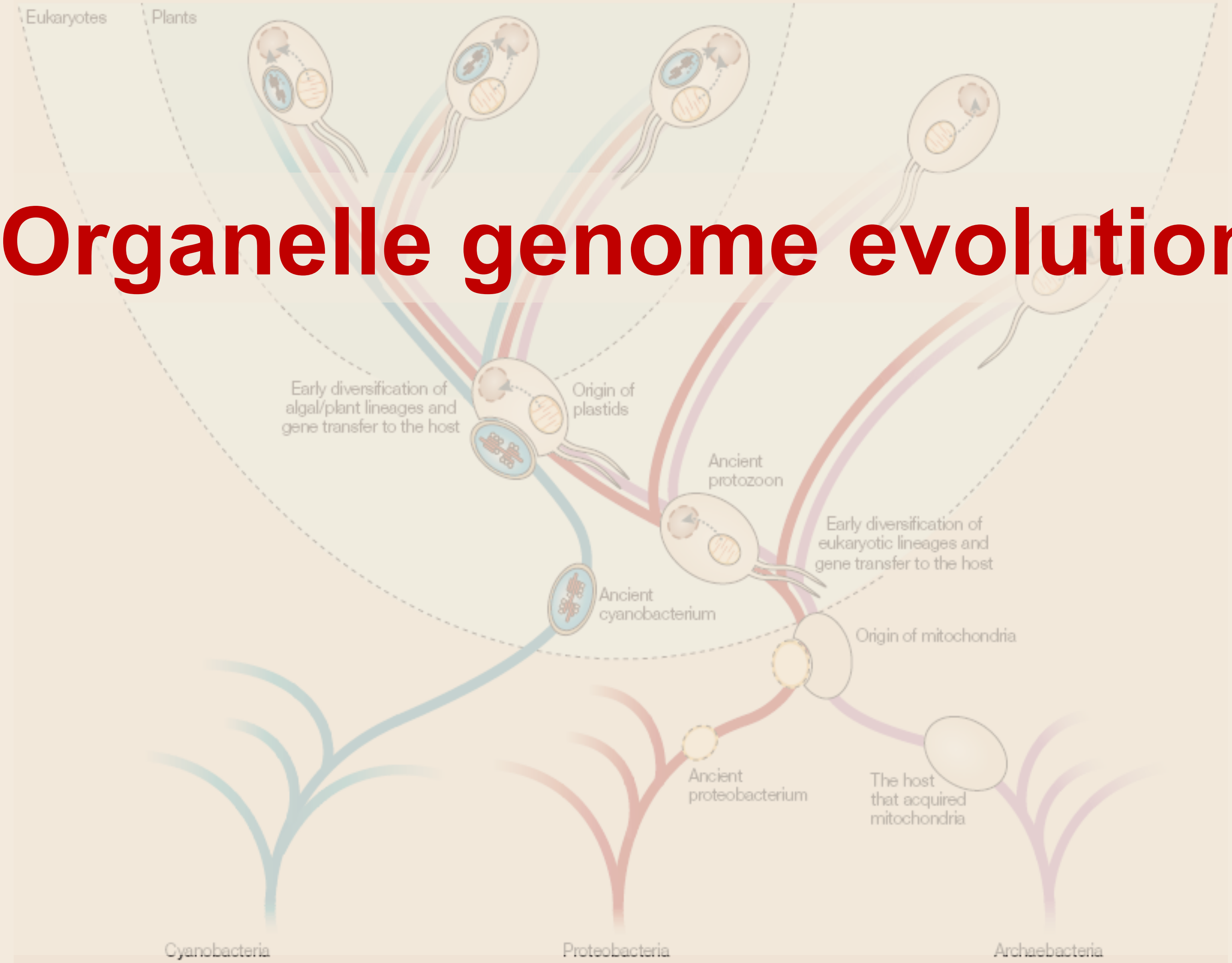
Organelle genome evolution



Plant of the day!

Rafflesia arnoldii

- largest individual flower (~ 1m)
- no true leafs, shoots or roots
- holoparasitic
- non-photosynthetic

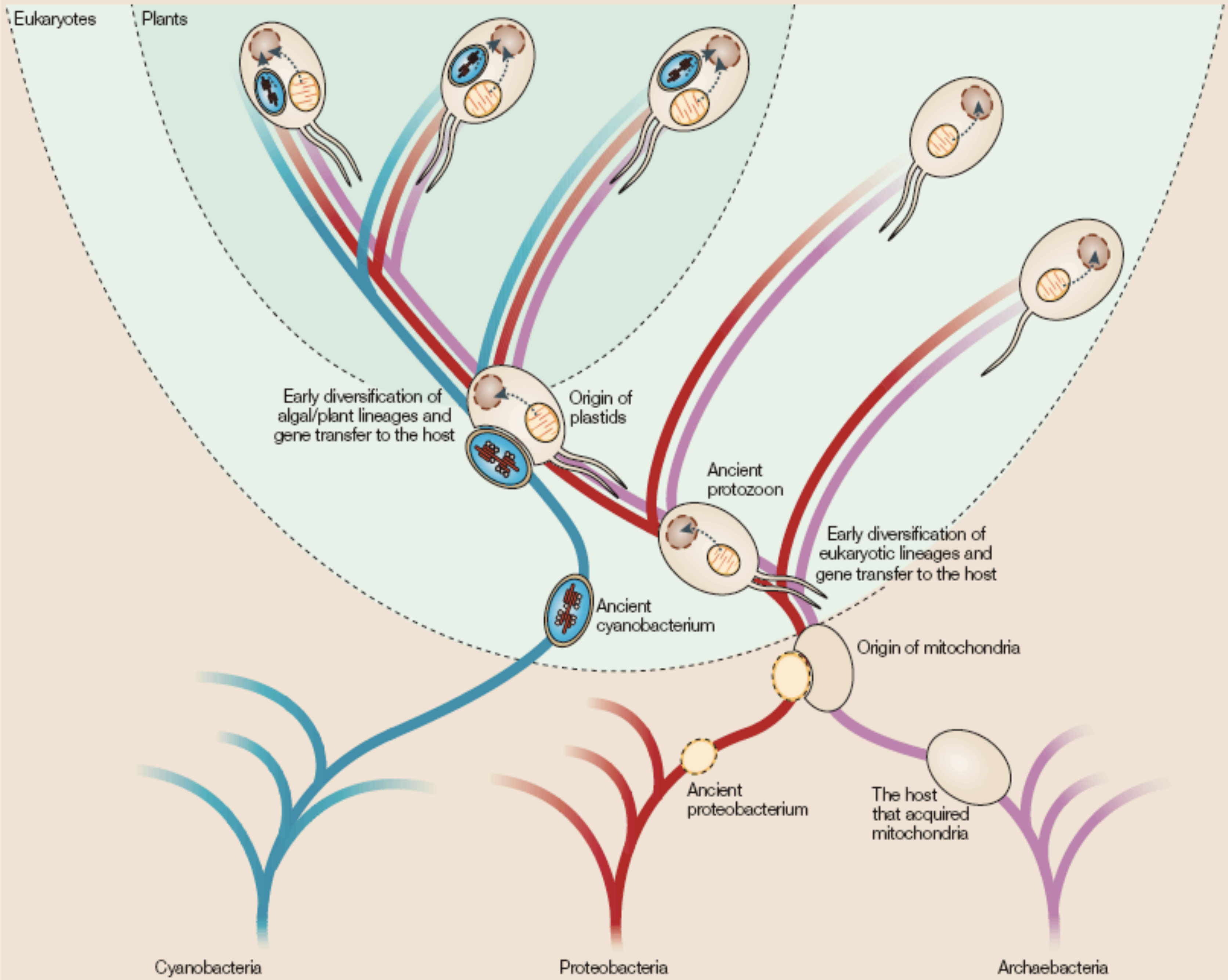
Big questions

- What is the origin of organelle genomes?
- What were the major steps in organelle genome evolution?
- Why are organelle genomes maintained?
- Is organelle genome variation neutral or adaptive?

The Endosymbiotic Theory

The Endosymbiotic Theory

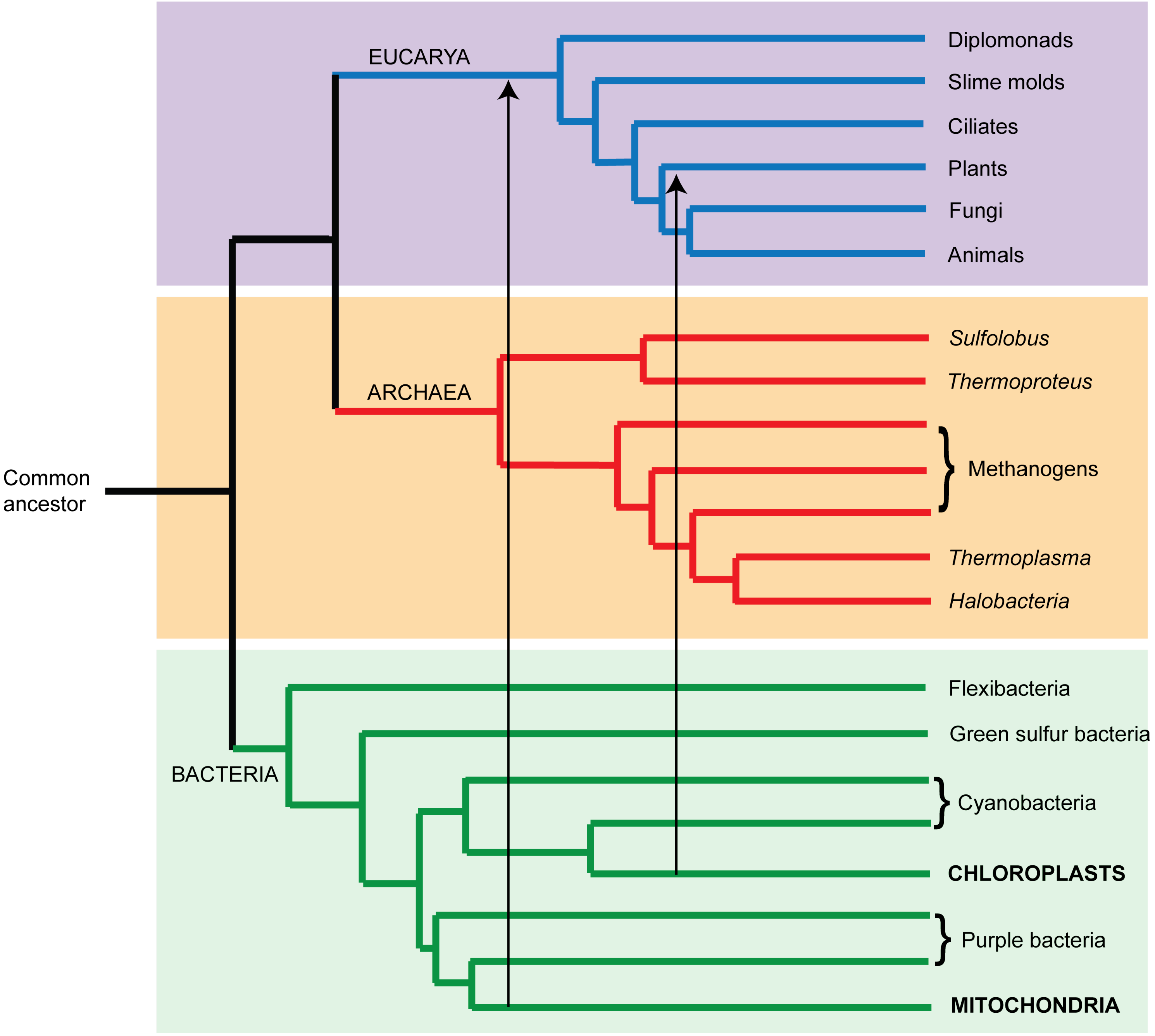
- MITOCHONDRIA: evolved from aerobic bacteria (α-proteobacteria) and a host
- CHLOROPLASTS: evolved from a heterotrophic eukaryote and a cyanobacteria



Timmis *et al*. (2004)

Evidence for the Endosymbiotic Theory

- Circular molecule
- No histones
- Protein synthesizing machinery (ribosomes, tRNA, rRNA)
- Some antibiotics block protein synthesis within the mitochondria and chloroplasts
- Structural similarity
- Reproduce through fission
- Strong phylogenetic evidence



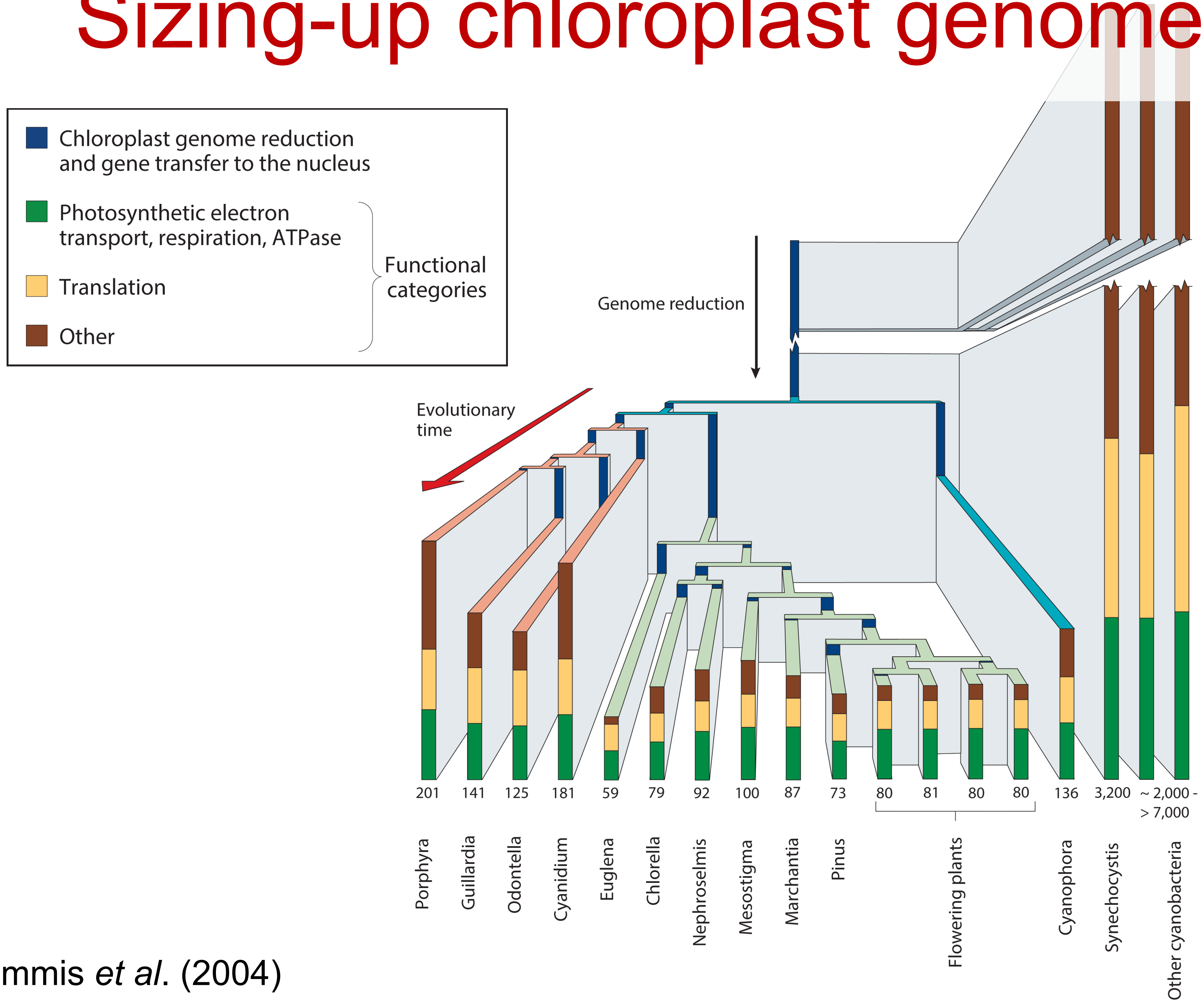
Futuyma (2009)

Organelle gene transfer

Sizing-up mitochondrial genomes

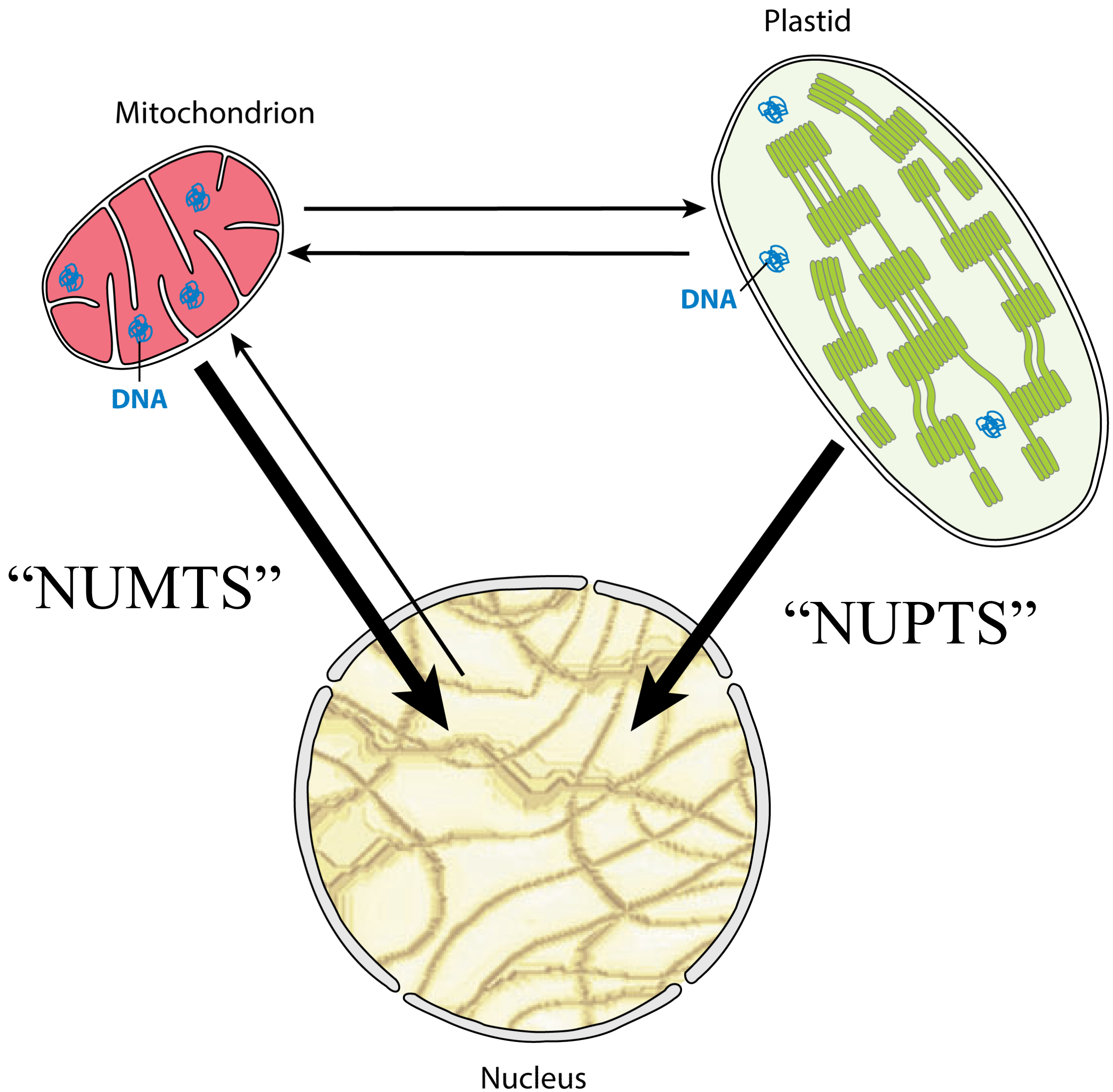
	kbp	# protein coding genes	
Plants and algae			
mt *Pylaiella littoralis*	59	52	NC_003055
mt *Marchantia polymorpha*	187	41	MPOMTCG
mt *Laminaria digitata*	38	39	AJ344328
mt *Cyanidioschyzon merolae*	32	34	NC_000887
mt *Arabidopsis thaliana*	367	31	MIATGENA
mt *Chondrus crispus*	26	25	MTCCGNME
mt *Scenedesmus obliquus*	43	20	NC_002254
Various protists and fungi			
mt *Reclinomonas americana*	69	67	NC_001823
mt *Malawimonas jakobiformis*	47	49	AF295546
mt *Naegleria gruberi*	50	46	NC_002573
mt *Rhodomonas salina*	48	44	NC_002572
mt *Dictyostelium discoideum*	56	40	NC_000895
mt *Phytophthora infestans*	38	40	NC_002387
mt *Acanthamoeba castellanii*	42	36	U12386
mt *Cafeteria roenbergensis*	43	34	NC_000946
mt *Monosiga brevicollis*	77	32	AF538053
mt *Physarum polycephalum*	63	20	AB027295
mt *Harpochytrium sp*	24	14	AY182006
mt *Candida albicans*	40	13	NC_002653
mt *Cryptococcus neoformans*	25	12	NC_004336
mt *Plasmodium falciparum*	6	3	NC_001677
α-proteobacteria			
Caulobacter crescentus	4017	3767	AE006573
Mesorhizobium loti	7596	7281	BA000012
Bradyrhizobium japonicum	~9100	~8300	BA000040

Sizing-up chloroplast genomes



Timmis *et al*. (2004)

Organelle gene transfer



modified from Kleine *et al*. (2009)

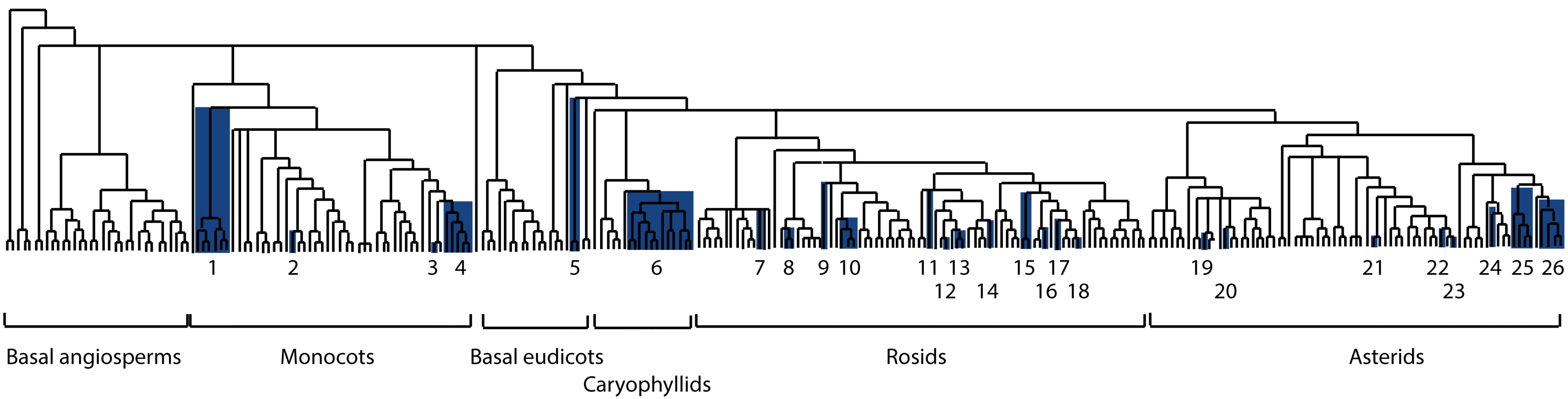
Recent organelle gene transfers

Comparisons of organelle genes and nuclear genes of the same species

- Gene transfer between cell compartments can occur
- This might be a continuous process
- The frequency of organelle-to-nucleus gene transfer

Mitochondrial Gene Transfer

• *rps*10 gene phylogeny ■ inferred transfers to the nucleus



modified from Adams *et al*. (2000)

Chloroplast Gene Transfer

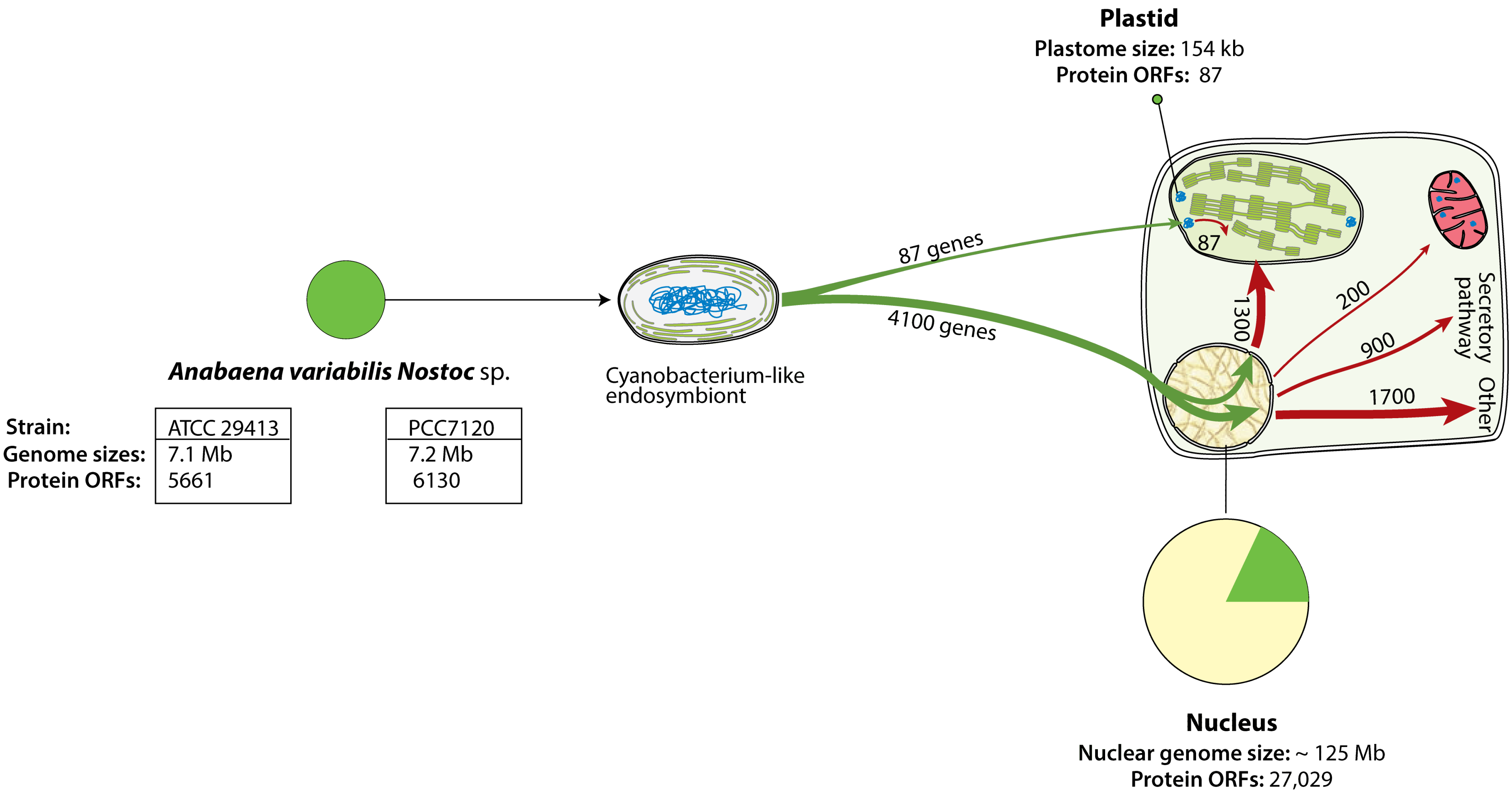
- *Inf*A (translation initiation factor) gene phylogeny (Millen *et al*. 2001)
- ~ 24 chloroplast-to-nucleus gene transfers
- mutational decay/loss of chloroplast sequence
- *de novo* mechanism for chloroplast targeting?

Ancient organelle gene transfers

Comparisons of nuclear, organelle and candidate prokaryotic ancestor genomes

- The scale of organelle-to-nucleus gene transfer
- The fate of imported genes over time

Organelle gene transfers (*Arabidopsis*)



modified from Kleine *et al.* (2009)

The fate of transferred genes

- products routed back to the donor organelle

- products are targeted to other cellular compartments

- functional replacement of equivalent host genes

  (= endosymbiotic gene replacement)

Mitochondrial Gene Transfer Rates

- rate estimates:
  - 1 plasmid transfer to nucleus in 20,000 yeast cells (integration rare)

Chloroplast Gene Transfer Rates

Rate estimates from tobacco chloroplasts
- 1 transfer in 5 million leaf cells
- 1 transfer in 16 000 pollen grains

Higher rates of transfer in the pollen?

Degradation of the organelle genomes in pollen could make DNA fragments available for uptake

How do organelle genes get into the nucleus?

- **<u>Bulk DNA</u>**

– Recombination between escaped organelle DNA and nuclear DNA
  - Experimental transfer in yeast
  - Non-coding sequence frequently transferred
  - Whole organelle sequences transferred

MUST HAPPEN

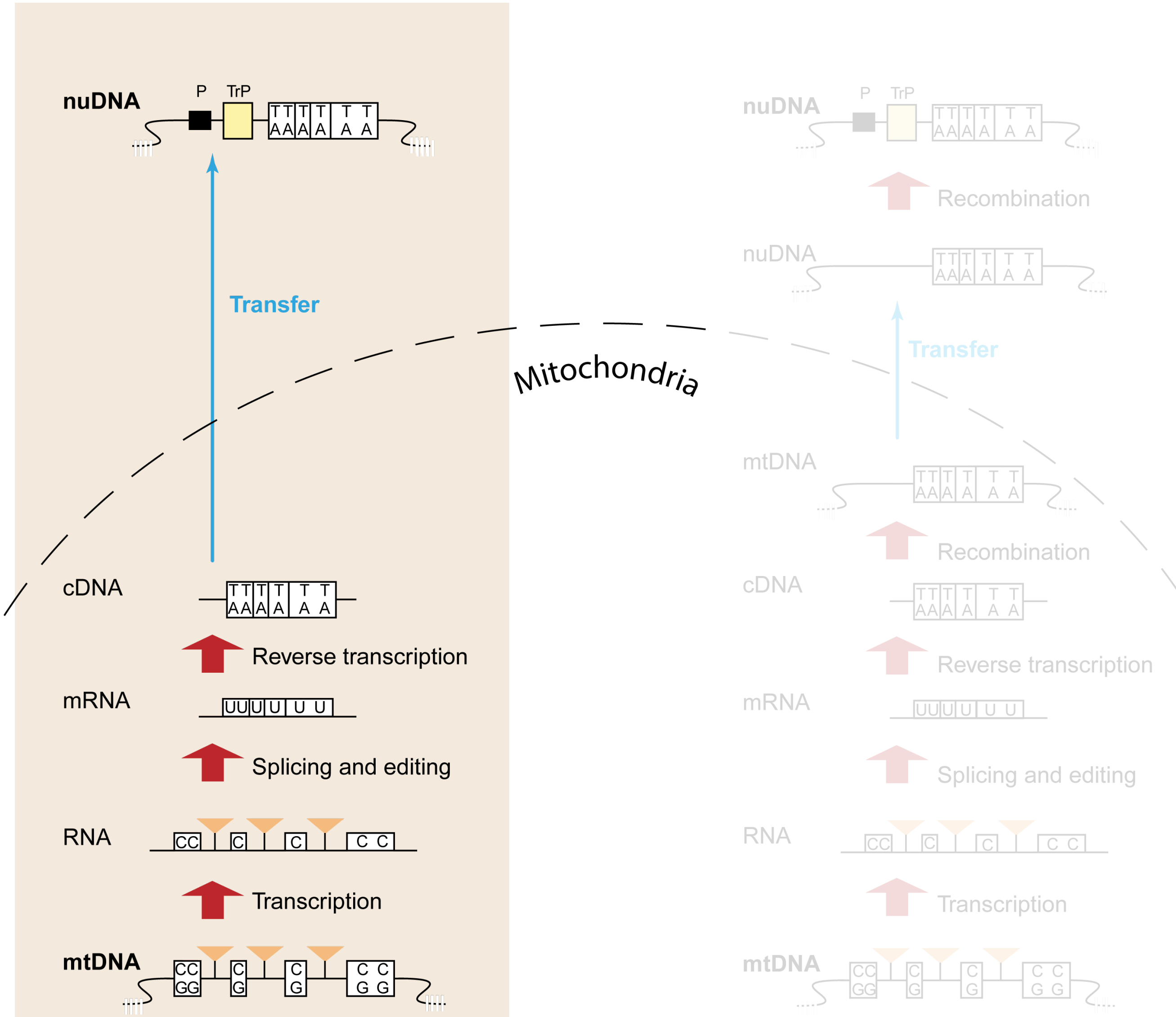
How do organelle genes get into the nucleus?

- **<u>cDNA intermediates</u>**
  - NUMTS and NUMPTS often lack organelle-specific introns and edited sites

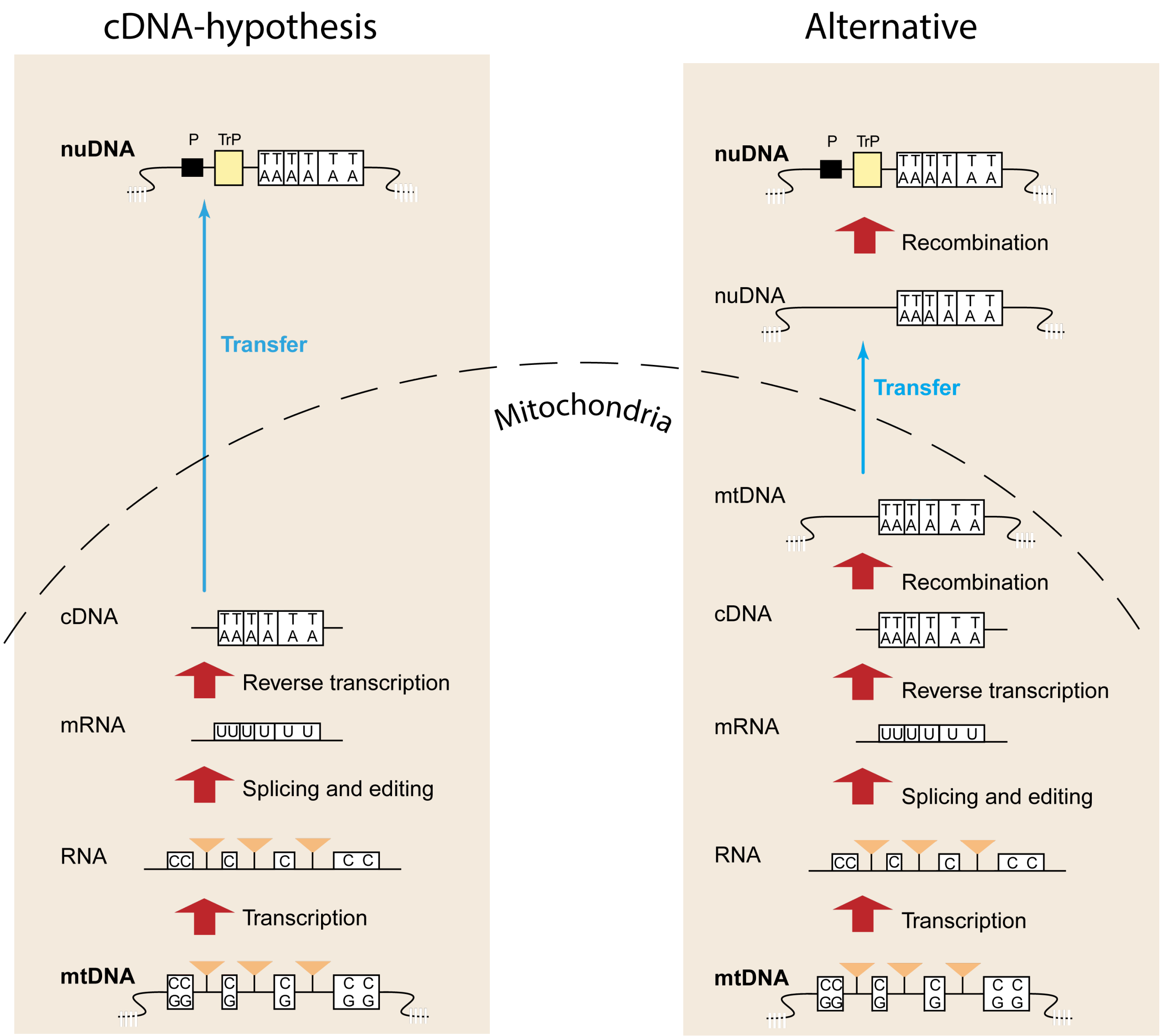
MAY HAPPEN

cDNA-hypothesis

Alternative



modified from Henze & Martin (2001)



modified from Henze & Martin (2001)

Why are organelle genomes maintained?

THINK – PAIR - SHARE

Why are organelle genomes maintained?

- Hydrophobicity -hydrophobic proteins are poorly imported
- Redox-control - fitness advantage if coding sequence and regulation are in same location
- Other constraints (RNA editing, genetic code)
- What about non-photosynthetic plants?


Rafflesia arnoldii
Lathraea clandestina
Orobanche lutea
Neottia nidus-avis

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- Hydrophobicity -hydrophobic proteins are poorly imported
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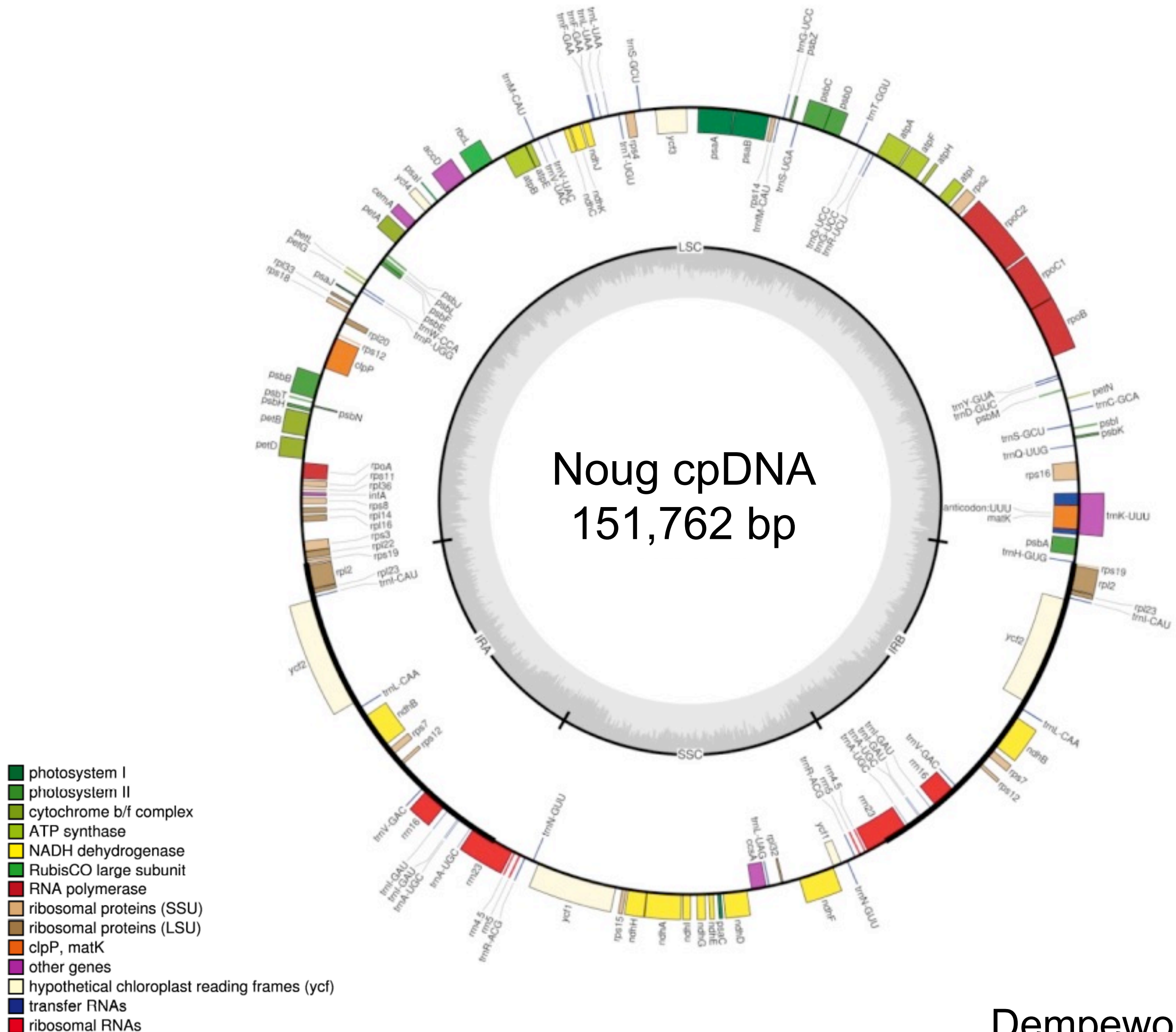
  - essential tRNAs (Barbrook *et al*. 2006)

Organelle genome evolution under changing environmental conditions

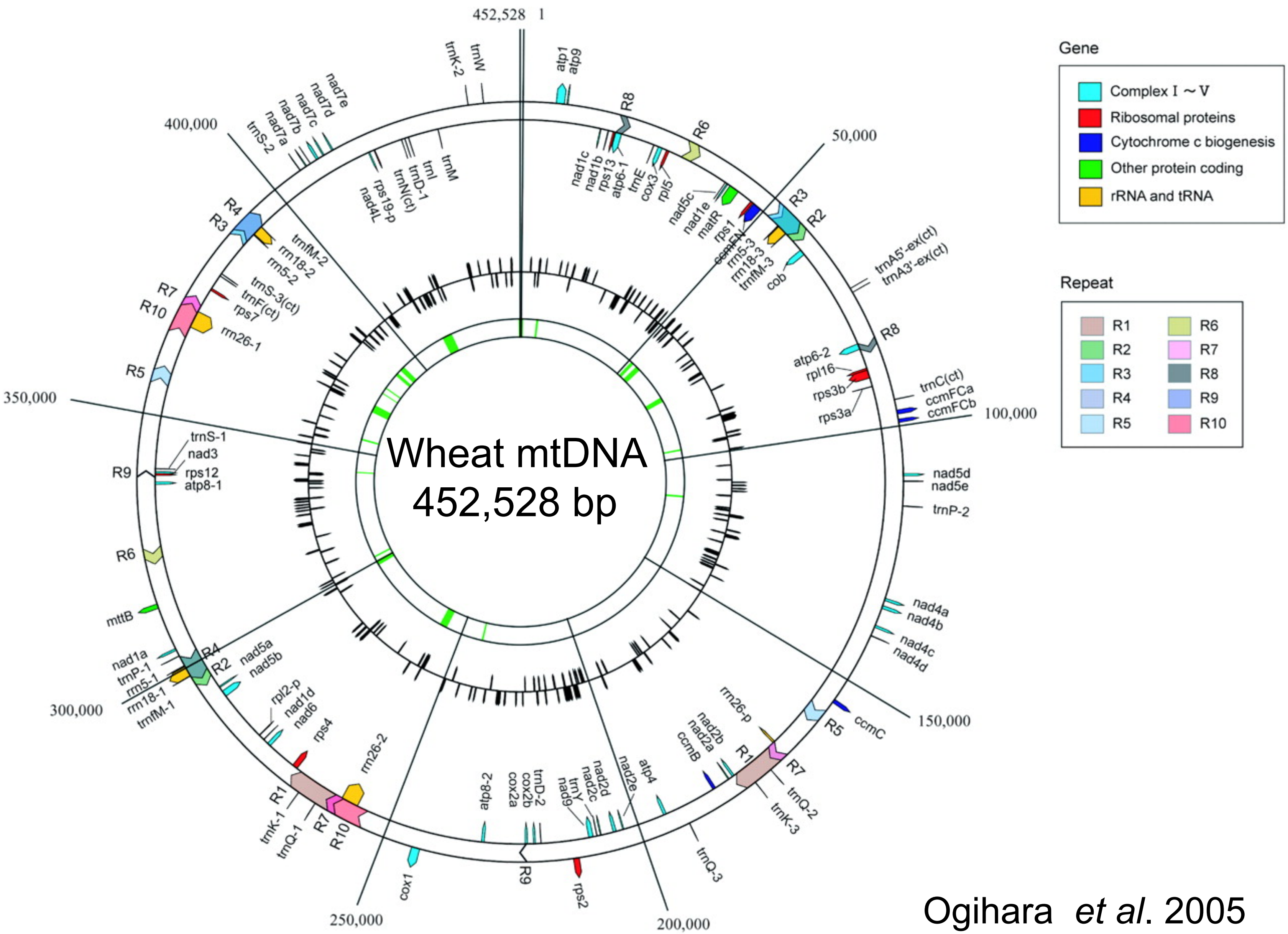
Structure of Plant cp Genomes



LSC – 84 kb
SSC – 18 kb
IR – 25 kb (each)

Dempewolf *et al*. 2010

Structure of Plant mt Genomes



Ogihara *et al*. 2005

Neutral organelle DNA variation

- organelle-encoded proteins are highly conserved

- limited coding potential of organelle genomes (compared to the nuclear genome)

- reduced rates of sequence evolution (in plants)

Rates of synonymous substitutions per million years

	Genome	Taxa compared	Rate
Plant	mt	Maize/wheat Monocot/dicot	0.2 – 0.3 0.8 – 1.1
	cp	Maize/wheat Monocot/dicot	1.1 – 1.6 2.1 – 2.9
	nuc	Spinach/Silene Monocot/dicot	15.8 – 31.5 5.8 – 8.1
Animal	mt	Human/chimpanzee Mouse/rat	21.8 – 43.7 18.2 – 54.5
	nuc	Human/chimpanzee Mouse/rat	0.9 – 1.9 3.9 – 11.8

Evolution of three genomes

	Genome	Sequence evolution	Structural evolution
Plant	mt	very slow	very fast
	cp	slow	very slow
	nuc	moderate	moderate
Animal	mt	very fast	very slow
	nuc	moderate	moderate

Adaptive organelle DNA variation?

Experimental evidence is accumulating:

- parallels between organelle capture and environmental variation
- experimental evolution of cytoplasm fitness effects
- direct tests of selection on organelle genes

Experimental evolution studies

Sambatti *et al*. (2008)

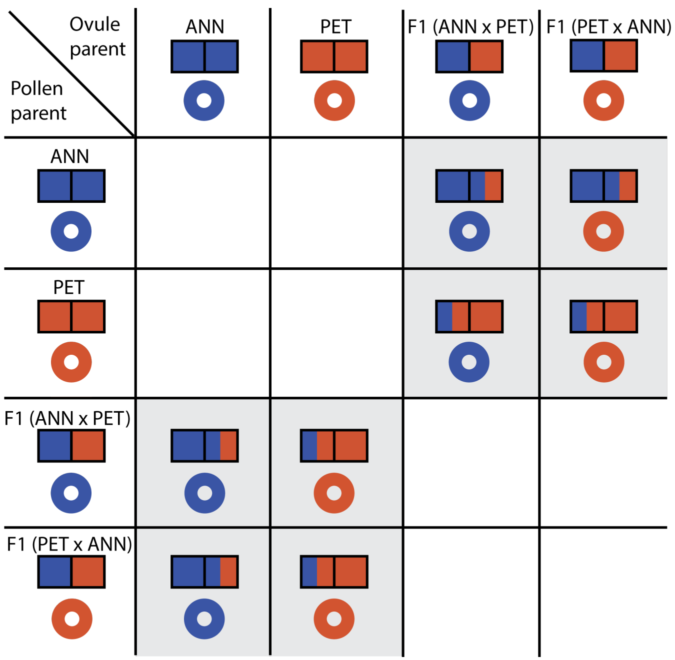
Helianthus petiolaris
- common in dry sandy soils

Helianthus annuus
- common in clay-based soils

Photos by J. Rick

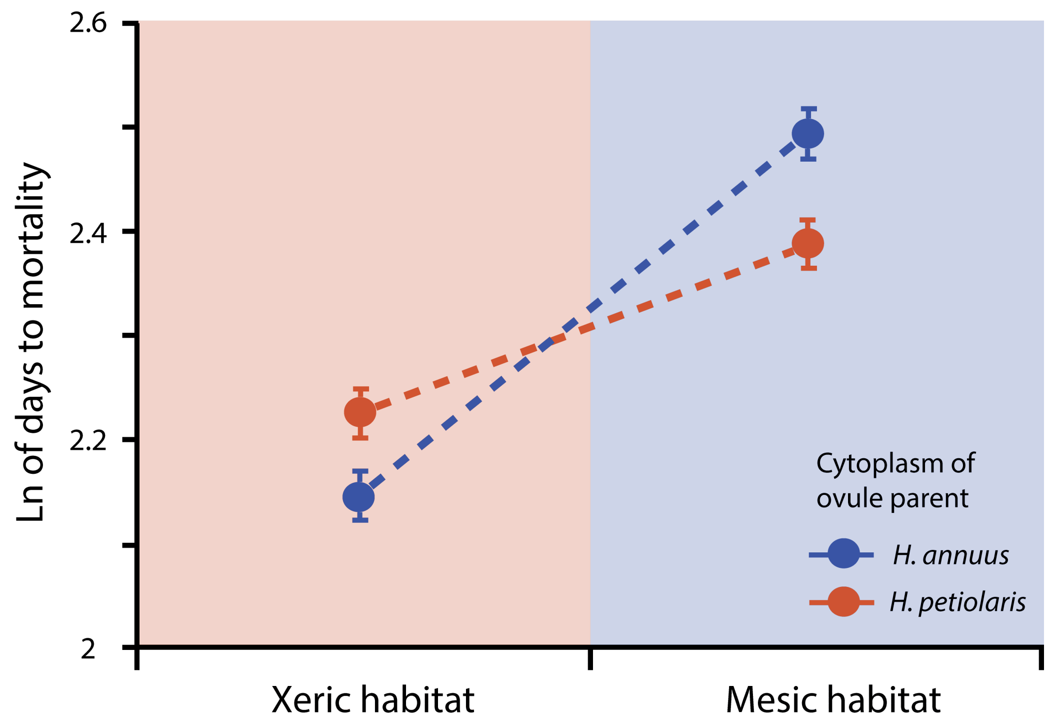
Experimental evolution studies

Crossing design



Backcrosses

Cytoplasm-by-habitat interaction



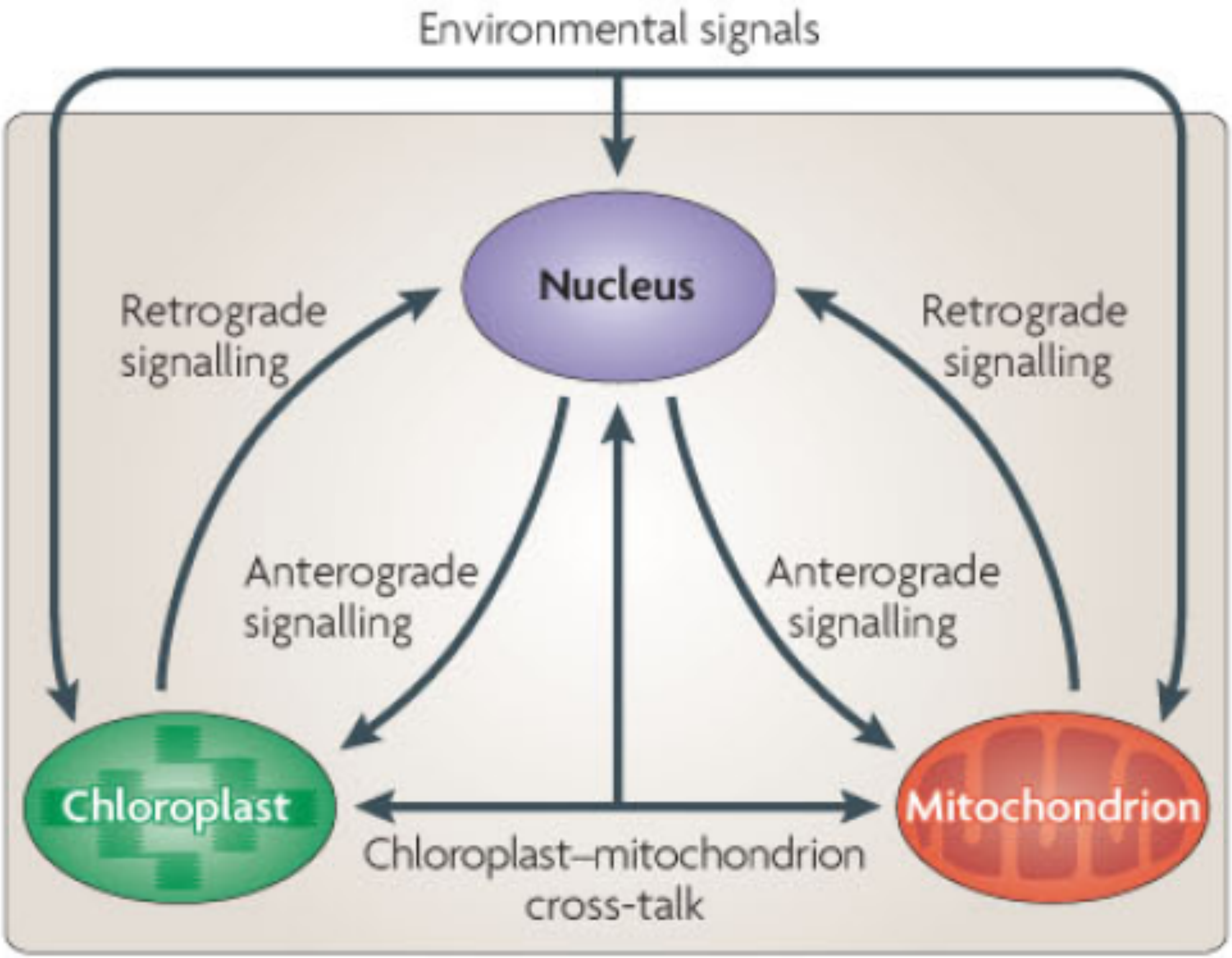
modified from Sambatti *et al*. (2008)

Tests of selection on organelle genes

- Kapralov & Filatov (2006)
- *Schiedea* genus (endemic to Hawaii)
- Species adapted to xeric conditions
- Positive selection detected at the cp *rbcL* gene

Schiedea globosa

Co-adaptation of genotype and plasmotype



Woodson & Chory (2008)

Unanswered questions

- To what extent have organelle gene transfers shaped nuclear genomes?
- Is organelle gene transfer just a quirk of evolution?
- How often does organelle genetic variation contribute to local adaptation?
- What are the agents and traits under divergent selection?