

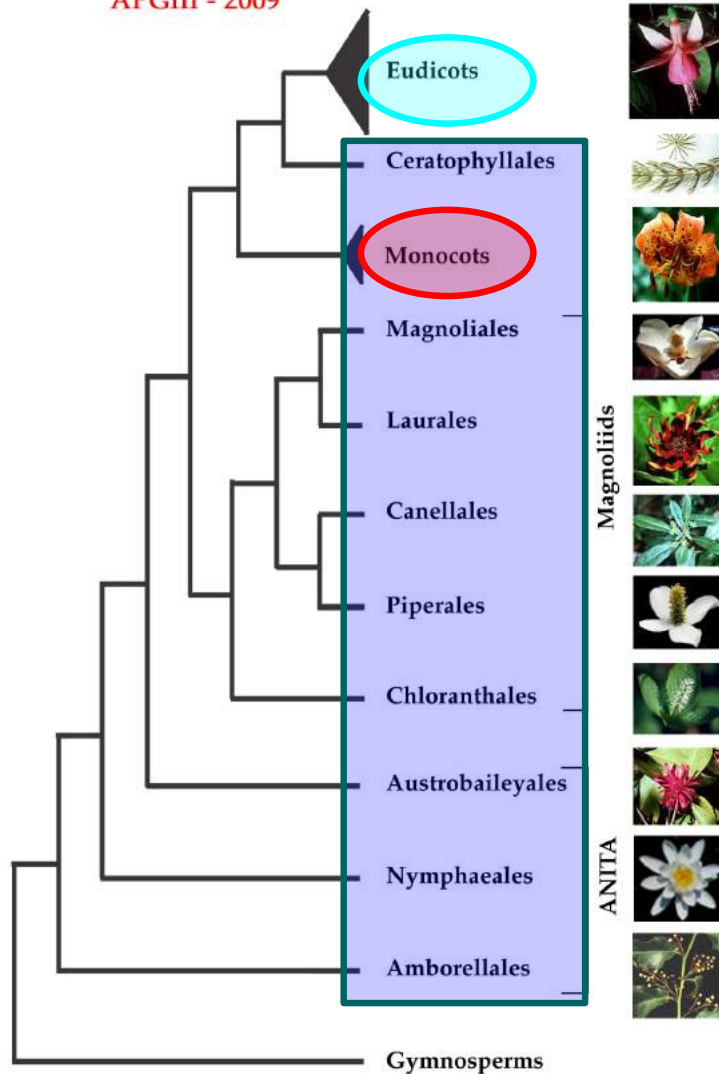
A close-up photograph of a yellow pitcher plant (Cephaelis Ipecacuanha) with a yellow crab spider (Thomisus sp.) perched on its surface. The background is a blurred green forest. The text "Diversity and Evolution of Monocots" is overlaid in yellow serif font at the top, and ". . . what, where, when, how . . ." is overlaid in yellow serif font in the middle.

# Diversity and Evolution of Monocots

. . . what, where, when, how . . .

# Monocots!

Basal Angiosperm Phylogeny  
APGIII - 2009



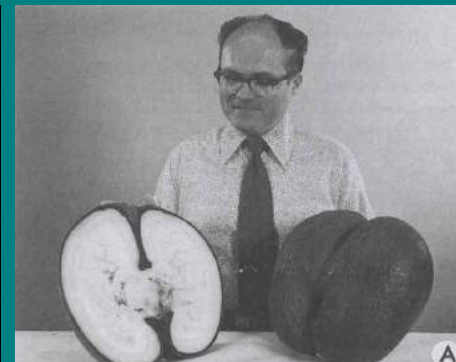
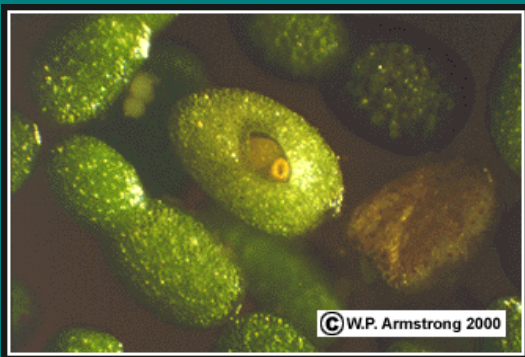
We will finish our survey of angiosperms by examining the **monocots** - a lineage of basal angiosperms

Basal angiosperm lineage, but is appearing to be **closer to eudicots** than most other basal angiosperms



# Monocots!

- Large group: ~ 60,000 species!
- Old lineage: ~134 mya
- Great diversity: habit, habitat, pollination, morphology
- Adaptive radiations:
  - (orchids—21,950 spp; grasses—10,035 spp)
- Smallest & largest seeds: orchids; *Lodoicea maldivica*
- Largest inflorescences (titan arum, palms, bromeliads)
- Smallest fruit, flower & flowering plant (*Wolffia*)





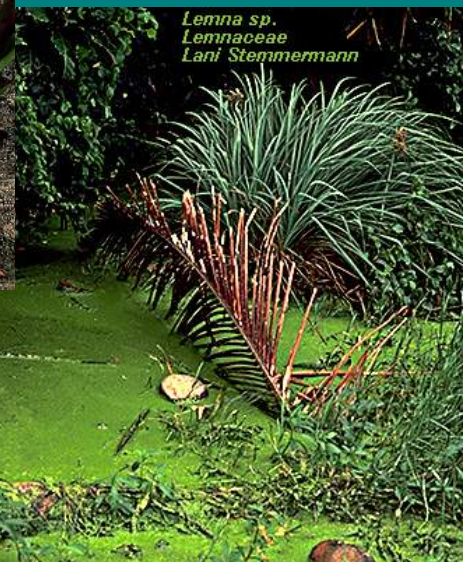
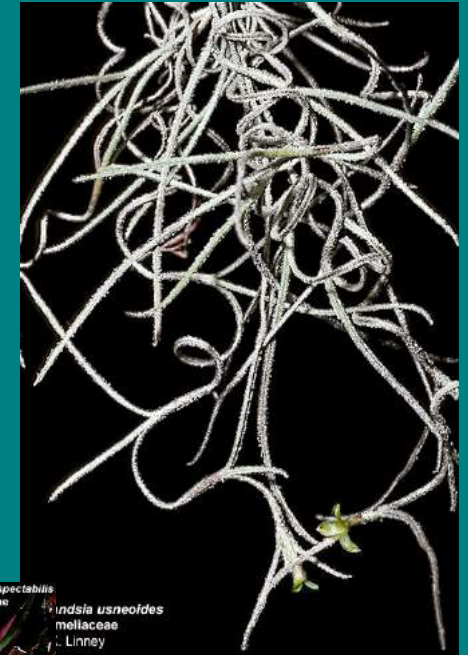
# Tremendous economic importance





# Diversity in ecology

- “Trees”, grasses, rosettes, vines, epiphytes...
- Carnivores, mycotrophs...
- Habitats: dry, wet, aquatic...
- Pollination: water, wind, zoophily





# Diversity of aquatic habits

emergent



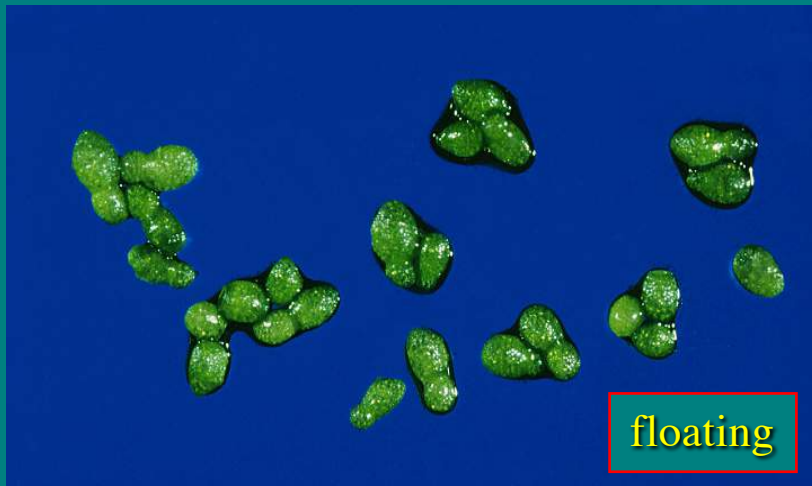
Emergent, floating, or submerged aquatic group of monocots

These are the first diverging monocots

submerged



floating





# Monocot “trees”

No vascular cambium activity  $\Rightarrow$  no true secondary growth (wood)

Anomalous secondary growth  $\Rightarrow$  “trees”



Dragon tree – a lily relative



Woody palm



# Monocot leaves



- **Parallel venation** (or derived forms) vs. pinnate or reticulate venation as in most dicots
- (more on this later)





# Monocot flower: common theme

3-merous

Tepals are common





# Diversity in pollination

Striking modifications & bracts:

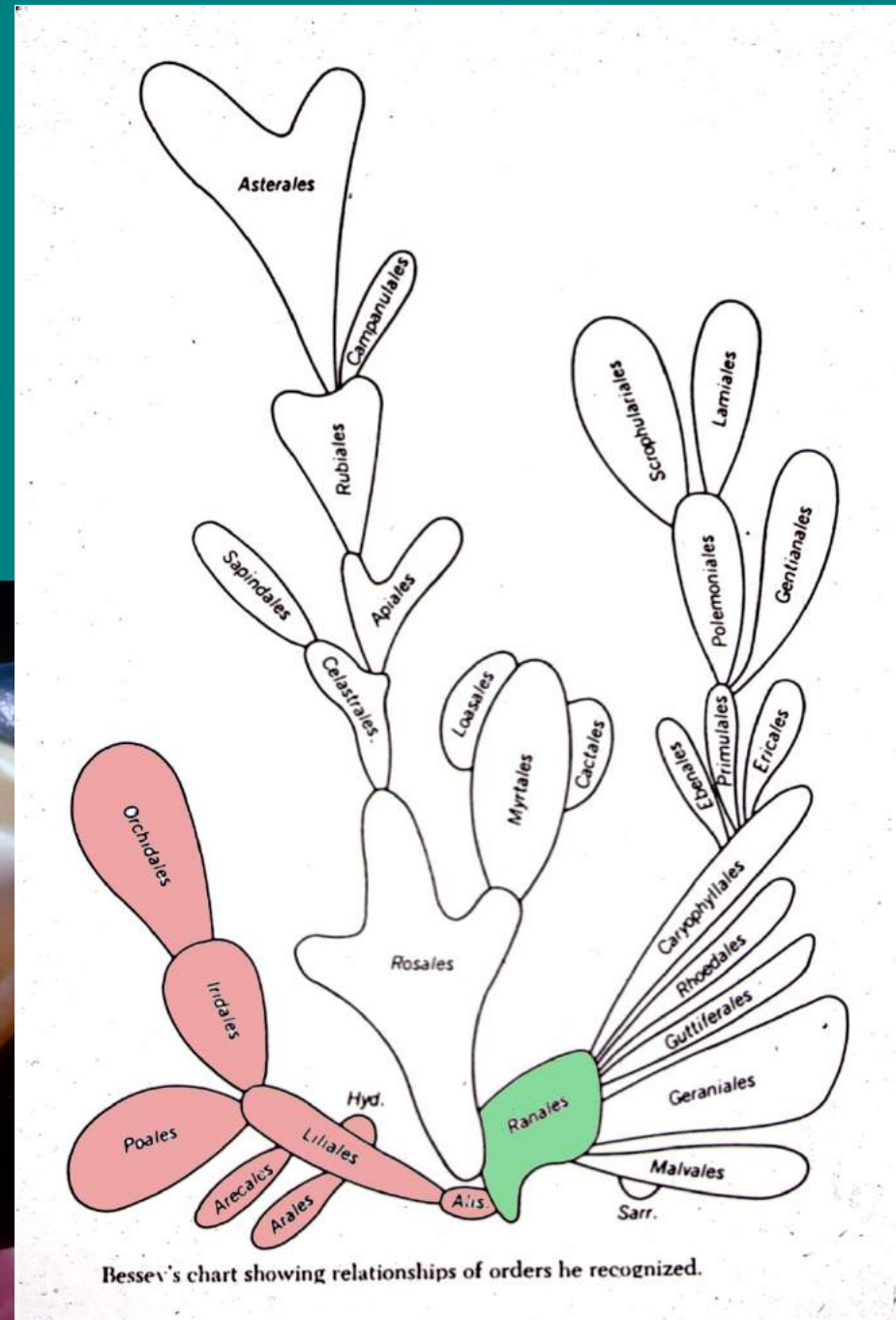
grasses, pulpits, orchids, spadices & more!





# Monocot Origins

Monocots have usually been considered as derived out of **basal angiosperms** - Ranales in the Bessey system or subclass Magnoliidae with Cronquist





# Monocot Origins

Crown group radiation: ~135+ mya [based on DNA evidence]

Pollen & leaf: possible early Aptian (Early Cretaceous), 113-125 mya

Oldest unambiguously assigned fossil: Araceae, 110-120 mya

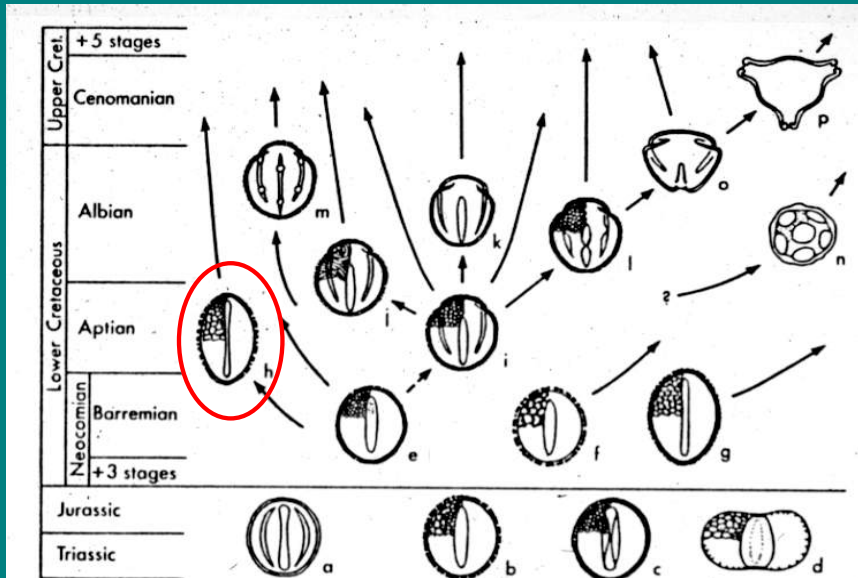


Figure 1 Time distribution and presumed relationships of principal Early Cretaceous and Cenomanian angiosperm pollen types (e-p), and selected pre-Cretaceous pollen types (a-d). a: *Eucommiidites*; b: Triassic reticulate-columellar monosulcate of Cornet (30); c: cycad-type alveolar monosulcate; d: saccate 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.

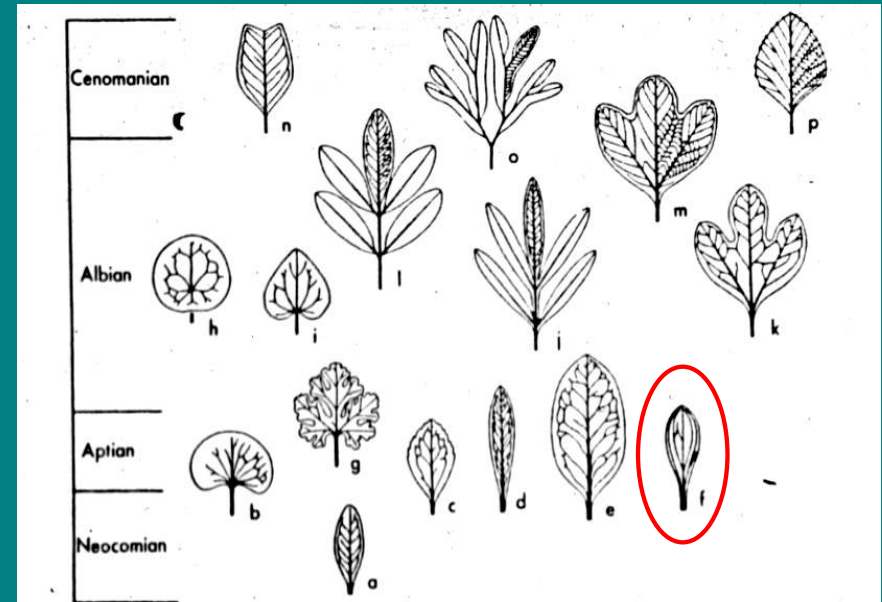
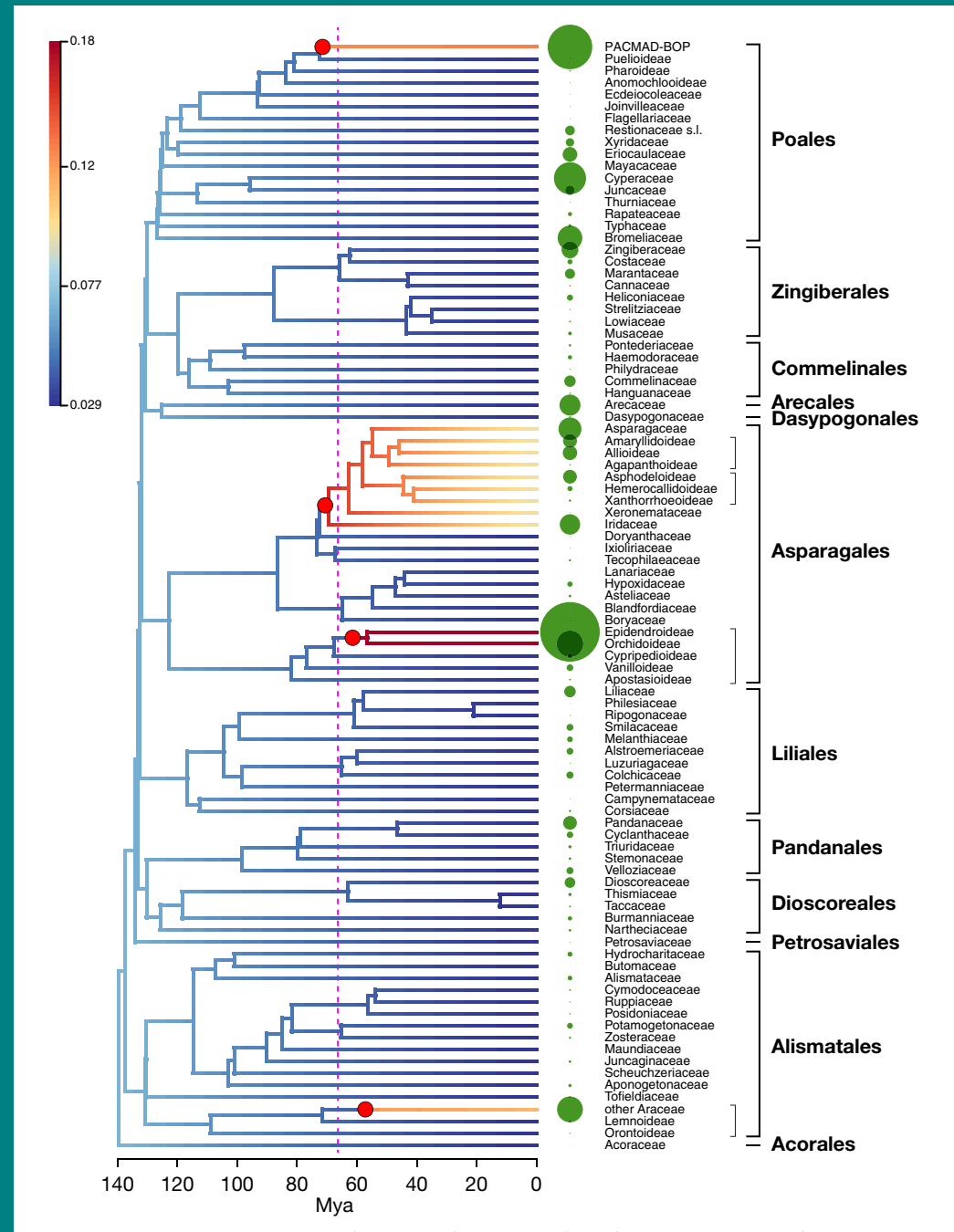


Figure 2 Principal Early Cretaceous and Cenomanian angiosperm leaf types. a: small, pinnately veined leaf of Vakhrameev (143); b: reniform; c: serrate; d: oblanceolate; e: *Ficophyllum*; f: *Acaciaephyllum*, a possible monocot; g: lobate reniform; h: peltate, actinodromous; i: ovate cordate; j: pinnatifid *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.



# Monocot Origins

- cpDNA genome phylogeny (Givnish et al. 2018)
- rapid radiation at base
- four large burst in species diversification





# Monocot leaf evolution



Classic idea of pre-monocot characteristics – Cronquist's view:

1. Herbs
2. Aquatic
3. Perianth not specialized
4. Uni-aperturate pollen
5. Apocarpy
6. Laminar placentation

**Nymphaeales**

Only non-monocot order with all these characteristics

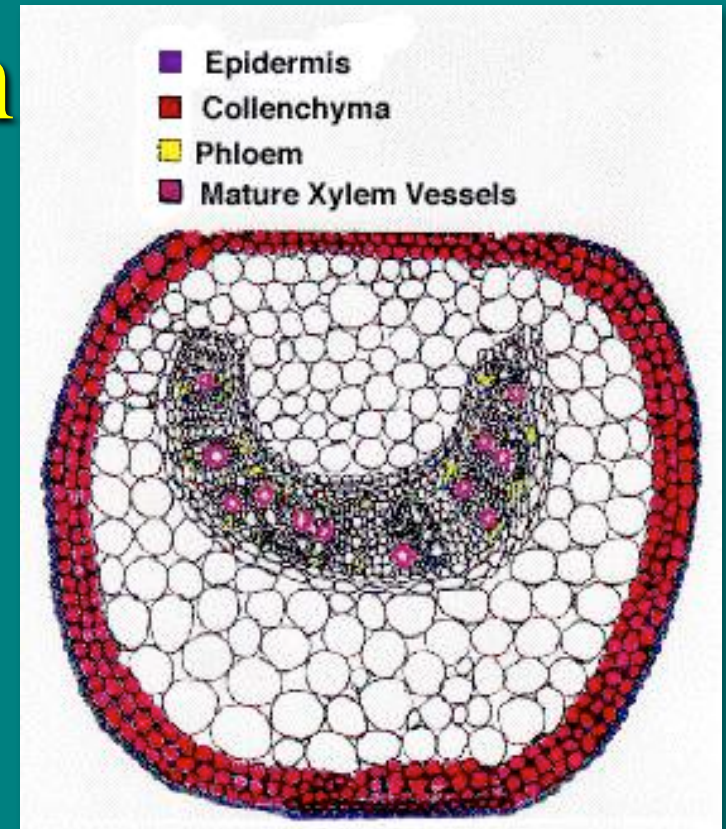


# Monocot leaf evolution



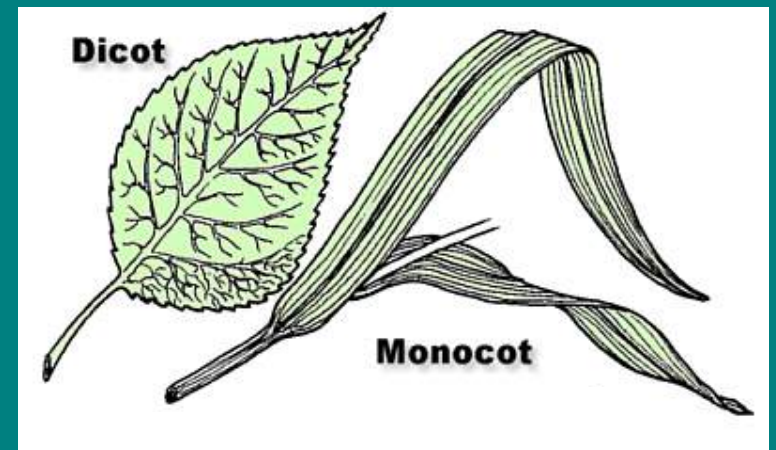
- monocot leaf morphology due to **aquatic ancestry**
- aquatic → terrestrial → aquatic pathways

# Monocot leaf evolution



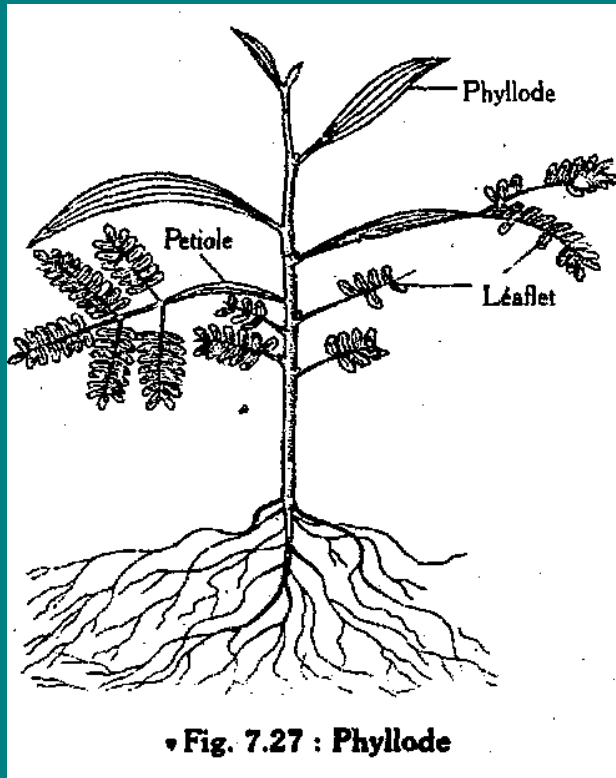
celery (left) and tomato (right) asterid petioles showing parallel vascular traces

- monocot leaf is derived from an expanded bladeless petiole





# Monocot leaf evolution

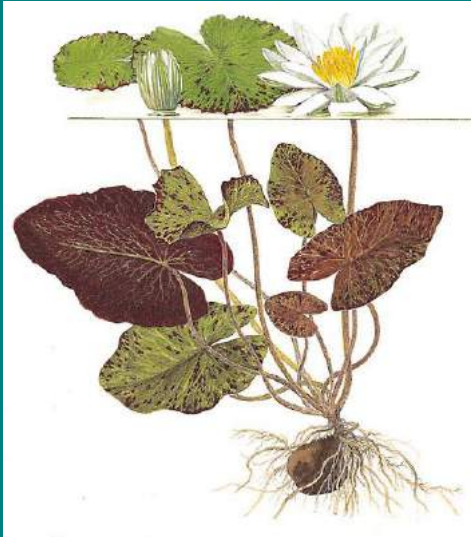


**Phyllode theory:** original monocot lacked a true leaf; only **expanded petiole**

**Phyllodes:** expanded **blade-less petioles** best seen in arid adapted woody legumes such as *Acacia*



# Monocot leaf evolution



→  
loss of blade  
& expansion  
of tissue  
between  
parallel veins  
of petiole

in aquatic habitat



→  
variable  
expansion of  
tissue  
between  
parallel veins



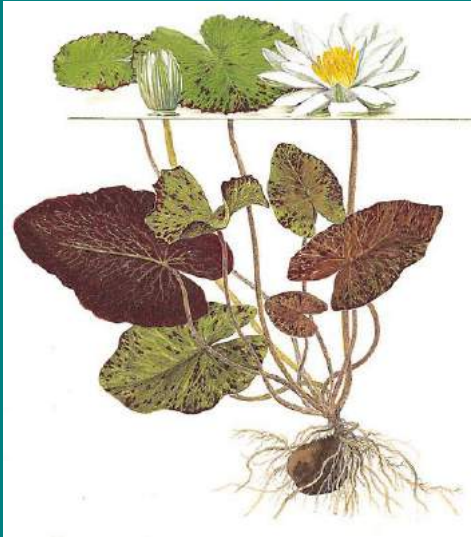
*Acorus*  
sweet flag



↙  
cross veins &  
'reticulated'  
blades



# Monocot leaf evolution



loss of blade  
& expansion  
of tissue  
between  
parallel veins  
of petiole

in aquatic habitat



variable  
divergence  
of parallel  
veins to leaf  
edge



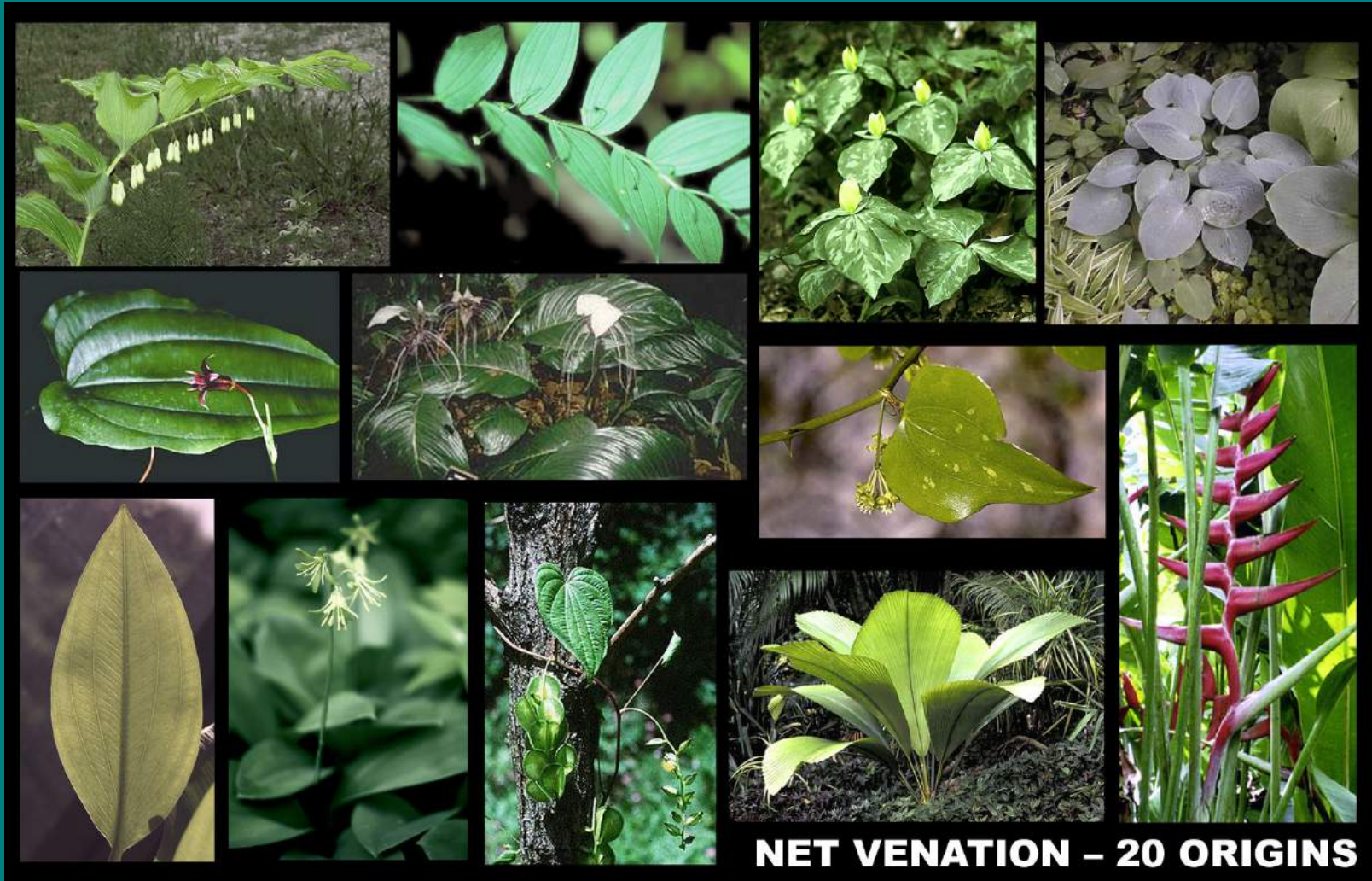
‘parallel-pinnate’  
venation of palms  
and bananas





# Monocot leaf evolution

functional ecological arguments for evolution of **broad leaves** and **fleshy fruits** of monocots **in shady understory** conditions (T. Givnish, 1984, 1999, 2002)

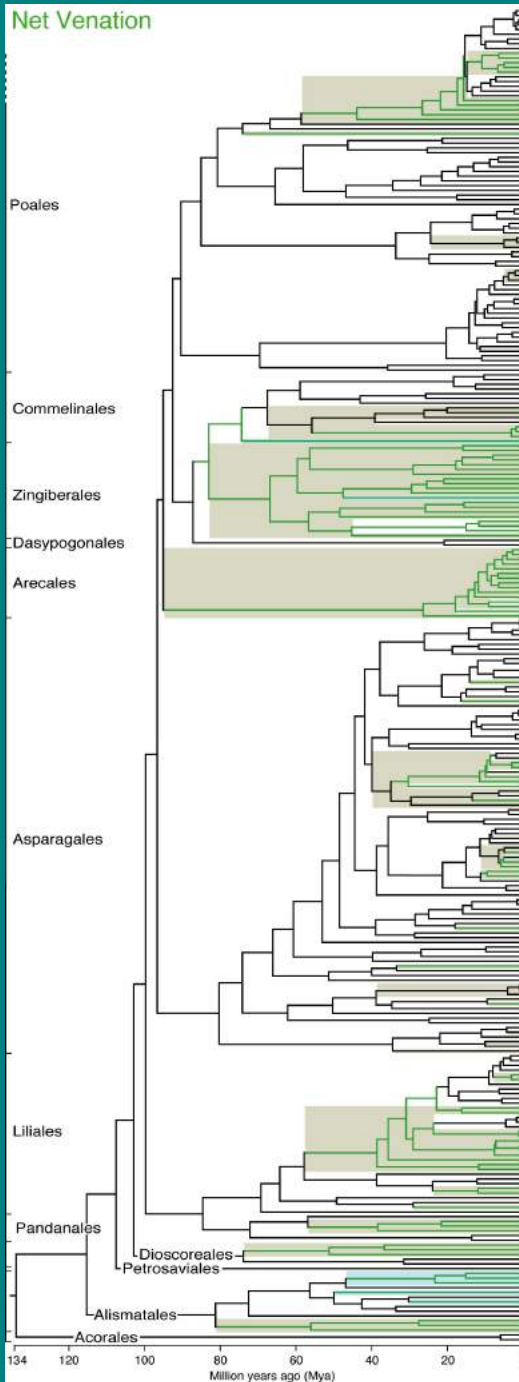


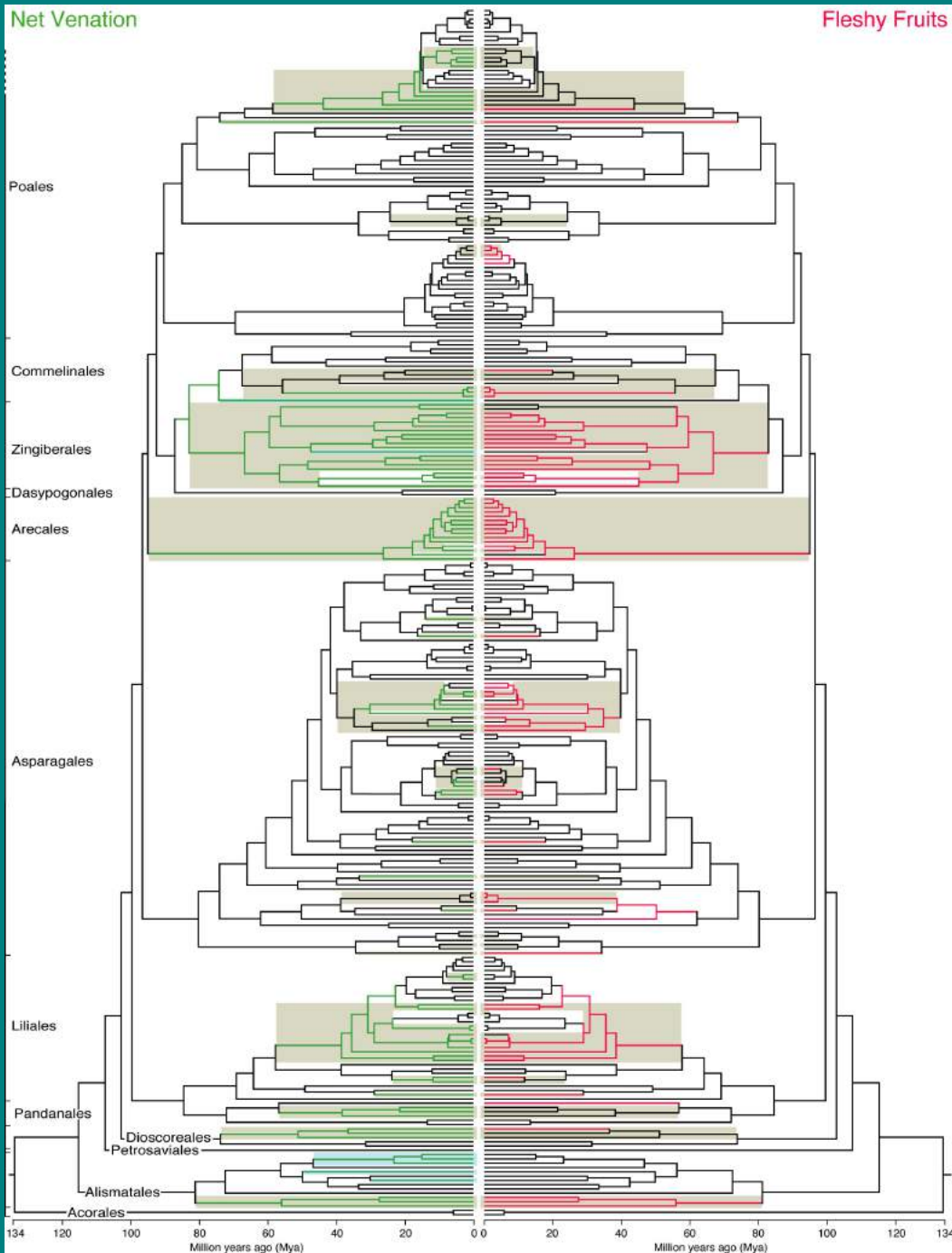
**NET VENATION – 20 ORIGINS**



# Concerted convergence

Occurrences of **net venation** are overlain on this monocot phylogeny





# Concerted convergence

Occurrences of **net venation** and **fleshy fruits** are overlain on this monocot phylogeny

Both features:

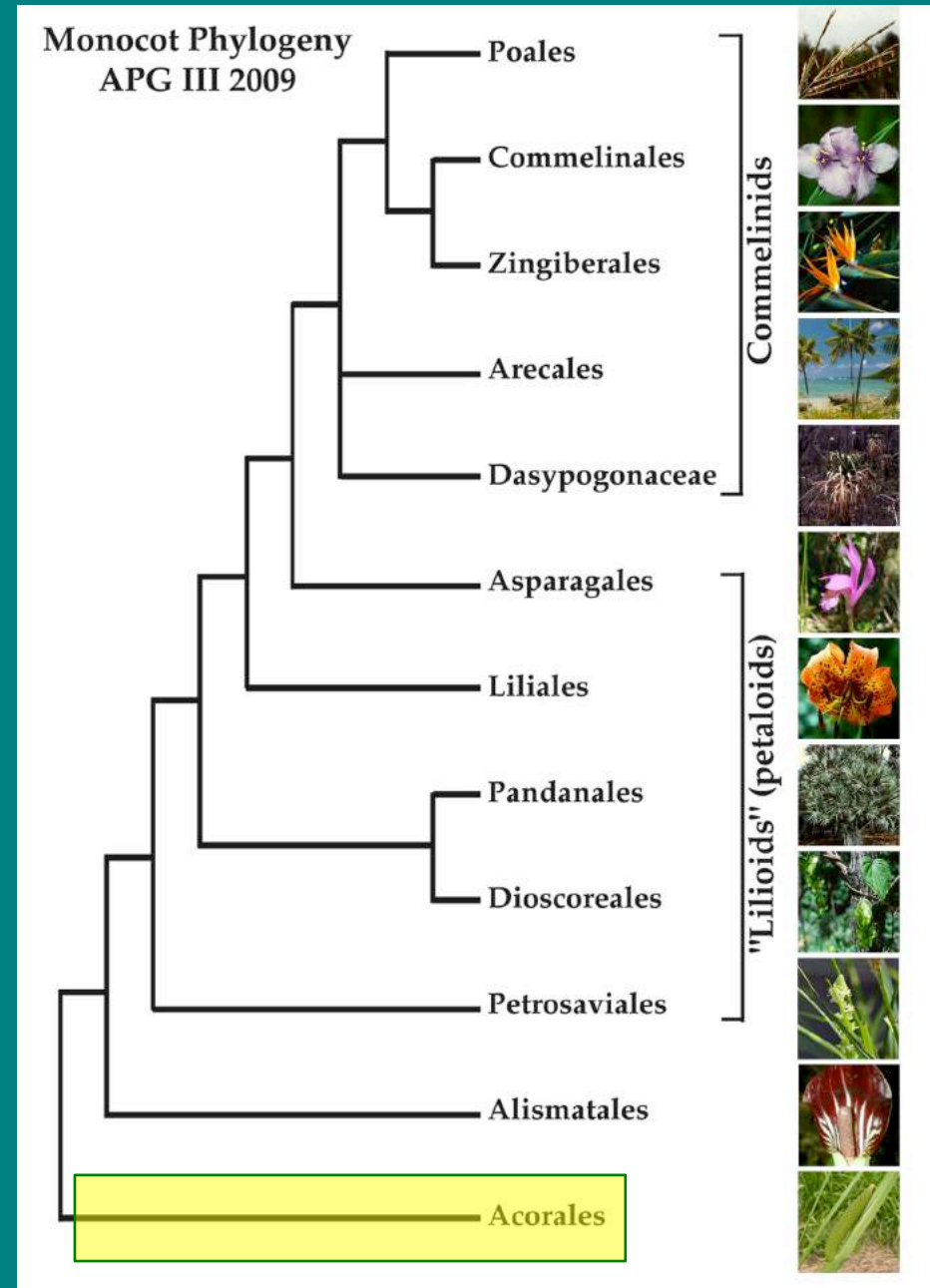
- arise multiple times
- are correlated with each other
- arise in **understory** clades



# Survey of monocots

## 4 main groups:

- **Acorales** - sister to all monocots
- **Alismatales**
  - inc. Aroids - jack in the pulpit
- “Lilioids” (lilies, orchids, yams):
  - non-monophyletic
  - petaloid
- **Commelinids**
  - Arecales – palms
  - Commelinales – spiderwort
  - Zingiberales – banana
  - Poales
    - pineapple
    - grasses & sedges



# Acorales (\*Acoraceae - sweet flag)

- Emergent aquatic plants with **ethereal oils** and no raphides

2 species:

*Acorus calamus*, Old World

*A. americanus*, New World

Both species in Wisconsin



*Acorus*  
sweet flag





# \*Acoraceae - sweetflag



Flat filaments



$P^6 \quad A^6 \quad \underline{G}^{(3)} \infty$  seeds

- Inflorescence with 'spathe' and spadix
- Flowers bisexual



*Acorus americanus* - sweet flag



# \*Acoraceae - sweetflag



Flat filaments



P<sup>6</sup> A<sup>6</sup> G<sup>(3)</sup> ∞ seeds

- Inflorescence with 'spathe' and spadix
- Flowers bisexual



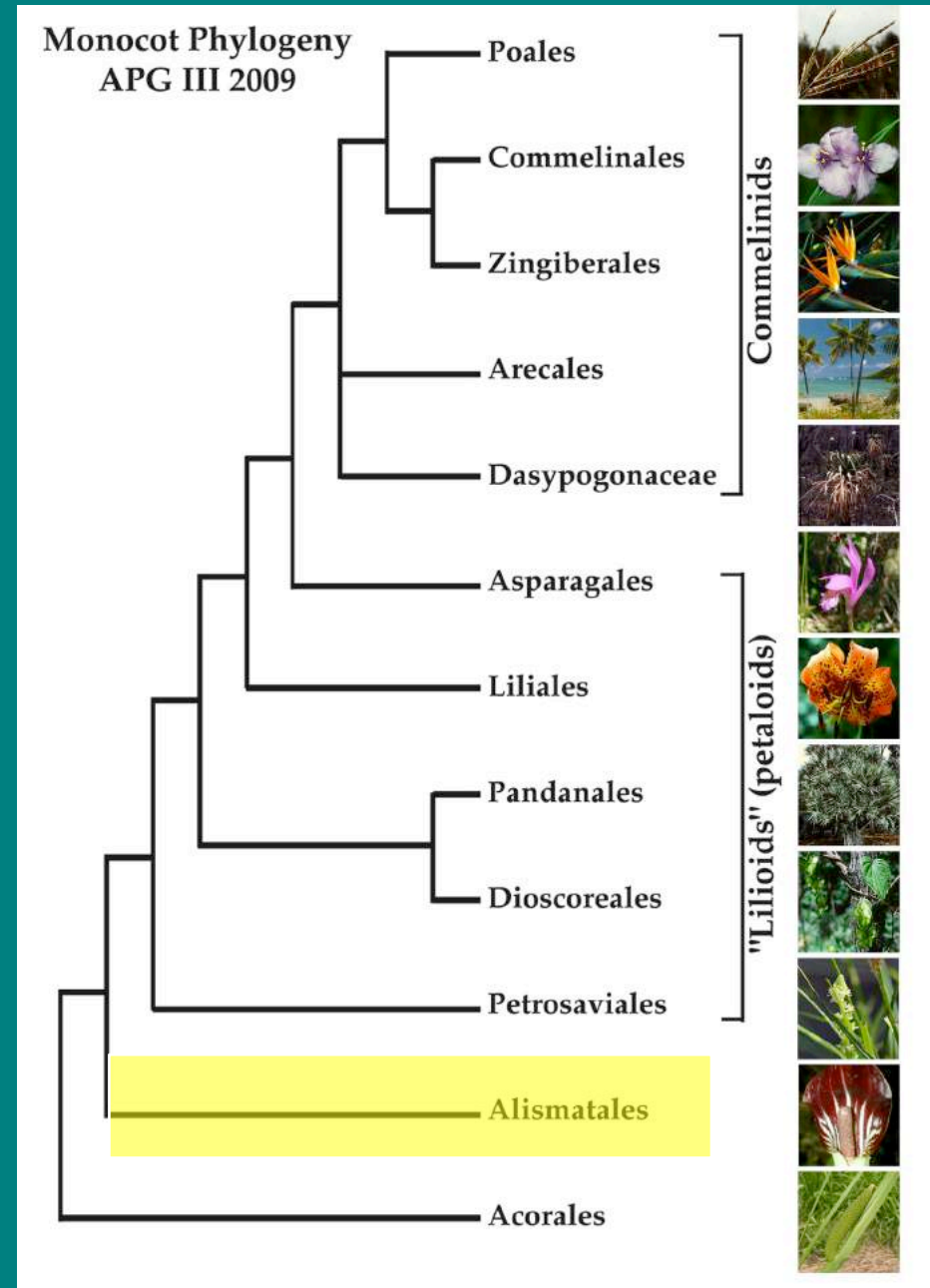
*Acorus americanus* - sweet flag



# Alismatales

## 4 main groups:

- Acorales - sister to all monocots
- Alismatales
  - inc. Aroids - jack in the pulpit
- “Lilioids” (lilies, orchids, yams)
  - non-monophyletic
  - petaloid
- Commelinids
  - Arecales – palms
  - Commelinales – spiderwort
  - Zingiberales – banana
  - Poales
  - pineapple
  - grasses & sedges



# Alismatales - aquatics

Recurring themes:

Aquatic  $\Rightarrow$  brackish  $\Rightarrow$  marine habitats

Insect  $\Rightarrow$  water pollination





# Alismatales - aquatics

emergent



Emergent, floating, or submerged aquatic group of monocots

submerged



floating





# Alismatales - aquatics



Showy flowers, insect-pollinated

Associated with the aquatic habit is the trend from insect-pollinated, showy flowers to water-pollinated, reduced flowers . . .

and increasing effort to vegetative rather than sexual reproduction

Reduced unisexual  
flowers, water-  
pollinated





# Alismatales - aquatics



Showy flowers, insect-pollinated

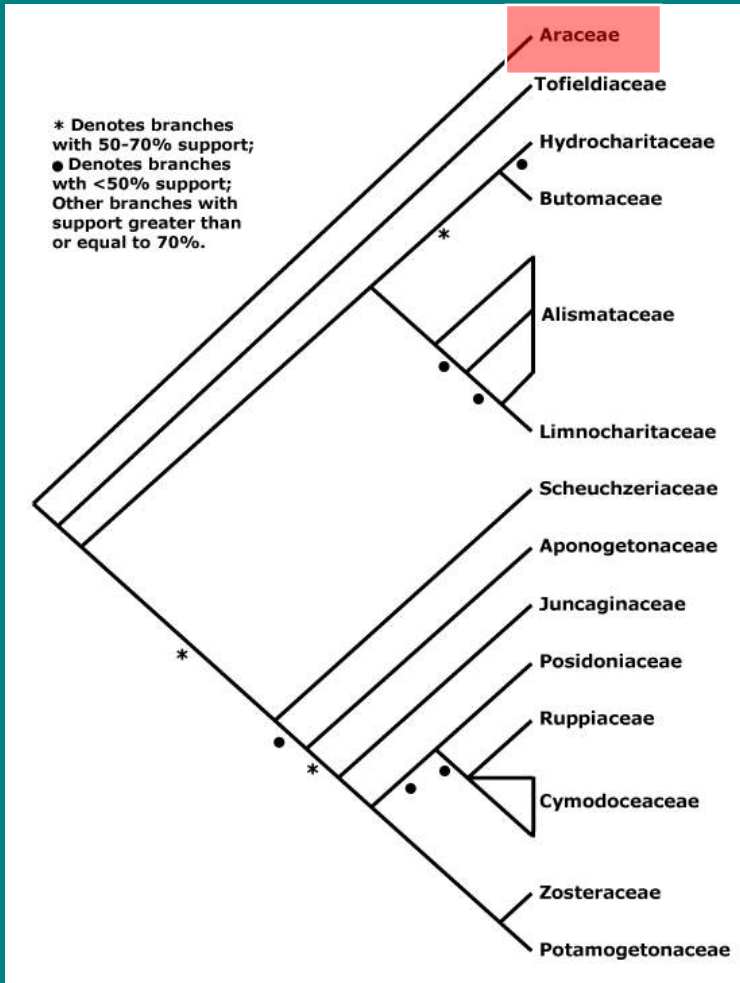
72% of Alismatales are **unisexual** - monoecious or dioecious

132 species are **hydrophilous** (*how many origins?*) – answer later

Reduced unisexual  
flowers, water-  
pollinated

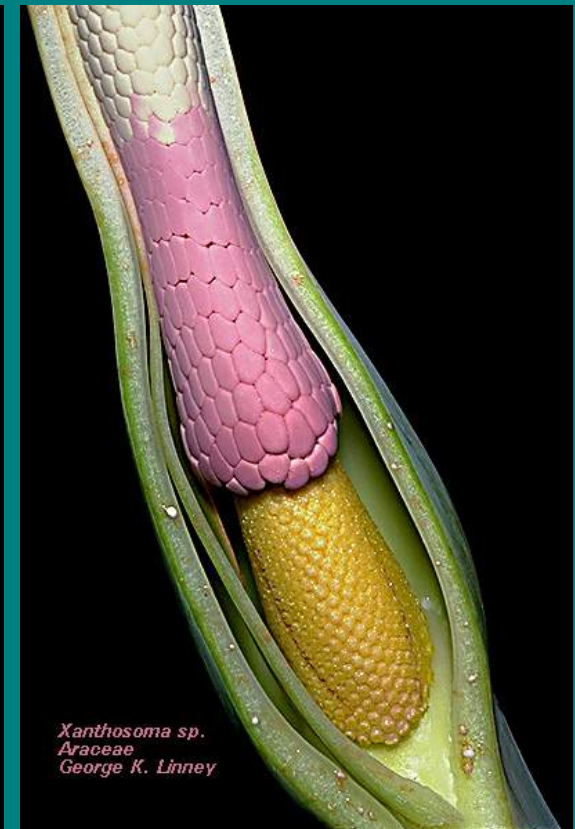


# \* Araceae - aroids



104 genera  
2,550 species

- Sister family to other Alismatales
- Tropical (to temperate)
- epiphytes, herbs, aquatic





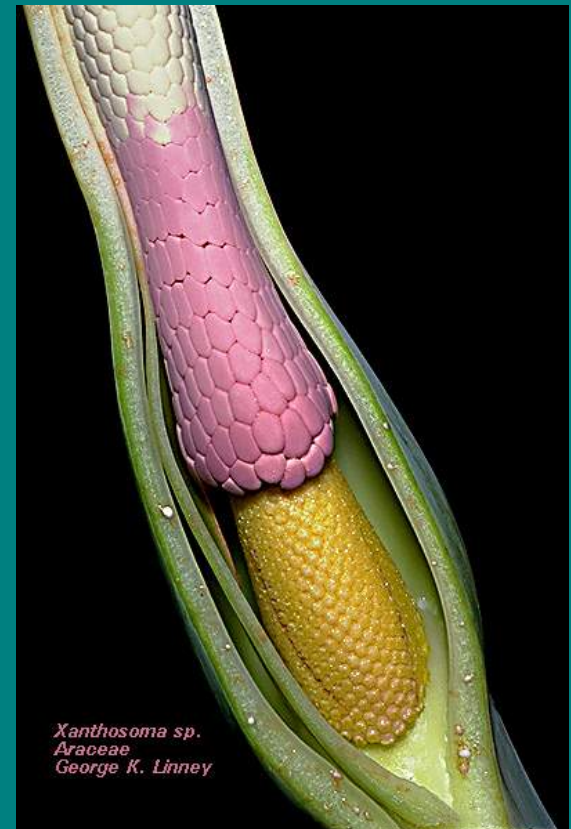
# \* Araceae - aroids

- raphides in vacuoles with mucilage
- Ca-oxalate (endo-osmosis)



- defining characteristic is the inflorescence of **spathe** and **spadix**

- spathe (or bract) is common in monocots



# \* Araceae - aroids



Inflorescence a fleshy **spadix**, surrounded by bract called the **spathe**

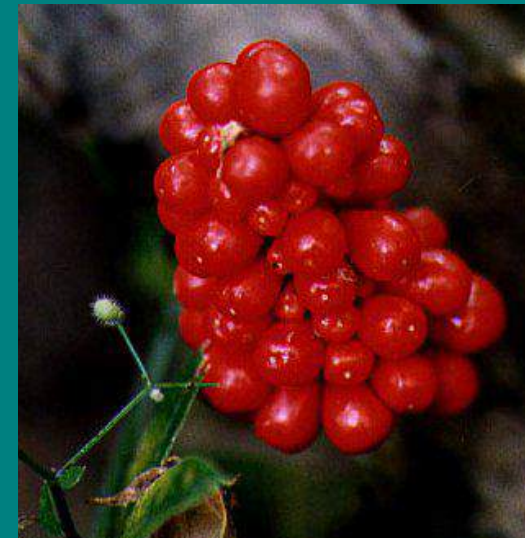
CA 0 CO 0 A 6- G (2-3)

Flowers unisexual or perfect  
Fruits berries clustered on spadix

spadix

spathe

(cut away)



*Symplocarpus foetidus* -  
skunk cabbage

*Arisaema triphyllum* - jack-in-the pulpit



# \* Araceae - aroids



L:female  
R:male



*Arisaema triphyllum* - jack-in-the pulpit  
[or jill-in-the-pulpit ?]



# \* Araceae - aroids



*Symplocarpus foetidus* - skunk cabbage



Cabbage-like leaves emerge later in the spring

**Foetid** smelling spathe and spadix emerges early in spring or late winter; attracts **carrion flies** by heating up and volatilizing off the odor



# \* Araceae - aroids



*Symplocarpus foetidus* -  
skunk cabbage



flesh flies –  
*Sarcophagidae*



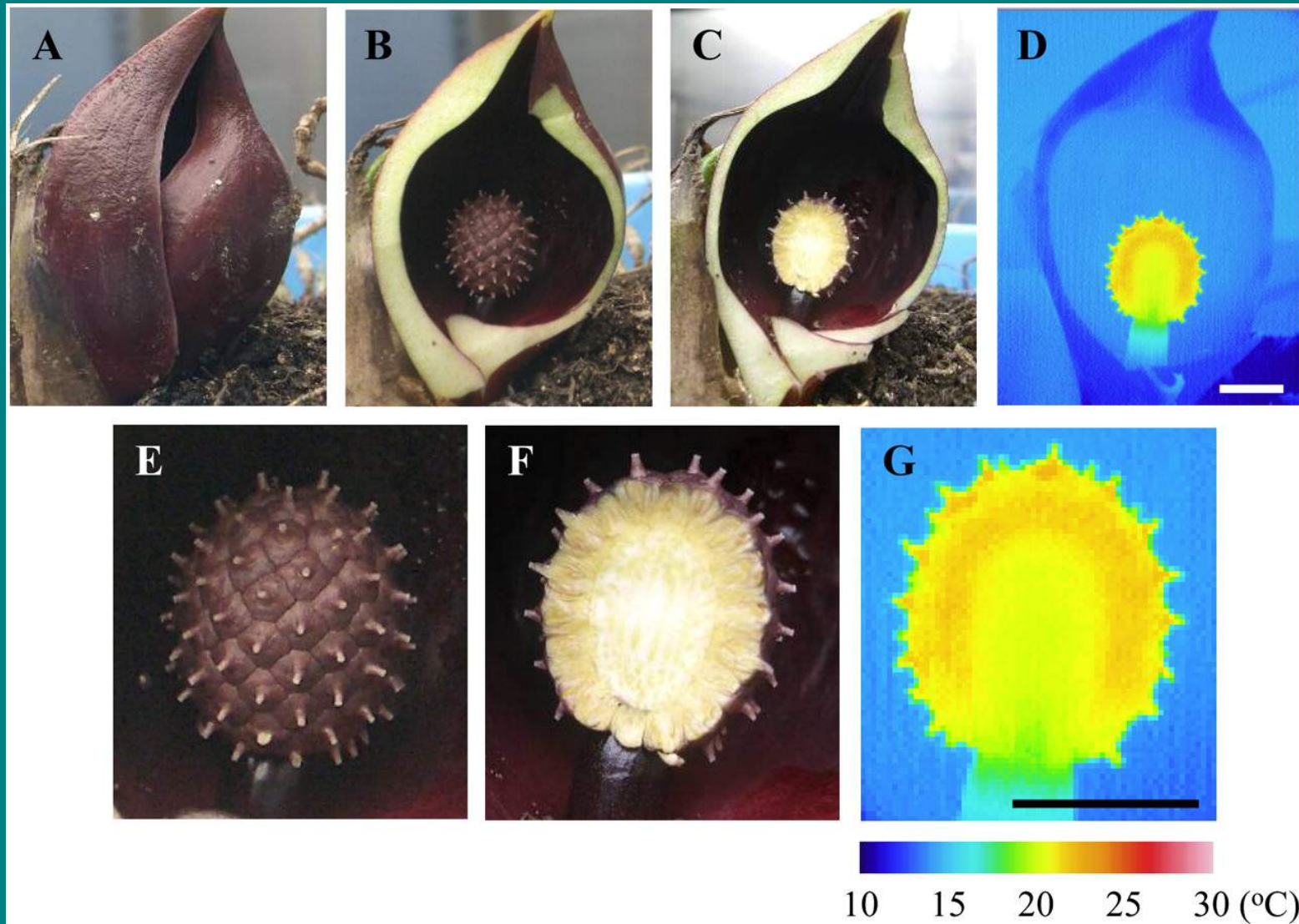
carrion flies –  
*Calliphoridae*

sapromyophily  
pollination



gnats -  
*Mycetophilidae*

# Endogenous heating of skunk cabbage (*S. renifolius*) spadix





# \* Araceae - aroids



*Calla palustris* - water arum

Only emergent aquatic member  
of the family in Great Lakes





# \* Araceae - aroids



*Monstera* - tropical aroid



# \* Araceae - aroids



*Zantedeschia*  
arum lily

funeral plants!

*Spathiphyllum*





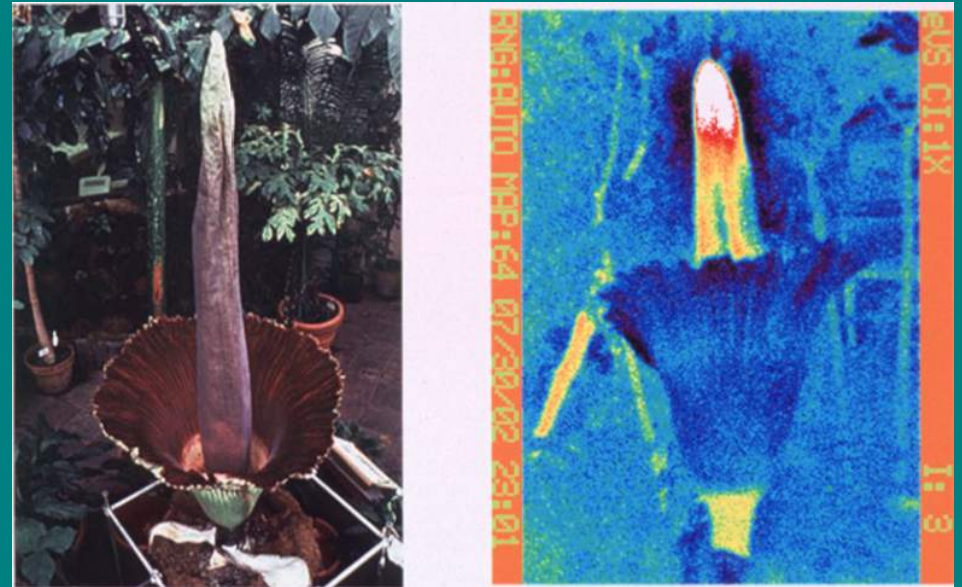
# \* Araceae - aroids

other strange aroids:

*Amorphophallus* - titan arum

*Pistia* - water lettuce

“*Lemnaceae*” - duckweeds





# \*Araceae (Lemnaceae - duckweeds)



*Lemna minor* - small duckweed

Floating or submersed aquatic \*family\*  
almost cosmopolitan in distribution;  
Vegetative reproduction primarily

Now known to be derived from within the  
Araceae

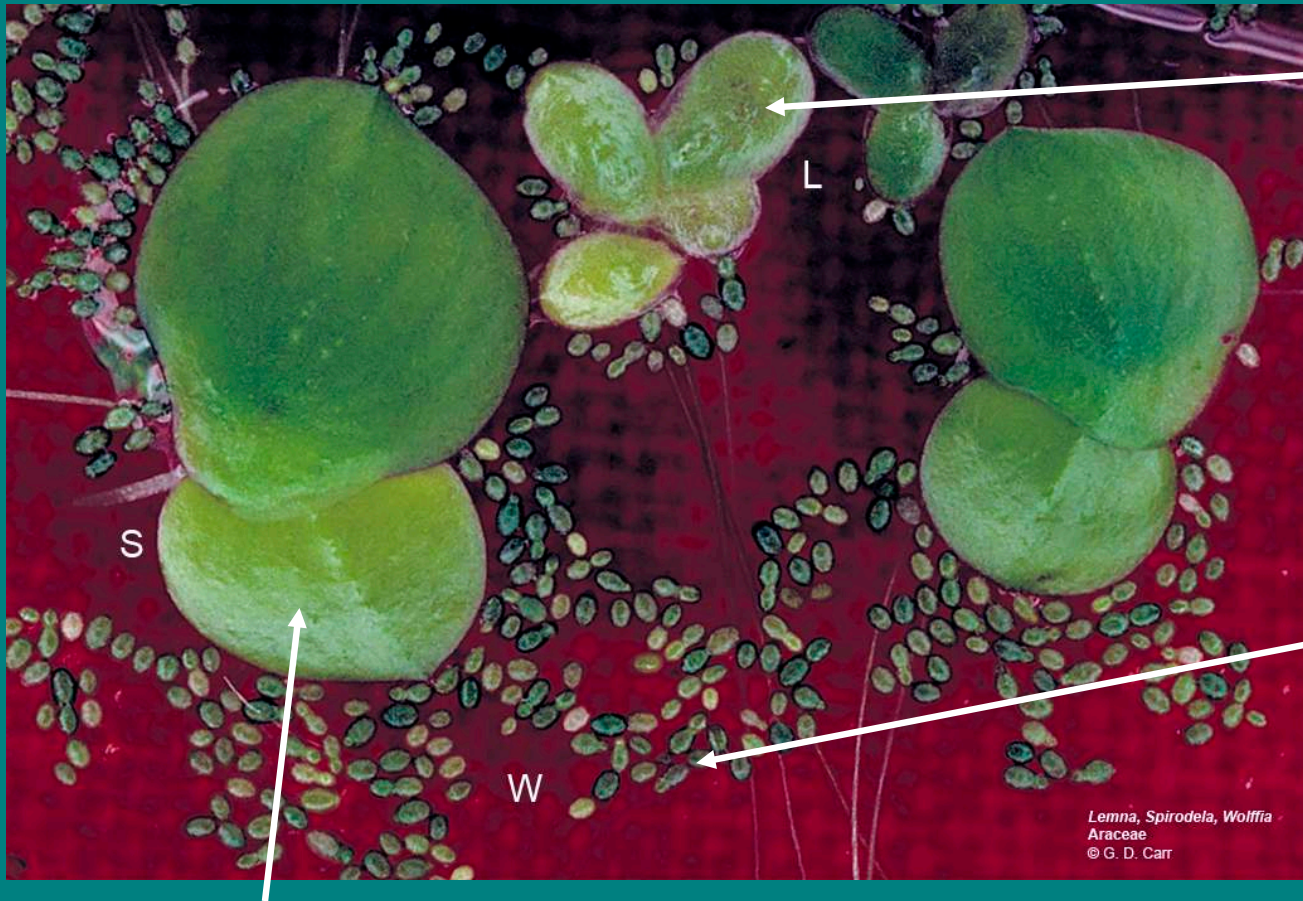
Includes the smallest  
angiosperm, and the smallest  
flower

Inflorescence reduced to 1  
female and 1-2 male flowers



*Lemna turionifera* - perennial duckweed

# \*Araceae (Lemnaceae - duckweeds)



*Lemna*

Smallest member of the family and the angiosperms:

*Wolffia columbiana* - water meal

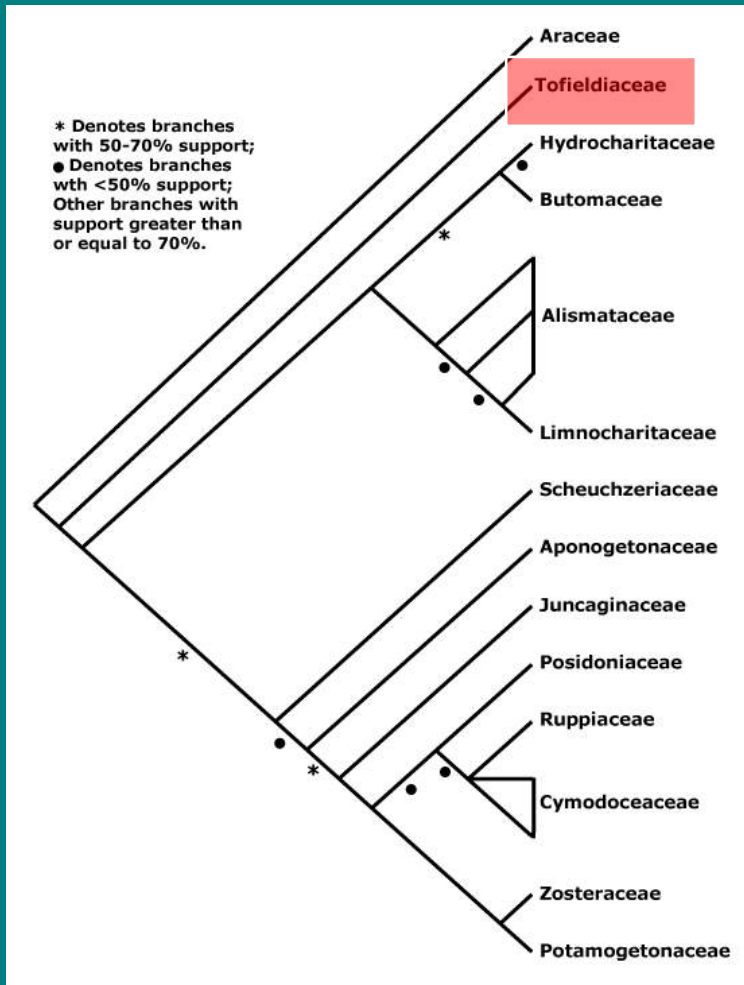
*Lemna, Spirodela, Wolffia*  
Araceae  
© G. D. Carr

*Spirodela polyrhiza*  
great duckweed

Largest member of the family



# Tofieldiaceae - asphodels

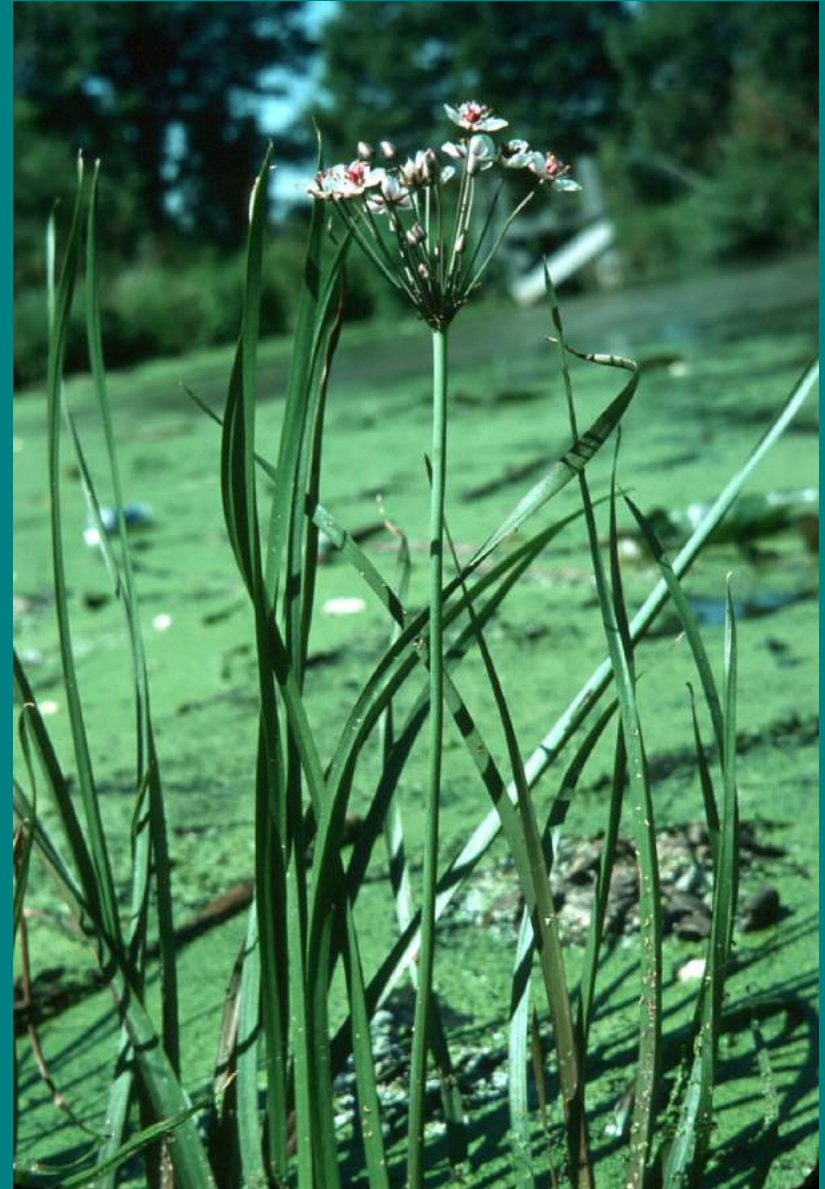


- Surprising inclusion!
- “Lilioid” flowers (Liliaceae s.l.)
- wet loving small herbs



# Butomaceae - flowering rush

- emergent aquatic family
- leaves show no obvious blade and petiole differentiation

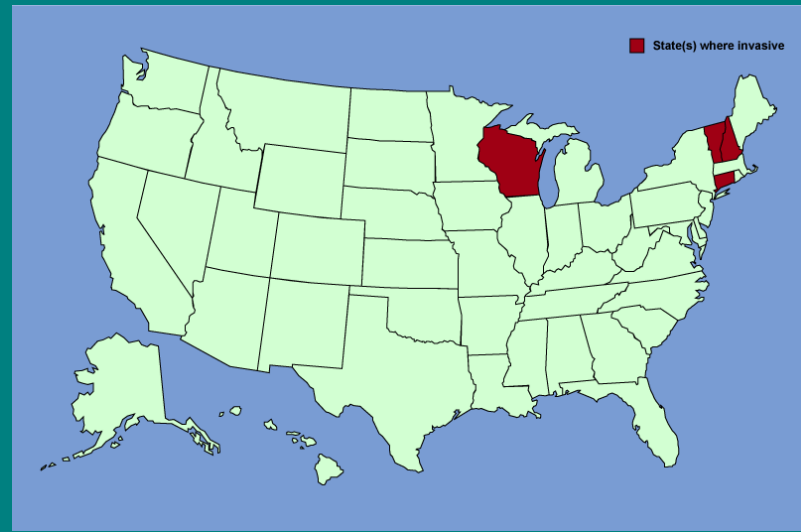




# Butomaceae - flowering rush

- flowers in umbels
- unsealed carpels - **follicles**
- introduced - invasive

CA 3 CO 3 A 9 G 6



*Butomus umbellatus* - flowering rush

# Alismataceae - water plantain



Aquatic or wetland family, especially in north temperate regions

Leaves long petioled, often with sagittate-shaped leaves

Tubers starchy, often edible



*Sagittaria* - arrowhead



# Alismataceae - water plantain

*Sagittaria* - arrowhead

CA 3 CO 3 A 6 - ∞ G 6 - ∞

Calyx of 3 green sepals, corolla of 3 white petals

**Apocarpic** in a head or ring

Perfect, monoecious, dioecious



# Alismataceae - water plantain

*Sagittaria* - arrowhead

CA 3 CO 3 A 6 - ∞ G 6 - ∞

Calyx of 3 green sepals, corolla of 3 white petals

**Apocarpic** in a head or ring

**Achenes** (head of achenes here)





# Alismataceae - water plantain



Similar to *Sagittaria*, but with carpels in one **ring** rather than globose head

*Alisma plantago-aquatica* - water plantain



# Potamogetonaceae - pondweed



Aquatic plants with dimorphic leaves, 25 species in Wisconsin difficult to identify, hybridize, and some are troublesome weeds



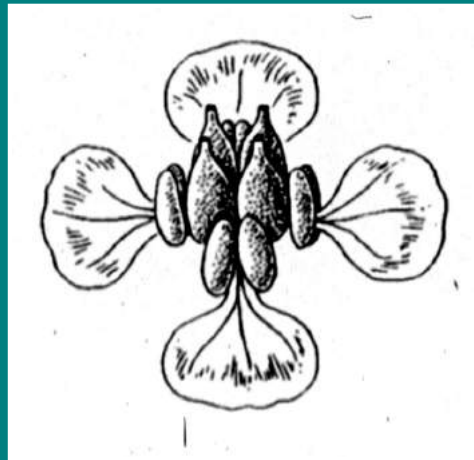
*Potamogeton* sp. - pondweed



# Potamogetonaceae - pondweed



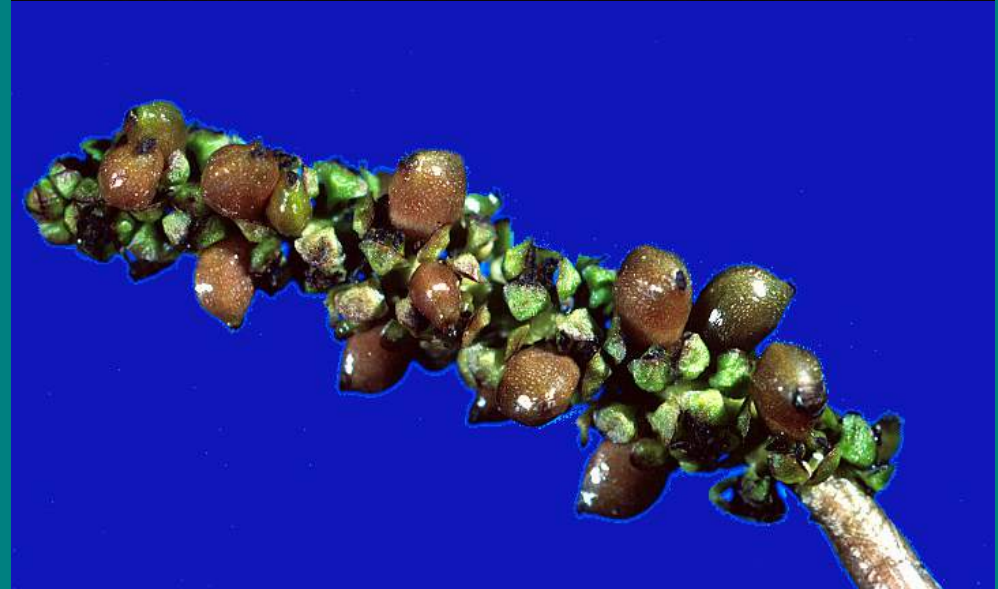
- perianth of 4 clawed segments if present
- gynoecium typically of 4 free, 1-ovuled carpels
- fruit drupe-like



CA 0,4 CO 0 A 4 G 4

*Potamogeton* sp. - pondweed

# Potamogetonaceae - pondweed



*Potamogeton nodosus* - pondweed

Flowers (top) and fruits (bottom)



# Hydrocharitaceae - frog bit



- submersed or floating aquatic plants
- various forms of **water pollination** present

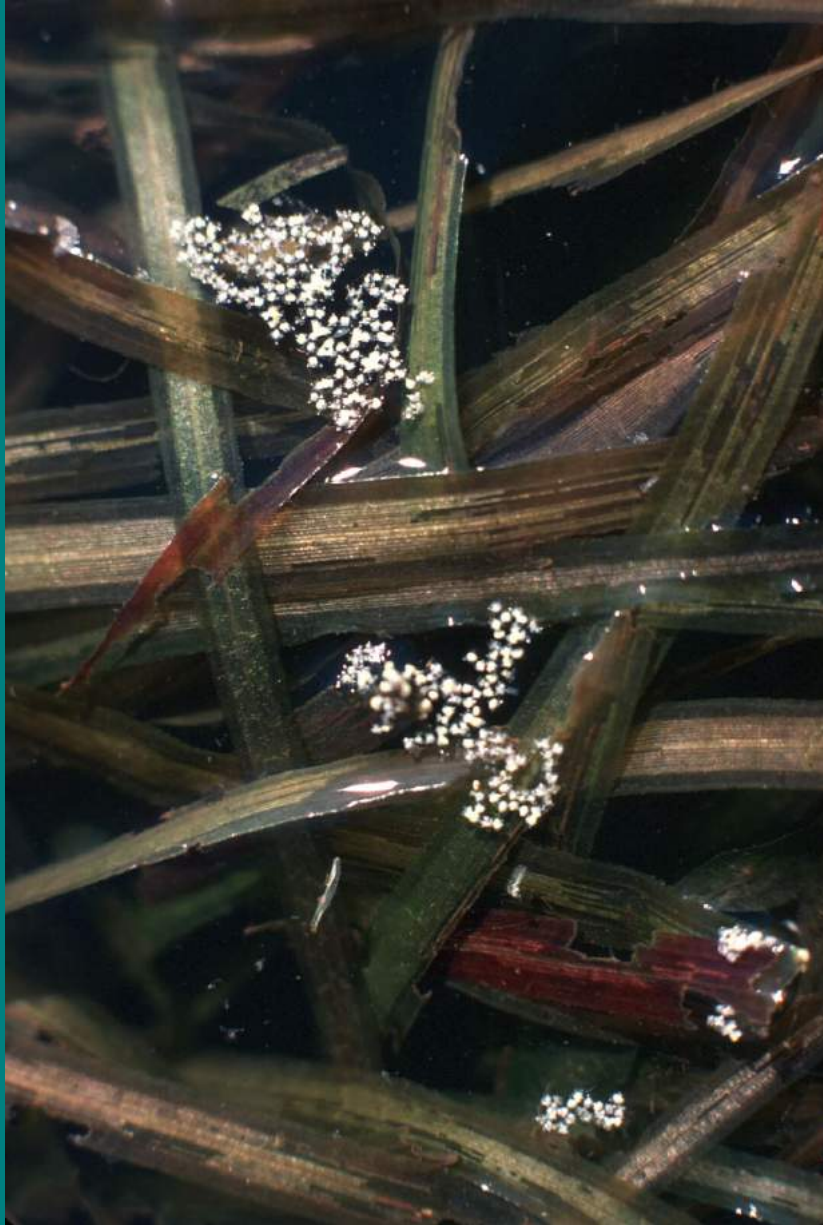


*Elodea canadensis* - waterweed



# Hydrocharitaceae - frog bit

*Vallisneria* (tapegrasses, eelgrasses) are composed of two species, one New World, one Old World



*Vallisneria americana* - tapegrass  
(with *Hydrilla verticillata*)

*Vallisneria americana* - tapegrass



# Hydrocharitaceae - frog bit



*Vallisneria spiralis* - tapegrass (OW)

Note the floating male flowers and one large female with 3 stigmatic areas on a long peduncle

- male flowers in clusters; female flower single
- **pollen water boat** floats and attaches to 3 broad stigma of the female flower
- flower retracts and forms fruit under water



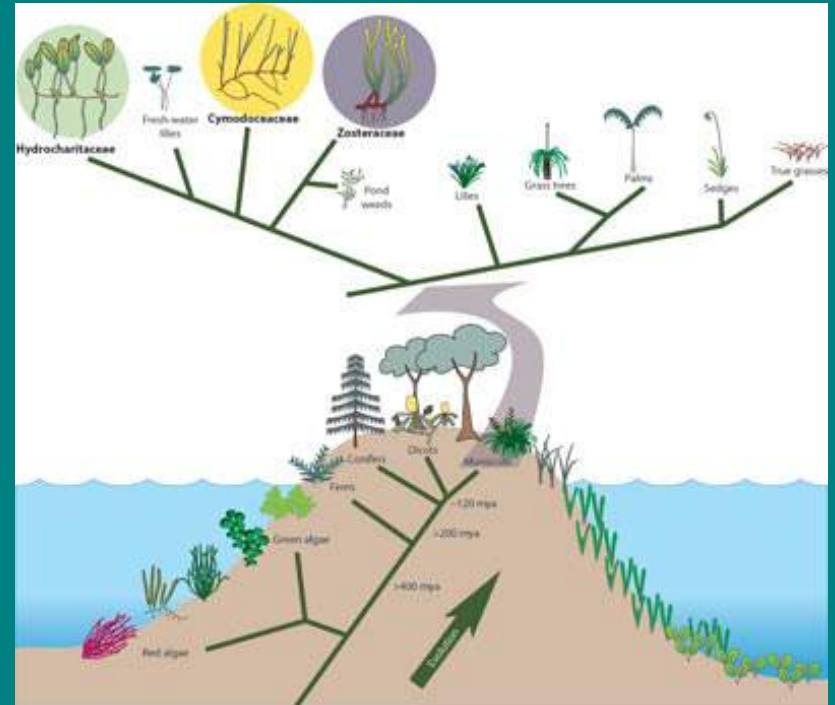
*Vallisneria americana* - tapegrass

# Evolution of Sea Grasses



Don Les' story of plants going back to the oceans 450 million years later

... another story of **convergence and divergence**



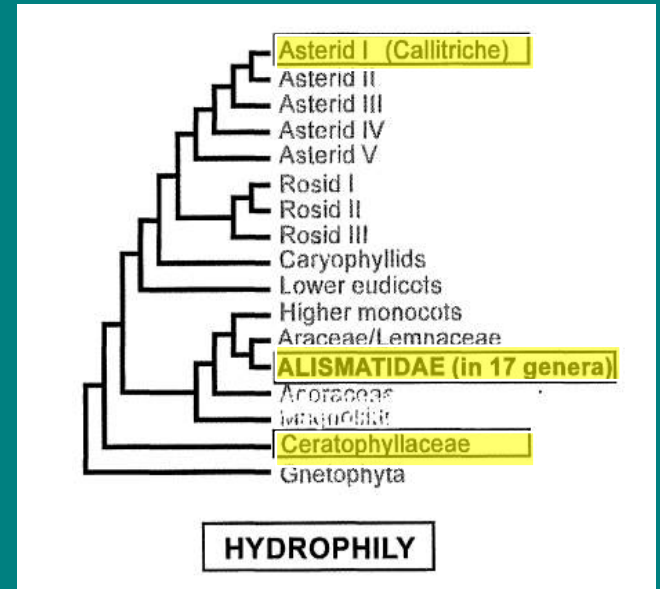
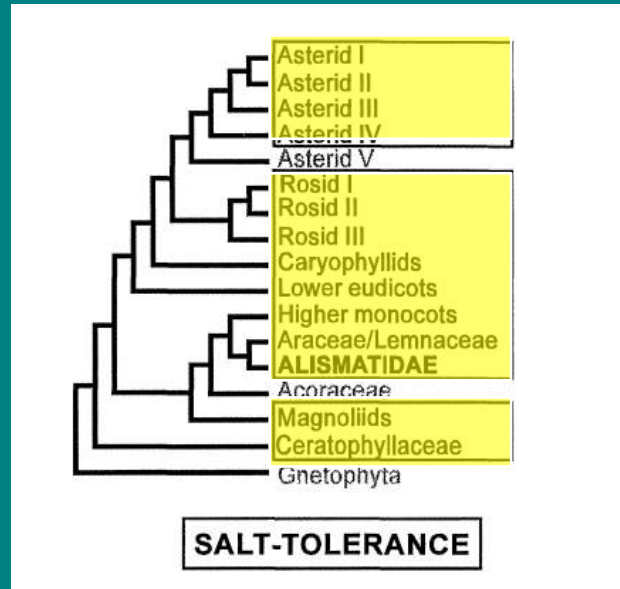
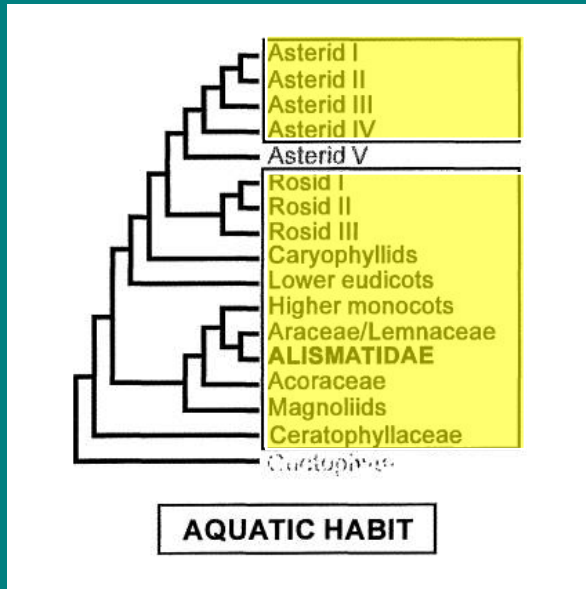


# Evolution of Sea Grasses

Aquatic

⇒ Salt Tolerant

⇒ Hydrophily



Aquatic plants found in most lineages

Salt tolerance also wide-spread

Water pollination restricted

*Callitriche*

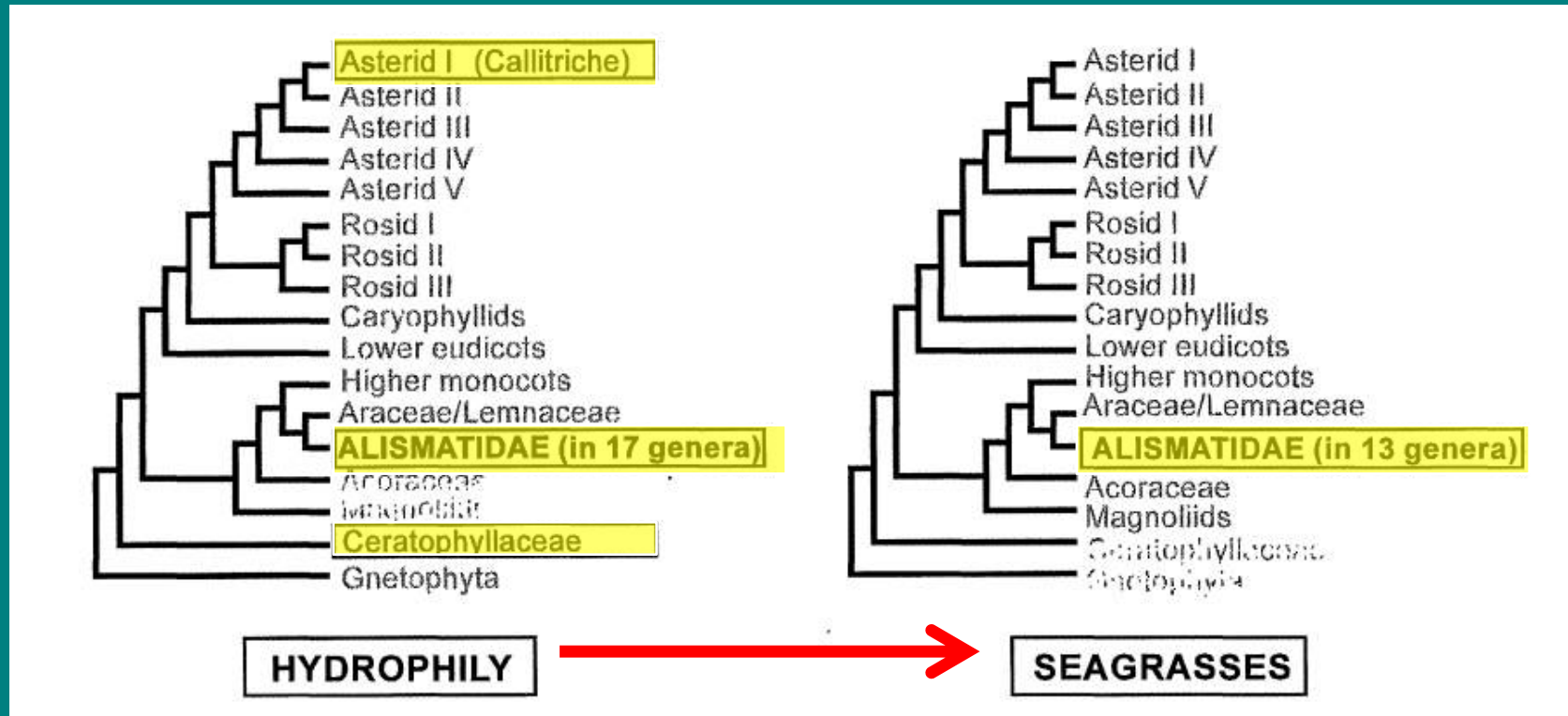


*Ceratophyllum*

# Evolution of Sea Grasses

⇒ Hydrophily

⇒ Marine

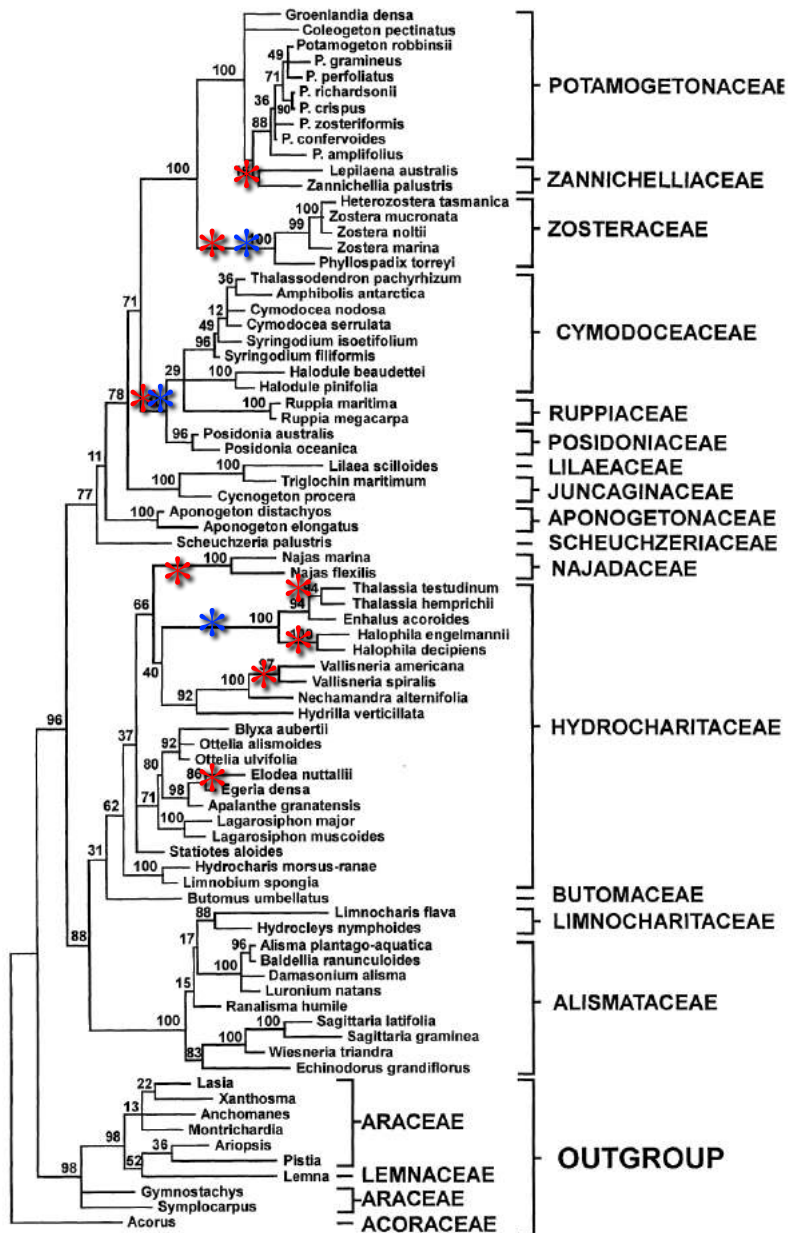


Seagrasses found in **only one lineage** of these aquatic, salt tolerant, and water pollinated lineages (order **Alismatales**)

**A single origin of seagrasses?**



# Evolution of Sea Grasses



- **hydrophily** originated 10 times in angiosperms

- 8 of these times independently in Alismatales!

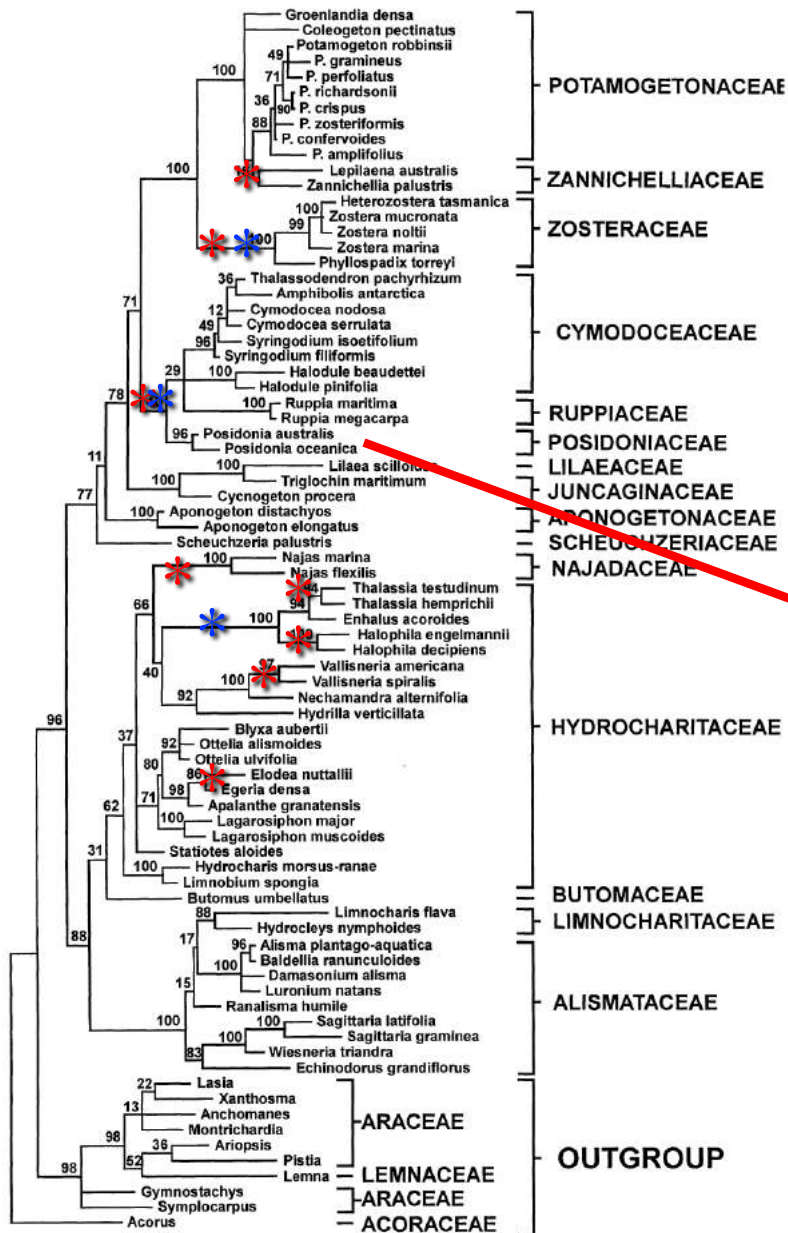
- **marine habitat** originated 3 times independently in Alismatales!

- marine habitat **correlated** with hydrophily

DNA based tree of Alismatales with water pollination and seagrasses mapped on

# Evolution of Sea Grasses

- oldest known clonal organism  
– 200,000 years old !



*Posidonia oceanica* L.

