

Tragopogon: A Model for the Study of Recent and Recurring Polyploidy

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Patrick Schnable,
Richard Buggs, Mike Chester, Joe Gallagher,
Wei Wu, and Srikar Chamala

Outline

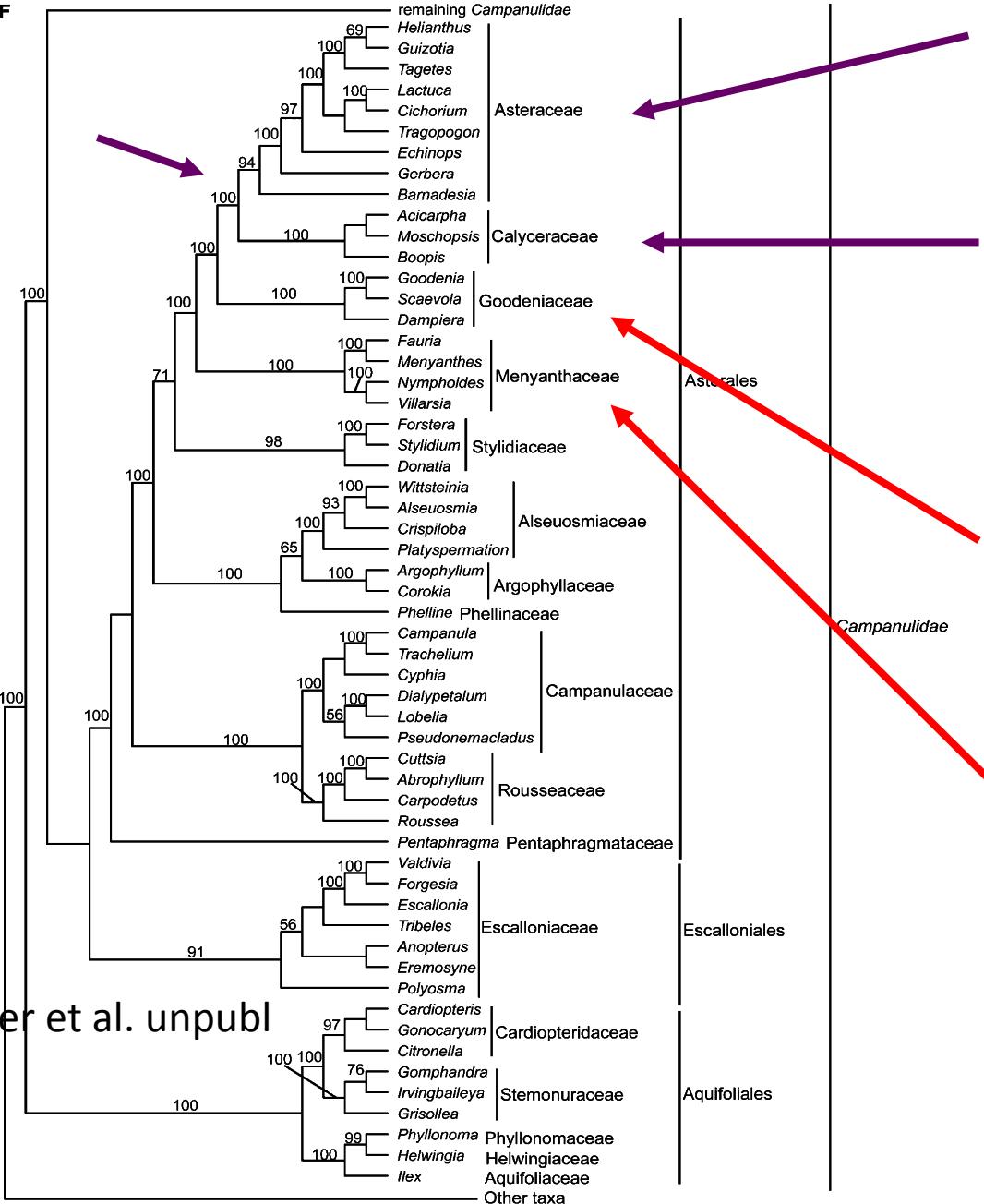
- Ancient polyploidy in Compositae
 - Genomic insights
 - Patterns of gene loss/retention
- Recent polyploidy events
 - Background—why these are important
 - Patterns of gene loss/retention
 - Compositae-wide rules
 - Extensive chromosomal variation

Polyplody in Compositae

- 570 genera, 58.3% of the 978 genera counted
- $2n = 4$ to 432 ($2x - 48x$) in the family
- Ancient polyploidy
- Recent polyploidy
- Unique opportunity to examine polyploidy over a range of ages from ancient to very recent

Ancient Polyploidy in Compositae + sister group

F



Compositae



Calyceraceae

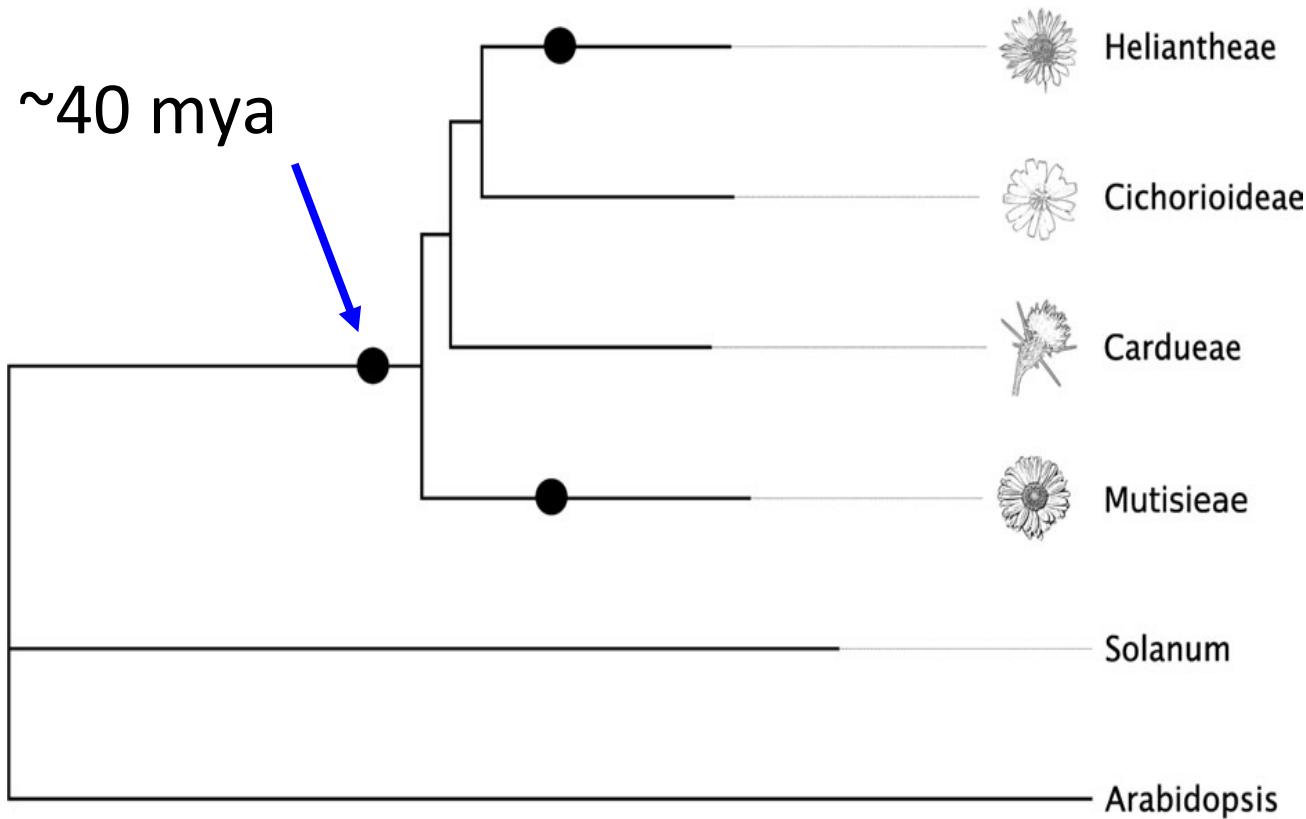


Goodeniaceae



Menyanthaceae

Ancient Polyploidy



Barker et al. 2008

0.2

FIG. 2.—Phylogeny of Compositae tribes and outgroups displaying observed paleopolyploid events and the rapid radiation of tribes. Branch lengths are mean rate corrected K_s values from 36 nuclear orthologs (supplementary table S1, Supplementary Material online). Black dots indicate inferred paleopolyploidizations in the evolution of the Compositae. Topology is a consensus phylogeny of the 36 nuclear orthologs (supplementary fig. S1, Supplementary Material online).

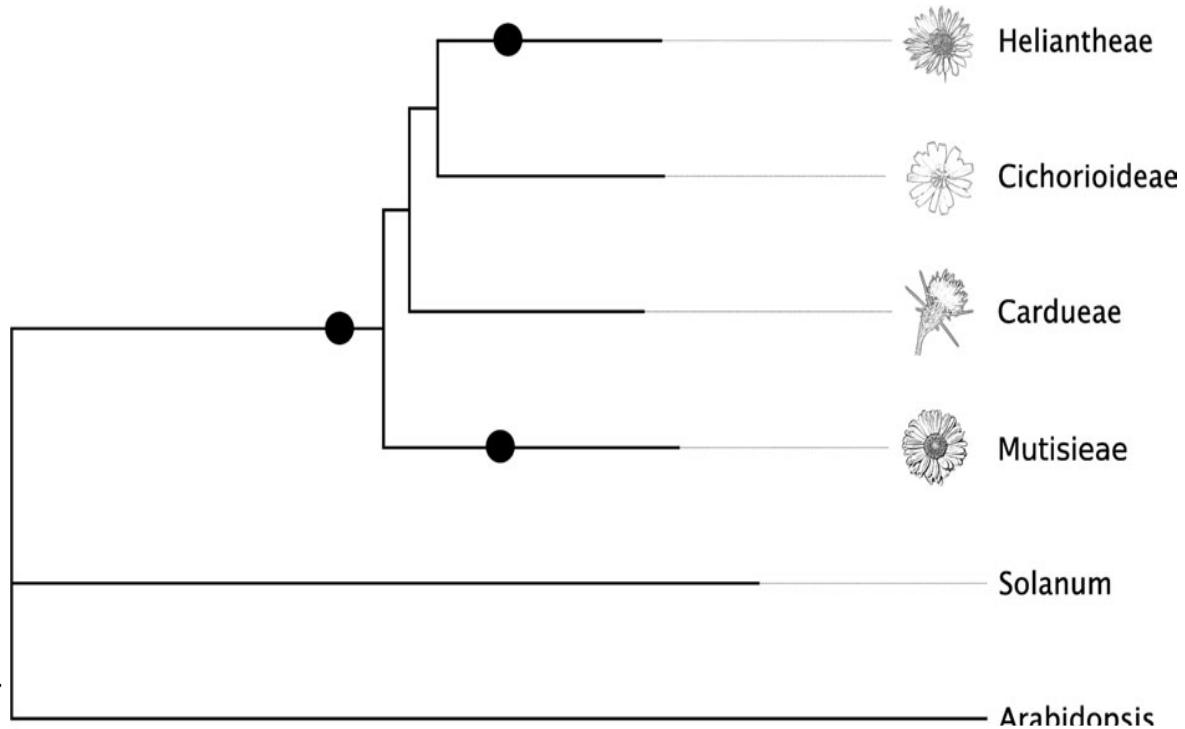
Compositae: Ancient Polyploidy

- Parallel retention of duplicate genes from the ancestral duplication across all tribes
- Pattern repeated for the Heliantheae duplication
- GO categories of genes retained in duplicate substantially different from those in *Arabidopsis*
- Genes annotated to structural components or cellular organization enriched among paleologs
- Genes associated with transcription factors underrepresented as duplicates
- Consistent patterns of gene retention

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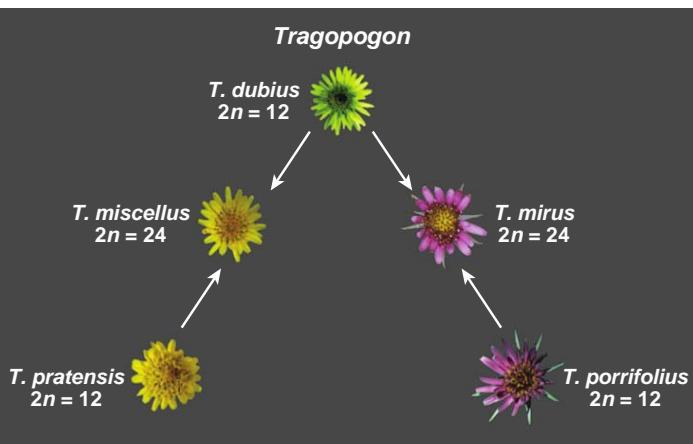
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Recent Polyploidy: last 100 years

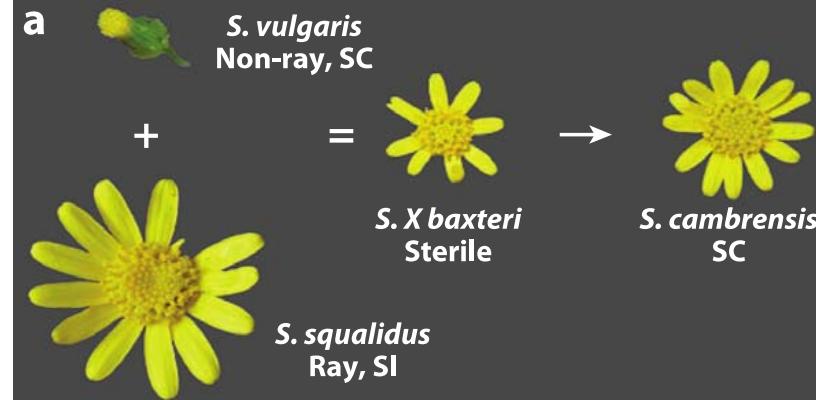


Tragopogon mirus

T. miscellus



Senecio camrensis (Welsh Ragwort)



Tragopogon: Man vs. Wild

T. dubius

$2n = 12$



T. miscellus

$2n = 24$



T. mirus

$2n = 24$



T. pratensis

$2n = 12$



T. porrifolius

$2n = 12$

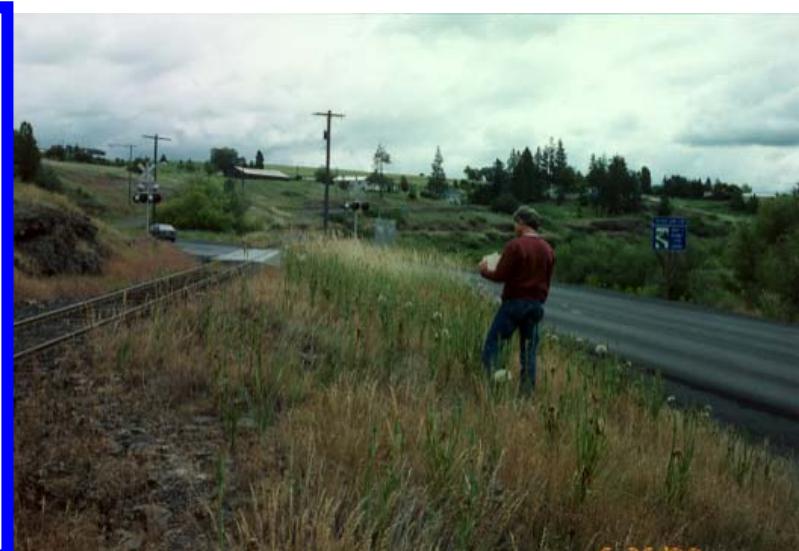
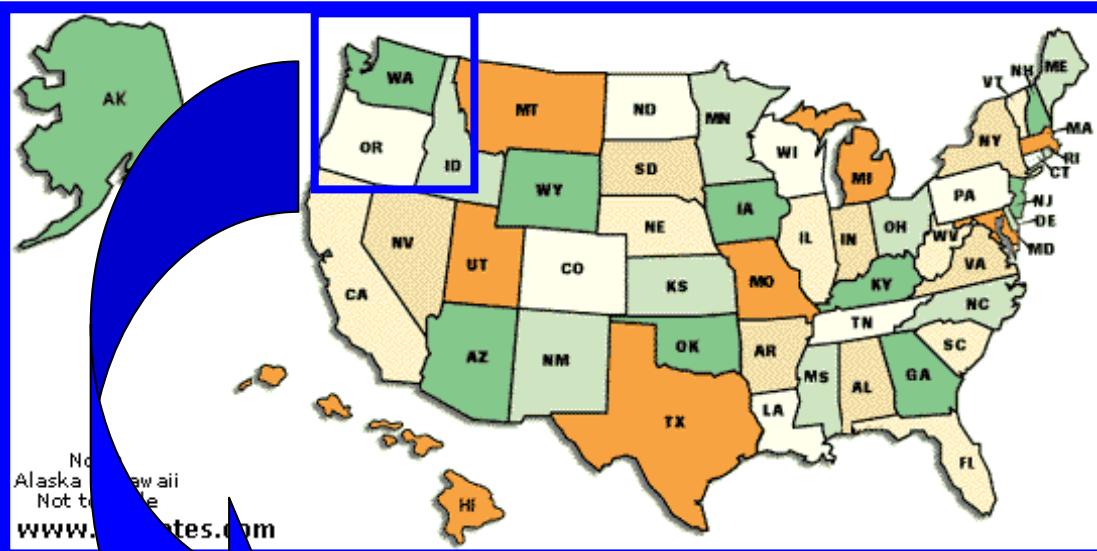
Tate et al. 2009

Tragopogon: A North American Success Story

- Diploids introduced from Europe early 1900s:
 - *T. dubius*, *T. porrifolius*, *T. pratensis*
- Allotetraploids *T. mirus* and *T. miscellus* discovered and named by Ownbey (1950)
 - ancestry of tetraploids is well documented
 - native to western N.A.
 - have not formed in Europe
 - less than 80 years old (40 gen.)
 - have formed repeatedly (>10)
 - very successful



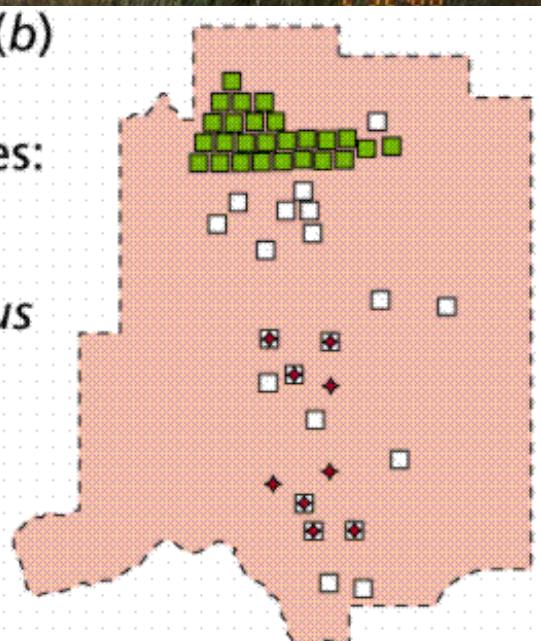
A Textbook Example of Polyploidy



Tetraploid hybrid species:

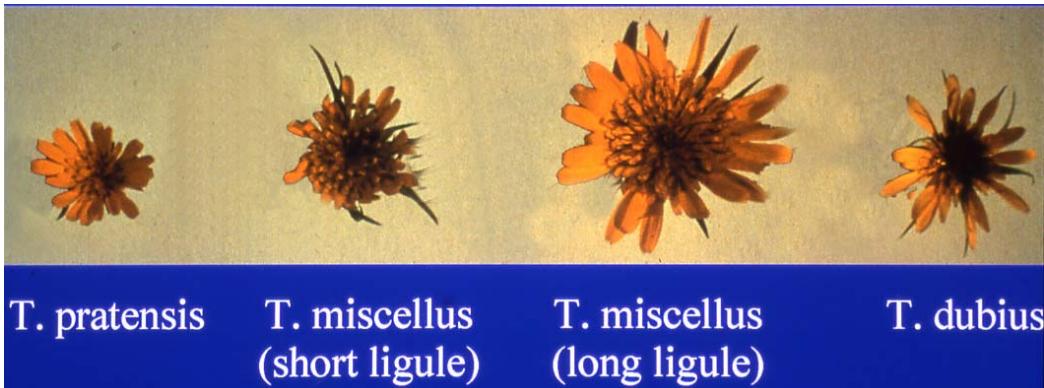
- *Tragopogon mirus*
- *Tragopogon miscellus*

Novak, Soltis, Soltis (1991)

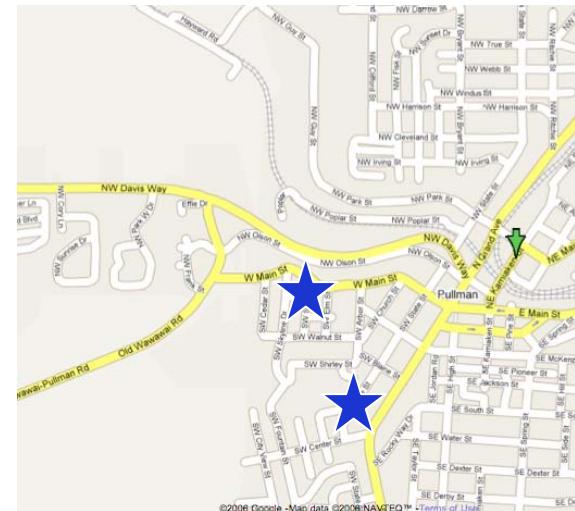


Molecular Markers: Origins of Species

- *T. mirus* 11+ origins
- *T. miscellus* 15+ origins
- Frequent multiple origins, in a short time period (<80 yrs)
- In a small geographic area (eastern WA and adjacent ID)
- Microsatellites—local scale, within small towns



Symonds et al. 2010



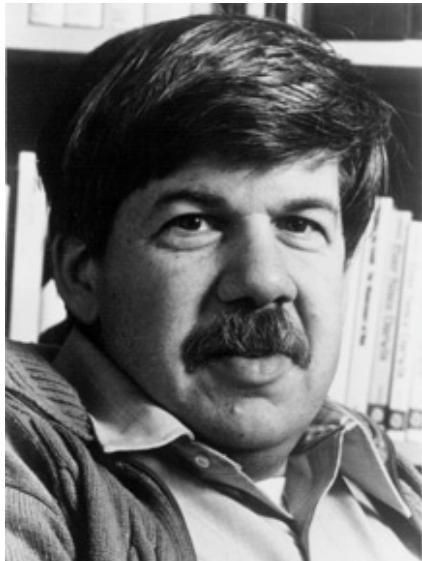
Recent Polyploidy in *Tragopogon*: Novel Research Possibilities

- Unique opportunity to examine the early stages of polyploidy in nature
- Are there rules to polyploidy that extend from 40 generations to 40 mya?
- Does evolution repeat itself?

Is evolution predictable?

Is evolution predictable?

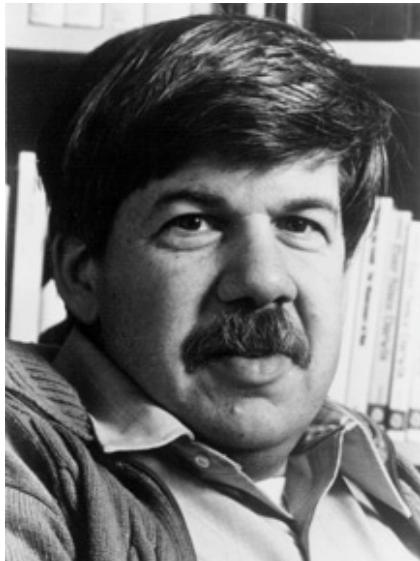
- NO



“Chains of historical events are so intricate,
so imbued with random and chaotic
elements, so unrepeatable in encompassing
such a multitude of unique objects, that
standard models of simple prediction and
replication do not apply” S. J. Gould

Is evolution predictable?

- NO



- YES



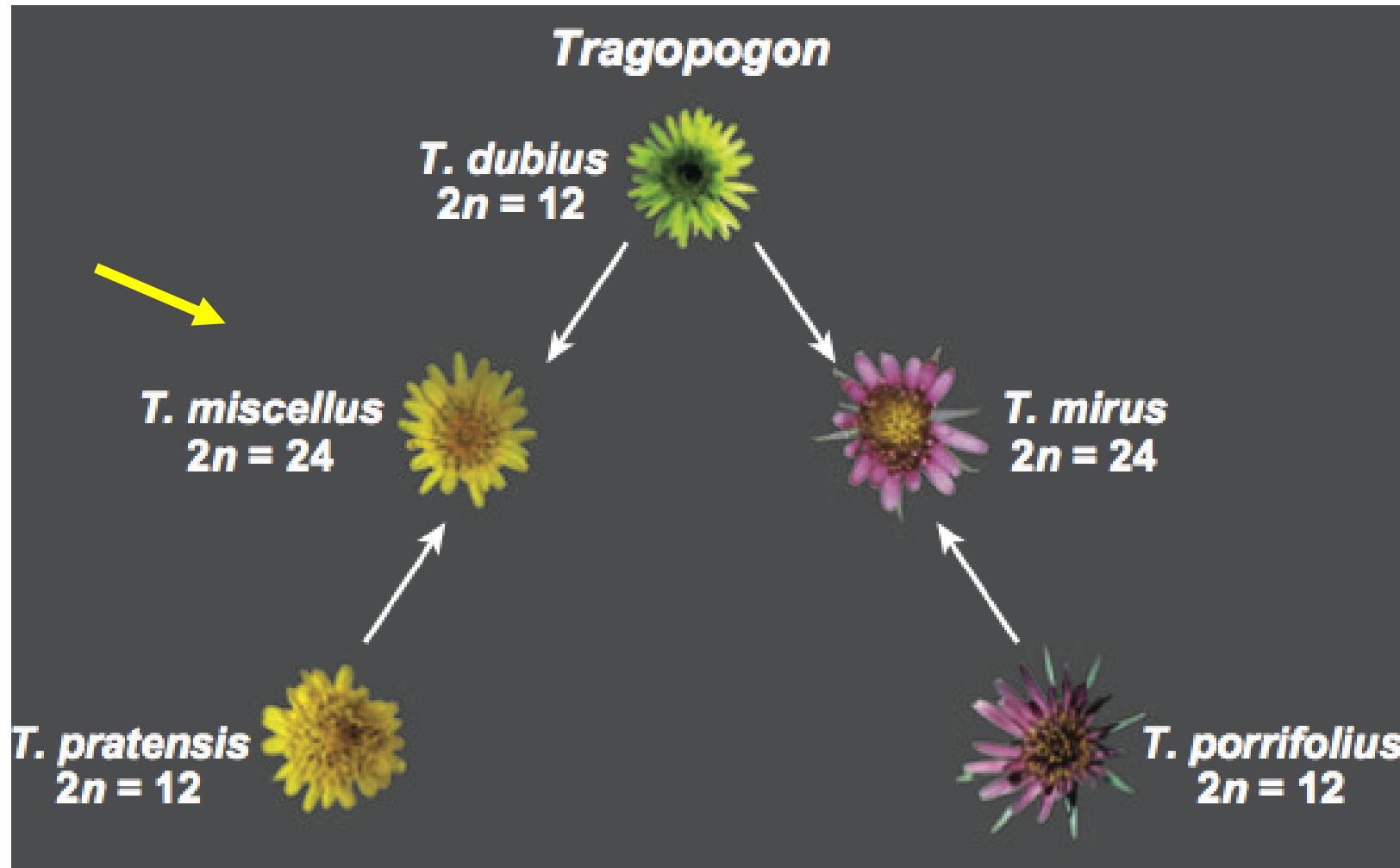
“Chains of historical events are so intricate, so imbued with random and chaotic elements, so unrepeatable in encompassing such a multitude of unique objects, that standard models of simple prediction and replication do not apply” S. J. Gould

Aspects of evolution are hard-wired, predictable

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Tragopogon Triangle



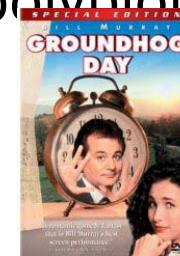
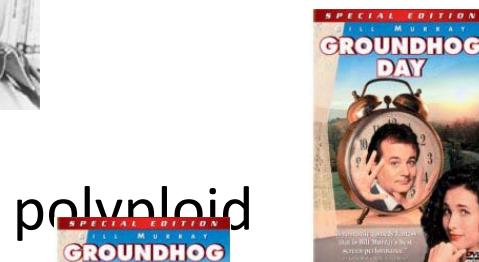
Homeolog Loss: one gene at a time

- 29 genes; 10 plants per multiple populations—5 years and 3 postdocs

- Homeolog loss is common
-

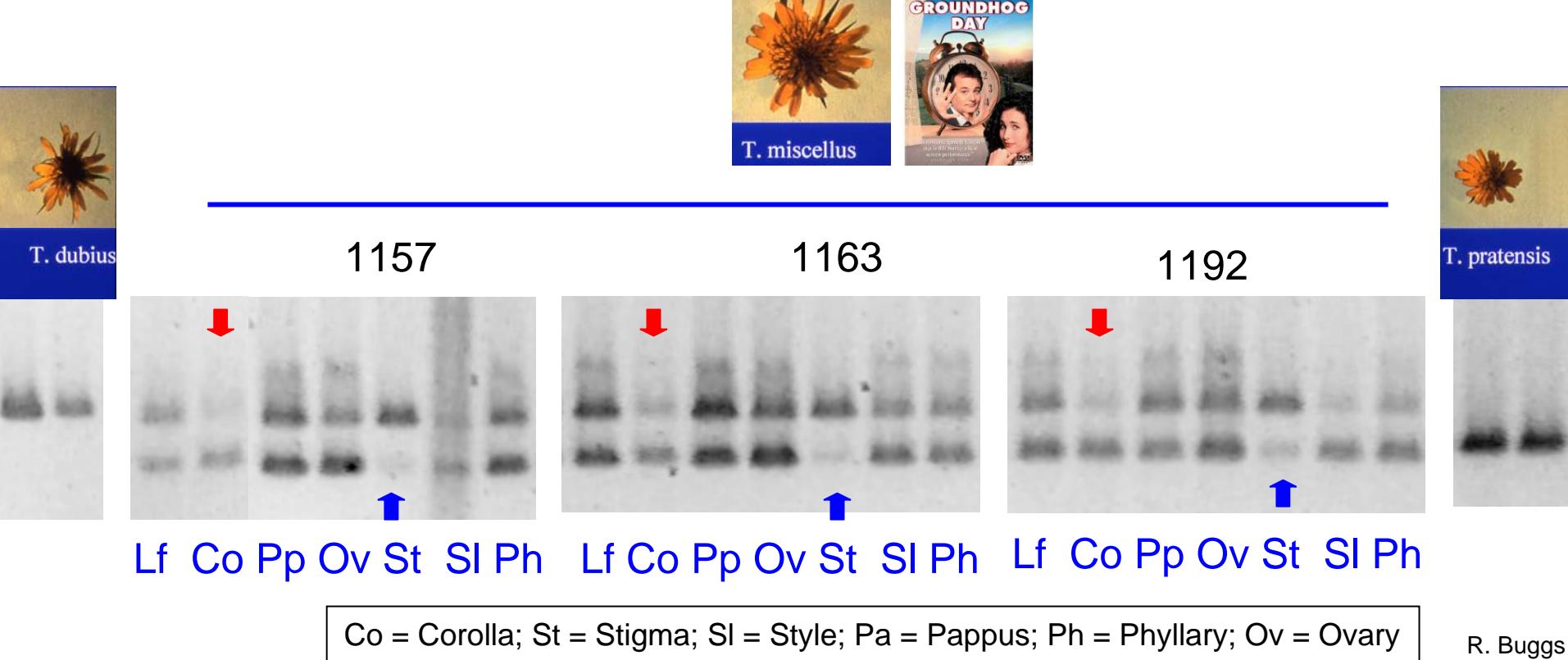


- Loss is stochastic within populations
- Same genes consistently undergo loss (9) in polyploid populations of separate origin
- Same genes (20) show no evidence of loss
- Loss often in the same direction (*T. dubius*)



But wait, there's more: Tissue-specific expression of homeologs

Suggests repeated subfunctionalization in T. miscellus



Tragopogon Genomics



Pat
Schnable

454 transcriptome sequencing

T. dubius (7 individuals)
T. pratensis (4 individuals)
T. porrifolius (4 individuals)

Assemble 454 reads into contigs

Call candidate SNPs in 454 contigs:

T. dubius v. *T. pratensis*
T. dubius v. *T. porrifolius*
T. pratensis v. *T. porrifolius*

Design Sequenom assays for a subset of SNPs

Validate Sequenom assays in genomic DNA of sequenced individuals

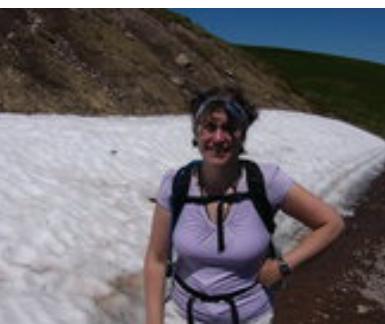
Illumina transcriptome sequencing

T. miscellus (3 individuals)
T. mirus (2 individuals)

Align Illumina reads to 454 contigs

Identify SNPs within allopolyploids showing unequal homeolog expression

Validate use of Sequenom assays for measuring relative homeolog expression



Brad
Barbazuk



Richard Bugs

Sequenom

Sequenom analysis

Sequenom analysis

Ingrid Jordon-Thaden

Genomics Summary

- Examined 70 homeolog-specific SNPs in 59 plants from five natural populations
- High frequency of single allele losses
 - ~20% of loci missing one or both alleles of a homeolog
 - 7% of original allele copies lost since polyploidization
- Repeated patterns of homeolog loss across populations
- Genes lost in clusters
- Gene ontology categories of the missing genes correspond with those lost after ancient WGD in Compositae
- Outcomes of WGD are predictable, even in <40 generations, perhaps due to the connectivity of gene products

Buggs et al. 2012



Tissue-Specific Silencing

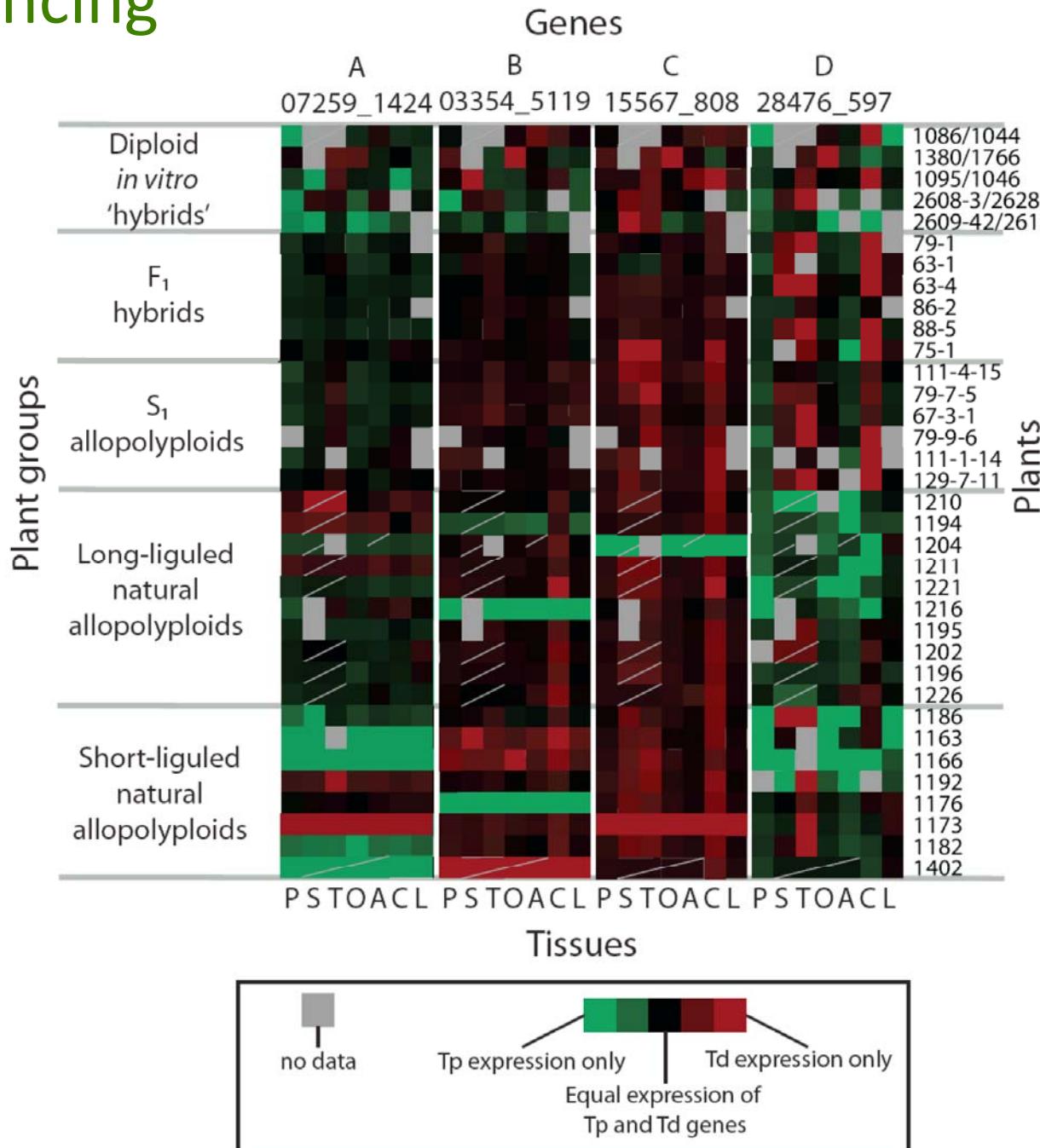
In *T. miscellus*

4 genes (columns) (144)

7 tissues (columns):

- phyllary
- style
- stigma
- ovary
- pappus
- corolla
- leaf

Many plants



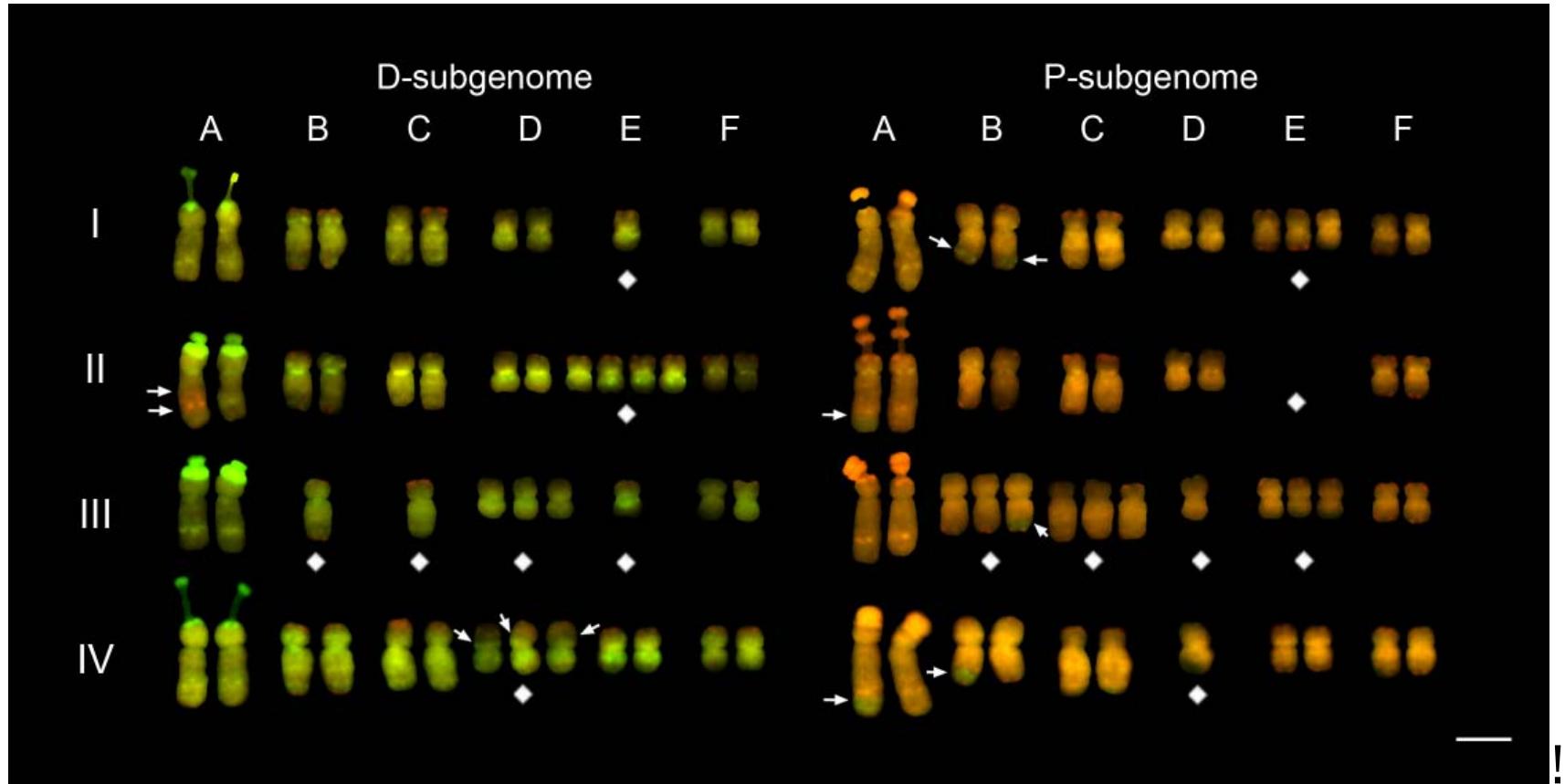
subfunctionalization

Buggs et al. 2011

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GISH in *Tragopogon miscellus*: extensive variation



Lim et al. 2008



Chester et al. 2012

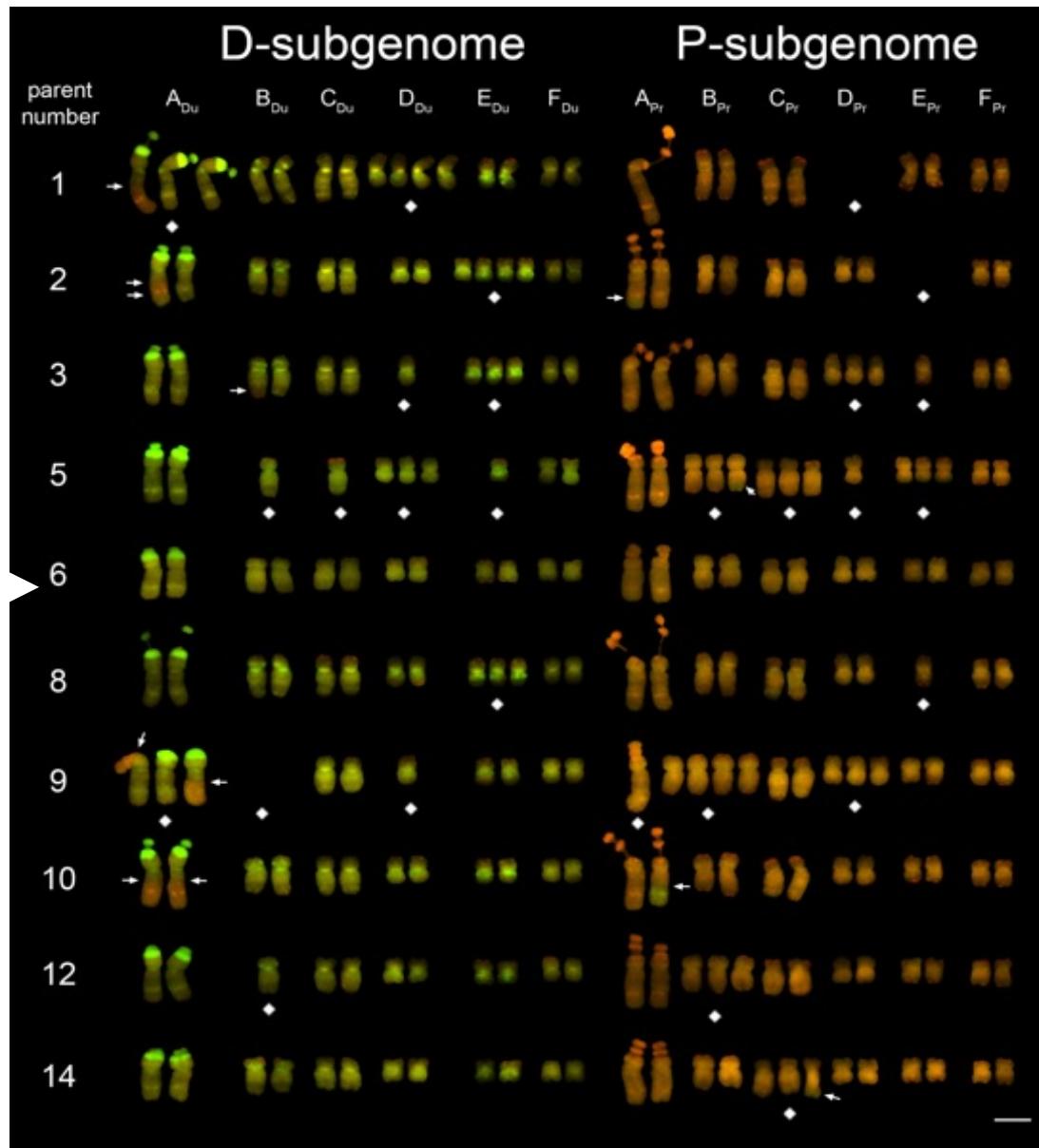
T. miscellus -- one population with GISH:

Chester et al. 2012

Only 1 plant has
expected additive
karyotype



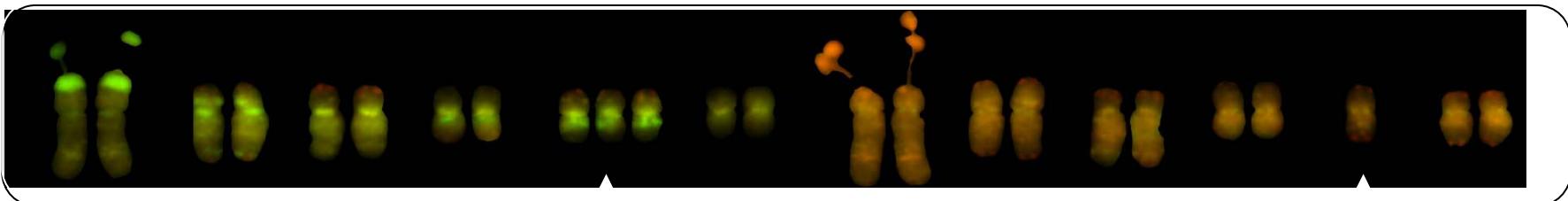
Mike Chester



Joe Gallagher

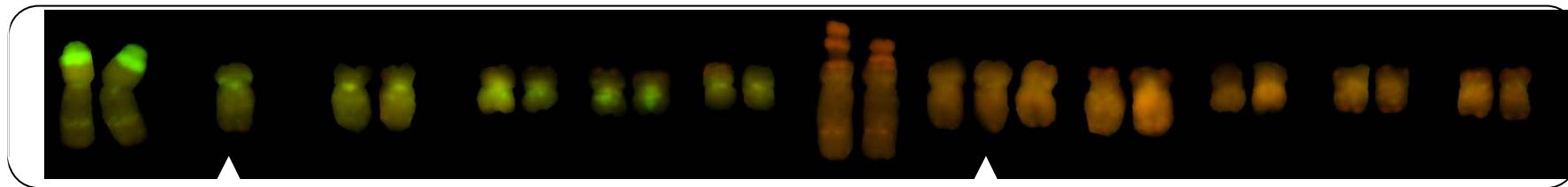
Chromosomes: Compensated Aneuploids

A B C D E F A B C D E F



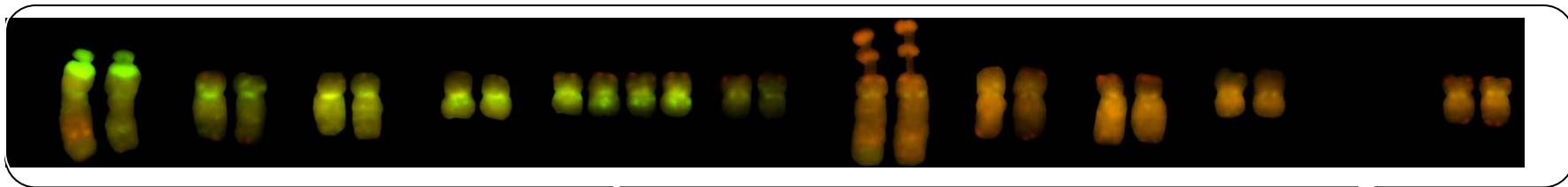
trisomy

monosomy



monosomy

trisomy

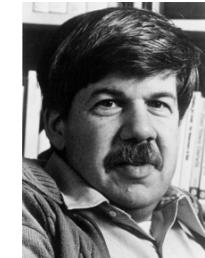


tetrasomy

nullisomy

Tragopogon Chromosomal Summary

- Recurring Aneuploidy (69%)
- Reciprocal trisomy-monosomy and tetrasomy-nullisomy repeated
- Intergenomic translocations (76%)
 - Repeated patterns
 - Unique features (stochastic)

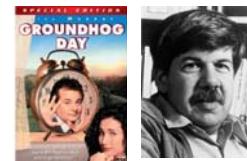


Summary: Does evolution repeat itself?

- Concerted evolution in the same direction (*T. dubius*)



- Chromosomal instability



- Same genes undergo loss/silencing



- Same genes show no evidence of loss/silencing



- Loss/silencing often in the same direction (*T. dubius*)



- Evidence for repeated subfunctionalization

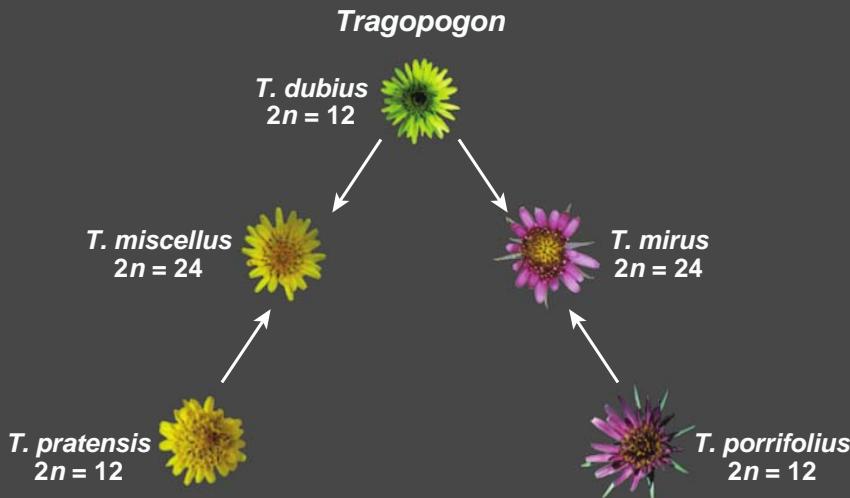


- But, within populations loss/silencing is stochastic



Tragopogon Polyploids: a continuum of ages

New North American polyploids



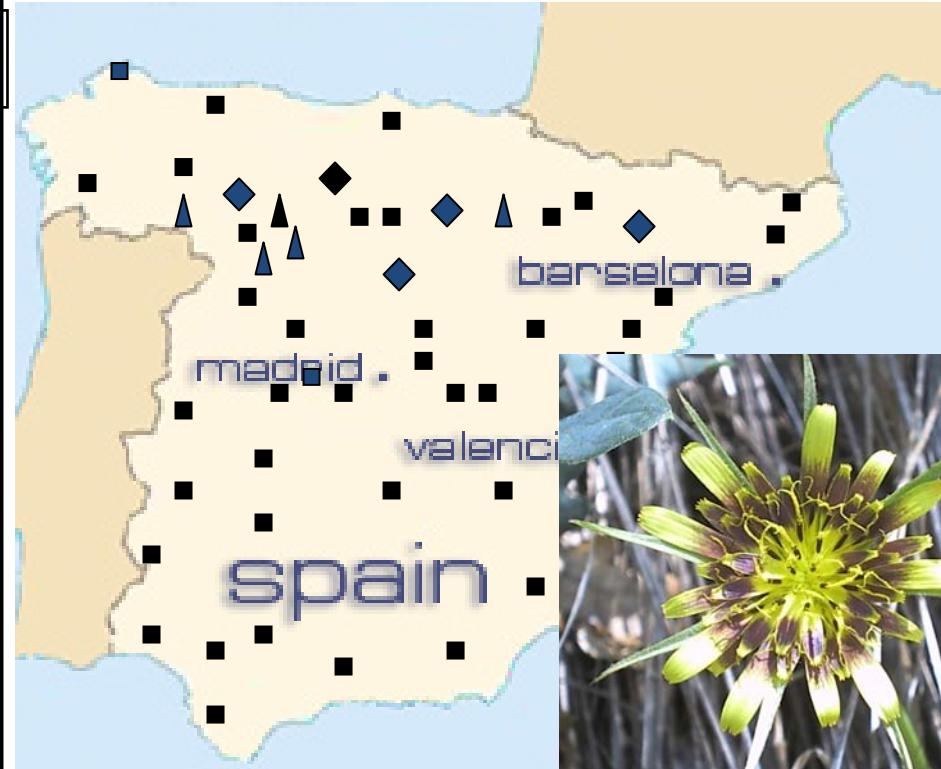
--F1 hybrids



-Resynthesized tetraploids



-Tetraploids < 80 years (40 gen)



4x *Tragopogon castellanus* (triangles)

2x *T. lamottei* (diamonds)

2x *T. crocifolius* (squares)



1 mya--Old Eurasian polyploid

Ingrid Jordon-Thaden

Traglodytes



Genomic tools quickly make a nonmodel system
that is a
good evolutionary model more of a model



“I want to be like
You, ou, ou...”



Stochastic loss of homeologs in *T. miscellus* plants from five natural populations.

