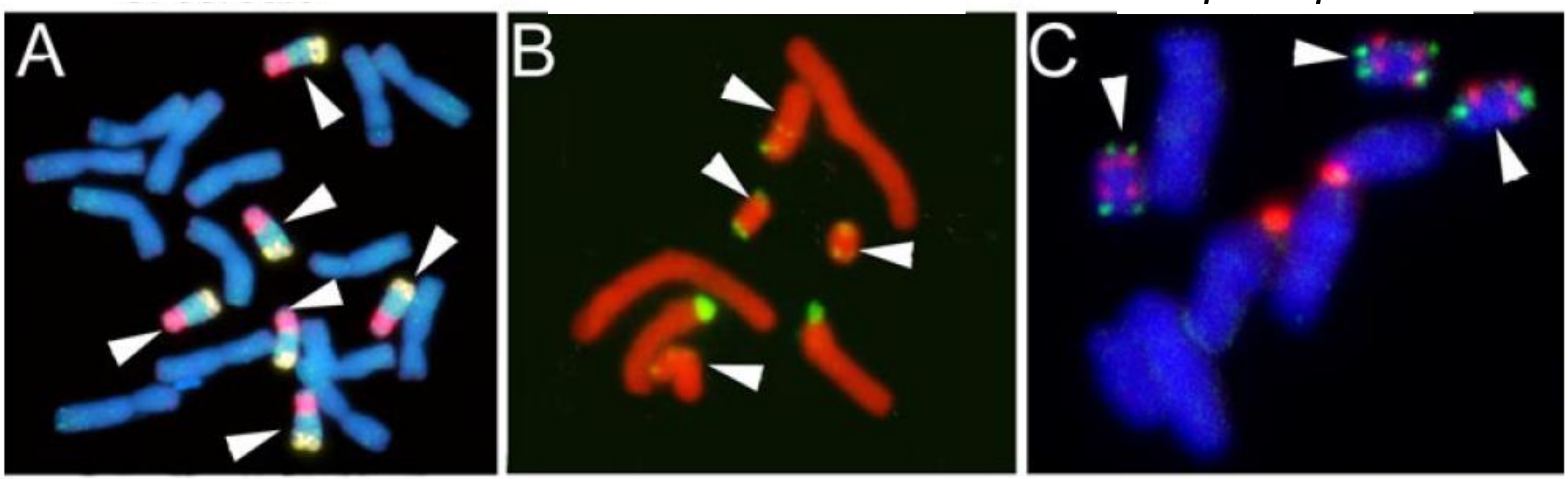
B chromosomes

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)

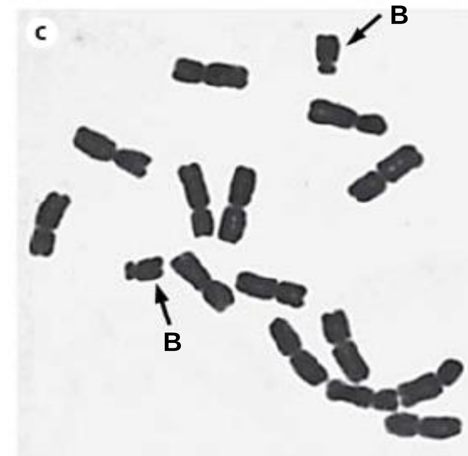
(6) neutral effects; negative and quantitative effects on the phenotype when present in high numbers (reduced fertility)

(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?

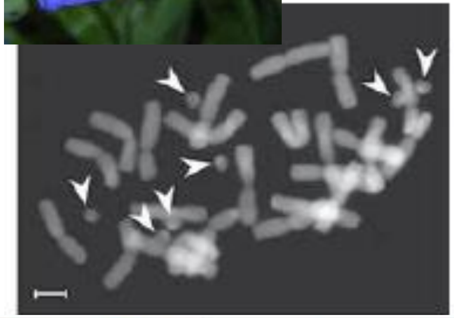
Bs in about 9% of angiosperm species
monocots: 8% (Poaceae, Liliales and Commelinales)
eudicots: 3% (Asteraceae)

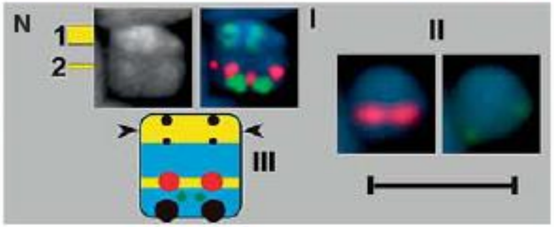
How many?

- 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 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

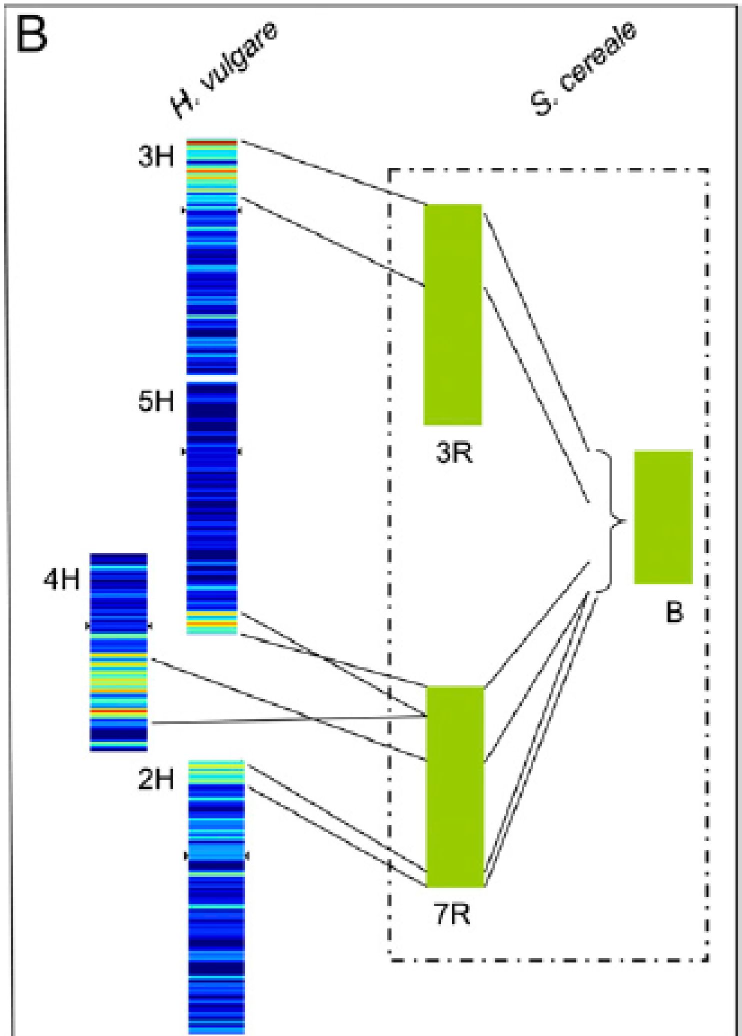
Mihaela Maria Martis[a], Sonja Klemme[b], Ali Mohammad Banaei-Moghaddam[b], Frank R. Blattner[b], Jiří Macas[c], Thomas Schmutzer[b], Uwe Scholz[b], Heidrun Gundlach[a], Thomas Wicker[d], Hana Šimková[e], Petr Novák[c], Pavel Neumann[c], Marie Kubaláková[e], Eva Bauer[f], Grit Haseneyer[f], Jörg Fuchs[b], 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



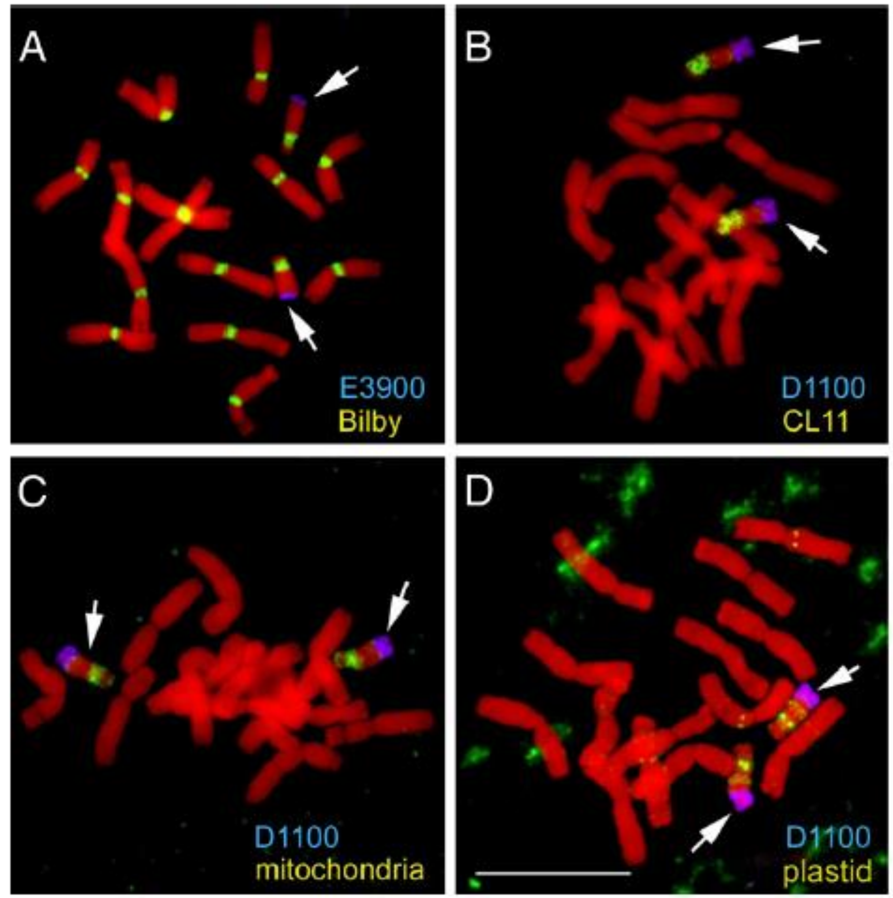
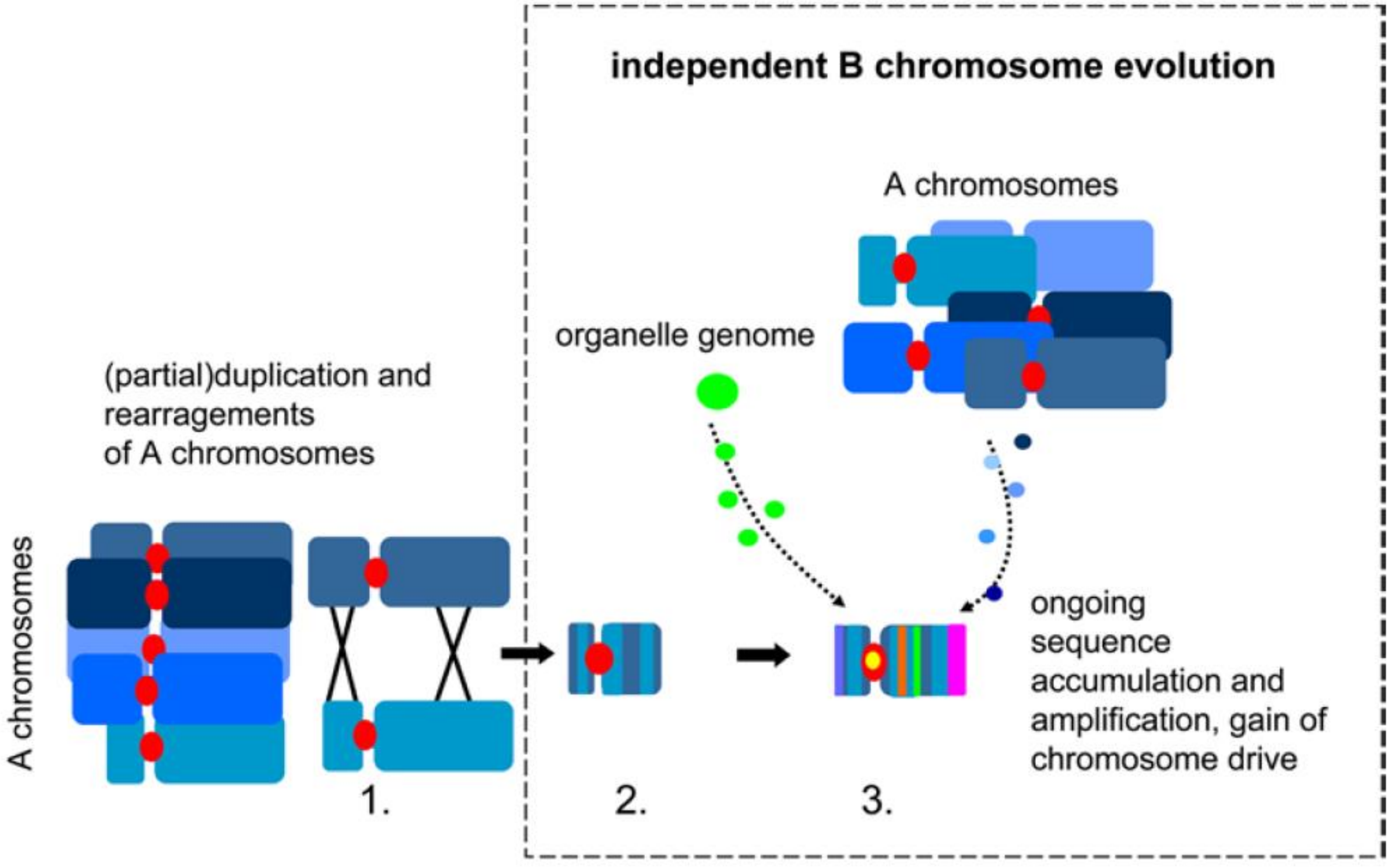


Fig. 2. FISH of rye mitotic metaphase chromosomes with the centromeric retrotransposons *Bilby* (*A*), the B-specific pericentromeric Ty1/copia repeat CL11 (*B*), mitochondrial DNA (*C*), and plastid DNA (*D*). B chromosome-specific satellite repeats E3900 and D1100 were used for identifications of the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

B chromosomes as a „genomic sponge“

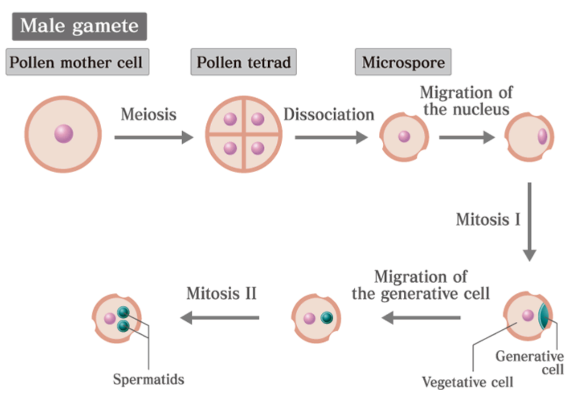
Model of Origin and Evolution of Rye B Chromosomes



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)

Post-meiotic chromosome drive in rye/*Aegilops*/maize (Poaceae), pollen grain mitosis I:



- ➢ **asymmetry of the mitotic spindle** (vegetative and generative nucleus) → the equatorial plate is nearer to the generative pole → Bs into the generative nucleus

- ➢ **Nondisjunction**: 2 chromatids of the B chromosome do not separate at anaphase and are included in the 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)

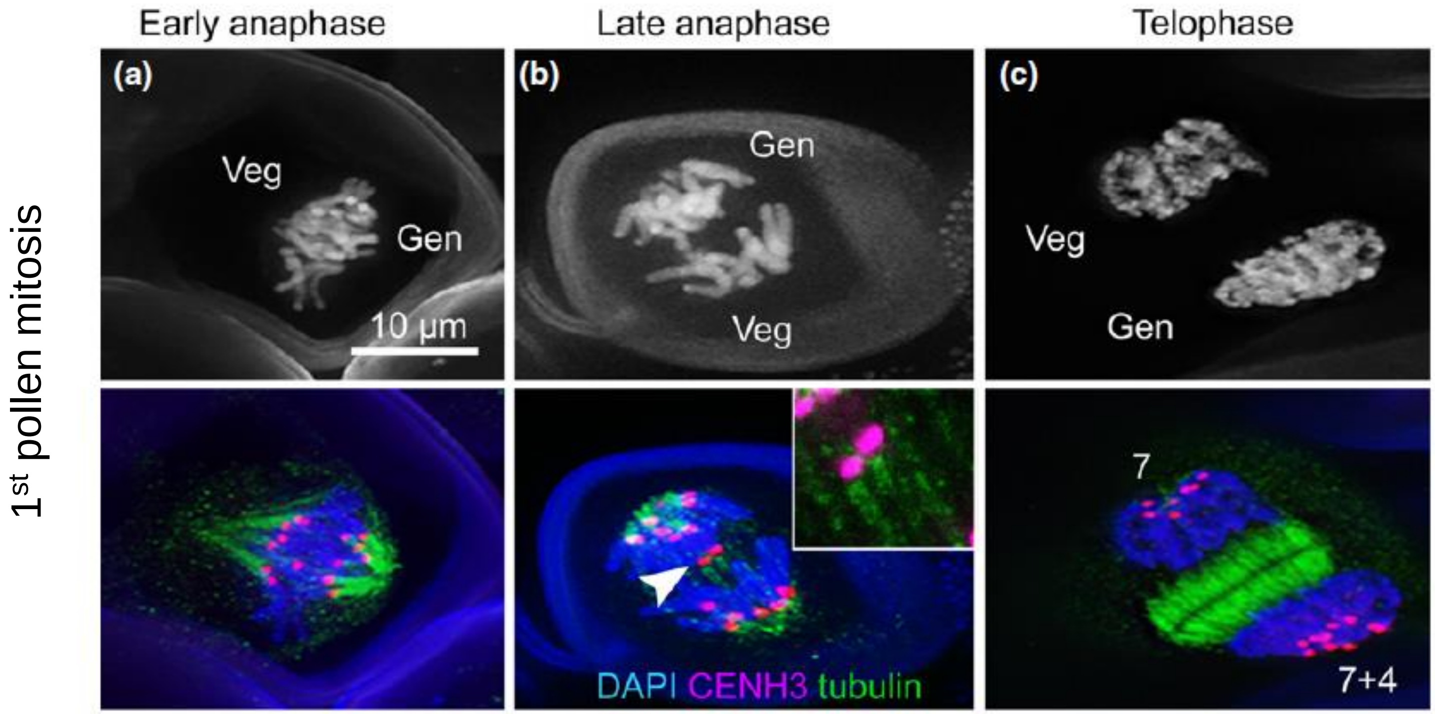
- ➢ **pollen grain mitosis II: both spermatids have an unreduced number of Bs**

- ➢ similar nondisjunction does not occur in the female gametophytes

Alternative explanation (in some other species?):
B-specific centromeric repeats acting as a neocentromere → „stronger centromeres“→ higher pulling force on the B centromere towards the generative pole

Post-meiotic B-chromosome drive

The accumulation of B chromosomes during pollen mitosis of *Aegilops speltoides* +2B.



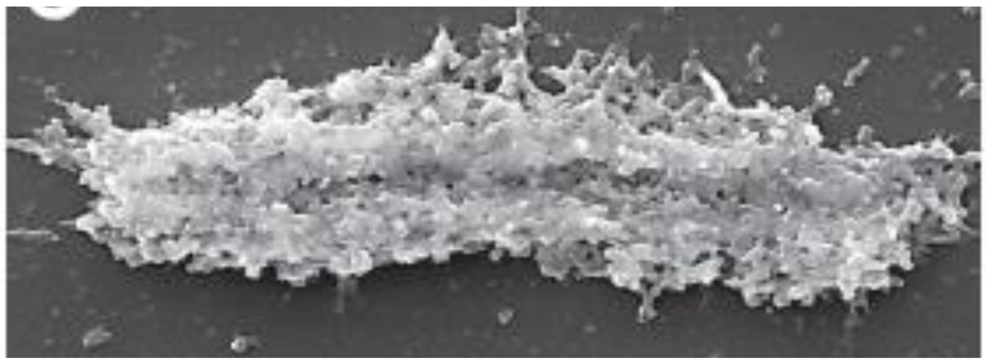
Formation of asymmetric spindle at early anaphase. The generative spindle (Gen) is short and blunt and the vegetative spindle (Veg) is long and sharp.

At late anaphase, nondisjunction of B sister chromatids (lagging chromosomes).

Pollen at late anaphase forming an asymmetric spindle midzone. Note the unequal number of CENH3 signals.

Wu et al. (2019) New Phytol

Holocentric chromosomes



Angiosperm species with holokinetic chromosomes

Juncaceae

Cyperaceae

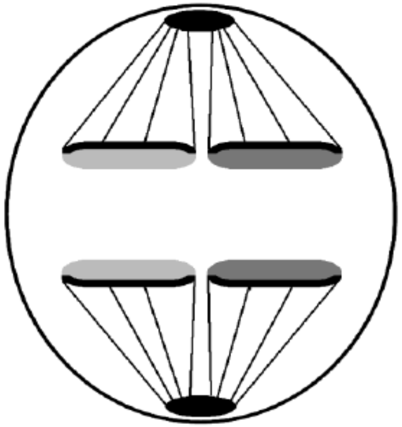
Myristica fragrans (Myristicaceae)

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

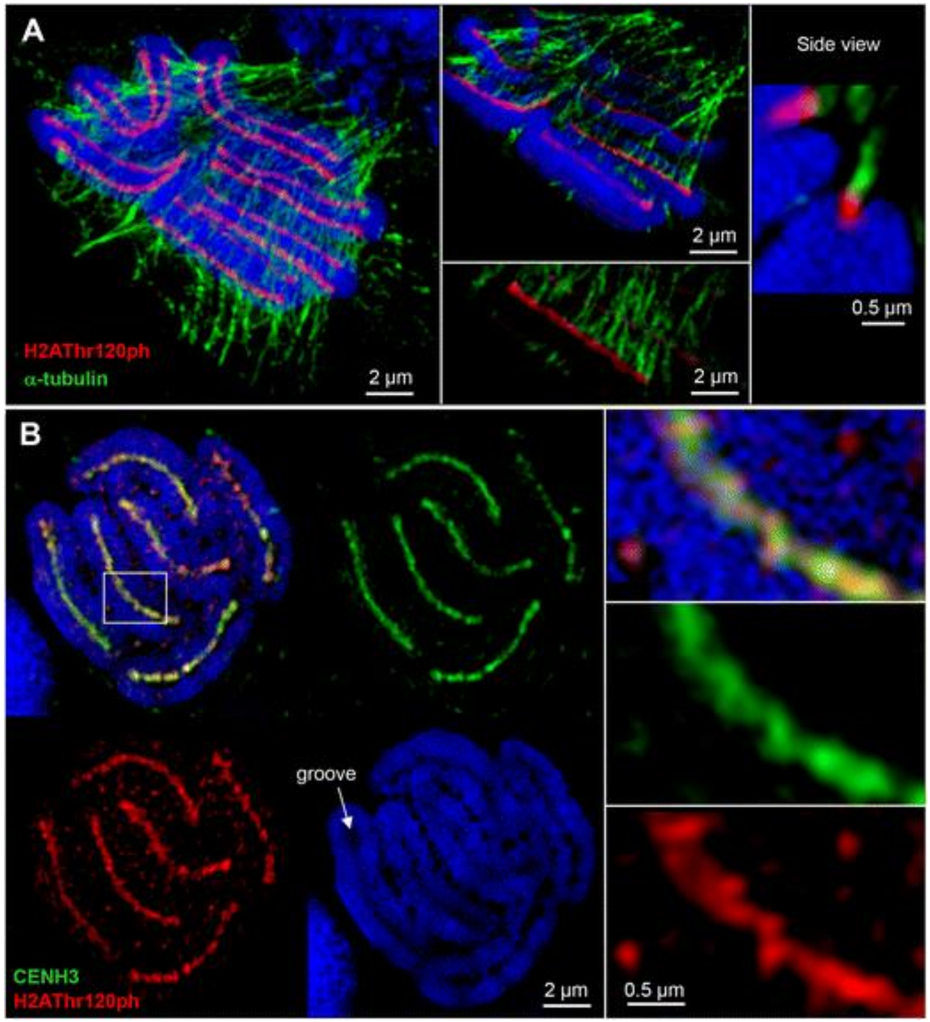
Variation in chromosome number in some holocentric plant genera

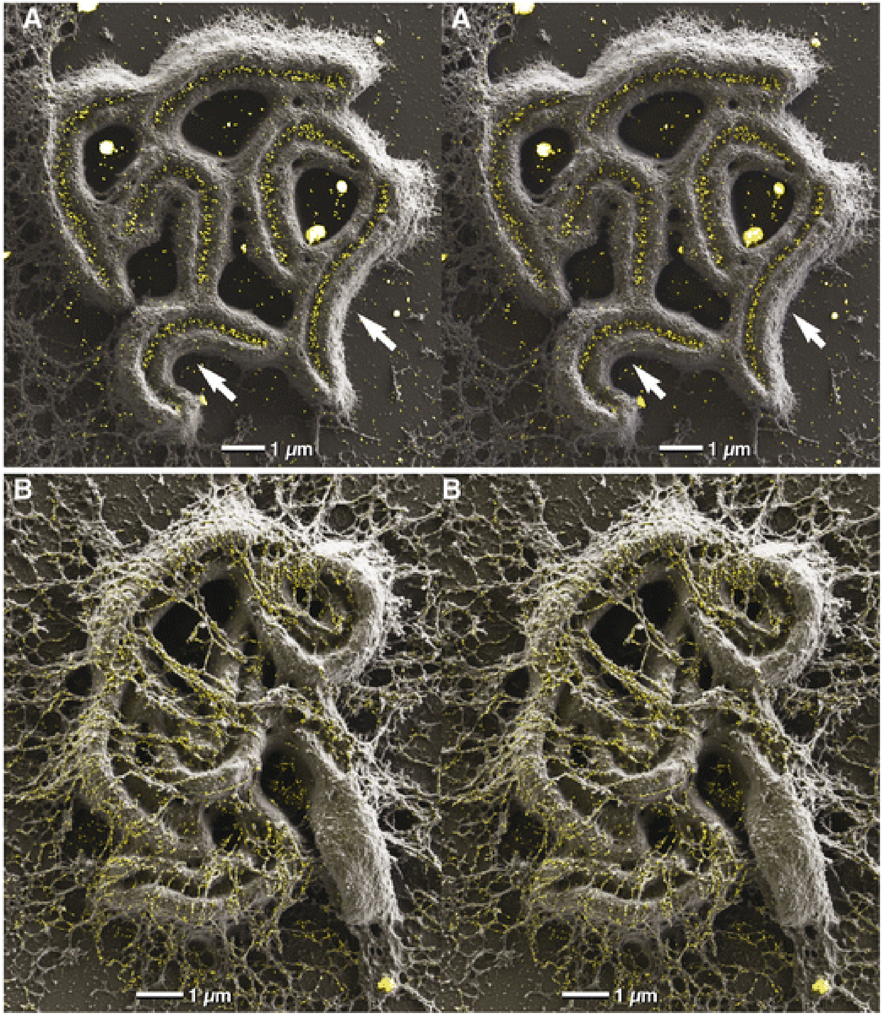
(Bureš et al. 2013)

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

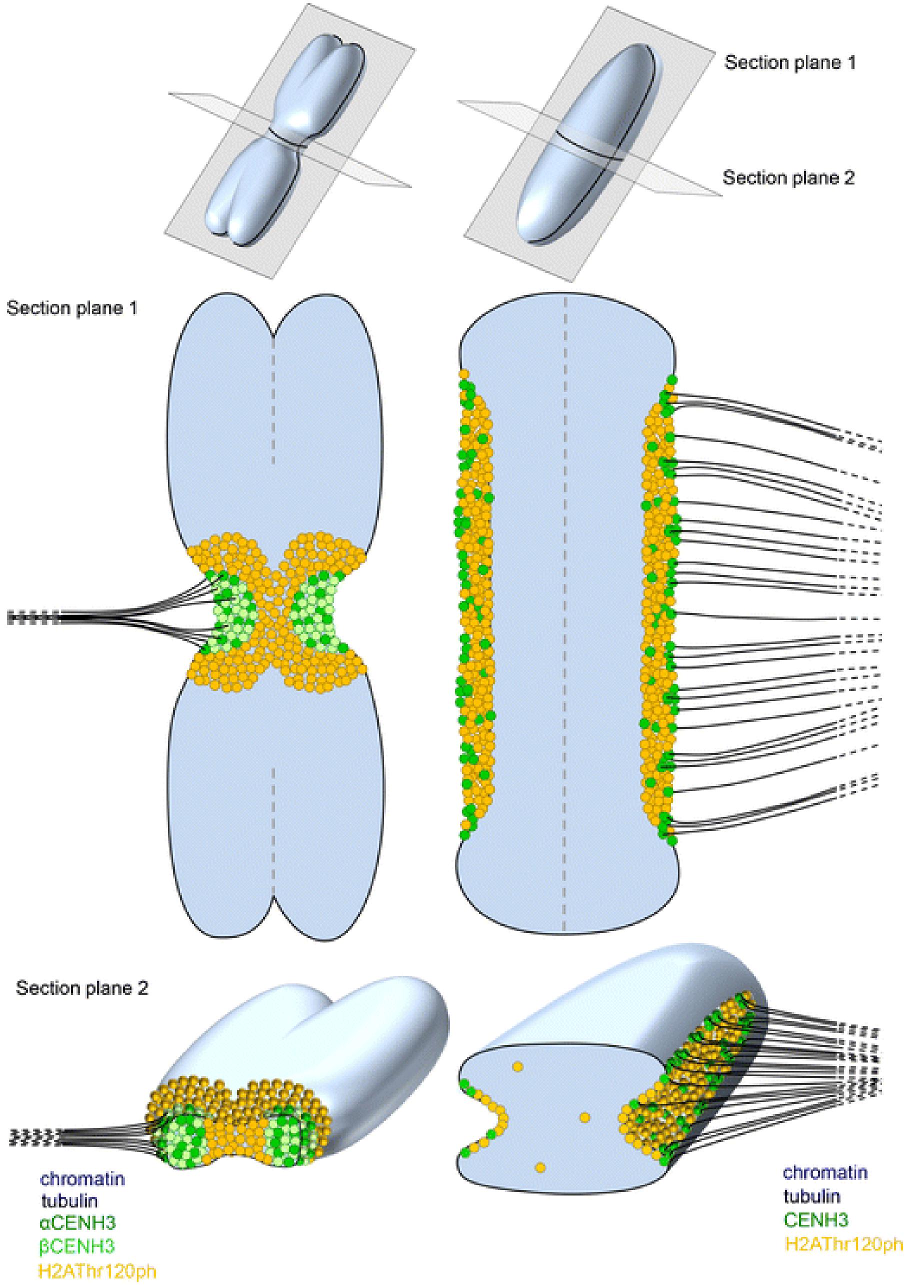
[a] Bolkovskikh et al. (1969)
[b] Golldblatt et al. (2010)
[c] Rivadavia et al. (2003)
[d] Tanaka and Tanaka (1979)
[e] Nordenskiöld (1951); Kirschner (1992)
[f] Roalson (2008)
[g] Rotreklová et al. (2011)
[h] Strandhede (1965b, 1966); Bureš (1998)
[i] Luceño et al. (1998); Vanzela et a. (2000, 2003)

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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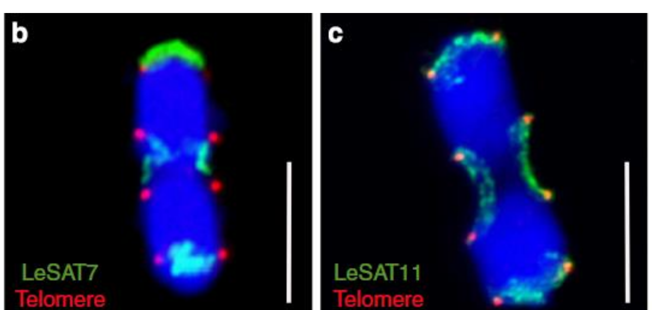
OPEN

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



...also in *Rhynchospora pubera* and *R. tenuis* (*Cyperaceae*)

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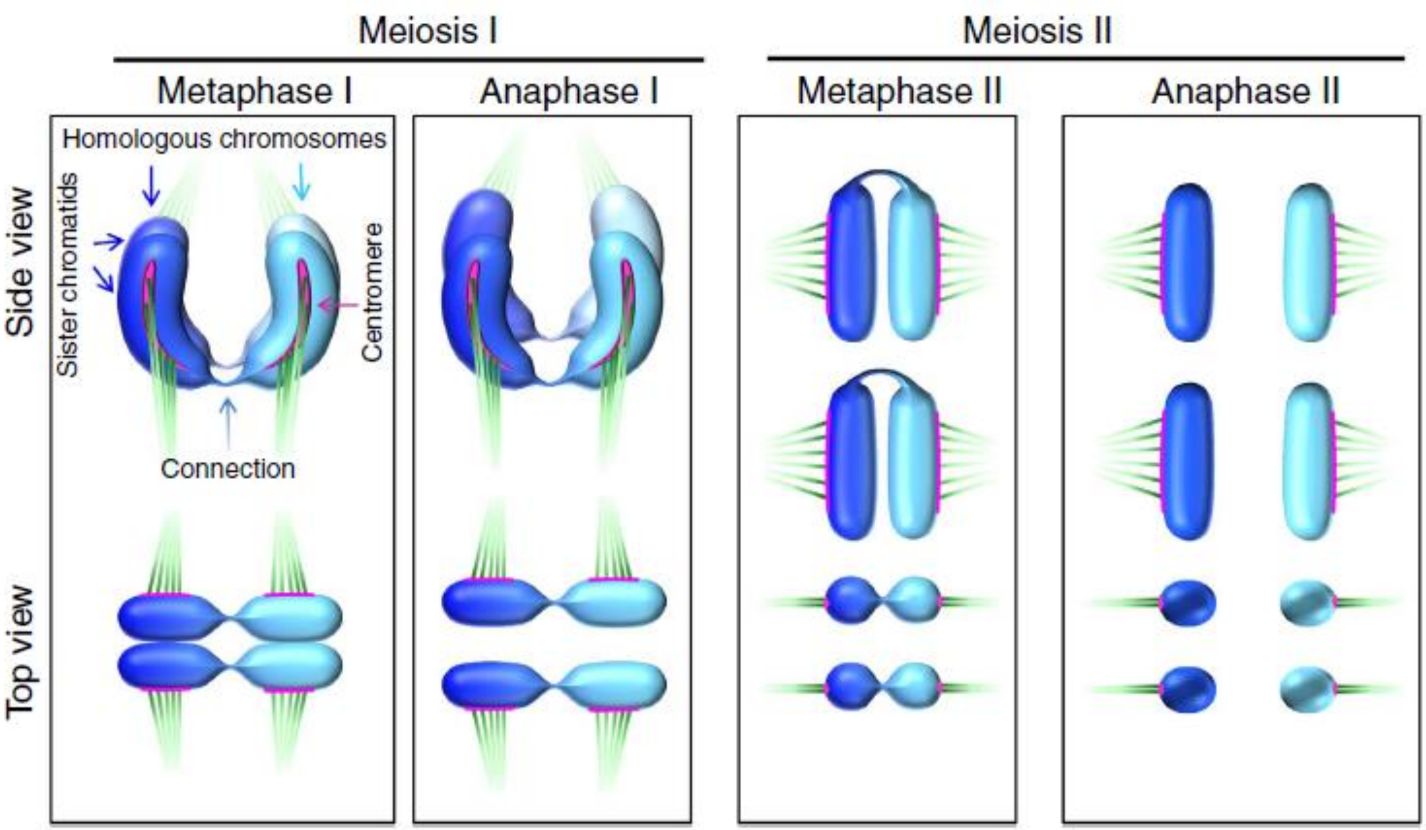

Chromosomes align at metaphase I in such a manner that **sister chromatids** rather than homologous chromosomes are **separated during meiosis I**. Homologous non-sister chromatids are terminally linked **by satellite DNA-enriched chromatin threads** until metaphase II to ensure faithful transmission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

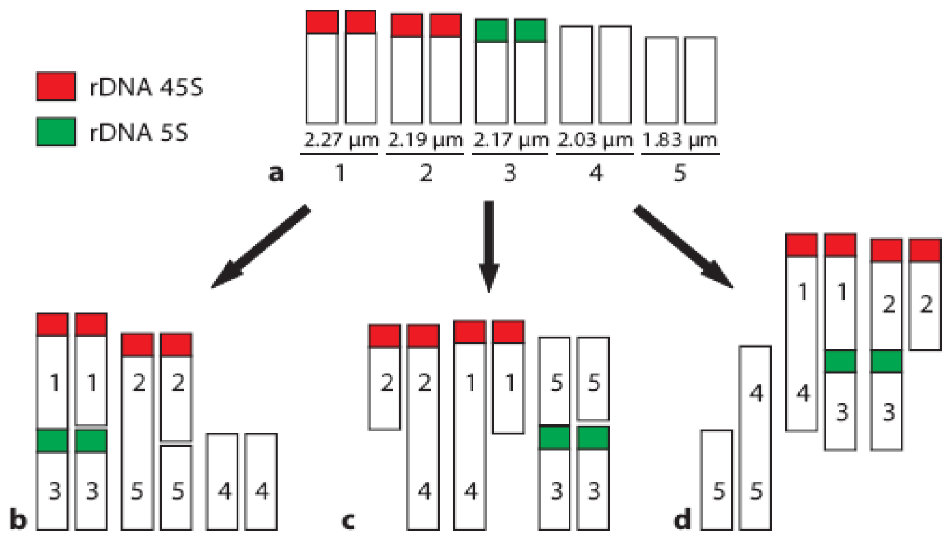

Fig. 3. Idiograms showing the symploidy pathways to formation of chromosome races in *Eleocharis maculosa*. The chromosome arrangement in the idiogram follows possible meiotic pairing. (**a**) Chromosome races with 2n = 10. The µm values correspond to the average of the size of each pair. (**b–d**) Chromosome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

2n = 10

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