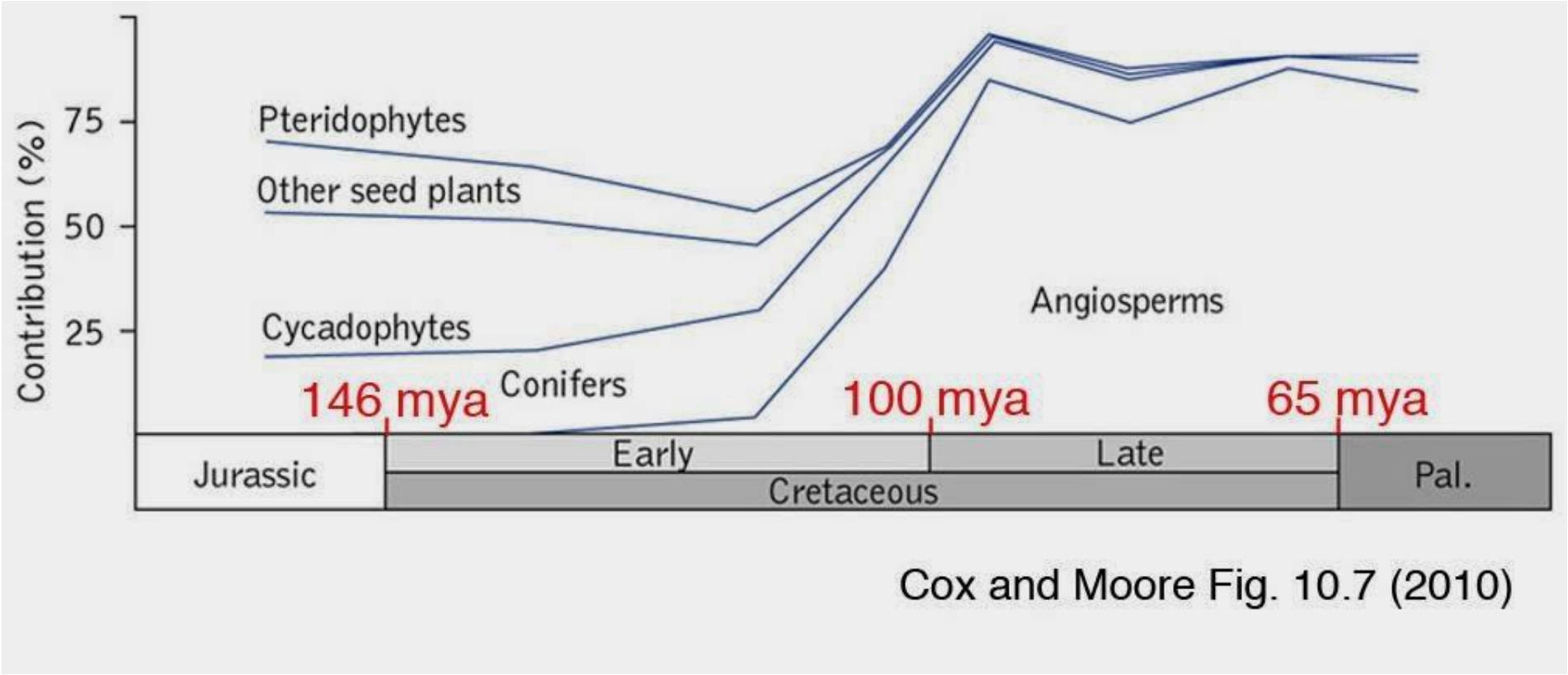
Biosystematika II

April 25th, 2019

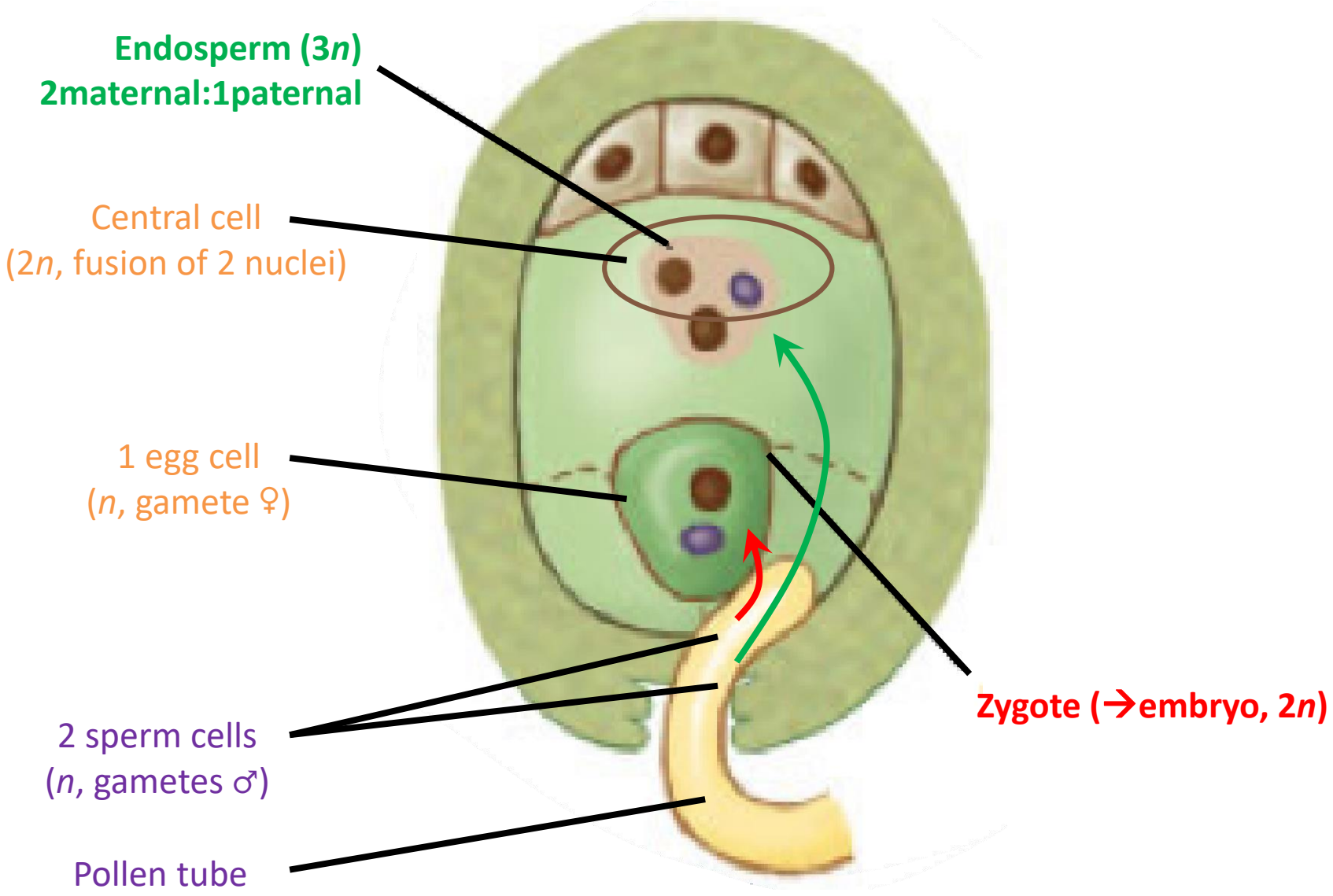
Clément Lafon Placette

Angiosperms dominate the current plant world



Cox and Moore Fig. 10.7 (2010)

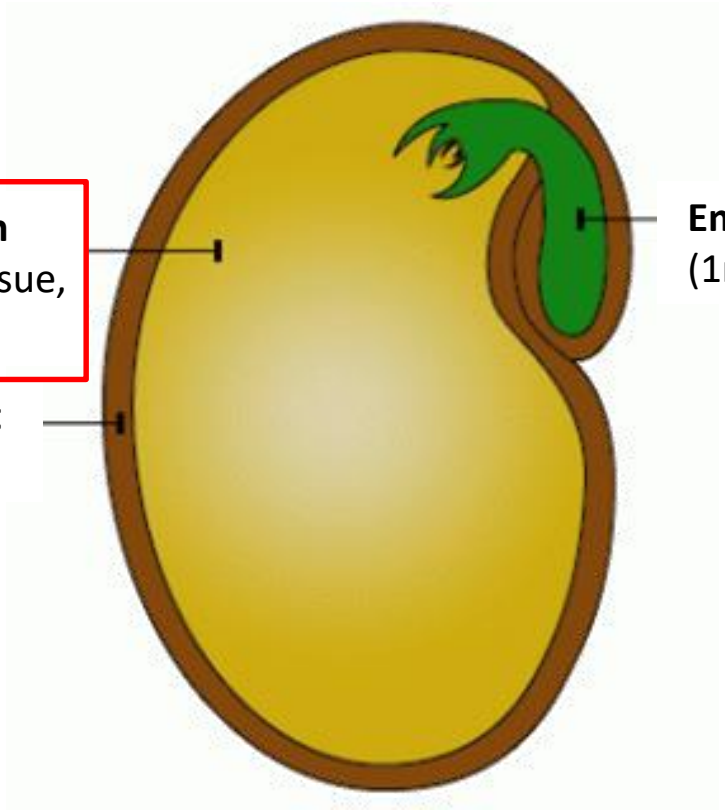
Double fertilization in Angiosperms



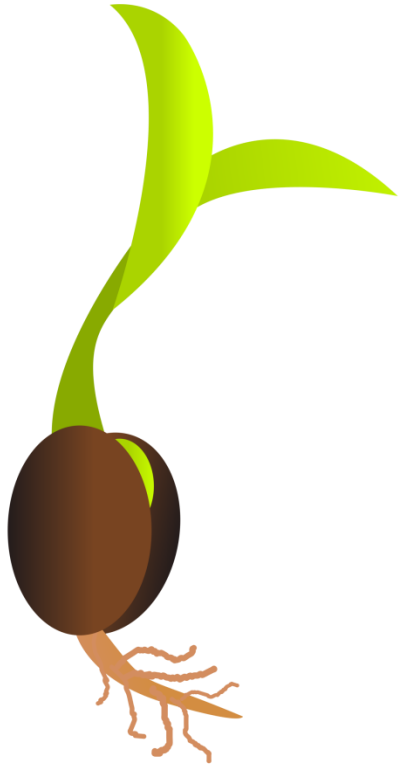
A seed is supposed to give rise to a new healthy seedling

endosperm
(nourishing tissue, 2m:1p)

seed coat
(2m:0p)



Embryo
(1m:1p)



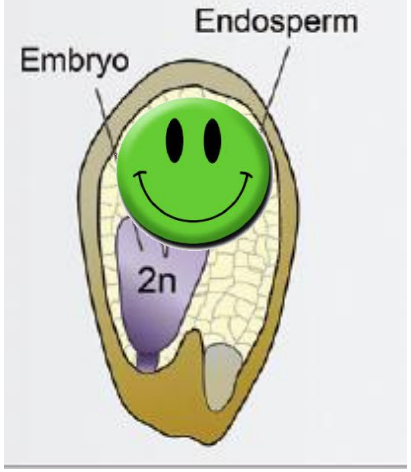
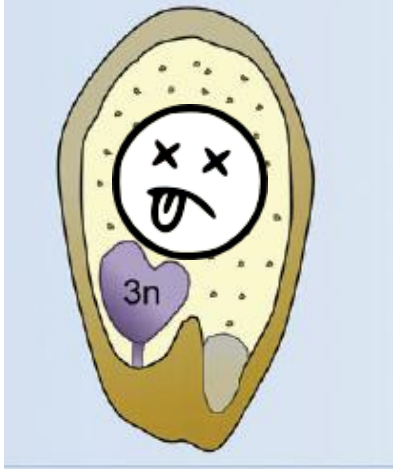
Next generation

The 2m:1p endosperm ratio can be disrupted

Cymbidium Fanfare
2x

Cymbidium Fanfare
4x

The endosperm: a genome dosage sensitive tissue

	Balanced ploidy 2x × 2x	**Maternal excess** 4x ♀ × 2x ♂	**Paternal excess** 2x ♀ × 4x ♂
Endosperm	**M:P** ratio: **2:1**	**M:P** ratio: **4:1**	**M:P** ratio: **1:1**
			
	Normal endosperm	Early cellularized Endosperm	Endosperm with failed cellularization

It's a relative dosage, not absolute. Homo-polyploids have more copies but remain 2m:1p

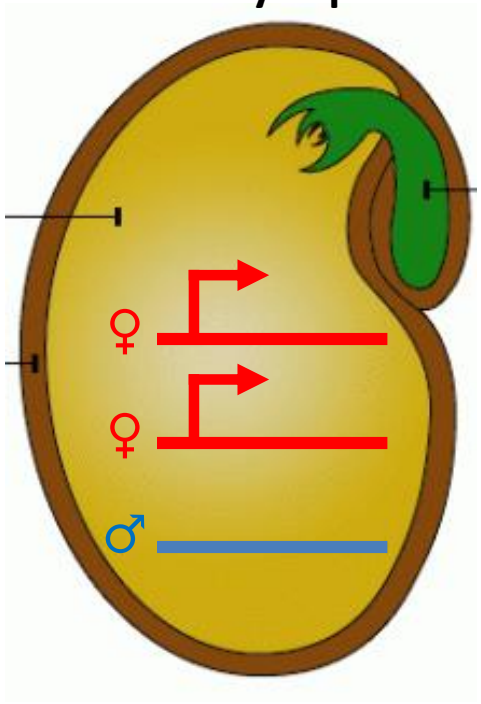
Parental genomes are not equivalent/they are complementary

Schatlowski and Köhler, 2012

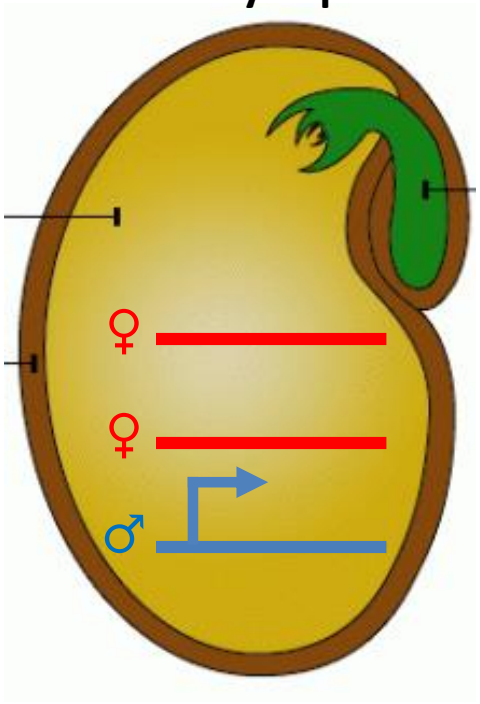
Parent-of-origin expression: genomic imprinting

Genomic imprinting is the epigenetic phenomenon by which certain genes are expressed in a parent-of-origin-specific manner

Maternally expressed



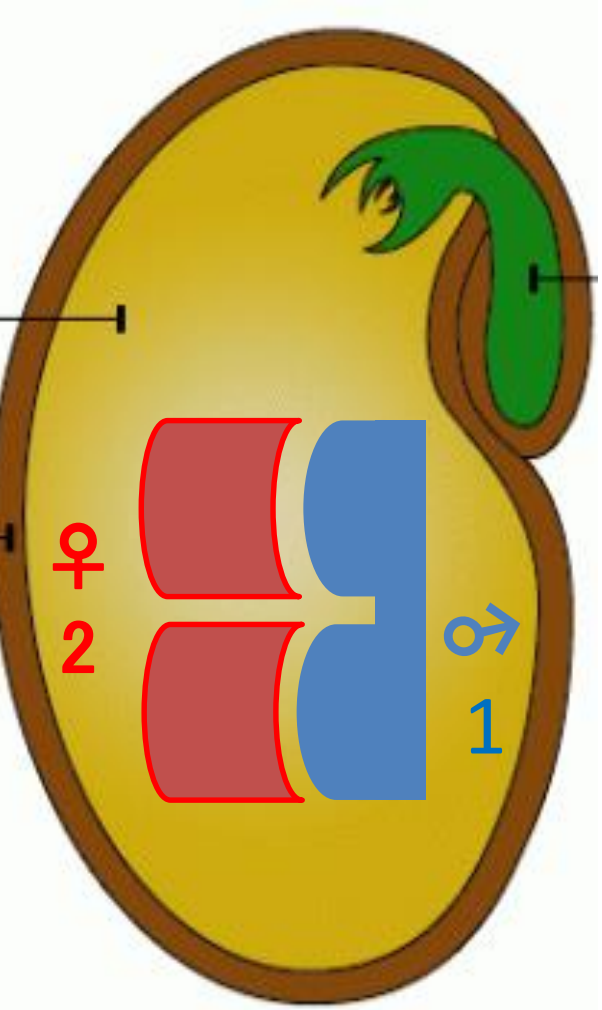
Paternally expressed



Complementarity/unequivalence of parental genomes

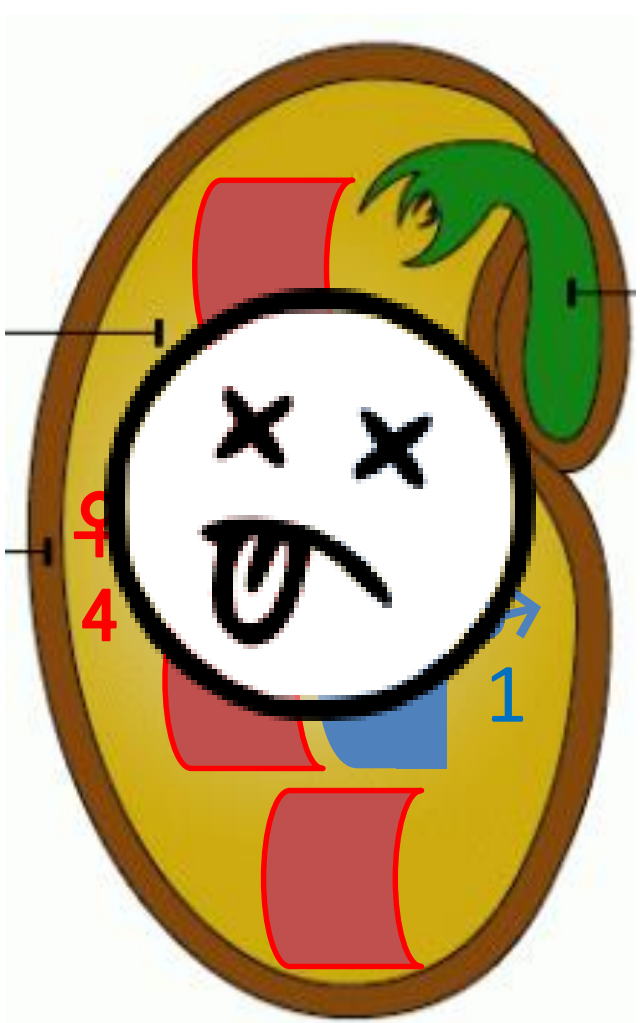
Balanced ploidy

2x × 2x



Maternal excess

4x ♀× 2x ♂



Paternal excess

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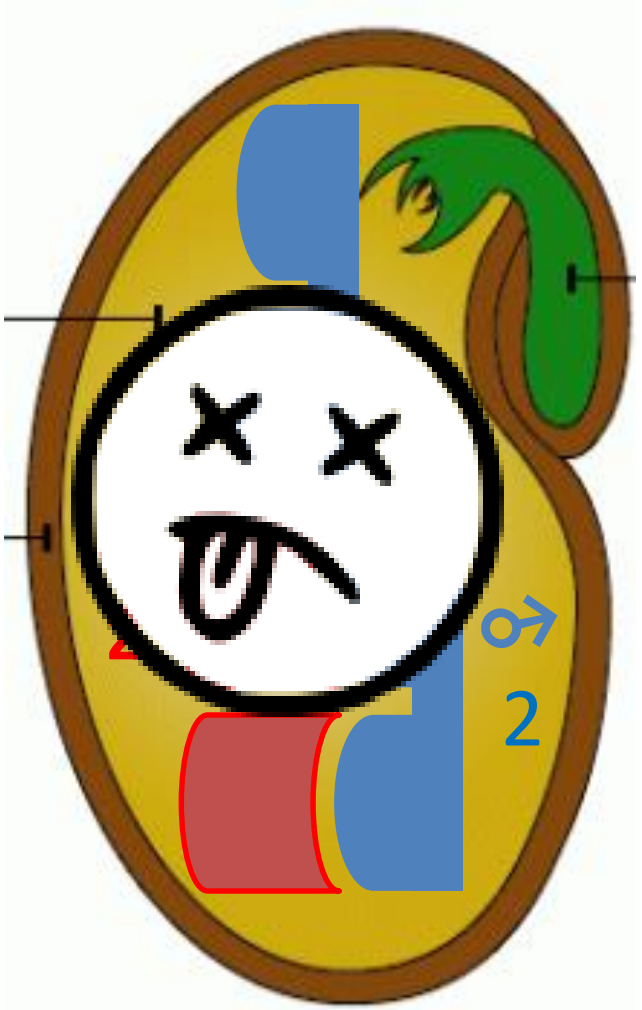


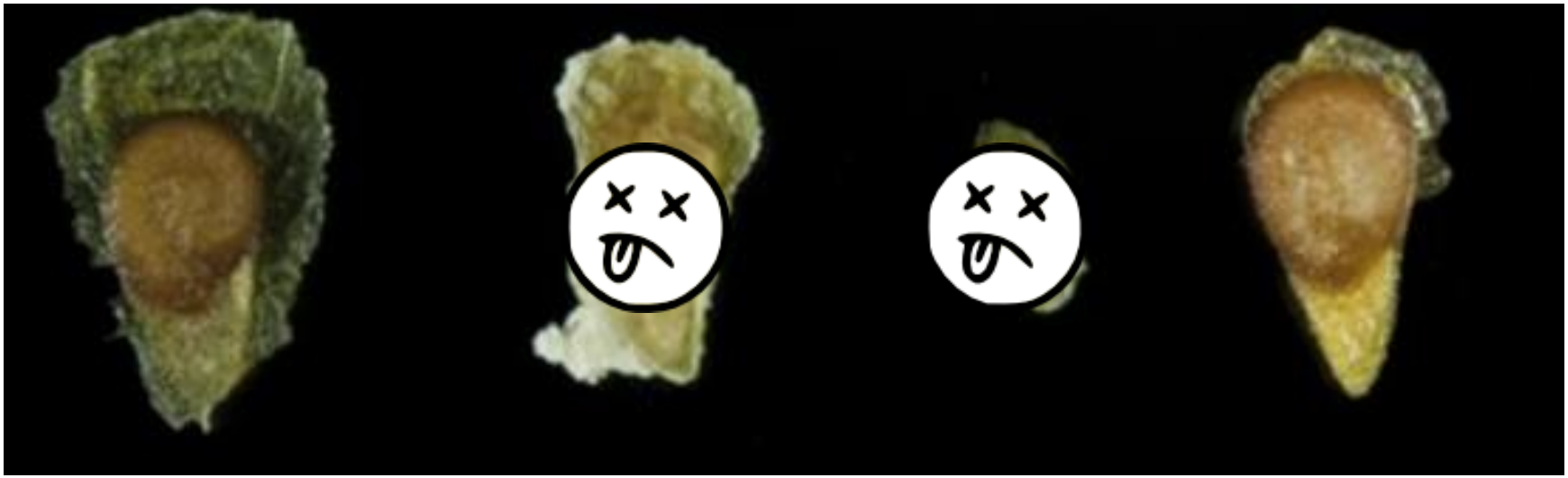
Hybrid seed lethality = reproductive barrier

S. chilense

S. chilense × *S. peruvianum*

S. peruvianum × *S. chilense*

S. peruvianum



Florez-Rueda et al., 2016

“What is a species and what is not?”

A cockadog (hassciencegonetoofar.com)

“Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups”

Ernst Mayr, 1963

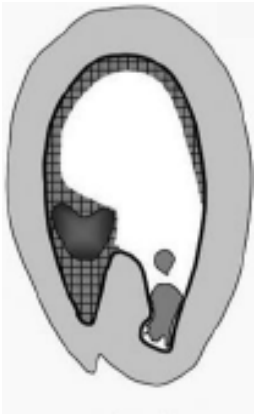
Exactly the same story in homoploid hybrid seeds

***A. lyrata*, 2x** × ***A. arenosa*, 2x** = **Hybrid**

***A. arenosa*, 2x** × ***A. lyrata*, 2x** = **Hybrid**

Lafon-Placette et al., 2018

The endosperm requires a specific relative dosage between maternal and paternal genomes (2:1)

	♀ 2*x* × ♂ 2*x*	♀ 4*x* × ♂ 2*x*	♀ 2*x Aa* × ♂ 2*x Al*	♀ 2*x* × ♂ 4*x*	♀ 2*x Al* × ♂ 2*x Aa*
Genome ratio	2m:1p	4m:1p	2m:1p	2m:2p	2m:1p
Genome balance	Normal	♀ excess	Normal	♂ excess	Normal
					
	Normal endosperm	Early cellularized endosperm		Endosperm with failed cellularization	

Reciprocal defects in interploid seeds within the same species = homoploid hybrid seeds!

A quantitative imbalance in interspecific (homoploid) hybrid seeds as well?

Tiwari et al., 2010

Increasing the ploidy of one parent rescues the hybrid seed: a quantitative rather than qualitative barrier

chromosomes doubling (drug induced, colchicine)

***C. rubella* (2x) × *C. grandiflora* (2x)**

***C. rubella* (4x) × *C. grandiflora* (2x)**

C. rubella × *C. grandiflora* hybrid seeds rescued!

Lafon-Placette and Hatorangan et al., 2018

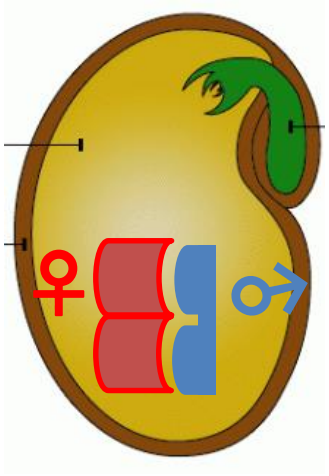



The Endosperm Balance Number (EBN) hypothesis

Johnston et al. 1980

chromosomes × 2
(drug induced)


***Solanum brevidens*, 2x**
EBN = 1



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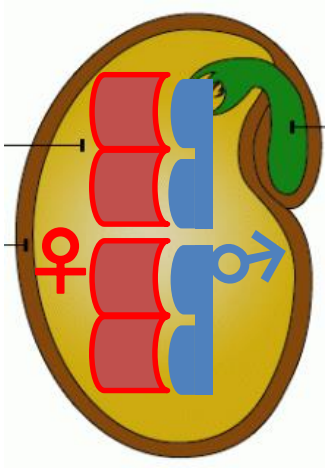
***S. stenotonum*, 2x**
EBN = 2



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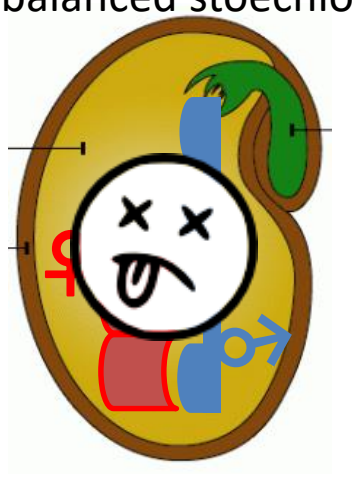
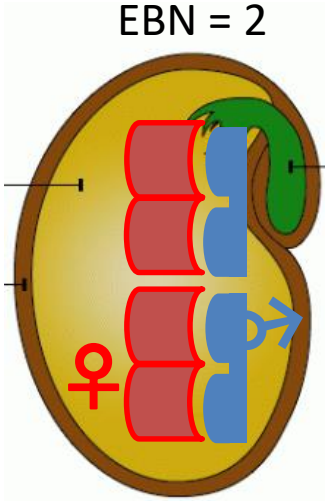
Hybrid seed, 2x
Imbalanced stoechiometry



***S. brevidens*, 4x**
EBN = 2



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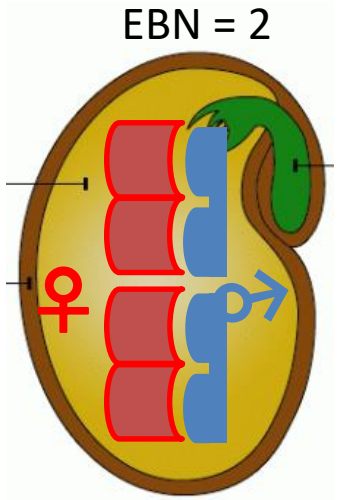
***S. stenotonum*, 2x**
EBN = 2



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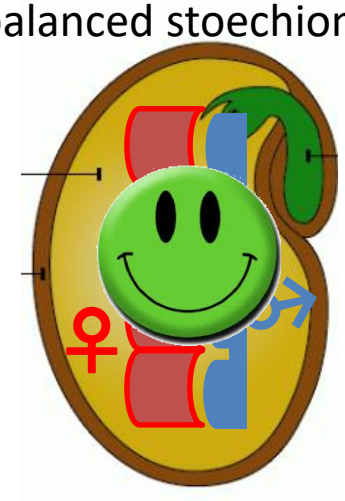
Hybrid seed, 3x
balanced stoechiometry



A problem of genome dosage between parental species

***A. lyrata*, 2x**
EBN = 1

***A. arenosa*, 2x**
EBN = 2

Hybrid seed, 2x
1 lyrata < 2 arenosa

Natural tetraploidization

***A. lyrata*, 4x**
EBN = 2

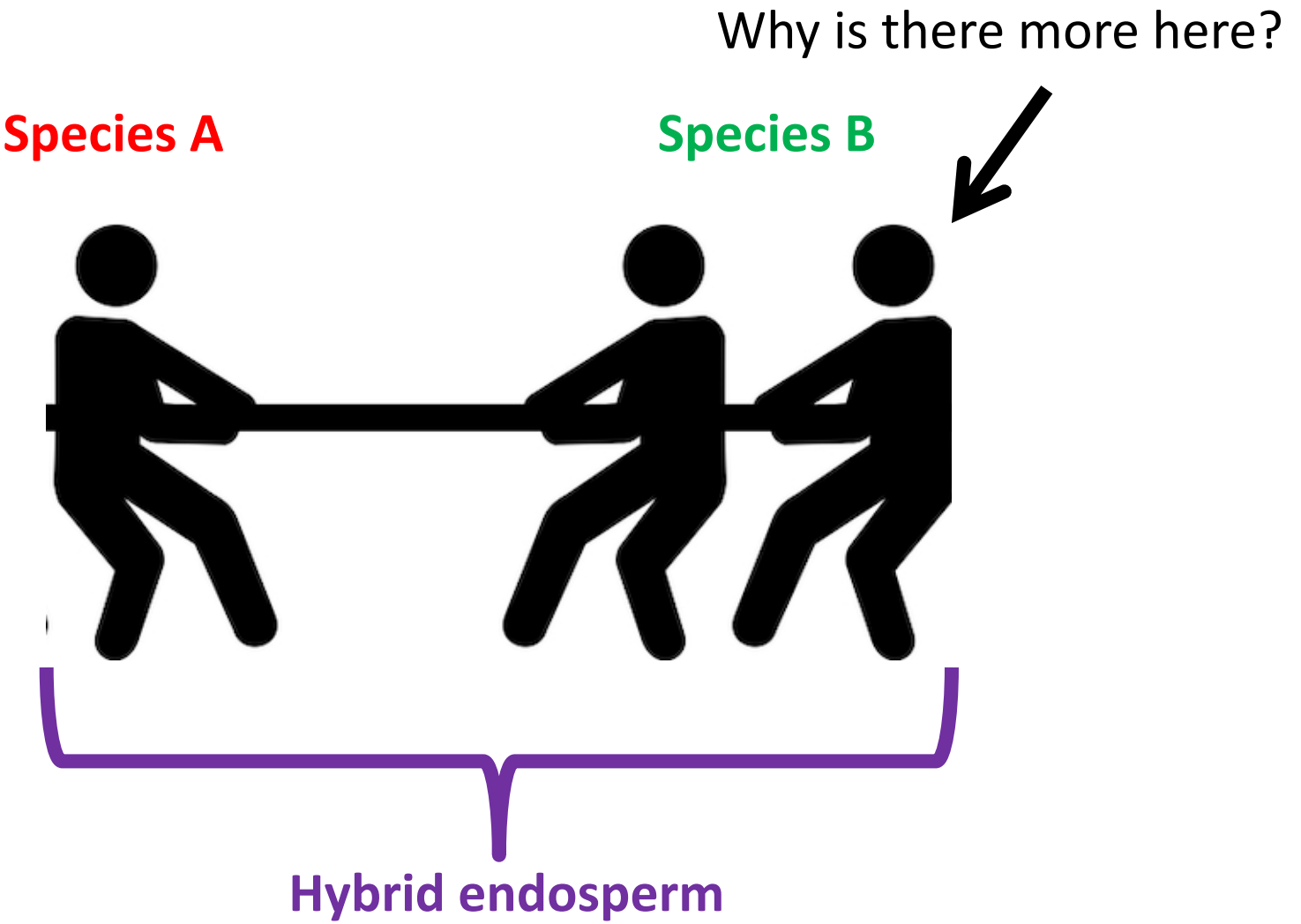
***A. arenosa*, 2x**
EBN = 2

Hybrid seed, 3x
2 lyrata = 2 arenosa

Johnston et al., 1980

Genome dosage imbalance → hybrid seed lethality: a widespread mechanism across angiosperms

Why do some species have higher EBN than others?



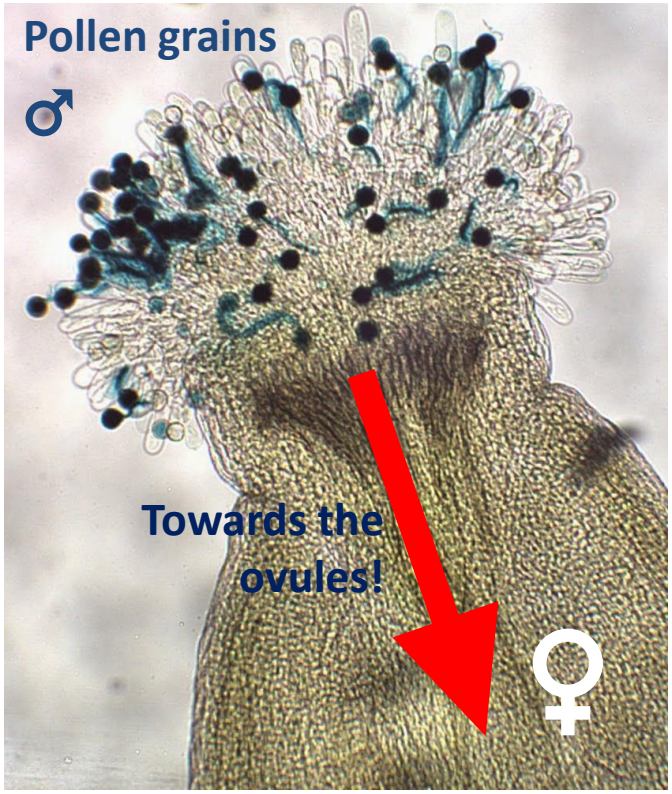
The “vendange en vert”

Unripe fruits, high acidity

Fruits grow bigger, higher sugar content

Competition between fruits/seeds for limited maternal resources…

Siblings from different males = competition for maternal resources



Seeds from male 1

Seeds from male 2

Seeds from male 3

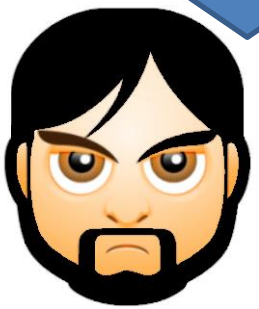
Seeds from male 4

The parental conflict theory

Genomic "message" to the developing progeny:

"Grow big and strong, use all maternal resources."

Positive selection

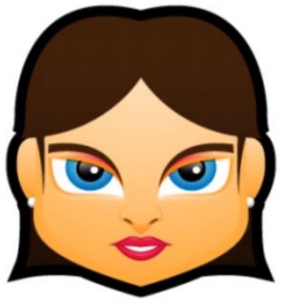


♂

♀

Genomic "message" to the developing progeny:

"Grow well, but leave some resources for the other progenies."



Positive selection

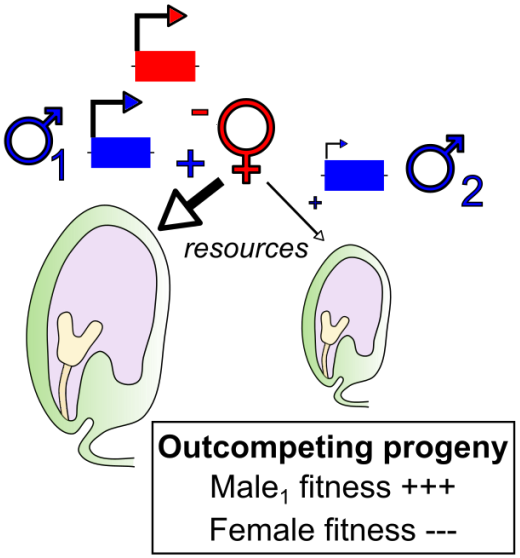
Evolution towards a "selfish"/ "demanding" influence

Conflict of interests

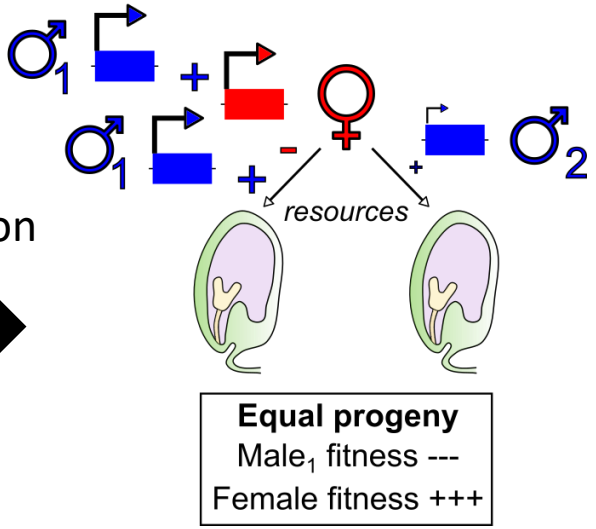
Evolution towards a "repressive"/ "equitable" influence

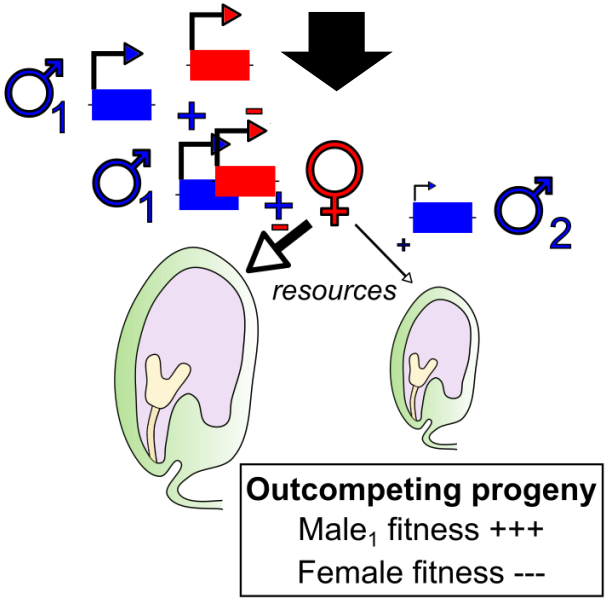
The parental conflict theory

A tug-of-war



Natural selection





Etc.

The Weak Inbreeder/Strong Outbreeder theory

Outbreeder

Siblings from different males

↓

Pressure for “selfish” males

↓

Pressure for “repressive” females

↓

High level parental conflict

↓

“Strong” parent
High EBN

Inbreeder

Siblings from mainly one male

↓

The mother plant is the male

↓

Same paternal and maternal interests

↓

Low level parental conflict

↓

“Weak” parent
Low EBN

The outbreeder parent overpowers the inbreeder one

=

EBN imbalance → endosperm-based hybrid seed lethality

Brandvain et Haig, 2005

Higher EBN in outbreeders: a clear trend in *Solanum*

Species	EBN	Ploidy	EBN in 2x	Mating type	Species	EBN	Ploidy	EBN in 2x	Mating type
Solanum acaule	1	2x	1	Self-compatible	*S. boliviense*	2	2x	2	Self-incompat.
S. brevidens	1	2x	1	SC	*S. bulbocastanum*	1	2x	1	SI
S. demissum	4	6x	1.33	SC	*S. cardiophyllum*	1	2x	1	SI
S. etuberosum	1	2x	1	SC	*S. chacoense*	2	2x	2	SI
S. fernandezianum	1	2x	1	SC	*S. chomatophilum*	2	2x	2	SI
S. iopetalum	4	6x	1.33	SC	*S. commersonii*	1	2x	1	SI
S. palustre	1	2x	1	SC	*S. gourlayi*	4	4x	2	SI
S. polyadenium	1	2x	1	SC	*S. infundibuliforme*	2	2x	2	SI
S. stoloniferum	2	4x	1	SC	*S. laxissimum*	2	2x	2	SI
S. verrucosum	2	2x	2	SC	*S. megistacrolobum*	2	2x	2	SI
S. moscopanum	4	6x	1.33	SC	*S. oplocense*	2	2x	2	SI
S. andreanum	2	2x	2	SC	*S. pinnatisectum*	1	2x	1	SI
S. hougasii	4	6x	1.33	SC	*S. raphanifolium*	2	2x	2	SI
S. guerreroense	4	6x	1.33	SC	*S. sparsipilum*	2	2x	2	SI
S. hjertingii	2	4x	1	SC	*S. stenotomum*	2	2x	2	SI
S. oxycarpum	2	4x	1	SC	*S. tuberosum*	4	4x	2	SI
S. agrimonifolium	2	4x	1	SC	*S. stenophyllidium*	1	2x	1	SI
S. colombianum	2	4x	1	SC	*S. santolallae*	2	2x	2	SI

Average EBN: 1.2

Average EBN: 1.72**

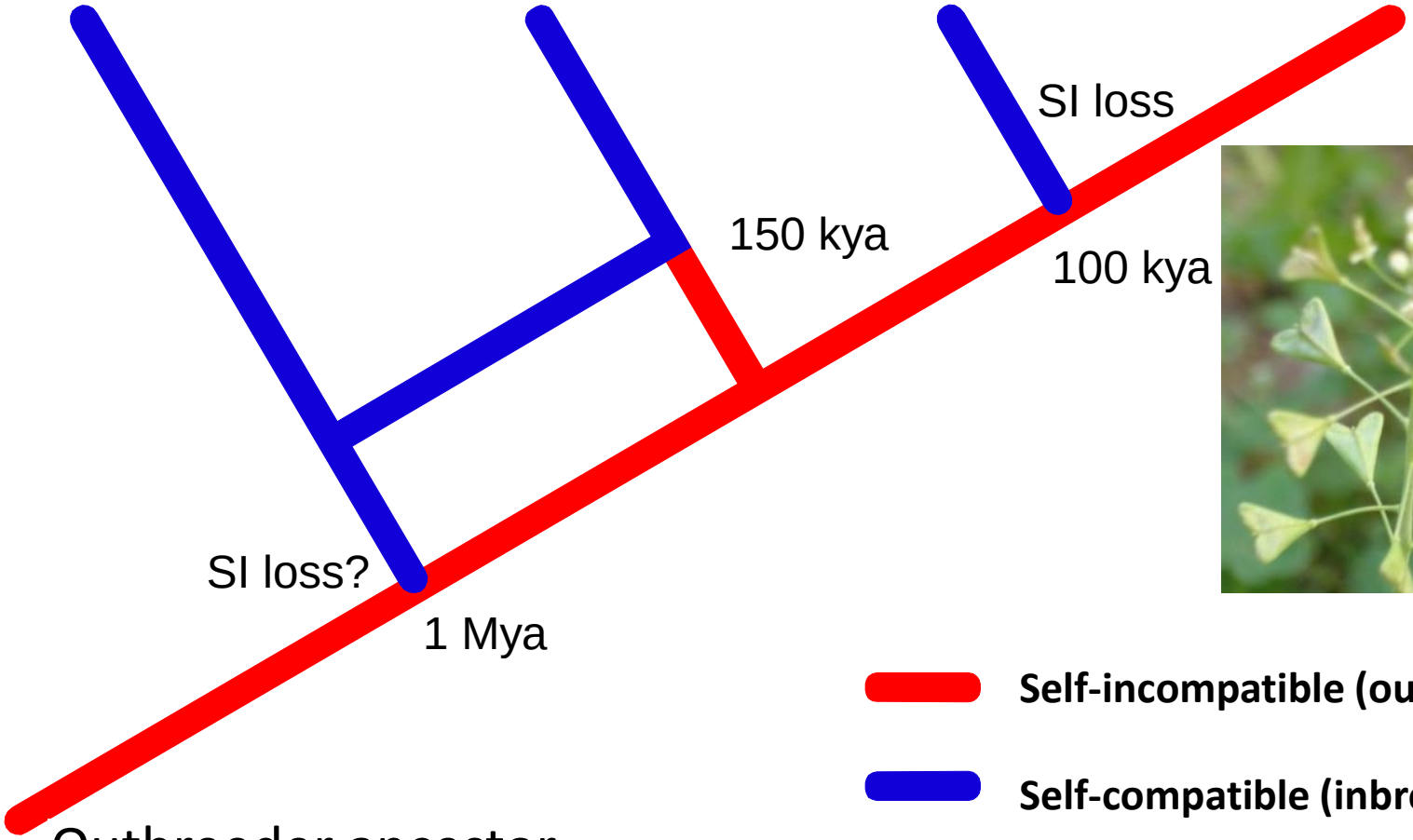
Lafon-Placette and Köhler, 2016

The *Capsella* genus




C. orientalis ***C. bursa-pastoris*** ***C. rubella*** ***C. grandiflora***

2*x* *4x* (allotetraploid) 2*x* 2*x*



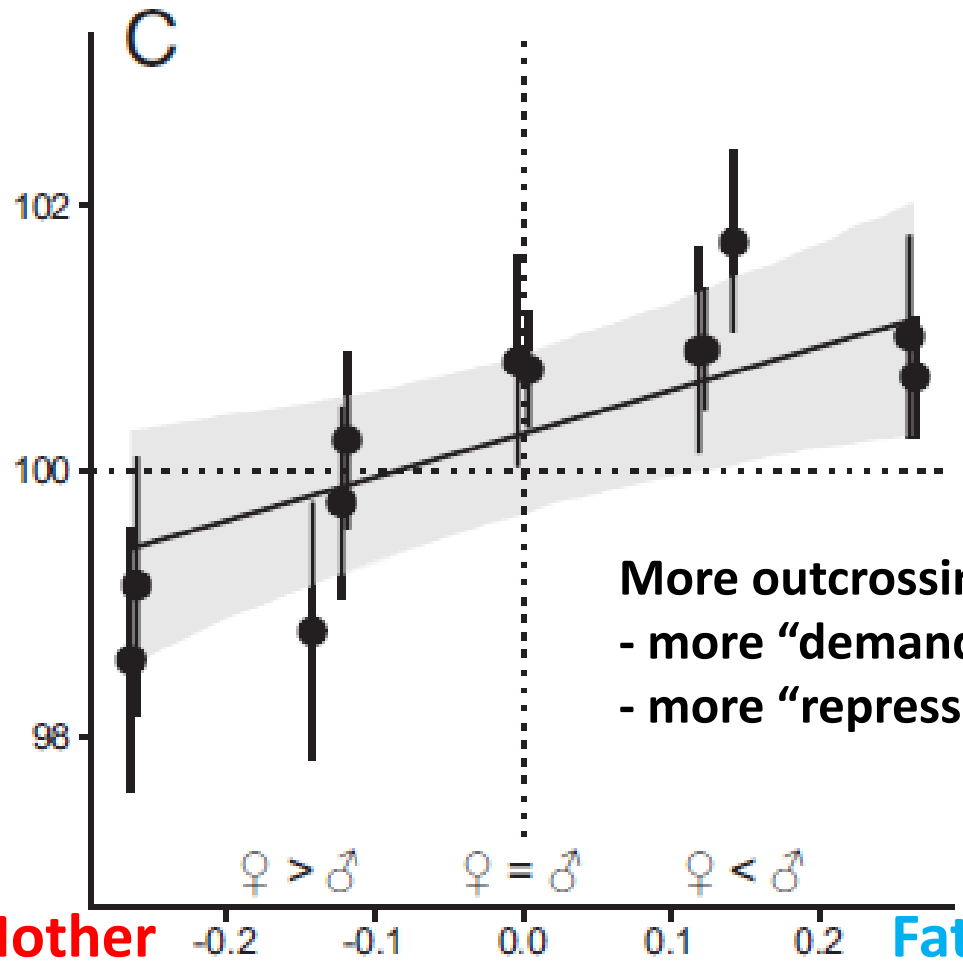
Self-incompatible (outbreeder)

Self-compatible (inbreeder)

Dalechampia scandens

Seems like a continuous phenomenon

Mixed-mating populations, with a range of outcrossing rates



More outcrossing =
- more "demanding" fathers
- more "repressive" mothers

Raunsgard et al., 2018

Not only outbreeder vs inbreeder

***A. lyrata*, 2x**

×

***A. arenosa*, 2x**

=

Hybrid

***A. arenosa*, 2x**

×

***A. lyrata*, 2x**

=

Hybrid

Lafon-Placette et al., 2018

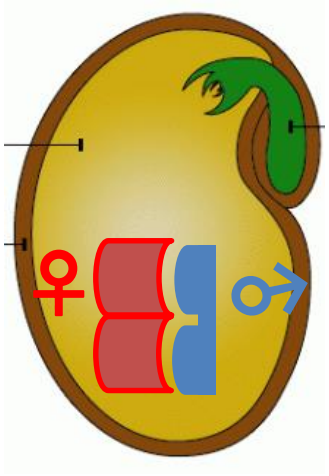



The Endosperm Balance Number (EBN) hypothesis

Johnston et al. 1980

chromosomes × 2
(drug induced)


***Solanum brevidens*, 2x**
EBN = 1



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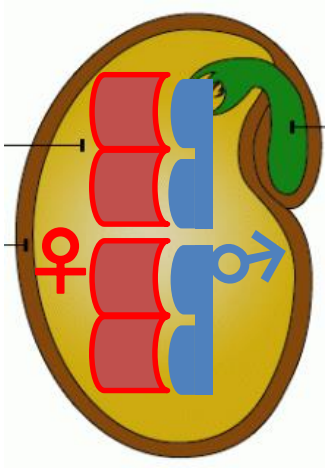
***S. stenotonum*, 2x**
EBN = 2



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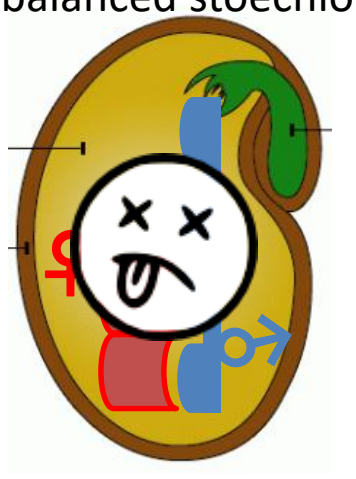
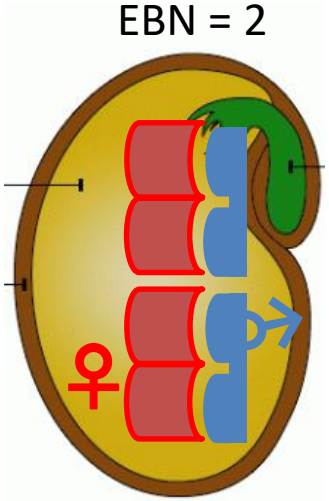
Hybrid seed, 2x
Imbalanced stoechiometry



***S. brevidens*, 4x**
EBN = 2



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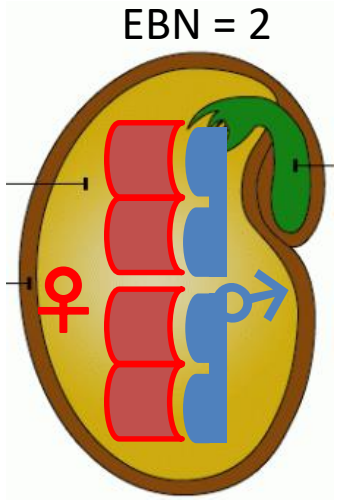
***S. stenotonum*, 2x**
EBN = 2



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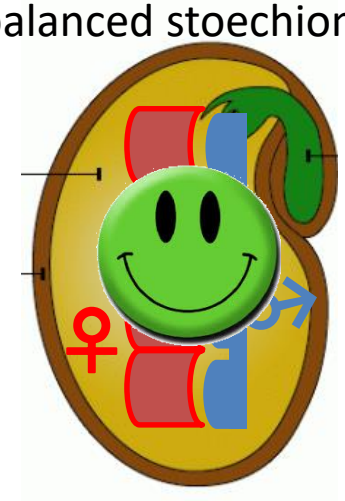
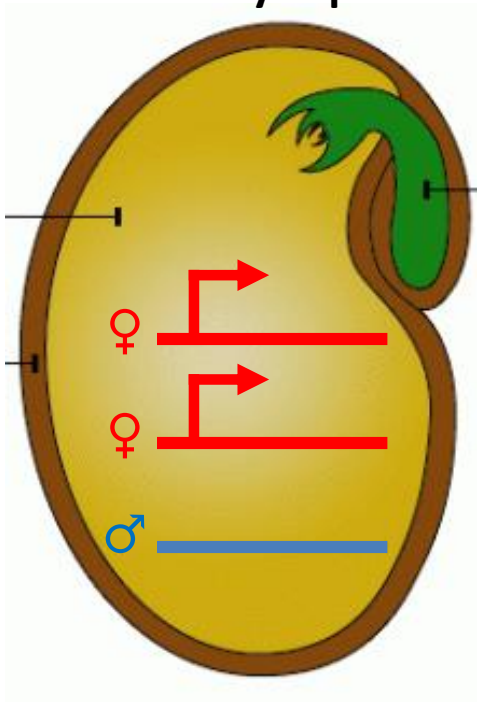
Hybrid seed, 3x
balanced stoechiometry



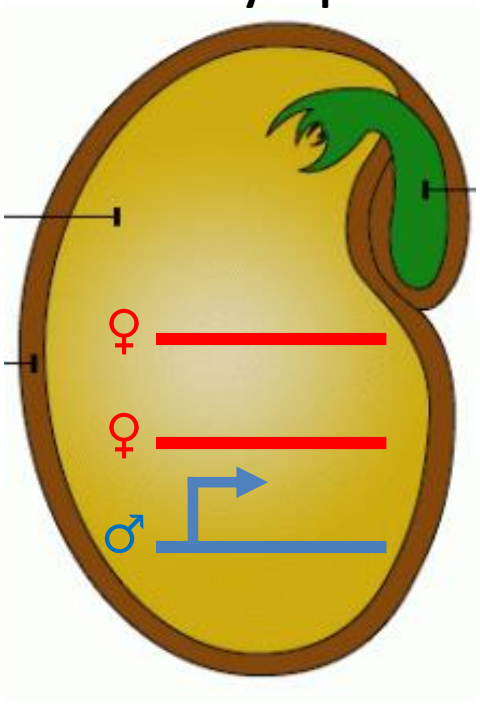
Is genomic imprinting involved?

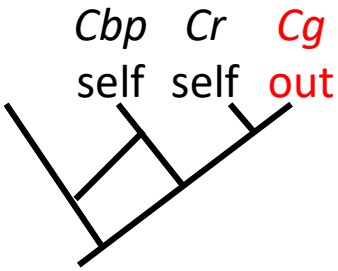
Genomic imprinting is the epigenetic phenomenon by which certain genes are expressed in a parent-of-origin-specific manner

Maternally expressed



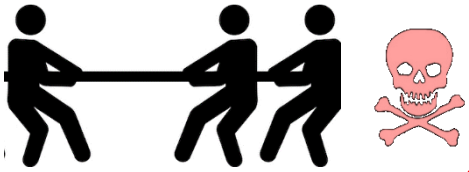
Paternally expressed



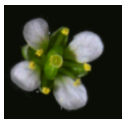


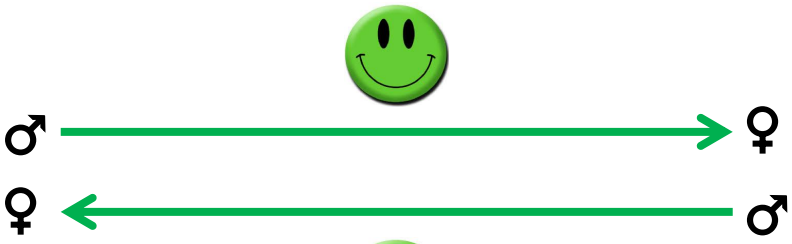
Bizarre love triangle

C. grandiflora
2*x*
outcrosser



C. bursa-pastoris
4*x*
selfer





C. rubella
2*x*
selfer