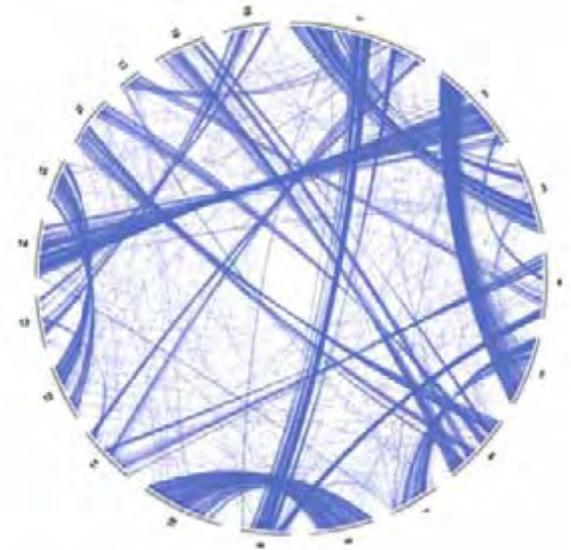
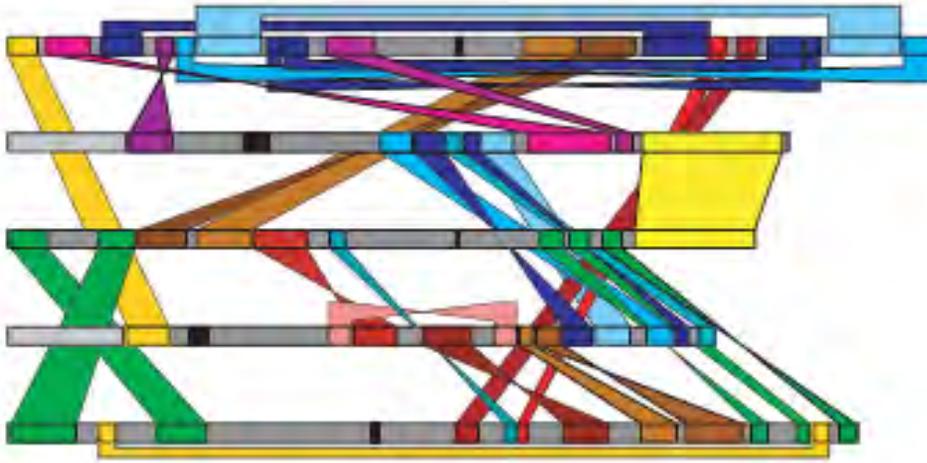
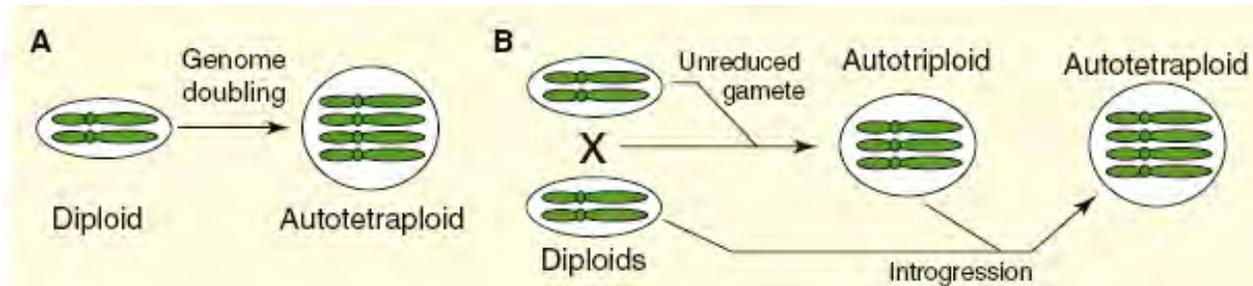


Whole-genome duplications and paleopolyploidy



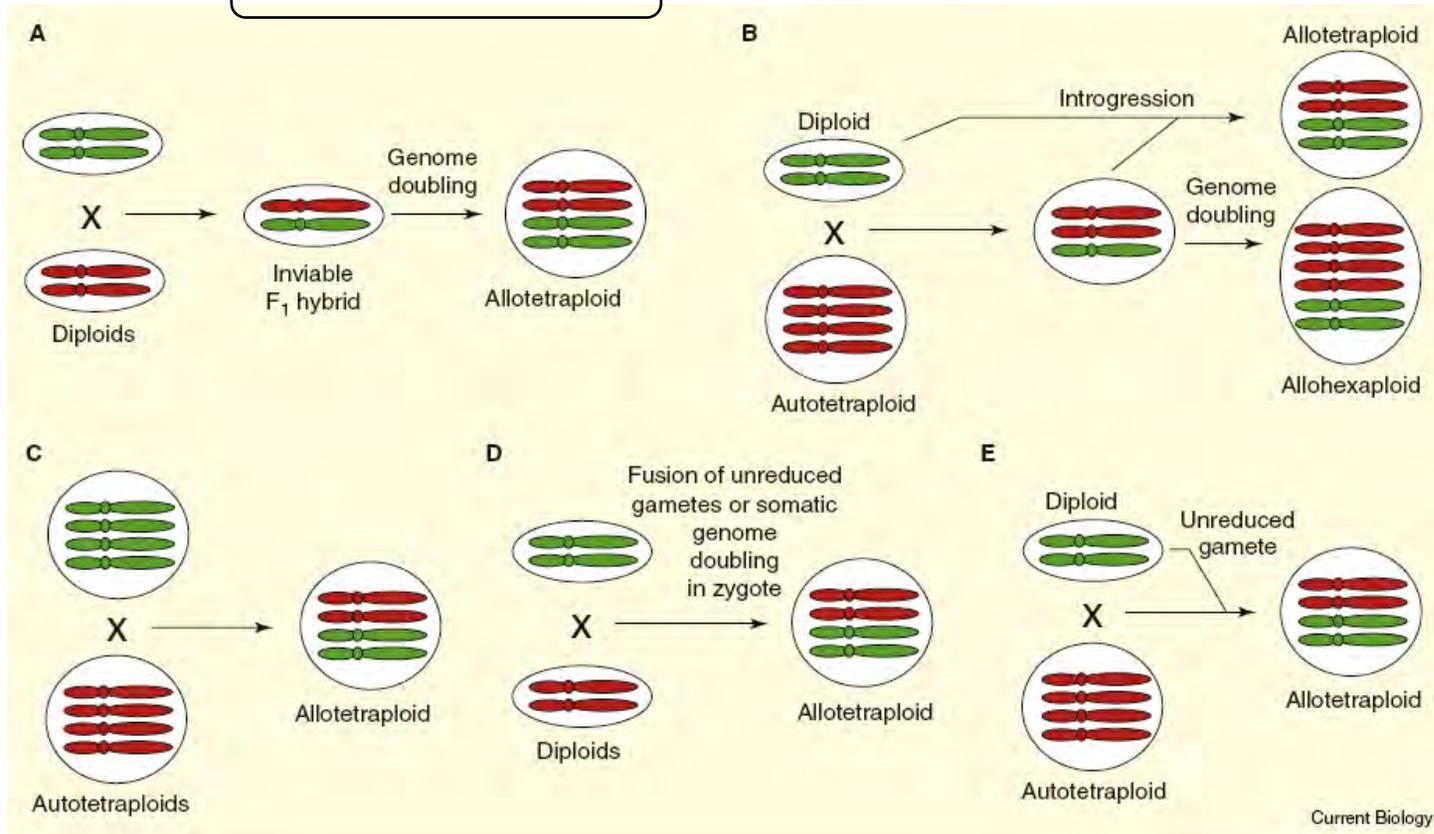
*Populus
trichocarpa*

Whole-genome duplications



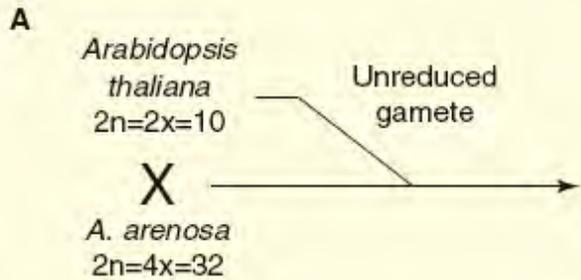
AUTOPOLYPLOIDY

ALLOPOLYPLOIDY

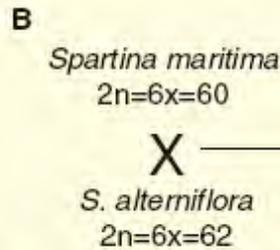


Current Biology

Examples of allopolyploid speciation



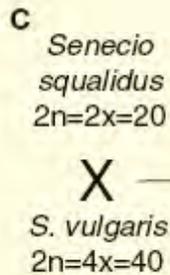
A. suecica
2n=4x=26



S. x townsendii
2n=6x=61
(Sterile)

Genome doubling

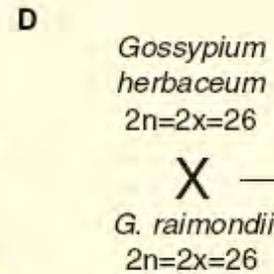
S. anglica
2n=12x=122
Fertile



S. x baxteri
2n=3x=30
(Sterile)

Genome doubling

S. cambrensis
2n=6x=60
Fertile



Diploid hybrid

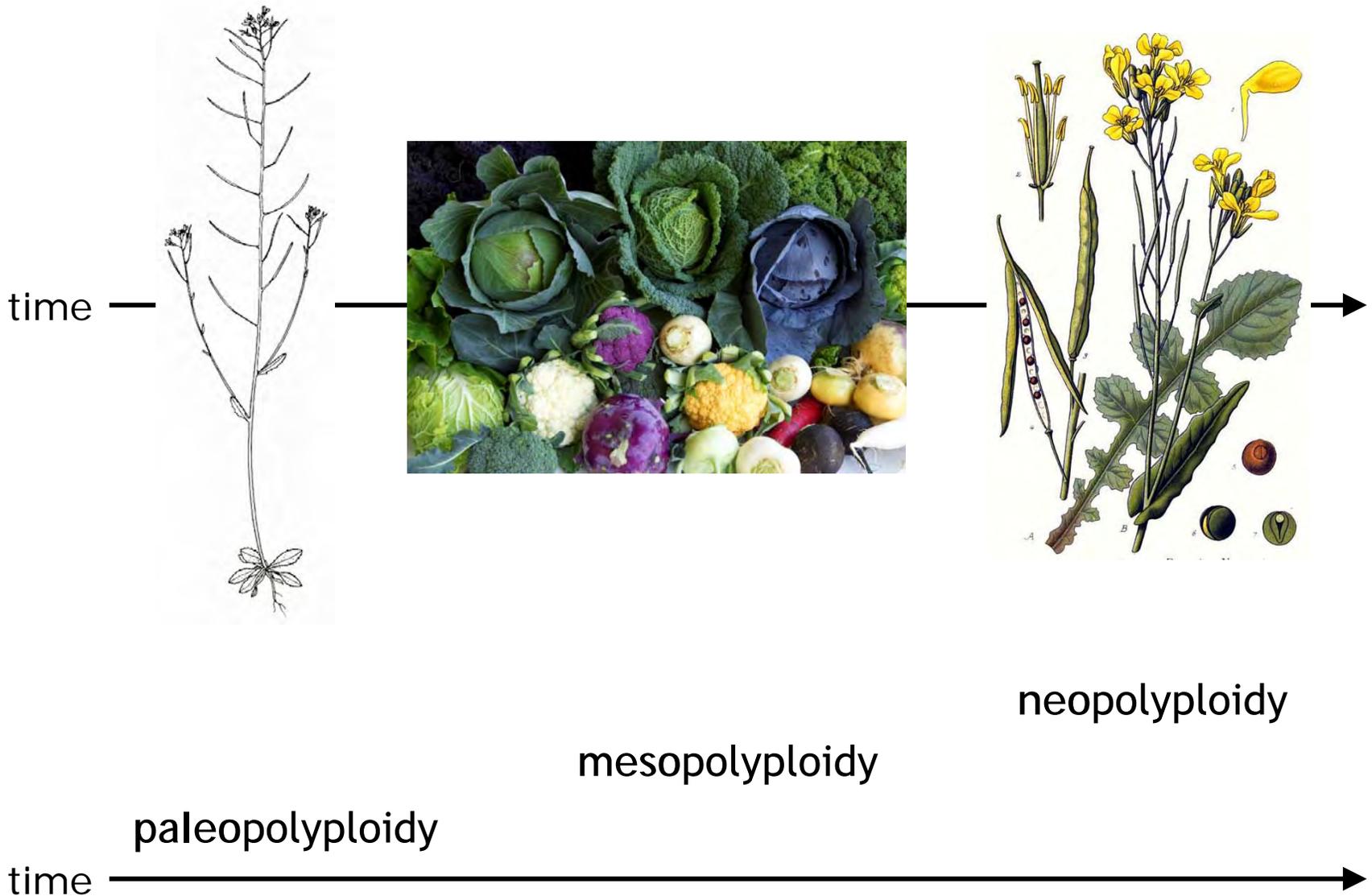
Genome doubling

G. hirsutum
2n=4x=52



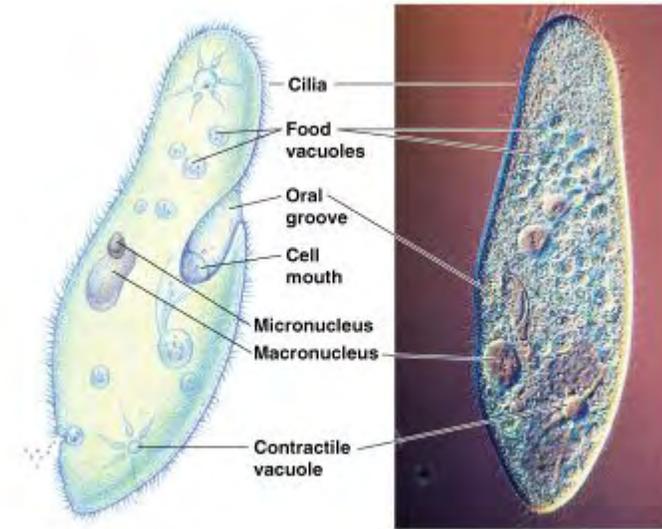
Current Biology

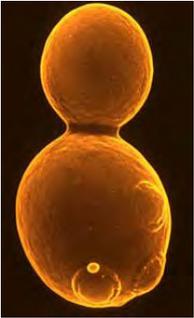
Whole-genome duplications of different age



Whole-genome duplications in protozoa

- Aury *et al.* (2006) analyzed the unicellular eukaryote *Paramecium tetraurelia*
- most of 40,000 genes arose through at least 3 successive whole-genome duplications (WGDs)
- most recent duplication most likely caused an explosion of speciation events that gave rise to the *P. aurelia* complex (15 sibling species)
- some genes have been lost, some retained
- many retained (duplicated) genes do not generate functional innovations but are important because of the gene dosage effect

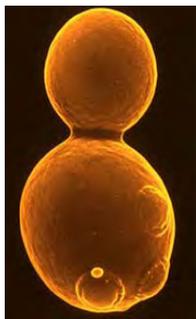




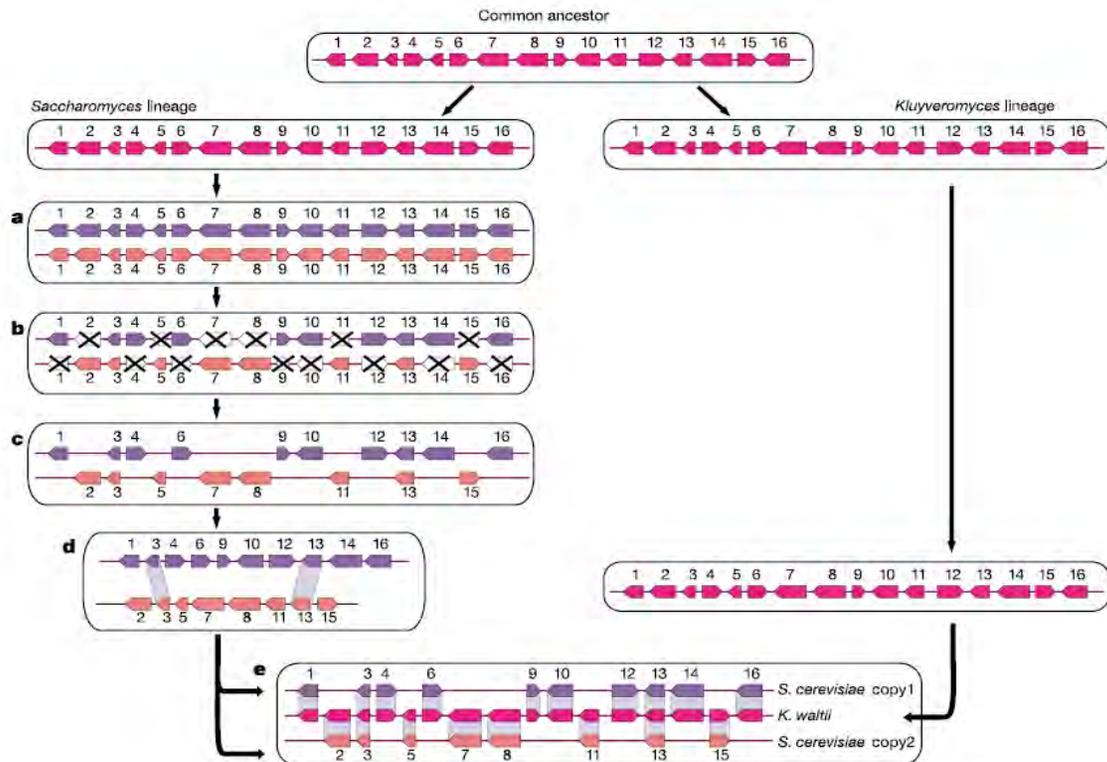
Whole-genome duplications in yeast

- genome comparison between two yeast species, *Saccharomyces cerevisiae* (n=16) and *Kluyveromyces waltii* (n=8)
- each region of *K. waltii* corresponding to two regions of *S. cerevisiae*
- the *S. cerevisiae* genome underwent a WGD after the two yeast species diverged
- in nearly every case (95%), accelerated evolution was confined to only one of the two paralogues (= one of the paralogues retained an ancestral function, the other was free to evolve more rapidly and acquired a derived function)

Whole-genome duplications in yeast

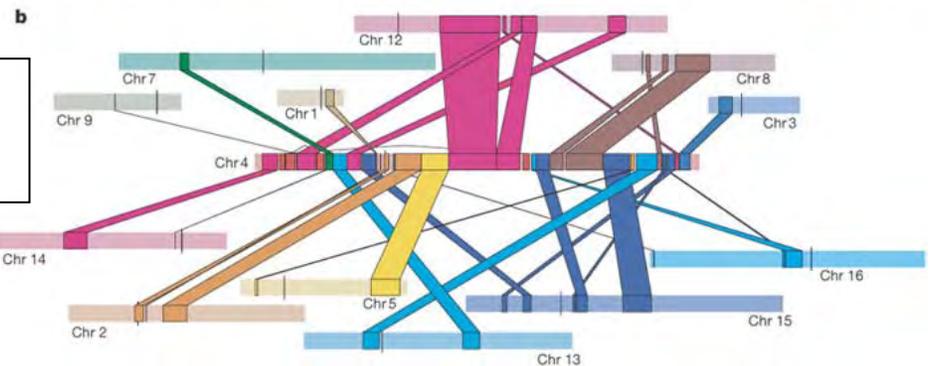
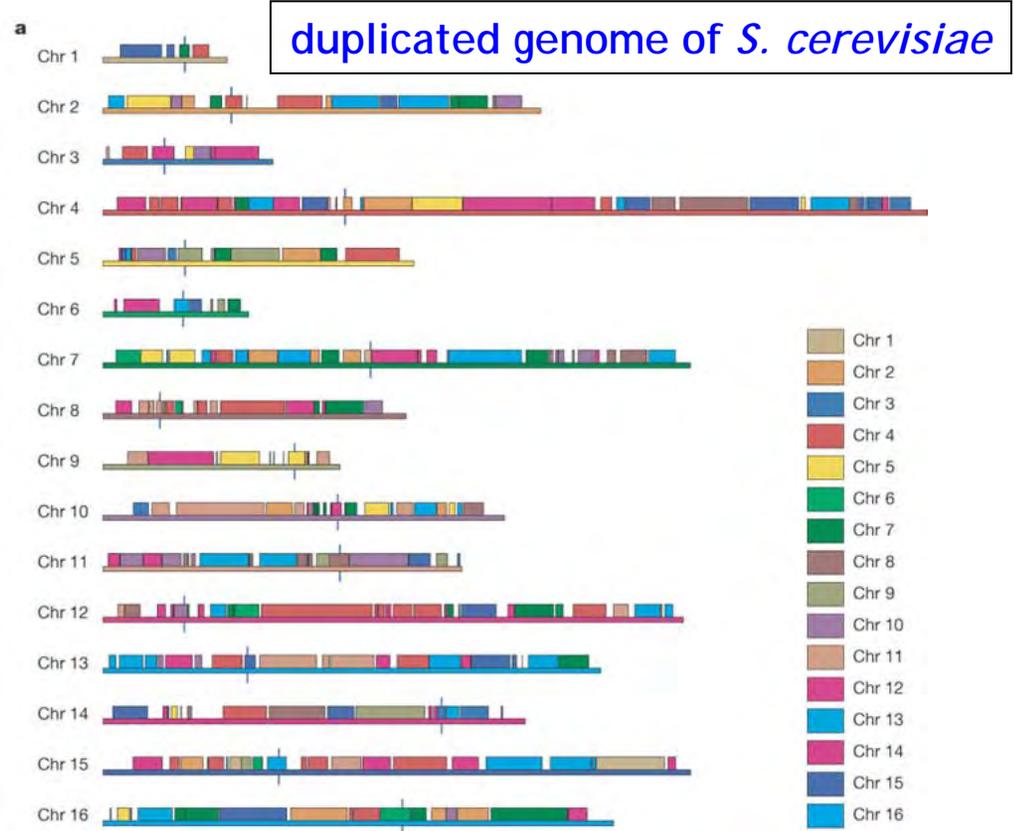
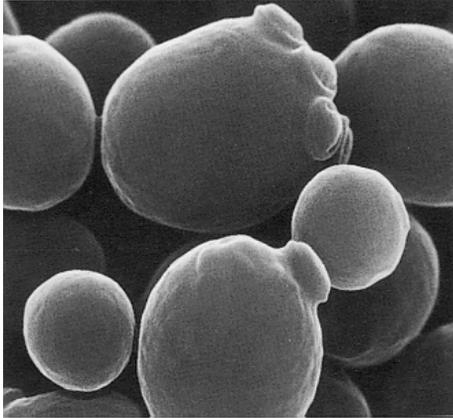


Kellis *et al.* 2004,
Nature 428



- a) after divergence from *K. waltii*, the *Saccharomyces* lineage underwent a genome duplication event (2 copies of every gene and chromosome)
- b) duplicated genes were mutated and some lost
- c) two copies kept for only a small minority of duplicated genes
- d) the conserved order of duplicated genes (nos. 3-13) across different chromosomal segments
- e) comparison between genomes of *S. cerevisiae* and *K. waltii* reveals the duplicated nature of the *S. cerevisiae* genome

Duplicated nature of the *S. cerevisiae* genome



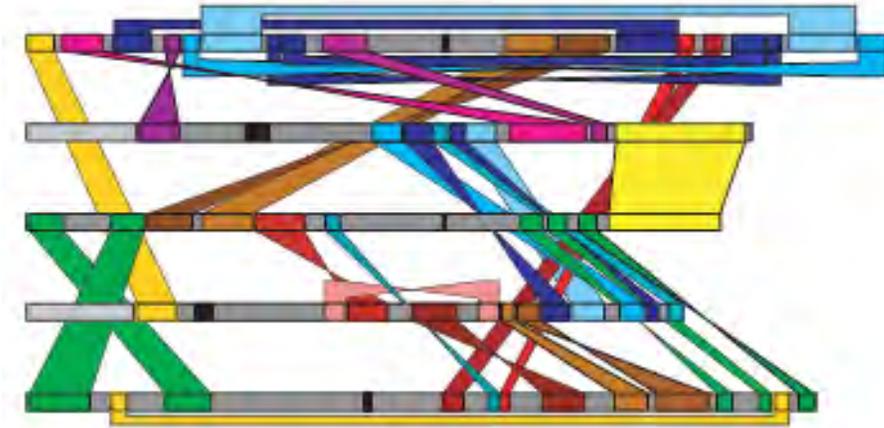
S. cerevisiae chromosome 4 with sister regions in other chromosomes

Is Arabidopsis a paleotetraploid?



Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*

The Arabidopsis Genome Initiative* AGI (2000)

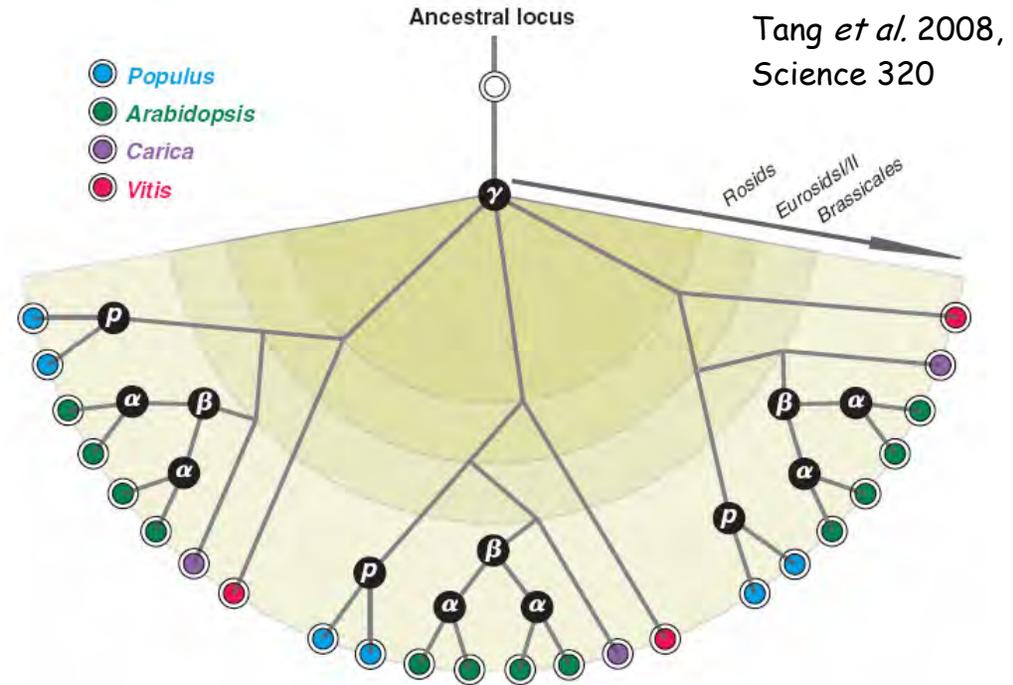
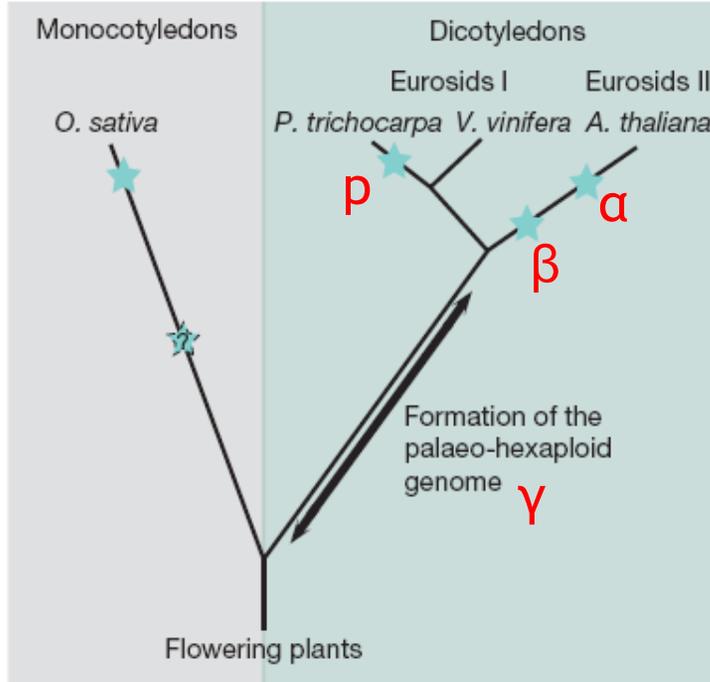


What does the duplication in the Arabidopsis genome tell us about the ancestry of the species? As the majority of the Arabidopsis genome is represented in duplicated (but not triplicated) segments, it appears most likely that Arabidopsis, like maize, had a tetraploid ancestor. ...The diploid genetics of Arabidopsis and the extensive divergence of the duplicated segments have masked its evolutionary history.

The grapevine genome sequence suggests ancestral hexaploidization in major angiosperm phyla

The French-Italian Public Consortium for Grapevine Genome Characterization*

Nature 449, 2007



The formation of the palaeo-hexaploid ancestral genome occurred after divergence from monocotyledons and before the radiation of the Eurosids. Star = a WGD (tetraploidization) event.

The γ triplication may have been an ancient auto-hexaploidy formed from fusions of three identical genomes, or allo-hexaploidy formed from fusions of three somewhat diverged genomes.

Tang et al. 2008, Genome Research

The draft genome of the transgenic tropical fruit tree papaya (*Carica papaya* Linnaeus)

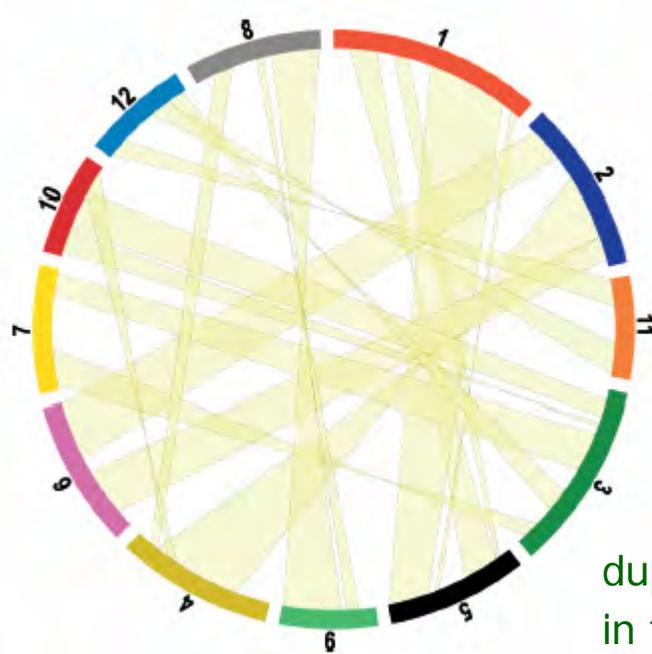
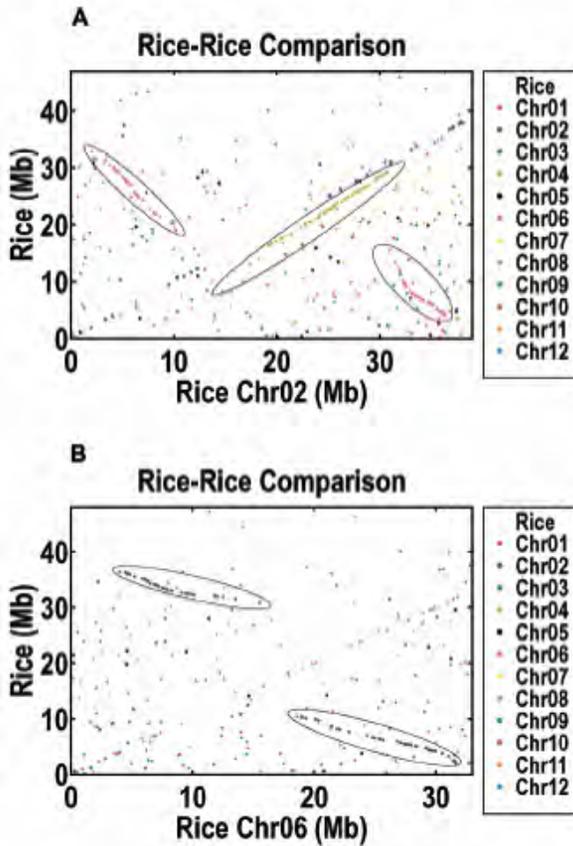
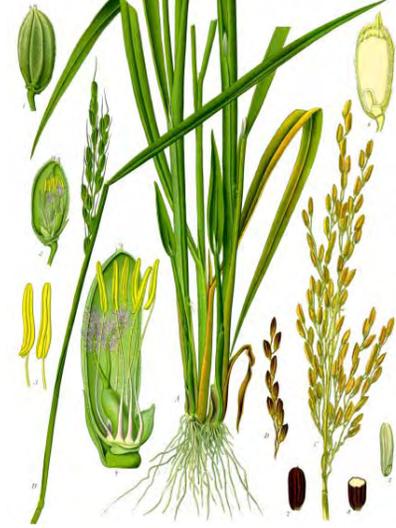
Ming et al. (2008) Nature 452

The papaya genome (372 Mb) is three times the size of the *Arabidopsis* genome, but contains fewer genes, including significantly fewer disease-resistance gene analogues. Comparison of the five sequenced genomes suggests a minimal angiosperm gene set of 13,311. A lack of recent genome duplication, atypical of other angiosperm genomes sequenced so far, may account for the smaller papaya gene number in most functional groups. Nonetheless, striking amplifications in gene number within particular functional groups suggest roles in the evolution of tree-like habit, deposition and remobilization of starch reserves, attraction of seed dispersal agents, and adaptation to tropical daylengths.



Papaya (*Caricaceae*) and *Arabidopsis* (*Brassicaceae*) belong to the Brassicales; both families diverged c. 72 million years ago

Genome duplications in rice (*Oryza sativa*)



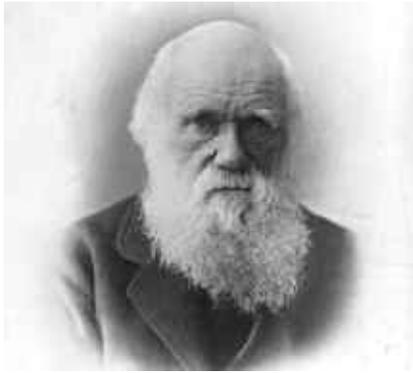
duplicated segments
in the rice genome

Duplicated segments of chromosomes 2 (A)
and 6 (B) in *Oryza sativa* subsp. *indica*.

Shown on the x-axis is the position of a gene on the indicated chromosome, and shown on the y-axis is the position of its homolog on any of the rice chromosomes, with chromosome number encoded by the colors indicated at the right.

Yu *et al.* (2005) The genomes of *Oryza sativa*: A history of duplications. PLoS Biol 3

Charles Darwin's abominable mystery solved?

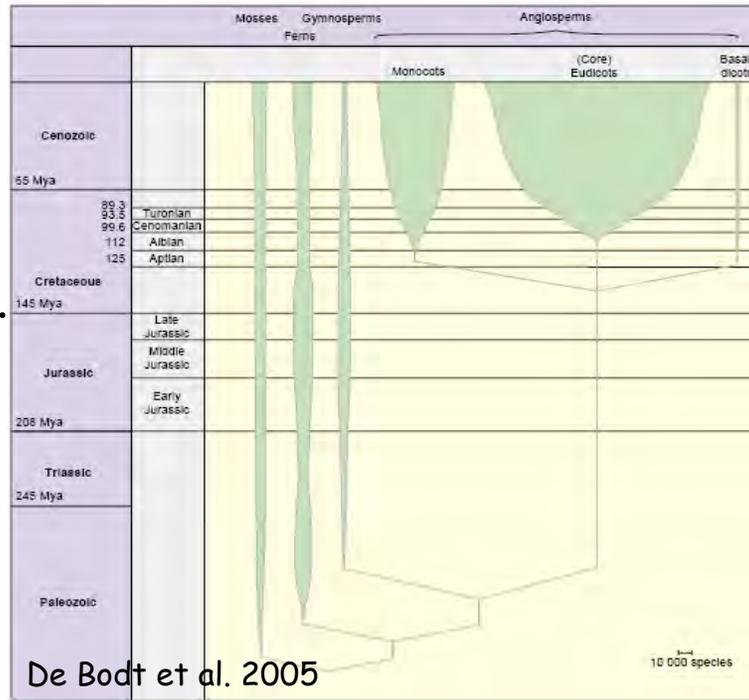


"The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery."
 (Charles Darwin in a letter to Sir Joseph Hooker, 1879)



Archaeoartus liaoningensis
 (140 million year old fossil)

The leaf-like structures on the stem are pods containing the seeds, a characteristic unique to flowering plants.



assumed ancient whole-genome duplication events

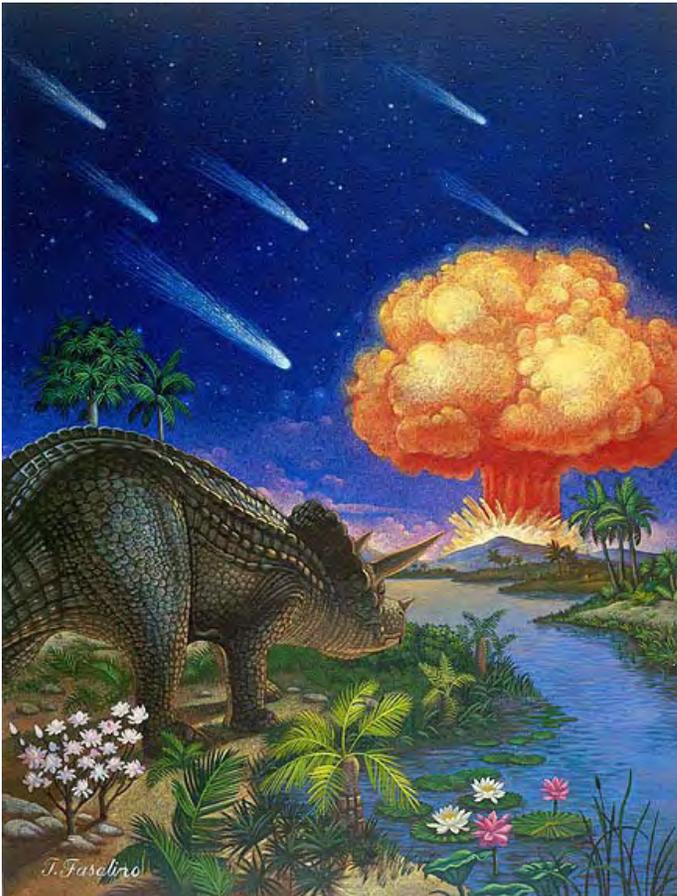
There is evidence of ancient polyploidy throughout the major angiosperm lineages. It means that a genome-scale duplication event probably occurred PRIOR to the rapid diversification of flowering plants

Plants with double genomes might have had a better chance to survive the Cretaceous–Tertiary extinction event

Jeffrey A. Fawcett^{a,b,1}, Steven Maere^{a,b,1}, and Yves Van de Peer^{a,b,2}

PNAS 106 (2009)

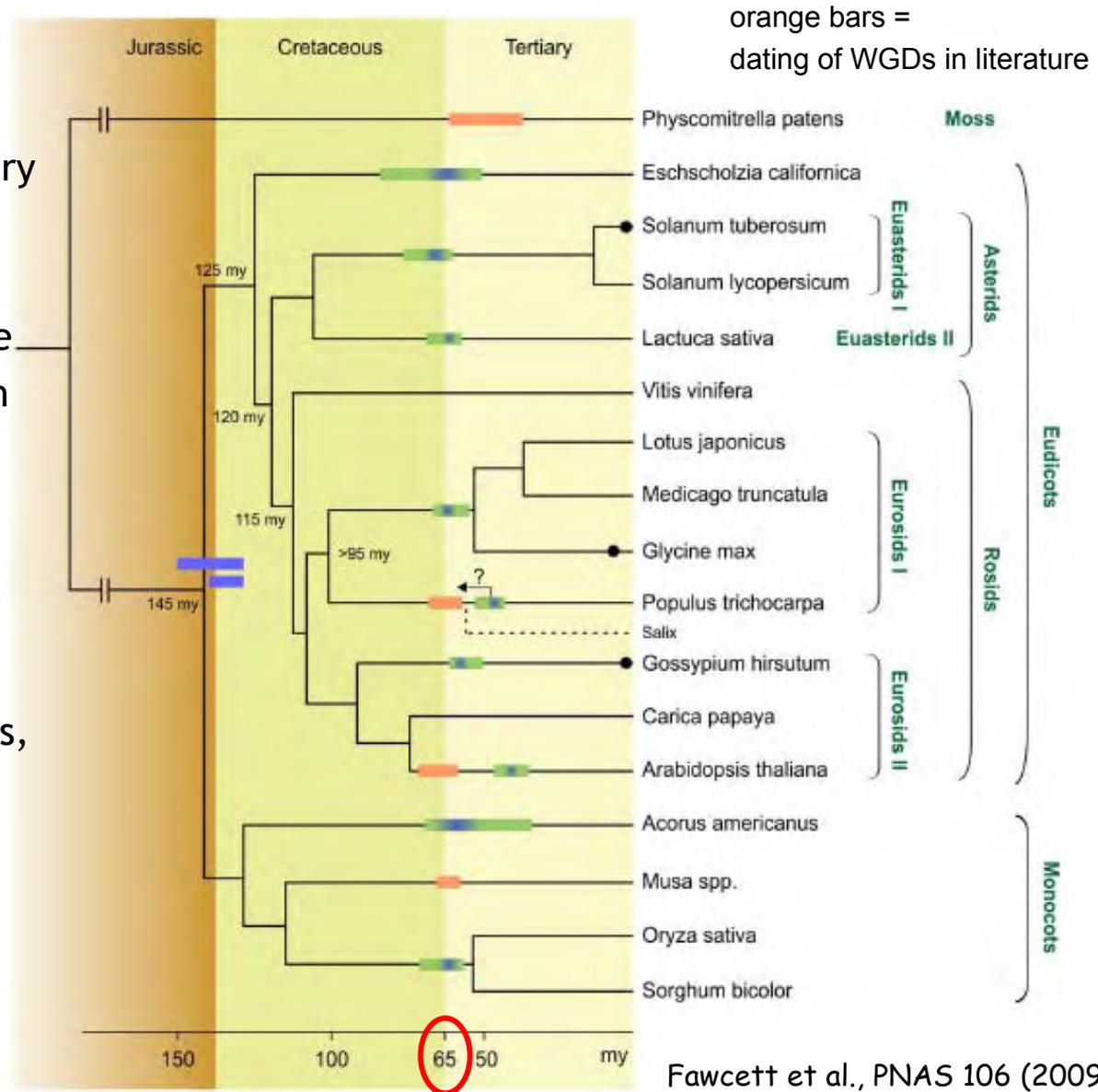
^aDepartment of Plant Systems Biology, Flanders Institute for Biotechnology, 9052 Gent, Belgium; and ^bDepartment of Plant Biotechnology and Genetics, Ghent University, 9052 Gent, Belgium



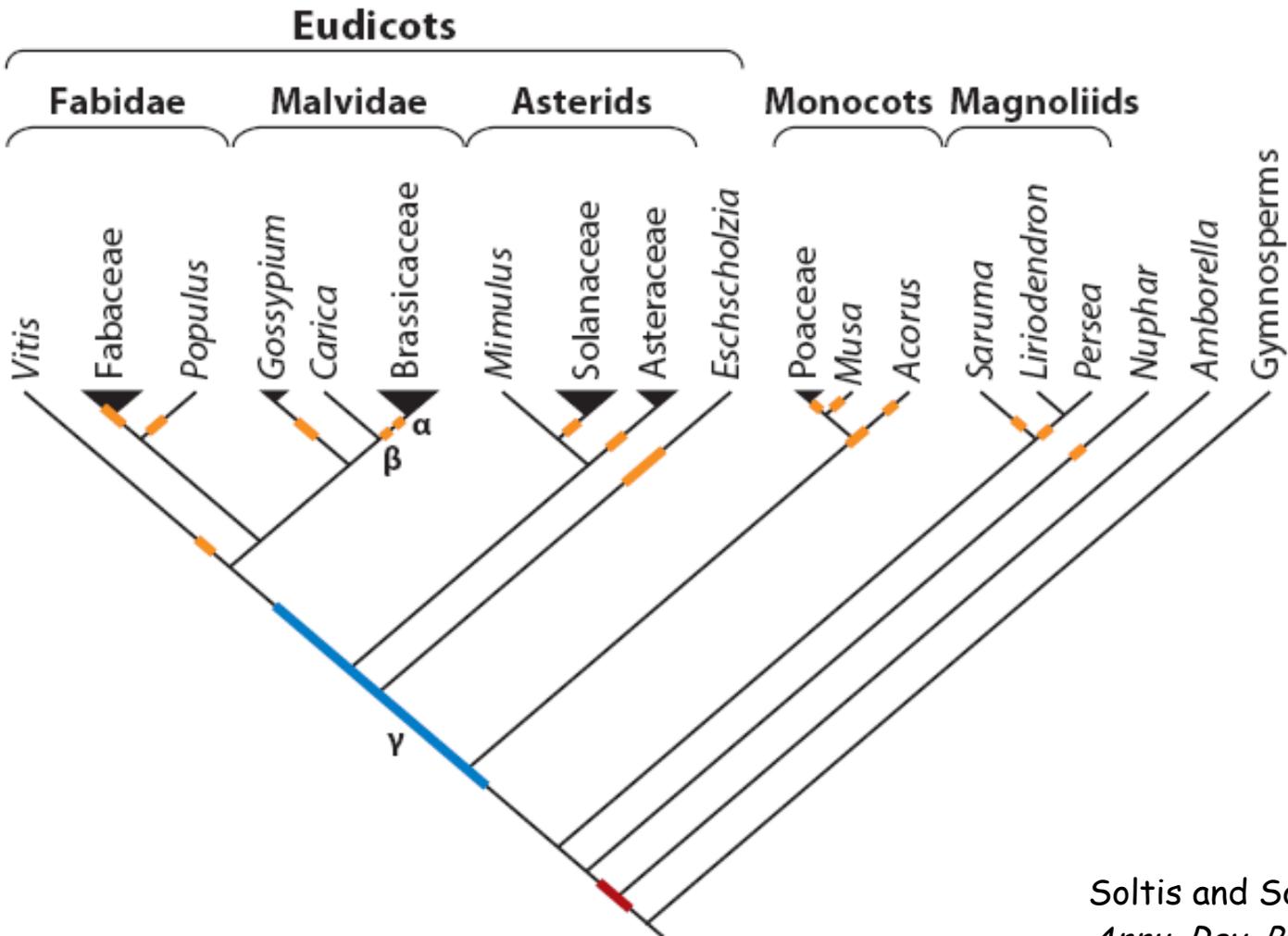
Could WGD event(s) help plants to survive the mass extinction (one or more catastrophic events such as a massive asteroid impact) at the Cretaceous–Tertiary boundary ?

Phylogenetic tree of flowering plants with assumed WGD events

- WGDs clustered around the Cretaceous-Tertiary (KT) boundary
- the KT extinction event - the most recent mass extinction (one or more catastrophic events such as a massive asteroid impact and/or increased volcanic activity)
- the KT extinction event - extinction of 60% of plant species, as well as a majority of animals, including dinosaurs



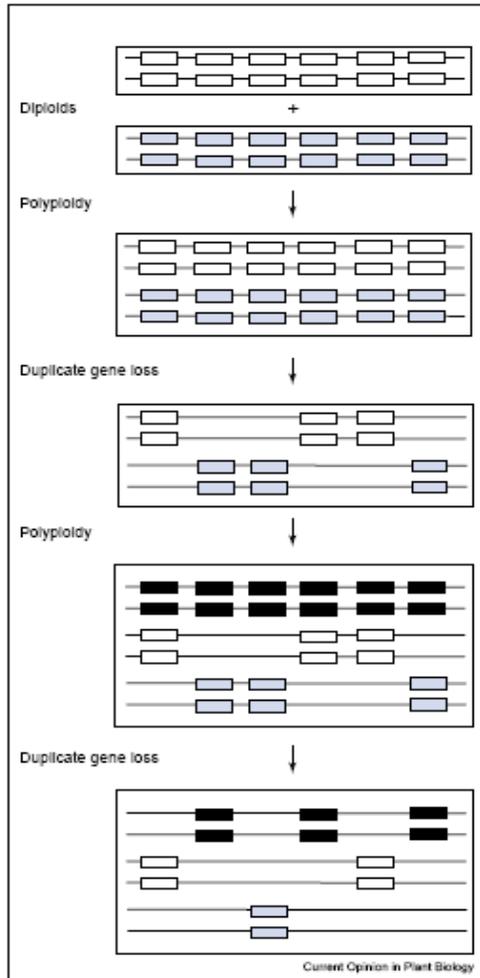
Whole-genome duplication (WGD) events in angiosperm evolution



Soltis and Soltis (2009),
Annu. Rev. Plant Biol.

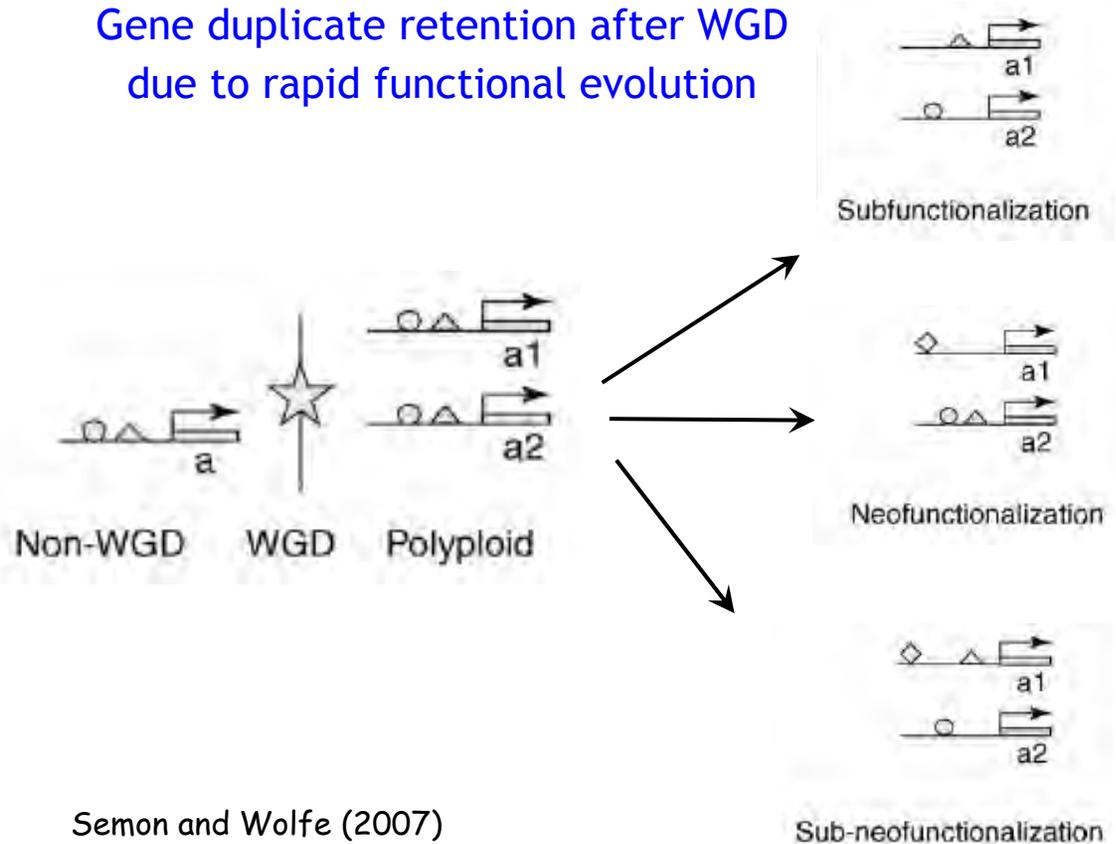
Whole-genome duplication, diploidization, and the consequences

Genome evolution through cyclic polyploidy



Adams and Wendel (2005)

Gene duplicate retention after WGD due to rapid functional evolution



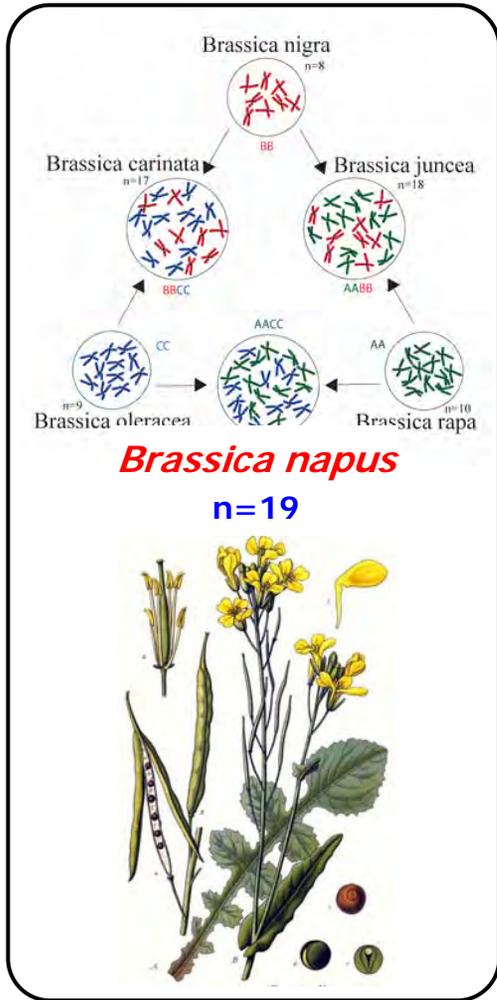
Semon and Wolfe (2007)

Gene-balanced duplications, like tetraploidy, provide predictable drive to increase morphological complexity

Michael Freeling^{1,3} and Brian C. Thomas²

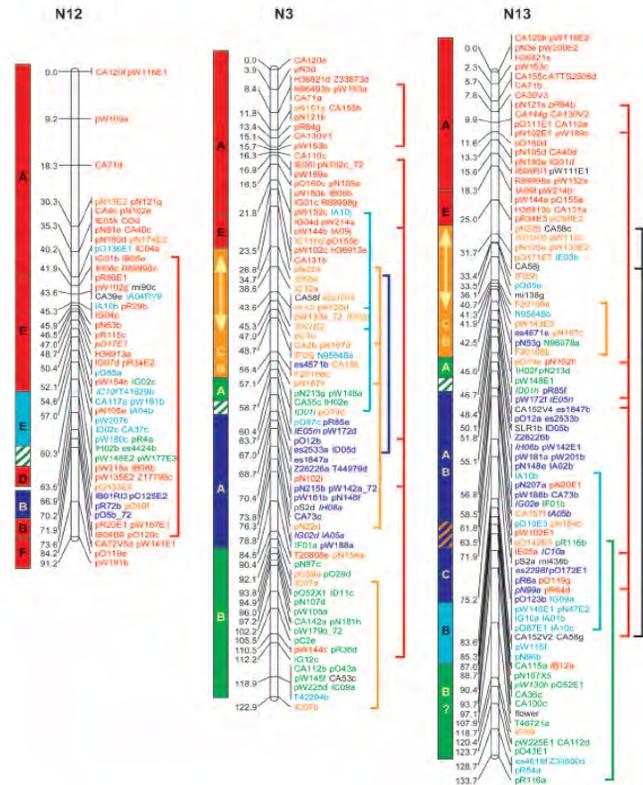
Genome Res 16 (2006)

Paleopolyploid evolution in *Brassica* and the Brassiceae



- comparative genetic analysis allowed the identification of a minimum of 21 conserved genomic units within the Arabidopsis genome, which can be duplicated and rearranged to generate the present-day *B. napus* genome

- the observed duplicated structure of the *B. napus* genome strongly suggests that the extant *Brassica* diploid species (n=8,9,10) evolved from a hexaploid ancestor



Paleopolyploid evolution in *Brassicaceae* analyzed by comparative chromosome painting

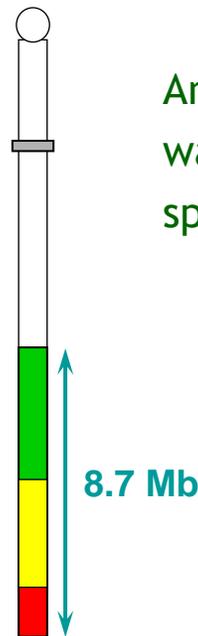
Chromosome triplication found across the tribe *Brassicaceae*

Martin A. Lysak,^{1,3,4} Marcus A. Koch,² Ales Pecinka,³ and Ingo Schubert³

¹Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, United Kingdom; ²Institute for Plant Sciences, University of Heidelberg, 69120 Heidelberg, Germany; ³Institute of Plant Genetics and Crop Plant Research (IPK), 06466 Gatersleben, Germany



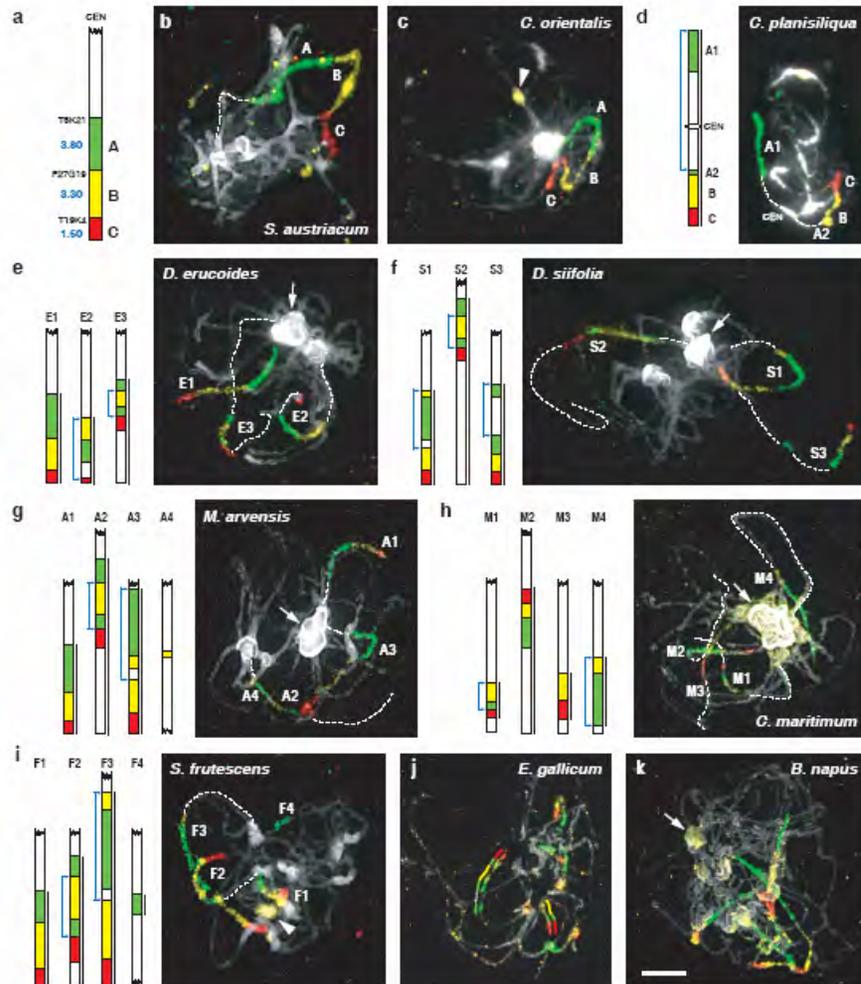
A. thaliana
chromosome 4



An 8.7-Mb BAC contig of *Arabidopsis thaliana*
was used for comparative painting in 21
species of the tribe *Brassicaceae*

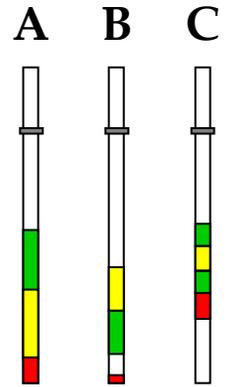
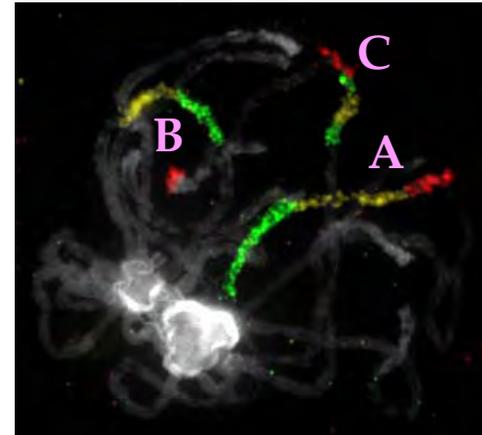
The 8.7-Mb segment was found triplicated in the majority of *Brassicaceae* species

$2n = 14, 16, 18, 20, 22, 28, 30, 34, 36, 38$



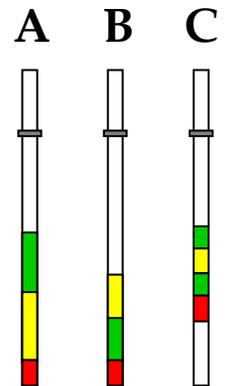
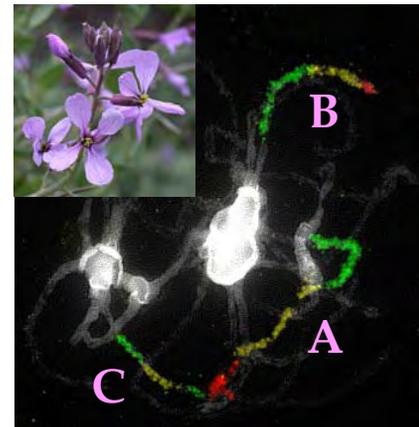
Diplotaxis erucoides

($2n=14$)

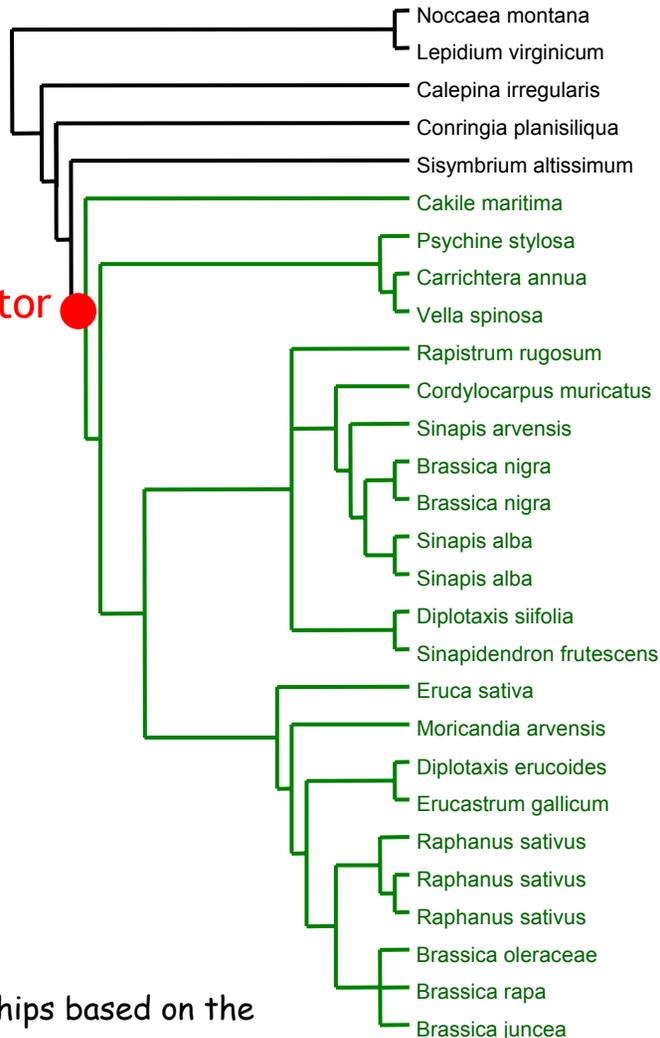


Moricandia arvensis

($2n=28$)

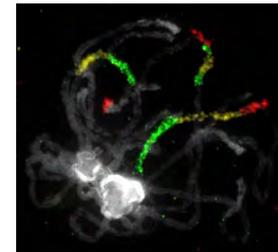


Congruence between cytogenetic and molecular phylogenetic data. *Brassicaceae* have a common hexaploid ancestor.



hexaploid ancestor ●

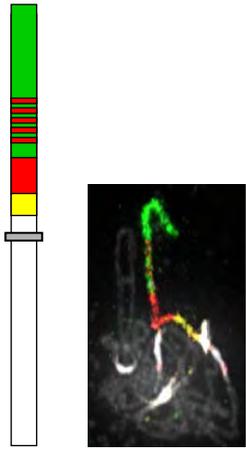
genome triplication



Phylogenetic relationships based on the chloroplast 5-*trnL* (UAA)-*trnF*(GAA) region

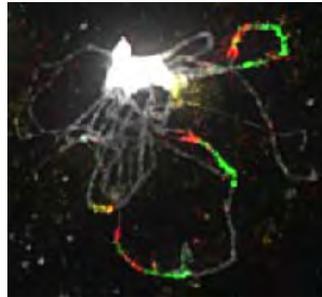
Further cytogenetic evidence of the paleohexaploidy event in the ancestry of *Brassicaceae*

BAC contig covering the upper arm of *A. thaliana* chromosome 3 used for comparative painting in *Brassicaceae* spp.



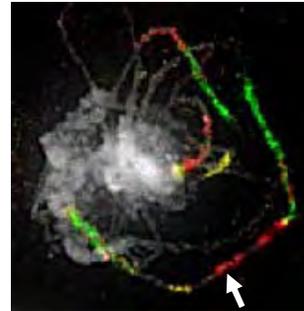
Morisia monanthos

(2n=14)

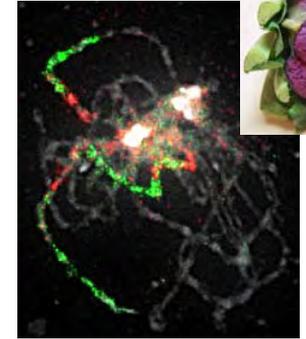


Physorhynchus chamaerapistrum

(2n=32)



translocation (→ fusion)



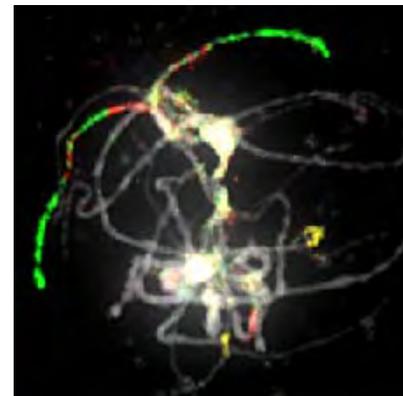
Brassica oleracea

(2n=18)



Orychophragmus violaceus

(2n=24)



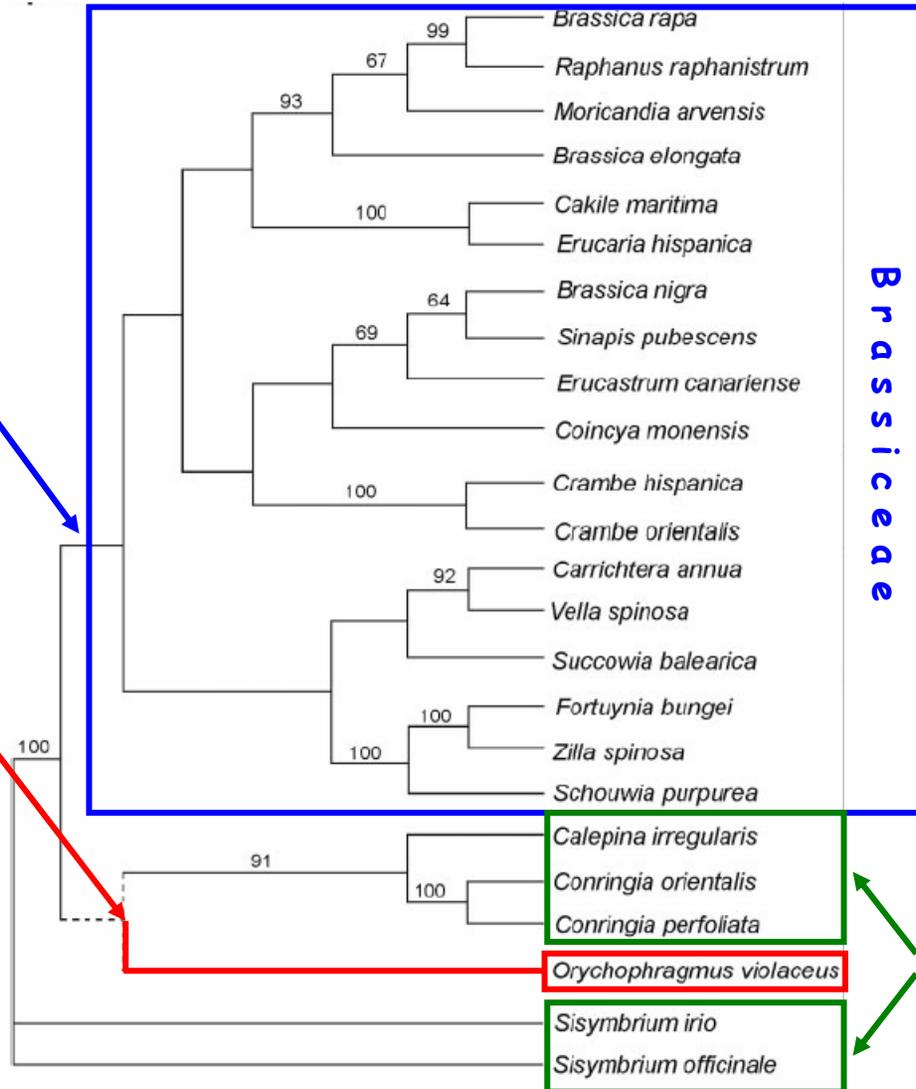
paleotetraploid ?

Congruence between phylogenetic and cytogenetic data?

Paleotetraploid origin of *Orychophragmus*

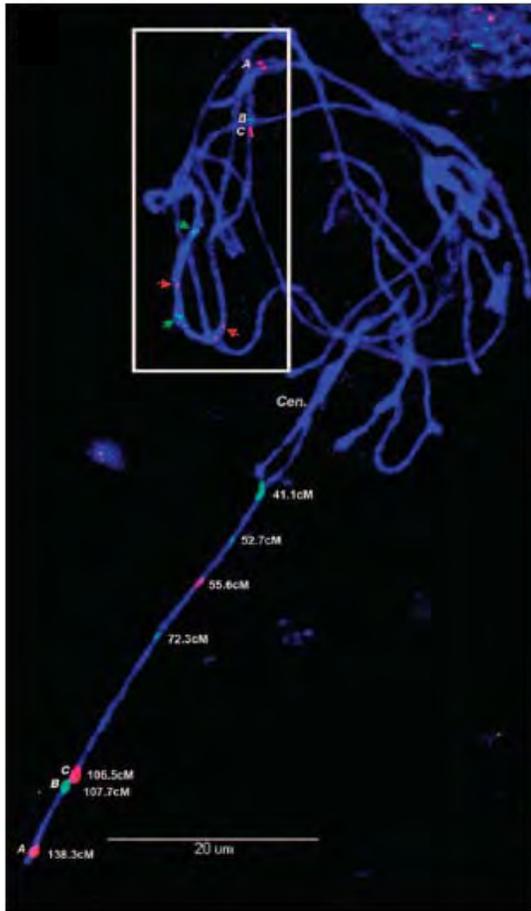
hexaploid ancestor
(Lysak *et al.* 2005)

tetraploid ancestor ?



"true" diploids
(Lysak *et al.* 2005)

'Recent' paleopolyploidy event in soybean (*Glycine max*)

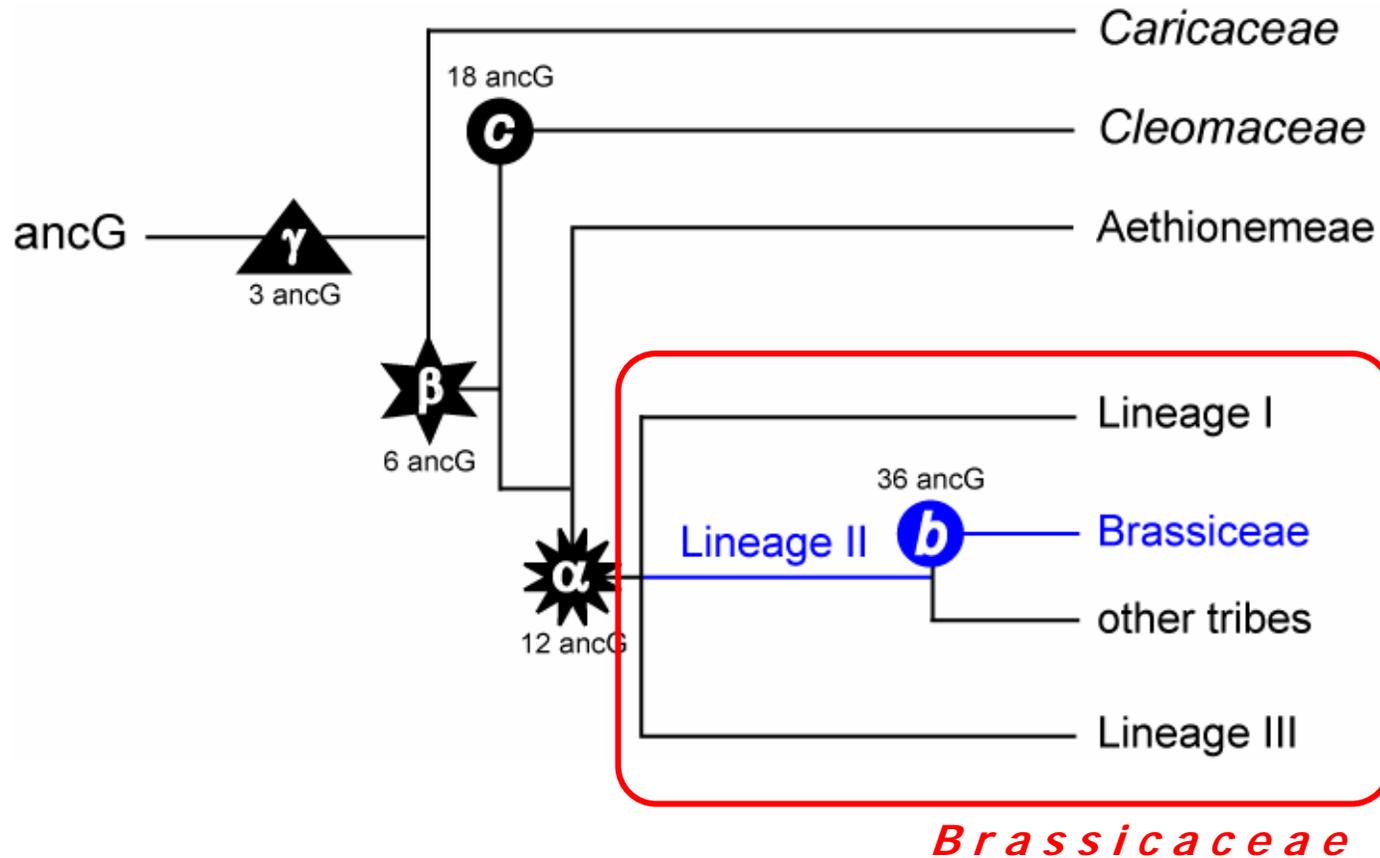


FISH mapping of seven BACs from chromosome 19 on pachytene chromosomes from soybean. BACs were localized on the long arm of chromosome 19. The inset highlights secondary signals from the putative homeologous chromosome.

- $2n=40$ karyotype, derived from at least two rounds of whole-genome duplication or polyploidy events
- cytogenetically, soybean behaves like a diploid and has disomic inheritance
- fluorescence *in situ* mapping of seven putatively gene-rich BACs from chromosome 19 revealed that there is extensive homeology with another chromosome pair



Whole-genome duplications in the evolution of flowering plants (and *Brassicaceae*)



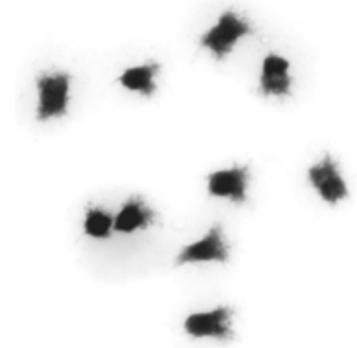
Karyotype evolution in Australian Camelinaeae species



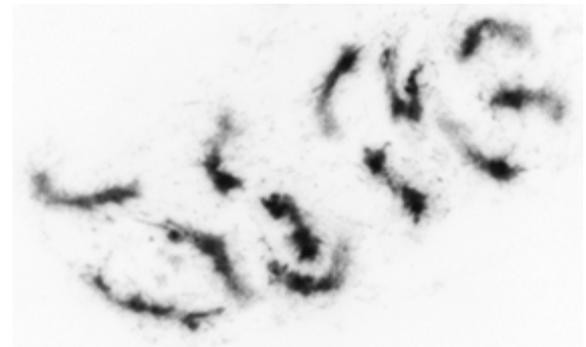
Stenopetalum nutans (n=4)



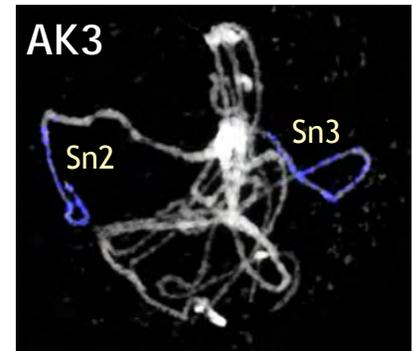
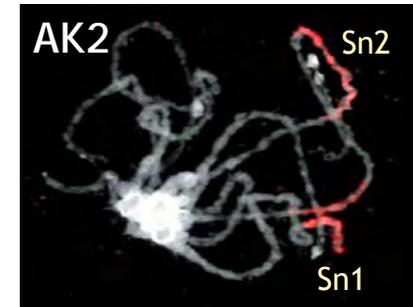
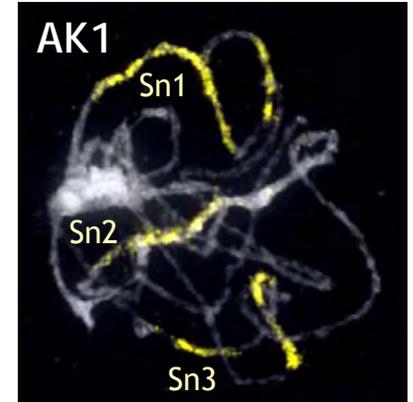
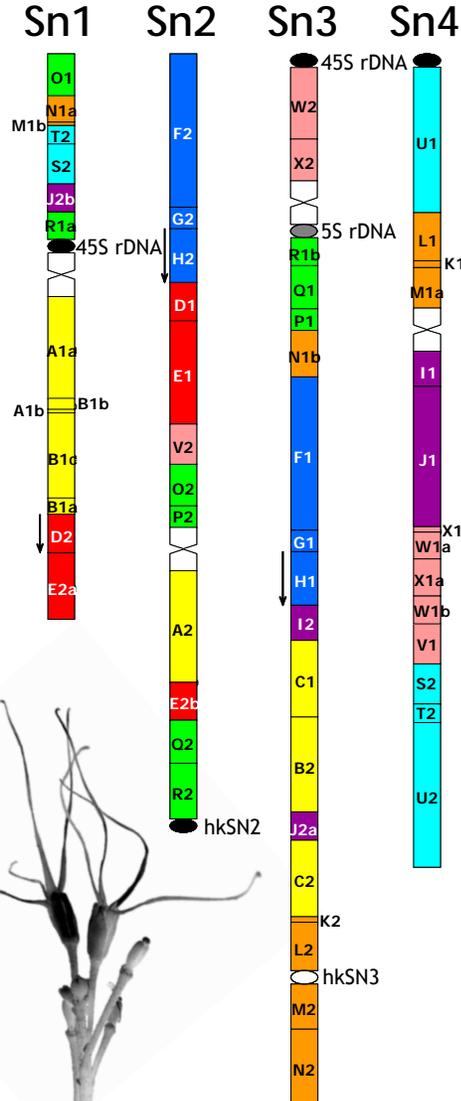
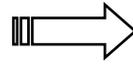
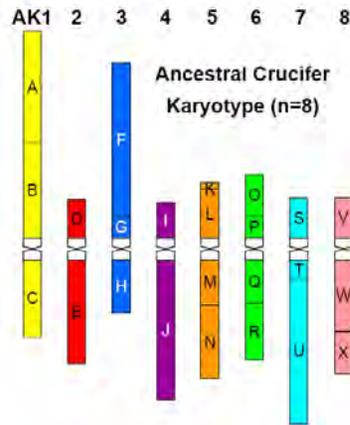
Arabidella eremigena (n=5)



Ballantinia antipoda (n=6)



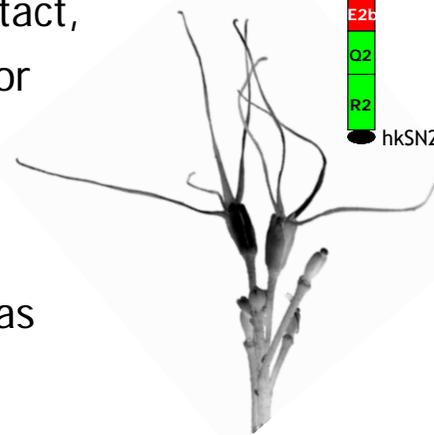
Australian Camelineae species experienced a whole-genome duplication followed by chromosome number reduction



All 24 genomic blocks (GBs) of the ACK (n=8) are duplicated in *Stenopetalum nutans*.

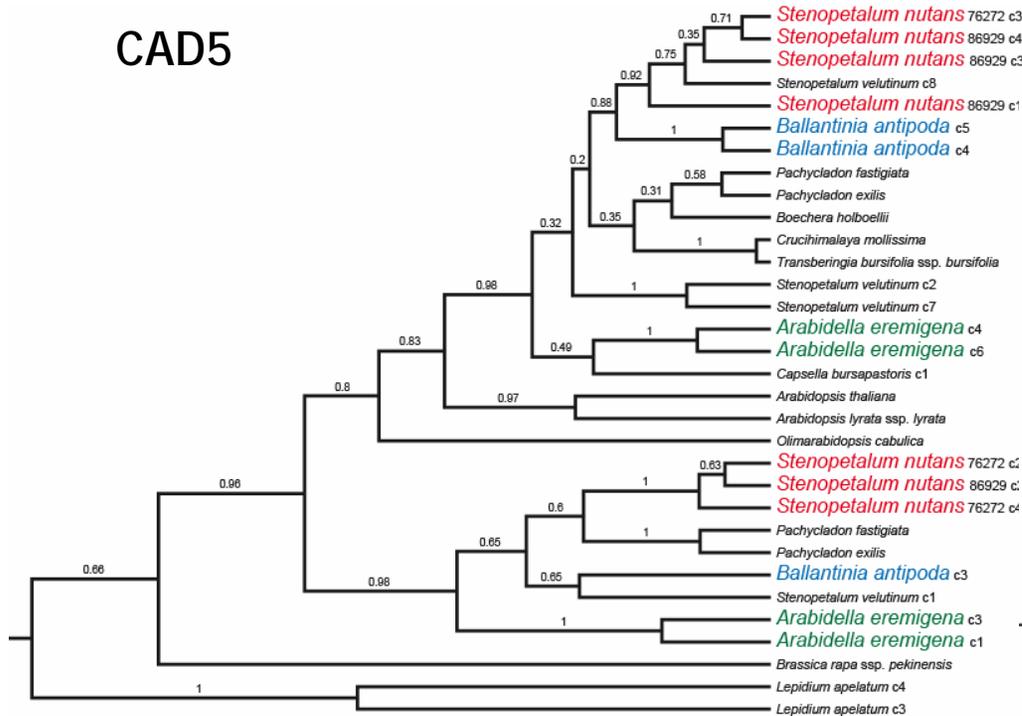
Out of 48 GBs, 39 remained intact, whereas 9 were split into two or three sub-blocks.

In *Ballantinia*, only 18 GBs are duplicated; 6 GBs were found as single copies.

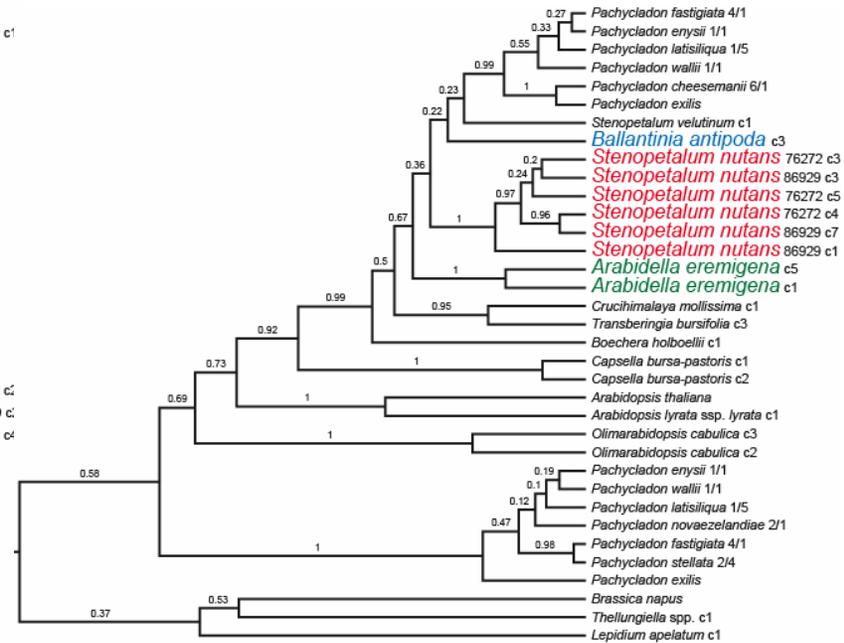


Analysis of single-copy nuclear genes shows the retention as well as the loss of gene paralogs after the WGD event(s)

CAD5

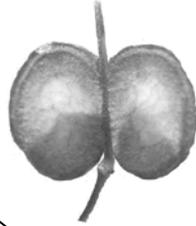
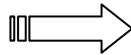


ms

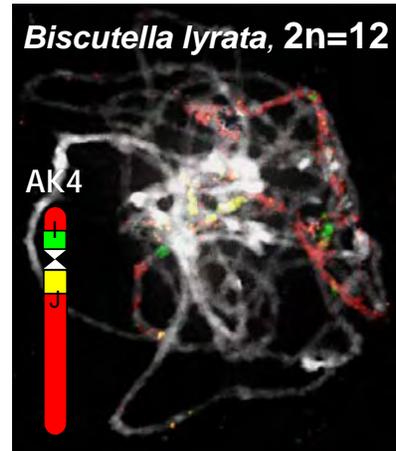


Mesopolyploid WGD events in *Brassicaceae* revealed by comparative chromosome painting

whole-genome
duplication



Biscutelleae



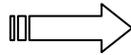
Cochlearieae

(*Cochlearia pyrenaica*, $2n=12$)

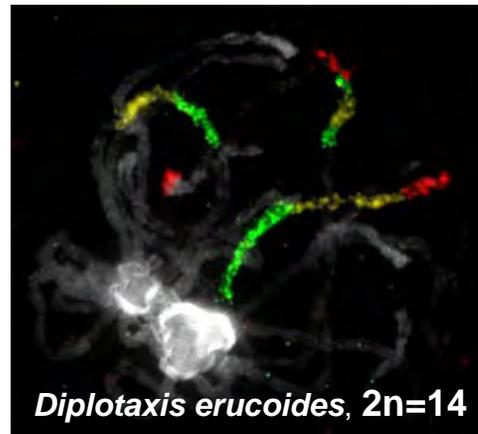
Iberideae

(*Iberis umbellata*, $2n=18$)

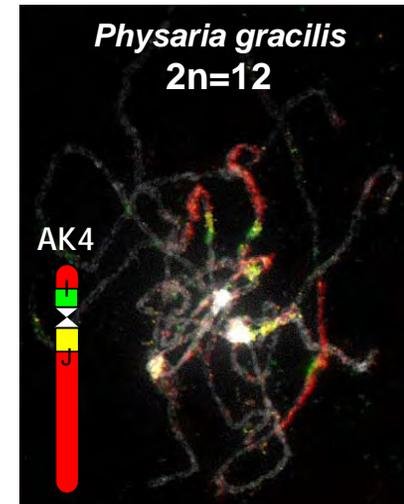
whole-genome
triplication



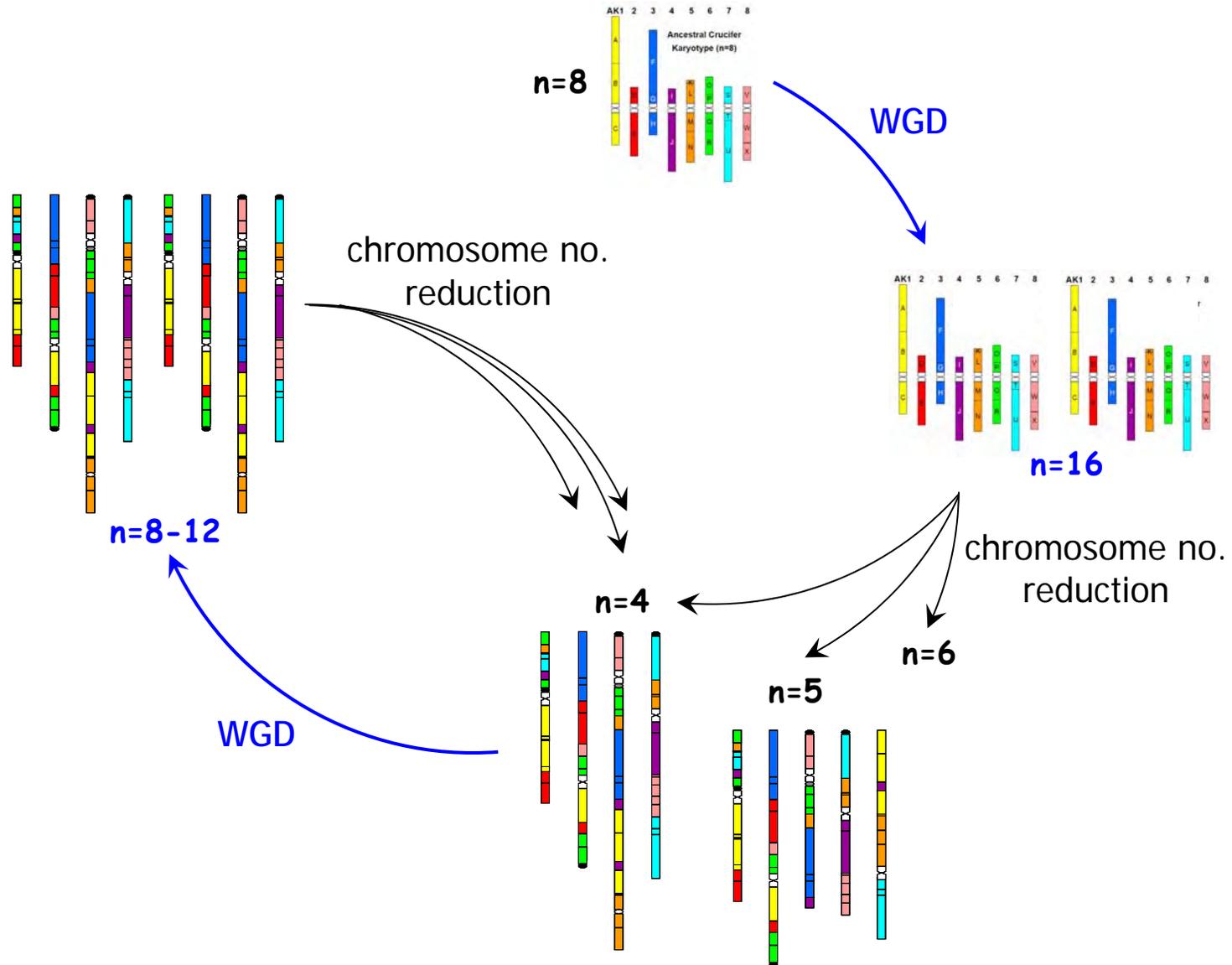
Brassicaceae



Physarieae



Model of genome evolution in *Brassicaceae*: cyclic whole-genome duplication and diploidization



Summary

'Many more, if not all, higher plant species, considered as diploids because of their genetic and cytogenetic behaviour, are actually ancient polyploids'

(Paterson *et al.* 2005)