The Diversification
of Flowering Plants:
Key Innovations and Radiations

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Goals of Presentation

• Overview of phylogenetic position of angiosperms among green plants
• Major clades of angiosperms
• Patterns of radiation
• Possible key innovations
A Phylogenetic Perspective: 
Green Plants

Chlorophytes

Streptophytes
Streptophytes

Charales

Embryophytes

Embryo
Multicellular sporophyte
Multicellular gametangia
Multicellular sporangia
Cuticle
Embryophytes

"Bryophytes"

Tracheophytes

Independent sporophyte
Vascular tissue
(tracheids)
Tracheophytes

Monilophytes

Seed Plants

Seed
Seed Plants

Extant Gymnosperms

Angiosperms

Flower: carpel
Double fertilization
Reduced gametophytes
Angiosperms: New Kids on the Block
The Angiosperms

• >250,000 species

• ~400 families

• Early Cretaceous origins, ~130 mya

• Sister to extant gymnosperms
Characteristics of Flowering Plants

- Double fertilization:
  - egg + sperm $\rightarrow$ zygote $(2n)$
  - egg + 2nd sperm $\rightarrow$ endosperm $(3n)$
- Closed carpels: enclose ovule
- Reduced gametophytes
- Sieve tubes and companion cells
- Stamens with 2 pairs of pollen sacs

Doyle & Donoghue (1986)
...the rapid rise and early diversification of angiosperms is “an abominable mystery”

--Charles Darwin,
letter to J. D. Hooker
22 July 1879
The Abominable Mystery

• **Fossil record:**
  – Floral diversity in early Cretaceous
  – Major lineages 130-90 mya
  – Ecological dominance 100-70 mya

• **Molecular dating:**
  – Origin of angiosperms ~200-140 mya
  – Many lineages date to early Cretaceous
  – All major lineages >100 mya
Early Cretaceous Angiosperms

Water Lilies ~125 mya

Modern *Nuphar* & *Victoria*

Friis et al. 2001
Early Cretaceous Angiosperms: *Archaefructus*

- ~125 mya
- China
- Spiral/whorled carpels
- Paired stamens
- Aquatic

Sun et al. (2002)
Overview of Angiosperm Phylogeny

- Molecular data from cp, mt, nu genomes
- Congruent
- Repeated patterns of resolution and polytomies
Basal Branches

rest

Austrobaileyales

Water Lilies

Amborella
Basal Branches

Alternative rootings
Early-branching Angiosperms

- Austrobaileyales
  - *Illicium*
- Water Lilies
  - *Cabomba*
- Amborella
Amborella trichopoda

- Shrub, cloud forests of New Caledonia
- Spiral phyllotaxis
- Indeterminate merosity
- Moderate number of parts
- Undifferentiated perianth
- Dioecious
Floral Diversity in Basal Angiosperms
Monocots

Poales: grasses
Arecales: palms
Zingiberales: gingers
Commelinales
Dasypogonaceae
Asparagales:
orchids, iris, hyacinth
Pandanales
Liliales: lilies
Dioscoreales
Petrosaviaceae
Alismatales
Acorales
A Sample of Monocots
Basal Angiosperms: Unresolved Placements

- Monocots
- Ceratophyllaceae
- Chloranthaceae

P. Endress
Pollen Types

Uniaperturate Pollen: basal angiosperms, including monocots; gymnosperms

Triaperturate Pollen: eudicots
Eudicots

- 75% of all angiosperm species
- Triaperturate pollen
- Origin of clade 125 mya
- Small basal lineages and large clade: core eudicots
Eudicots

Core Eudicots

Buxaceae
Trochodendraceae
Sabiaceae
Proteales
Ranunculales

rest
A Sample of Eudicots
Asterids
- Campanulids
  - Lamiids
    - Ericales
    - Cornales
Rosids
Recurring Theme: Radiations

Base of angiosperms

Monocots

Core Eudicots

Rosids

Eurosids I

Eurosids II

Myrtales
Geraniales
Crossosomatales
Saxifragales
Traits Tested for Association with Angiosperm Diversification

- Pollination syndrome
- Geographic range
- Dispersal mode
- Habit
- Dioecy
- Chromosome number
- Life history

Davies et al., 2004
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Davies et al., 2004

No significant associations!

Simple explanations for angiosperm radiation are inadequate -- Darwin’s abominable mystery
Recurring Theme: Radiations

Base of angiosperms

Monocots

Core Eudicots

Rosids

Adaptive or not????
Possible Key Innovations

- Vessels: nearly all angiosperms
- Closed carpels: nearly all angiosperms
- Genome duplication??:
  - all angiosperms
  - Eudicots or core eudicots??
- Synorganized flowers: core eudicots
- Nitrogen-fixing symbiosis: N-fixing clade of rosids
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From Endress & Igersheim, 2000
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Origin of Nitrogen-Fixing Symbiosis
Origin of Symbiosis with Nitrogen-fixing Bacteria

- 10 families have N-fixing symbioses
- Previously considered distantly related
- Suggested “simple” molecular basis

- BUT...
• All 10 families united in single clade in rosids
• Other families lacking N-fixing symbioses
• “Predisposition” for evolution of symbiosis
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Flowering Plants: Phylogeny

- Large clade
- United by several features
- Arose in early Cretaceous, diversified shortly thereafter
- *Amborella* or *Amborella* + water lilies sister to rest of clade
- Position of monocots still uncertain
- ~75% of angiosperms are eudicots
- Series of radiations
Flowering Plants: Innovations

- Vessels
- Closed carpels
- Genome duplications??
- Synorganized flowers
- Nitrogen-fixing symbiosis
- **Others?**
  - Genome duplications
  - Evolution of floral regulators
- **Are microevolutionary processes (e.g., mutation, drift, selection) responsible for macroevolutionary patterns?**
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