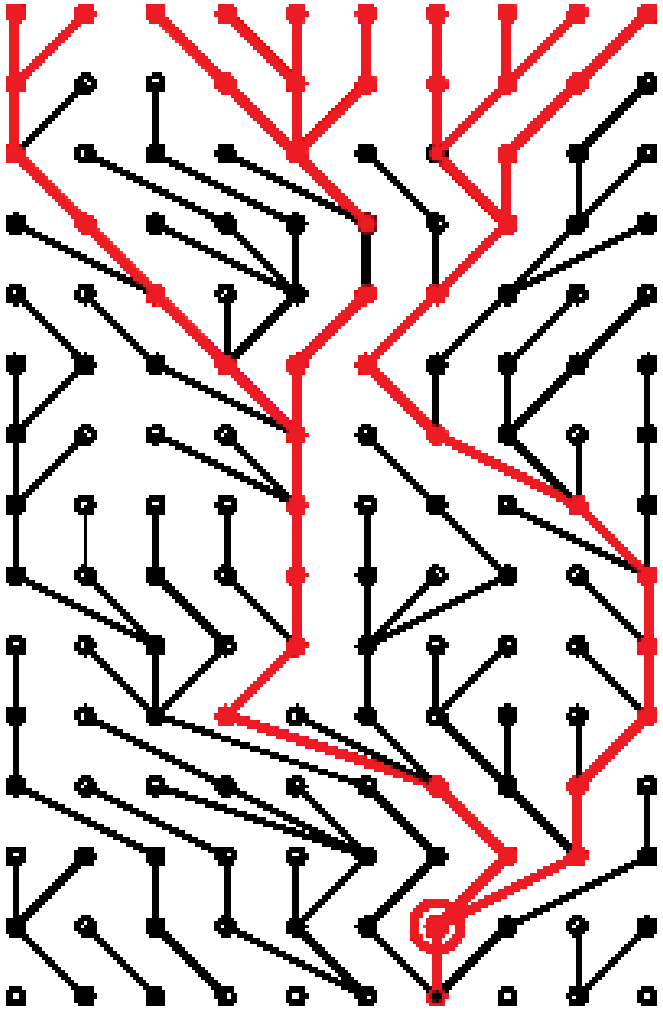


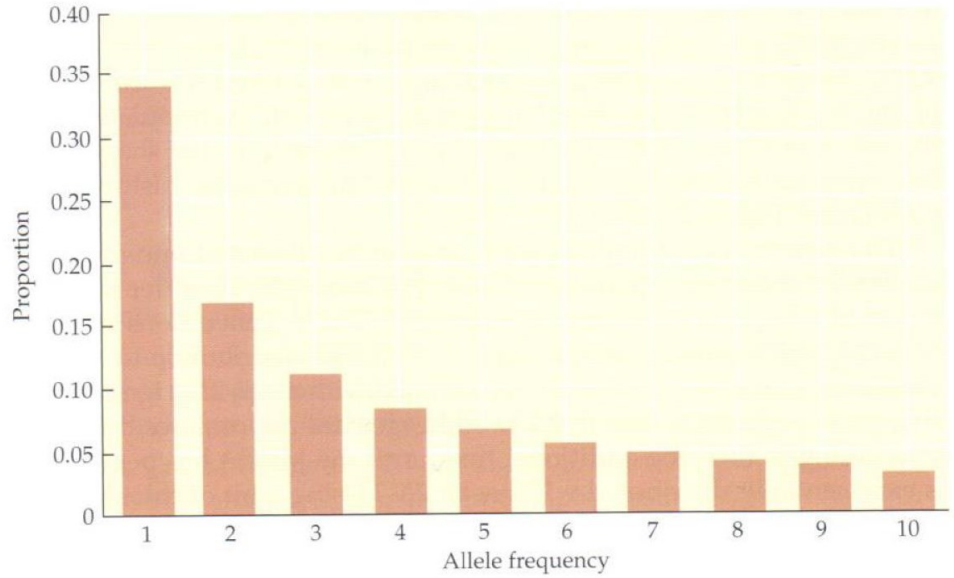
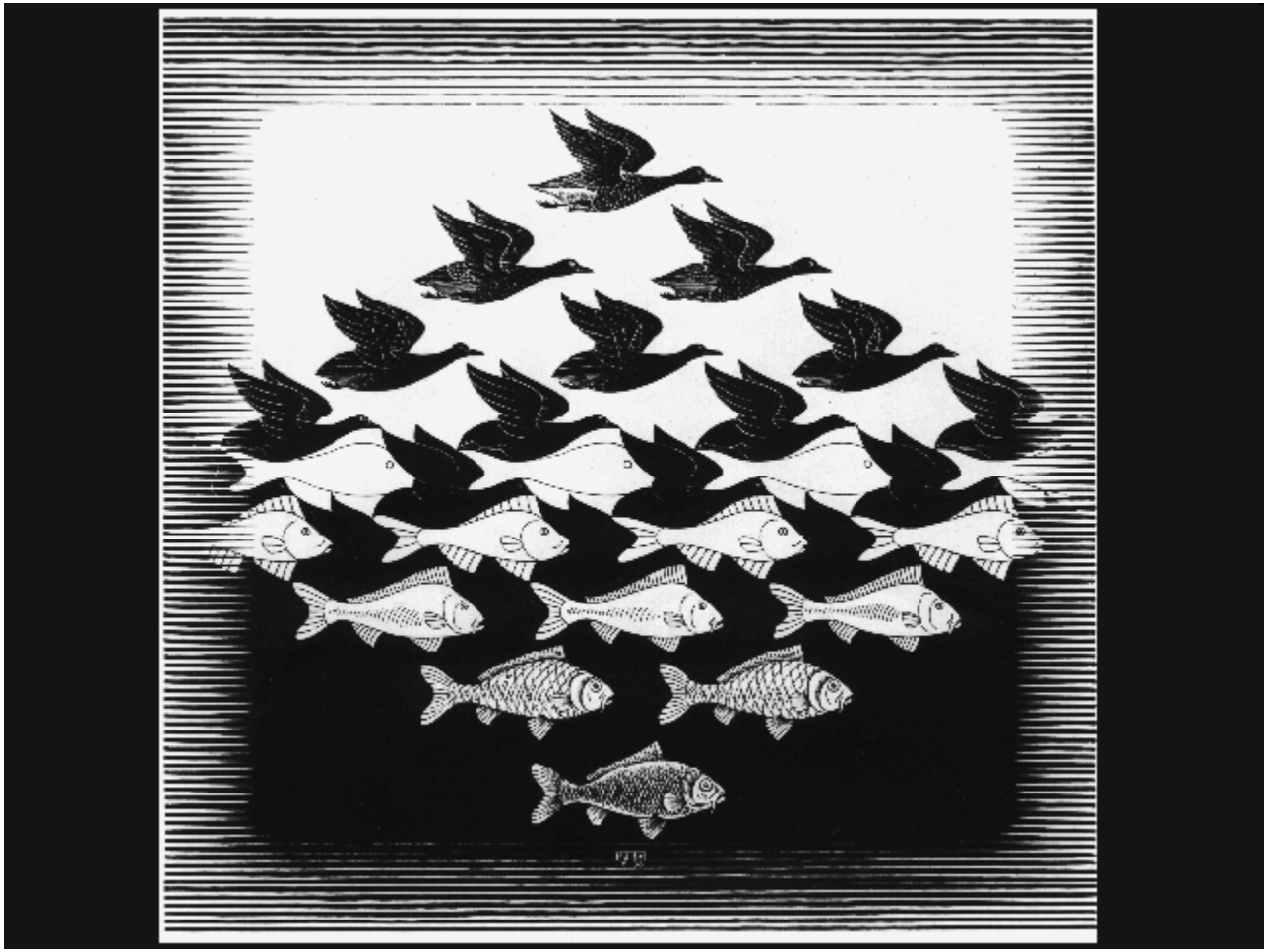


Figure 3.9 The expected site frequency spectrum (SFS) for a sample of $n = 10$ haploid individuals under the standard neutral coalescence model with infinite sites mutation.

Genetika speciace



- Příroda je diskontinuitní
- Jedince většinou zařadíme do druhů

- Biological nature is discontinuous
- Species exist

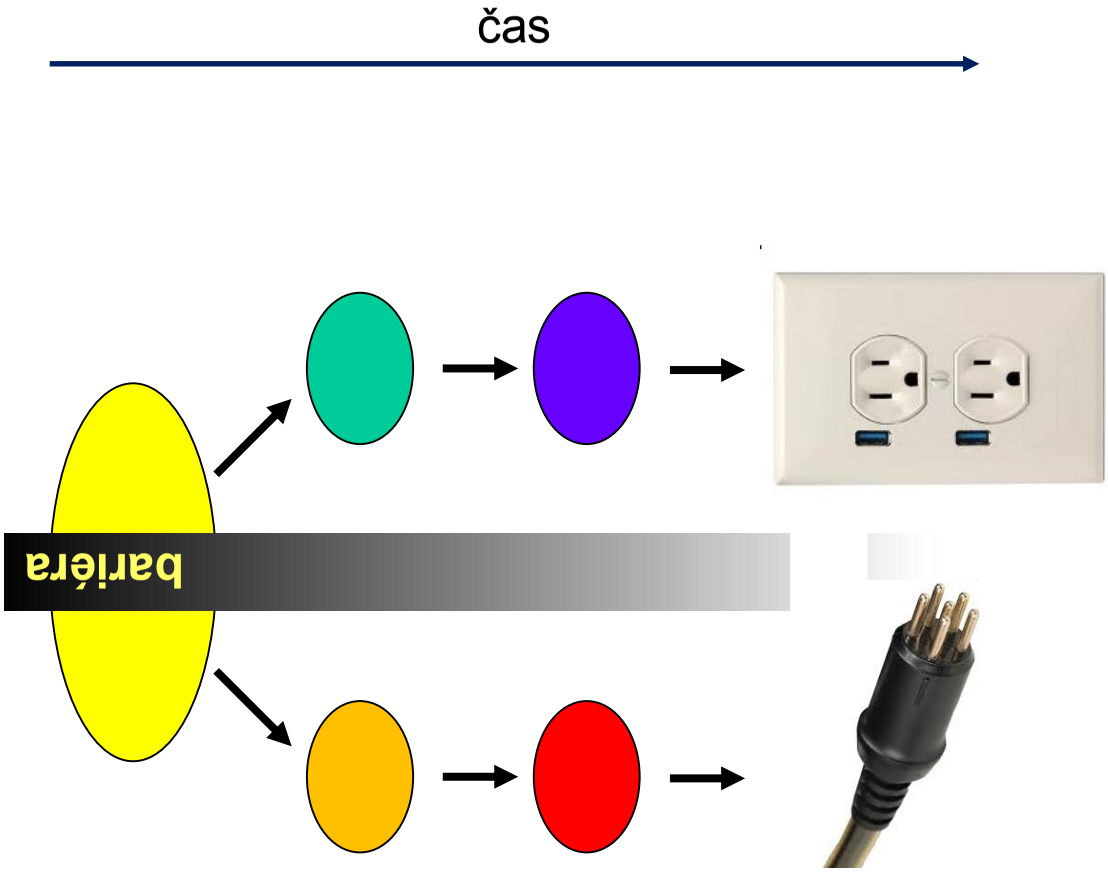
- How do we define them?
- Why do they exist?

Biologické pojetí druhu

- Druh je skupina populací, mezi kterými může dojít ke křížení a které jsou **reprodukčně izolovány** od jiných populací.

- *The biological meaning of species is thus quite apparent: The segregation of the total genetic variability of nature into discrete packages, so called species, which are separated from each other by **reproductive barriers**. (E. Mayr)*

- → **Reprodukčně izolační bariéry**


bariéra
čas

Neúplná izolace

- I jasné druhy se spolu občas kříží
- Modely speciace s tokem genů

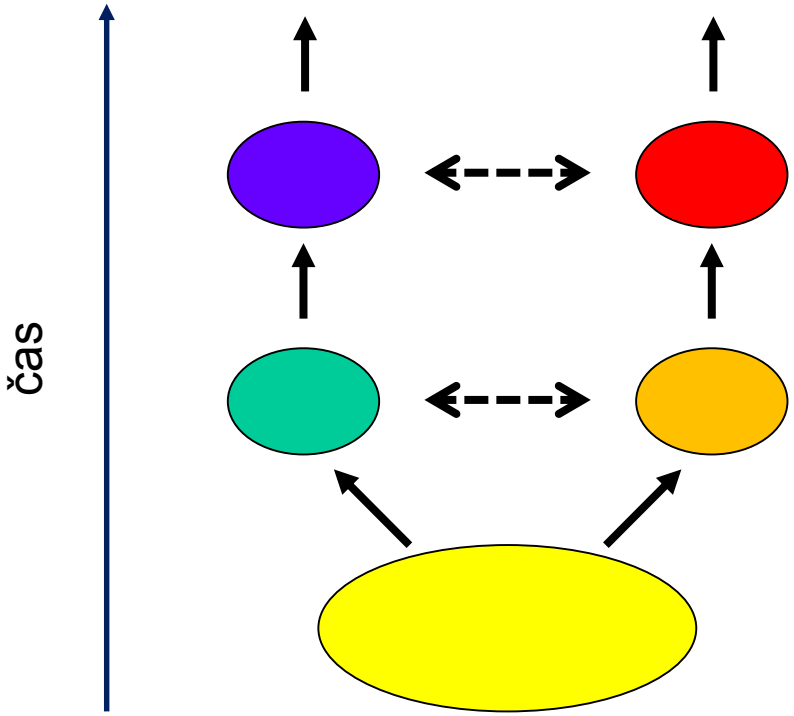
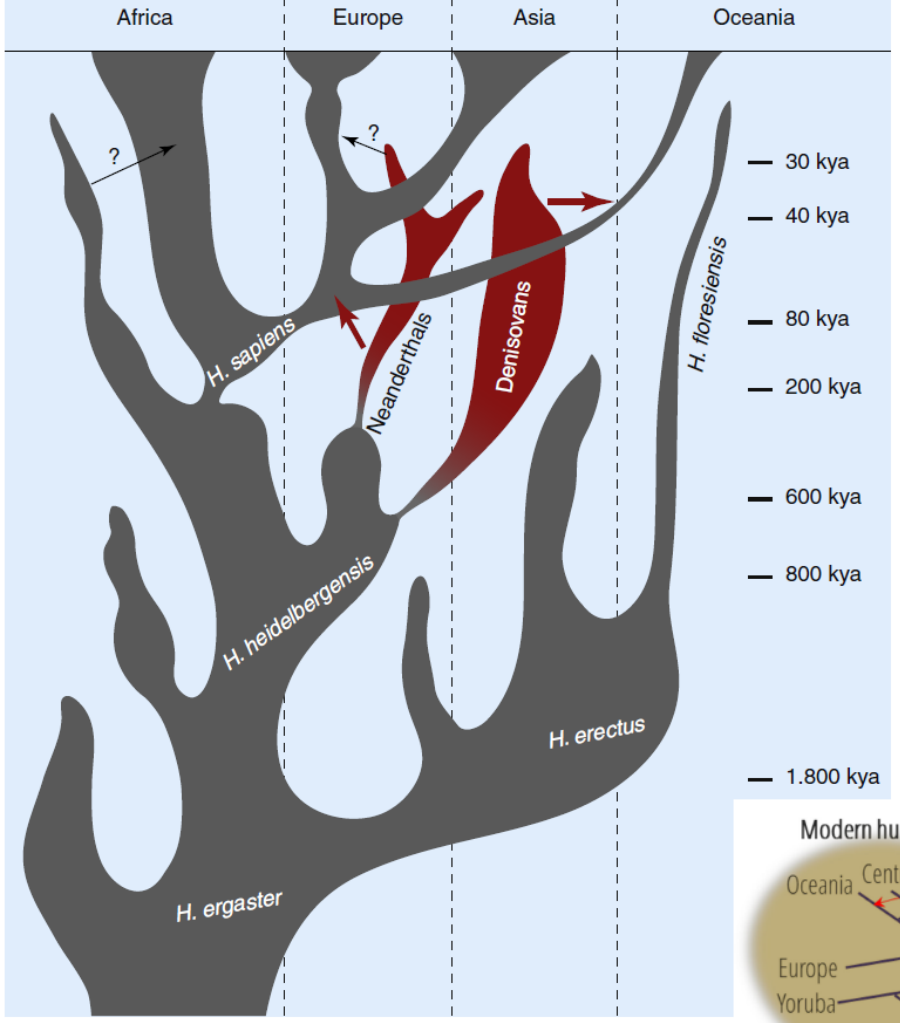


Table 1 Reported cases of record holders that produce viable hybrids despite their long time of separation in various linages based on the published articals

Lineage	Family	Time of divergence (million years ago)	References
Fishes	Lepisosteidae	33–100	Hedges et al., 2006; Herrington et al., 2008.
	Centrarchidae	35	Bolnick and Near, 2005.
Frogs	Hylidae	22–80	Karl et al., 1995; Smith et al., 2005.
Lizards	Iguanidae	10–20	Rassmann, 1997.
Snakes	Pythonidae	35	Hoser, 1988; Rawlings et al., 2008.
	Colubridae	30	Hedges et al., 2006; LeClere et al., 2012.
Turtles	Cheloniidae	50–63	Karl et al., 1995; Naro-Maciel et al., 2008.
Crocodiles	*Crocodylus*	10	Polet et al., 2002; Brochu, 2003.
Birds	Anatidae	28	Gonzalez et al., 2009.
Mammals	Balaenopteridae	5– 8	Hedges et al., 2006; Glover et al., 2013.
	Delphinidae	8	Hedges et al., 2006; Zhang et al., 2014.



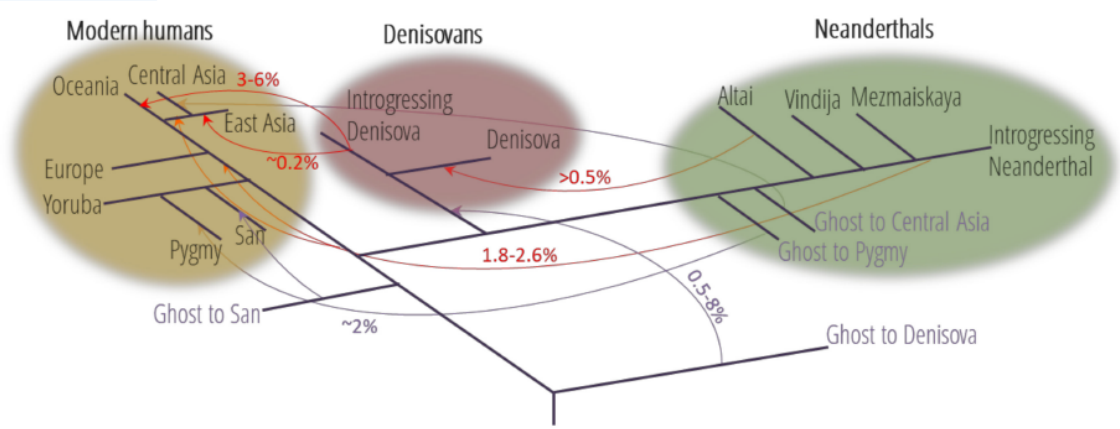
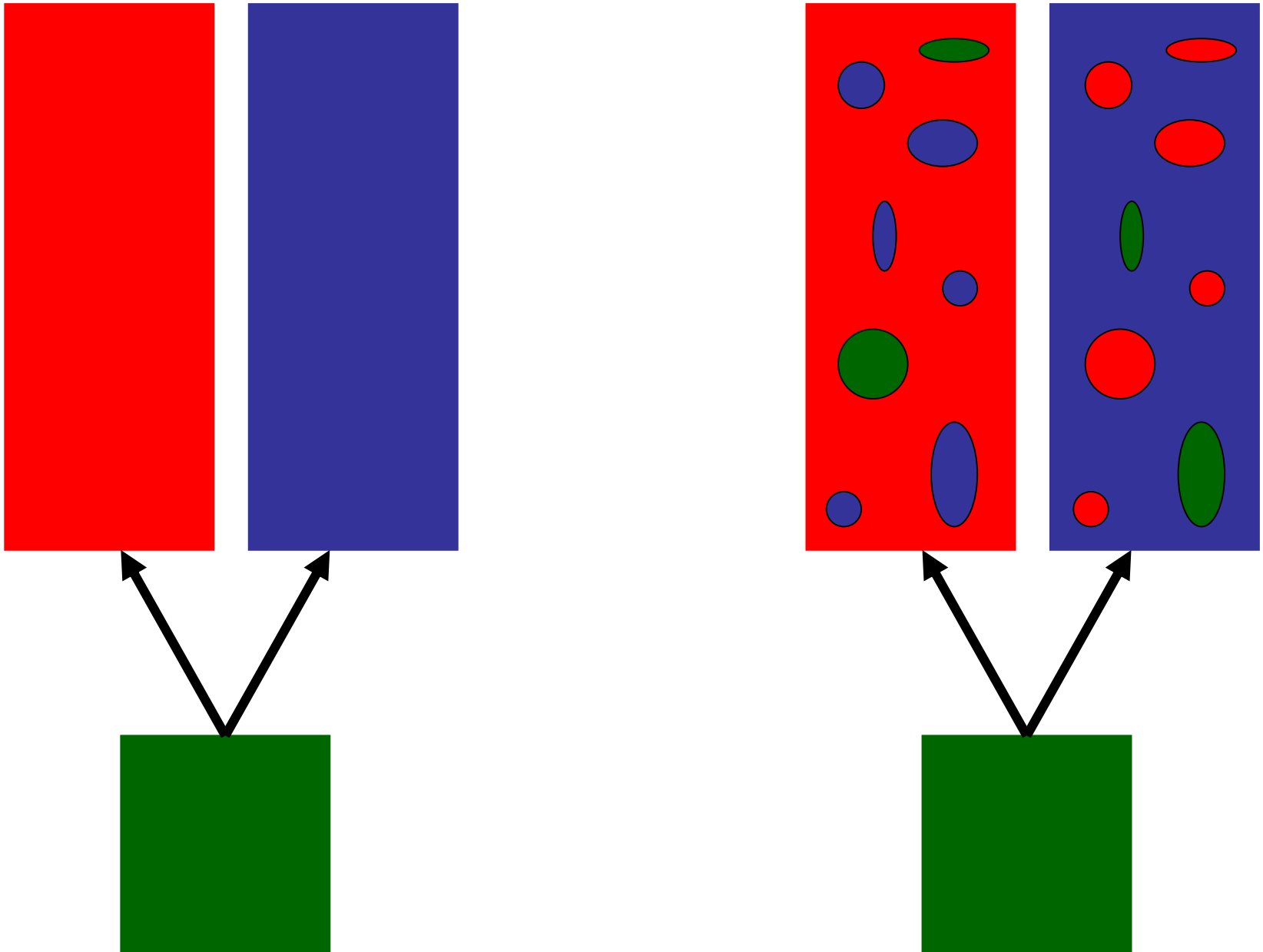


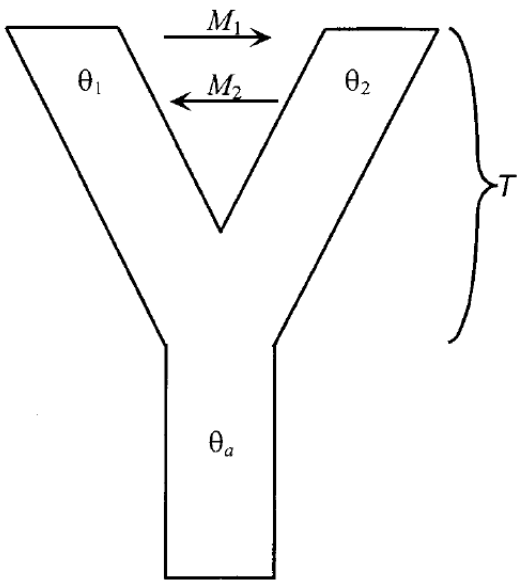
Figure 1. Family tree of the four groups of early humans living in Eurasia 50,000 years ago and the inferred gene flow between the groups due to interbreeding (based on [12–16]). The direction and estimated magnitude of inferred gene flow events are shown. Branch lengths and timing of gene flows are not scaled. Light violet color indicates introgression events from unknown archaic populations (Ghost).

Homogenní nebo „děravé“ druhy



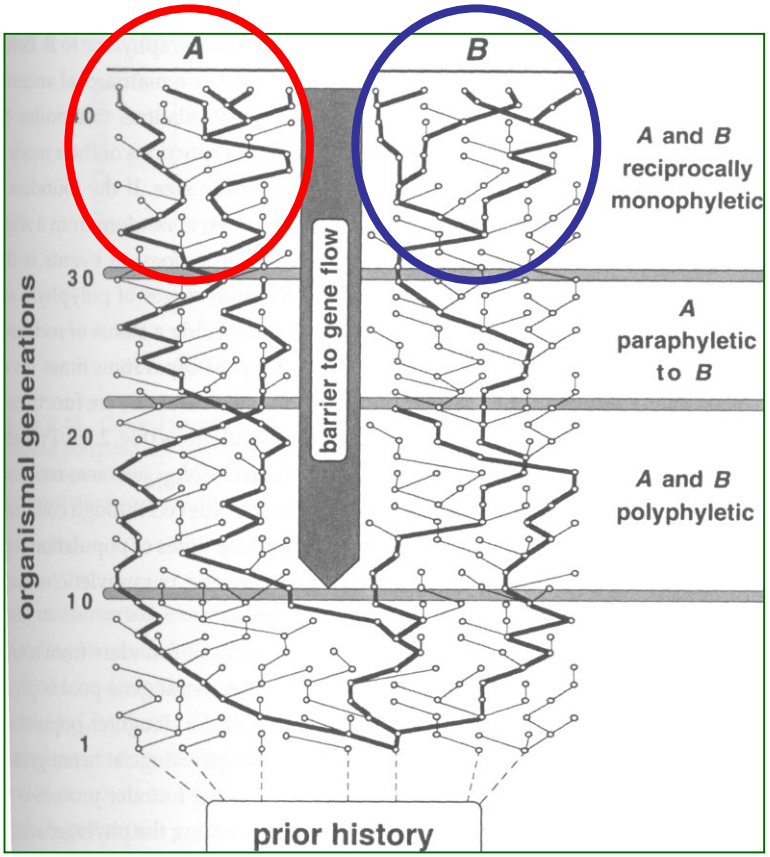
Proč jsou druhy „děravé“?

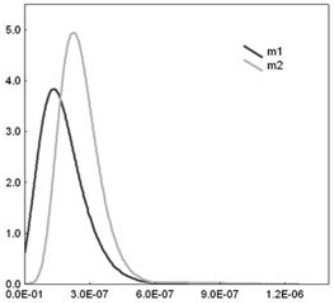
- přetrvávání ancestrálního polymorfismu
- introgrese (občasné křížení s jiným druhem)
- nové modely: izolace s migrací



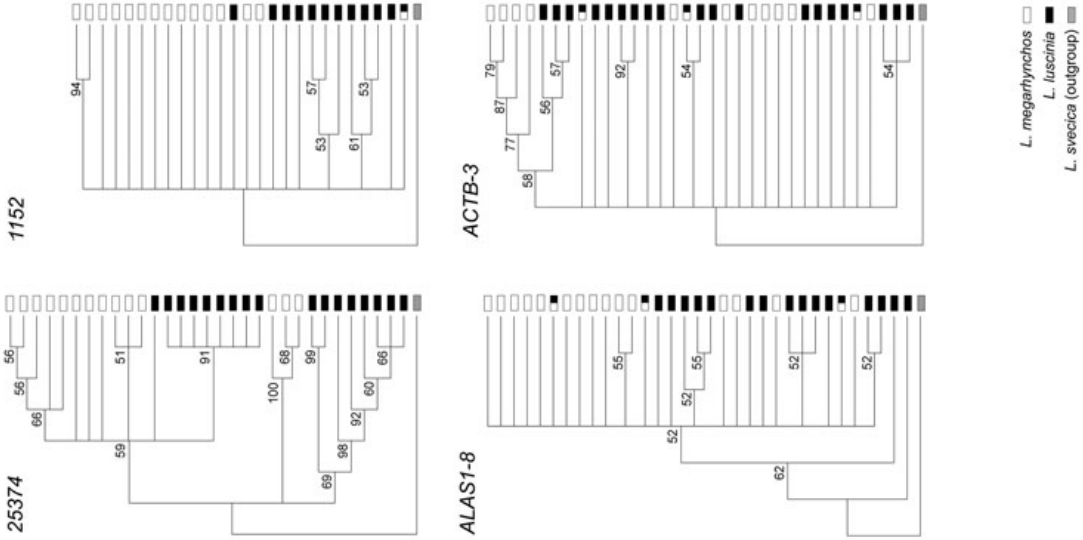
Přetrvávání ancestrálního polymorfismu

Lineage sorting
→ reciproční monofylie

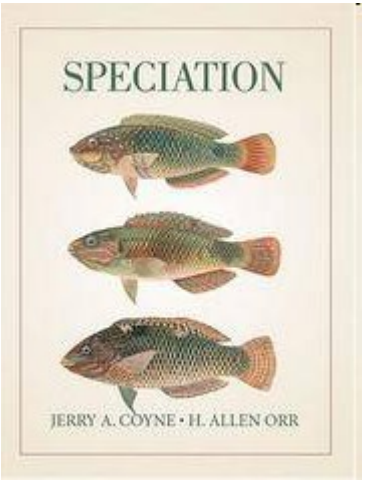




slavík obecný a s. tmavý – divergence 1,8 mil let



- **Kdy fungují reprodukčně izolační bariéry**?
  - **Před kopulací**
    (Premating isolating bariers)
  - **Po kopulaci před vznikem zygoty**
    (Postmating, prezygotic isolating bariers)
  - **Po vzniku zygoty**
    (Postzygotic isolating bariers)



Klasifikace dle Coynne & Orr 2004: Speciation

- → Reproductive isolating bariers
  - **Premating** isolating bariers
    (behavioral, ecological, mechanical)
  - **Postmating, prezygotic** isolating bariers
    (copulatory behavioral isolation, competitive gametic isolation)
  - **Postzygotic** isolating bariers

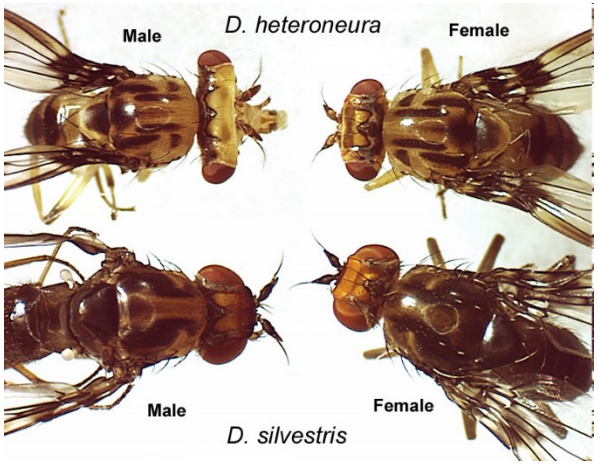
Behavioral isolating bariers

Ostrinia zavíječ
izolace díky feromonu
jeden lokus

- Námluvy, atrahování pomocí feromonů
- Genetic evolutionary forces
  - Selection on preference
  - Selection on trait
  - → produkt více genů
  - Vzácně však i jediný gen

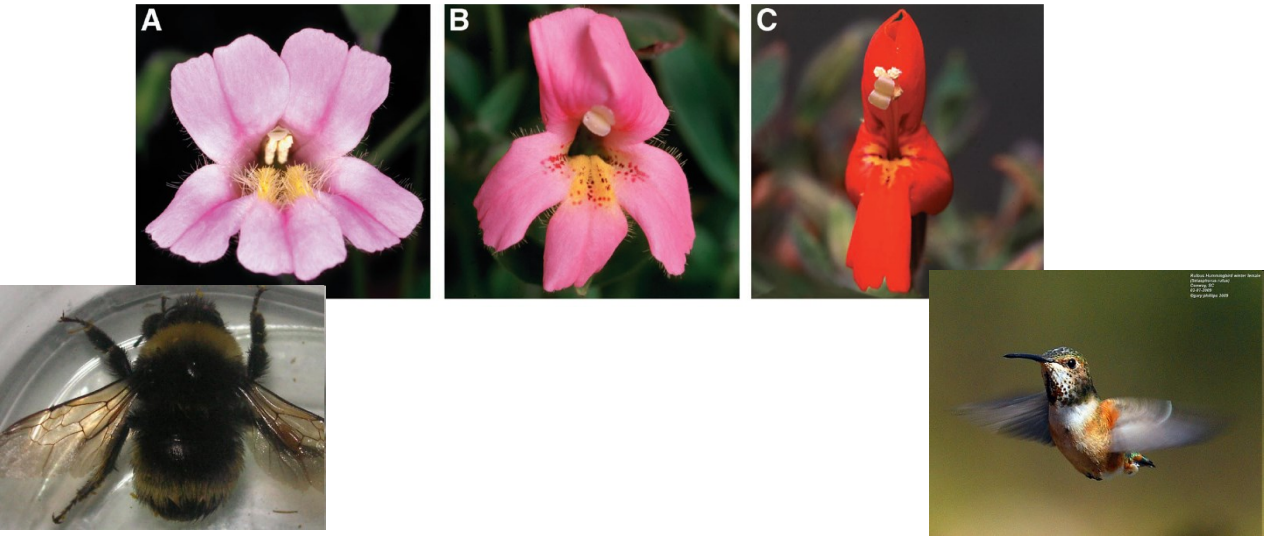
Magic trait – současně znak i preference

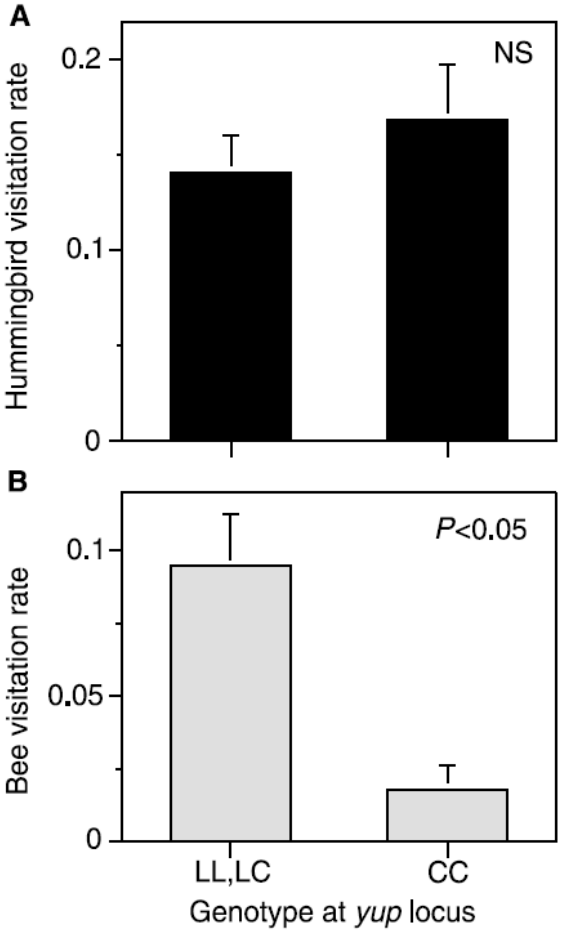
Laupala
cvrčení - více genů



D. silvestris and D. heteroneura
tvar hlavy důležitý při dvoření – více genů

bee-pollinated *Mimulus lewisii* and its hummingbird-pollinated congener *M. cardinalis*





Mimulus Kejklířka

- → Reproductive isolating bariers
  - **Premating isolating bariers (behavioral, ecological, mechanical)**
  - **Postmating**, prezygotic isolating bariers (copulatory behavioral isolation, competitive gametic isolation)
  - **Postzygotic** isolating bariers

Postmating, prezygotic isolating bariers

- **Noncompetitive isolation**
  - Poor movement, viability or storage of sperm in foreign reproductive tract
  - Poor crosss-attraction of gametes
  - Intrinsic gametic incompatibility

- **Competitive isolation**
  - Conspecific sperm (pollen) precedence

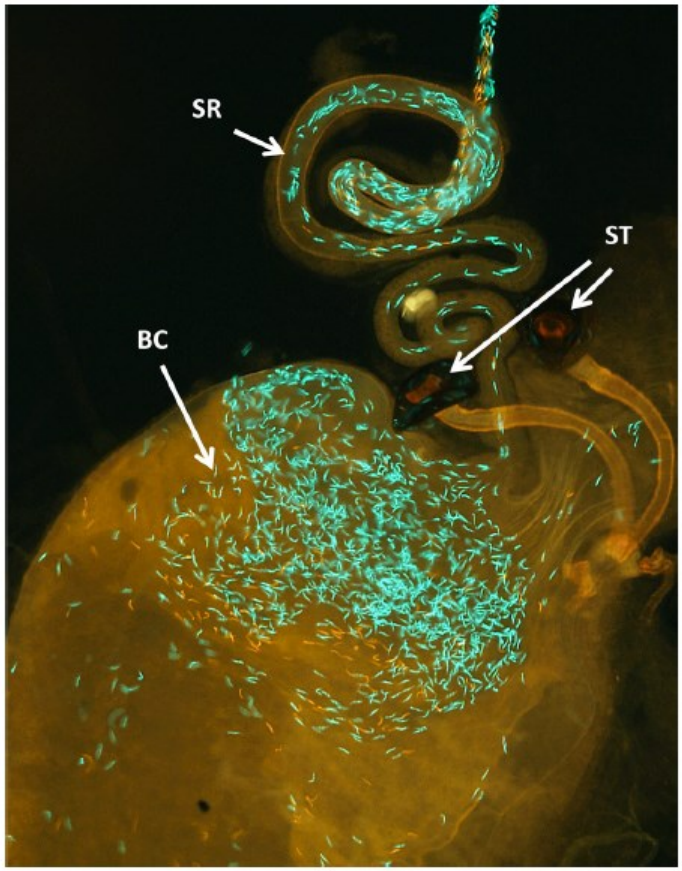
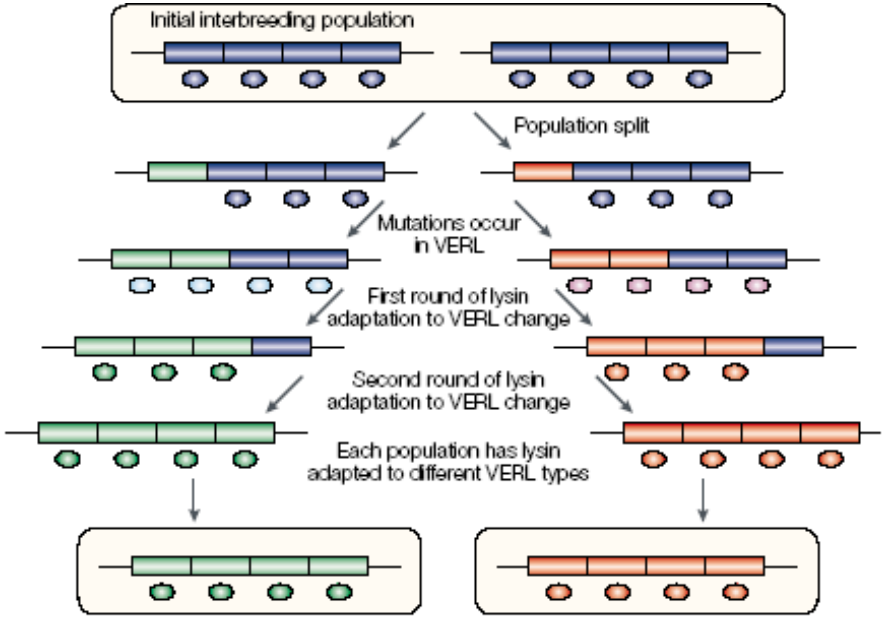


Figure 1. The image shows the lower reproductive tract (with ovaries excluded) of a twice-mated female *Drosophila simulans*. The female mated first with a heterospecific, *D. mauritiana* male producing sperm heads tagged with a red fluorescent protein (RFP). The female remated 2 days later to a *D. simulans* male producing sperm heads tagged with green-tagged (GFP) (the long sperm tails of *D. simulans* are not visible). The reproductive tract was dissected shortly after the second mating. The image shows green-headed conspecific sperm occupying the bursa copulatrix (BC; large region that serves as the site of insemination) and the female sperm-storage organs (the long, tubular seminal receptacle [SR], and the paired spermathecae [ST]). Numerous, red *D. mauritiana* sperm were displaced from the storage organs to the bursa copulatrix at the time of remating. Photo by Scott Pitnick.

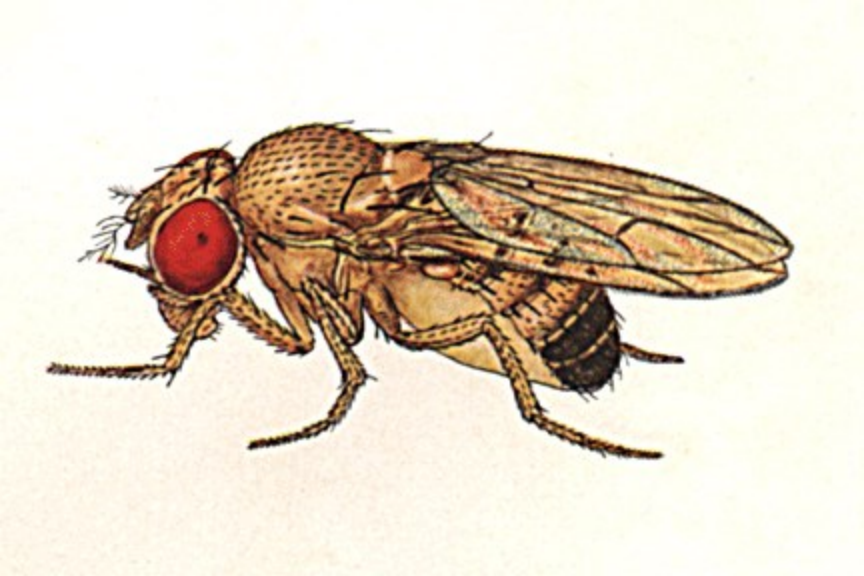
Lysin

Haliotis, Tegula

- Spermie vypouští před oplozením na povrch vitelinní membrány (obalu vajíčka) protein lysin
- Extrémně odlišná sekvence lysinu u různých druhů, pozitivní selekce ($d_N/d_S > 1$)
- Ve vitelinní membráně membráně receptor pro lysin VERL (fibrózní struktura), na něj se druhově specificky váže lysin → VERL ztrácí kohezi → otvor, kterým pronikne spermie dovnitř k buněčné membráně vajíčka
- VERL neutrální evoluce (22 repeatů)



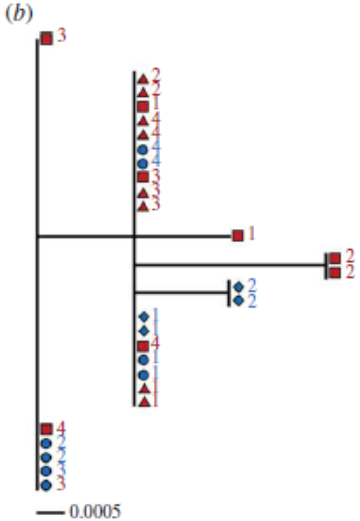
Drosophila

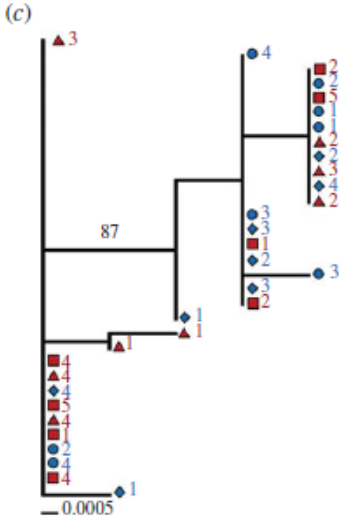


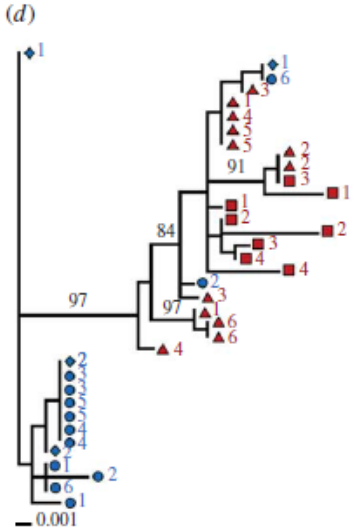
- Při kopulaci ♂ předá kromě spermií i přibližně 83 proteinů
- Dvakrát větší diversita než jiné proteiny *Drosophily*
- Protein přídatné žlázy *Acp26Aa* – jeden z proteinů s nejrychlejší evolucí u *Drosophily*
- *D. suzukii* a *D. pulchrella* normálně po mezidruhové kopulaci nevznikne potomstvo.
  Při přidání proteinů z přídatných žláz ze stejného druhu, jako je ♀
  → vznik hybridů

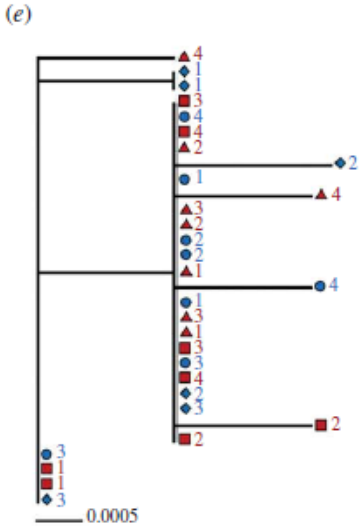
Andrés et al. 2008

Gryllus firmus and *Gryllus pennsylvanicus*









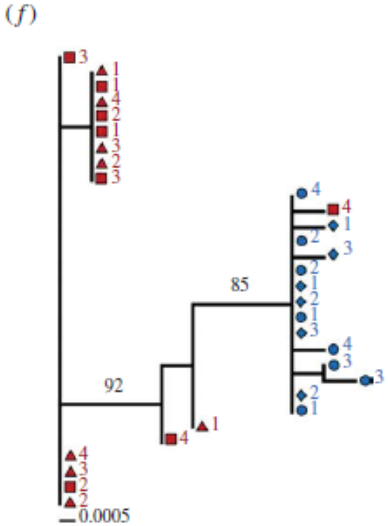


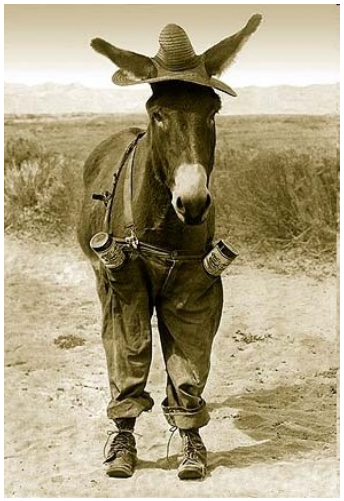
Figure 1. Contrasting DNA gene genealogies between control ((*b*) *COQ7* and (*c*) *GuKc*; *PPase* not shown owing to absence of variation) and seminal protein genes ((*d*) *AG-0005F*, (*e*) *AG-0308F* and (*f*) *AG-0334P*). (*a*) The map shows the approximate location of the hybrid zone (dashed line) between *G. firmus* (blue) and *G. pennsylvanicus* (red), and the location of the populations sampled in this study. Numbers on the branches represent bootstrap support values over 75%. Numbers after symbols represent the identity of the individuals sequenced. Scale bars represent divergence measured as substitutions per nucleotide. Note the scale differences between *AG-0005F* and all other loci.

Postzygotické izolační bariéry

- **Vnější**
  - Ecologická neživotaschopnost *(ecological inviability)*
  - Behaviorální sterilita
- **Vnitřní**
  - Hybridní neživotaschopnost
  - Hybridní sterilita

Helianthus

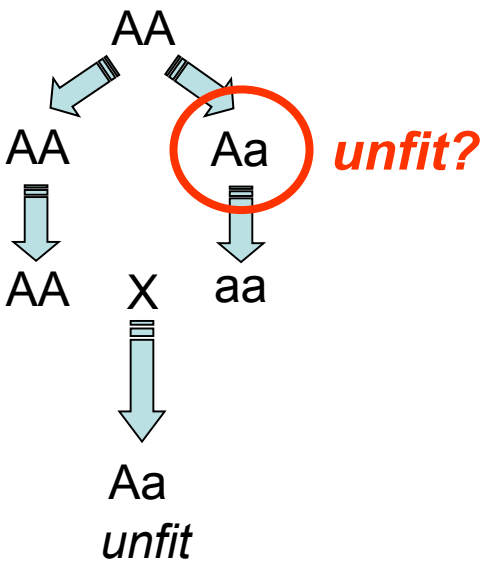
Schizocosa ocreata and S. rovneri

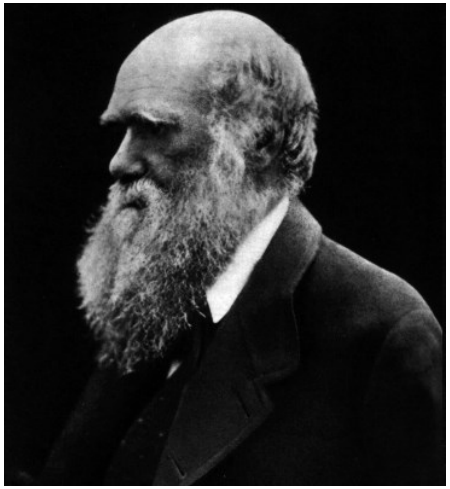


Inviable - unable to survive or develop normally

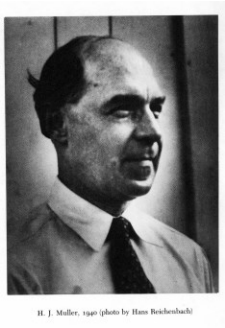
Vnitřní postzygotické izolační bariéry

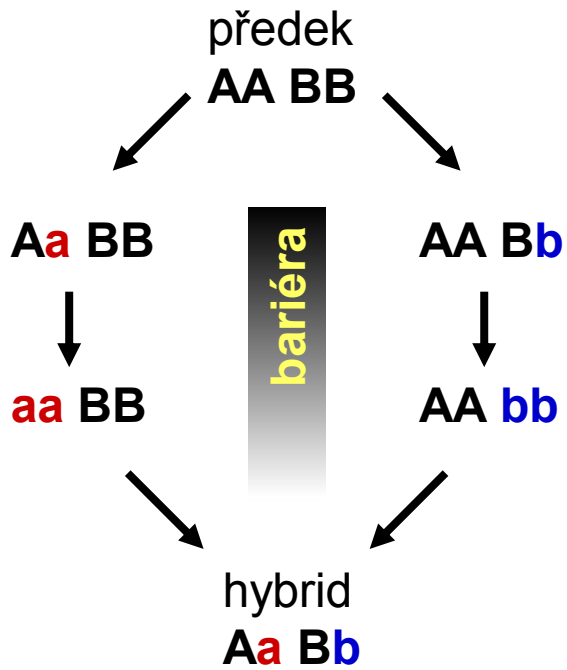
- Darwinovo dilema

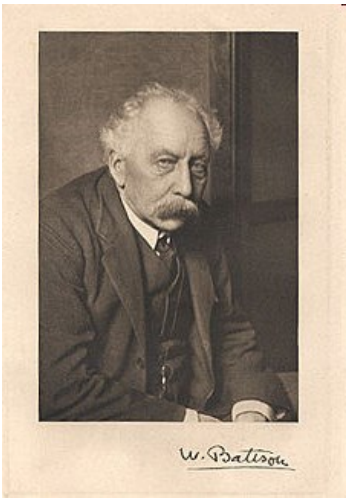




Model Dobzhanského a Mullera
(BDM model)







BDM model

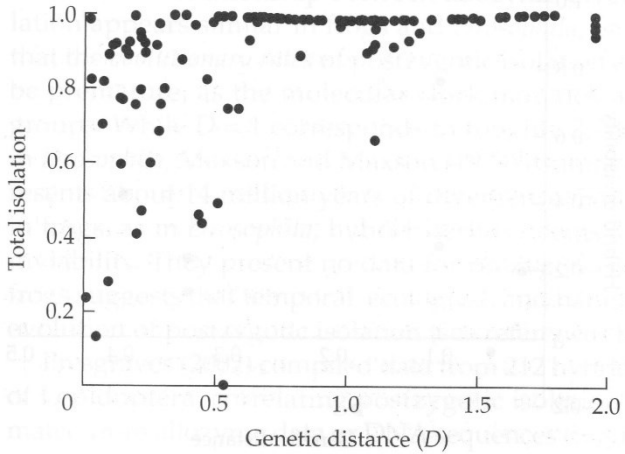
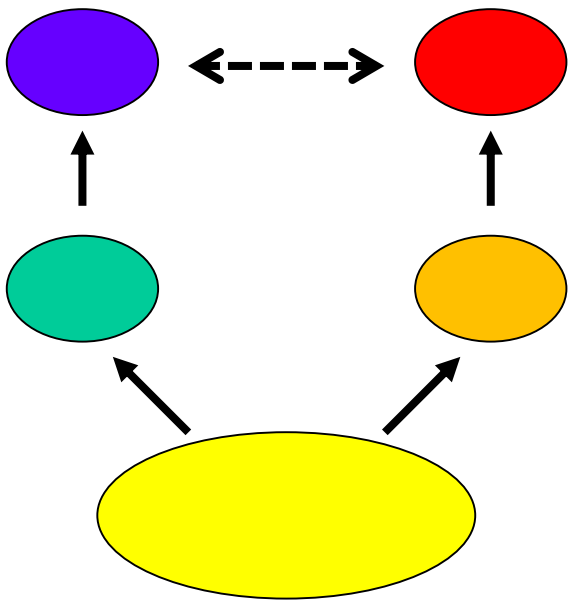
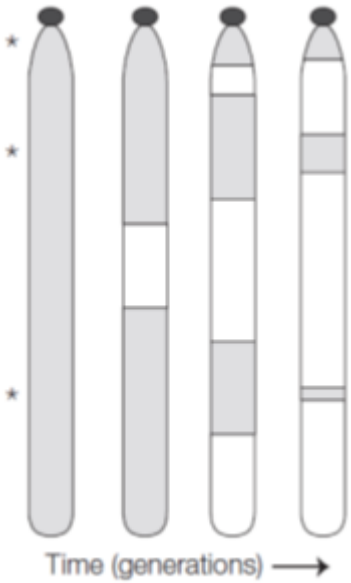


Figure 2.3 Time course for the evolution of "total" reproductive isolation (behavioral + postzygotic isolation) between pairs of *Drosophila* species. (From Coyne and Orr 1997.)

- Interakce i více než 2 genů
- I slabý efekt
  – kumulativní působení
  mnoha nekompatibilit
- „Snowball effect"
  efekty se lavinovitě nabalují
- Nutnost studovat druhy ve stavu vzniku
  (jen částečná reprodukční izolace)




Time (generations)

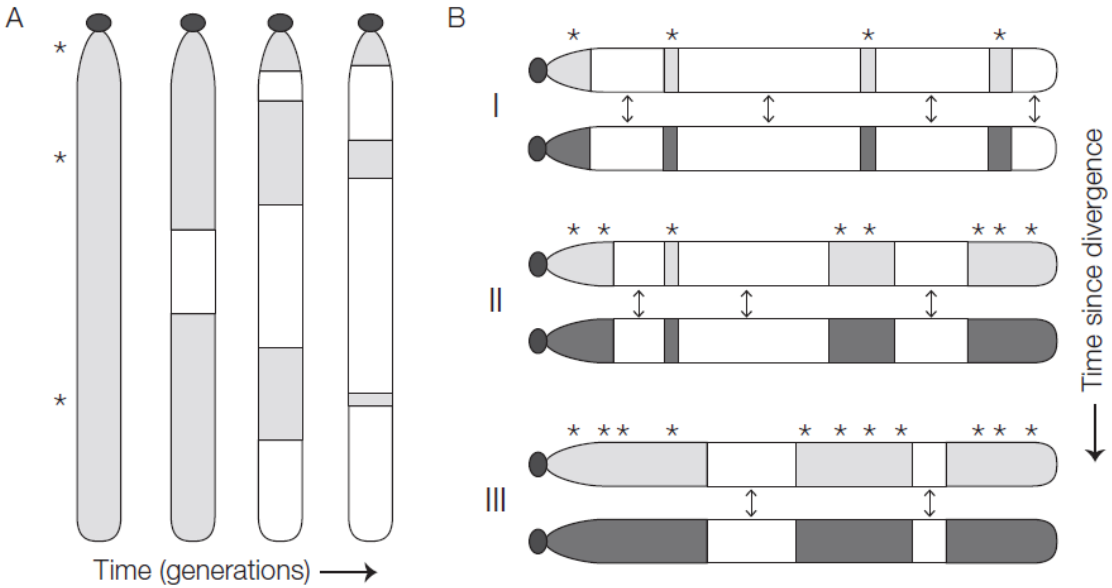
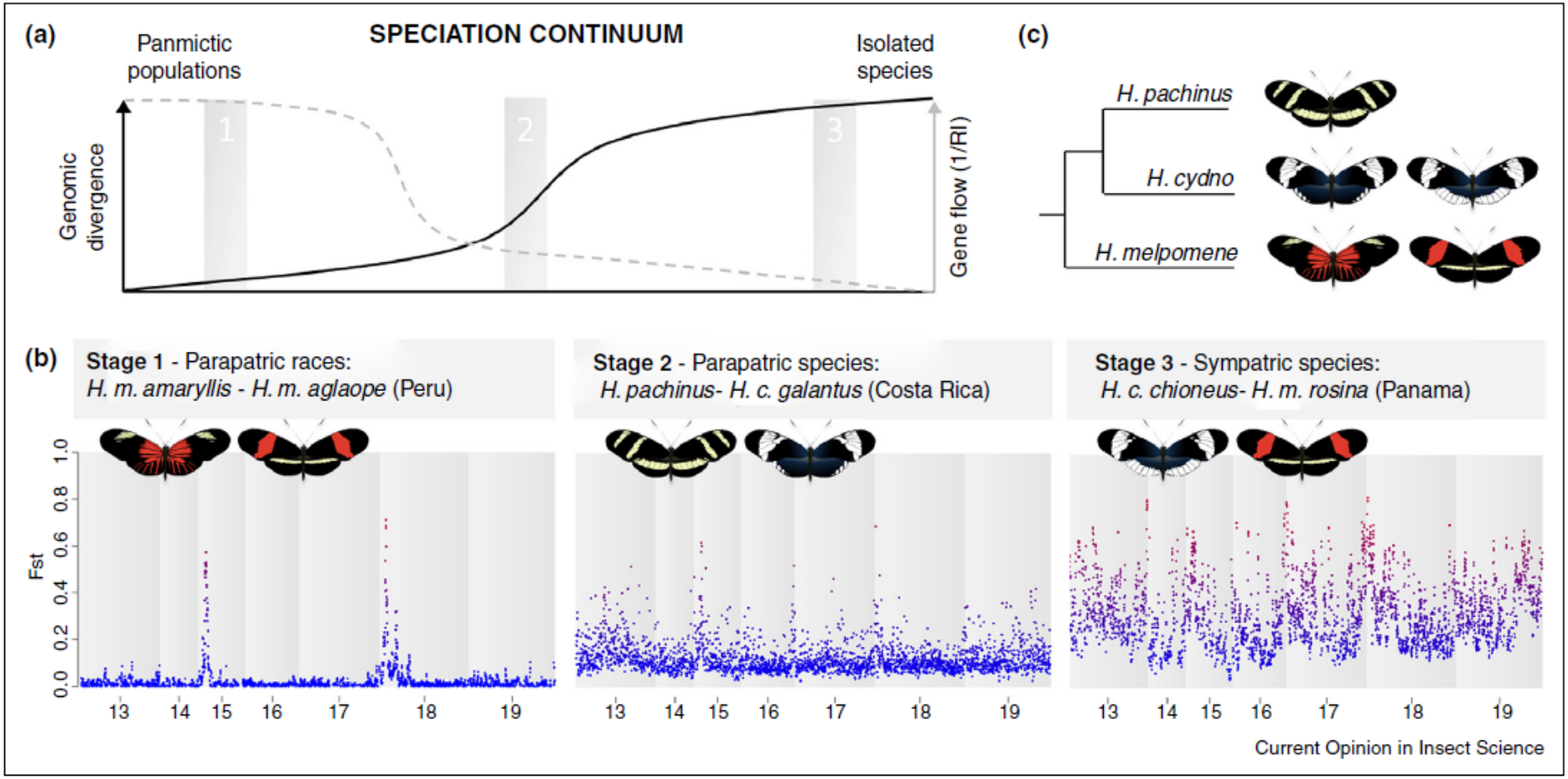


Figure 1. Classic illustrations of the semipermeable nature of species boundaries. (**A**) Gene flow following secondary contact as depicted by Barton and Hewitt (1981). The vertical bars represent a chromosome with 3 loci contributing to reproductive barriers (indicated by *). Immediately after contact, linkage disequilibrium along the chromosome will be high, but over time recombination breaks down associations among loci. Barrier genes or genes under divergent selection will remain differentiated (light gray regions), whereas alleles at loci that are neutral (white regions) will be exchanged between species. Many generations of recombination in hybrid zones allow fine-scale mapping of genes contributing to reproductive isolation and estimates of the strength of selection on individual alleles. (**B**) The idea that the genomes of diverging lineages become less permeable over time, as shown by Wu (2001). Each pair of horizontal bars represents chromosomes of 2 diverging lineages. Very recently diverged species (pair I) may have few genes contributing to reproductive isolation (indicated by *). These regions will remain differentiated (represented by light and dark gray regions), whereas gene exchange can occur in other parts of the genome (white regions). With increasing genetic divergence (chromosome pairs II and III), an increasing number of loci contribute to reproductive barriers, thus restricting gene flow for a greater proportion of the genome.



Arias et al. 2016

Postzygotické izolační bariéry

- **Dvě empirická pravidla** *(Two rules of speciation)*

- **Haldaneovo pravidlo**

  When in the offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous (heterogametic, i.e., XY or ZW) sex.

  Problémy u hybridů jsou převážně u heterogametického pohlaví

- **Velký efekt chromosomu X** *(Large X effect)*

  Genes having large effect on postzygotic isolation often map to the Chr X

  Geny postzygotické izolace jsou často na Chr X.

  Ptáci – Chr Z

Haldane's rule

- The dominance theory

Autosomal loci

aaBB X **AAbb**

samice *samec*

a *is incompatible with* **b**

aABb Both factors dominant → inviability

A is X-linked

aaBB X **Abb**

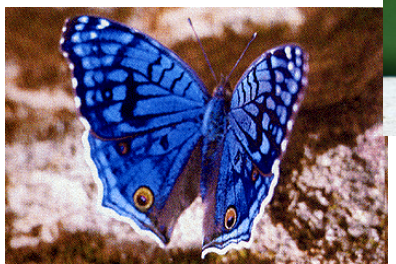
samice *samec*

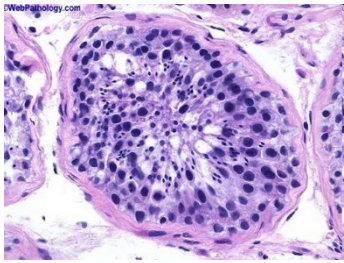
dominant **aABb** **aBb** dominant and recessive

samice *samec*

Faster male theory

- Spermatogenesis – inherently sensitive process
- Sexual selection – faster evolution of male-expressed genes
- Insects: groups where females mate with many males
  → higher rates of speciation
- ? Lepidoptera, birds ?





Velký efekt chromosomu X *(Large X effect)*

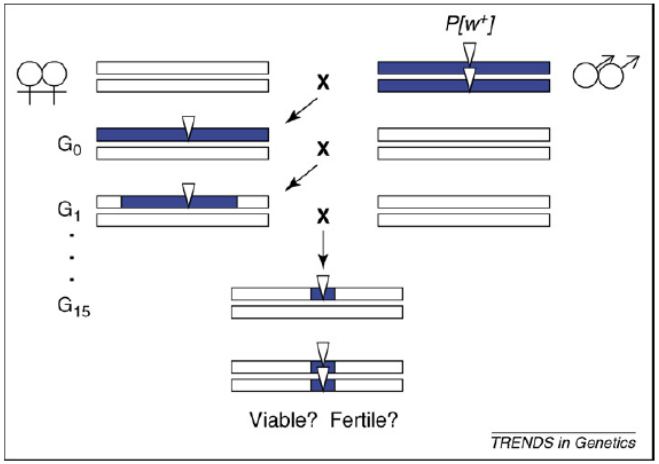
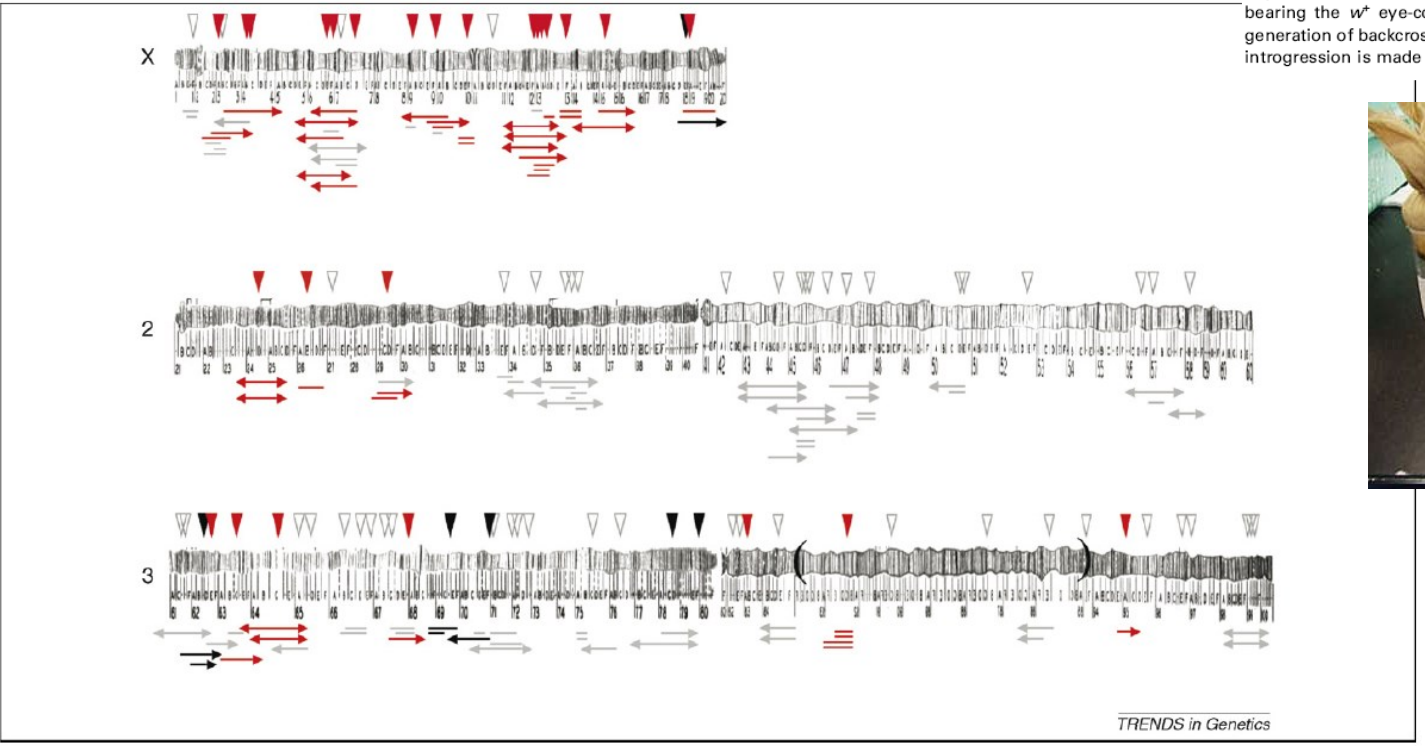


Figure 2. Introgression analyses of hybrid incompatibilities. Introgression studies move small chromosomal regions from one species (purple bars) into the genomic background of a closely related sister species (white bars) by repeated backcrossing through fertile hybrid females. Introgressed chromosomal segments typically bear a selectable dominant genetic marker (e.g. a *P*-element bearing the w^+ eye-color marker and become progressively smaller with each generation of backcrossing. After several generations of backcrossing, the foreign introgression is made homozygous and tested for its effects on hybrid fitness.



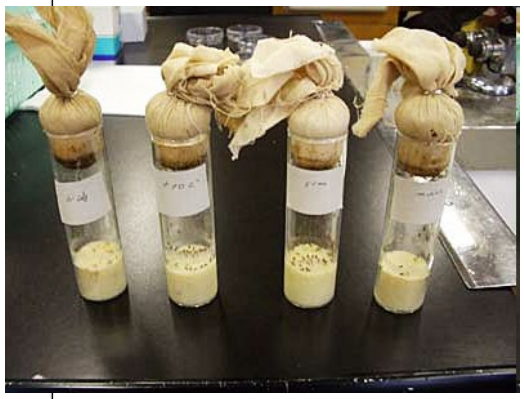


Figure 3. The X chromosome is a hotspot for hybrid male sterility factors. The density of introgressions from *Drosophila mauritiana* that cause hybrid male sterility (red triangles) in an otherwise *Drosophila sechellia* genomic background is four times higher on the X chromosome than on chromosomes 2 and 3. A chromosomal inversion is bracketed by parentheses on chromosome arm 3R. Gray and black triangles mark fertile and hybrid lethal introgressions, respectively. Introgression sizes are depicted beneath the chromosomes (modified from Ref. [16]).

Velký efekt chromosomu X *(Large X effect)*

- ? Rychlejší evoluce Chr X *(faster X-theory)*
- *Mus, Drosophila* sporné výsledky
- Platí pro Chr Z u ptáků a motýlů
- Pozor, pro např. X dále platí:
  - Není rekombinace u samců
  - Nižší Ne

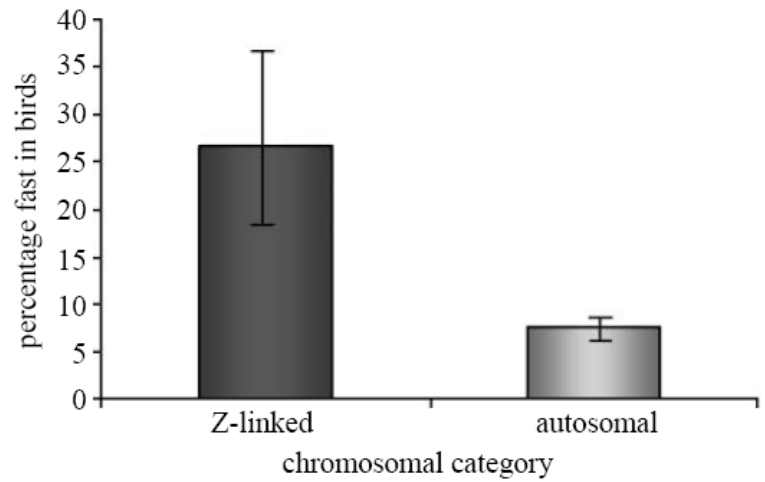
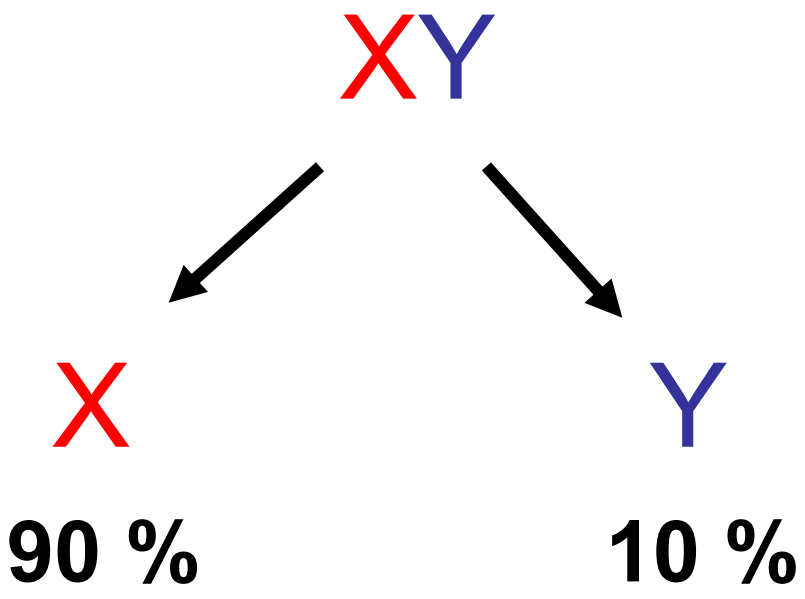


Figure 2. The percentage of Z-linked and autosomal genes, respectively, identified as evolving faster in birds than in mammals. Error bars represent 95% confidence intervals of the proportions.

Velký efekt chromosomu X *(Large X effect)* a intragenomický konflikt *(drive)*

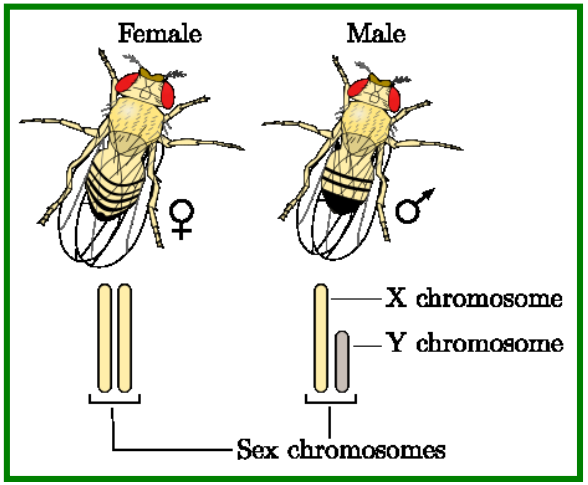
Drive a pohlavní chromosomy

- → vychýlení poměru pohlaví
- → evoluce supresorů na Y i autosomech



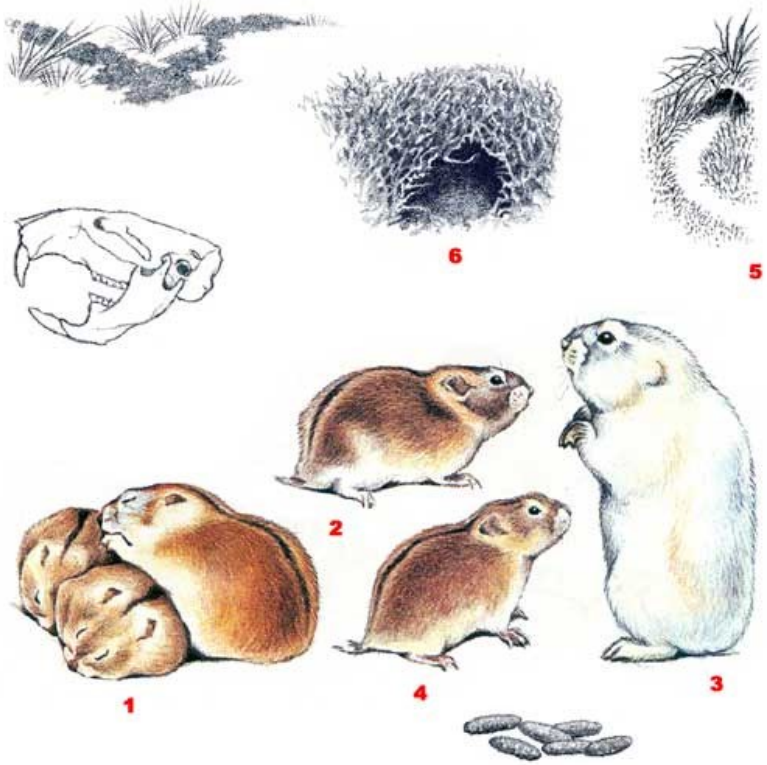
Killer X^K

- *Drosophila*
- Snížení produkce spermií na méně než polovinu
- → tedy i některé X^K spermie zničeny
- Inverze (proti rekombinaci s X)
- Evoluce supresorů na Y i autosomech
- Se supresory 54-58% dcer
- Bez supresorů 80-100%



U některých komárů Killer Y
Větší Y podobný X

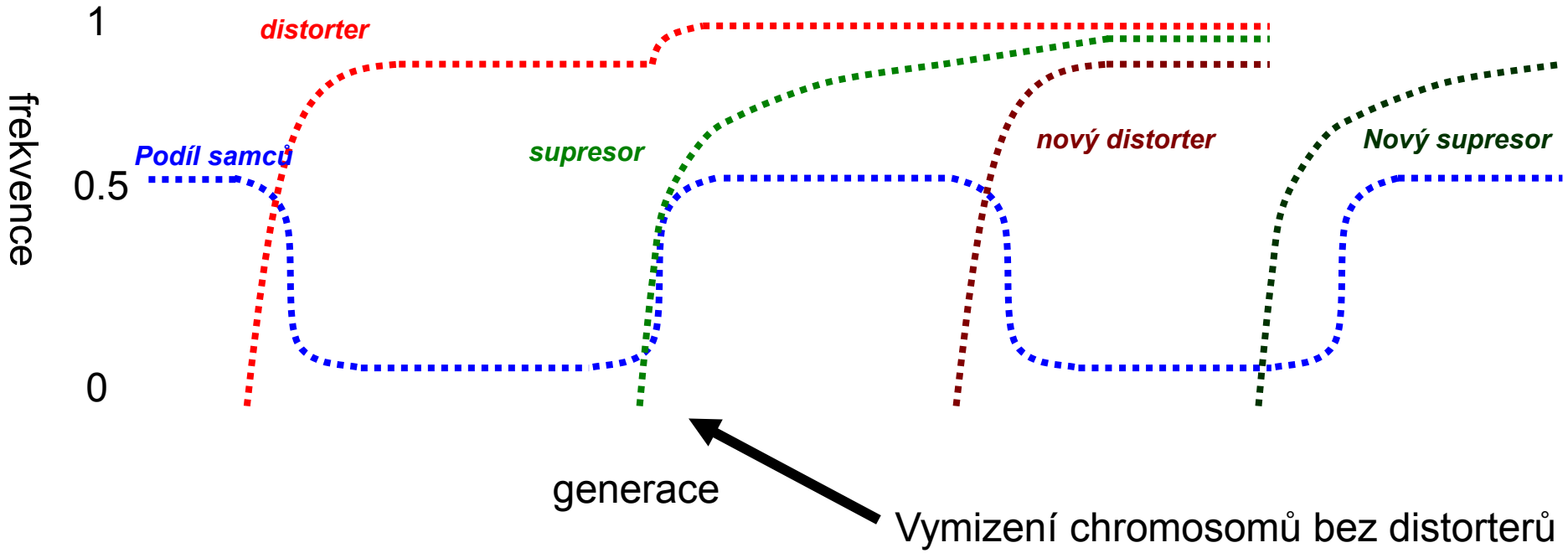
Feminizující X* u lumíků

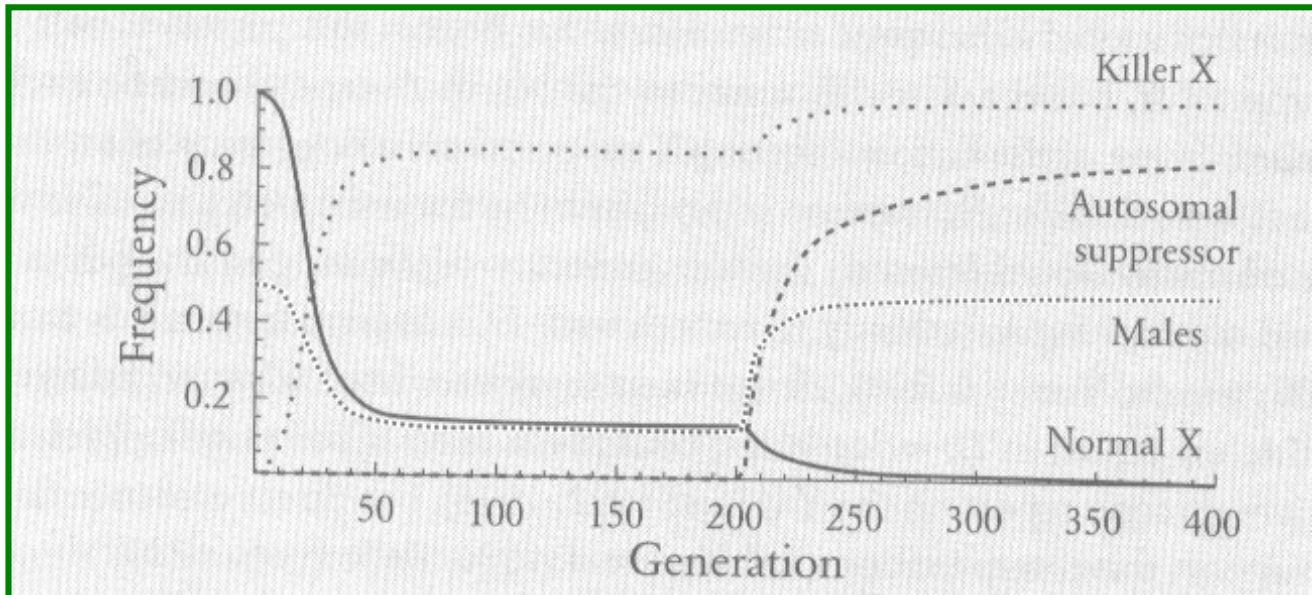


- *Dicrostonyx torquatus*
- XX, XX*, X*Y samice
- XY samci
- X*Y →Y vajíčka,
  YY zygota zahyne

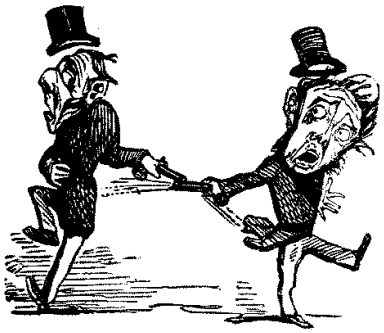
- XY samci mají více synů: 56%

- *Myopus schisticolor*
- X*Y samice produkují jen X*vajíčka
  (a ne Y vajíčka)
- X*Y samice zdatnější než XX* a XX
- Rodí se až 80% samic, z nich až 40% X*Y


1
0.5
0
frekvence
distorter
Podíl samců
supresor
nový distorter
Nový supresor
generace
Vymizení chromosomů bez distorterů

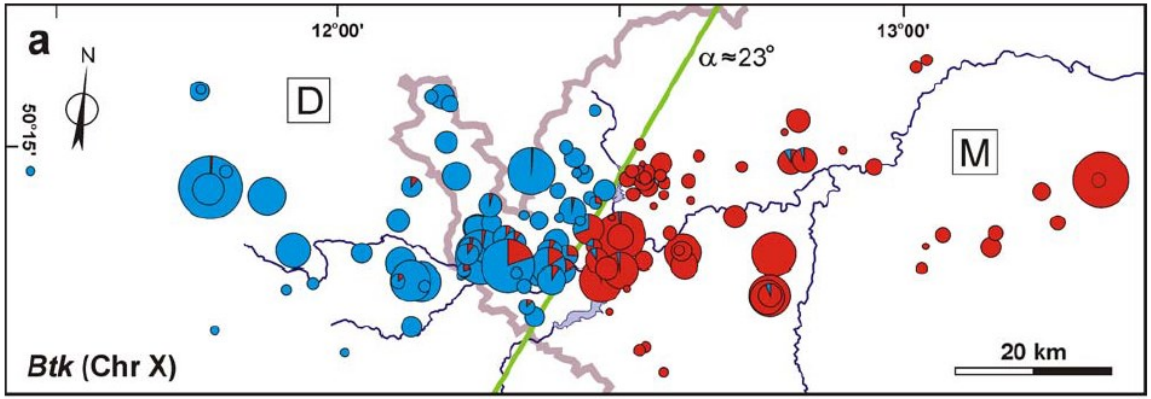

Killer X
Autosomal suppressor
Males
Normal X
Frequency
1.0
0.8
0.6
0.4
0.2
50
100
150
200
250
300
350
400
Generation

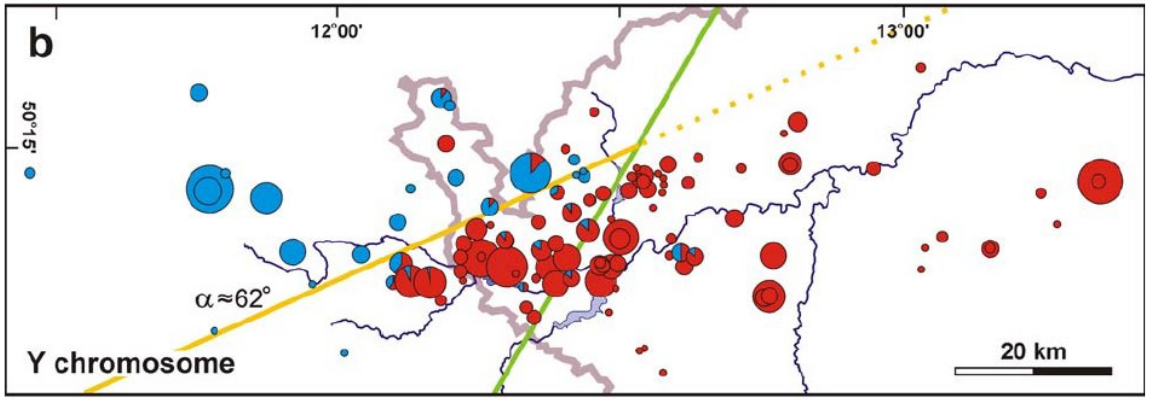
Drive a vznik bariér

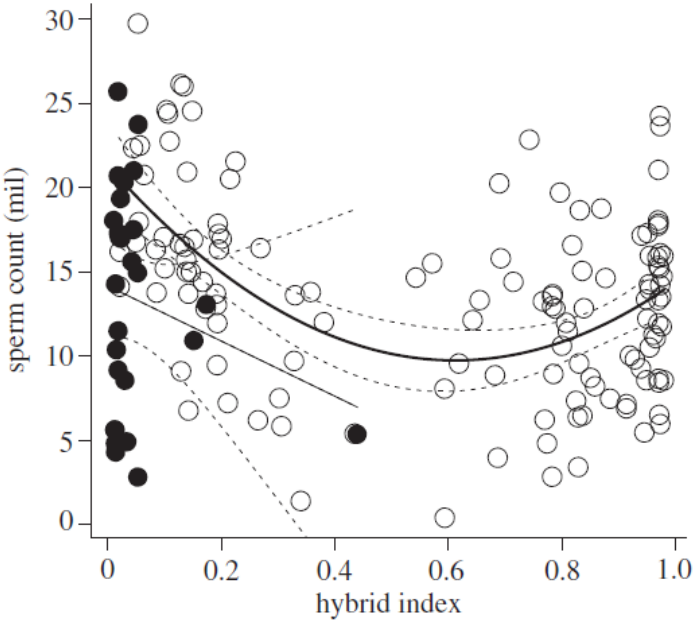


- Nezávislé „vlny“ distorterů a supresorů u různých druhů
- U hybridů distortery opět bez supresorů → drive
- Různé distortery → sterilita
- Teoreticky předpovězeno (Frank 1991, Hurst & Pomiankowski 1991)
- Potvrzeno u octomilek
- *Too much yin*, *Overdive*
  drive i sterilita hybridů
- → silná reprodukční bariéra

Anti-speciation gene: a gene that constrains speciation by mediating increased gene flow and reduced reproductive isolation between populations.
Conflictual speciation: a mechanism of speciation whereby genomic conflicts drive the evolution of reproductive isolation.

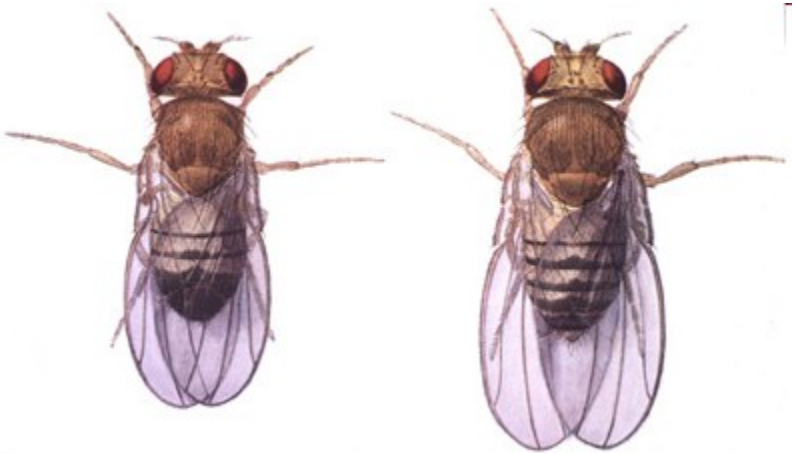






Jiné mechanismy

Translokace genů



- *Drosophila*
- *JYAlpha* zásadní pro funkci spermií
- *D. melanogaster* Chr 4
- *D. simulans* Chr 3

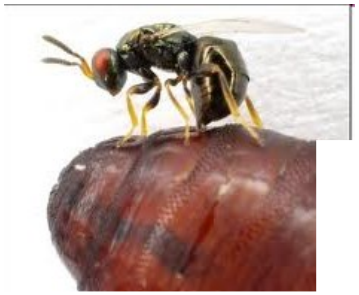
…a další

- Odlišné bloky heterochromatinu u rodičovských druhů → poruchy mitózy → smrt hybridů

- Odlišná transkripční inaktivace Chr X v časných stadiích spermatogeneze → sterilita

- Interakce s prostředím:
  zvýšení teploty → zesílení bariér

- Transposony, cytonukleární konflikty, imprinting…



Coupling – kombinace bariér

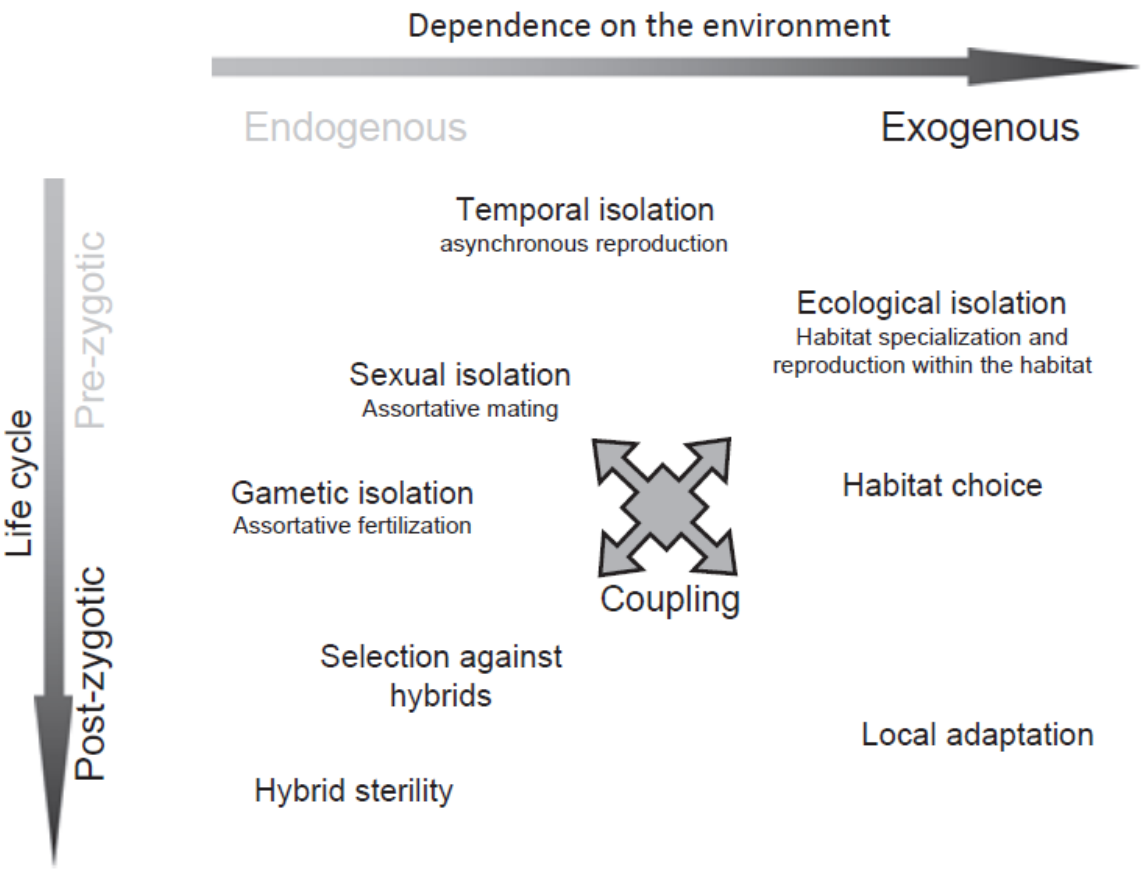
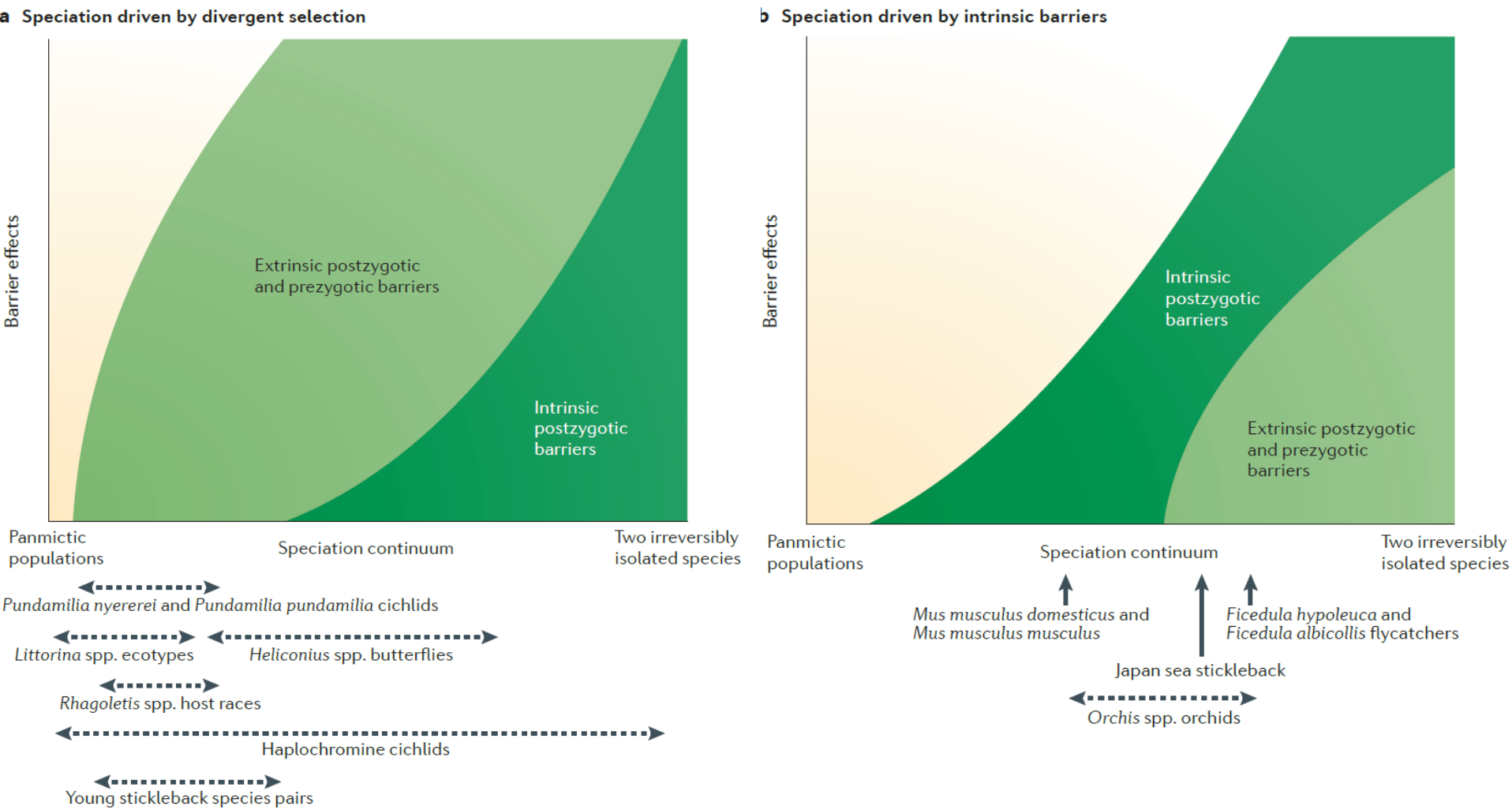


Fig. 1 Coupling can bring together the effects of barriers of any type. Four major domains of reproductive isolation are defined by the prezygotic–postzygotic and endogenous–exogenous axes but some forms of isolation do not fall neatly into these domains.

Reinforcement - Selection for the strengthening of prezygotic barriers to avoid the production of unfit hybrids between taxa that have previously evolved some postzygotic isolation.


a Speciation driven by divergent selection
Barrier effects
Extrinsic postzygotic and prezygotic barriers
Intrinsic postzygotic barriers
Panmictic populations
Speciation continuum
Two irreversibly isolated species
Pundamilia nyererei and Pundamilia pundamilia cichlids
Littorina spp. ecotypes
Heliconius spp. butterflies
Rhagoletis spp. host races
Haplochromine cichlids
Young stickleback species pairs
b Speciation driven by intrinsic barriers
Barrier effects
Intrinsic postzygotic barriers
Extrinsic postzygotic and prezygotic barriers
Panmictic populations
Speciation continuum
Two irreversibly isolated species
Mus musculus domesticus and Mus musculus musculus
Ficedula hypoleuca and Ficedula albicollis flycatchers
Japan sea stickleback
Orchis spp. orchids

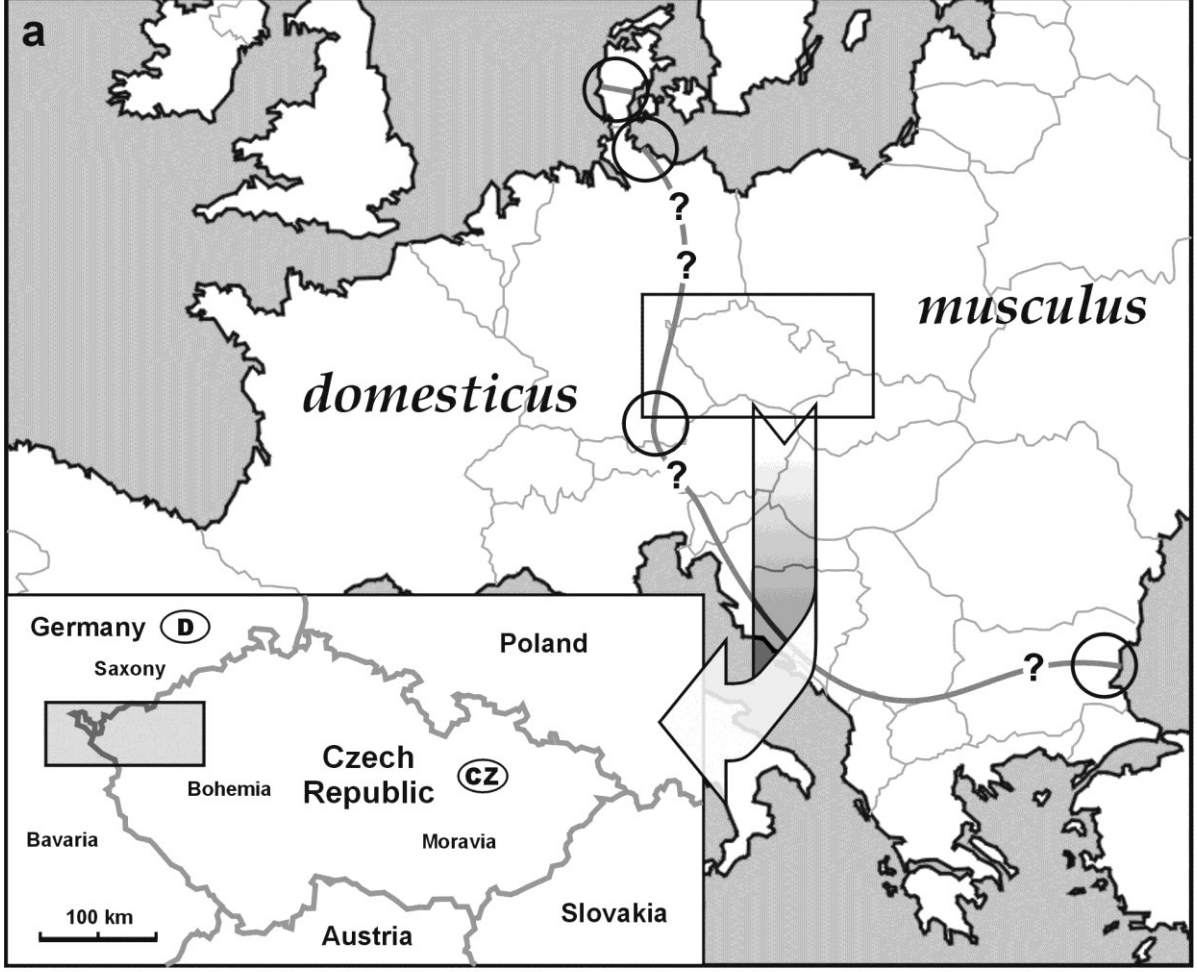
Experimental hybridization

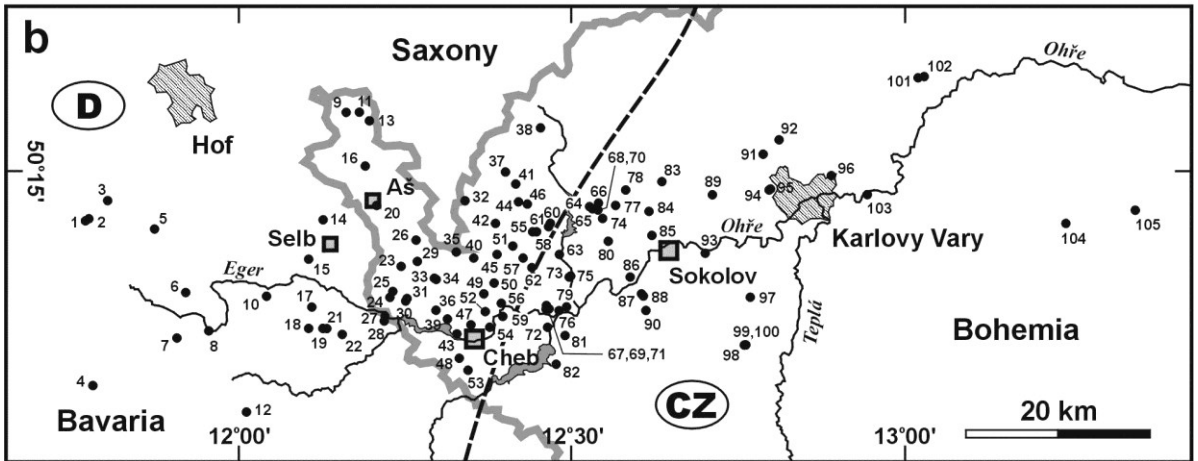
Speciační geny

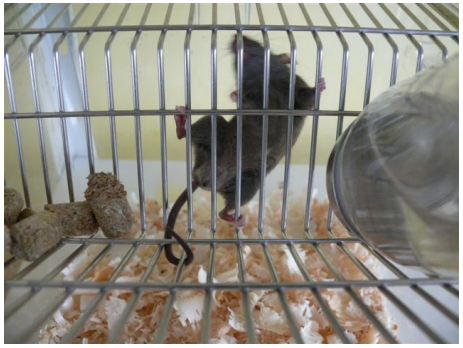
- *Xiphophorus*
  - *Xmrk-2*
- *Drosophila*
  - *OdsH*
  - *Hmr*
  - *Nup96*
  - *Lhr*
  - *a další*
- *Myš*
  - *Prdm9*
- Normální (ne nové) geny
- Nejrůznější funkce
- Nutná interakce s jinými geny (BDM model)
- Rychlá evoluce

Experimental hybridization

Natural hybridization


a
musculus
domesticus
?
?
?
?
Germany
D
Saxony
Poland
Czech
Republic
CZ
Bohemia
Bavaria
Moravia
100 km
Austria
Slovakia


b
Saxony
D
Hof
50°15'
Aš
Selb
Eger
Ohře
Ohře
Karlovy Vary
Sokolov
Teplá
Bohemia
Cheb
67,69,71
CZ
Bavaria
12°00'
12°30'
13°00'
20 km



Clines

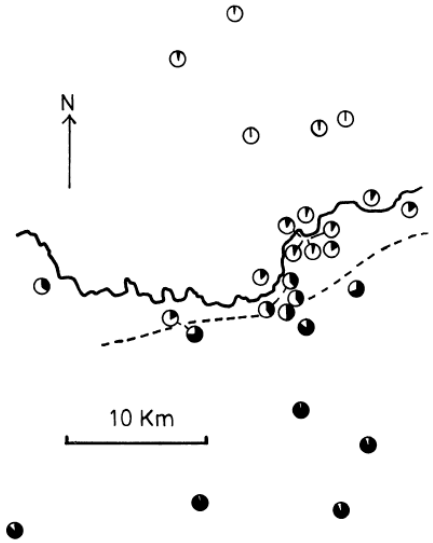
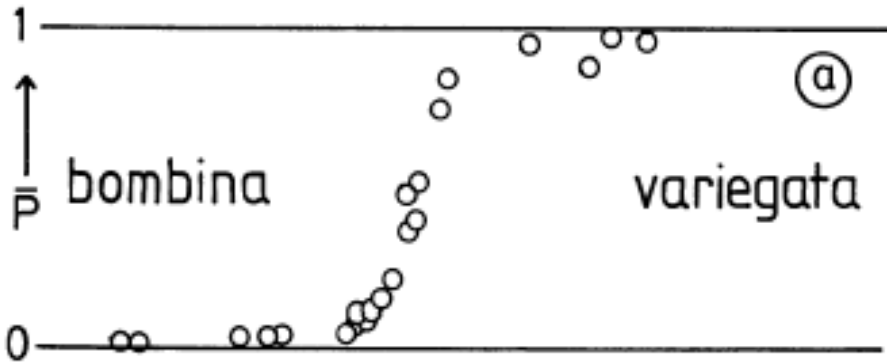
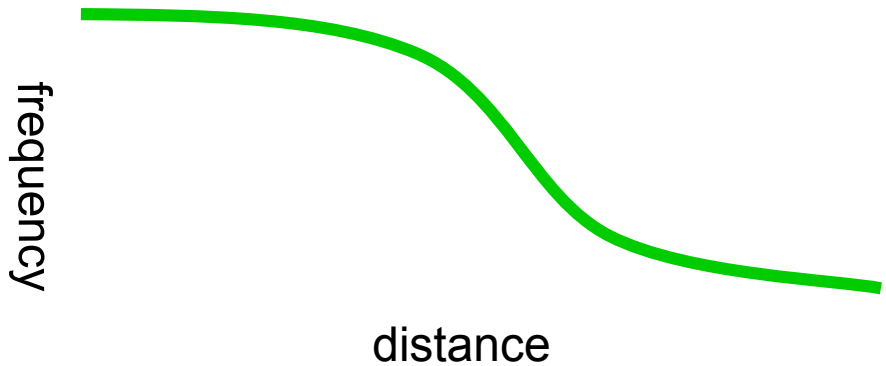
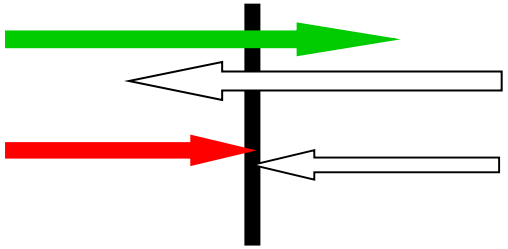


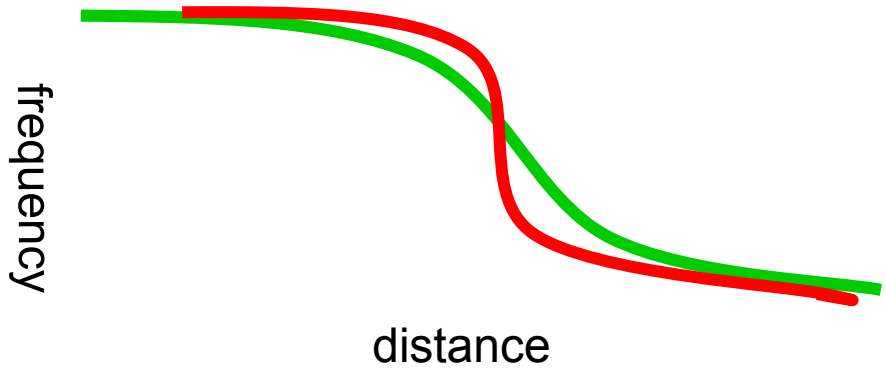
FIG. 2. The average frequency of *variegata* alleles across the transect near Cracow. The morphological hybrid zone (Michałowski, 1958) is indicated by the dotted line, and the Vistula by the thicker line.

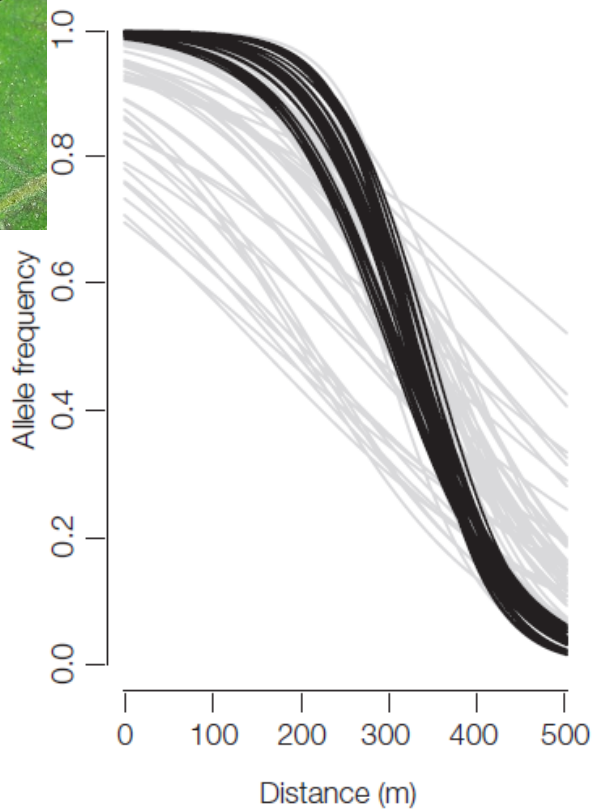




frequency
distance







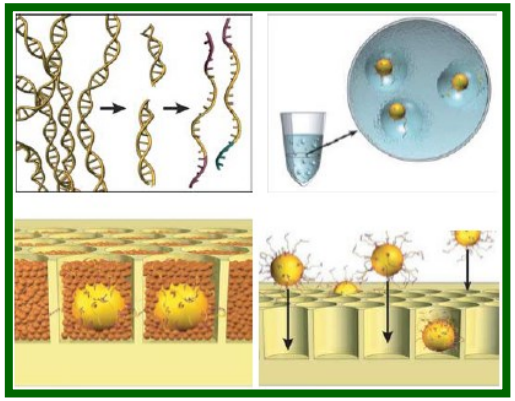
N. Barton
Teorie HZ

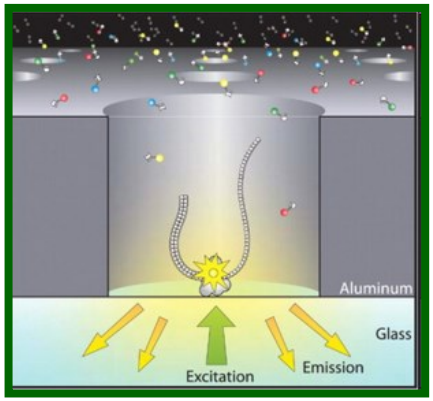
Kolik genů na začátku způsobí bariéru?

- Laboratoře
  - Jeden či několik genů

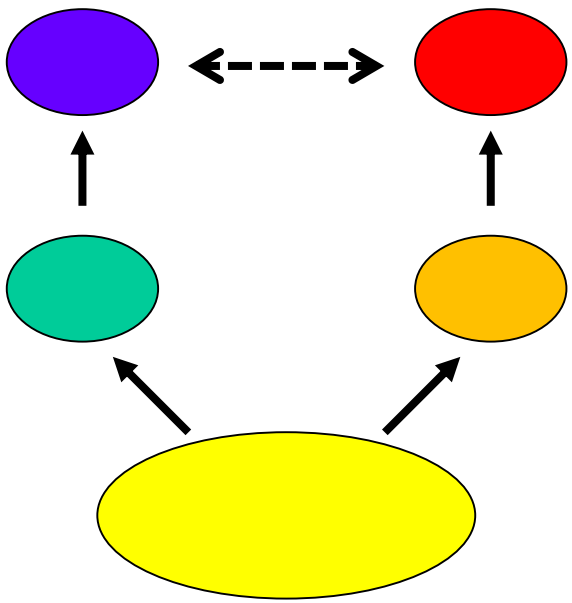
- Příroda, hybridní zóny
  - Desítky až stovky genů

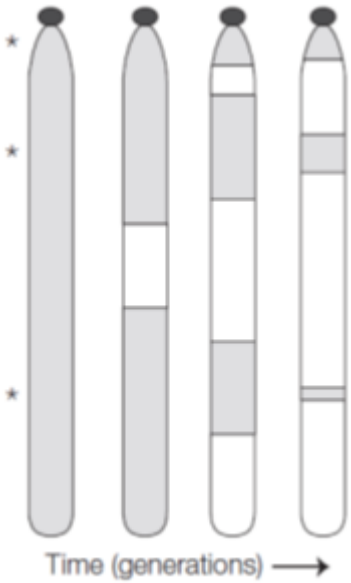
Populační genetika → populační genomika

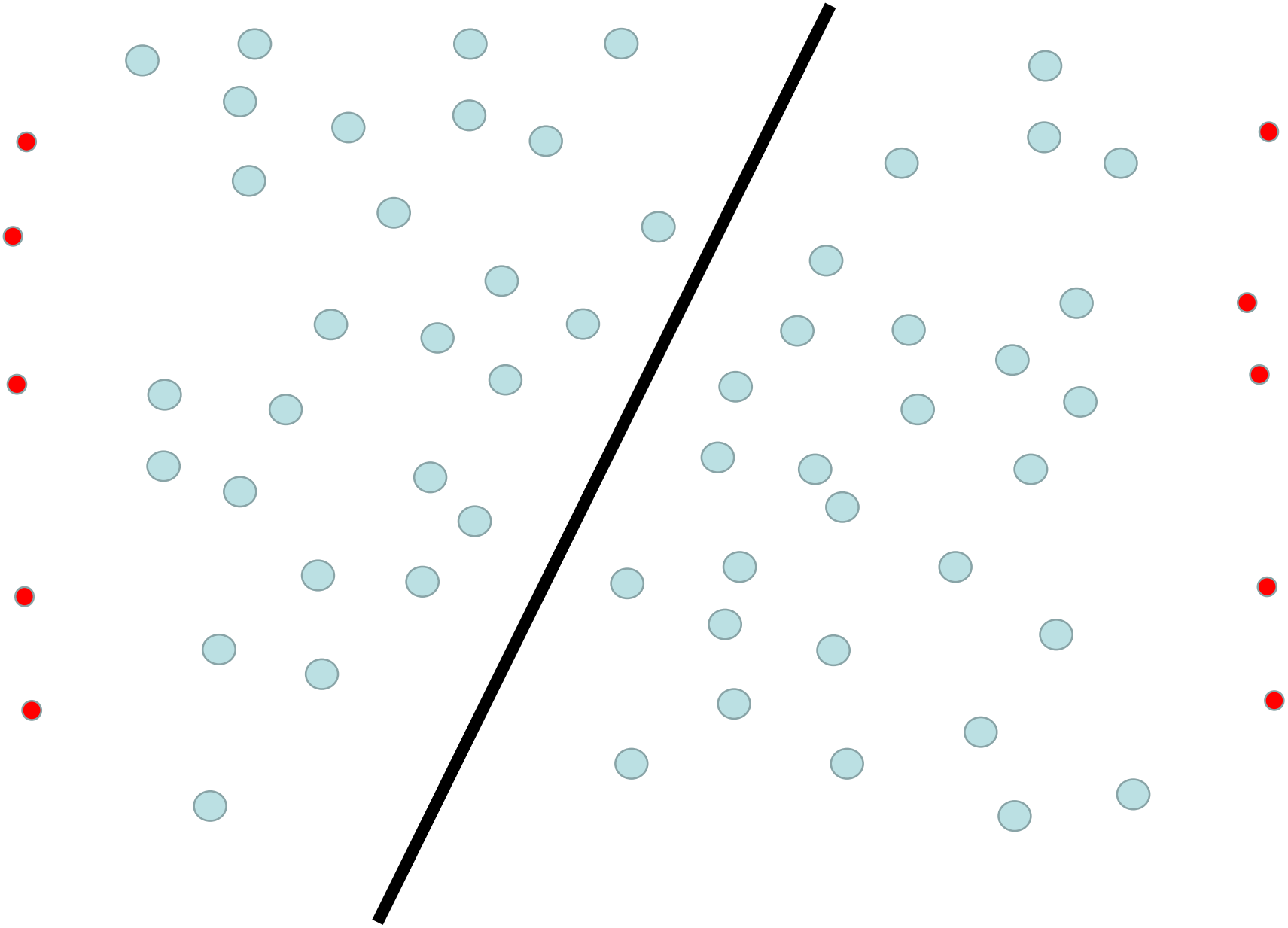




3rd-gen sequencing




Time (generations)



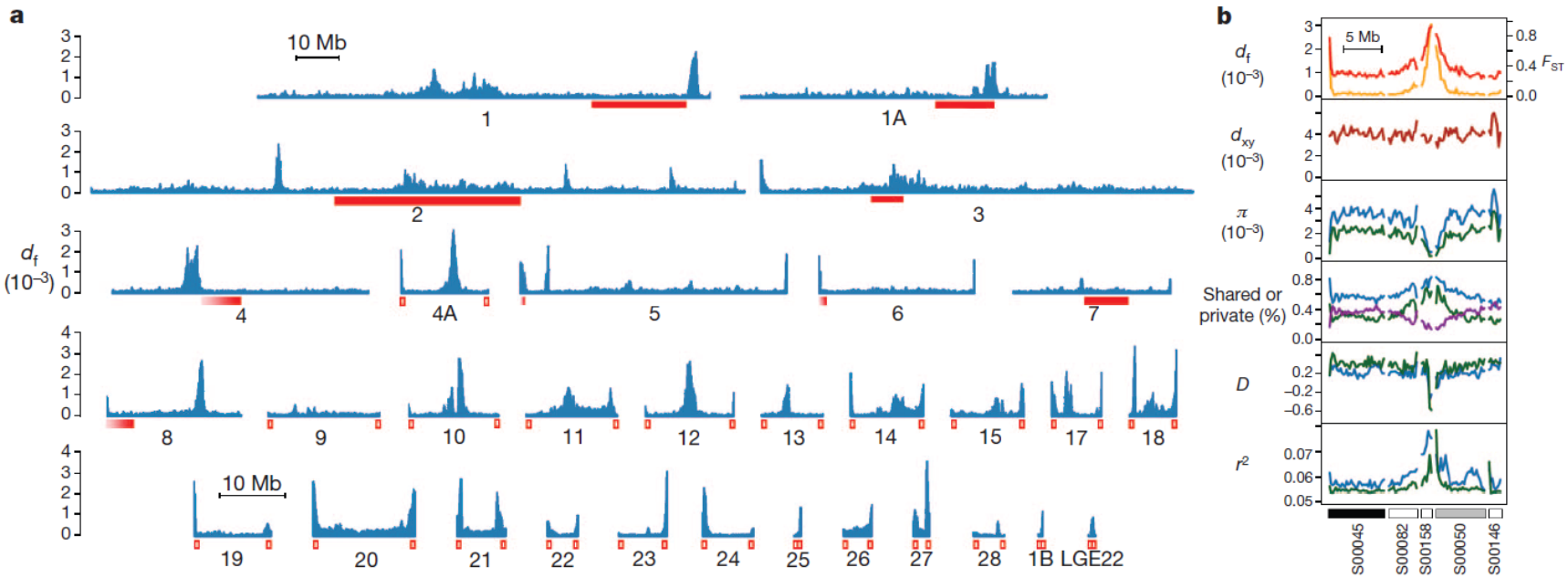
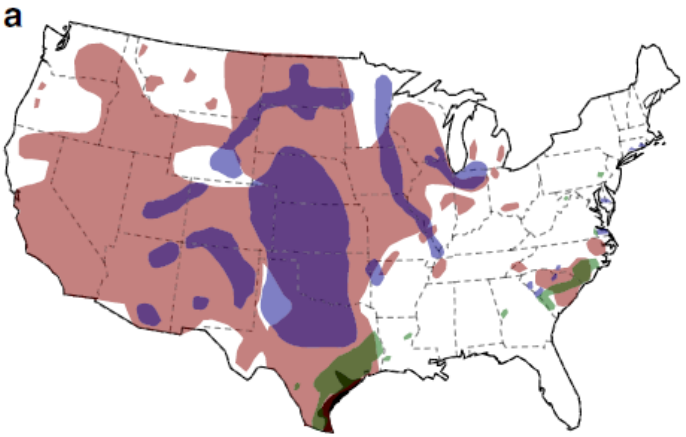


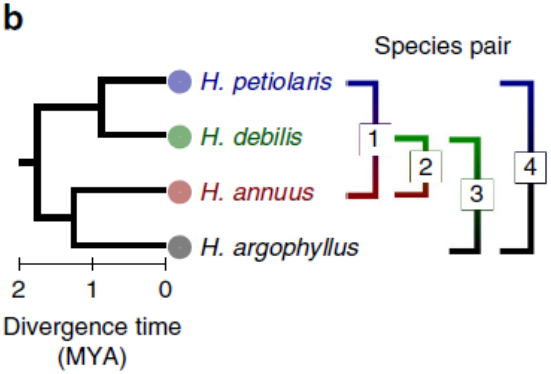
Figure 2 | The genomic landscape of species divergence in flycatchers. **a**, Distribution of divergence measured as the density of fixed differences per bp for 200-kb windows across the genome. Chromosomes are listed in numerical order and are separated by gaps. Red horizontal bars show the approximate location of centromeres in homologous chromosomes of zebra finch. Open read symbols are used to indicate that avian microchromosomes are generally acro- or telocentric; both ends of these chromosomes are labelled as the orientation is not known. For chromosomes 4, 6 and 8, there is a lack of an *in situ* mapped marker 5′ of the centromere in zebra finch. **b**, Distribution of population genomic parameters along an example chromosome (chromosome 4A). The plots show the density of fixed differences per bp (d_f) (yellow), F_{ST} (red), the total between-species sequence divergence (d_{xy}), nucleotide diversity (π) for each species, the proportion of shared polymorphisms among sites polymorphic in at least one species (purple), the proportion of private polymorphisms among sites polymorphic within species (private and shared polymorphisms shown in the same panel), Tajima's *D*, and linkage disequilibrium (r^2). For π, private polymorphisms, *D* and r^2, species-specific estimates are given for collared flycatcher in blue and for pied flycatcher in green. Assigned scaffolds are shown under the plot: black, denoting scaffolds ordered and oriented by the collared flycatcher linkage map; grey, scaffolds ordered with the collared flycatcher linkage map and oriented through comparative mapping with zebra finch; white, scaffolds ordered and oriented through comparative mapping with zebra finch.

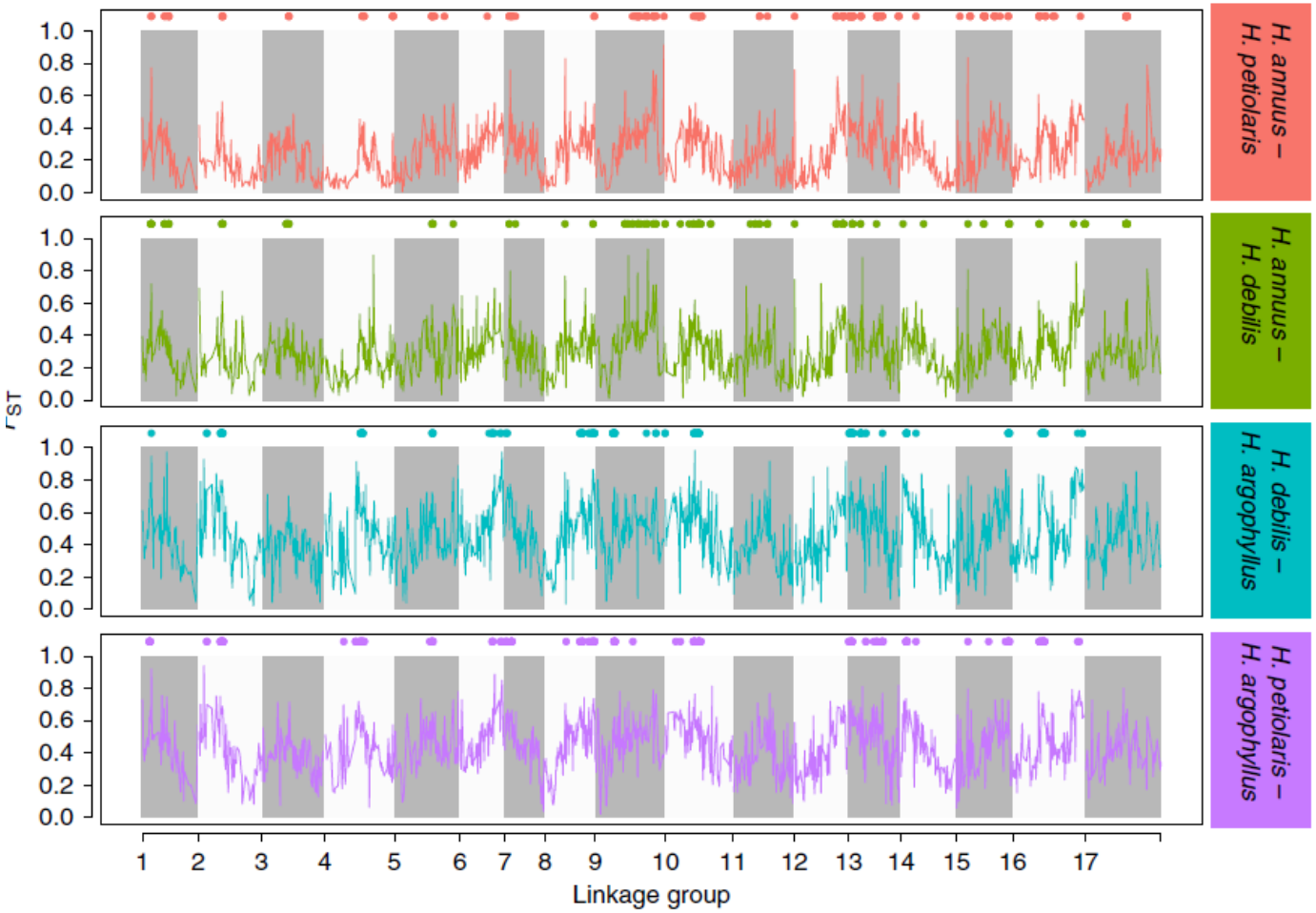
Islands of speciation ? = ? Islands of divergence

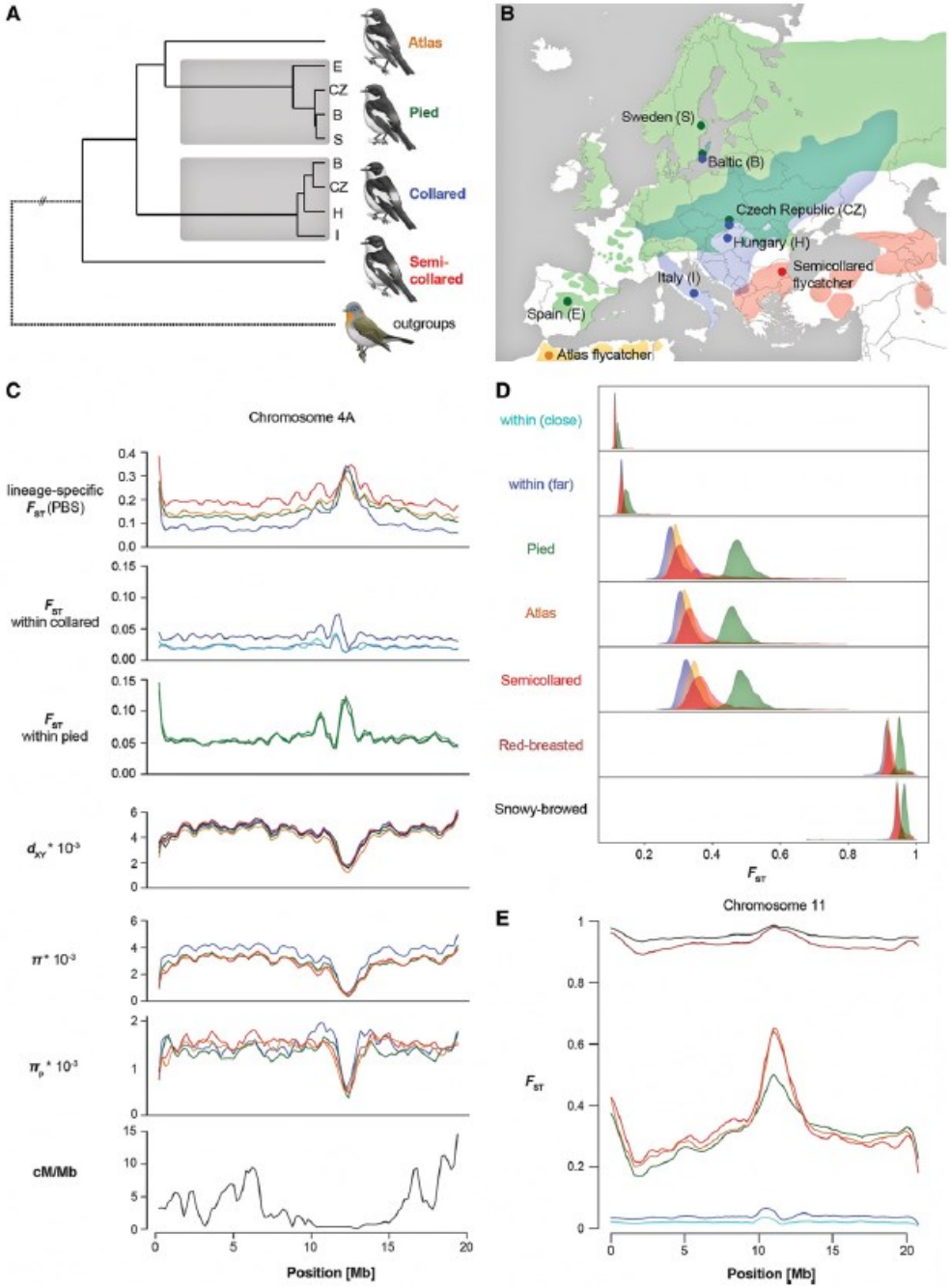
Table 1. Definitions of some newer terms being used to describe patterns and processes of genomic divergence.

term	definition
genomic island of divergence	a region of the genome, of any size, whose divergence exceeds neutral background expectations
divergence hitchhiking	a term used to describe the process by which physical linkage to a divergently selected gene(s) increases genomic divergence for regions adjacent to a selected site on a chromosome. The process is based on a site under divergent selection between populations creating a localized region of reduced gene flow around it in the genome, enhancing the potential to maintain or accumulate differentiation (both neutral and selected) at linked sites
genome hitchhiking	a term used to describe the process by which genetic divergence across the genome is facilitated, even for loci unlinked to those under selection, by a global reduction in average genome-wide gene flow that divergent selection causes
outlier loci	exceptionally differentiated gene regions, usually those that are differentiated beyond background levels/neutral expectations. Outlier loci are generally interpreted as being affected by divergent selection and/or causing reproductive isolation, but this has rarely been directly tested


a


b
Species pair
H. petiolaris
H. debilis
H. annuus
H. argophyllus
1
2
3
4
2
1
0
Divergence time
(MYA)


1.0
0.8
0.6
0.4
0.2
0.0
r_{ST}
H. annuus –
H. petiolaris
H. annuus –
H. debilis
H. debilis –
H. argophyllus
H. petiolaris –
H. argophyllus
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Linkage group


A
Atlas
E
CZ
B
S
Pied
B
CZ
H
I
Collared
Semi-collared
outgroups
B
Sweden (S)
Baltic (B)
Czech Republic (CZ)
Hungary (H)
Italy (I)
Spain (E)
Semicollared flycatcher
Atlas flycatcher
C
Chromosome 4A
lineage-specific F_{ST} (PBS)
F_{ST} within collared
F_{ST} within pied
d_{XY} * 10^{-3}
π * 10^{-3}
π_p * 10^{-3}
cM/Mb
Position [Mb]
D
within (close)
within (far)
Pied
Atlas
Semicollared
Red-breasted
Snowy-browed
F_{ST}
E
Chromosome 11
F_{ST}
Position [Mb]

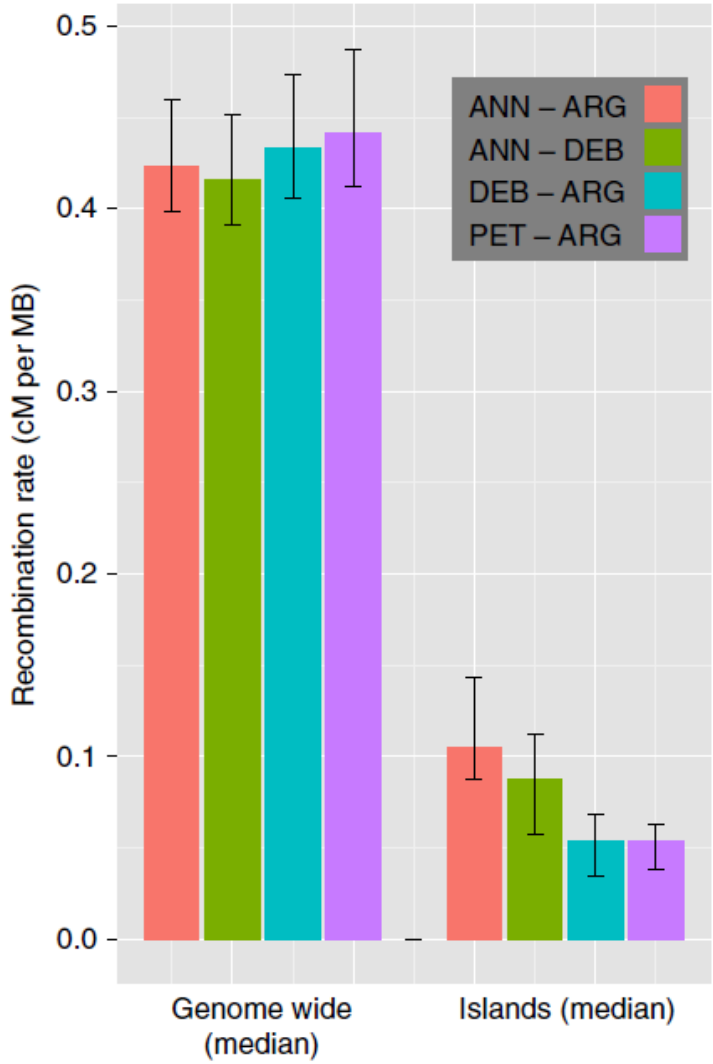
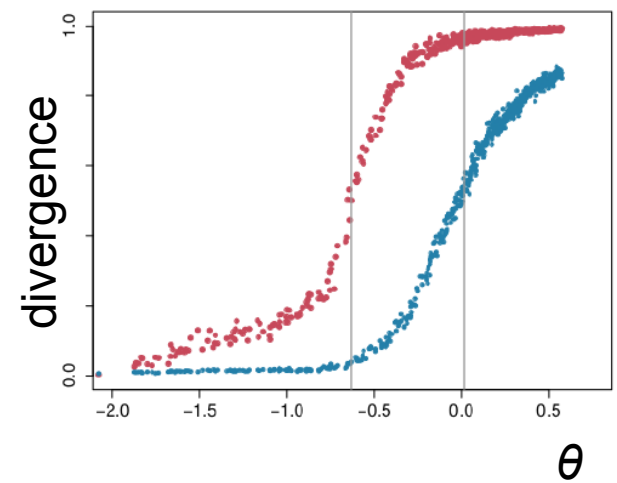
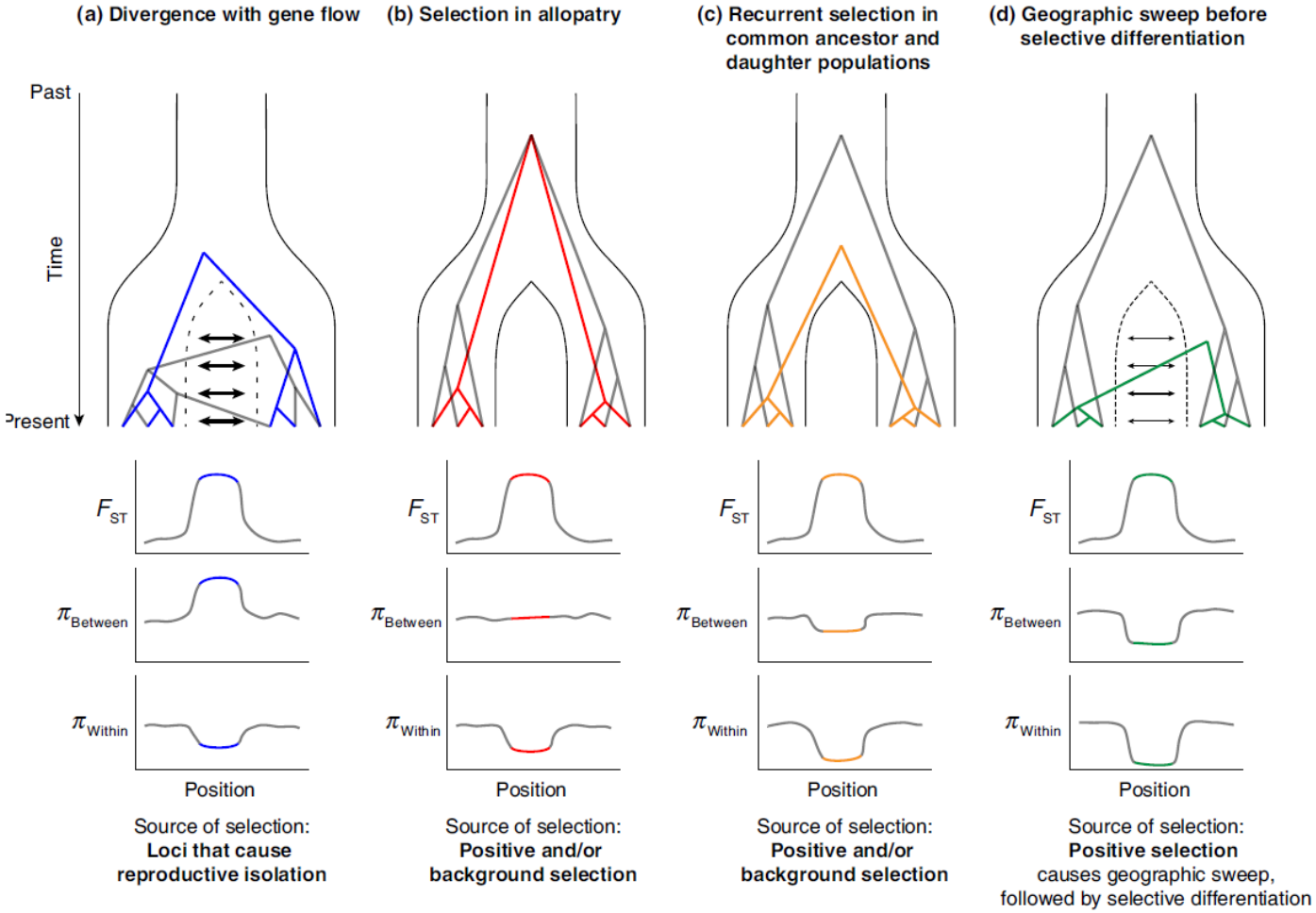
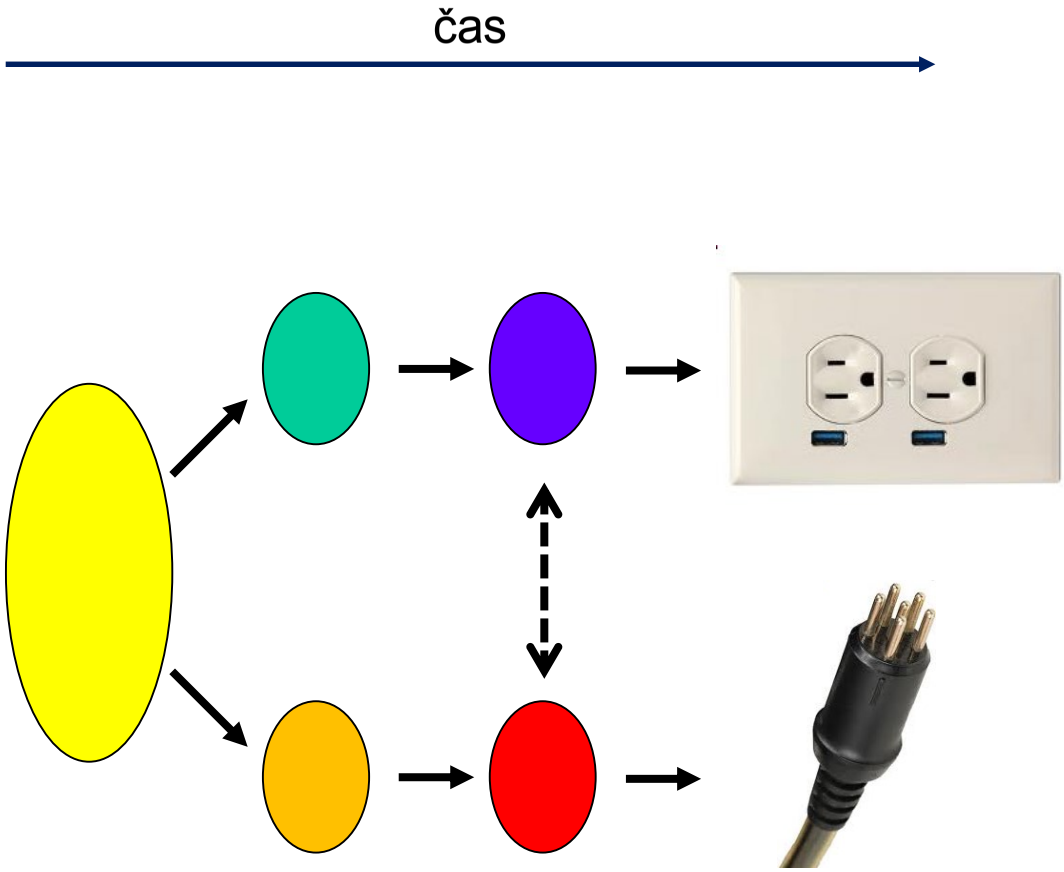


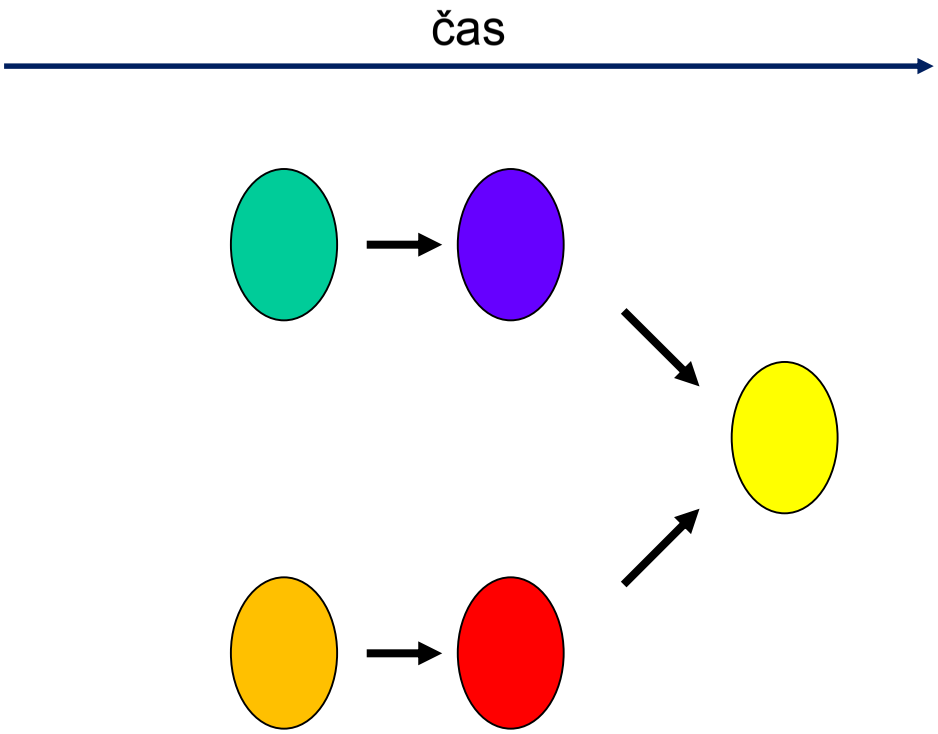
Figure 4 | Recombination rates. Median recombination rates calculated genome wide and solely for islands of divergence (error bars: 95% confidence interval of the median) for each species pair.

Barton's coupling coefficient
$\theta = s/r$




(a) Divergence with gene flow
(b) Selection in allopatry
(c) Recurrent selection in common ancestor and daughter populations
(d) Geographic sweep before selective differentiation
Past
Time
Present
F_{ST}
$\pi_{Between}$
π_{Within}
Position
Source of selection:
Loci that cause reproductive isolation
Source of selection:
Positive and/or background selection
Source of selection:
Positive and/or background selection
Source of selection:
Positive selection
causes geographic sweep, followed by selective differentiation


čas

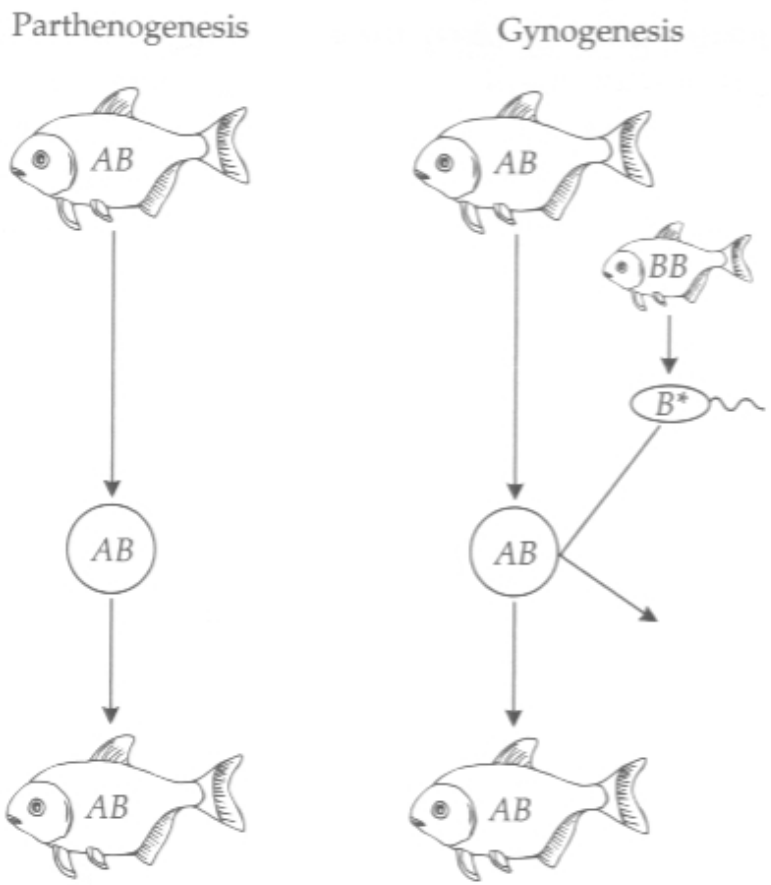

čas

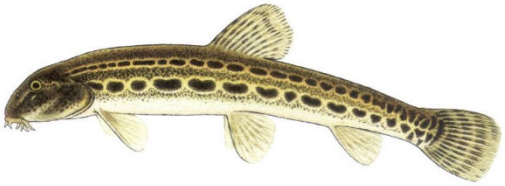
Taxony hybridního původu

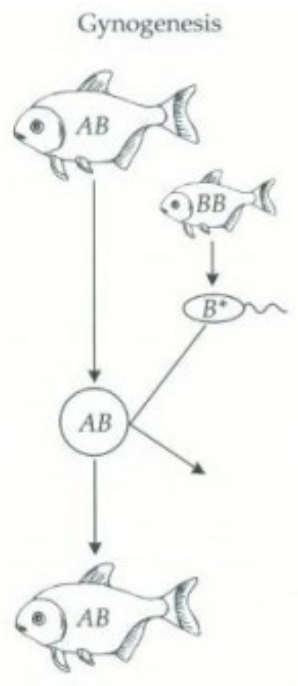
- Běžné u rostlin
- F1 ale i následné back-crossy
- Většinou pak asexuální rozmnožování (apomixie)
- Např. *Sorbus bohemica, S. portae-bohemicae, S. albensis*

Speciace hybridizací
→ většinou zvláštní rozmnožování

- Partenogeneze
- Gynogeneze
- Genomic exclusion





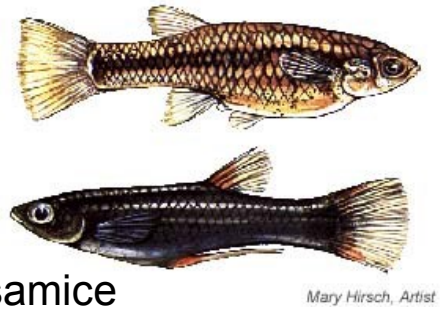


Ambystoma
kombinace genomu až 4 druhů
genom ze spermie asi občas použit
kleptogeneze

Genomic exclusion

- **Hybridogeneze**
  - Jen mezidruhoví hybridi
  - Hybridi diploidní
  - Haploidní genom jednoho druhu zničen při gametogenezi (nebo dříve)

Poeciliopsis monacha



  - ***Poeciliopsis*** (živoroděnky) – hybridi: jen samice
  - Mitóza s monopolárním vřeténkem (před meiosou!)
  - Při křížení *P. monacha* s *P. occidentalis* nebo *P. lucida* hybridní samice přenáší jen genom *monacha* (klonálně!)

  - (gynogeneze – také většinou u mezidruhových hybridů)

Vodní skokani rodu *Pelophylax* (dříve v rodu *Rana*)

P. lessonae LL

P. esculentus LR

P. ridibundus RR

P. esculentus LR

Sympatrie s P. lessonae LL

LR

↓ Odstranění genomu L

~~L~~R

↓ Duplikace R

RR

↓ Gametogeneze

R

L → ↓ Křížení s *P. lessonae*

LR

Sympatrie s P. ridibundus RR

LR

↓ Odstranění genomu R

L~~R~~

↓ Duplikace L

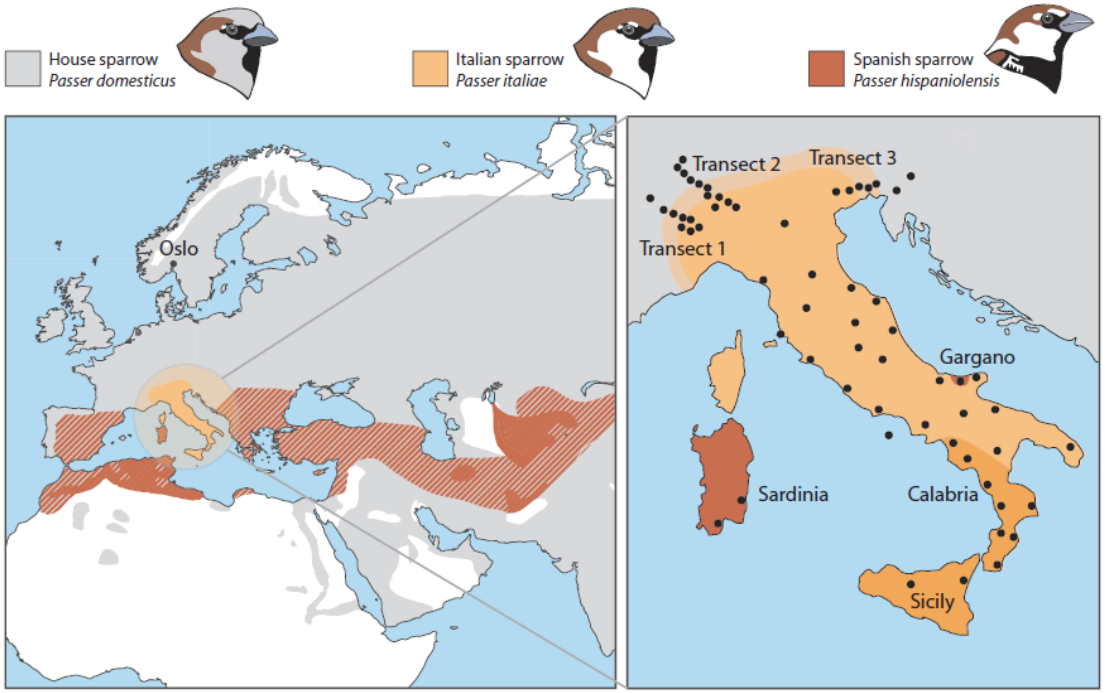
LL

↓ Gametogeneze

L

R → ↓ Křížení s *P. ridibundus*

LR

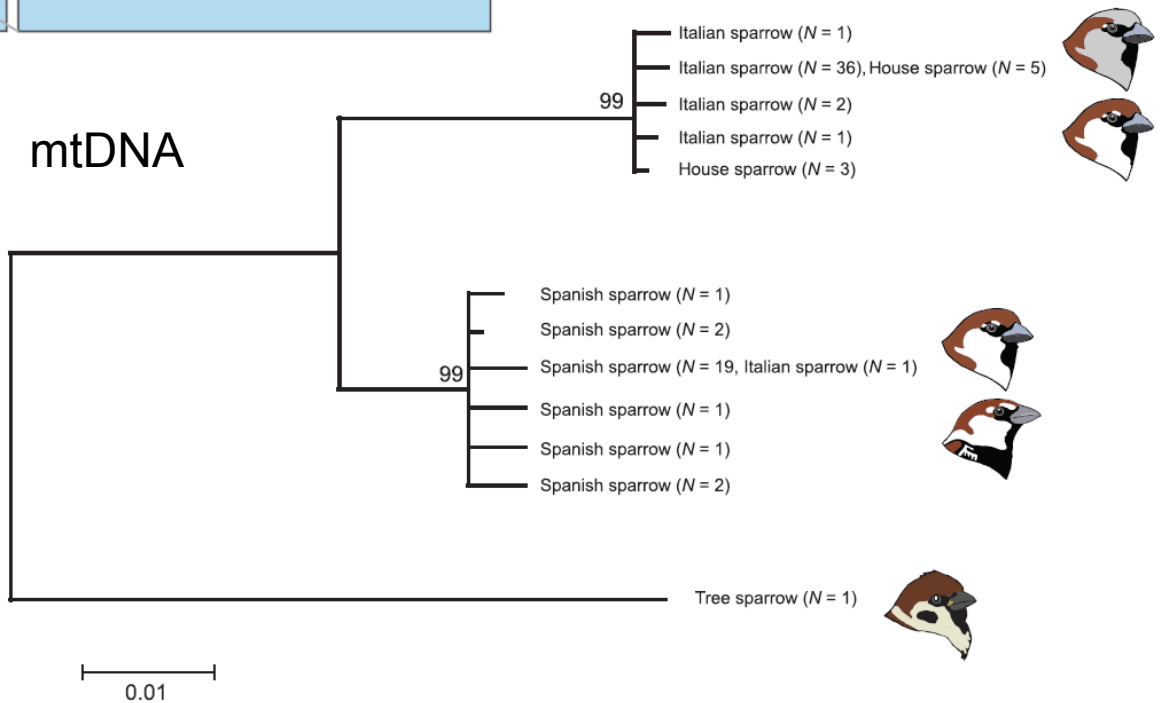


Italští vrabci

hybridní taxon
mnohanásobný vznik
fenotypicky homogenní

Setophaga auduboni
lesňáček žlutokorunkatý

mtDNA



Existují vůbec druhy? Pokud ano, tak jak je potom definovat?

Box 1. Species concepts[a]

- Agamospecies Concept
- Biological Species Concept*
- Cladistic Species Concept
- Cohesion Species Concept*
- Composite Species Concept
- Ecological Species Concept*
- Evolutionary Significant Unit*
- Evolutionary Species Concept*
- Genealogical Concordance Concept
- Genetic Species Concept*
- Genotypic Cluster Concept
- Hennigian Species Concept*
- Internodal Species Concept
- Morphological Species Concept
- Non-dimensional Species Concept
- Phenetic Species Concept
- Phylogenetic Species Concept (Diagnosable Version)*
- Phylogenetic Species Concept (Monophyly Version)
- Phylogenetic Species Concept (Diagnosable and Monophyly Version)
- Polythetic Species Concept
- Recognition Species Concept*
- Reproductive Competition Concept*
- Successional Species Concept
- Taxonomic Species Concept

Reference

a Mayden, R.L. (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In *Species: the Units of Biodiversity* (Claridge, M.F. *et al.*, eds), pp. 381–424, Chapman & Hall

*Concepts that make reference to biological processes (e.g. reproduction and competition) that occur among organisms within species (and less so between species) and that contribute to a shared process of evolution within species.

PROGRESS TOWARD A GENERAL SPECIES CONCEPT

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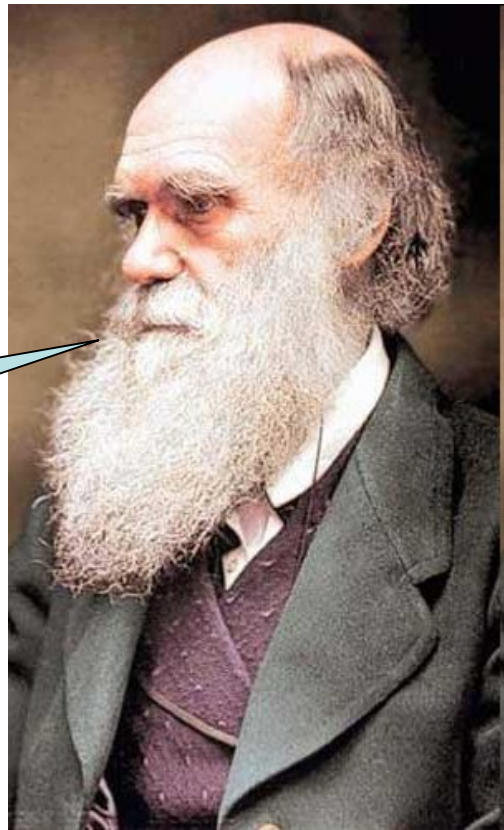
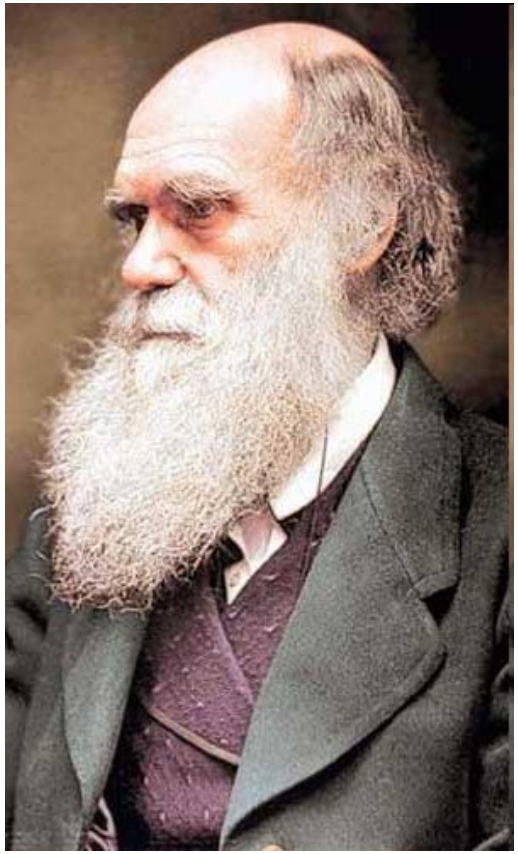
It is really laughable to see what different ideas are prominent in various naturalists minds, when they speak of “species”; … It all comes, I believe, from trying to define the indefinable.

Darwin 1856



A rediscovered first edition of Charles Darwin's (1809-1882) On the Origin of Species by Means of Natural Selection sold at Christie's in London for £103,250 / $170,569 / €114,298 / Photo: Christie's Images Ltd. 2009.



- On the Origin of Species

- An Abstract of an Essay on the Origin of Species **and Varieties** by Means of Natural Selection

Shrnutí

- Izolace populací → reprodukční bariéry
- Často náhodné procesy (BDM model)
- Speciace je možná i při (částečném) toku genů
- Intragenomický konflikt
- Již známe konkrétní hráče (geny, mechanismy)
- Už v prvotních fázích - interakce mnoha genů
- Významná role hybridizace