



# 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

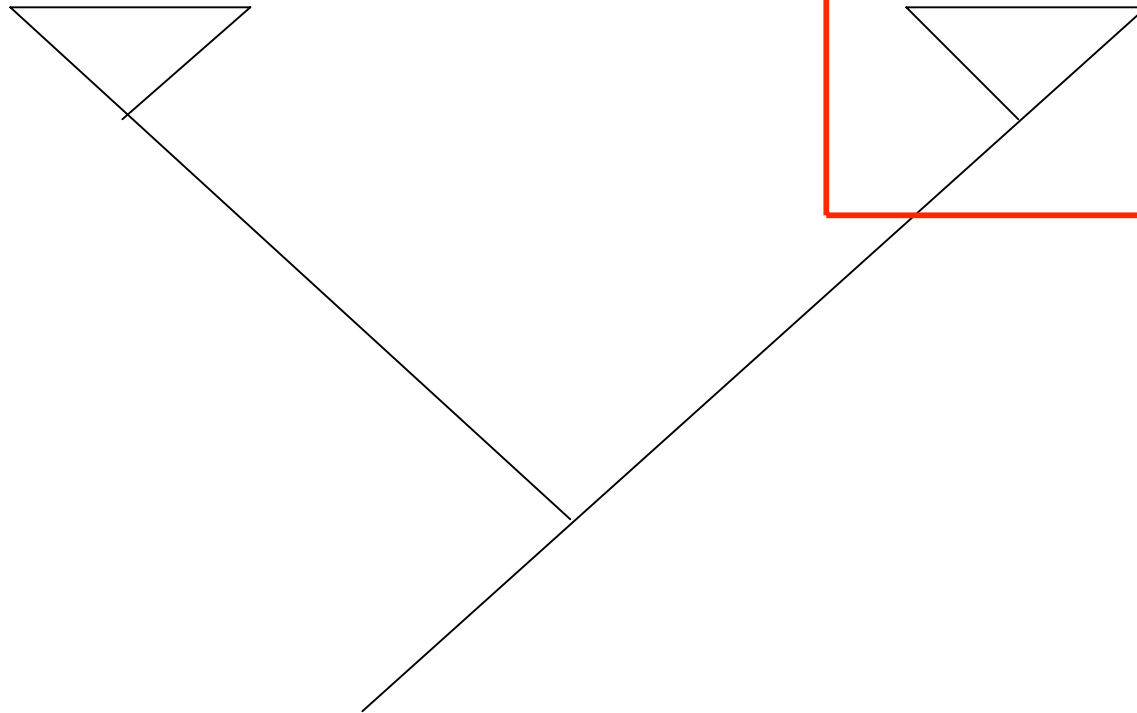
# A Phylogenetic Perspective: Green Plants



Chlorophytes



Streptophytes



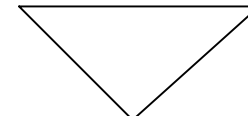
# Streptophytes



Charales

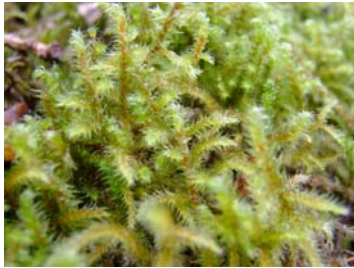


Embryophytes



- Embryo
- Multicellular sporophyte
- Multicellular gametangia
- Multicellular sporangia
- Cuticle

# Embryophytes

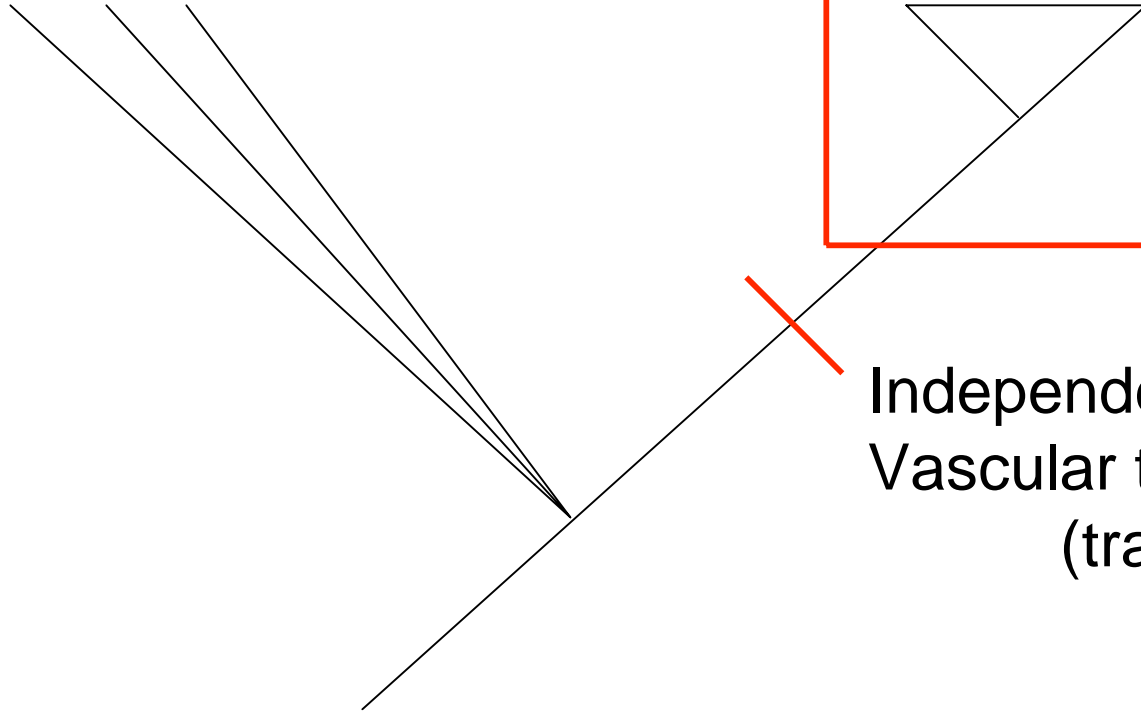


“Bryophytes”



Tracheophytes

Independent sporophyte  
Vascular tissue  
(tracheids)



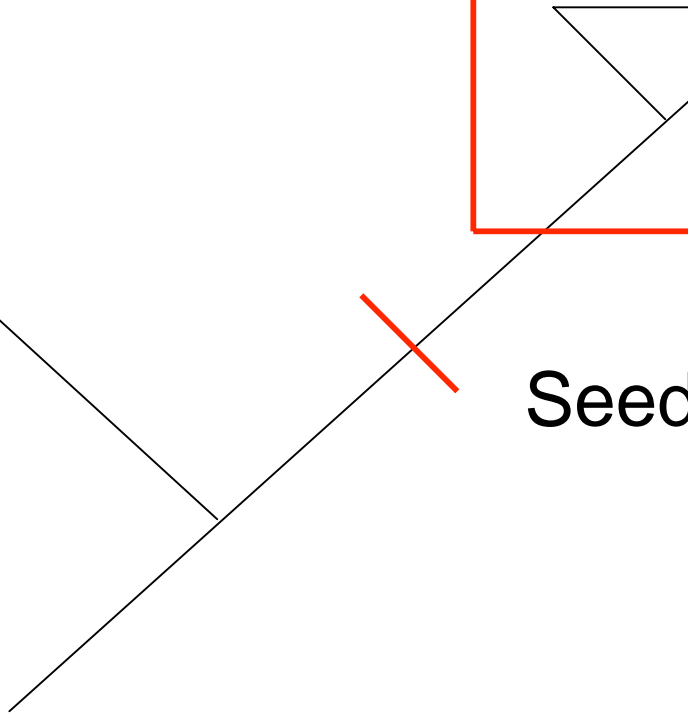
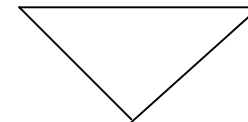
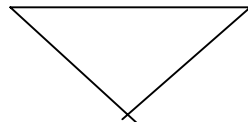
# Tracheophytes



Monilophytes



Seed Plants



Seed

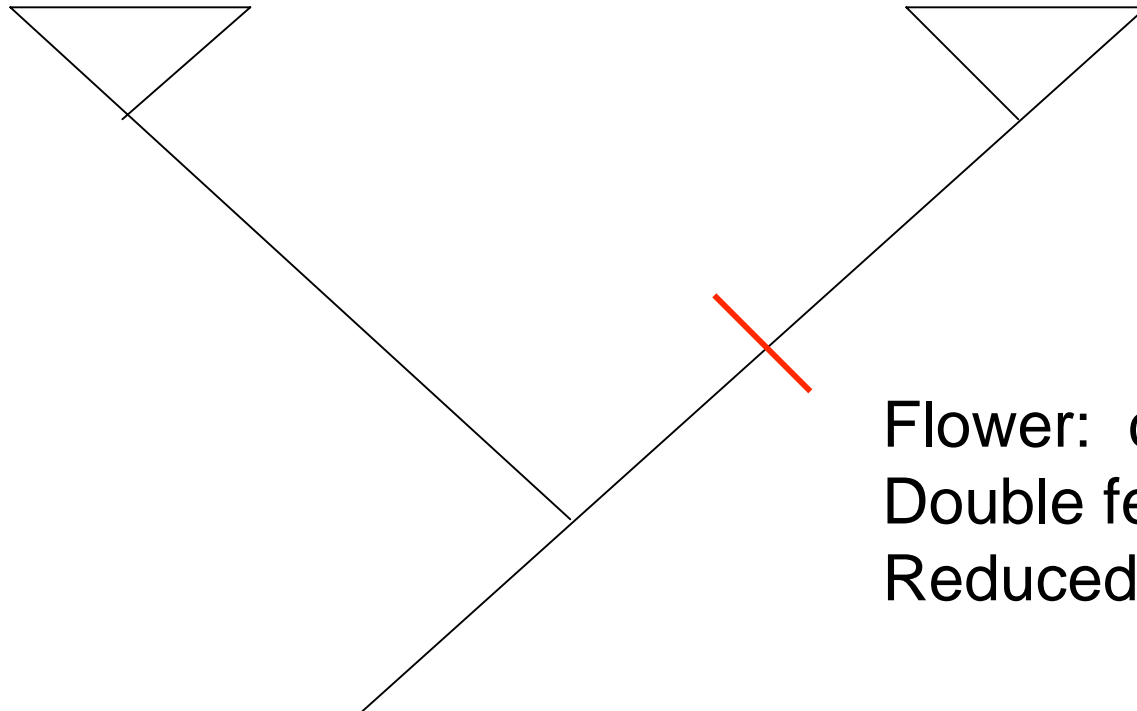
# Seed Plants



Extant  
Gymnosperms

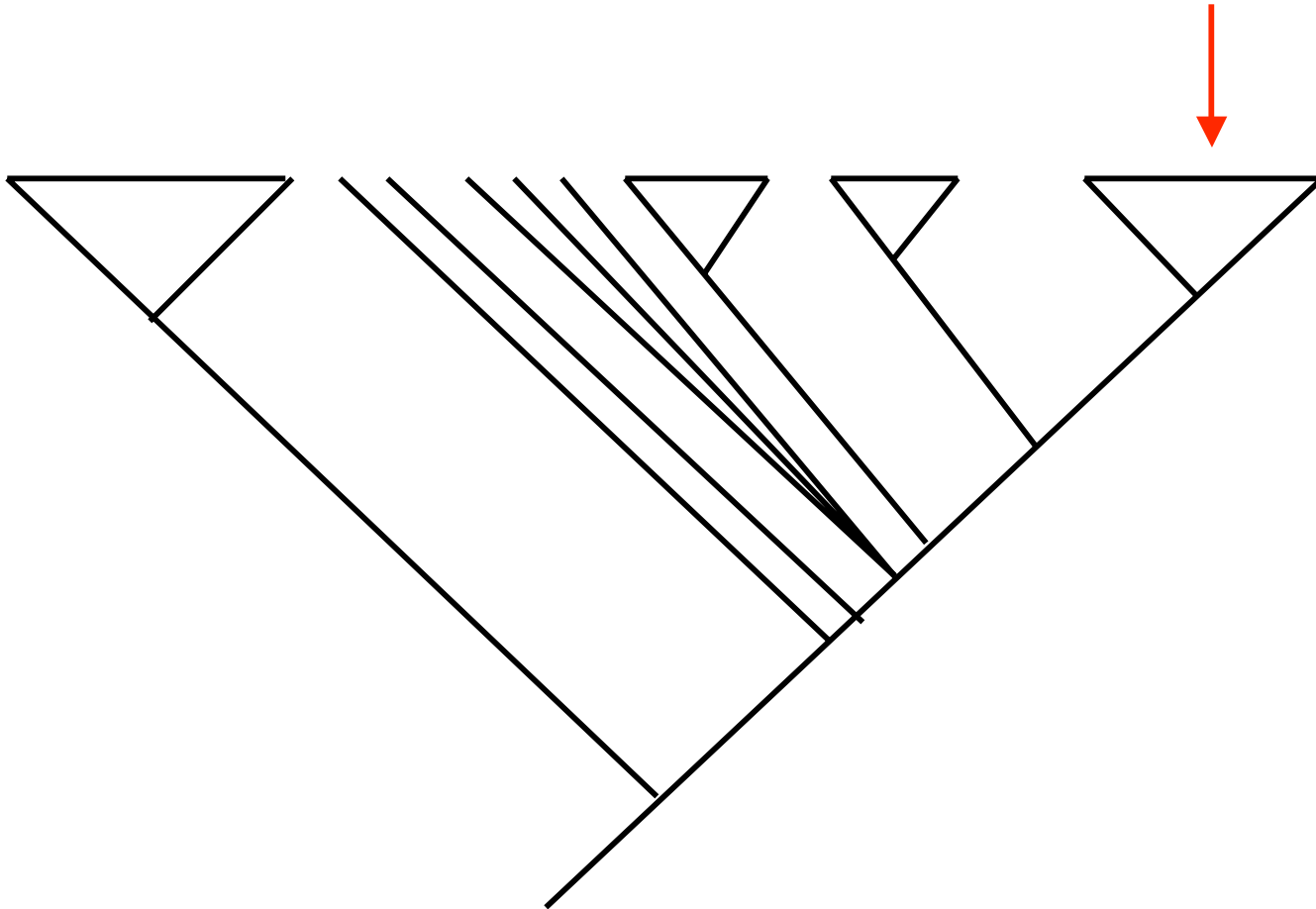


Angiosperms



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 → zygote ( $2n$ )
  - egg + 2nd sperm → 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: *Archaeoфраuctus*



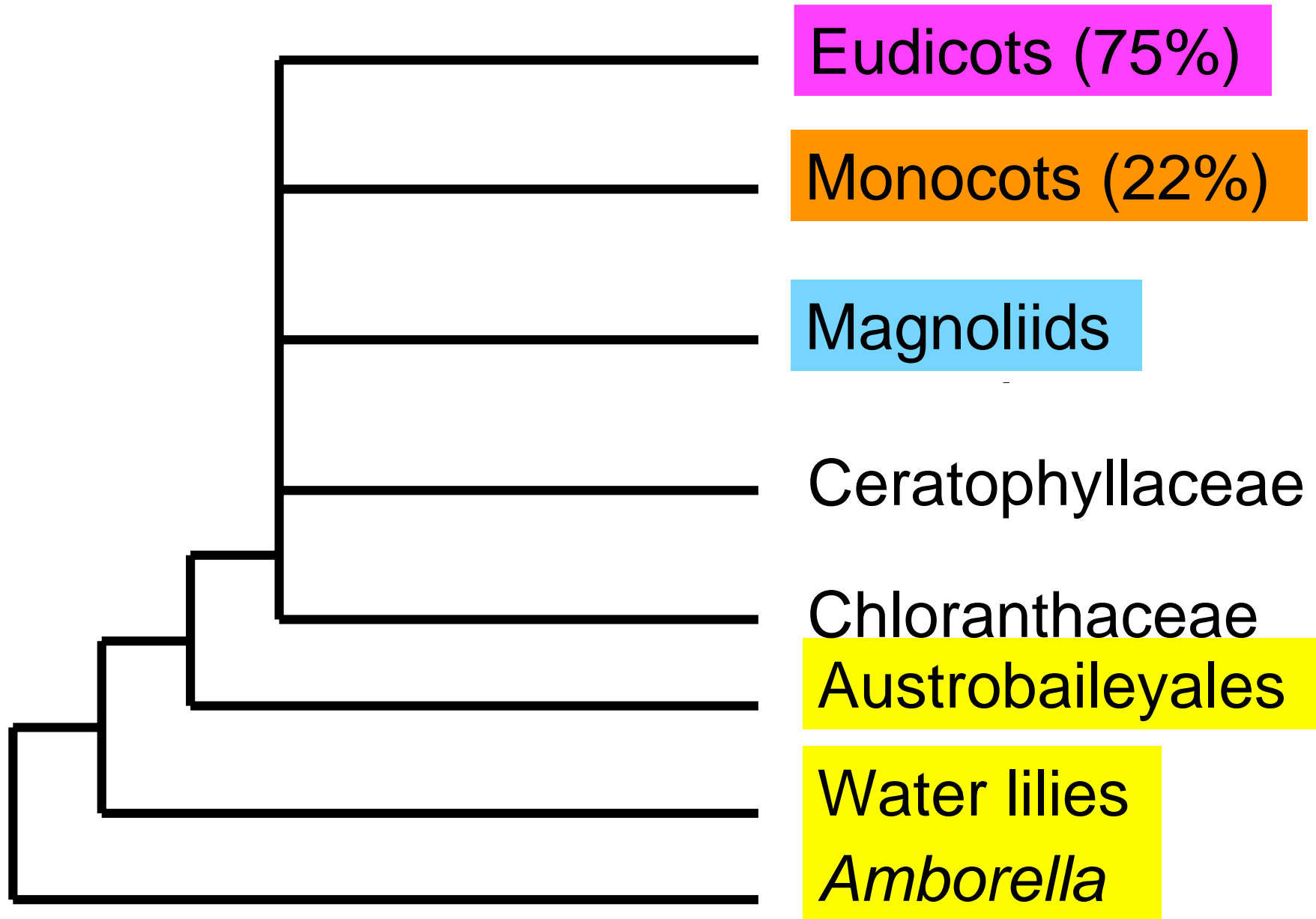
- ~125 mya
- China
- Spiral/whorled carpels
- Paired stamens
- Aquatic

Sun et al. (2002)

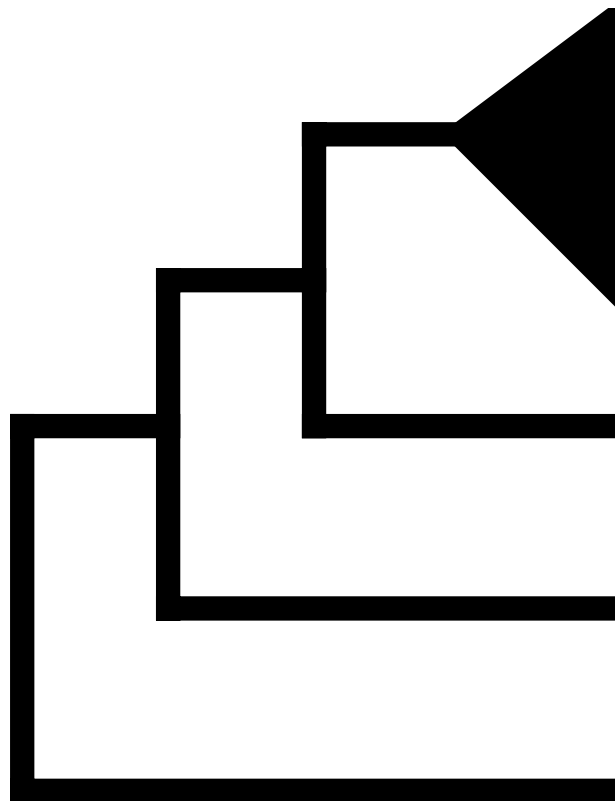
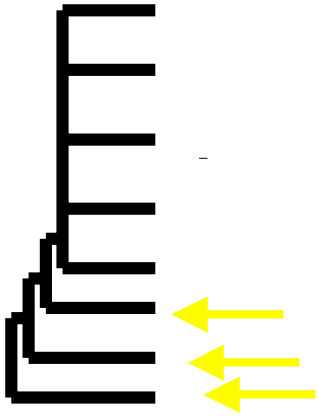
# Overview of Angiosperm Phylogeny

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

# Summary of Angiosperm Phylogeny



# Basal Branches



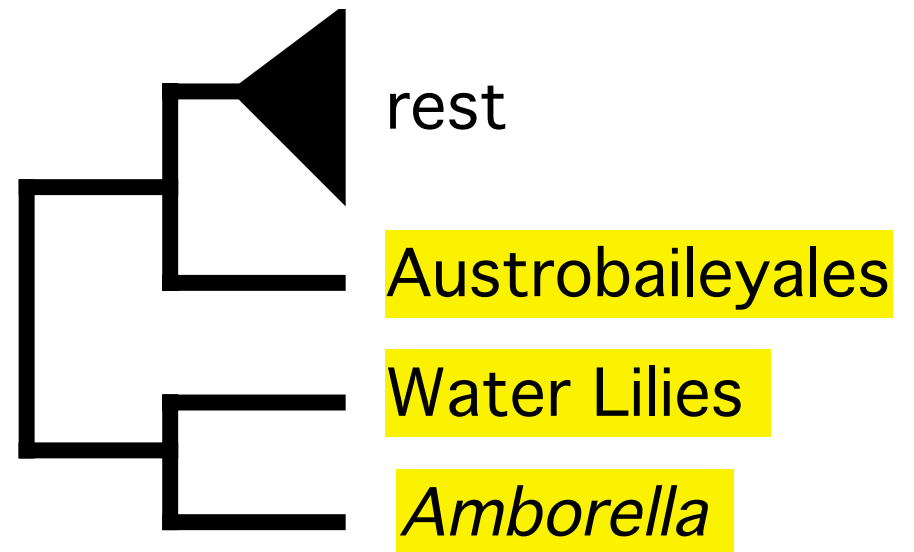
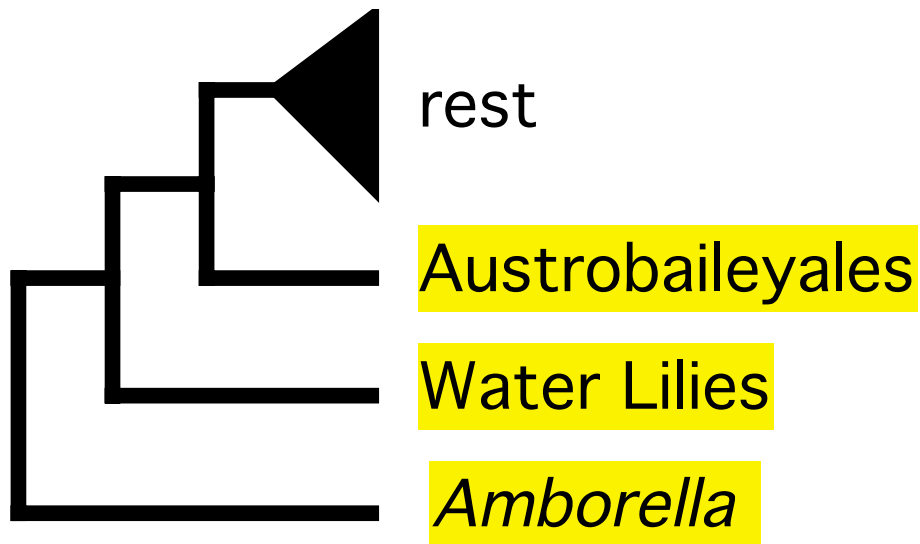
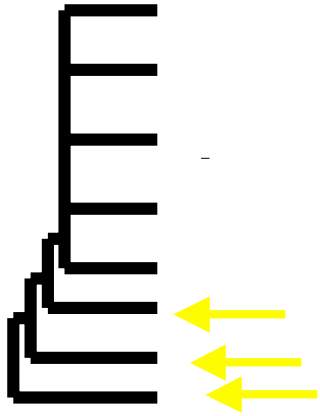
rest

Austrobaileyales

Water Lilies

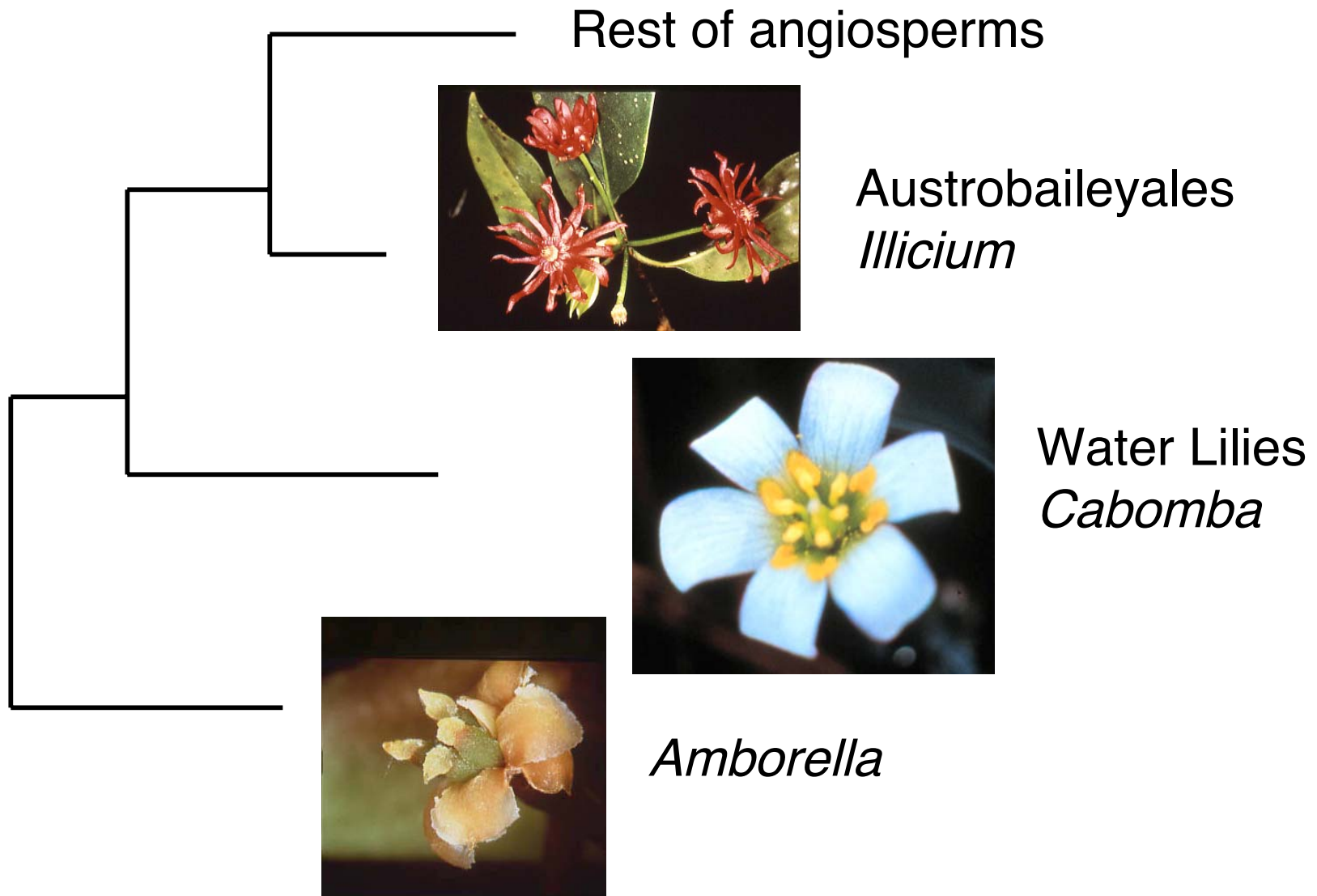
*Amborella*

# Basal Branches



Alternative rootings

# Early-branching Angiosperms



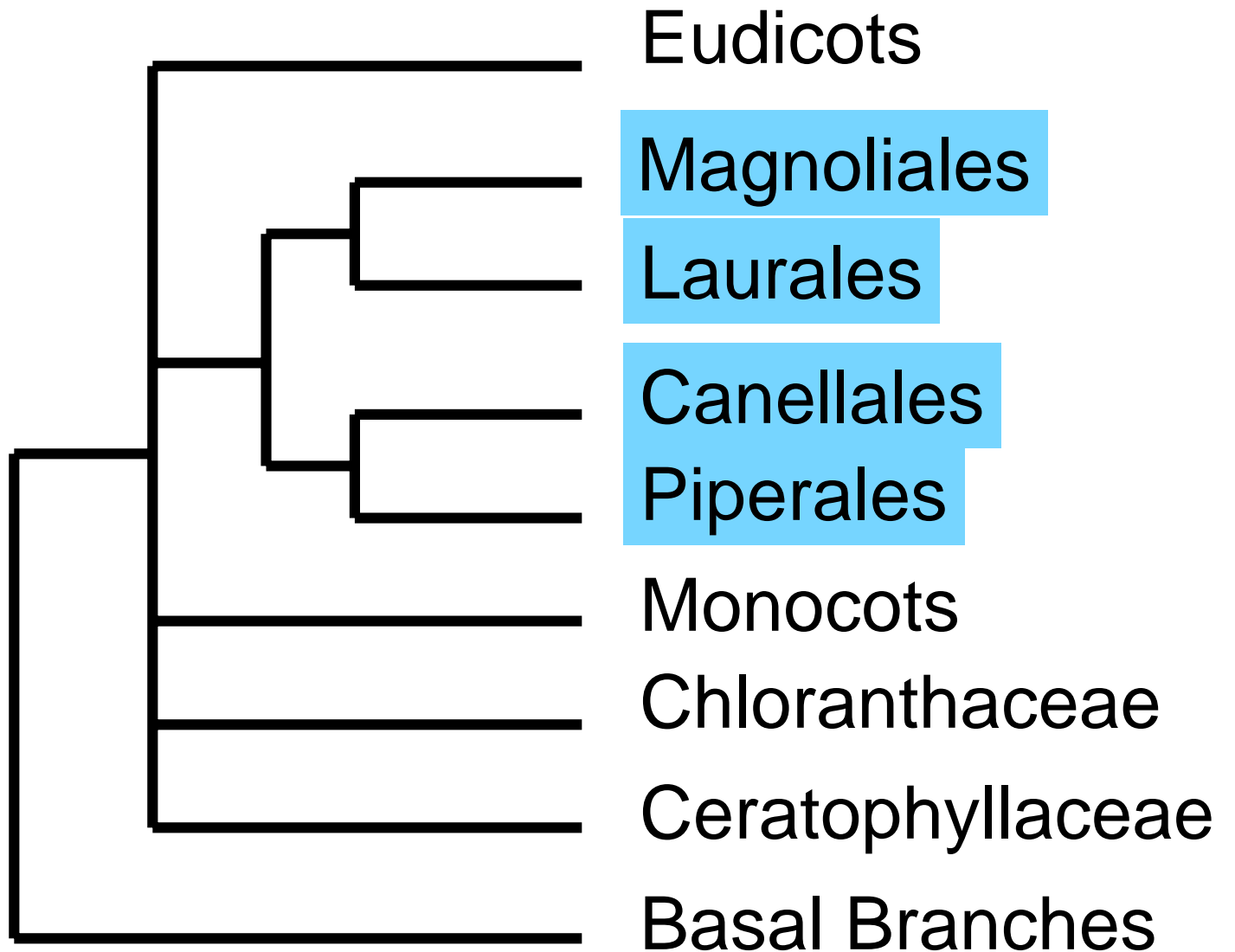
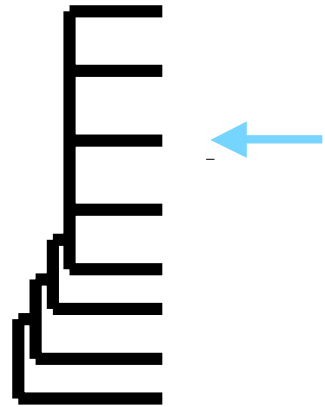
# *Amborella trichopoda*



Sandy Floyd

- Shrub, cloud forests of New Caledonia
- Spiral phyllotaxis
- Indeterminate merosity
- Moderate number of parts
- Undifferentiated perianth
- Dioecious

# Magnoliids



# Magnoliids

Magnoliales



Piperales



Lurales

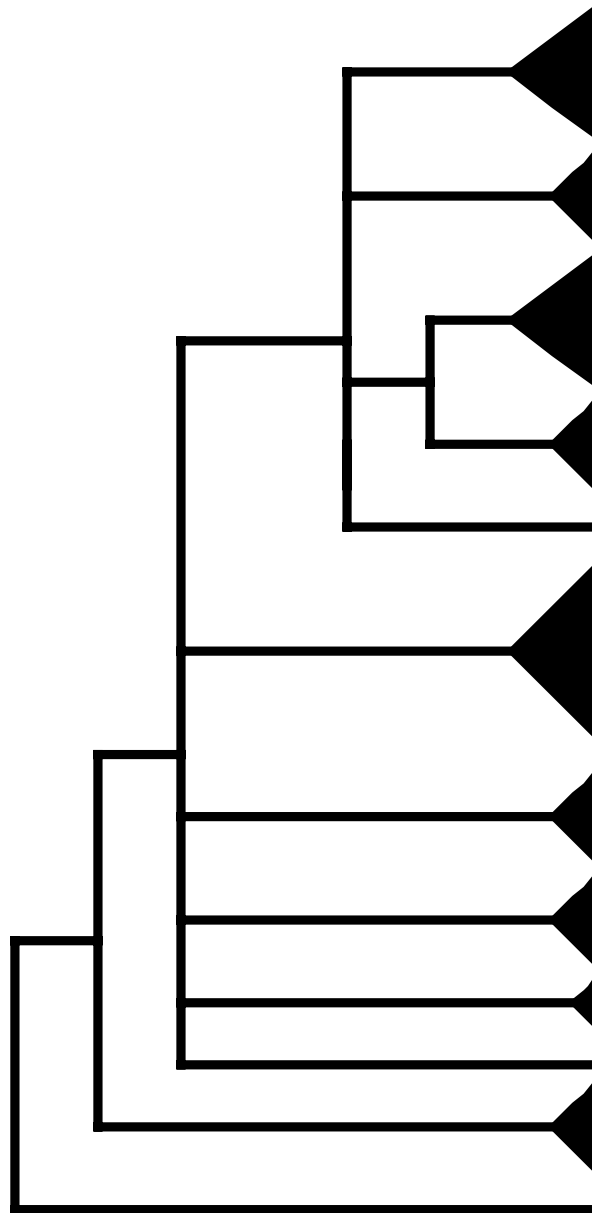
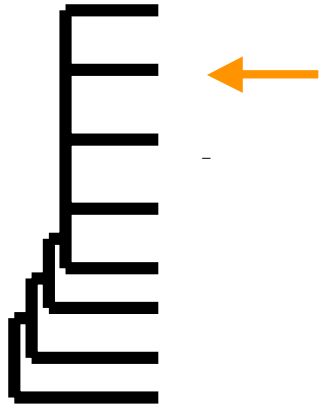


Canellales

# Floral Diversity in Basal Angiosperms



# Monocots



Poales: **grasses**

Arecales: **palms**

Zingiberales: **gingers**

Commelinales

Dasygongonaceae

Asparagales:  
**orchids, iris, hyacinth**

Pandanales

Liliales: **lilies**

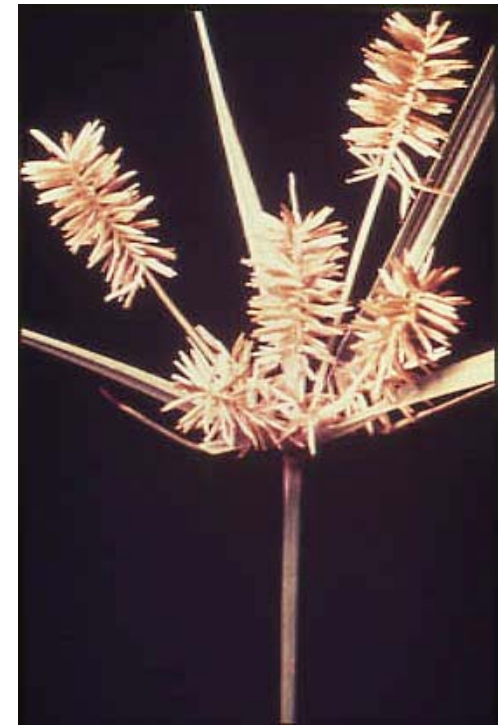
Dioscoreales

Petrosaviaceae

Alismatales

Acorales

# A Sample of Monocots

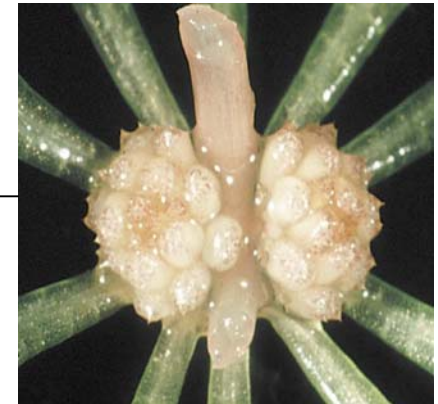


# Basal Angiosperms: Unresolved Placements

- Monocots



- Ceratophyllaceae



P. Endress

- Chloranthaceae



P. Endress

# Pollen Types



Uniaperturate Pollen:  
basal angiosperms,  
including monocots;  
gymnosperms

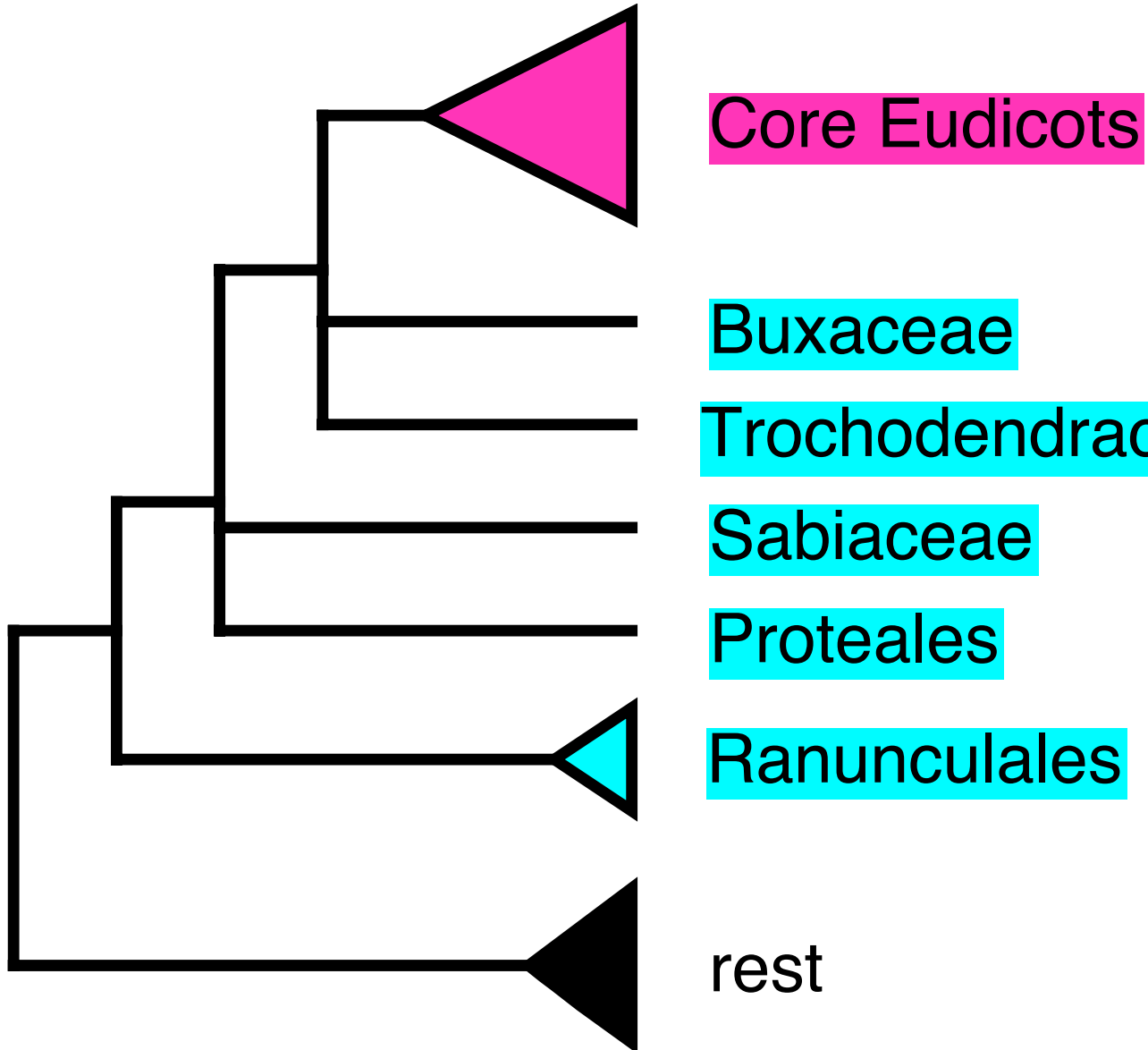
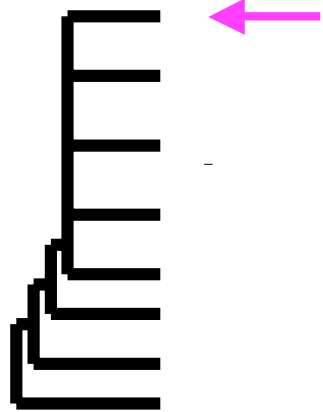


Triaperturate Pollen:  
eudicots

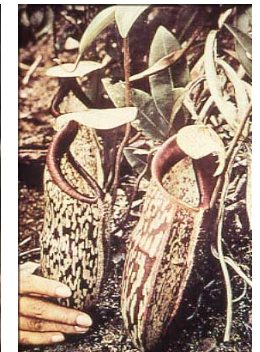
# Eudicots

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

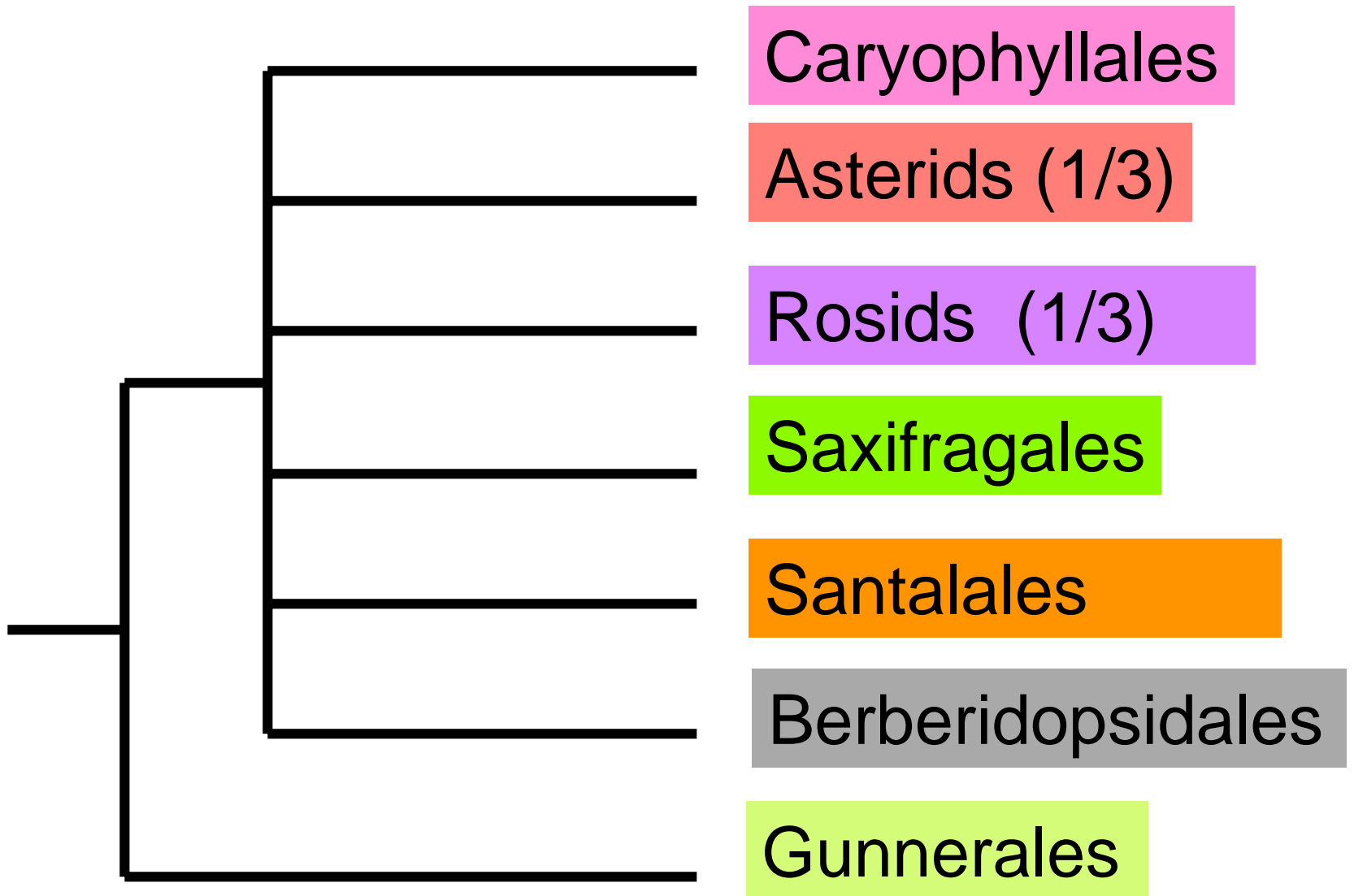
# Eudicots



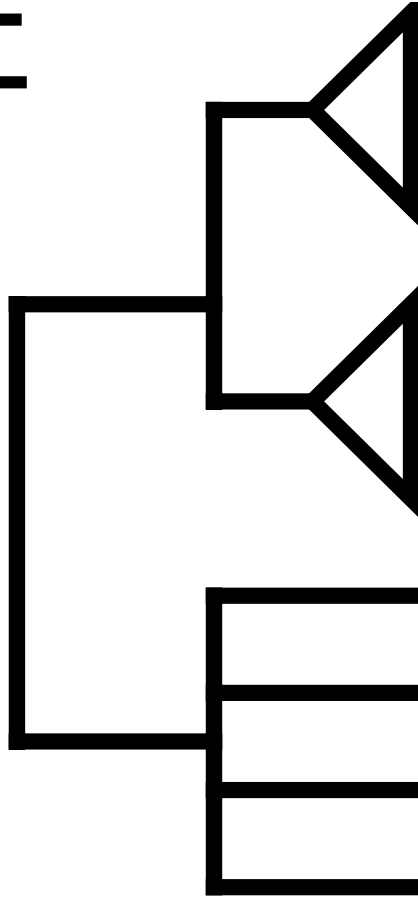
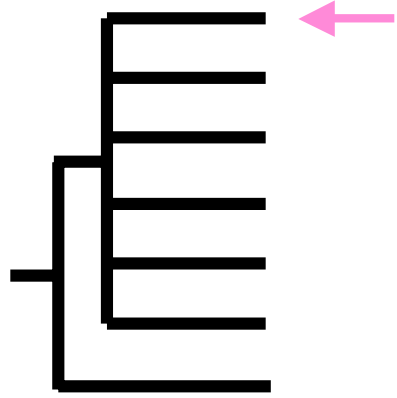
# A Sample of Eudicots



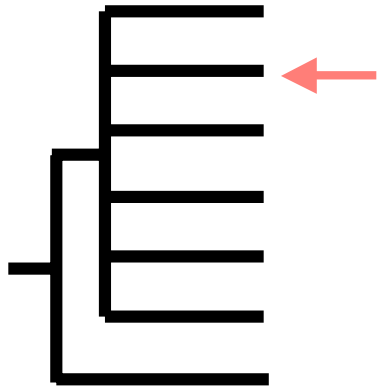
# Core Eudicots



# Caryophyllales



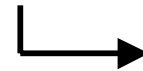
# Asterids



Campanulids →



Lamiids



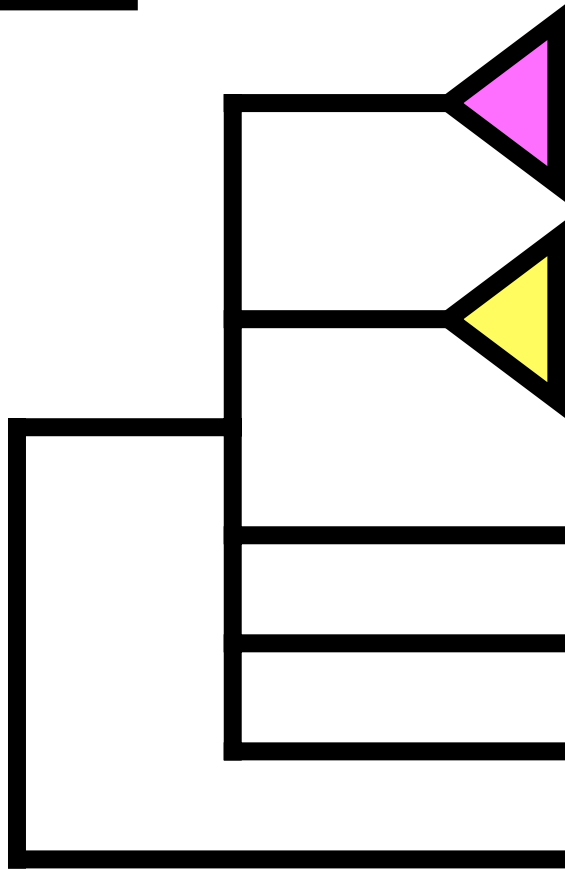
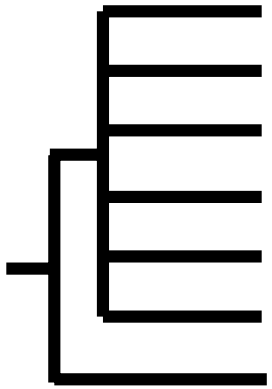
Ericales



Cornales



# Rosids



Eurosids I

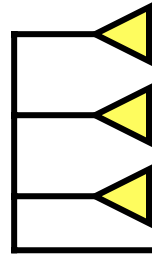
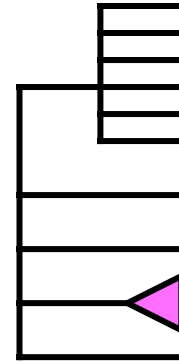
Eurosids II

Myrtales

Geraniales

Crossosomatales

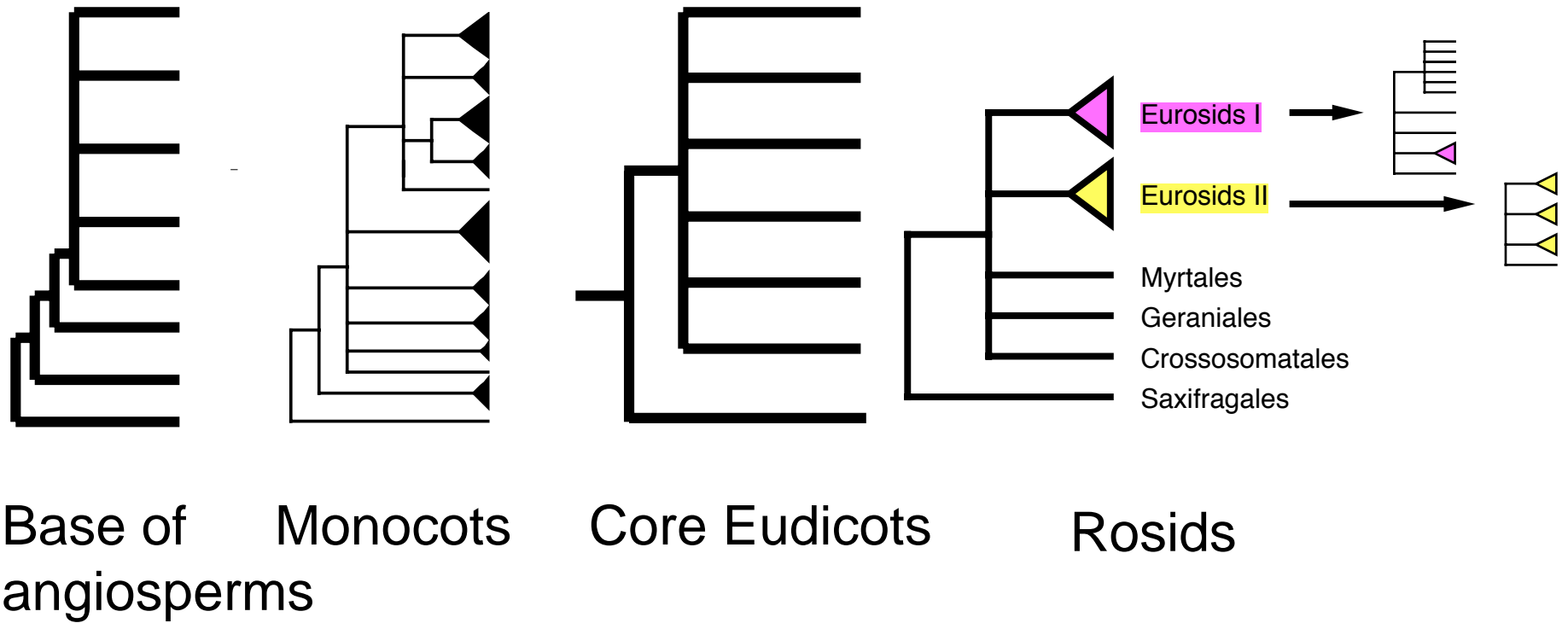
Saxifragales



# Rosids



# Recurring Theme: Radiations



# Traits Tested for Association with Angiosperm Diversification

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

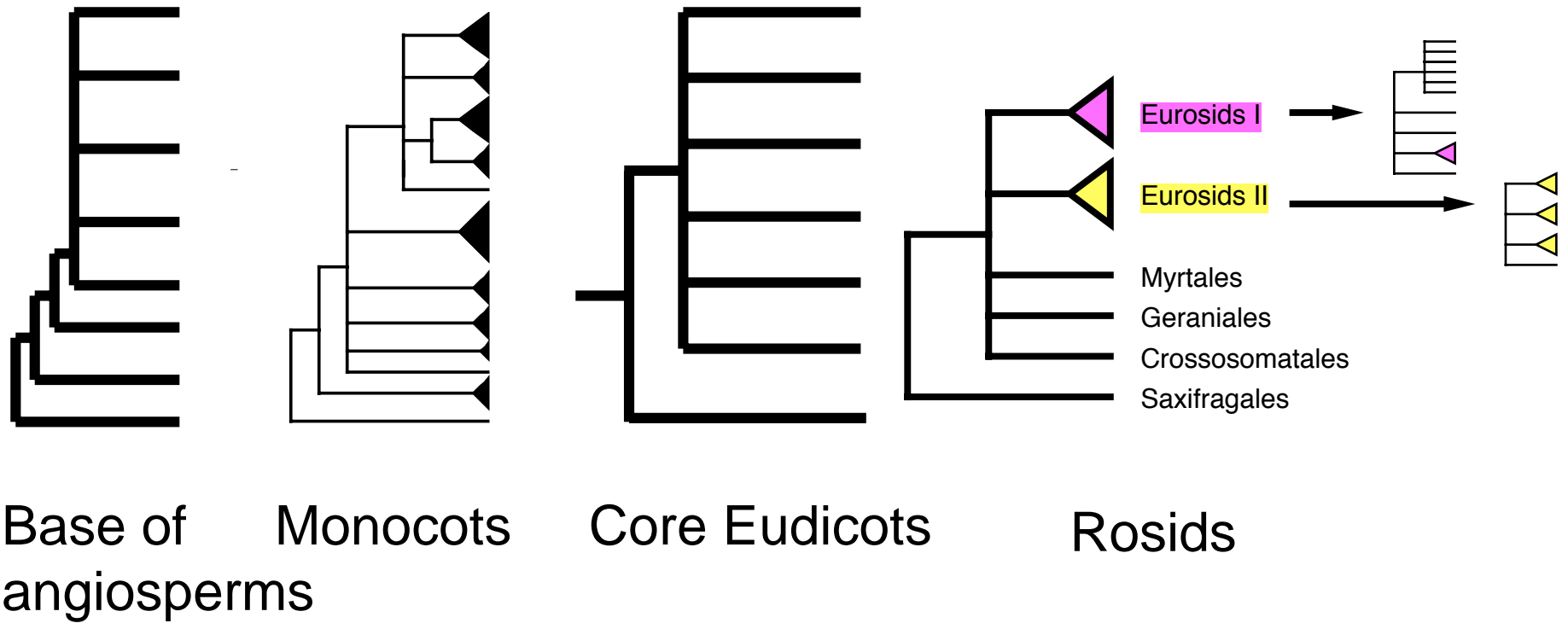
Davies et al., 2004

# Traits Tested for Association with Angiosperm Diversification

- Pollination syndrome
- Geographic range **No significant associations!**
- Dispersal mode **Simple explanations for angiosperm radiation are inadequate --**
- Habit **Darwin's abominable mystery**
- Dioecy
- Chromosome number
- Life history

Davies et al., 2004

# Recurring Theme: Radiations



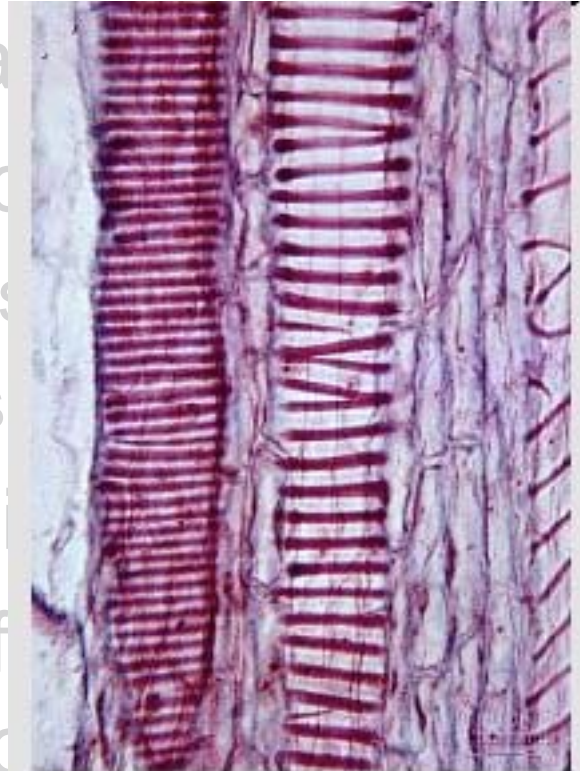
*Adaptive or not????*

# 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

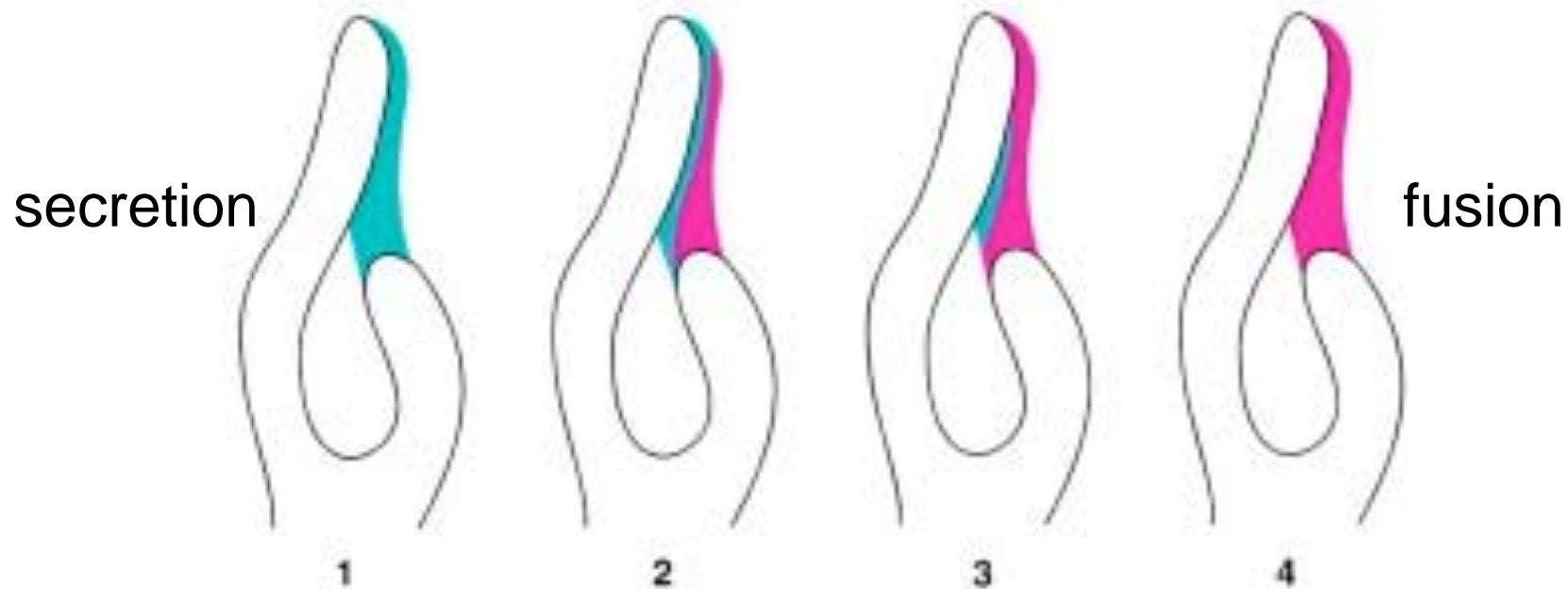
# Possible Key Innovations

- Vessels: nearly all angiosperms
- Closed cambium: all angiosperms
- Genome C-value: all angiosperms
  - all angiosperms
  - Eudicots
- Synangium: more eudicots
- Nitrogen-fixing clade of rosettes: N-fixing



# Possible Key Innovations

- Vessels: nearly all angiosperms
- Closed carpels: nearly all angiosperms



*From Endress & Igersheim, 2000*

# 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

# Possible Key Innovations



- Synorganized flowers: core eudicots
- Nitrogen-fixing symbiosis: N-fixing clade of rosids

# Possible Key Innovations

- Vessels: nearly all angiosperms
- Closed carpels: nearly all angiosperms
- Genome duplication??:
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  - Eudicots or core eudicots??
- Synorganized flowers: core eudicots
- **Nitrogen-fixing symbiosis: N-fixing clade of rosids**

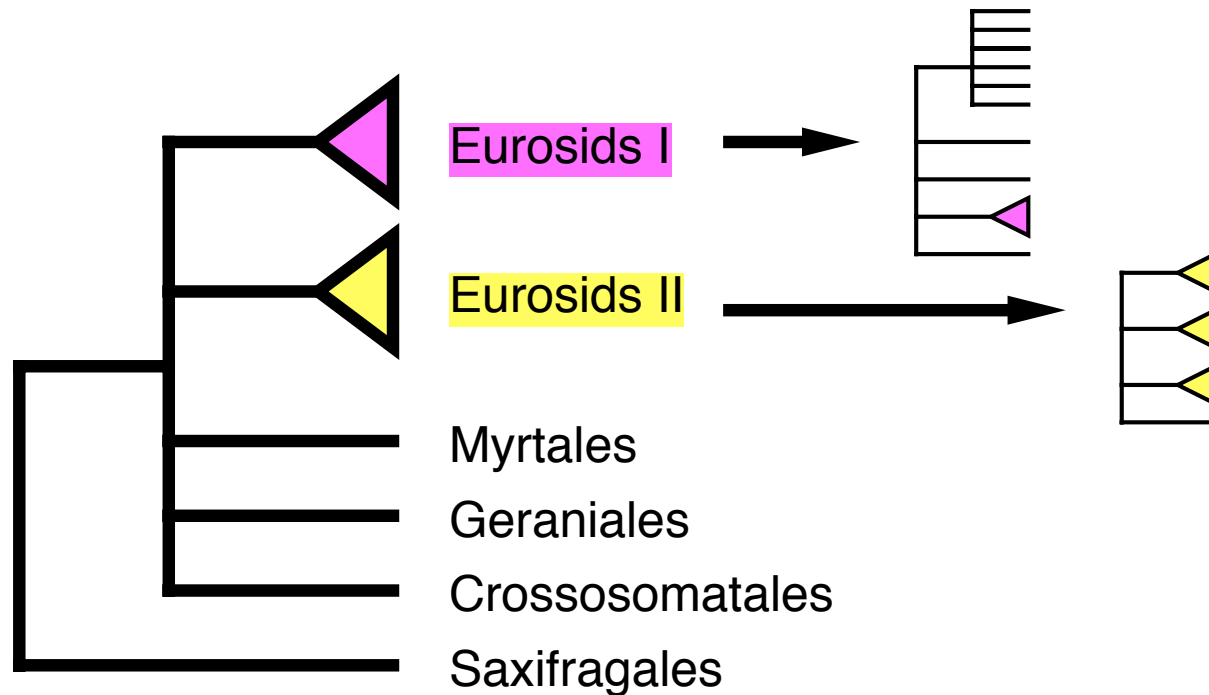
# Origin of Nitrogen-Fixing Symbiosis



# 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



# 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

# 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?*



# Acknowledgments

- Doug Soltis and Mark Chase
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- NSF, including AToL grant on angiosperm phylogeny