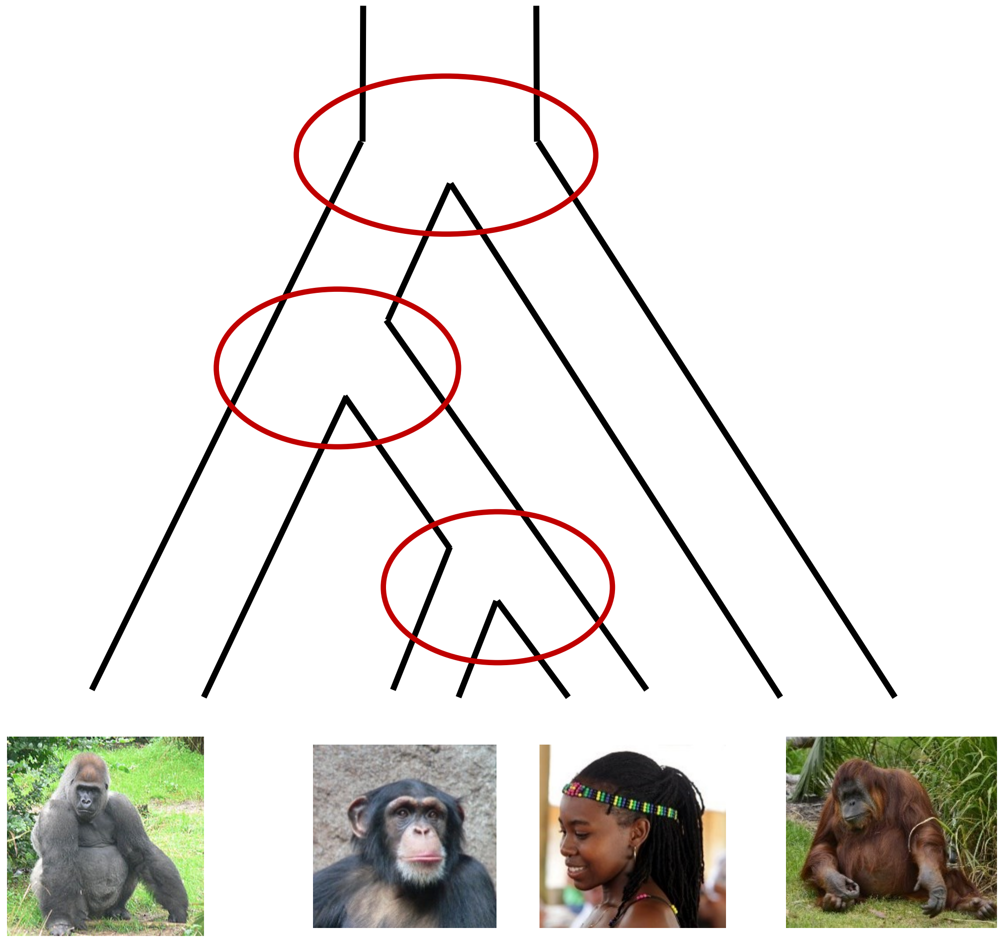
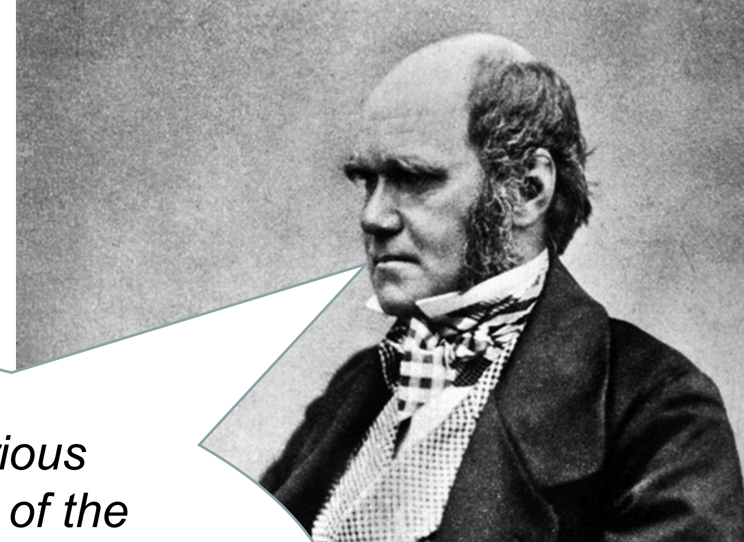
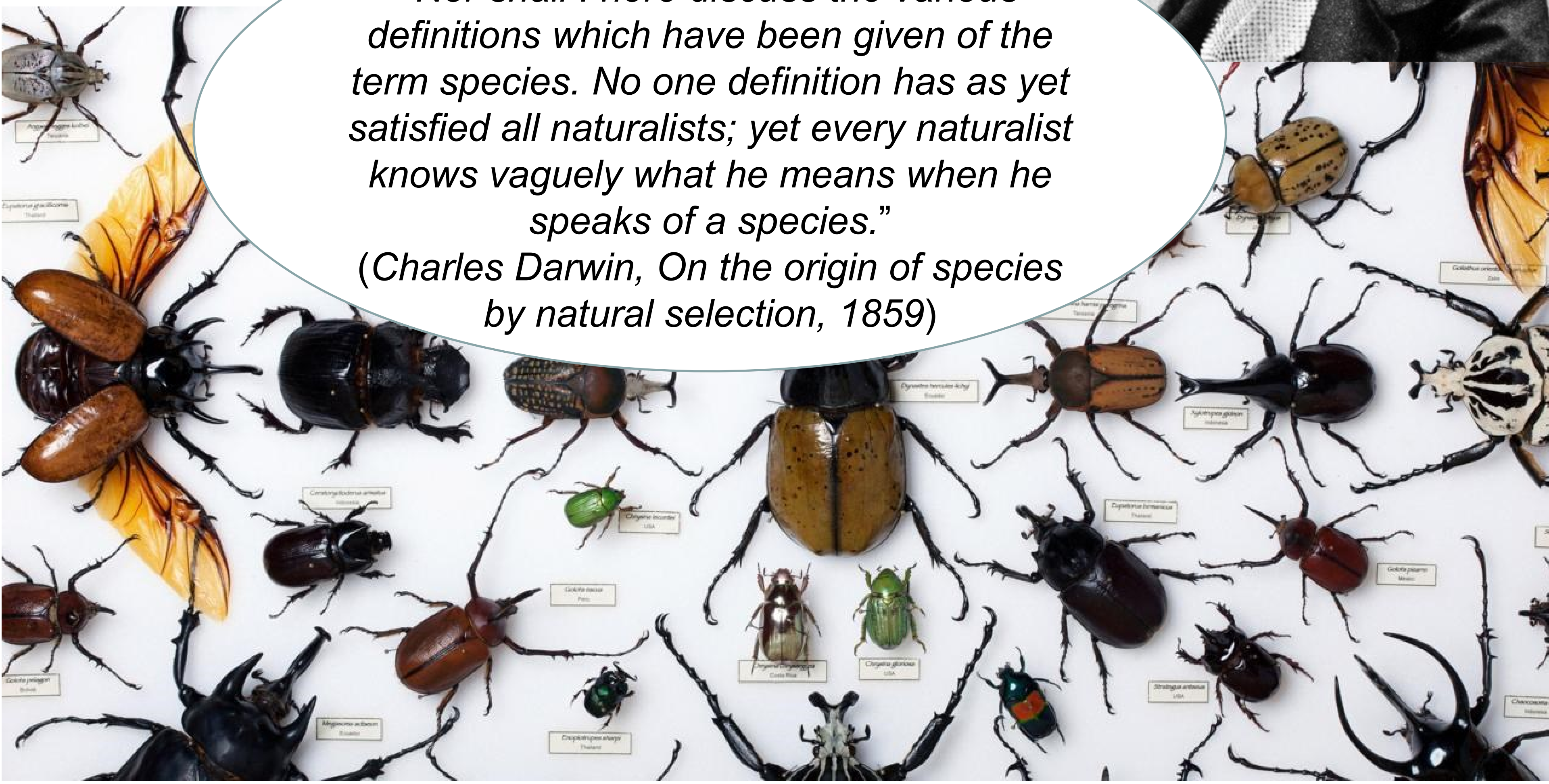
Speciation



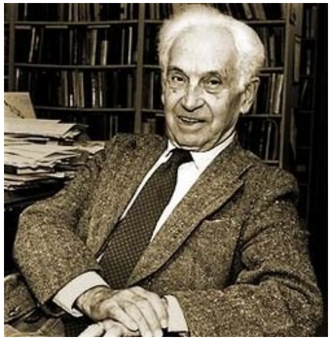
Biological diversity is discontinuous.
Species objectively exist.
But how to define them?





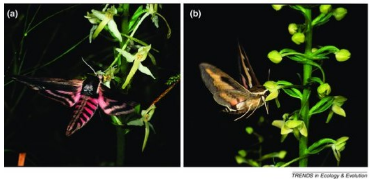
“Nor shall I here discuss the various definitions which have been given of the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species.”
(*Charles Darwin, On the origin of species by natural selection, 1859*)

What is species?



Biological species concept (Ernst Mayr, 1942)

- A group of organisms that can successfully interbreed and produce fertile offspring. A species' integrity is maintained by interbreeding within a species as well as by reproductive barriers between organisms in different species.



Reproductive isolation
- prezygotic
  - precopulatory
  - postcopulatory
- postzygotic
  - intrinsic (sterility and inviability of hybrids)
  - extrinsic

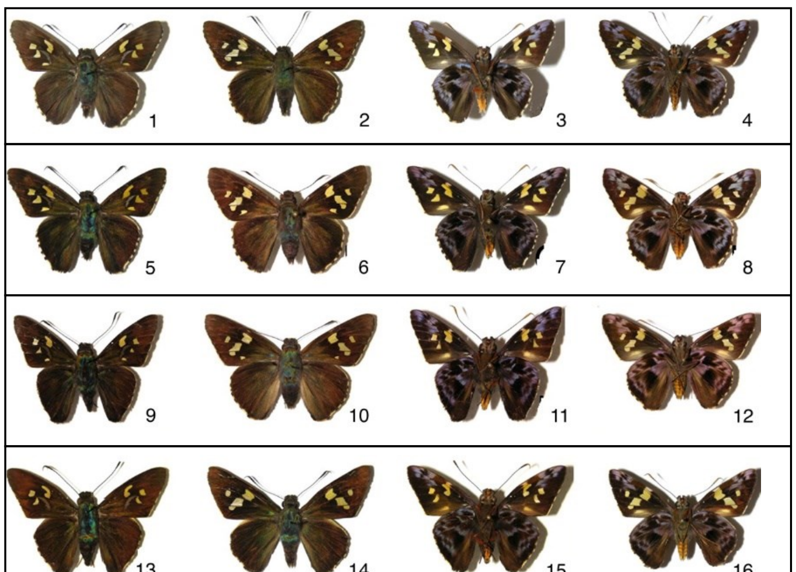
Morphological species concept

Groups of individuals that are morphologically similar to one another and are morphologically distinct from other such groups..

Cryptic species

dorsal ventral

M F M F



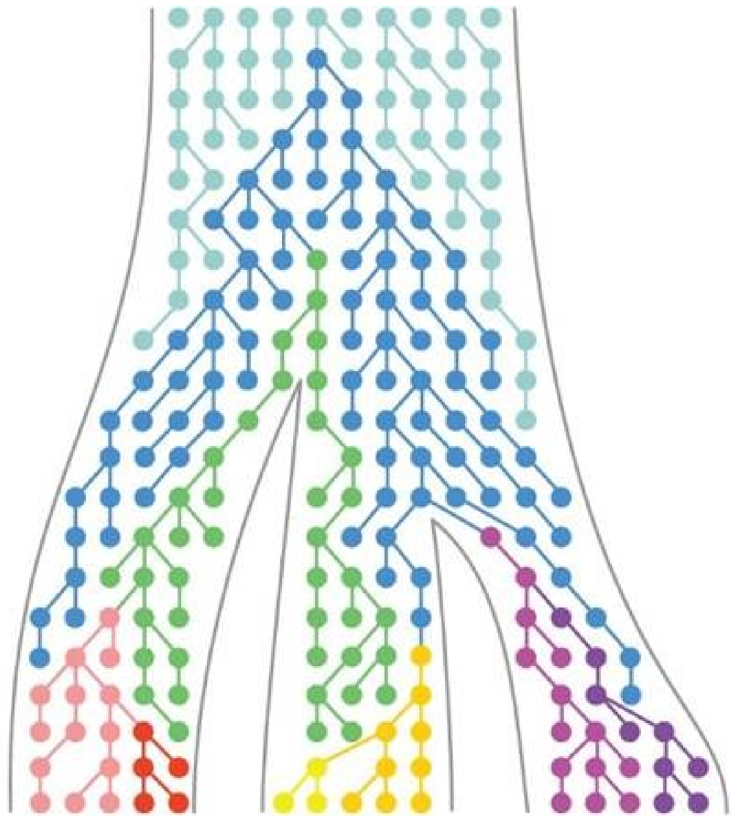
Four cryptic species of *Perichares* butterflies

Polytypic species

The western yellow wagtail (***Motacilla flava***)

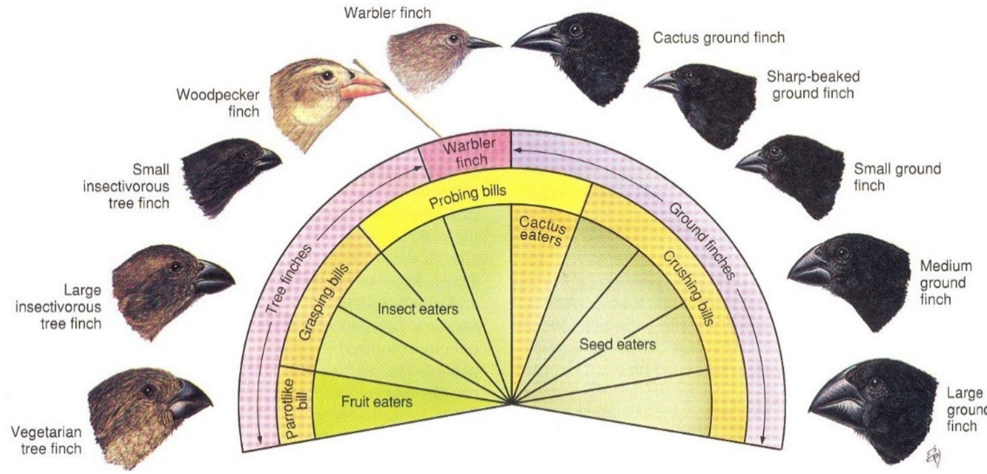
Genealogical/phylogenetic species concept

A group of organisms whose members are all more closely related to each other than they are to any organisms outside the group and share a unique common ancestor.

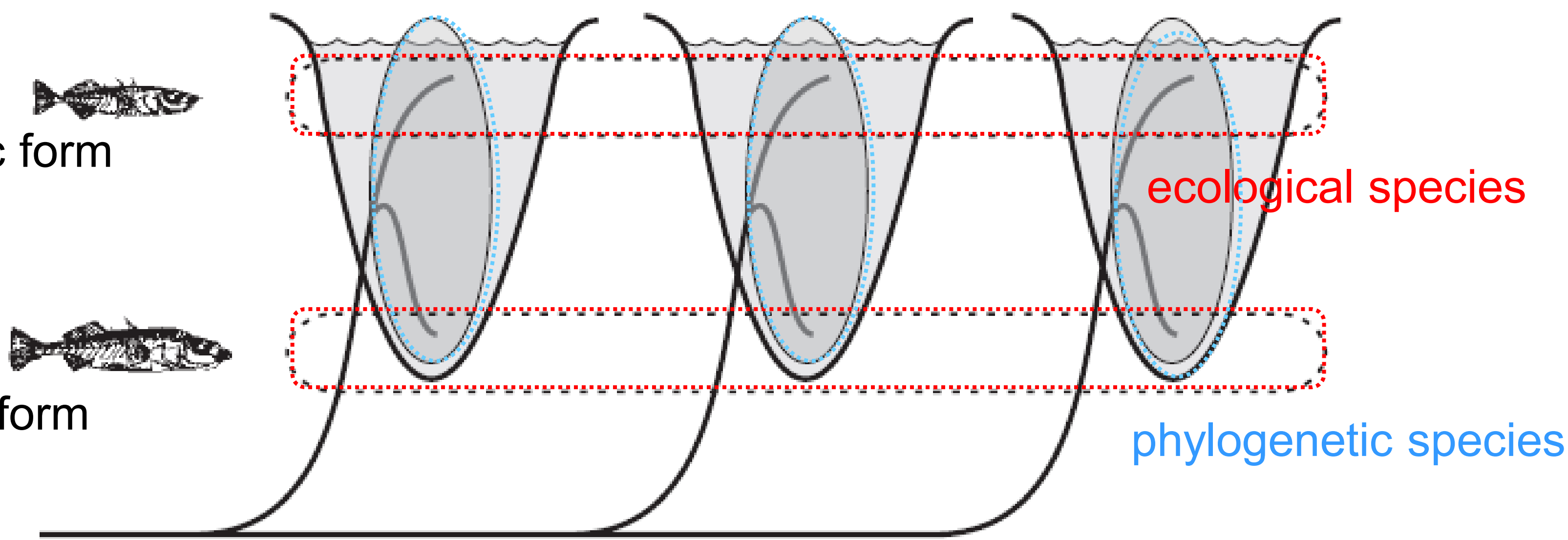


Ecological species concept

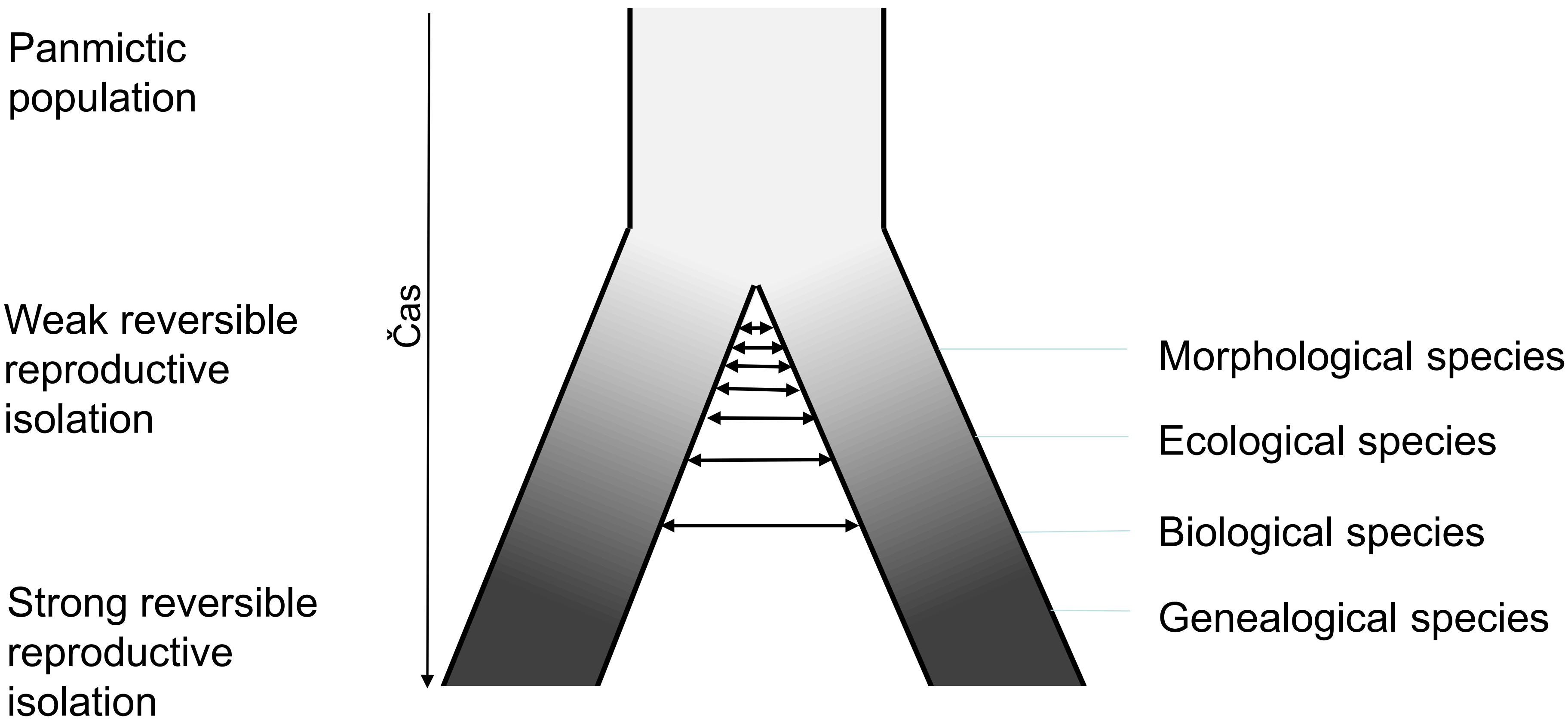
A goup of organisms that share the ecological niche.



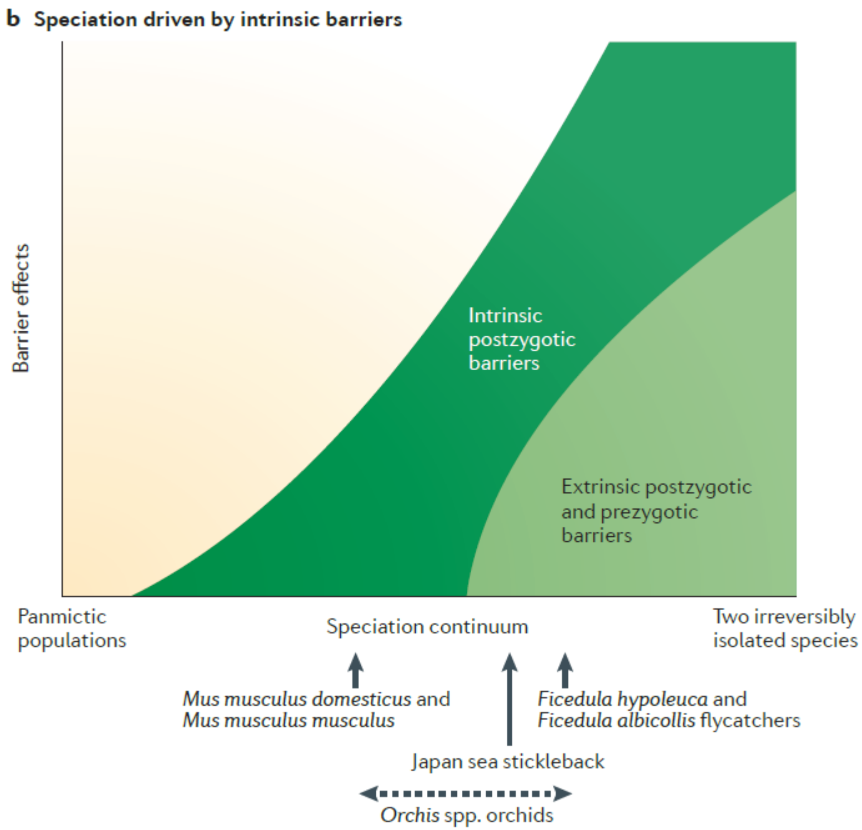
Three-spined stickleback

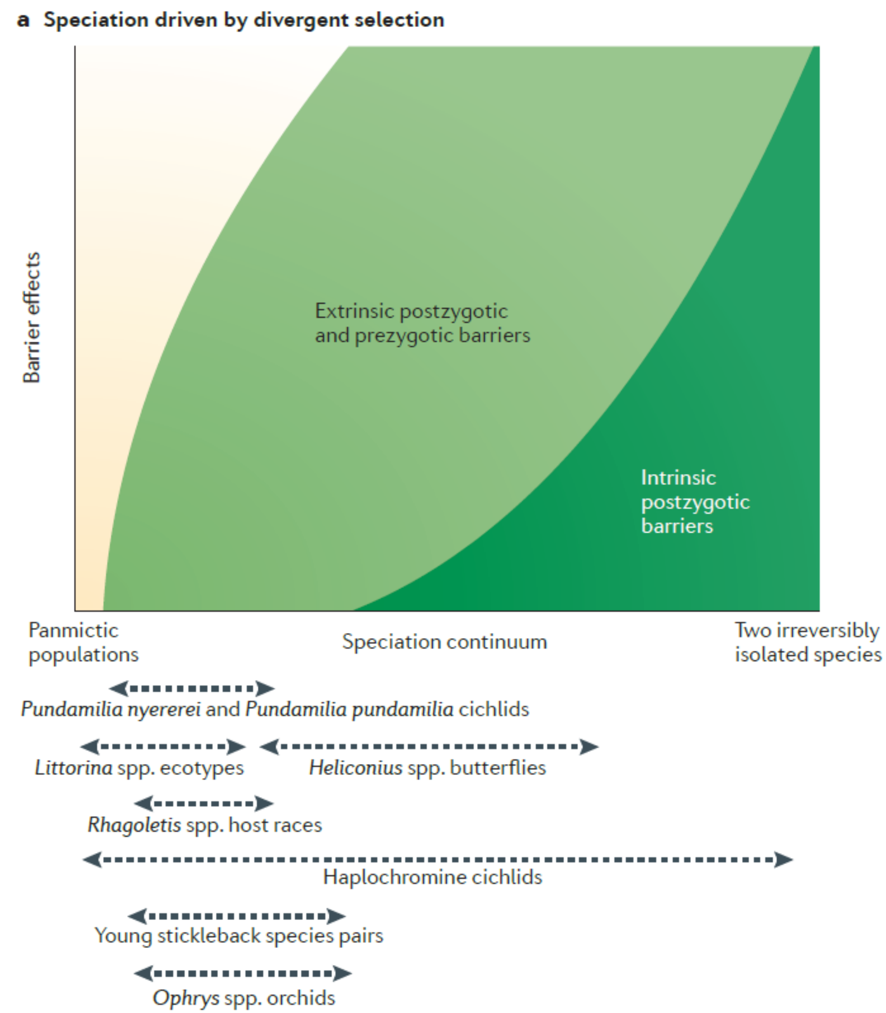


Speciation continuum

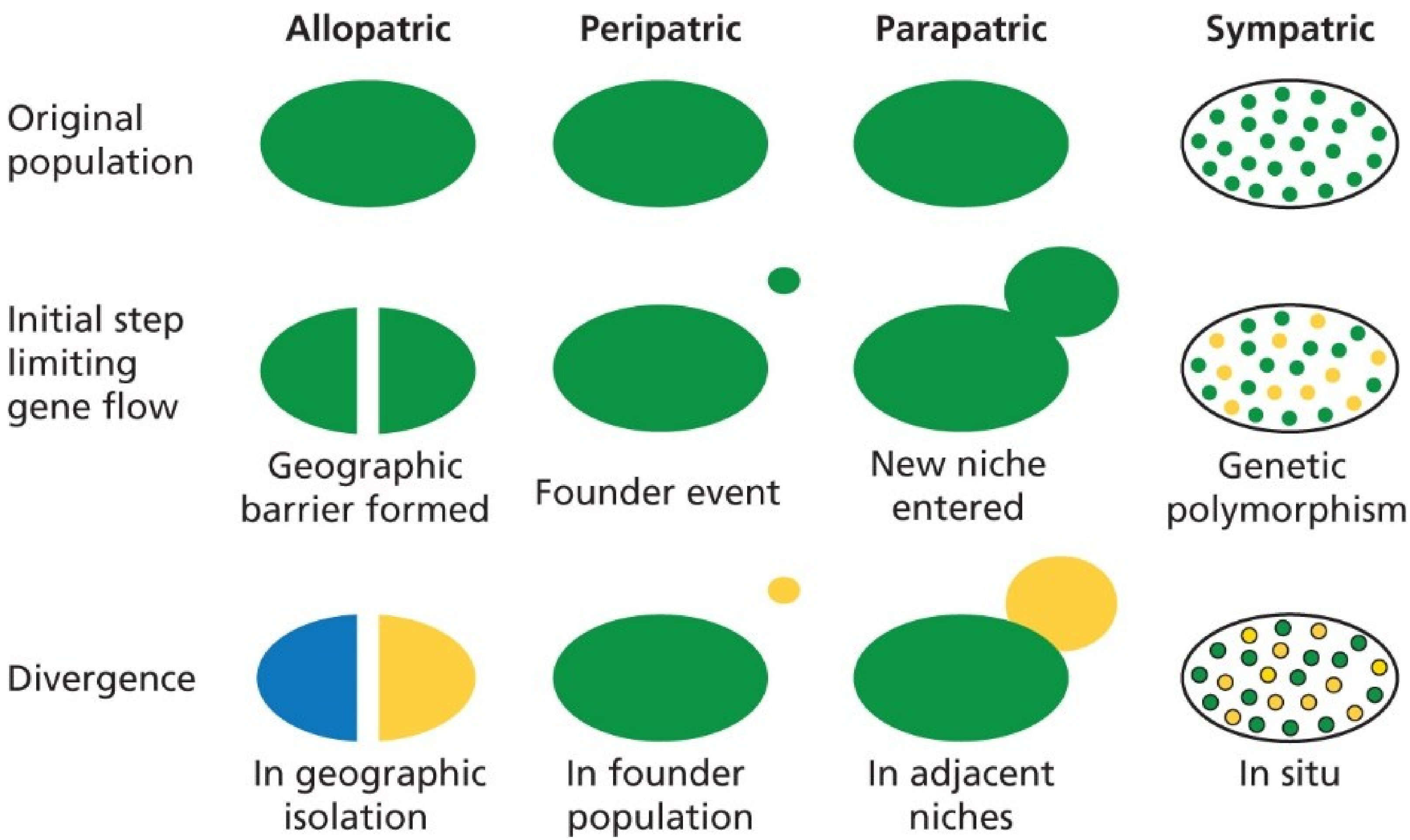


Speciation driven by intrinsic barriers vs. speciation driven by extrinsic postzygotic and prezygotic barriers (ecological speciation and speciation by sexual selection)



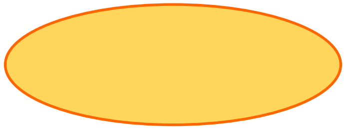


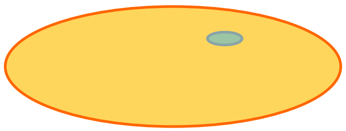
Speciation



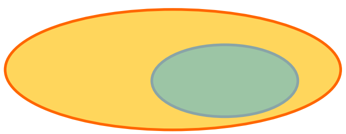
Allopatric
Peripatric
Parapatric
Sympatric
Original population
Initial step limiting gene flow
Geographic barrier formed
Founder event
New niche entered
Genetic polymorphism
Divergence
In geographic isolation
In founder population
In adjacent niches
In situ

Sympatric speciation

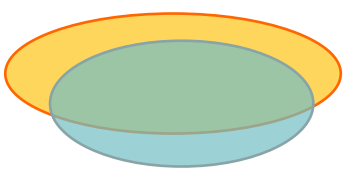




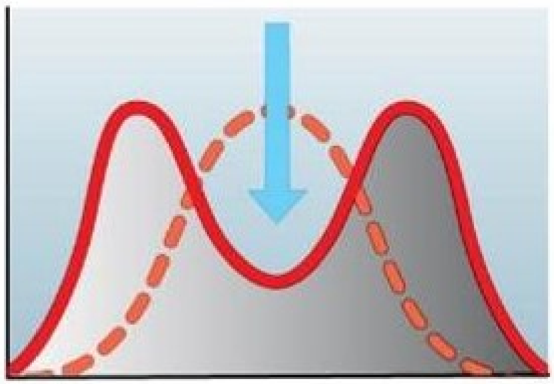
Genetic polymorphism



Reproductive isolation arise in the face of gene flow in sympatry



Charles Darwin

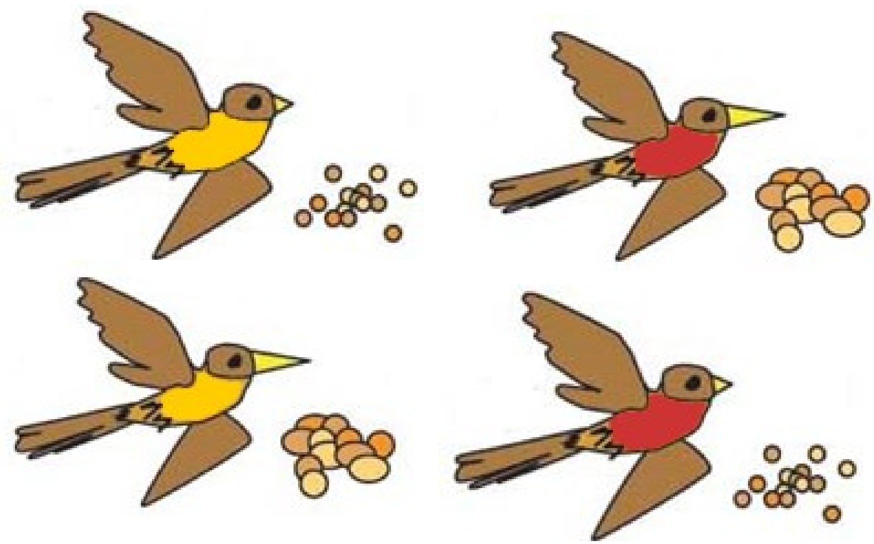


Disruptive selection

Assortative mating

Problems with sympatric speciation

Recombination between genes for:
(1) ecological traits under disruptive selection,
(2) female preferences

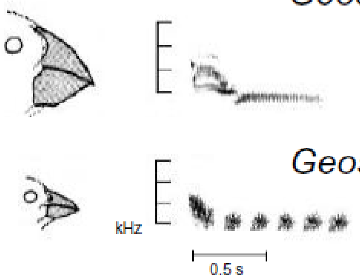


vrtule (*Rhagoletis pomonella*)

Magic traits

Geospiza magnirostris

Geospiza fuliginosa



Sympatric speciation

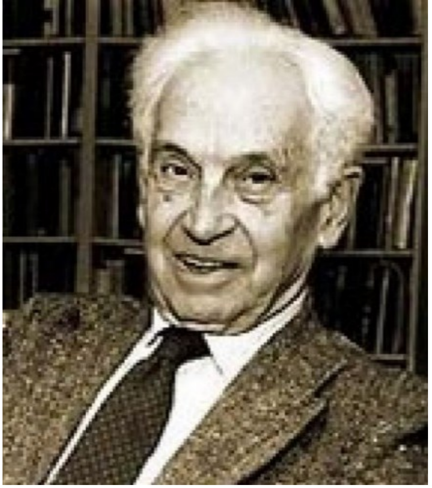
Two palm species on the isand of lord Howa in Pacific.

Savolainen et al. (2006), Nature.

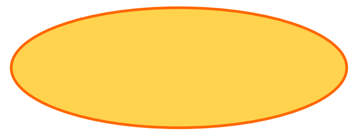
Cichlids in crater lakes

Barluenga et al. (2006), Nature.

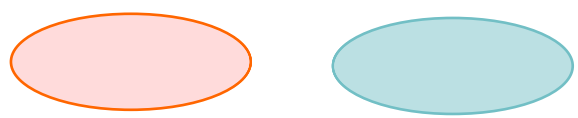
Allopatric speciation



Ernst Mayr

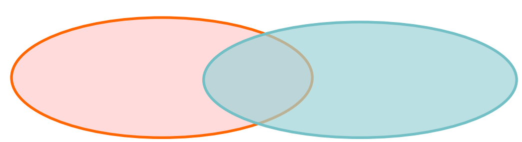


Geographic barrier

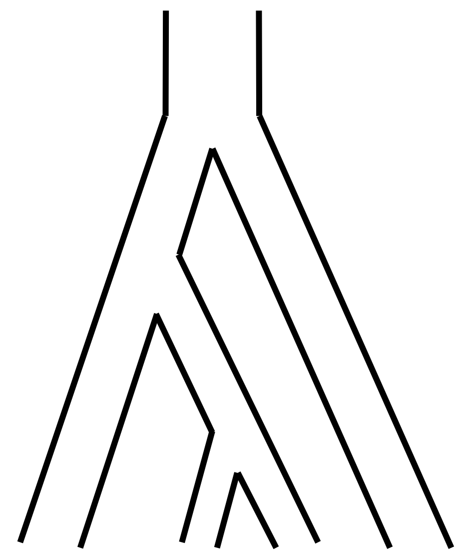


Reproductive barrier arise without gene flow in allopatry

After secondary contact species do not interbreed or produce sterile or inviable hybrid progeny

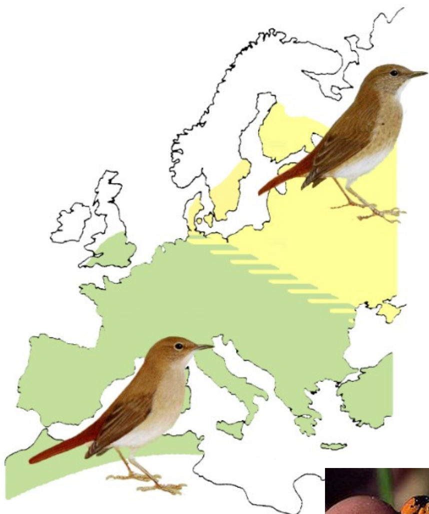


Divergence without gene flow

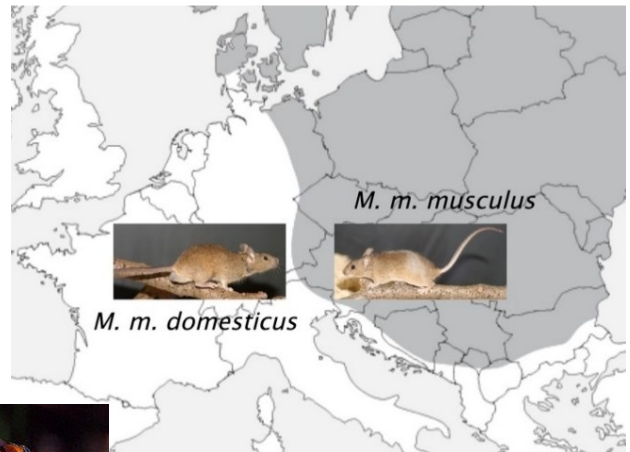


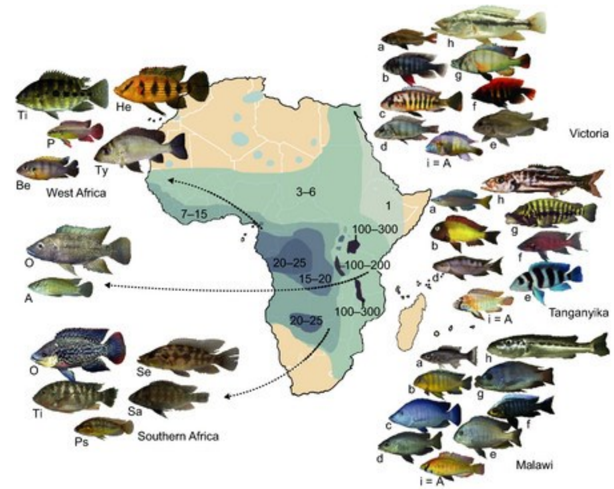
Interspecific hybridization after secondary contact

Luscinia megarhynchos
Luscinia luscinia



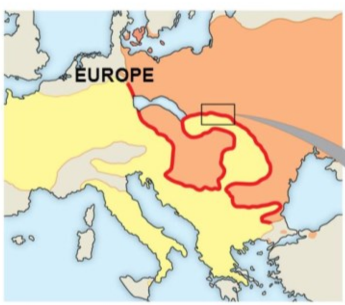
Mus musculus domesticus
Mus musculus musculus

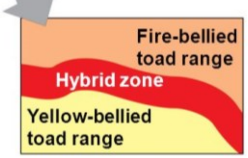




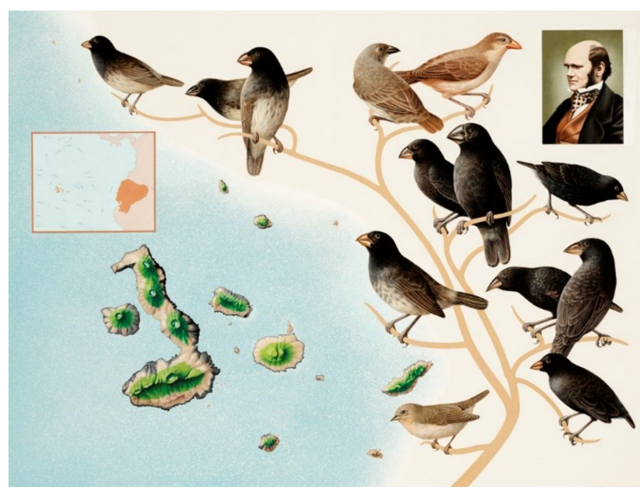
Cichlids

Bombina bombina
Bombina variegata

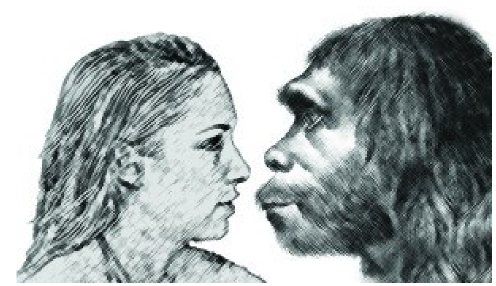




Darwin Finches

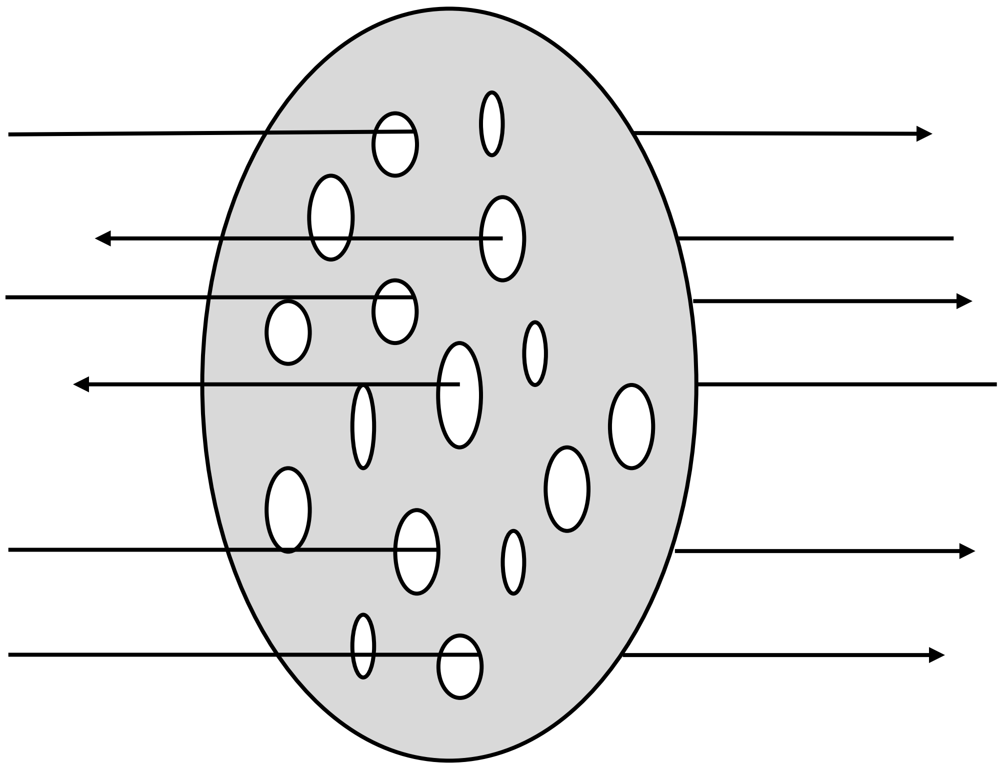


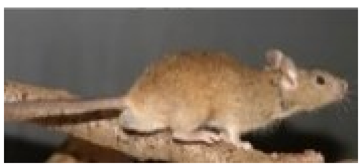
Homo sapiens
Homo neanderthalensis



Semi-permeable species boundary

species 1



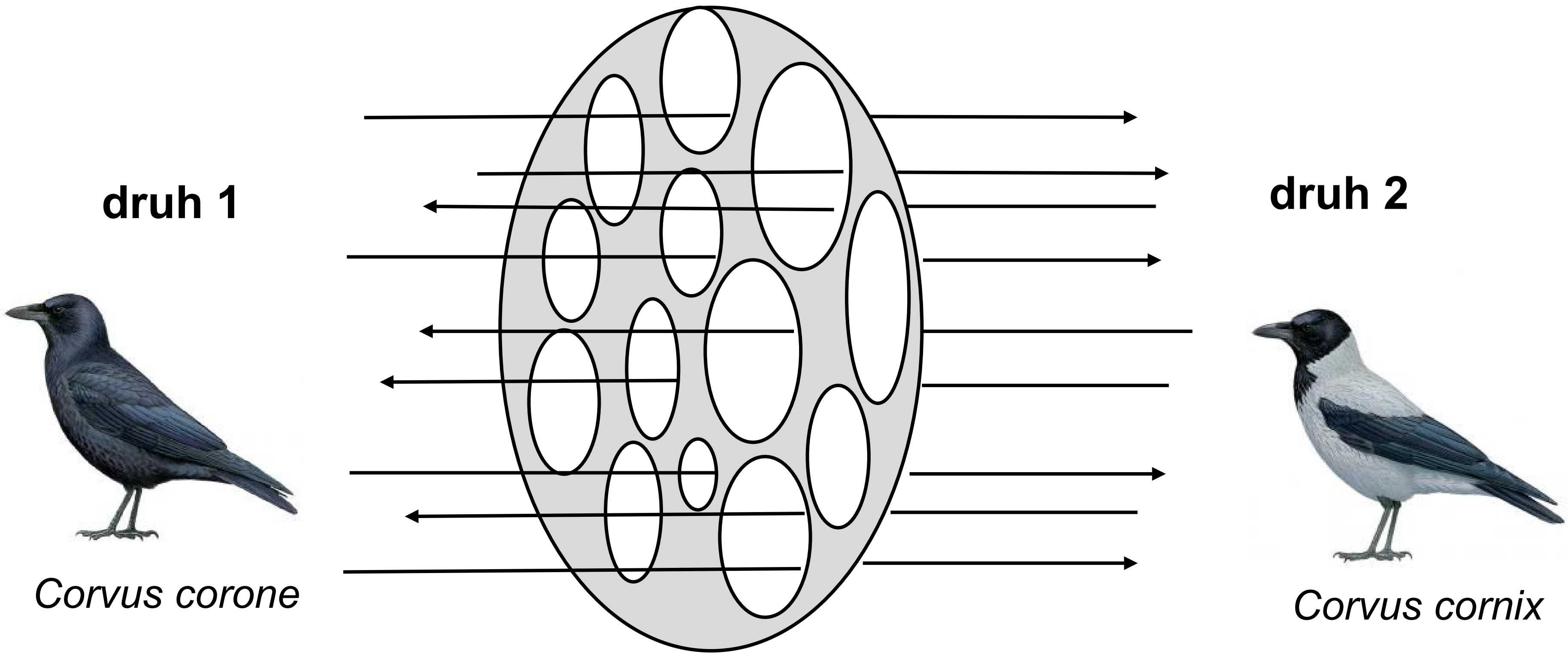


M. m. domesticus

species 2

M. m. musculus

Semi-permeable species boundary

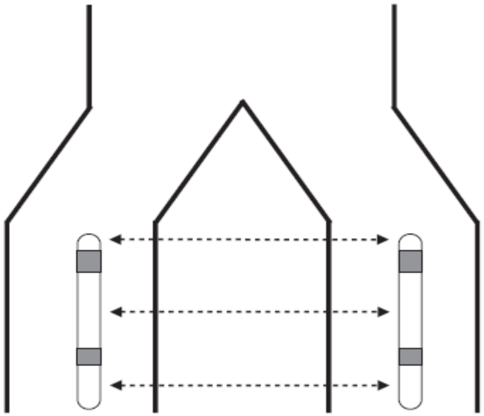


Genic species concept (Chung-I Wu, 2001)

- Reproductive isolation can be underlined by small part of the genome.
- Species as a coadapted gene complexes.

Speciation islands

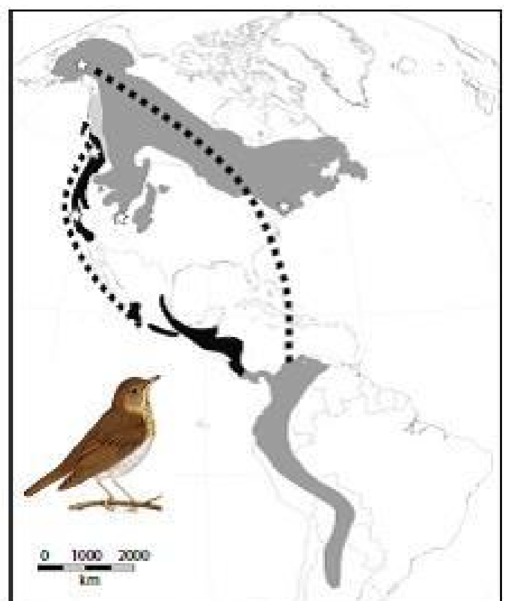
Increase in F_{ST} a D_{XY}

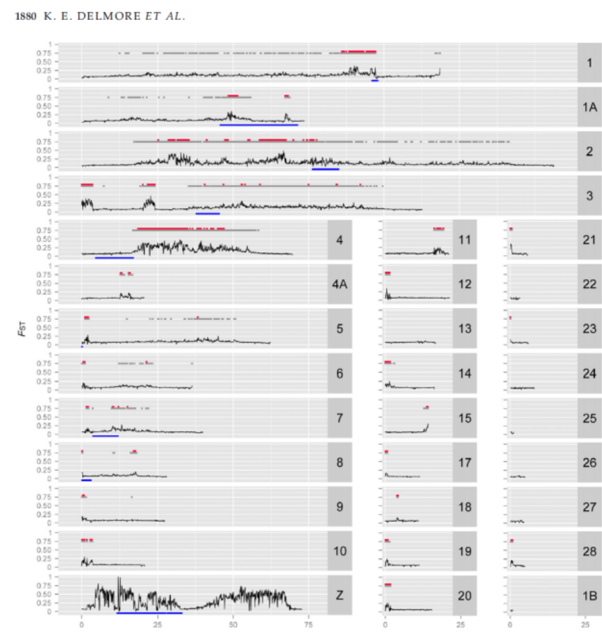


Speciation-with-gene-flow

Migration homogenizes much of the genome

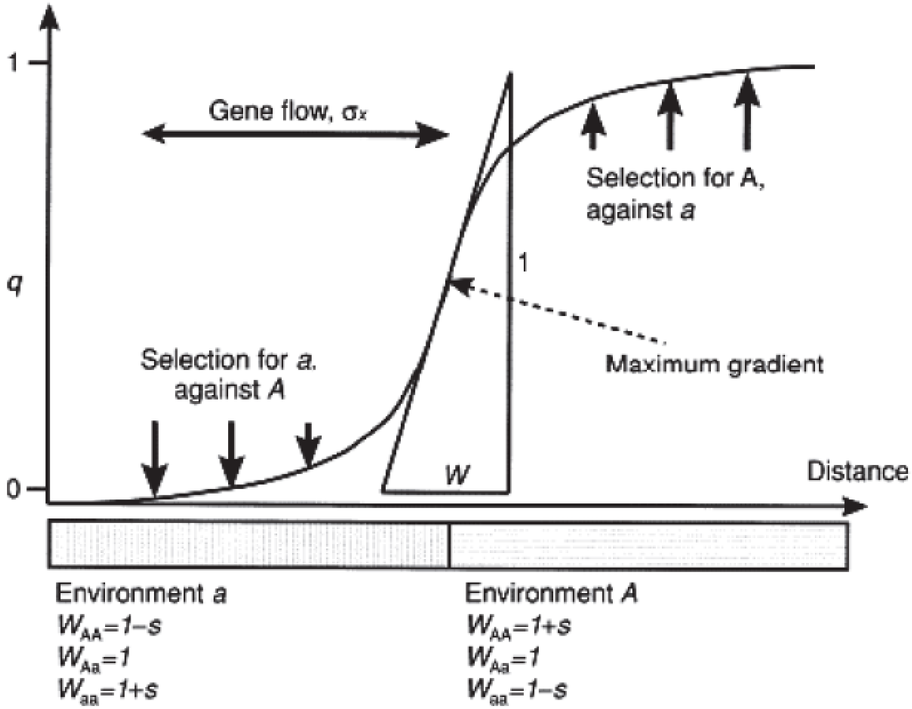
Swainson's Thrush

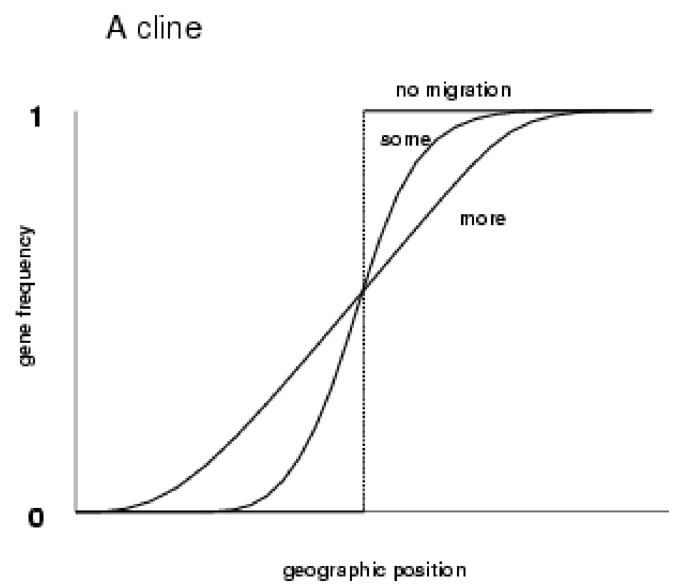




Delmore et al. 2015. Mol.Ecol.

Geographic clines

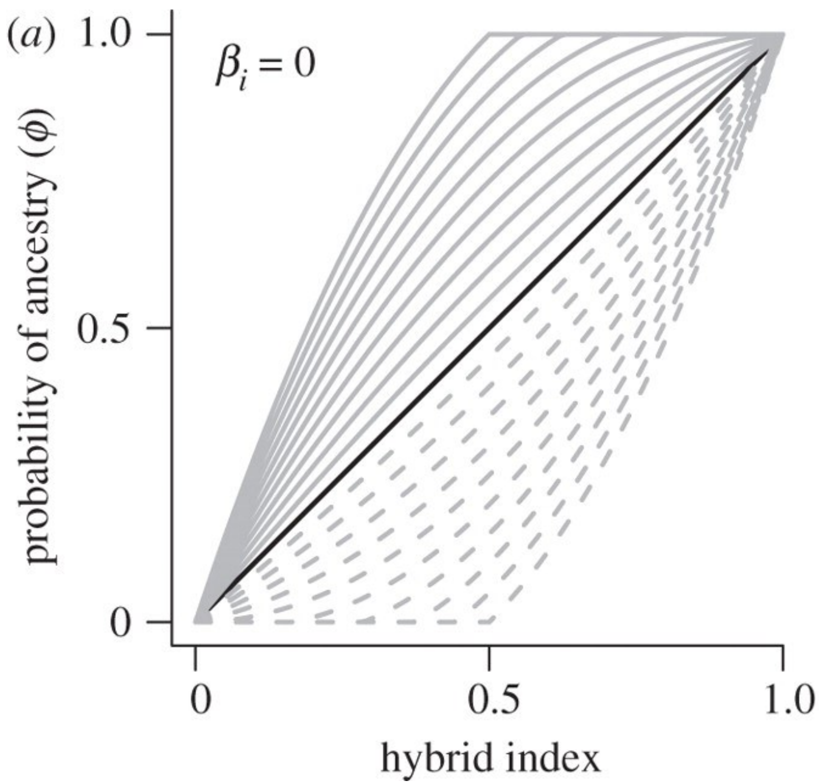


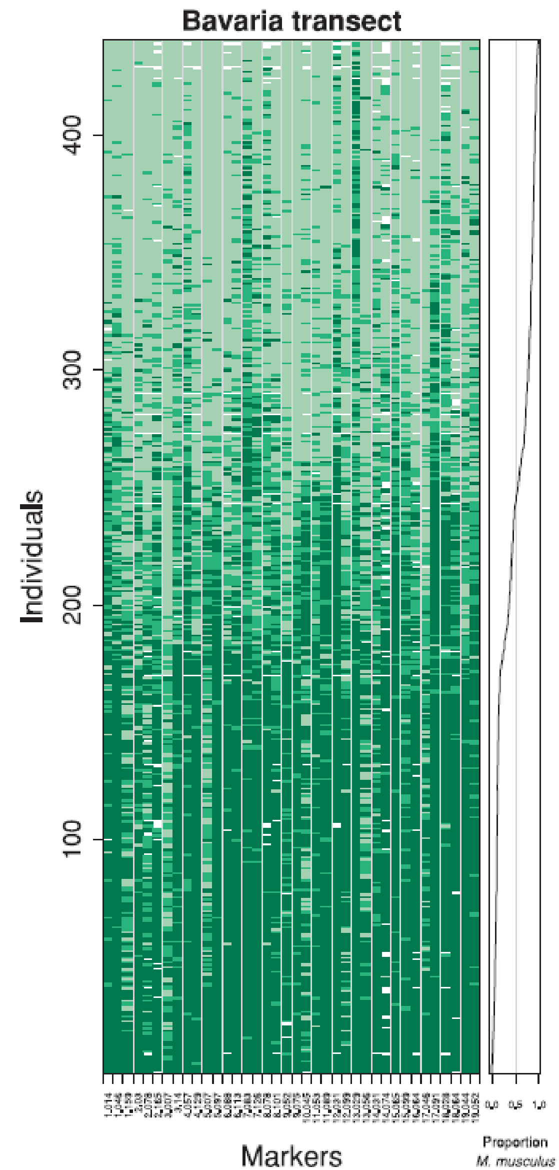


- measure the movement of alleles across hybrid zones.
- Enable to compare levels of introgression for different markers.

Genomic clines

- Measure the movement of alleles into different genomic backgrounds.

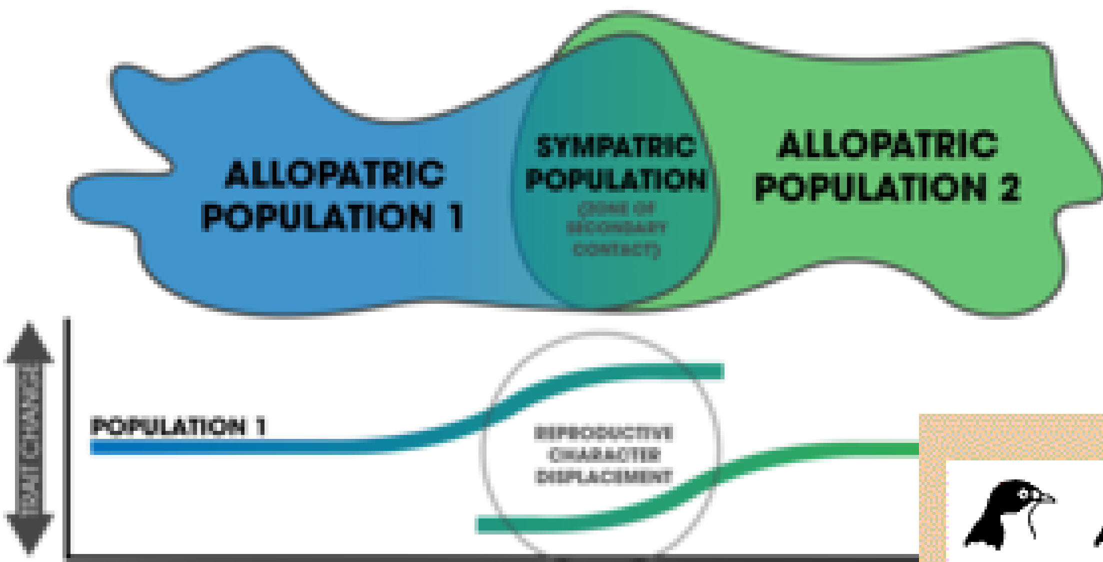


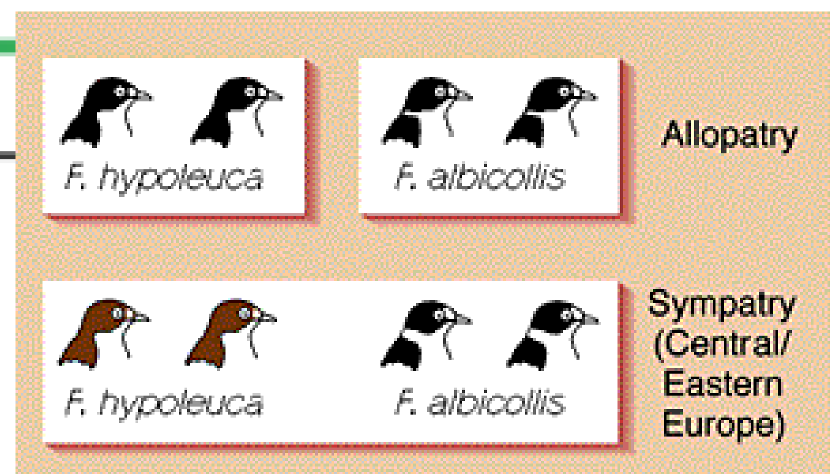


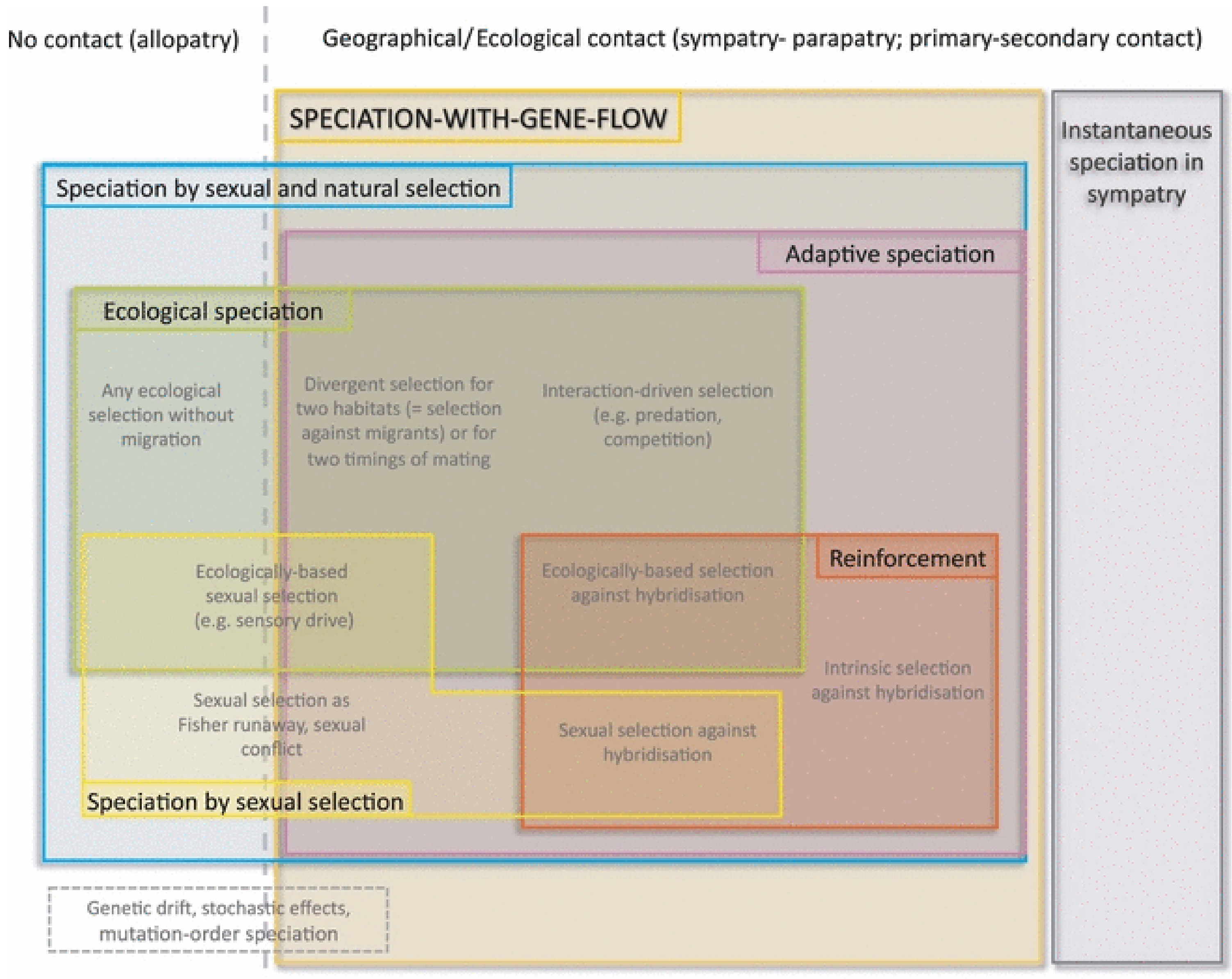
How to complete speciation after secondary contact

Reinforcement

- Origin of prezygotic barrier due to selection against hybridization

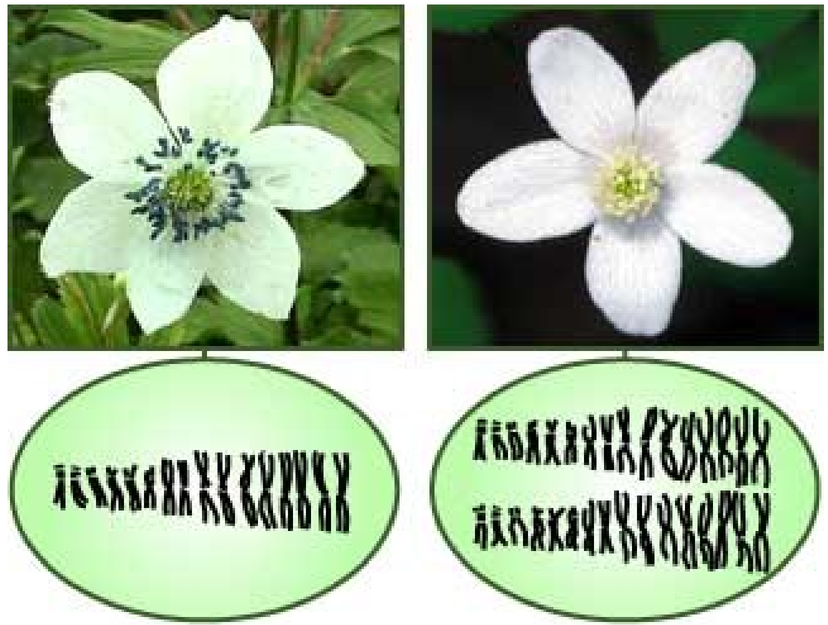






Smadja and Butlin. MolEcol. 2011

Instantaneous sympatric speciation by polyploidization

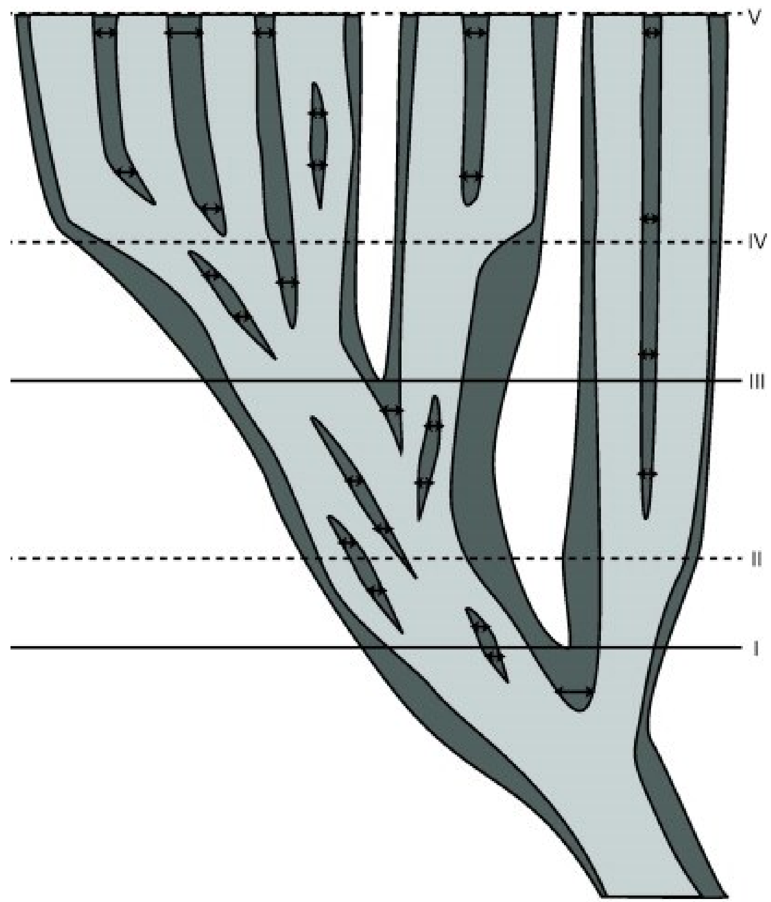


2n 4n

- Whole genome duliplication will instantaneously create reproductive isolation betwen 2n and 4n plants as 3n hybrids will be sterile.

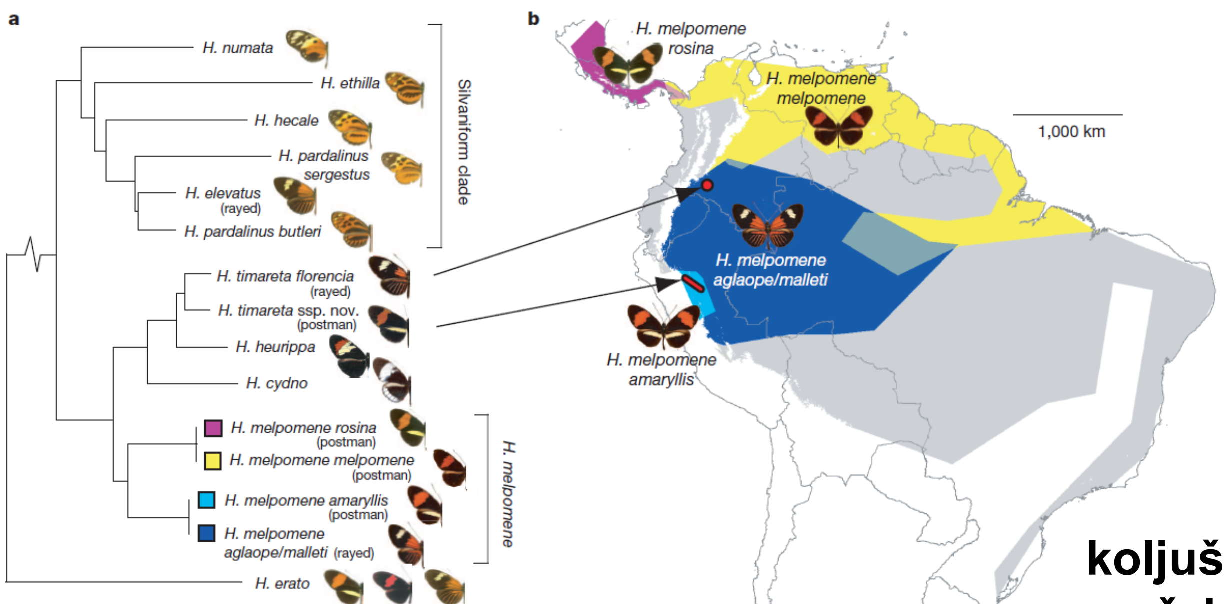
Divergence with gene flow

- Evolution of complete reproductive isolation is often a slow process.
- Many closely related species are not fully reproductively isolated.
- Species in various stages of origin



Evolutionary consequences of interspecific hybridization

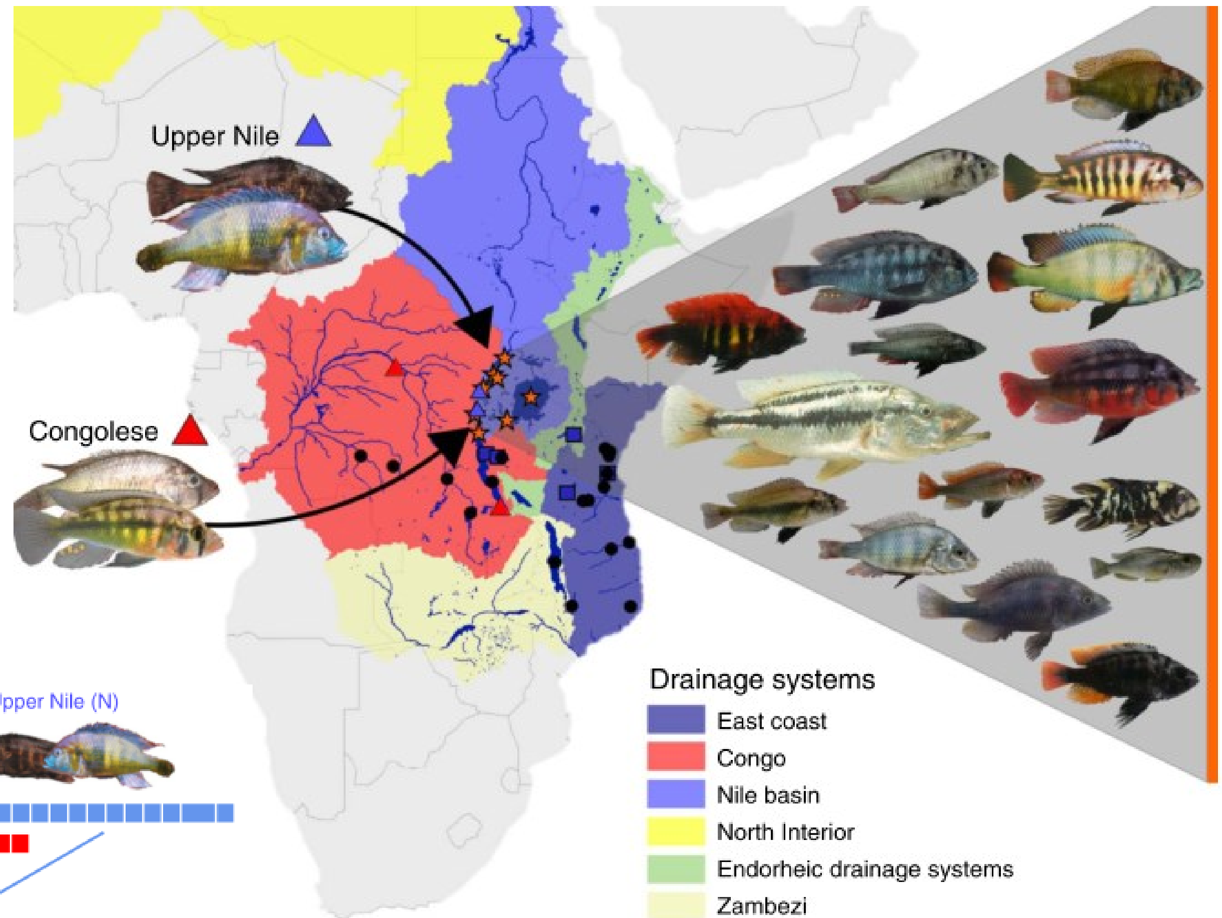
Important source of genetic variation, speed up adaptive evolution
Paralel evolution

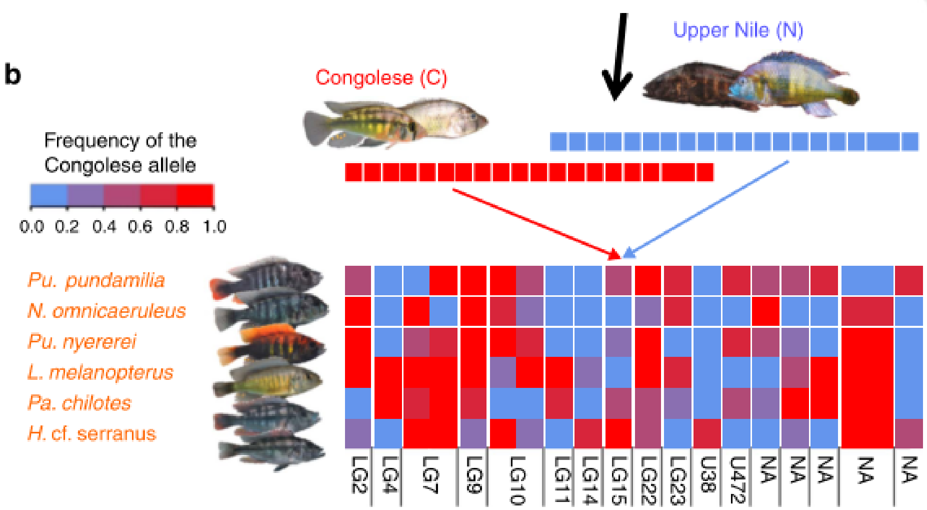


koljuška tříostná, forma mořská (nahoře) a říční (dole)

Facilitates adaptive radiation

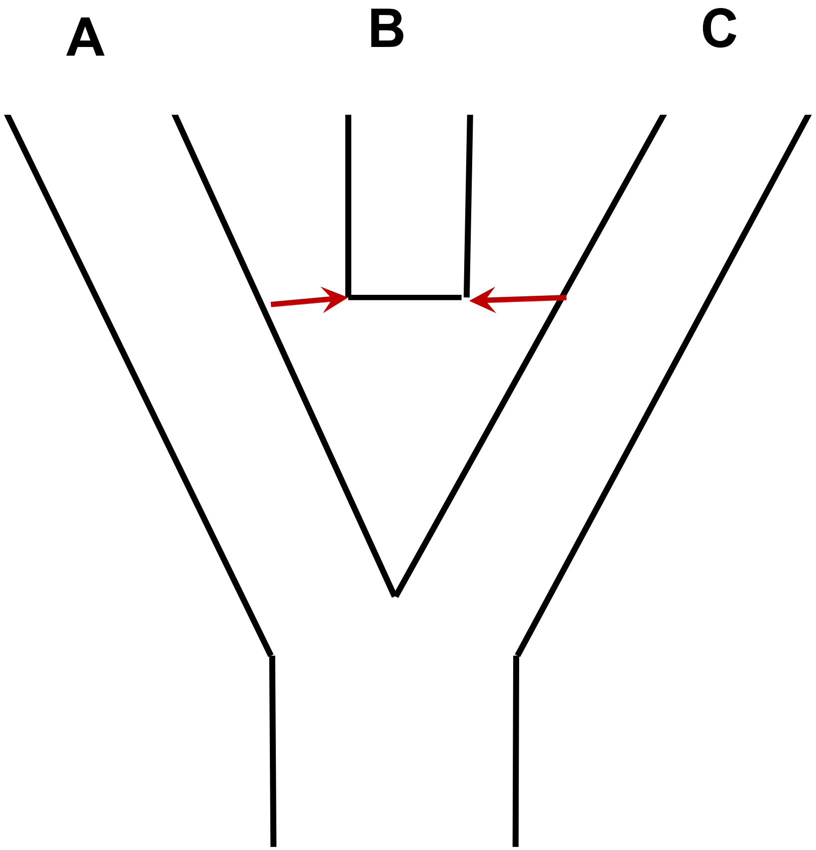
- Mixing up genetic variation





Meier, et al. 2017 *Nat. Comm.*

Hybridization can lead to the origin of new hybrid species

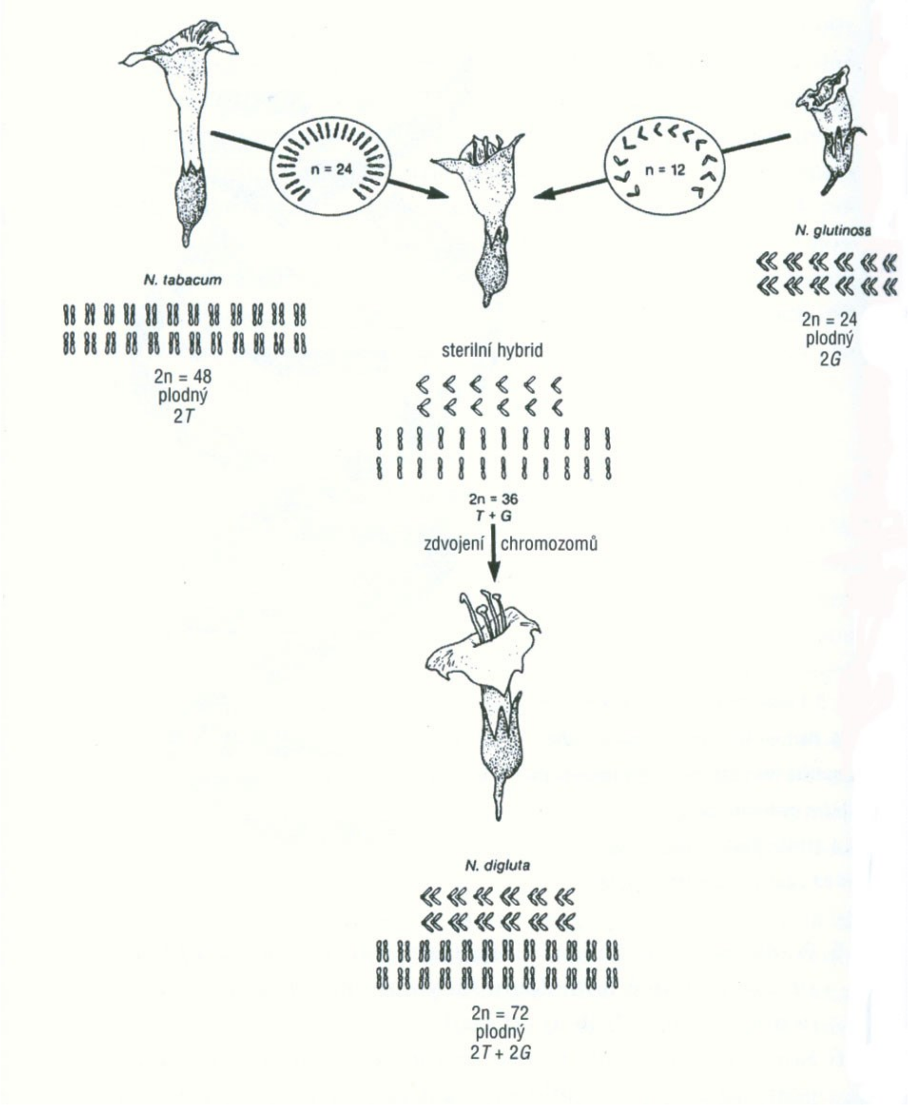


Polyploid hybrid speciation

- Whole genome duplication in hybrid.
- Will restore the fertility of hybrids.

At the same time will create reproductive barrier between hybrid and parental species.

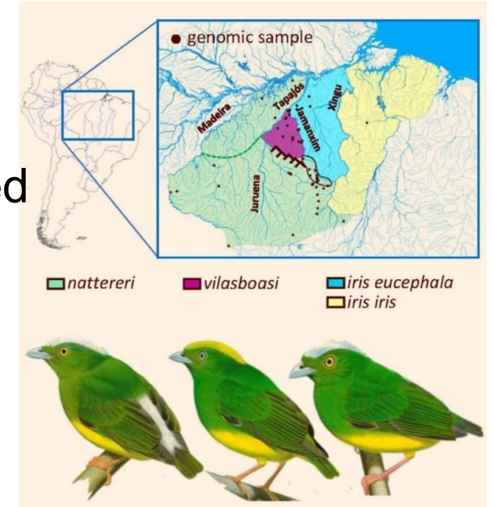
- ~ 15% of angiosperm plants originated by polyploid hybrid speciation.

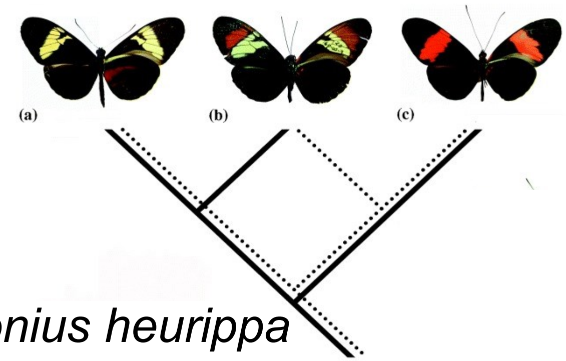


Homoploid hybrid speciation

- Without changes in ploidy.
- Reproductive isolation between parental species and hybrid species can arise if hybrids have different phenotype, occupy different ecological niche or are geographically isolated.

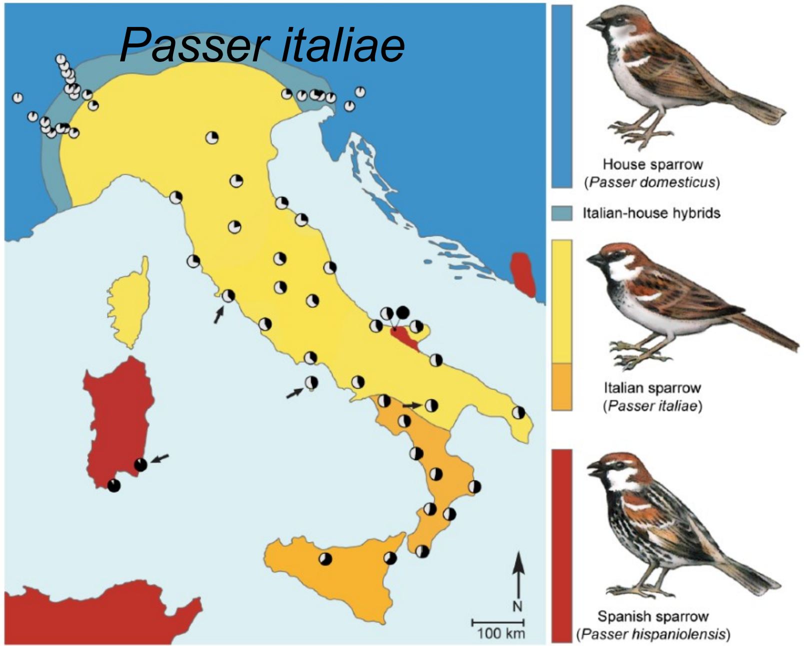
Golden crowned manakin

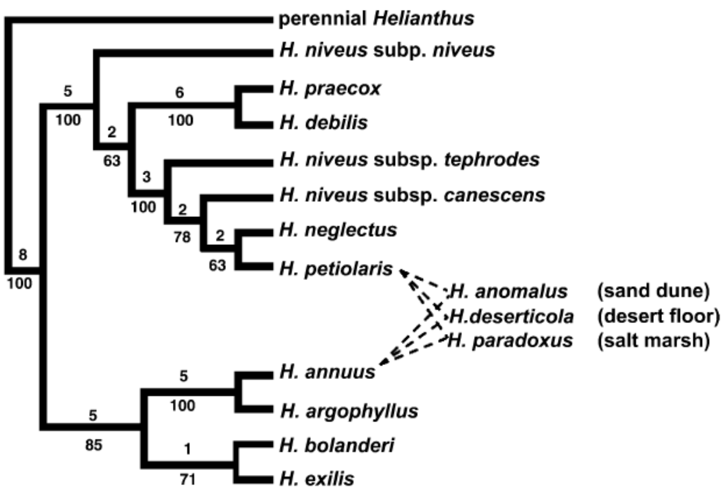




Heliconius heurippa

Passer italiae

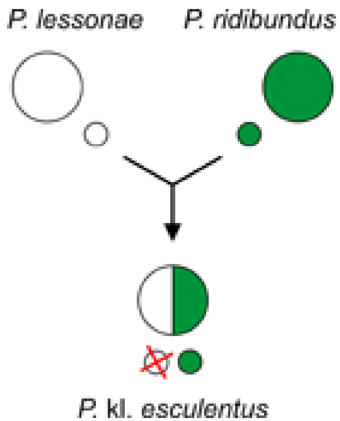




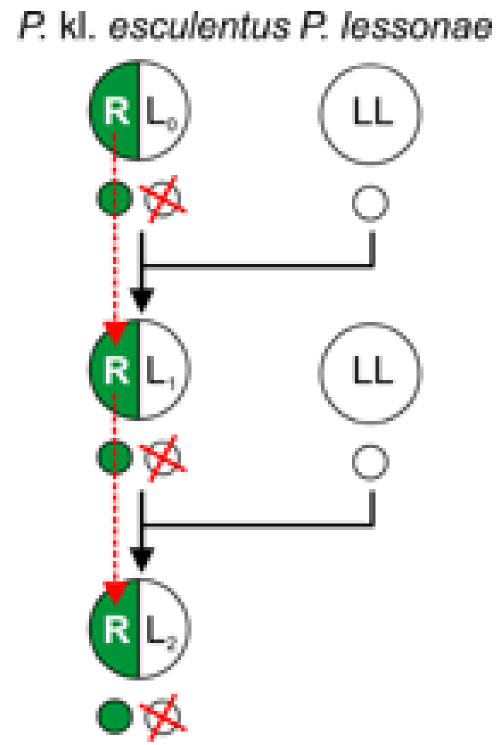
Hybridogenesis

Pelophylax ridibundus

Pelophylax lessonae



Pelophylax esculentus

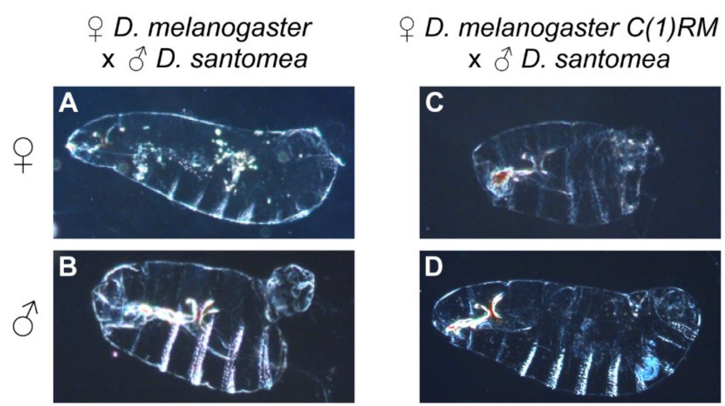


Intrinsic postzygotic isolation

Hybrid sterility

Oryza sativa

Hybrid inviability

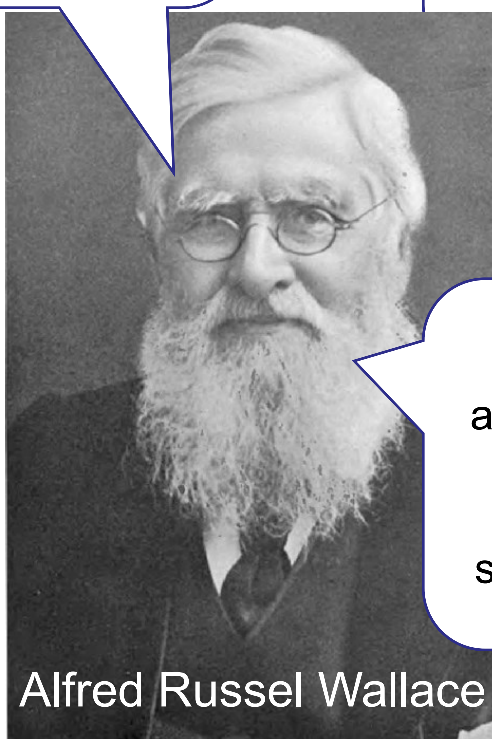


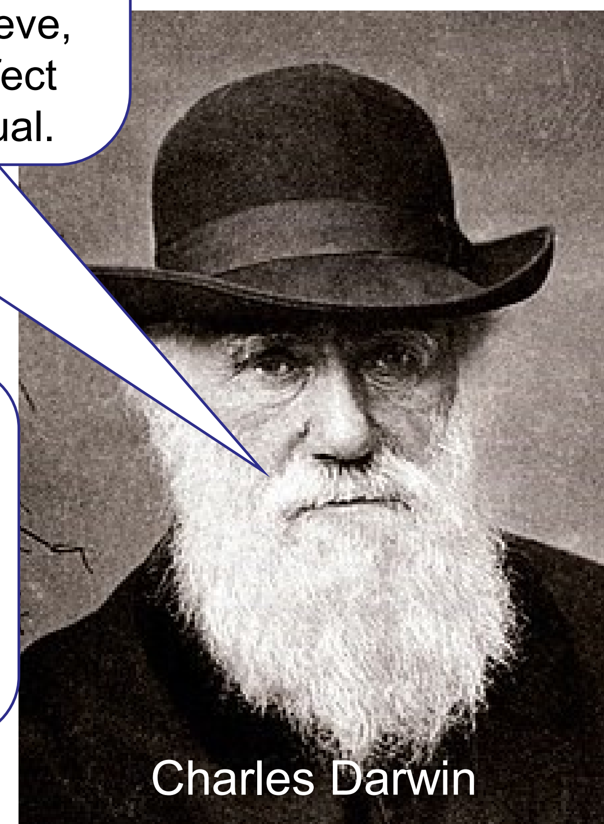
Origin of intrinsic postzygotic isolation

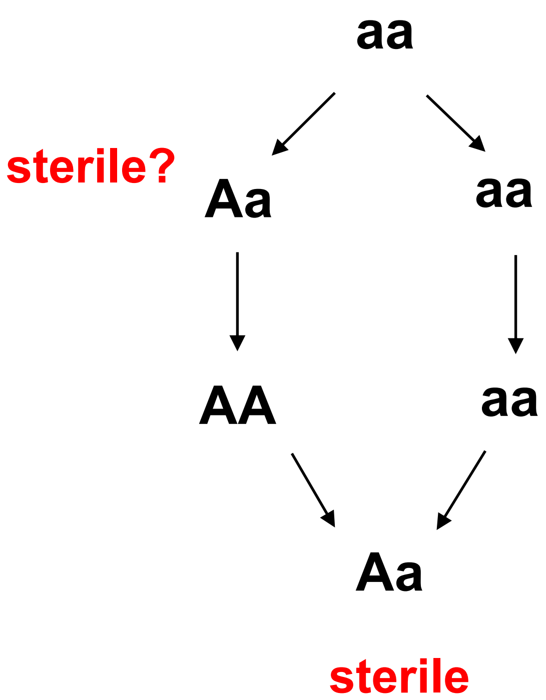
Could you imagine that hybrid sterility arose by natural selection?

No man could have more earnestly wished for the success of natural selection in regard to sterility, than I did…. I always felt sure it could be worked out, but always failed in detail. The cause being as I believe, that natural selection cannot effect what is not good for the individual.

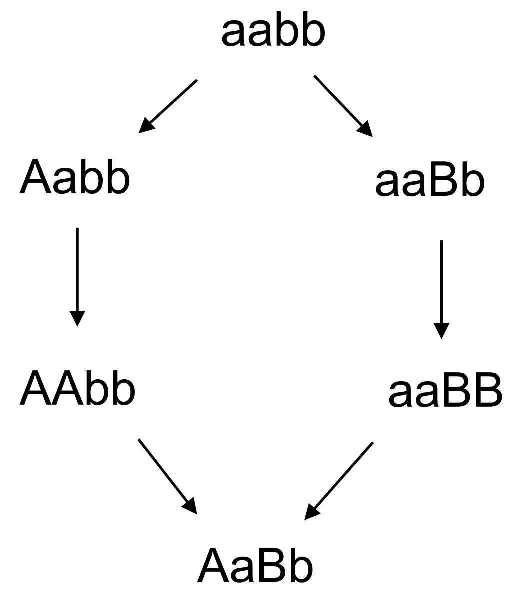
I am sorry you should have given yourself the trouble to answer my ideas on sterility… I now think there is about an even chance that natural selection may or not be able to accumulate sterility.



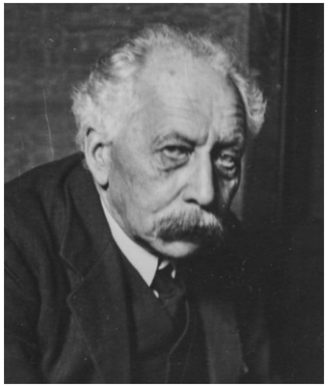




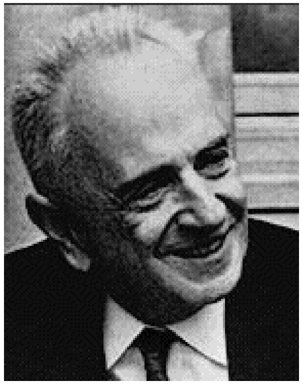
(Bateson)-Dobzhansky-Muller incompatibilities



- Intrinsic postzygotic isolation does not arise adaptively, but as a consequence of species genetic divergence after isolation.



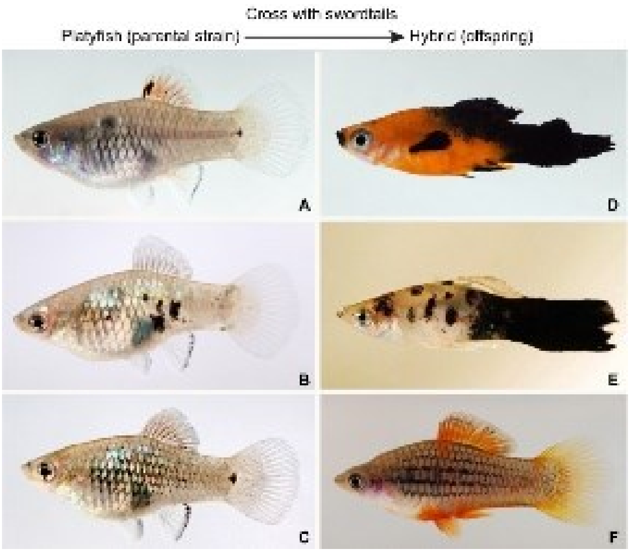
William Bateson



Theodosius Dobzhansky

Herman J. Muller

Speciation genes



Xiphophorus
Xmrk-2 (hybrid inviability)
Malign melanomas in hybrids

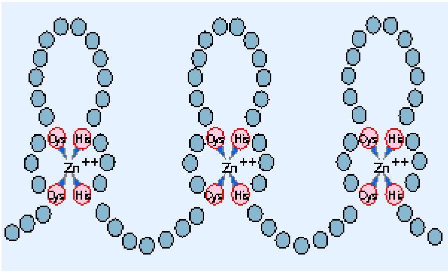
House mouse
Prmd9 (hybrid sterility)

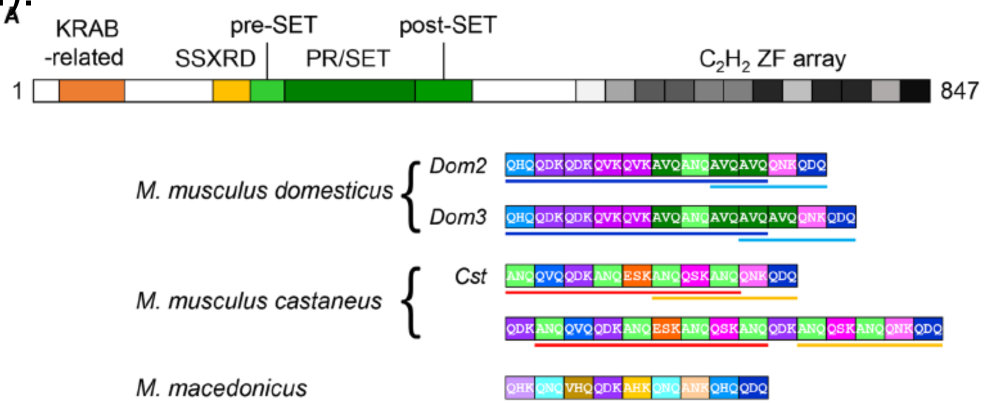
Drosophila
Overdrive (hybrid sterility)
OdsH (hybrid sterility)
Nup96 (hybrid inviability)
Hmr (hybrid inviability)
…..

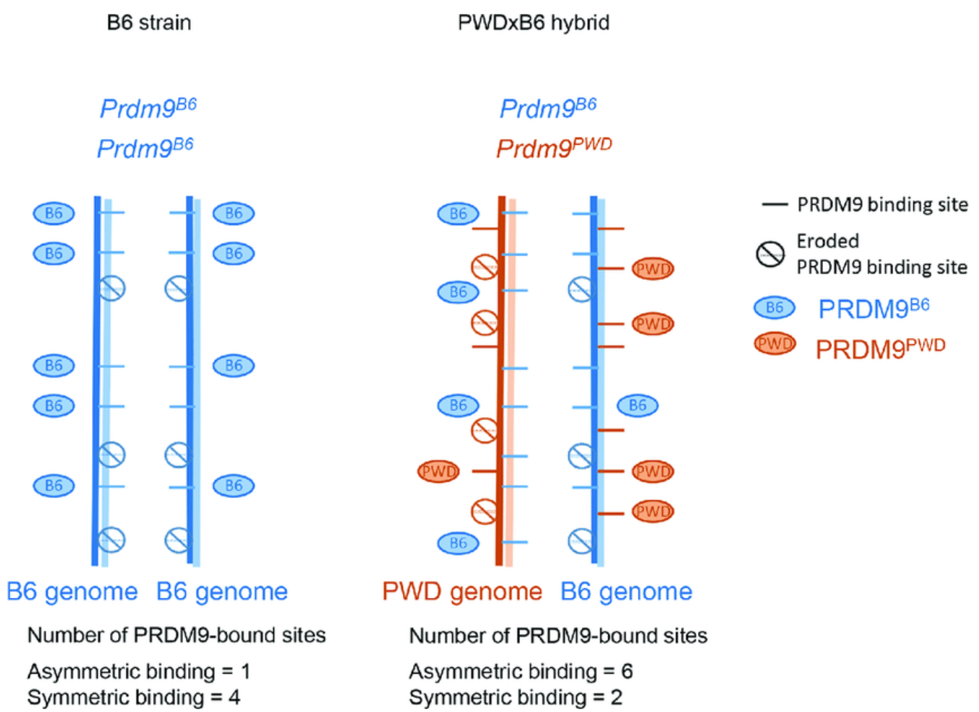
- Fast molecular evolution usually due to positive selection

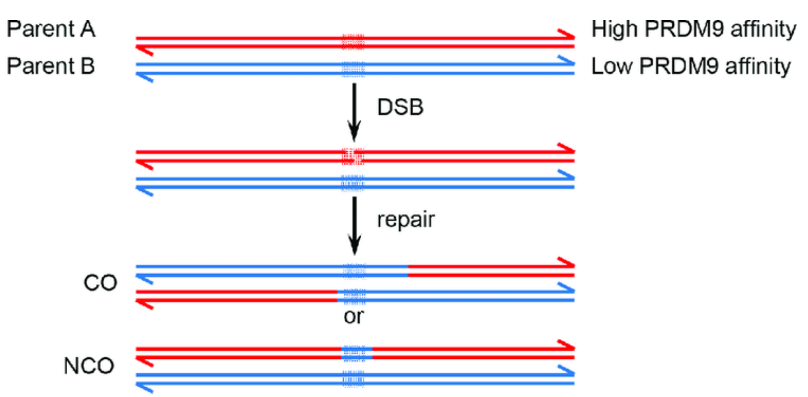
Prdm9

- Hybrid male sterility gene in house mouse.
- DNA binding protein (zinc-finger domain). Determines the position of double strand breaks in meiosis (hotspots of recombination).
- Fast molecular evolution due to gene conversions.







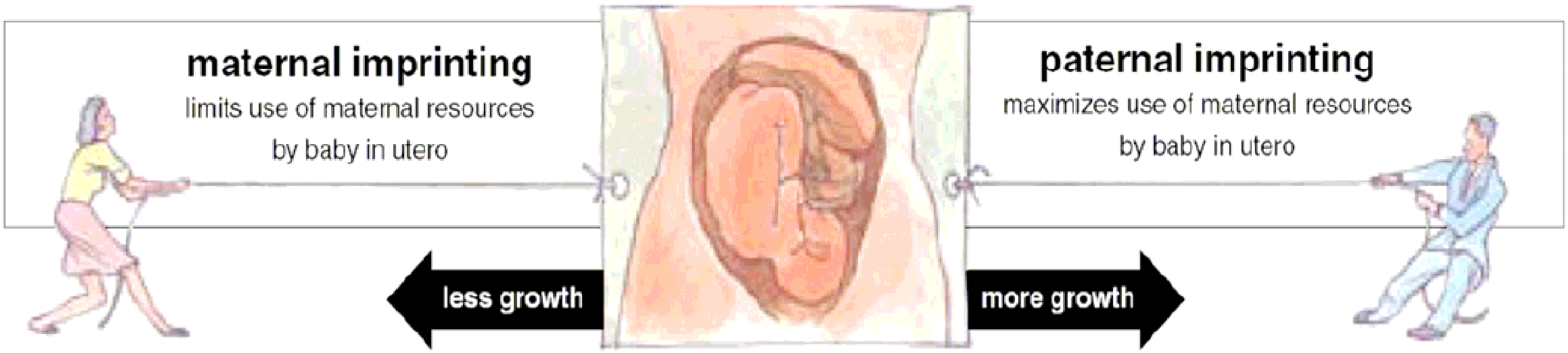


Asymetrical gene conversion.

Mihola et al. 2009

Parental conflict, genomic imprinting and hybrid inviability in mammals

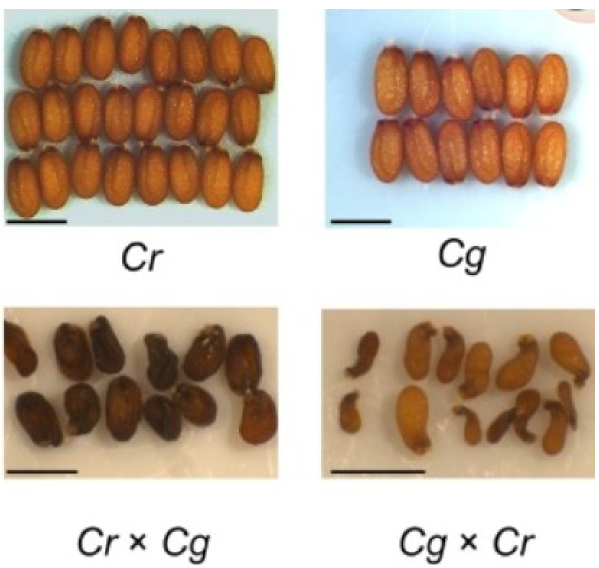
- Hybrid inviability arise relatively quickly in mammals compared to other vertebrates.

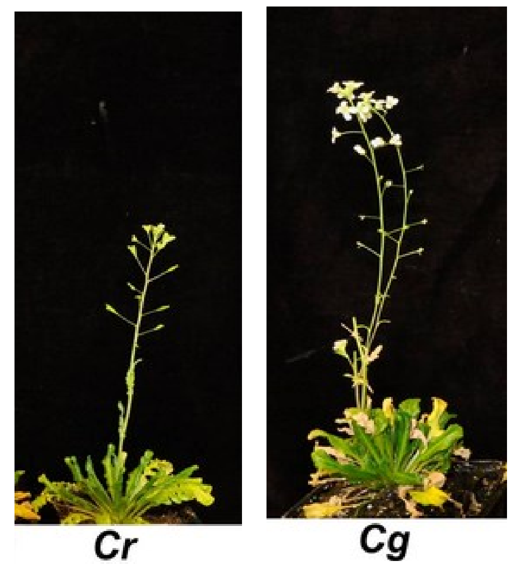


- **Hybrid placental dysplasia in hybrids**

  M. musculus x M. spretus
  - smaller placenta
  M. sprestus x M. musculus
  - larger placenta

Abnormal endosperm development in agiosperm hybrids





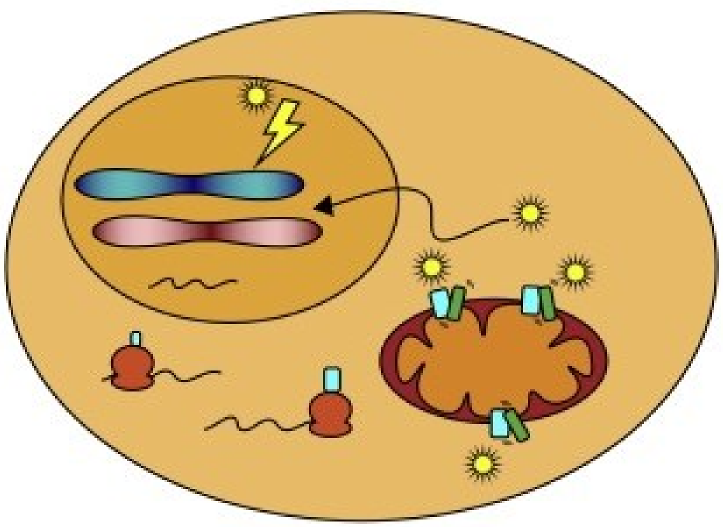
Capsella rubella a *C. grandiflora*

Reberning et al. 2015
Lafon-Placette and Kohler, 2016

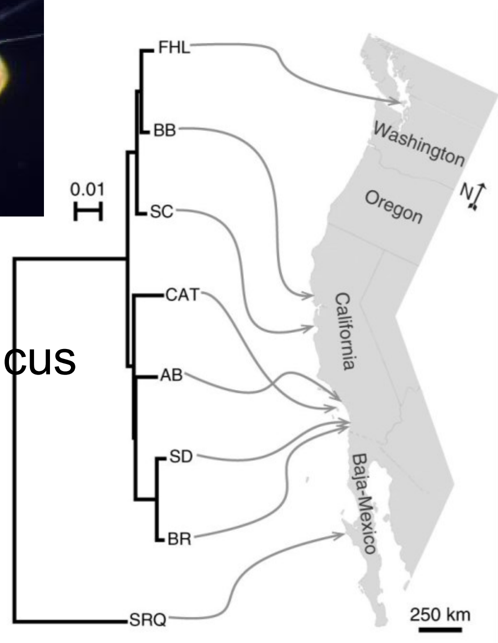
Mito-nuclear inkompatibilities

- Proteins important for oxidative phosphorylation are partially coded in mtDNA and partially in nucleus.

- Relatively fast molecular evolutoin of mtDNA in mammals.
- Incompatibilities between mtDNA and nuclear genes can lead to suboptimal electron transfer and higher production of oxygen radicals.



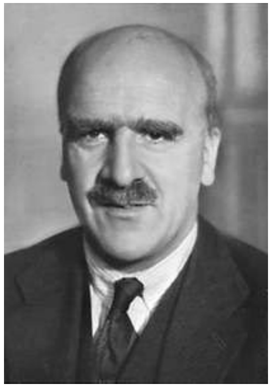
marine cope-pod
Tigriopus californicus



Two rules of speciation

Haldane's rule

When in the F1 offspring of two different species one sex is absent, rare, or sterile, that sex is the heterogametic sex (1922).

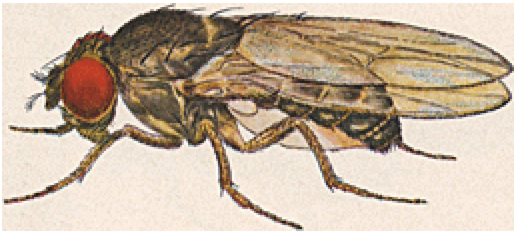


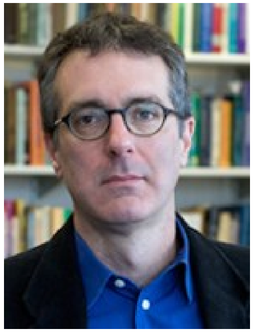
John B. S. Haldane

Two rules of speciation

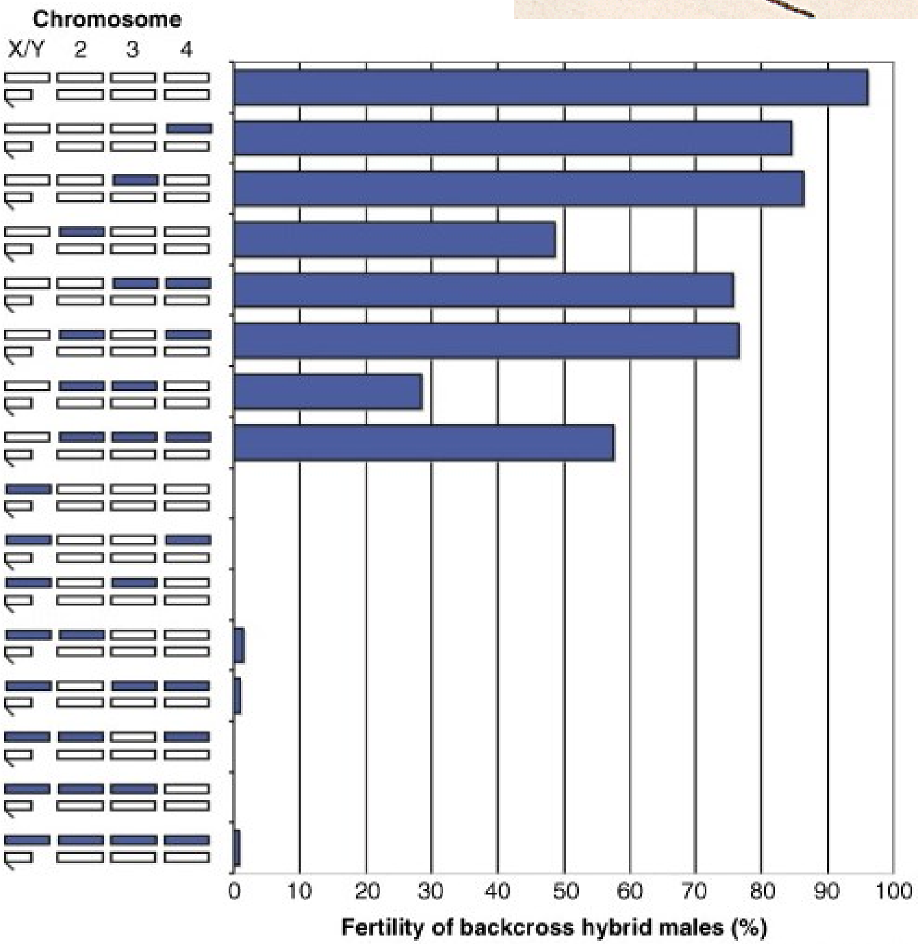
Large X effect

- X chromosome have a disproportionately large effect on intrinsic postzygotic isolation (sterility) compared to autosomes.



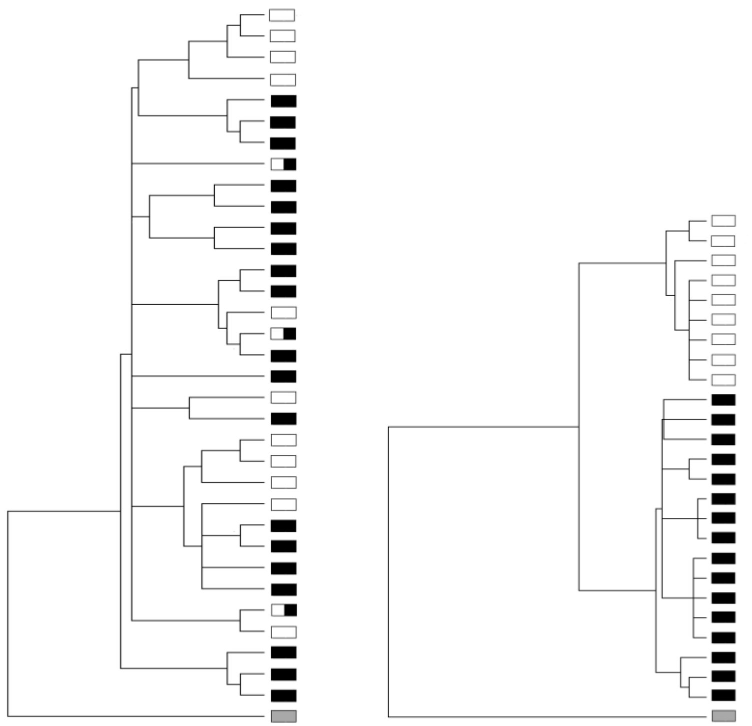


H. Allen Orr



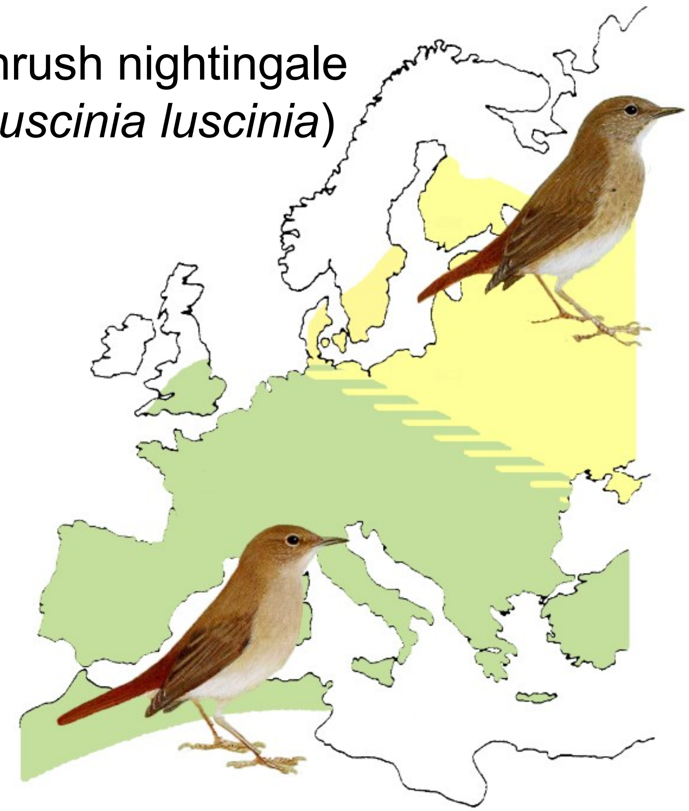
Orr HA, 1989

The large Z effect



autosomal locus Z-linked locus

Thrush nightingale
(*Luscinia luscinia*)



Common nightingale
(*Luscinia megarhynchos*)

Storchová et al. 2010

Dominance theory

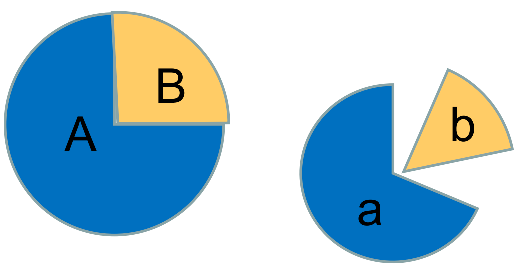
Homogametic sex

AABB

AAbb aaBB

AaBb

fertile



A,a… autosom
B,b….X chrom.

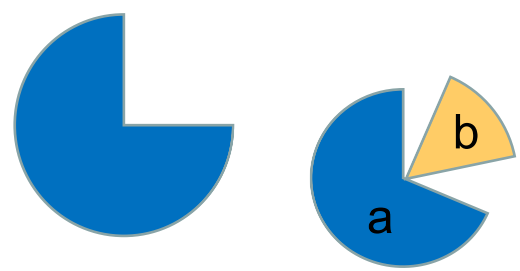
Heterogametic sex

AAB

AAb aaB

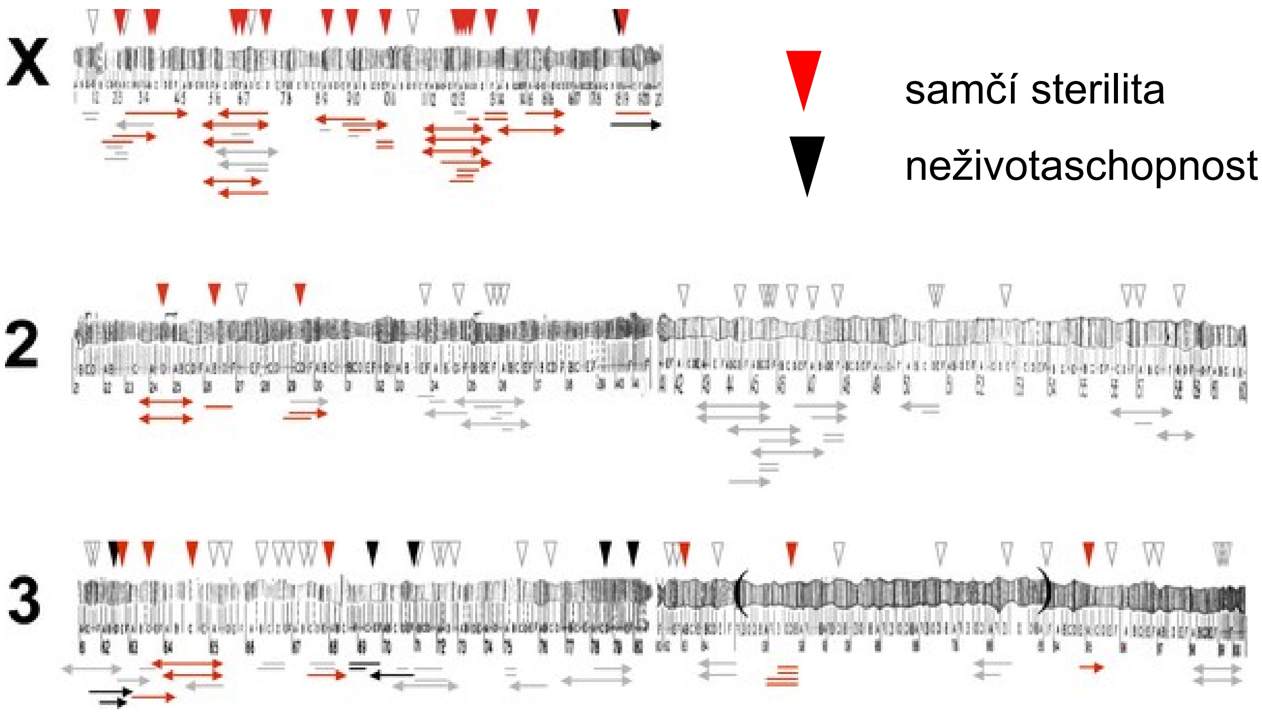
Aab

sterile



Genes for hybrid sterility are more common on the X even if recessive autosomal incompatibilities are counted.

Homozygotní introgrese z *D. mauritiana* do *D. sechellia*



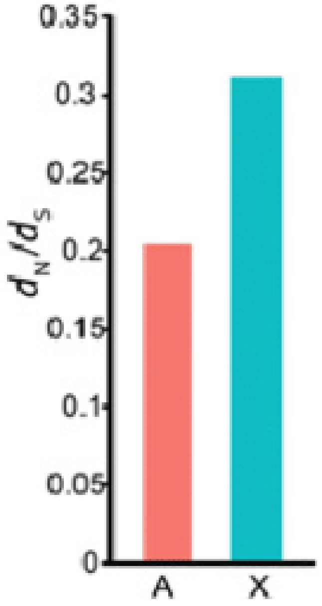
Masly and Presgraves, 2007

Another causes of the Haldane’s rule and the large X/Z effect

Faster molecular evolution on the X/Z chromosomes

i. Faster fixation of recessive advantageous mutations on the hemizygous X/Z.

ii. Lower Ne and stronger genetic drift cause faster fixation of mildly disadvantageous mutations.



Another causes of the Haldane's rule and the large X/Z effect

Meiotic drive

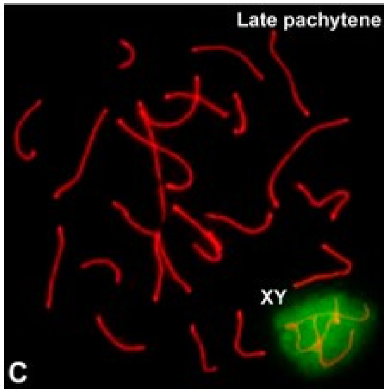
Fast co-evolution between meiotic drivers on sex chromosomes and their suppressors. In hybrids can cause sterility.

- Hybrid male sterility.
- Caused by gene **Overdrive**. Normally causes meiotic drive on the X. Fast evolution due to reccurent positive selection (high dN/dS).

Drosophila pseudoobscura
Subspecies from Colombia (Bogotá) and US*A*

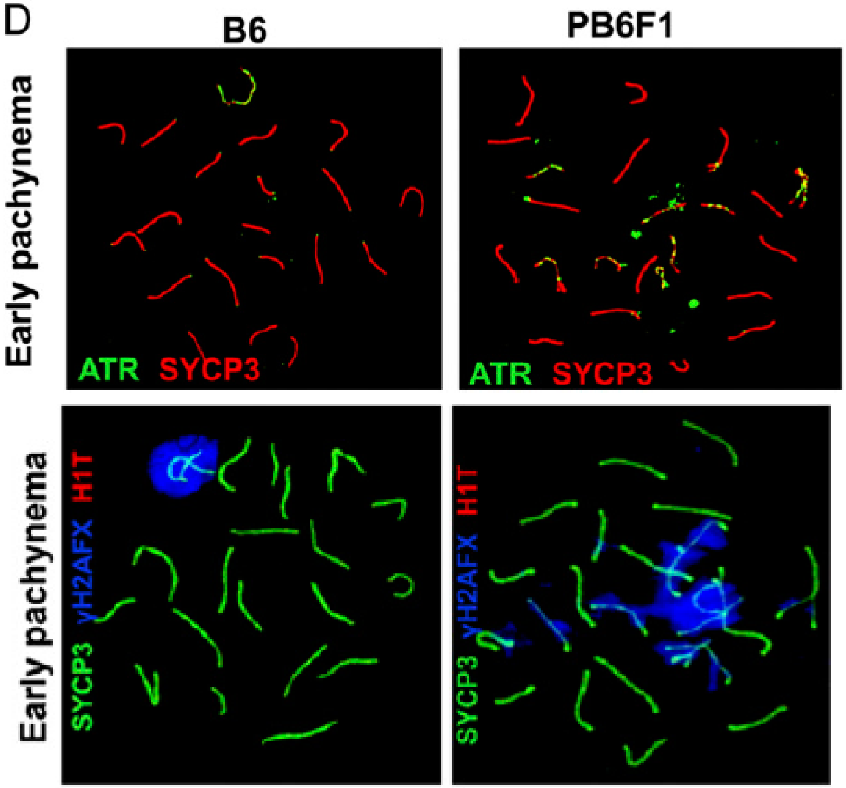
Phadnis and Orr, 2009

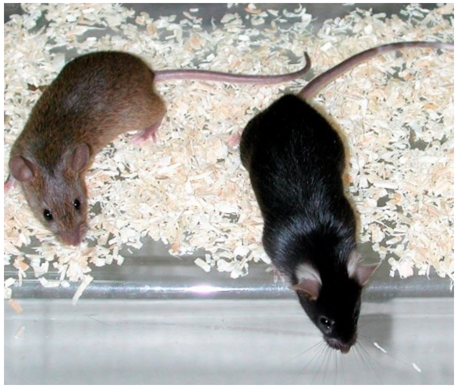
Another causes of the Haldane's rule and the large X/Z effect



sex body

Failure of sex chromosome inactivation during meiosis





PWD/Ph
(*M.m.musculus*)

C57BL/6J
(M.m.domesticus)

- Hybrid males sterile.
- Asynapsis of homologous chromosomes in pachytene. In males at the same time failure of sex chromosome inactivation.

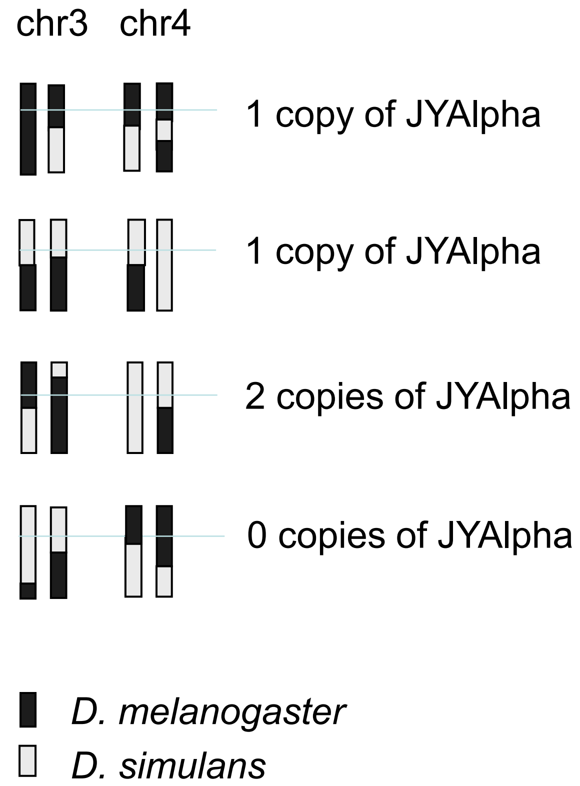
Bhattacharyya et al. (2013) PNAS

Translocation of genes as a cause of intrinsic postzygotic isolation

- JYAlpha gene

- On chr 3 in Drosophila melanogaster
- On chr 4 in Drosophila simulans

- Part of F2 hybrids lack JYAlpha -> sterility

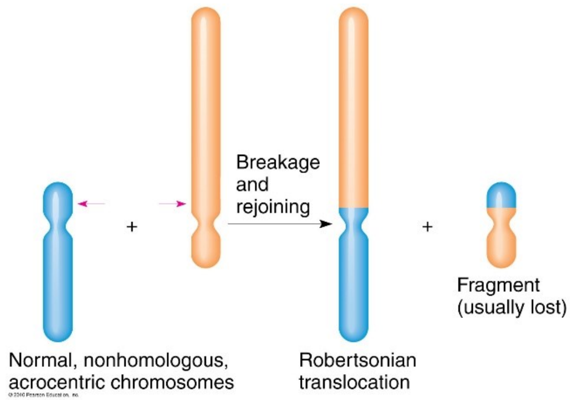


Masly et al. 2006

Chromosomal speciation

- Changes in karyotypes (chromosomal rearrangements, fussions, fissions) cause problems with chromosome pairing and segregation during meiosis in hybrids (underdominance).
- Underdominant rearrangements are, however, unlikely to be fixed in the population unless they arise in very small populations inbreeding populations.
- Sterility can be caused by interaction of more rearrangements

Robertsonian translocations in mice

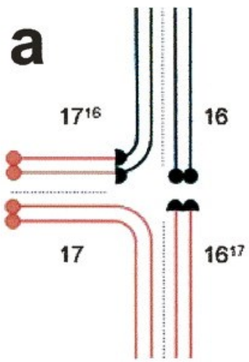


Mus musculus domesticus has more than 40 distinct local chromosomal races, characterized by about 100 types of Rb chromosomes with different arm combinations.

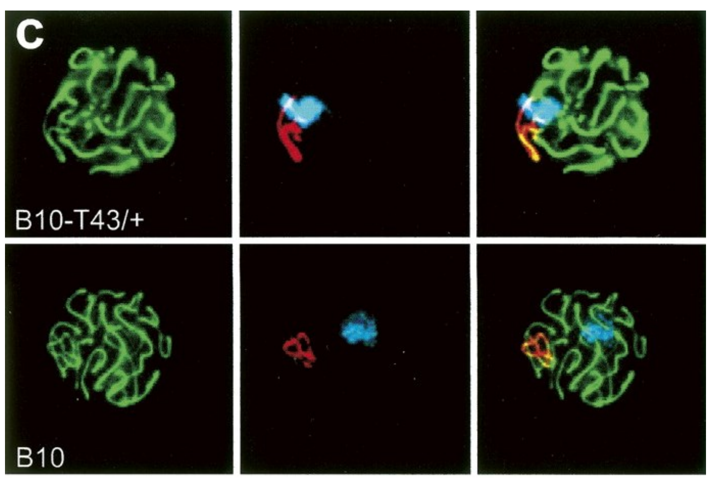
- Hybrids between species differing in single Robersonian translocation may be fertile, but doubly heterozygous for two Robertsonian translocations involving the same chromosome are often sterile.

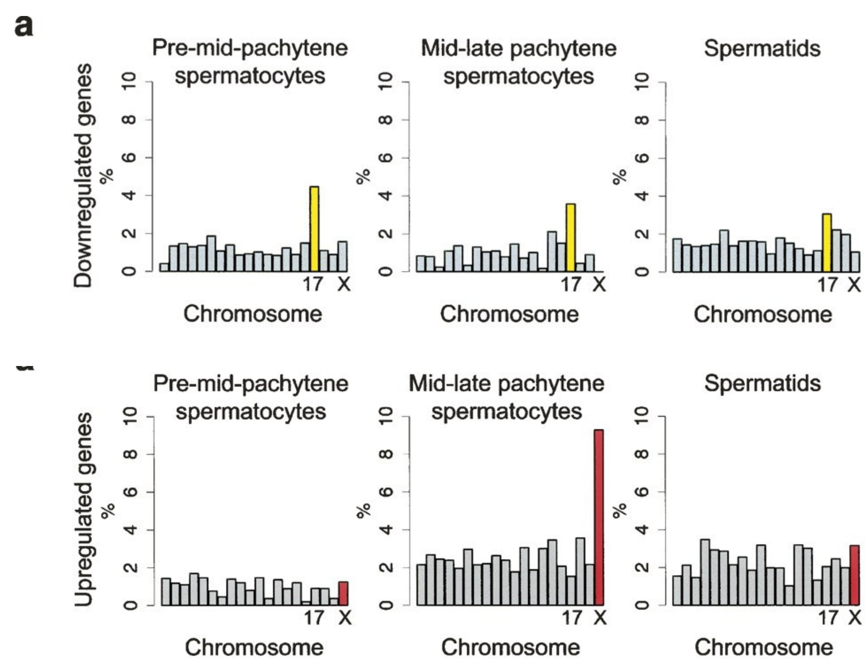
Chromosomal rearrangements and Haldane’s rule

Many Robersonian translocations, reciprocal autosome translocations and X-autosome translocations causes sterility of hybrid males, but not females (Haldane’s rule).



Sterile males heterozygous for chromosomal rearangements show incomplete meiotic synapsis, meiotic silencing of unsynapsed chromosomes and disturbance of X chromosome inactivation.

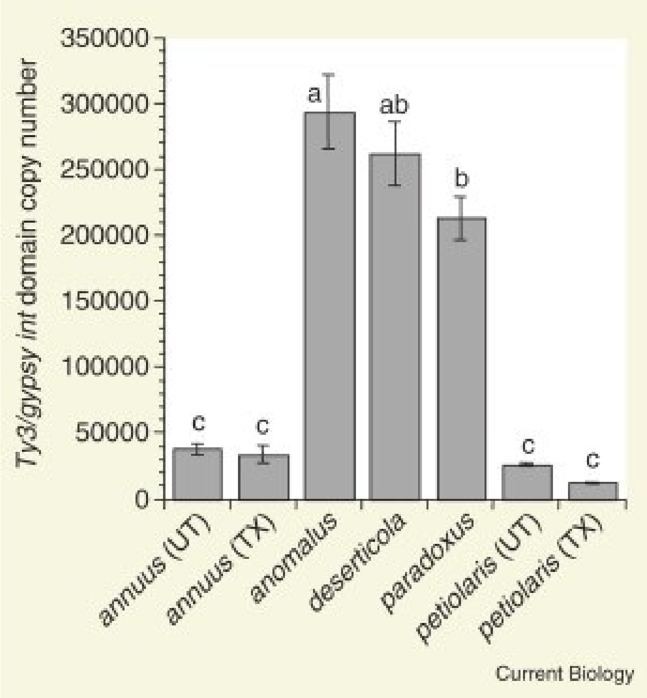


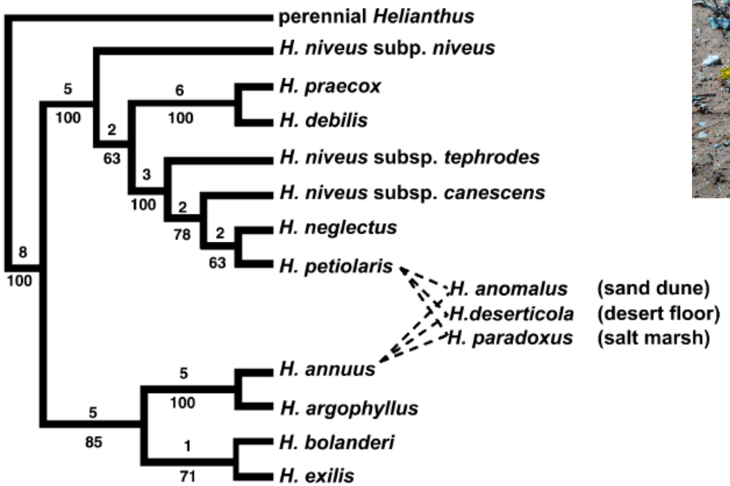


Homolka et al. 2007

Transposon derepression in interspecific hybrids

- Transposable elements are repressed by small RNAs (piRNAs) in the germline.
- Mismatch between paternally transmitted transposon and maternally inherited piRNAs can lead to transposon activation.





Ungerer et al. 2006

Proc. Natl. Acad. Sci. USA
Vol. 92, pp. 8050–8054, August 1995
Genetics

Diverse transposable elements are mobilized in hybrid dysgenesis in *Drosophila virilis*

(regulation of transposition)

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Communicated by Matthew Meselson, Harvard University, Cambridge, MA, May 25, 1995 (received for review April 4, 1995)

ABSTRACT We describe a system of hybrid dysgenesis in *Drosophila virilis* in which at least four unrelated transposable elements are all mobilized following a dysgenic cross. The data are largely consistent with the superposition of at least three different systems of hybrid dysgenesis, each repressing a different transposable element, which break down following the hybrid cross, possibly because they share a common pathway in the host. The data are also consistent with a mechanism in which mobilization of a single element triggers that of others, perhaps through chromosome breakage. The mobilization of multiple, unrelated elements in hybrid dysgenesis is reminiscent of McClintock's evidence [McClintock, B. (1955) *Brookhaven Symp. Biol.* 8, 58–74] for simultaneous mobilization of different transposable elements in maize.

Undermethylation associated with retroelement activation and chromosome remodelling in an interspecific mammalian hybrid

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Genetic models[1,2] predict that genomic rearrangement in hybrids can facilitate reproductive isolation and the formation of new species by preventing gene flow between the parent species and hybrid (sunflowers are an example[3]). The mechanism underlying hybridization-induced chromosome remodelling is as yet unknown, although mobile element activity has been shown to be involved in DNA rearrangement in some dysgenic *Drosophila* hybrids[4,5]. It has been proposed that DNA methylation evolved as a means of repressing the movement of mobile elements (the host defence model[6,7]). If such a protective mechanism were to fail, mobile elements could be activated, and could cause major and rapid genome alterations[8,9]. Here we demonstrate the occurrence of genome-wide undermethylation, retroviral element amplification and chromosome remodelling in an interspecific mammalian hybrid (*Macropus eugenii* × *Wallabia bicolor*). Atypically extended centromeres of *Macropus eugenii* derived autosomes in the hybrid were composed primarily of an unmethylated, amplified retroviral element not detectable in either parent species. These results, taken with the observation of deficient methylation and *de novo* chromosome change in other mammalian hybrids, indicate that the failure of DNA methylation and subsequent mobile-element activity in hybrids could facilitate rapid karyotypic evolution.

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***Drosophila buzzatii* and *D. koepferae* coexist in the arid zones of Bolivia and the Argentine Northwest.**

- Mobilization of TEs has been described in interspecific hybrids.
- TE deregulation very likely due to fast divergence in piRNA pathway proteins and piRNA (signs of positive selection, differential experssion between species).

GCAT TACG GCAT *genes*

MDPI

Article

Drosophila Interspecific Hybridization Causes a Deregulation of the piRNA Pathway Genes

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