

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

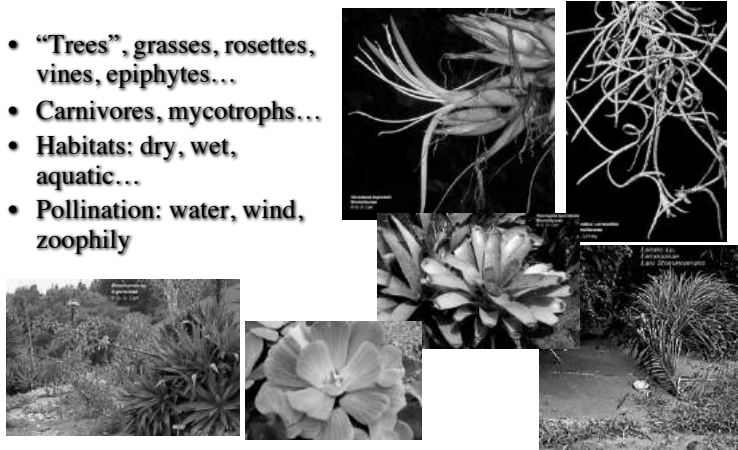
Monocots!

- 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

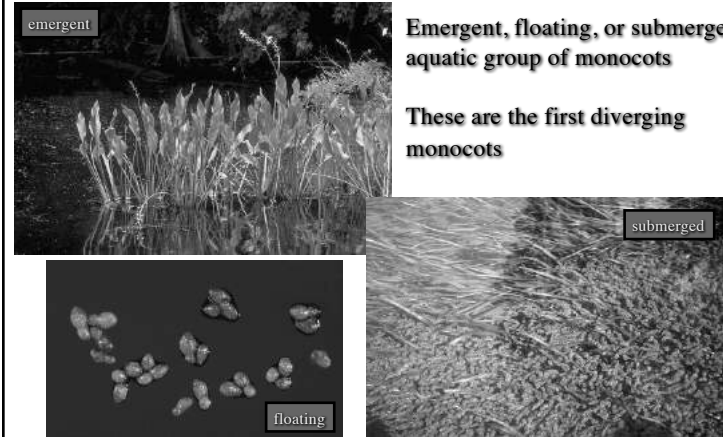
- “Trees”, grasses, rosettes, vines, epiphytes...
- Carnivores, mycotrophs...
- Habitats: dry, wet, aquatic...
- Pollination: water, wind, zoophily



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

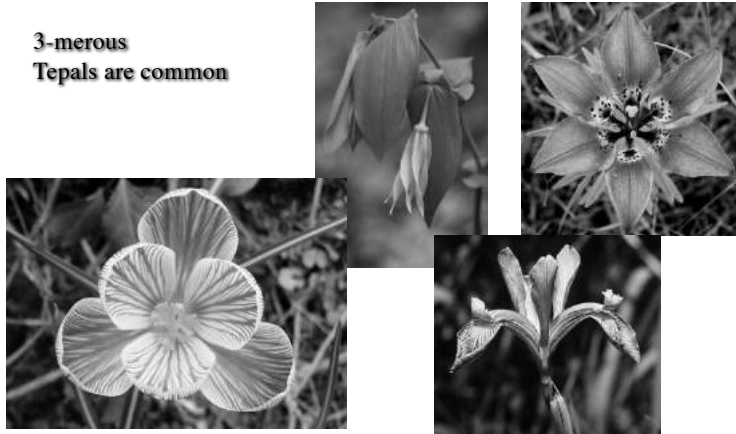
Monocot leaves

- 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



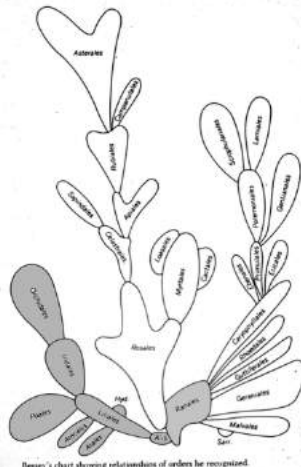
Diversity in pollination

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



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

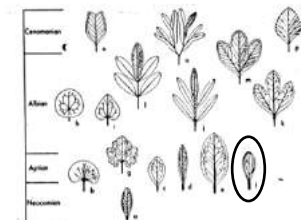
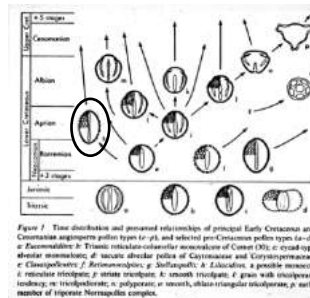
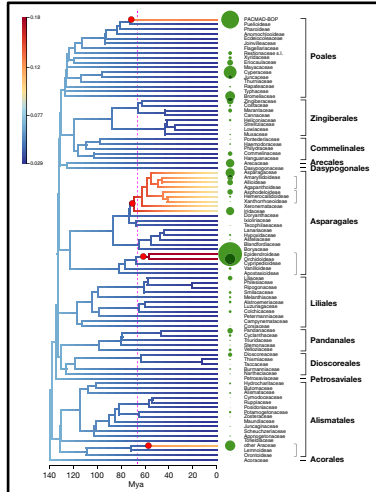


Figure 1 Time distribution and presumed relationships of principal Early Cretaceous and Cretaceous angiosperm pollen types (a-i) and selected pre-Cretaceous pollen types (a-d) at Flacamballidites; b: Triassic reticulate-colporate monolete pollen of Cretaceous (C1); c: oval type abaxial monolete; d: square abaxial pollen of Cretaceous and Cretaceous; e: Clavopollenites; f: Retinaculopollenites; g: Saccopollenites; h: Alveolates, a possible monolete; i: reticulate tricolpate; j: minute tricolpate; k: smooth tricolpate; l: grain with multiporate tendency; m: tricolpate; n: polycolpate; o: smooth, elliptical tricolpate; p: early member of triporate Neoretales complex.

Figure 2 Principal Early Cretaceous and Cretaceous angiosperm leaf types: a: small, pinnately veined leaf of Valdebarones (14); b: cordate, c: serrate; d: obtusolate; e: Ficus-like; f: Arctostaphylos; g: possible monolete; h: lobate cordate; i: palmate, acuminately; j: ovate cordate; k: pinnately bipinnate; l: early pinnate; m: compound; n: bipinnate; o: later pinnate, with rigidly organized base venation; p: Lycopodium; q: dichotomously compound; r: secondary simple pinnate derivative.

Monocot Origins

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



Monocot leaf evolution

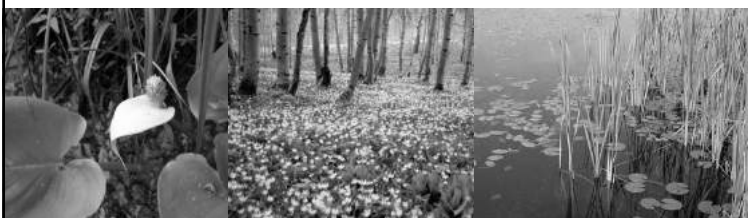


Classic idea of pre-monocot characteristics – Cronquist's view:

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

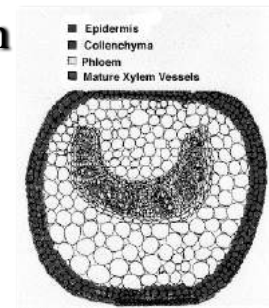
Nymphaeales
Only non-monocot
order with all these
characteristics

Monocot leaf evolution



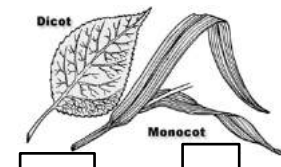
- monocot leaf morphology due to aquatic ancestry
- aquatic → terrestrial → aquatic pathways

Monocot leaf evolution

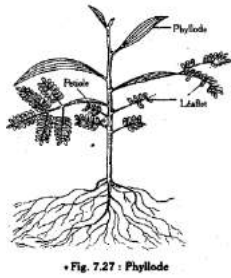


celery (left) and tomato (right) asterid petioles showing parallel vascular traces

- monocot leaf is derived from an expanded bladeless petiole



Monocot leaf evolution

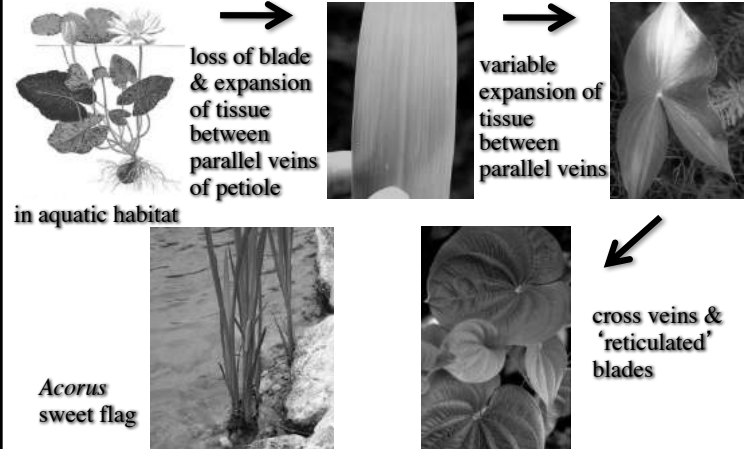


Phyllode theory: original monocot lacked a true leaf; only expanded petiole

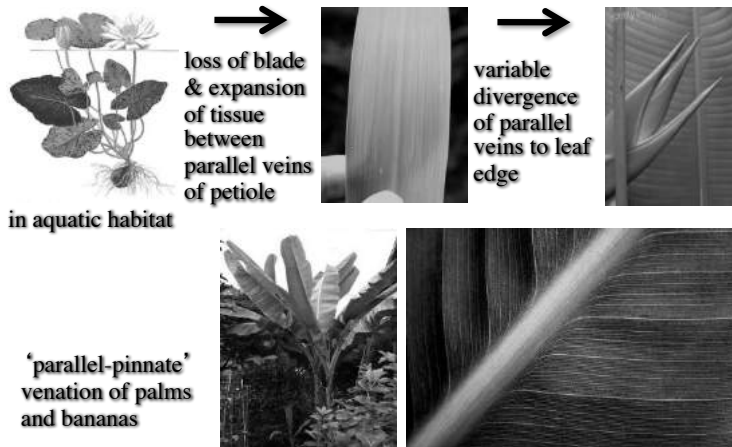
Phyllodes: expanded blade-less petioles best seen in arid adapted woody legumes such as *Acacia*



Monocot leaf evolution

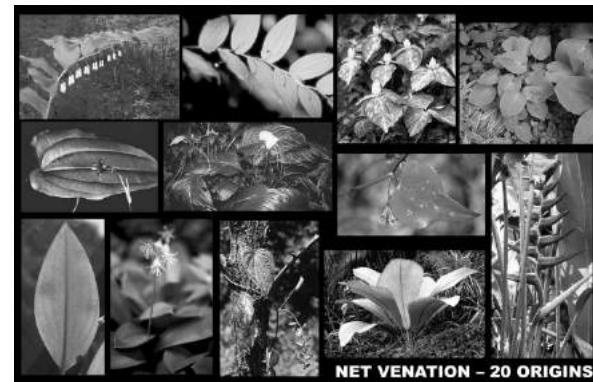


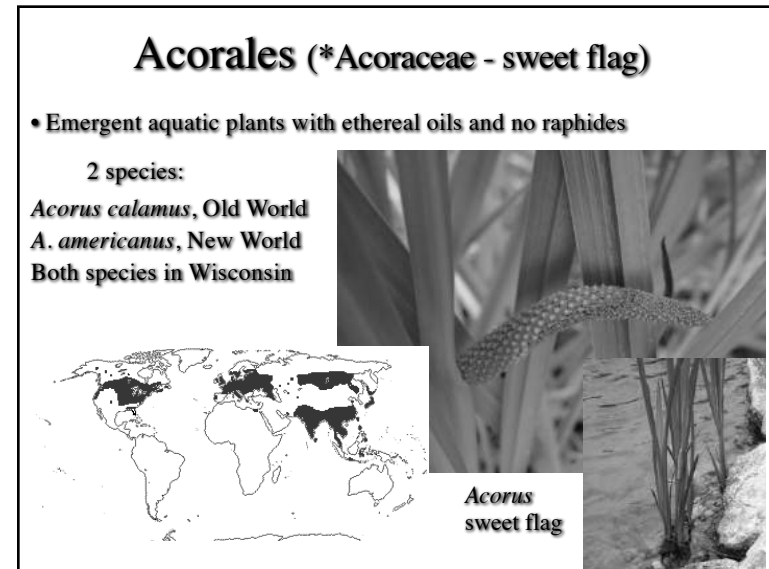
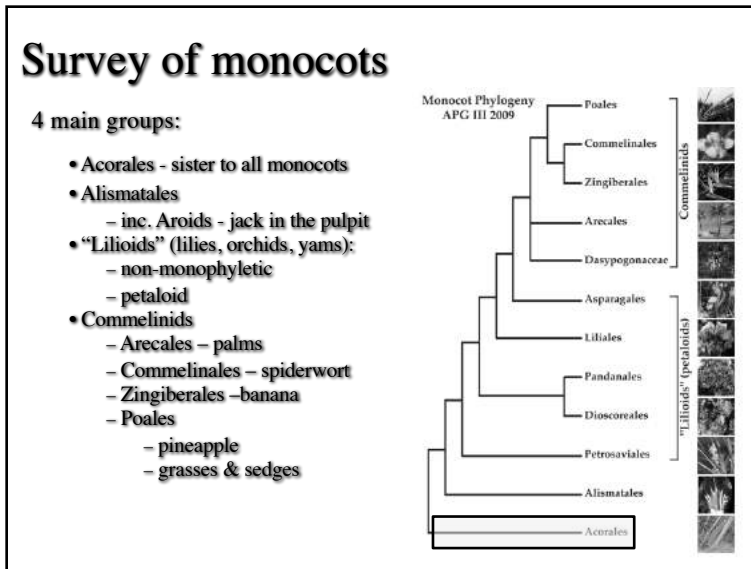
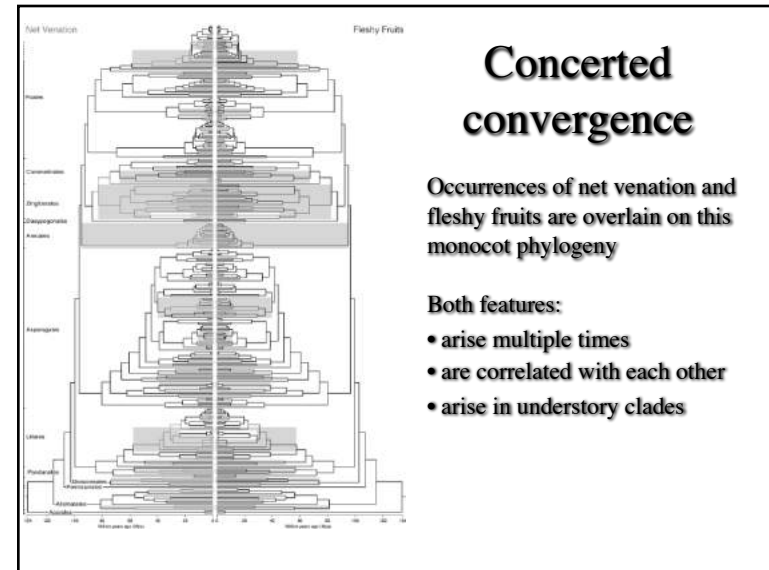
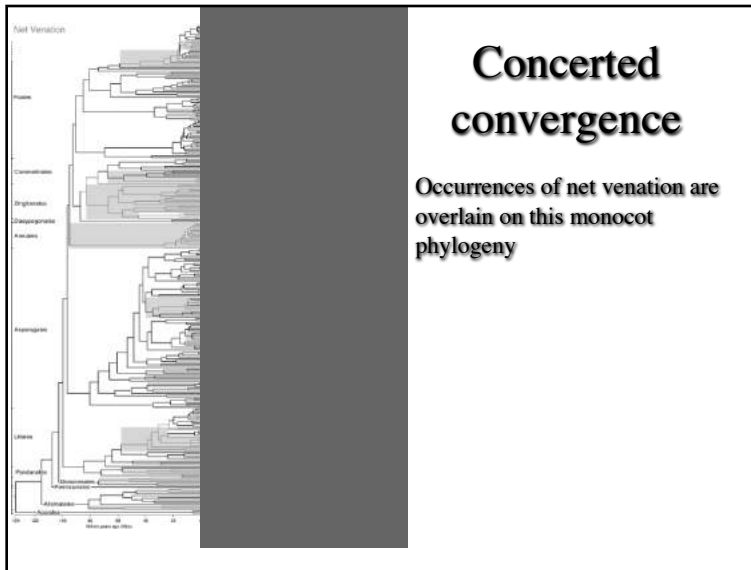
Monocot leaf evolution



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)





*Acoraceae - sweetflag



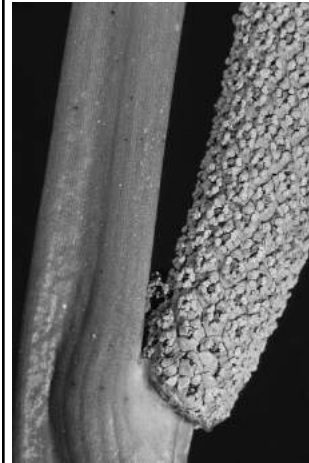
Flat filaments
 P^6 A^6 $\underline{G}^{(3)}$ ∞ seeds

- Inflorescence with 'spathe' and spadix
- Flowers bisexual



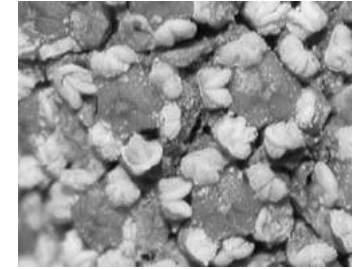
Acorus americanus - sweet flag

*Acoraceae - sweetflag



Flat filaments
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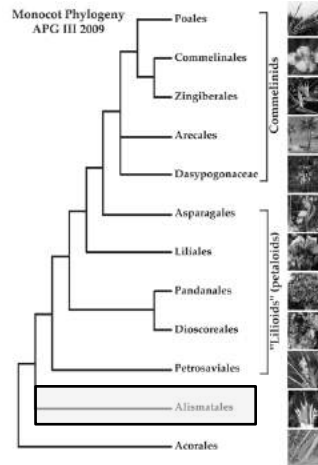


Acorus americanus - sweet flag

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

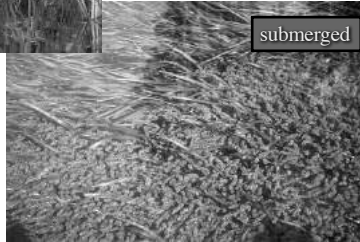
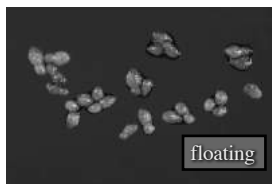
Insect \Rightarrow water pollination



Alismatales - aquatics



Emergent, 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

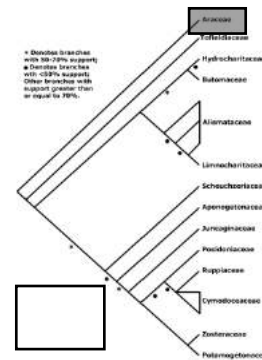
72% of Alismatales are unisexual - monoecious or dioecious

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



Reduced unisexual flowers, water-pollinated

*Araceae - aroids

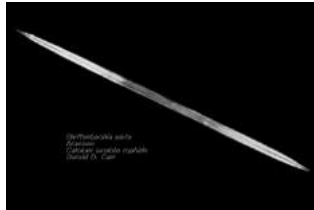


104 genera
2,550 species

- 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

CA0 CO0 A6- 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



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

Symplocarpus foetidus - skunk cabbage

***Araceae - aroids**



Symplocarpus foetidus -
skunk cabbage



flesh flies –
Sarcophagidae



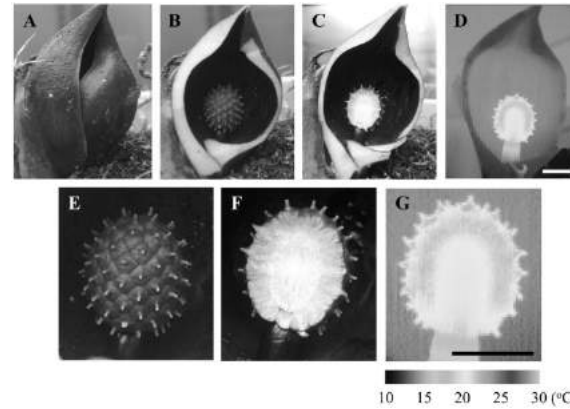
carrion flies –
Calliphoridae



gnats -
Mycetophilidae

sapromyophily
pollination

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



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

***Araceae - aroids**



Calla palustris - water arum

Only emergent aquatic member
of the family in Great Lakes



***Araceae - aroids**



Monstera deltoidea
Araceae
Gerald D. Carr

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)**



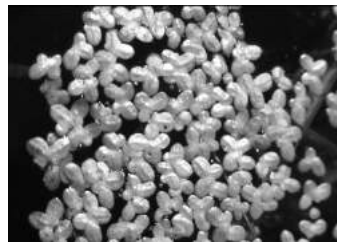
Lemna minor - small duckweed

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

Now known to be derived from within the
Araceae

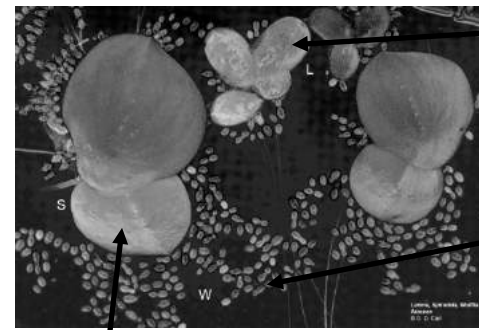
Includes the smallest
angiosperm, and the smallest
flower

Inflorescence reduced to 1
female and 1-2 male flowers



Lemna turionifera - perennial duckweed

***Araceae (Lemnaceae - duckweeds)**



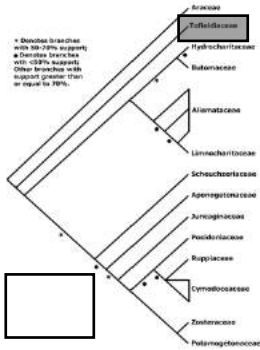
Lemna

Smallest member
of the family and
the angiosperms:

Wolffia columbiana -
water meal

Spirodela polyrhiza Largest member of the family
great duckweed

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

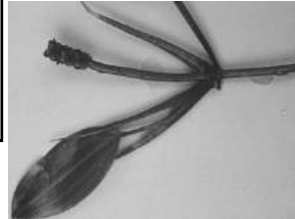
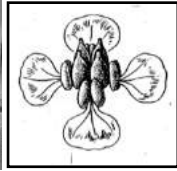


Potamogeton sp. - pondweed

Potamogetonaceae - pondweed



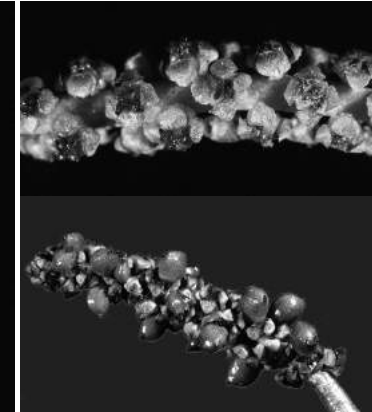
- perianth of 4 clawed segments if present
- gynoecium typically of 4 free, 1-ovuled carpels
- fruit drupe-like



CA0,4 CO0 A4 G4

Potamogeton sp. - pondweed

Potamogetonaceae - pondweed



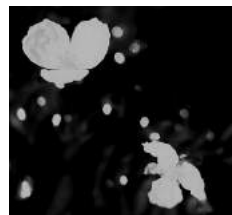
Potamogeton nodosus - pondweed

Flowers (top) and fruits (bottom)

Hydrocharitaceae - frog bit

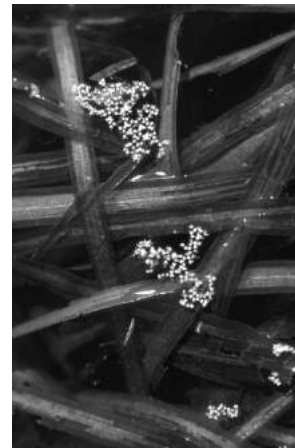


- submersed or floating aquatic plants
- various forms of water pollination present

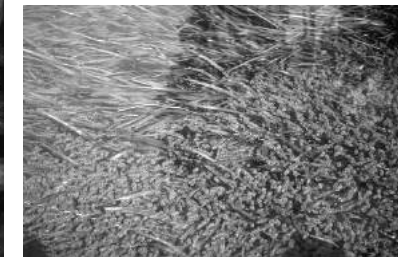


Elodea canadensis - waterweed

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



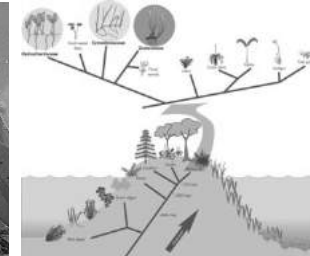
Vallisneria americana - tapegrass

Evolution of Sea Grasses



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

... another story of convergence and divergence

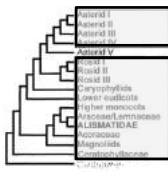


Evolution of Sea Grasses

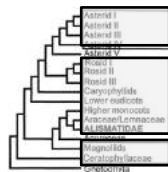
Aquatic

⇒ Salt Tolerant

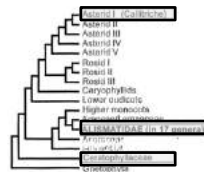
⇒ Hydrophily



AQUATIC HABIT



SALT-TOLERANCE



HYDROPHILY

Aquatic plants found in most lineages

Salt tolerance also wide-spread

Water pollination restricted

Callitriche

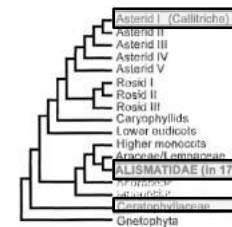


Ceratophyllum

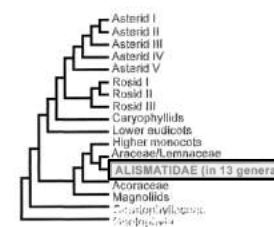
Evolution of Sea Grasses

⇒ Hydrophily

⇒ Marine



HYDROPHILY

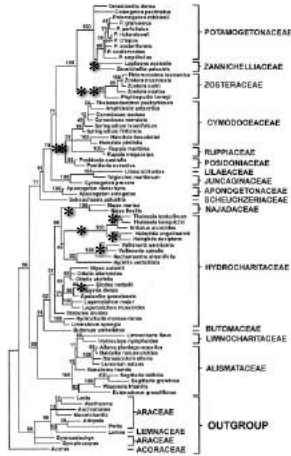


SEAGRASSES

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

A single origin of seagrasses?

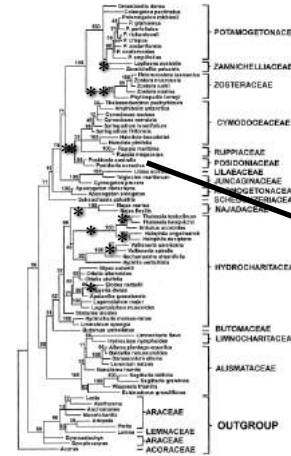
Evolution of Sea Grasses



- 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.

