Darwin’s Abominable Mystery
...origin of angiosperms...


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
Gymnosperm Dominance

Angiosperms have NOT always dominated

Fossil Record as seen by Charles Darwin
- tree-like lycopsids, horsetails, primitive gymnosperms - the Carboniferous
- ferns, cycads, ginkos, 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

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

% of total fossils

PTERIDOPHYTES
OTHER SEED PLANTS
CYCADOPHYTES
CONIFERS
ANGIOSPERMS

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 2017 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?
the 2017 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
- 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

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

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: 47mya
- genus Fuchsia (Onagraceae) first seen 30mya in Oligocene

Leaf Record

- consistent trends emerge with leaf fossils
- Neocomian (130mya) Rogersia (basal angiosperm) simple, pinnately veined, entire
• consistent trends emerge with leaf fossils

• early Aptian (125mya) 
  *Archaefructus* (basal angiosperm) palmately compound

• Aptian to Albian (120-110mya) = magnoliids (pinnate veins), cordates (palmate veins), monocots (parallel veins)

• early Aptian (125mya) 
  *Archaefructus* (basal angiosperm) palmately compound

great leaf diversity within 15my

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

  Platanoid - lobed
  Sapindopsis - compound

• by Upper Cretaceous (100mya) 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 98-95mya
Magnoliaceae with stingless bee – 90mya

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

Flower Record

- what are the earliest fossil flowers?

1990 - Leo Hickey

- 120 mya - Australia
- small, unisexual flowers
- placed into Piperales (pepper, wild ginger)
Flower Record
• what are the earliest fossil flowers?

1996 - Chris Hill
• Bevhalstia pebja
• 130 mya - England
• small, 25cm aquatic herb
• dissected leaves
• most not convinced it is an angiosperm

1998 - David Dilcher & Chinese colleagues
• Archaeofructus
• 125 [135 1st] mya - China
• small, dissected leaves
• stamens and carpels on long axis

2015 - David Dilcher & Spanish colleagues
• Montsechia
• 125-130 mya - Pyrenes
• aquatic, fruiting

Flower Record
• what are the earliest fossil flowers?
• morphology phylogenetic analyses place it before Amborella

Flower Record
• what are the earliest fossil flowers?
Flower Record

• what are the earliest fossil flowers?
  2011 - David Dilcher & Chinese colleagues again
  • Leefructus
  • 122mya - China
  • first Eudicot
  • Ranunculaceae?

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 - 130mya
   • DNA - some molecular clocks suggest >200mya

Magallón 2010

stem node with living gymnosperms
• crown node of living angiosperms

Stem lineage
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

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

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

4. From what Gymnosperms did they arise?
   - no consensus based on extant lineages!
     - conifers
     - cycads
     - ginkoes
     - gnetales

- **Gnetales** have been the favorites for some time (vessels, double fertilization, broad leaves) . . .
  - Ephedra
  - Gnetum
  - Welwitschia

*but this “Anthophyte” hypothesis is strongly rejected by DNA sequence data!
• more likely that Angiosperms arose from a now extinct Gymnosperm lineage such as Bennettitales or other "seed fern" groups.

**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?

• does the timing of Angiosperm & pollinator radiations fit?

No & Yes — Angiosperms co-opted already diverging animal lineages in Early Cretaceous.
Darwin’s Abominable Mystery

.. would he be satisfied had he lived to be 208 ? . .

Yes . . . but questions remain