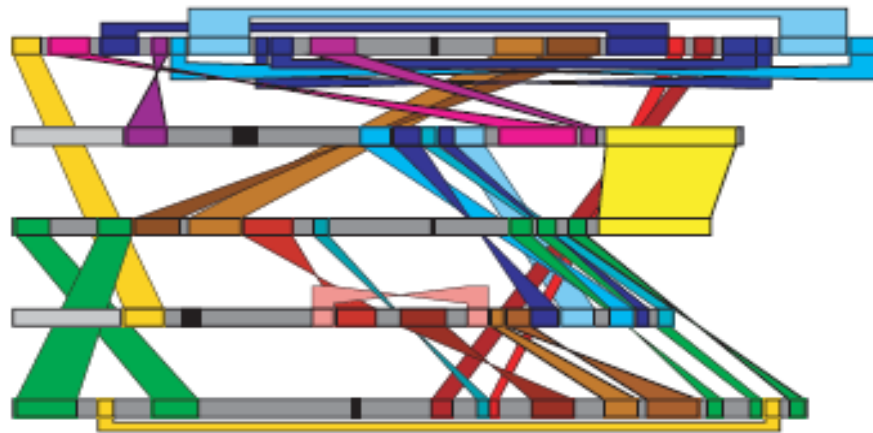
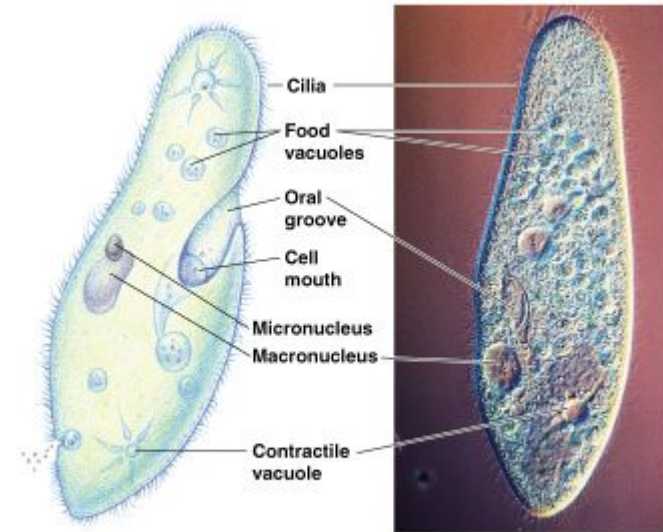


Whole-genome duplications and paleopolyploidy



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
- 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

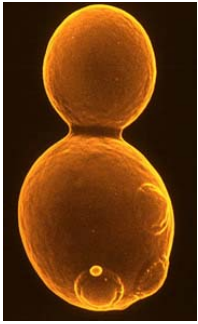




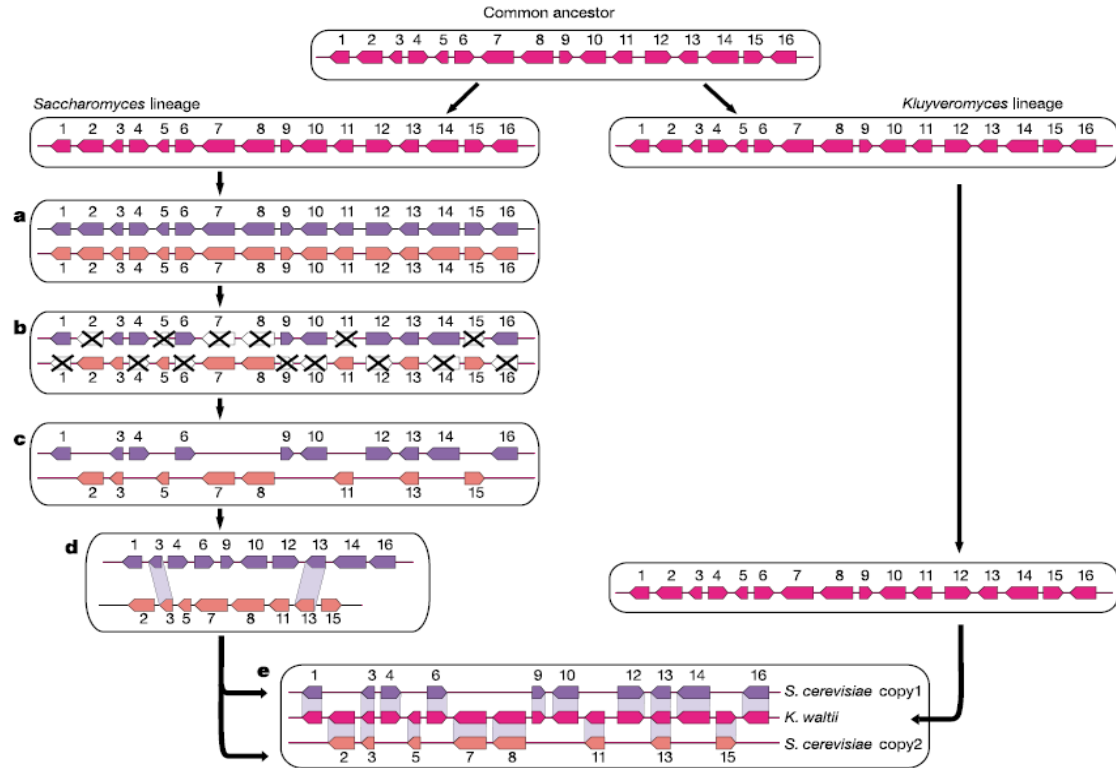
Whole-genome duplications in yeast

- 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 whole-genome duplication 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

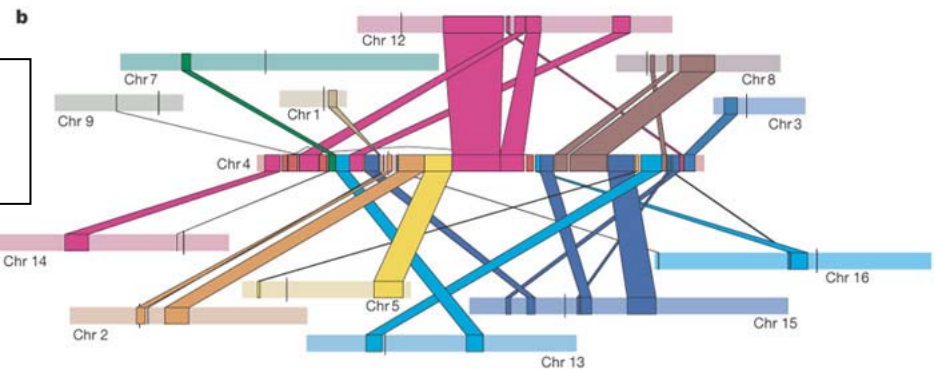
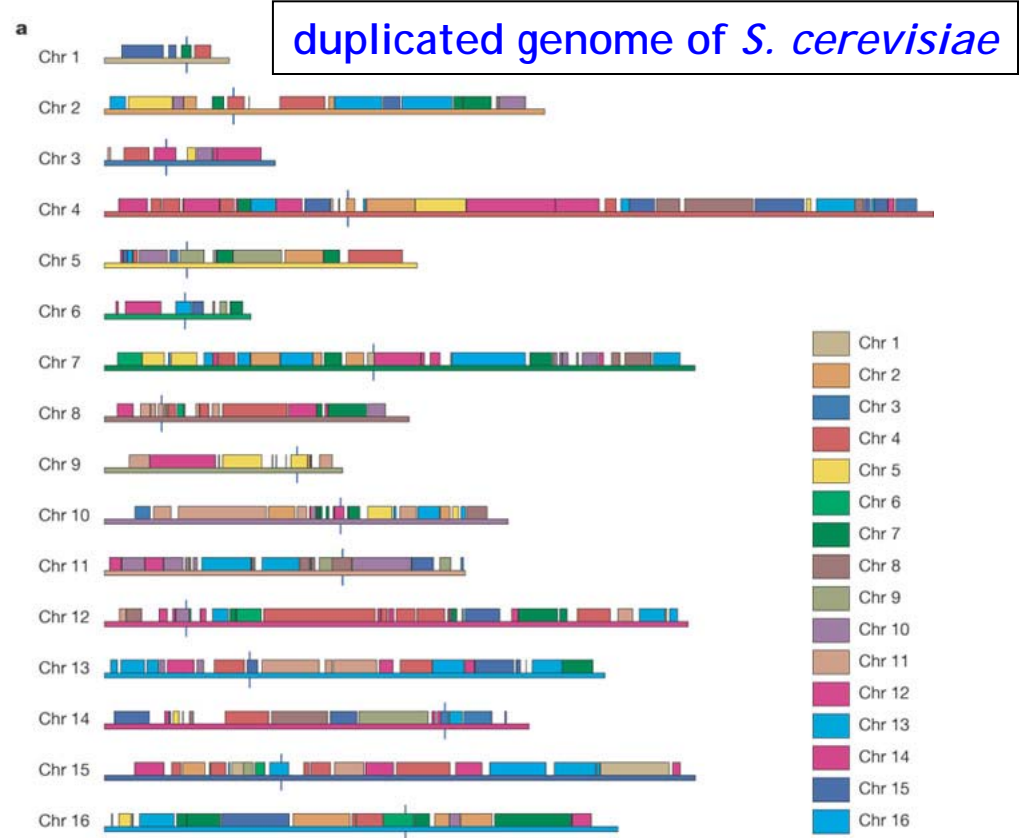
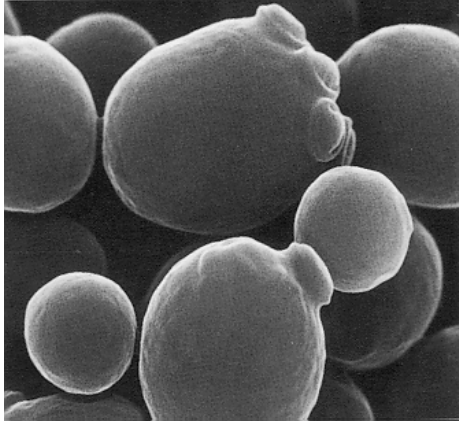


Kellis *et al.* 2004,
Nature 428



- after divergence from *K. waltii*, the *Saccharomyces* lineage underwent a genome duplication event (2 copies of every gene and chromosome)
- duplicated genes underwent mutations and some were lost
- two copies were kept for only a small minority of duplicated genes
- the conserved order of duplicated genes (nos. 3-13) across different chromosomal segments
- 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

Charles Darwin's abominable mystery solved?

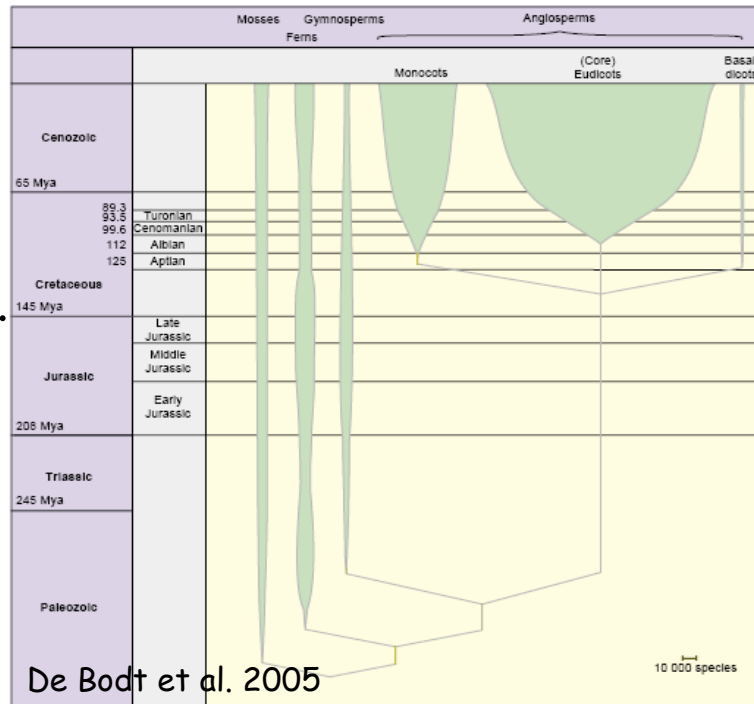


"The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery."
 (Charles Darwin in a letter to Sir Joseph Hooker, 1879)



Archaeoфрактus 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

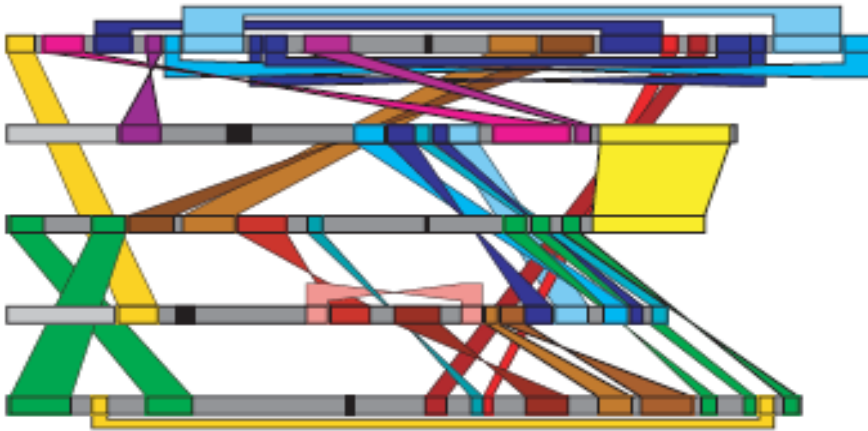
There is evidence of ancient polyploidy throughout the major angiosperm lineages. It means that a genome-scale duplication event probably occurred PRIOR to the rapid diversification of flowering plants

Is Arabidopsis a paleotetraploid?



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

The Arabidopsis Genome Initiative*

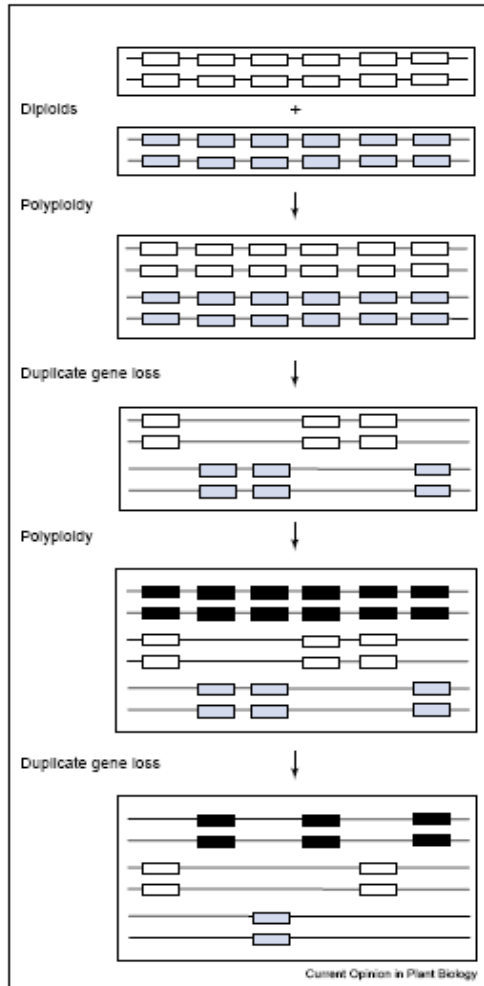


AGI (2000)

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.

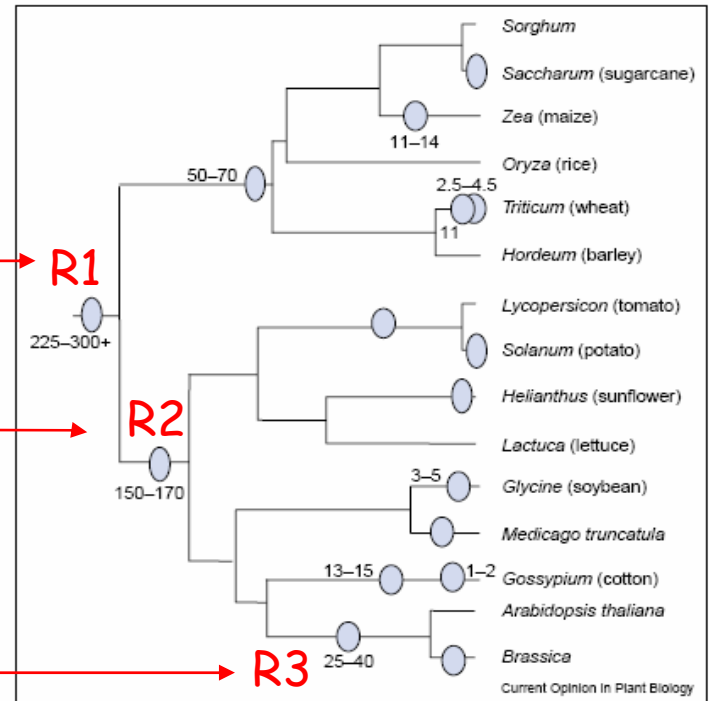
Whole-genome duplication, diploidization, and the consequences

Genome evolution through cyclic polyploidy



Adams and Wendel (2005)

inferred
paleopolyploidy
events



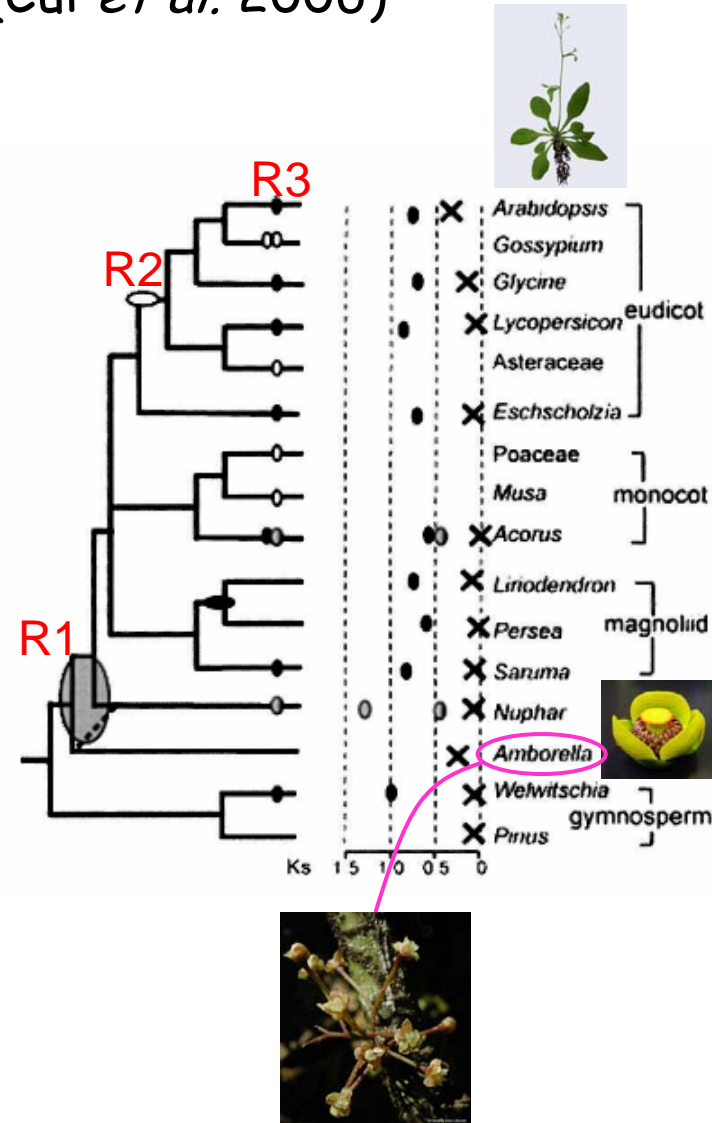
Gene-balanced duplications, like tetraploidy, provide predictable drive to increase morphological complexity

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

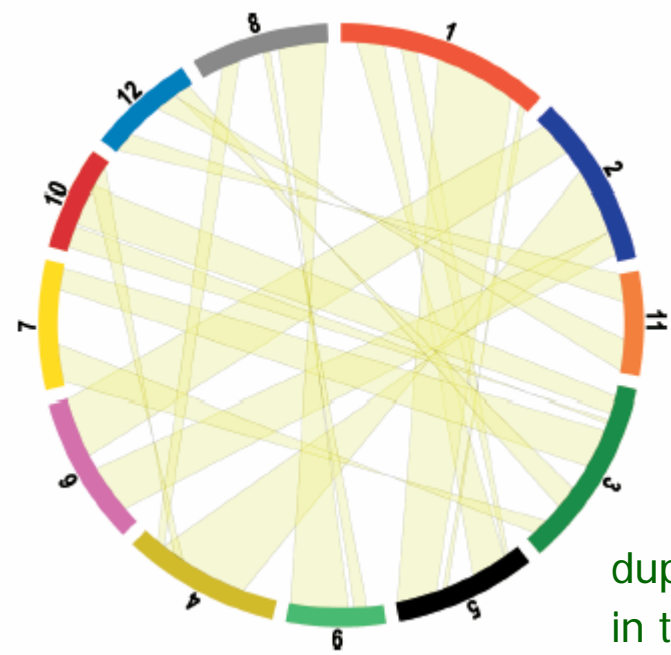
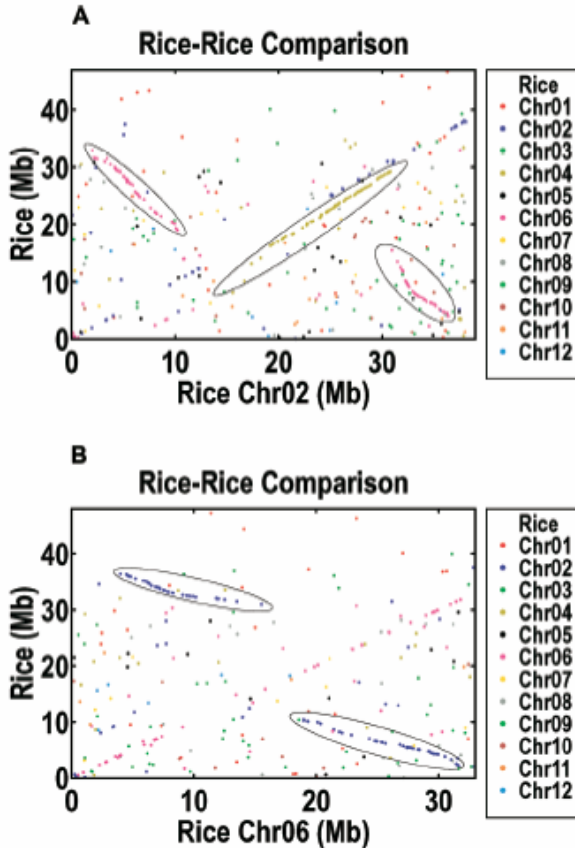
Genome Res 16 (2006)

Widespread genome duplications throughout the history of flowering plants (Cui *et al.* 2006)

- evidence for ancient genome-wide duplications in the basal angiosperm lineages including *Nuphar advena* (*Nymphaeaceae*) and the magnoliids *Persea americana* (*Lauraceae*), *Liriodendron tulipifera* (*Magnoliaceae*), and *Saruma henryi* (*Aristolochiaceae*)
- independent genome duplications in the basal eudicot *Eschscholzia californica* (*Papaveraceae*) and the basal monocot *Acorus americanus* (*Acoraceae*)
- independent duplications documented for ancestral grass (*Poaceae*) and core eudicot lineages (**R2 duplication**)
- gymnosperms: equivocal evidence for ancient polyploidy in *Welwitschia mirabilis* (Gnetales) and no evidence for polyploidy in pine (*Pinus*), although gymnosperms generally have much larger genomes than angiosperms!
- an ancient duplication in *Nuphar* may represent a genome duplication (**R1**) in the common ancestor of all or most extant angiosperms, except *Amborella*



Whole-genome duplication in rice (*Oryza sativa*)



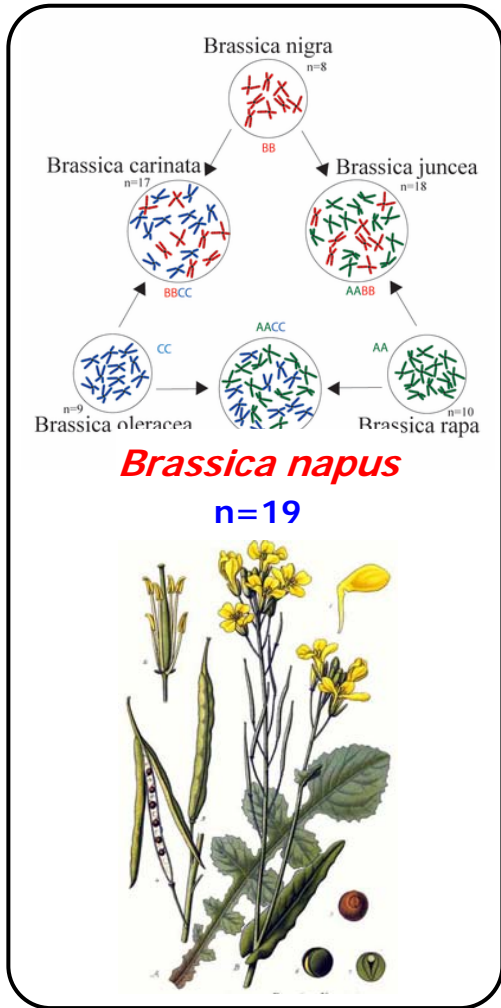
duplicated segments
in the rice genome

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.

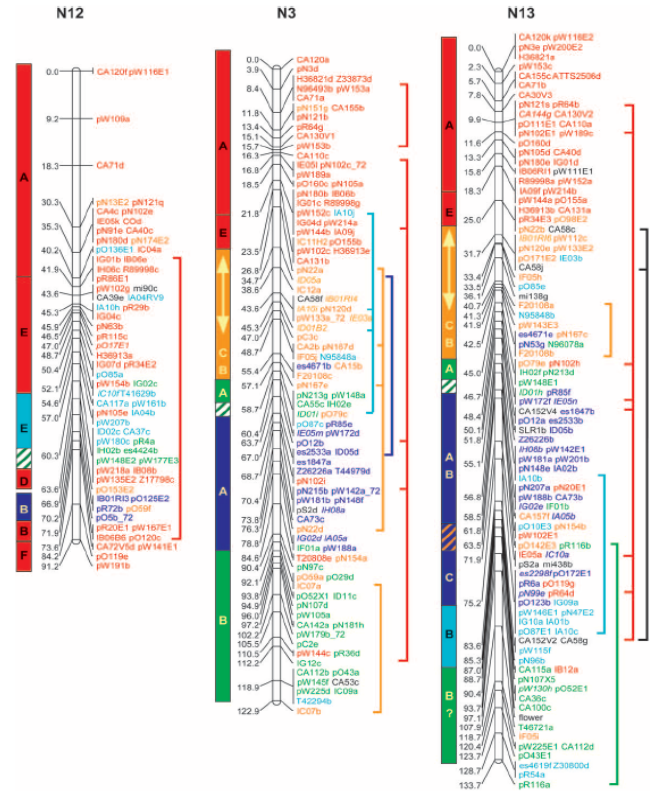
Yu *et al.* (2005) The genomes of *Oryza sativa*: A history of duplications. PLoS Biol 3

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

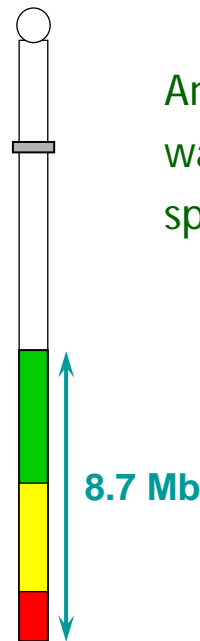
Chromosome triplication found across the tribe *Brassicaceae*

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



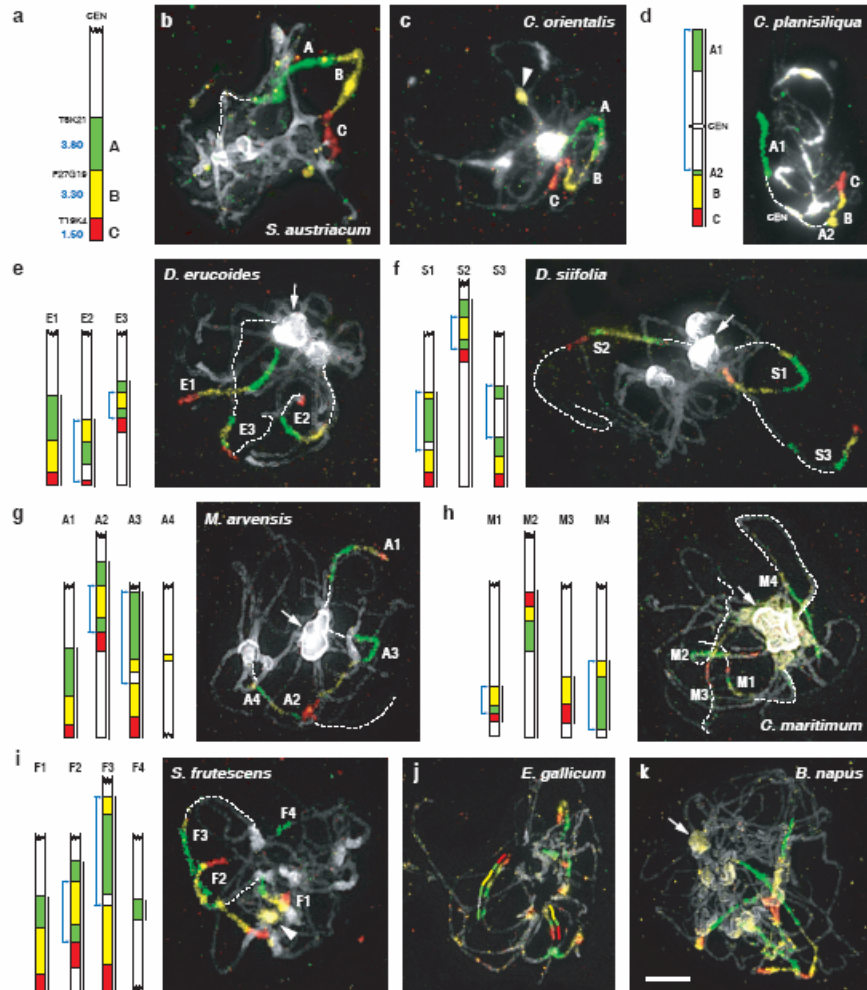
A. thaliana
chromosome 4



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

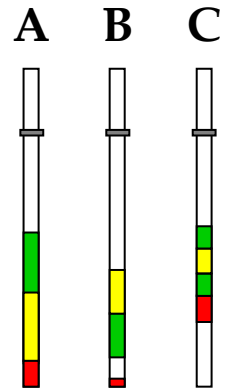
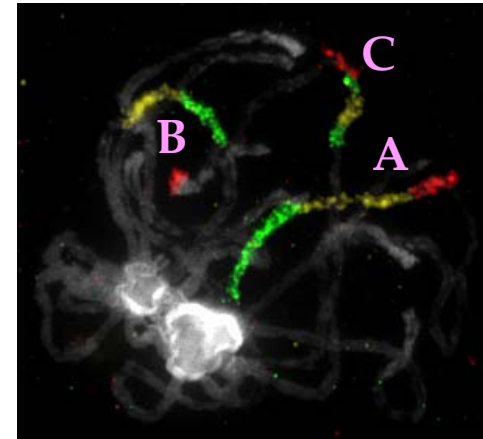
The 8.7-Mb segment was found triplicated in the majority of *Brassicaceae* species

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



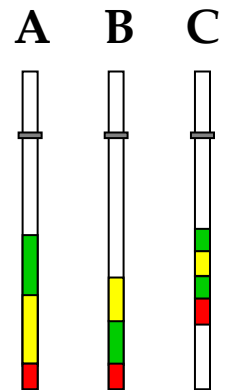
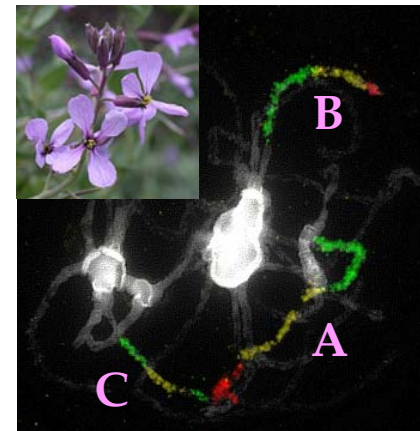
Diplotaxis erucoides

($2n=14$)

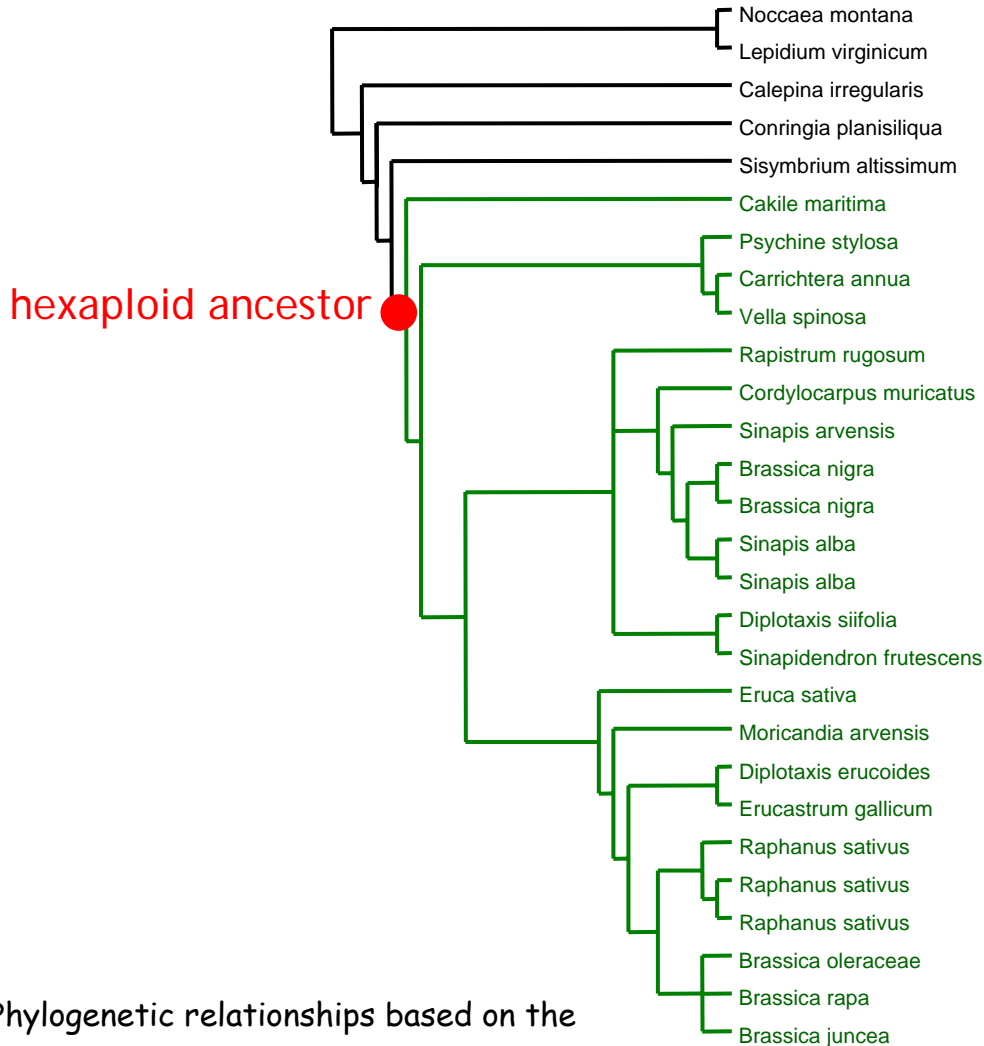


Moricandia arvensis

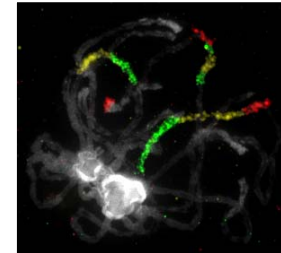
($2n=28$)



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



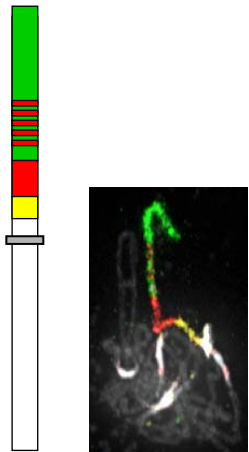
genome triplication



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

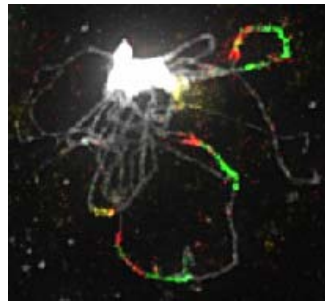
Further cytogenetic evidence of the paleohexaploidy event in the ancestry of *Brassicaceae*

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



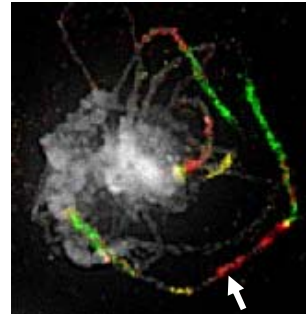
Morisia monanthos

(2n=14)

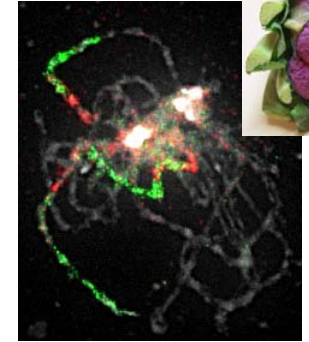


Physorhynchus chamaerapistrum

(2n=32)



translocation (→ fusion)



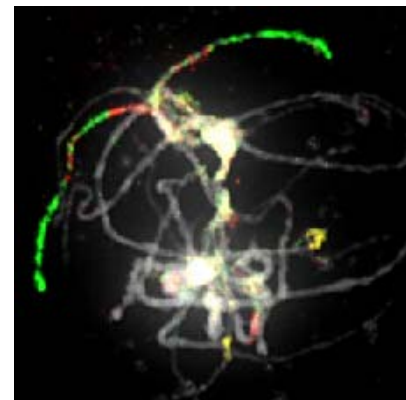
Brassica oleracea

(2n=18)



Orychophragmus violaceus

(2n=24)



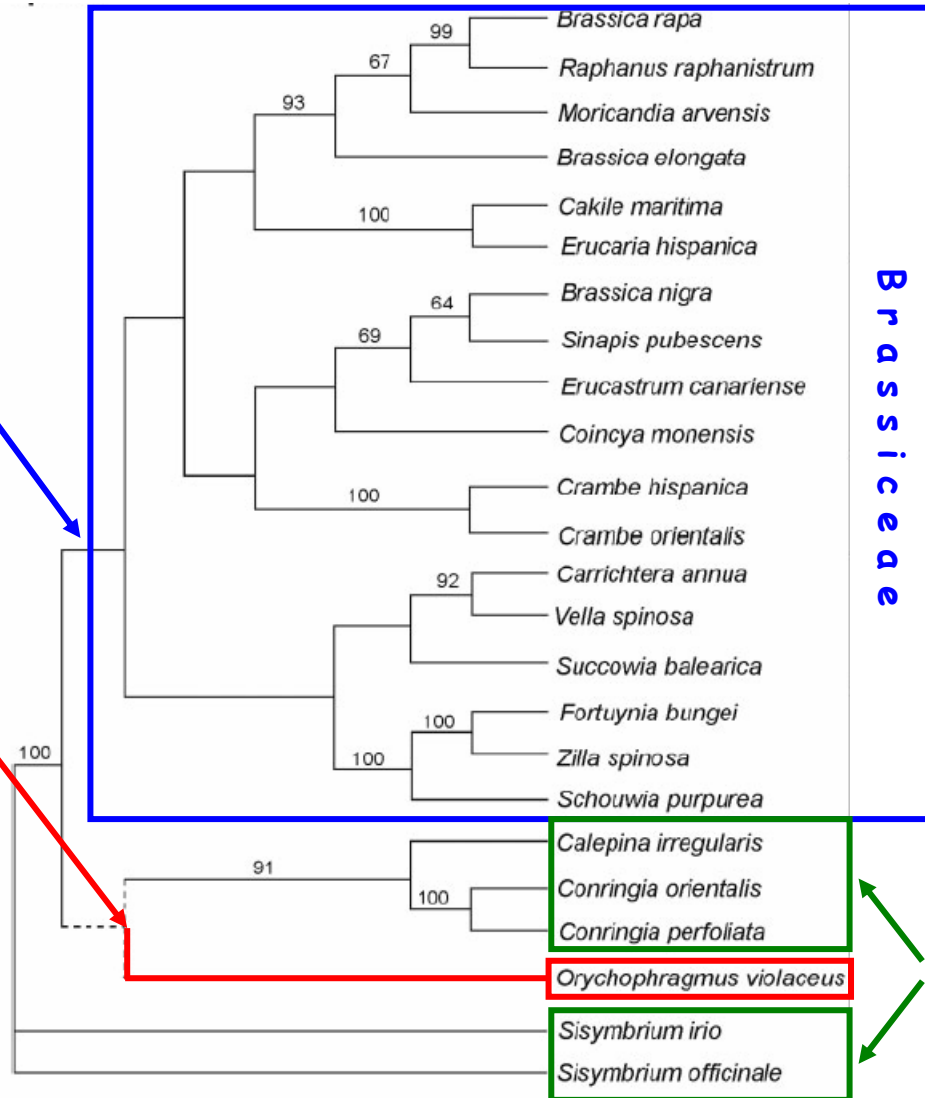
paleotetraploid ?

Congruence between phylogenetic and cytogenetic data?

Paleotetraploid origin of *Orychophragmus*

hexaploid ancestor
(Lysak *et al.* 2005)

tetraploid ancestor ?



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

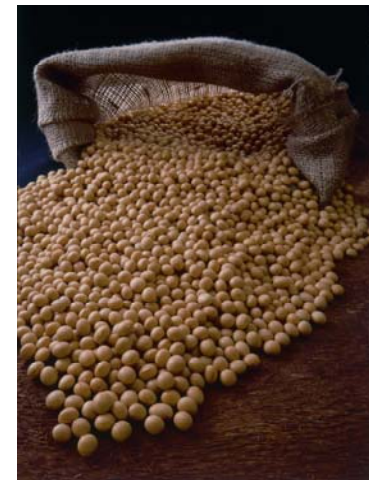
modified from Warwick & Sauder 2005

'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



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)