Darwin's Abominable Mystery

. . . origin of angiosperms . . .

Read Saquet et al. 2017. The ancestral flower of angiosperms and its early diversification. Nature Communications

Great Mysteries to Zoologists

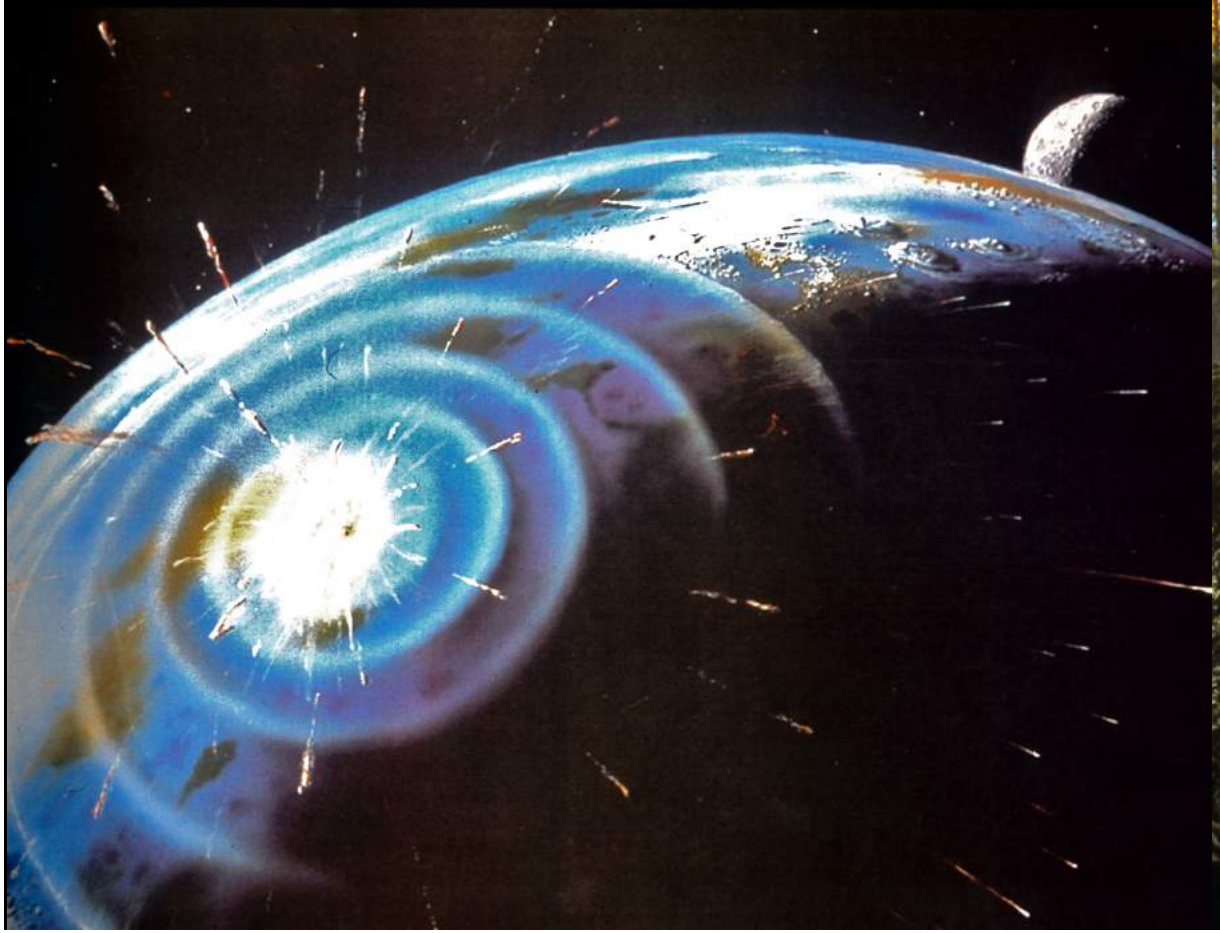
Rise of the birds from a dinosaur lineage

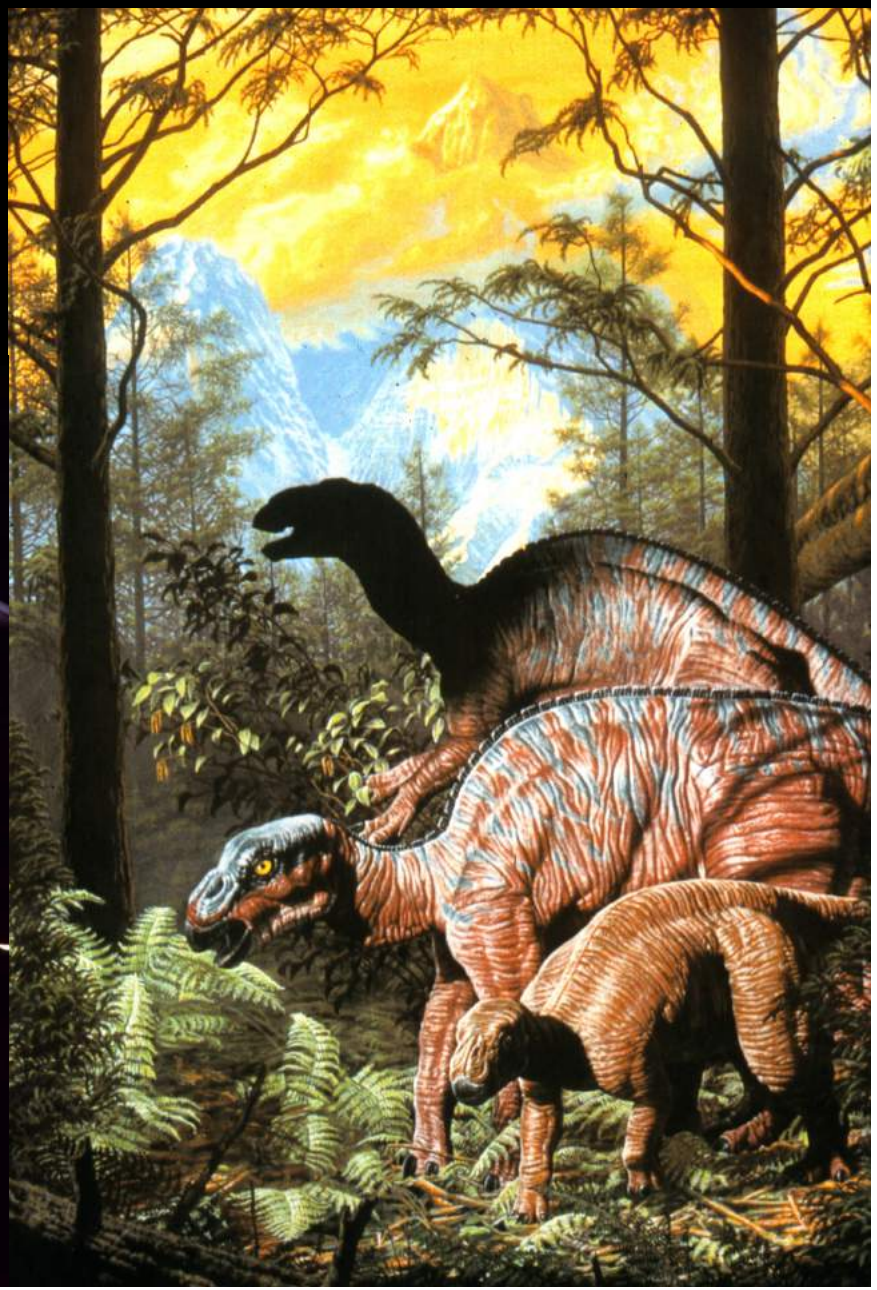
Archaeopteryx

Great Mysteries to Zoologists

Demise of the non-avian dinosaur lineage

Edmontosaurus

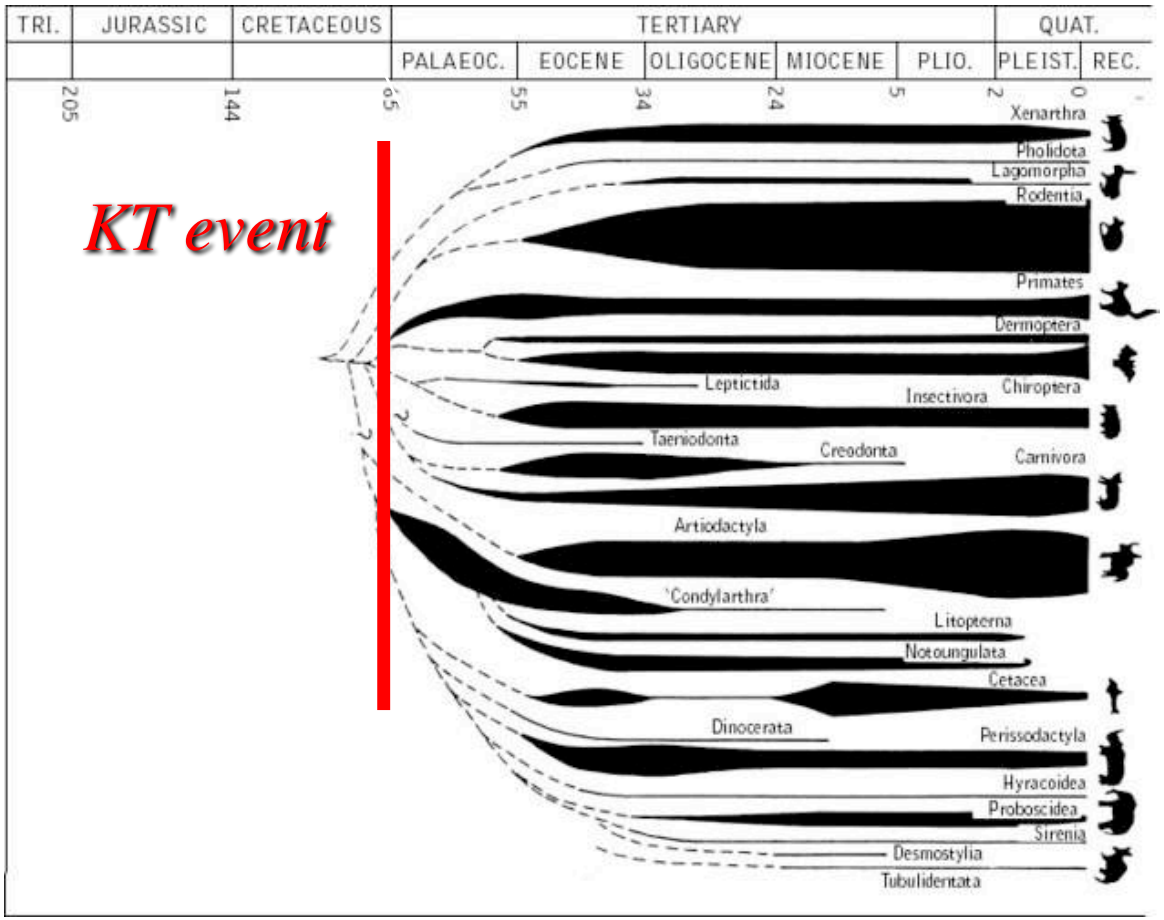




Great Mysteries to Zoologists

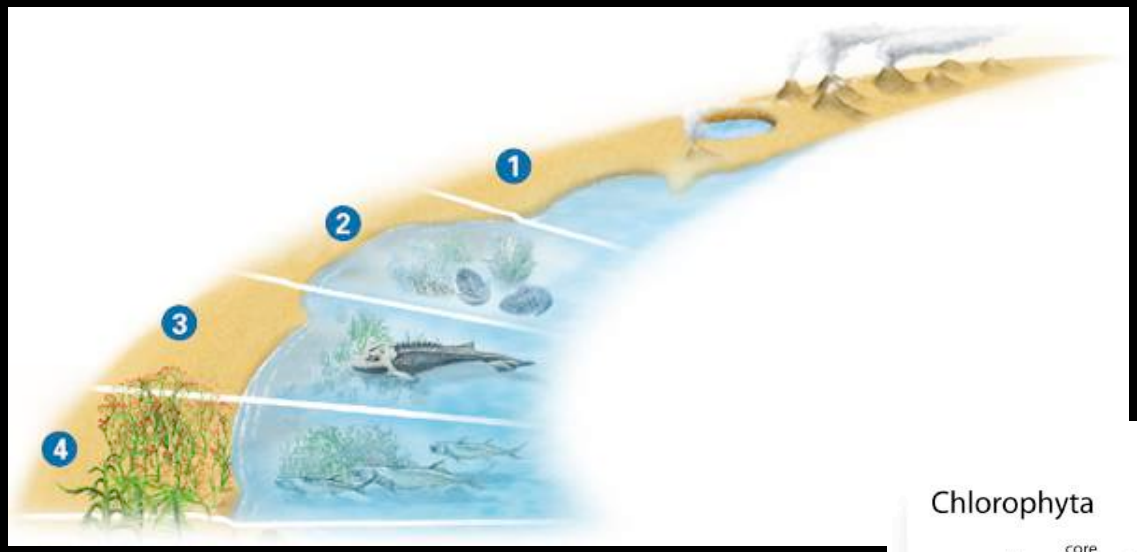
Adaptive radiation of mammals after dinosaurs

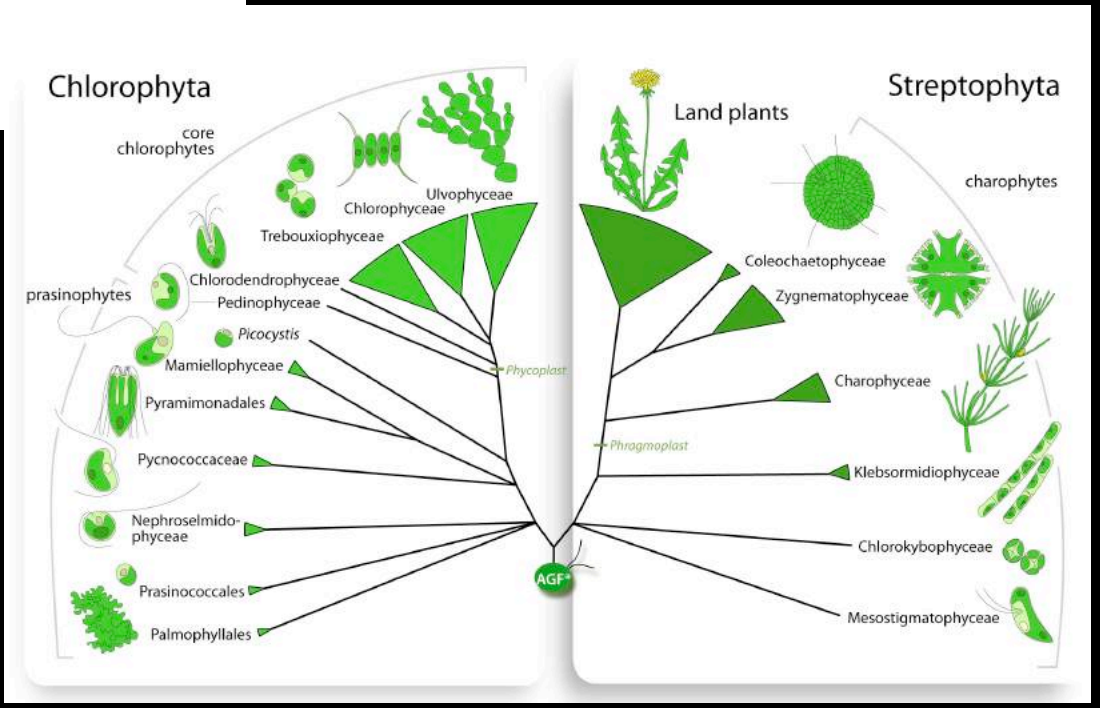
Eocene in Kansas



Great Mysteries to Botanists

Origin of land plants





Greatest Mystery to Botanists

Origin and rise of angiosperms

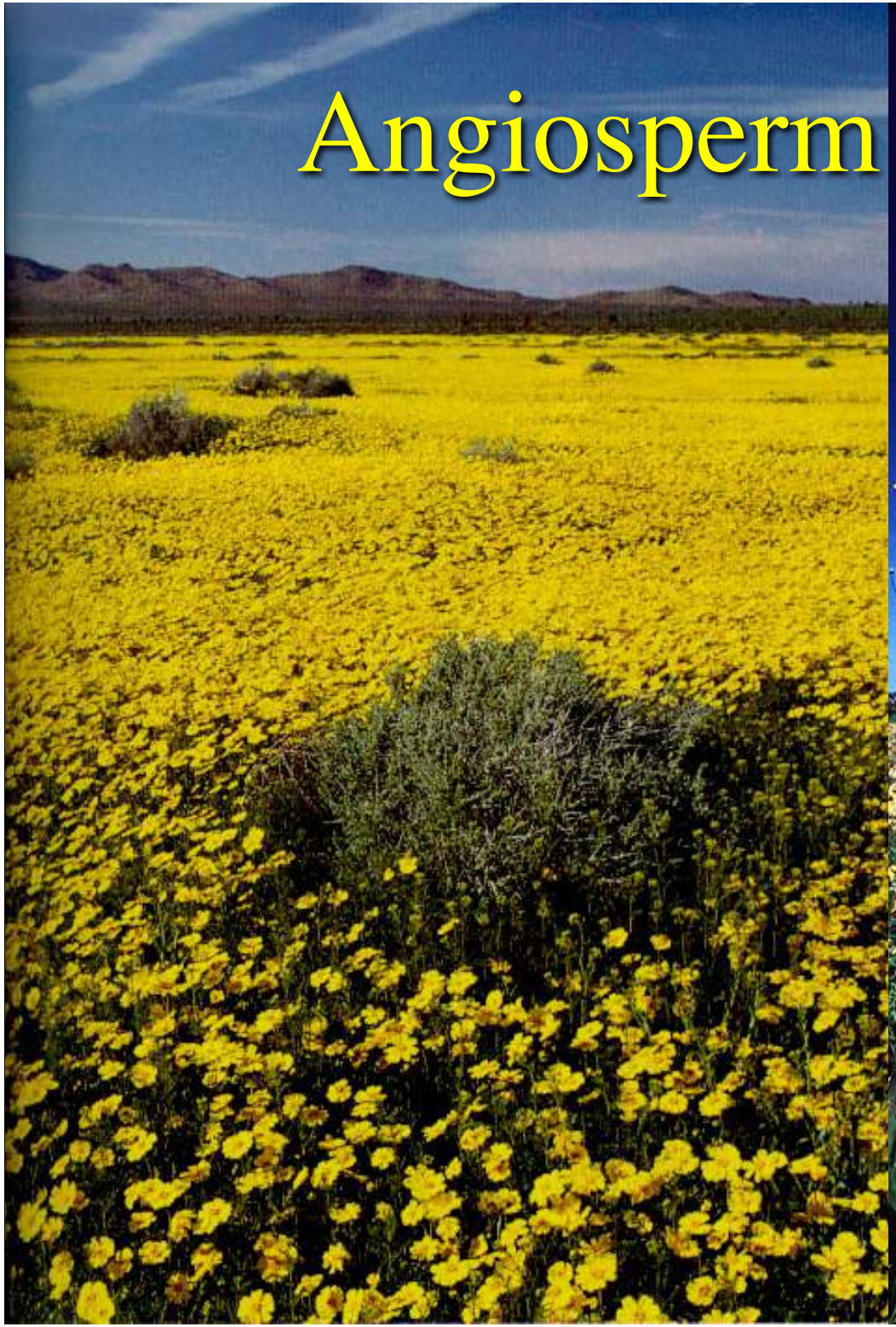
Angiosperm Dominance

Angiosperm Dominance

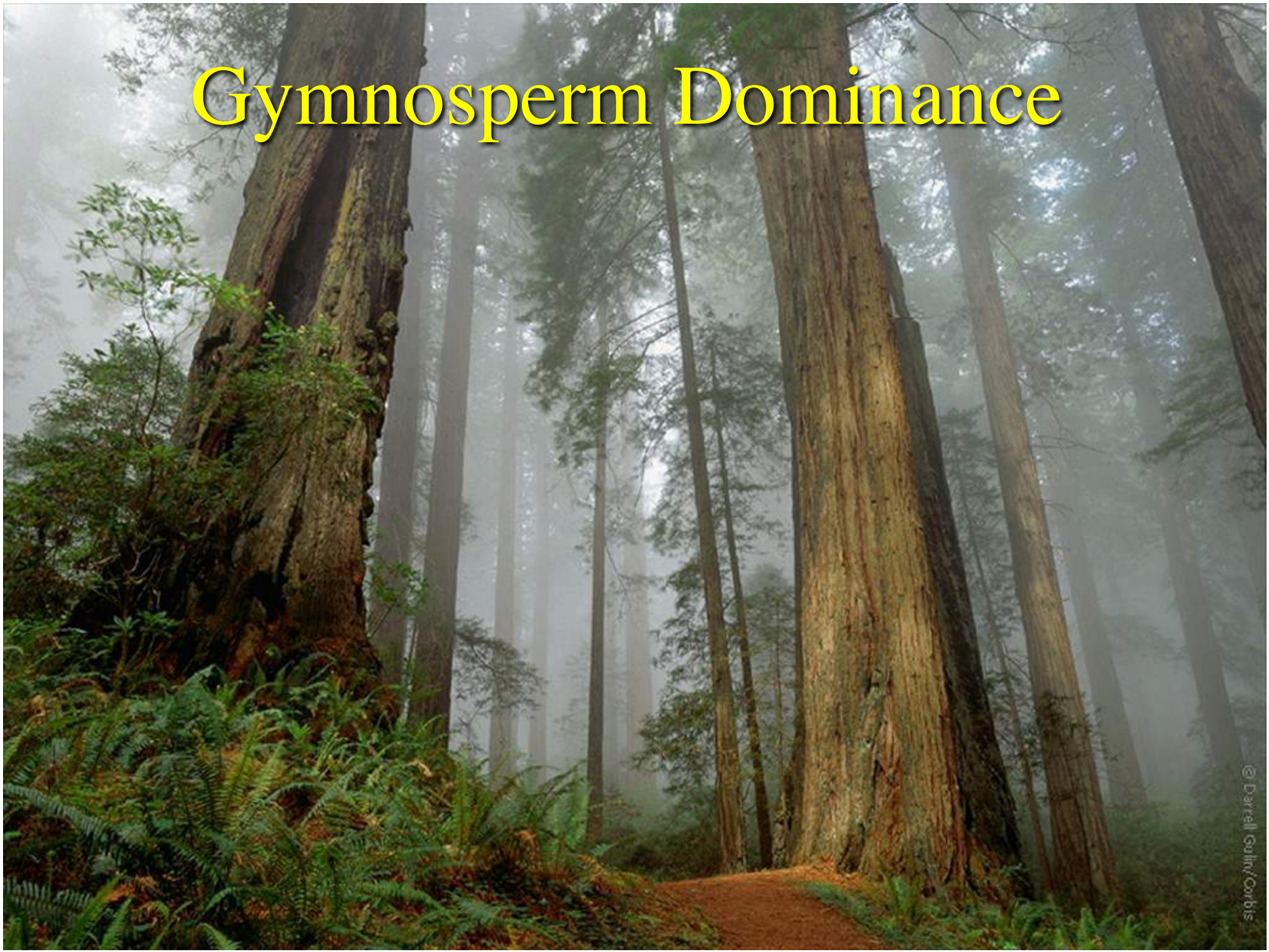
Angiosperm Dominance


Angiosperm Dominance

Angiosperm Dominance

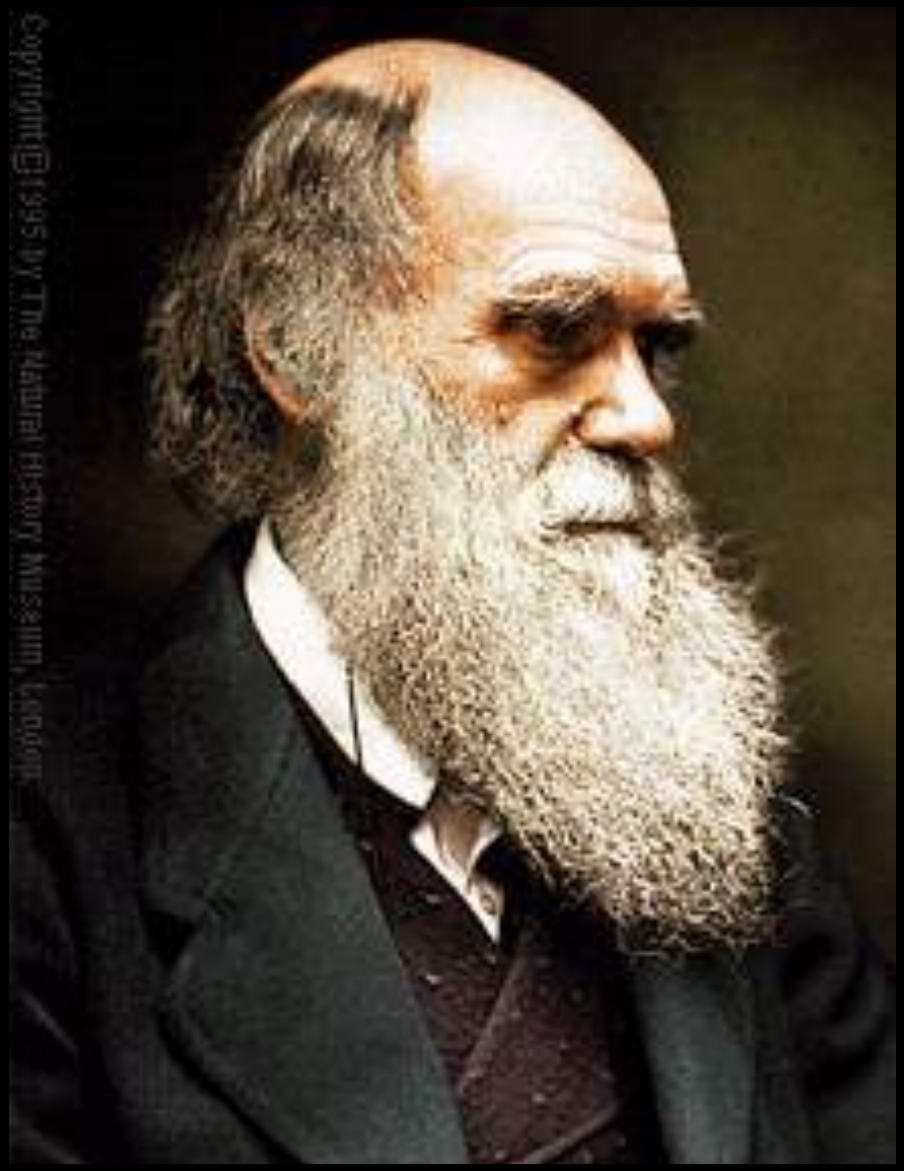


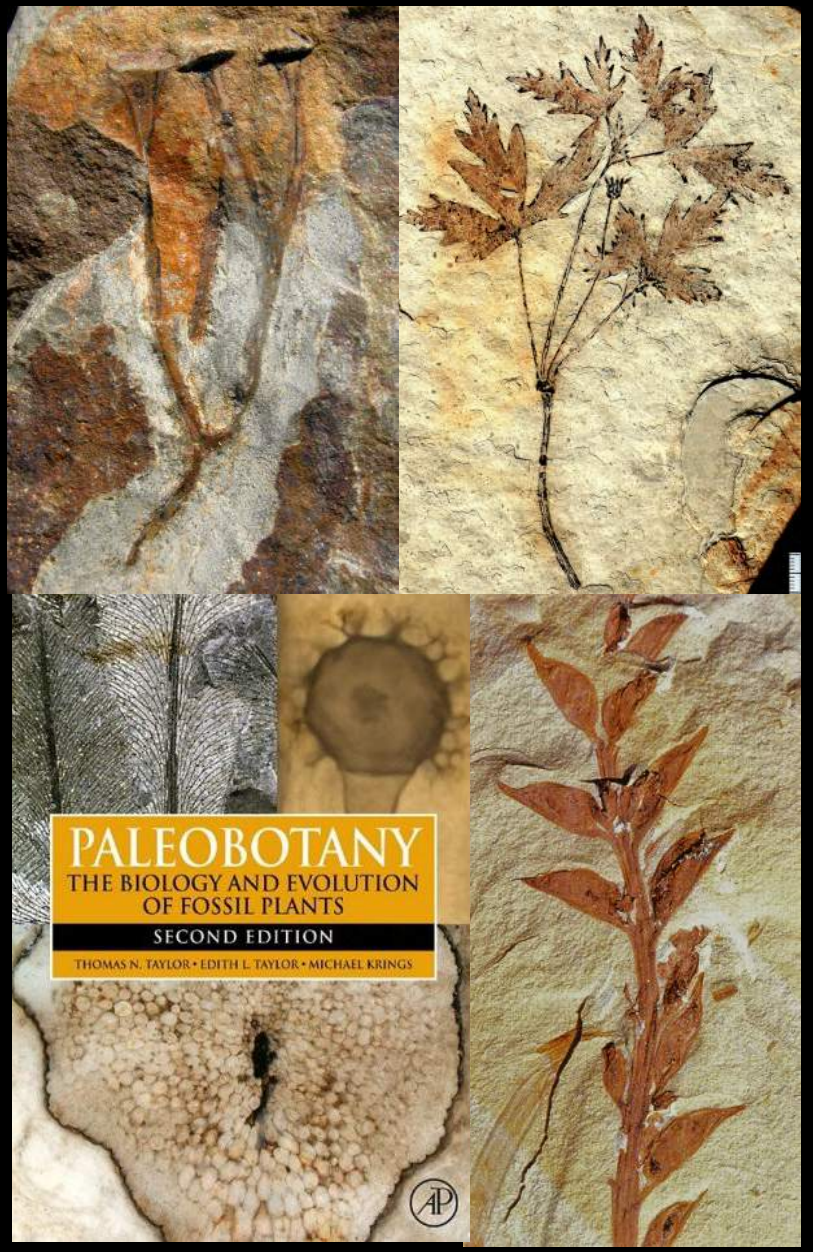
Gymnosperm Dominance



Gymnosperm Dominance

Angiosperms have NOT always dominated

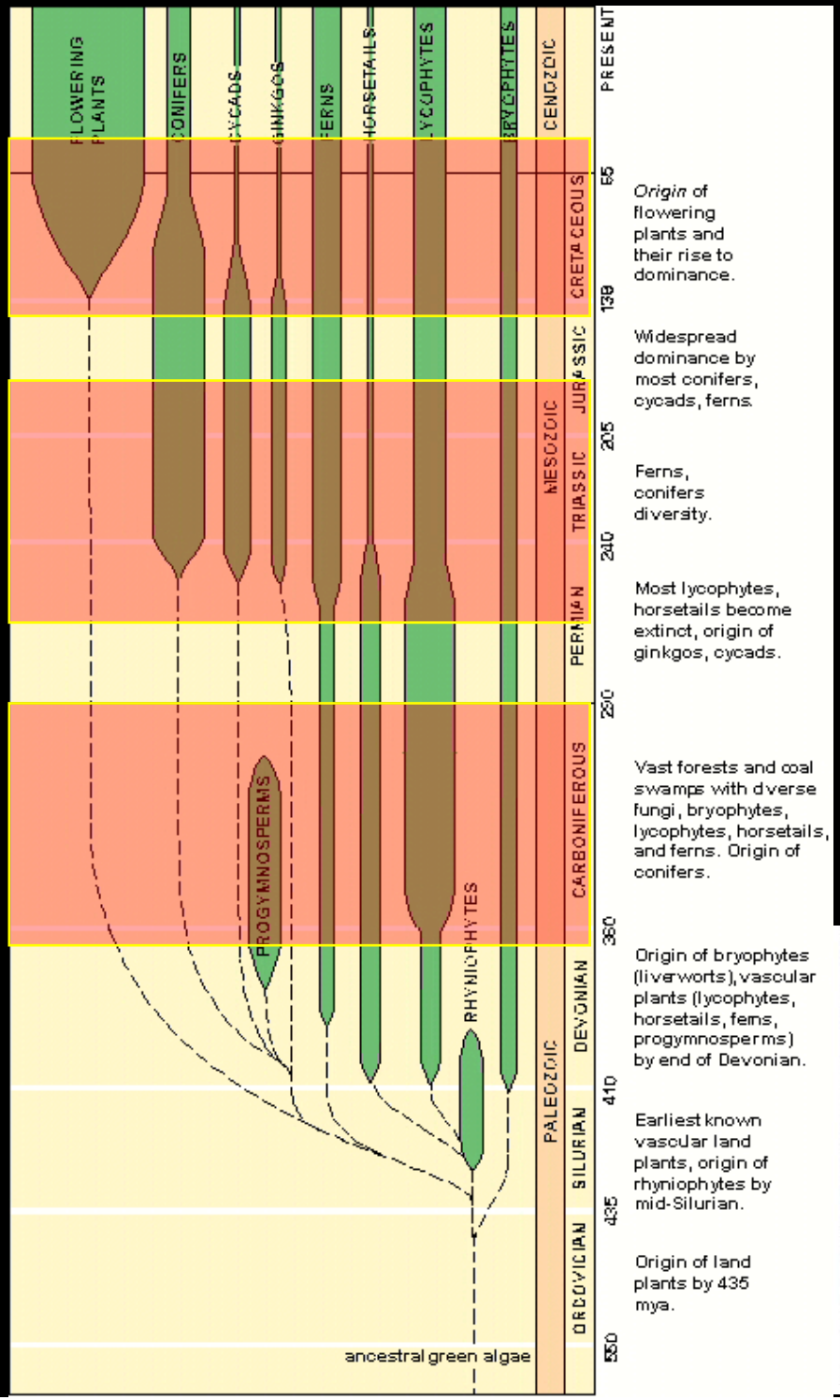




Fossil Record

as seen by Charles Darwin

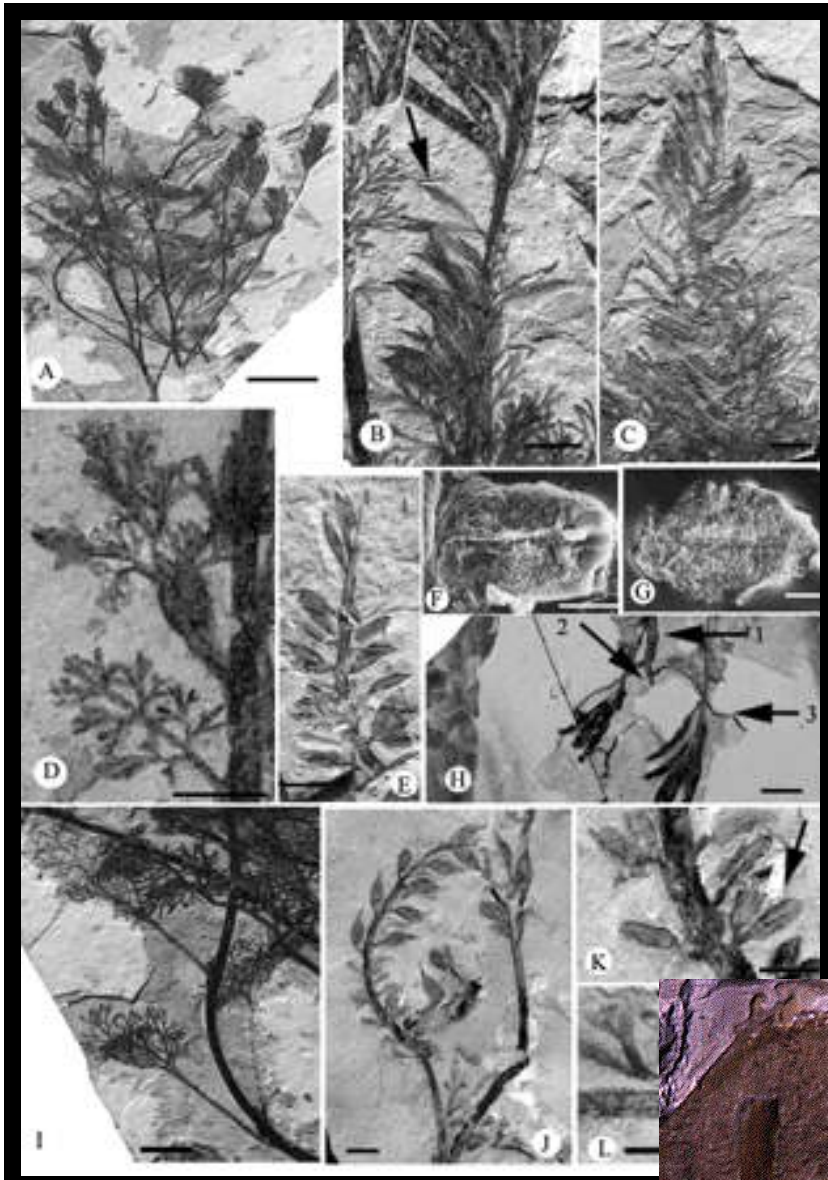
- tree-like lycopods, horsetails, primitive gymnosperms - the Carboniferous
- ferns, cycads, ginkgos, conifers - the Triassic/Jurassic
- flowering plants suddenly show up at start of Cretaceous



Fossil Record

as seen by Charles Darwin

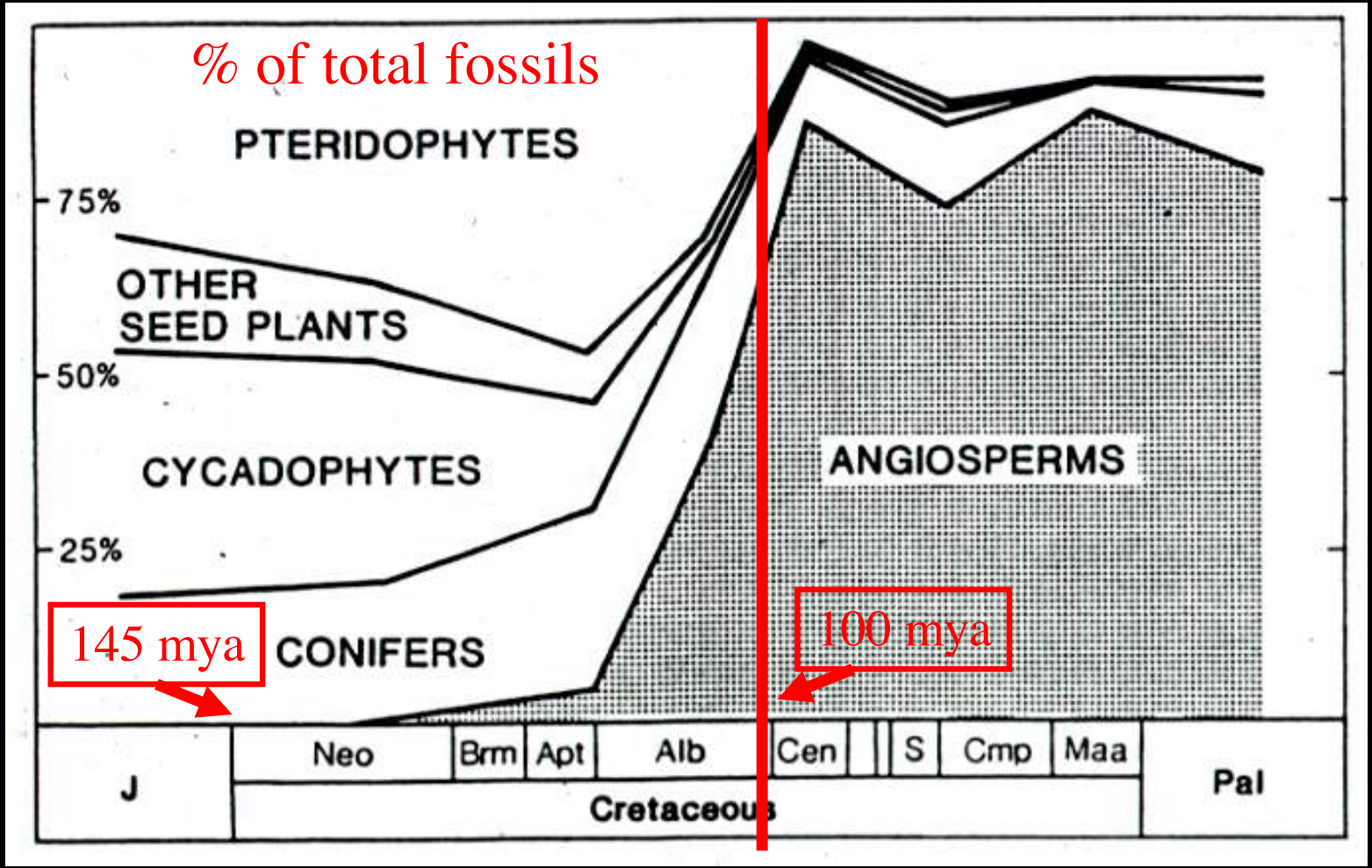
- by mid-Cretaceous, 50 families of angiosperms seen
  - including 5 monocot
  - including 4 ament/catkin bearing



Fossil Record

as seen by Charles Darwin

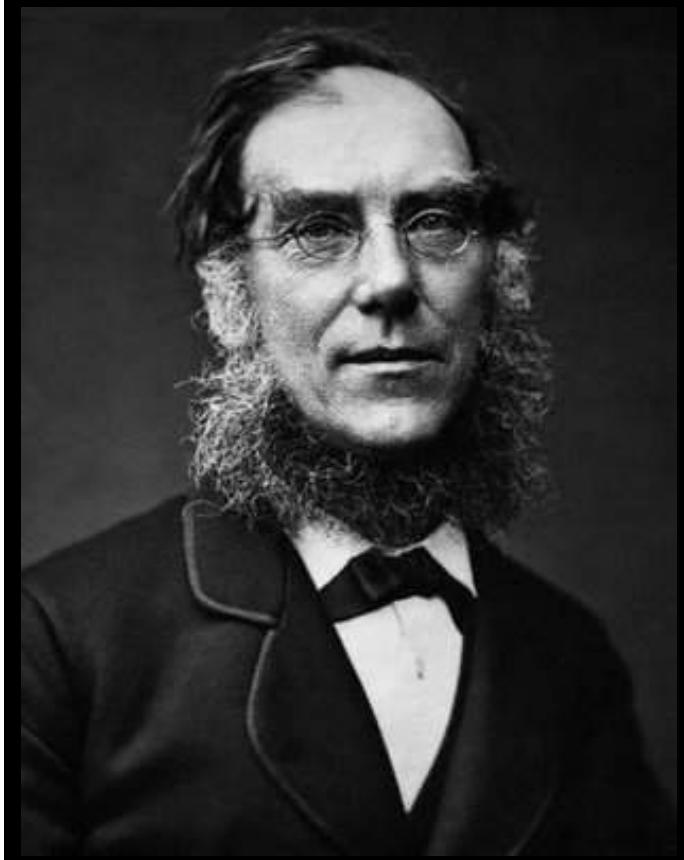
- by mid-Cretaceous, angiosperms also dominate the face of the earth (based on fossil diversity)



the Abominable Mystery

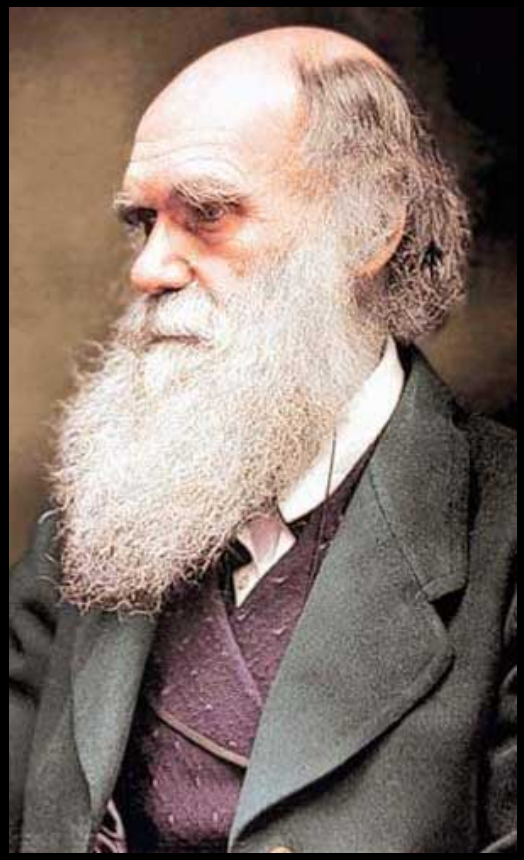
*"The rapid development, as far as we can judge, of all the higher plants within recent geological time is **an abominable mystery**"*

(Darwin, 1879, in a letter to Hooker)



Joseph Dalton Hooker

Director of the Kew Royal Botanic Garden and good friend of Darwin (the only acknowledged person in the "*Origin of Species*")



the Abominable Mystery

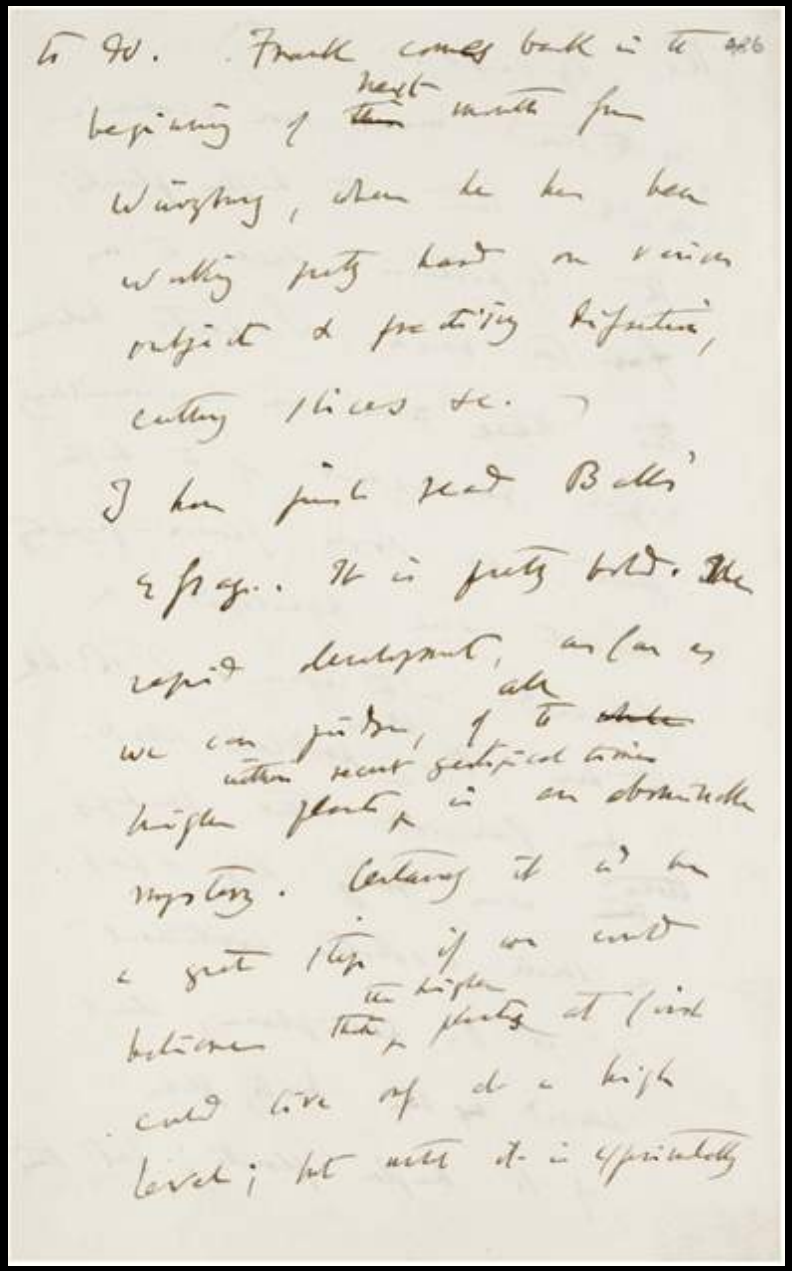
(page 3, letter of 22 July 1879)

- Continues with speculations on how to answer the mystery

  - originated in alpine conditions

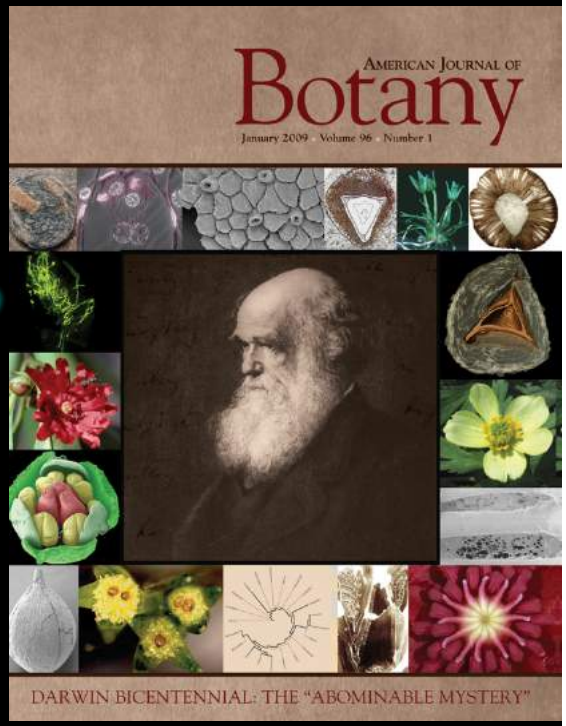
  - originated in isolated tropical island

  - arose in response to rise of ‘flower-frequenting insects’



the 2019 Questions

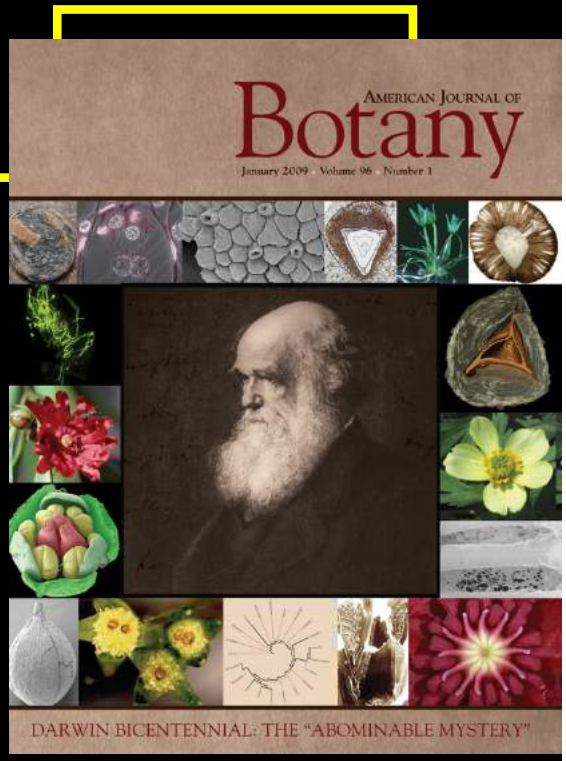
1. **When** did the Angiosperms arise?
2. **What** were the first Angiosperms?
3. **Where** did the Angiosperm arise?
4. **From what** Gymnosperm clade did the Angiosperms arise ?
5. **Why** did they take over the world's flora?



2009 AJB volume

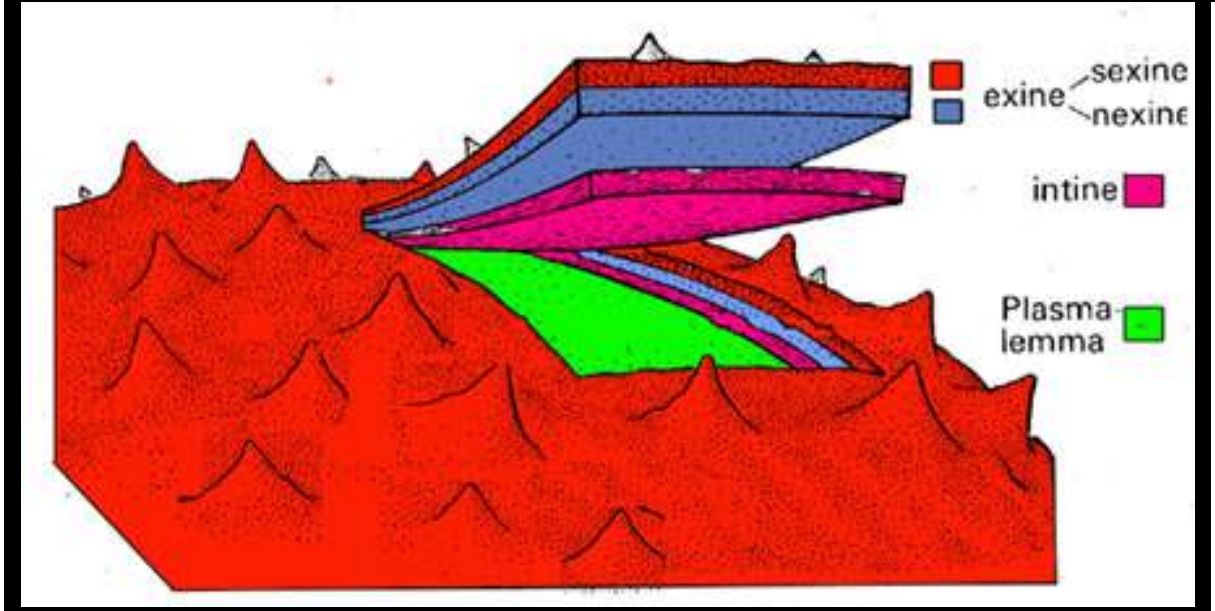
the 2018 Evidence

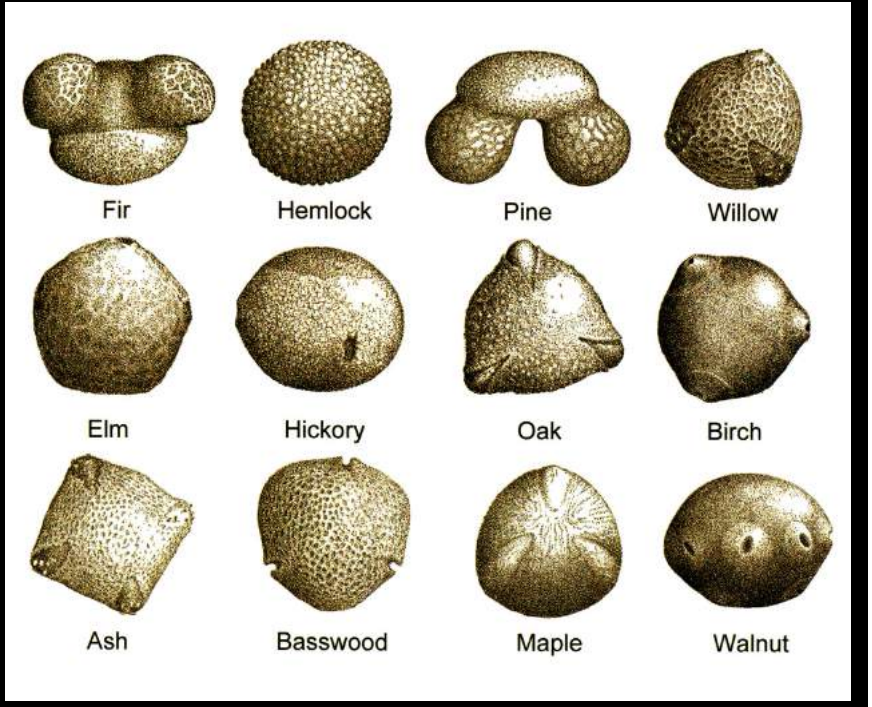
1. Modern fossil record
2. Geographical distributions
3. Morphological phylogenetics
4. Evo-devo studies of flowers
5. Molecular phylogenetics
6. Molecular “clocks”



Pollen Record

- **ubiquitous** - preserves well due to **exine** layer
- often **diagnostic** to specific gymnosperm or angiosperm groups





Pollen Record

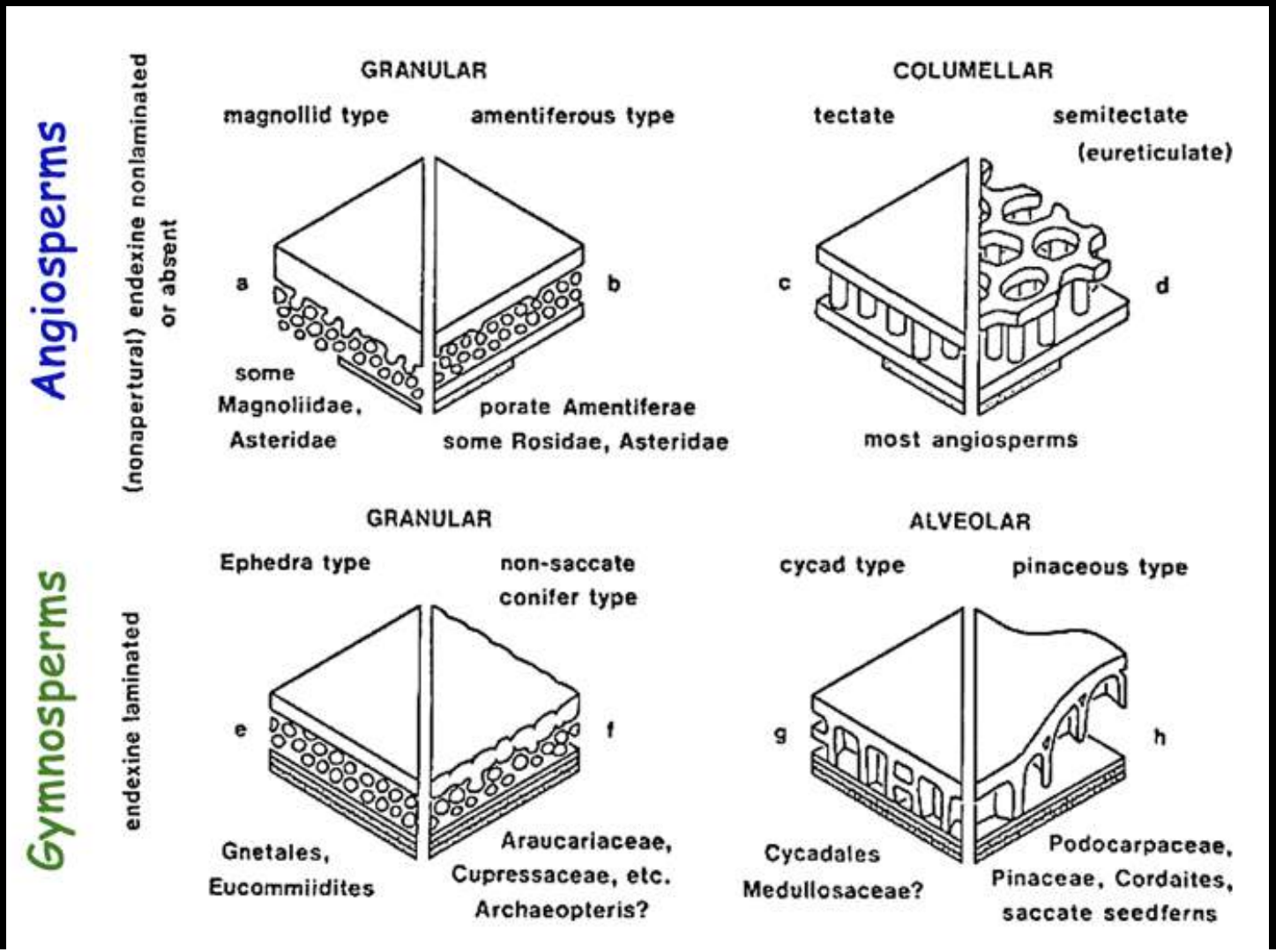
- **ubiquitous** - preserves well due to **exine** layer
- often **diagnostic** to specific gymnosperm or angiosperm groups
- but **different levels** of production and fossilization

- little *Senecio* pollen in tropics

- abundant pine pollen in lake sediments

Pollen Record

- gymnosperm vs. early angiosperm pollen differentiation often **requires TEM vs. SEM** visualization - both one pored



Pollen Record

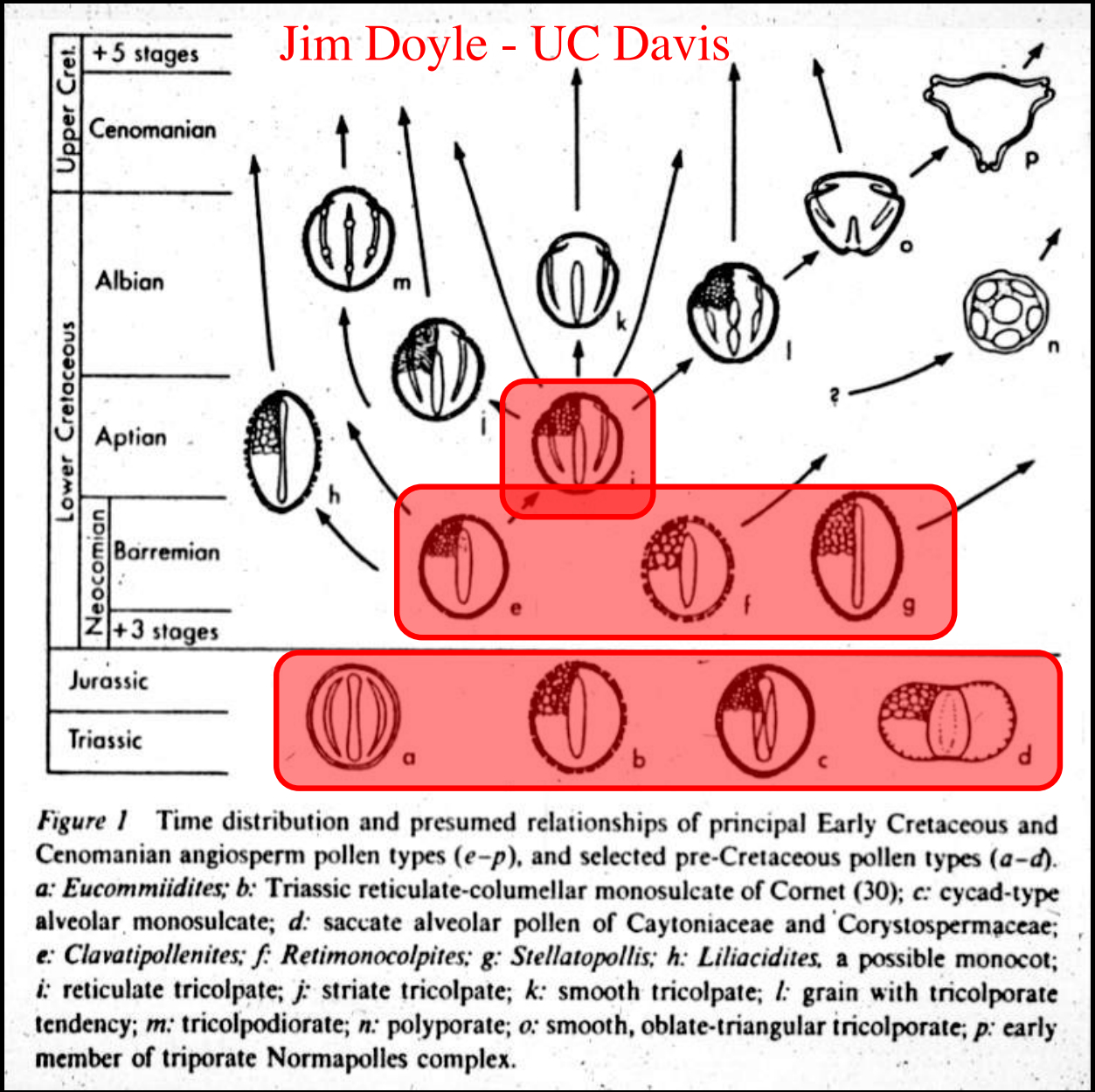
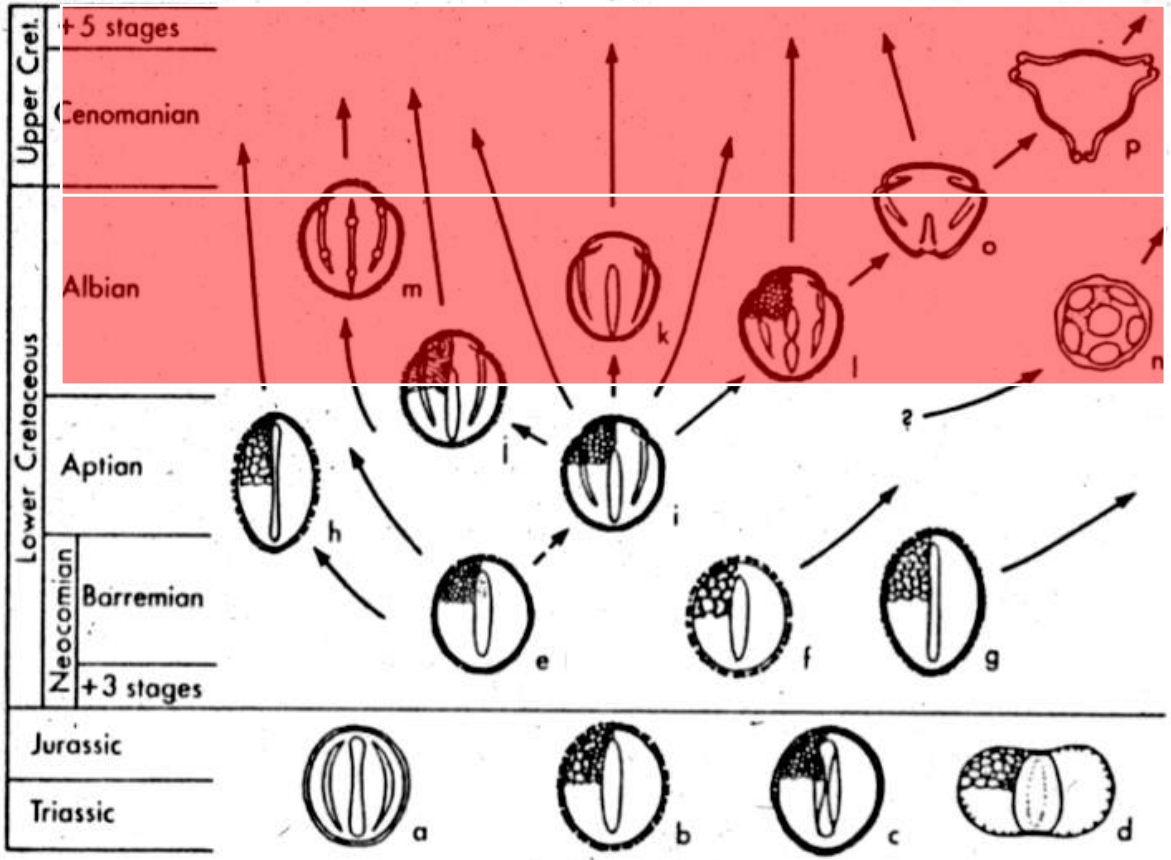


Figure 1 Time distribution and presumed relationships of principal Early Cretaceous and Cenomanian angiosperm pollen types (*e–p*), and selected pre-Cretaceous pollen types (*a–d*). *a: Eucommiidites; b:* Triassic reticulate-columellar monosulcate of Cornet (30); *c:* cycad-type alveolar monosulcate; *d:* saccate alveolar pollen of Caytoniaceae and Corystospermaceae; *e: Clavatipollenites; f: Retimonocolpites; g: Stellatopollis; h: Liliacidites,* a possible monocot; *i:* reticulate tricolpate; *j:* striate tricolpate; *k:* smooth tricolpate; *l:* grain with tricolporate tendency; *m:* tricolpodiorate; *n:* polyporate; *o:* smooth, oblate-triangular tricolporate; *p:* early member of triporate Normapolles complex.

- all pre-Cretaceous pollen = gymnosperm
- Neocomian (130 mya) = oldest angiosperm single pored pollen (basal angiosperms)
- Barr.-Aptian (125 mya) = oldest tricolpate pollen (eudicots)

Pollen Record



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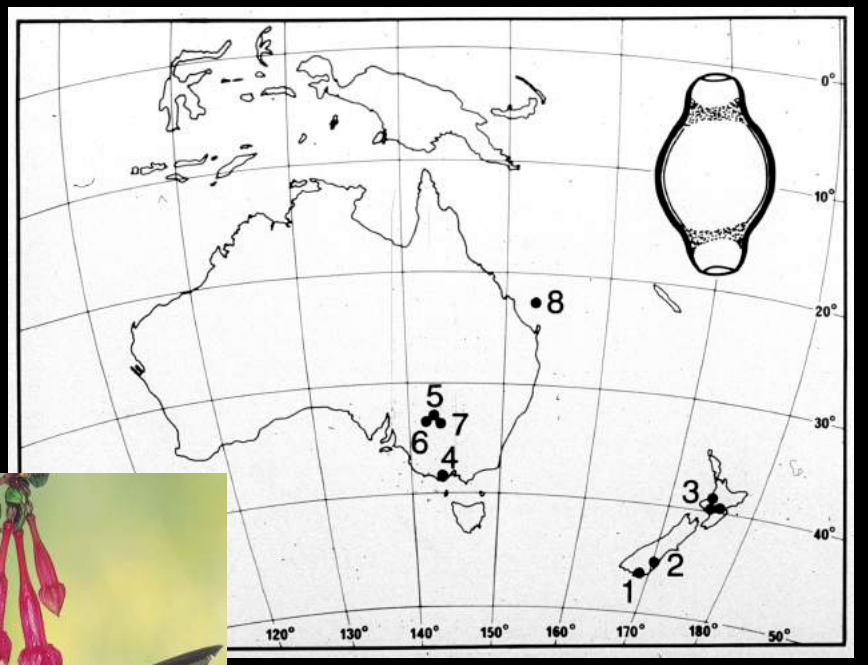
Albian (110 mya) diversity

- magnoliids
- monocots
- cordate-leaved eudicots
- aments - wind pollinated

Upper Cretaceous (100 mya) - angiosperm pollen dominates

Pollen Record

• pollen diversification continues through Upper Cretaceous into Tertiary



• family Asteraceae first seen in mid Eocene: 47 mya

• genus *Fuchsia* (Onagraceae) first seen 30 mya in Oligocene

Leaf Record

- consistent trends emerge with leaf fossils

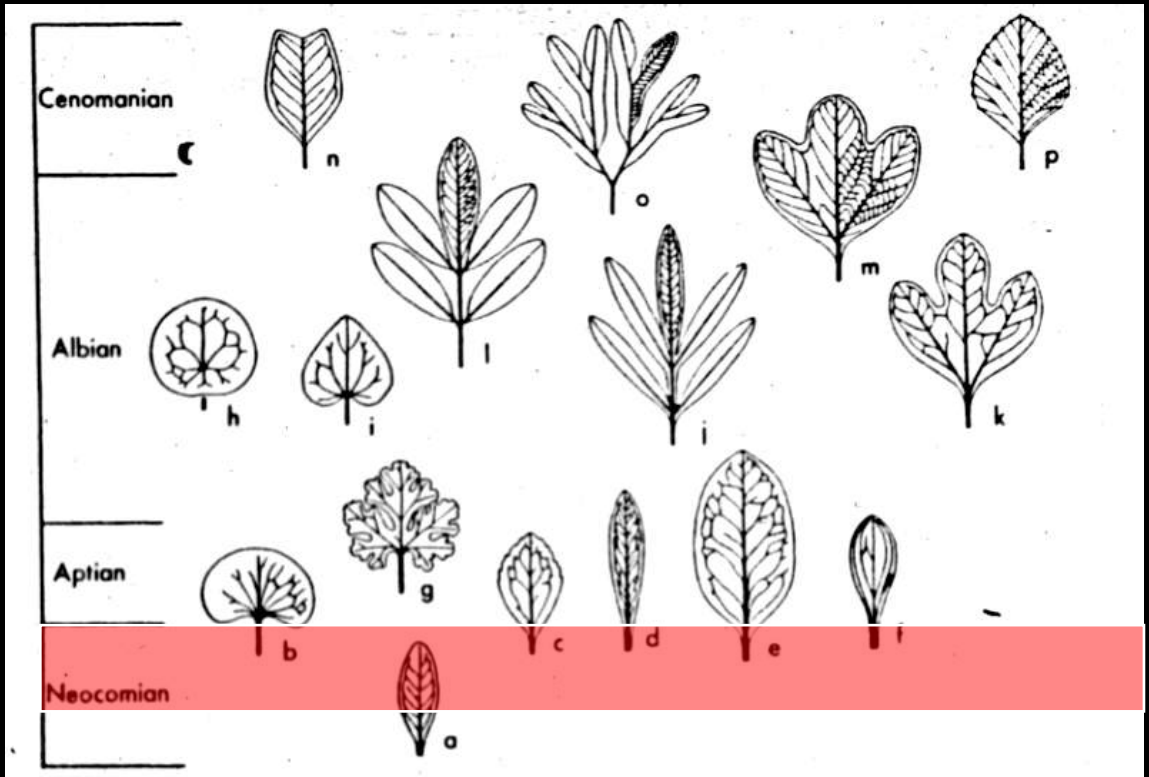
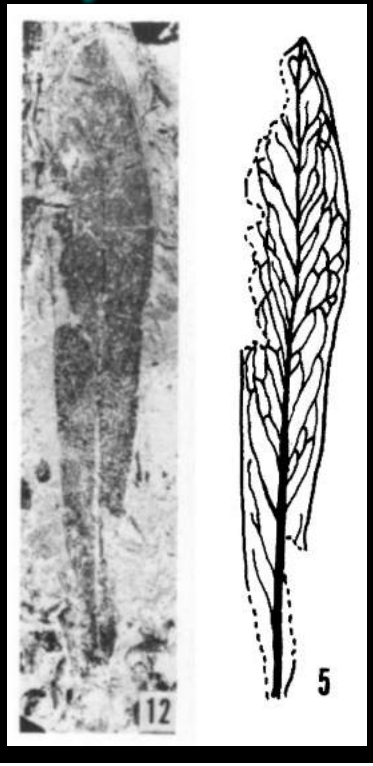


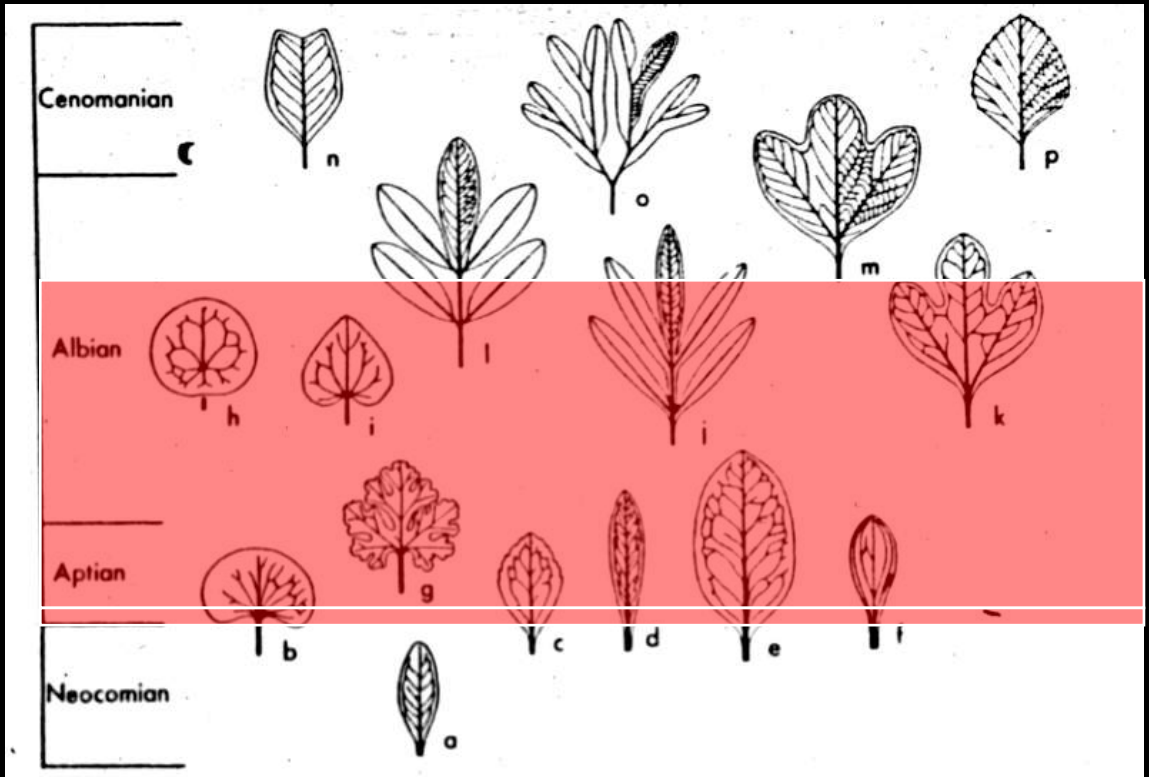
Figure 2 Principal Early Cretaceous and Cenomanian angiosperm leaf types. *a:* small, pinnately veined leaf of Vakhrameev (143); *b:* reniform; *c:* serrate; *d:* oblanceolate; *e: Ficophyllum; f: Acaciaephyllum,* a possible monocot; *g:* lobate reniform; *h:* peltate, actinodromous; *i:* ovate cordate; *j:* pinnatifid *Sapindopsis; k:* early plantanoid; *l:* compound *Sapindopsis; m:* later plantanoid, with rigidly organized fine venation; *n: Liriophyllum; o:* dichotomously compound; *p:* secondarily simple platanoid derivative.

- Neocomian (130 mya) *Rogersia* (basal angiosperm) simple, pinnately veined, entire



Leaf Record

- consistent trends emerge with leaf fossils



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- early Aptian (125 mya) *Archaefructus* (basal angiosperm) palmately compound
- Aptian to Albian (120-110 mya) = magnoliids (pinnate veins), cordates (palmate veins), monocots (parallel veins)

Leaf Record

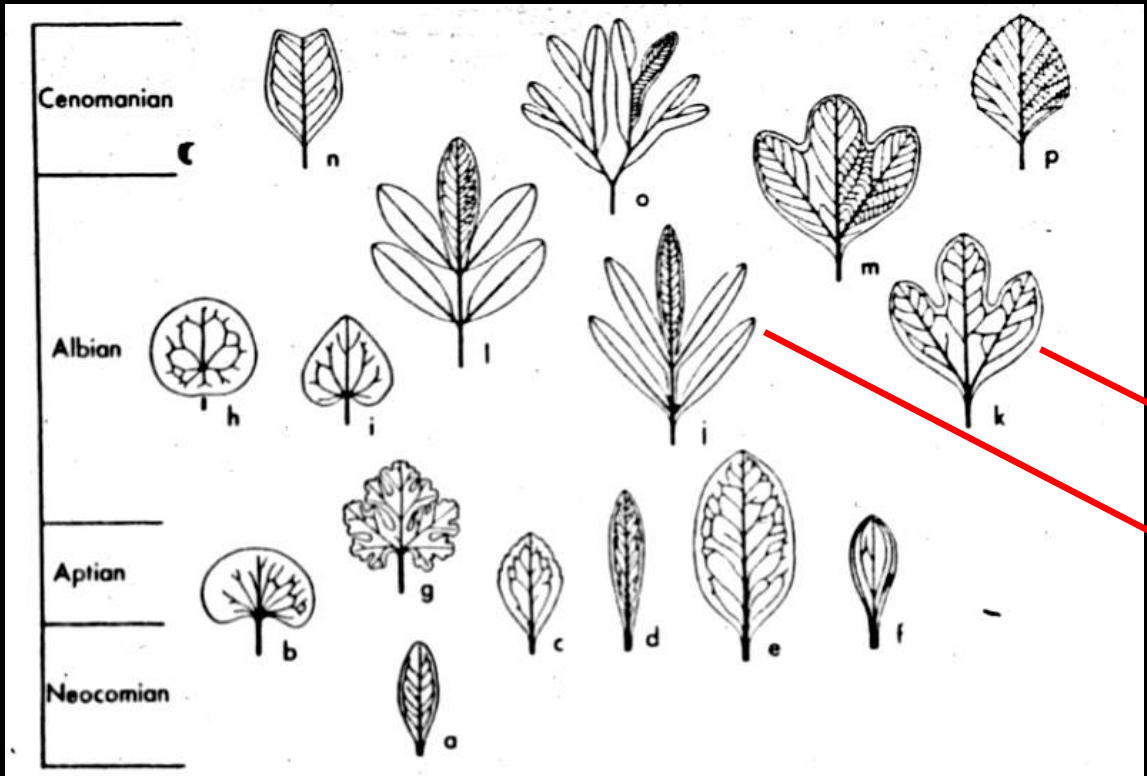
- consistent trends emerge with leaf fossils

great leaf diversity within 15my

- early Aptian (125 mya) *Archaefructus* (basal angiosperm) palmately compound
- Aptian to Albian (120-110 mya) = magnoliids (pinnate veins), cordates (palmate veins), monocots (parallel veins)

Leaf Record

- consistent trends emerge with leaf fossils



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- by Upper Cretaceous (100 mya) a variety of **primitive eudicot leaves** are seen

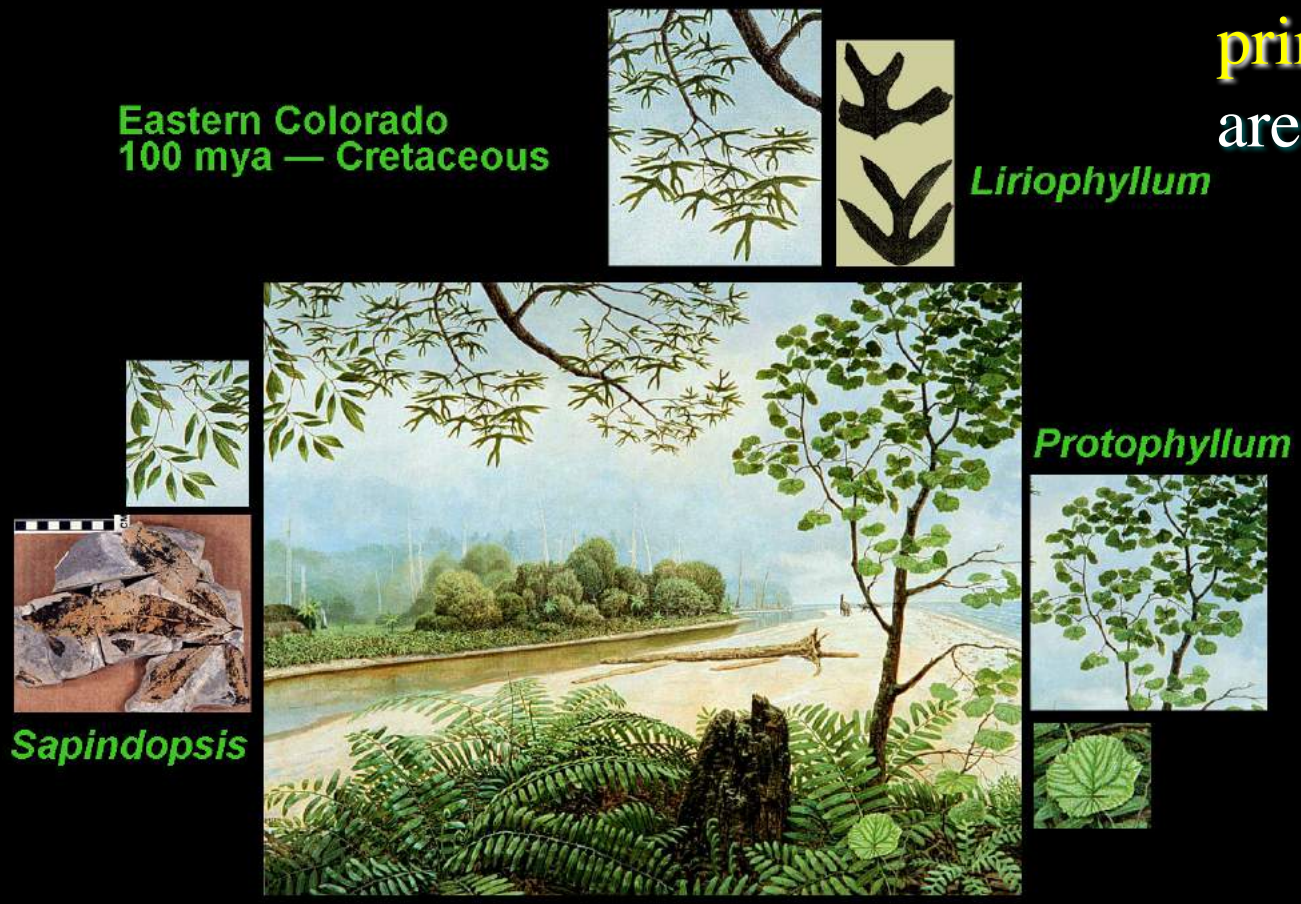
Platanoid - lobed

Sapindopsis - compound

Leaf Record

- consistent trends emerge with leaf fossils

- by Upper Cretaceous (100 mya) a variety of **primitive eudicot leaves** are seen



Flower Record

• the "Magnolia = primitive" idea has biased the way paleobotanists have looked at the fossil record

1. bisexual flower
2. ∞ spirally arranged stamens & carpels
3. ∞ perianth parts
4. cone-like receptacle
5. beetle pollination

• what does the fossil record actually say?

Flower Record

• large flowered, insect-pollinated flowers are seen (such as these 98-90 mya mid-late Cretaceous fossils) . . .

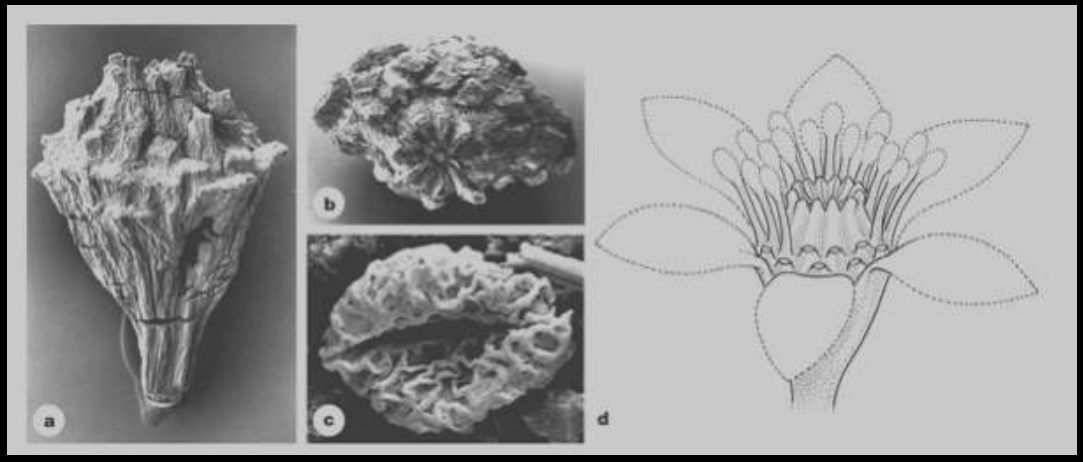
Archaeanthus (Magnoliaceae) – from Kansas 98-95 mya

Magnoliaceae with stingless bee – 90 mya

Flower Record

• large flowered, insect-pollinated flowers are seen (such as these 95-85 mya late Cretaceous fossils) . . .

. . . but the earliest and most numerous are small, bisexual or unisexual, wind or insect-pollinated



Science Times

The New York Times

In Tiny Fossils, Botanists See Flowery World

Empty Lot Yields Trove of Ancient Plants

By CAROL KAESUK YOON

Flower Record

- what are the earliest fossil flowers?

Fossil, After 120 Million Years, Is Believed the Oldest Flower

By JOHN NOBLE WILFORD

A tiny fossilized plant, barely one inch tall and resembling today's black pepper plant, has been identified by scientists at Yale University as the oldest known flower. It lived 120 million years ago and its flower was probably a drab green or beige — hardly the thing to inspire nosegays for dinosaurs.

Botanists were not so much surprised to find a fossil flower more than five million years older than anything previously discovered as they were by the plant's humble size and appearance. Textbooks and museum murals depicting scenes of prehistoric life, reflecting the traditional hypothesis, usually picture showy magnolia-like flowers with large, shiny foliage.

Because the fossil had characteristics of the two major branches of modern flowering plants, scientists said the plant could be their common ancestor and represent a kind of missing link needed to understand plant evolution. Nearly all the world's plants that bear seed, about a half million species, are likely descendants of the small plant.

"This insignificant-looking flowering herb is packed with information about plant evolution that could be of incalculable value," said Dr. Leo J. Hickey, a paleobiologist at Yale University who made the discovery with Dr. David W. Taylor, a Yale botanist.

Plant Grows Near Melbourne

The discovery, being reported today in the journal Science, was made after Dr. Taylor saw a published description of the fossil, which had been dug up in southeastern Australia near Melbourne and labeled a fern. Examining detailed photographs of the fossil under a microscope, Dr. Taylor and Dr. Hickey identified the plant as a flowering angiosperm — with fruit surrounding its seeds.

"We're looking at the origin of flowering plants, which are the dominant plants on earth," Dr. Hickey said yesterday in a telephone interview.

The scientists said the plant grew in scraggly underbrush on the edge of a pond in the Koonwarra area of Australia; it had a mild climate and probably was a perennial with an underground stem. Similar flowering plants can be found today in marshes. Gardeners as well as botanists might recognize similarities between the Koonwarra plant and wild yams, cat briar, lizard's tail, and the black pepper plant.

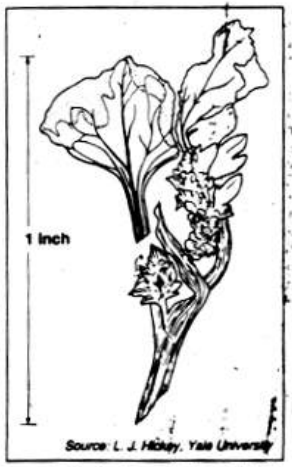
Dr. Peter Crane, an authority on plant evolution at the Field Museum of Natural History in Chicago, said the finding was "certainly interesting and important." But he cautioned that the fossil was not well preserved, which could prevent scientists from determining the plant's structure in more detail.

More Diversity in Early Flowers

"We're starting to see pretty clearly that by no means everything then was put together like a magnolia flower," Dr. Crane said. "There was more diversity in early flowering plants. If anything, the evidence favors the view that magnolias evolved slightly later than had been assumed."

The earliest flowering plants may date back to 130 or 140 million years ago, scientists estimate. It has been determined that some fossil pollen from that period came from flowering plants. But the full plants and flowers of anything that old have yet to be identified.

Most current studies have concentrated on flowering plants from about 100 million years ago, when they were becoming abundant forms of vegetation. The dogma, as Dr. Crane put it, had been that the primordial flowers probably grew on shrubs or trees. In addition to the flowers resembling the southern magnolia, plants of that early period were members of modern groups composed of avocado, bay leaves and sycamore.



The New York Times/Hank Iken/Feb. 9, 1990

Artist's rendering of the fossil of the oldest known flower, called the Koonwarra plant.

THE NEW YORK TIMES **NATIONAL** FRIDAY, FEBRUARY 9, 1990

1990 - Leo Hickey

- 120 mya - Australia
- small, unisexual flowers
- placed into Piperales (pepper, wild ginger)

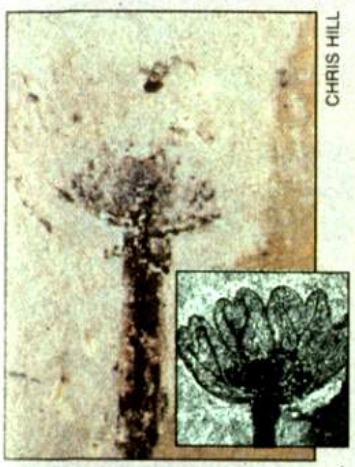
Flower Record

- what are the earliest fossil flowers?

The World's Oldest Flower

A British scientist claims to have discovered the world's oldest flower in 130-million-year-old clay rocks in the south of England.

Flowering plants or angiosperms, which range from grasses to oaks, reproduce via ovules borne in an enclosed cavity. They have dominated the world's vegetation for the last 65 million years, but paleobotanists still argue over fundamental questions such as which group is the most primitive and from what did they evolve.



Ancient bloom. Cretaceous flower imprint in English clay. Inset: computer-enhanced image. Actual size is 7 mm.

Some scientists have suggested that the earliest flowering plants were large, woody, magnolialike shrubs. But the new find, reported by paleobotanist Chris Hill in the February issue of *Cretaceous Research*, bolsters the notion, first suggested by U.S. scientists 6 years ago, that the plants started small.

Hill was prompted to search rock formations called Weald Clay in southern England after reading a report in *Science* (9 February 1990, p. 702) by David Taylor and Leo Hickey of Yale University. Their analysis of angiospermlike fossil plants from this geologic period, the Cretaceous, in Australia indicated that early flowering plants may have been simple, fragile herbs with small reproductive organs—that is, flowers.

Hill's plant fossil, found at the Smokejacks Brickworks in Surrey, seems to fulfill this prediction. It was a relatively small (25 cm high) herb. Most important, it combines a primitive fernlike anatomy and leaves with more advanced branching and small flowerlike reproductive structures. It probably lived in water (it was found in waterland sediment, and some leaves resemble those of modern aquatic plants). Hill, who has christened his find *Bevhalstia pebja*, says that its form is quite unlike any other plant from the Early Cretaceous.

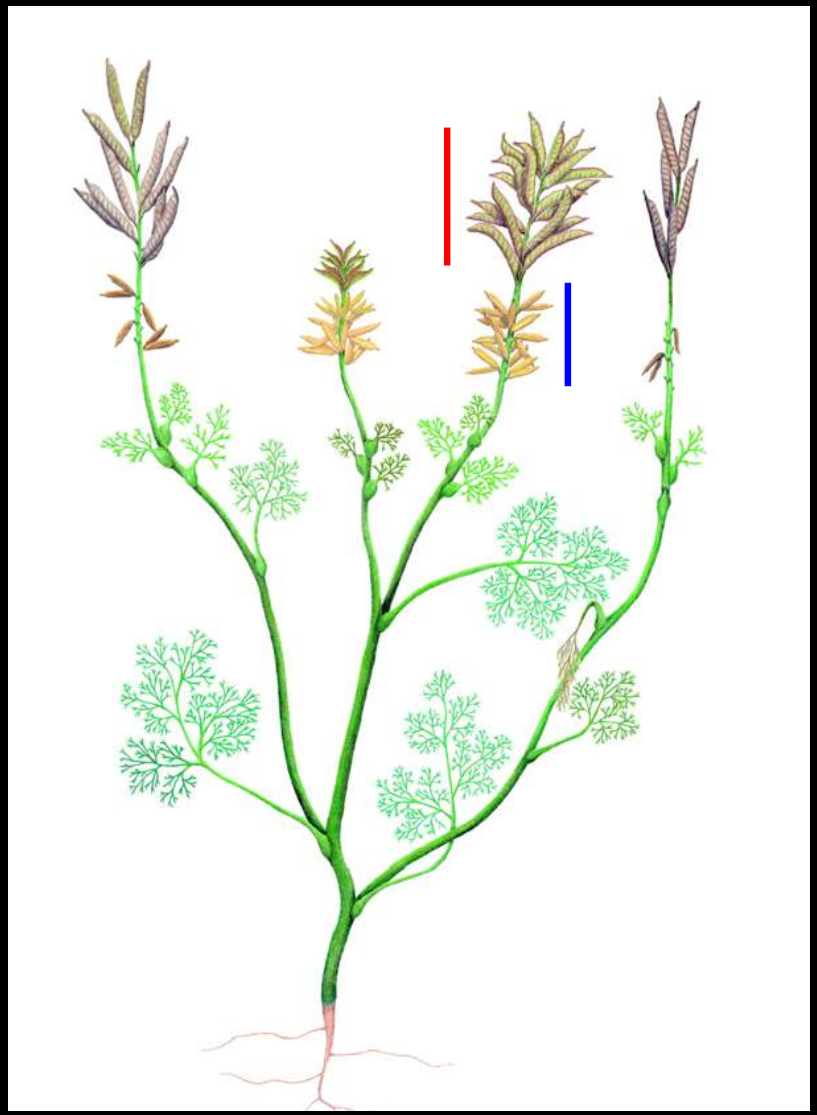
David Batten, an expert on Cretaceous pollen at the University of Wales, says the find is "interesting because it forms a continuation of the macrofossil record of angiospermlike plants deeper into the Lower Cretaceous." Pollen believed to be from angiosperms had already been located at this level, but no flowers. Now that Hill has found a flower, the hunt is on for pollen that will clinch its identification.

1996 - Chris Hill

- *Bevhalstia pebja*
- 130 mya - England
- small, 25cm aquatic herb
- dissected leaves
- *most not convinced it is an angiosperm*

Flower Record

- what are the earliest fossil flowers?

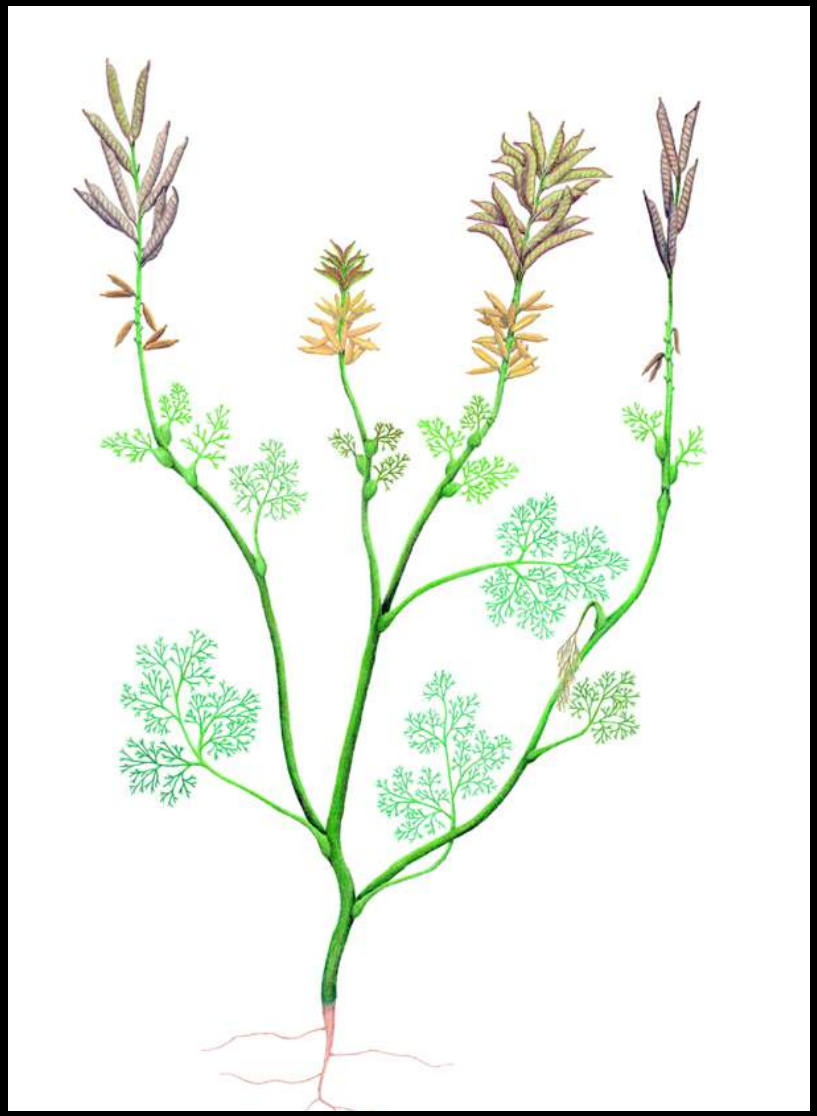


1998 - David Dilcher & Chinese colleagues

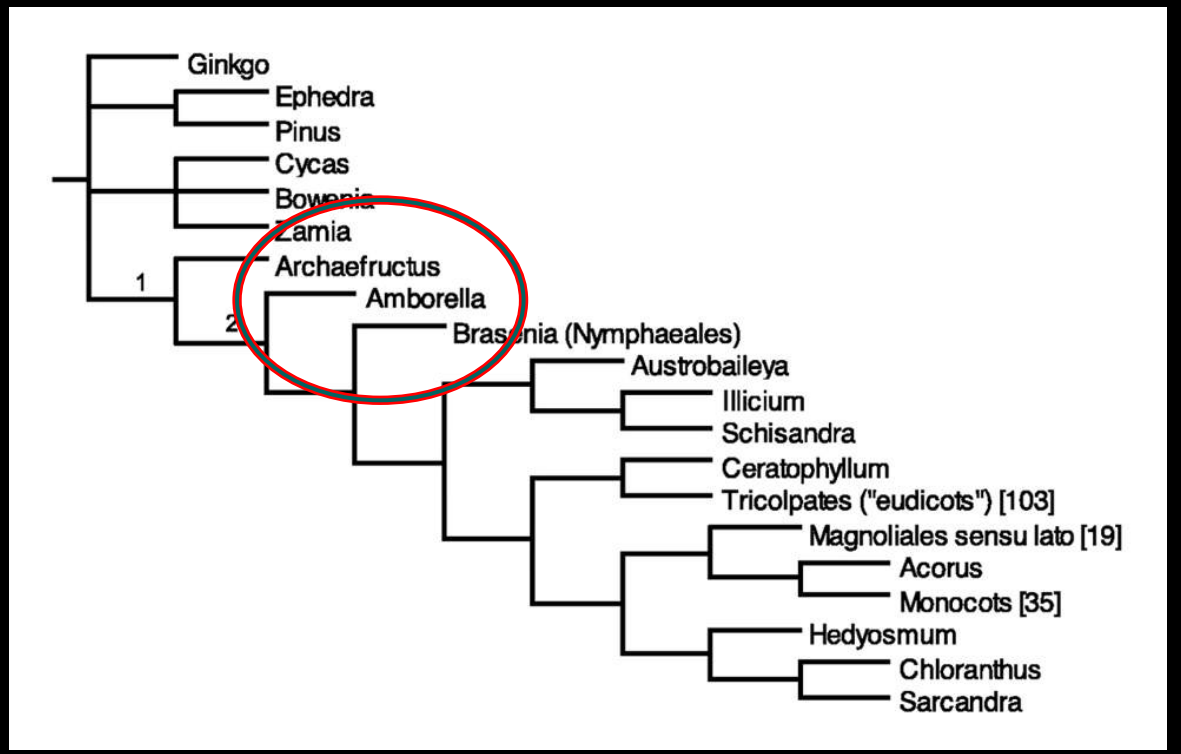
- *Archaefructus*
- 125 [135 1st] mya - China
- small, dissected leaves
- stamens and carpels on long axis

Flower Record

- what are the earliest fossil flowers?



- morphology phylogenetic analyses place it before *Amborella*



Flower Record

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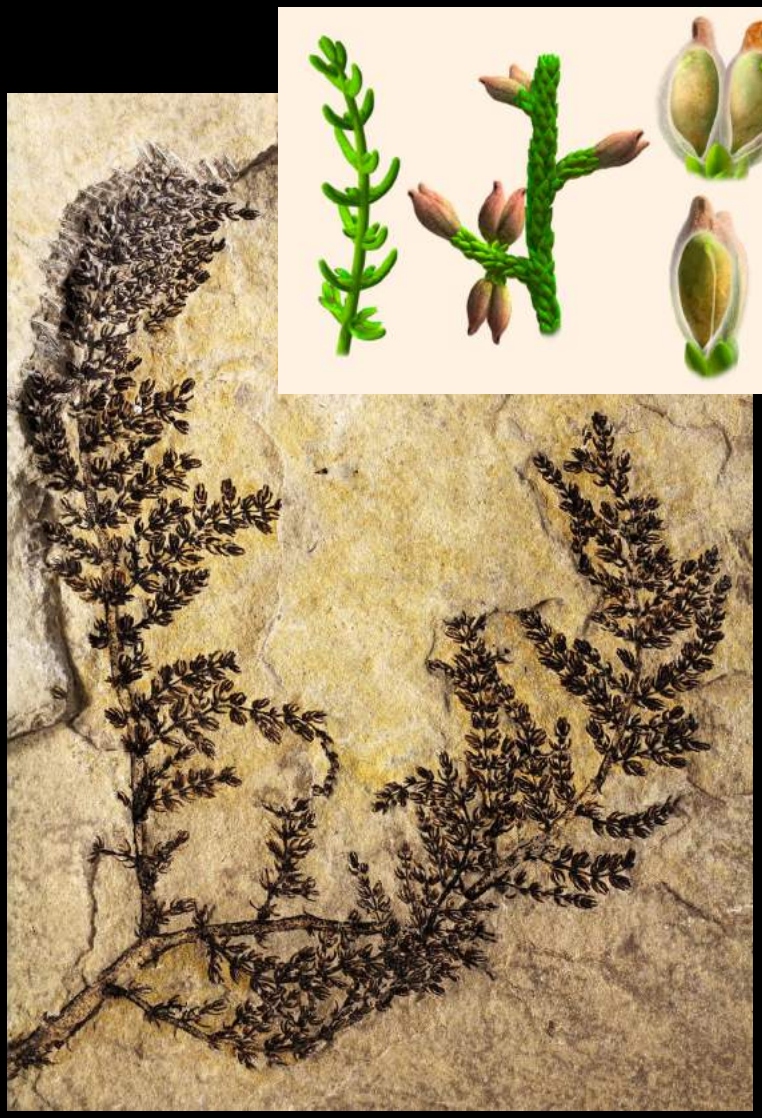
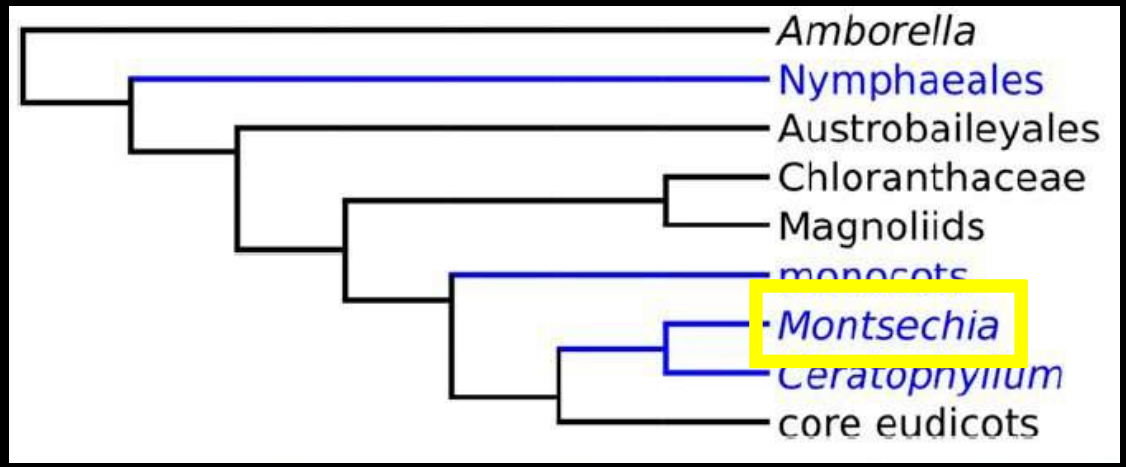


2015 - David Dilcher & Spanish colleagues

- *Montsechia*
- **125-130 mya - Pyrenes**
- aquatic, fruiting



Flower Record

- what are the earliest fossil flowers?

2018 – Qiang Fu & Chinese colleagues

- *Nanjinganthus*
- **174 mya Jurassic! - China**

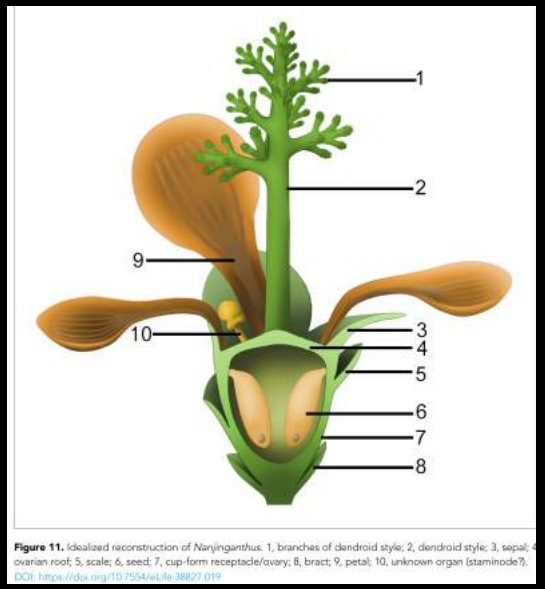


Figure 11. Idealized reconstruction of *Nanjinganthus*. 1, branches of dendroid style; 2, dendroid style; 3, sepal; 4 ovarian roof; 5, scale; 6, seed; 7, cup-form receptacle/ovary; 8, bract; 9, petal; 10, unknown organ (staminode?).
DOI: https://doi.org/10.7554/eLife.38827.019

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RESEARCH ARTICLE

An unexpected noncarpellate epigynous flower from the Jurassic of China

Qiang Fu[1], Jose Bienvenido Diez[2], Mike Pole[3], Manuel García Ávila[2,4], Zhong-Jian Liu[5]*, Hang Chu[6], Yemao Hou[7], Pengfei Yin[7], Guo-Qiang Zhang[5], Kaihe Du[8], Xin Wang[1]*

Flower Record

- what are the earliest fossil flowers?

2018 – Qiang Fu & Chinese colleagues

- *Nanjinganthus*
- **174 mya Jurassic! - China**
- fierce debate!

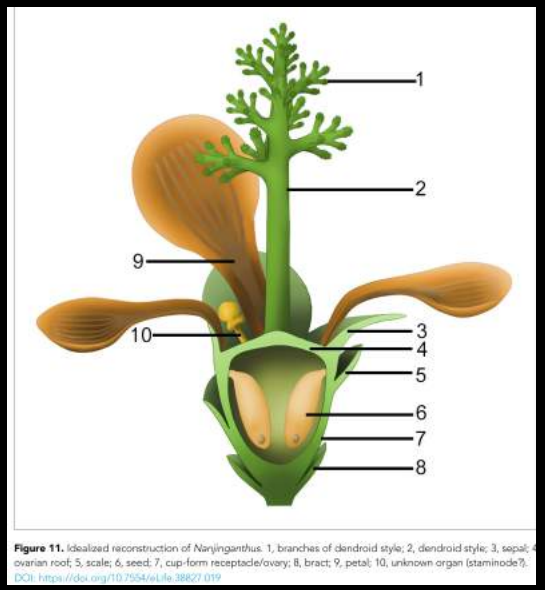


Figure 11. Idealized reconstruction of *Nanjinganthus*. 1, branches of dendroid style; 2, dendroid style; 3, sepal; 4 ovarian roof; 5, scale; 6, seed; 7, cup-form receptacle/ovary; 8, bract; 9, petal; 10, unknown organ (staminode?).
DOI: https://doi.org/10.7554/eLife.38827.019

Hunting the Snark: the flawed search for mythical Jurassic angiosperms

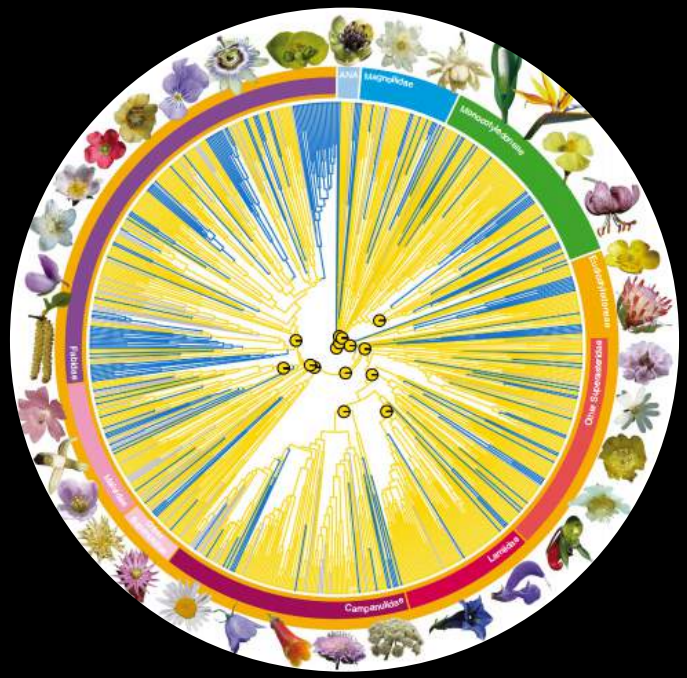
Richard M. Bateman

Jodrell Laboratory, Royal Botanic Gardens Kew, Richmond, Surrey, TW9 3DS, U.K.

Flower Record

- what did the earliest flower look like based on morphological analyses?

2017 – Herve Sauquet et al. (reading!)

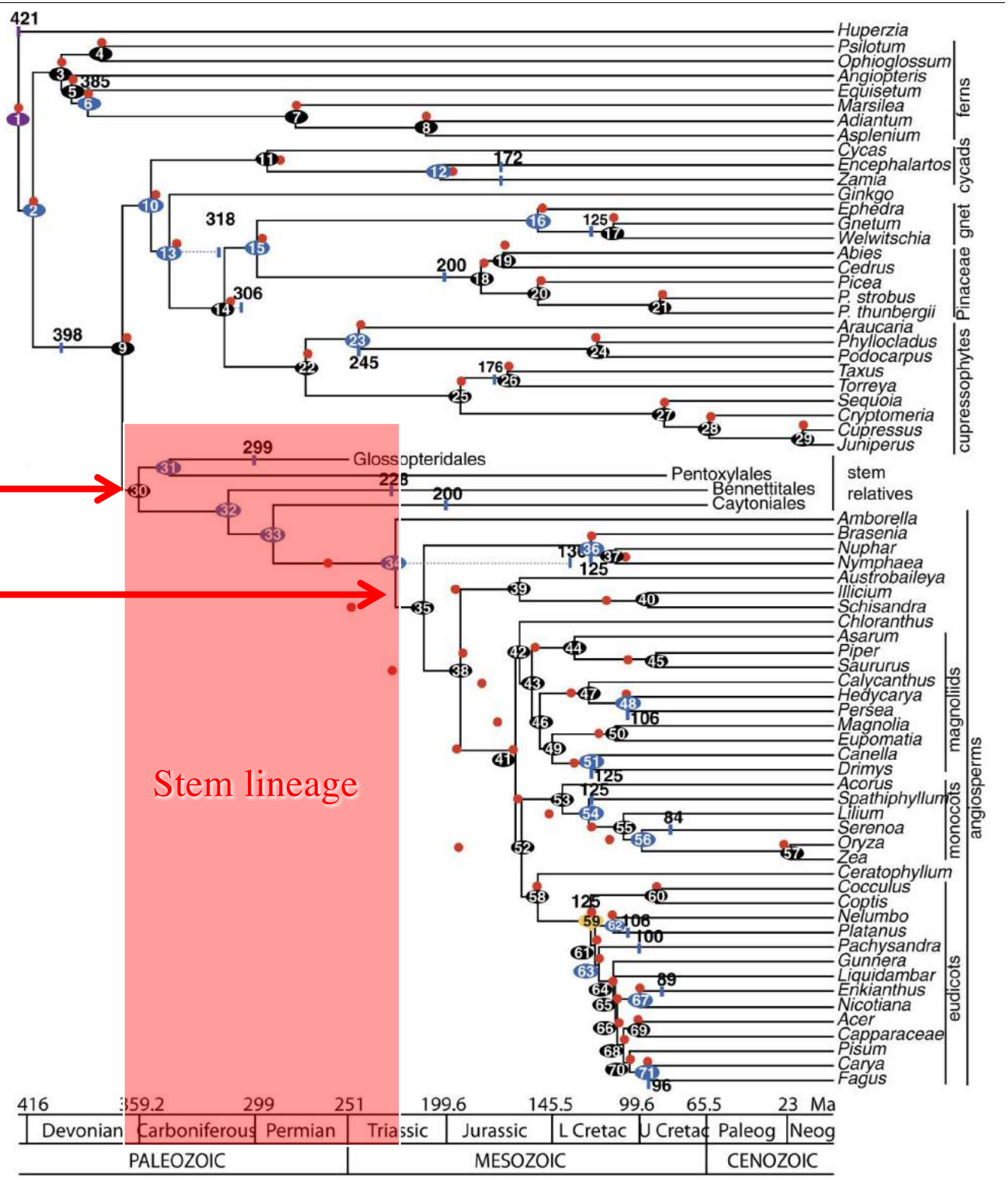


Summary of Angiosperm Evolution

1. When did the Angiosperms arise?

- Fossils - after boundary of Jurassic and Cretaceous – 130 mya
- DNA - some molecular clocks suggest >200 mya

- stem node with living gymnosperms — 350 mya
- crown node of living angiosperms — 225 mya



Magallón 2010

Summary of Angiosperm Evolution

1. When did the Angiosperms arise?

- perhaps older but unseen (in fossil record) radiation of angiosperms
- perhaps older radiation but we can't tell them apart from ancestors (share features of gymnosperms and some but not all of angiosperms)
- perhaps "molecular clock" methods are flawed – not really that old

Summary of Angiosperm Evolution

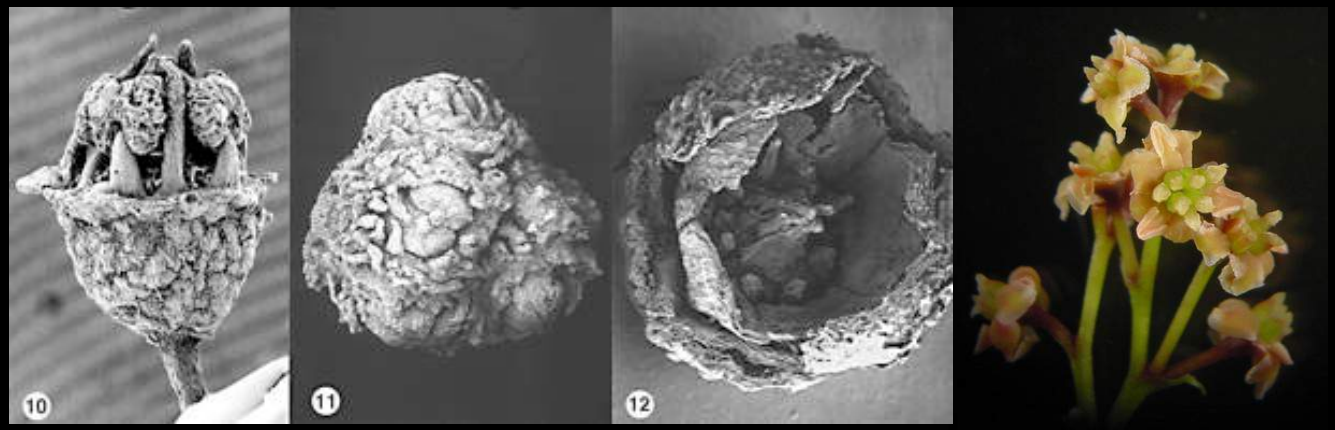
2. What were the first Angiosperms?

- "*Magnolia* = primitive" not justified
- *Amborella* and water lilies are first extant taxa to separate

Summary of Angiosperm Evolution

2. What were the first Angiosperms?

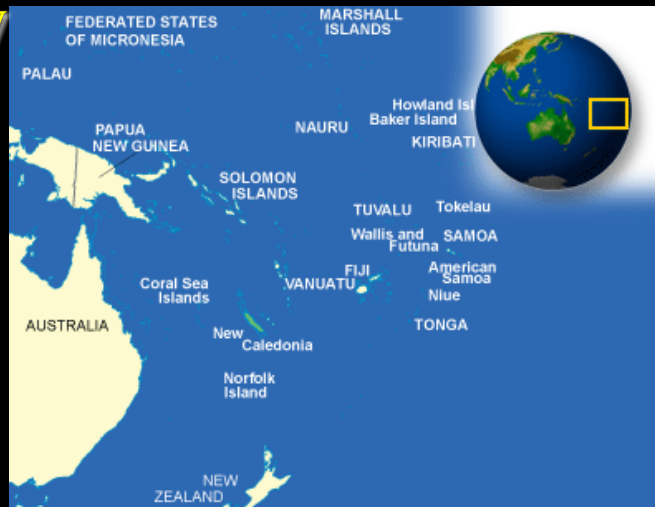
- "*Magnolia* = primitive" not justified
- *Amborella* and water lilies are first extant taxa to separate
- earliest extinct fossils are small, probably aquatic plants



Summary of Angiosperm Evolution

3. Where did the Angiosperms arise?

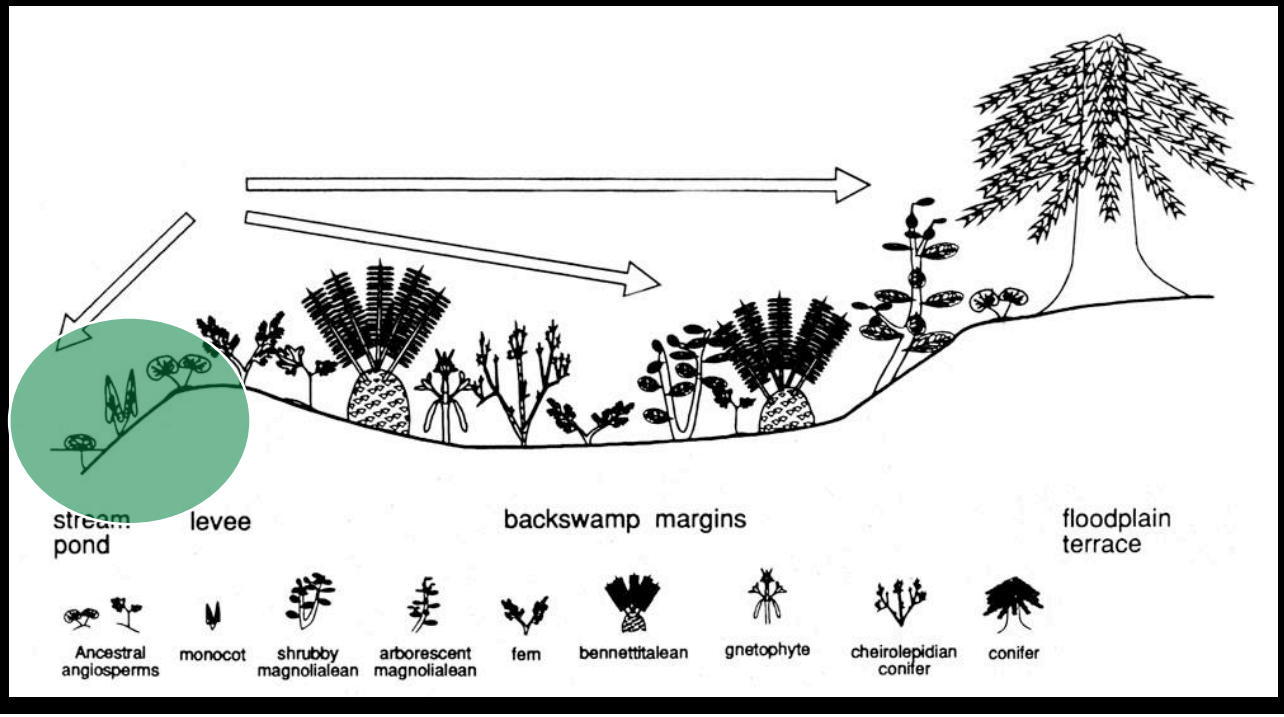
- Australasia if based on earliest diverging extant families
- earliest (extinct) fossils come from many areas - China, England, Australia (most tropical or subtropical or warm temperate in early Cretaceous)



Summary of Angiosperm Evolution

3. Where did the Angiosperms arise?

- likely in wet margins of gymnosperm dominated forests

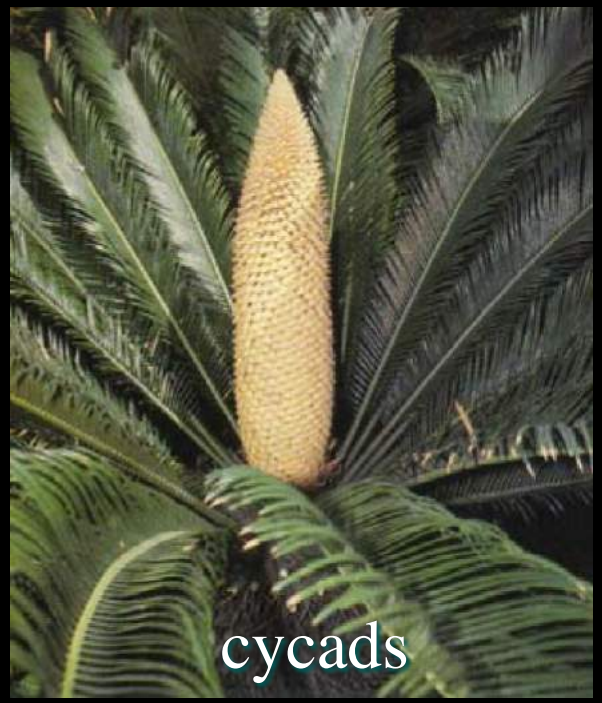


Summary of Angiosperm Evolution

4. From what Gymnosperms did they arise?

- no consensus based on extant lineages!


conifers


cycads


ginkgoes


gnetales

• Gnetales have been the favorites for some time (vessels, double fertilization, broad leaves) . . .

Gnetum

Ephedra

Welwitschia

• but this "Anthophyte" hypothesis is strongly rejected by DNA sequence data!

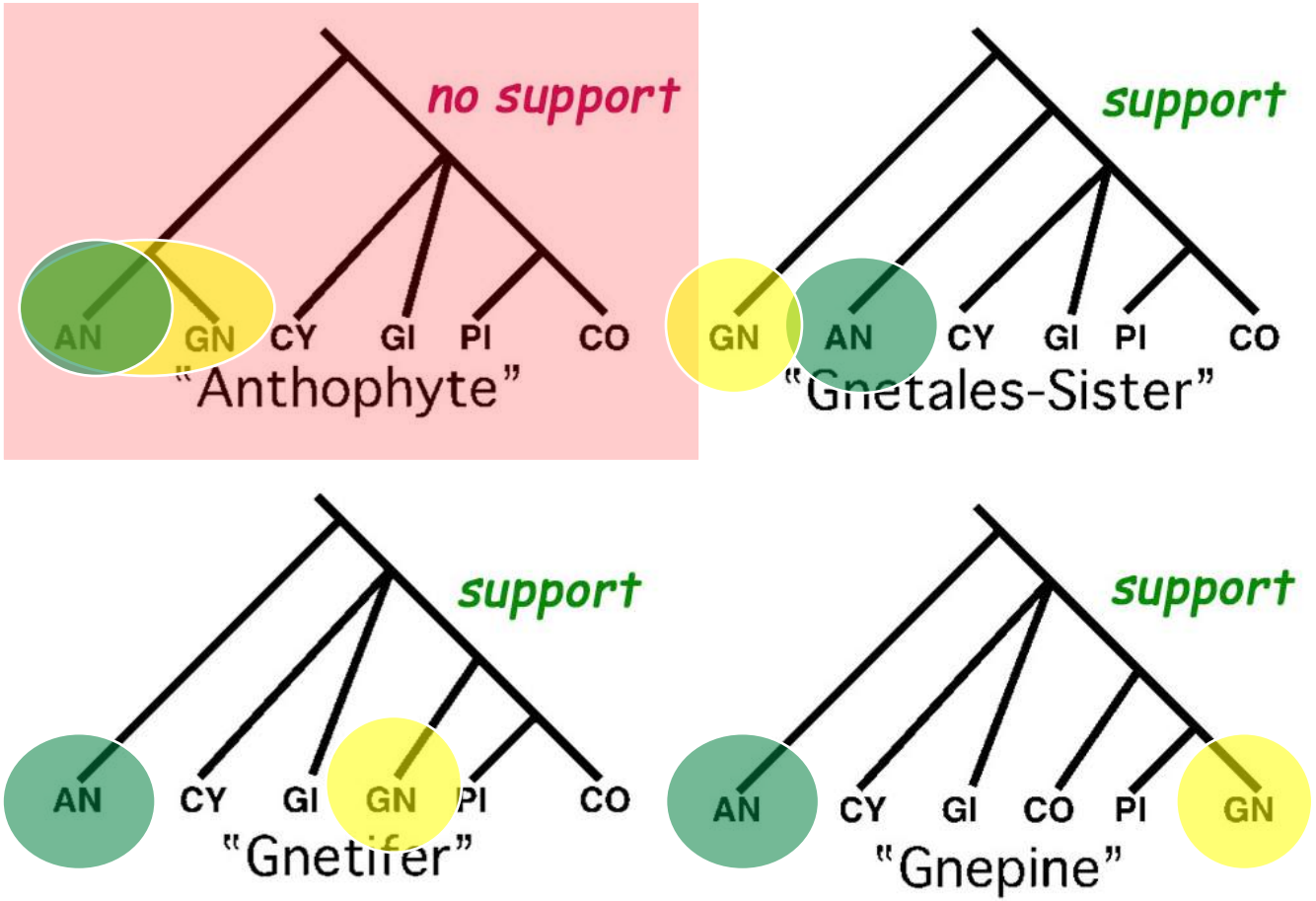
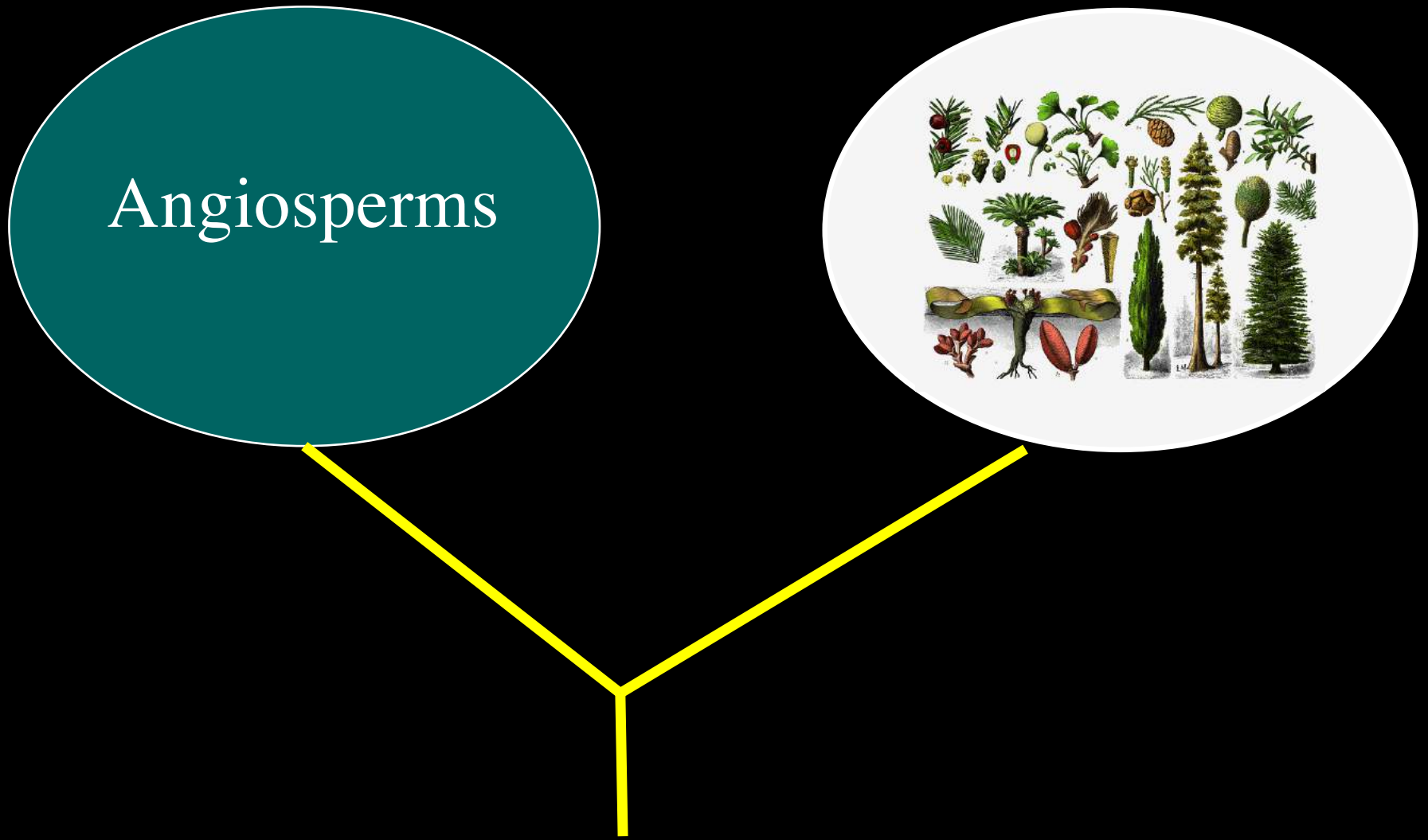
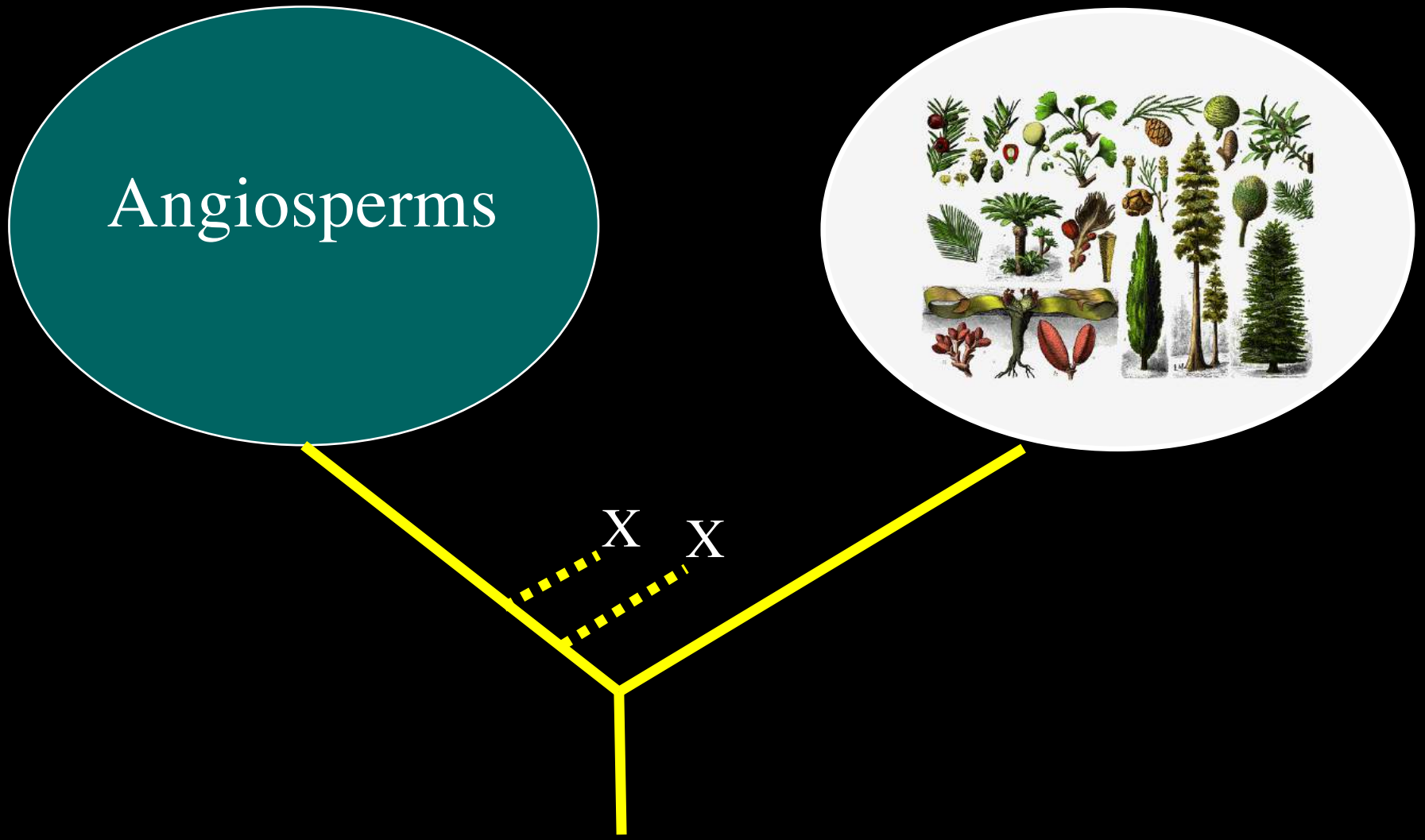


Fig. 1. Four major hypotheses of relationships among extant seed plant lineages. AN = angiosperms; CY = cycads; GI = *Ginkgo*; GN = Gnetales; PI = Pinaceae; CO = non-Pinaceae conifers.

- 2018 Next Generation Sequence data place ALL living gymnosperms as a monophyletic lineage



• likely that Angiosperms arose from a now **extinct** Gymnosperm lineage



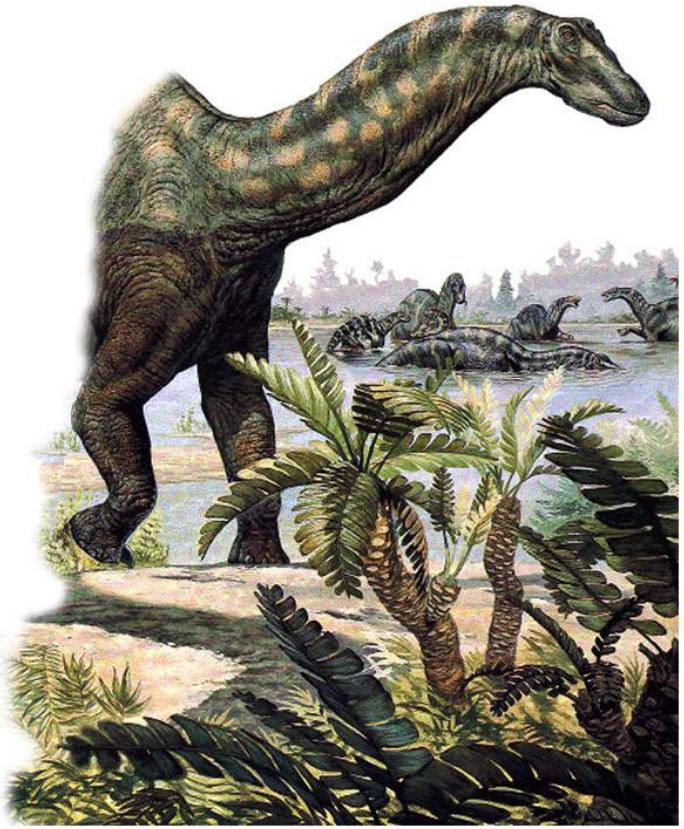
- likely that Angiosperms arose from a now **extinct** Gymnosperm lineage such as **Bennettitales** or other "**seed fern**" groups

Bennettitales (Cycadeoid or "cycad like")
Seed "Ferns"

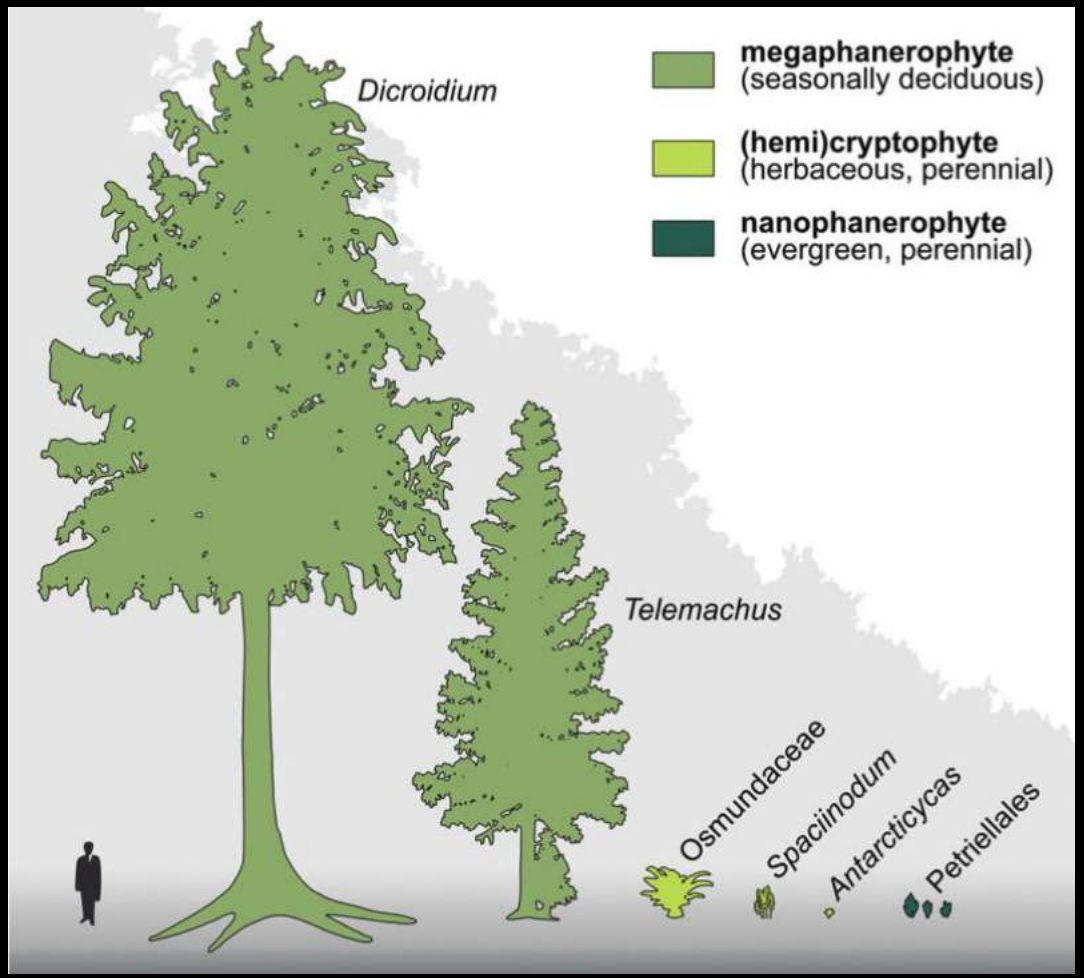
Williamsonia

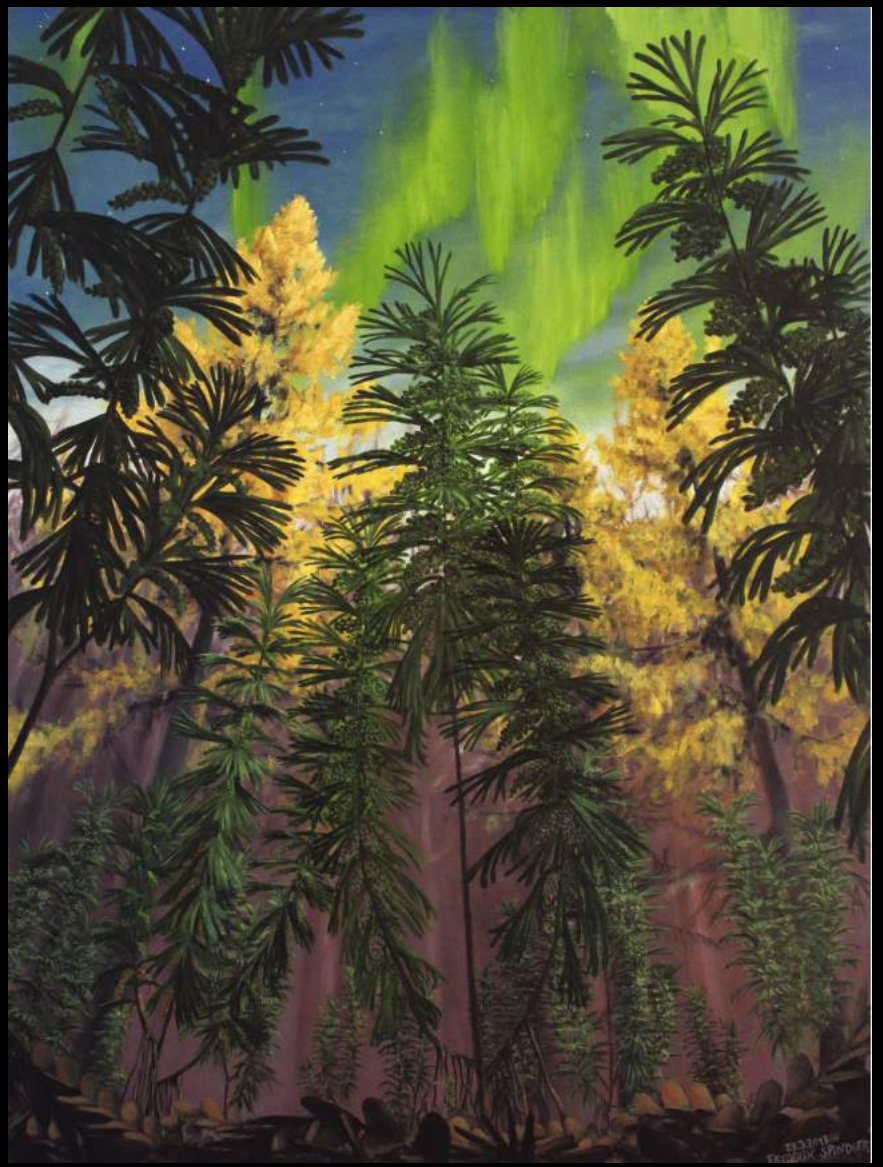
Seed fern fossils - 320 mya

Pentoxylon (Jurassic)



- likely that Angiosperms arose from a now **extinct** Gymnosperm lineage or the understory Petriellales





Summary of Angiosperm Evolution

5. Why did Angiosperms dominate quickly?

- BIG story! We will deal with it throughout the course
- vessel elements?
- mycorrhizal interactions with fungi?
- the flower as a "key innovation"?
- genome duplication(s)?
- co-evolution with animal pollinators?






Darwin's Abominable Mystery

. . would he be satisfied had he lived to be 210 ? . .

Yes . . . but questions remain