Diversity and Evolution of Monocots

...what, where, when, how...
Monocots!

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 (*Wolfia*)
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, 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!
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
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-apperturate 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

variable expansion of tissue between parallel veins

cross veins & ‘reticulated’ blades

in aquatic habitat

Acorus sweet flag
Monocot leaf evolution

- 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
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)
Concerted convergence

Occurrences of net venation are overlain on this phylogeny.
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

**Concerted convergence**
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
Acoraceae - sweetflag

- Inflorescence with ‘spathe’ and spadix
- Flowers bisexual

Acorus americanus - sweet flag

Flat filaments

P⁶ A⁶ G(3)∞ seeds
Acoraceae - sweetflag

- Inflorescence with ‘spathe’ and spadix
- Flowers bisexual

\[ P^6 \quad A^6 \quad G^{(3)} \infty \text{ seeds} \]

Acorus americanus - sweet flag
Alismatales

4 main groups:

• Acorales - sister to all monocots
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  – inc. Aroids - jack in the pulpit
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  – non-monophyletic
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    – pineapple
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Alismatales - aquatics

Recurring themes:

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

Insect $\Rightarrow$ water pollination
Emergent, floating, or submerged aquatic group of monocots
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
72% of Alismatales are **unisexual** - monoecious or dioecious

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

Showy flowers, insect-pollinated

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

**Symplocarpus foetidus** - skunk cabbage

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

*Araceae - aroids

L: female
R: male
*Araceae - aroids*

*Symlocarpus 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 volatizing off the odor.
*Araceae - aroids*

- Symplocarpus foetidus - skunk cabbage
- Carrion flies – Calliphoridae
- Flesh flies – Sarcophagidae
- Gnats – Mycetophilidae

Sapromyophily
Pollination
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
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)

*Smallest member of the family and the angiosperms:*

- *Wolffia columbiana - water meal*
- *Spirodela polyrhiza - great duckweed*

*Largest member of the family*

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

Tofieldiaceae - asphodels

Triantha glutinosa
Butoomaceae - flowering rush

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

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

Butomus umbellatus - flowering rush

[Map showing states where invasive]

CA 3  CO 3  A 9  G 6
**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**

*Calyx of 3 green sepals, corolla of 3 white petals*

*Apocarpic in a head or ring*

*Perfect, monoecious, dioecious*

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*Sagittaria - arrowhead*

CA 3  CO 3  A 6 - ∞  G 6 - ∞
Alismataceae - water plantain

*Sagittaria* - arrowhead

Calyx of 3 green sepals, corolla of 3 white petals

Apocarpic in a head or ring

Achenes (head of achenes here)
Similar to *Sagittaria*, but with carpels in one ring rather than globose head.
Potamogetonaceae - pondweed

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

*Potomogeton sp.* - pondweed
Potamogetonaceae - pondweed

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

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

Vallisneria americana - tapegrass
(with Hydrilla verticillata)

Vallisneria americana - tapegrass
**Vallisneria americana** - tapegrass

- 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 spiralis** - tapegrass (OW)

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

**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 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.