Diversity and Evolution of Caryophyllids

...carnations, cacti, chenopods...
Caryophyllids

What are caryophyllids?

• First of the core eudicots we will examine: Caryophyllids, Rosids, Asterids

• = order Caryophyllales

• APG III in 2009 places caryophyllids as sister lineage to the asterids – but probably dates back to 110-100 mya
What are caryophyllids?

- 34 families & 11,155 species = 6% of eudicot diversity

- Unusual (!) group of families not all previously thought to form a natural order

- Share one character? sepals only - “petals” if present appear to be of staminal origin
What are caryophyllids?

- Exhibit unusual adaptations to “stressful” environments — desert or arid regions: high salt, low water, xerophytes

saltbush- Amaranthaceae  cacti- Cactaceae
Caryophyllids

What are caryophyllids?

- Exhibit unusual adaptations to “stressful” environments — salt marshes, halophytes

Glasswort - Amaranthaceae
Caryophyllllids

What are caryophyllllids?

• Exhibit unusual adaptations to “stressful” environments — alpine, tundra, cushion plants

chickweed- Caryophyllllaceae  spring-beauty- Montiaceae
Caryophyllids

What are caryophyllids?

- “new” (unplaced) members to the group include desert families
Caryophyllllids

What are caryophyllids?

• “new” (unplaced) members to the group include desert families

*Simmondsia chinensis*
jojoba
*Simmondsiaceae*
Sonoran Desert endemic
Caryophyllids

What are caryophyllids?

• “new” (unplaced) members to the group include desert families

*Tamarix* - tamarisk
*Tamaricaceae*
What are caryophyllids?

• “new” (unplaced) members to the group include desert families

*Halophytum*

Halophytaceae
Caryophylllids

Suite of morphological and/or physiological adaptations for life in the arid world - succulence, no leaves, C₄ and CAM photosynthesis, salt excretion

C₄ and Crassulacean Acid Metabolism
Caryophylllids

What are caryophylllids?

- troublesome “weeds”

*Tamarix* - tamarisk  
*Gypsophila* - baby’s-breath
Caryophylllids

What are caryophylllids?

• some, but not all, of the carnivorous plants - low N
• why this incredible diversity – ecology, physiology, habit, color?
We performed climate occupancy ancestral reconstruction analyses on the phylogeny of 2843 taxa that included taxa with at least three sampled geographic coordinates (Figs 1–3). We conducted these analyses for visualization and for comparison with diversification and WGD results (see later). Results for individual bioclimatic variables and principal components can be found in Figs S2–S4. Bioclimatic variable 1 (mean annual temperature, Fig. 1) showed that there are several strong phylogenetic patterns of clades with preferences for colder or warmer regions. For example, Polygonaceae, Caryophyllaceae, and Montiaceae each are dominated by taxa with preferences for cold environments, although each also contains early-diverging taxa with preferences for warm environments. By contrast, taxa inhabiting warm environments predominate in Cactaceae, Amaranthaceae, Aizoaceae, the carnivorous clade (Droseraceae, Drosophyllaceae, Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae), and the phytolaccoid clade (Nyctaginaceae, Phytolaccaceae, Petiveriaceae, Sarcobataceae, and Agdestis). Bioclimatic variable 12 (mean annual precipitation) showed a comparatively consistent pattern of relatively dry to intermediately wet clades throughout the group. Indeed, only a few clades inhabiting wet ecosystems (in this case, the wet tropics) exist in the Caryophyllales, specifically small groups within the carnivorous clade, the phytolaccoids, early-diverging Polygonaceae, and other small groups throughout the Caryophyllales. The principal component loadings are presented in Figs 2 and S5. Principal component 1 (PCA1) showed significant differentiation throughout the Caryophyllales, as, for example, early-diverging Polygonaceae vs the rest of Polygonaceae, early diverging Caryophyllaceae vs the rest of Caryophyllaceae, phytolaccoids vs Aizoaceae, and Portulacineae relatives vs Cactaceae, to name a few. These results generally reflect the extensive ecological diversification throughout the group. They also reflect significant diversification in the temperate regions of the world, especially within the Caryophyllaceae and Polygonaceae, contrasted with extensive diversification in the succulent lineages (especially Aizoaceae and Cactaceae) found in relatively dry and warm environments.

- why this incredible diversity – ecology, physiology, habit, color?
- whole genome duplications & diversification shifts?
Caryophyllids

- focus on "core Caryophyllales"
- examine all carnivorous plants later – Halloween lecture!

[check out botanical Halloween costumes for Extra Credit]

- also look at Polygonaceae - smart weed family

Core Caryophyllales

Angiosperm Phylogeny Website
www.mobot.org/MOBOT/Research/APweb/welcome.html
Core Caryophyllales

- defined by 5 features but with some reversals

Caryophyllid clade

Core Caryophyllales
Core Caryophyllales

1. betalains

N containing – very different from flavonoids
Core Caryophyllales

2. free-central placentation (or basal) = “Centrospermae”
Core Caryophyllales

2. free-central placentation (or basal) = “Centrospermae”

... generates capsule fruits

capsule pyxis utricle
Core Caryophyllales

3. curved embryo in ovule = campylotropous

campylotropous ovule

micropyle
Core Caryophyllales

4. pollen shed in trinucleate stage vs. most common 2-nucleate
Core Caryophyllales

5. sieve tube plastids with crystal proteins surrounded by protein filaments
Core Caryophyllales

Caryophyllid clade

• problematic for family circumscription / recognition
• examine 3 groups

Core Caryophyllales
*Caryophyllaceae - Carnations

- carnation or pink family - herbs, often weedy

*Lychnis coronaria* - mullein pink
*Caryophyllaceae - Carnations

- **dichasium inflorescence** – usually a **cyme**

*Minuartia* - sandwort

Note 3 way split, middle branch is oldest flower
*Caryophyllaceae - Carnations

- dichasium inflorescence – usually a cyme
- leaves opposite, swollen nodes
*Caryophyllaceae - Carnations

CA 5, (5) CO 5 A 5,10 G (2-5)

- 5 merous flowers, calyx fused +/-
- corolla not fused, often lobed (staminal origin?)
*Caryophyllaceae - Carnations

CA 5, (5) CO 5 A 5,10 G (2-5)

- anthers of 1-2 whorls
- 1 pistil of 2-5 carpels
*Caryophyllaceae - Carnations

CA 5, (5)  CO 5  A 5,10  G (2-5)

- free-central or axile placentation
- capsule fruit opening by teeth or valves
*Caryophyllaceae - Carnations

Huge family, 87 genera, 2300 species; widespread but characteristic of temperate and warm temperate regions of the Northern Hemisphere.

Minuartia michauxii
sand rockwort
*Caryophyllaceae - Carnations

*Cerastium - mouse-ear chickweed

Cerastium vulgatum
Caryophyllaceae
Gerald D. Carr
*Caryophyllaceae - Carnations

Silene cucubalus
bladder campion

Silene vulgaris
white campion

Dianthus armeria
dep tford pink
*Caryophyllaceae - Carnations

*Saponaria officinalis* - bouncing bet, soapwort
*Amaranthaceae - amaranths*

- herbs, often **halophytes** or **weeds**, worldwide
- 174 genera & 2,050 species
- includes **chenopods** (old Chenopodiaceae)

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*Chenopodium - lamb’s quarter*

*Salicornia - glasswort*
*Amaranthaceae - amaranths*

- flowers small, bracted, congested, lacking corolla
- bisexual or unisexual, monoecious or dioecious

Chenopodium - lamb’s quarter
*Amaranthaceae - amaranths*

- fruit is 1-seeded circumscissile capsule (utricle) or basal seeded achene
- calyx is persistent around the fruit
*Amaranthaceae - amaranths

- native, weedy, and horticultural species
*Amaranthaceae - amaranths

- native, weedy, and horticultural species

*Cycloloma atriplicifolium – winged pigweed*
*Amaranthaceae - amaranths

- native, weedy, and horticultural species

_Bassa (Kochia) - summer cypress

_Beta vulgaris - beet
*Amaranthaceae - amaranths

- native, weedy, and horticultural species

*Celosia - cock’s comb*  
*Gomphrena - globe amaranth*
*Amaranthaceae - amaranths*

- desert specialists & tumbleweed
- invasives

*Atriplex - saltbush*  
*Salsola - Russian thistle*
* ‘Portulacaceae’ - Purslanes

- belongs to a **succulent** group of families
- family boundaries obscure - e.g. Montiaceae = spring beauties

*Portulaca - purslane*
* ‘Portulacaceae’ - Purslanes

- herbs, succulents
- world-wide, especially western N. America, 50 genera, 500 species
* ‘Portulacaceae’ - Purslanes

CA 2  CO 5+  A 5+  G (2-5)

- 5 merous flowers (petals?)
- capsule of various types
* ‘Portulacaceae’ - Purslances

Portulaca grandiflora  
rock rose (Argentina)

Claytonia megarhiza  
w. NAm alpine

Claytonia virginica  
spring beauty

Claytonia now in family Montiaceae
* ‘Portulacaceae’ - Purslanes

**Phemeranthus**

- **fame flower**

**Montiaceae**

**Phemeranthus rugospermus**
*Cactaceae - cacti

- New World stem succulents protected by spines
- 100 genera / 1400 species
*Cactaceae - cacti

- fleshy, succulent, often epiphytes
- **no leaves**, except *Pereskia*
- **spines** or glochids at areoles
*Cactaceae - cacti*  

![P∞ A∞ G (4)](image)

- ‘hypanthium’ with many tepals
- ∞ stamens
- epigynous flower
**Cactaceae - cacti**

- placentation parietal (rare!)
- berry fruit

\[ P \infty A \infty G (4) \]
Cactaceae - cacti

- great diversity: columnar, prickly pear, barrel, vines
- relationships emerging
*Cactaceae - cacti

• Caribbean “Pereskia” at base of family! – now called Rhodocactus
*Cactaceae - cacti

- Caribbean “Pereskia” at base of family! – now called Rhodocactus
- then S. American Pereskia
*Cactaceae - cacti

• Caribbean “Pereskia” at base of family! – now called *Rhodocactus*

• then S. American *Pereskia*

• then the rest of American taxa
*Cactaceae - cacti

**Selenicereus grandiflorus**
Queen-of-the-night
25 cm diameter flowers!

**Lophophora williamsonia**
peyote (mescaline)
*Cactaceae - cacti

- upper midwest cacti

*Opuntia macrorhiza* - plains prickly-pear

*Opuntia humifusa* - eastern prickly-pear
Didiereaceae - African ‘cacti’

- Madagascar & east Africa
- convergent also with American Fouquieriaceae (ocotillo)
*Phytolaccaceae - pokeweed

- Small family of trees/shrubs of tropical and temperate regions

Phytolacca americana - pokeweed
*Phytolaccaceae - pokeweed*

- small petaloid sepals only
- stamens 2X sepals
- carpels +/- fused, each with one ovule

Phytolacca octandra

CA 5  CO 0  A 10  G (5+)
*Phytolaccaceae - pokeweed*

- racemes
- berry fruits
- often poisonous
- dyes (poke = puccoon: Algonquian for red/orange dye)

*Phytolacca americana* - pokeweed

*Rivinia* - bloodberry
**Polygonaceae - smartweeds**

- also look at Polygonaceae - smart weed family
- 61 genera / 1,100 species

*Persicaria amphibia – water smartweed*
*Polygonaceae - smartweeds*

- herbs (few shrubs) of wet or arid regions

*Persicaria hydropiper* - water pepper  
*Persicaria amphibia* – water smartweed
**Polygonaceae - smartweeds**

- herbs (few shrubs) of wet or arid regions
- alternate, simple leaves at swollen nodes
- modified stipules as sheath = ocrea

*Persicaria amphibia* – water smartweed
*Polygonaceae - smartweeds

- flowers congested
- basically 3 merous, tepals petaloid
- one-seeded, three-angled achene

Persicaria amphibia – water smartweed
*Polygonaceae - smartweeds

- Rumex and Persicaria (Polygonum) largest genera

Persicaria - smartweed

Rumex crispus - curly doc

Rumex orbicularis - water doc
*Polygonaceae - smartweeds

- horticulturally important

Rheum rhabarbarum
Garden rhubarb
locally adventive

Fagopyrum esculentum
buckwheat