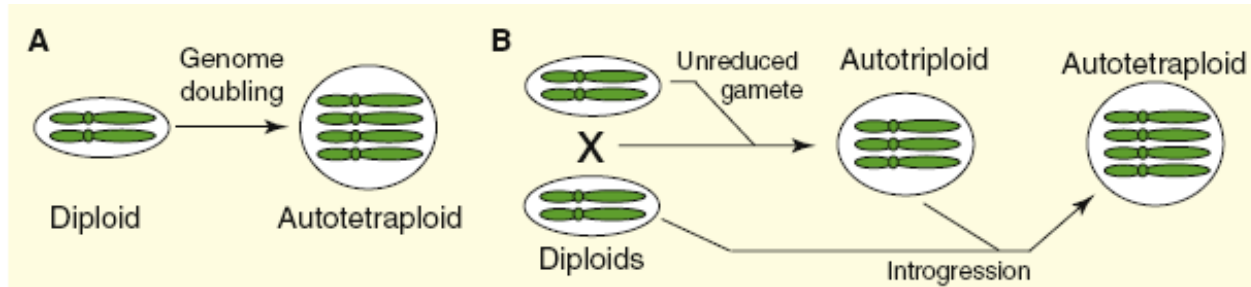


(Paleo)Polyploidy – When Things Get Bigger

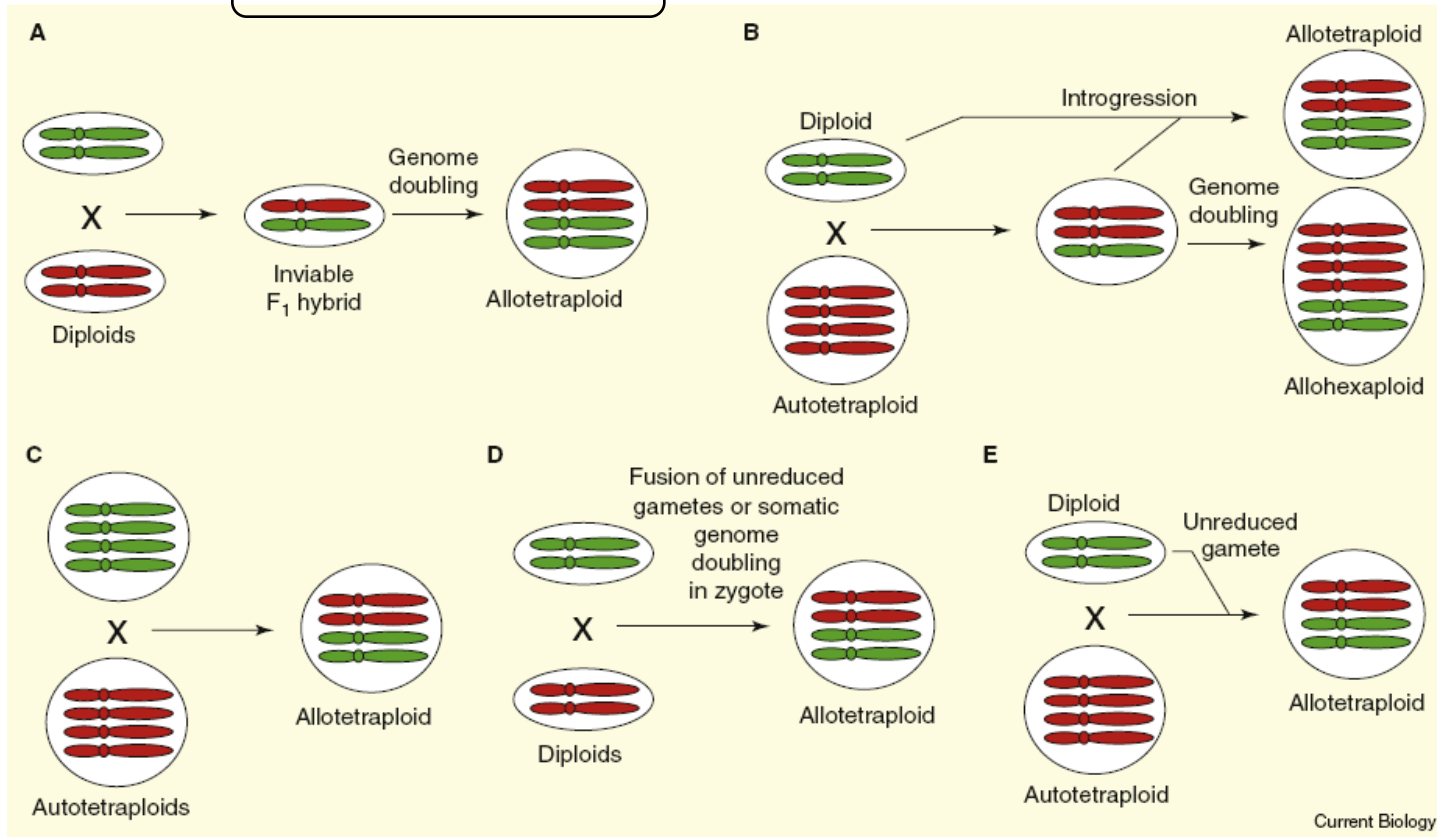


Whole-genome duplications



AUTOPOLYPLOIDY

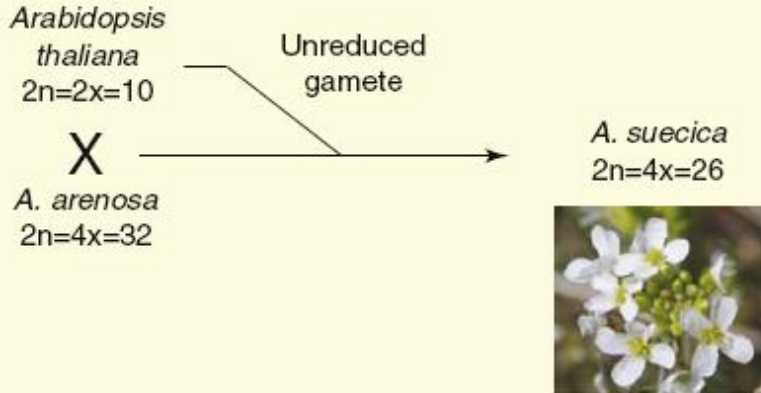
ALLOPOLYPLOIDY



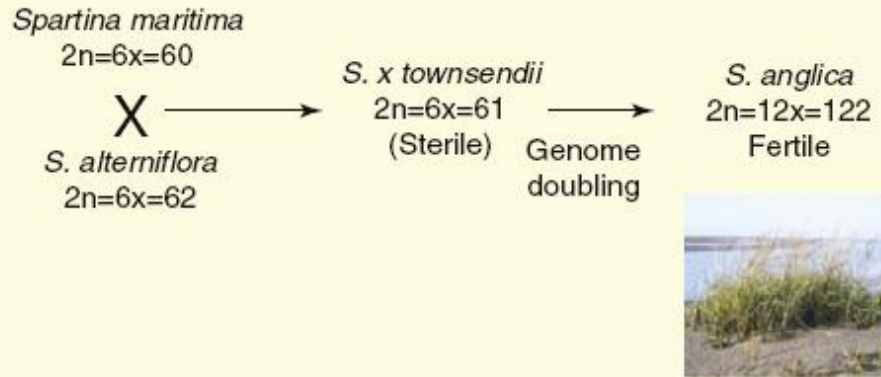
Current Biology

Examples of allopolyploid speciation

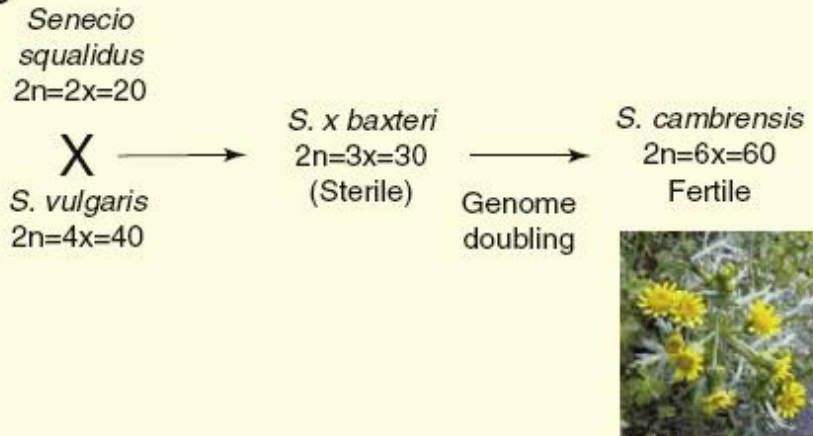
A



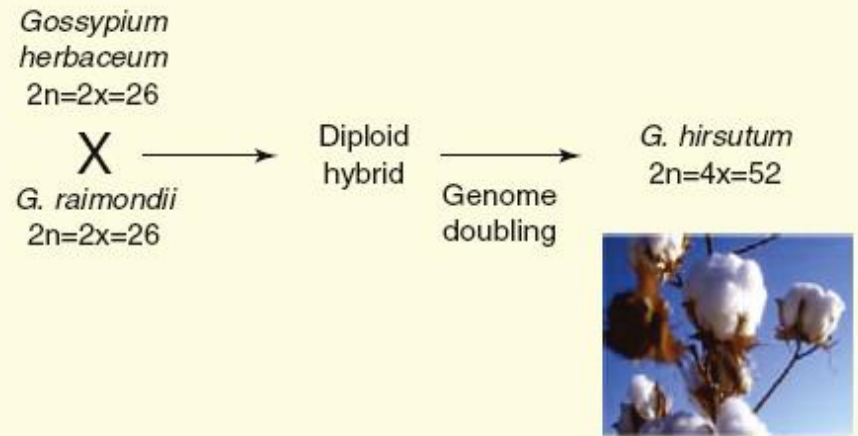
B



C



D



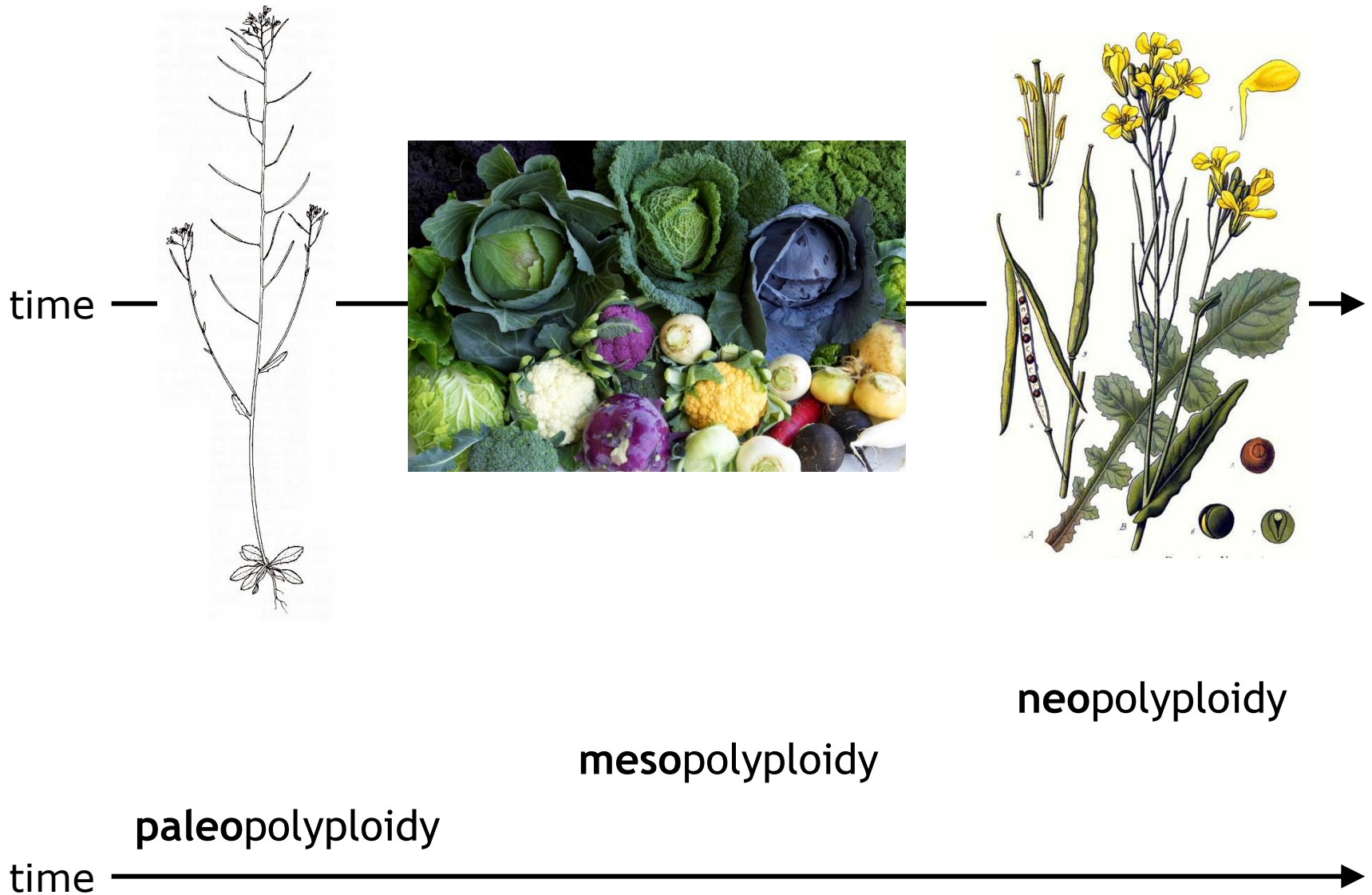
Current Biology

Evolutionary significance of polyploidy

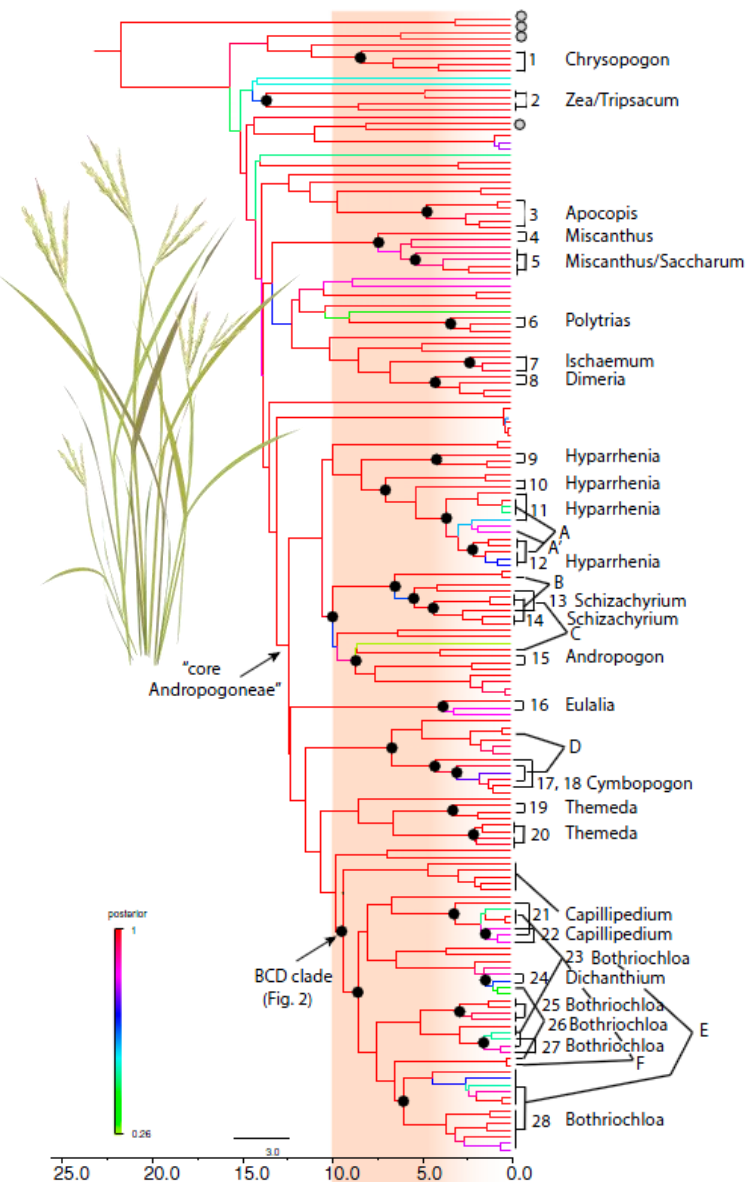


Leitch & Leitch (2008) *Science* 320

Whole-genome duplications of different age

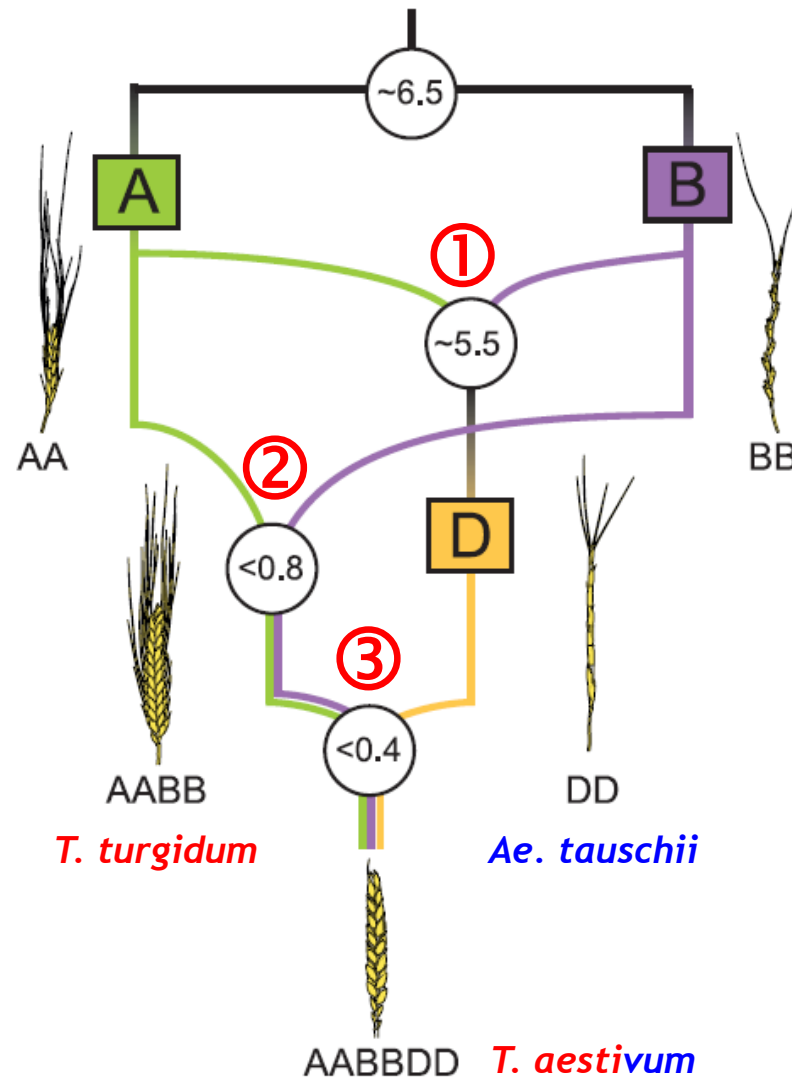


Allopolyploidy, diversification, and the Miocene grassland expansion



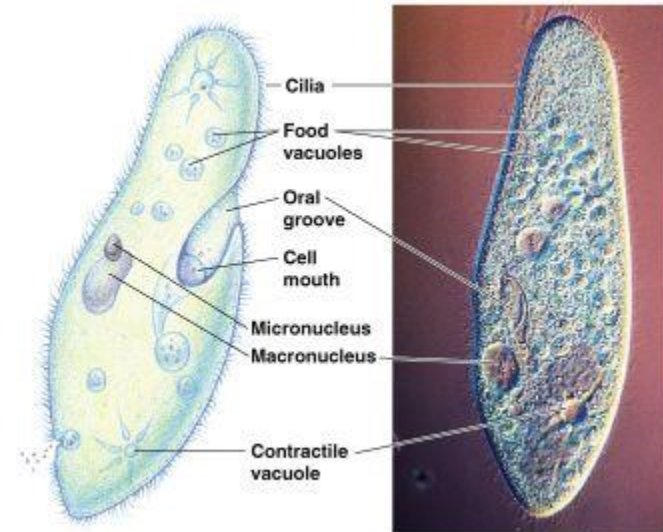
- Most of the allopolyploidization events identified here occurred in the Late Miocene, simultaneous with or following the well documented expansion of the C4 grasslands.
- The dominant species of modern C4 grasslands are members of Andropogoneae, and most are allopolyploid. Many of these ecological dominants whose origin is dated to about 10.5 million years ago (mya) correlates closely with the date when C4 species came to dominate grasslands in Africa and Southern Asia (Pakistan), also estimated about 10-11 mya; the expansion in North America is dated about 7 mya.
- Allopolyploidy is thus correlated with ecological success.

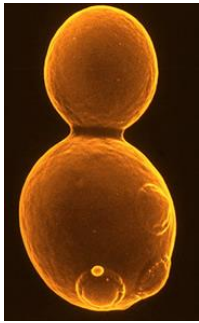
Model of the phylogenetic history of bread wheat (*Triticum aestivum*; AABBDD). Three rounds of hybridization/polyploidization.



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

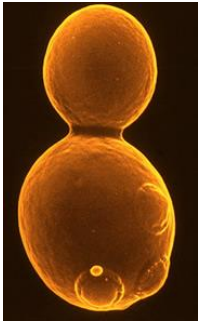




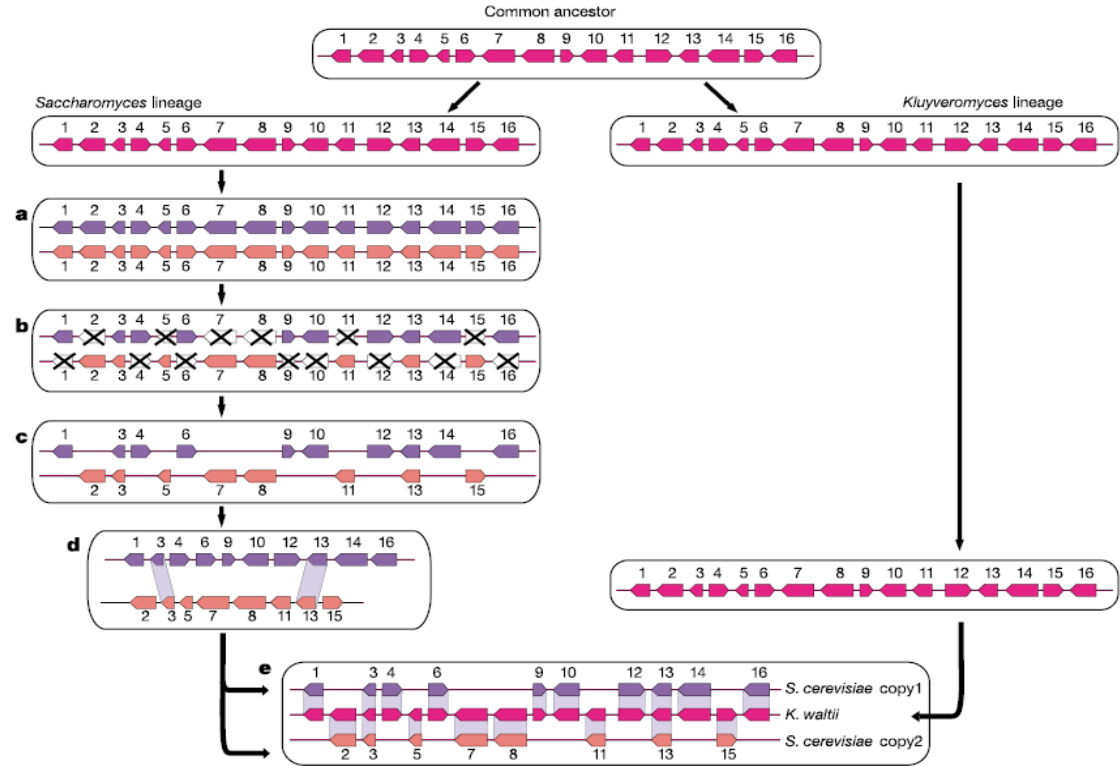
Whole-genome duplications in yeast

- 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

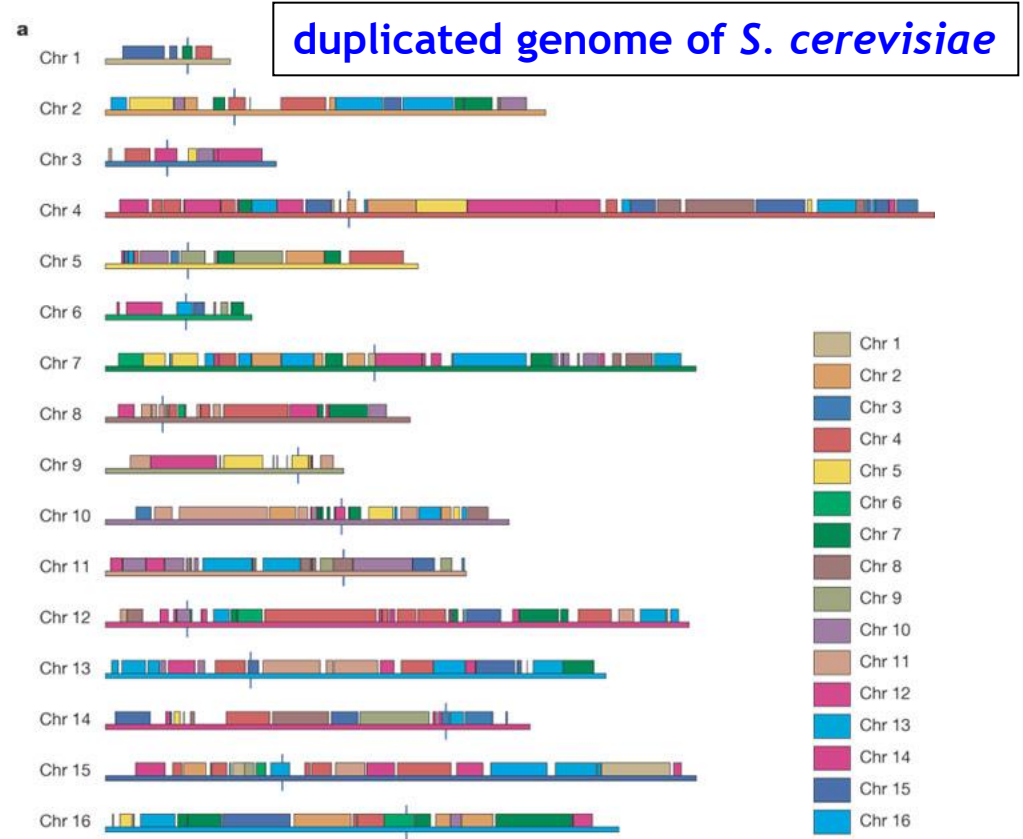
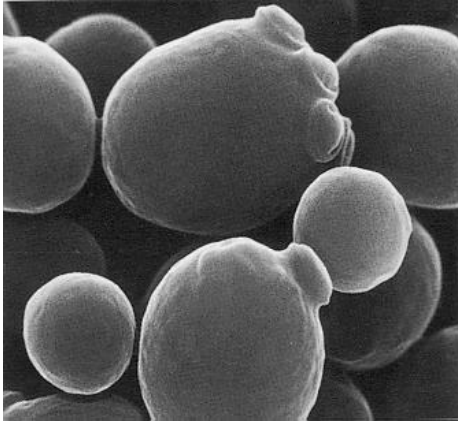


Kellis *et al.* 2004,
Nature 428

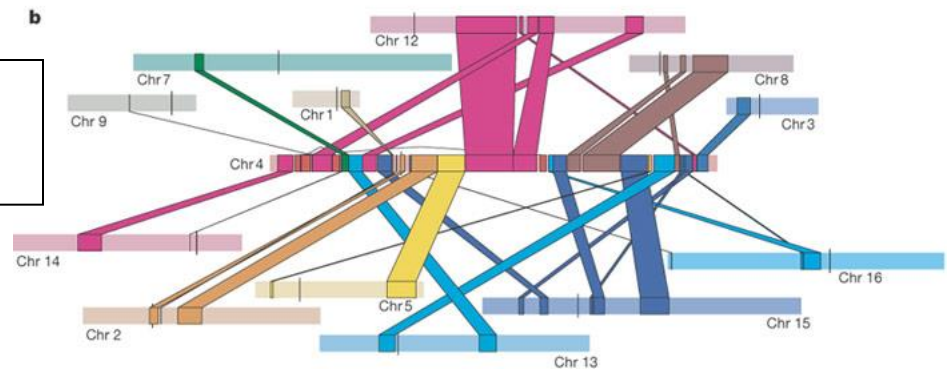


- a) after divergence from *K. waltii*, the *Saccharomyces* lineage underwent a genome duplication event (2 copies of every gene and chromosome)
- b) duplicated genes were mutated and some lost
- c) two copies kept for only a small minority of duplicated genes
- d) the conserved order of duplicated genes (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**

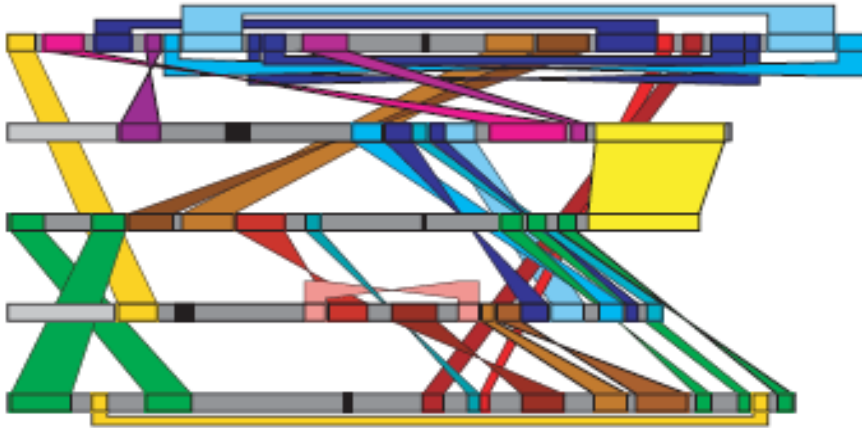


First evidence of a WGD in plants



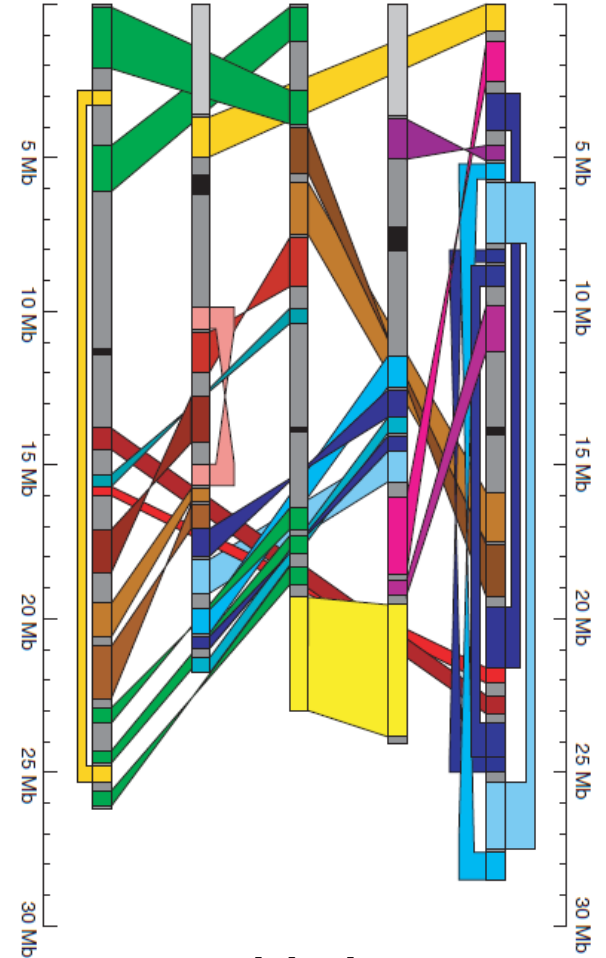
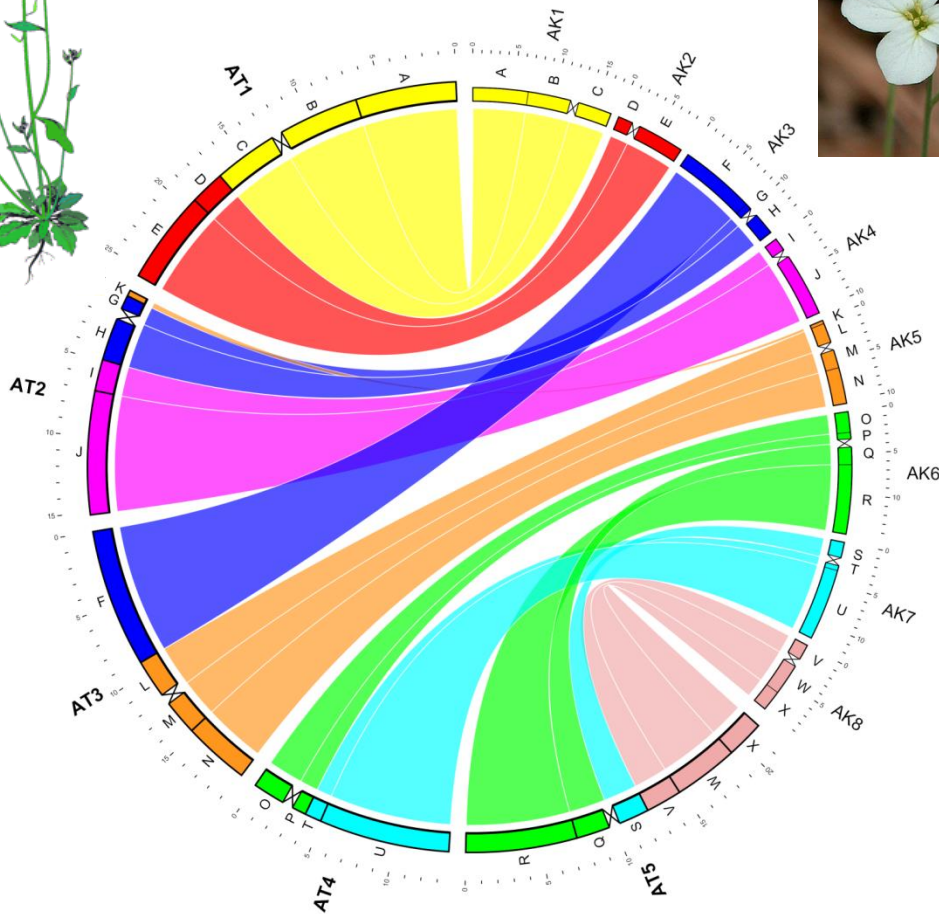
Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*

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.

Arabidopsis Species Are „Paleotetraploids“ with 8 or 5 Chromosomes

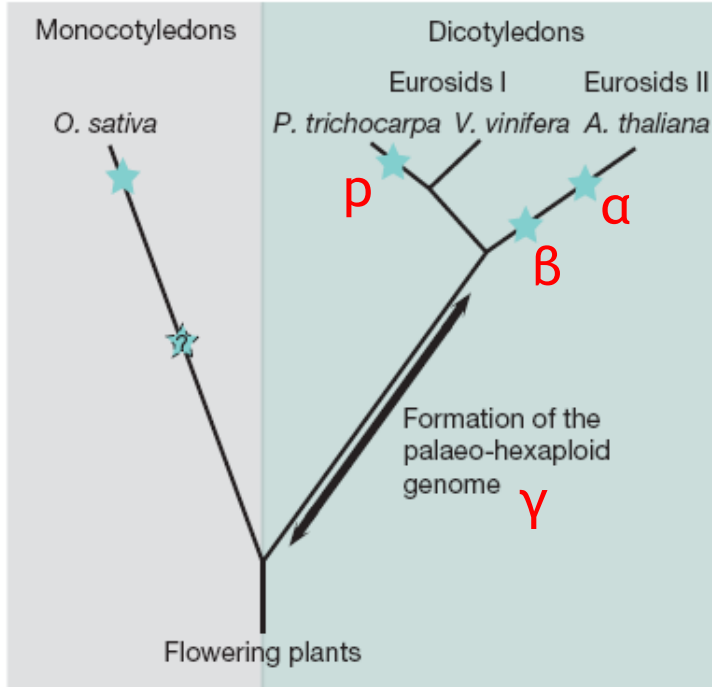


segmental duplications in the *A. thaliana* genome

The grapevine genome sequence suggests ancestral hexaploidization in major angiosperm phyla

The French-Italian Public Consortium for Grapevine Genome Characterization*

Nature 449, 2007



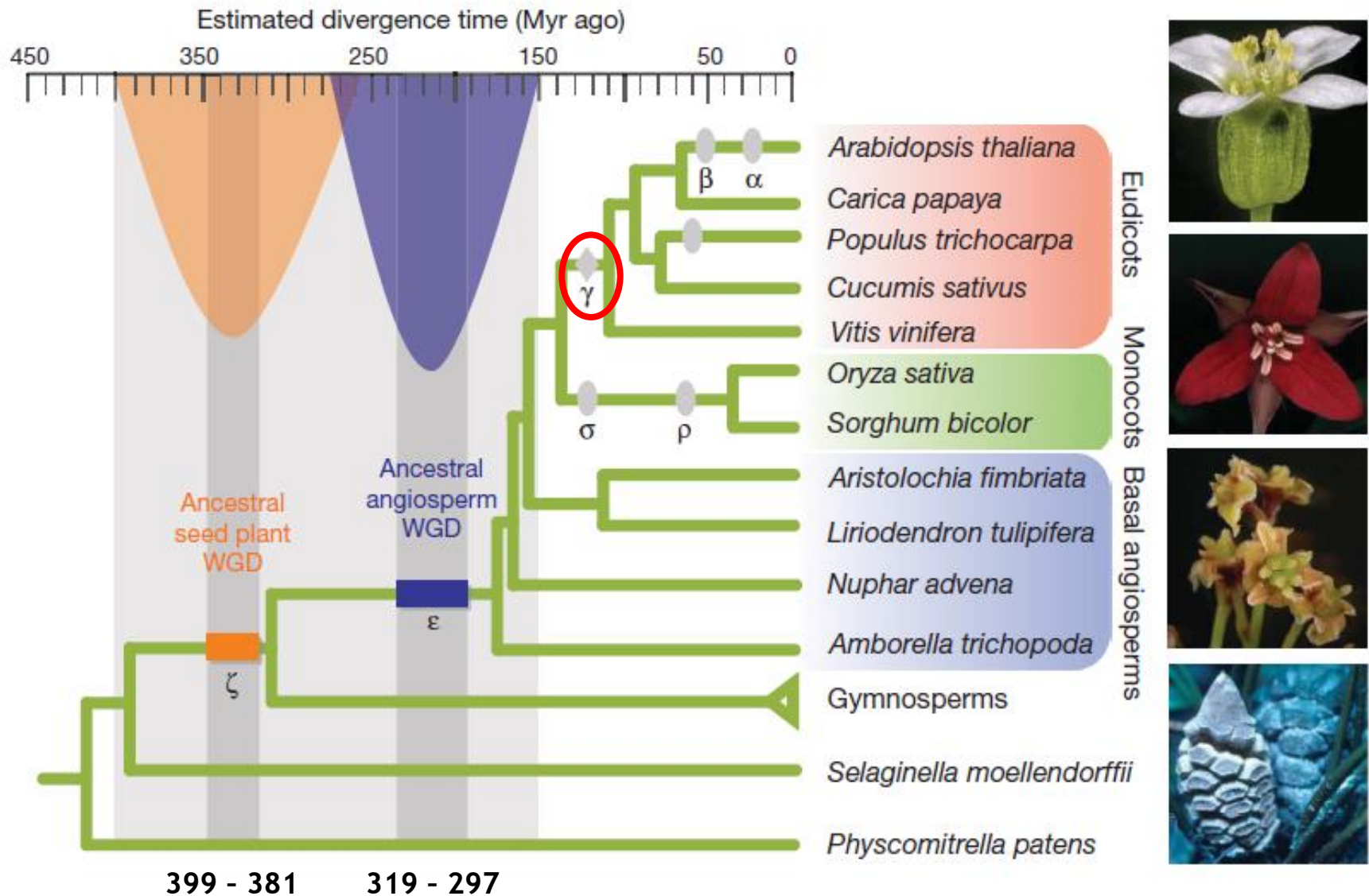
The **γ triplication** may have been an ancient **auto-hexaploidy** formed from fusions of three identical genomes, or **allo-hexaploidy** formed from fusions of three somewhat diverged genomes.

Tang *et al.* 2008, *Genome Research*

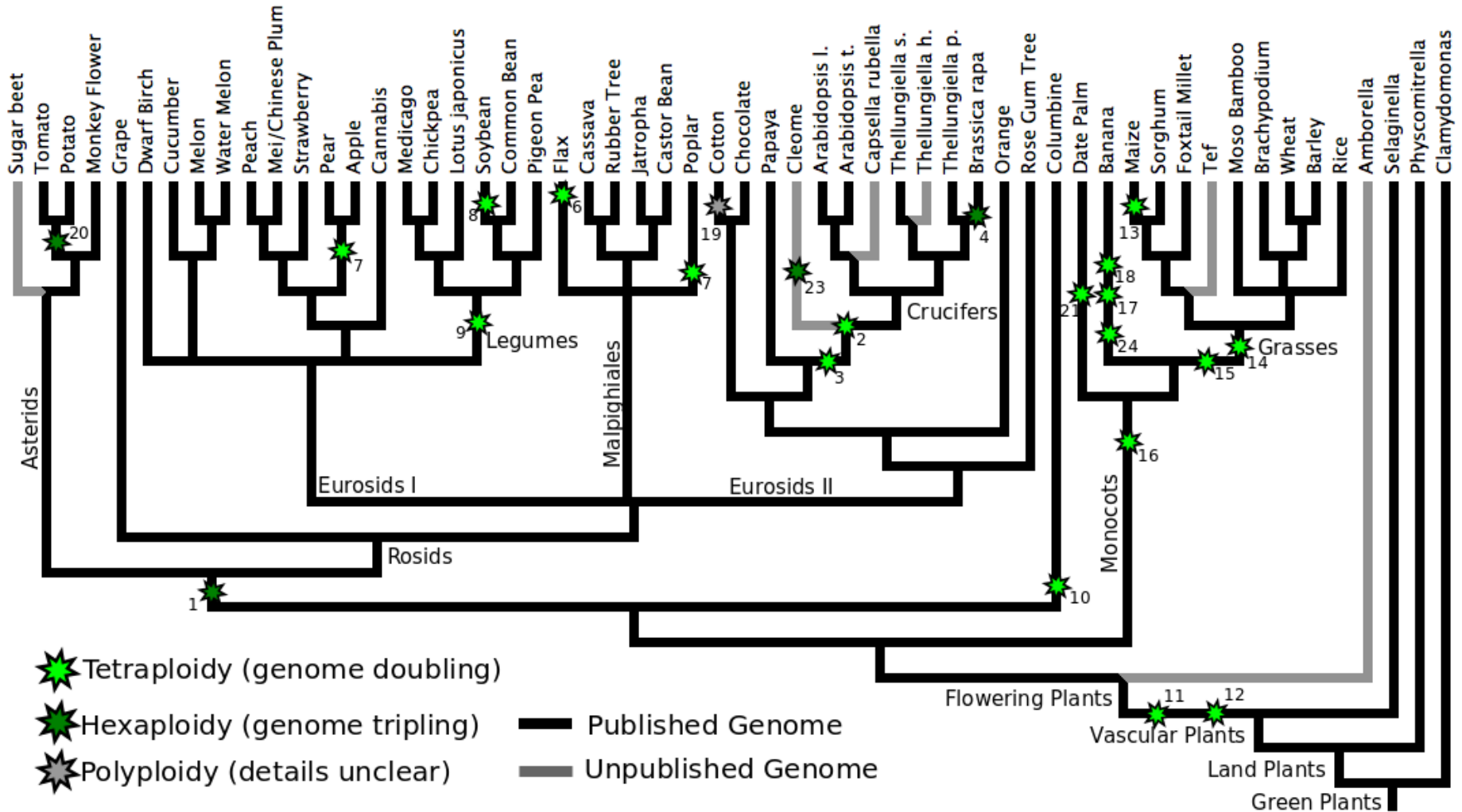
The formation of the palaeo-hexaploid ancestral genome occurred after divergence from monocots and before the radiation of the Eurosids. Star = a WGD (tetraploidization) event.



WGD events in seed plants and angiosperms

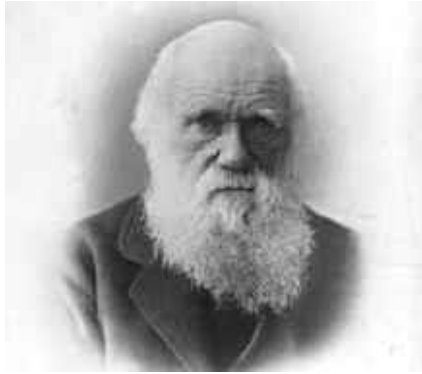


Phylogenetic Tree of Sequenced Genomes with Whole Genome Duplications Marked



CoGePedia (<http://genomevolution.org/wiki/>)

Charles Darwin's abominable mystery solved?

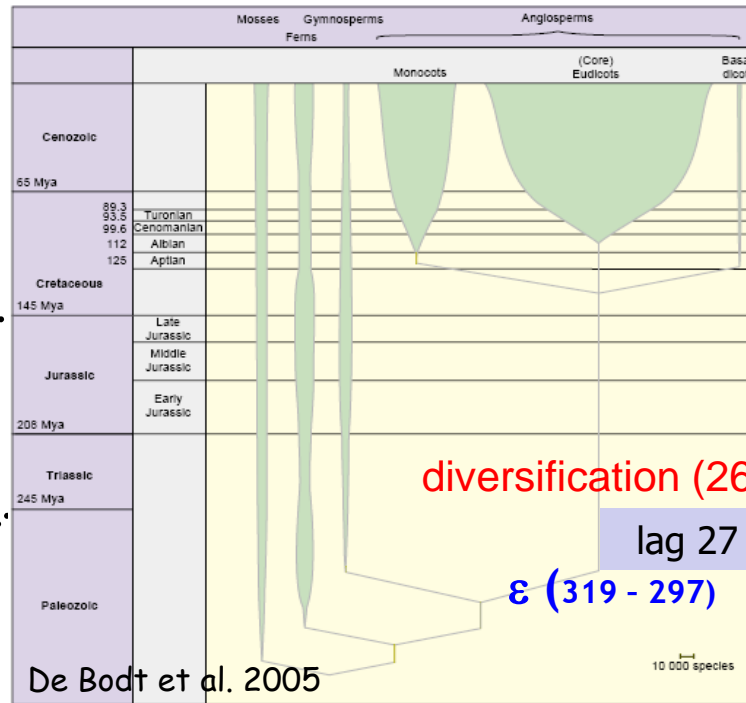
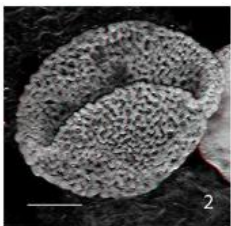


"The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery."
 (Charles Darwin in a letter to Sir Joseph Hooker, 1879)

Archaeofructus liaoningensis
 (140 million year old fossil)



Afropollis
 (245 million year old angiosperm pollen)



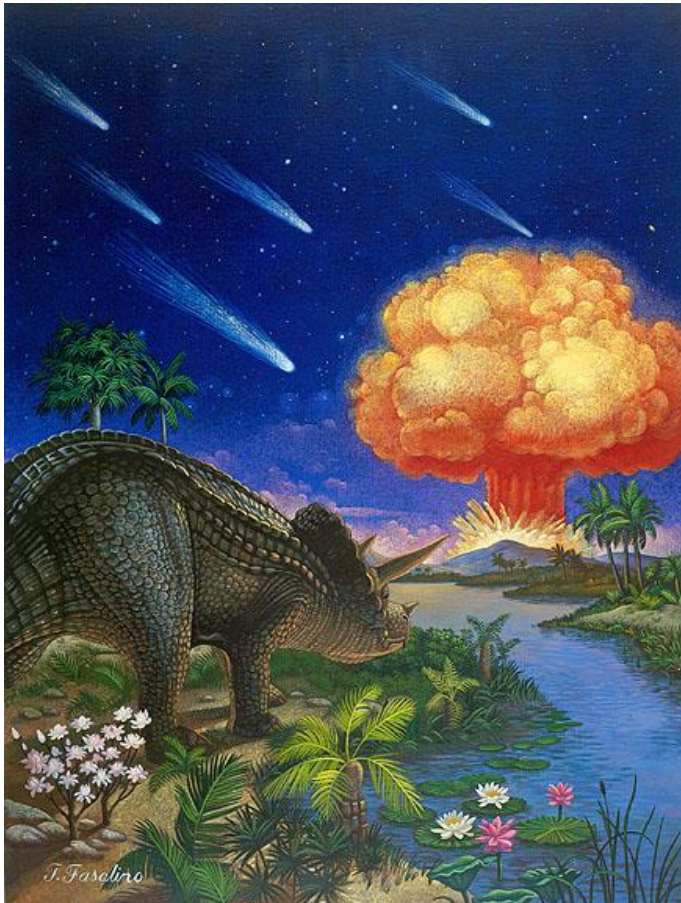
There is evidence of ancient polyploidy throughout the major angiosperm lineages. It means that a genome-scale duplication event probably occurred PRIOR to the rapid diversification of flowering plants

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 ?

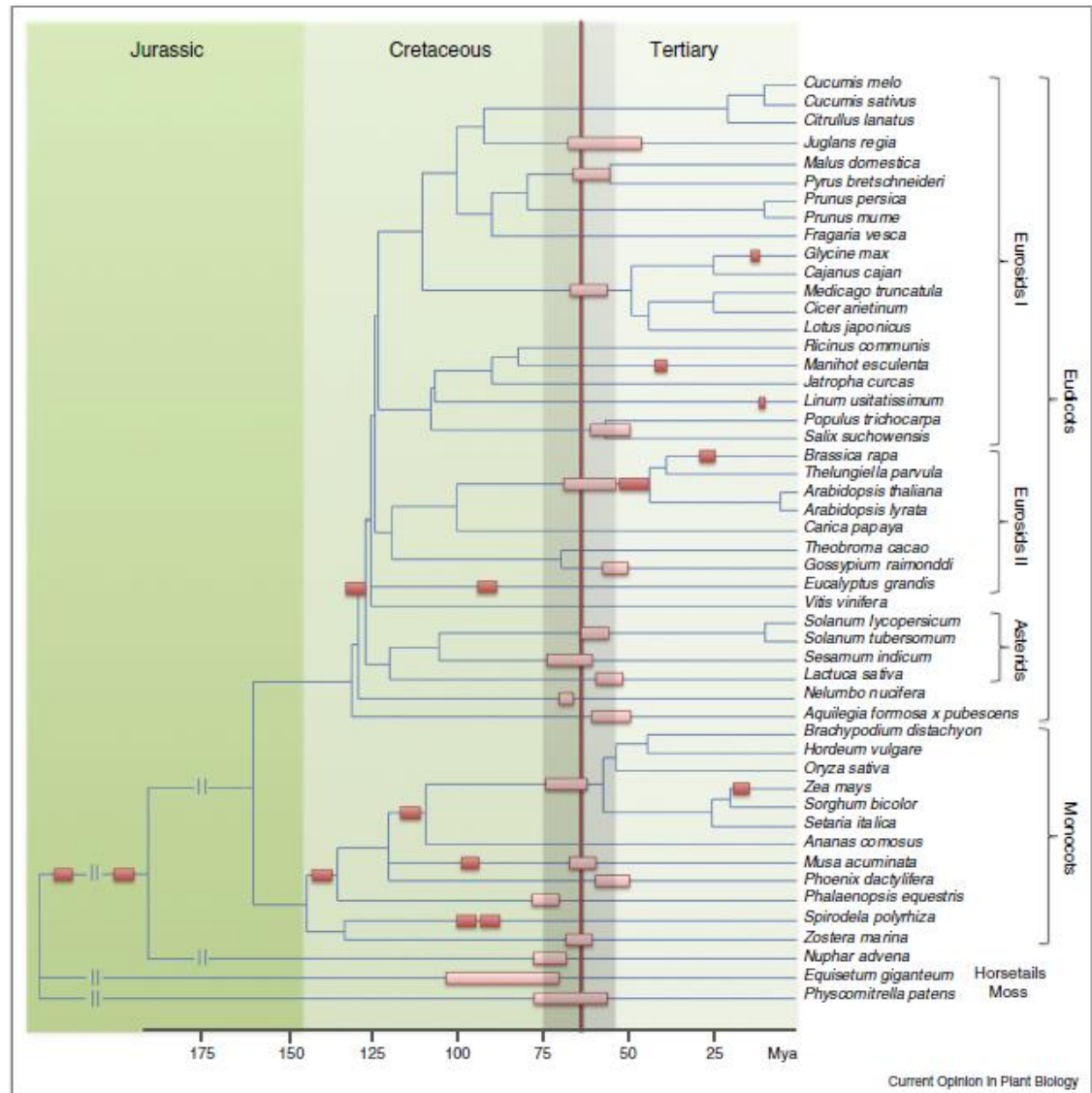
Analysis of 41 plant genomes supports a wave of successful genome duplications in association with the Cretaceous–Paleogene boundary

Kevin Vanneste,^{1,2} Guy Baele,³ Steven Maere,^{1,2} and Yves Van de Peer^{1,2,4}

Genome Res (2014)

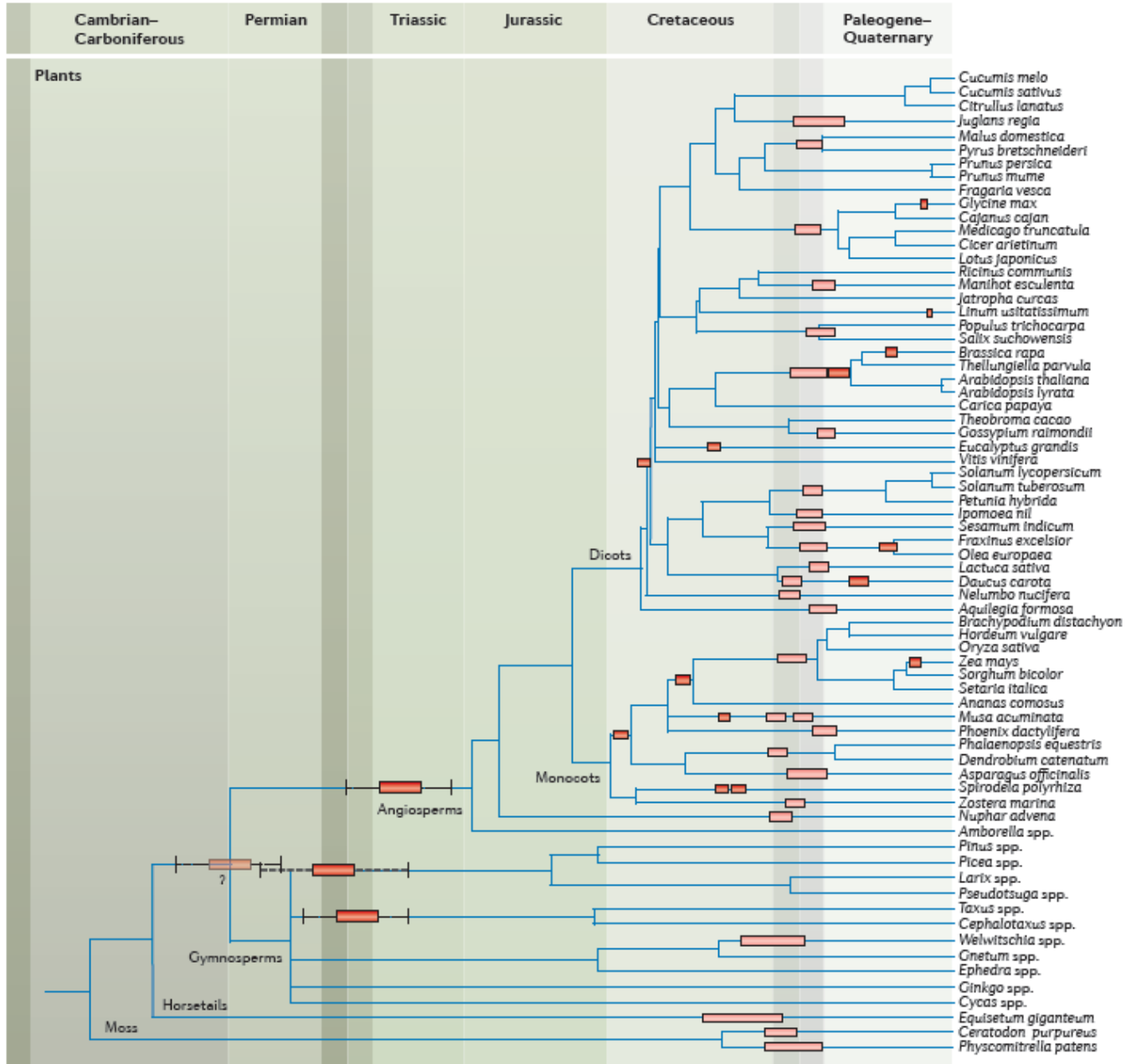
Possible establishment of polyploid plants following the K/Pg mass extinction (66 million y. ago)

- 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

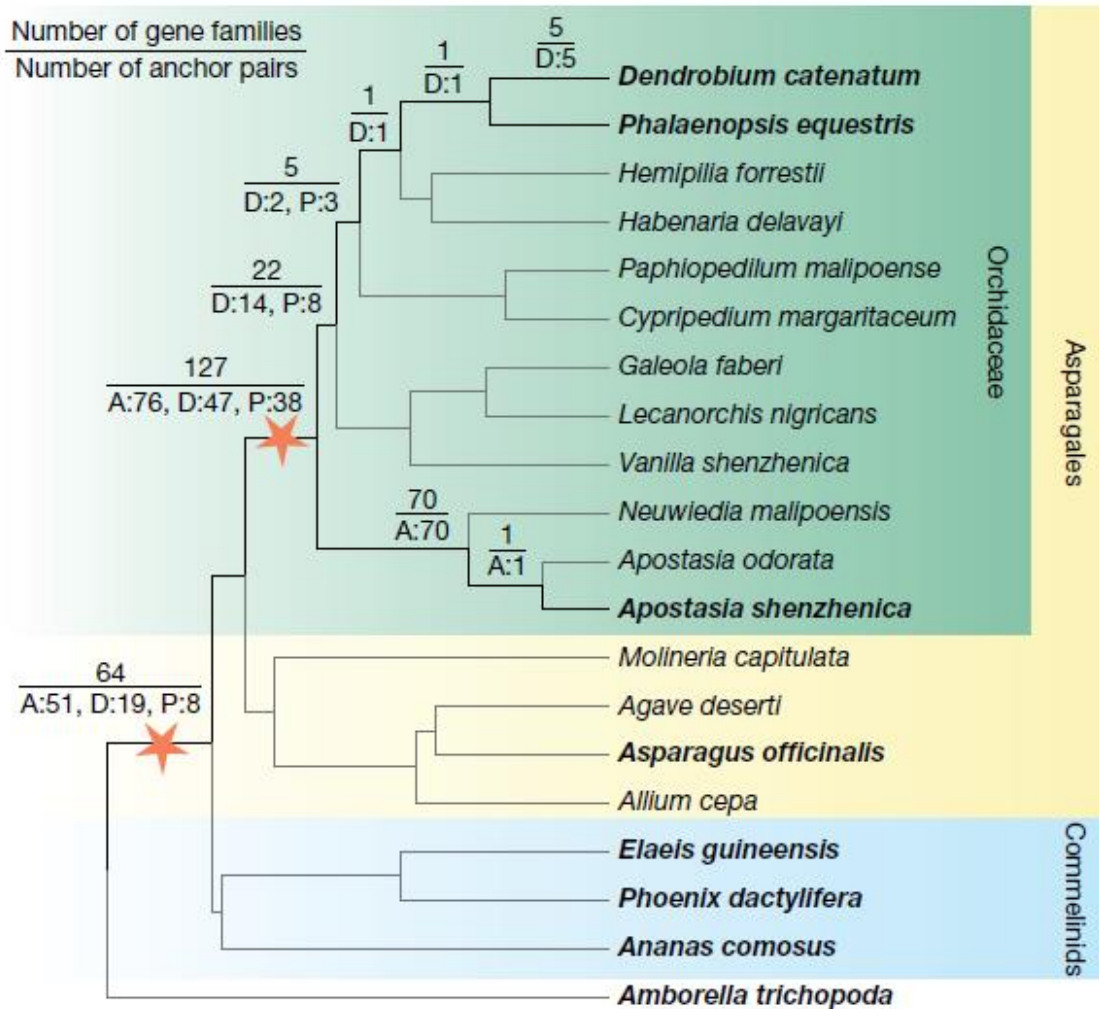


Lohaus and Van de Peer (2016) Curr Opin Pl Biol

Whole-genome duplication in land plants



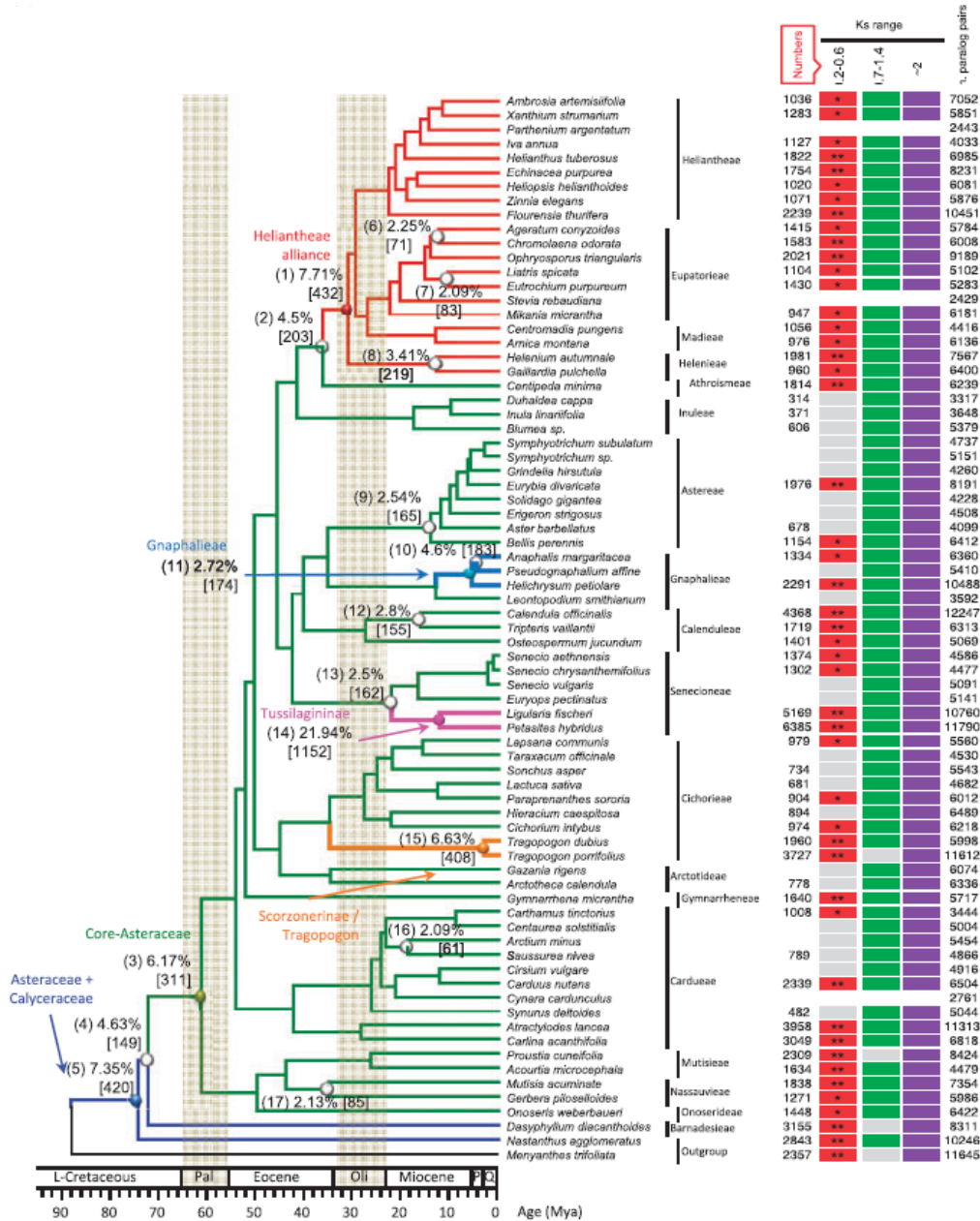
Orchids probably share a common WGD driving the early divergence of the family



- largest vascular plant family
- c. 28,000 species
- 736 genera



Multiple WGDs across the Asteraceae family tree

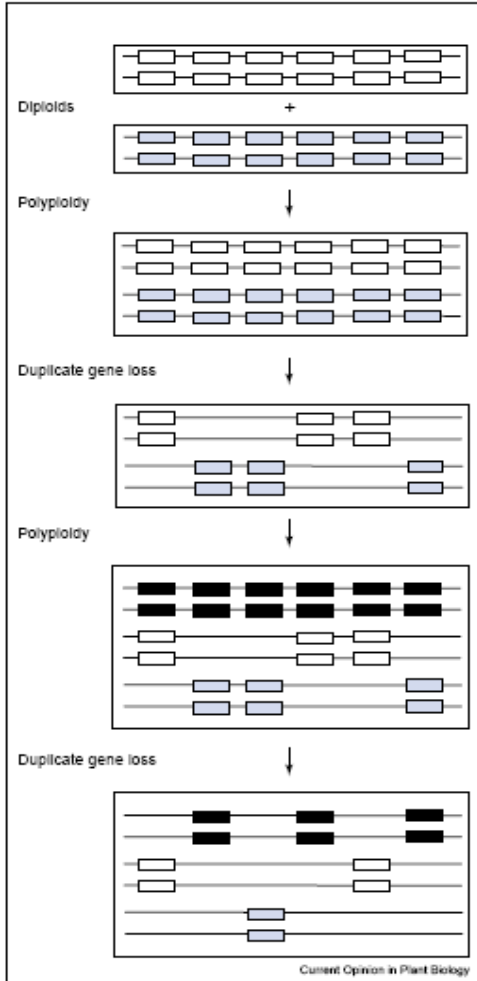


- the second largest family of vascular plants
- some 24,700 species
- enormous karyological variation - >180 different mitotic chromosome counts
- chromosome numbers from n = 2 to c. n = 216



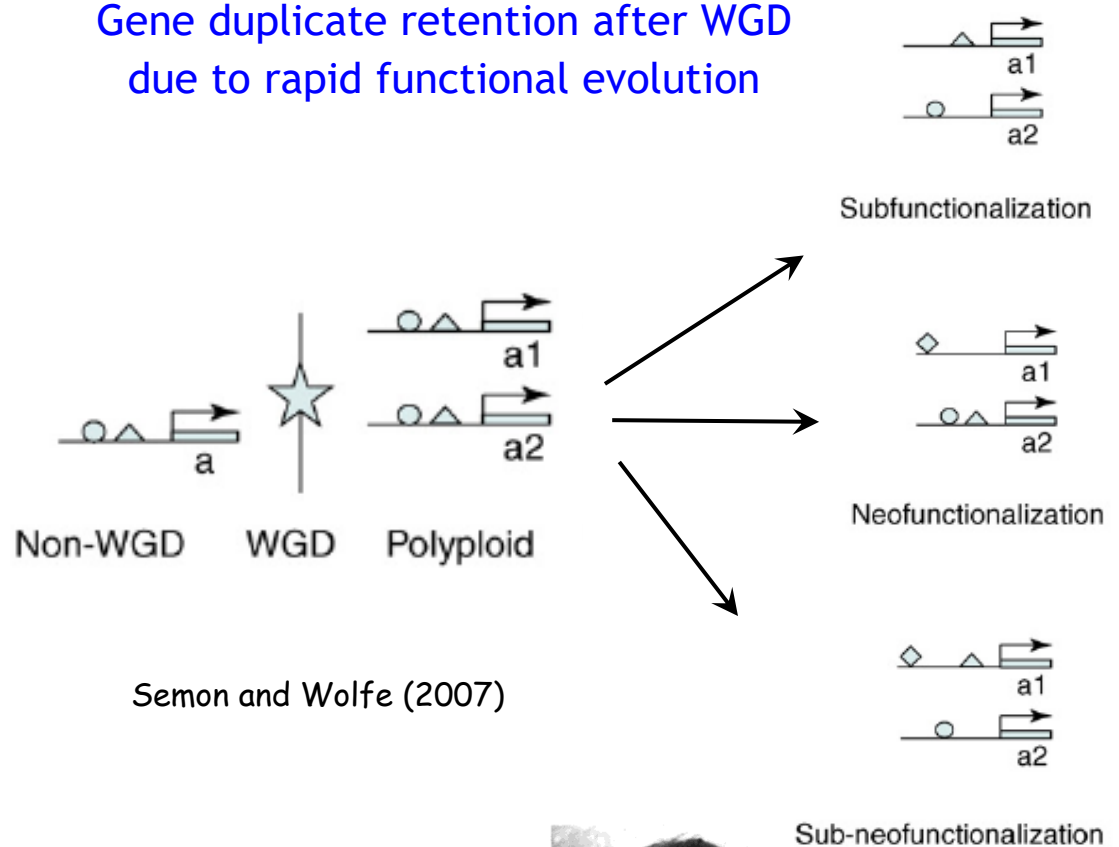
Whole-genome duplications, diploidization, and the consequences

Genome evolution through cyclic polyploidy

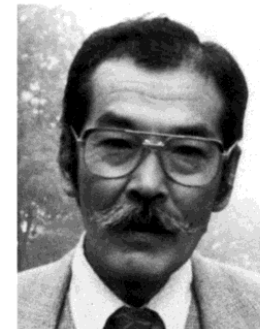


Adams and Wendel (2005)

Gene duplicate retention after WGD due to rapid functional evolution

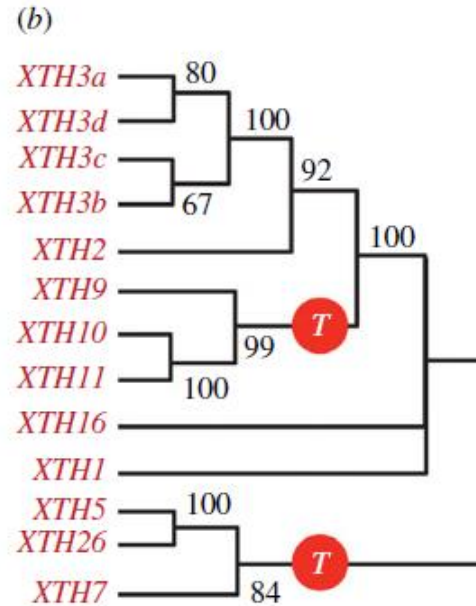
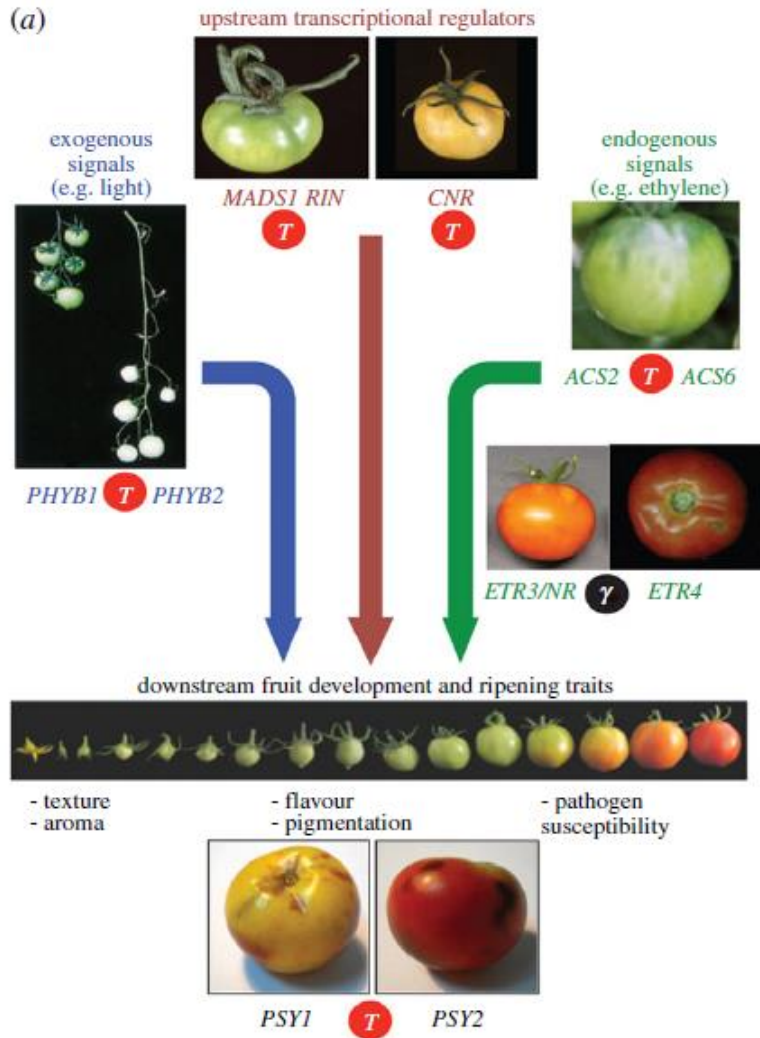


Semon and Wolfe (2007)



Sun and Ohno

Consequences of WGD events: the Solanaceae-specific genome triplication (49 million y. ago) contributed to the evolution of the tomato fruit

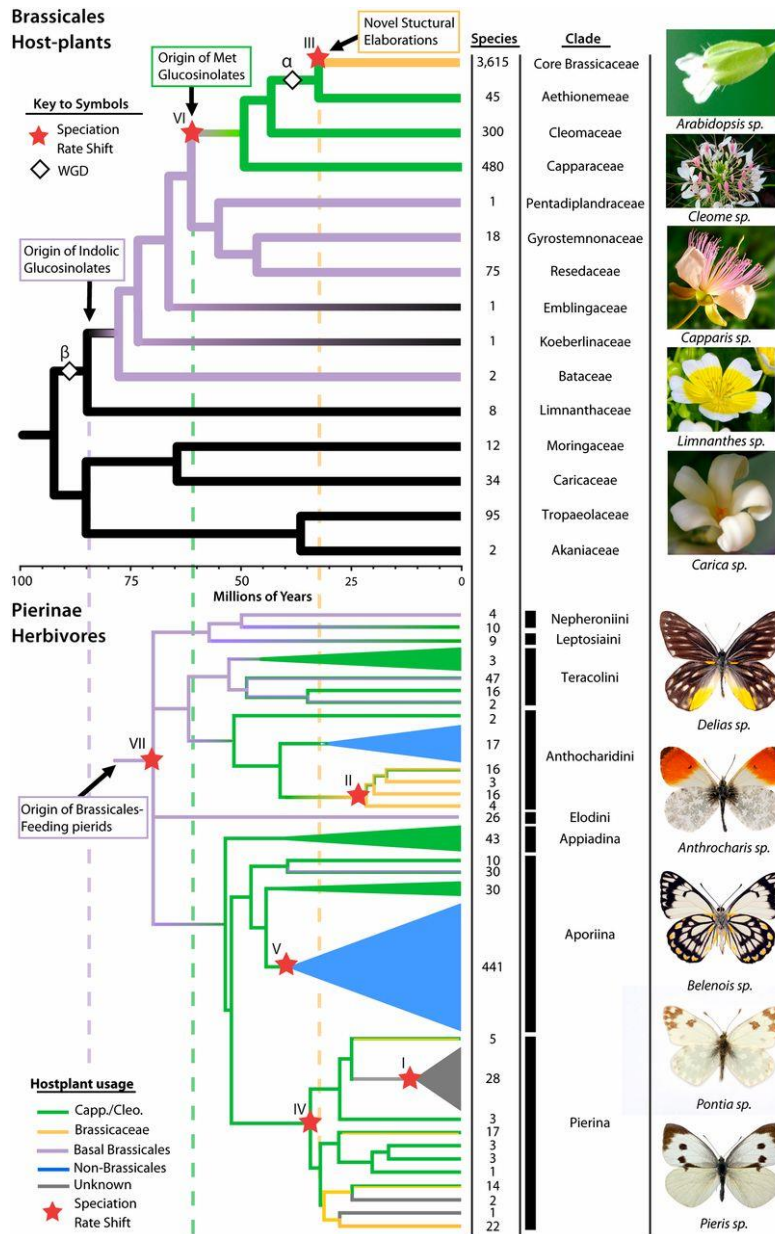


phylogeny of xyloglucan endotransglucosylase/hydrolases (XTHs)

T Solanaceae-specific genome triplication

γ core eudicot shared hexaploidy

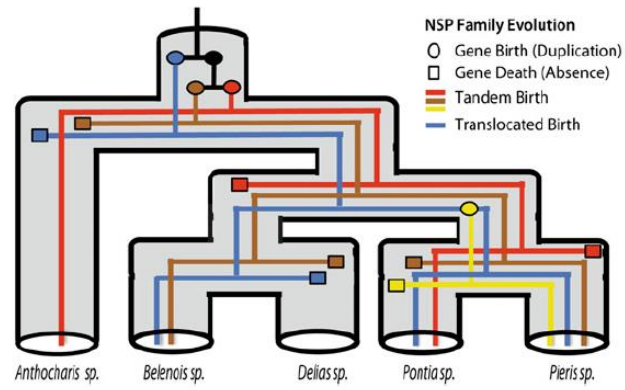
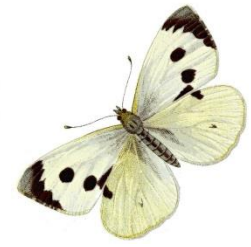
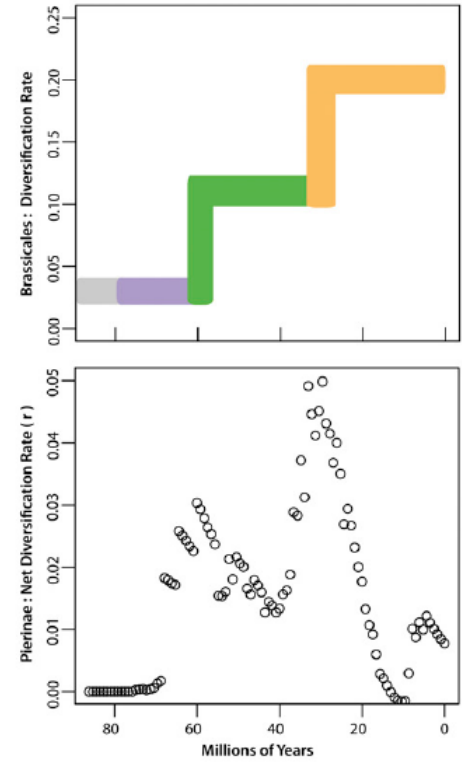
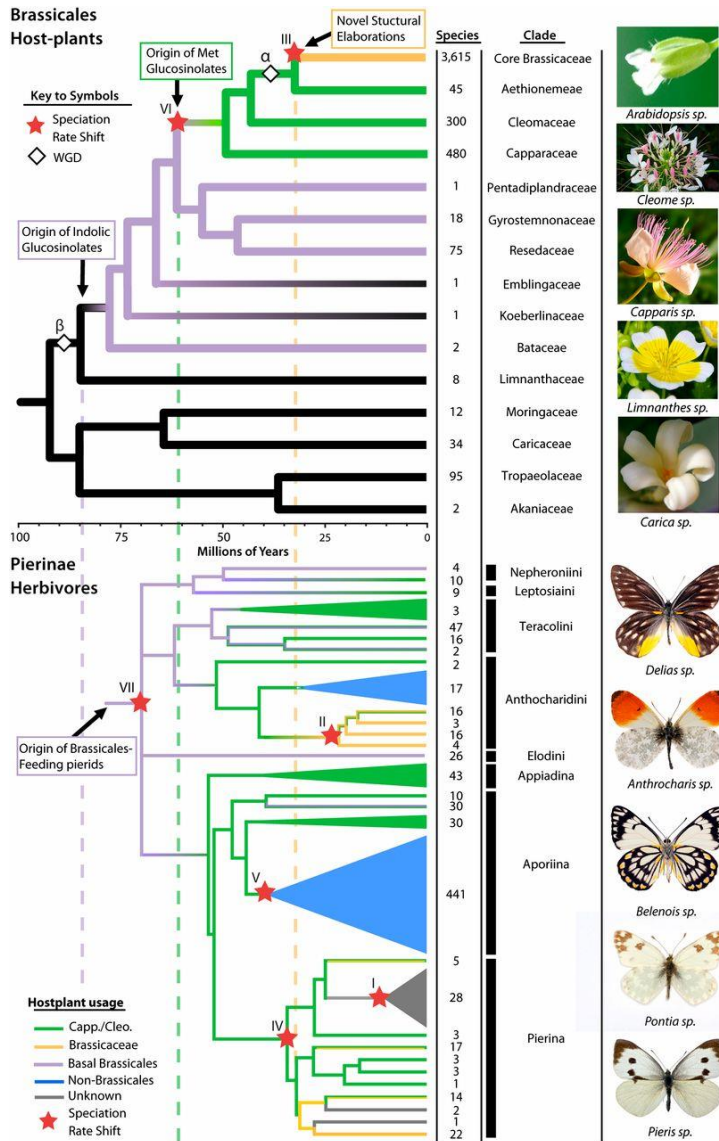
Gene and genome duplications, key innovations and coevolution



- WGDs (core Brassicales, Brassicaceae)
- chemical arms race
- plants - glucosinolates
- butterflies - countertactic (detoxification)
- repeated escalation of key innovations (glucosinolate synthesis) → diversification in Brassicales plants and Pierinae butterflies over 80 million years

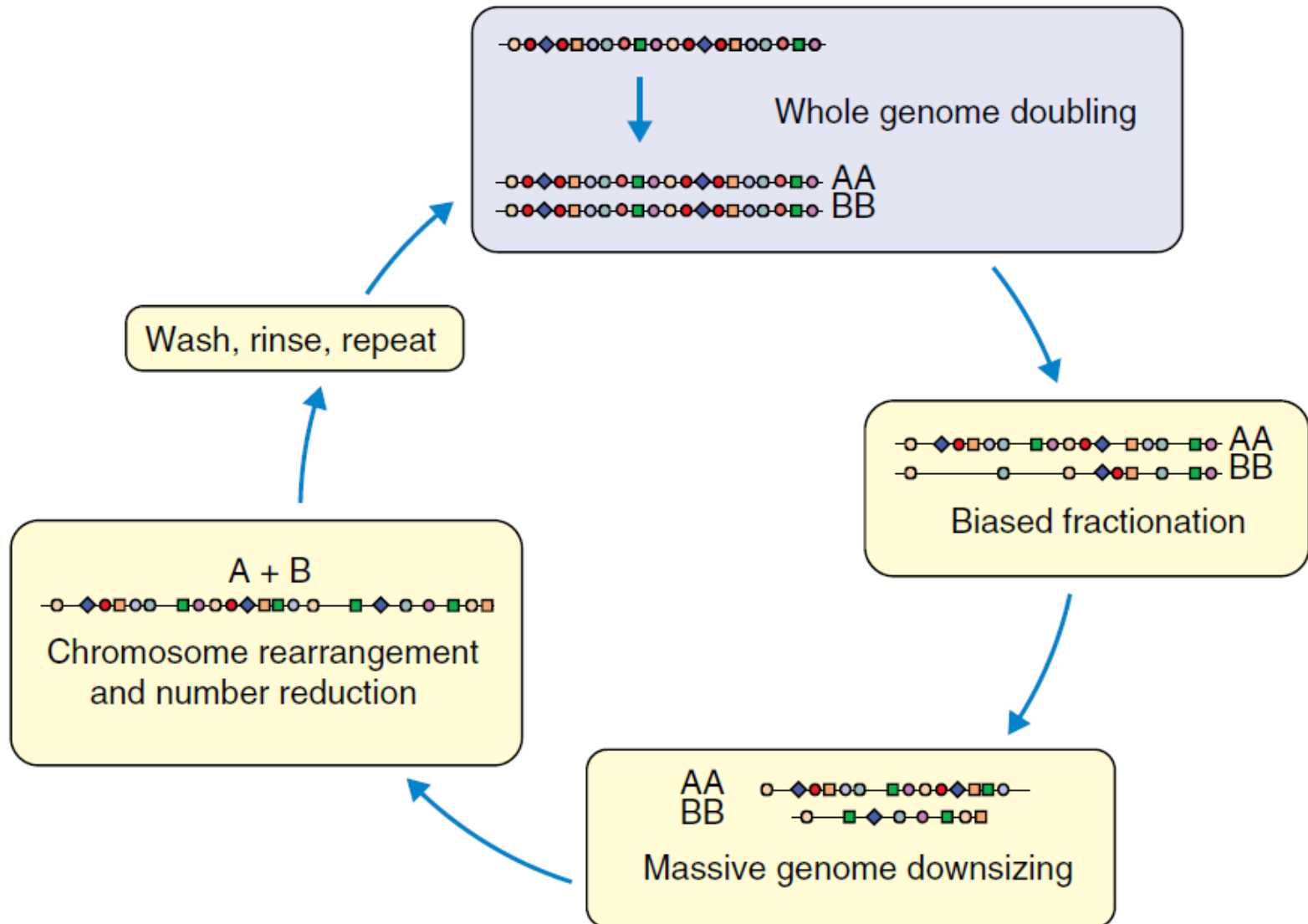


Gene and genome duplications, key innovations and coevolution

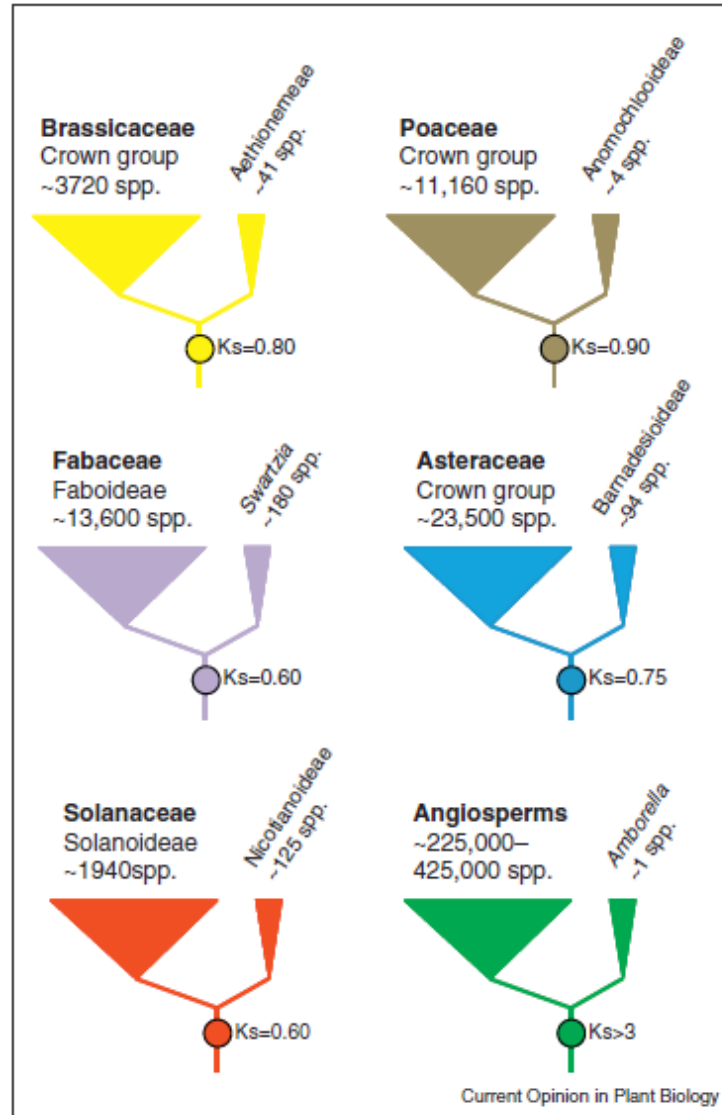


Whole-genome duplication and **diploidization**

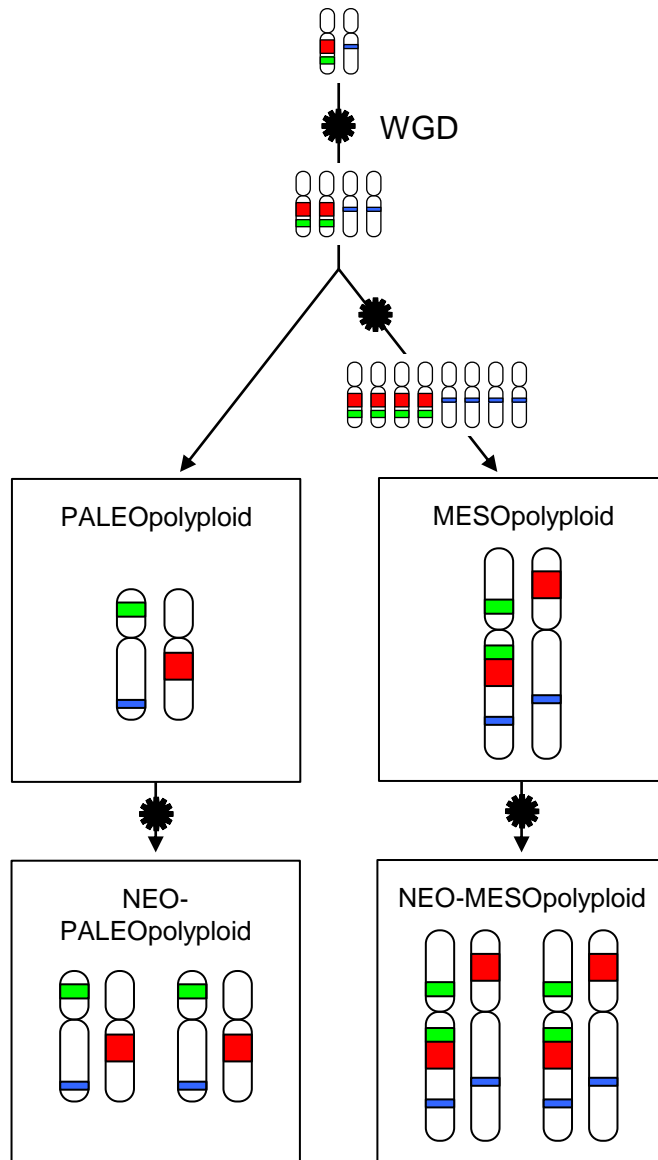
Whole-genome duplication and diploidization



The WGD Radiation Lag-Time Model

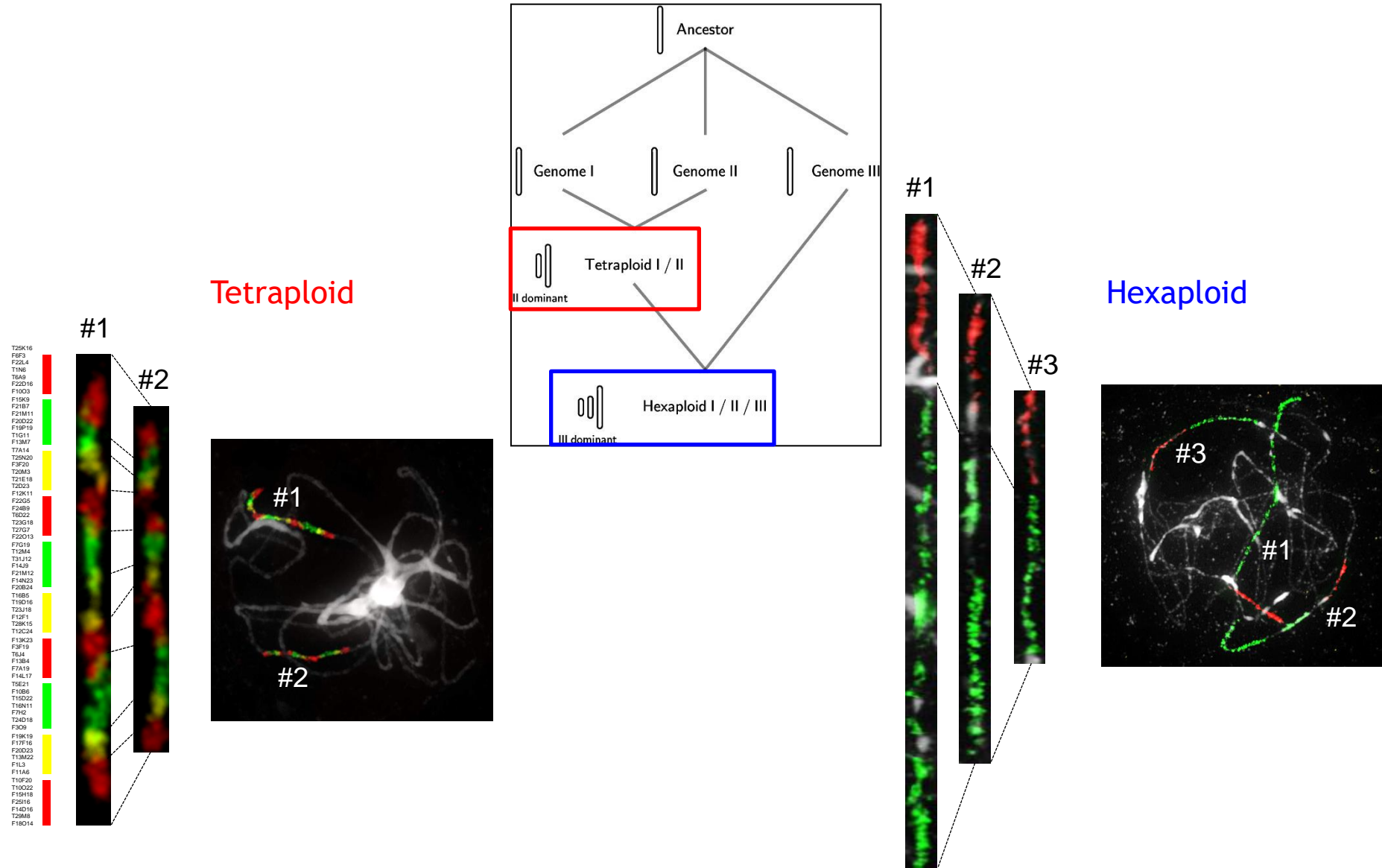


Cytogenomic features of post-polyploid genome diploidization



- recurrent WGDs
- different age of WGDs
- different diploidization rates

Cytogenetic evidence for biased subgenome fractionation during post-polyploid diploidization.



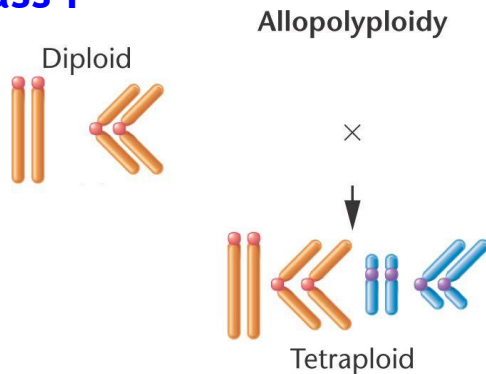
Two Evolutionarily Distinct Classes of Paleopolyploidy

Olivier Garsmeur,^{†,1} James C. Schnable,^{†,2} Ana Almeida,² Cyril Jourda,¹ Angélique D'Hont,^{*,†,1} and Michael Freeling^{*,†,2}

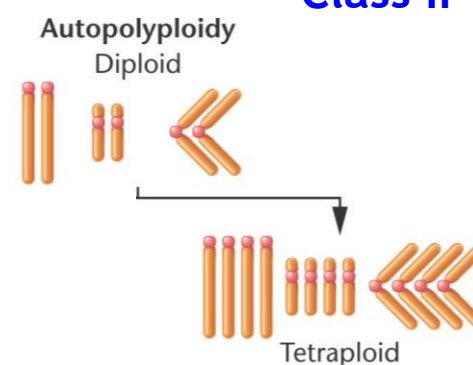
Table 2. Fractionation Pattern and Genome Dominance in Eight Species.

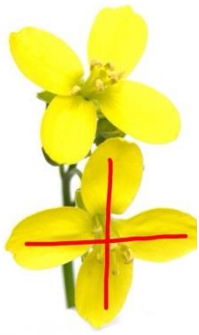
Species	WGD Class	Substitution Rate (Ks)	Bias Ratio between Duplicate Regions	Fractionation Pattern	Genome Dominance	Expression Data from
Medicago	I	0.87	1.23	Biased	No data	
Sorghum	I	0.95	1.24	Biased (Schnable et al. 2012)	Yes	Dugas et al. (2011)
Arabidopsis	I	0.76	1.17	Biased (Thomas et al. 2006)	Yes	Gan et al. (2011)
Brassica	I	0.34	1.47	Biased (Wang et al. 2011)	Yes (Cheng et al. 2012)	
Maize	I	0.17	1.46	Biased (Woodhouse et al. 2010)	Yes (Schnable et al. 2011)	
Poplar	II	0.23	1.05	Unbiased	No data	
Soybean	II	0.15	1.03	Unbiased	No	Schmidt et al. (2011)
Banana	II	0.39	1.06	Unbiased	No	D'Hont et al. (2012) and supplementary table S4, Supplementary Material online

Class I

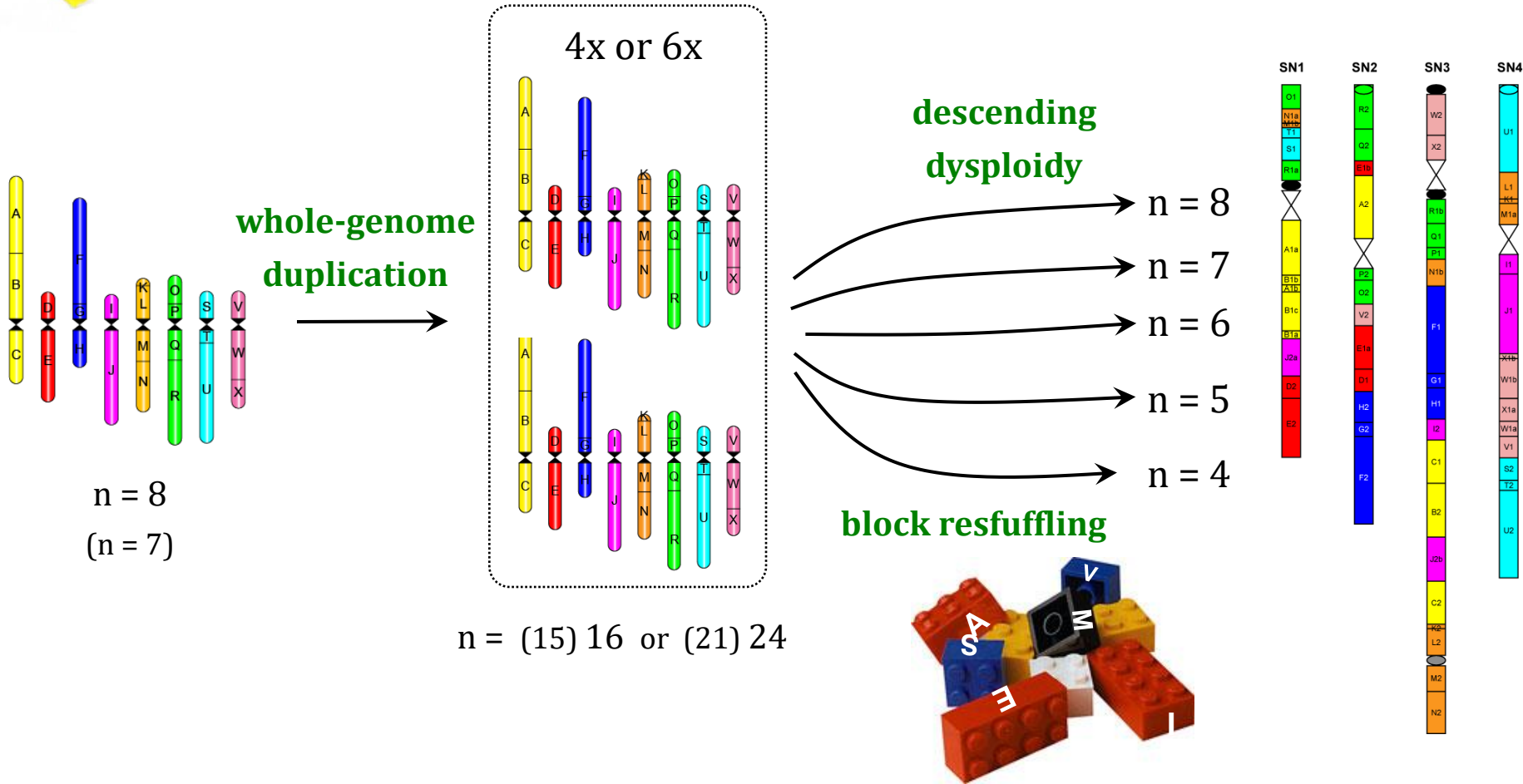


Class II



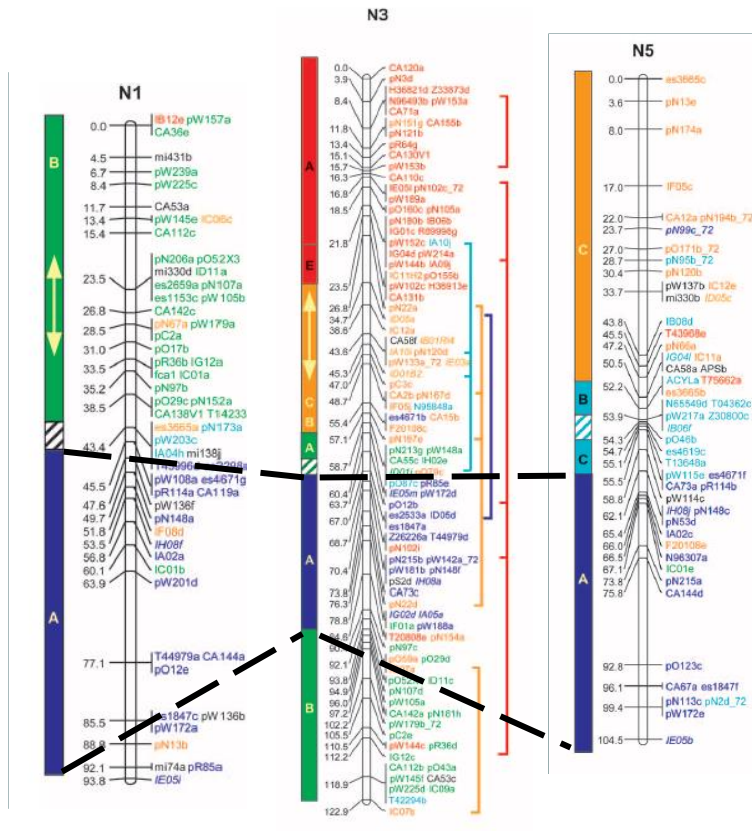


Evolution of the Ancestral Crucifer Genome – ANCIENT POLYPLOIDS



Brassicas Are Ancient Hexaploids (Mesopolyploids)

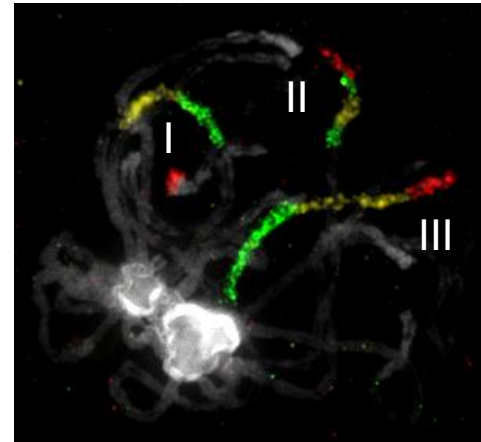
Brassica napus (AACC, n = 19), A genome (N1-N10)



Parkin et al. (2005) Genetics

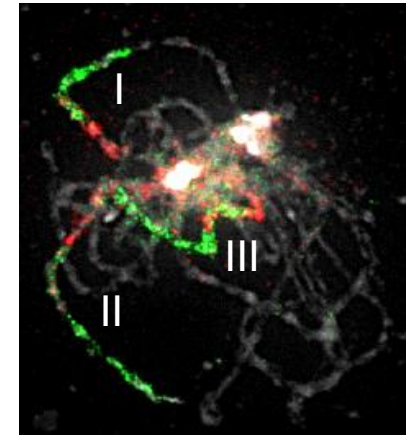
Diplotaxis erucoides

2n = 14



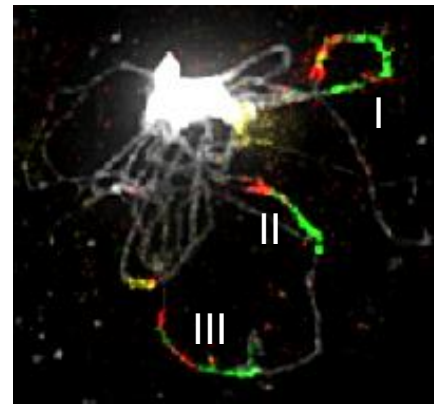
Brassica oleracea

2n = 18



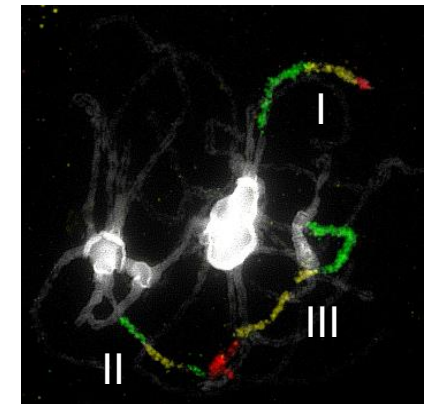
Morisia monanthos

2n = 14



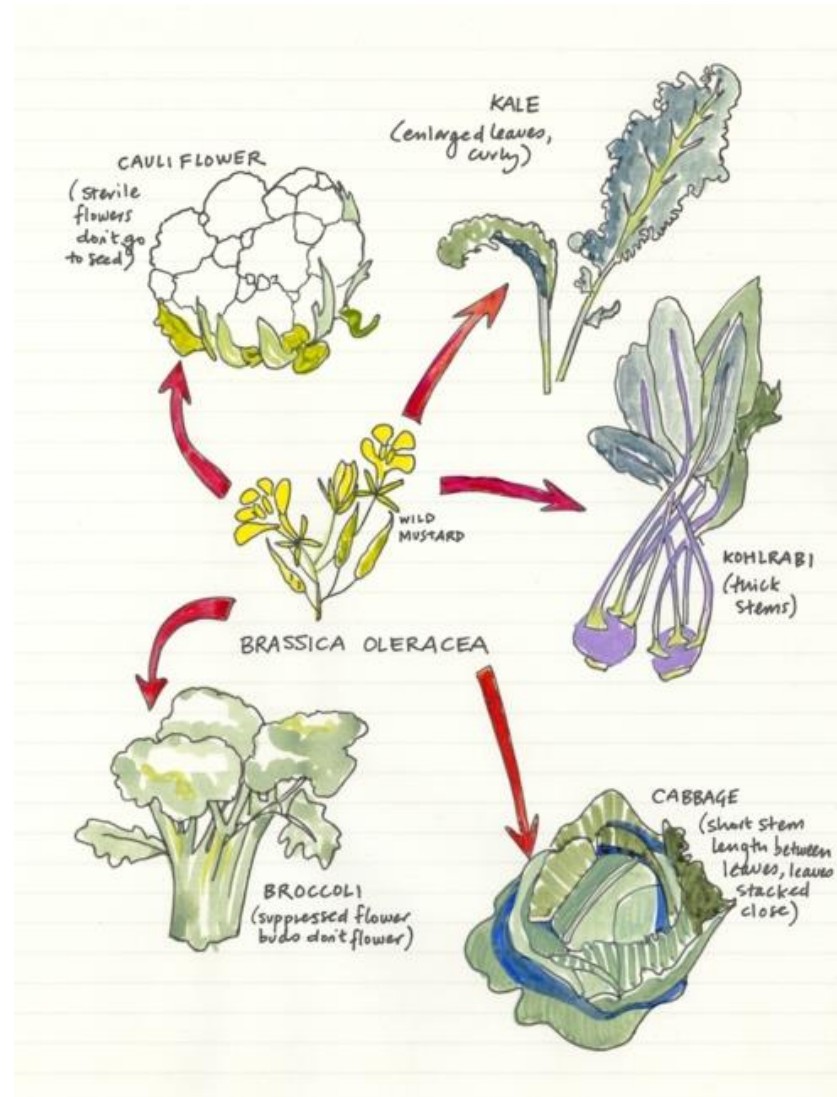
Moricandia arvensis

2n = 28



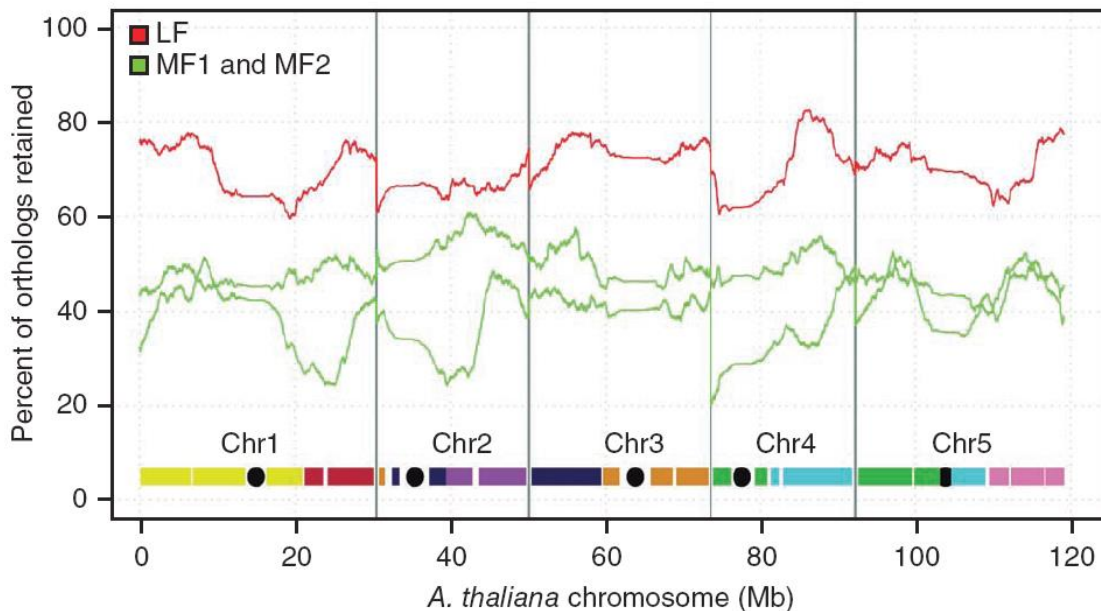
Lysak et al. (2005) Genome Res, (2007) Plant Physiol

Diploidization in *Brassica* is marked by the asymmetrical evolution of polyploid genomes



The genome of the mesopolyploid crop species *Brassica rapa*

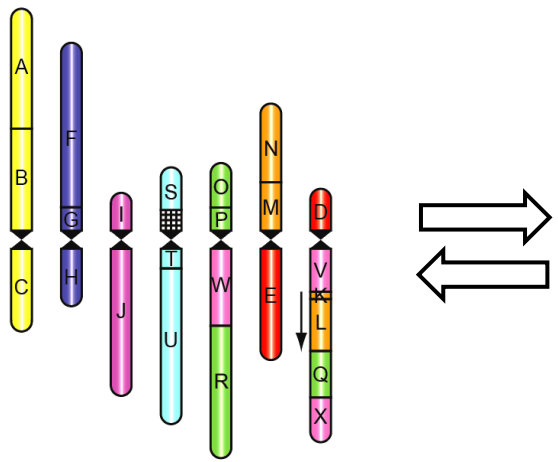
The *Brassica rapa* Genome Sequencing Project Consortium



The density of orthologous genes in **three subgenomes** (LF, MF1 and MF2) of *B. rapa* compared to *A. thaliana*.

Three *B. rapa* Subgenomes Contain Genome Block Associations Unique to the tPCK Ancestral Genome

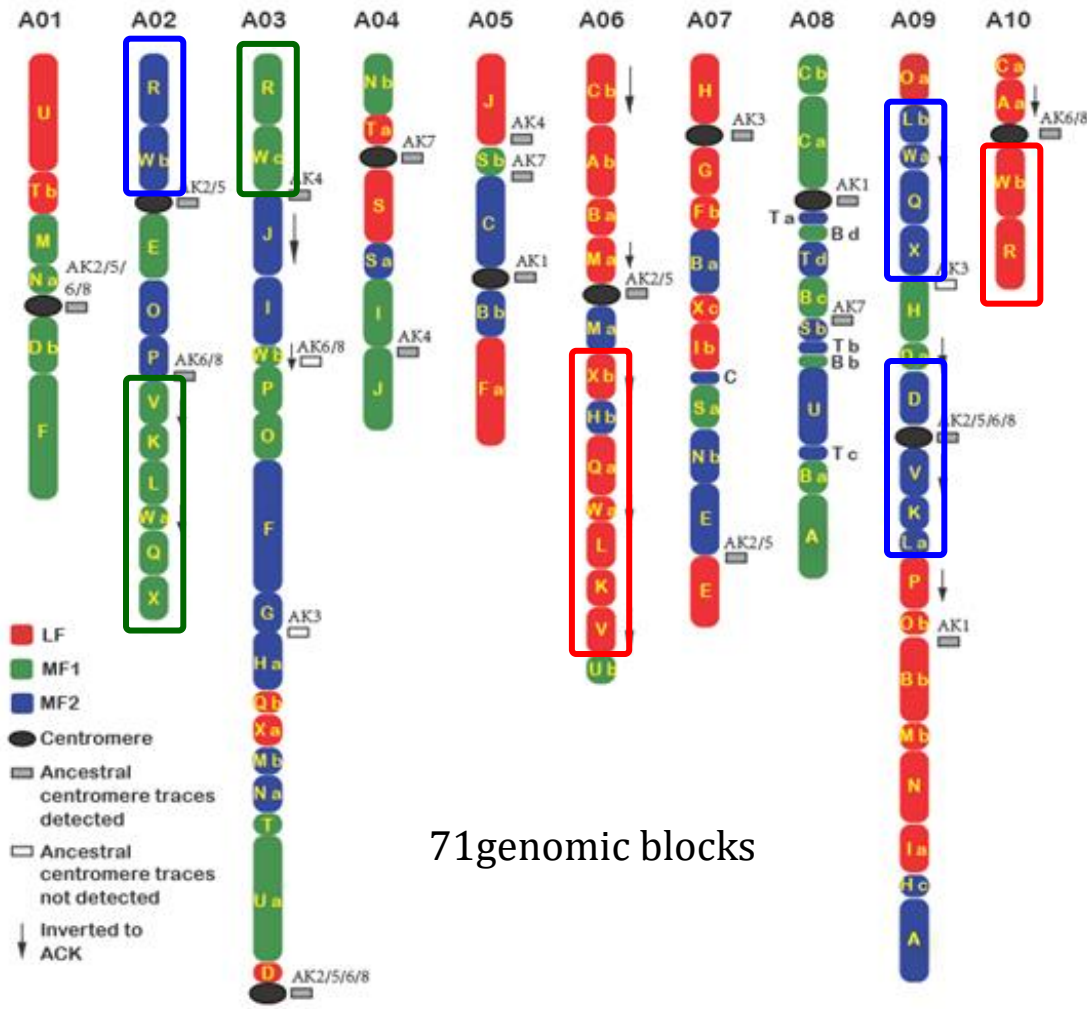
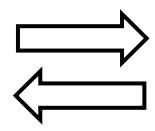
n = 7



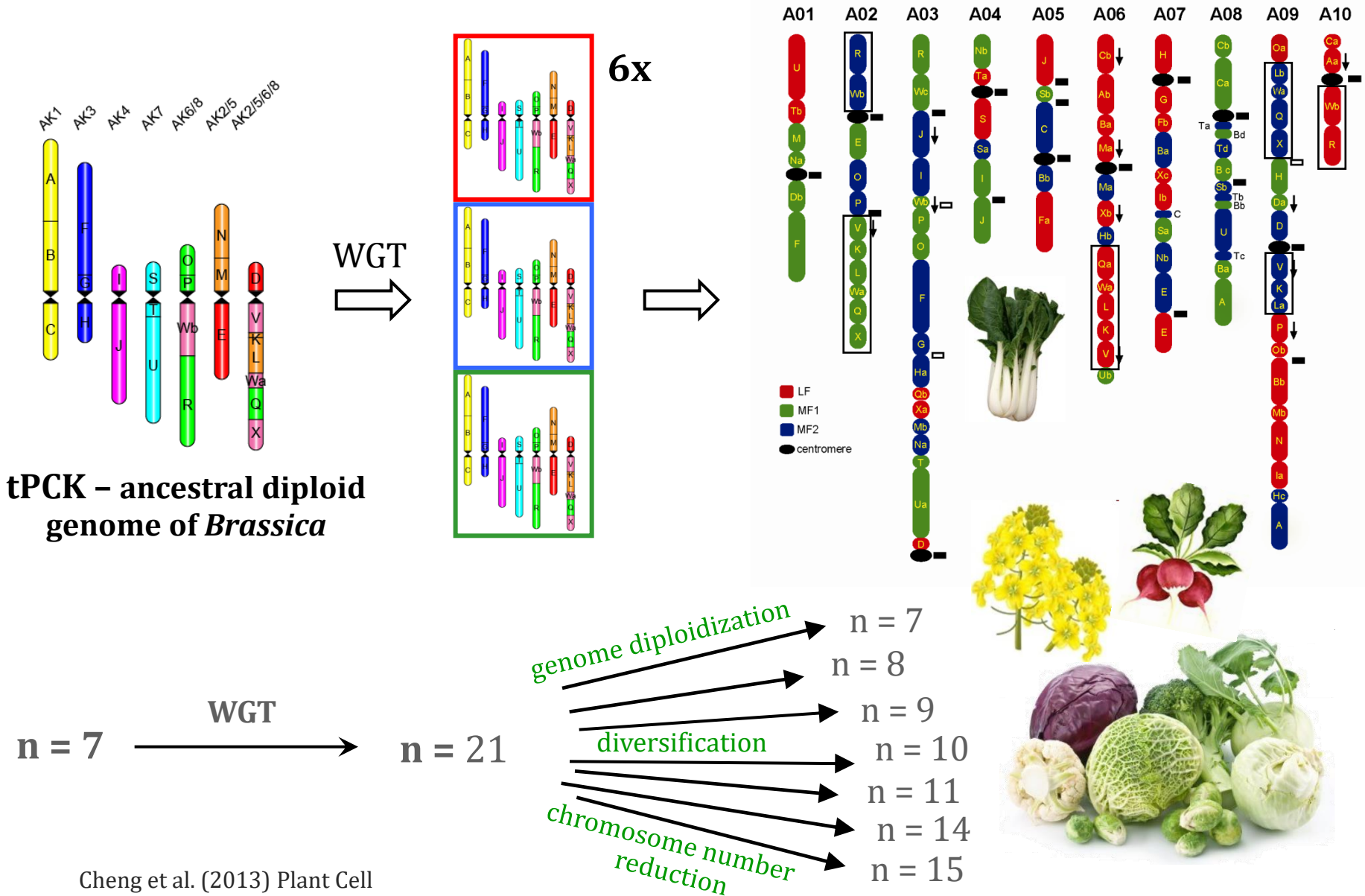
translocation

Proto-Calepineae Karyotype



tPCK



Whole-Genome Triplication Spurred Genome and Taxonomic Diversity in *Brassica* and Tribe Brassiceae

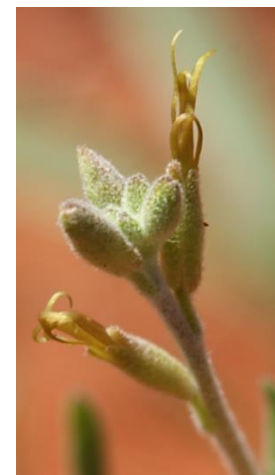


Multispeed genome diploidization and diversification after an ancient allopolyploidization

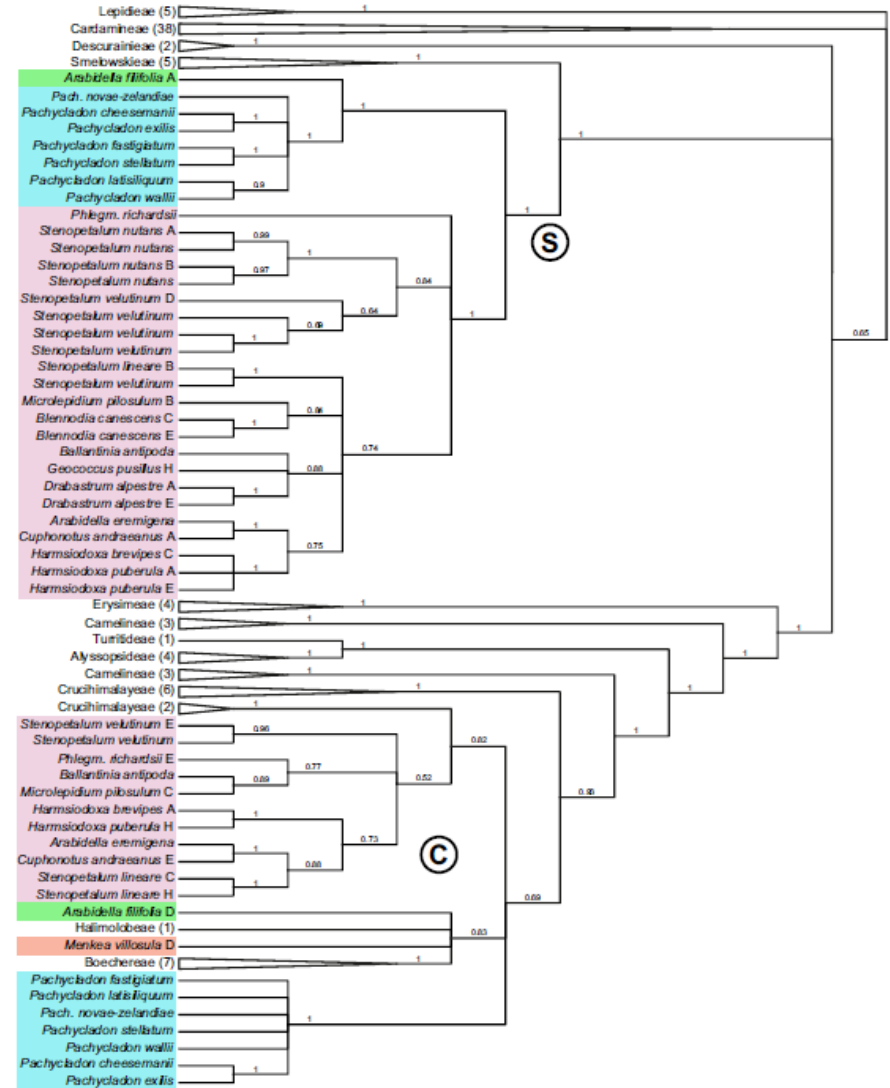
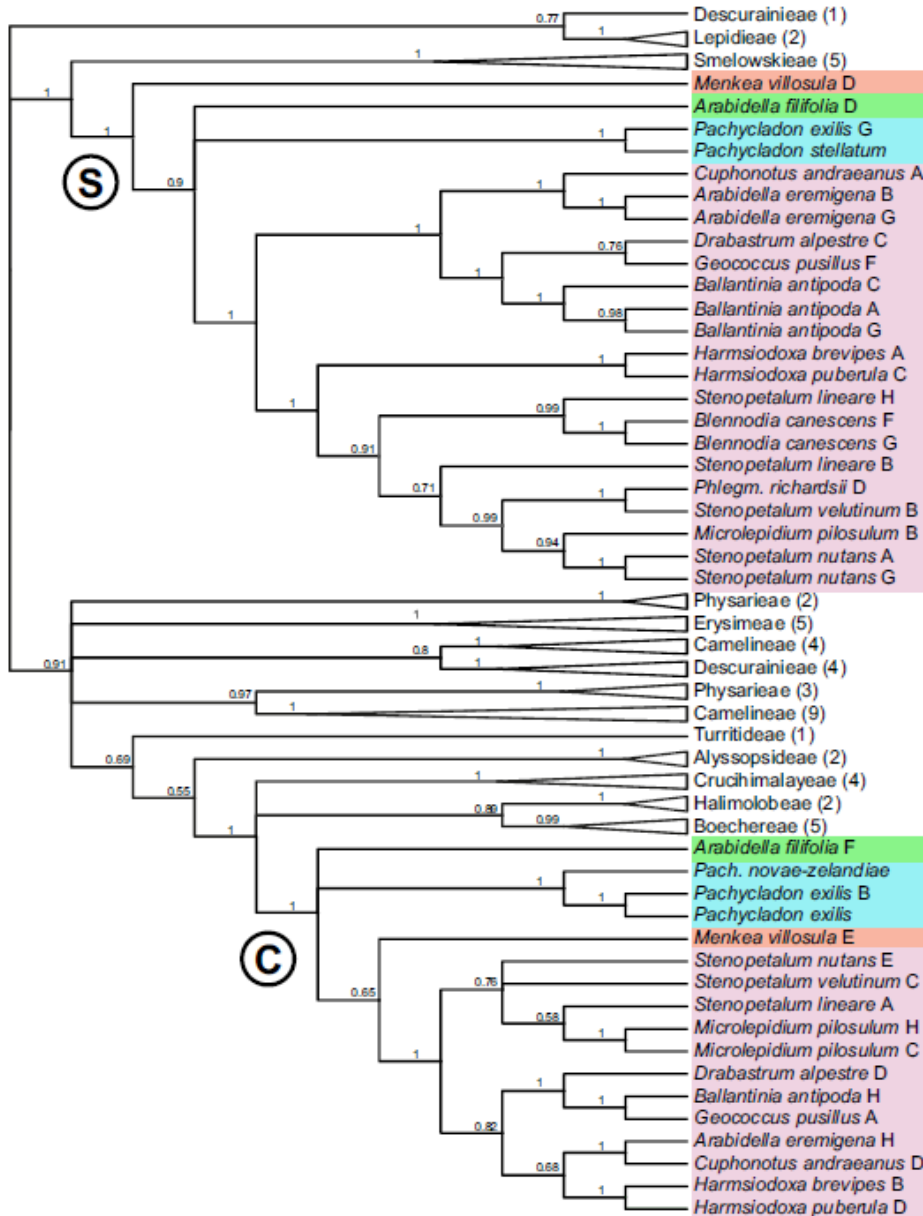
Terezie Mandáková¹  | Milan Pouch¹ | Klára Harmanová¹ | Shing Hei Zhan² | Itay Mayrose³ | Martin A. Lysak¹ 

Australia: 15 genera, 47 species

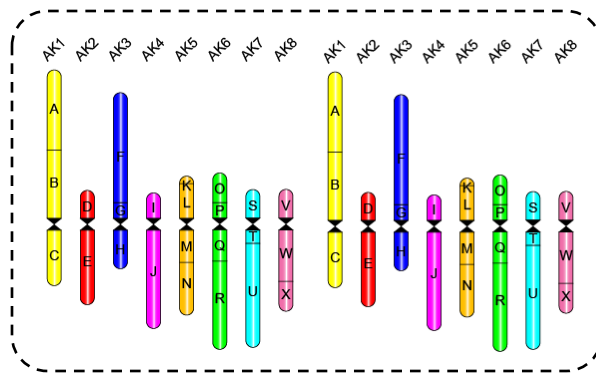
New Zealand: *Pachycladon*, 11 species



The allopolyploid origin evidenced by single-copy nuclear gene phylogenies



16 chromosomes
48 blocks

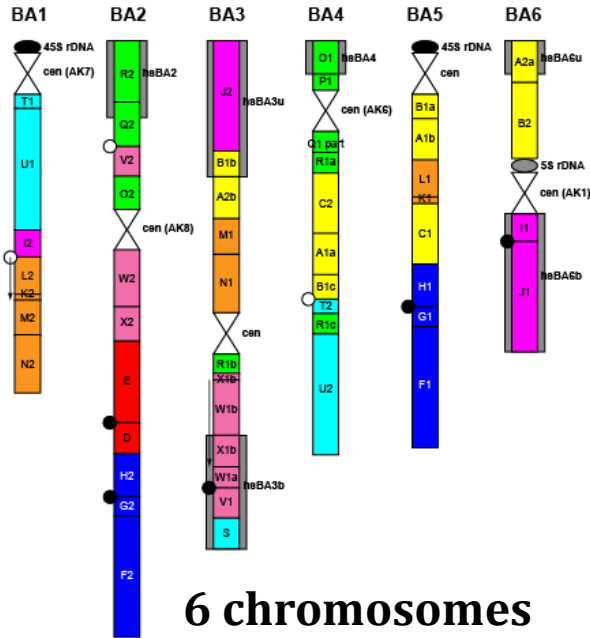


ACK, 4x

~ 6 - 9 mya

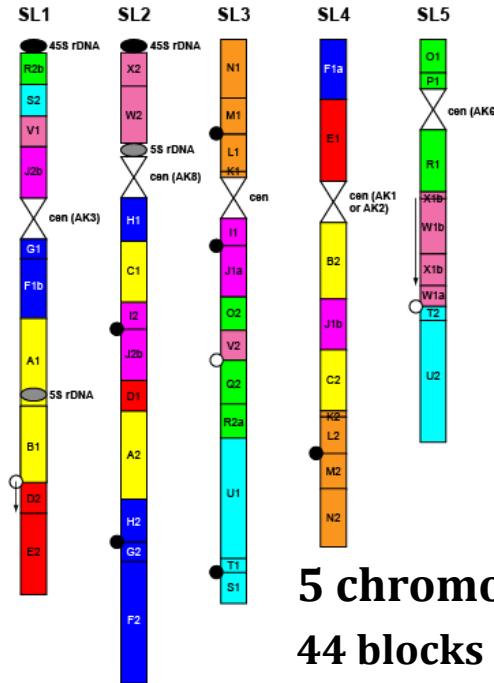
Ballantinia antipoda

Stenopetalum nutans

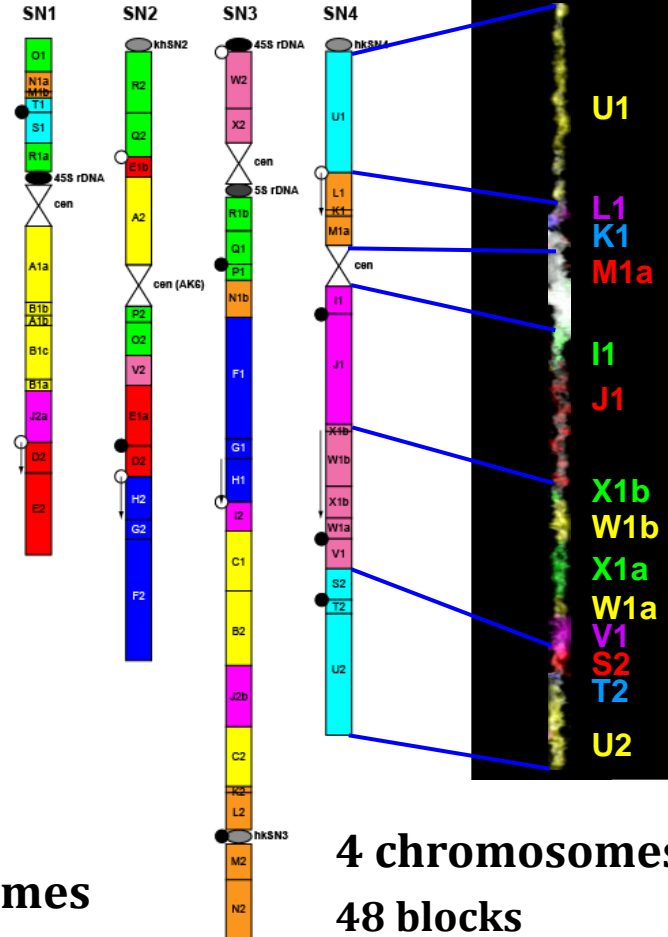


6 chromosomes
40 blocks

Stenopetalum lineare



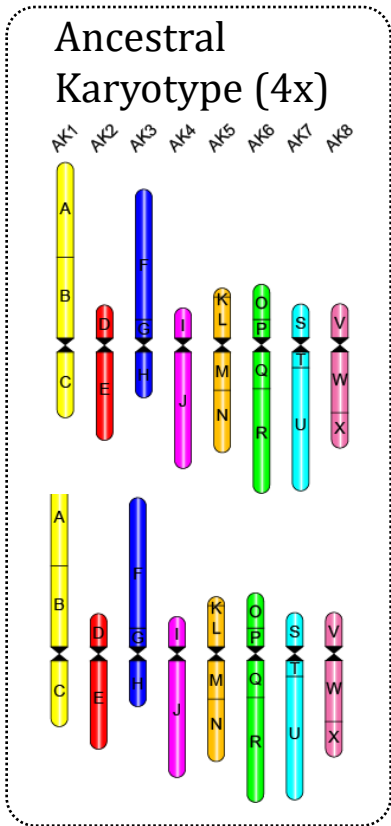
5 chromosomes
44 blocks



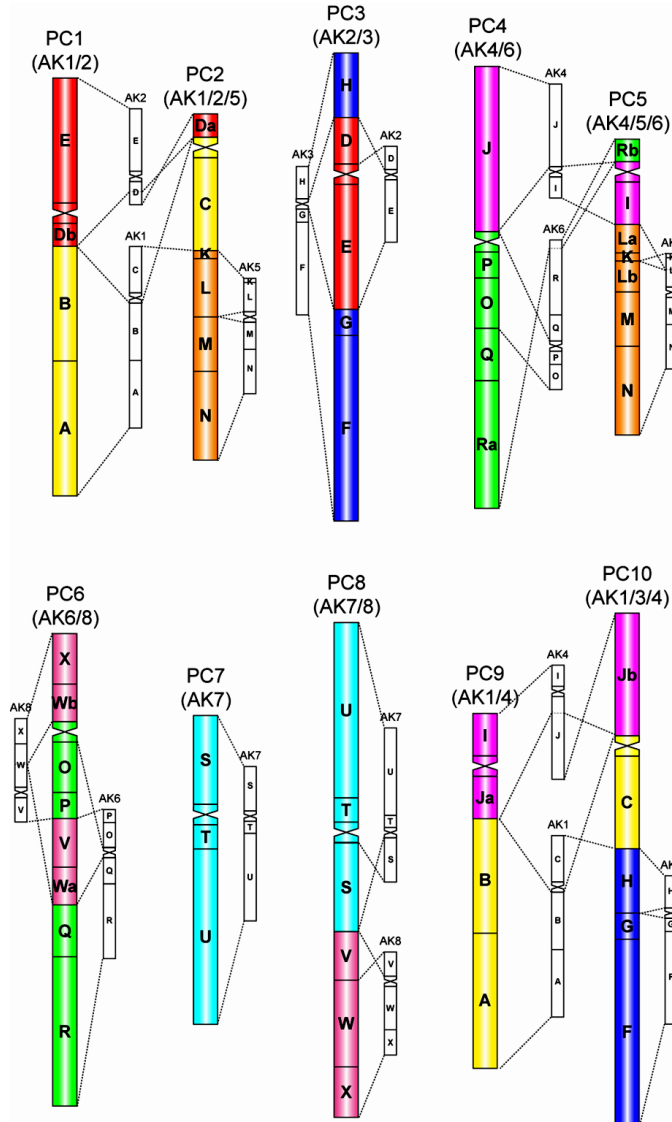
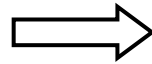
4 chromosomes
48 blocks

Polyploid Origin of *Pachycladon* (n=10)

~ 1 - 2 mya



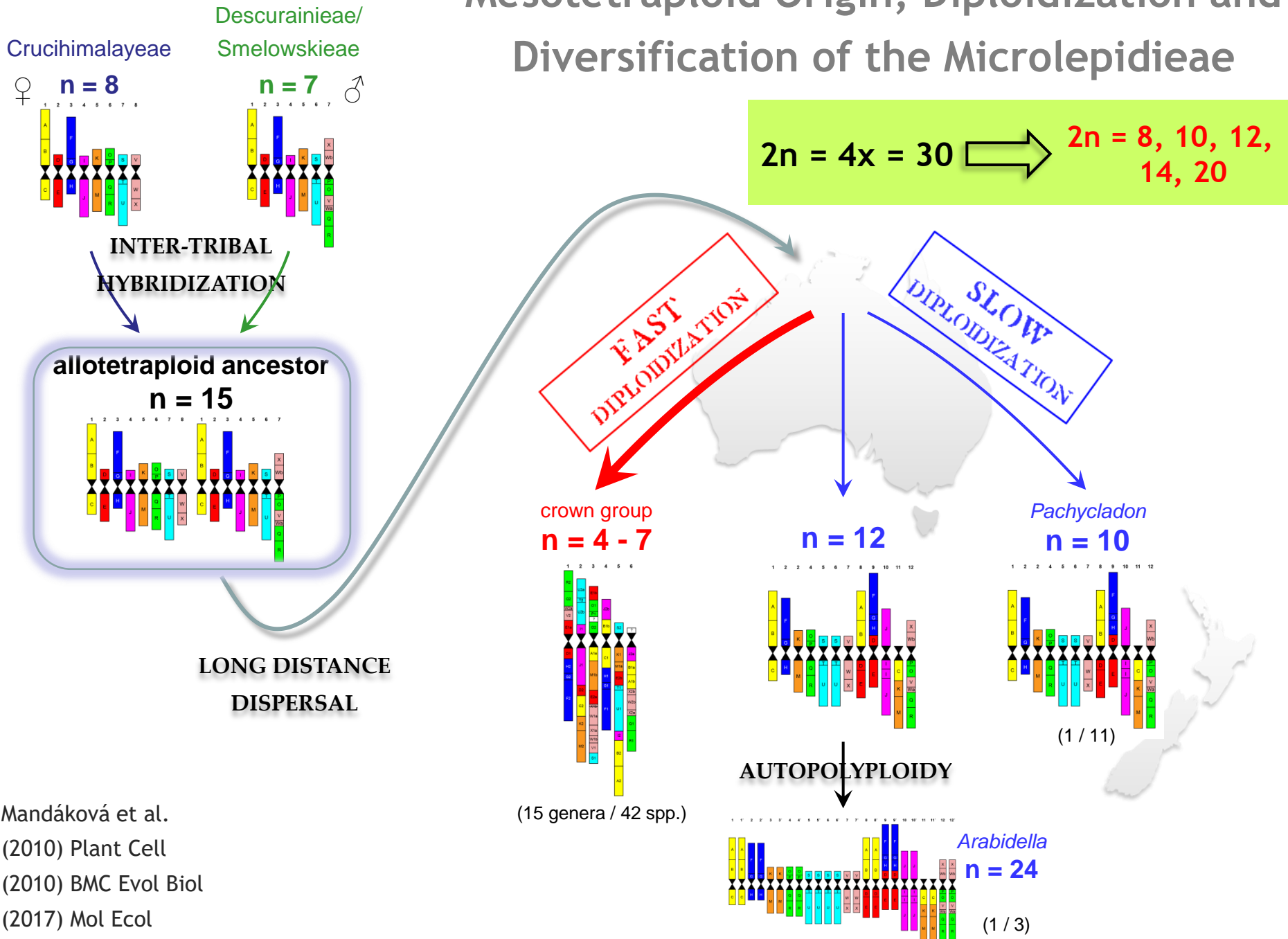
16 chromosomes
48 blocks



10 chromosomes
48 blocks

P. ensyii
P. novae-zelandiae
P. cheesemani
P. exile

Mesotetraploid Origin, Diploidization and Diversification of the Microlepidieae



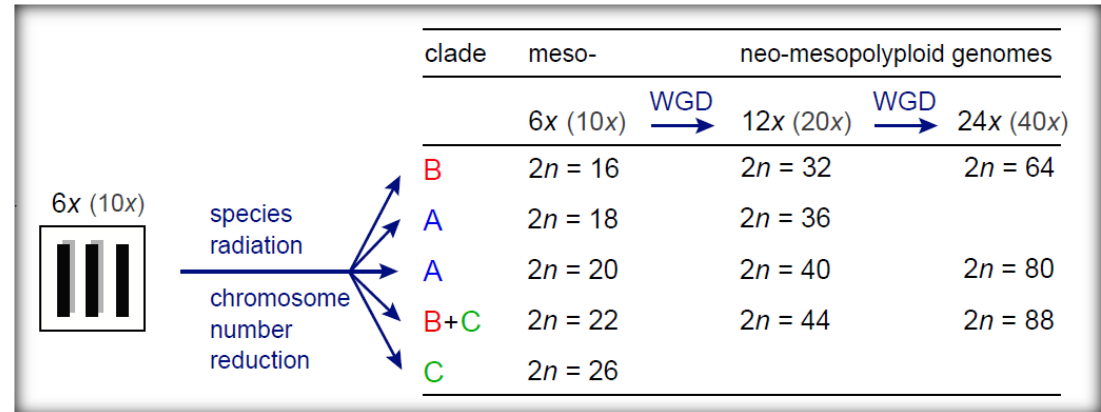
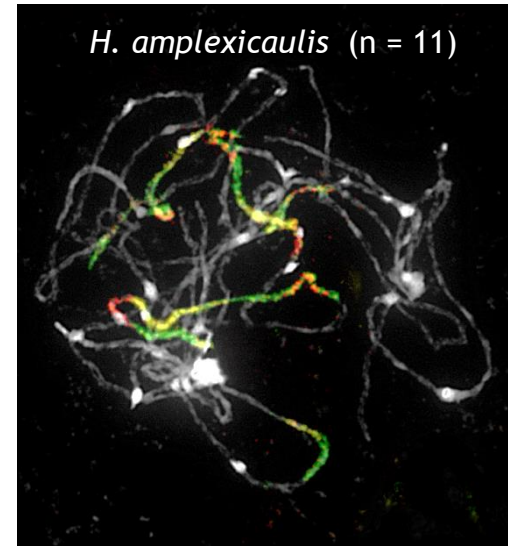
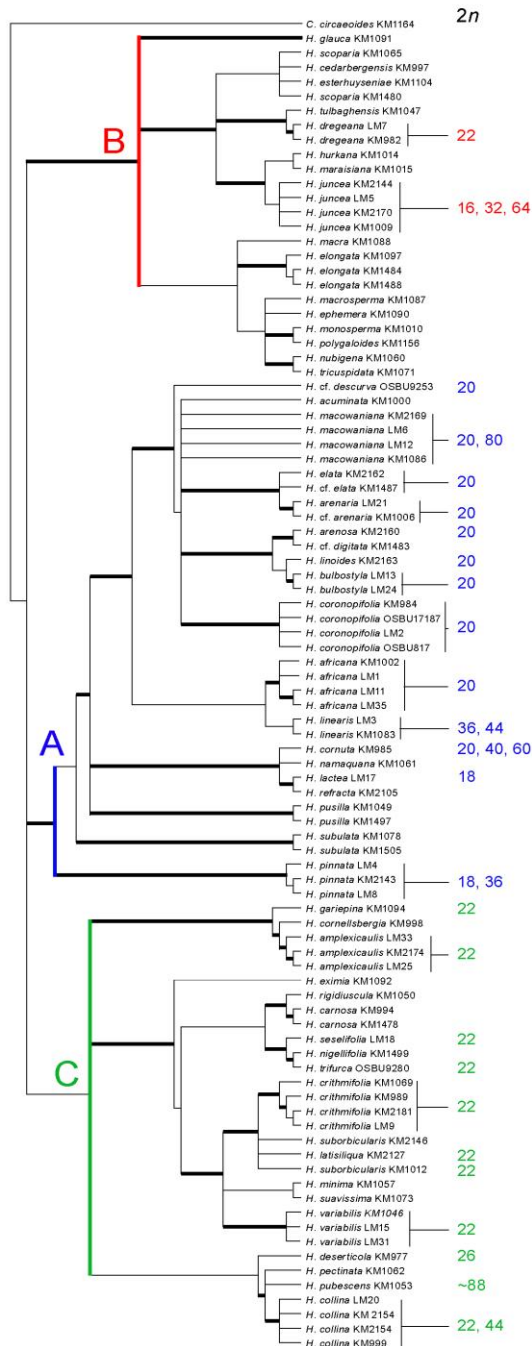
Mandáková et al.
 (2010) Plant Cell
 (2010) BMC Evol Biol
 (2017) Mol Ecol

Does Ancient Polyploidy Explain the Rapid Species Radiation in *Heliophila* ?

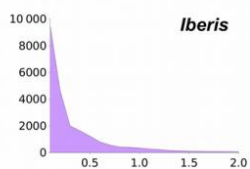
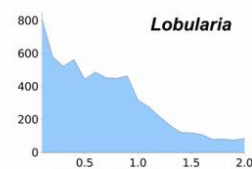
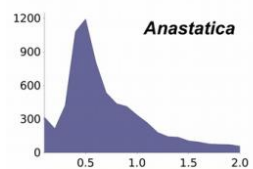
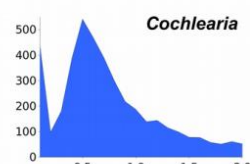
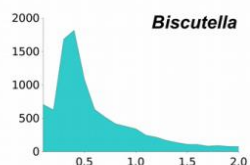
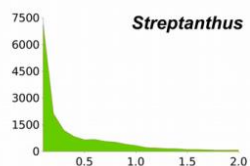
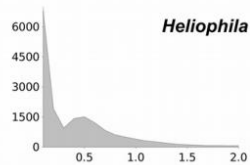
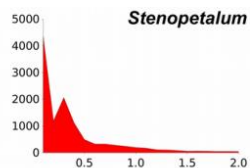
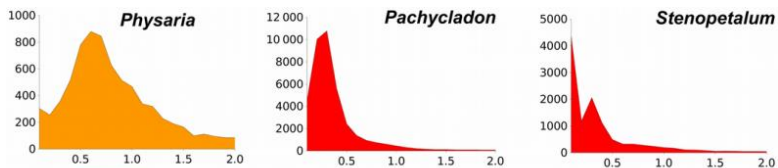
c. 90 (-100) endemic spp.



Whole-Genome Triplication in the Southern African Tribe Heliophileae

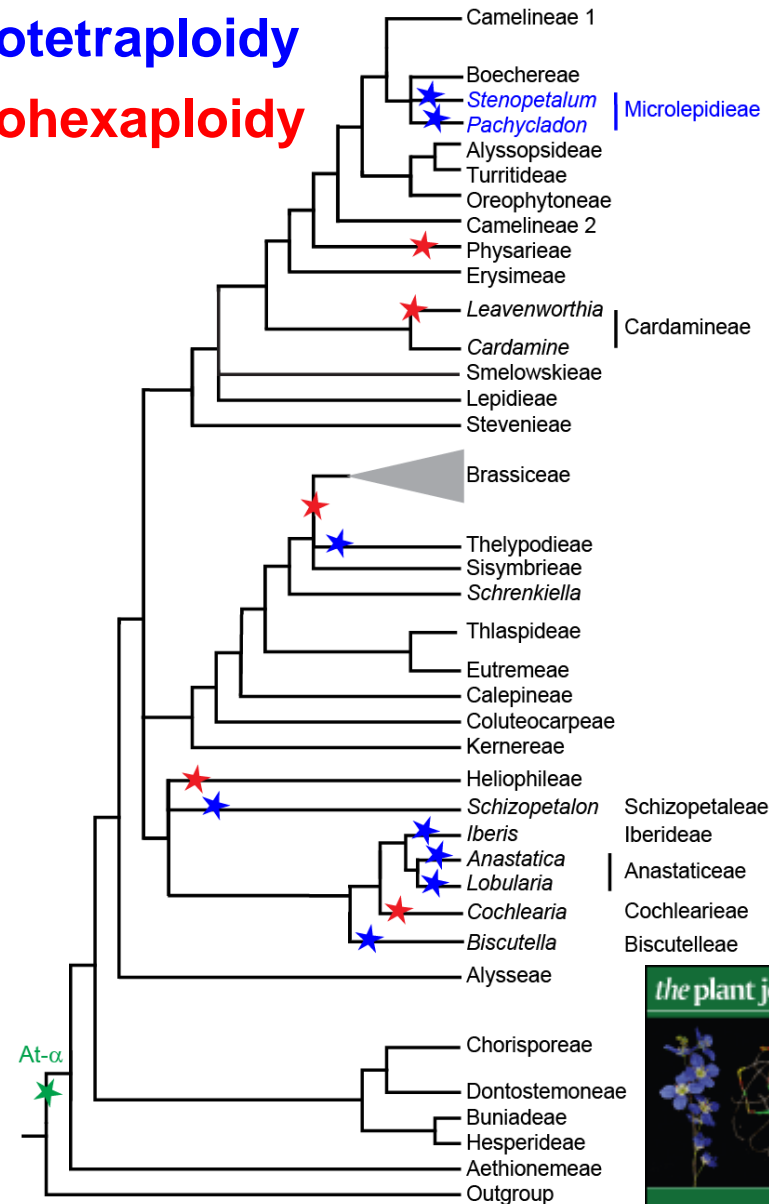
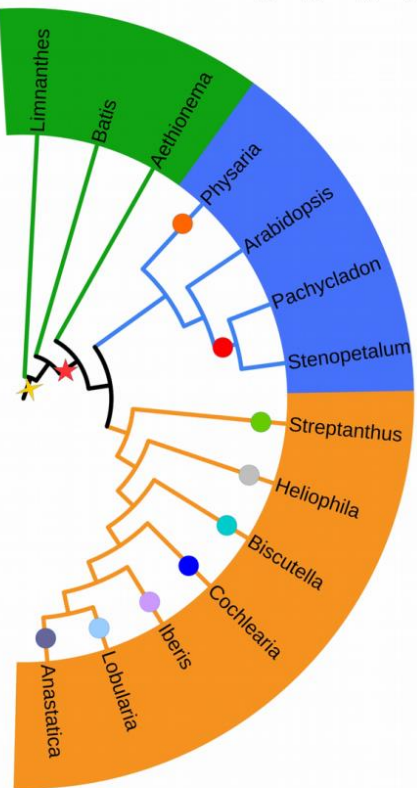


Lineage-Specific Mesopolyploid WGDs in Brassicaceae



★ mesotetraploidy

★ mesohexaploidy



Existing species and genomic diversity of many Brassicaceae clades result from post-polyploid diploidizations

meso TETRAPLOIDS



Thelypodieae

26 g.: 244 spp.

n = 14

→ n = (10, 12) 14

Biscutelleae

2: 46 (or more)



16

→ 6, 8, 9



Microlepidieae

17: 56

15

→ 4, 5, 6, 7, 10, 12

meso HEXAPLOIDS



Brassicaceae

47: 227

21

→ 7, 8, 9, 10, 11, 12, 13, ...

Heliophileae

1: 100



21 or 24

→ (8, 9) 10, 11 (13)



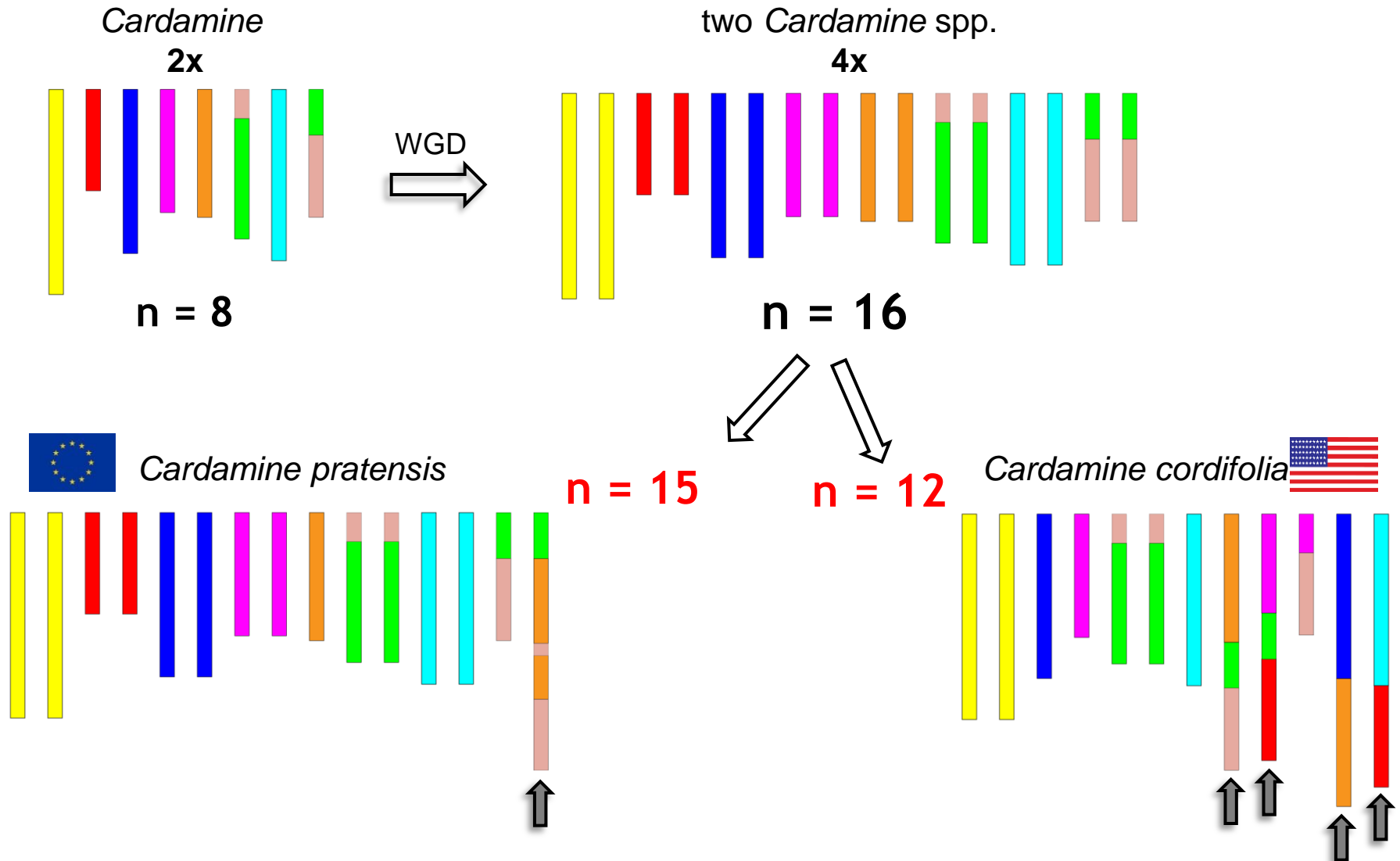
Physarieae

7: 133

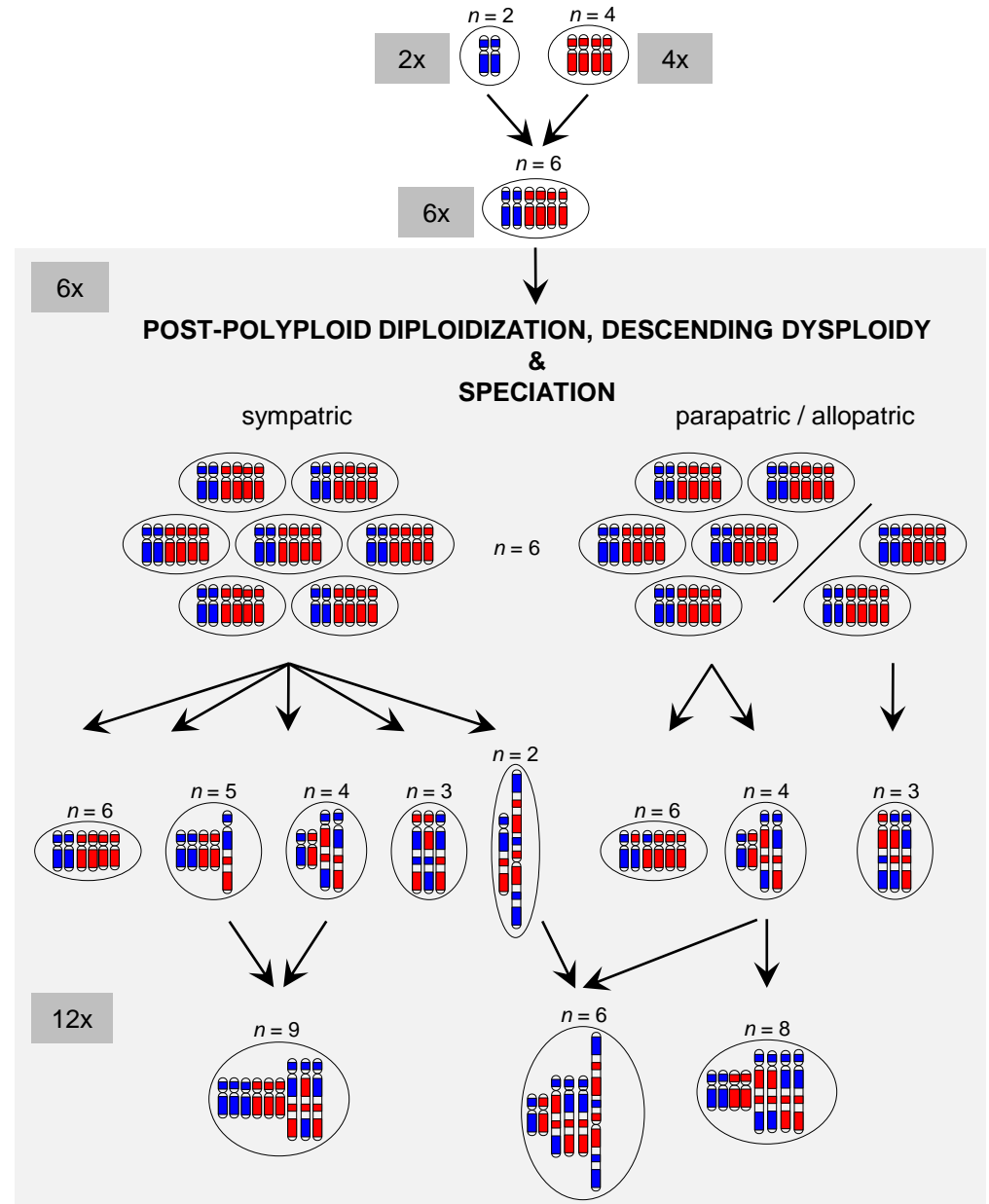
24

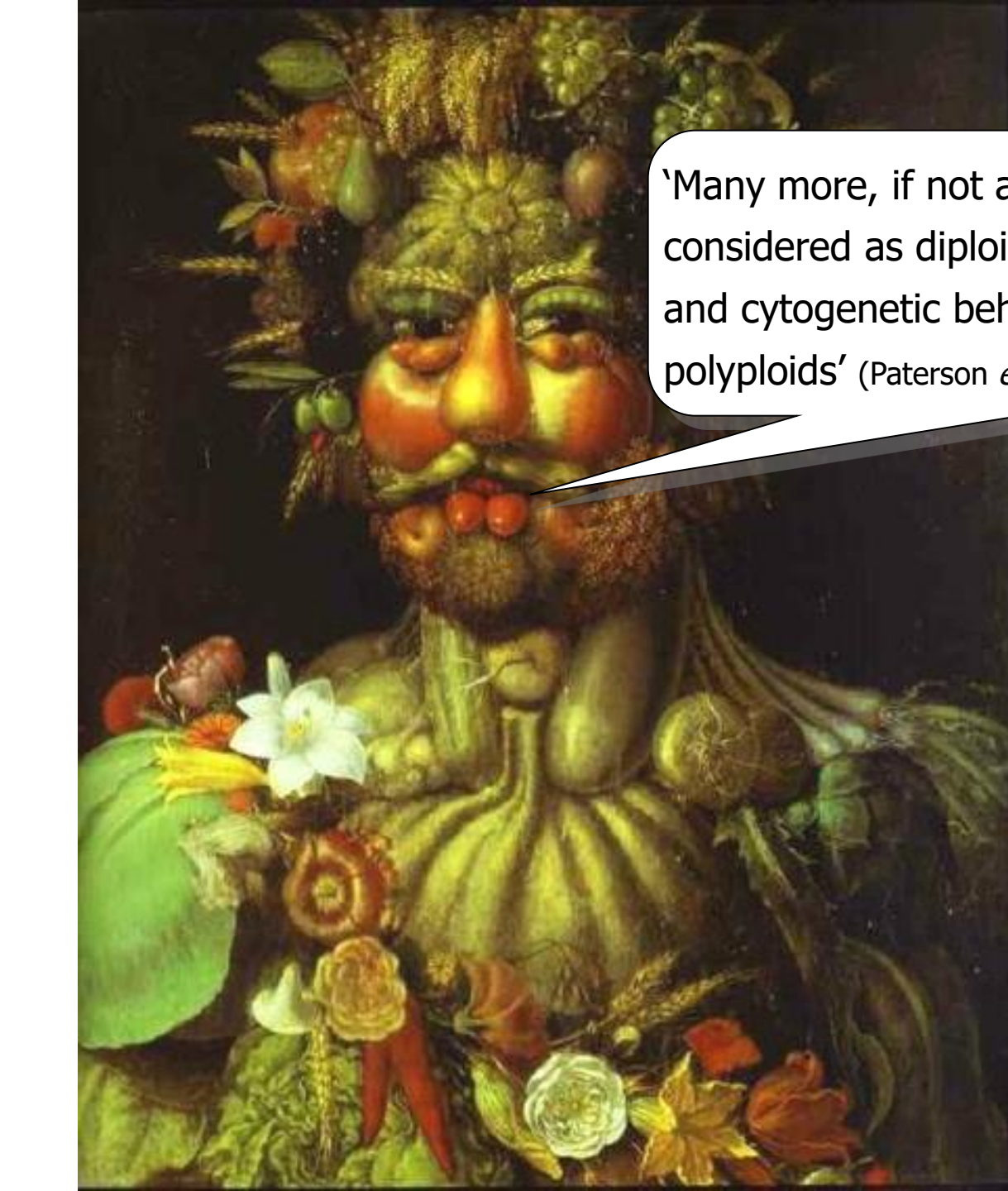
→ 4, 5, 6, 7, 10, 12

Two hypotetraploid *Cardamine* species: recent and starting diploidizations via descending dysploidy



Speciation and diversification driven by post-polyploid diploidization via descending dysploidy



A detailed still life painting where the central figure is a man's face and upper torso, meticulously constructed from a variety of fruits and vegetables. The face features a large, pointed nose made of a pear, a beard of raspberries, and lips of strawberries. The chest is covered in green vegetables like zucchini and eggplant. The background is dark, making the vibrant colors of the produce stand out. A speech bubble is overlaid on the right side of the image.

'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).