

B chromosomes



B chromosomes



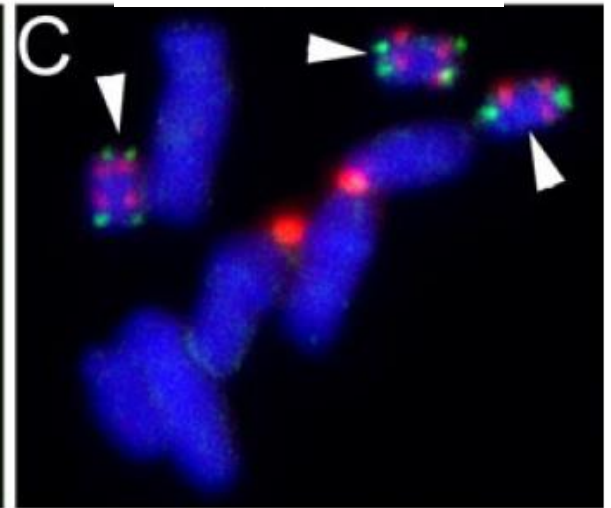
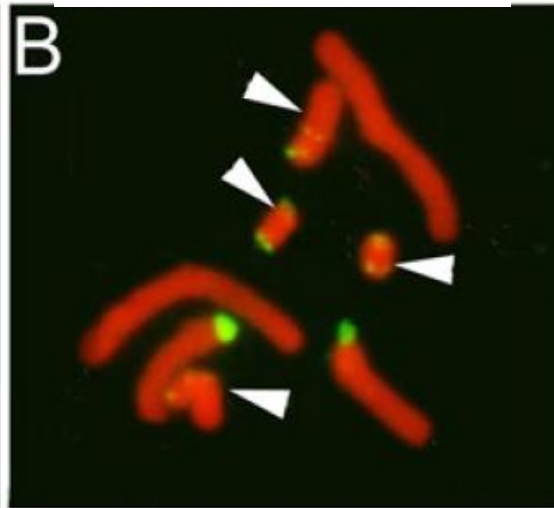
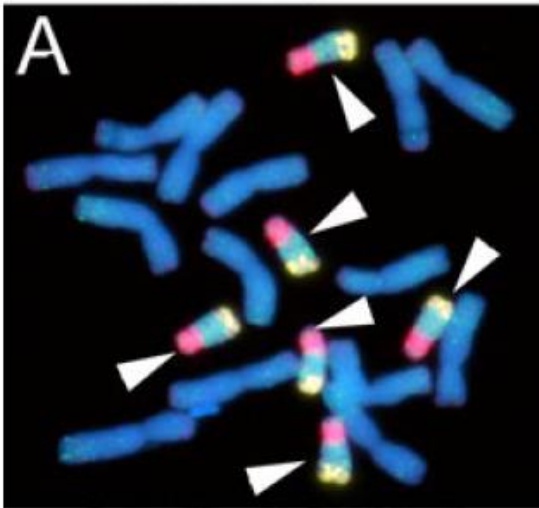
rye (*Secale cereale*)



*Brachycome
dichromosomatica*

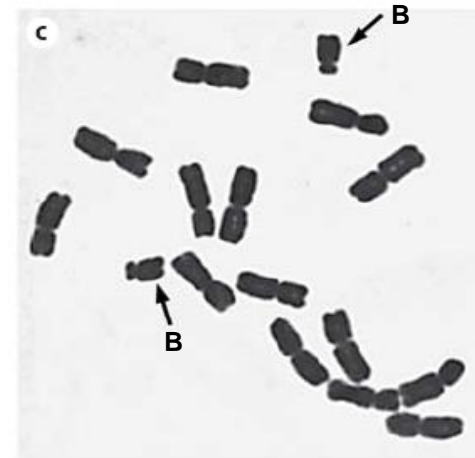


Crepis capillaris



B chromosomes

- (1) dispensable
- (2) usually smaller than A chromosomes
- (3) do not pair/recombine with A chromosomes at meiosis
- (4) their inheritance is irregular, non-Mendelian (univalents)
- (5) meiotic elimination in some species is counter-balanced by processes of drive at mitosis, and less frequently at meiosis (equilibrium frequencies in populations)
- (6) neutral effects; negative and quantitative effects on the phenotype when present in high numbers (reduced fertility)
- (7) they lack any known major gene loci, but rDNA sequences are known in a few species
- (8) they contribute greatly to intraspecific genome size variation
- (9) they have no obvious adaptive properties
- (10) their mode of origin remains a mystery



14 A and 2 B chromosomes in rye

B chromosomes

The occurrence of Bs across angiosperms seems to be not random: their presence is correlated with genome size - higher frequency in families with large genomes

How frequent?

Bs in about 9% of angiosperm species

monocots: 8% (Poaceae, Liliales and Commelinales)

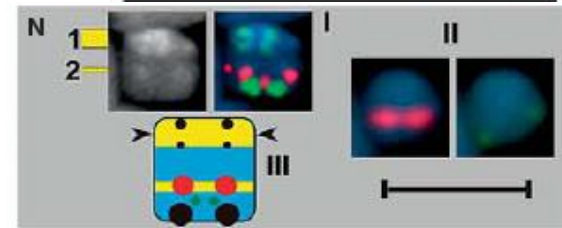
eudicots: 3% (Asteraceae)

How many?

- usually in low numbers (0-5)
- exceptions: *Silene maritima* (0-15), *Brachycome lineariloba* (0-22) or *Allium schoenoprasum*
- more Bs than As in maize ($2n = 20 \text{ As} + 0-34 \text{ Bs}$)
- number can vary between tissues: grasses *Aegilops speltoides* and *Ae. mutica* - Bs exist in aerial organs but not in roots



H Golczyk (2012) CGR

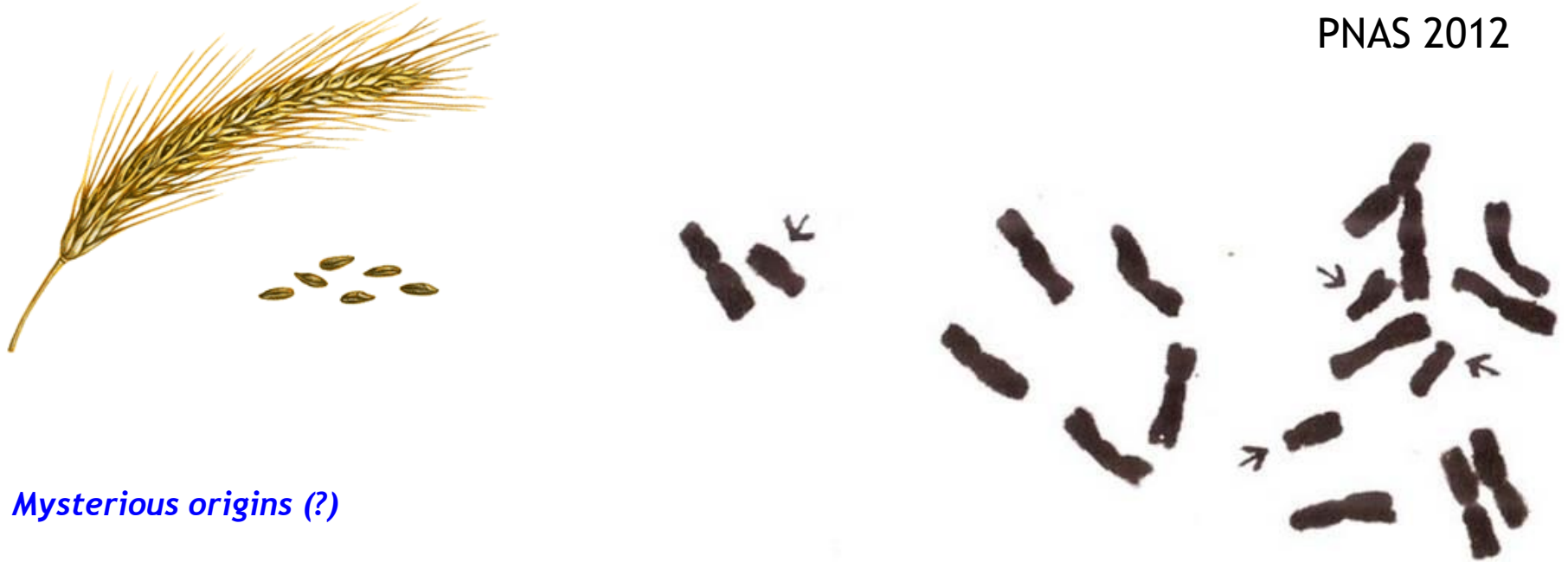


Tradescantia virginiana
($2n=24$)

Selfish supernumerary chromosome reveals its origin as a mosaic of host genome and organellar sequences

Mihaela Maria Martis^a, Sonja Klemme^b, Ali Mohammad Banaei-Moghaddam^b, Frank R. Blattner^b, Jiří Macas^c, Thomas Schmutzer^b, Uwe Scholz^b, Heidrun Gundlach^a, Thomas Wicker^d, Hana Šimková^e, Petr Novák^c, Pavel Neumann^c, Marie Kubaláková^e, Eva Bauer^f, Grit Haseneyer^f, Jörg Fuchs^b, Jaroslav Doležel^e, Nils Stein^b, Klaus F. X. Mayer^a, and Andreas Houben^{b,1}

PNAS 2012



Mysterious origins (?)

- Seem to arise in different ways in different species
- Generally thought to originate from A chromosomes
- Proposed origins (examples): from centric fragments after an unequal reciprocal translocation or by excision from A chromosomes

Multichromosomal Origin of Rye B Chromosomes and Sequences Located on B Chromosomes

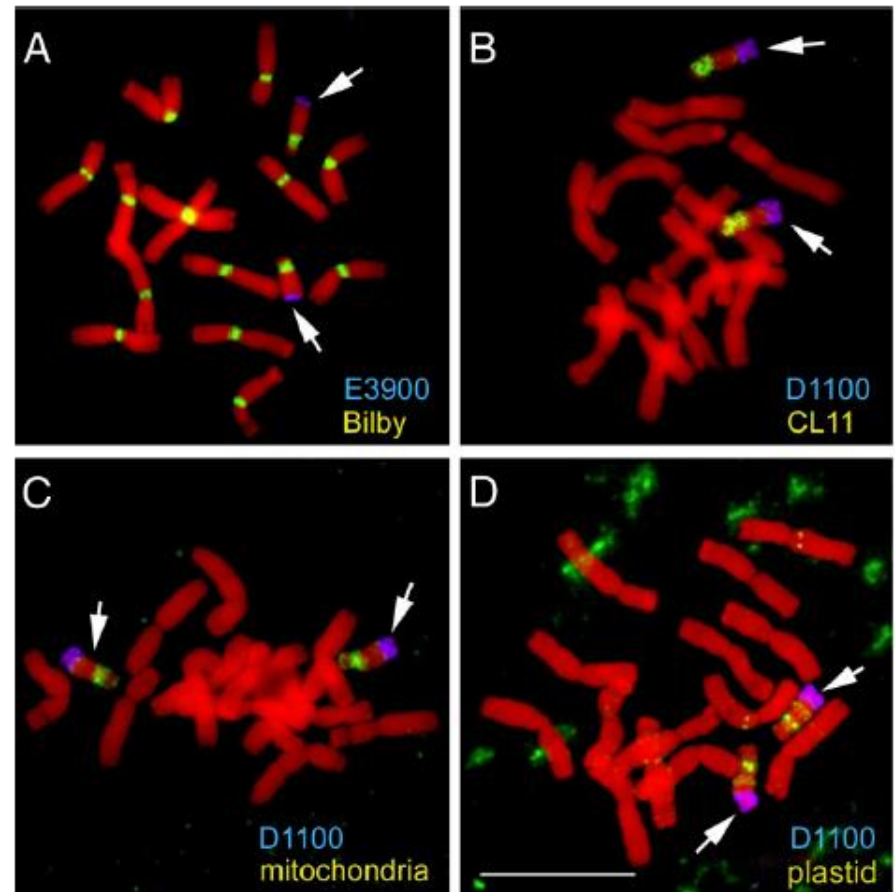
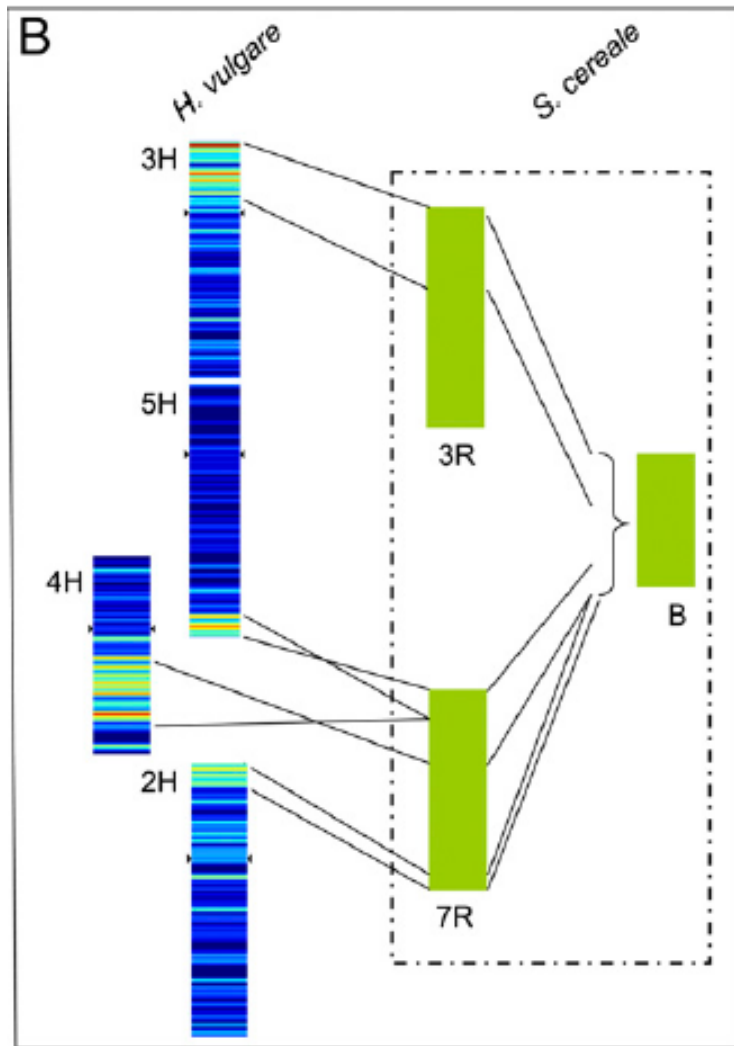
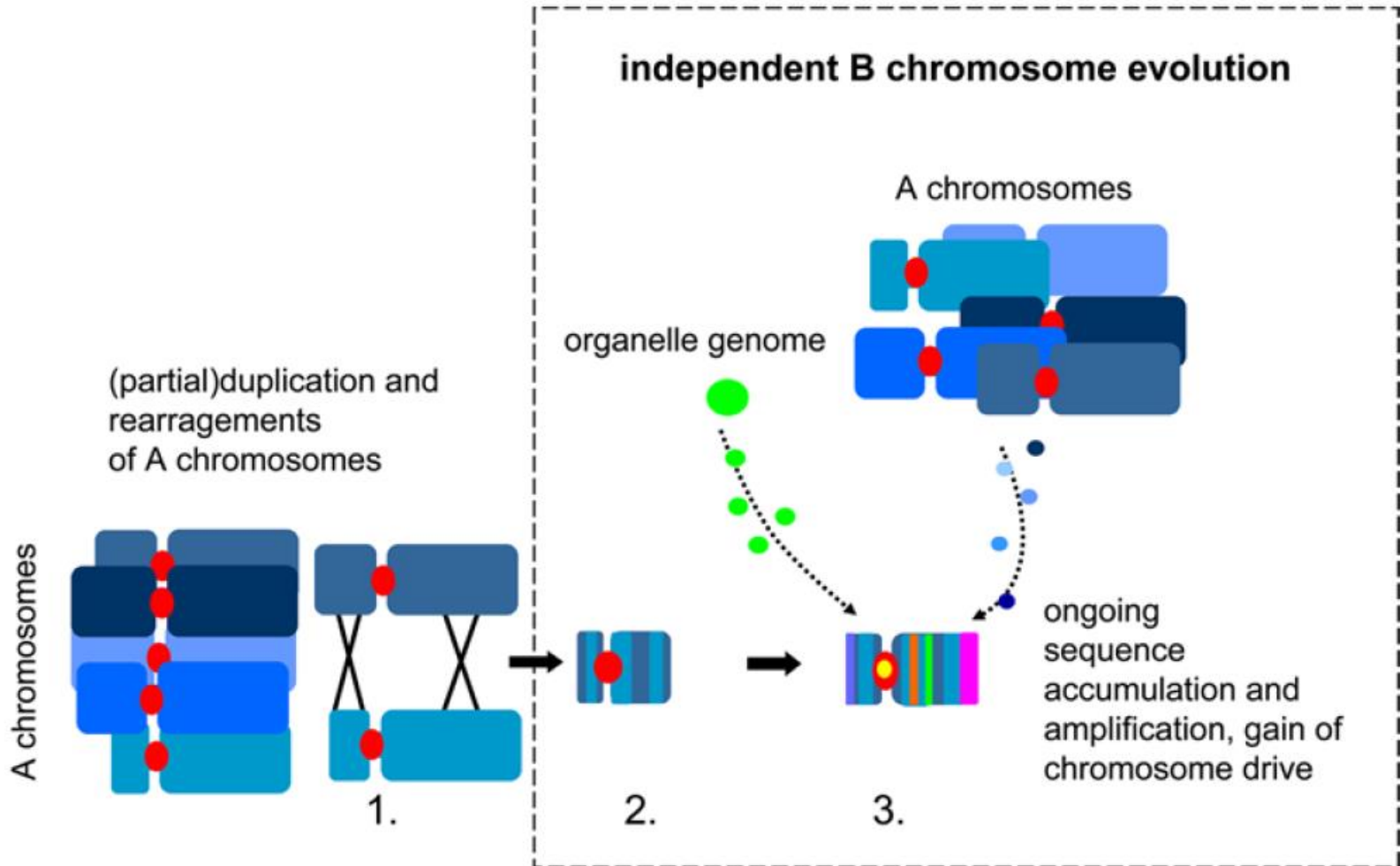


Fig. 2. FISH of rye mitotic metaphase chromosomes with the centromeric retrotransposons *Bilby* (A), the B-specific pericentromeric Ty1/copia repeat CL11 (B), mitochondrial DNA (C), and plastid DNA (D). B chromosome-specific satellite repeats E3900 and D1100 were used for identifications of the Bs. The Bs are indicated by arrows. (Scale bar: 10 μ m.)

B chromosomes as a „genomic sponge“

Model of Origin and Evolution of Rye B Chromosomes



How a supernumerary B chromosome survives over time?

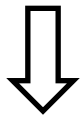
- ❖ transmission higher than Mendelian → kept in populations
- ❖ drive (pre-meiotic, meiotic, post-meiotic) = preferential maintenance of Bs
- ❖ post-meiotic drive common in plants during gametophyte maturation (examples: rye, maize)

Rye

Pollen grain mitosis I: 2 chromatids of the B chromosome do not separate at anaphase and are included in the generative nucleus

Pollen grain mitosis II: both spermatids have an unreduced number of Bs

(- a similar nondisjunction process may occur in the female gametophytes)

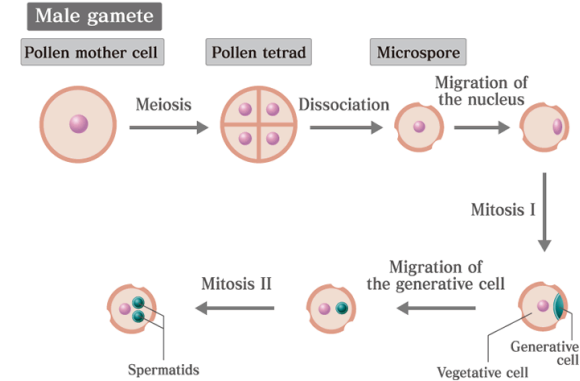


Pollen grain mitosis I:

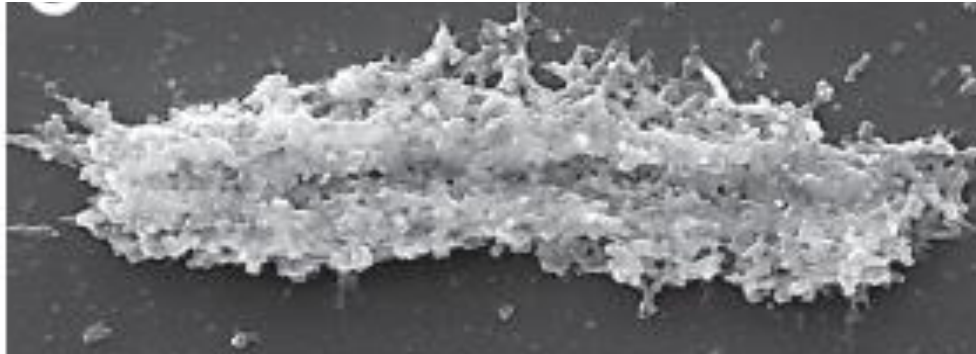
Asymmetry of the mitotic spindle (→ vegetative and generative nucleus)

Nondisjunction control factor on B chromosome (sequence unknown) → ? noncoding RNA influencing the differential sister-chromatid cohesion of As and Bs (= B chromosome chromatids not separated)

? B-specific centromeric repeats acting as a neocentromere (centromeric drive → nondisjunction)



Holocentric chromosomes



Angiosperm species with holokinetic chromosomes

Juncaceae

Cyperaceae

Myristica fragrans (Myristicaceae)

Drosera (Droseraceae)

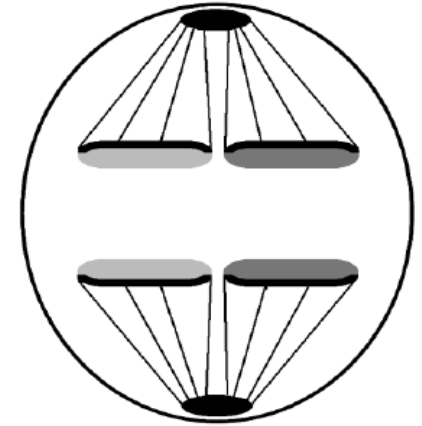


Chionographis (Melanthiaceae)



Holocentric chromosomes

difuse kinetochor →



chromosome segregation
in anaphase

- holocentric vs. monocentric chromosomes
- holocentrics: huge variation in chromosome numbers [the largest number of chromosomes in animals ($2n = 446$) is found in the blue butterfly *Polyommatus atlantica* with holokinetic chromosomes]
- in c. 5,500 angiosperm species
- chromosome numbers from $n=2$ up to $n=110$
- chromosome fission (agmatoploidy) and fusion (symploidy)
→ extensive chromosome number variation

Variation in chromosome number in some holocentric plant genera

(Bureš et al. 2013)

Family / Genus	Range	Haploid chromosome number (n)
Droseraceae		
<i>Drosera</i> ^{a, b, c}	13.3-fold	3–7, 9–17, 20, 23, 30, 32, 36, 40
Melanthiaceae		
<i>Chionographis</i> ^d	1.8-fold	12, 21, 22
Juncaceae		
<i>Luzula</i> ^{a, b, e}	14.0-fold	3, 6–16, 18, 21, 23, 24, 26, 31, 33, 35, 36, 42
<i>Juncus</i> ^{a, b}	10.6-fold	9, 10, 13, 15–24, 30, 32, 34, 35, 40, 42, 45, 50, 53, 54, 60, 66, 67, 85
Cyperaceae		
<i>Carex</i> ^{f, g}	11.6-fold	5–47, 50, 52–58
<i>Eleocharis</i> ^{f, h}	36.0-fold	3–16, 18–30, 36–44, 47–50, 68, 86–92, 100, 108
<i>Cyperus</i> ^f	22.4-fold	5, 8, 9, 12, 13, 15–32, 34–45, 47–50, 52–60, 62–64, 66–69, 76, 80, 93, 98, 104, 110, 112
<i>Rhynchospora</i> ^{f, i}	12.5-fold	2, 4–13, 15, 18–22, 24, 25

^a Bolkovskikh et al. (1969)

^b Golldblatt et al. (2010)

^c Rivadavia et al. (2003)

^d Tanaka and Tanaka (1979)

^e Nordenskiöld (1951); Kirschner (1992)

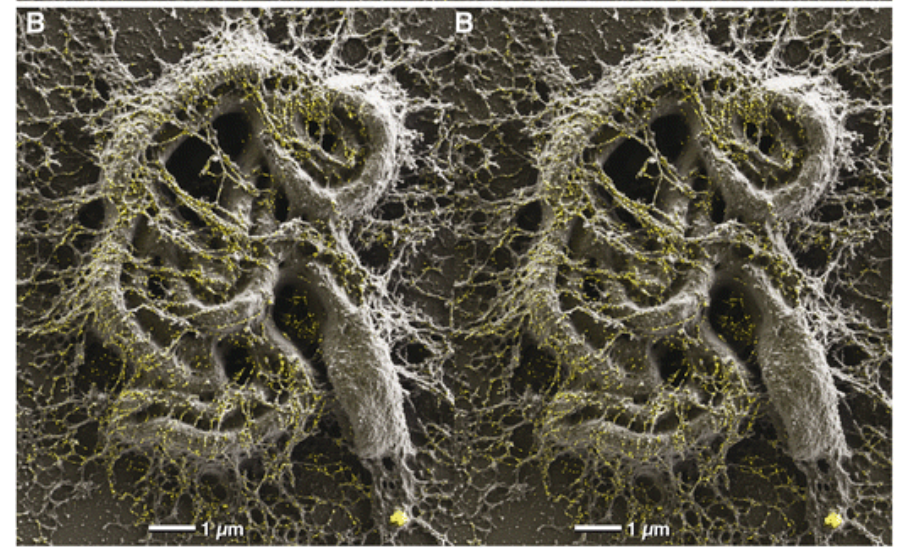
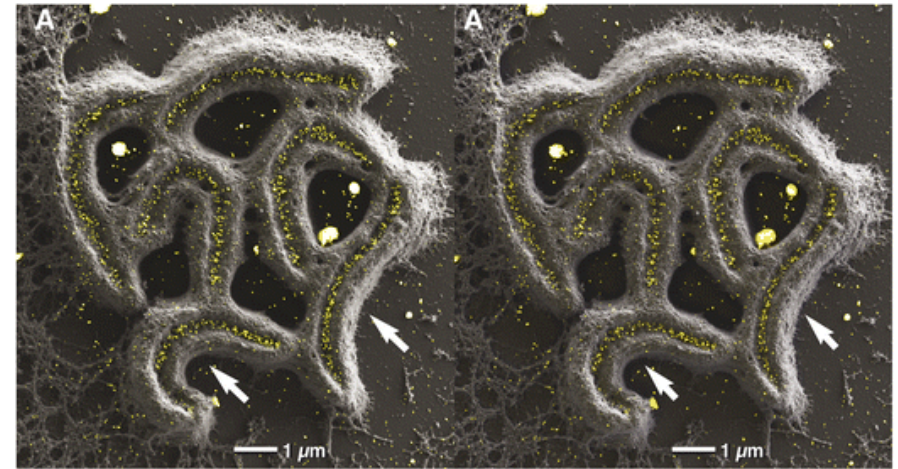
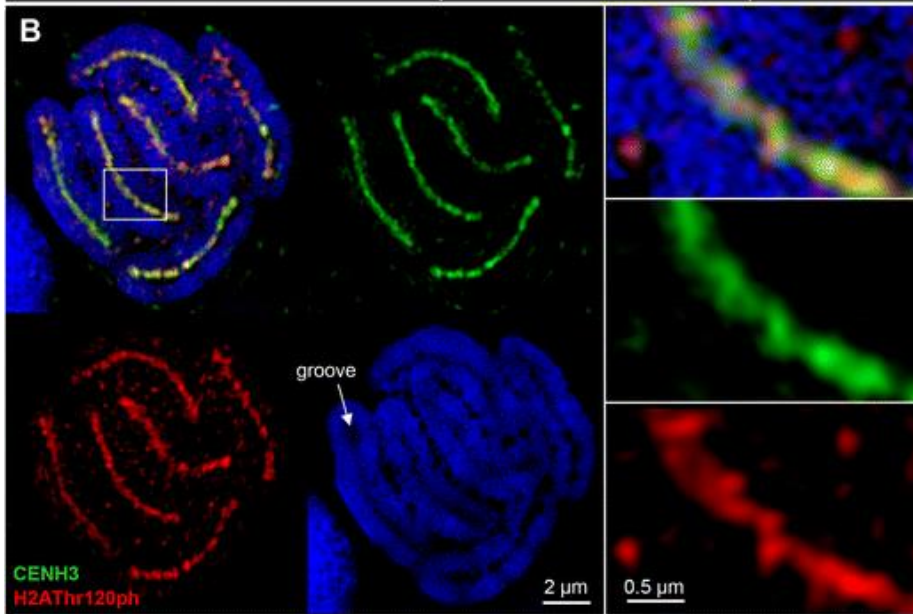
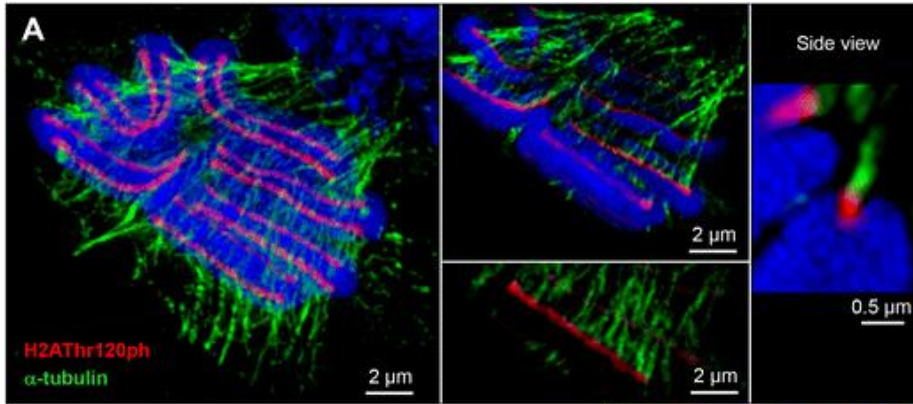
^f Roalson (2008)

^g Rotreklová et al. (2011)

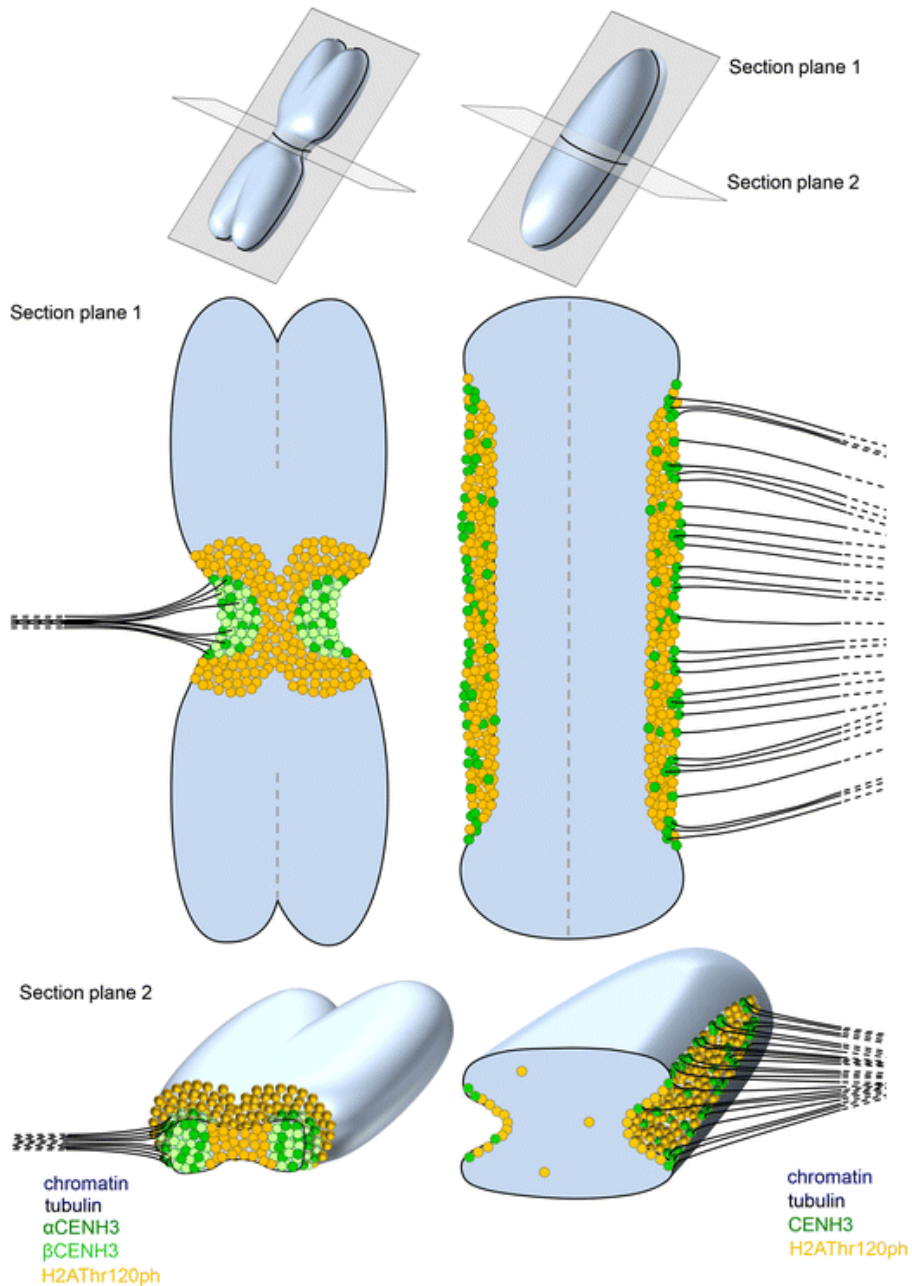
^h Strandhede (1965b, 1966); Bureš (1998)

ⁱ Luceño et al. (1998); Vanzela et al. (2000, 2003)

Holocentric chromosomes, centromeres and microtubules



Model of the centromere organization of mono- and holocentric plant chromosomes



Microtubules (tubulin) attach at CENH3, but not at H2AThr120ph. The microtubule bundle formation is less pronounced at holocentromeres.

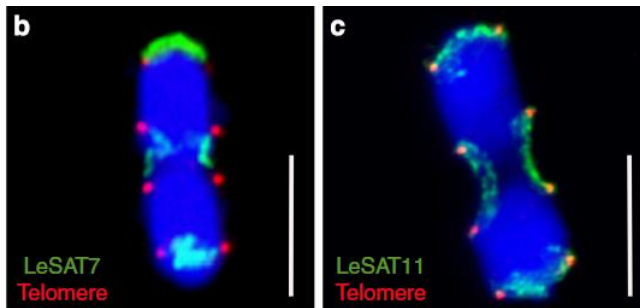
active centromeres have H2AThr120ph - phosphorylation of threonine 120 of histone H2A

Alternative meiotic chromatid segregation in the holocentric plant *Luzula elegans*

Stefan Heckmann^{1,*†}, Maja Jankowska^{1,*}, Veit Schubert¹, Katrin Kumke¹, Wei Ma¹ & Andreas Houben¹



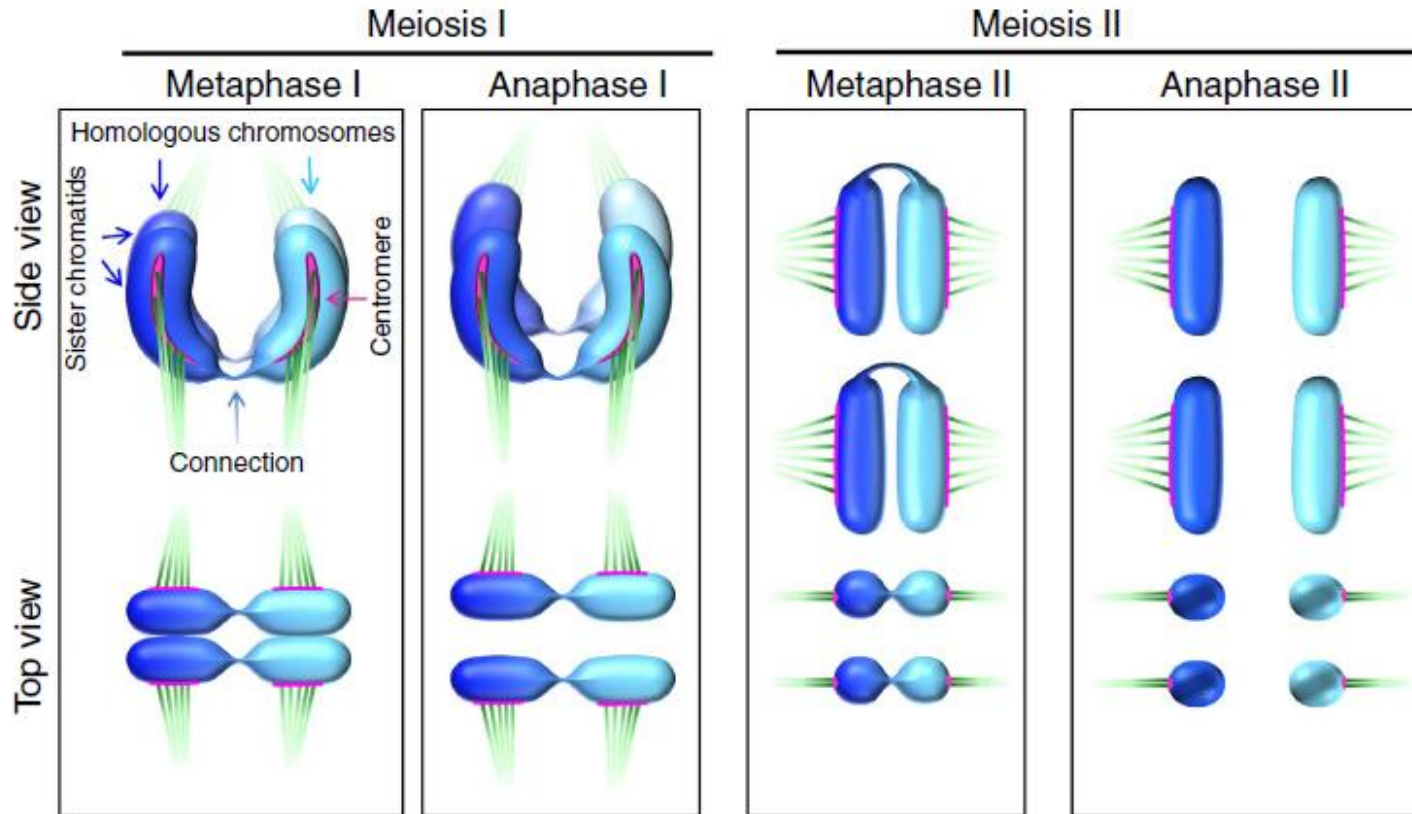
- chromosomes are structurally and functionally holocentric throughout meiosis
- an inverted sequence of sister chromatid segregation occurs during meiosis
- terminal satellite DNA repeat-enriched chromatin threads assist the pairwise movement and the linkage of homologous non-sister chromatids up to metaphase II to enable the faithful formation of haploid gametes





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Chromosomes align at metaphase I in such a manner that **sister chromatids** rather than homologous chromosomes are **separated during meiosis I**. Homologous non-sister chromatids are terminally linked by **satellite DNA-enriched chromatin threads** until metaphase II to ensure faithful transmission of holocentric chromatids.

Holocentric chromosomes in *Eleocharis*

Chromosome reduction in *Eleocharis maculosa* (Cyperaceae)

C.R.M. da Silva^{a,b} M.S. González-Elizondo^c A.L.L. Vanzela^a

CGR 122 (2008)

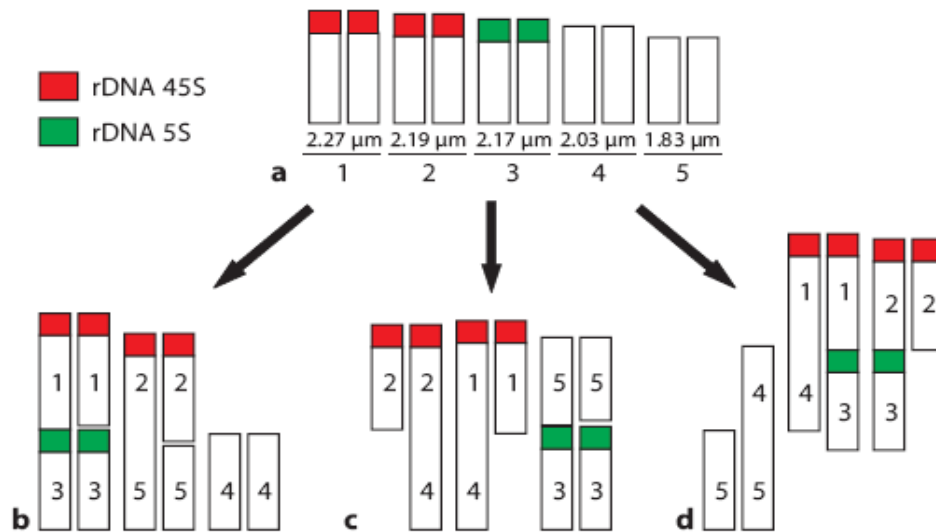
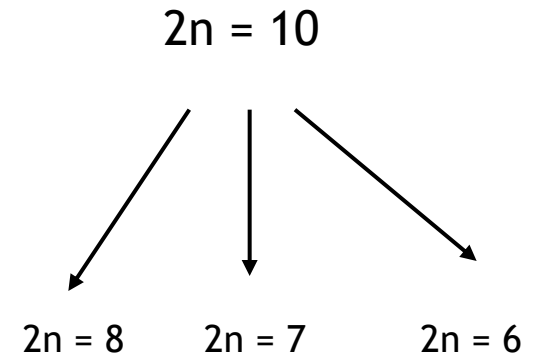


Fig. 3. Idiograms showing the symploidy pathways to formation of chromosome races in *Eleocharis maculosa*. The chromosome arrangement in the idiogram follows possible meiotic pairing. (a) Chromosome races with $2n = 10$. The μm values correspond to the average of the size of each pair. (b-d) Chromosome race with $2n = 8$, 7 and 6, respectively.



Holocentric chromosomes

- holocentric vs. monocentric chromosomes
- in c. 5,500 angiosperm species
- chromosome numbers from $n=2$ up to $n=110$
- chromosome fission (agmatoploidy) and fusion (symploidy)
→ extensive chromosome number variation

- **enigma of *Luzula* karyotypes**

- „euploid“ chromosome numbers based on $x=6$
- large (L), medium (M) and small (S) chromosomes; relation is $1L = 2M = 4S$
- large chromosomes: 4 ploidy levels (2x with 12L, 4x with 24L, 6x with 36L, 8x with 48L)
medium chromosomes: 24M
small chromosomes: 48S (*L. sudetica*)
- concerted fission/agmatoploidy
- mechanism unknown

