Evolutionary trends and mechanisms of chromosome number variation


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Basic or base chromosome number (x)

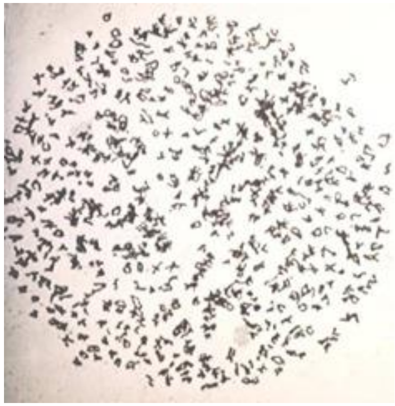
- a relative concept [x has to be related to a certain taxonomic unit, e.g. genus or (sub)family]
- monobasic taxa (single x number), dibasic taxa (two x nos.) and polybasic taxa (>2 x nos.)
- are there any evolutionary trends in chromosome number changes?
- are the same chromosome number and similar karyotype structure indicative of close phylogenetic relationship?
- can polybasic taxa be regarded as monophyletic?
- is the most common basic chromosome number automatically the ancestral one?

Asteraceae – example of a polybasic family

Table 4. Tri- and polybasic genera in the Astereae.

Genus	Region	"Basic" chromosome numbers
Amellus L.	(Africa)	$x = 6, 8, 9$ (diploid)
Aphanostephus DC.	(N. Am.–Mex.)	$x = 3, 4, 5$ (diploid)
Aster L.	(cosmopolitan)	$x = (4–)5, 7, 8, 9, 13$ (polyploid to $16x$)
Astranthium Nutt.	(N. Am.–Mex.)	$x = 3, 4, 5, 6, 8, 9$, etc. (dysploid; polyploid to $6x$?)
Brachyscome Cass.	(Austr., N.Z., N.G.)	$x = 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13$, etc. (dysploid; polyploid to $18x$?)
Calotis R. Br.	(New Zealand)	$x = 4, 7, 8, 9$, etc. (polyploid to $14x$?)
Chrysopsis Nutt.	(N. Am.)	$x = 4, 5, 9$ (polyploid to $6x$)
Felicia Cass.	(Africa)	$x = 5, 6, 8, 9$ (diploid and tetraploid)
Haplopappus Cass. sensu lato	(N. Am.–S. Am.)	$x = 2, 3, 4, 5, 6, 7, 8, 9$, etc. (dysploid; polyploid to $18x$?)
Machaeranthera Nees	(N. Am.–Mex.)	$x = 2, 4, 5, 8, 9$? (dysploid; diploid and tetraploid)
Psilactis A. Gray	(N. Am.–S. Am.)	$x = 4, 5, 9$ (perhaps dibasic with dysploidy; diploid)

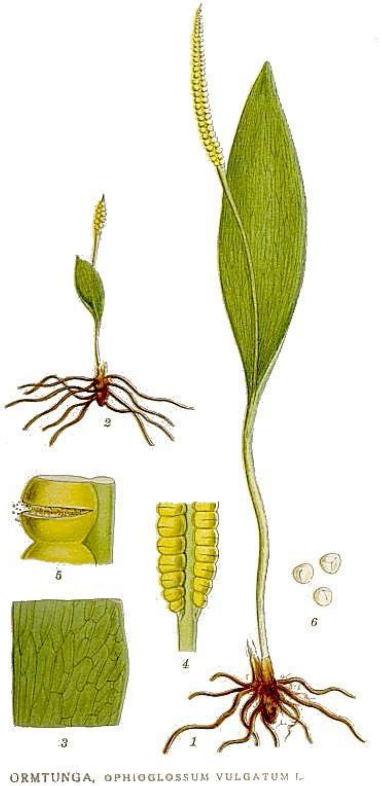
Chromosome number variation

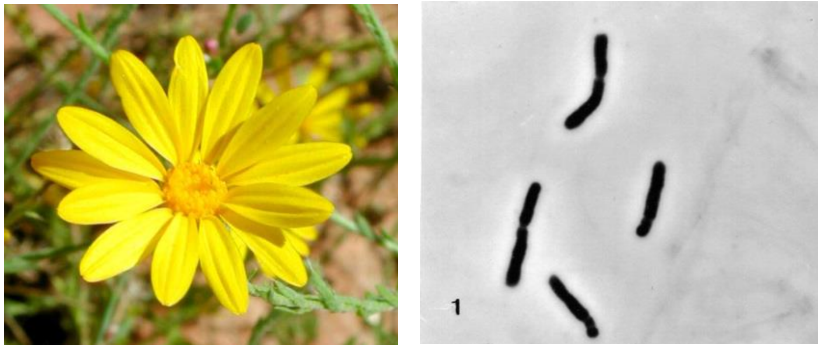


Chromosome numbers of plants vary enormously over a 360-fold range.

n = 2 in five angiosperm species

n = 630 in the fern *Ophioglossum reticulatum*



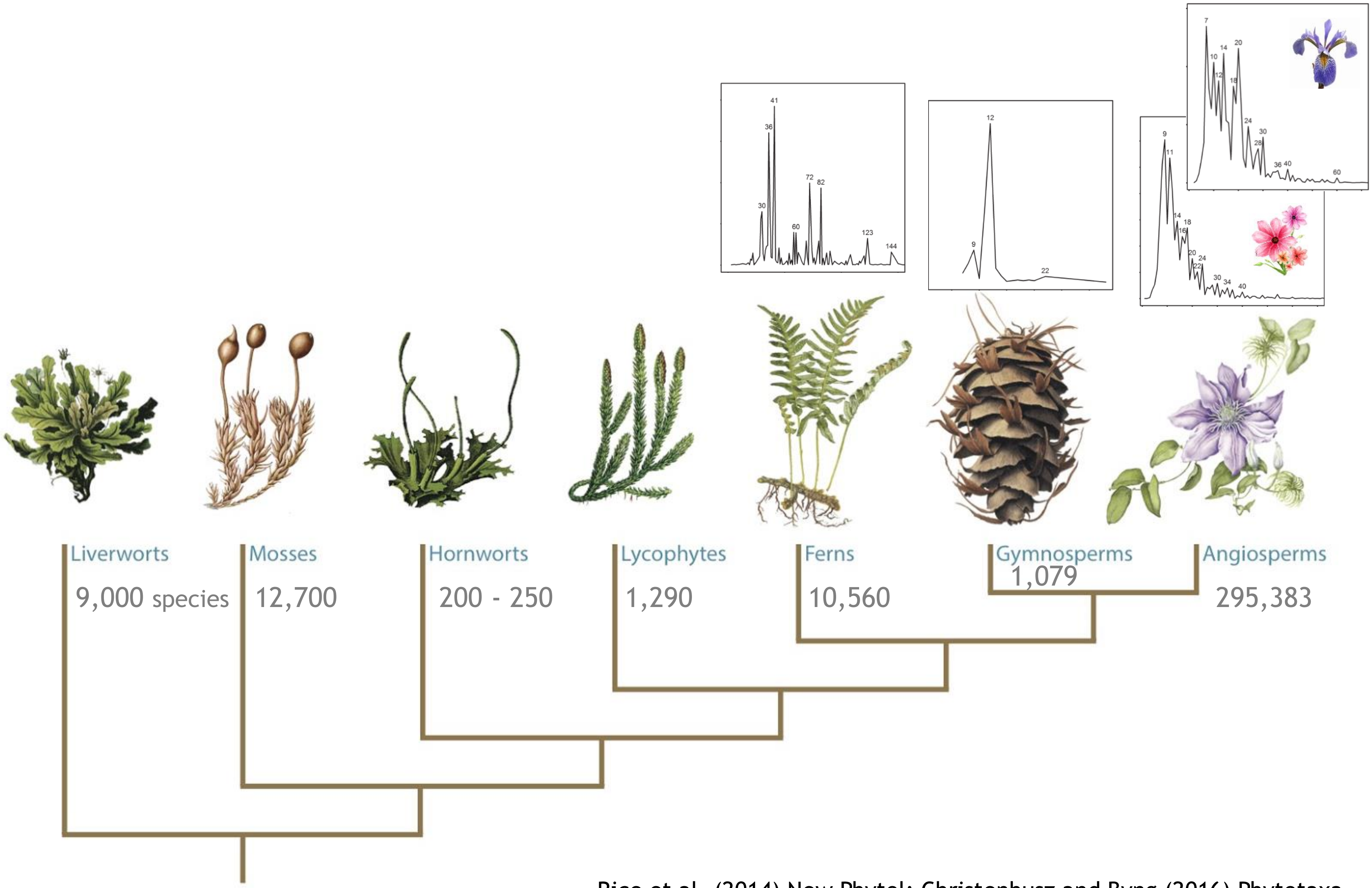


Haplopappus gracilis

Chromosome number variation

- Stasis
- Decrease (descending dysploidy)
- Increase (polyploidy and ascending dysploidy)

Chromosome Number Diversity Across Land Plants



Liverworts
9,000 species

Mosses
12,700

Hornworts
200 - 250

Lycophytes
1,290

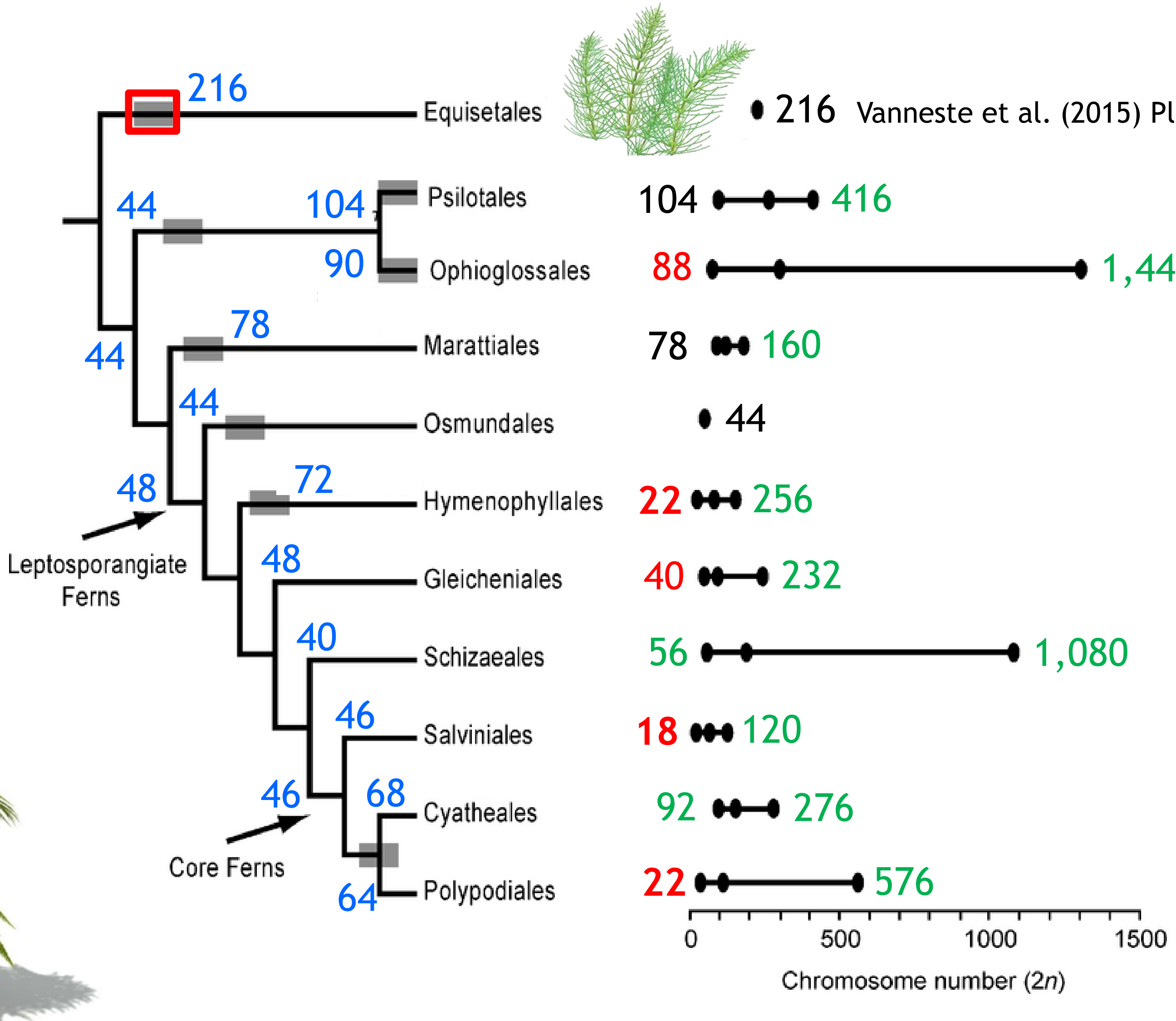
Ferns
10,560

Gymnosperms
1,079

Angiosperms
295,383

Rice et al. (2014) New Phytol; Christenhusz and Byng (2016) Phytotaxa

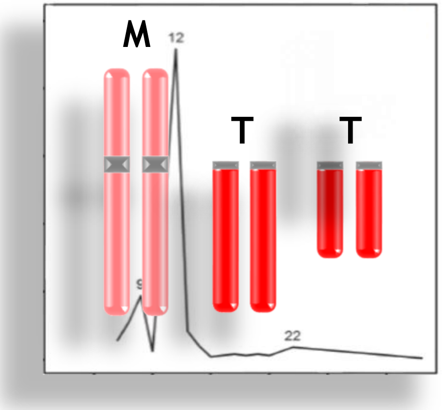
Fern „Polyploidy Paradox“: high chromosome nos., but no clear evidence. Multiple WGDs and Dysploidies ?

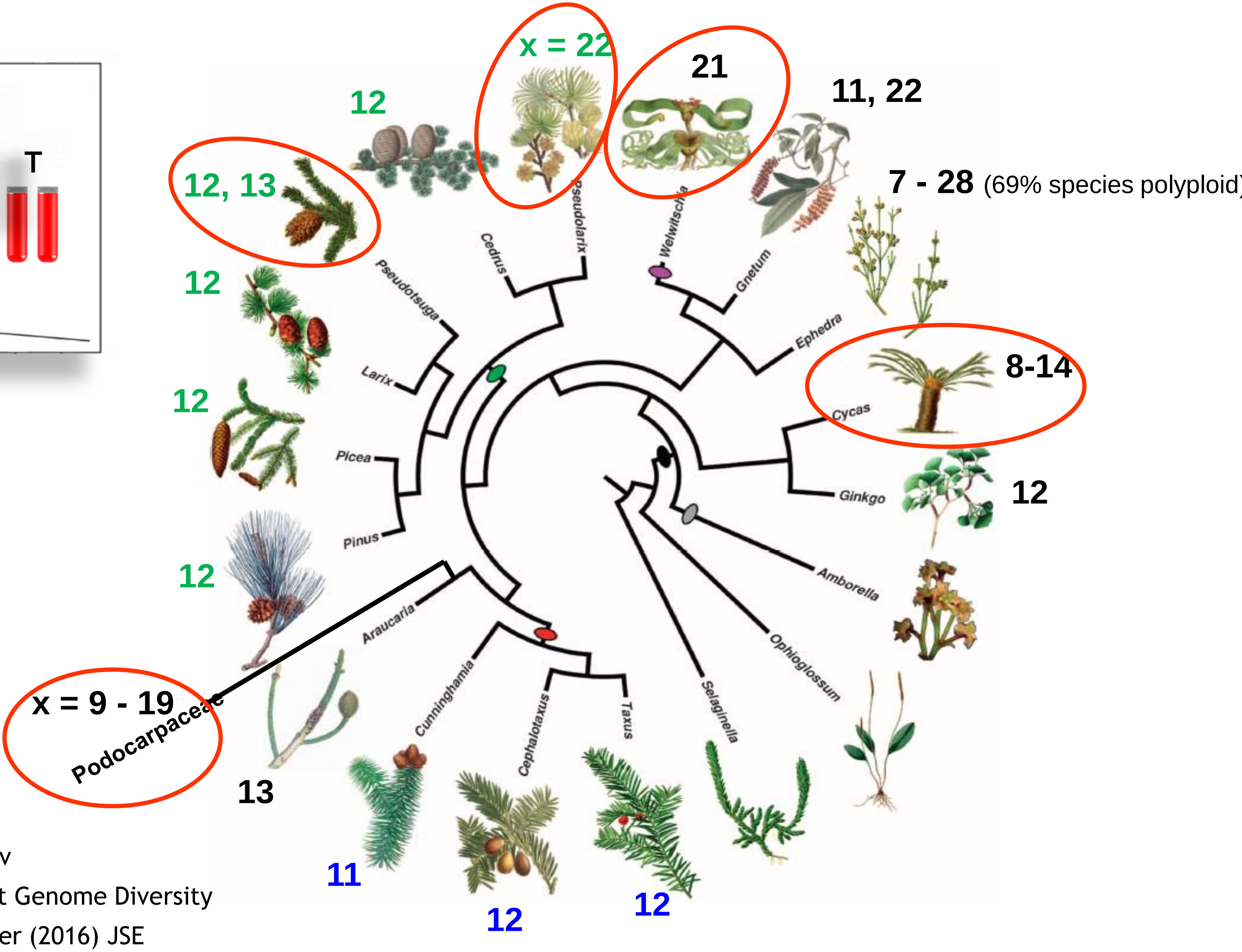


Vanneste et al. (2015) Plant Cell

Clark et al. (2016) New Phytologist

Reduced Chromosome Number Diversity and Rare Neopolyploids in Gymnosperms



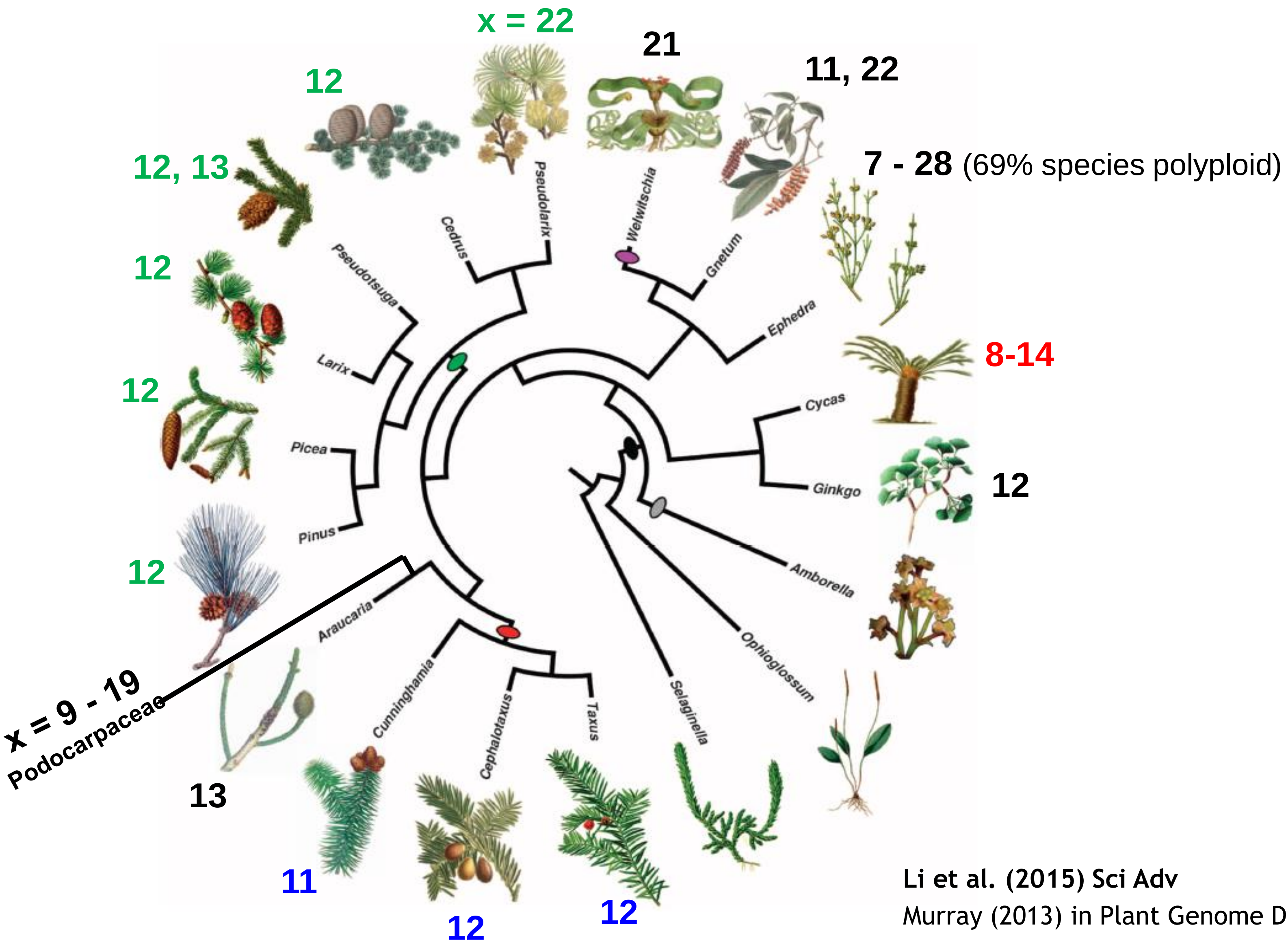


Li et al. (2015) Sci Adv

Murray (2013) in Plant Genome Diversity

Ickert-Bond and Renner (2016) JSE

Ancient Whole-Genome Duplications in Gymnosperms



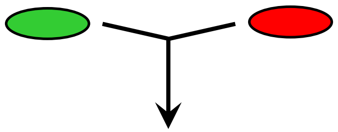
Li et al. (2015) Sci Adv

Murray (2013) in Plant Genome Diversity

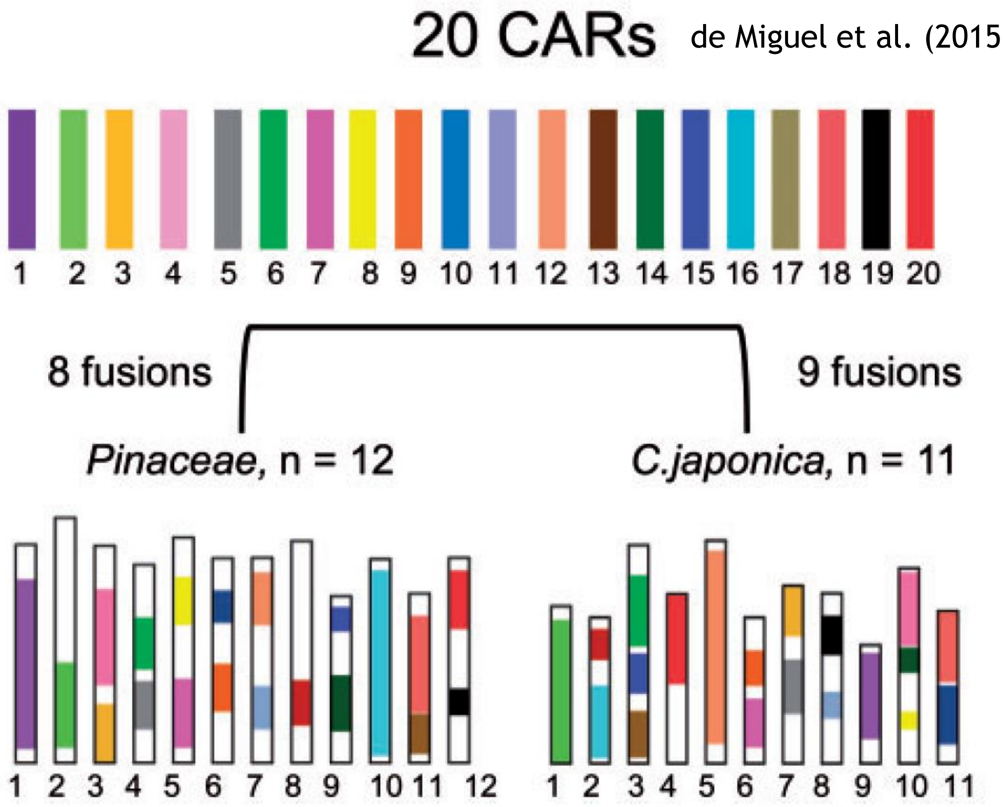
Ickert-Bond and Renner (2016) JSE

Post-Polyploidy Chromosomal Schuffling in Coniferales ?

2 independent WGDs ?



Li et al. (2015)



de Miguel et al. (2015)

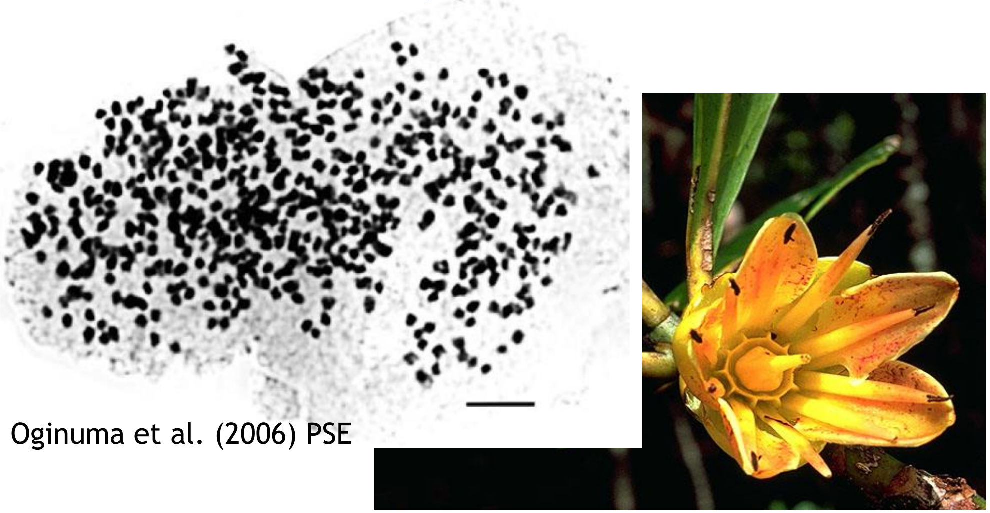
de Miguel et al. (2015) GBE; Li et al. (2015) Sci Adv

A 160-Fold Variation of Chromosome Numbers in Angiosperms

Haplopappus gracilis
n = 2

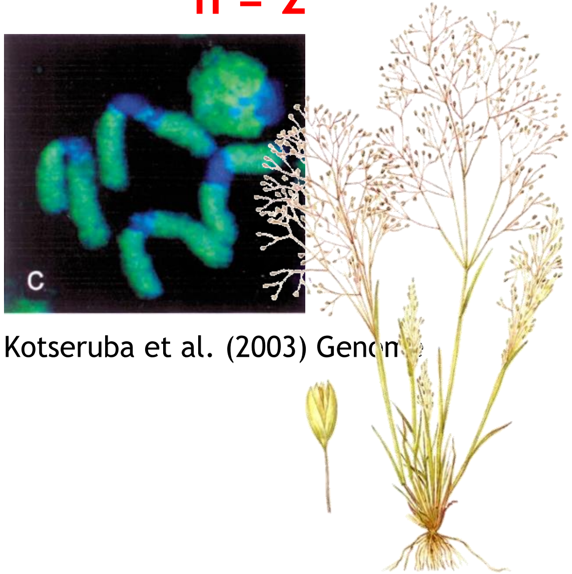
Jackson et al. (2002) Am J Bot

Strasburgeria robusta
n = 250



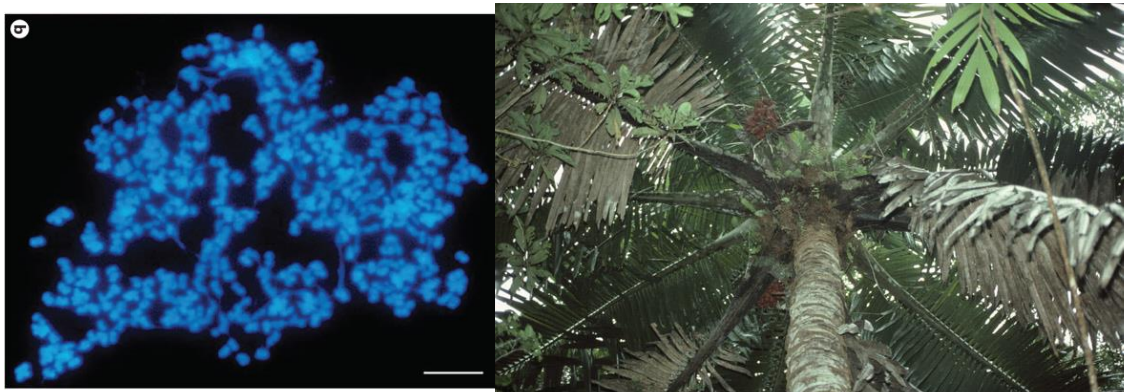
Oginuma et al. (2006) PSE

Zingeria biebersteiniana
n = 2



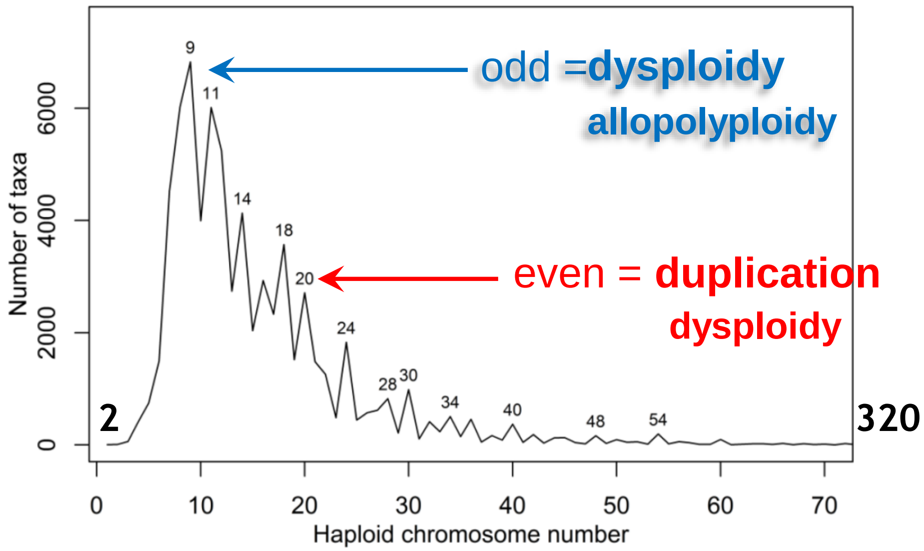
Kotseruba et al. (2003) Genome

Voanioala gerardii
n = 303



Röser et al. (2015) CGR

Distribution of Haploid Chromosome Numbers in Angiosperms Was Shaped by Polyploidy and Subsequent Dysploidy



odd =**dysploidy**

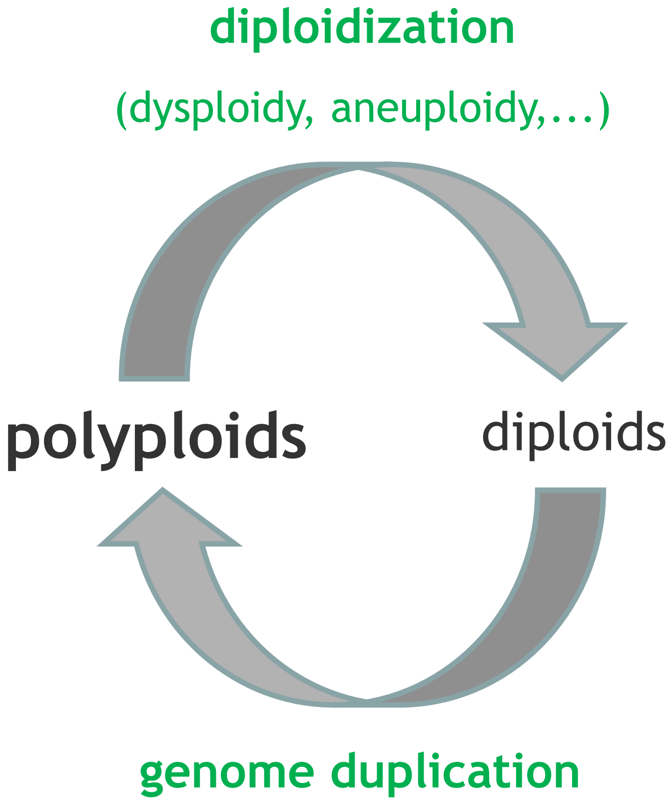
allopolyploidy

even = **duplication**

dysploidy

Table 3 Major groups even vs odd chromosome counts[a]

Clade	Number of total counts	Percentage of even counts
Angiosperm	70 338	56%
Monocots	15 528	58%
Eudicots	53 492	55%
Monilophytes	2986	63%
Lycophytes	220	53%
Gymnosperms	488	59%
Bryophytes	1446	48%



diploidization

(dysploidy, aneuploidy,...)

polyploids

diploids

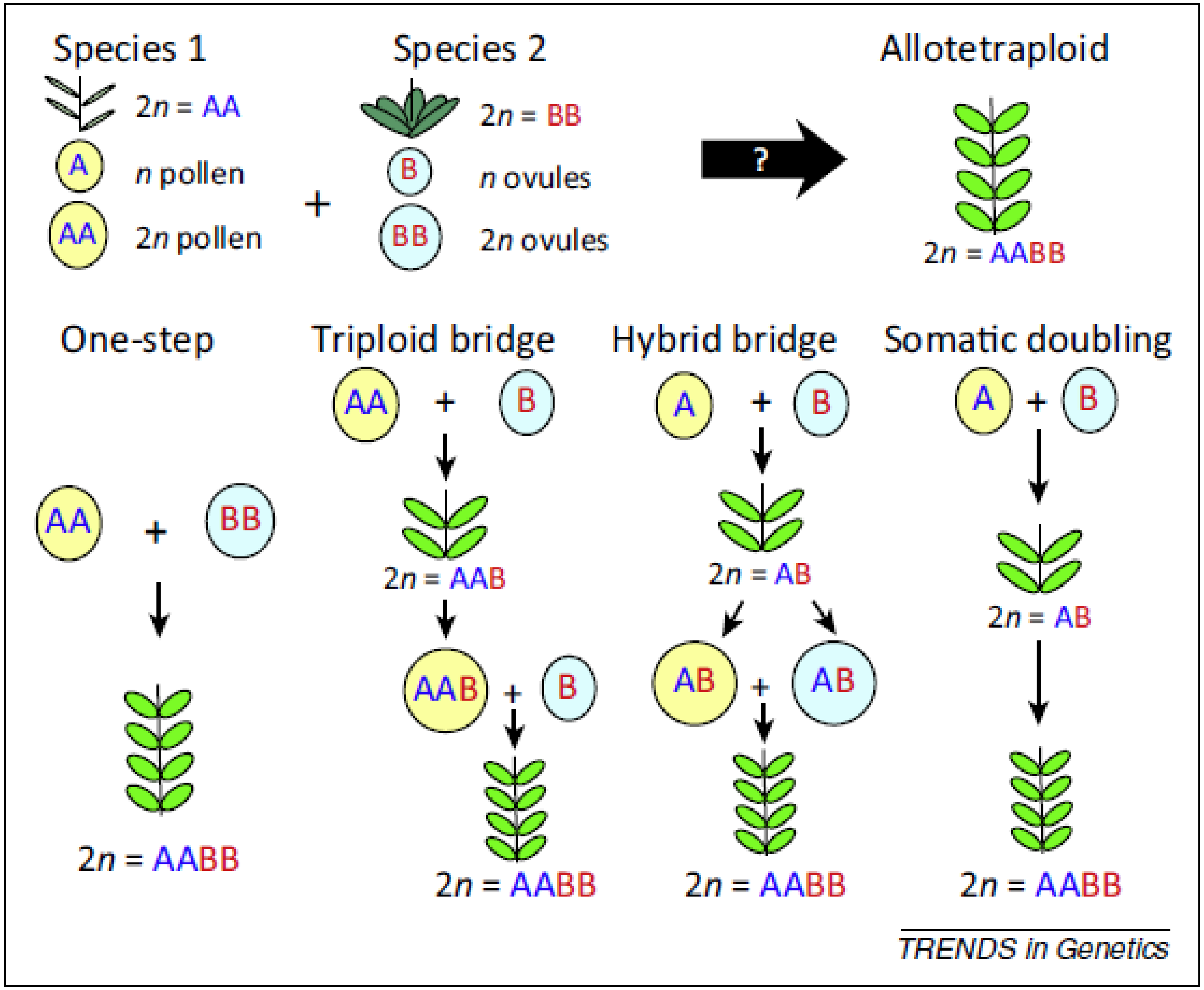
genome duplication

Otto and Whitton (2000) Annu Rev Genet; Rice et al. (2014) New Phytol

Chromosome number variation

- Stasis
- Decrease (descending dysploidy)
- Increase (polyploidy and ascending dysploidy)

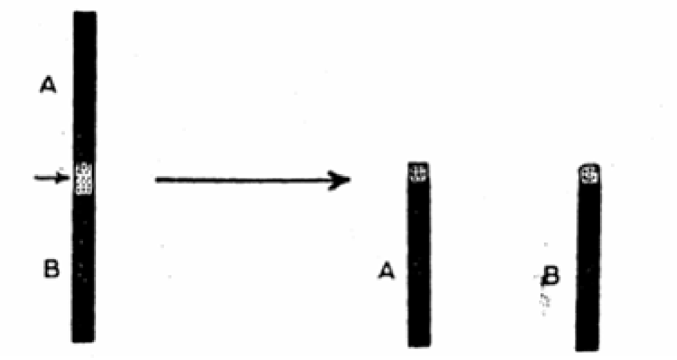
Allopolyploidy (and of course autopolyploidy)



TRENDS in Genetics

Ascending dysploidy

1. Centric fission (1 metacentric chromosome → 2 telocentrics)



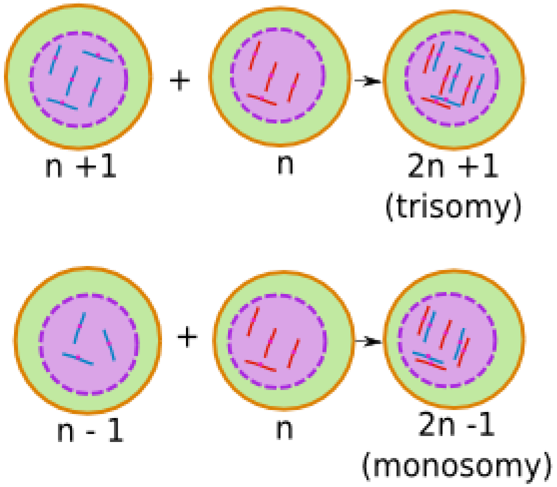
probably in orchids, cycads...

2. Meiotic misdivision (non-disjunction)

- misdivision resulting in a tetrasomic plant (2n+2)

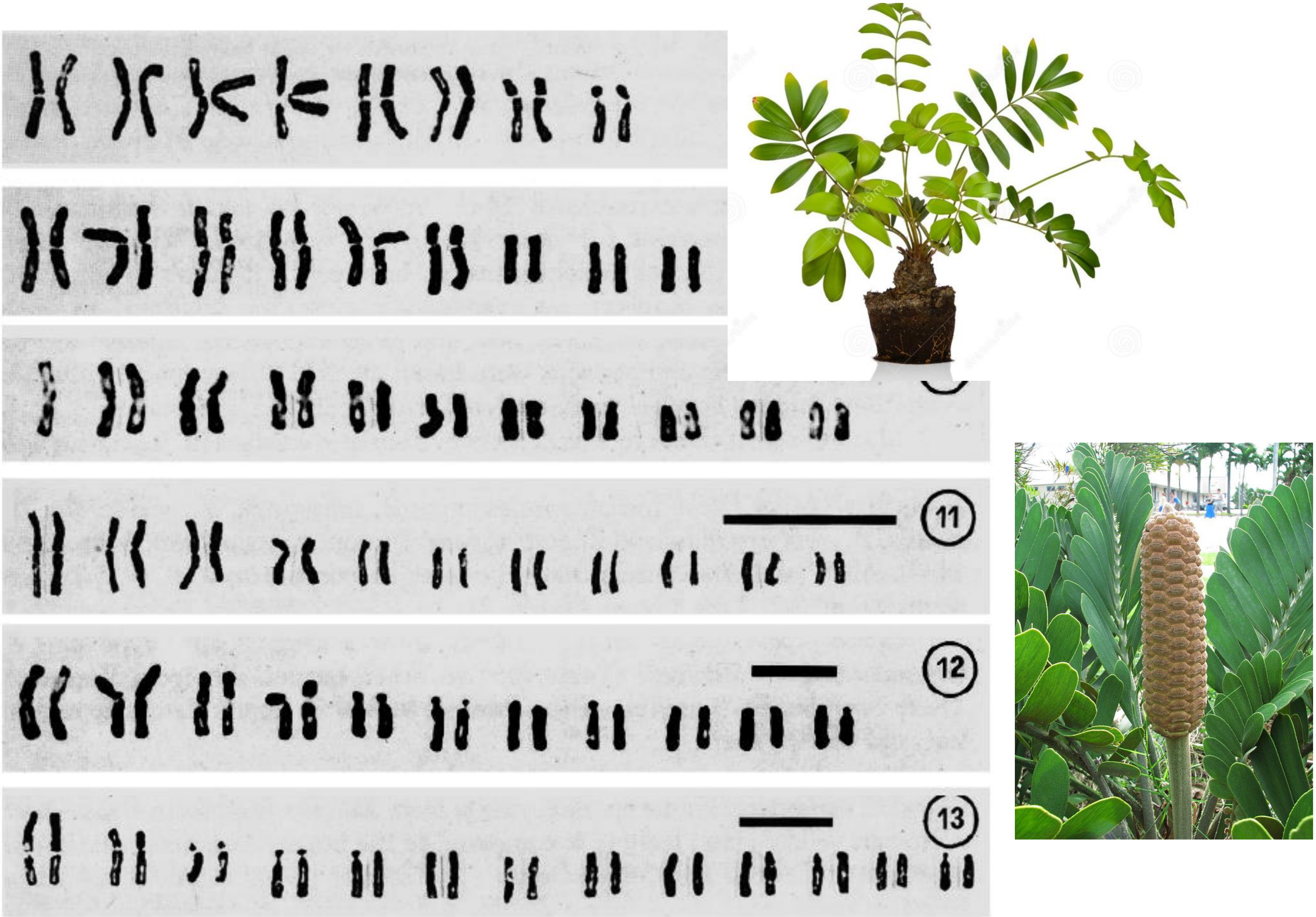
(or first trisomy: 2n+1 followed by tetrasomy, 2n+2)

or monosomic plant (2n-1, this is descending dysploidy)

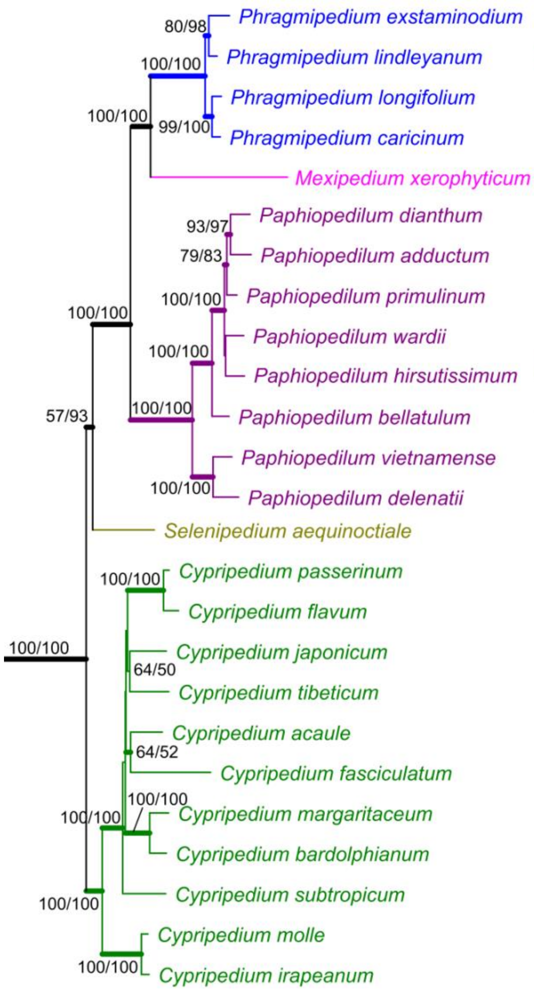


- the extra chromosome can diverge from their homologues through a translocation with non-homologous chromosomes

Centric fissions → telocentric chromosomes in cycads (*Zamia*)



Centric Fissions Increase Chromosome Number in Seed Plants



18 → **30**

26

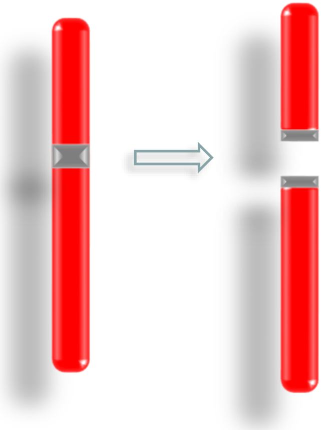
→ **32**

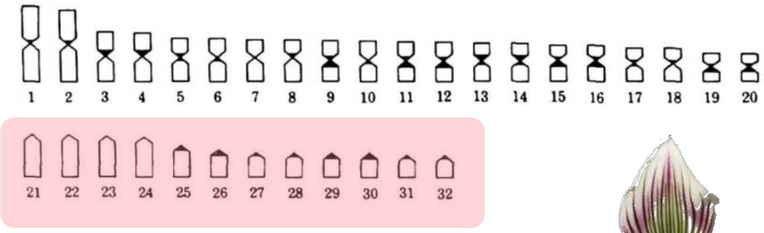
26

→ **42**

20

20





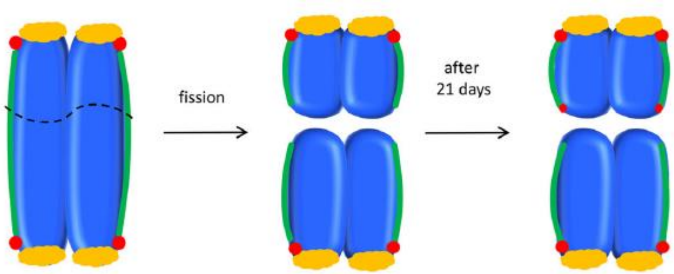
Guo et al. (2012) Plos ONE; Karasawa and Tanaka (1980) Cytologia
Cox et al. (1998) Am J Bot; Leitch et al. (2009) Ann Bot

Centric Fissions Are Rare in Seed Plants Despite Evidence of Efficient Chromosome Healing

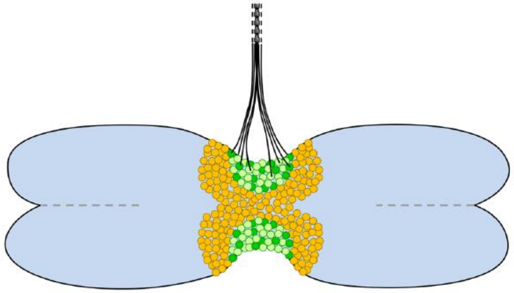
„Sticky“ chromosome ends can be stabilized by *de novo* telomere formation or „chromosome healing.“

bread wheat, ditelosomic Dt 3AS
courtesy of B. Friebe (Koo et al. 2015, PLoS ONE)

Luzula elegans
Jankowska et al. (2015) Chromosoma

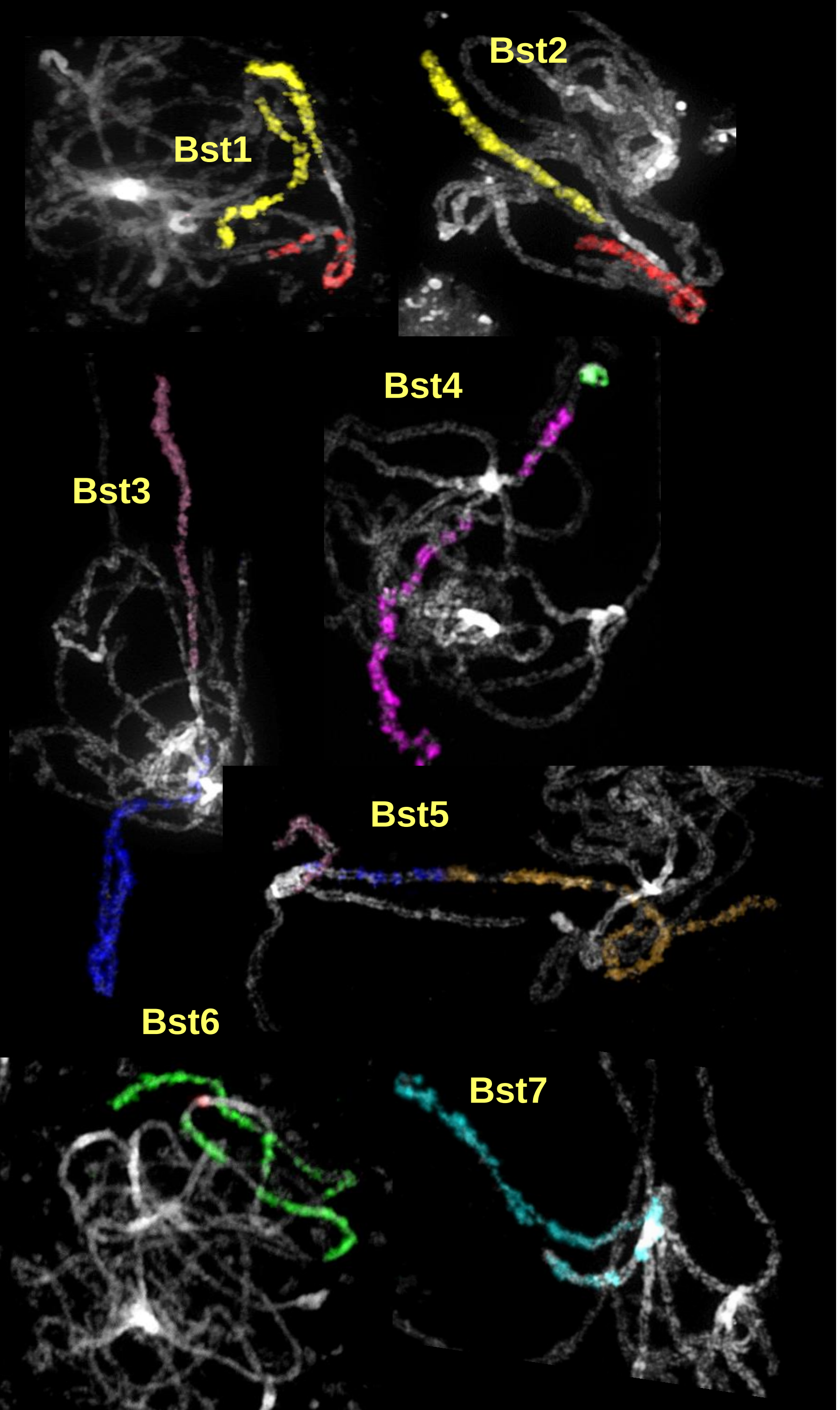


Telocentrics can be „unstable“…

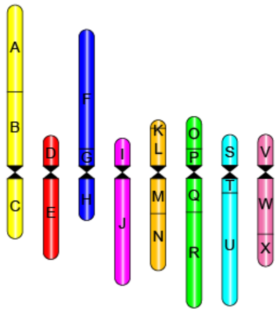


Wanner et al. (2015) Chromosoma

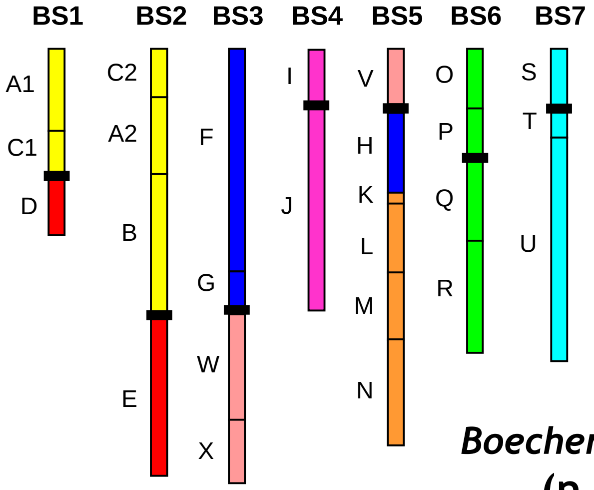
McClintock (1941), Marks (1957), Brighton (1978), Schubert et al. (1992), Slijepcevic and Bryant (1998), Tsujimoto et al. (1999), Jankowska et al. (2015), Koo et al. (2015), Wanner et al. (2015), Rocha et al. (2016)



Boechera genomes originated from eight ancestral chromosomes



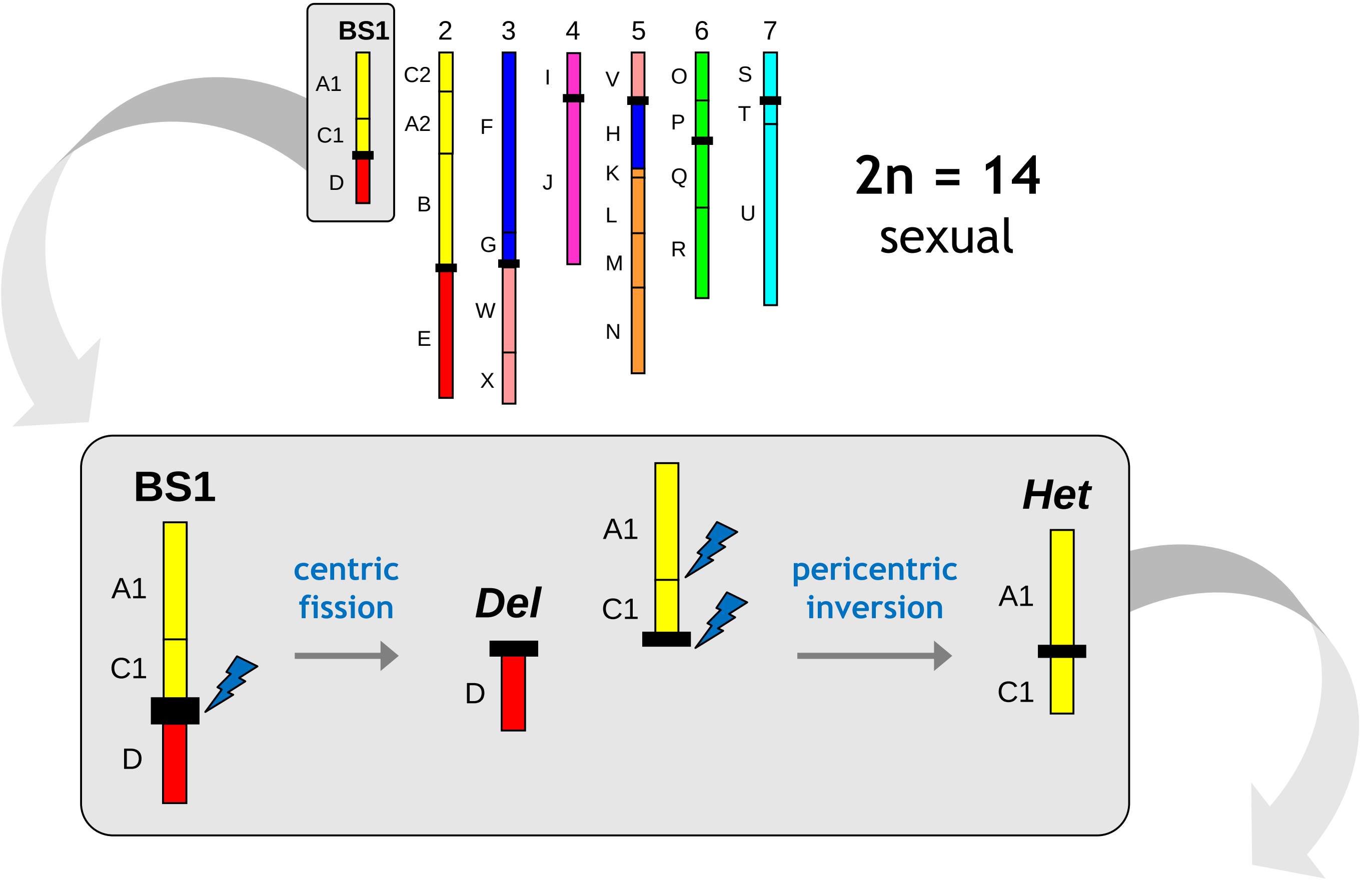
descending dysploidy
n = 8 → n = 7



Boechera stricta
(n = 7)

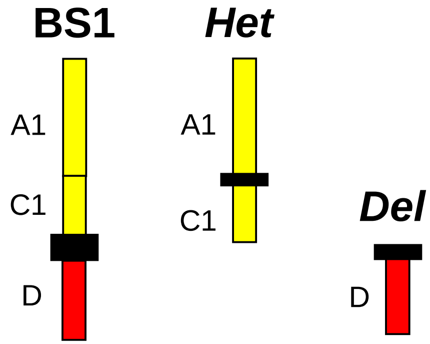
Mandáková et al. (2016) Plant J

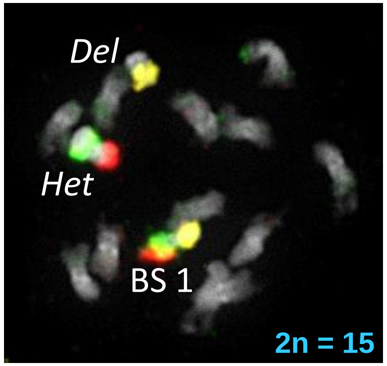
Ascending dysploidy by centric fission fixed due to apomixis



2n = 14
sexual

2n = 15
apomict





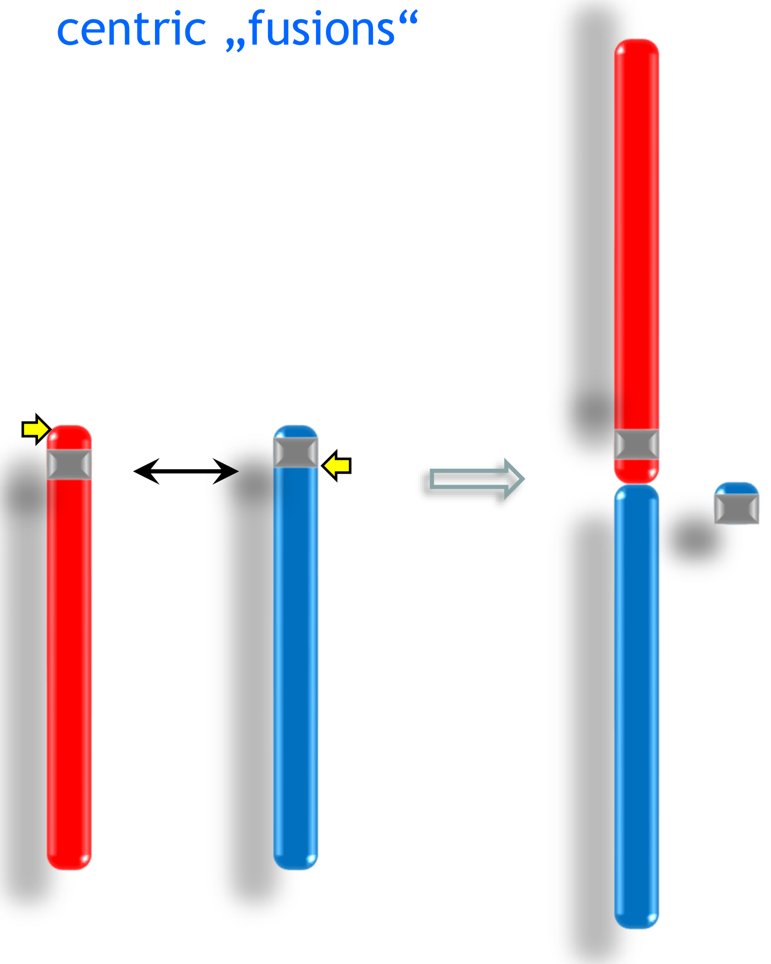
Mandáková et al. (2016) Plant J

Chromosome number variation

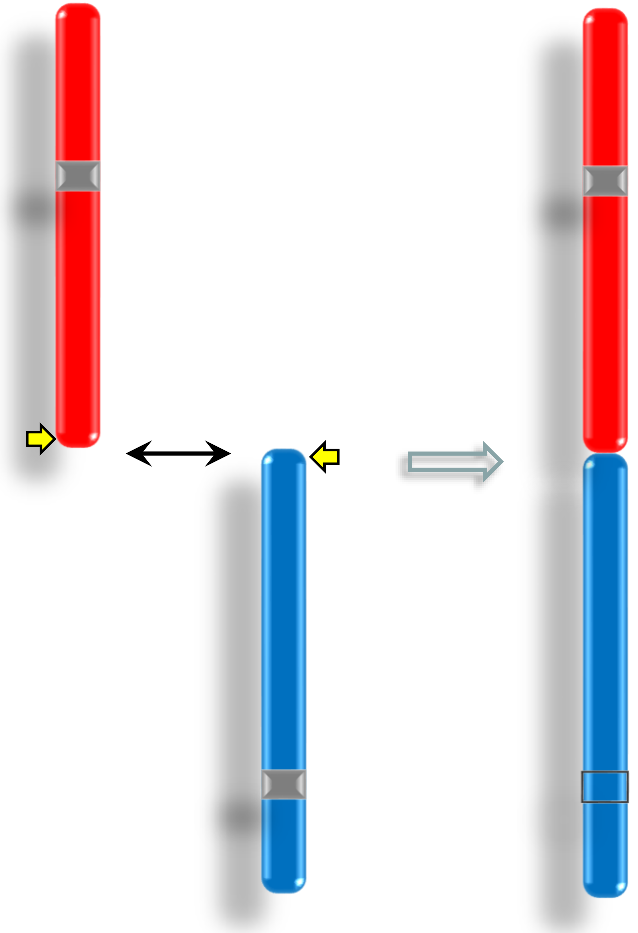
- Stasis
- Decrease (descending dysploidy)
- Increase (polyploidy and ascending dysploidy)

Descending Dysploidy via Terminal Chromosome Translocations

Roberstonian(-like) translocations / centric „fusions“



End-to-end translocations / „fusions“

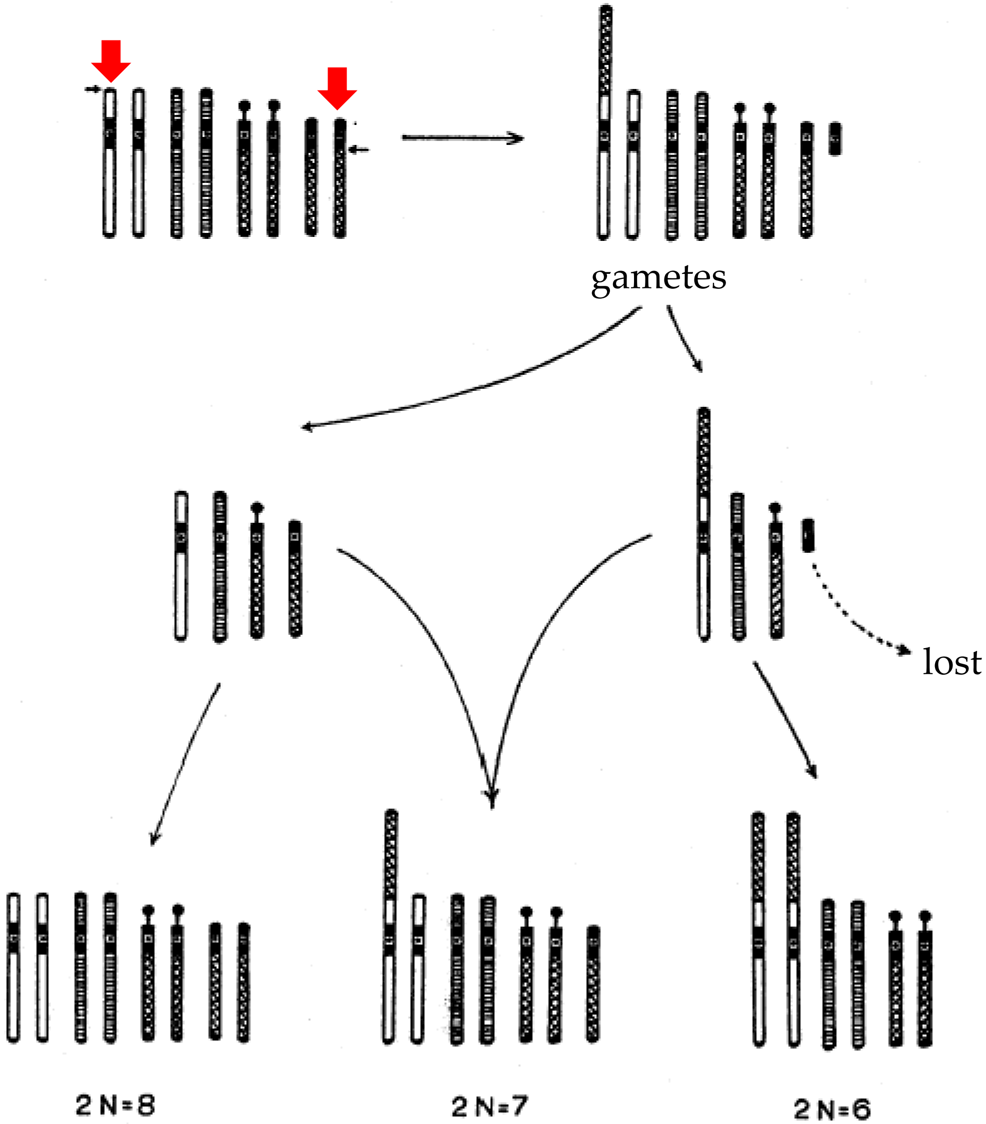


Robertsonian (unequal reciprocal) translocation and meiotic seqregation

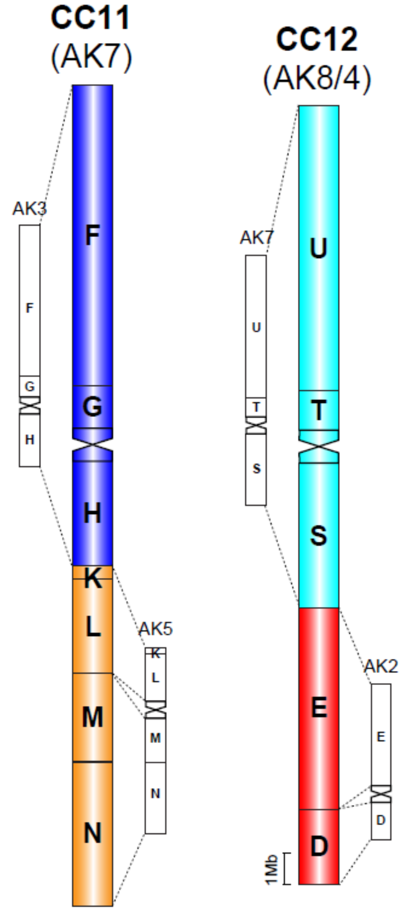
2n = 8

chromosome
number
reduction

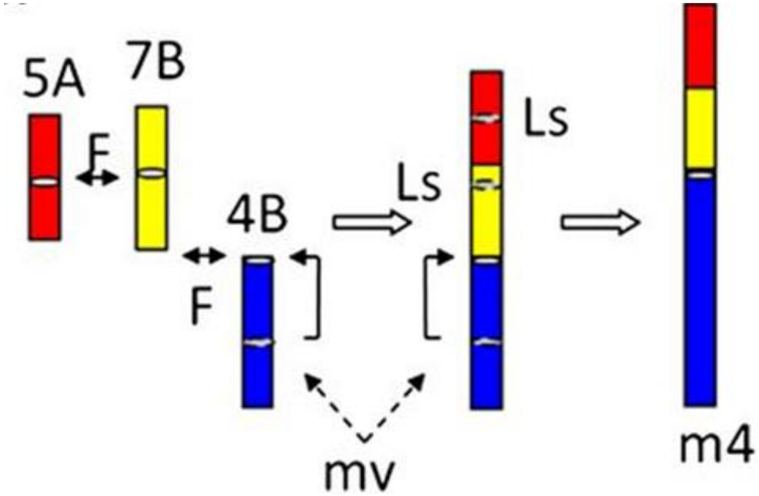
2n = 8 or 7 or 6



End-to-End Translocations in Plants Are Probably More Common Than Previously Thought

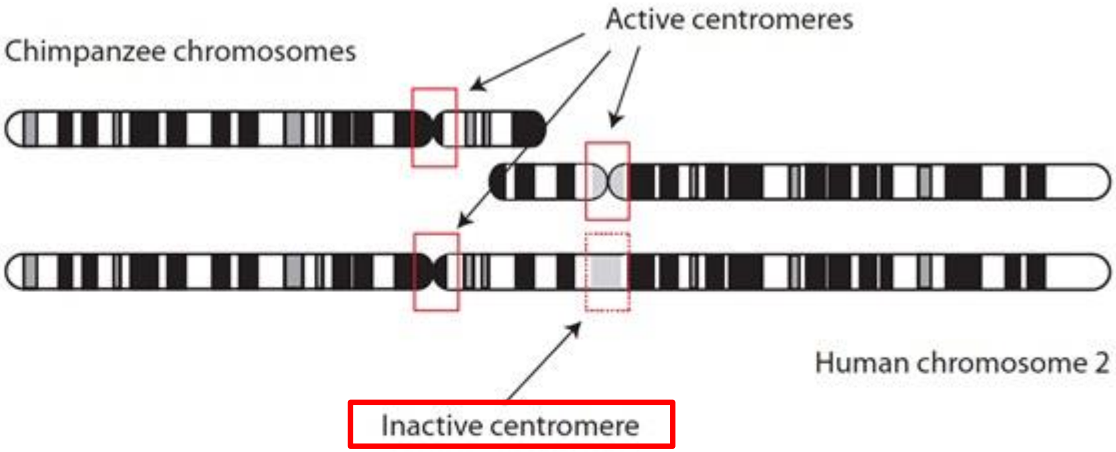


Mandáková et al. (2016) Am J Bot



Wang and Bennetzen (2012) PNAS

Chromosome „fusion“ – the origin of the human (dicentric) chromosome 2

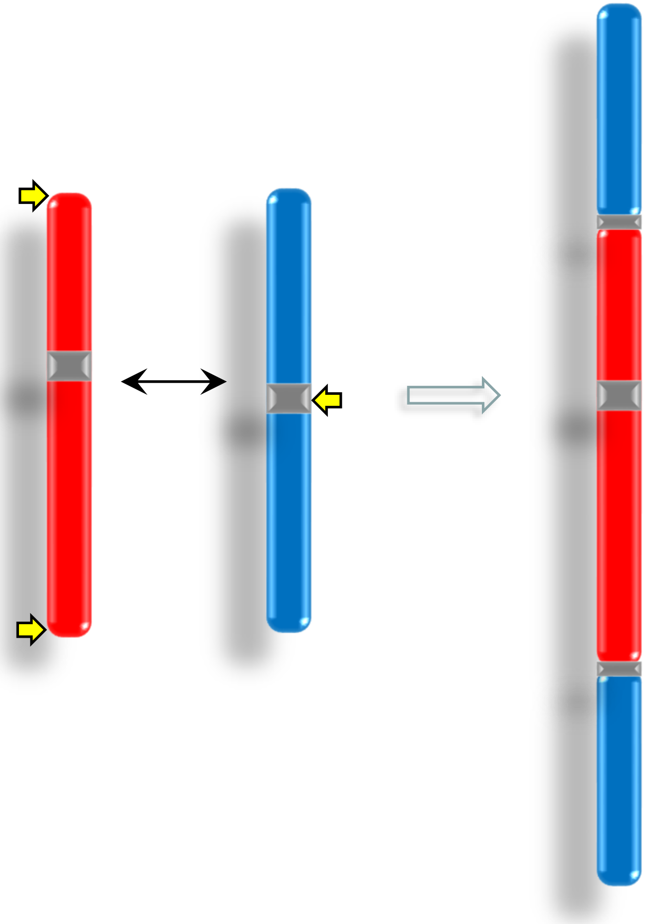


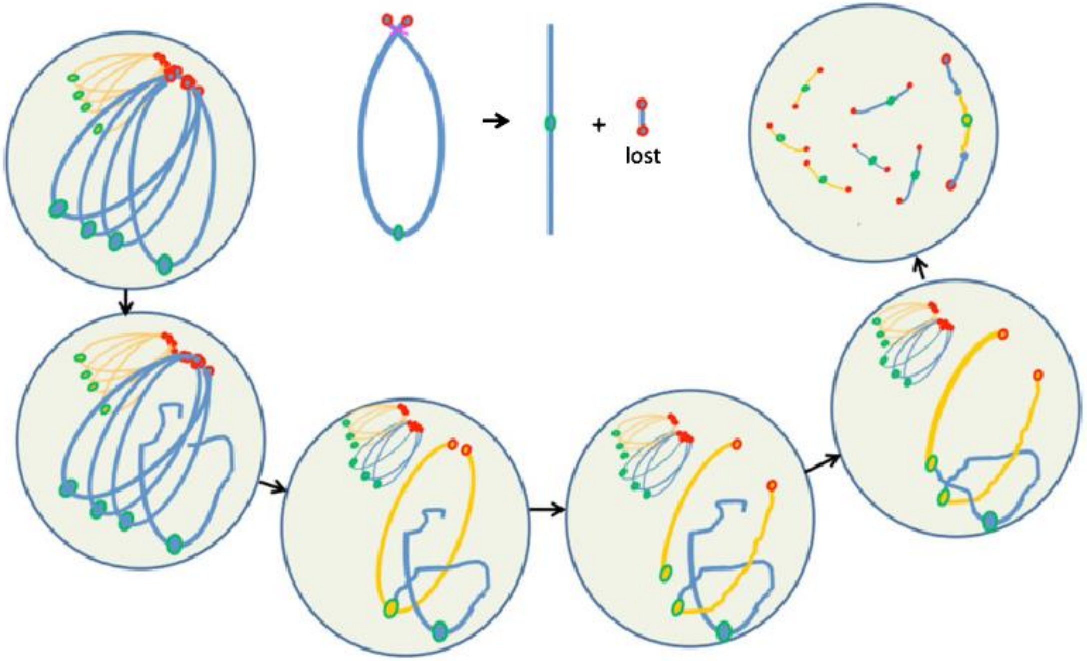
Two optionss how the „fusion‟ chromosome 2 was stabilized

- the ancestral centromere (AC) was either epigenetically inactivated or centromere-determining sequences were excised
- the excision is more probable – what mechanism?
- recombination-based excision, most likely in one step (similar human clinical cases...)

Chiatante et al. (2017), MBE

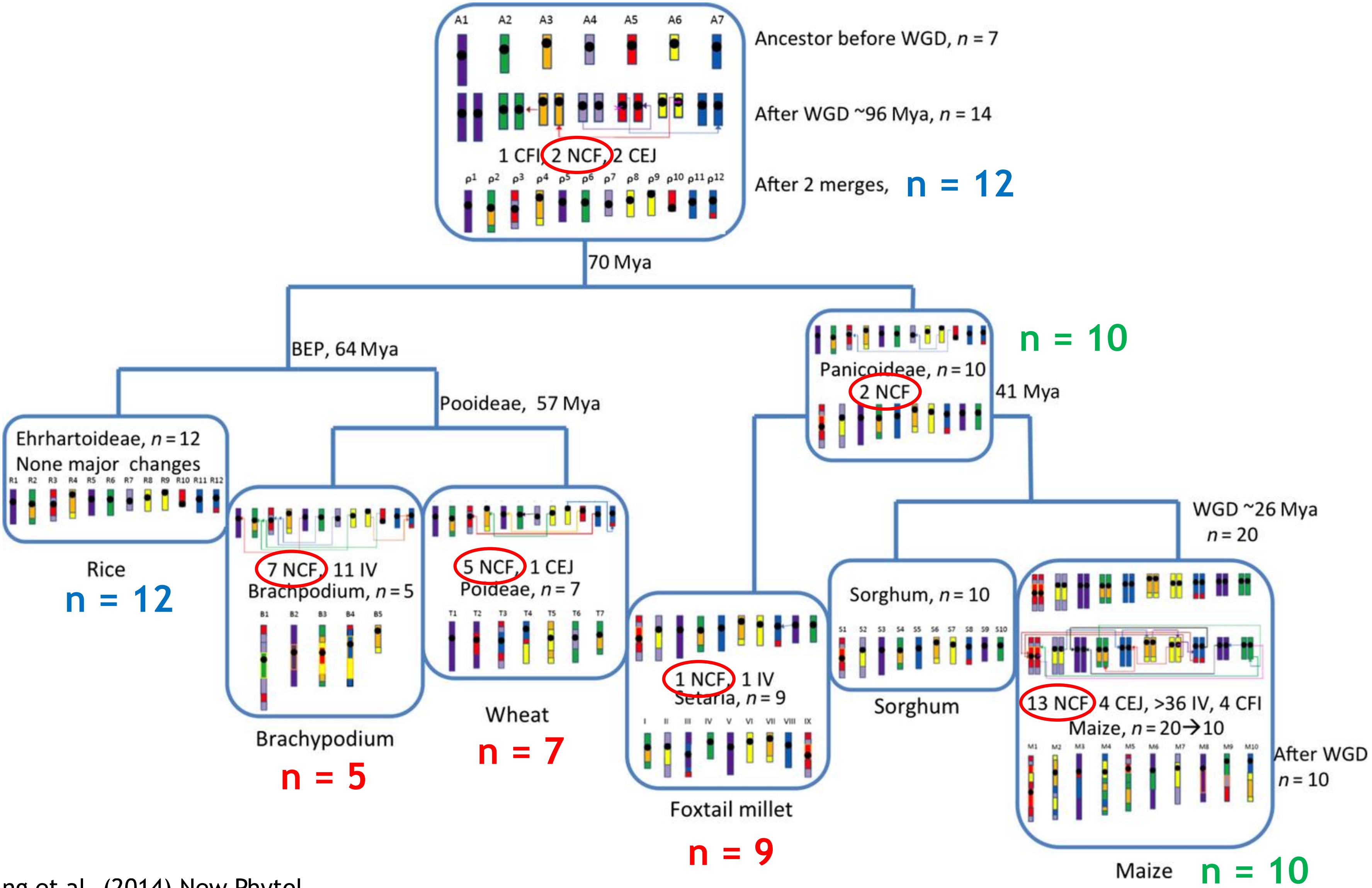
Descending Dysploidy in Grasses is Mediated by Nested Chromosome Insertions (NCIs)





Wang et al. (2014) New Phytol

Nested Chromosome Insertions Repeatedly Mediated Descending Dysploidy in Grasses

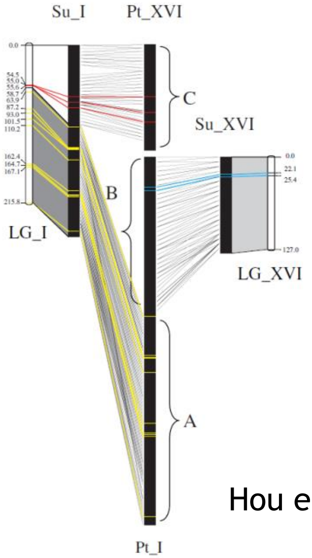


Wang et al. (2014) New Phytol

Did Nested Chromosome Insertions Occur Only in Grasses ?

Populus / Salix

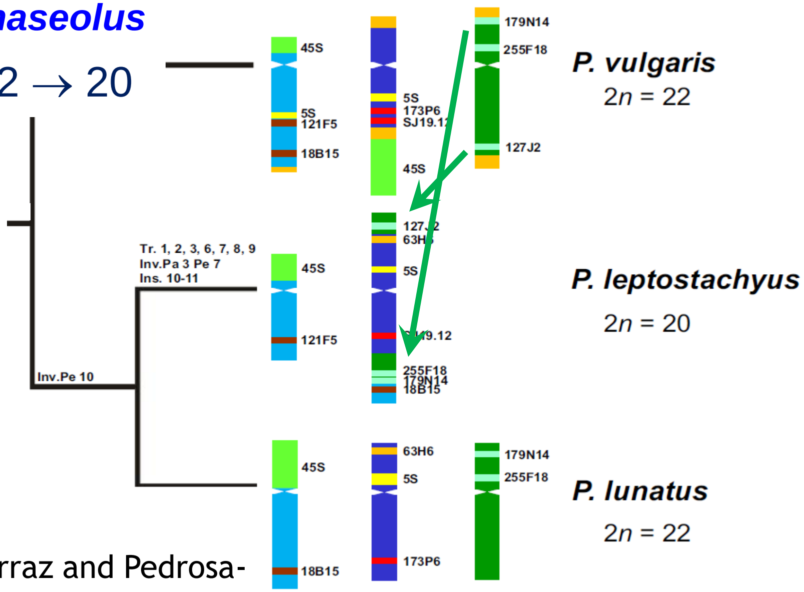
19 – 19



Hou et al. (2016) GBE

Phaseolus

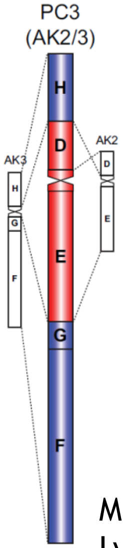
22 → 20



Fonsêca, Ferraz and Pedrosa-Harand (2016) Chromosoma

Pachycladon exilis

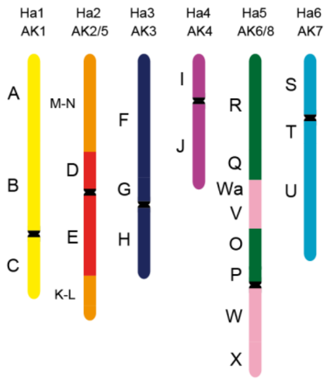
15 (16) → 10



Mandáková, Heenan and Lysak (2010) BMC Evol Biol

Hornungia alpina

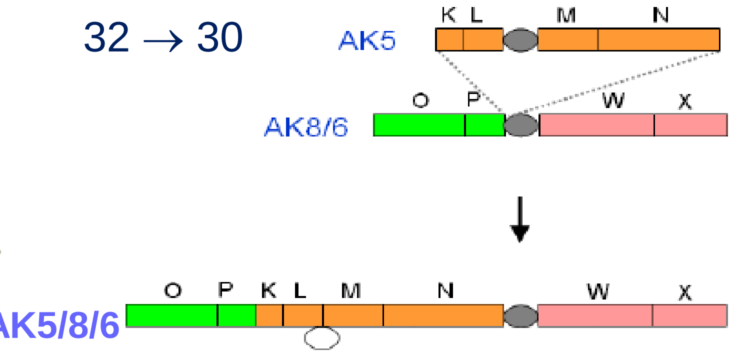
8 → 6



Lysak et al. (2006) PNAS

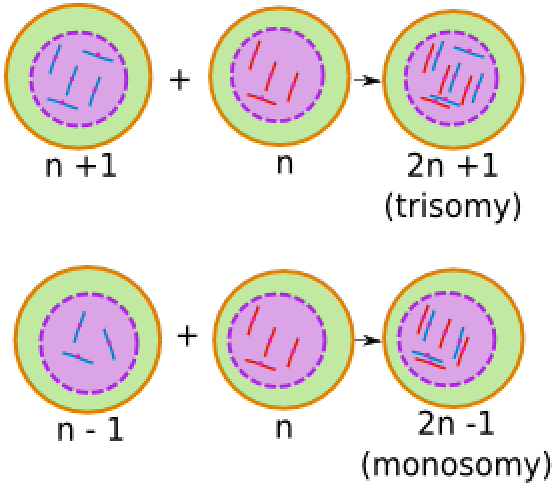
Cardamine pratensis

32 → 30



Mandáková et al. (2013) Plant Cell

Chromosome number change due to aneuploidy



Odd basic chromosome numbers in Rosaceae (x=7, 8 and 7; x=17 in the tribe Pyreae)

the Pyreae have long been considered an example of allopolyploidization between species related to extant Spiraeoideae (x = 9) and Amygdaleoideae (x = 8) taxa

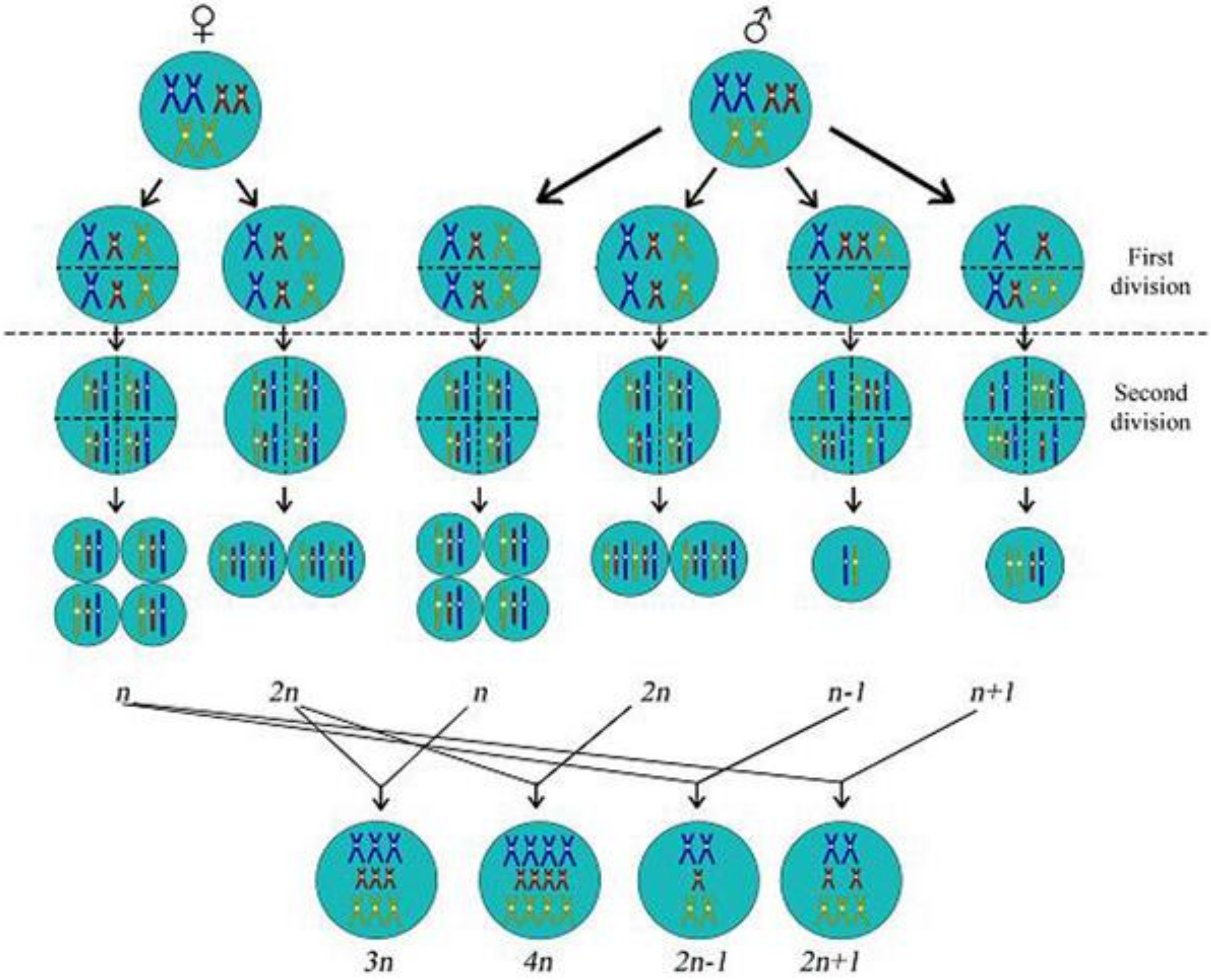
the diploid apple tree - *Malus* (Considine et al.)

- all tetraploid seedlings were derived from 2*n* ova fertilized with 2*n* spermatozoa
- all triploids from 2*n* ova fertilized with *n* spermatozoa
- **all aneuploids from *n* ova fertilized with aneuploid spermatozoa**

Thus ova only contributed euploidy while spermatozoa contributed a range of cytotypes, including aneuploidy, to non-diploid seedlings in the diploid *Malus*.

Considine MJ et al. (2012) Molecular Genetic Features of Polyploidization and Aneuploidization Reveal Unique Patterns for Genome Duplication in Diploid *Malus*. PLoS ONE 7(1): e29449.

Schematic Summary of the Features of Gametic Combinations for Apple Polyploidization in Diploid *Malus*



Odd basic chromosome numbers in the Pyreae (x=17)

Three-step scenario to the odd basic chromosome number in *Malus*:

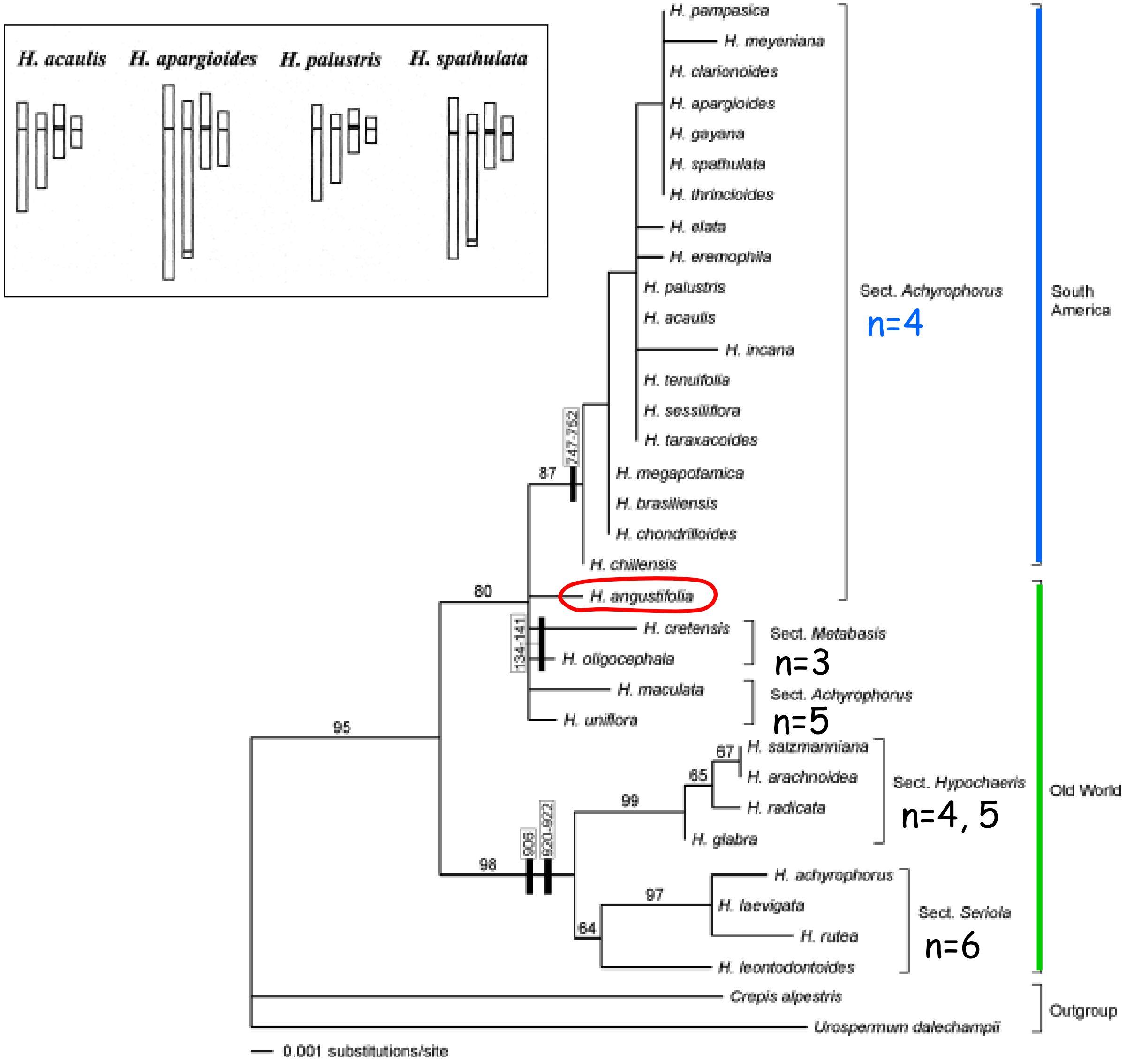
(aneuploidization - eupolyploidization - diploidization)

- aneuploidization of two sister taxa ($x = 9$, $2n = 18$) to $2n = 17$ ($x = 9$)
- whole-genome duplication in both ova and spermatozoa → tetraploids ($x = 9$, $4n = 34$)
- diploidization → the extant diploid state ($x = 17$, $2n = 34$) (diploid-like meiosis)

Aneuploidization can result in speciation with both odd and even basic chromosome numbers, while eupolyploidization can ONLY contribute to even basic chromosome numbers.

Chromosome number evolution in phylogenetic contexts

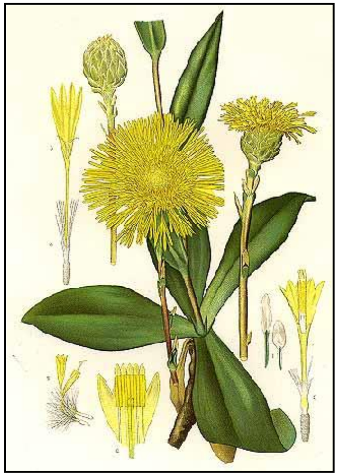
Descending dysploidy in *Hypochaeris* (*Asteraceae*)



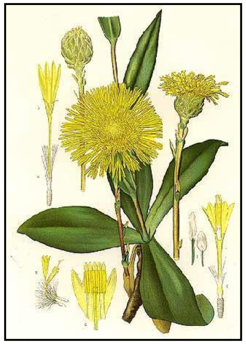
Descending dysploidy in *Podolepis* (*Asteraceae*)

- the extraordinary series of chromosome numbers, n = 12, 11, 10, 9, 8, 7 and 3 (dysploidy)

- chromosome number of n = 10 is the most common in the genus, and thus, x = 10 was regarded as the ancestral chromosome base number for the genus



Descending dysploidy in *Podolepis* (*Asteraceae*)



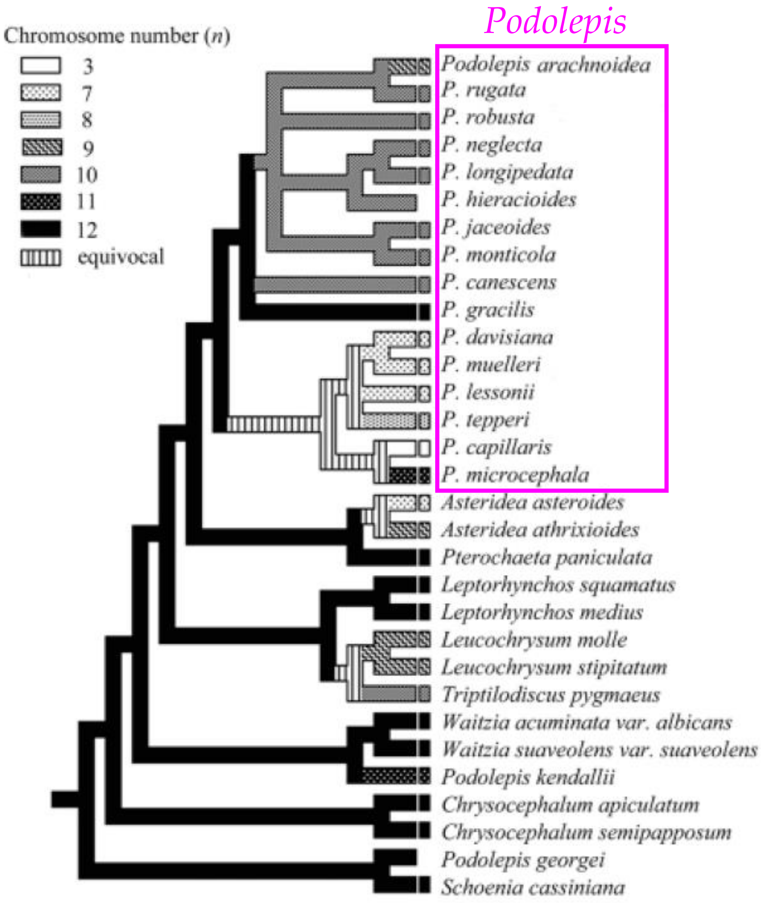
- the haploid chromosome number of *n* = 12 is the most common in the related genera (*Chrysocephalum*, *Waitzia*, *Leptorhynchos*, *Pterochaeta*)

- **according to the phylogenetic analysis, the ancestral chromosome base number in the genus *Podolepis* may be *x* = 12**

- chromosome number reduction has occurred in three lineages:
  - from *n* = 12 to *n* = 10 and 9 in the subclade A
  - from *n* = 12 to *n* = 8 and 7 in the subclade B1
  - from *n* = 12 to *n* = 11 and 3 in the subclade B2

- the low chromosome numbers of *n* = 8, 7 and 3 were found only in annual species which were distributed in semi-arid regions

- comparing the karyotypes between the taxa with *n* = 12 (in *Waitzia* and *Chrysocephalum*) and *n* = 10 (perennial *Podolepis*), **the increase in the number of large chromosomes accompanies the decrease in the number of medium-sized chromosomes** in *Podolepis* → **the reduction in chromosome number has been achieved by the unequal reciprocal translocations, followed by the loss of the short translocation product**



Chromosome number pattern congruent with phylogenetic relationships: *Ranunculaceae*

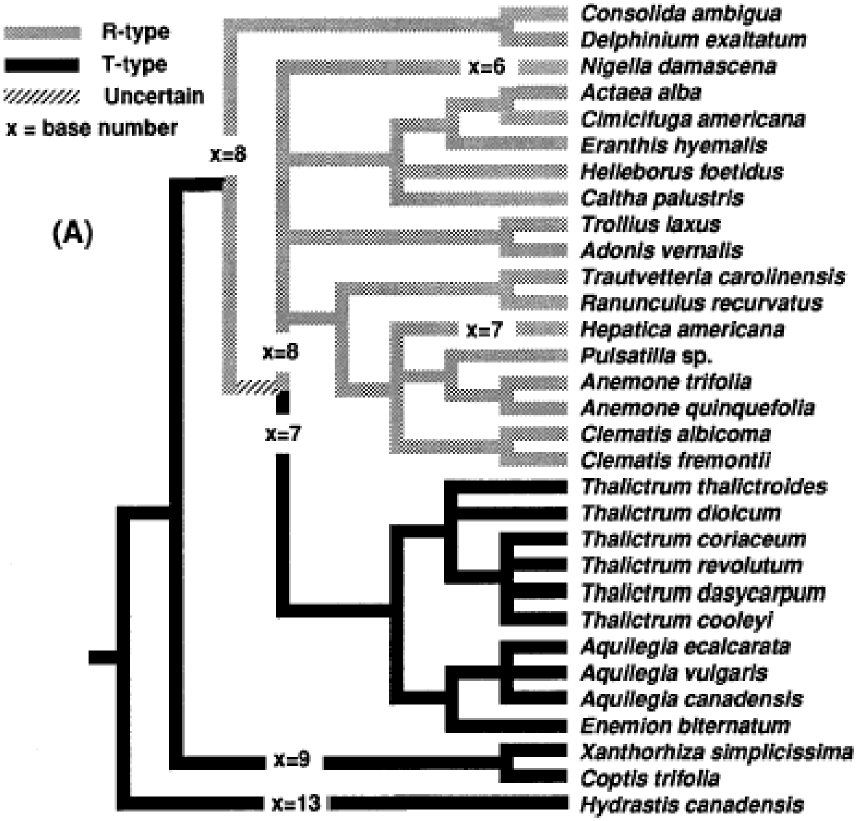
- Langlet (1927, 1932) recognized two subfamilies of *Ranunculaceae* (*Ranunculoideae* and *Thalictroideae*) on the basis of cytological characters, including chromosome size and basic number

- the *Ranunculus* group of genera (R-chromosome group) has large and long chromosomes with a basic number of 8

- the *Thalictrum* group (T-chromosome group) has short and small chromosomes with a basic number of 7 or 9

- Ro et al. (1997): chromosome type and base number are congruent with the inferred molecular (rDNA) phylogeny

- fruit type (often used for the higher classification) was not congruent with karyological data and phylogenetic patterns

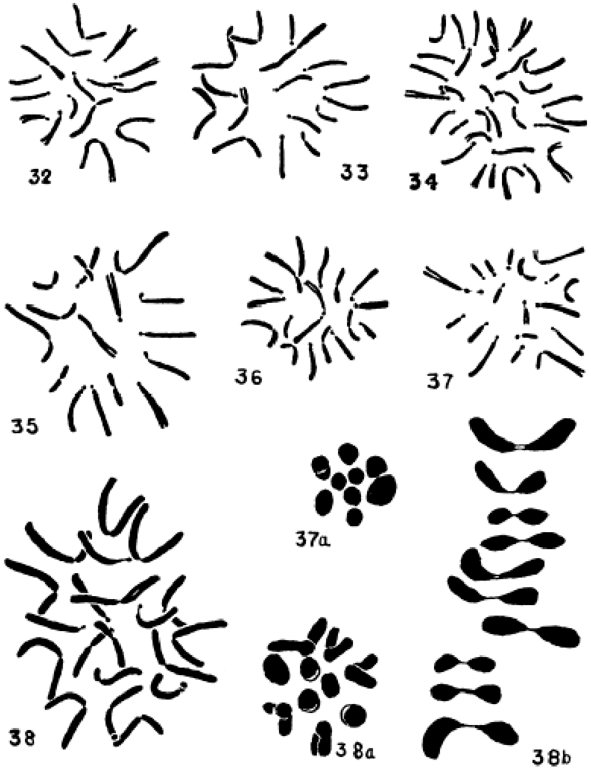


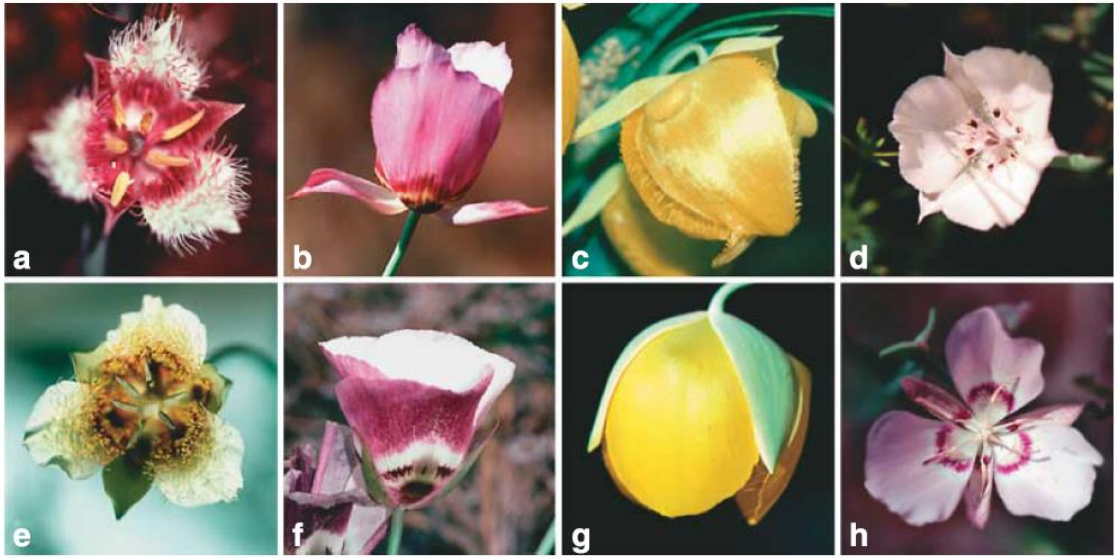
Descending and ascending (?) dysploidy in *Calochortus* (*Liliaceae*)

- c. 67 spp.

- chromosome numbers n = 6, 7, 8, 9, and 10

- molecular phylogenetic study carried out to test the monophyly of the three sections and 12 subsections erected by Ownbey (1940) based on morphology and chromosome number





Descending and ascending (?) dysploidy in *Calochortus* (*Liliaceae*)

- the ancestral chromosome number of *Calochortus* is *x* = 9
- descending aneuploidy (9 → 8, 7, 6)
- ascending aneuploidy (9 → 10) BUT is this true or the phylogeny is wrong?

Patterson and Givnish (2003)