Hybridization in Compositae

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Tennessee – not Texas, but we still grow them big!

Ayres Hall – University of Tennessee campus in Knoxville, Tennessee
University of Tennessee

Tennessee

Leucanthemum vulgare – Inspiration for school colors (“Big Orange”)
Changing view of hybridization: once consider rare, now known to be common in some groups

Hotspots (Ellstrand et al. 1996. Proc Natl Acad Sci, USA 93: 5090-5093)
Comparison of 5 floras (British Isles, Scandanavia, Great Plains, Intermountain, Hawaii):
Asteraceae only family in top 6 in all 5

### Table 3. Six families and four genera with the most hybrids in five biosystematic floras

<table>
<thead>
<tr>
<th>Flora</th>
<th>Families (rank)*</th>
<th>Hybrids</th>
<th>Genera (Family)</th>
<th>Hybrids</th>
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</thead>
<tbody>
<tr>
<td>British Isles</td>
<td>Scrophulariaceae (6)</td>
<td>88</td>
<td>Euphrasia (Scrophulariaceae)</td>
<td>71</td>
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<tr>
<td></td>
<td>Salicaceae (20)</td>
<td>55</td>
<td>Salix (Salicaceae)</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>Rosaceae (3)</td>
<td>53</td>
<td>Epilobium (Onagraceae)</td>
<td>43</td>
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<tr>
<td></td>
<td>Onagraceae (25)</td>
<td>46</td>
<td>Rosa (Rosaceae)</td>
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</tr>
<tr>
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<td>Poaceae (2)</td>
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<td><strong>Asteraceae</strong> (1)</td>
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<tr>
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<td>Cyperaceae (4)</td>
<td>30</td>
<td>Carex (Cyperaceae)</td>
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<tr>
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<td>25</td>
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<tr>
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<td>Salicaceae (17)</td>
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<td>Viola (Violaceae)</td>
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<td>Calamagrostis (Poaceae)</td>
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<td>Dryopteridaceae (31)</td>
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<td>Great Plains</td>
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<td>Amaranthus (Amaranthaceae)</td>
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<td>Aster (Asteraceae)</td>
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<td></td>
<td>Rosaceae (7)</td>
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<td>Rosa (Rosaceae)</td>
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<td>Fabaceae (3)</td>
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<td>Verbena (Verbenaceae)</td>
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<td>Amaranthaceae (31)</td>
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<td></td>
<td>Verbenaceae (34)</td>
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<td>Intermountain†</td>
<td><strong>Asteraceae</strong> (1)</td>
<td>43</td>
<td>Penstemon (Scrophulariaceae)</td>
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<td>Scrophulariaceae (3)</td>
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<td>Poaceae (1)</td>
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<td>Castilleja (Scrophulariaceae)</td>
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<td>Cyperaceae (4)</td>
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<td>Hawaii</td>
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<td>Dubautia (Asteraceae)</td>
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<td>Rubiaceae (7)</td>
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<td>Clermontia (Campanulaceae)</td>
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<td>Lamiaceae (5)</td>
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</table>

*In terms of species number.
†See text.
Overview of Presentation – Selected Aspects of Hybridization

1. More rather than less – an example from the flower garden

2. Allopolyploidy – a changing view

3. Temporal diversity – *Eupatorium* (thoroughworts)

4. Hybrid speciation/lineages – Liatrines (blazing stars)

5. Complications for phylogeny estimation – Helianthinae (sunflowers)
Hybrid: offspring between two genetically different organisms

Evolutionary Biology: usually used to designated offspring between different species “Interspecific Hybrid”

“Species” – problematic term, so some authors include a description of their species concept in their definition of “hybrid”: 
Recognition of Hybrids:

1. Morphological “intermediacy”
   
   Actually – mixture of discrete parental traits + intermediacy for quantitative ones

   In practice: often a hybrid will also exhibit traits not present in either parent, transgressive
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4. Conflicting phylogenies based on different genes
   Plants: plastid DNA vs. nuclear DNA (often ITS/ETS loci)

Note – DNA sequence data have made possible increased sensitivity to detect hybrids/past hybridization
Internal Transcribed Spacer Region – nuclear ribosomal DNA
Internal Transcribed Spacer Region – nuclear ribosomal DNA

ITS REGION

ITS5

79F

5.8sR

ITS4

18S rDNA

ITS1

5.8S

ITS2

26S rDNA

ITS1

ITS2
Internal Transcribed Spacer Region – nuclear ribosomal DNA

ITS REGION

ITS5

79F

ITS1

ITS2

5.8S

18S rDNA

26S rDNA

ITS4

ITS – ok for phylogeny – great for identification
Example – $F_1$ hybrids from the garden:
Example – $F_1$ hybrids from the garden:

What is *Eupatorium aromaticum* ‘Joicus Variegated’?

Note – *Eupatorium aromaticum* = *Ageratina aromatic*a
Names in Green – Eupatorium s.l.
Perityleae Outgroup
Ageratina herbacea
Ageratina glechnophylla
Ageratina aromatica
Ageratina wrightii
Ageratina (7 spp)
Pachythamnus crassirameus
Kaunia saltensis
Neomirandea araliifolium
Hofmeisteria fasciculata
Bartlettina (4 spp)
Stevia plummerae
Stevia rebaudiana
Microspermum nummular
Shinnersia rivularis
Trichocoronis wrightii
Sclerolepis uniflora
Mikania scandens
Brickellia coulteri
Brickellia problematica
Brickellia grandiflora
Pleurocoronis pluriseta
Malperia tenuis
Brickeliasmum fendleri
Carminatia tenuiflora
Eupatorium (30 spp)
Eutrochium (5 spp)
Garberia heterophylla
Trilisa paniculata
Litrisa carnosa
Hartwrightia floridana
Carphephorus corymbosus
Carphephorus tomentosus
Liatris (25 spp)
Steviopsis vigintiseta
Peteravenia malvaefolia

Eupatoriine ITS Phylogeny → Eupatorium restricted to ca. 30 spp. of North America/Asia

Flyriella parryi
Viereckia tamaulipensis
Grisebachianthus libanotica
Grisebachianthus lantanifol.
Koanophyllum polytechicum
Koanophyllum ayapanoides
Ageratum (6 spp)
Conoclinium (5 spp)
Tamaulipa azurea
Critonia sexangularis
Kyrsteniopsis spinacifolia
Chromolaena (4 spp)
Chromolaena odorata
Chromolaena laevigata
Chromolaena morii
Praxelis kleinoides
Praxelis decumbens
Aristiqueta salvia
Isocarpha oppositifolia
Adenostemma involucratum
Pygits tanactifolia
Bejaranao balansae
Barrossoa betoneactifolia
Platypanthera mellisifol.
Trichogonia menthaefolia
Trichogonia sp.
Trichogonia salvaeofolia
Trichogonia sp.
Conocliniopsis prassifolius
Acritopappus hagei
Bishopiella elegans
Lithothamnus ellipticus
Campuloclinium chlorolepis
Campuloclinium hirsutum
Heterocondylus pumilus
Acanthostyles buniifolius
Symphyopappus brasiliensis
Campovassouria cruciata
Graziela dimorpholepis
Neocabrera serrulata
Ophryosporus triangularis
Helogyne tacaquirensis
What is “Eupatorium (Ageratina) auromaticum ‘Joicus Variegated’”?
ITS-2 sequence data – “Eupatorium auromaticum” = hybrid *Eupatorium serotinum* / *E. altissimum*

Direction of sequencing

**Eupatorium “auromaticum”**

“stutter” caused by length polymorphism

2 bp insertion vs. all other *Eupatorium*

**Eupatorium serotinum**

**Eupatorium altissimum**

2 bp insertion vs. all other *Eupatorium*
Hybrids in the Garden – Conclusions:

1. Hybrids are common
2. Hybrids are more detectable with molecular tools
3. Caution in using material from Botanical Gardens!

“Eupatorium greggii” – *Conoclinium dissectum x C. coelestinum*

“Solidaster luteus” – *Solidago canadensis x S. ptarmicoides*

“Conoclinium coelestinum ‘Alba’ Syn. Eupatorium coelestinum x C. dichotomum”
Outcome of Hybridization: allopolyplody

**Allopolyplody**

2 diploid parents - **Species 1 (AA)** and **Species 2 (BB)**

F1 hybrid is sterile - chromosomes don’t pair normally

\[
\text{AA} \quad \rightarrow \quad \text{AB} \quad \xrightarrow{\text{Chromosome doubling}} \quad \text{AABB}
\]

Diploid parents | Sterile hybrid | Fertile tetraploid

NOTE: tetraploid is reproductively isolated from parents -> potential for immediate speciation
Tragopogon Polyploid Complex

Fig. 11-13
Raven et al., Biology of Plants, 7th ed.
Tragopogon Polyploid Complex

3 Parent Species – All Eurasian Natives

All diploid
x=6
c’somes
(2n=12)
Tragopogon Polyploid Complex

New Polyploid Species

PPxDD → PD

T. mirus (g)

Hybrid

T. dubius (a)

2n=24

T. pratensis (c)

DD

SS

In North America – after 1930
Tragopogon Polyploid Complex

New Polyploid Species

T. dubius

T. mirus

T. pratensis

Hybrids

T. porrifolius

T. miscellus

In North America – after 1930

2 new species!
How frequently does polyploidy lead to an entirely new evolutionary lineage?

→ New genomic data suggest that this may be more significant than suspected.

Ancestral polyploidy events in seed plants and angiosperms.

Fig. 4.1. Chromosomal base number evolution in Asteraceae. Hypothesized base numbers are superimposed on the summary tree of the supertree (=metatree) phylogeny presented by Funk et al. (2005).
Whole Genome Duplication in Compositae?

Fig. 4.1. Chromosomal base number evolution in Asteraceae. Hypothesized base numbers are superimposed on the summary tree of the supertree (=metatree) phylogeny presented by Funk et al. (2005).

Phylogeny of Compositae tribes and outgroups displaying observed paleopolyploid events and the rapid radiation of tribes.


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Outcome of Hybridization: allopolyploidy + apomixis $\rightarrow$ apomictic complex

Famous examples in Compositae: *Taraxacum, Hieracium*
Outcome of Hybridization: allopolyplody + apomixis → apomictic complex

Famous examples in Compositae: *Taraxacum, Hieracium*

Another example: *Eupatorium* in eastern North America

*Eupatorium paludicola*  
*Eupatorium altissimum*
Eupatorium album – apomictic complex unraveled with DNA sequence data
North American Eupatorium – ITS-based phylogeny

E. album 31 samples

E. petaloideum 4 samples

Eupatorium album vs. E. petaloideum - Different Species? – the complicating influence of hybrids

<table>
<thead>
<tr>
<th>Character</th>
<th>album (including hybrids)</th>
<th>petaloideum</th>
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</thead>
<tbody>
<tr>
<td>phyllary glands</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>leaf glands</td>
<td>sparse-abundant</td>
<td>sparse</td>
</tr>
<tr>
<td>leaf size</td>
<td>35-105 mm</td>
<td>35-60 mm</td>
</tr>
</tbody>
</table>
Eupatorium album vs. E. petaloideum – Hybrids Recognized → Different Species!

<table>
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<tr>
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<th>album</th>
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<td>abundant</td>
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</tr>
<tr>
<td>leaf size</td>
<td>65-105 mm</td>
<td>35-60 mm</td>
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</table>

![Eupatorium album](image1.jpg) ![Eupatorium petaloideum](image2.jpg)
Eupatorium album/E. petaloideum - a pair of cryptic species

album - occurs in pine flatwood communities on poorly drained soils

petaloideum - occurs in upland well drained sites in oak-hickory communities
Eupatorium album var. subvenosum - a hybrid, but not of *album*
Eupatorium “album” var. subvenosum
<table>
<thead>
<tr>
<th>Species</th>
<th>Sequence Read Direction</th>
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<tbody>
<tr>
<td><strong>Eupatorium petaloideum</strong></td>
<td><img src="image1" alt="Sequence Read" /></td>
</tr>
<tr>
<td><strong>Eupatorium subvenosum</strong></td>
<td><img src="image2" alt="Sequence Read" /></td>
</tr>
<tr>
<td><strong>Eupatorium hyssopifolium</strong></td>
<td><img src="image3" alt="Sequence Read" /></td>
</tr>
</tbody>
</table>
Eupatorium album

Eupatorium petaloideum

Eupatorium subvenosum

Eupatorium hyssopifolium

ITS 2 region:
Blue arrows: polymorphism, either album or petaloideum with hyssopifolium

Red arrows: polymorphism - diagnostic for petaloideum, not album, with hyssopifolium
North American Eupatorium – ITS-based phylogeny

Use of cloning to establish identity of copies

**Eupatorium subvenosum**

ITS clones:
hyssopifolium / petaloideum
Eupatorium album – a hybrid complex

E. sullivaniae – album x lancifolium

E. vaseyi – petaloideum x sessilifolium

E. fernaldii – petaloideum / sessilifolium / perfoliatum

E. subvenosum – petaloideum x hyssopifolium
What is the biological meaning?

1. Initial divergence $\rightarrow$ album-type morphology
2. Secondary divergence $\rightarrow$ album vs. petaloideum [“cryptic species”]
3. Tertiary divergence $\rightarrow$ hybridization with other species

Question: did range expansion occur before or after hybridization?

Scenario 1: parent species expand ranges, hybridization occurs, hybrids outcompete parents in part of range

Scenario 2: parent species contact, hybridize, hybrids able to expand ranges beyond potential of parents
ITS sequence data – notable polymorphisms

Chromolaena morii - ITS

Campovassouria cruciata (monotypic) - ITS
Homoploid Hybridization – Example from Liatrinae (Eupatorieae)
Eupatorieae  ITS Phylogeny → **Liatrinae** sister to **Eupatorium/Eutrochium**

**Names in Pink – Liatrinae**
Liatrinae – History of Generic Circumscription

Liatris               Liatris               Liatris                 Liatris                Liatris
Carphephorus                          Carphephorus                              Carphephorus
Litrísa
Trilisa               Trilisa                                                                    Trilisa
Garberia
Hartwrightia
Kuhniinae
*Kuhnia, Adenostyles, Carphochaete*
Liatrinae – molecular phylogeny based on ca 10 kb of combined ITS/ETS and plastid DNA sequence data
Liatrinae – molecular phylogenetic analysis – ITS/ETS only
Liatrinas – molecular phylogenetic analysis
## Liatrinae – morphological analysis of “hybrid” lineages

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Trilisa</em></th>
<th><em>Litrisa</em></th>
<th><em>Carphephorus</em></th>
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<td>Phyllary series</td>
<td>2</td>
<td>2-3</td>
<td>3-5</td>
</tr>
<tr>
<td>Flowers/head</td>
<td>4-15</td>
<td>5-10</td>
<td>9-30</td>
</tr>
<tr>
<td>Pales</td>
<td>few or none</td>
<td>few or none</td>
<td>usually present</td>
</tr>
<tr>
<td>Corolla color</td>
<td>pinkish-purple</td>
<td>pinkish-purple</td>
<td>pinkish-purple</td>
</tr>
<tr>
<td>Corolla lobe l/w</td>
<td>1.25-1.5</td>
<td>1.5</td>
<td>1.5-2.5</td>
</tr>
<tr>
<td>Anther appendage</td>
<td>unlobed</td>
<td>notched</td>
<td>notched</td>
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<tr>
<td>Cypselae ribs</td>
<td>8</td>
<td>8-10</td>
<td>10</td>
</tr>
<tr>
<td>Cypselae hairs</td>
<td>simple + glands</td>
<td>simple + glands</td>
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</tr>
<tr>
<td>Pappus bristles</td>
<td>1 series</td>
<td>2 series</td>
<td>2-3 series</td>
</tr>
<tr>
<td>Leaf punctation</td>
<td>absent</td>
<td>present</td>
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[Image of tree diagram showing phylogenetic relationships among species involved]
Liatrinas – morphological analysis of “hybrid” lineages

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<th>Hartwrightia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phyllary series</td>
<td>2</td>
<td>2-3</td>
<td>3-5</td>
<td>1*</td>
</tr>
<tr>
<td>Flowers/head</td>
<td>4-15</td>
<td>5-10</td>
<td>9-30</td>
<td>7-10</td>
</tr>
<tr>
<td>Pales</td>
<td>few or none</td>
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<td>usually present</td>
<td>none</td>
</tr>
<tr>
<td>Corolla color</td>
<td>pinkish-purple</td>
<td>pinkish-purple</td>
<td>pinkish-purple</td>
<td>whitish*</td>
</tr>
<tr>
<td>Corolla lobe l/w</td>
<td>1.25-1.5</td>
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<td>1.5-2.5</td>
<td>1*</td>
</tr>
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<td>notched</td>
<td>notched</td>
<td>none*</td>
</tr>
<tr>
<td>Cypselae ribs</td>
<td>8</td>
<td>8-10</td>
<td>10</td>
<td>5*</td>
</tr>
<tr>
<td>Cypselae hairs</td>
<td>simple + glands</td>
<td>simple + glands</td>
<td>simple + glands</td>
<td>glands only*</td>
</tr>
<tr>
<td>Pappus bristles</td>
<td>1 series</td>
<td>2 series</td>
<td>2-3 series</td>
<td>none*</td>
</tr>
<tr>
<td>Leaf punctation</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>absent</td>
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Liatrinae – morphological analysis of “hybrid” lineages

<table>
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Liatrinae Summary

Homoploid hybrid speciation $\rightarrow$ *Litrisa* (intermediate morphology)

$\rightarrow$ *Hartwrightia* (transgressive)

Both species: different habitat than putative progenitor lineages
Liatrinae Summary

Homoploid hybrid speciation → *Litrisa* (intermediate morphology)

→ *Hartwrightia* (transgressive)

Both species: different habitat than putative progenitor lineages

Liatrinae Summary

Homoploid hybrid speciation $\rightarrow$ *Litrisa* (intermediate morphology) $\rightarrow$ *Hartwrightia* (transgressive)

Both species: different habitat than putative progenitor lineages

"normal" phylogeny – diverging branches

hybrid speciation – reversal of divergence

Wide Hybridization?
Inferred Wide Hybridization in Helianthinae - Sunflowers

Schilling EE & JL Panero. 2011
Inferred Wide Hybridization in Helianthinae - Sunflowers

Viguiera dentata – type of genus
Inferred Wide Hybridization in Helianthinae - Sunflowers

Viguiera dentata – type of genus

Type of Aldama

Rhysolepis

ITS/ETS
Inferred Wide Hybridization in Helianthinae - Sunflowers

Mexico

North America

Helianthus annuus – Domesticated Sunflower
Inferred Wide Hybridization in Helianthinae - Sunflowers

Mexico
North America
South America - Andes
South America - widespread
Inferred Wide Hybridization in Helianthinae - Sunflowers

North America

Mexico

ITS/ETS

Plastid DNA
Inferred Wide Hybridization in Helianthinae - Sunflowers

Mexico

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Inferred Wide Hybridization in Helianthinae - Sunflowers

**ITS/ETS**

*Simsia* – 11 (24) species

*Tithonia diversifolia*
*Tithonia rotundifolia*
*Tithonia tubaeformis*
*Tithonia thurberi*
*Tithonia longiradiata*
*Tithonia pedunculata*
*Tithonia koelzii*

**Plastid DNA**

*Simsia* – flattened cypselae

*Tithonia* – fistulose peduncle

**Aldama** – 19 (118) species

*Aldama* – solid peduncle, convex cypselae
INTERGENERIC HYBRID BETWEEN CULTIVATED SUNFLOWER (*Helianthus annuus* L.) AND *Tithonia rotundifolia* (Mill.) Blake

M. Humberto Reyes-Valdés¹*, Martha Gómez-Martínez¹, Octavio Martínez², Fernando Hernández Godínez²

1. How Wide Can Hybridization Be?

2. ITS/ETS
Hybridization – Current Approaches:

Sampling in depth – Genomic Level Sequencing Approaches

→ 1000’s of genes, few samples

vs.

Sampling in breadth

Both needed to develop a synthesis
Summary

Hybridization in Compositae is common and widespread

→ Short term diversity
→ Hybrid-derived species
→ New lineages

Many of problems and challenges remain!
Extra slides after this
**ITS Sequence – Hartwrightia contains numerous autapomorphies**

| Taxon      | 26 | 34 | 40 | 44 | 60 | 69 | 70 | 76 | 81 | 90 | 100 | 101 | 118 | 126 | 190 | 215 | 233 | 244 | 256-7 | 393 | 445 | 453 | 462 | 466 | 468 | 481 | 543 | 588 | 603 | 613-4 | 626 | 643 |
|------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Carpephorus| A  | C  | A  | C  | A  | C  | C  | T  | A  | T  | C  | A  | C  | T  | T  | T  | -- | T  | A  | G  | T  | T  | T  | T  | C  | T  | A  | T  | A  | T  | T  |
| Litrisa    | C  | C  | A  | A  | G  | C  | G  | T  | A  | C  | C  | G  | T  | A  | A  | T  | C  | C  | -- | C  | A  | G  | T  | T  | T  | T  | C  | C  | C  | -- | T  | T  |
| Trilisa    | C  | T  | A  | A  | G  | C  | T  | T  | A  | C  | C  | G  | T  | T  | A  | T  | C  | C  | -- | C  | C  | A  | T  | A  | A  | G  | C  | T  | A  | -- | T  | G  |
| Hartwrightia| C  | T  | C  | A  | G  | T  | T  | A  | T  | C  | T  | G  | T  | T  | T  | T  | T  | C  | C  | GT | C  | C  | A  | C  | A  | A  | G  | T  | T  | A  | -- | C  | G  |

* indicates the presence of autapomorphies.
Liatrines – morphological analysis of “hybrid” lineages

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Carphephorus tomentosus</em></th>
<th><em>Carphephorus bellidifolius</em></th>
<th><em>Trilisa</em></th>
</tr>
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<tr>
<td>Phyllary series</td>
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Outcome of Hybridization: 1. production of hybrid swarm
