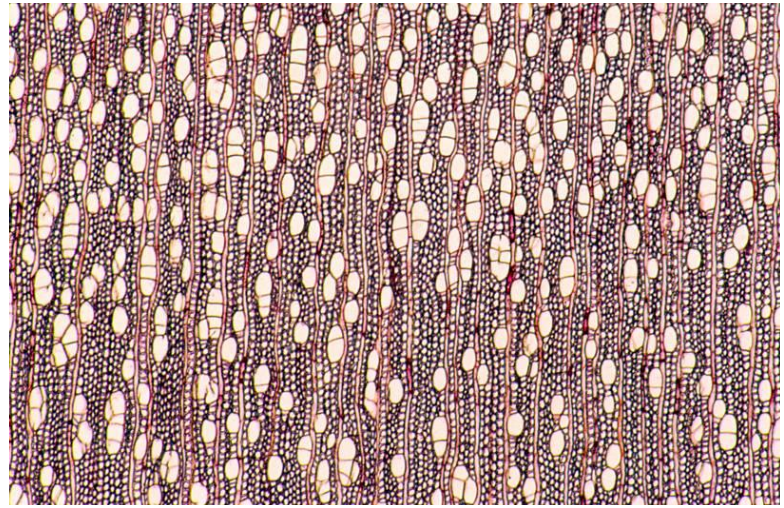
Ring-porous hardwood

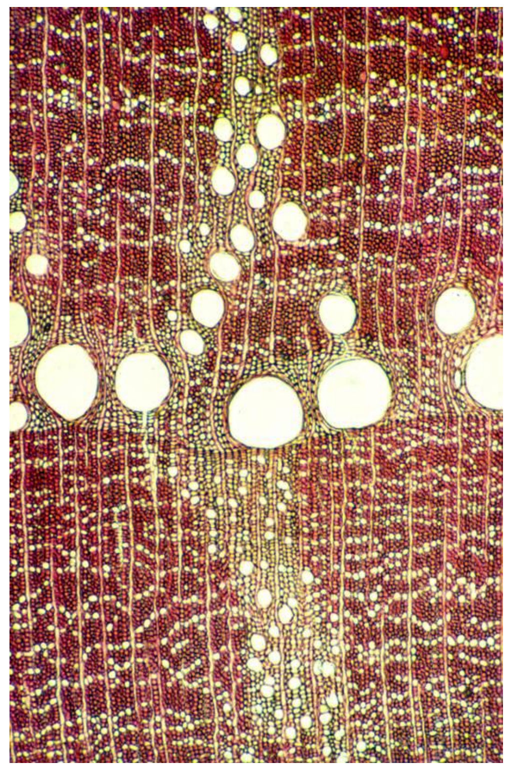
Dicot Woods





Tropical diffuse-porous tree (*Shorea*) and climber (*Serjania*)

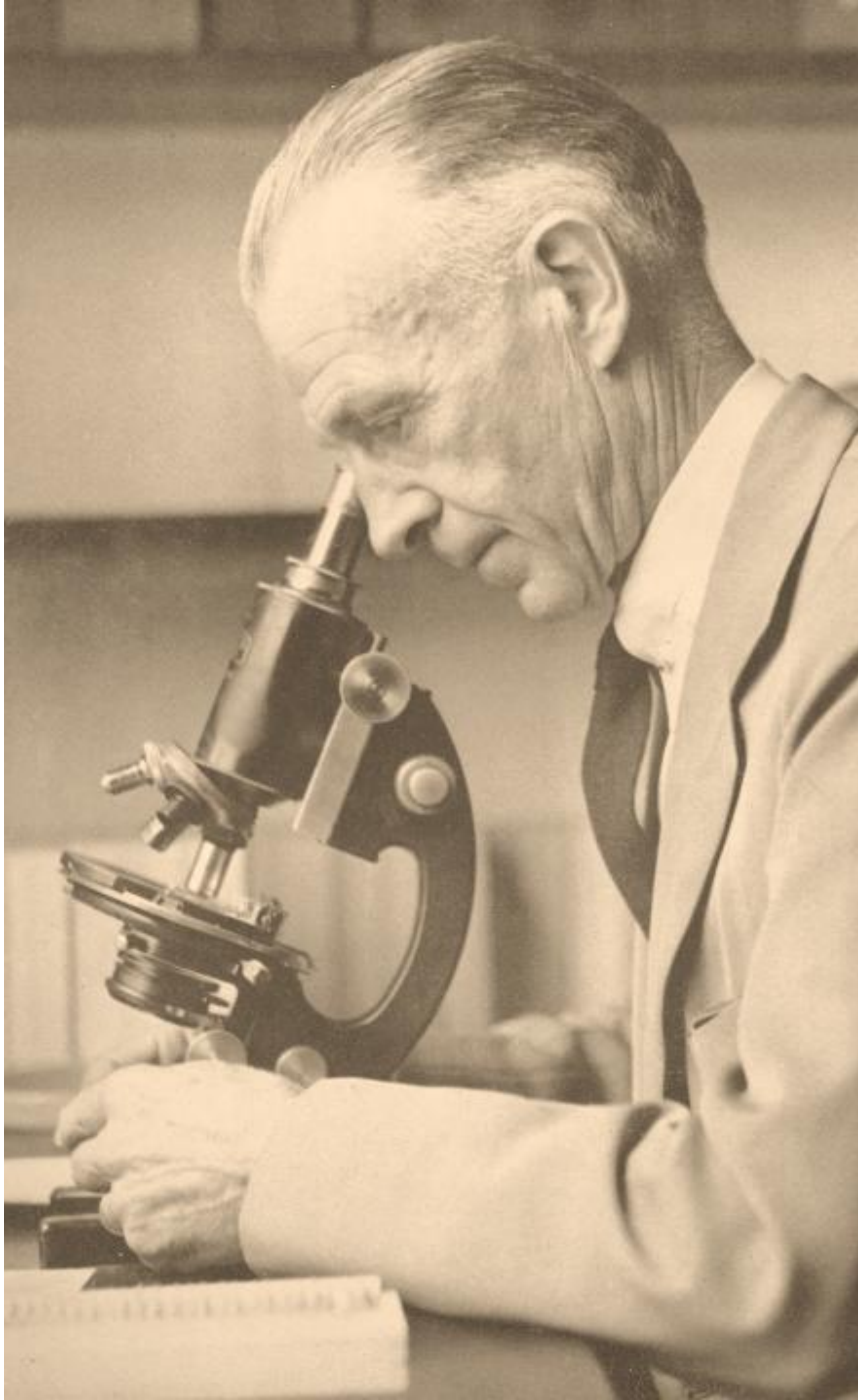




Temperate diffuse-porous (*Aesculus*) and ring-porous (*Quercus*) trees

I.W. Bailey (1884—1967)

- **Xylem evolution**
- Fossil woods
- Wood properties (preservatives)
- Tree pathology
- Wood Identification
- Cambium
- Cell wall structure
- Vestured pits



1918

Bailey & Tupper

Size variation in tracheary cells = Major trends in xylem evolution

"Inspirational"

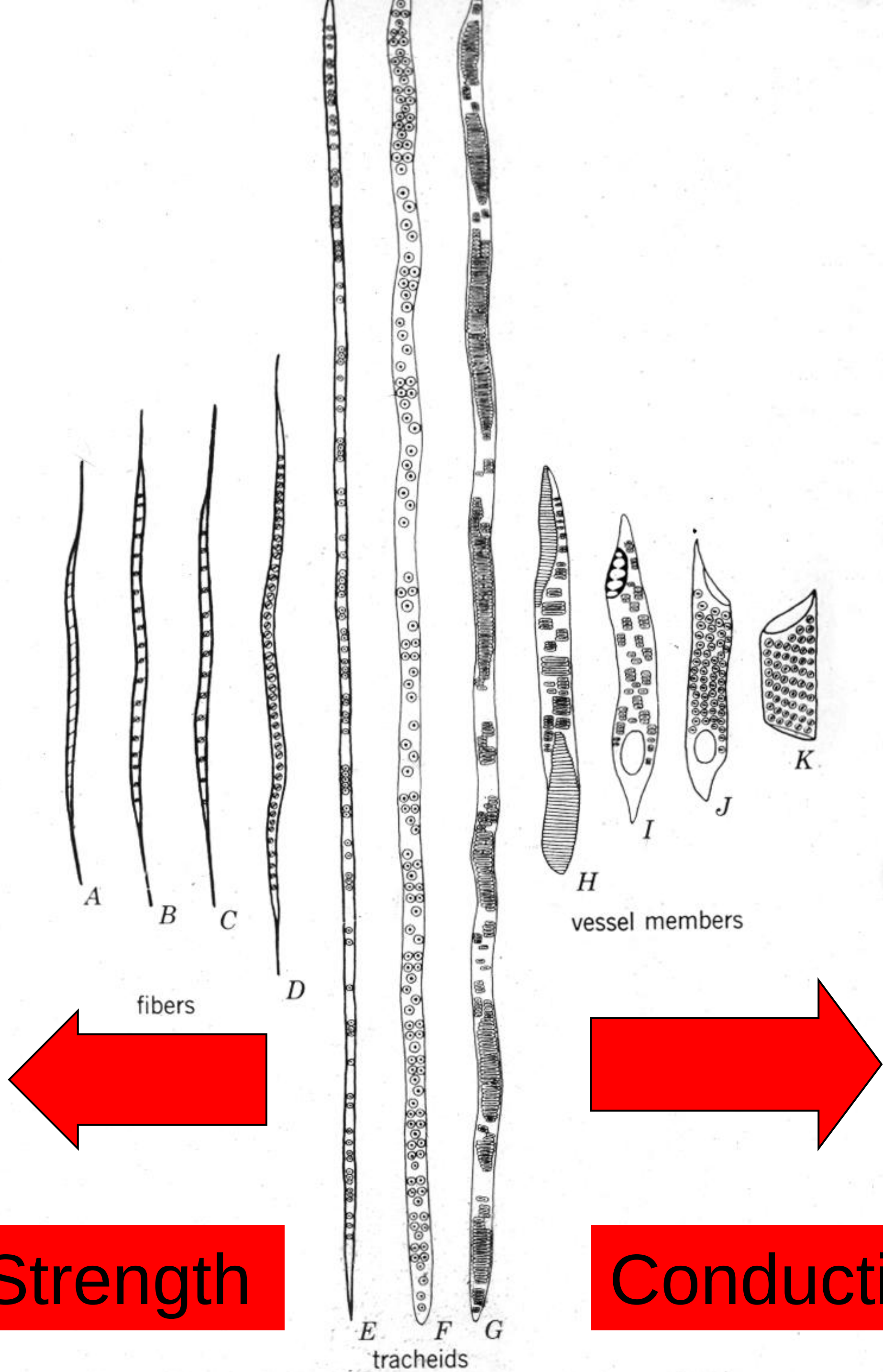
Pieter Baas and others

or:

"Outdated and unnecessary" ??

Marc Olson –Botan. Rev. 2012 (and others)

Swamy, 1954



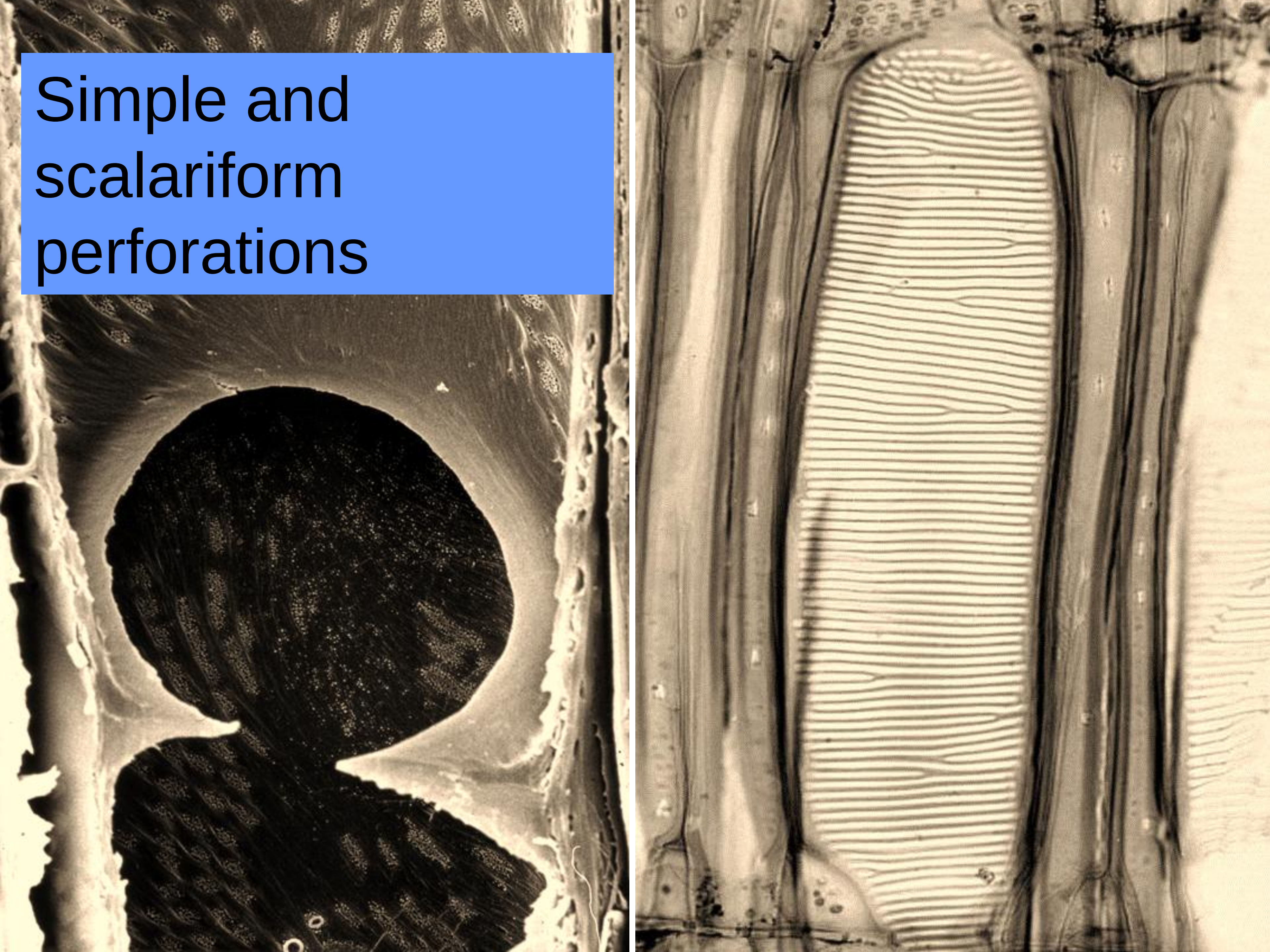
Wood evolution from vesselless gymnosperms to vessel-bearing angiosperms

Division of labour

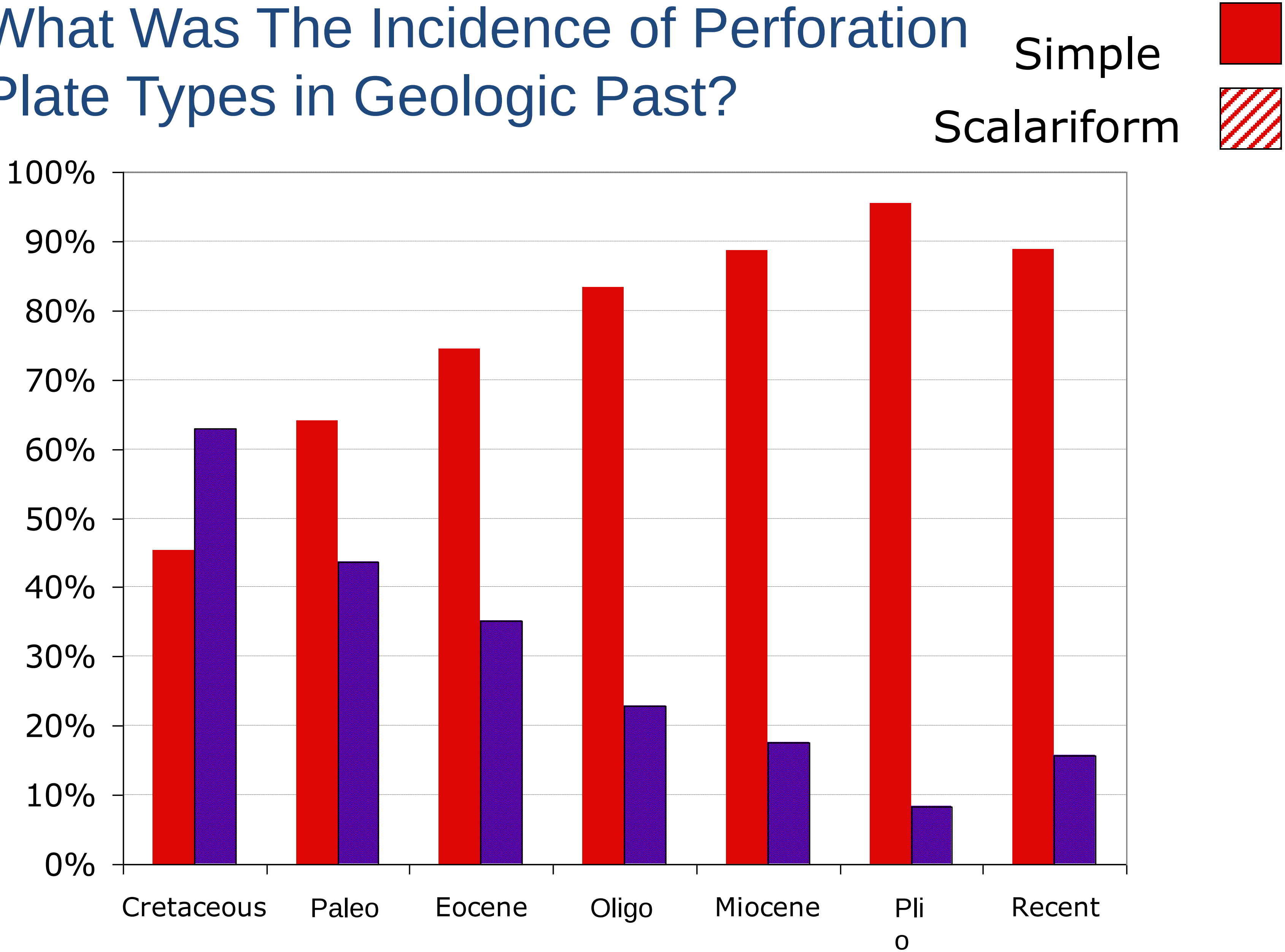
Strength

Conductivity

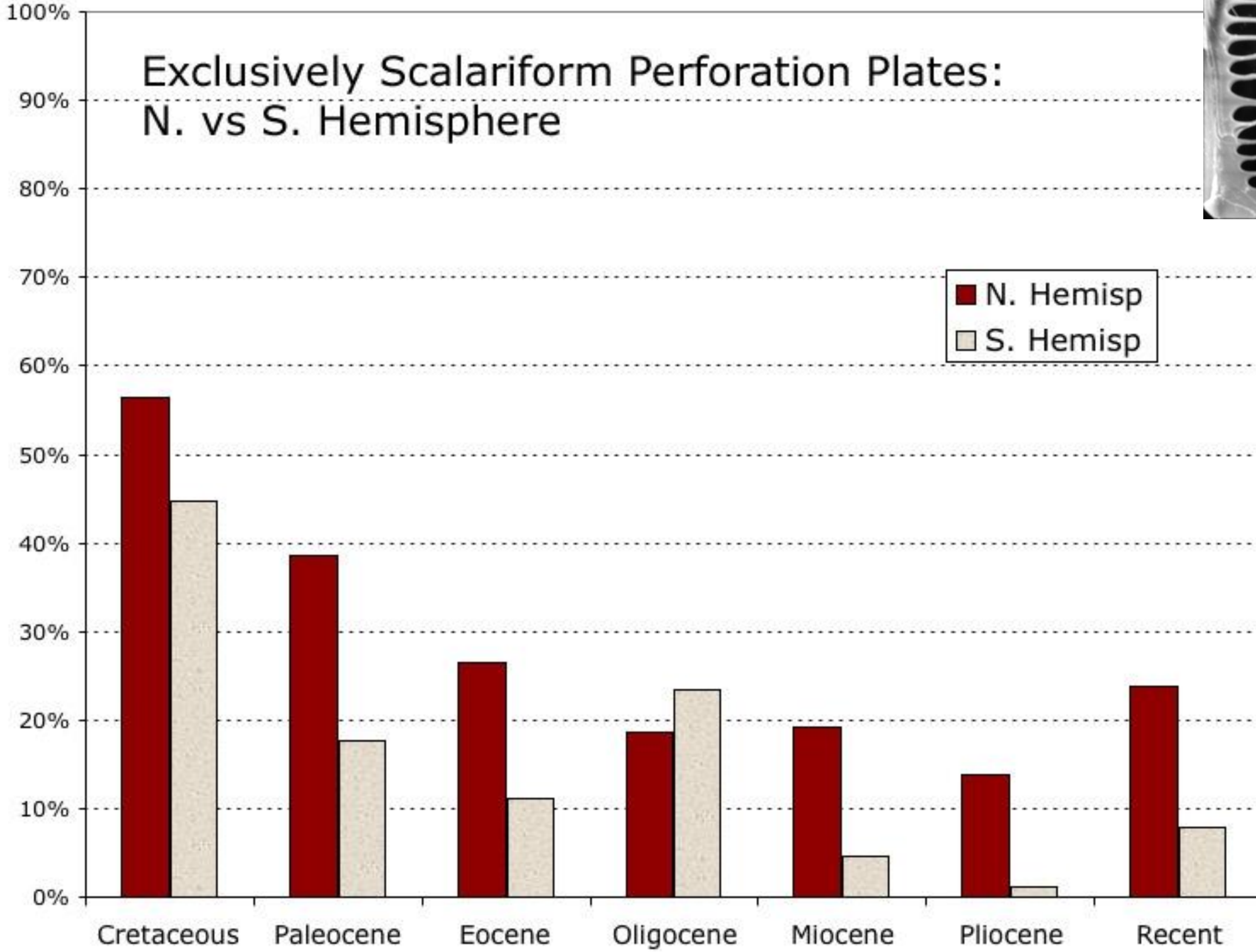
Simple and scalariform perforations

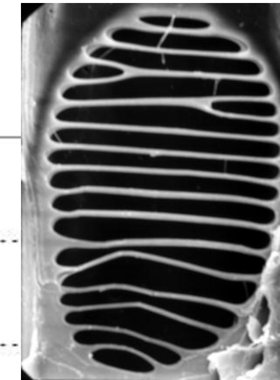


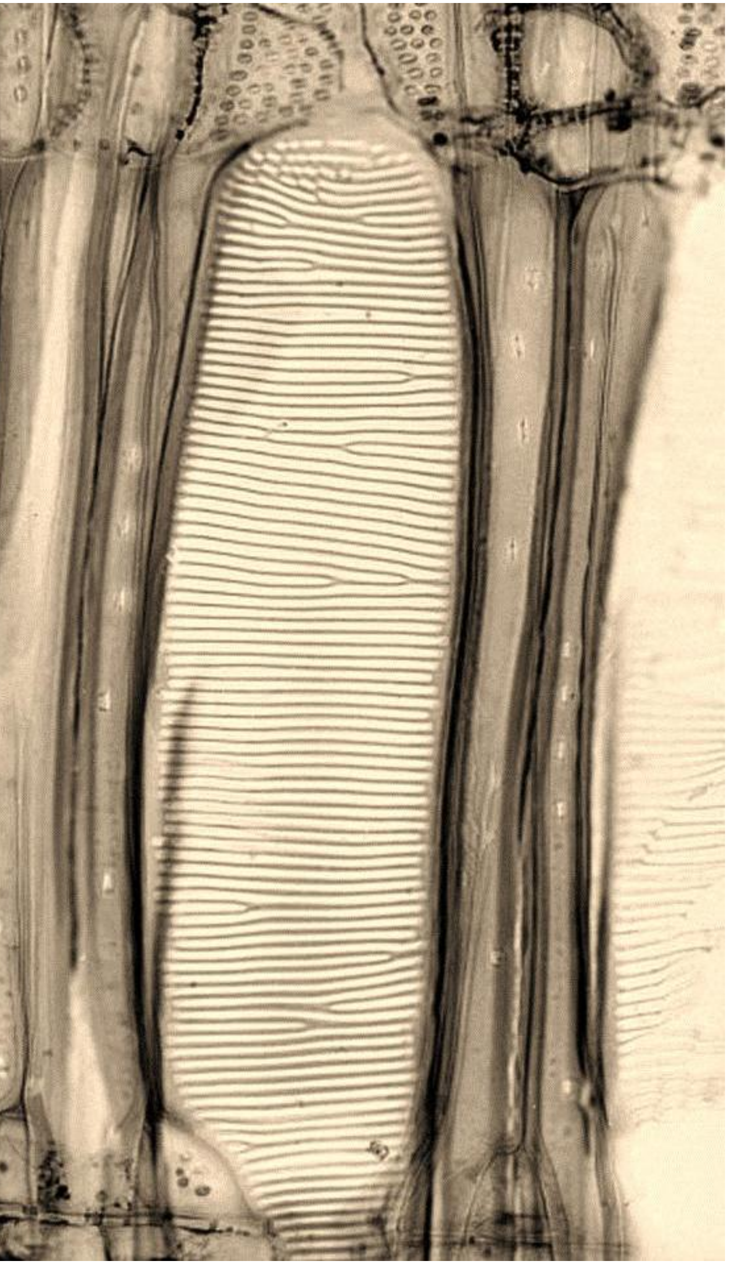
What Was The Incidence of Perforation Plate Types in Geologic Past?

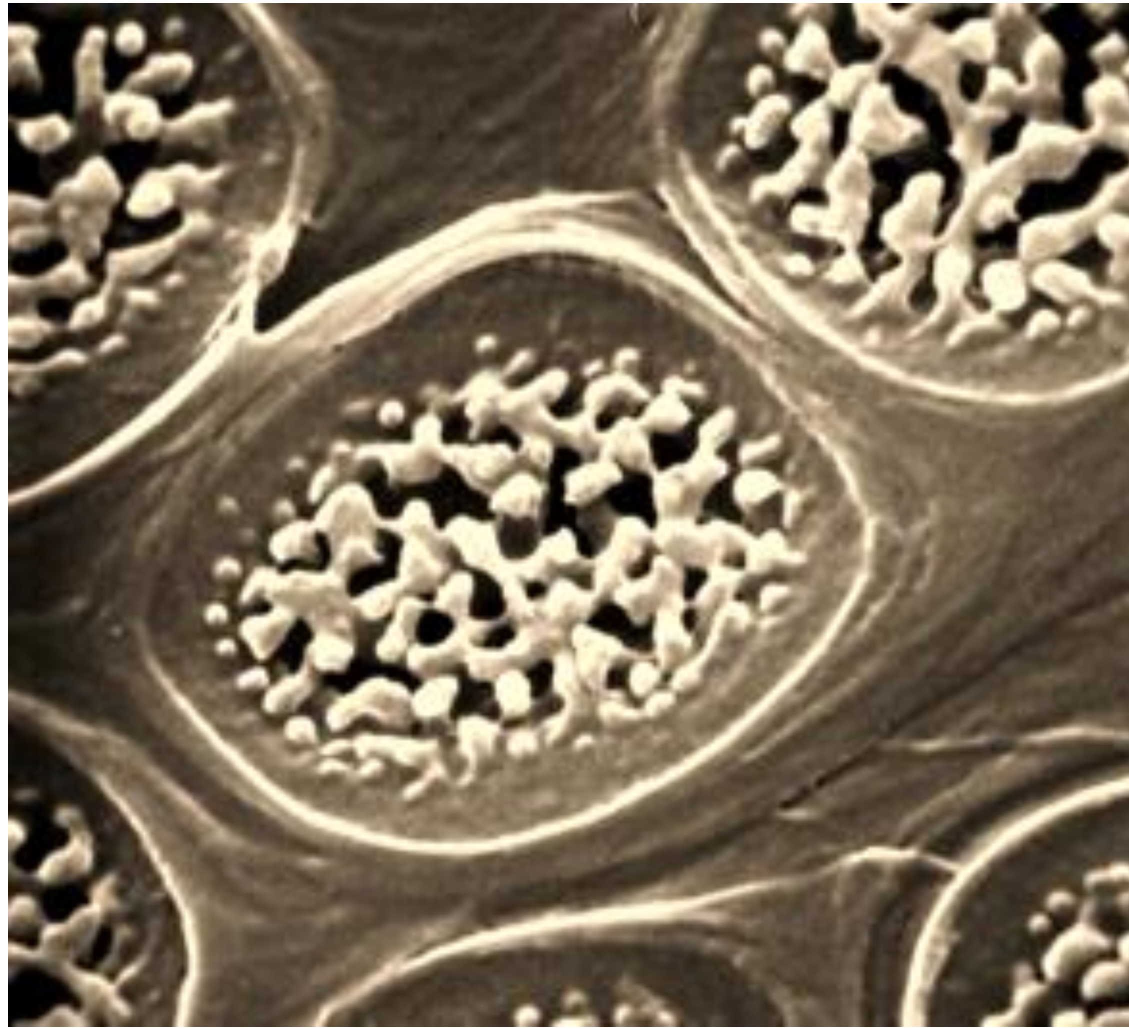


Cretaceous - Recent


Exclusively Scalariform Perforation Plates:
N. vs S. Hemisphere
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
N. Hemisp
S. Hemisp
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Recent



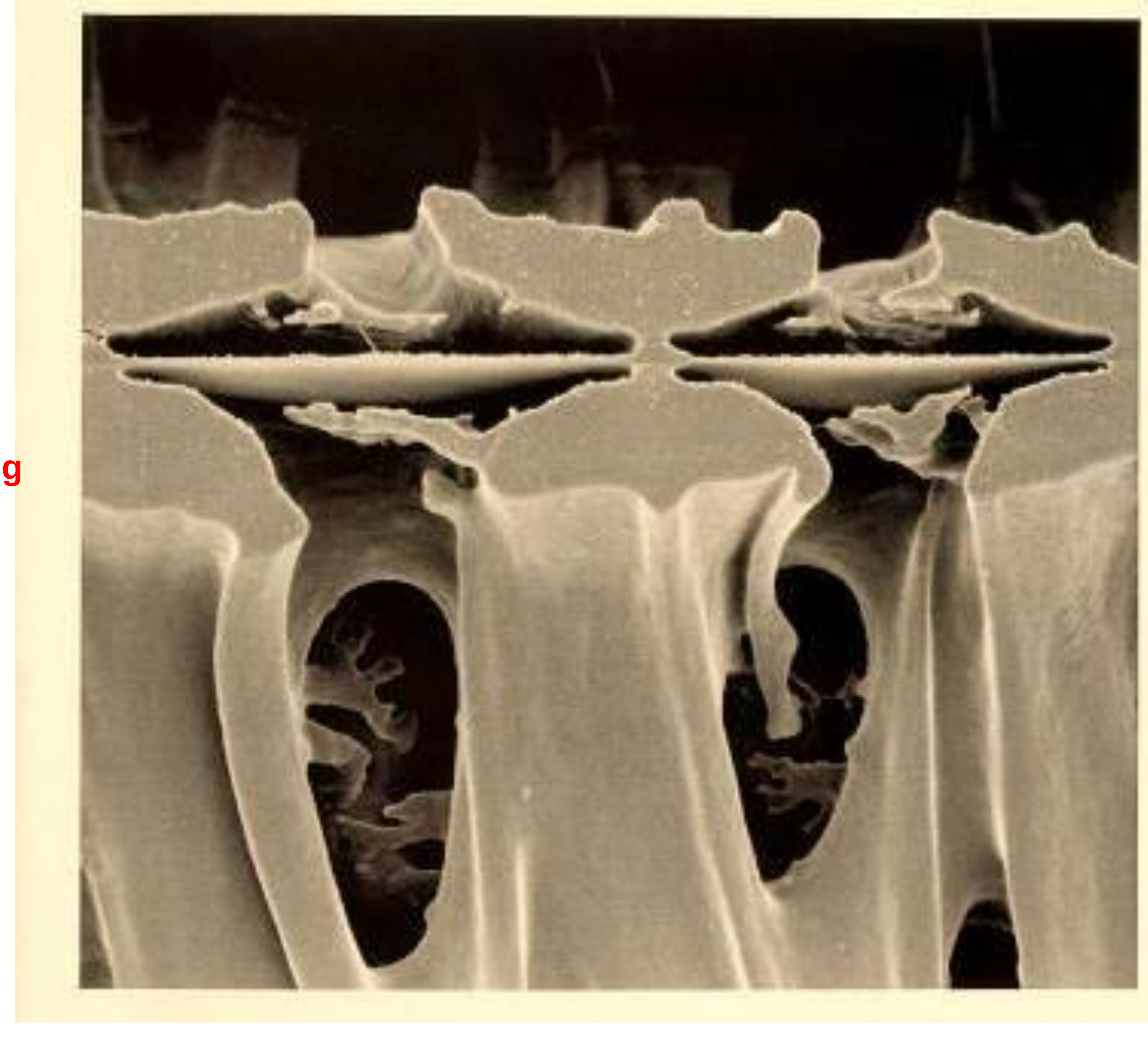




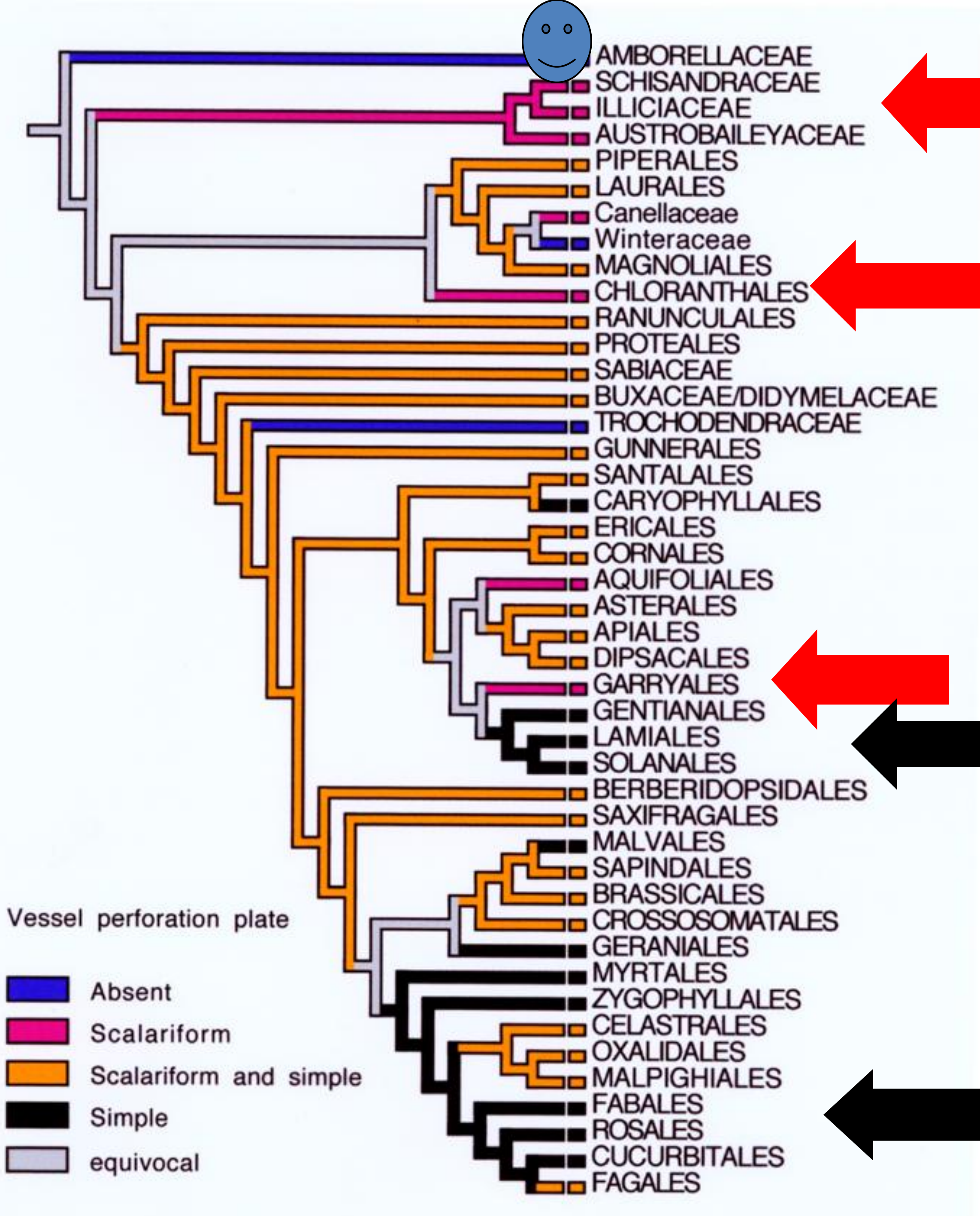
Scalariform perforation & Vestured pits

Photo by S. Noshiro, Perforation Plate in *Davidia*

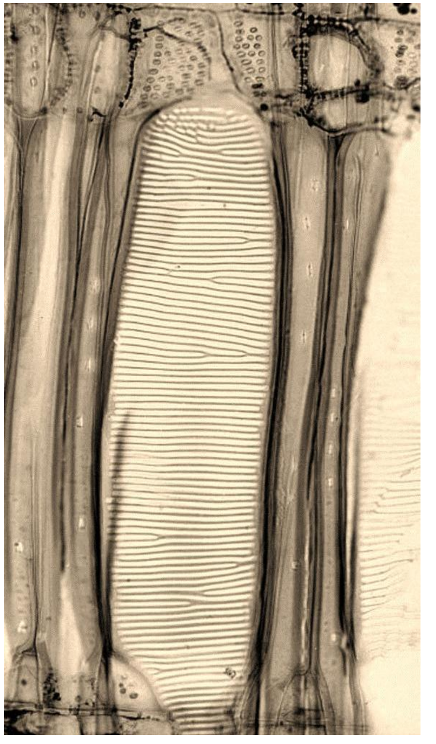
Do Vestures reduce cavitation risk?

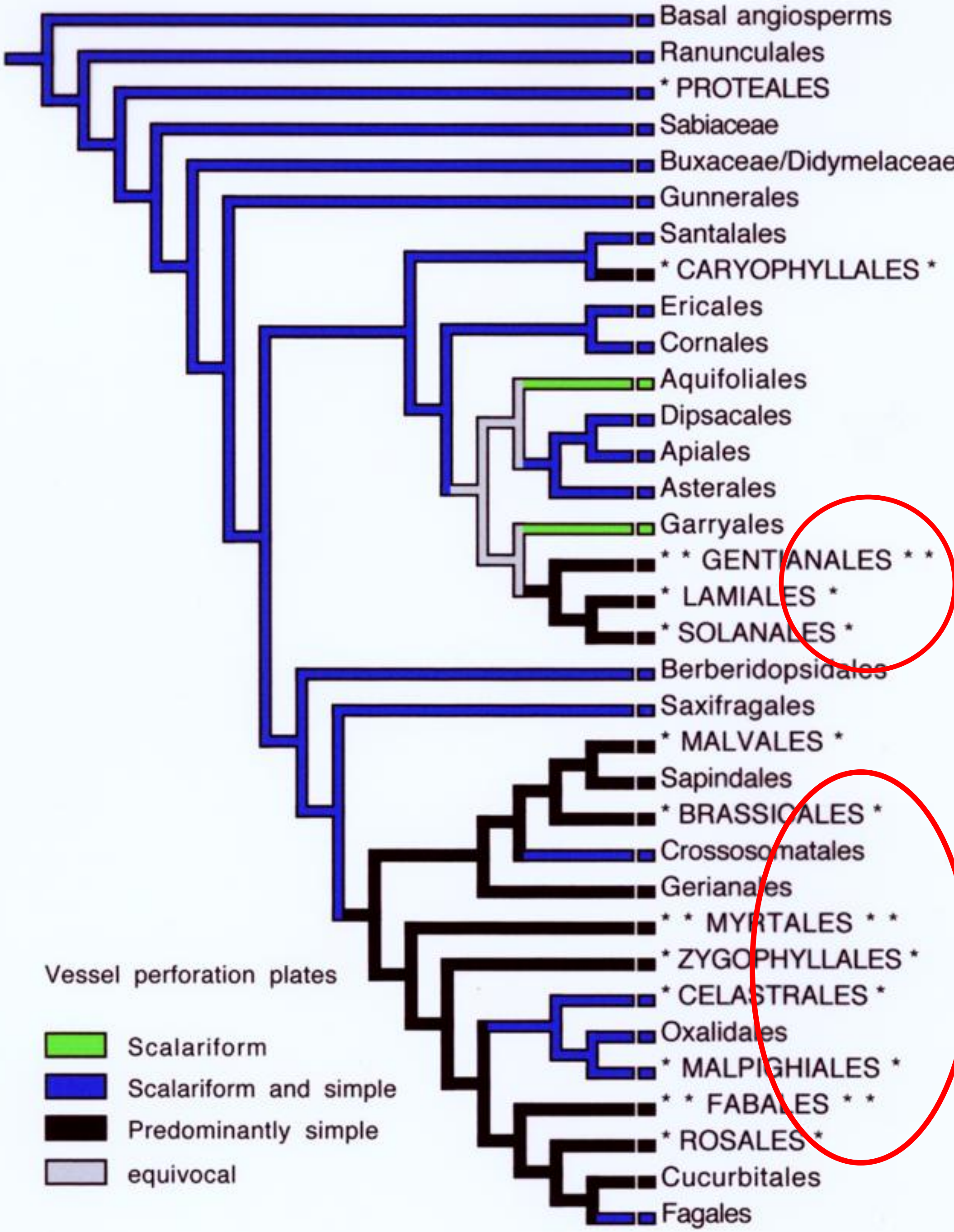


Zweypfenning 1978



Scalariform perforations plotted on the Soltis tree are much more common in basal clades

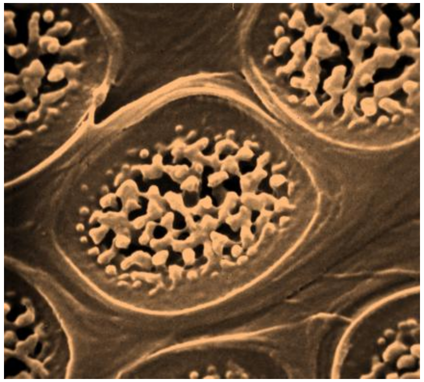




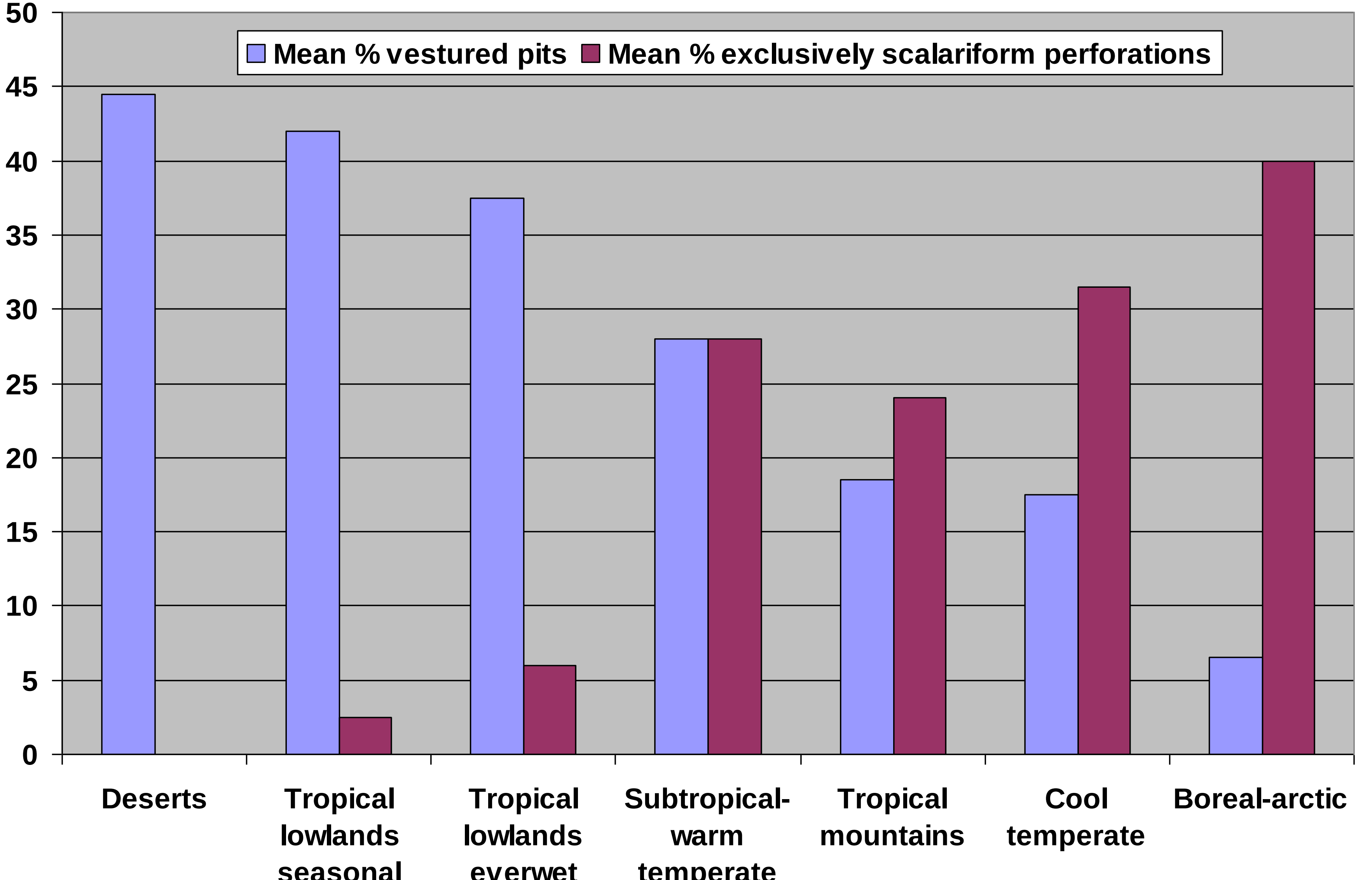
vestured

pits (**)

on Soltis tree

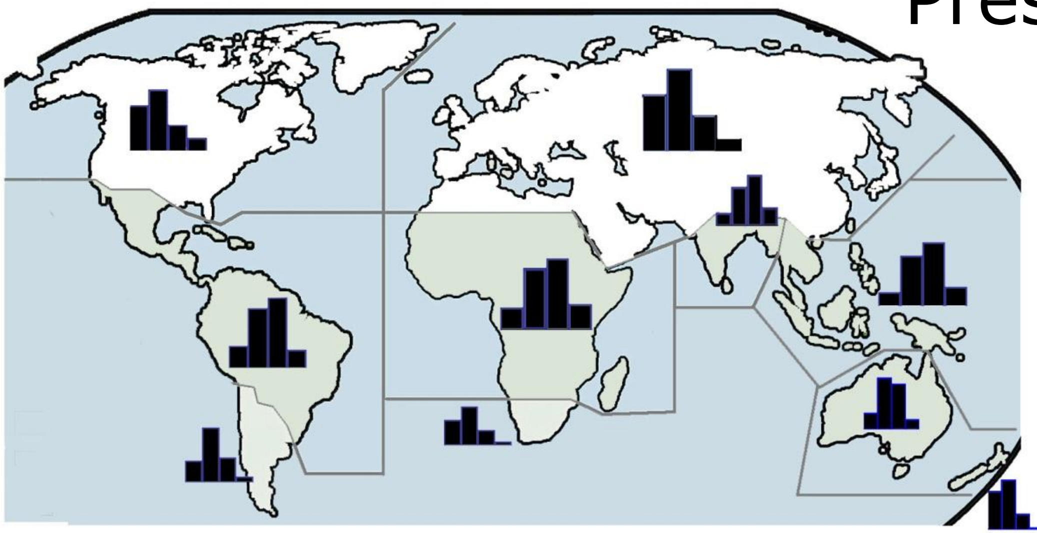


Ecological trends in (vestured pits and) scalariform perforations (purple)



Jansen et al.2004, PNAS

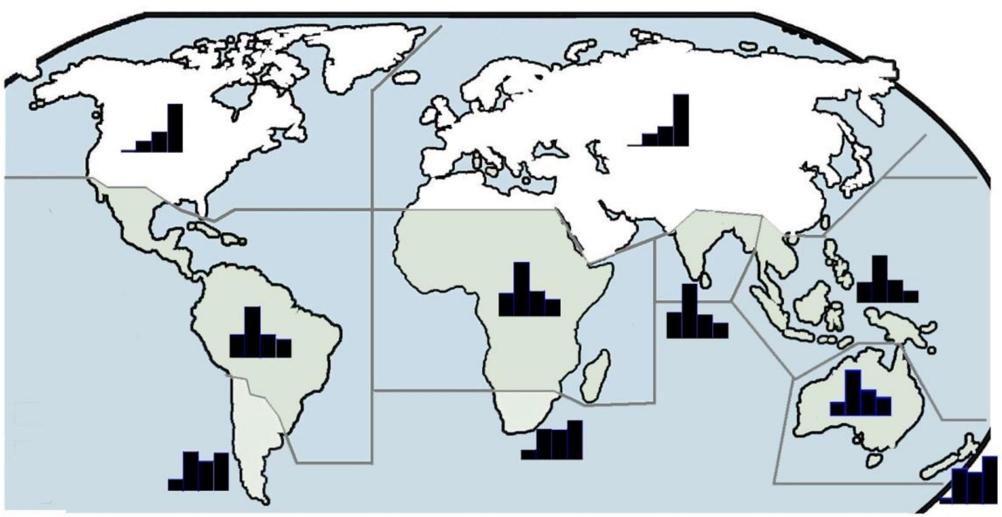
Present-Day Woods



North America, Temperate Asia, Europe similar to one another

Tropical America, Africa, SE Asia similar to one another

< 50 µm , 50 - 100 µm, 100 - 200 µm, > 200 µm --Mean Vessel Diameter

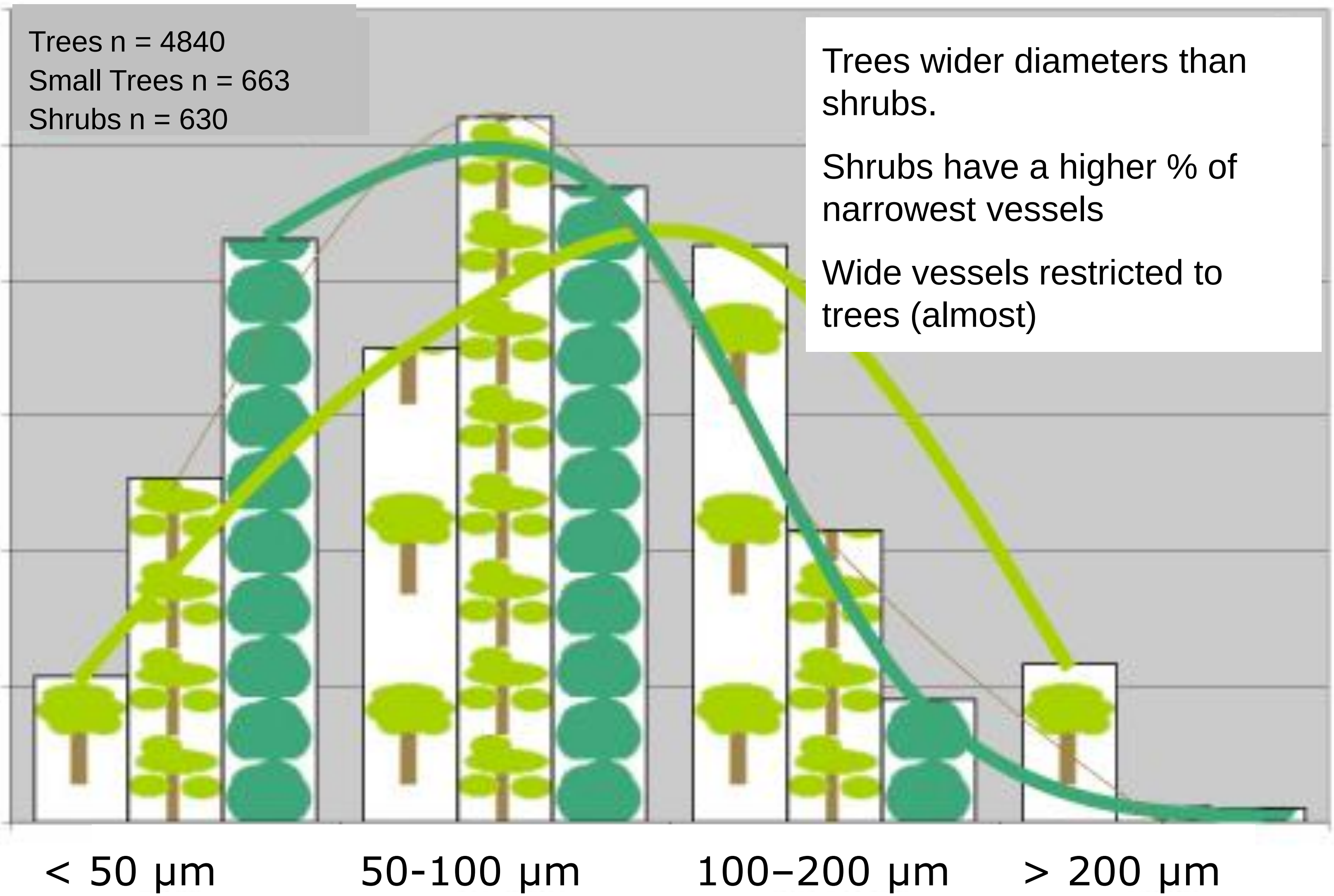


Regions with high proportions of narrow vessels have low proportions of 'few vessels per sq. mm'

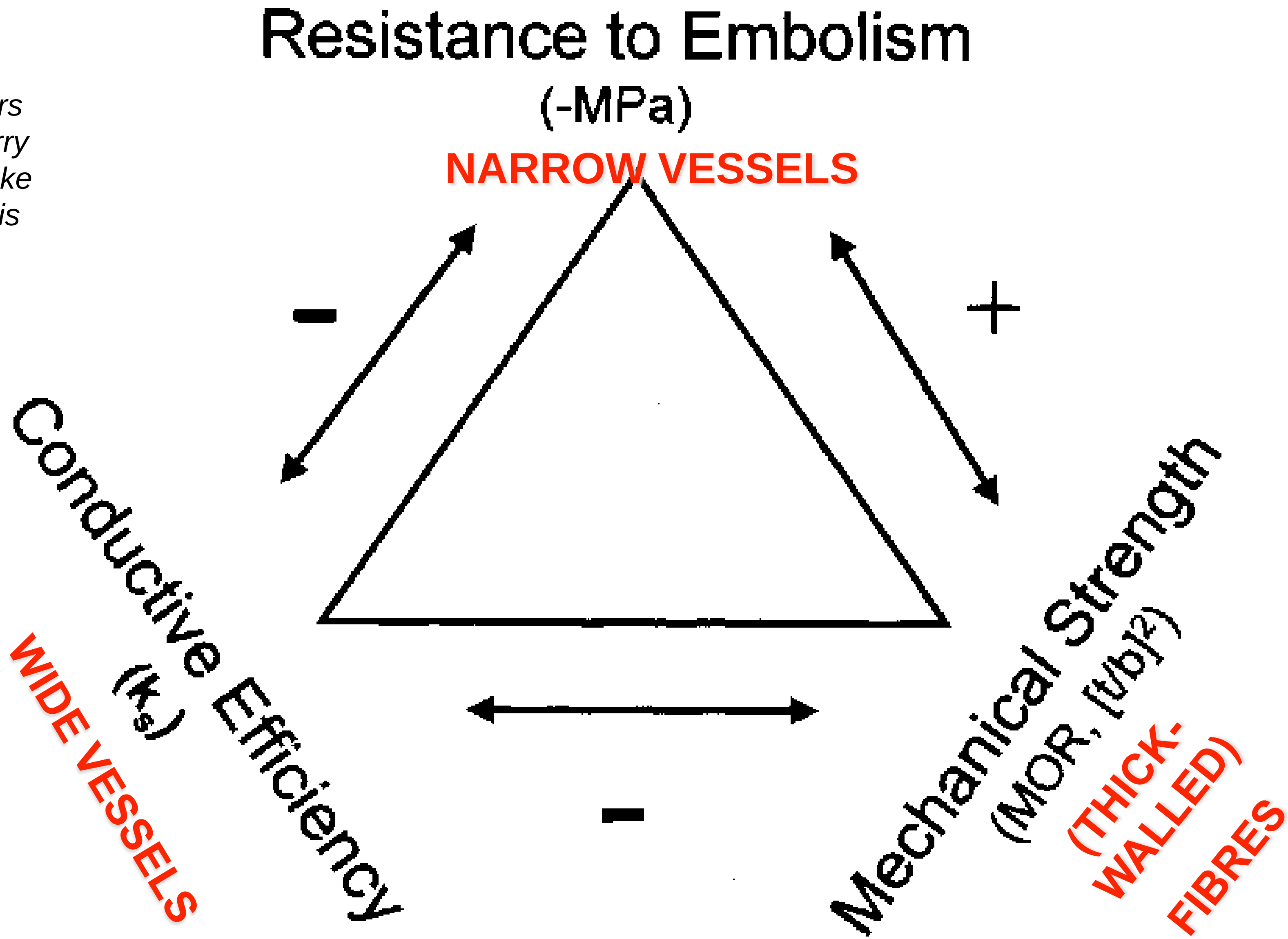
< 5 , 5 - 20, 20 - 40, > 40-- Vessels per sq. mm

Wheeler, Baas, Rodgers 2007 IAWA J

Vessel
Mean Tangential Diameter in Trees / Small Trees / Shrubs



Work of
F. Ewers
J. Sperry
U. Hacke
S. Davis



Triangle of wood functions and trade-offs

Summary of functional ecological trends

1. In tropical - temperate - boreal - arctic gradients:
   Scalariform perforations become more common
   Element length decreases
   Vessel diameter decreases
   Vestured pits become rarer

2. In mesic - xeric gradients:
   Scalariform perforations become very rare
   Element length decreases
   Vessel diameter decreases
   Vestured pits become more common

Confounding for temperature and moisture proxies!

Also clade dependent (phylogeny)

Additional Wood Anatomical Proxies for Warmer Climates

- Storied structure **+**
- Ring porosity **–**
- Parenchyma rare or absent **–**
- Paratracheal parenchyma **+**
- Marginal parenchyma **–**
- Septate fibres **+**
- Homocellular rays **–**

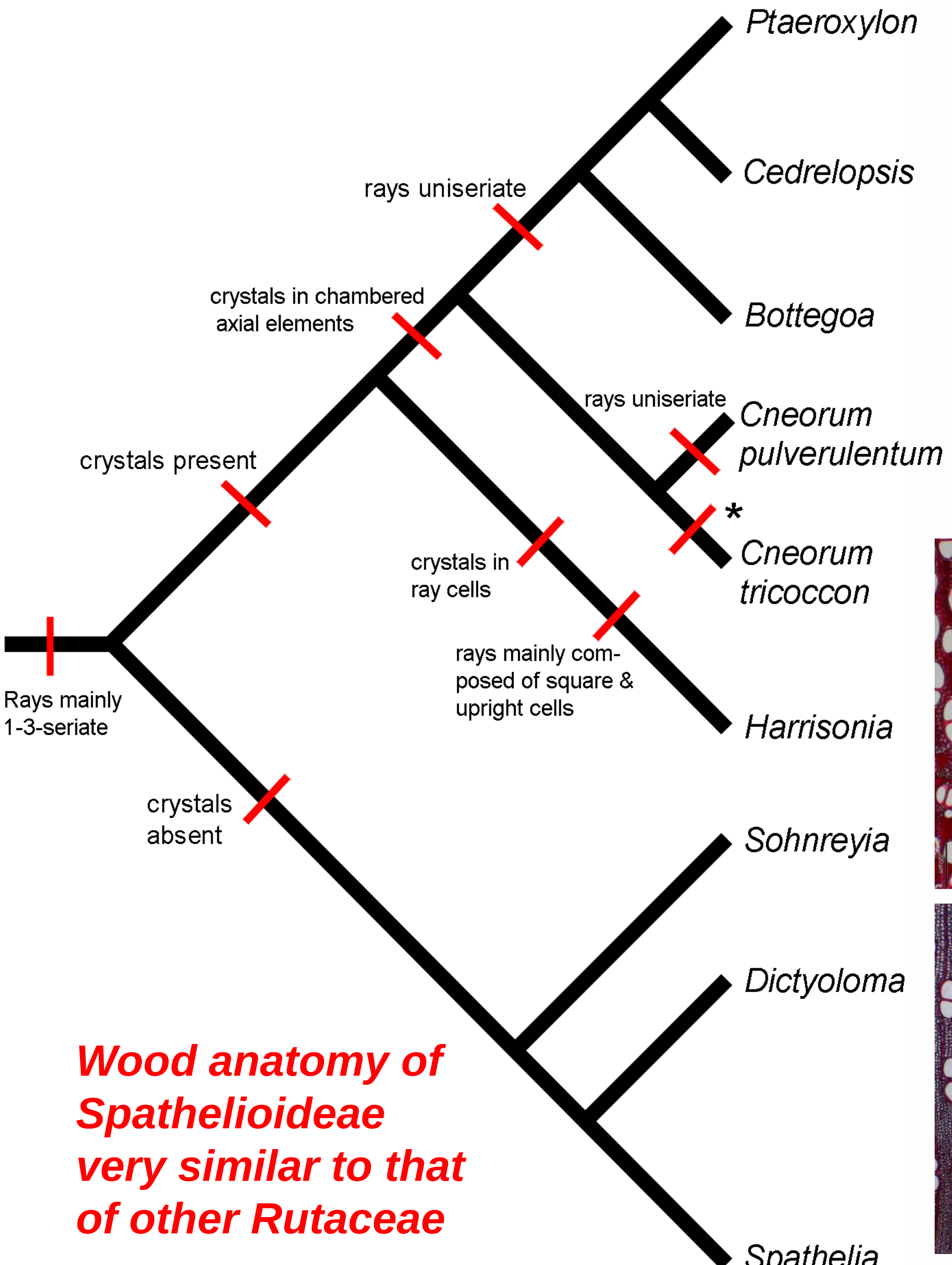
Wiemann et al. 1999; Wheeler et al. 1993, 2007

Scale matters!

- Within wild *Olea europaea* in Europe vessel density is positively related with MAT (Téral & Mengüal 1999)
- Within world flora vessel density negatively related with MAT (Wheeler et al. 2007)

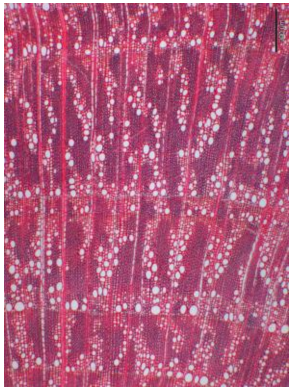
Interim Conclusion No. I

- Wood anatomy contains very strong ecologically adaptive signals (temperature, water, etc.)
- Some of these signals (perforation type, vestured/nonvestured pits) also contain very strong phylogenetic signals
- Conclusion: adaptive evolution is driver of wood anatomical diversification
- Research questions have to take into account spatial, temporal, and taxonomic scales

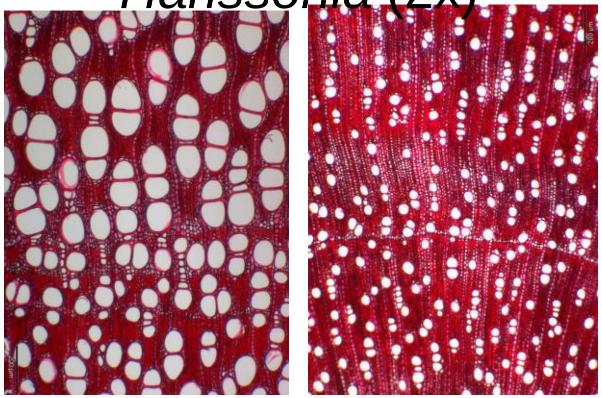


Wood anatomy of Spathelioideae very similar to that of other Rutaceae

* Cneorum tricoccon

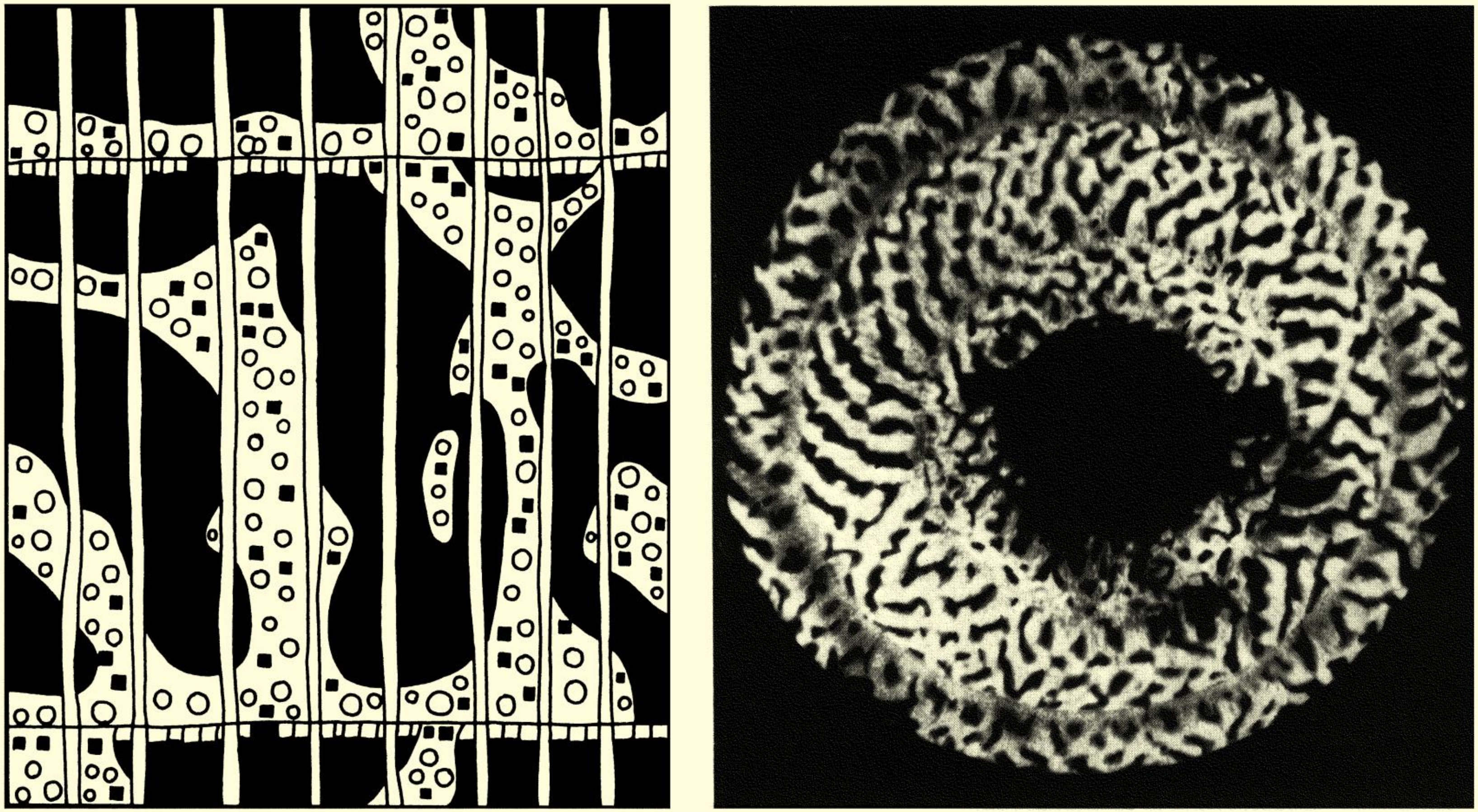


Harissonia (2x)



Dictyoloma

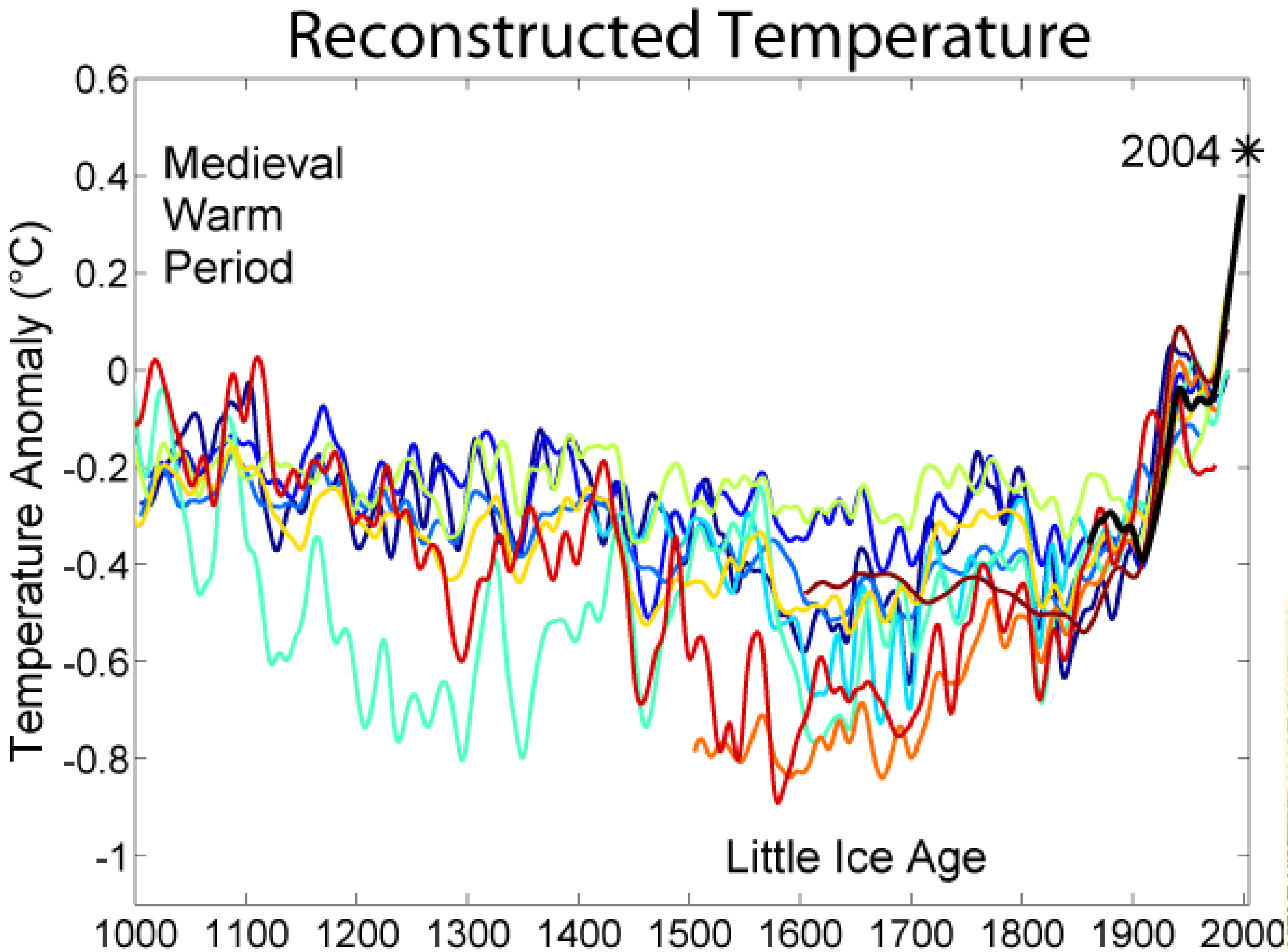
H.J. Braun (1963, 1970)- Functional Type *Rhamnus*

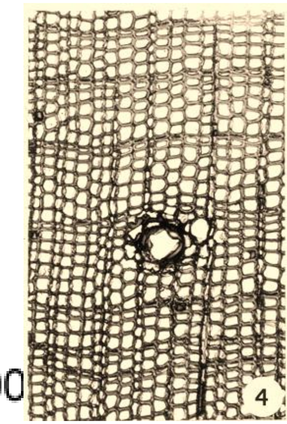


Rationale for Links between Climate and Wood Evolution

- Photosynthesis ~ Gas Exchange ~ Stomatal opening ~ Transpiration
- High CO_2 ~ Low stomatal frequency ~ Lower demands on conductivity
- Climate ~ water vapour deficit ~ drought stress ~ cavitation
- Conductivity ~ 4^{th} Power Conduit Radius ~ vessel density
- Resistance to flow: perforation plates & pit membranes
- Cavitation resistance (drought stress) : vessel diameter, vestured pits, pit membrane ultrastructure?
- Cavitation resistance (freeze-thaw cycle): vessel diameter, scalariform perforations
- Forest Canopy transpiration regulates climate
  - Jarmila Pittermann 2010

Wood Anatomy and Climate Change 1: Tree rings

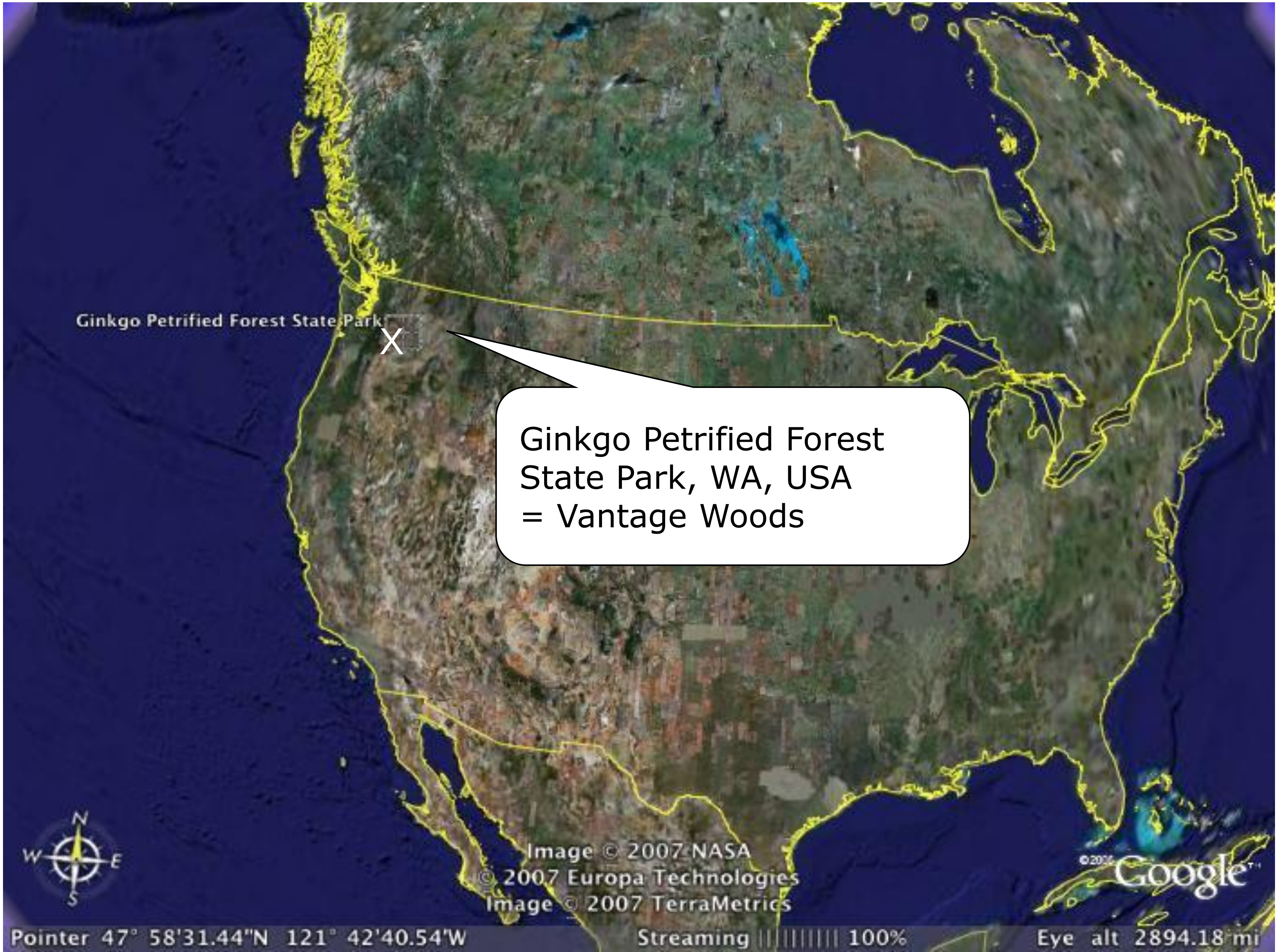




Wood Anatomy and Climate Change 2: Vantage Fossil Wood example

- Rich Mid-Miocene assemblage (Wheeler & Dillhoff, 2009, *IAWA Journal Supplement* 7)
- Mean Annual Temperature reconstruction based on qualitative wood anatomical proxies

Vantage Woods 15.5 my,mid-Miocene



Estimating MAT °C using wood physiognomy

MAT = 24.78 + 36.57 (% storied rays) - 15.61 (% marginal parenchyma) - 16.41 (% axial parenchyma rare to absent)

Wiemann, M.C., E.A. Wheeler, S.R. Manchester, & K.M. Portier. 1998. Dicotyledonous wood anatomical characters as predictors of climate. Palaeogeography, Palaeoclimatology, Palaeoecology 139: 83--100.

Wiemann, M.C., S.R. Manchester, & E.A. Wheeler. 1999. Paleotemperature estimation from dicotyledonous wood characters. Palaios 14: 460--474.

33 Dicot Wood Types From Main Vantage Locality

If treat Vantage *Fraxinus* as a tendency to storied rays, MAT estimate of **12.8 ^{o}C**,

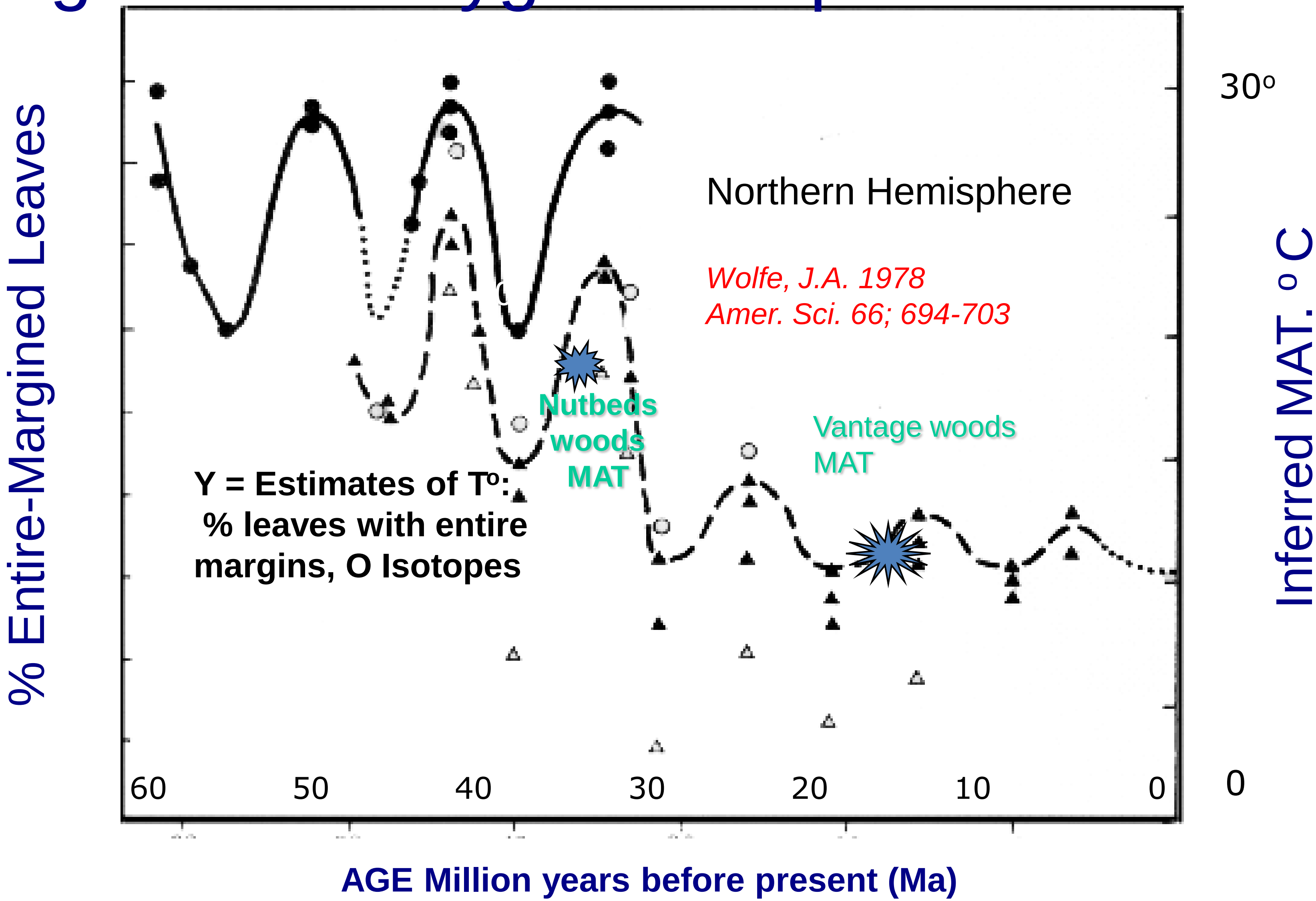
If storied rays absent, the MAT estimate is **12.1 ^{o}C**

Recent Temperate Deciduous Broad-leaved Forests of China have MAT of 10 -- 14.6 ^{o}C

Recent Mixed Mesophytic Forests of China have MAT of 11.4--16.4 ^{o}C

Wang, Chi-Wu. 1961. The Forests of China. Maria Moors Cabot Foundation Publication No. 5

Past climate change inferred from leaf margins and Oxygen isotopes



Experimental Studies

- Increased temperature results in:
  - increased wood density
  - lower vessel diameter
  - lower flow resistance (lower sap viscosity)
- Increased CO_2 results in:
  - increased growth
  - decreased wood density
  - lower vessel diameter

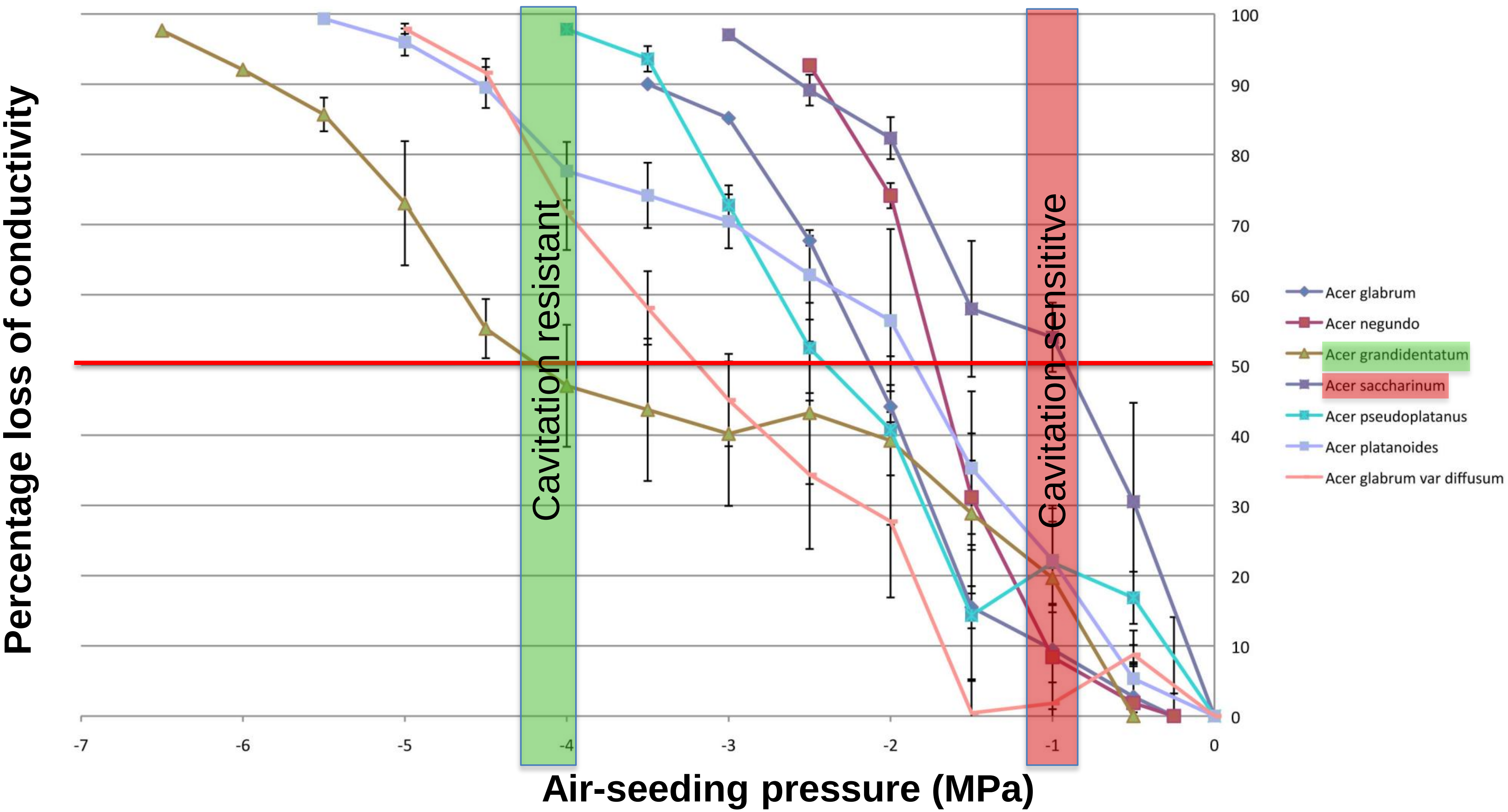
Caution: limitations of short term experiments

Interim Conclusion 2

- Wood anatomy contains wealth of climatic signals from past and present
- Wood anatomical profiles of species assemblages are underutilised as environmental proxies
- *Is this the full story??*

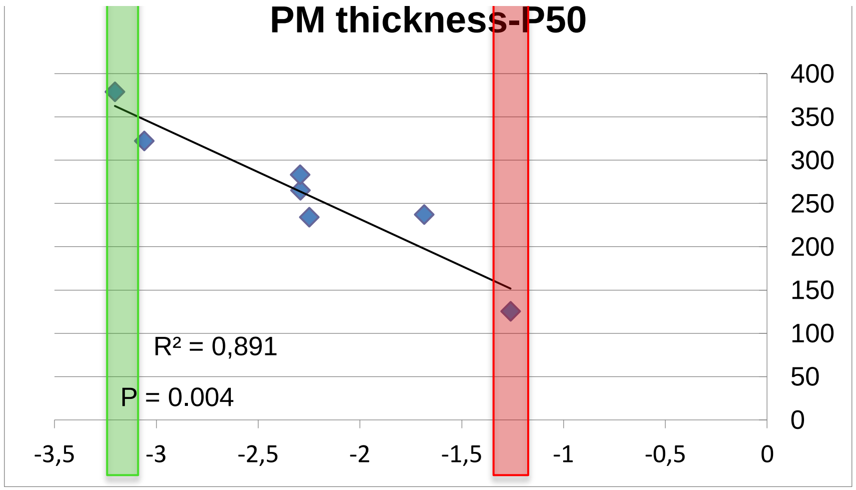
Cavitation resistance

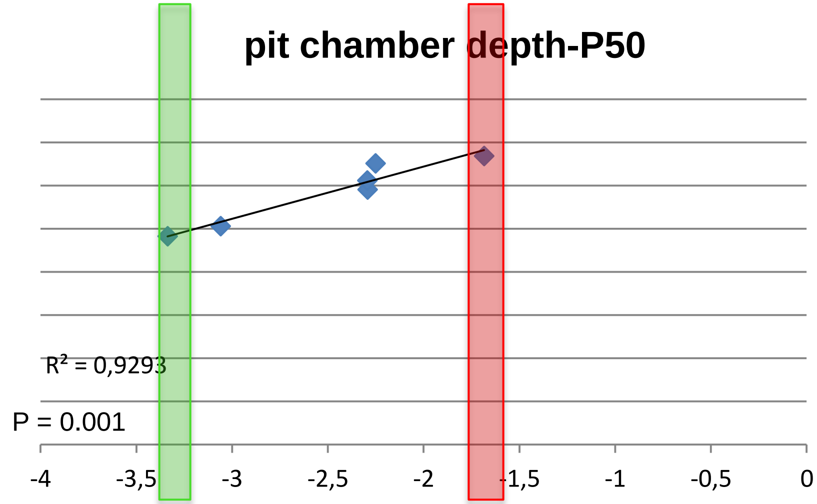
Vulnerability curves vs. P50

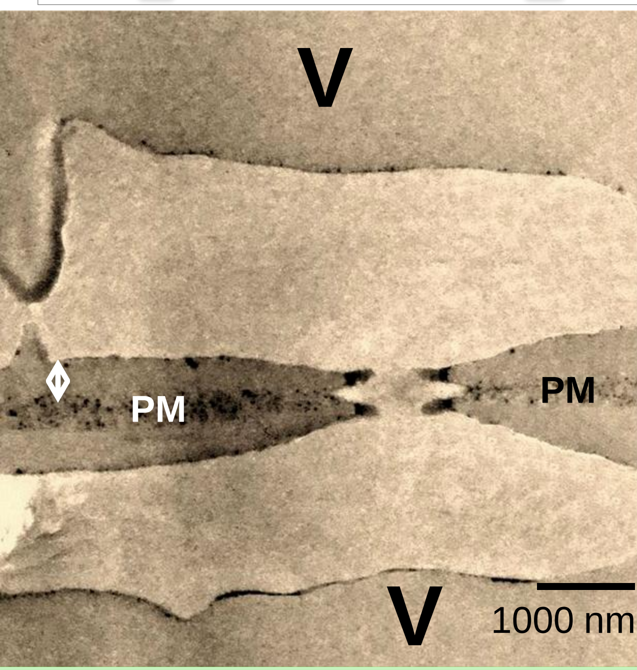


Lens et al. 2011. *New Phytologist* 190: 709-723

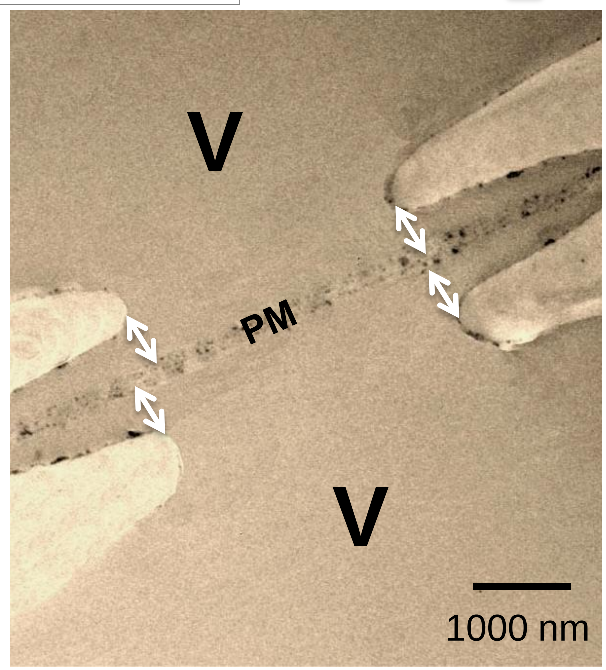
Acer



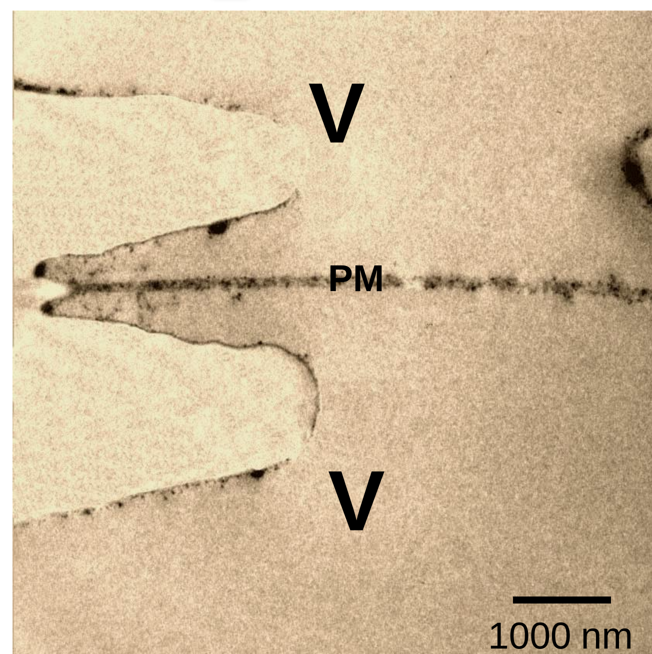




A. grandidentatum P50: -3.19MPa



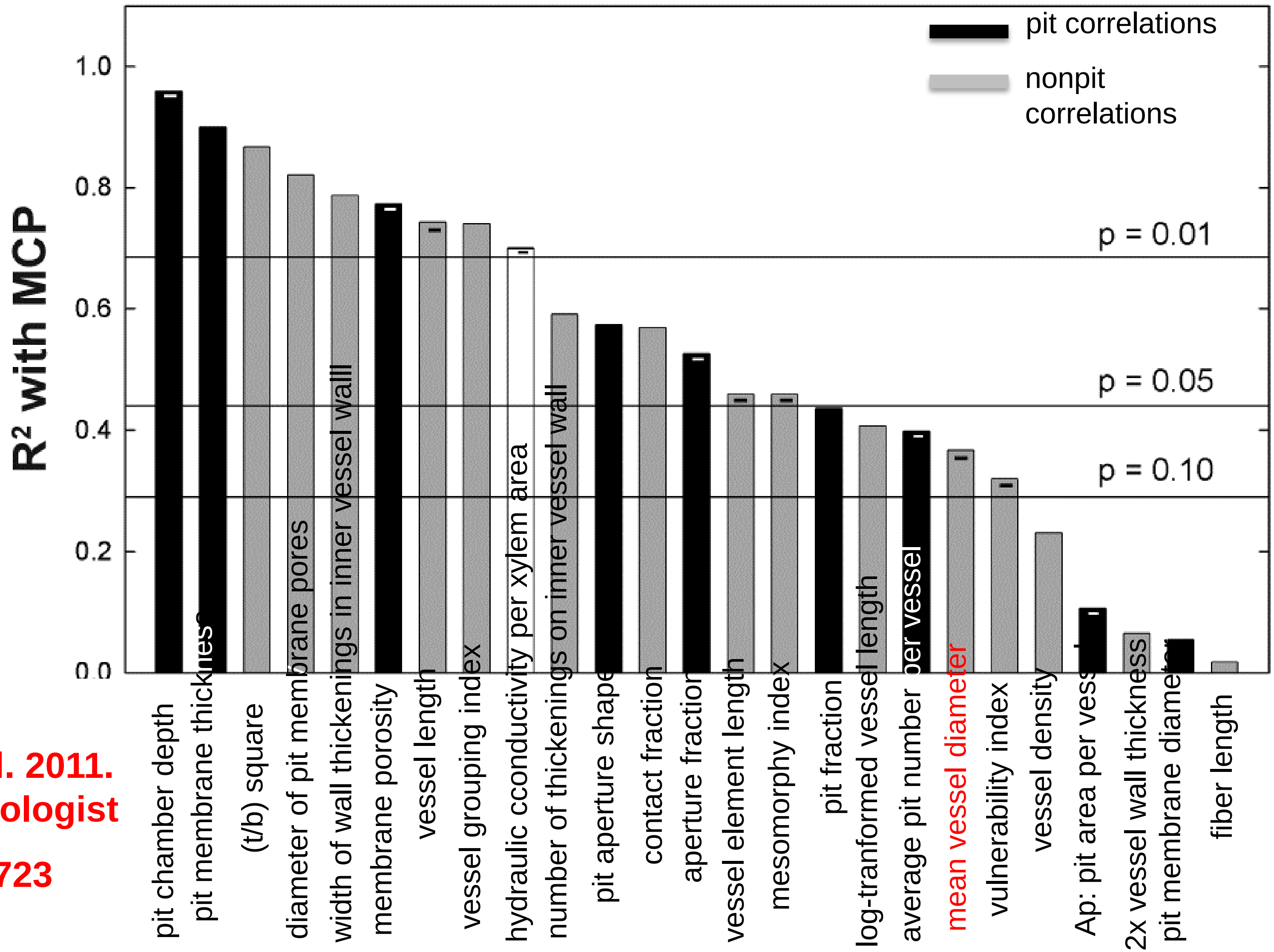
A. platanoides P50: -2.29MPa



A. saccharinum P50: -1.26MPa

Lens et al. 2011. *New Phytologist* 190: 709-723

Tight correlation between ultrastructural IV pit characters and Mean Cav. Press. in *Acer*



Lens et al. 2011. New Phytologist

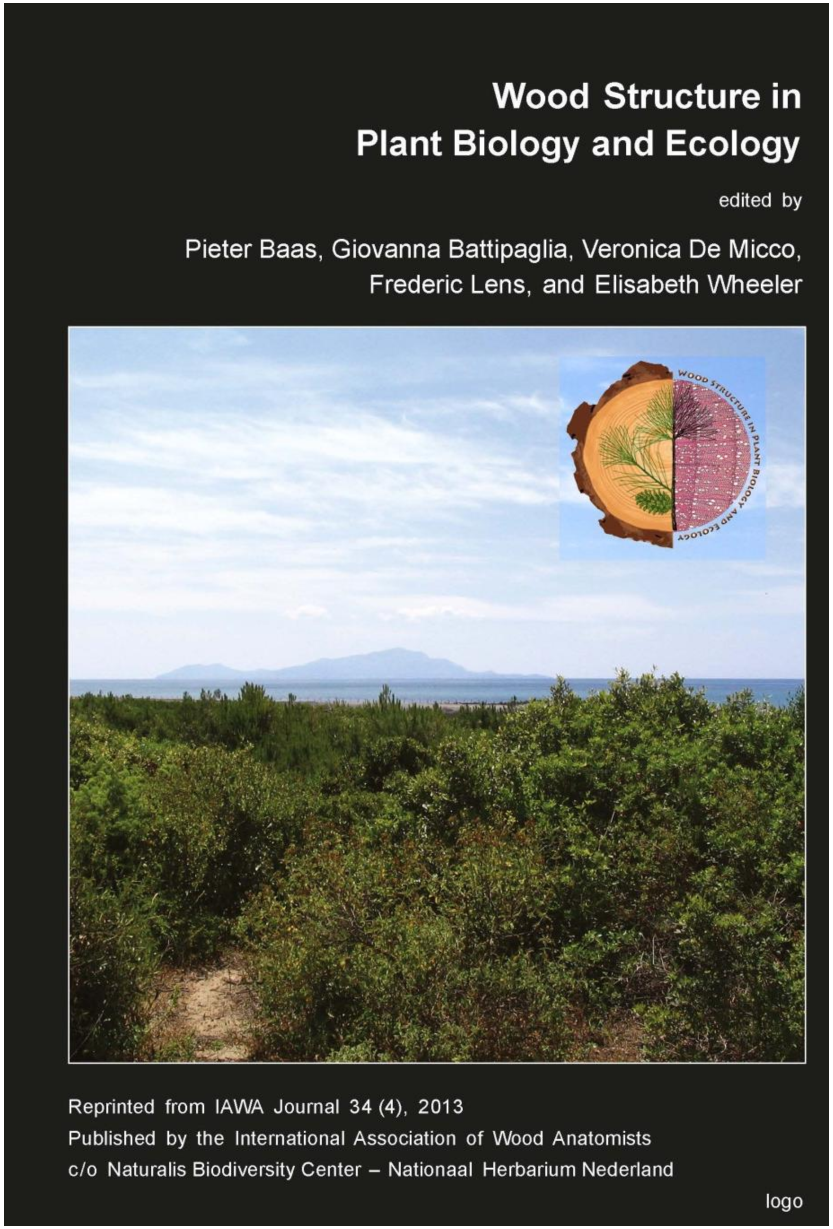
190: 709-723

Conclusions no. 3

- Major breakthroughs in last 10 years about understanding roles of pit membrane ultrastructure and thickness (Choat, Sano, Jansen, Lens, a.o.).
- Experimental evidence for role of other attributes: perforation type, helical wall thickenings, vessel grouping – what is more to come?
- Vessel diameter-vessel density trade-offs exist, but only explain a small fraction of efficiency-safety trade-offs!
- Vessel diameter could be fully dependent on tree size (tapering conduit model of Anfodillo)?

Special IAWA Journal Issue 2013

- Proceedings of COST-Action STREeSS and IAWA/IUFRO meeting in Naples, April 2013
- Twelve papers: reviews, new methods to observe functional traits, and integrative physiological and anatomical studies
- Guest editors Veronica de Micco, Giovanna Battipaglia and Frederic Lens



Thank You and thanks to:

- Frederic Lens
- Peter Gasson
- Elisabeth Wheeler
- Steven Jansen