



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*)



Diversity in ecology

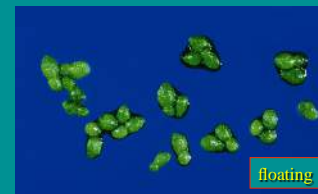
- Trees, grasses, rosettes, vines, epiphytes...
- Carnivores, mycotrophs...
- Habitats: dry, wet, aquatic...
- Pollination: water, wind, zoophily



Diversity of aquatic habits

Emergent, floating, or submerged aquatic group of monocots

These are the first diverging monocots



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

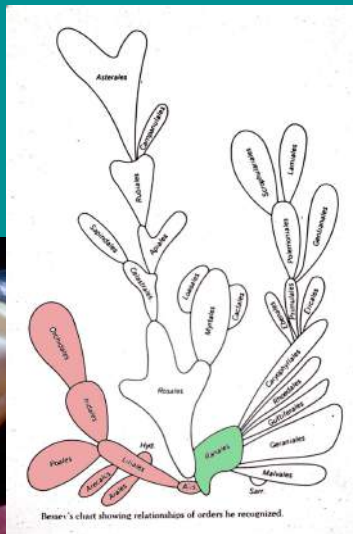
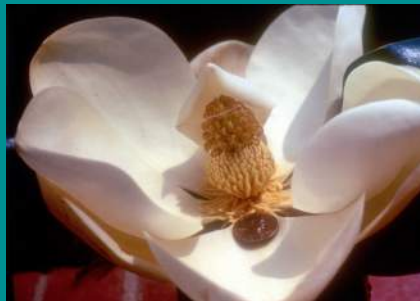
Striking modifications & bracts:
grasses, pulpits, orchids, spadices & more!



Agave sp.
Antonie
© G. D. Carr

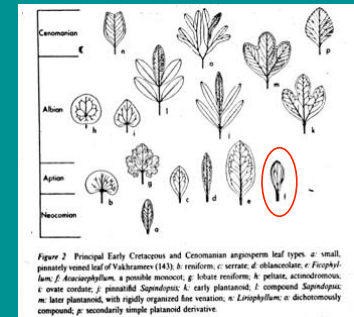
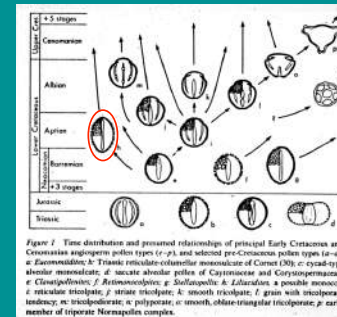
Monocot Origins

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



Fossil record

Crown group radiation: ~134 mya [based on DNA evidence]
Pollen & leaf: possible early Aptian (Early Cretaceous), 113-125 mya
Oldest unambiguously assigned fossil: Araceae, 110-120 mya



Cronquist's view

Classic idea of pre-monocot characteristics:

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



Nymphaeales

Only non-monocot order with all these characteristics

Cronquist's view



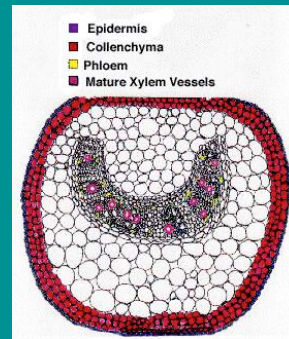
- monocot leaf morphology due to **aquatic ancestry**

• aquatic → terrestrial → aquatic pathways

Cronquist's view

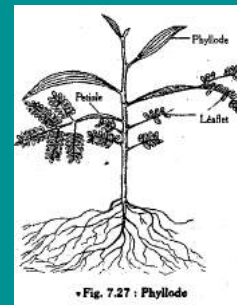


celery (left) and tomato (right) asterid petioles showing parallel vascular traces



- monocot leaf is derived from an **expanded bladeless petiole**

Monocot leaves – phyllode theory



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



Phyllodes: expanded **bladeless petioles** best seen in arid adapted woody legumes such as *Acacia*

Monocot leaves – phyllode theory



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

variable expansion of tissue between parallel veins

in aquatic habitat



Acorus
sweet flag



cross veins & 'reticulated' blades

Monocot leaves – phyllode theory



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

variable divergence of parallel veins to leaf edge

in aquatic habitat

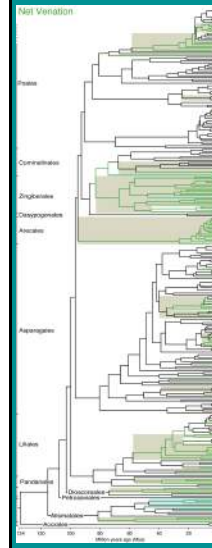


'parallel-pinnate' venation of palms and bananas



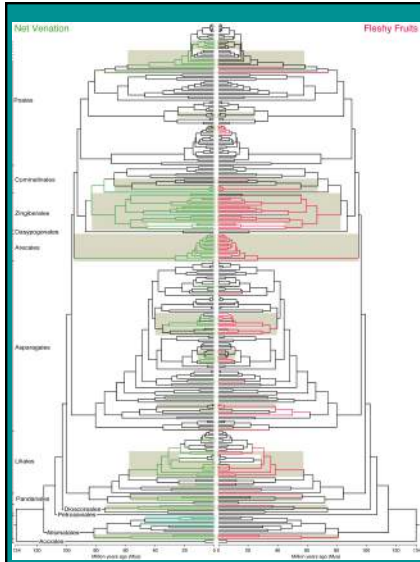
Net venation & fleshy fruits

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



Concerted convergence

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



Concerted convergence

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

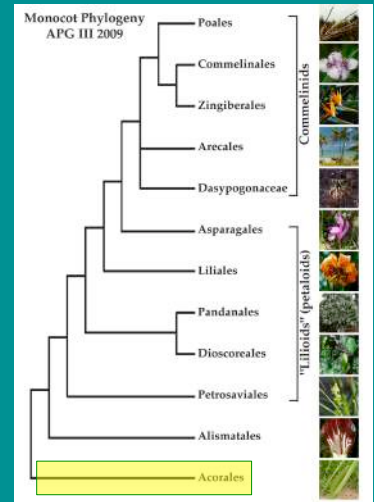
Both features:

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

Survey of monocots

4 main groups:

- **Acorales** - sister to all monocots
 - inc. Aroids - jack in the pulpit
- **Alismatids**
 - non-monophyletic
 - petaloid
- **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

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

- Inflorescence with 'spathe' and spadix
- Flowers bisexual



Acorus americanus - sweet flag

*Acoraceae - sweetflag



- Flat filaments
- P^6 A^6 $\underline{G}^{(3)} \infty$ seeds
- Inflorescence with 'spathe' and spadix
 - Flowers bisexual
 - Cellular endosperm (dicot-like)

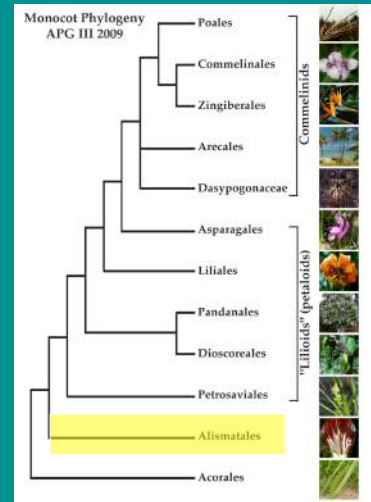


Acorus americanus - sweet flag

Alismatales

4 main groups:

- Acorales - sister to all monocots
- Alismatids
 - 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, floating, or submerged aquatic group of monocots



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

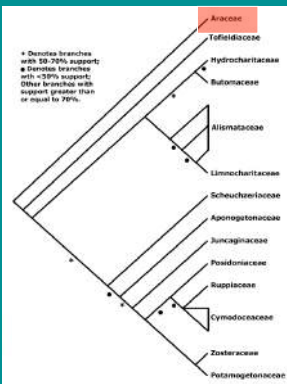
72% of Alismatales are **unisexual** - monoecious or dioecious

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

Reduced unisexual flowers, water-pollinated



*Araceae - aroids

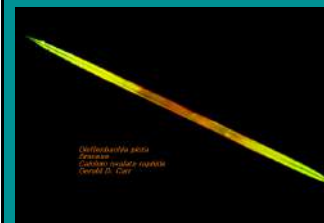


- Sister family to other Alismatales
- Tropical (to temperate)
- epiphytes, herbs, aquatic

104 genera
2,550 species



*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

sapromyophily
pollination

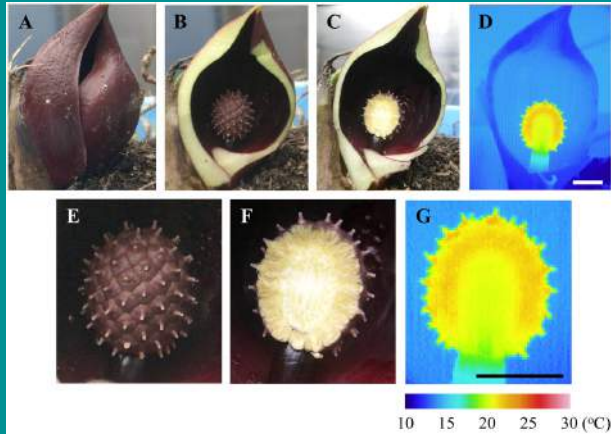


carrion flies –
Calliphoridae



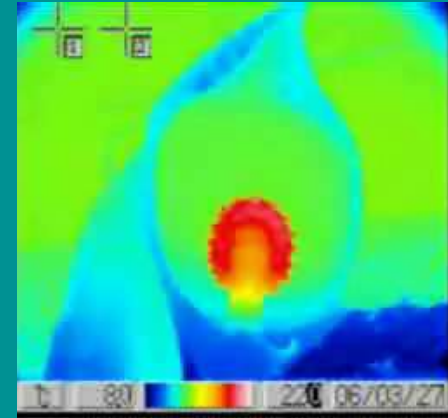
gnats –
Mycetophilidae

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



Onda Y. et.al. Plant Physiol. 2008:146:636-645

Cyclical heating of the skunk cabbage spadix in the male phase



*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)



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

Now known to be derived from within the
Araceae

Lemna minor - small duckweed

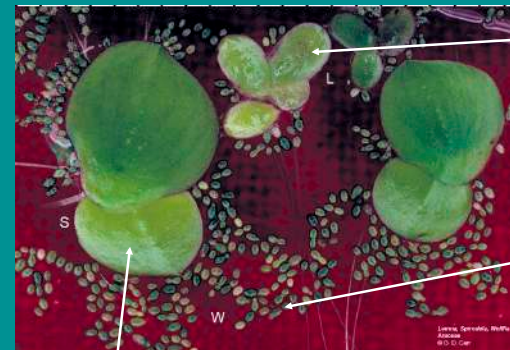
Includes the smallest
angiosperm, and the smallest
flower

Inflorescence reduced to 1
female and 1-2 male flowers



Lemna turionifera - perennial duckweed

*Araceae (Lemnaceae - duckweeds)



Lemna

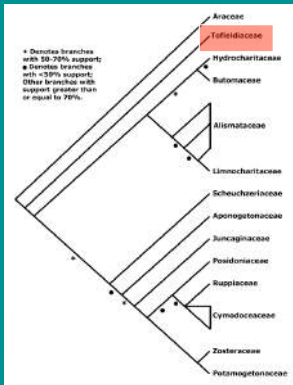
Smallest member
of the family and
the angiosperms

Wolffia columbiana -
water meal

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

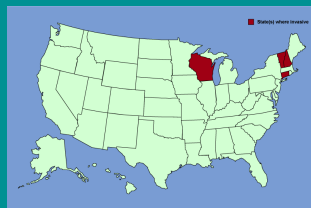
- emergent aquatic family
- leaves show no obvious blade and petiole differentiation



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



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

Alisma plantago-aquatica
Alismataceae
© G. D. Carr



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

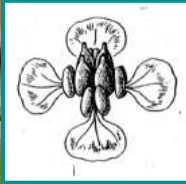


Potamogeton sp. - pondweed

Potamogetonaceae - pondweed



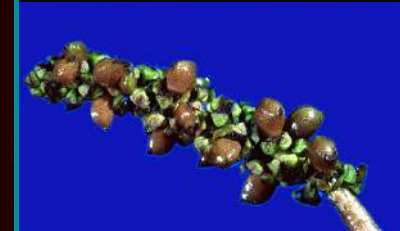
- perianth of 4 clawed segments if present
- gynoecium typically of 4 free, 1-ovuled carpels
- fruit drupe-like



CA 0,4 CO 0 A 4 G 4

Potamogeton sp. - pondweed

Potamogetonaceae - pondweed



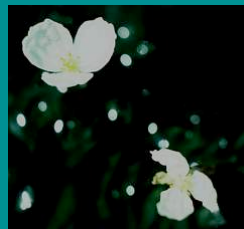
Potamogeton nodosus - pondweed

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



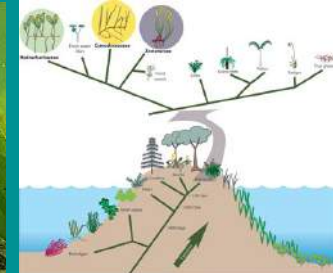
Vallisneria americana - tapegrass

Evolution of Sea Grasses



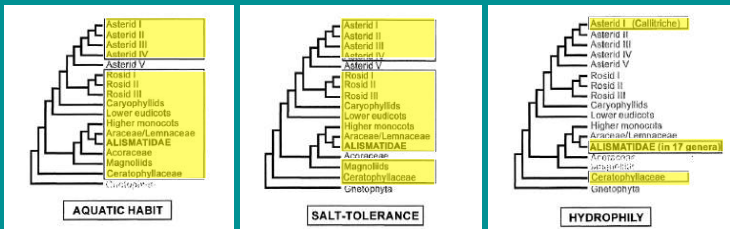
Don Les' story of plants going back to the oceans 450 million years later

. . . 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

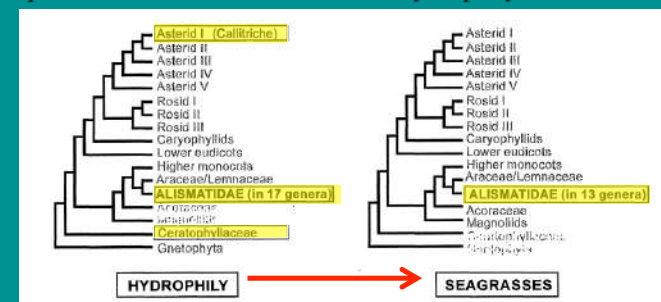
Callitriche



Ceratophyllum

Evolution of Sea Grasses

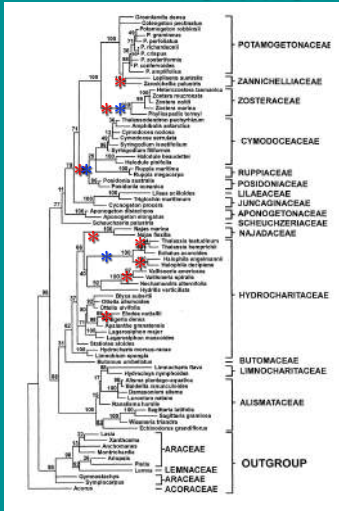
Aquatic ⇒ Salt Tolerant ⇒ Hydrophily ⇒ Marine



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

A single origin of seagrasses?

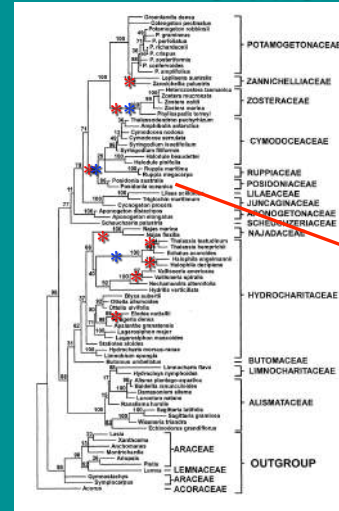
Evolution of Sea Grasses



- **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.

