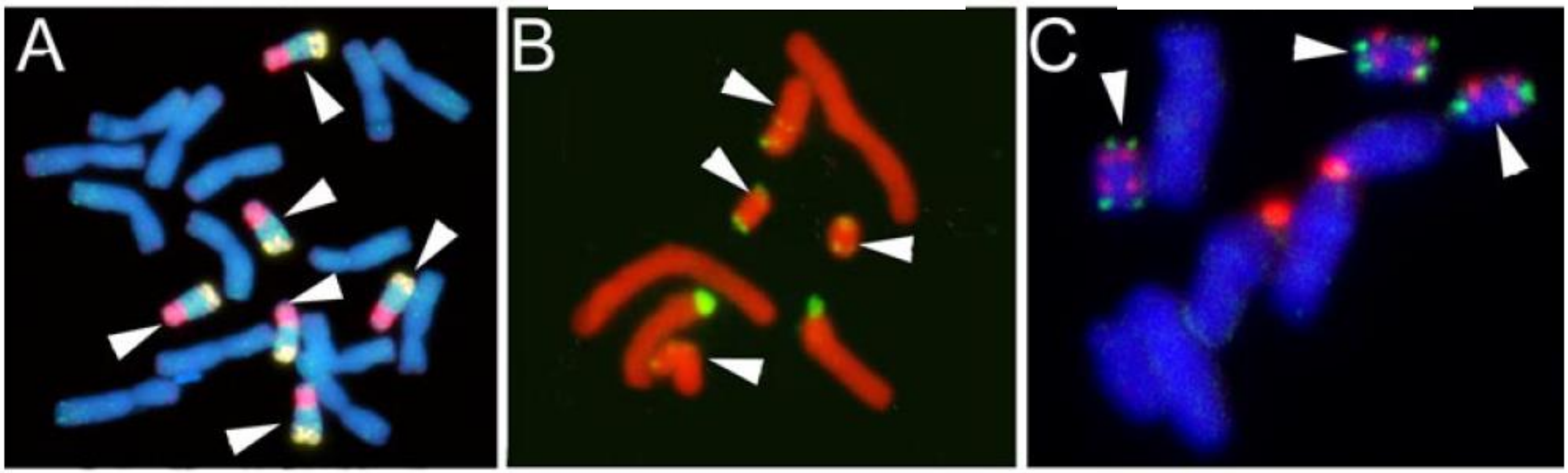
B chromosomes

B chromosomes

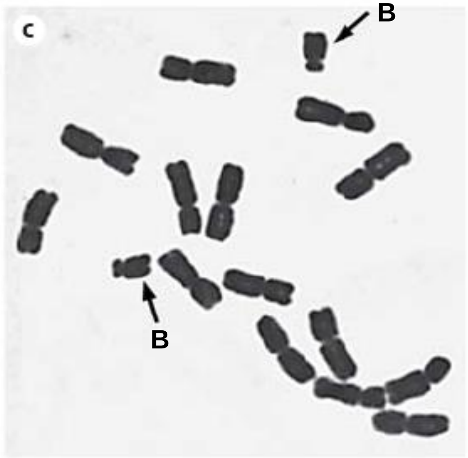
rye (*Secale cereale*)

Brachycome dichromosomatica

Crepis capillaris



B chromosomes



14 A and 2 B chromosomes in rye

(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, mainly in the gametophytes, 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

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

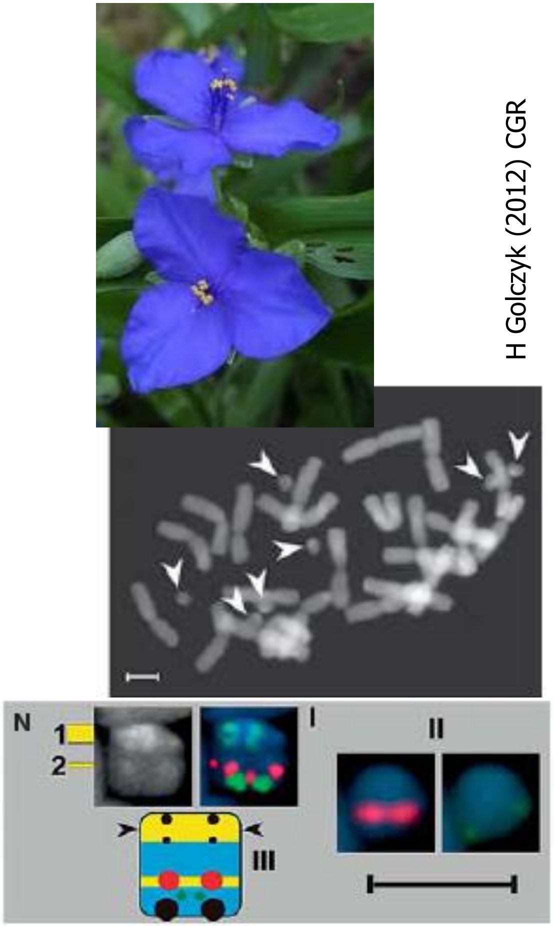
How frequent?

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 As + 0-34 Bs)
- number can vary between tissues: grasses *Aegilops speltoides*

and *Ae. mutica* - Bs exist in aerial organs but not in roots



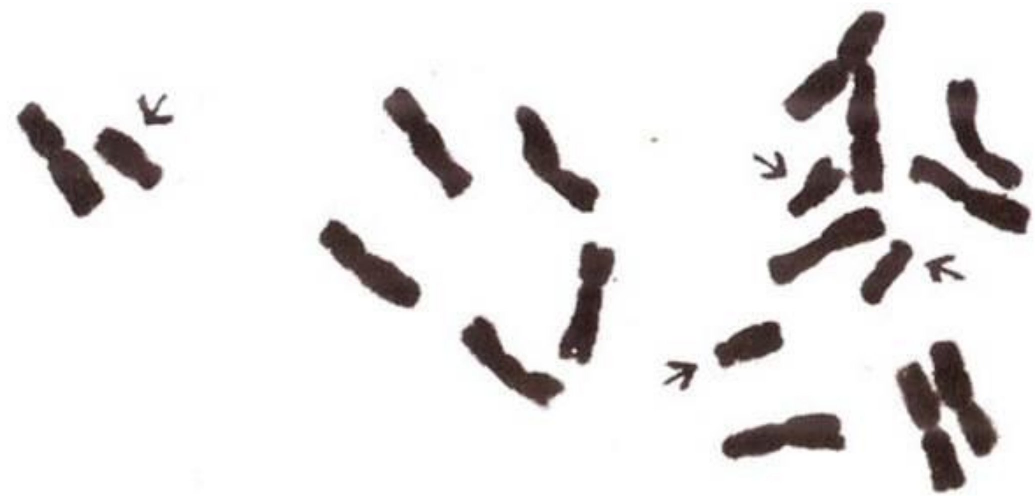
H Golczyk (2012) CGR

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]

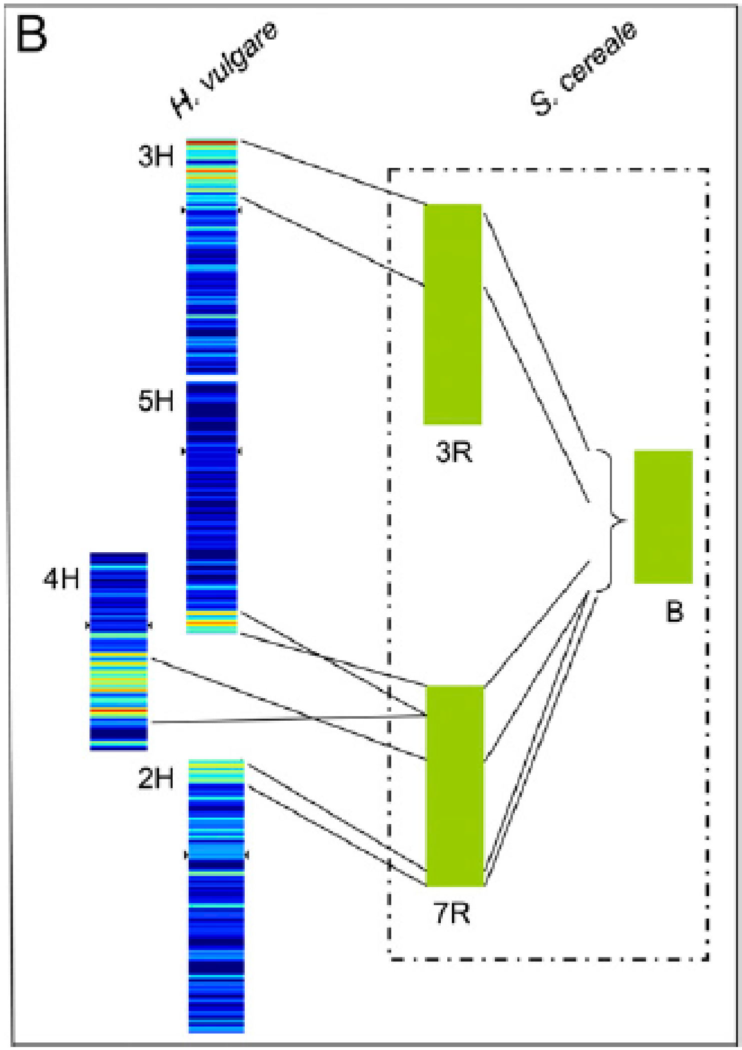
PNAS 2012



Mysterious origins (?)

- Seem to arose 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



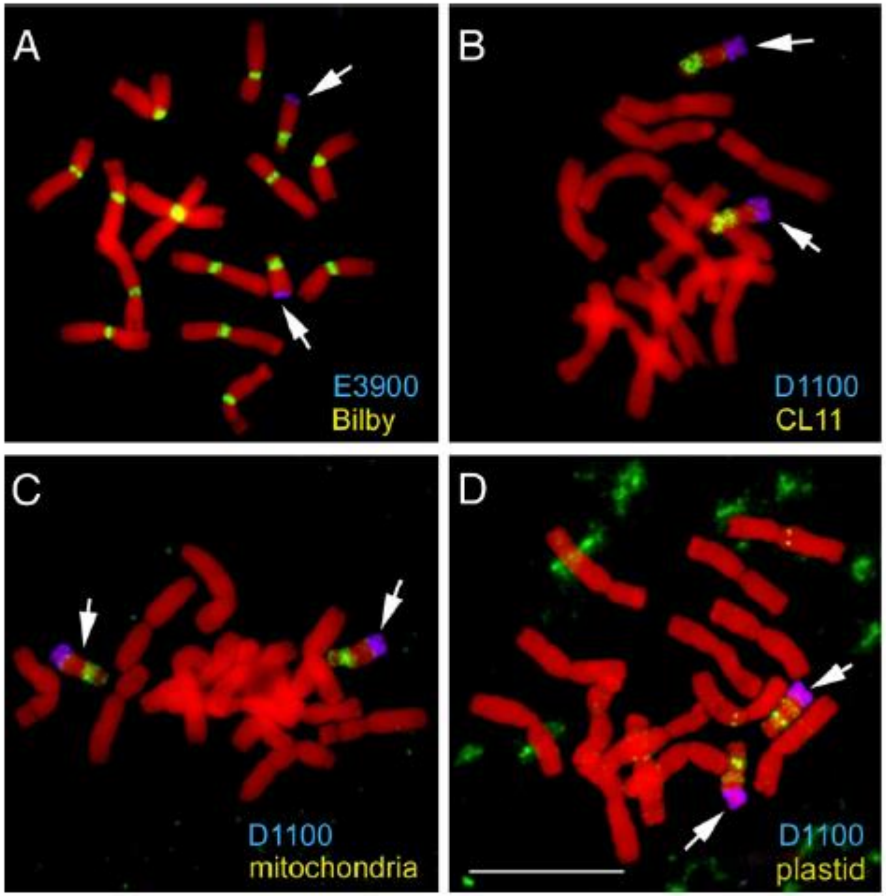
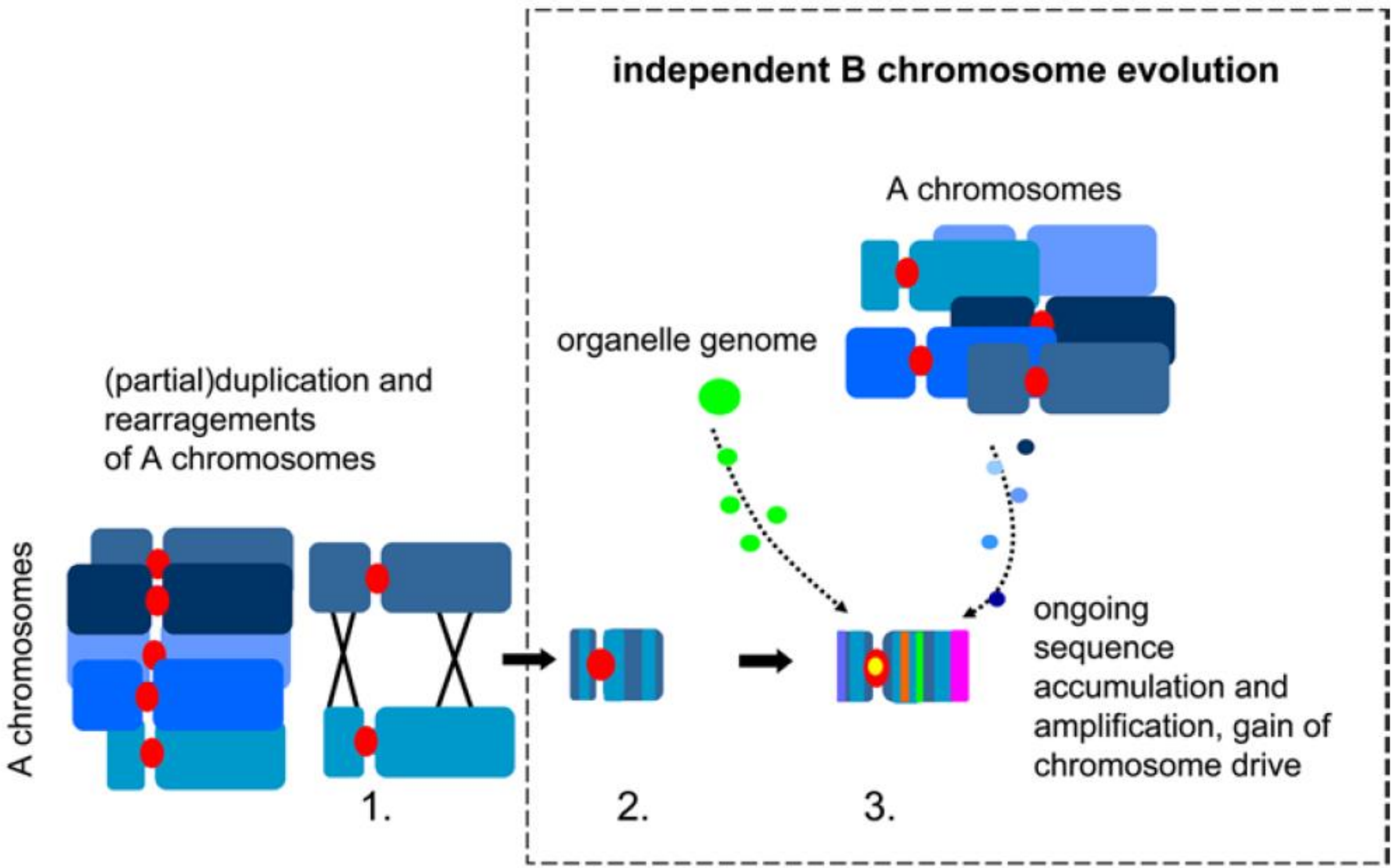


Fig. 2. FISH of rye mitotic metaphase chromosomes with the centromeric retrotransposons *Bilby* (*A*), the B-specific pericentromeric Ty1/copia repeat CL11 (*B*), mitochondrial DNA (*C*), and plastid DNA (*D*). B chromosome-specific satellite repeats E3900 and D1100 were used for identifications of the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

B chromosomes as a „genomic sponge“

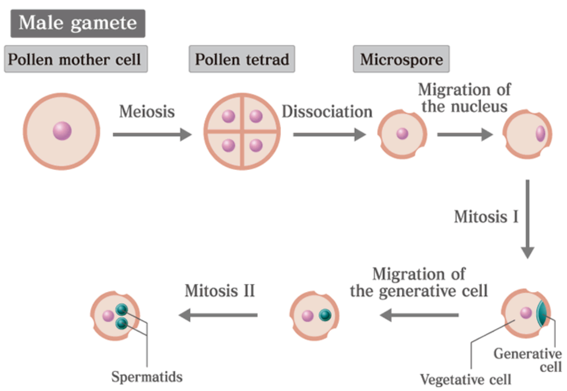
Model of Origin and Evolution of Rye B Chromosomes



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)

⇩

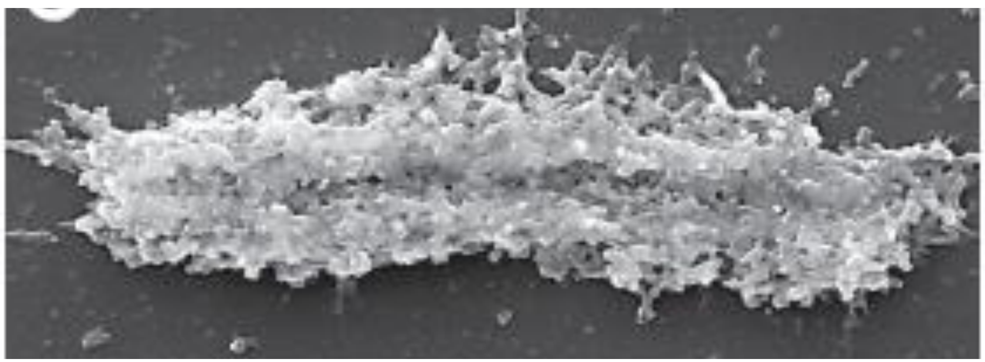
Pollen grain mitosis I:

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

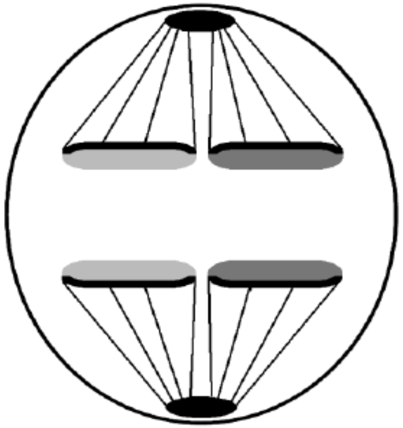
Myristica fragrans (Myristicaceae)

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

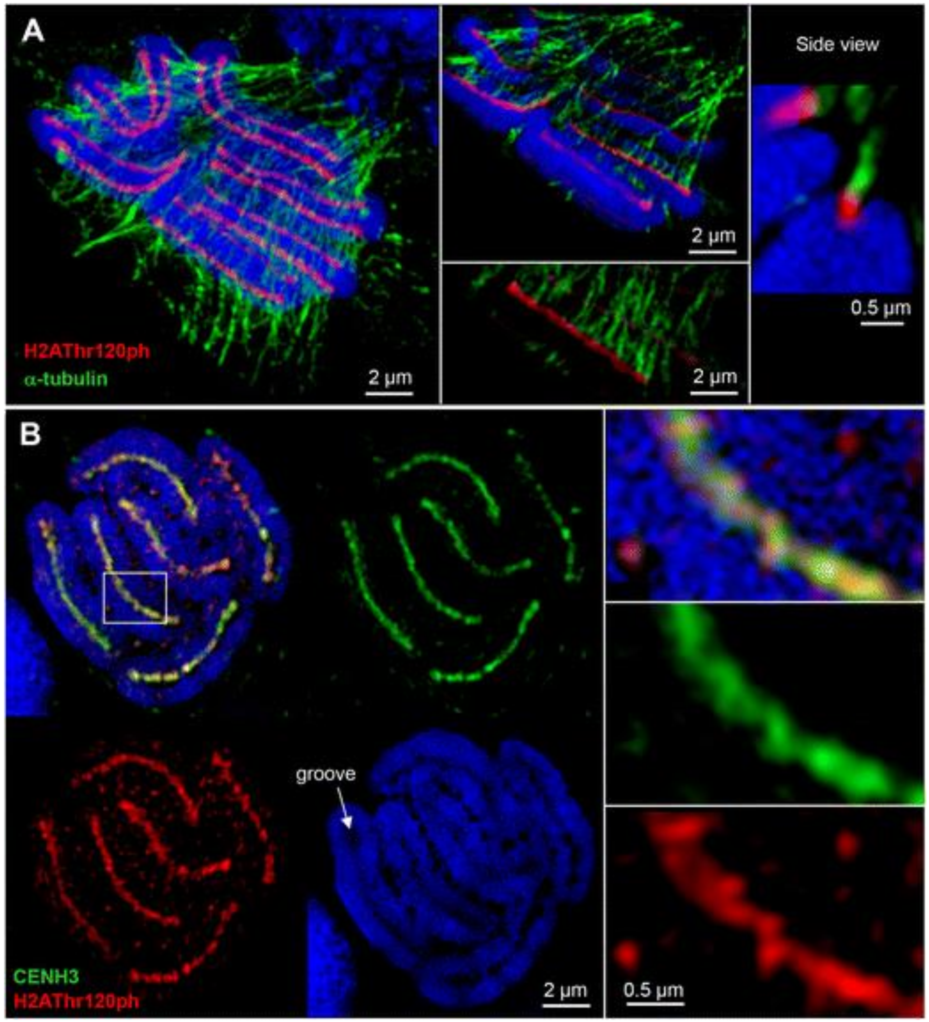
Variation in chromosome number in some holocentric plant genera

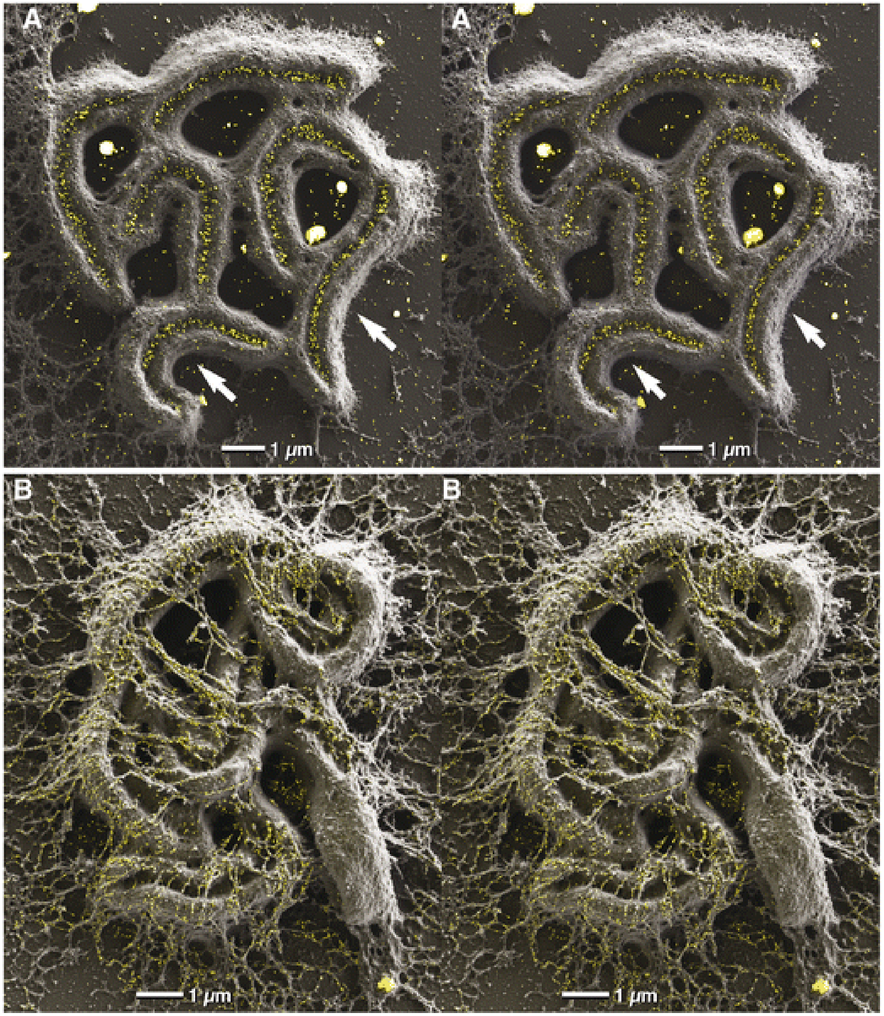
(Bureš et al. 2013)

Family / Genus	Range	Haploid chromosome number (n)
Droseraceae		
Drosera[a, b, c]	13.3-fold	3–7, 9–17, 20, 23, 30, 32, 36, 40
Melanthiaceae		
Chionographis[d]	1.8-fold	12, 21, 22
Juncaceae		
Luzula[a, b, e]	14.0-fold	3, 6–16, 18, 21, 23, 24, 26, 31, 33, 35, 36, 42
Juncus[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		
Carex[f, g]	11.6-fold	5–47, 50, 52–58
Eleocharis[f, h]	36.0-fold	3–16, 18–30, 36–44, 47–50, 68, 86–92, 100, 108
Cyperus[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
Rhynchospora[f, i]	12.5-fold	2, 4–13, 15, 18–22, 24, 25

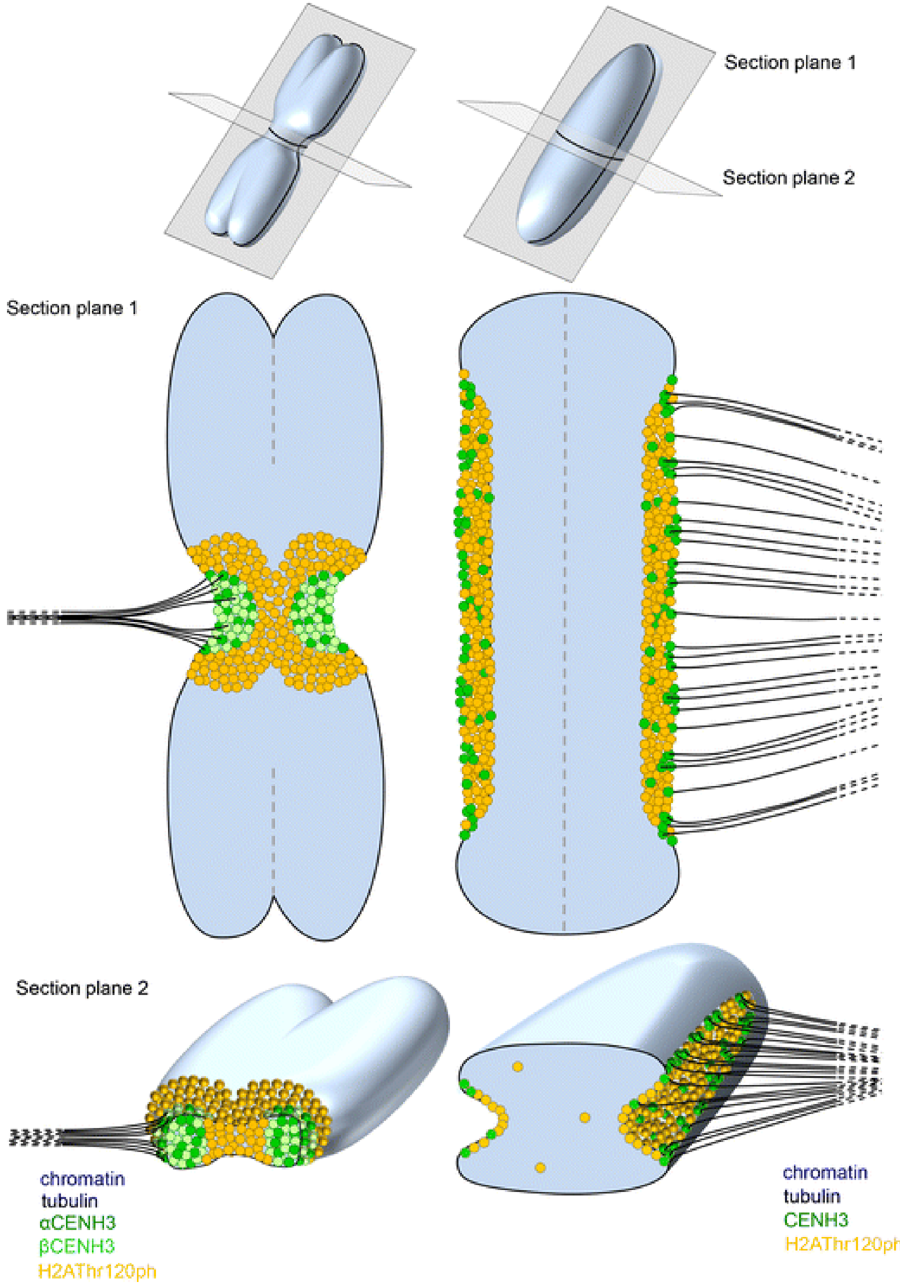
[a] Bolkovskikh et al. (1969)
[b] Golldblatt et al. (2010)
[c] Rivadavia et al. (2003)
[d] Tanaka and Tanaka (1979)
[e] Nordenskiöld (1951); Kirschner (1992)
[f] Roalson (2008)
[g] Rotreklová et al. (2011)
[h] Strandhede (1965b, 1966); Bureš (1998)
[i] Luceño et al. (1998); Vanzela et a. (2000, 2003)

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

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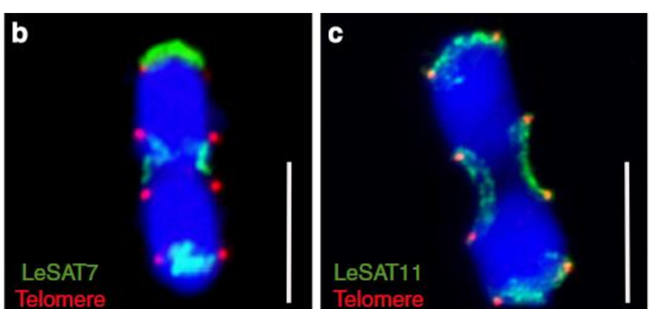
Alternative meiotic chromatid segregation in the holocentric plant *Luzula elegans*

Stefan Heckmann[1,*,†], Maja Jankowska[1,*], Veit Schubert[1], Katrin Kumke[1], Wei Ma[1] & Andreas Houben[1]

- 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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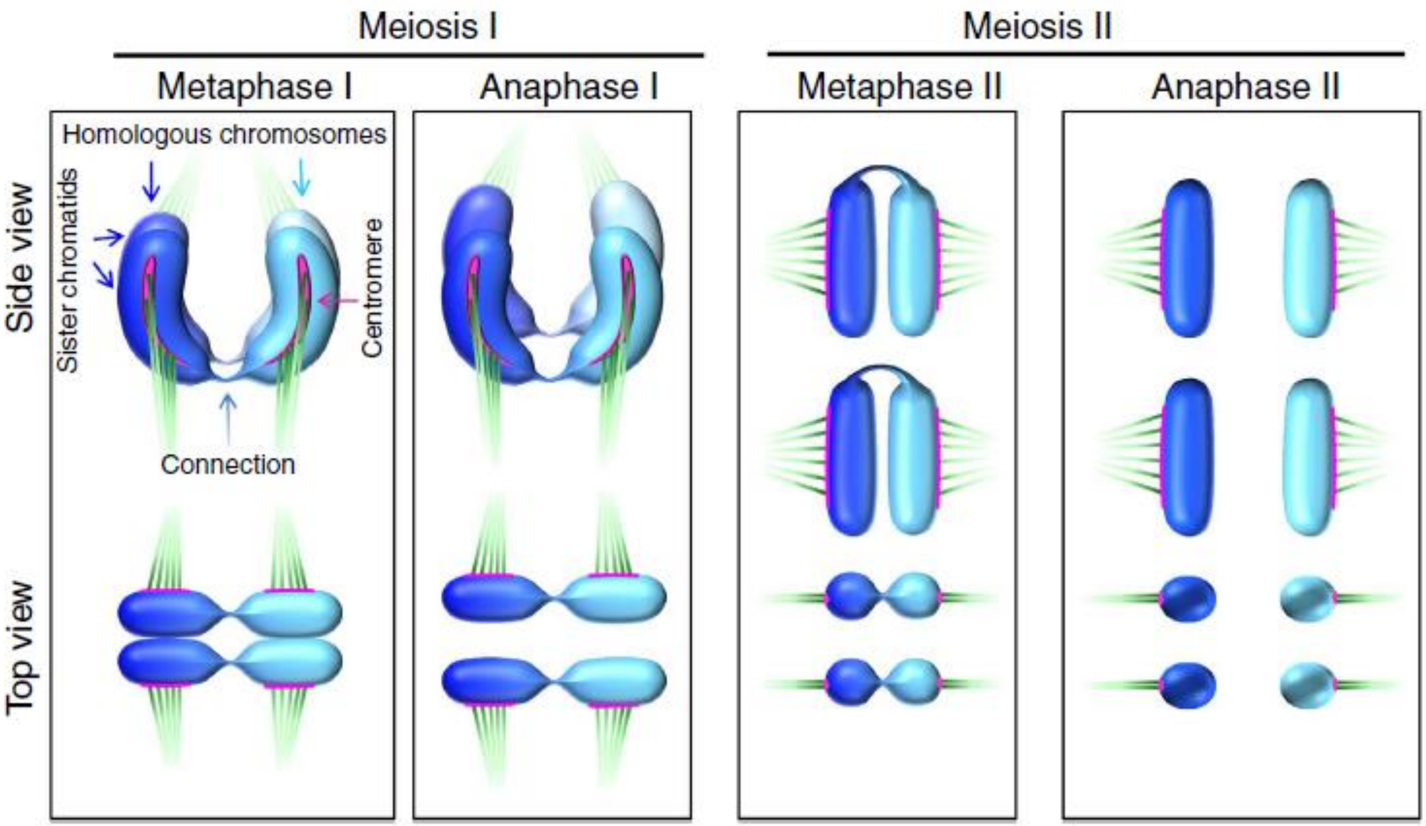

Chromosomes align at metaphase I in such a manner that **sister chromatids** rather than homologous chromosomes are **separated during meiosis I.** Homologous non-sister chromatids are terminally linked **by satellite DNA-enriched chromatin threads** until metaphase II to ensure faithful transmission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

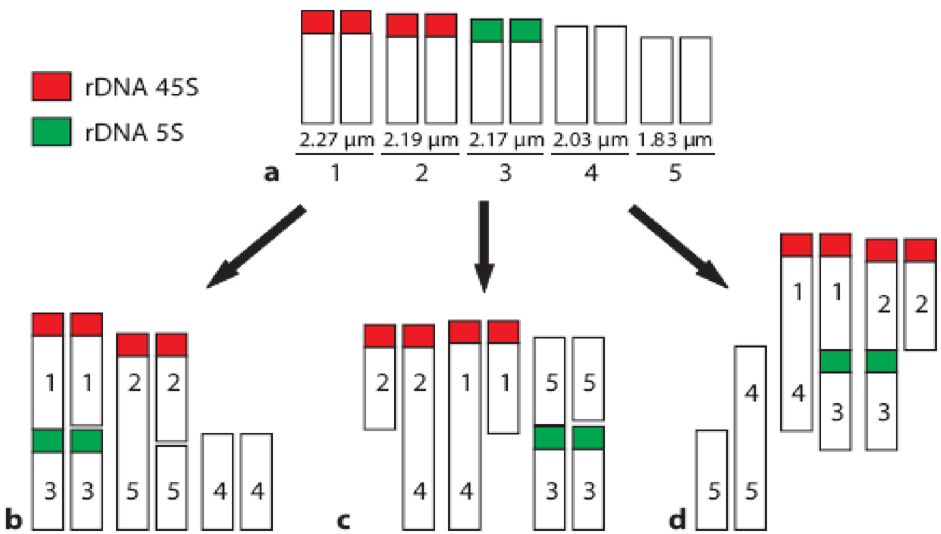

Fig. 3. Idiograms showing the symploidy pathways to formation of chromosome races in *Eleocharis maculosa*. The chromosome arrangement in the idiogram follows possible meiotic pairing. (**a**) Chromosome races with 2n = 10. The µm values correspond to the average of the size of each pair. (**b–d**) Chromosome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

2n = 10

2n = 8 2n = 7 2n = 6

Holocentric chromosomes

1081. Luzula spicata DC.
Spiked Woodrush.

- 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