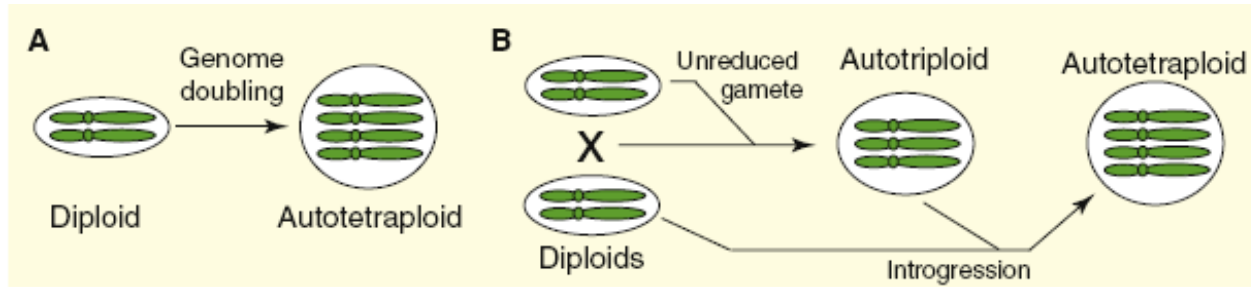


(Paleo)Polyploidy – When Things Get Bigger

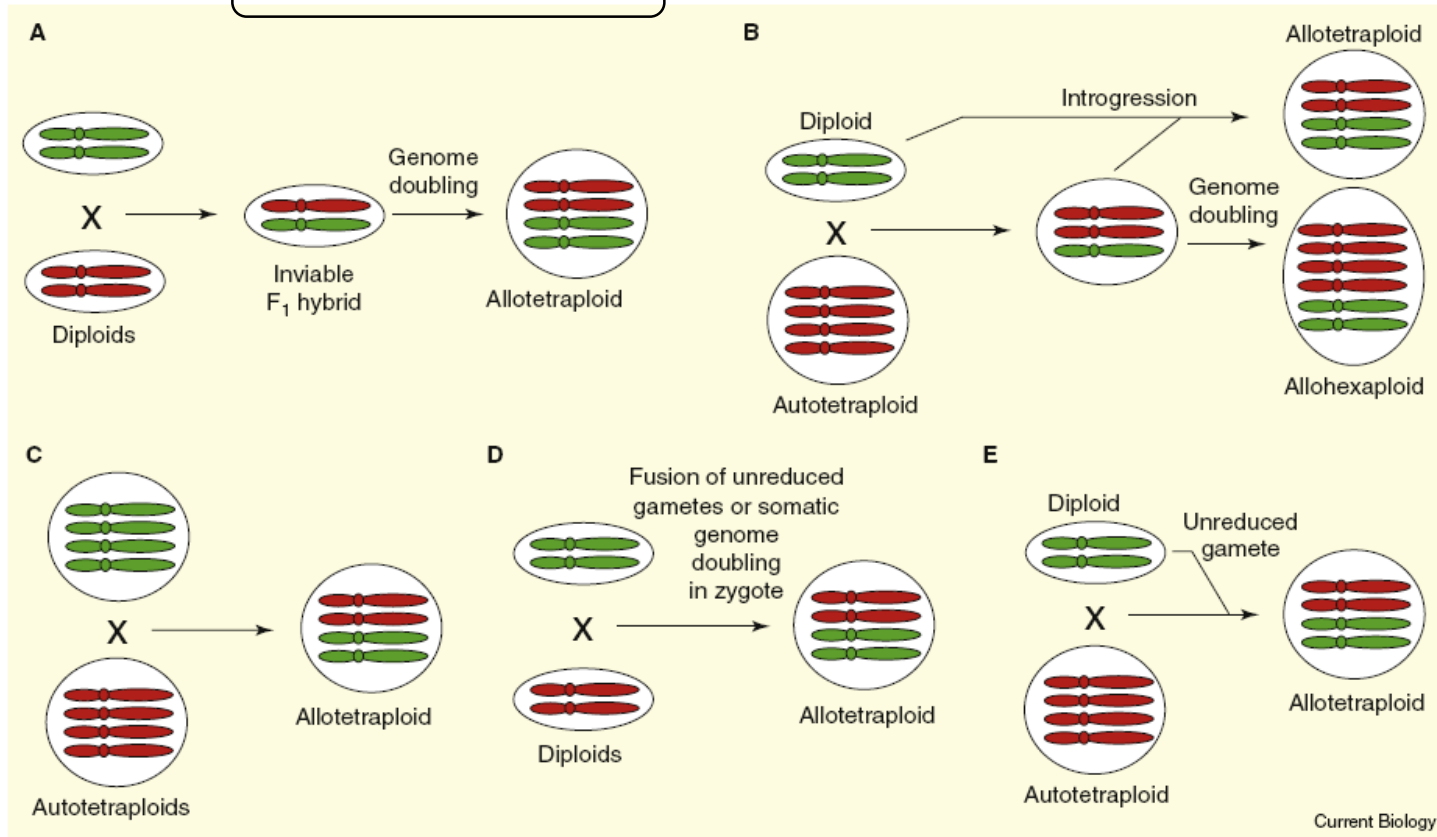


Whole-genome duplications



AUTOPOLYPLOIDY

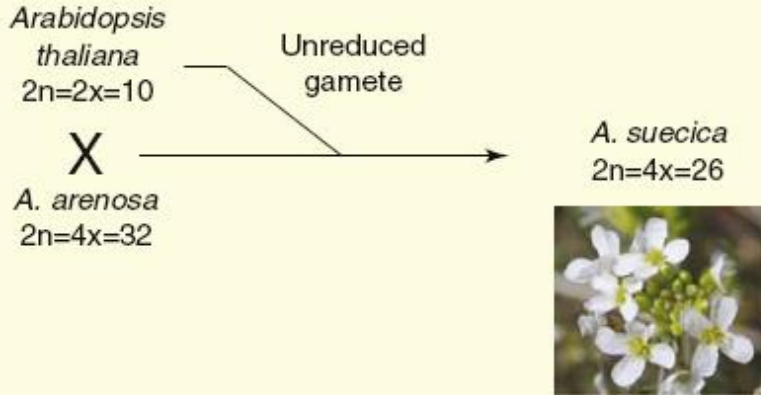
ALLOPOLYPLOIDY



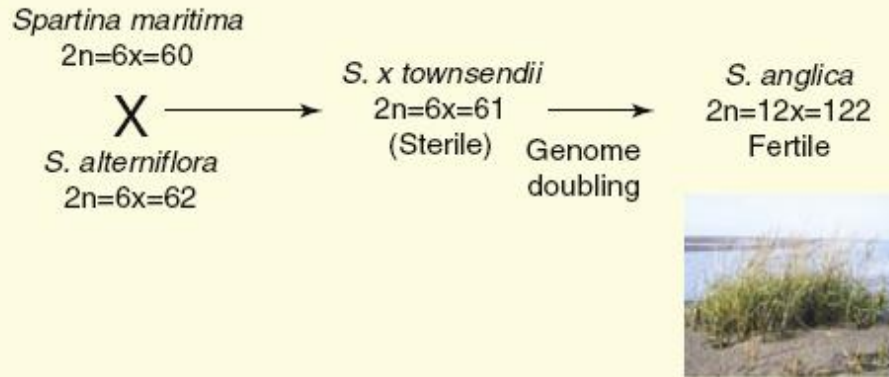
Current Biology

Examples of allopolyploid speciation

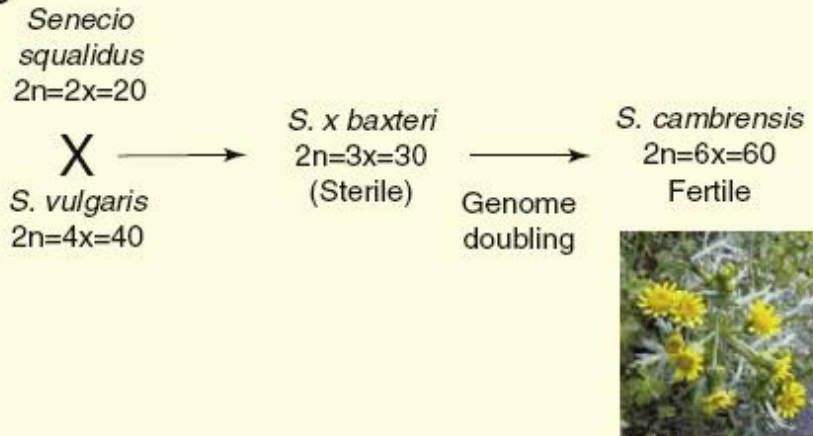
A



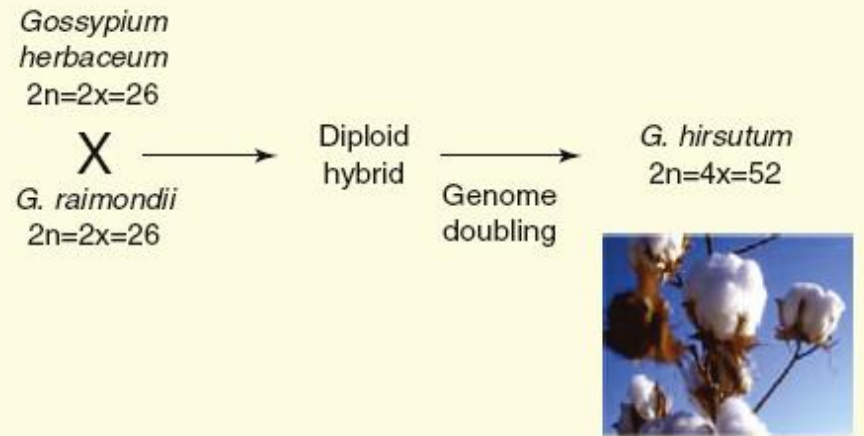
B



C



D



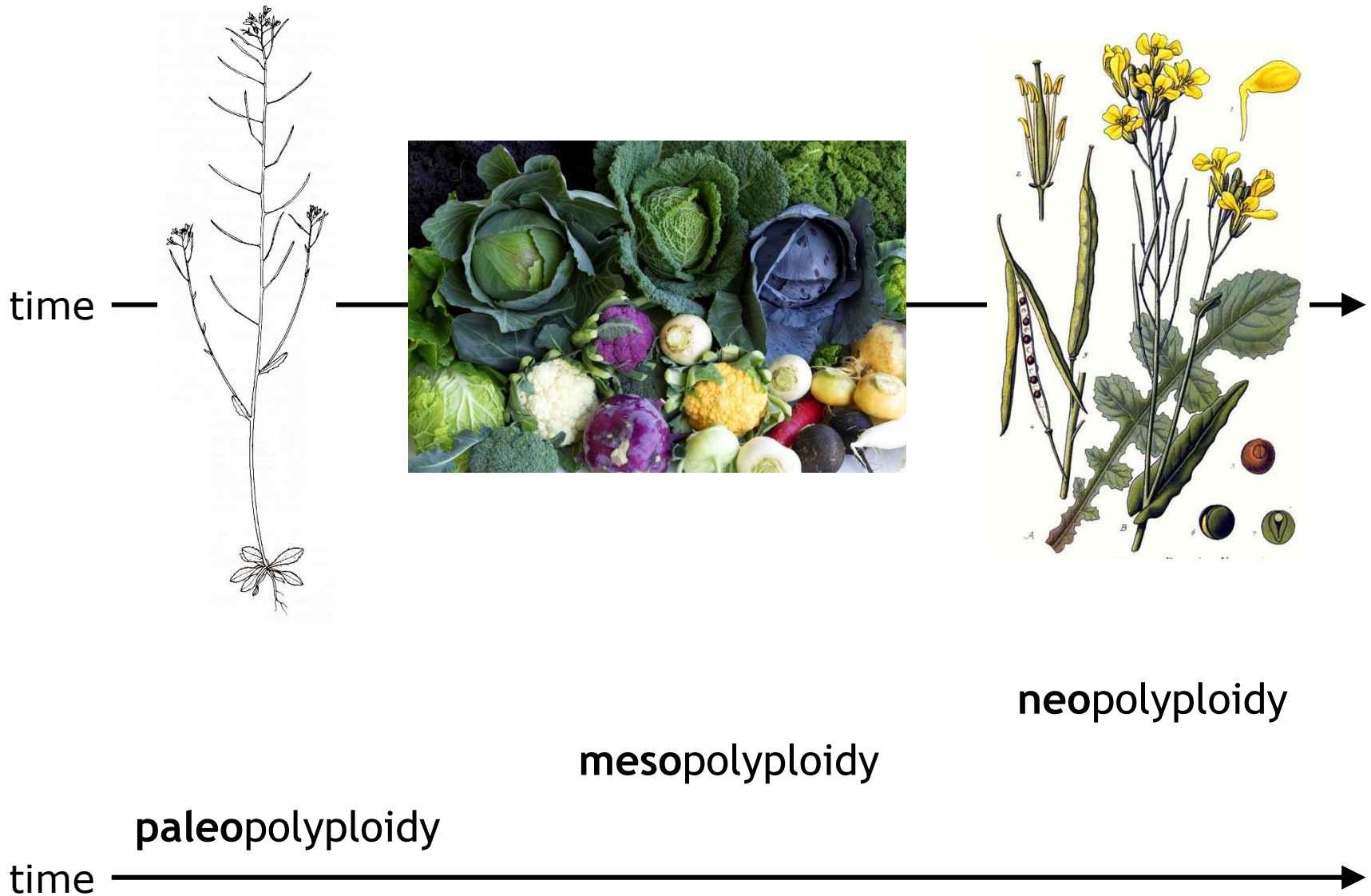
Current Biology

Evolutionary significance of polyploidy

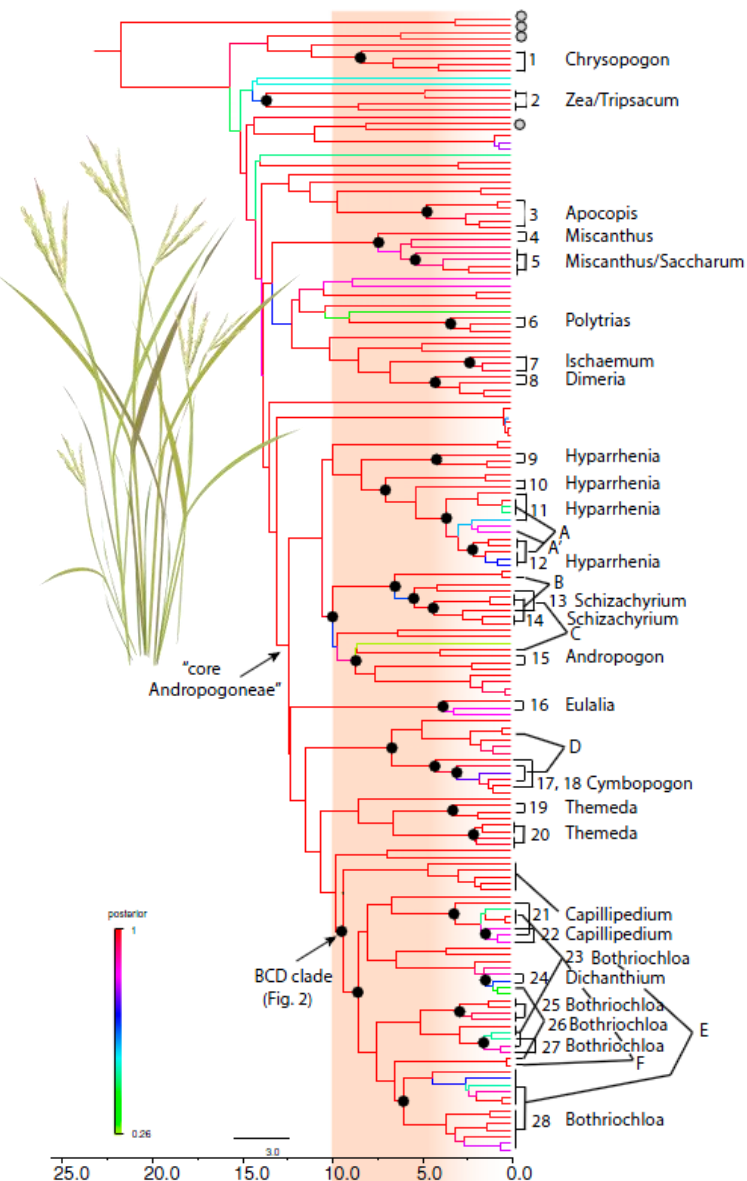


Leitch & Leitch (2008) *Science* 320

Whole-genome duplications of different age

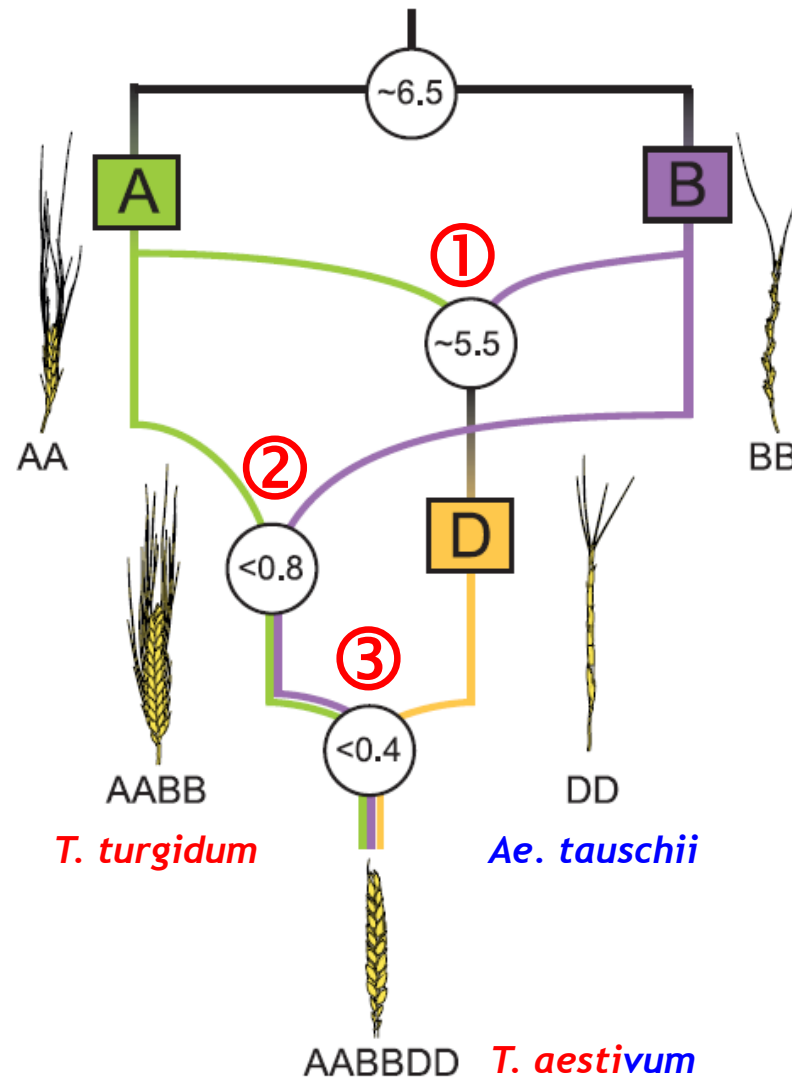


Allopolyploidy, diversification, and the Miocene grassland expansion



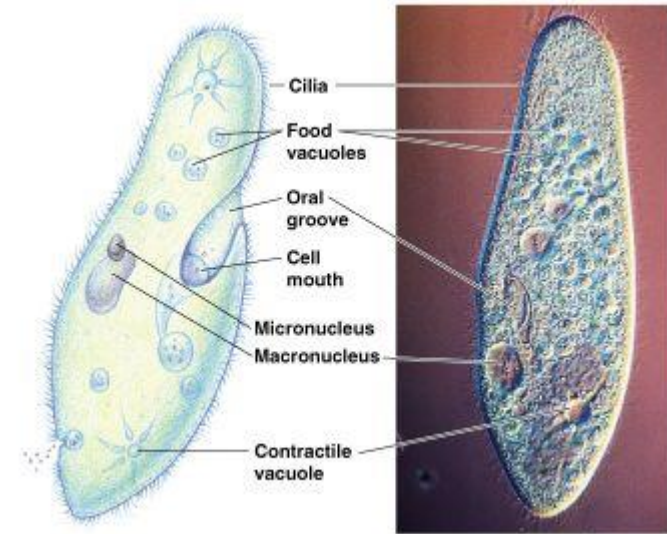
- Most of the allopolyploidization events identified here occurred in the Late Miocene, simultaneous with or following the well documented expansion of the C4 grasslands.
- The dominant species of modern C4 grasslands are members of Andropogoneae, and most are allopolyploid. Many of these ecological 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.

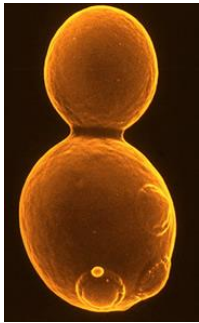
Model of the phylogenetic history of bread wheat (*Triticum aestivum*; AABBDD). Three rounds of hybridization/polyploidization.



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

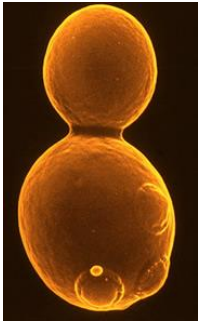




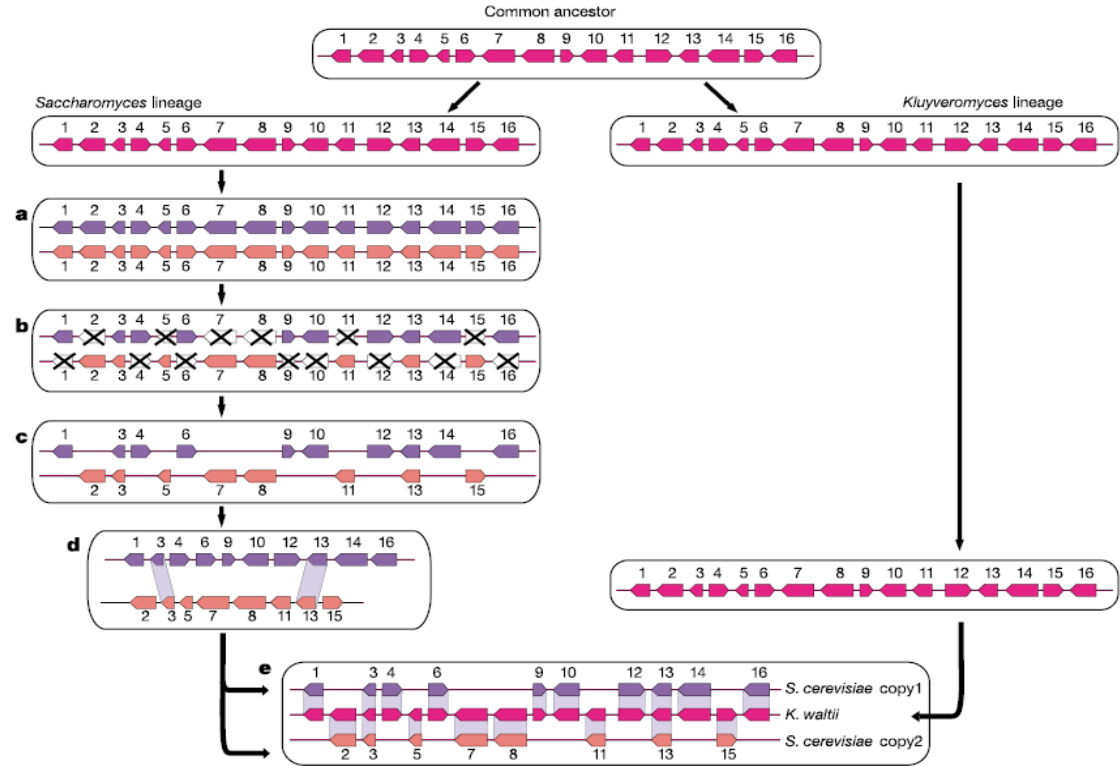
Whole-genome duplications in yeast

- 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

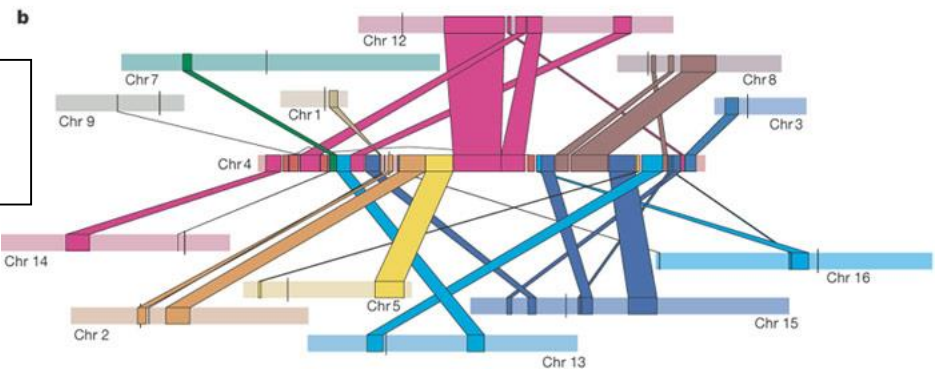
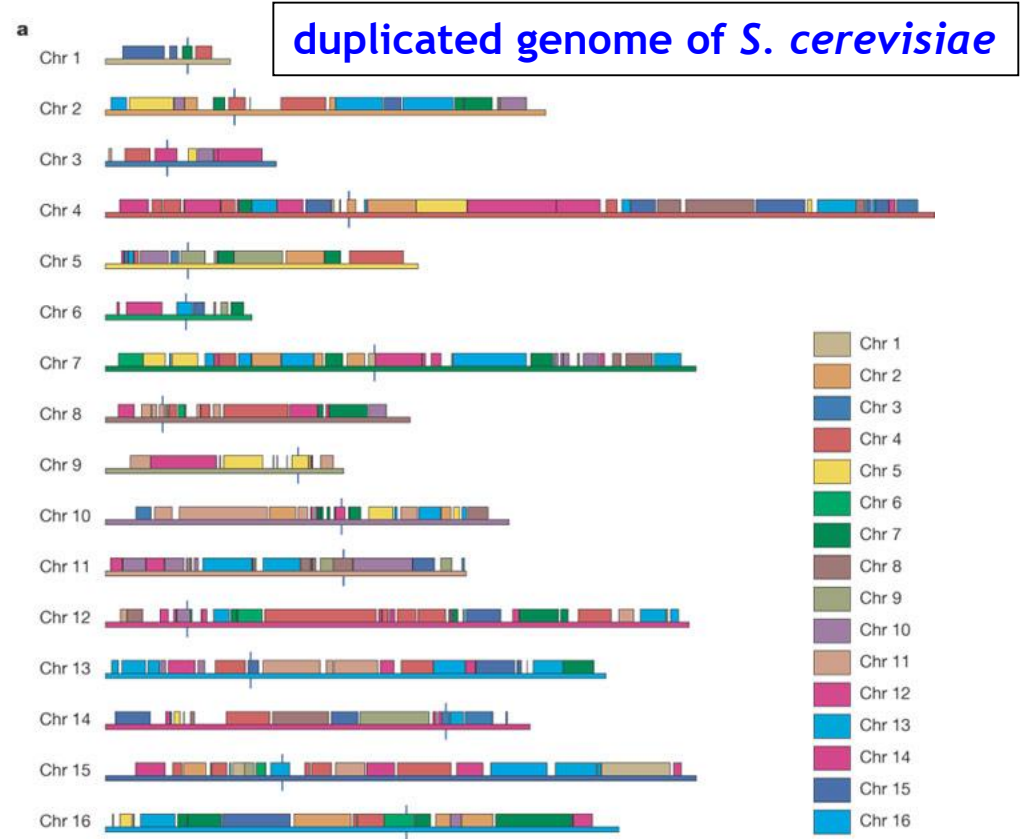
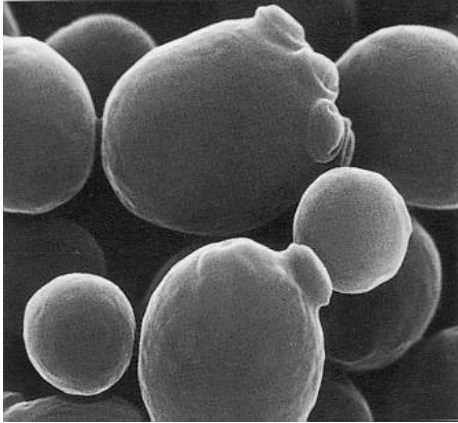


Kellis *et al.* 2004,
Nature 428



- 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



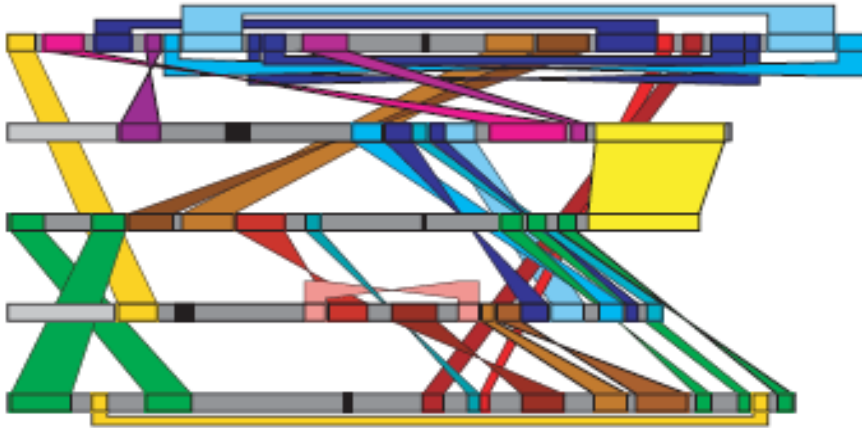
S. cerevisiae chromosome 4 with
sister regions in other chromosomes

First evidence of a WGD in plants



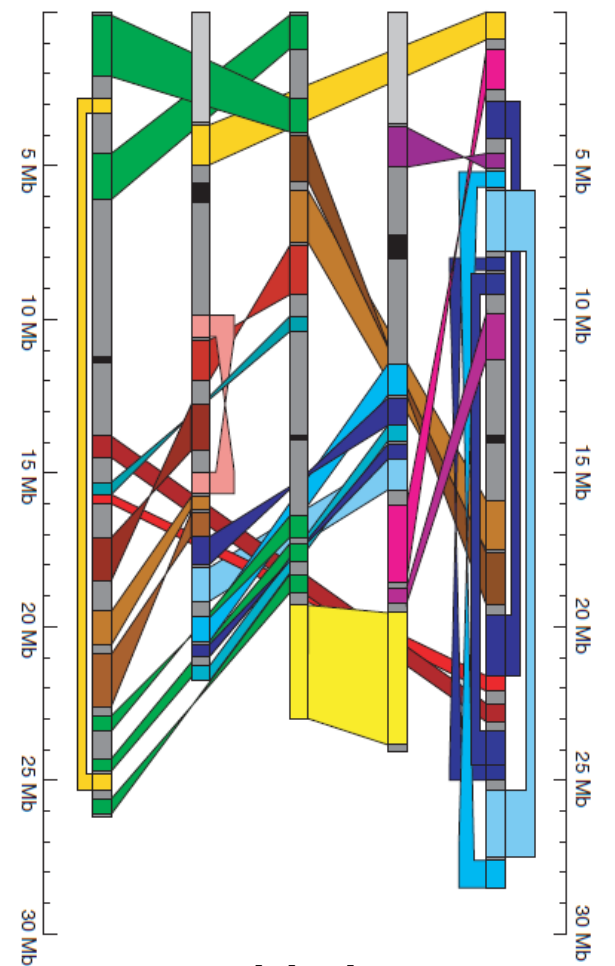
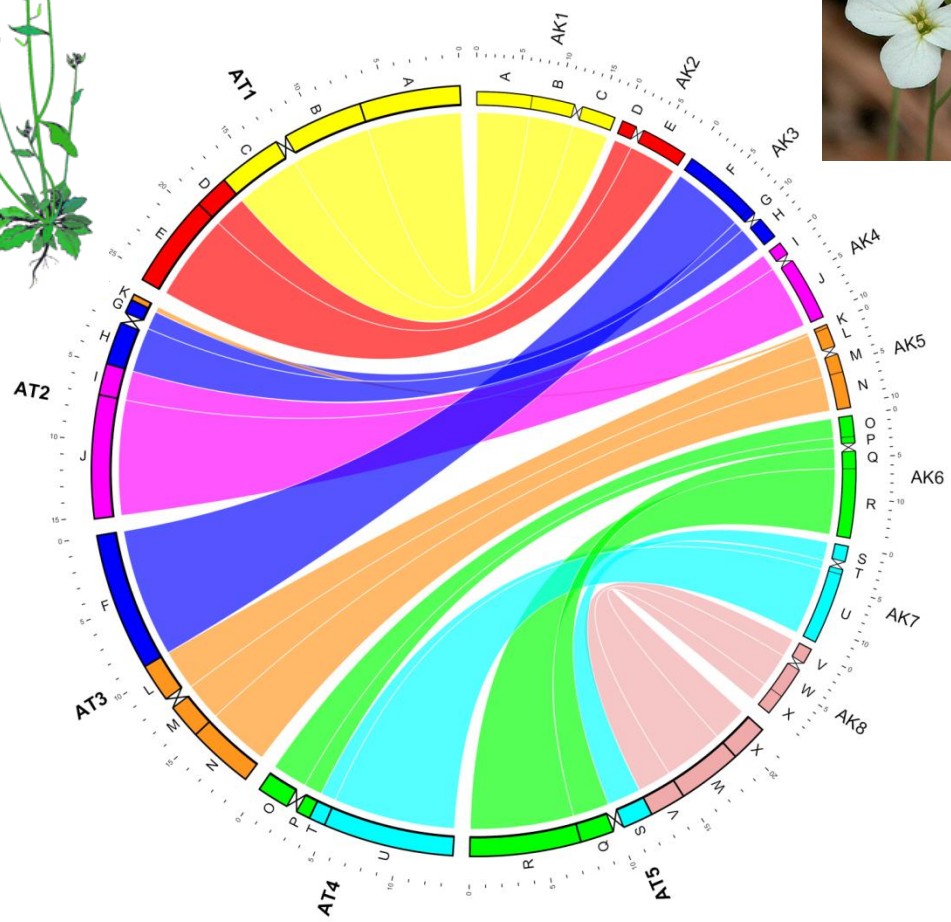
Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*

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

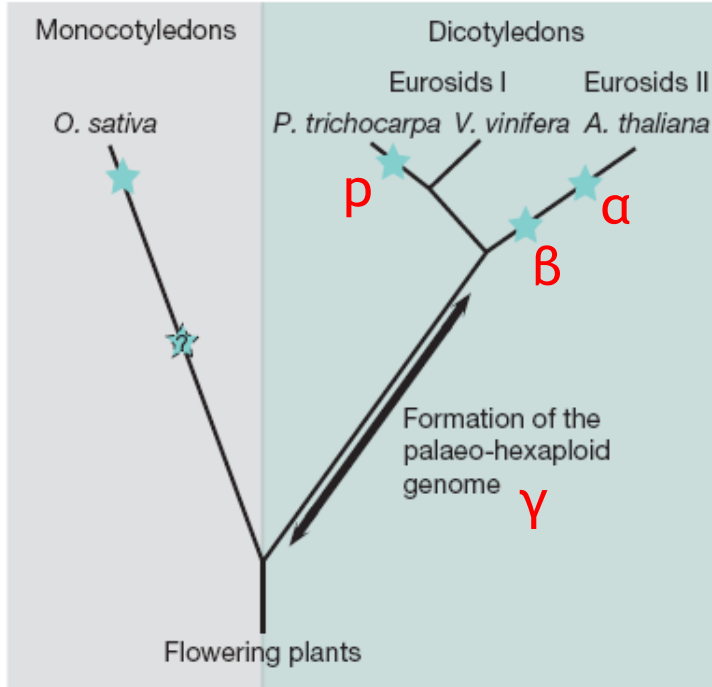


segmental duplications in the *A. thaliana* genome

The grapevine genome sequence suggests ancestral hexaploidization in major angiosperm phyla

The French-Italian Public Consortium for Grapevine Genome Characterization*

Nature 449, 2007



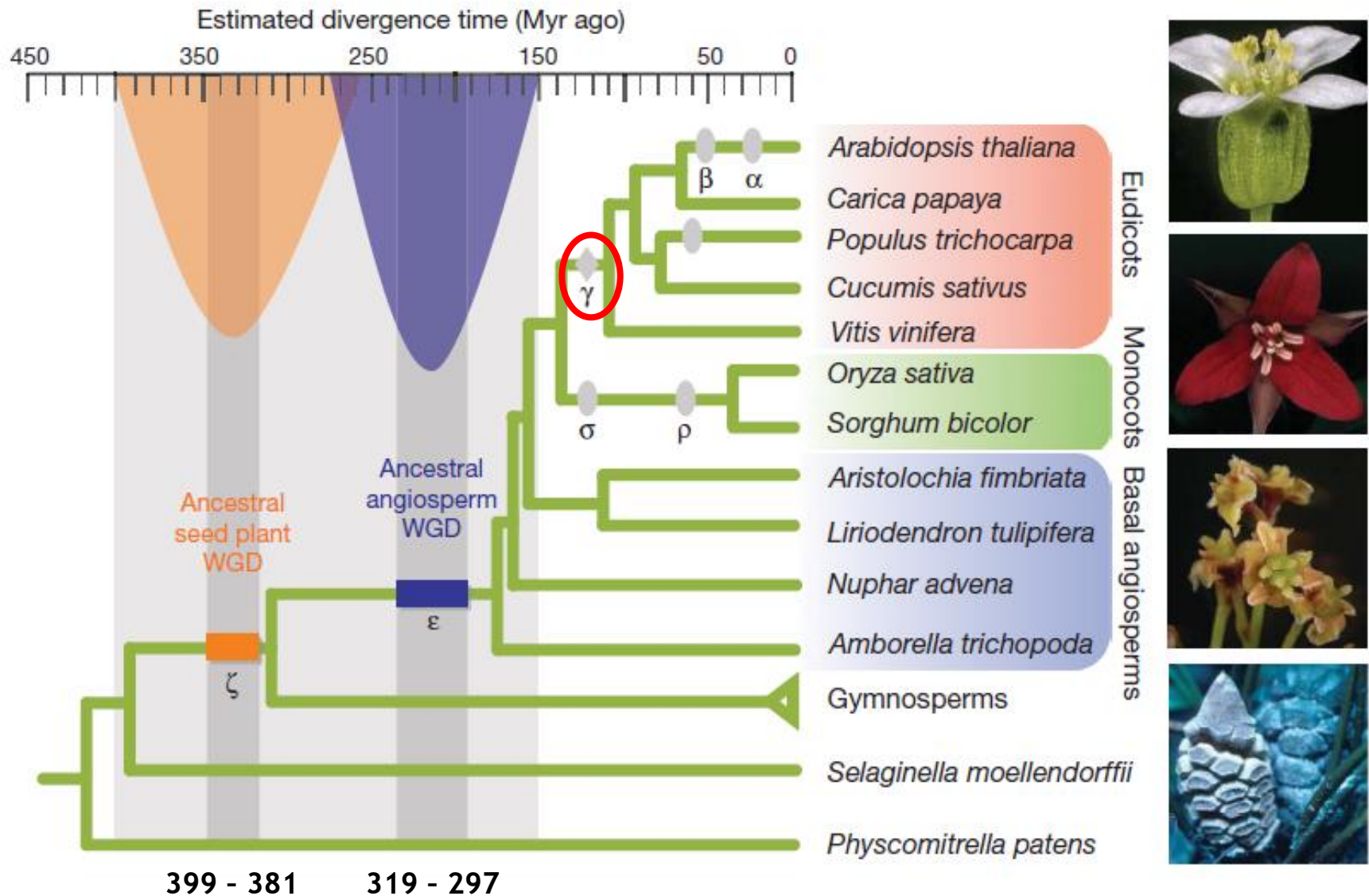
The **γ triplication** may have been an ancient **auto-hexaploidy** formed from fusions of three identical genomes, or **allo-hexaploidy** formed from fusions of three somewhat diverged genomes.

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

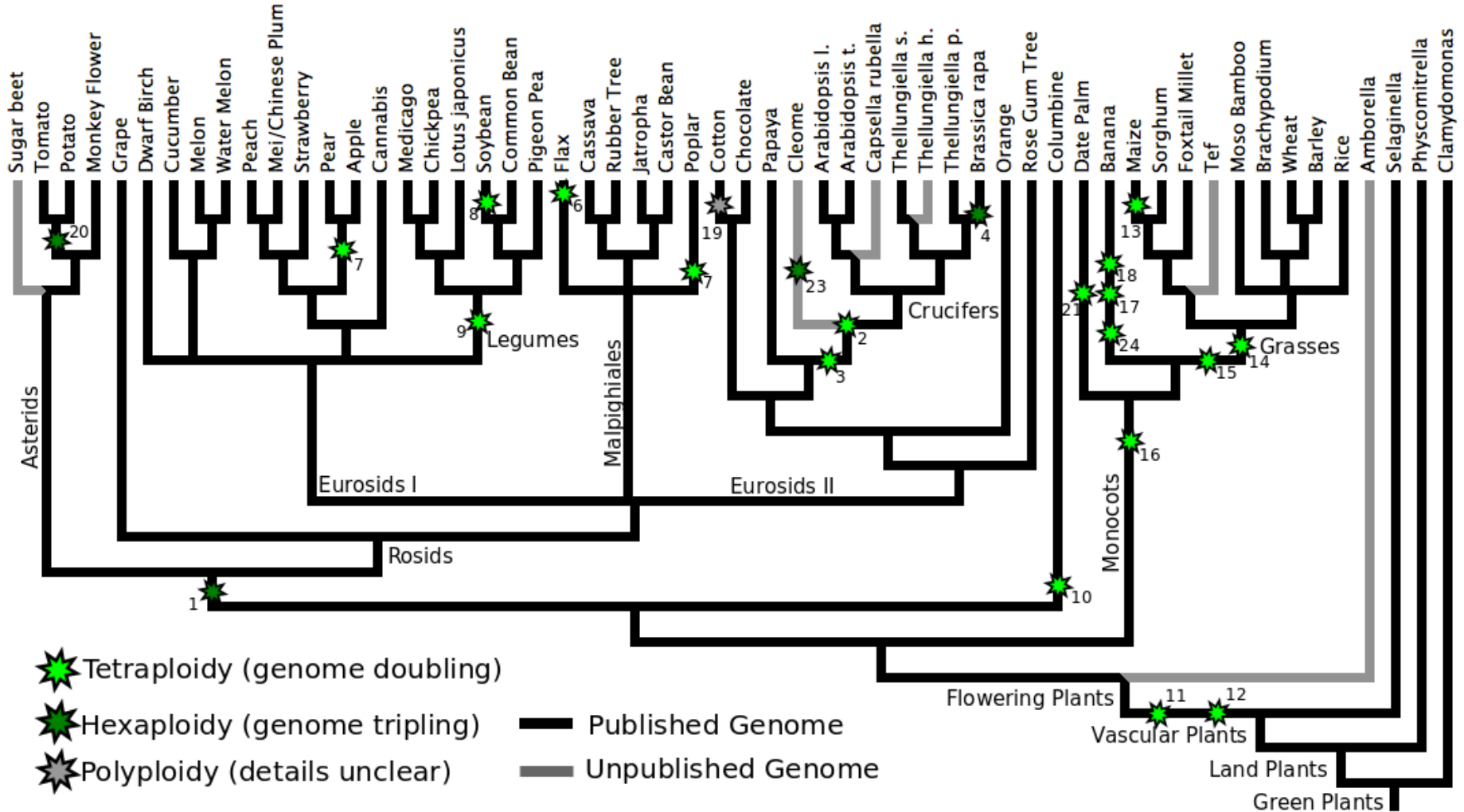
The formation of the palaeo-hexaploid ancestral genome occurred after divergence from monocots and before the radiation of the Eurosids. Star = a WGD (tetraploidization) event.



WGD events in seed plants and angiosperms

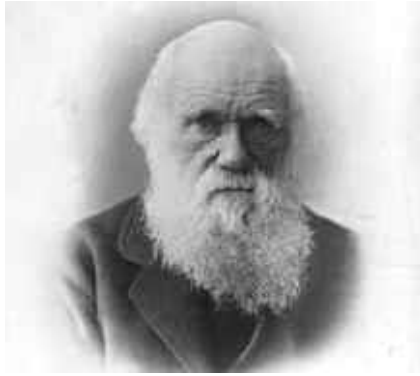


Phylogenetic Tree of Sequenced Genomes with Whole Genome Duplications Marked



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

Charles Darwin's abominable mystery solved?

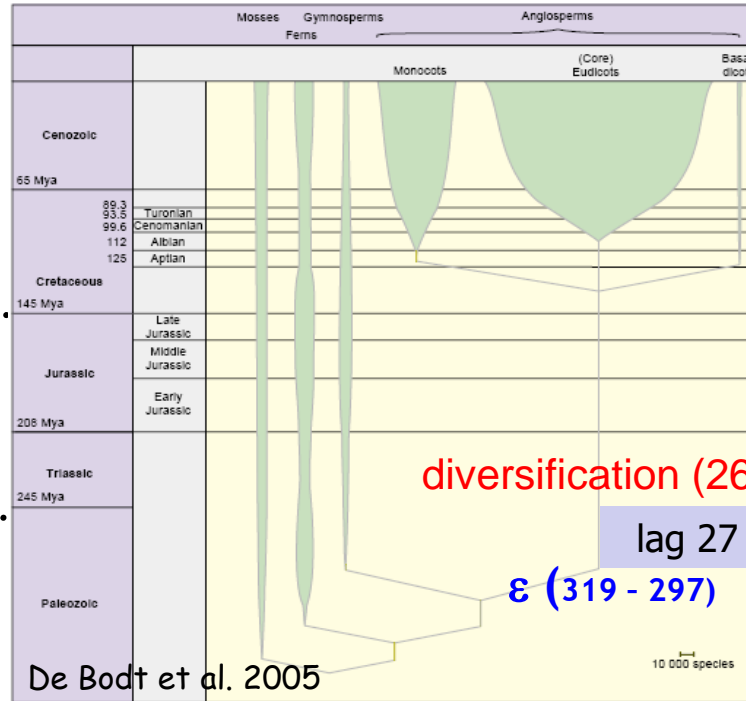
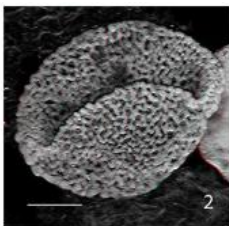


"The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery."
 (Charles Darwin in a letter to Sir Joseph Hooker, 1879)

Archaeofructus liaoningensis
 (140 million year old fossil)



Afropollis
 (245 million year old angiosperm pollen)



assumed ancient whole-genome duplication events (e.g. γ - gamma WGD)

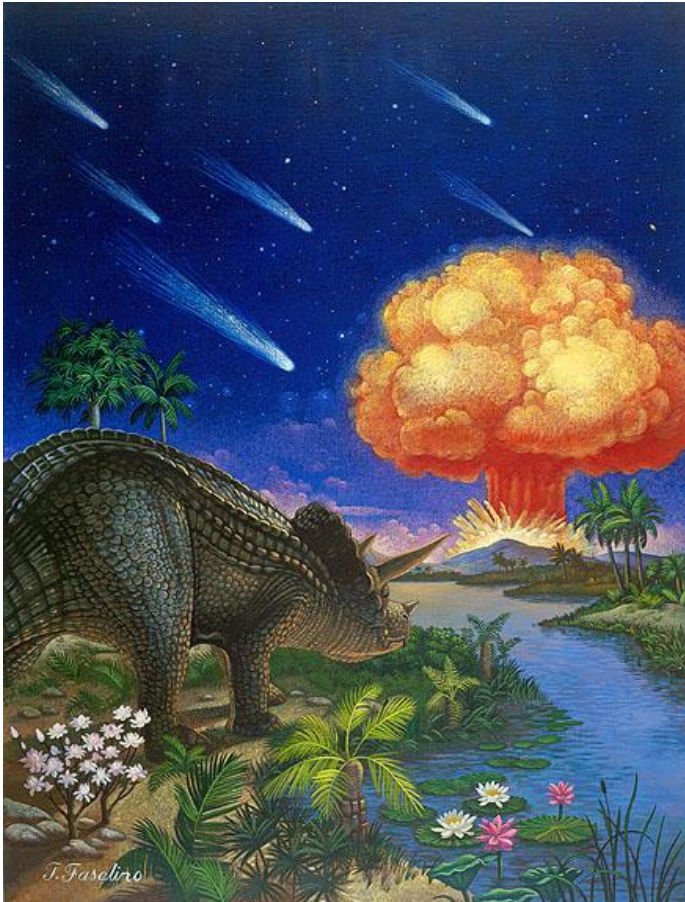
There is evidence of ancient polyploidy throughout the major angiosperm lineages. It means that a genome-scale duplication event probably occurred PRIOR to the rapid diversification of flowering plants

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 ?

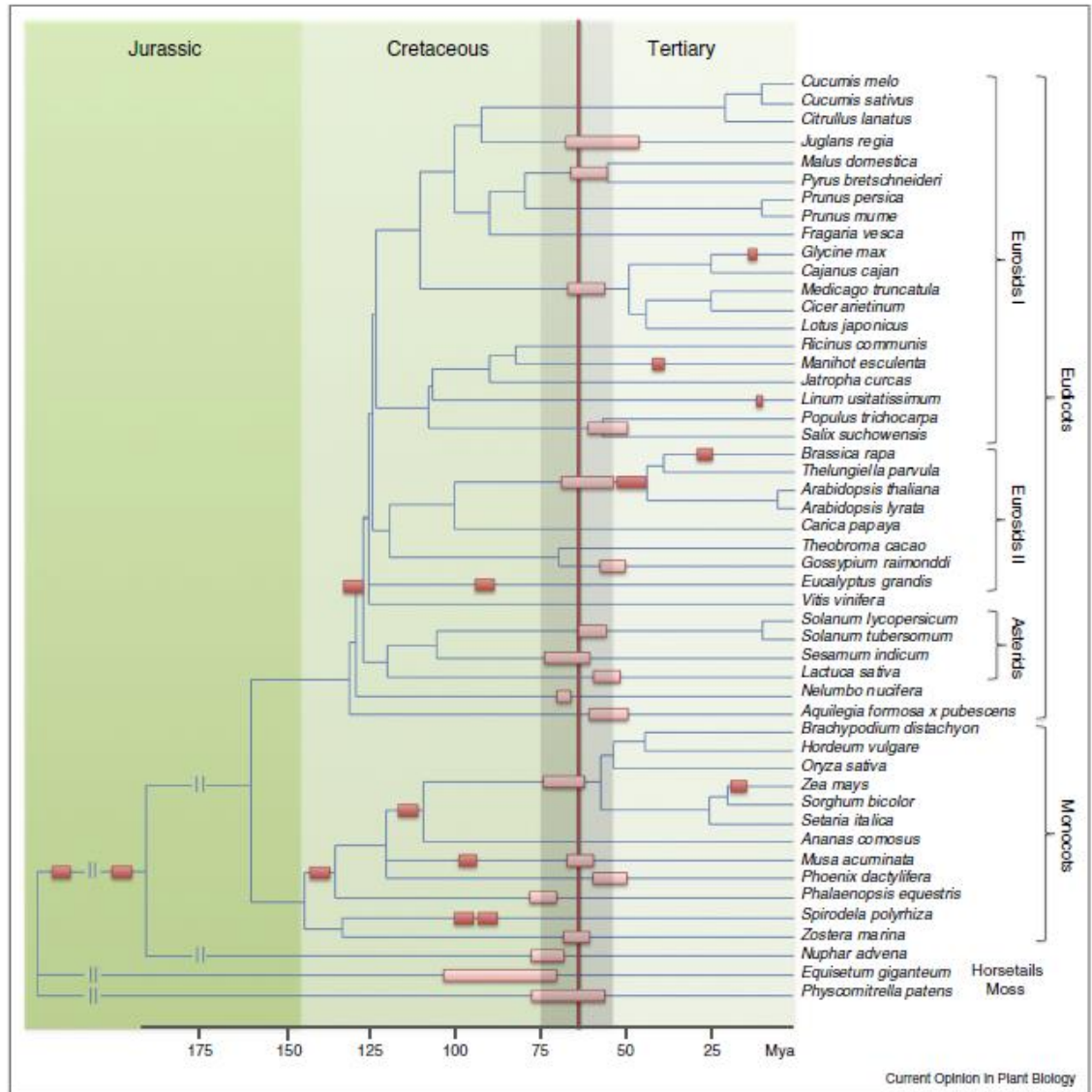
Analysis of 41 plant genomes supports a wave of successful genome duplications in association with the Cretaceous–Paleogene boundary

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

Genome Res (2014)

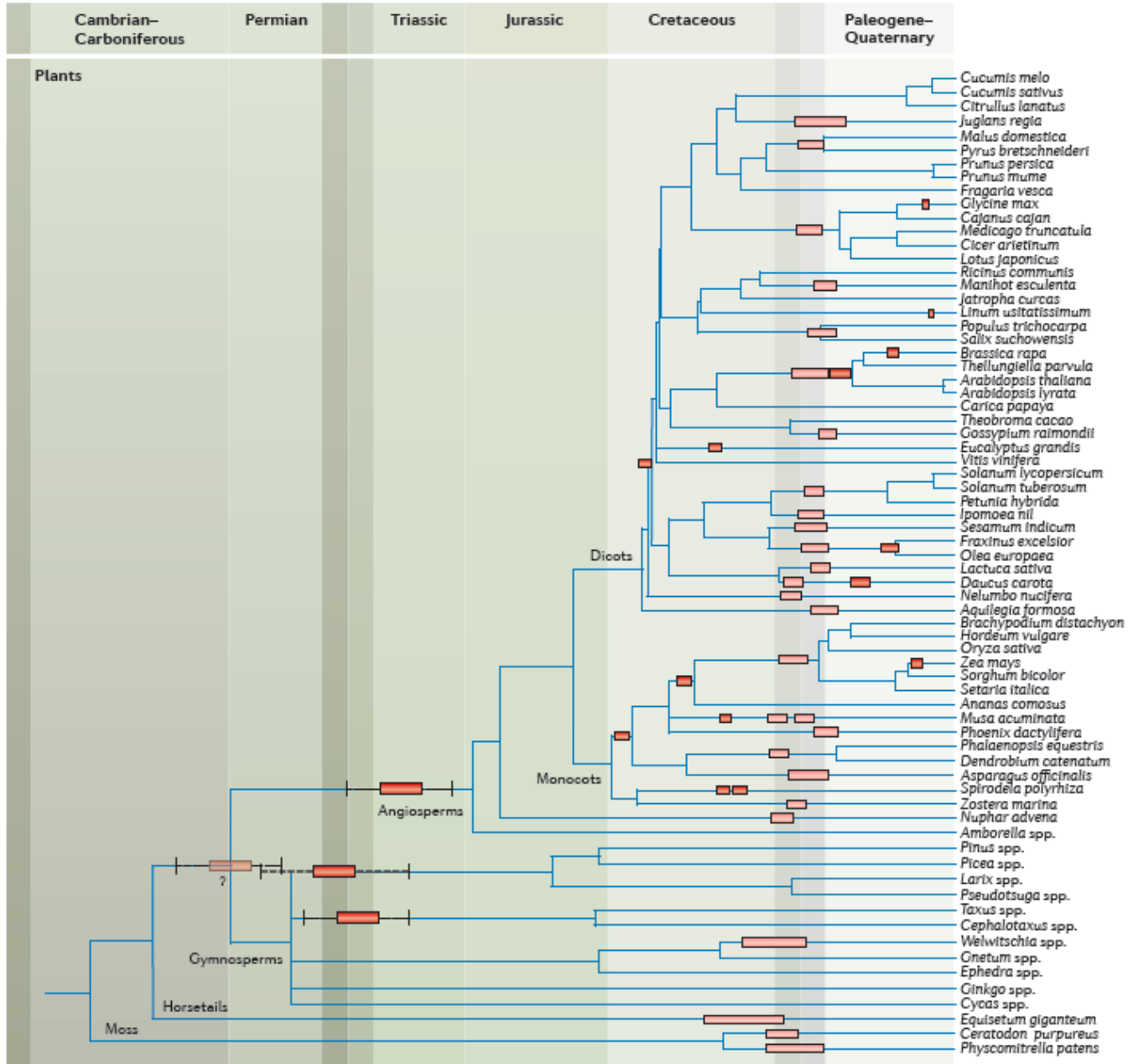
Possible establishment of polyploid plants following the K/Pg mass extinction (66 million y. ago)

- 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

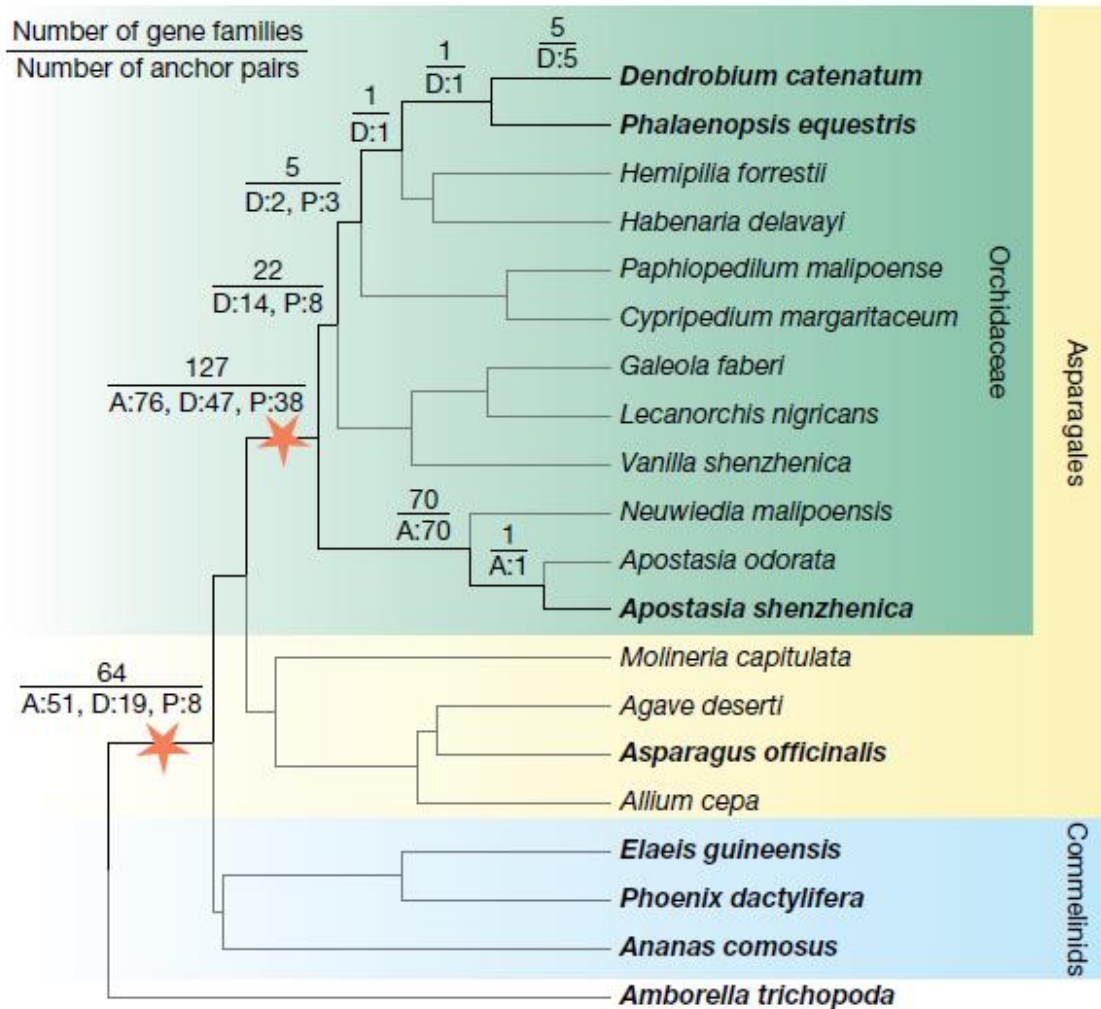


Lohaus and Van de Peer (2016) Curr Opin Pl Biol

Whole-genome duplication in land plants



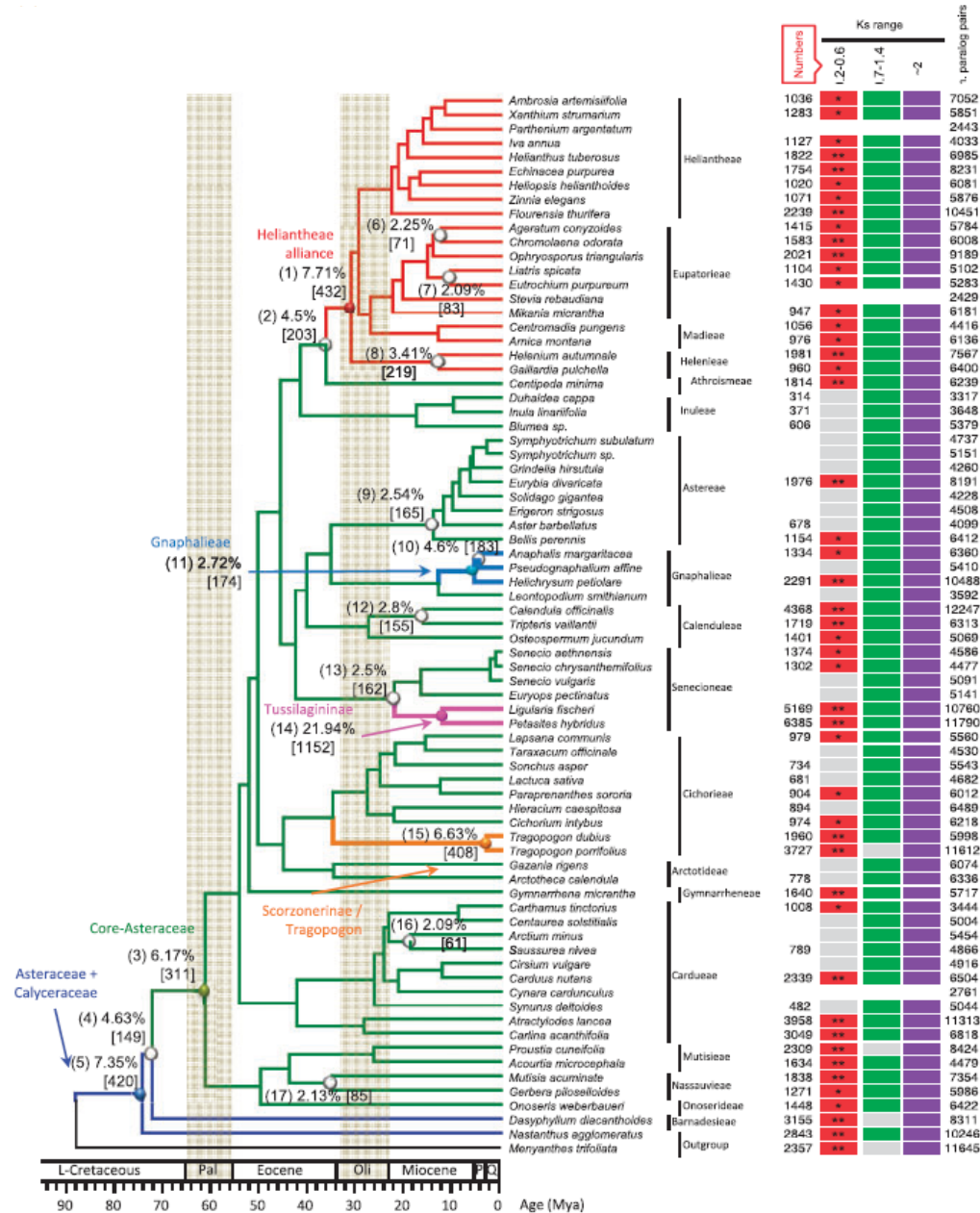
Orchids probably share a common WGD driving the early divergence of the family



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



Multiple WGDs across the Asteraceae family tree



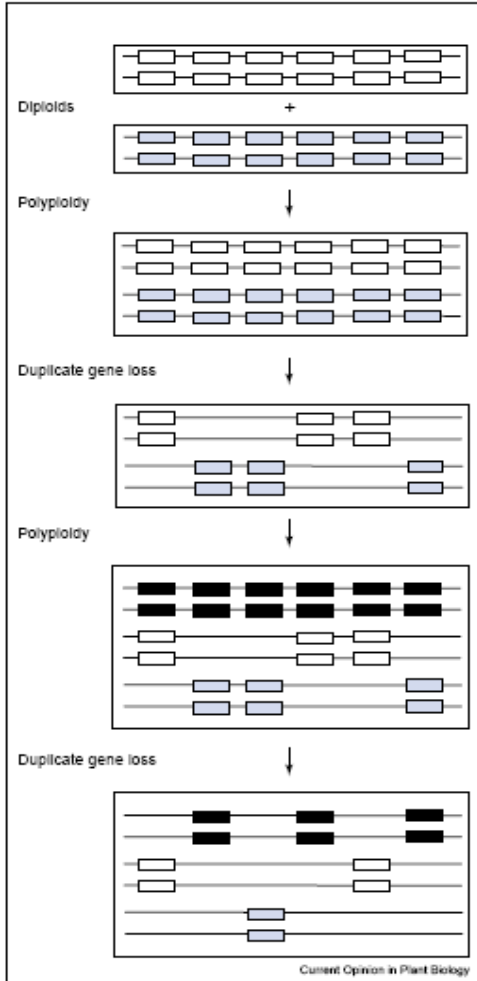
Numbers	Ks range			paralog pairs
	0.6	1.7-1.4	>2	
1036	**			7052
1283	**			5851
1127	**			2443
1822	**			4033
1754	**			6985
1020	**			8231
1071	**			6081
2239	**			5876
1415	**			10451
1583	**			5784
2021	**			6008
1104	**			9189
1430	**			5102
				5283
				2429
947	**			6181
1056	**			4416
974	**			6136
1981	**			7867
960	**			6400
1814	**			6239
314				3317
371				3648
606				5379
				4737
				5151
				4260
1976	**			8191
				4228
				4508
678	**			4099
1154	**			8412
1334	**			6360
				5410
2291	**			10488
				3592
4368	**			12247
1719	**			6313
1401	**			5069
1374	**			4586
1302	**			4477
				5091
				5141
5169	**			10760
6385	**			11790
979	**			5580
				4530
734	**			5543
681	**			4682
904	**			6012
804	**			6489
974	**			6218
1960	**			5998
3727	**			11612
				8074
778	**			6336
1640	**			5717
1008	**			3444
				5004
				5454
789	**			4866
				4916
2339	**			6504
				2761
482	**			5044
3958	**			11313
3049	**			8818
2309	**			8424
1634	**			4479
1838	**			7354
				5086
1271	**			5988
				6422
1448	**			8311
3155	**			10246
2843	**			11645
2357	**			

- 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



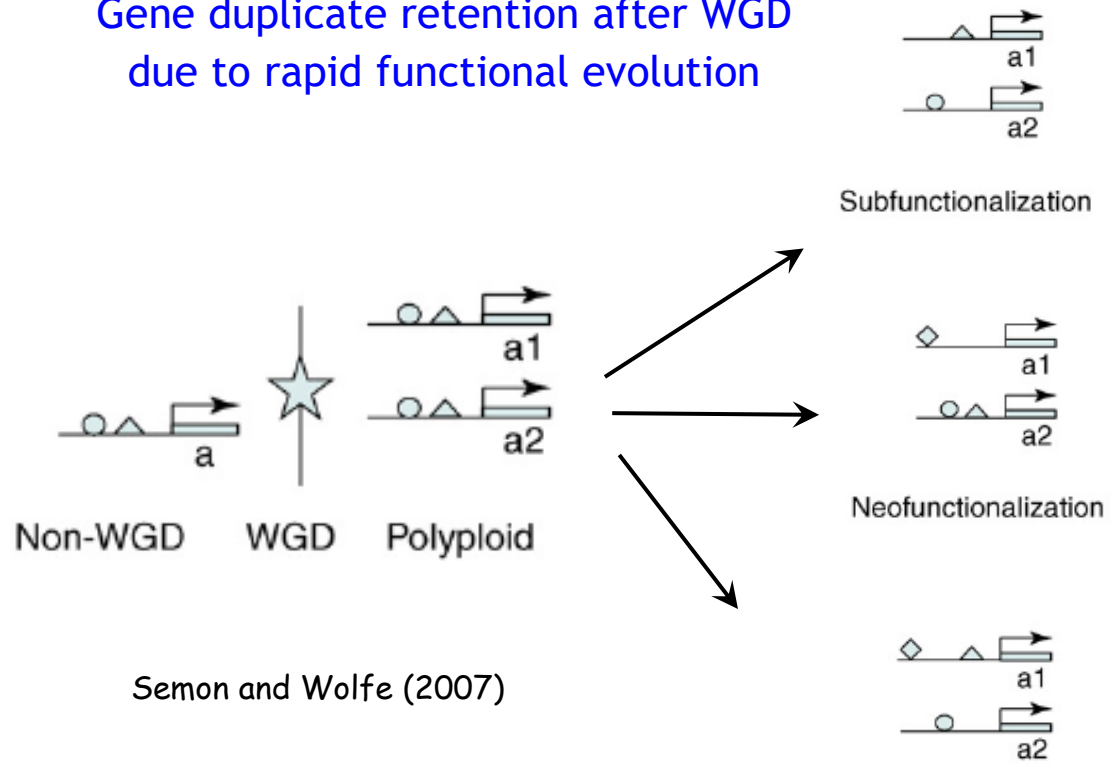
Whole-genome duplications, diploidization, and the consequences

Genome evolution through cyclic polyploidy

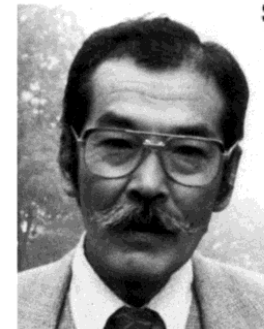


Adams and Wendel (2005)

Gene duplicate retention after WGD due to rapid functional evolution

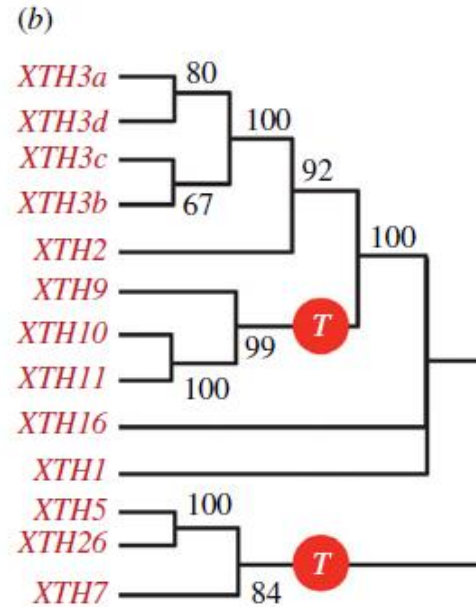
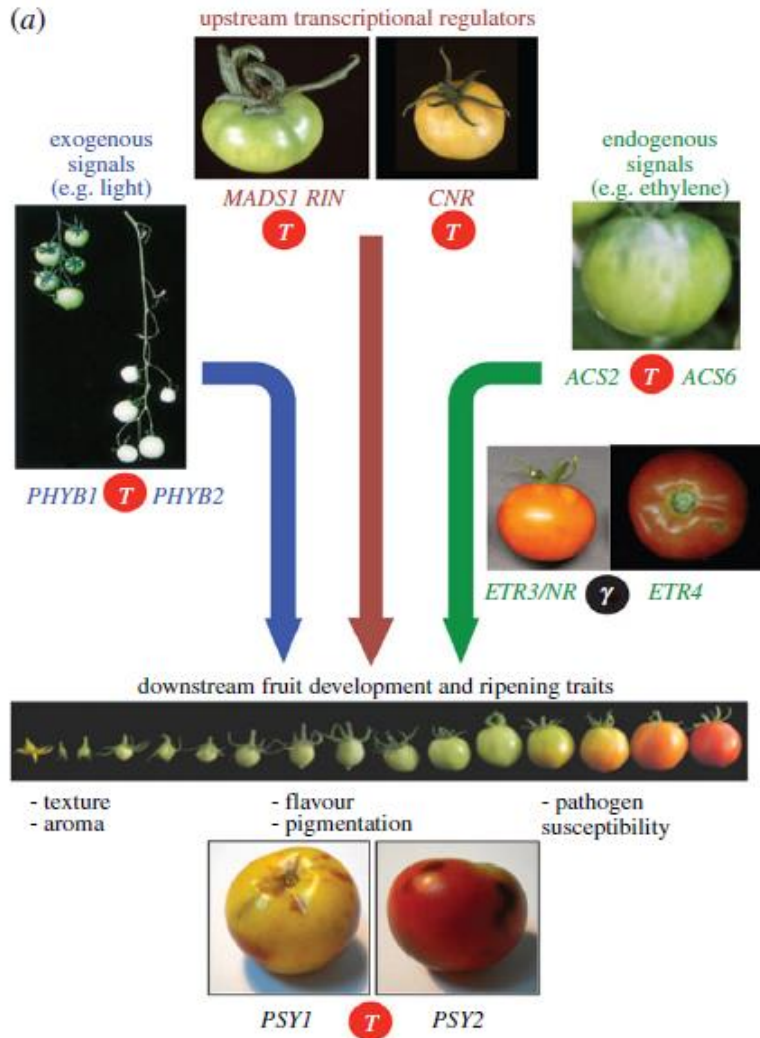


Semon and Wolfe (2007)



Sun and Ohno

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

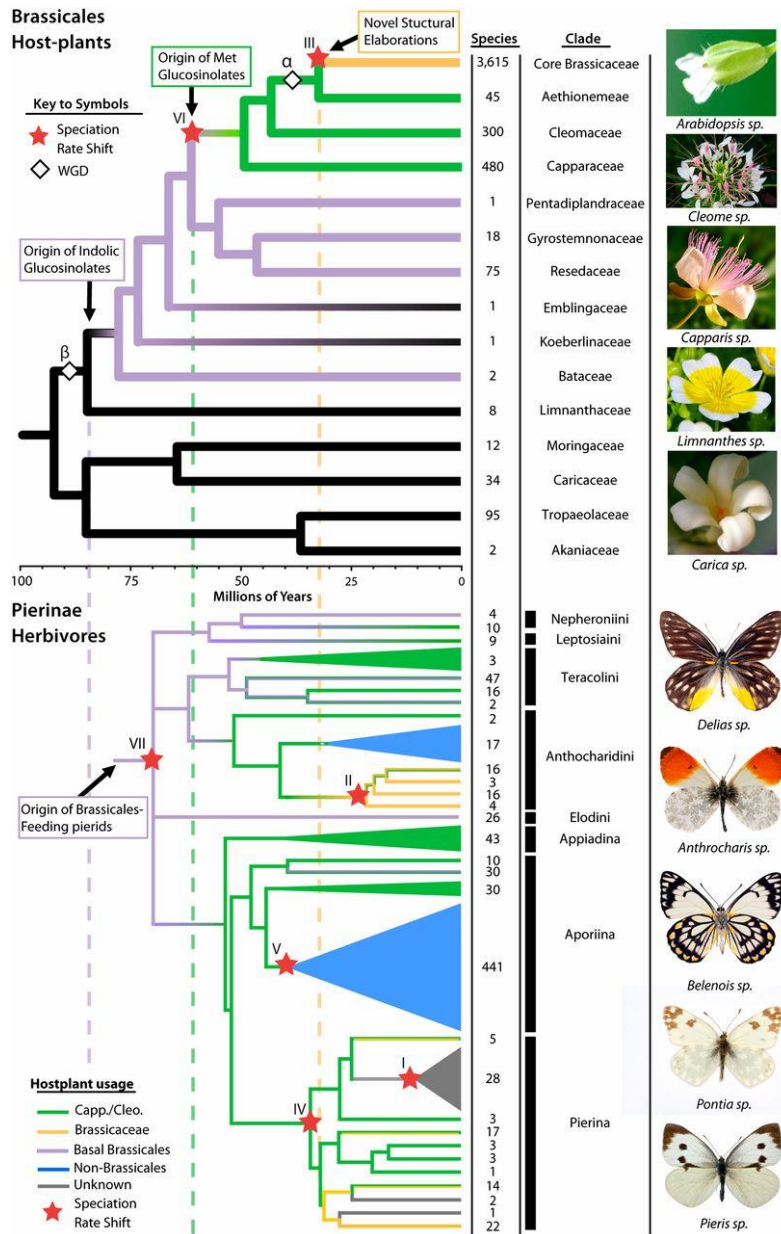


phylogeny of xyloglucan endotransglucosylase/hydrolases (XTHs)

T Solanaceae-specific genome triplication

γ core eudicot shared hexaploidy

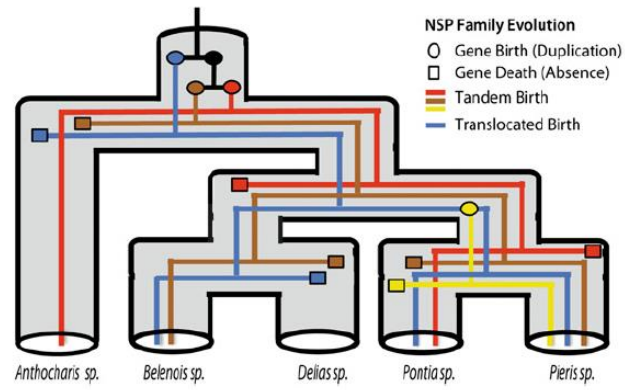
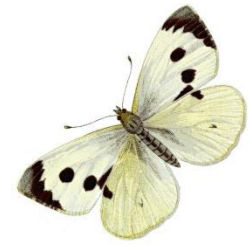
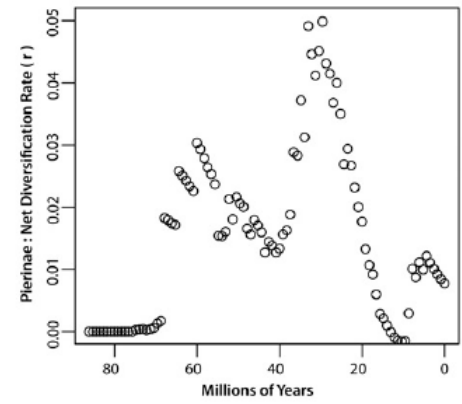
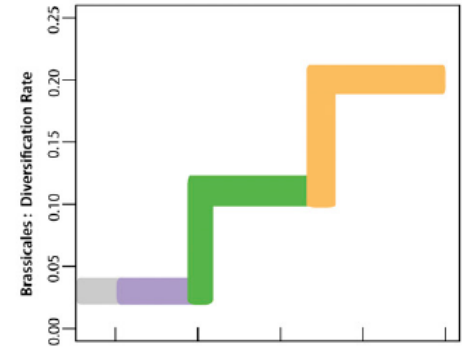
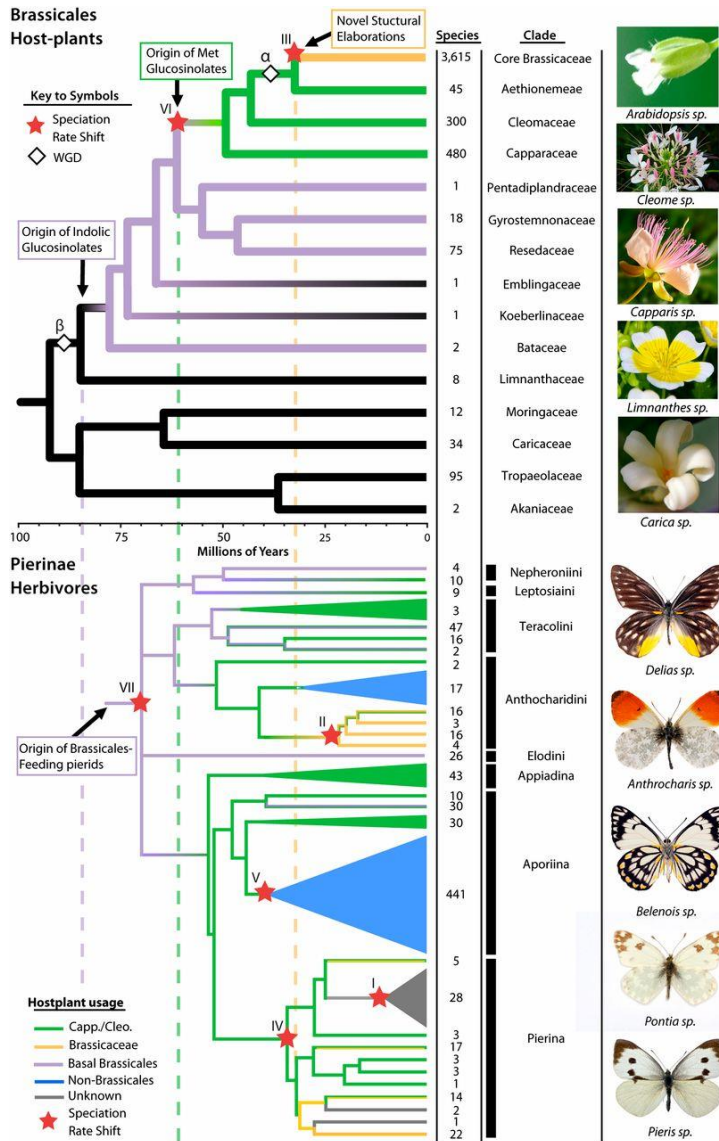
Gene and genome duplications, key innovations and coevolution



- 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

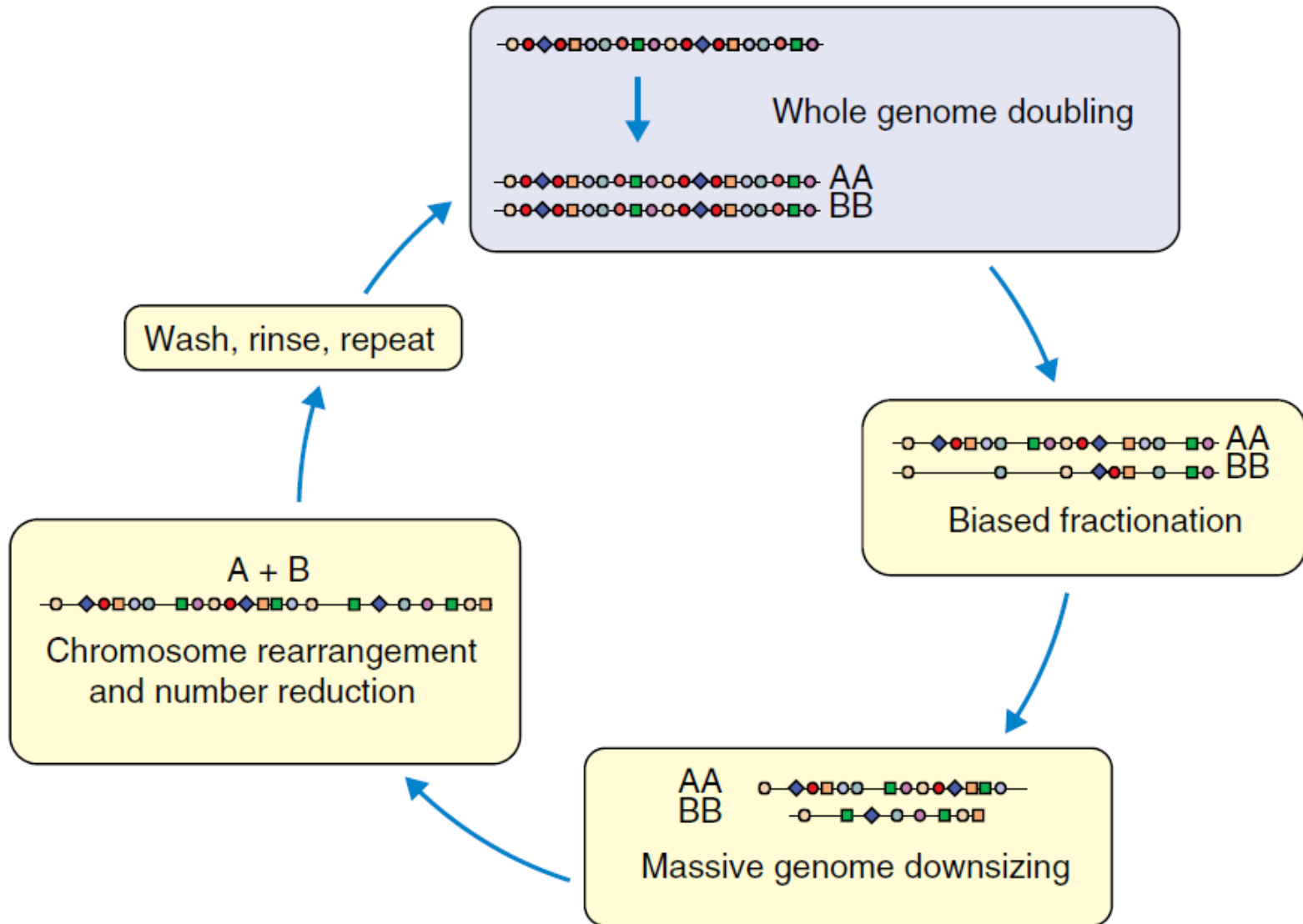


Gene and genome duplications, key innovations and coevolution

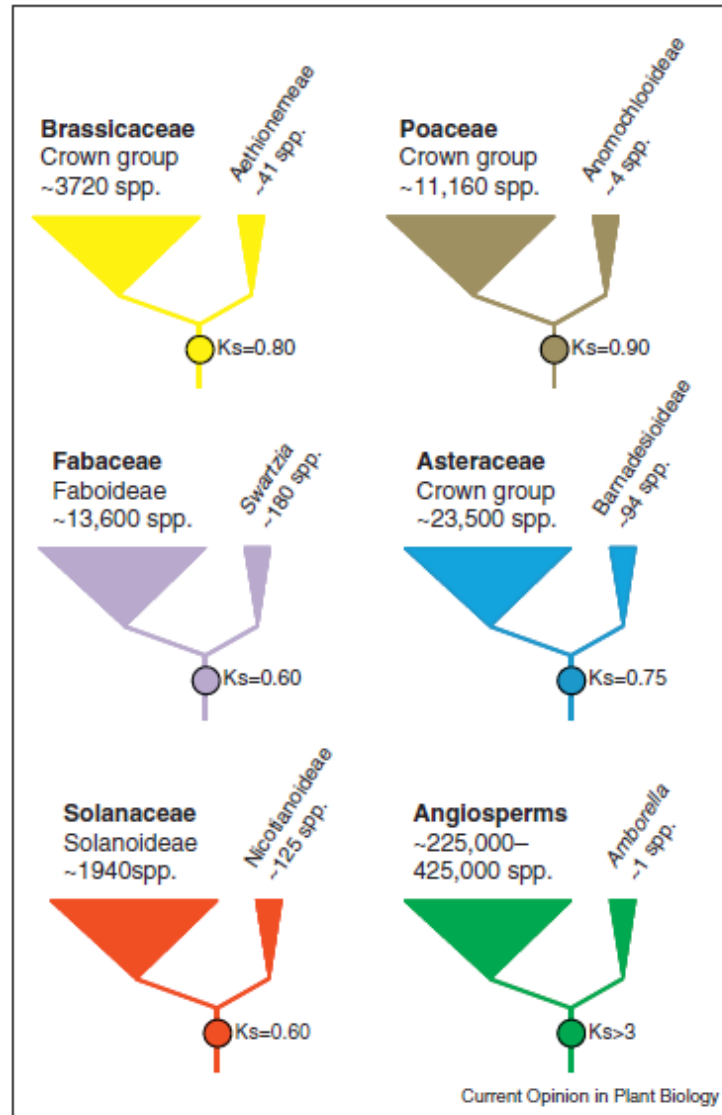


Whole-genome duplication and **diploidization**

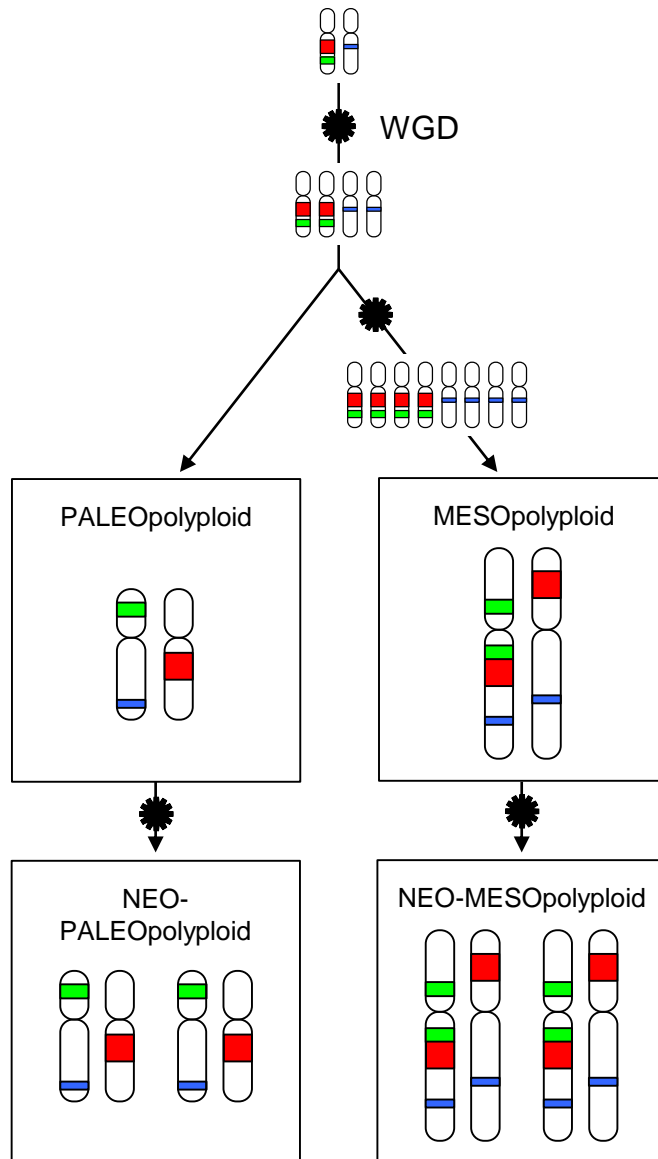
Whole-genome duplication and diploidization



The WGD Radiation Lag-Time Model

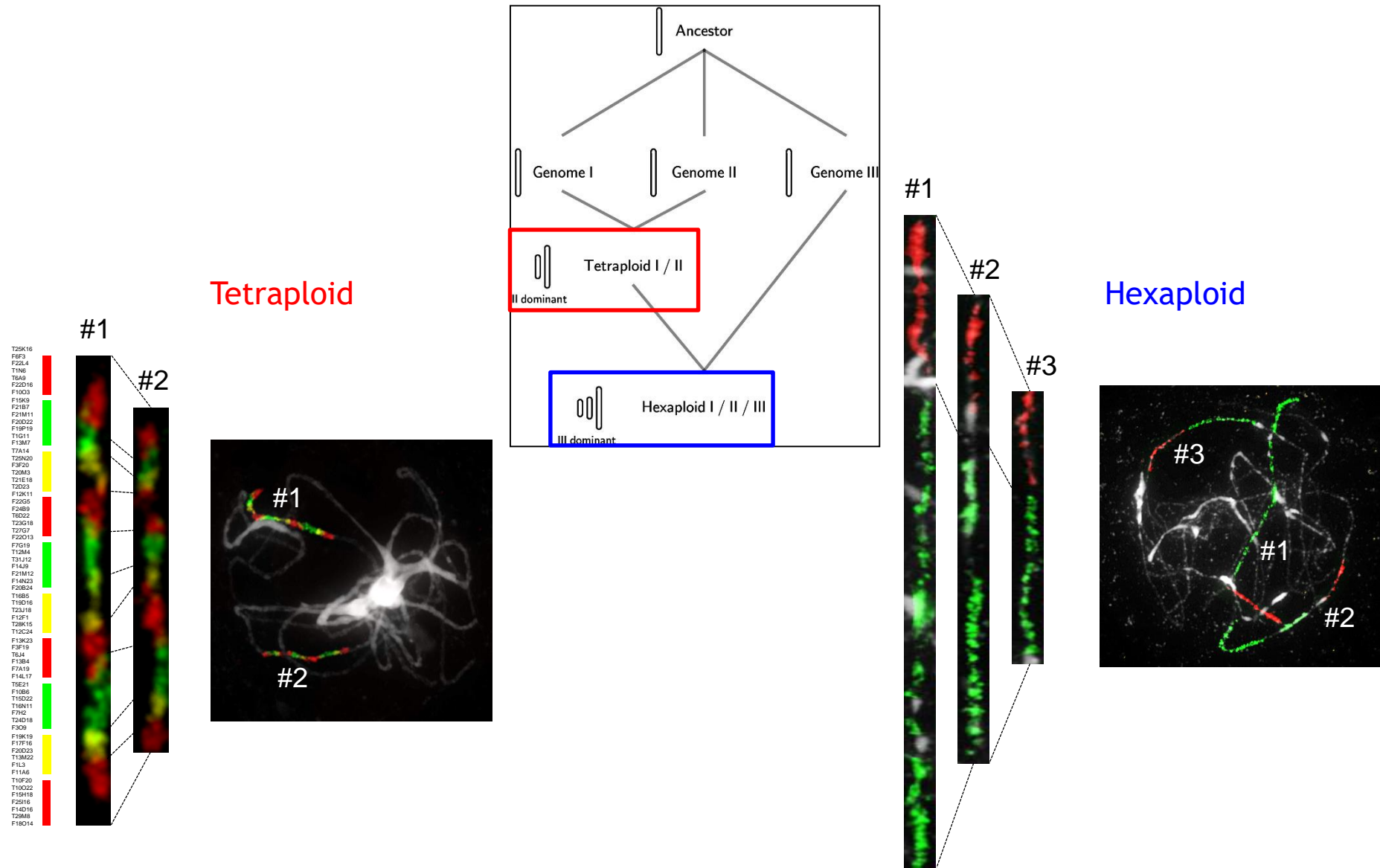


Cytogenomic features of post-polyploid genome diploidization



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

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



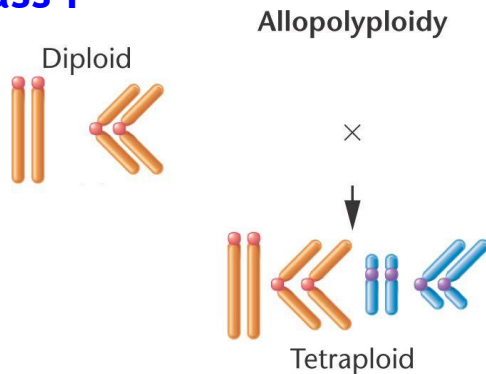
Two Evolutionarily Distinct Classes of Paleopolyploidy

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

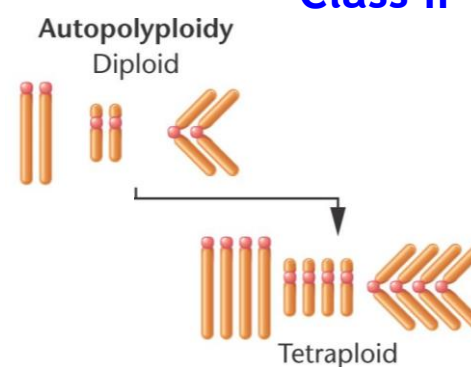
Table 2. Fractionation Pattern and Genome Dominance in Eight Species.

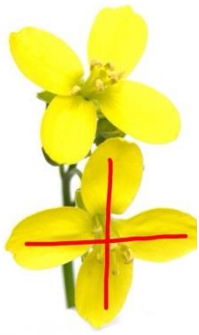
Species	WGD Class	Substitution Rate (Ks)	Bias Ratio between Duplicate Regions	Fractionation Pattern	Genome Dominance	Expression Data from
Medicago	I	0.87	1.23	Biased	No data	
Sorghum	I	0.95	1.24	Biased (Schnable et al. 2012)	Yes	Dugas et al. (2011)
Arabidopsis	I	0.76	1.17	Biased (Thomas et al. 2006)	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

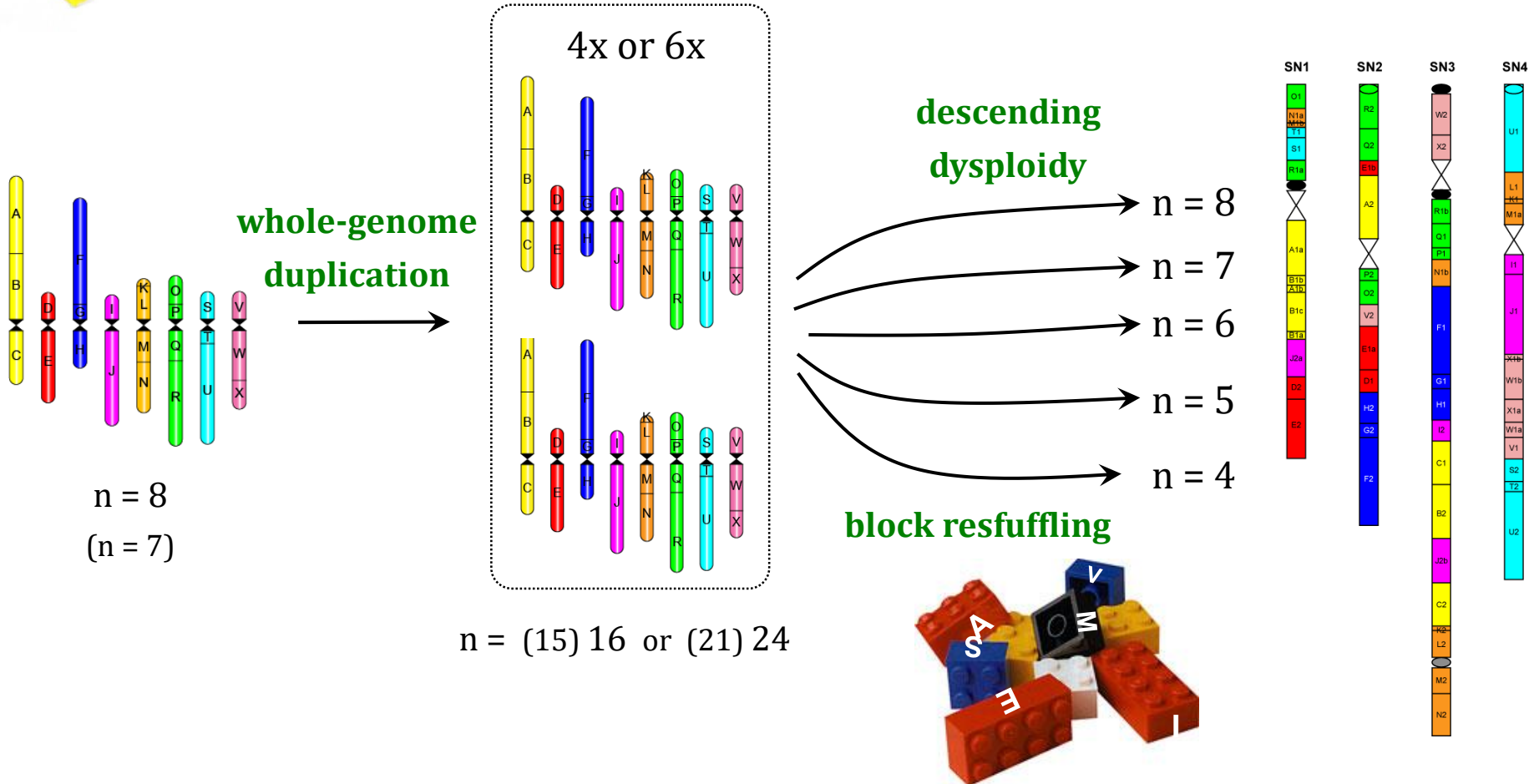


Class II



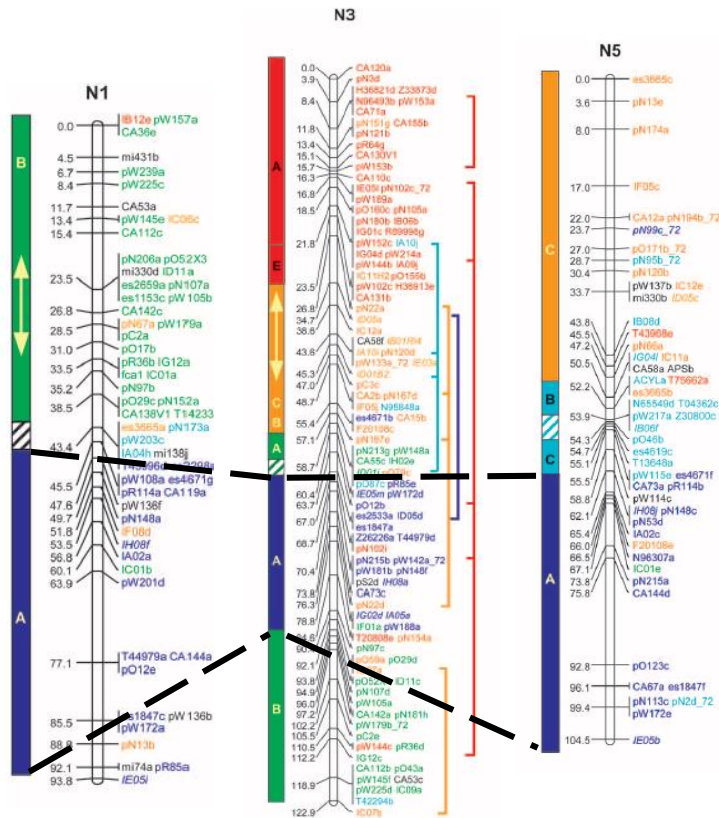


Evolution of the Ancestral Crucifer Genome – ANCIENT POLYPLOIDS



Brassicas Are Ancient Hexaploids (Mesopolyploids)

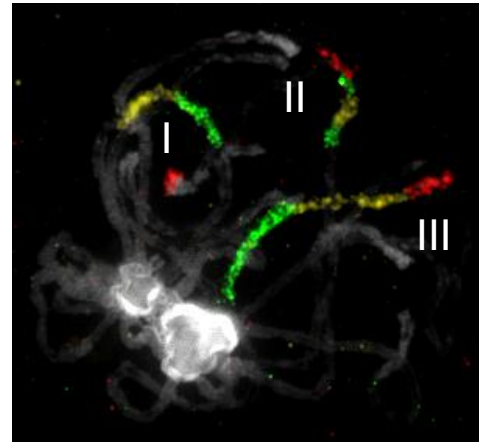
Brassica napus (AACC, n = 19), A genome (N1-N10)



Parkin et al. (2005) Genetics

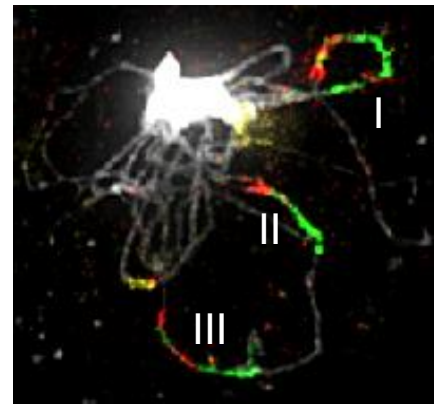
Diplotaxis erucoides

2n = 14



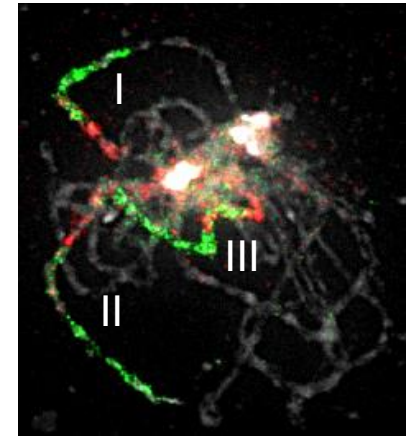
Morisia monanthos

2n = 14



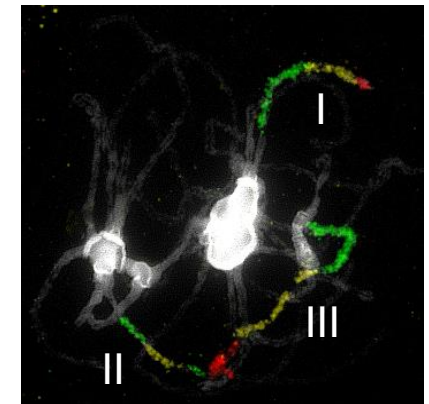
Brassica oleracea

2n = 18



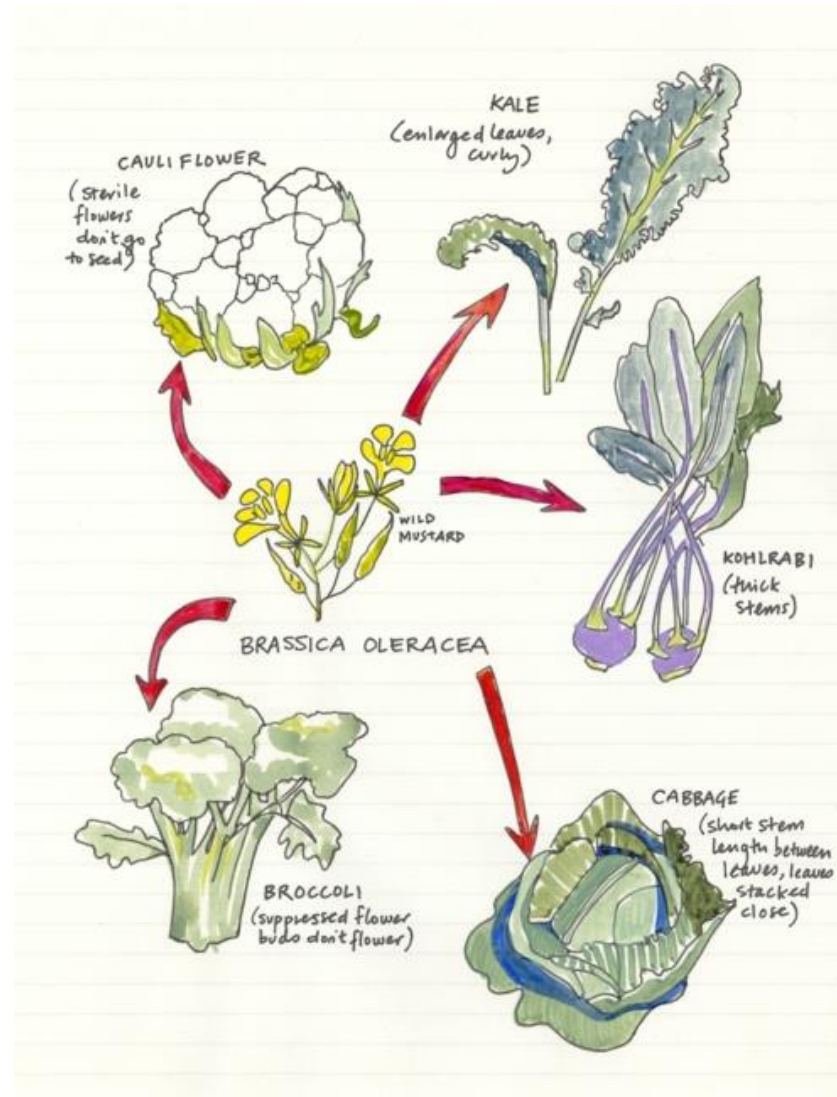
Moricandia arvensis

2n = 28



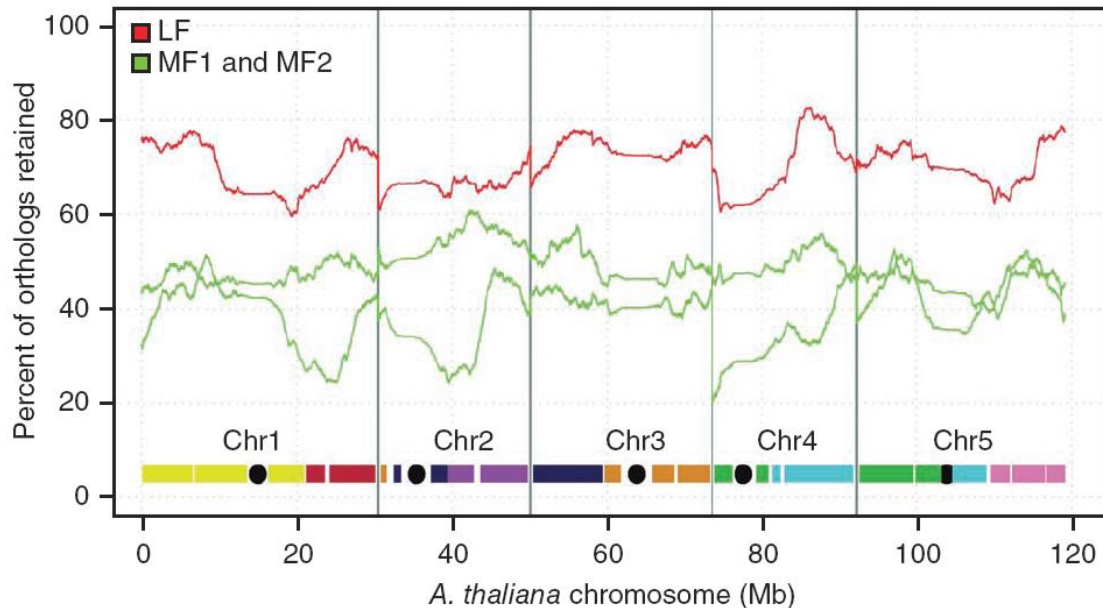
Lysak et al. (2005) Genome Res, (2007) Plant Physiol

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



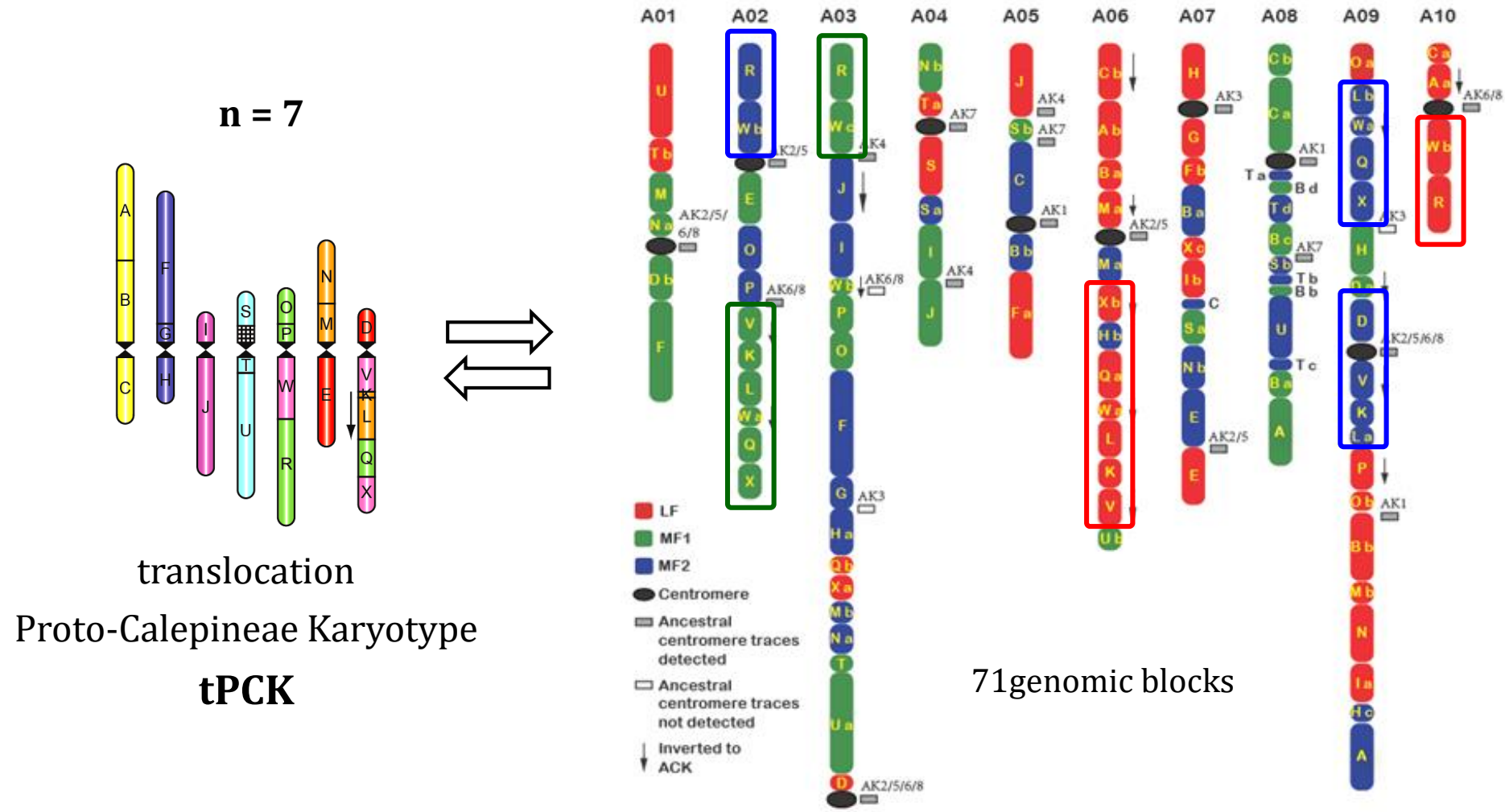
The genome of the mesopolyploid crop species *Brassica rapa*

The *Brassica rapa* Genome Sequencing Project Consortium

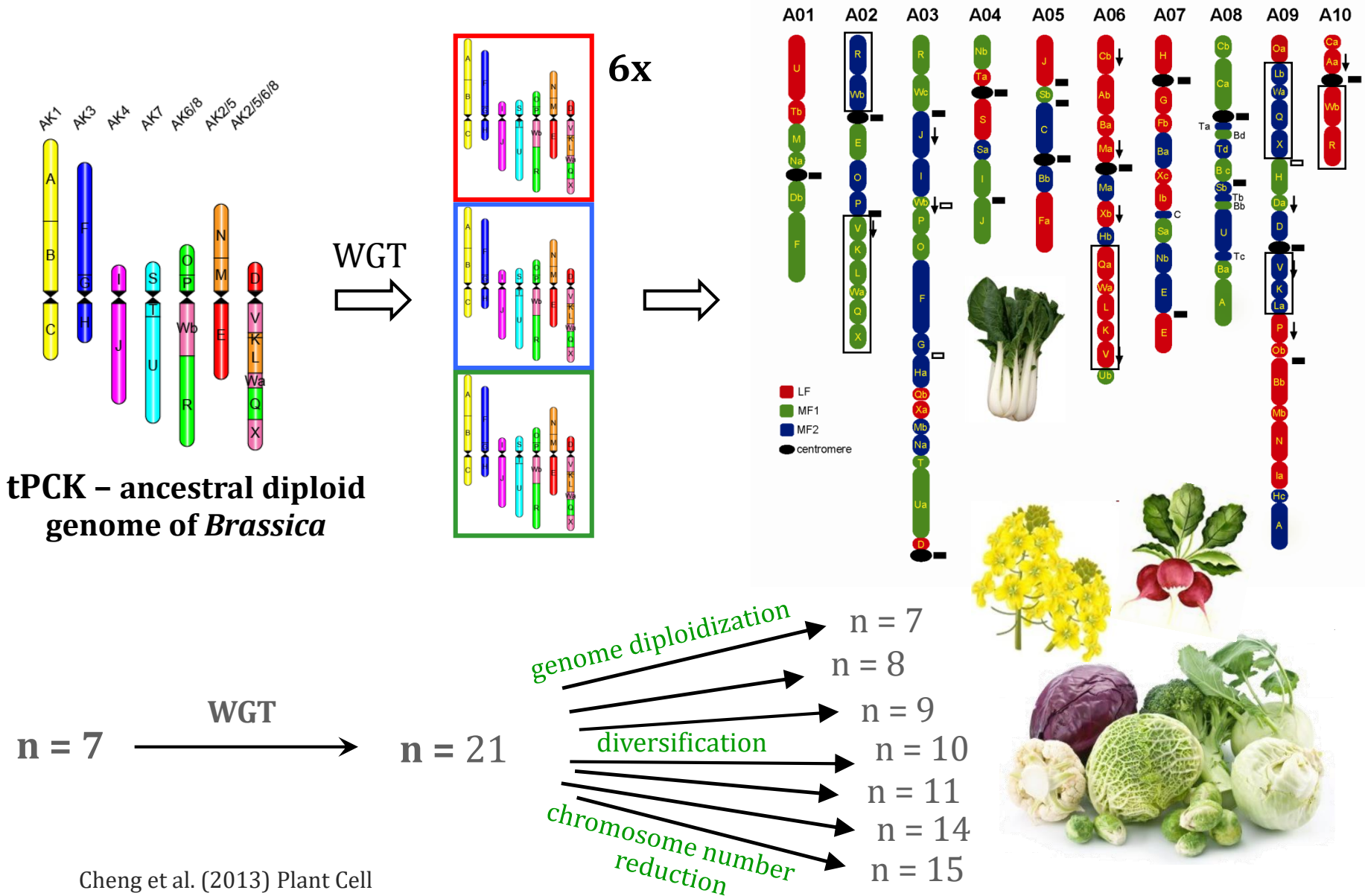


The density of orthologous genes in **three subgenomes** (LF, MF1 and MF2) of *B. rapa* compared to *A. thaliana*.



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



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

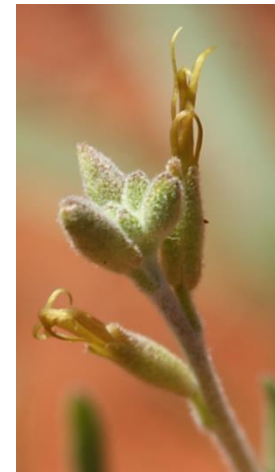


Multispeed genome diploidization and diversification after an ancient allopolyploidization

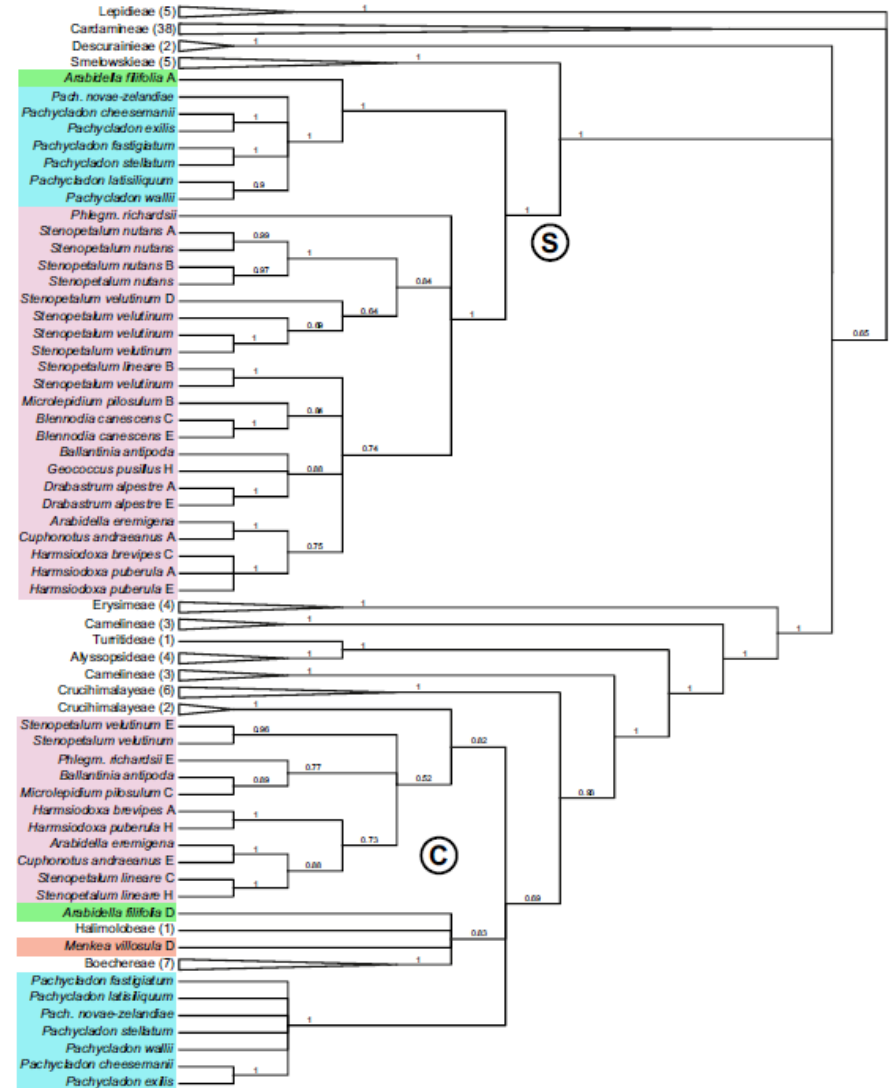
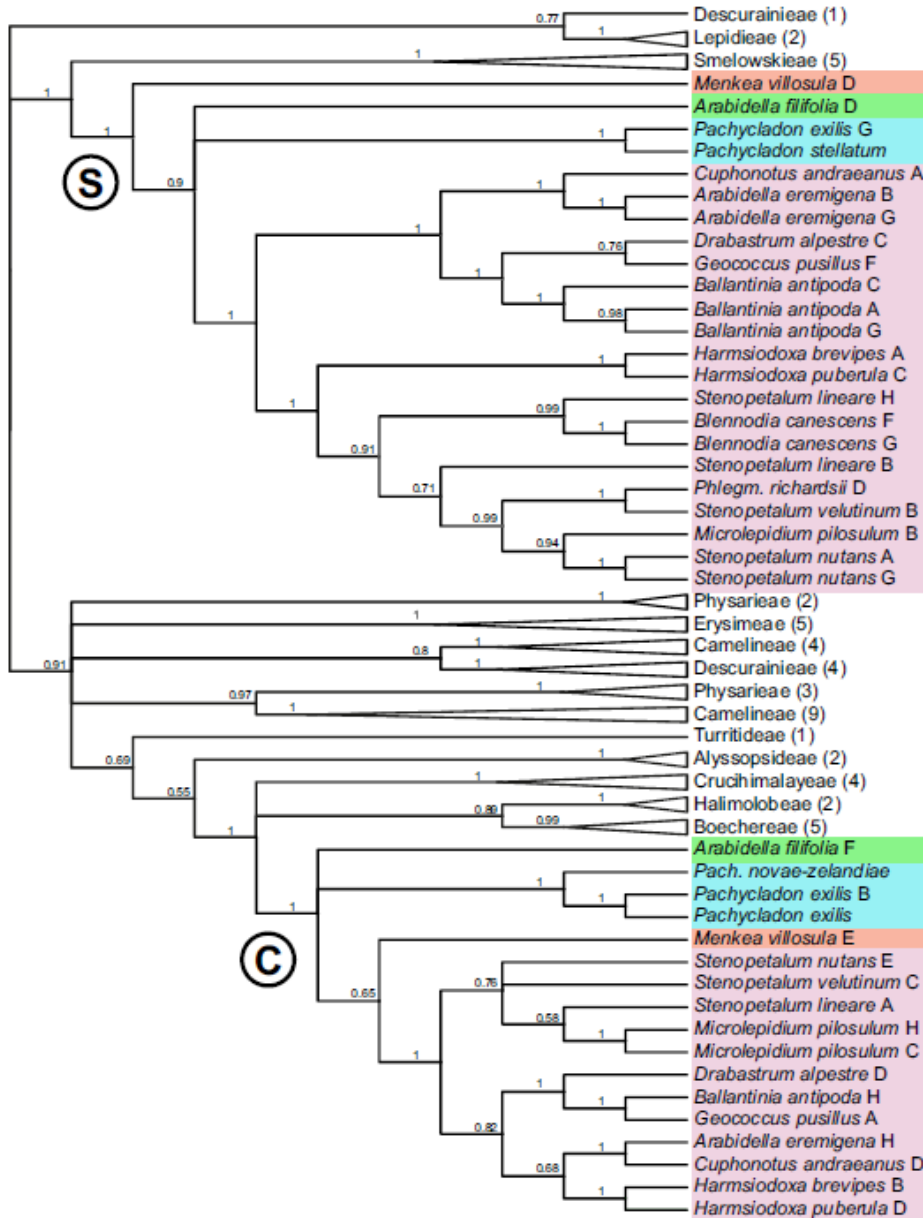
Terezie Mandáková¹  | Milan Pouch¹ | Klára Harmanová¹ | Shing Hei Zhan² | Itay Mayrose³ | Martin A. Lysak¹ 

Australia: 15 genera, 47 species

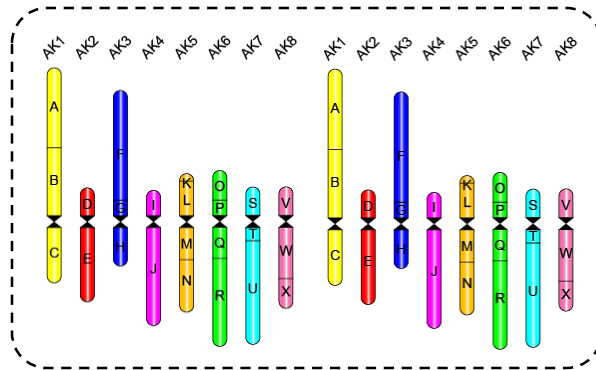
New Zealand: *Pachycladon*, 11 species



The allopolyploid origin evidenced by single-copy nuclear gene phylogenies



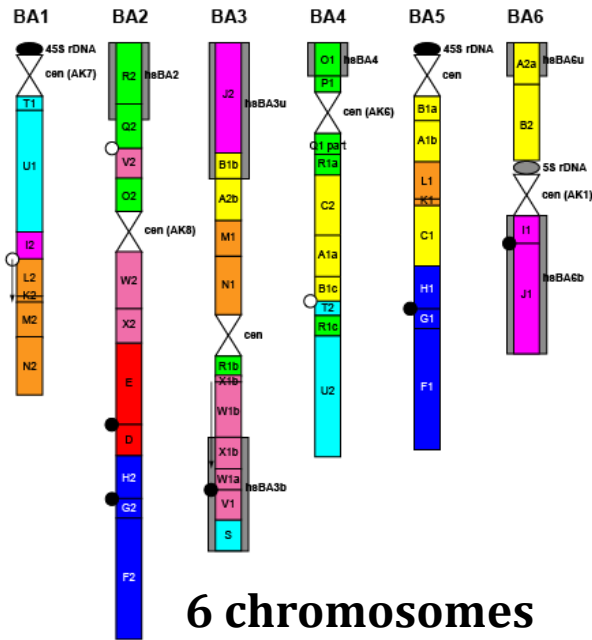
16 chromosomes
48 blocks



ACK, 4x

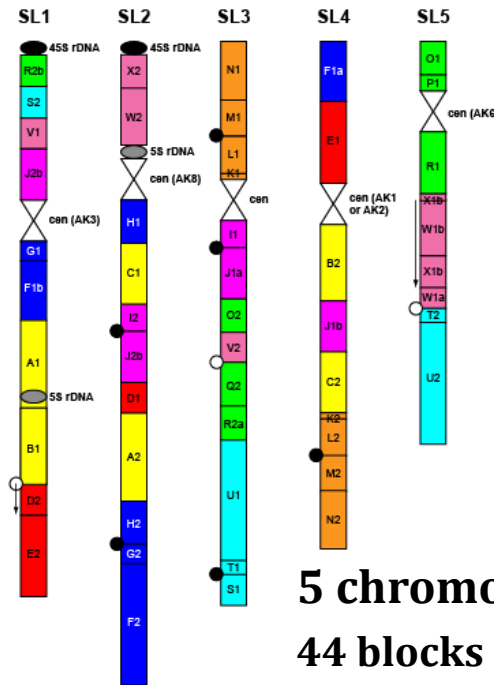
~ 6 - 9 mya

Ballantinia antipoda



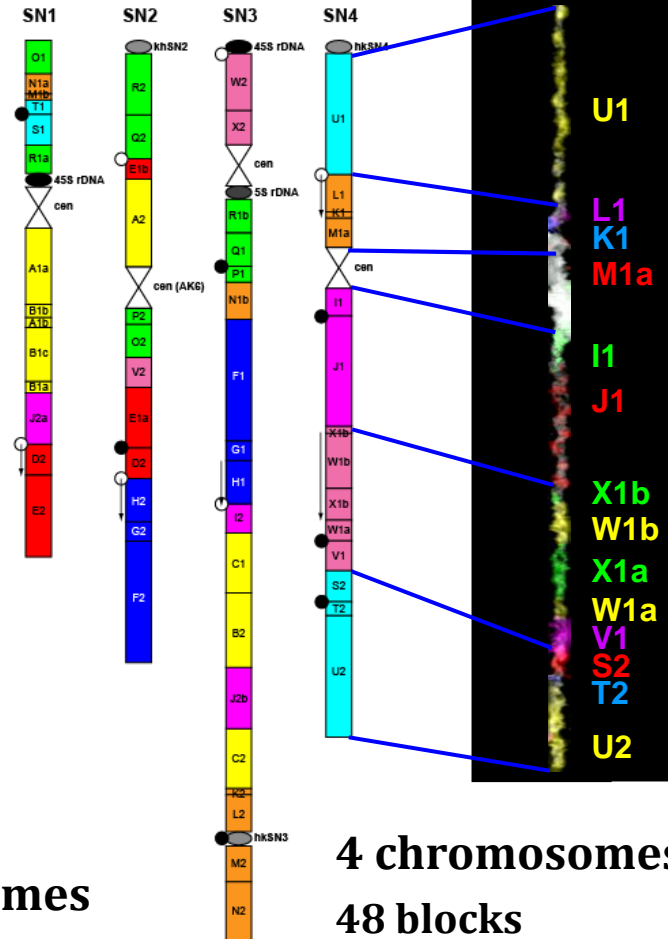
6 chromosomes
40 blocks

Stenopetalum lineare



5 chromosomes
44 blocks

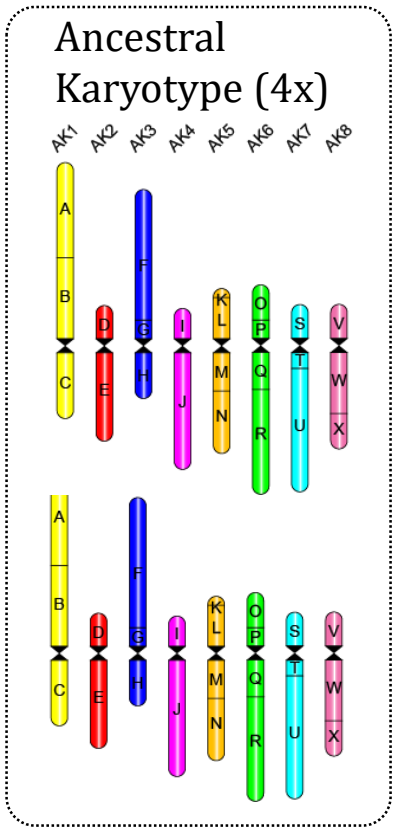
Stenopetalum nutans



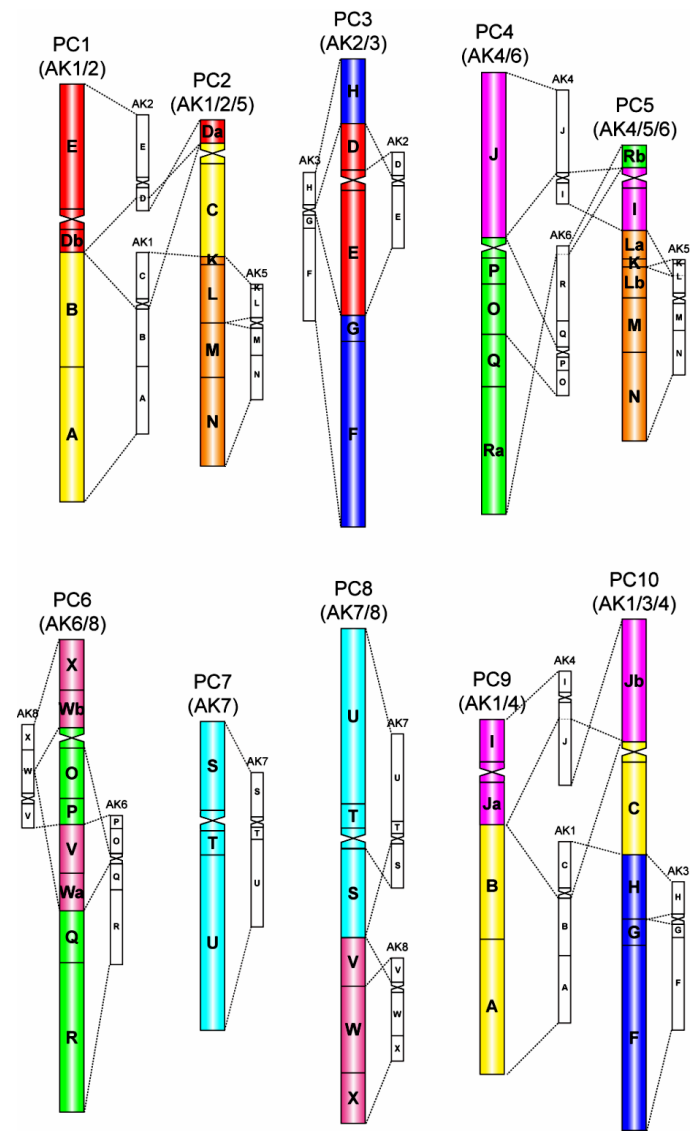
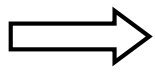
4 chromosomes
48 blocks

Polyploid Origin of *Pachycladon* (n=10)

~ 1 - 2 mya



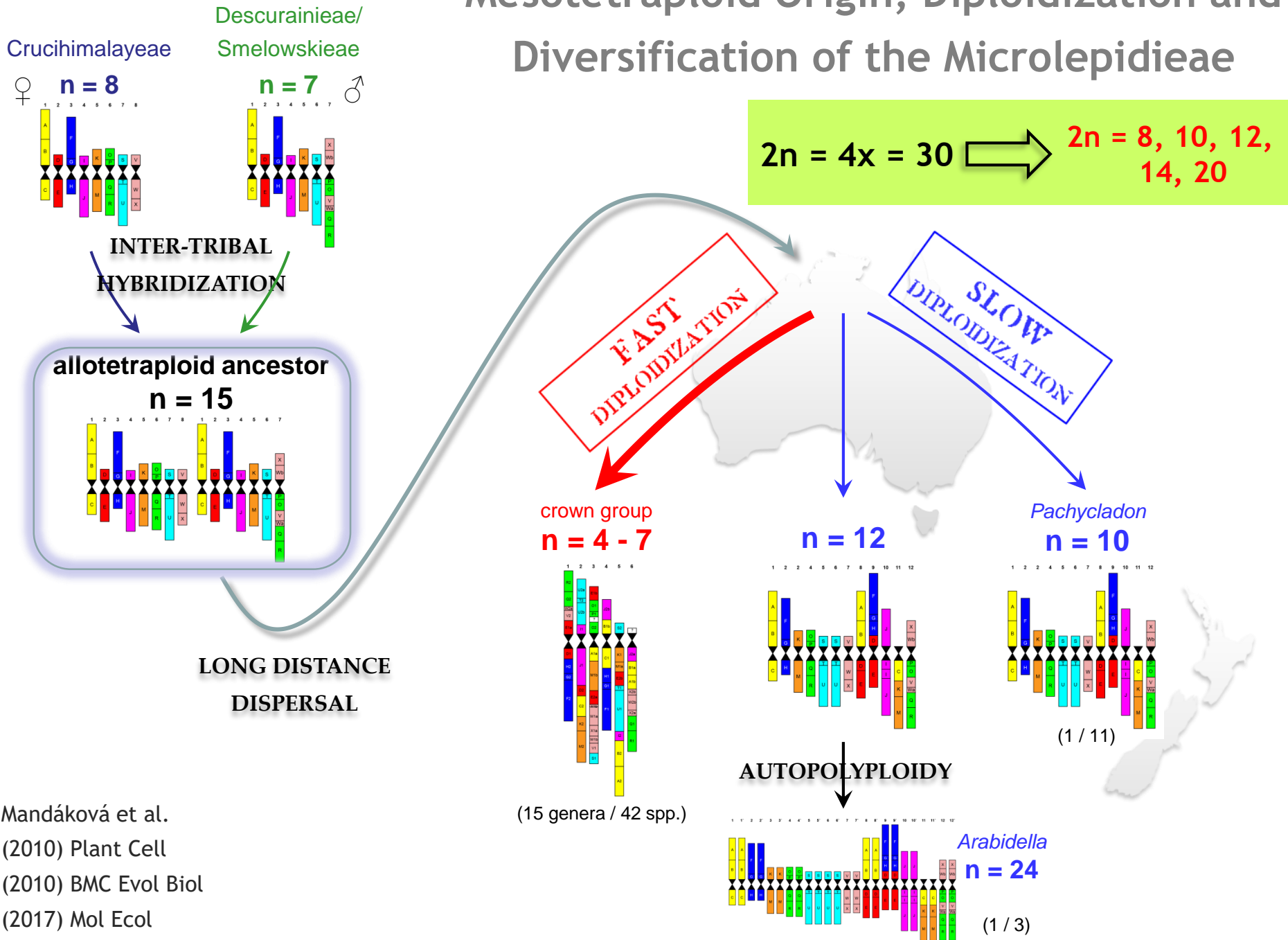
16 chromosomes
48 blocks



10 chromosomes
48 blocks

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

Mesotetraploid Origin, Diploidization and Diversification of the Microlepidieae



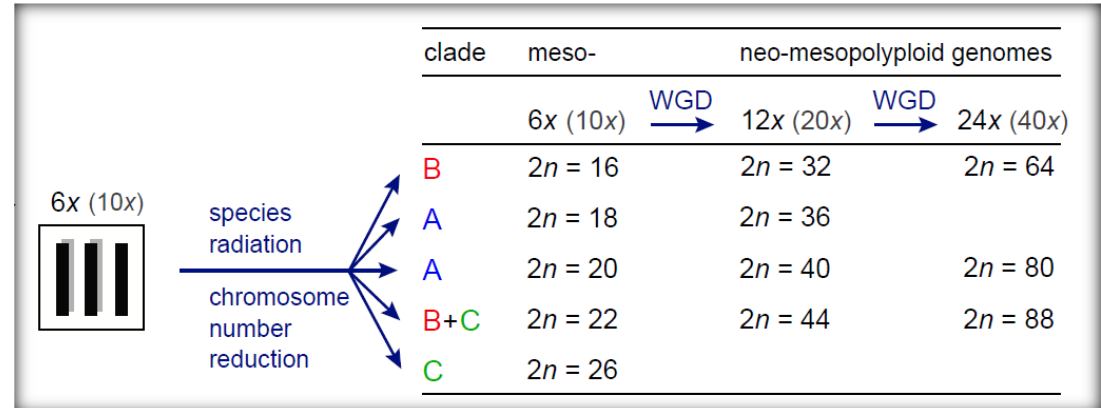
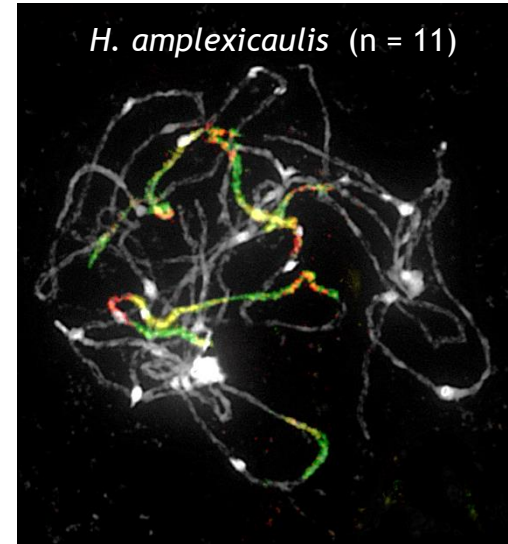
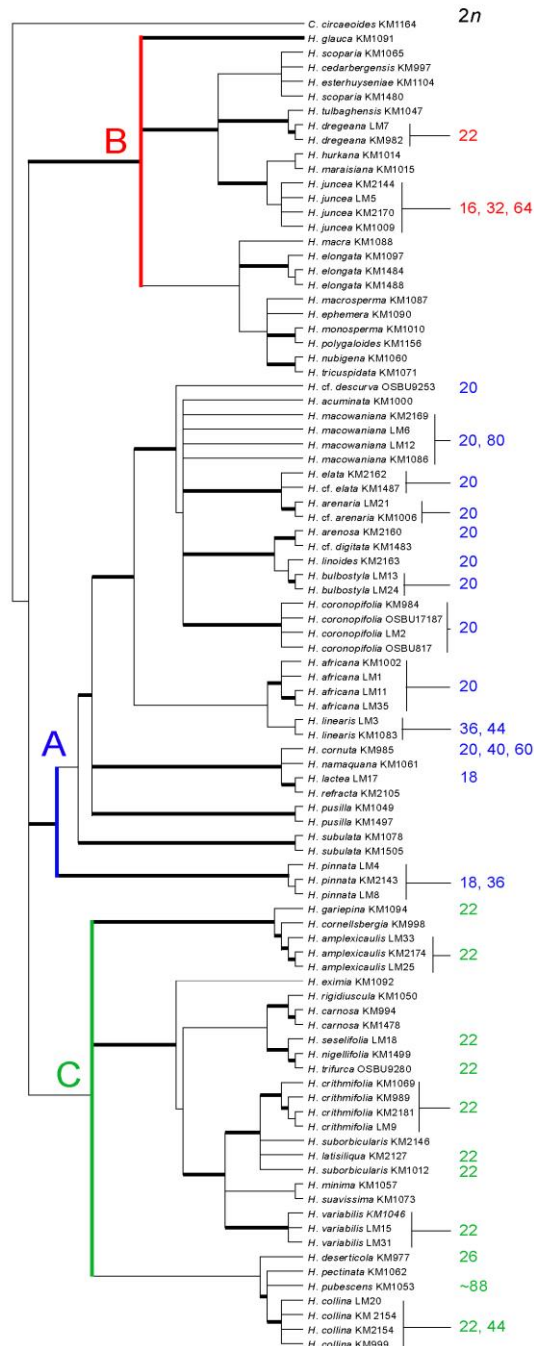
Mandáková et al.
 (2010) Plant Cell
 (2010) BMC Evol Biol
 (2017) Mol Ecol

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

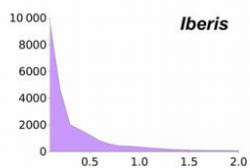
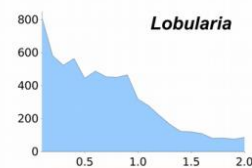
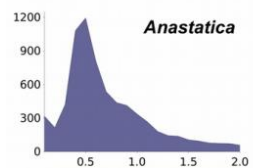
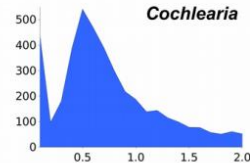
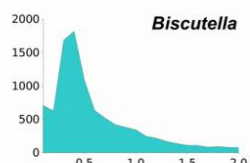
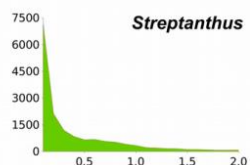
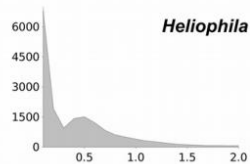
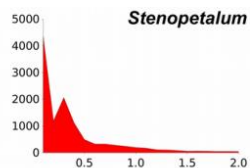
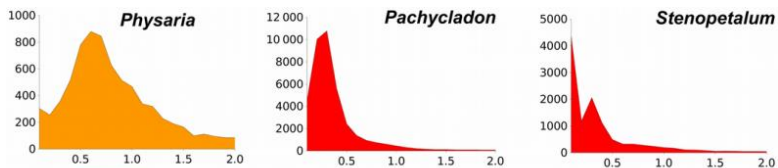
c. 90 (-100) endemic spp.



Whole-Genome Triplication in the Southern African Tribe Heliophileae

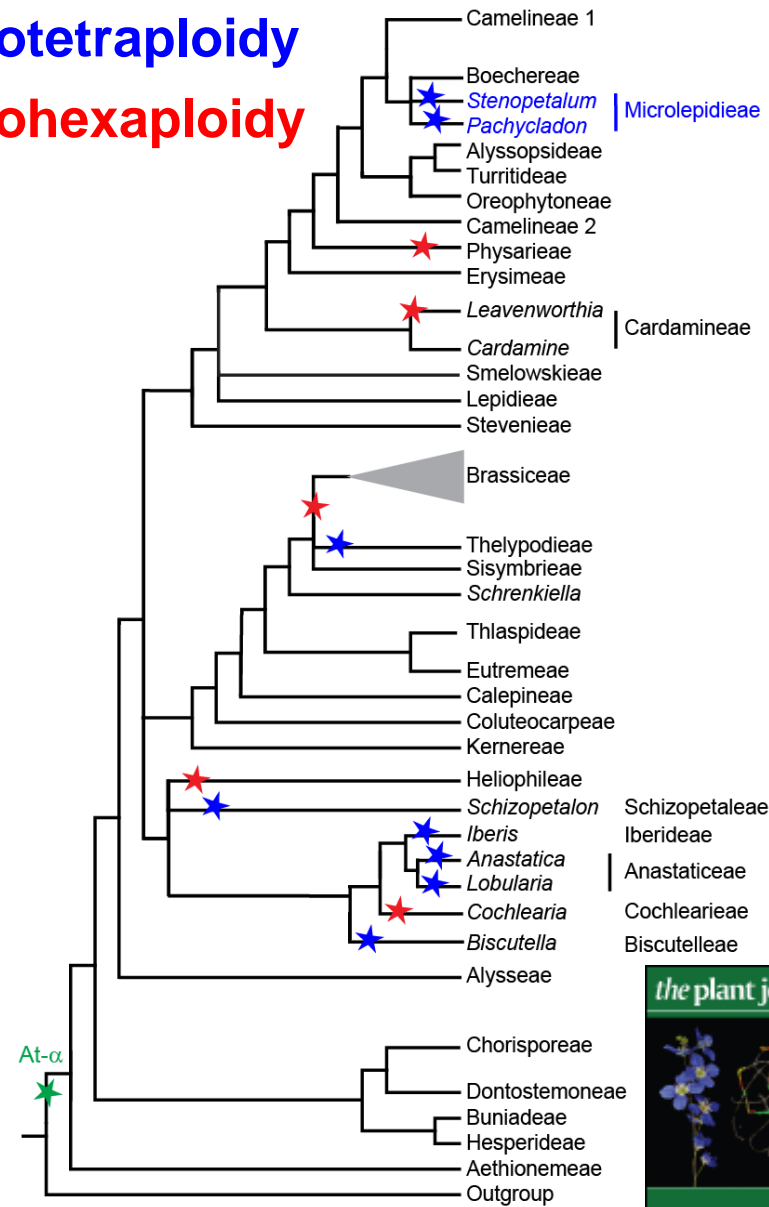
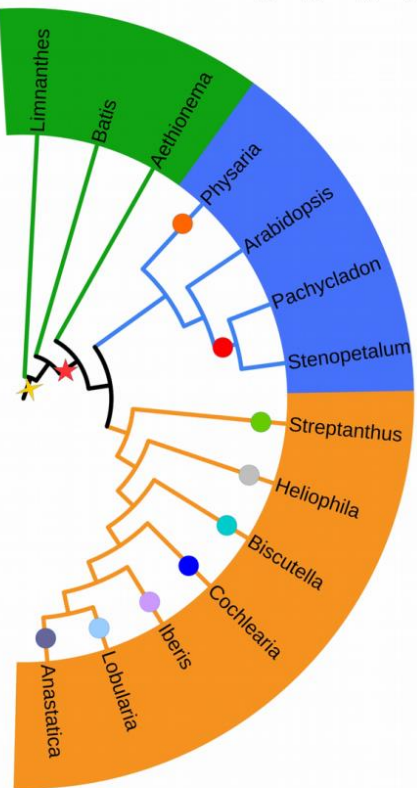


Lineage-Specific Mesopolyploid WGDs in Brassicaceae



★ 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)



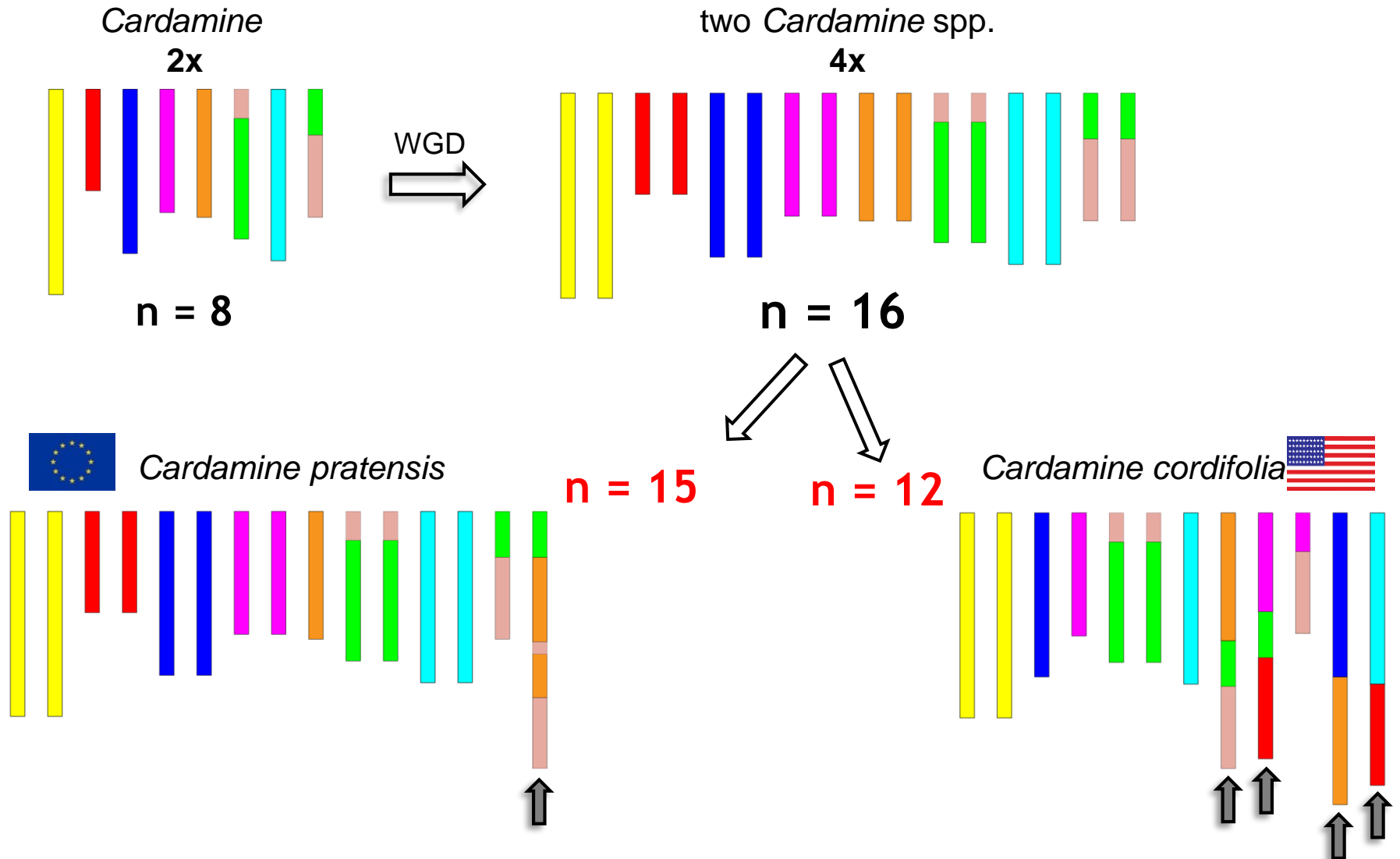
Physarieae

7: 133

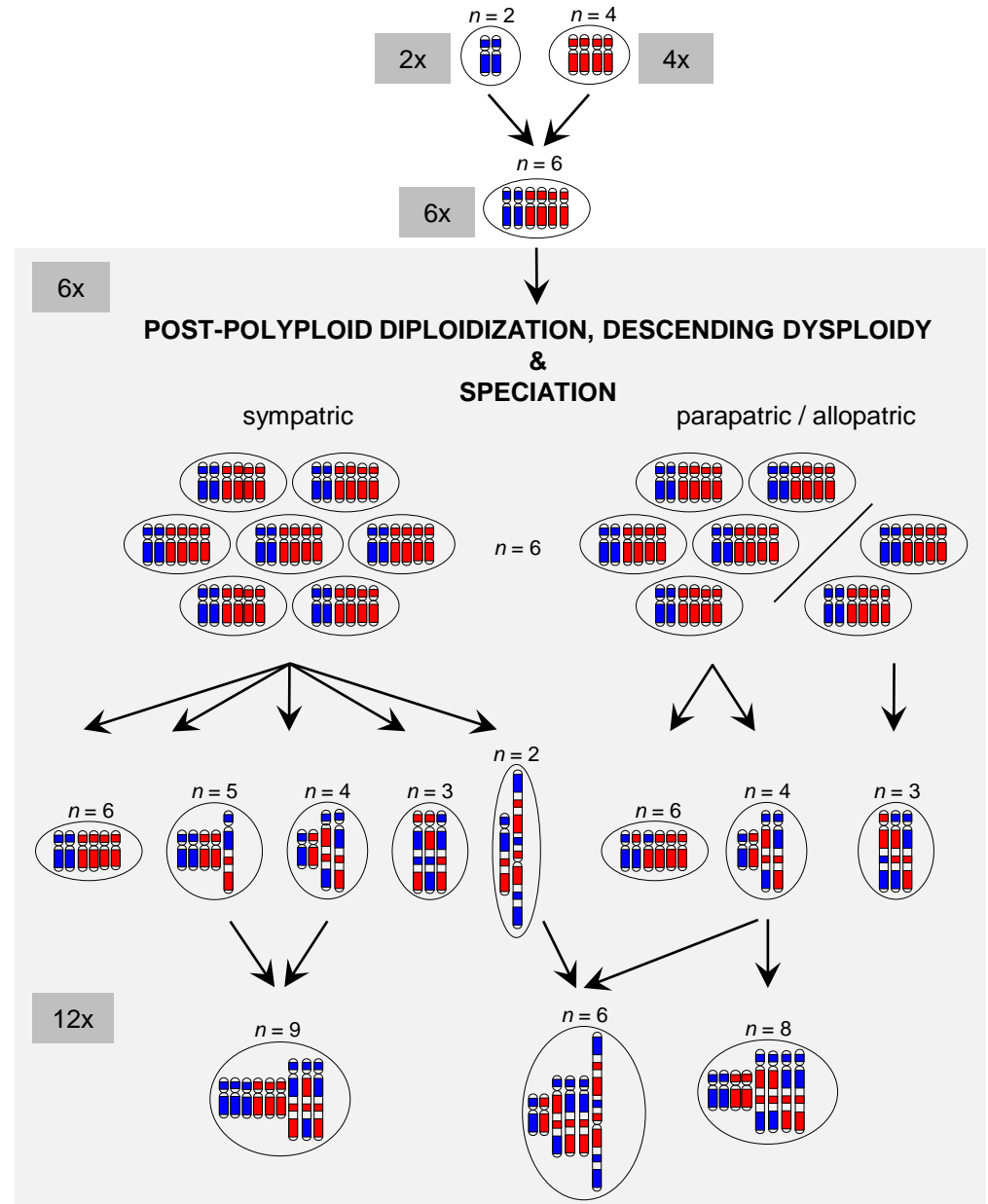
24

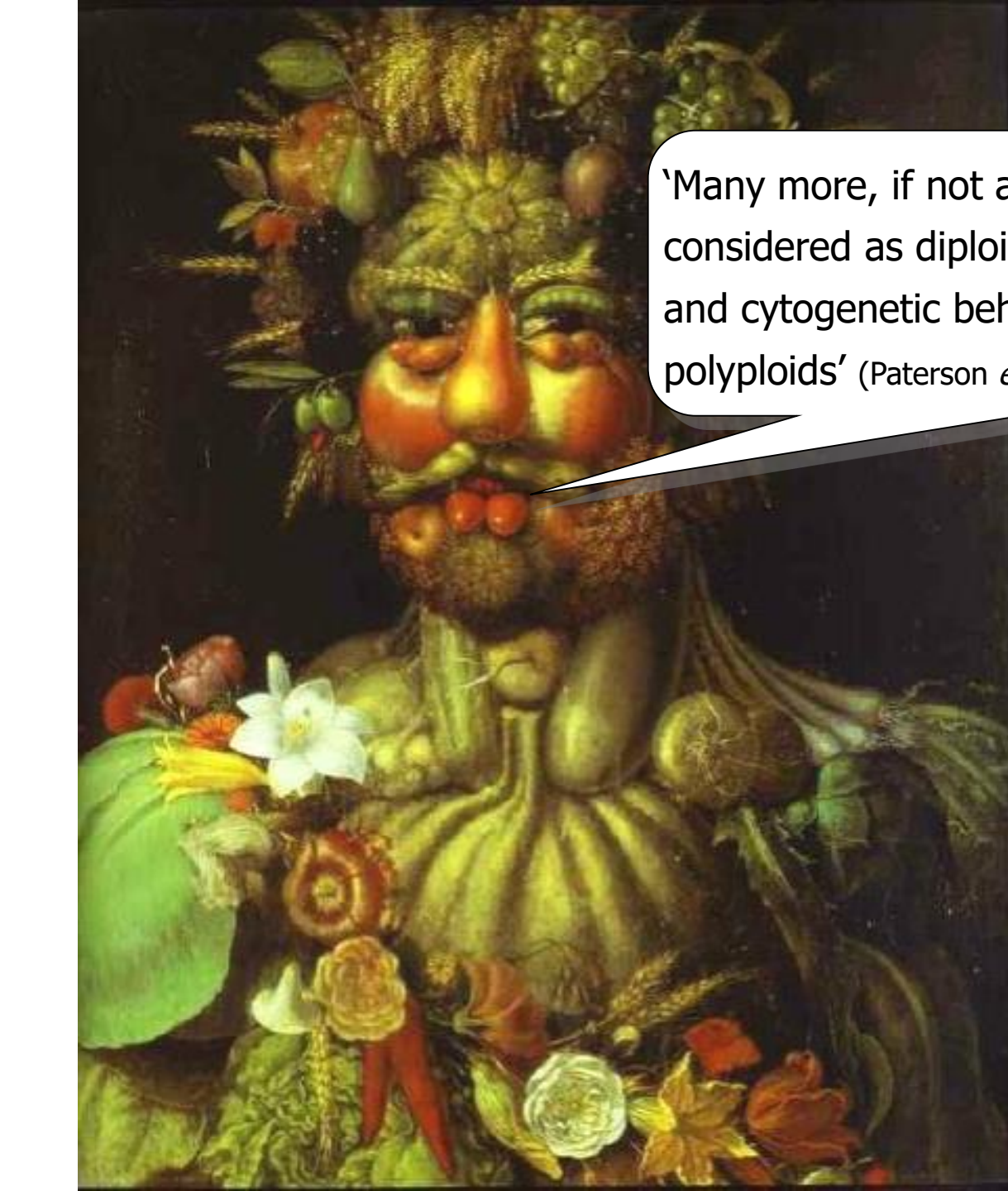
→ 4, 5, 6, 7, 10, 12

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 a man's face is intricately constructed from a variety of fruits and vegetables. The nose is a large, golden pear, the lips are two small red tomatoes, and the beard is a dense cluster of small red berries. The man's torso is formed by a large, ribbed green vegetable, possibly a zucchini or squash. 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, containing text about polyploidy in plants.

'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).