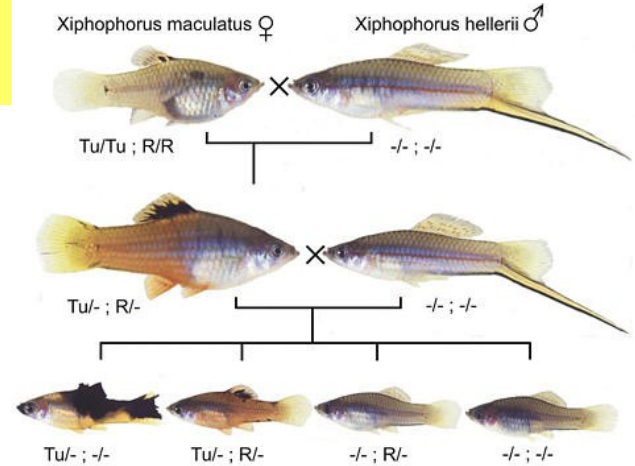
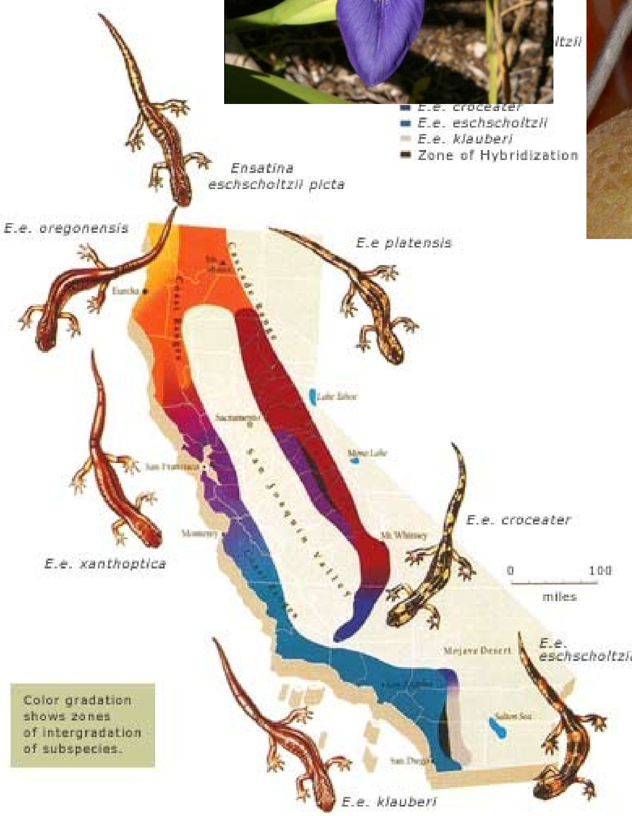
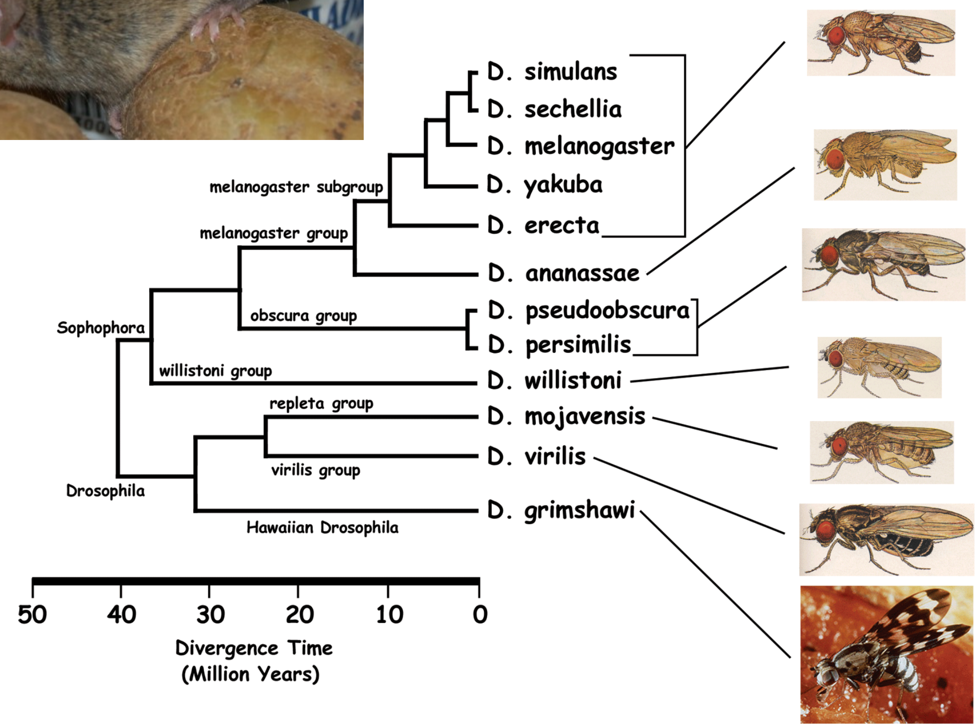
SPECIATION


Xiphophorus maculatus ♀
Xiphophorus hellerii ♂
Tu/Tu ; R/R
-/- ; -/-
Tu/- ; R/-
-/- ; -/-
Tu/- ; -/-
Tu/- ; R/-
-/- ; R/-
-/- ; -/-


E.e. croceater
E.e. eschscholtzii
E.e. klauberi
Zone of Hybridization
Ensatina eschscholtzii picta
E.e. oregonensis
E.e platensis
E.e. xanthoptica
E.e. croceater
0
100
miles
E.e. eschscholtzii
E.e. klauberi
Color gradation shows zones of intergradation of subspecies.


D. simulans
D. sechellia
D. melanogaster
D. yakuba
D. erecta
D. ananassae
D. pseudoobscura
D. persimilis
D. willistoni
D. mojavensis
D. virilis
D. grimshawi
melanogaster subgroup
melanogaster group
obscura group
Sophophora
willistoni group
repleta group
virilis group
Drosophila
Hawaiian Drosophila
50
40
30
20
10
0
Divergence Time
(Million Years)

What is species?

How do species arise?



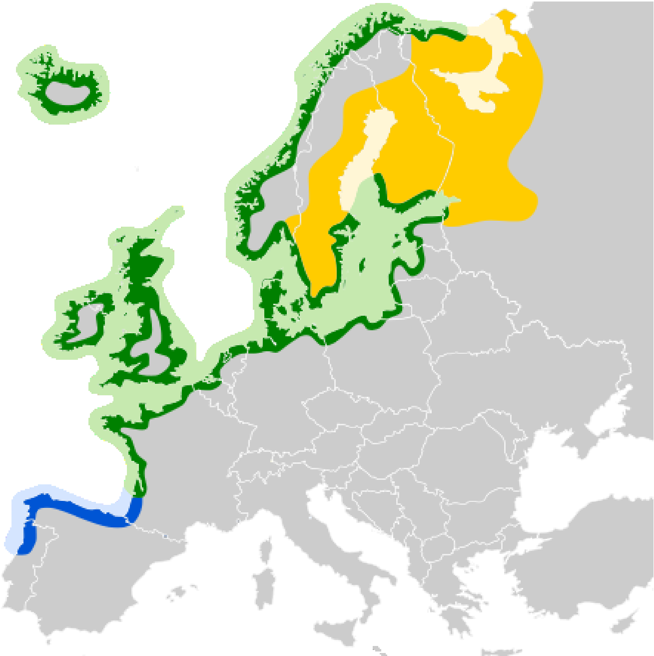
Eurasian nuthatch (*Sitta europea*)

x

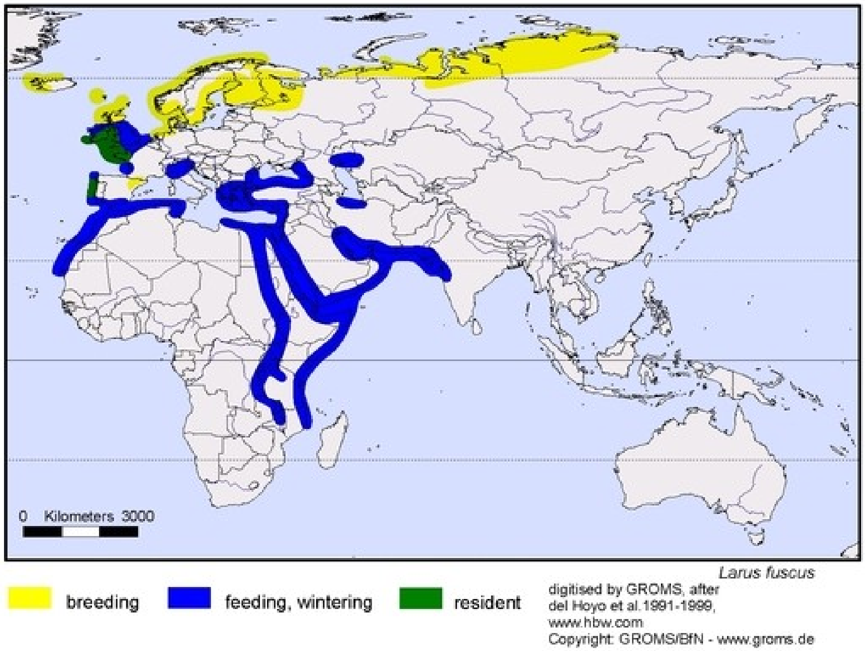
common treecreeper
(*Certhia familiaris*)

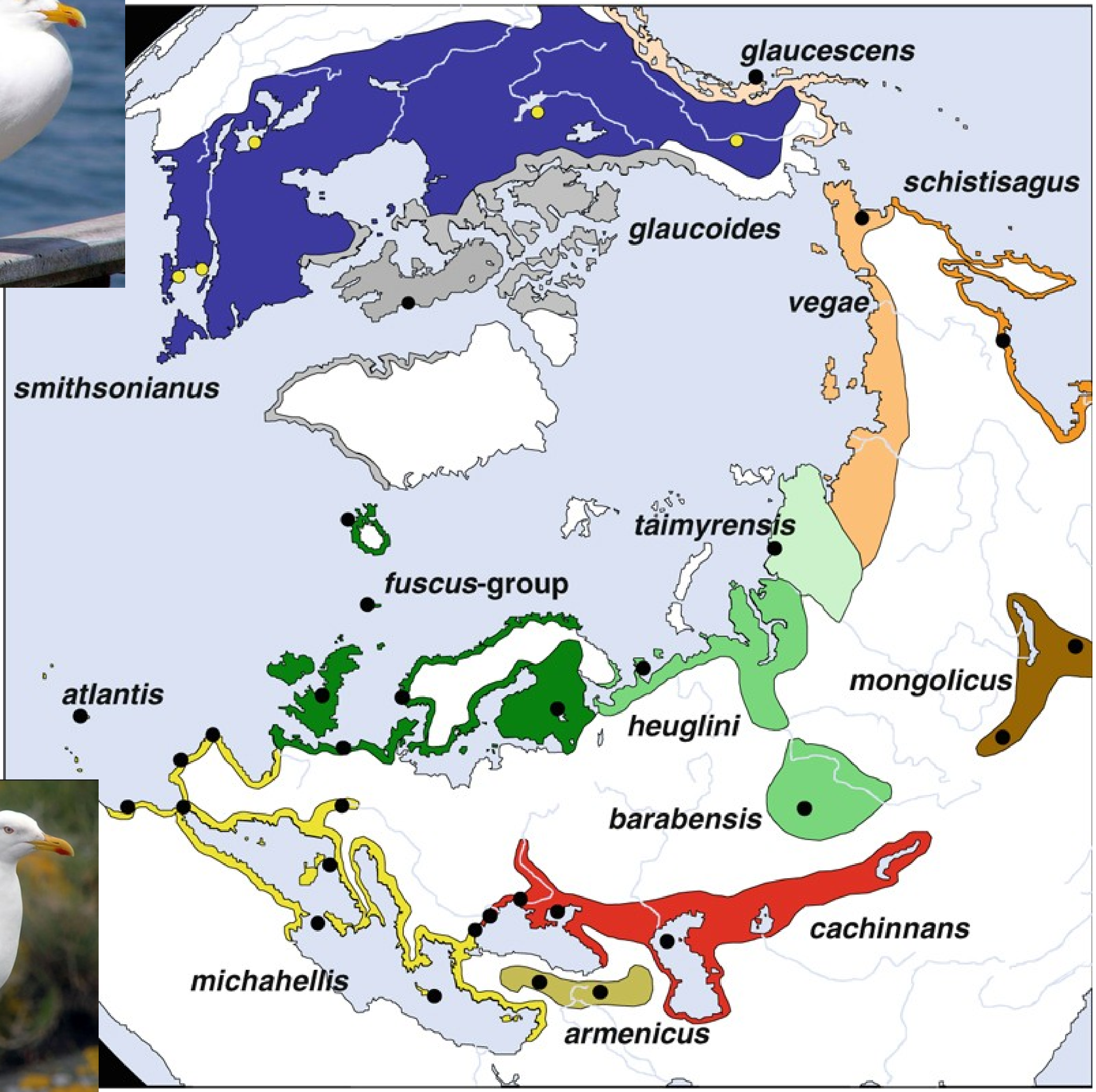
Mechanisms maintaining species integrity

European herring gull
(*Larus argentatus*)



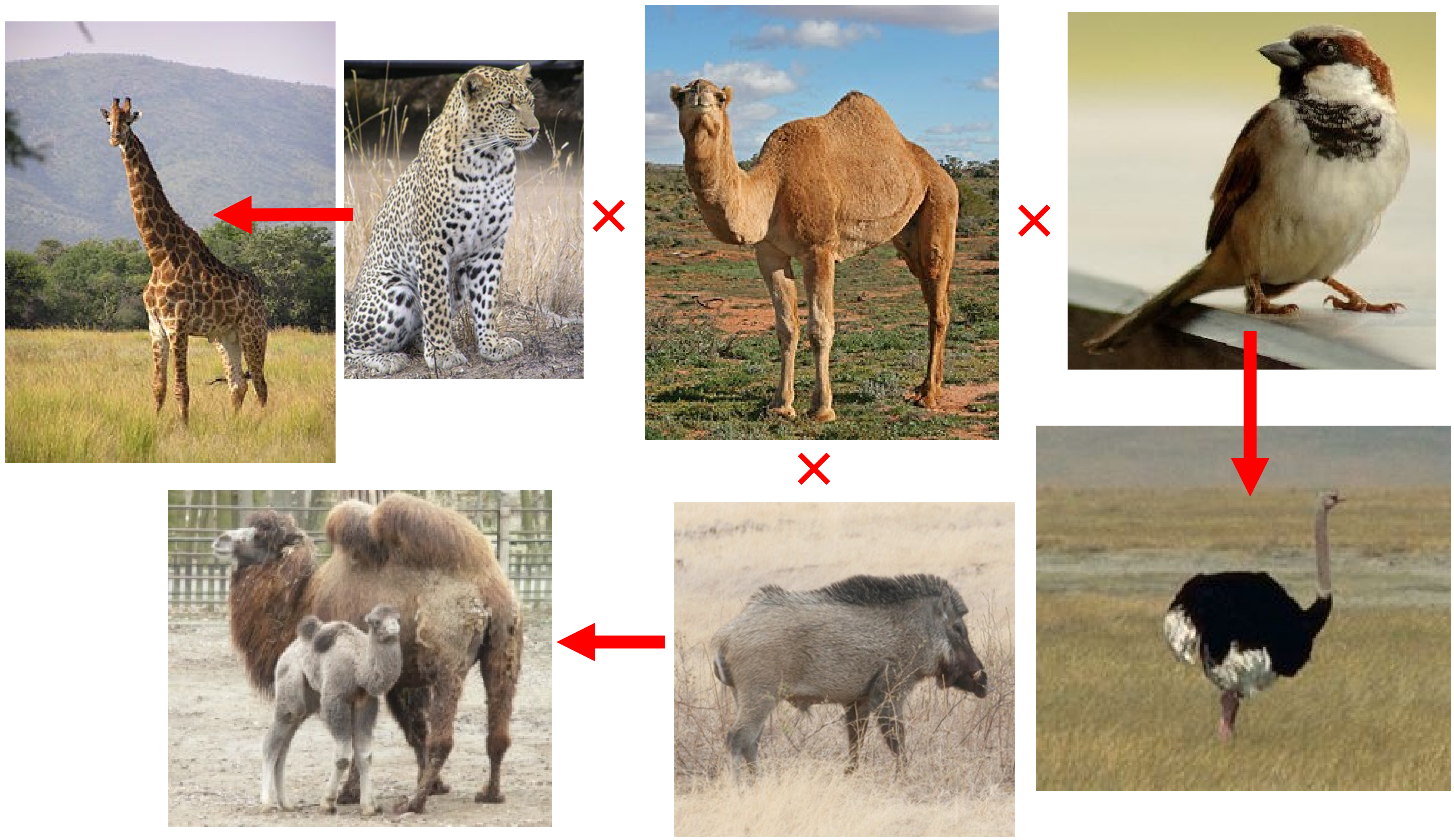
lesser black-backed gull
(*L. fuscus*)




glaucescens
schistisagus
glaucoides
vegae
smithsonianus
taimyrensis
fuscus-group
atlantis
mongolicus
heuglini
barabensis
cachinnans
michahellis
armenicus

Antics:

species unstable and highly variable

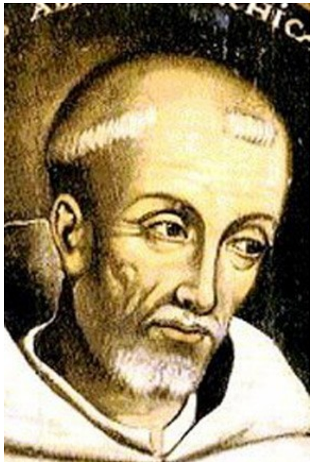


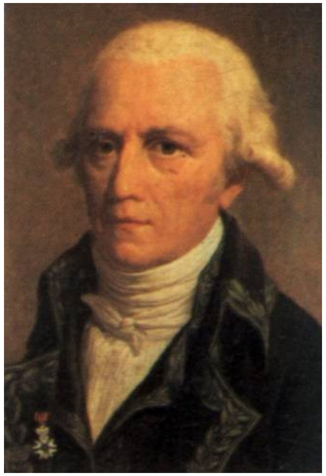
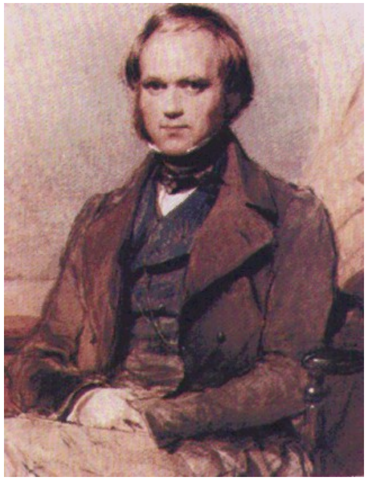
Are species real entities?

nominalists:

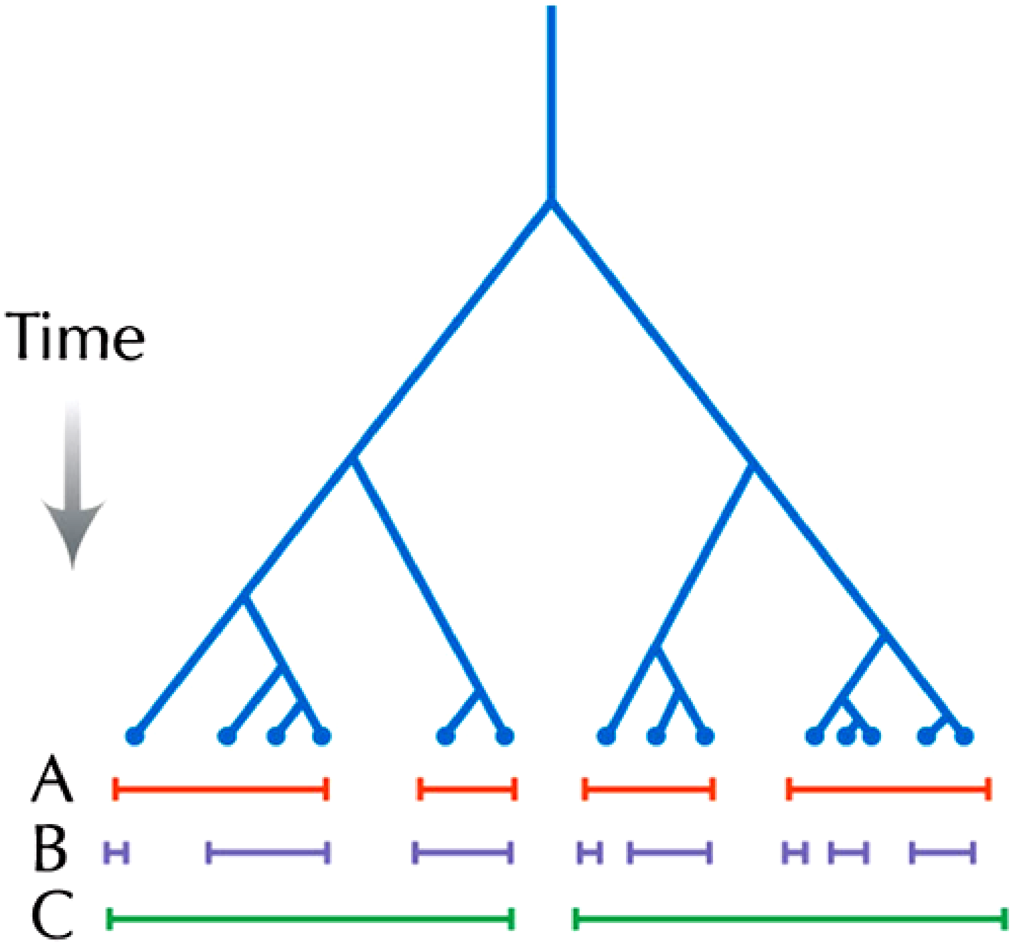
no universals and abstract objects (= only words), only particulars exist

eg. William of Ockham, popular in France in the 1700s (young Buffon and Lamarck), Darwin



species are human abstractions, artificially dividin natural continuum according to Darwin classification of organisms to a large extent arbitrary:



realists:

only universals are real, particulars are derived, random, variable, and ephemeral

eg. Plato

species really exist in nature

New Guinea tribes:

Karam people → almost identical discrimination of bird species with western taxonomists (but bats considered as birds)

Rofaifo people → only two names for mammals (small = Hunembe, big = Hefa); cassowary considered as a mammal

× human brain same in aborigines and professional taxonomists

free hybridization within species × rare between species

Problem: definition should be both <u>universal</u> and <u>operational</u>

Typological (essentialist) concept

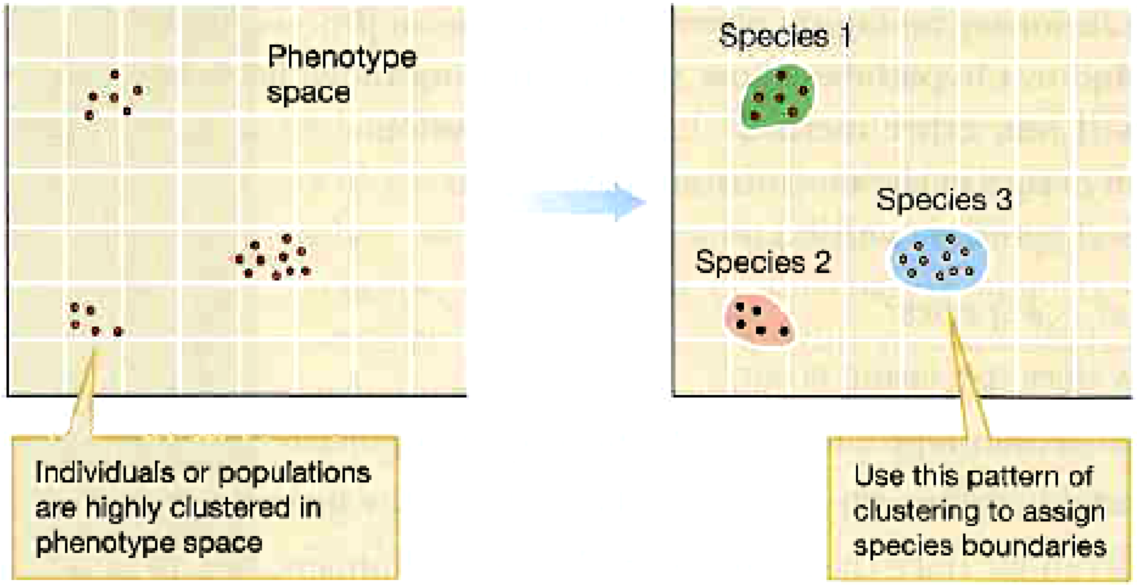
Plato´s world of ideas: assumption of existence of limited number of types (universals)

species composed of idividuals having the same essence

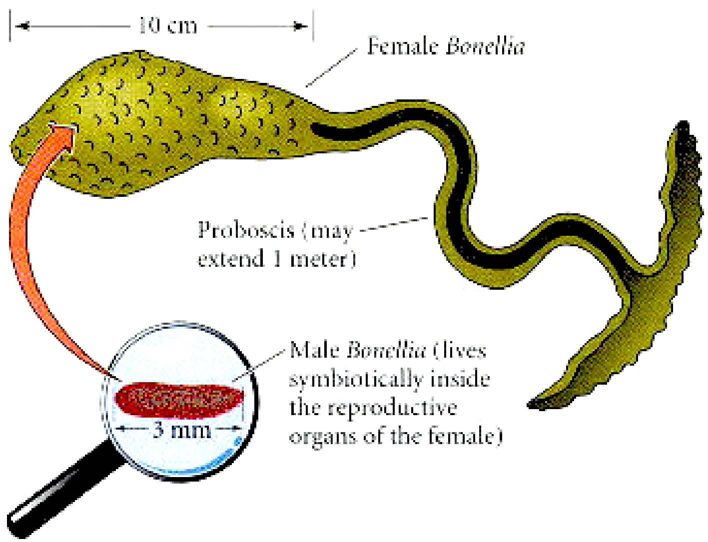
variability strongly limited, results from imperfekt expression of the idea

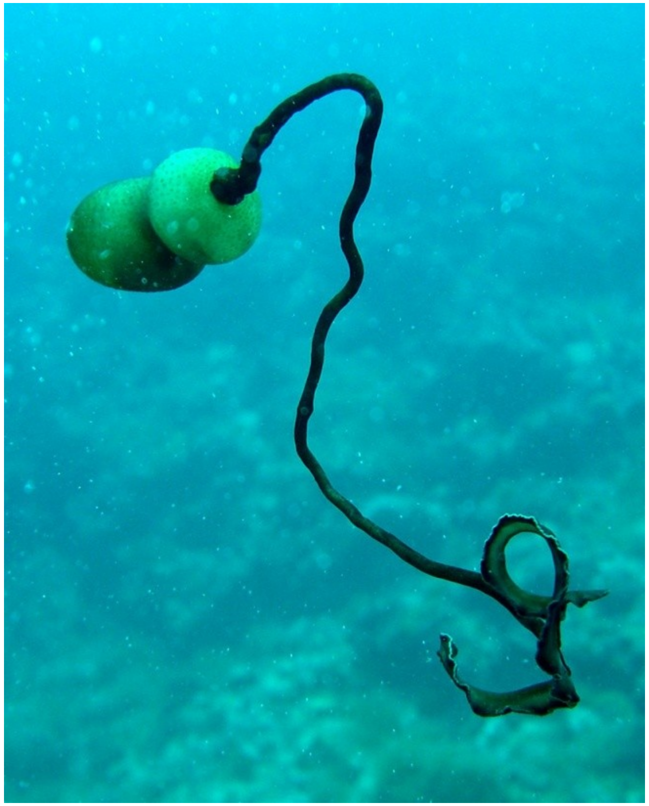
each species separated from others by sharp boundary

constant in time

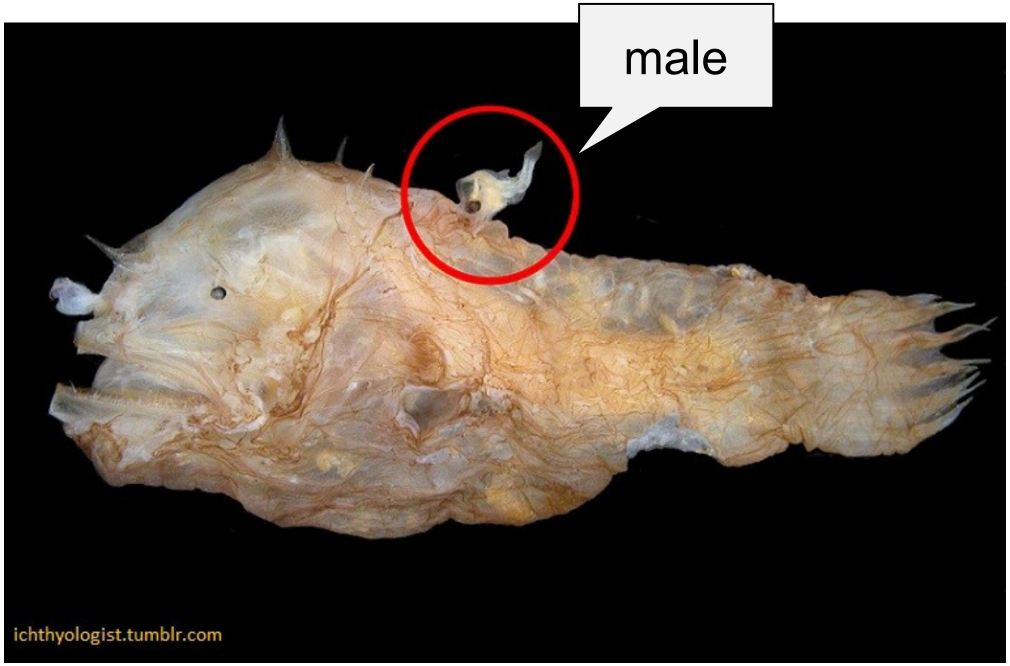


× sexual dimorphism



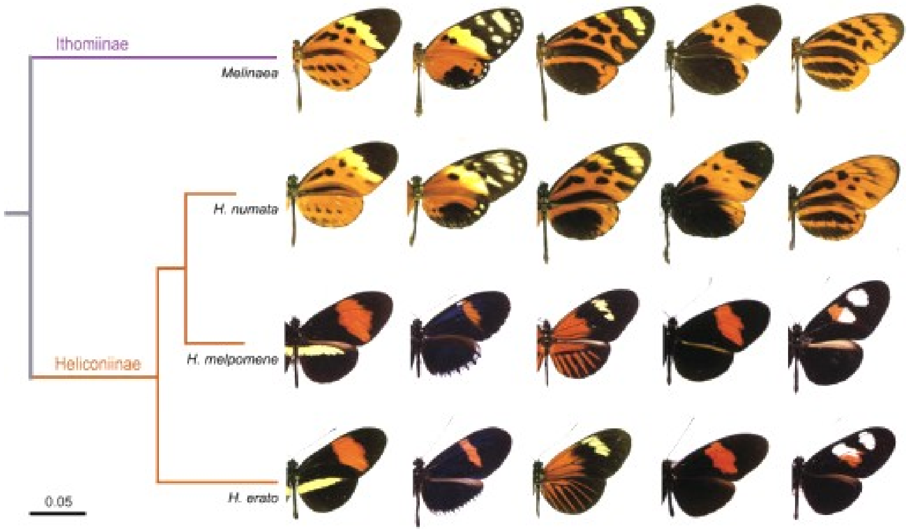


Bonellia viridis



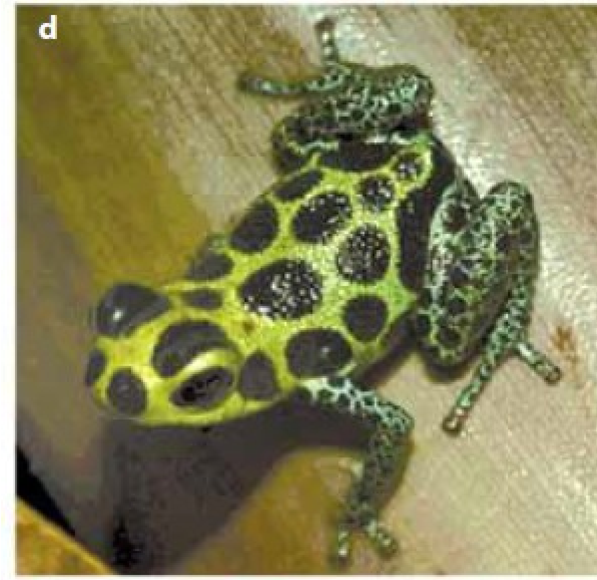
angler
(*Lophius piscatorius*)

× polymorphism, different ontogenetic stages



Heliconius spp.

Papilio polyxenes

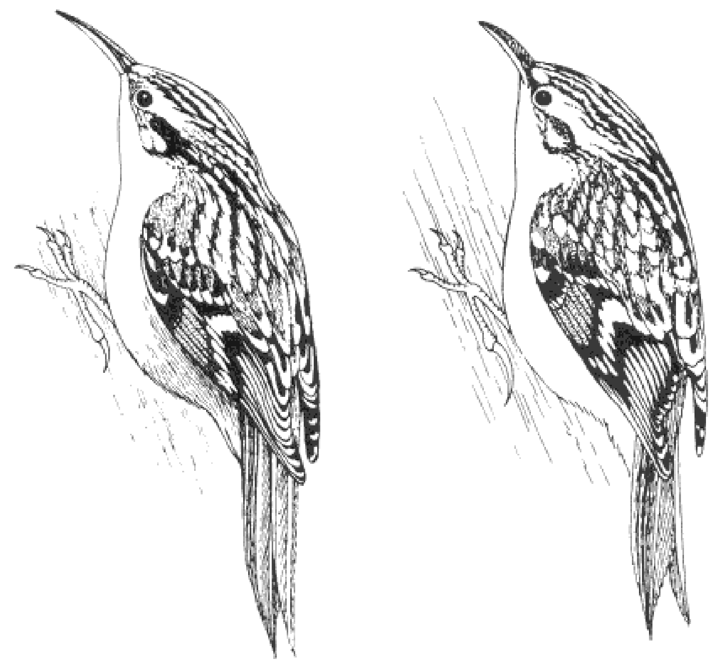


Ranitomeya imitator

× sibling species, cryptic species

Drosophila persimilis/
D. pseudoobscura

Pipistrellus pipistrellus/P. pygmaeus

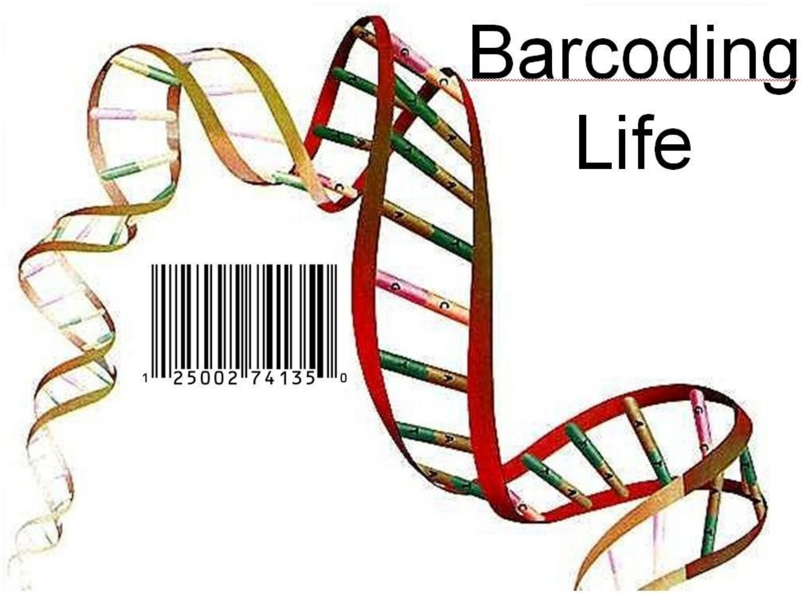


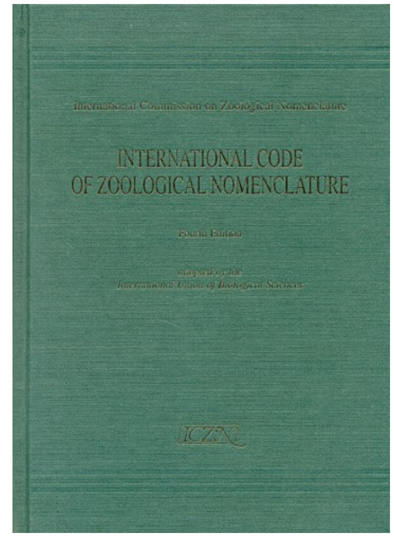
Certhia brachydactyla/C. familiaris

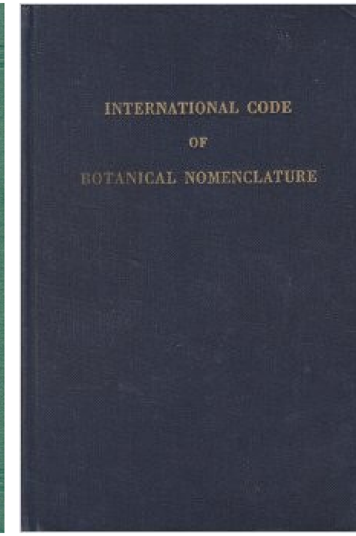
Typological species still in nomenclatorial practice:

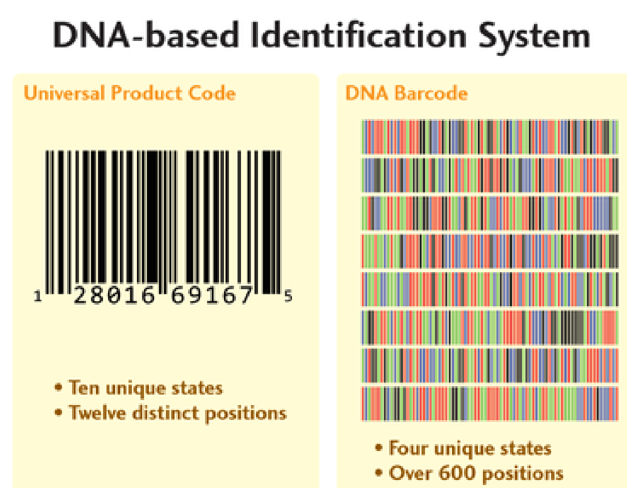
type specimen = <u>holotype</u>, type series, type locality

barcoding







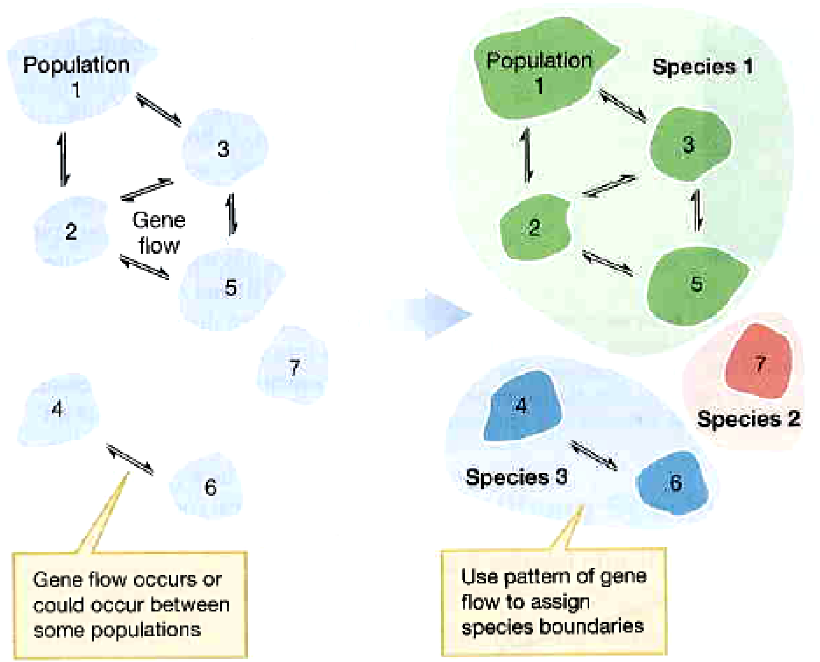


Biological species concept (BSC)

T. Dobzhansky, H. Muller, J. Huxley, E. Mayr

species as gene pools, reproductive communities
reproductively isolated from others

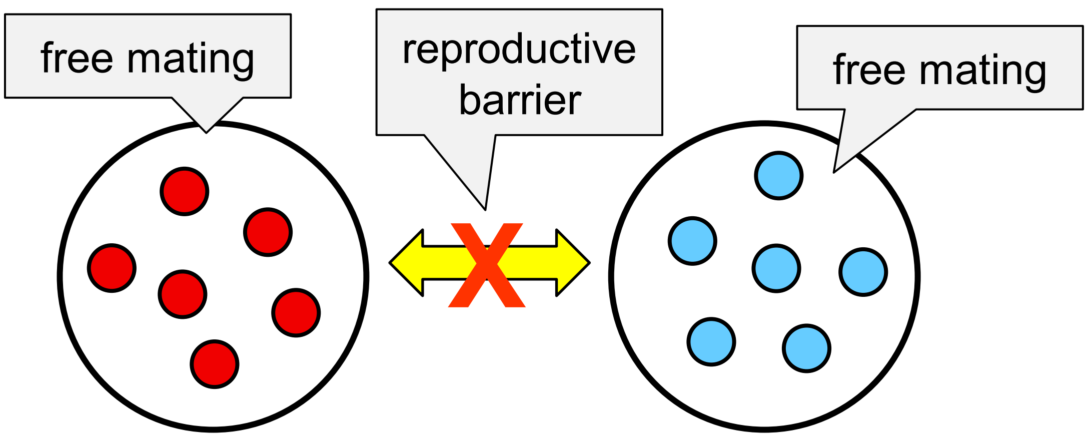
no constant, „essential“ characters



E. Mayr

Ernst Mayr (1942):

Species are groups of interbreeding natural populations that are reproductively isolated from others such groups.



Limitations and problems of biological species:

only sexual organisms

problems in allopatry („potential“ hybridization) ⇒ auxiliary morphological and genetic criteria (degree of divergence ~ degree of reproductive isolation)

problems in palaeontology – populations are not contemporary

hybridization between „good“ species (*Bombina bombina* × *B. variegata*)

auxiliary criteria (DNA sequences)

Quercus gambelii

grisea + *gambelii* = <u>syngameon</u>

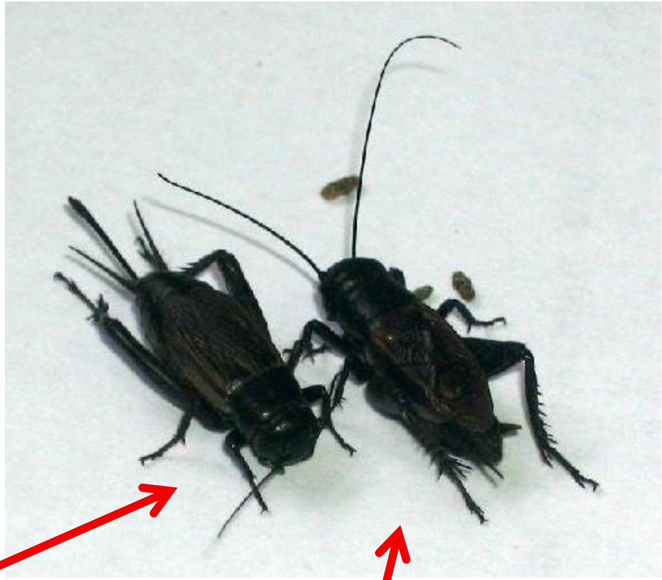
Q. grisea

Reproductive barriers

formerly reproductively isolating mechanisms = RIM ... today we prefer the term reproductive barriers (RIM imply „in order to“)!

1. Prezygotic

A) pre-copulatory:



partners do not meet:

seasonal (temporal)

eg. fireflies, crickets *Gryllus pennsylvanicus* (autumn) × *G. veletis* (spring) ecological (habitat):

Viola arvensis (chalk soils) × *V. tricolor* (acidic soils),

hybrids limited to neutral or weakly acidic soils

Reproductive barriers

1. Prezygotic

A) pre-copulatory:

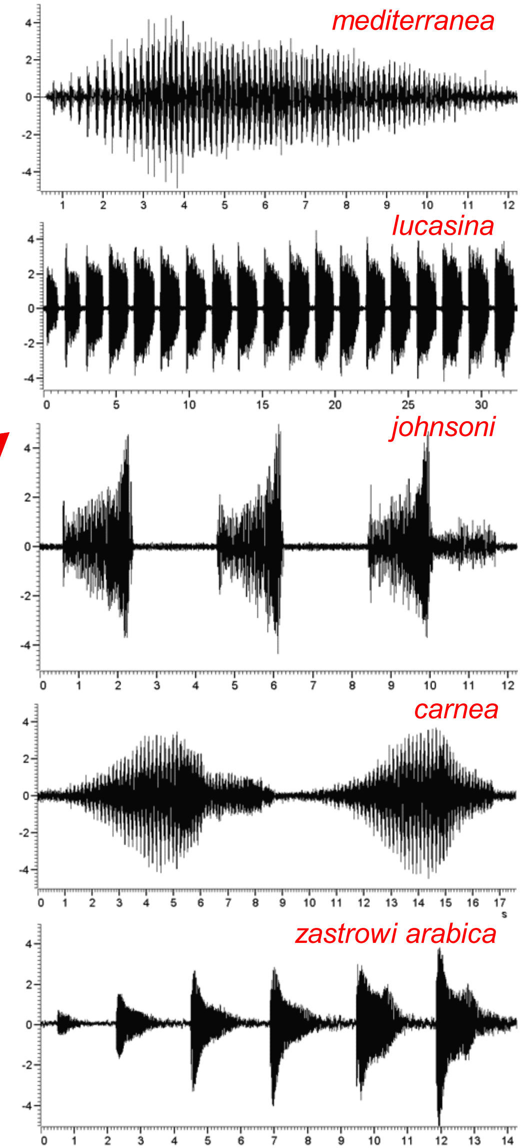
<u>partners meet but do not mate</u>:

ethological, behavioral, sexual

signals:

- acoustic

lacewing (*Chrysoperla*)



1. Prezygotic

A) pre-copulatory:

<u>partners meet but do not mate</u>:

ethological, behavioral, sexual

signals:
- acoustic
- chemical
- light

1. Prezygotic

A) pre-copulatory:

partners meet but do not mate:

ethological, behavioral, sexual

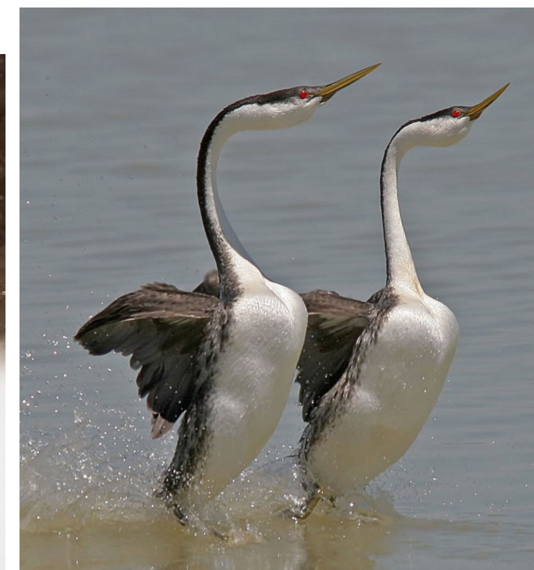
signals:
- acoustic
- chemical
- light
- behavioral (eg. wedding dances)

grey-crowned crane (*Balearica regulorum*)

great bustard (*Otis tarda*)

black-necked stilt (*Himantopus mexicanus*)

red-crowned crane (*Grus japonensis*)



western grebe
(*Aechmophorus occidentalis*)

Reproductive barriers

signals:

- acoustic
- chemical
- light
- behavioral (eg. wedding dances)
- different pollinators in plants

1. Prezygotic

B) post-copulatory:

<u>partners mate but without transfer of gametes</u>:

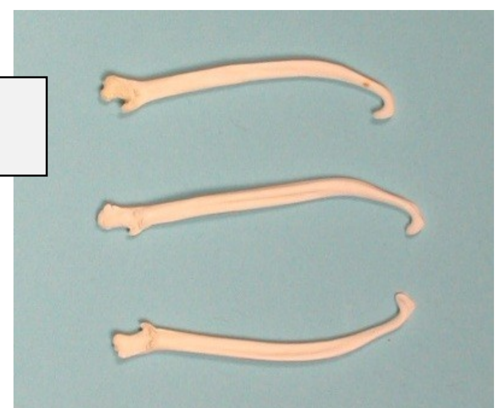
mechanical:

- especially plants; in animals shape of genitalia

cat

fox

walrus (fossil: 1,2 m and recent: 56 cm)



mink

racoon

1. Prezygotic

B) post-copulatory:

transfer of gametes occur but without fertilization:

gametic incompatibility

external fertilization: esp. marine invertebrates (mollusks, echinoderms)

internal fertilization: eg. *Drosophila* – sperm cannot survive in spermatheca of females of other species

plants: pollen tube grows through style

2. Postzygotic

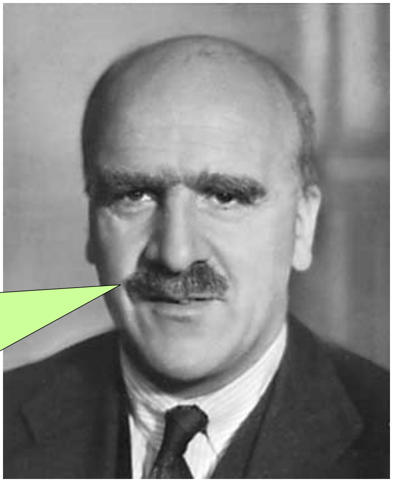
inviability of F1 hybrids

sterility of F1 hybrids

reduced viability or fertility of F2 or backcrosses
= hybrid dysgenesis

Haldane´s rule:

When in the F1 offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous (heterogametic) sex.*)



*) *Drosophila* – males (XY); *Abraxas* – females (WZ)

Haldane´s rule explains Large X effect: genes having large impact on postzygotic reproductive isolation are usually located on X chromosome

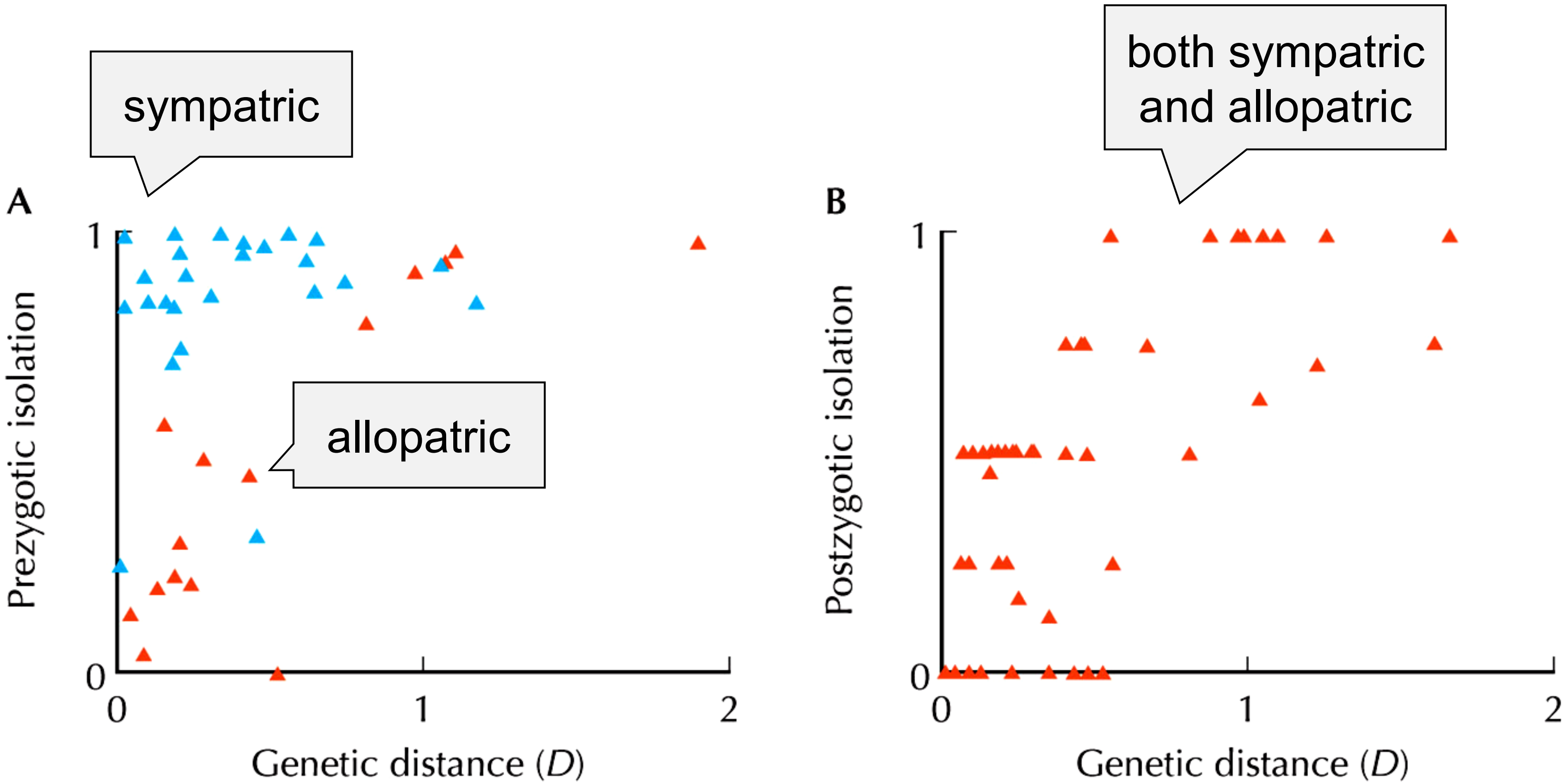
dominance theory
(Muller 1940, 1942; Orr 1997):

males – both <u>dominant</u> and <u>recessive</u> alleles of X-linked genes

females – only <u>dominant</u> alleles

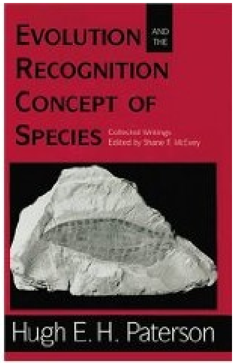
Drosophila pseudoobscura × *D. persimilis*

Rate of prezygotic isolation between allopatric species is similar to rate of postzygotic isolation ...



... prezygotic isolation between sympatric/parapatric species arises more rapidly

Concepts related to biological species:



Recognition species concept

Hugh E.H. Paterson (1985)

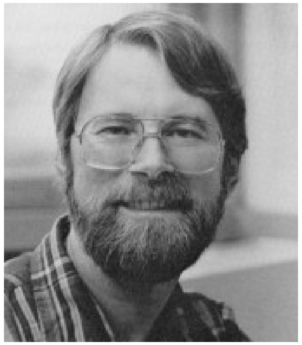
empasizes shared fertilization system rather than isolation:

specific mate recognition system (SMRS)

courtship, timing of mating, choice of condition, coloration, endocrine system, shape of copulatory organs, gametic compatibility, …

reproductive isolation as a byproduct

Concepts related to biological species:



Cohesion species concept

Alan R. Templeton (1989)

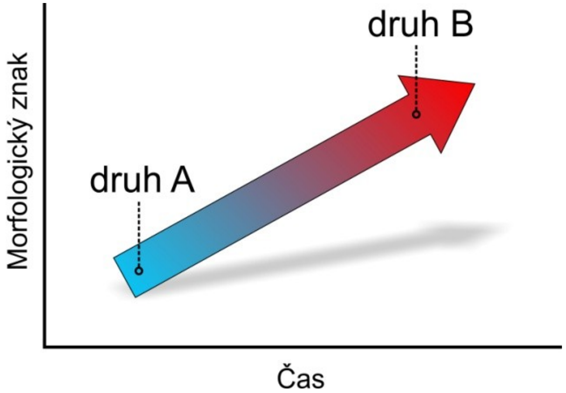
empasizes mechanisms maintaining morphological stability of populations

cohesion mechanisms: gene flow, stabilizing selection, ontogenetic constraints, reproductive isolation

aplication also to asexual organisms, possibility of interspecific hybridization

Evolutionary species concept

attempts for vertical species concepts



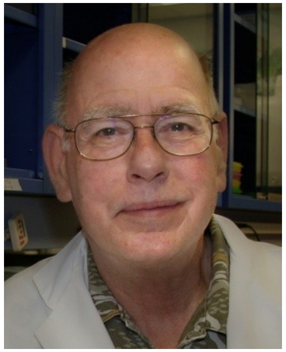
George Gaylord Simpson (1961):

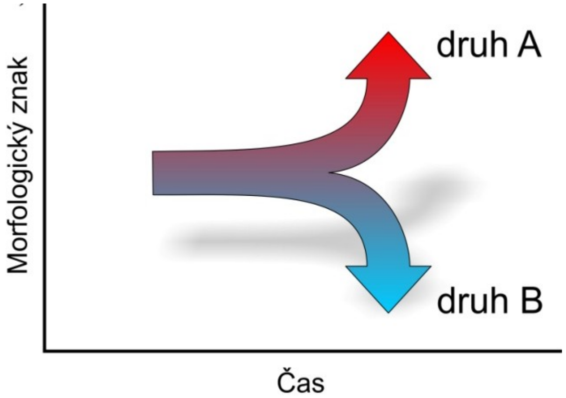
phyletic speciation, chronospecies

asexual organisms

temporal perspective

biological species is a part of it





Edward O. Wiley (1978):

„A species is a lineage of ancestral descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.“

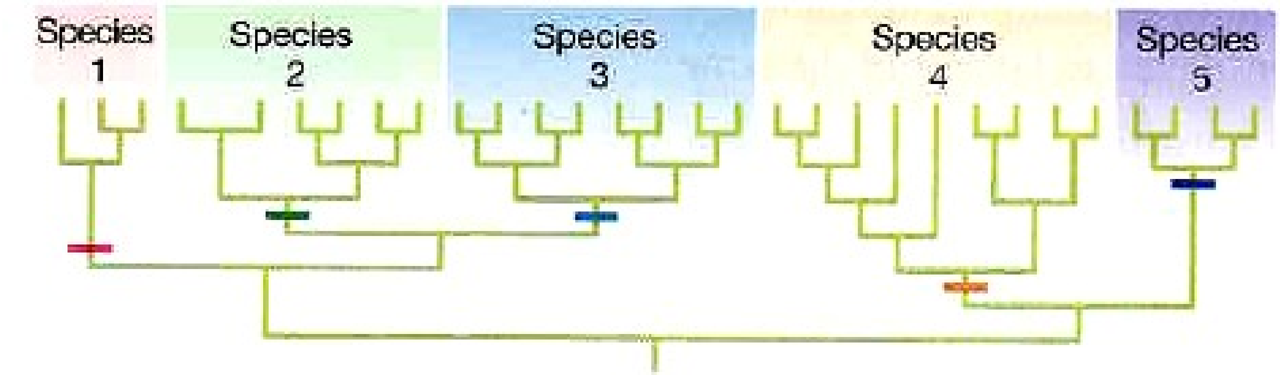
contrary to Simpson´s concept Wiley admits only cladogenesis, ie. splitting speciation

Phylogenetic species concept

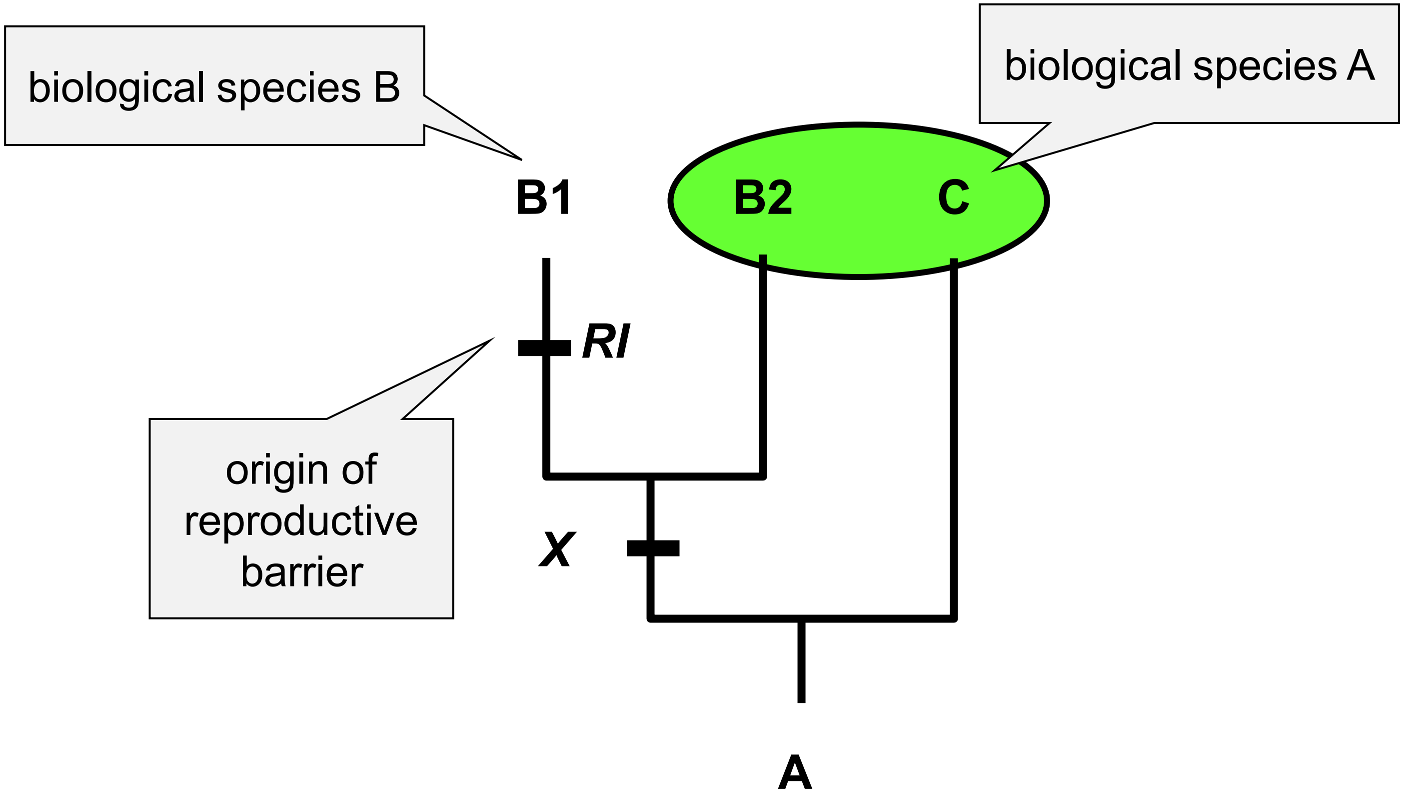
emphasis on diagnostic criteria → but which ones?

⇒ primary inference of phylogeny (synapomorfies)

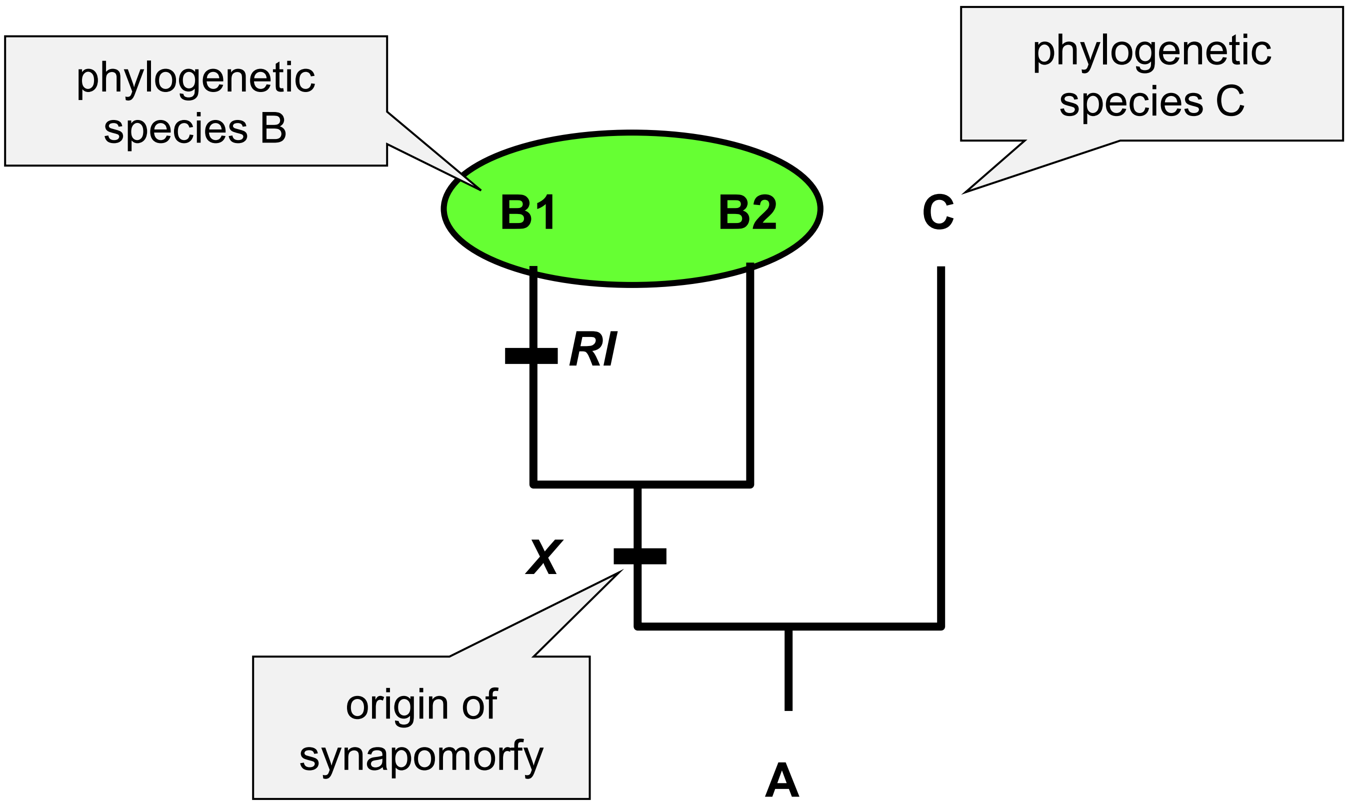
Phylogenetic species = smallest monophyletic group distinguished by a shared derived trait



Relation of biological and phylogenetic species:



Relation of biological and phylogenetic species:



SPECIATION

geography:	allopatric	allopatric
	(isolation)	peripatric
		allo-parapatric (reinforcement)
	sympatric	parapatric
	(no isolation)	sympatric

mechanism:
- drift
- selection
- sexual selection
- hybridisation
- polyploidisation

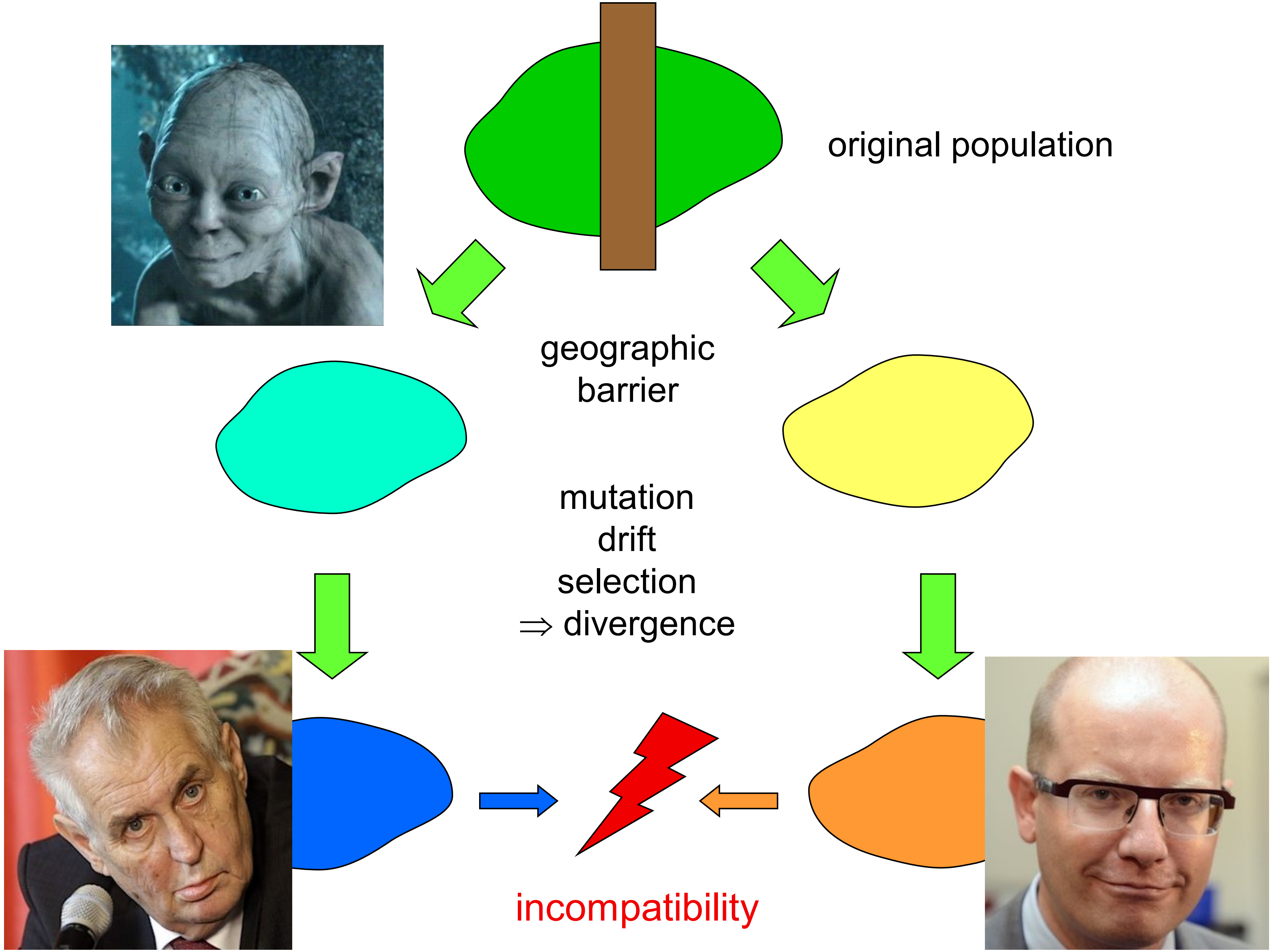
genetic elements: genes *vs*. chromosomes (stasipatric speciation)

Allopatric speciation

geographic isolation

advancing divergence: mutation, drift, selection, sexual selection

reproductive barriers as a byproduct


original population
geographic
barrier
mutation
drift
selection
⇒ divergence
incompatibility

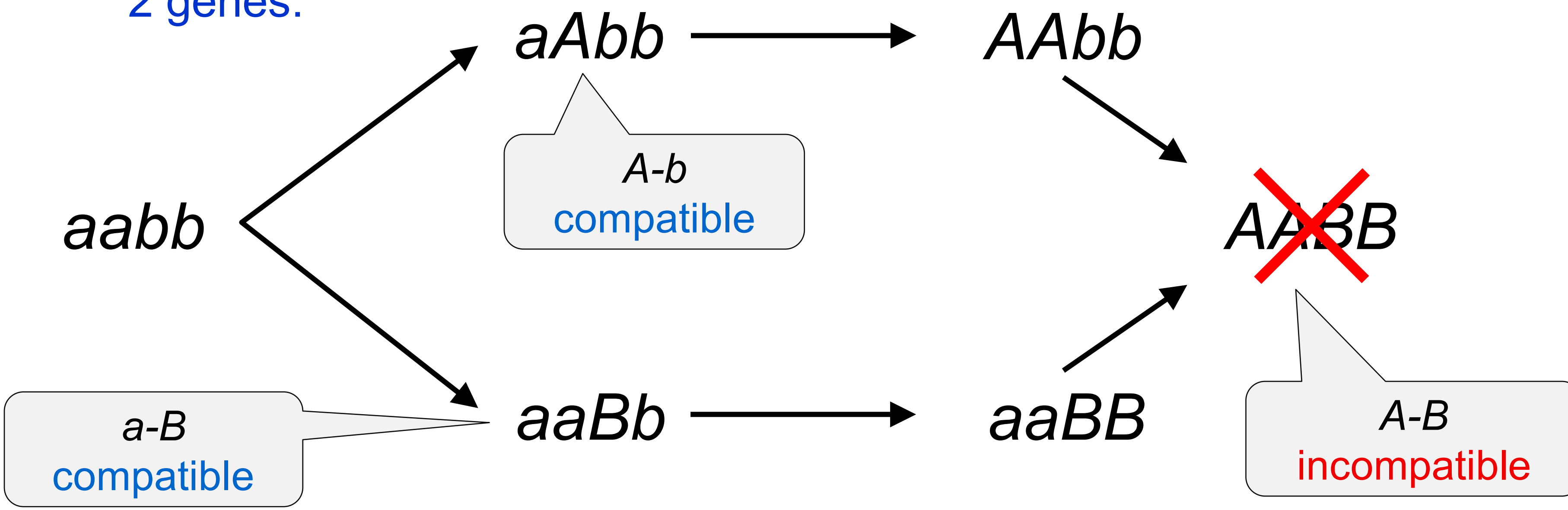
Dobzhansky-Muller model:

W. Bateson

T. Dobzhansky

H. Muller

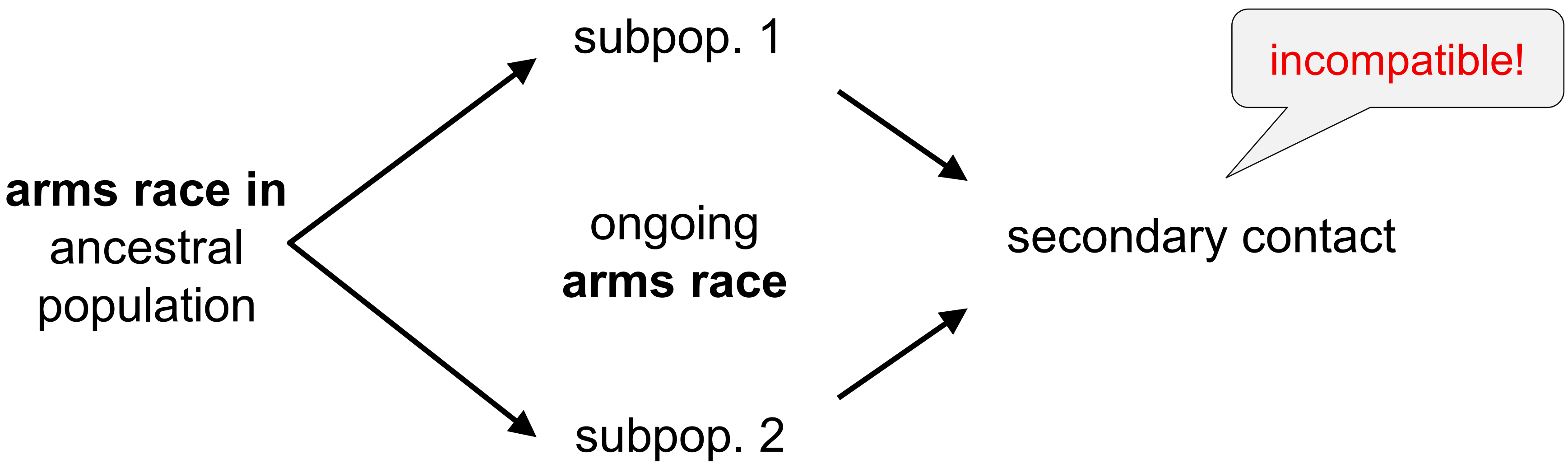
2 genes:



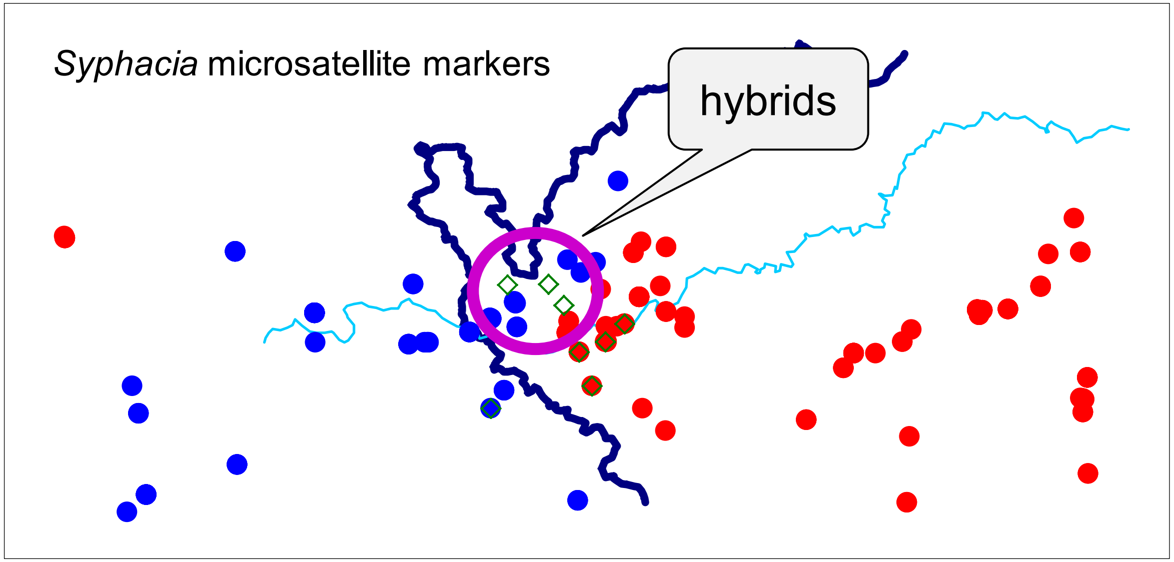
large population

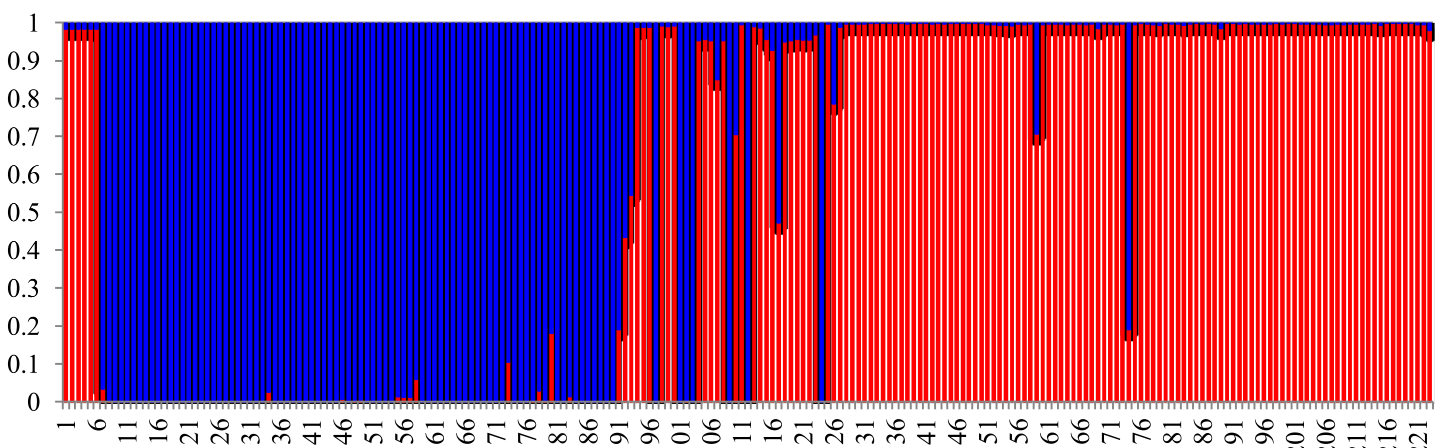
allopatric speciation usually slow (exceptions: sexual selection, genetic conflict)

genetic conflict:



co-speciation (parasite-host):





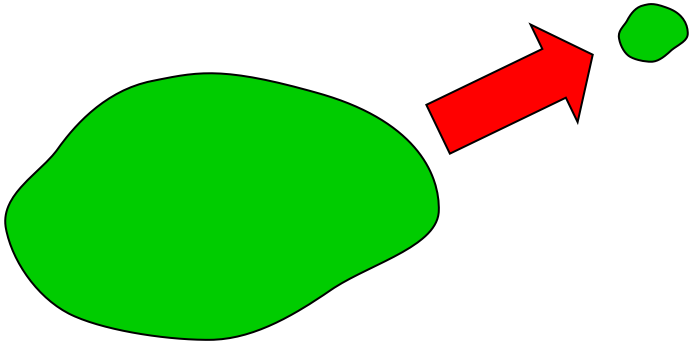
J. Goüy de Bellocq

Wasimuddin

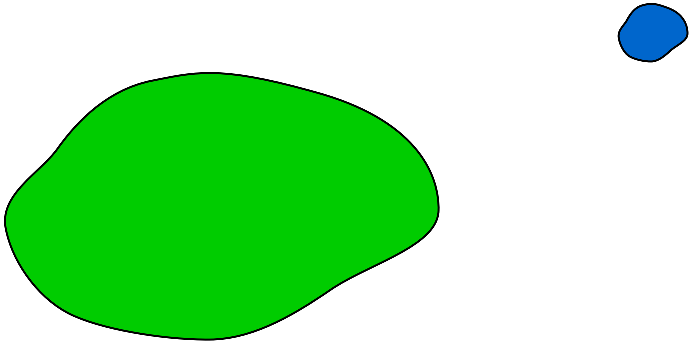
Peripatric speciation (founder-effect speciation)

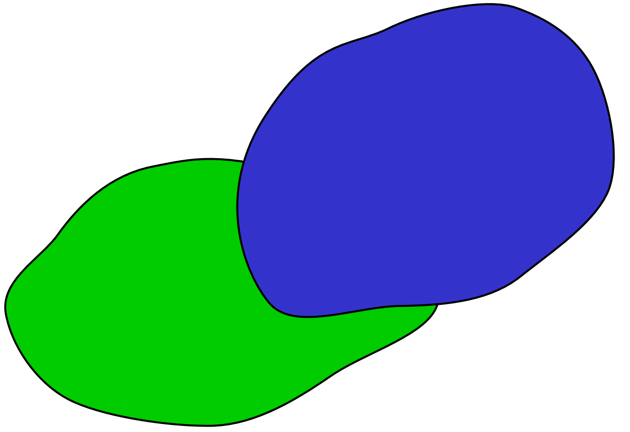
Mayr: founder effect

island organisms, peripheral isolates (extinction-recolonisation)



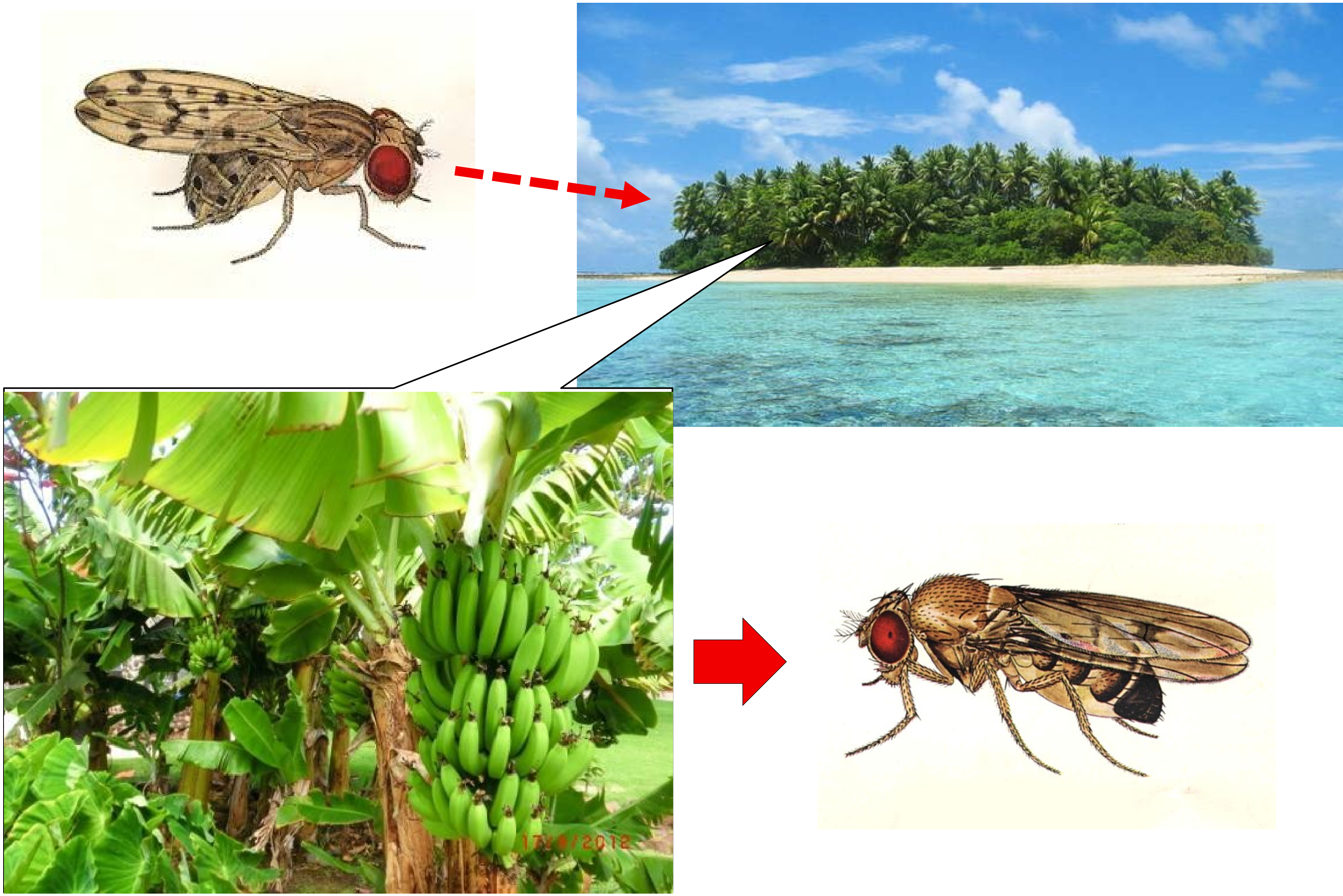
genetic revolution $\Rightarrow$ rapid speciation





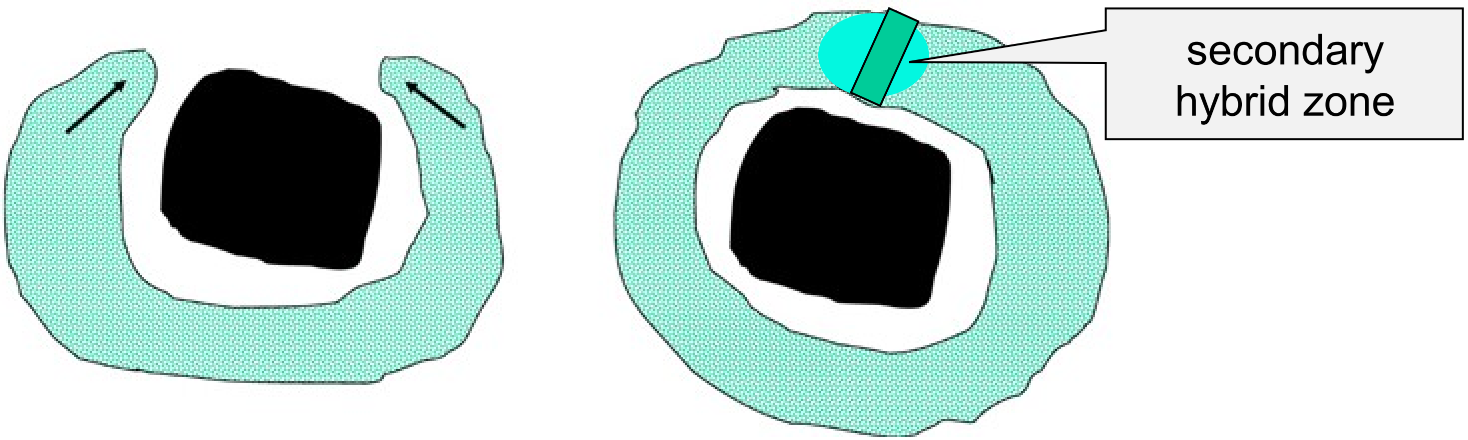
founder-flush model: *Drosophila*

colonisation of a novel environment – no selection ⇒ rapid divergence



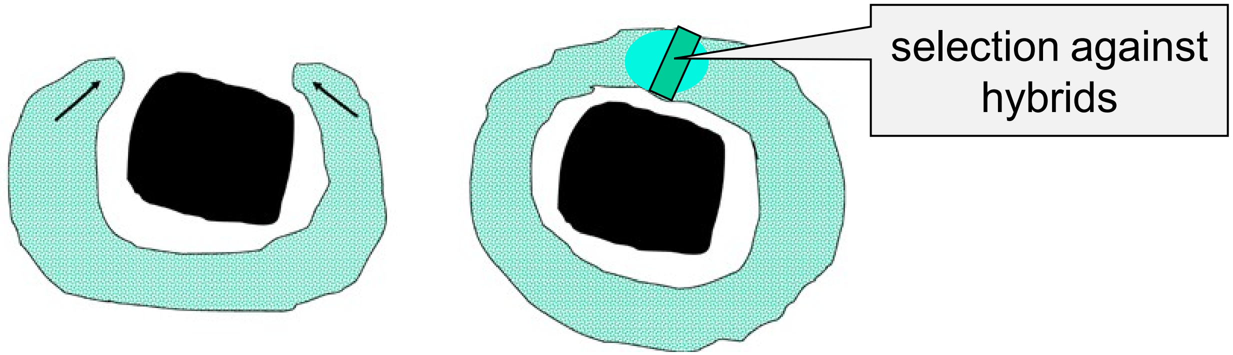
Allo-parapatric speciation (reinforcement speciation)

A. R. Wallace, R. A. Fisher, T. Dobzhansky



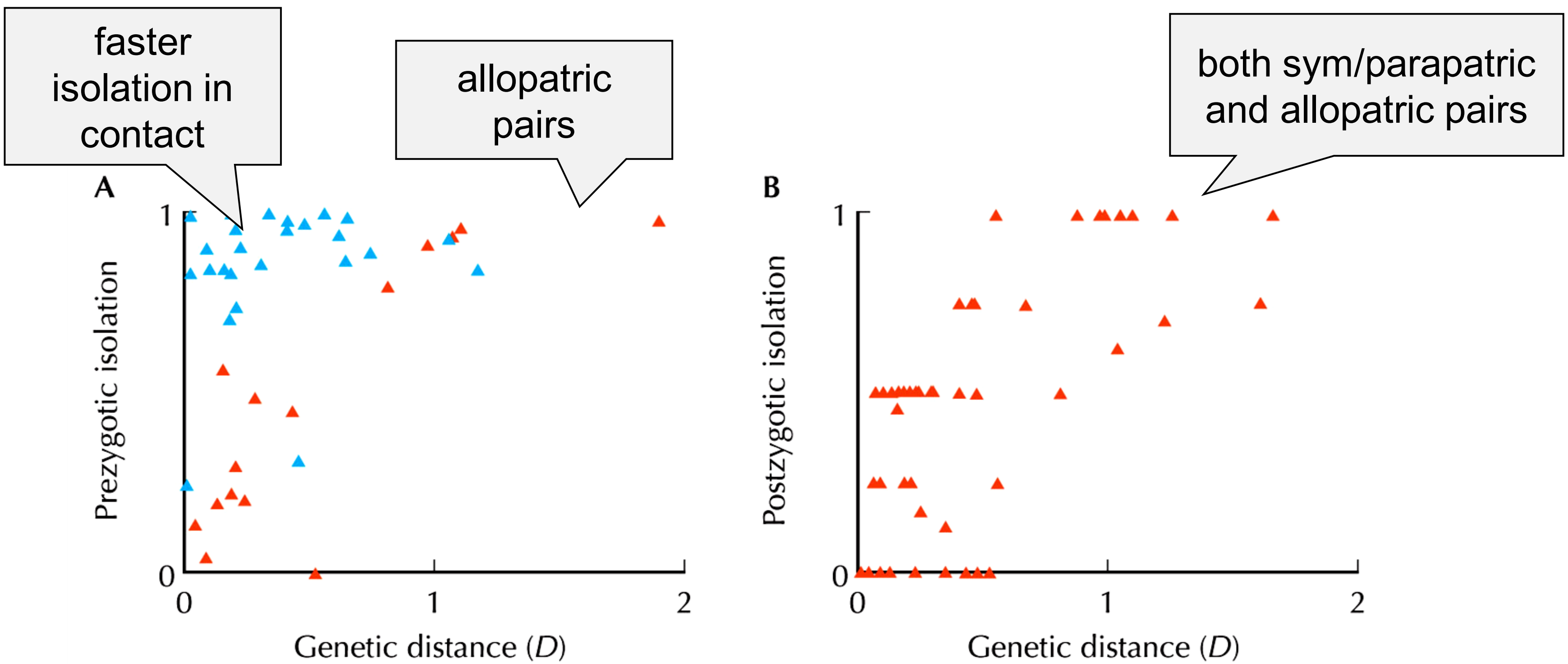
initial geographic isolation

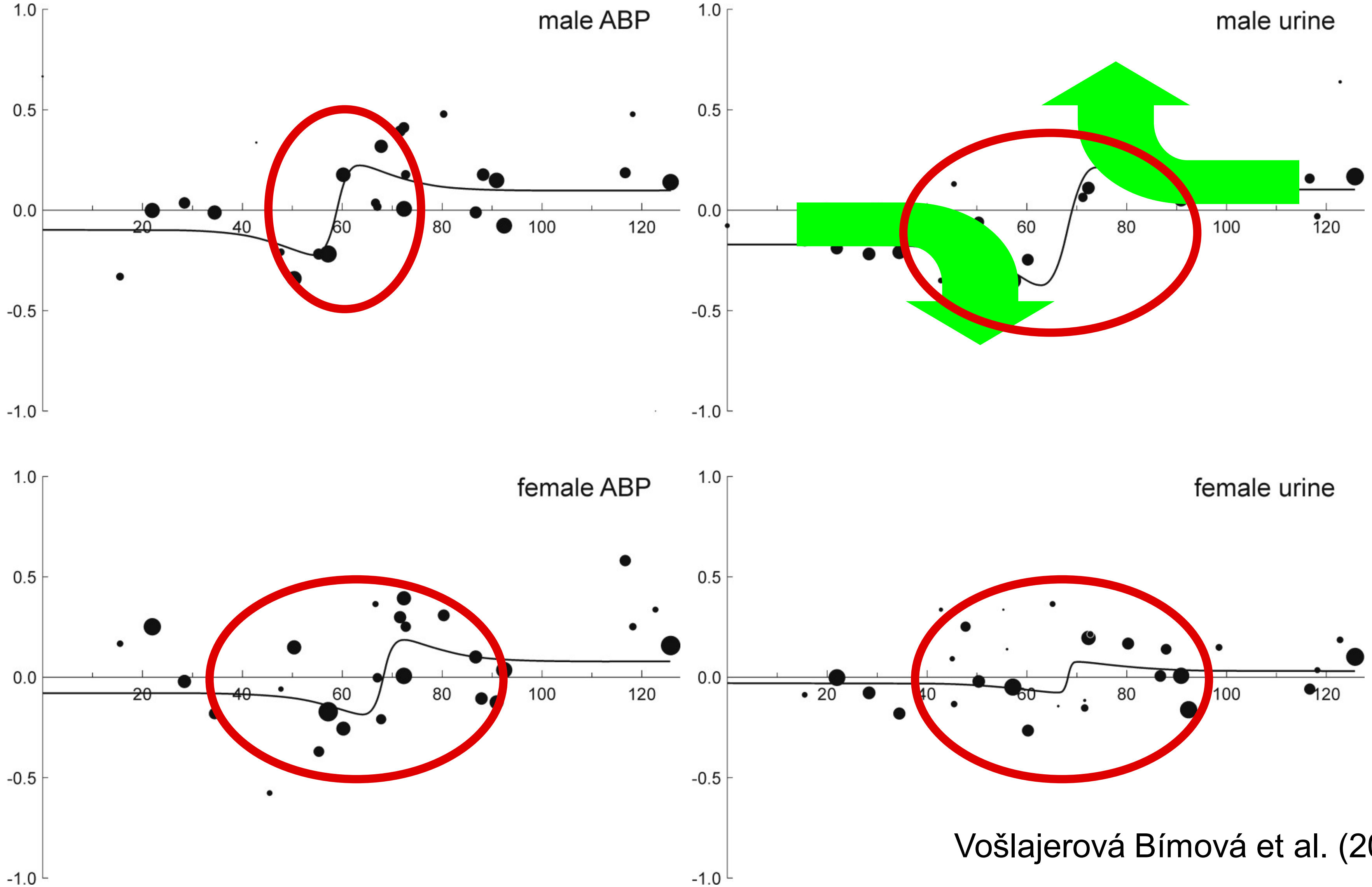
reproductive isolation incomplete → secondary hybrid zone



selection against hybrids ⇒ formation of prezygotic barrier

→ strenghtening of isolation (reinforcement) = Wallace´s effect

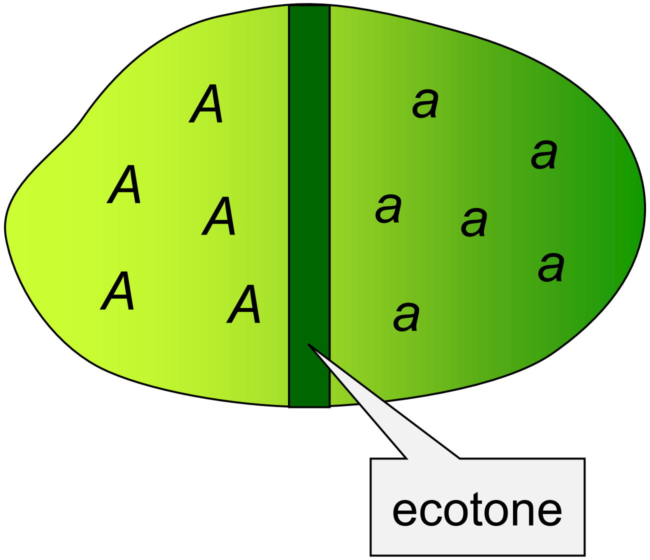




Vošlajerová Bímová et al. (2011)

Both female and male preference show reinforcement in the zone centre ⇒ prezygotic barrier probably contributes to reproductive isolation

Parapatric speciation



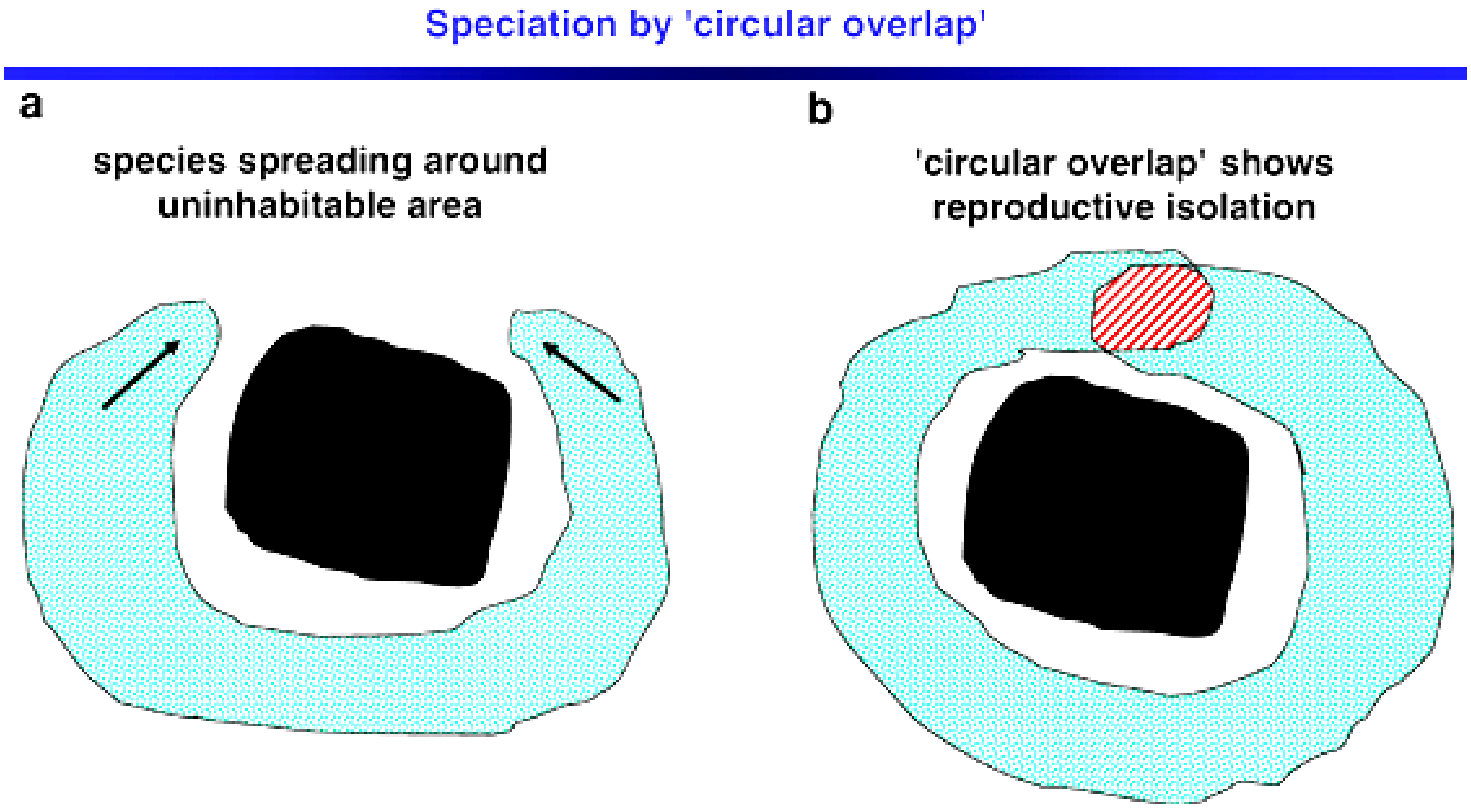
environmental gradient ⇒ genetic gradient

⇒ primary hybrid zone

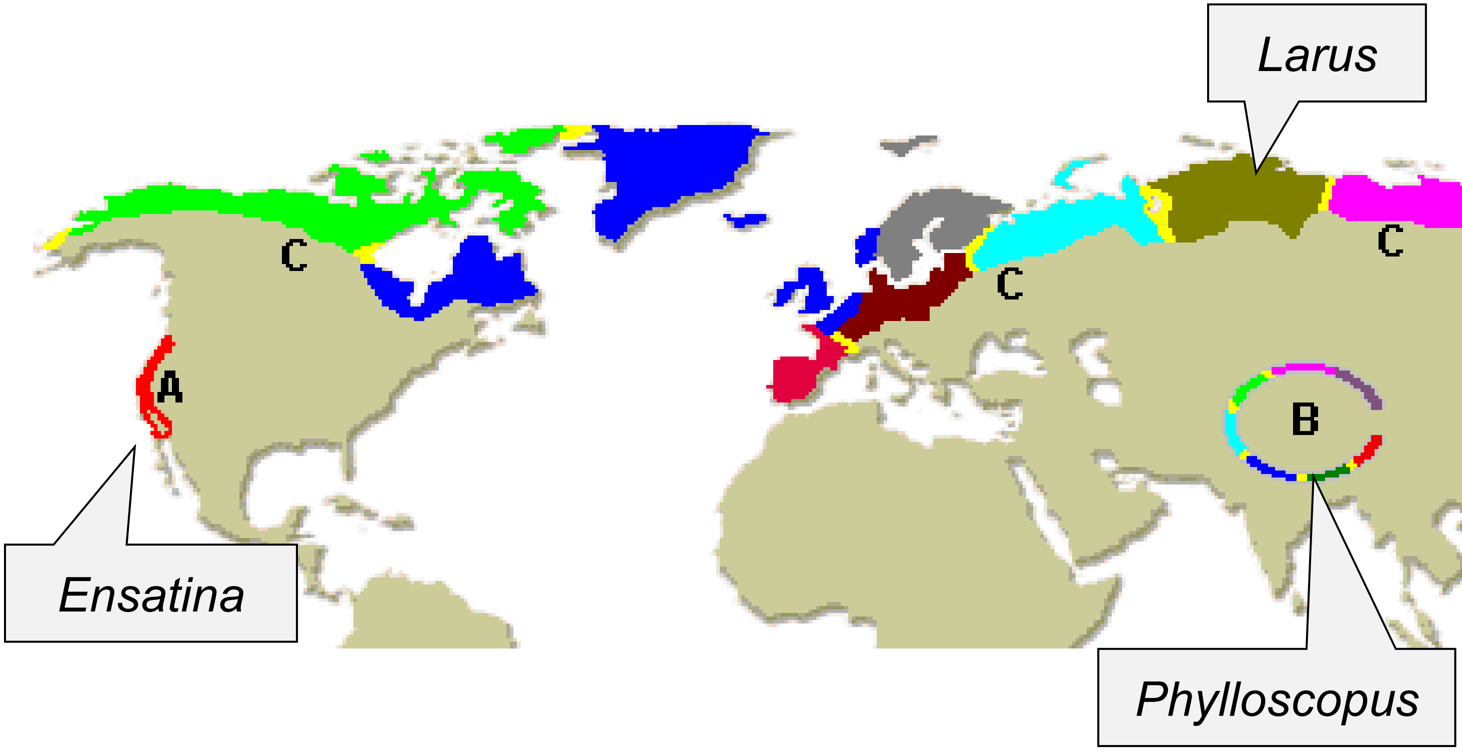
different selection in the two parts ⇒ genetic divergence even with gene flow

Sometimes difficult to distinguish allopatric and parapatric speciation:

ring species

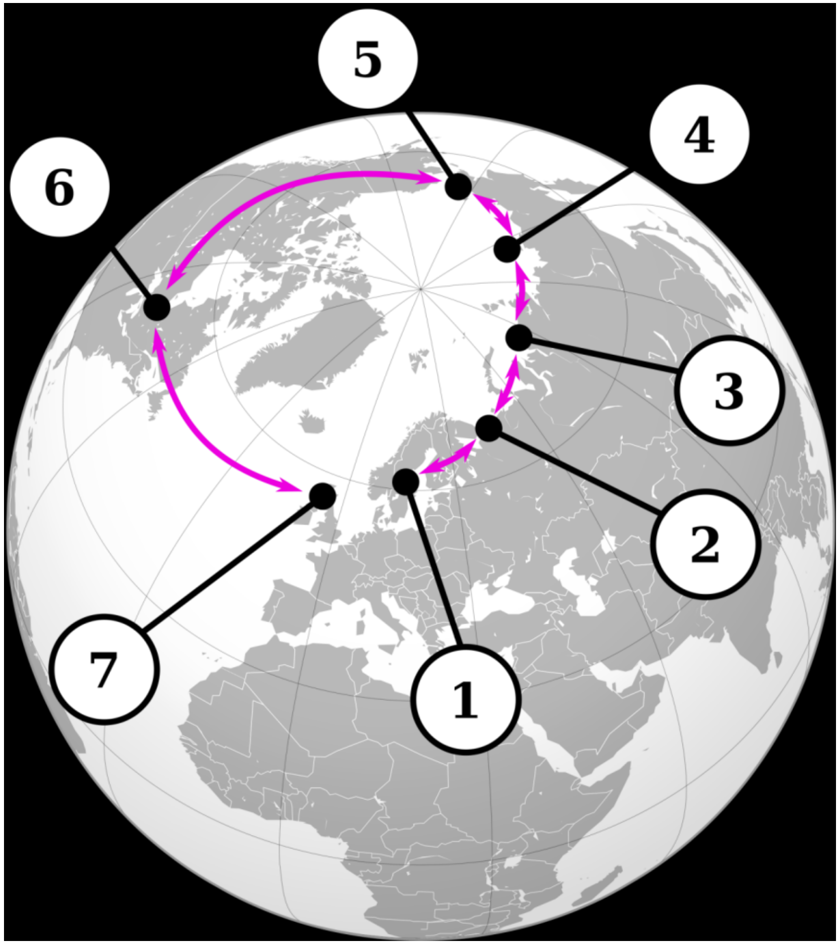


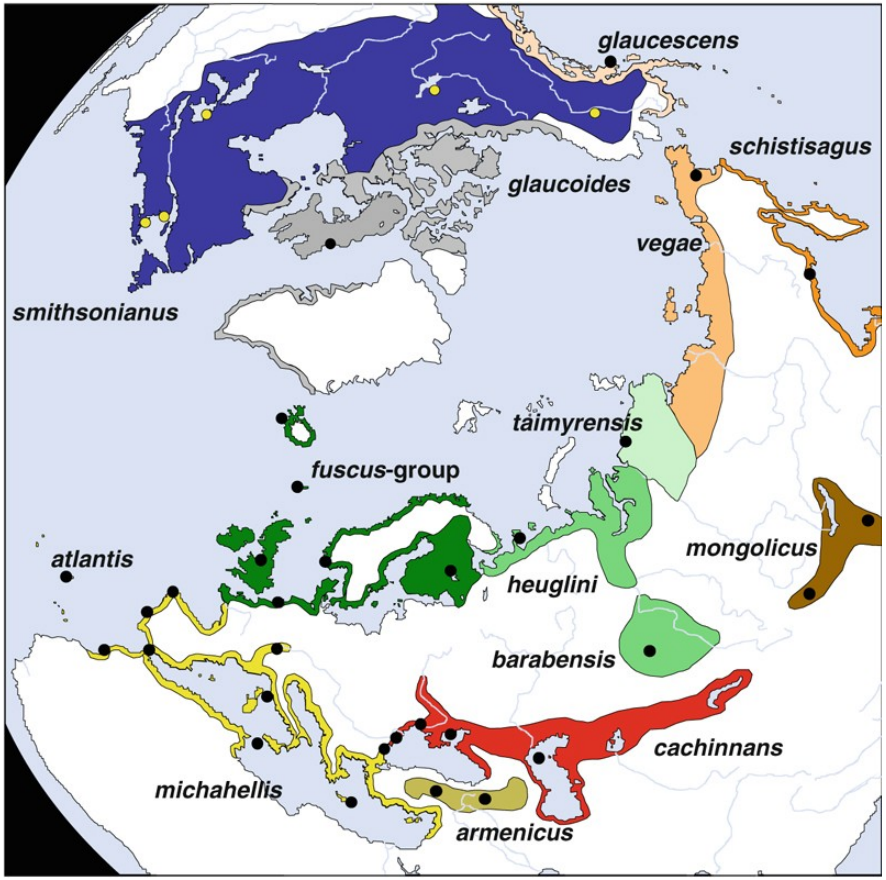
ring species:



ring species:

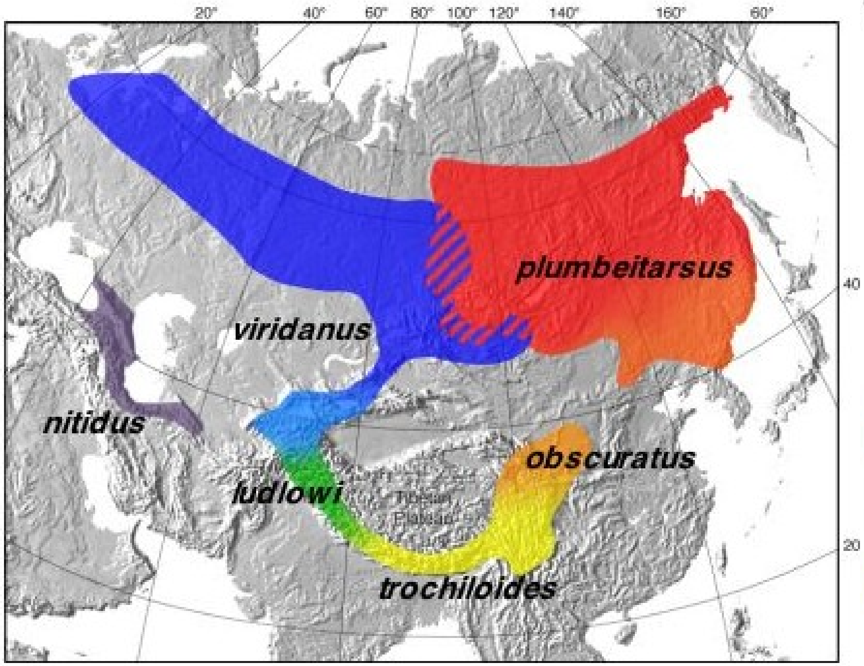
European herring gull (*Larus argentatus*) and lesser black-backed gull (*L. fuscus*)

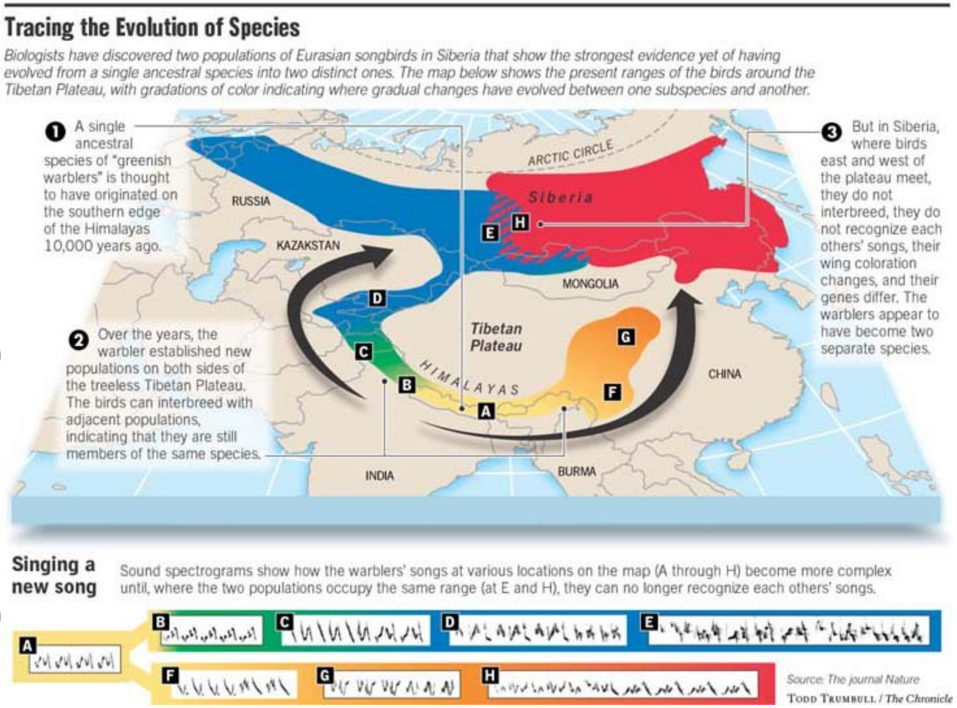




ring species:

greenish warbler (*Phylloscopus trochiloides*)

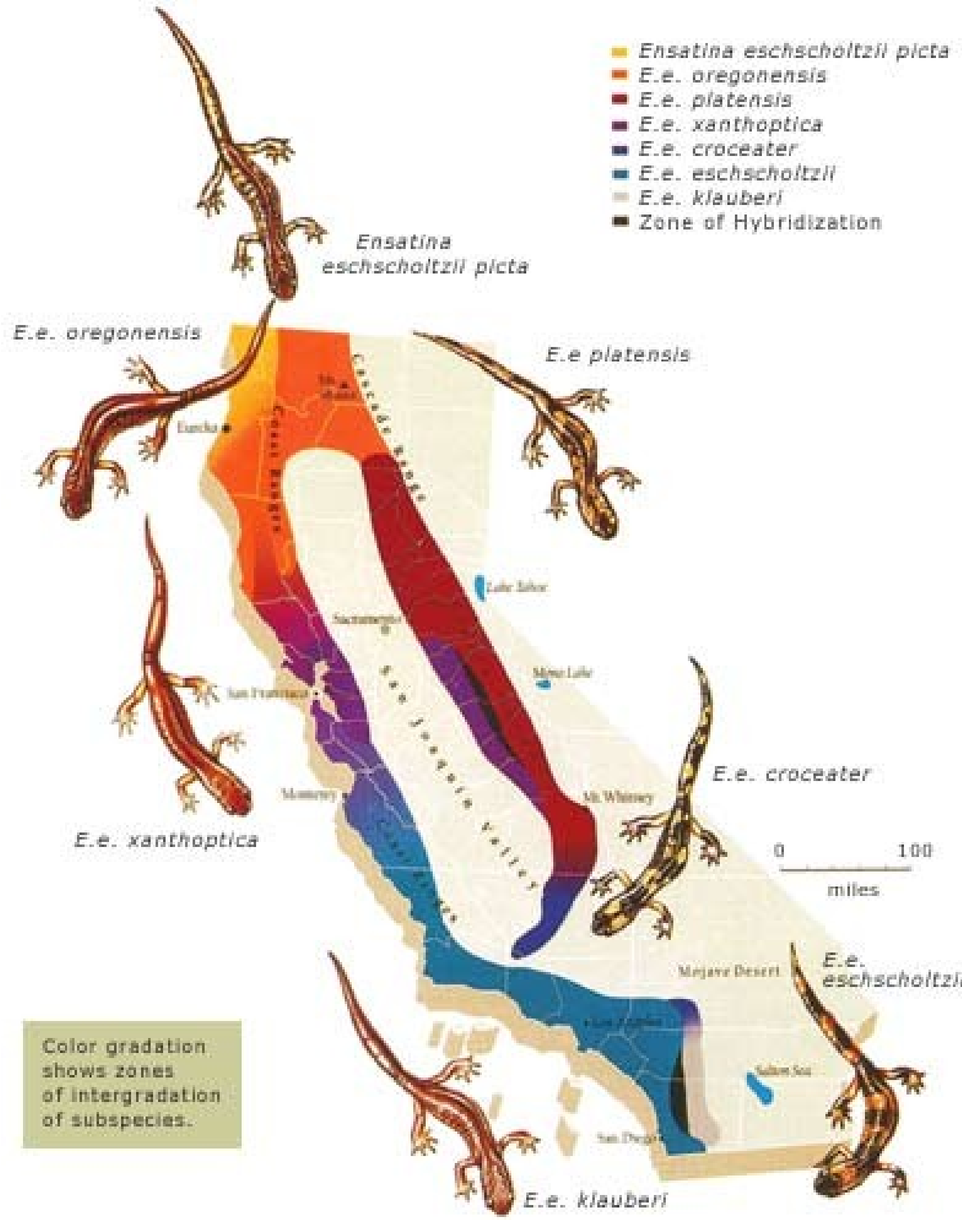




ring species: *Ensatina eschscholtzii*

Ensatina e. xanthoptica

Ensatina e. klauberi

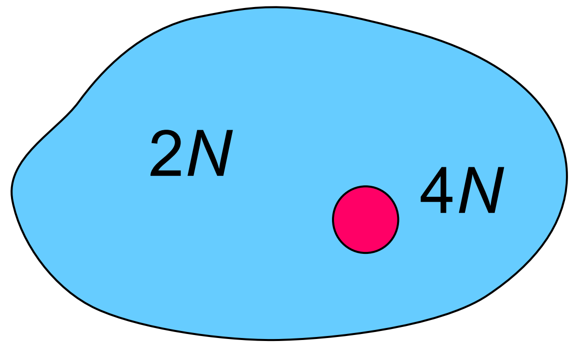


Sympatric speciation

Polyploidisation

$2N \rightarrow 4N$
$2N \times 4N = 3N$

aneuploid hybrids



Host shift

R. pomonella

apple magot (*Rhagoletis pomonella*):

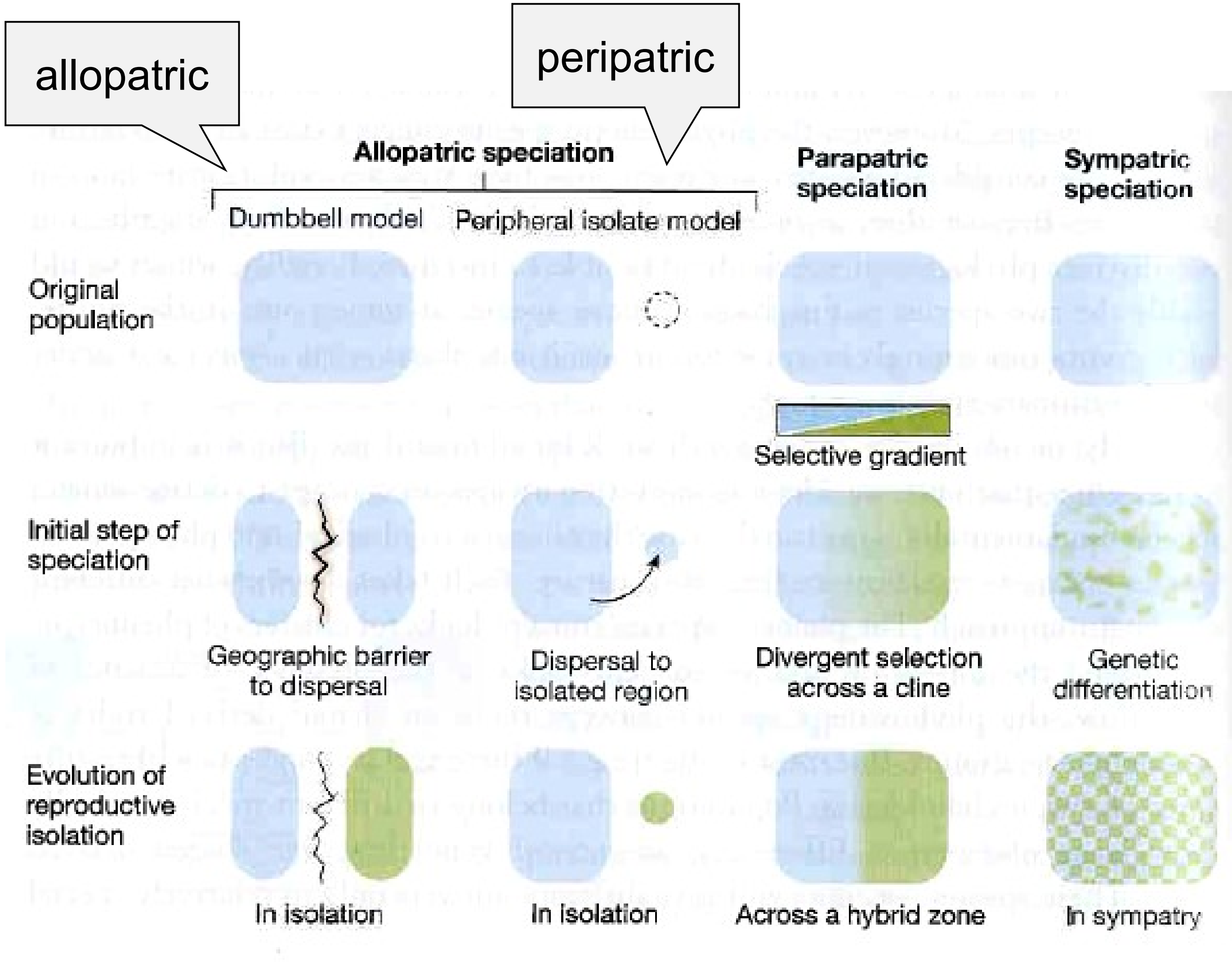
hawthorn → 1866 apple → ca. 1960 cherry

peer, rose, plum etc.

assortative mating, genetic differences, different incubation period (seasonal isolation)

absence of postzygotic mechanisms

Final overview:

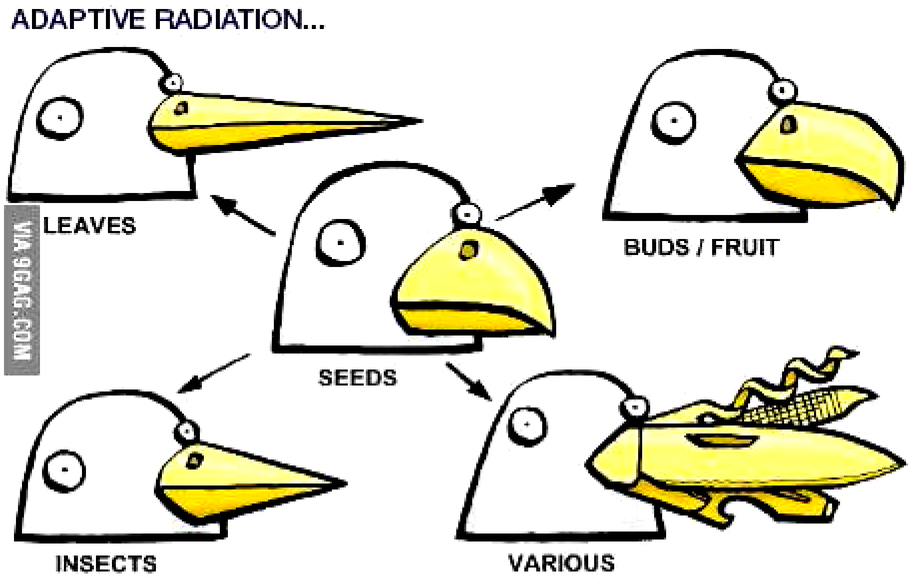


Rate of speciation:

allopatric speciation usually slow

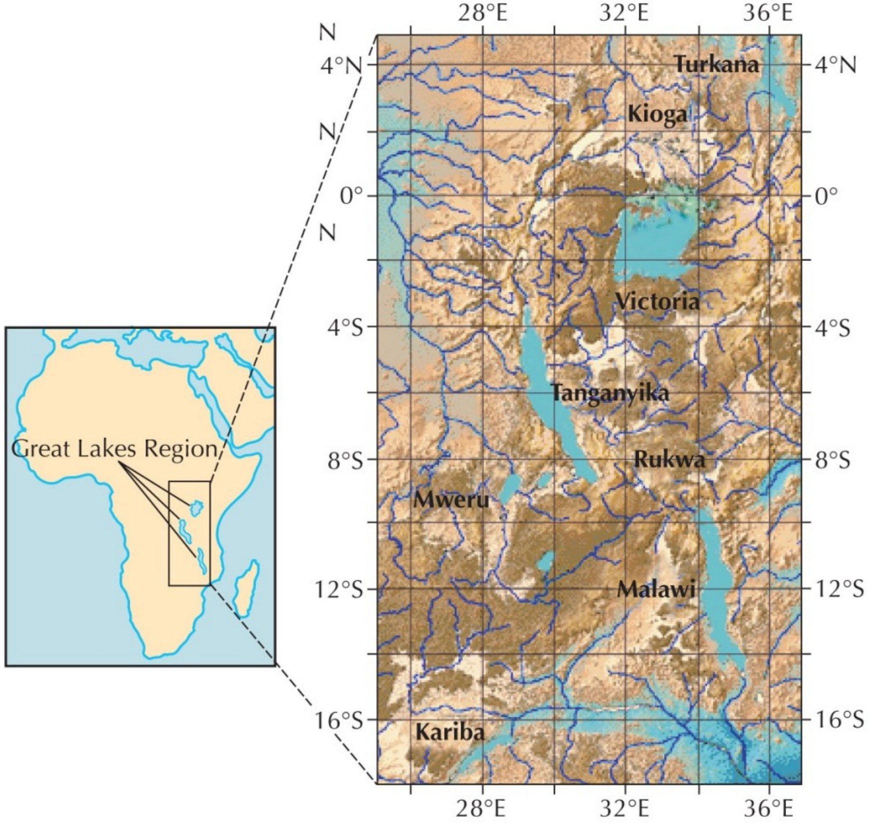
rapid speciation and adaptive radiation:

- Darwin´s finches
- fruit flies in Hawaii
- cichlids in African lakes



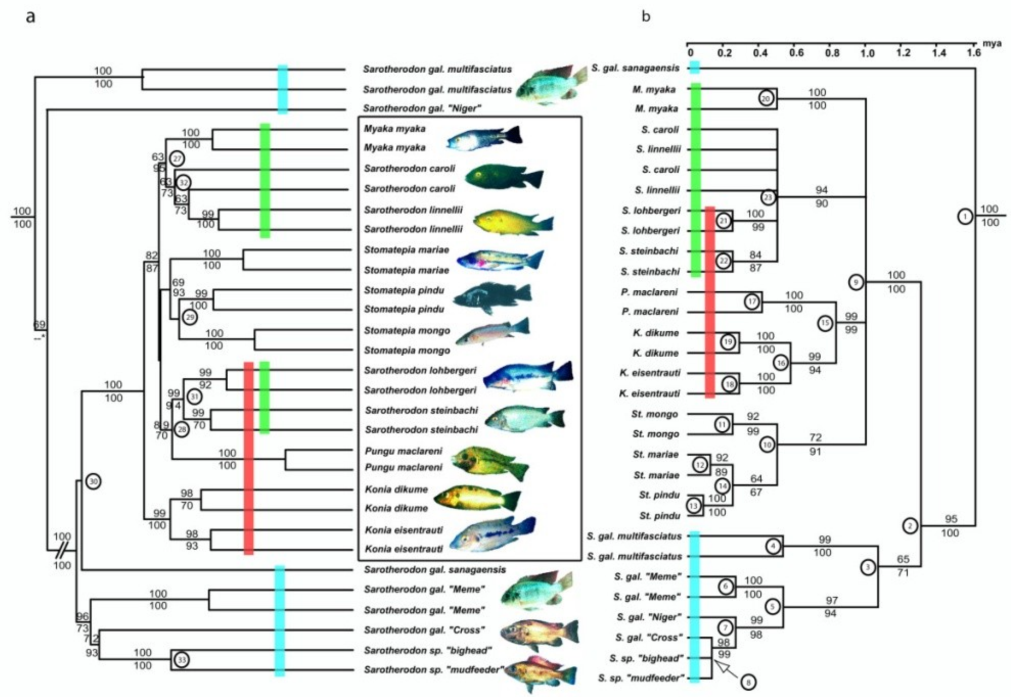
Great Rift Valley – Viktoria, Malawi, Tanganyika;

Viktoria: 400 000 years, 17 300 – drying, 14 700 re-creation;
molecular clock: ancestor of cichlids – 100 000 years



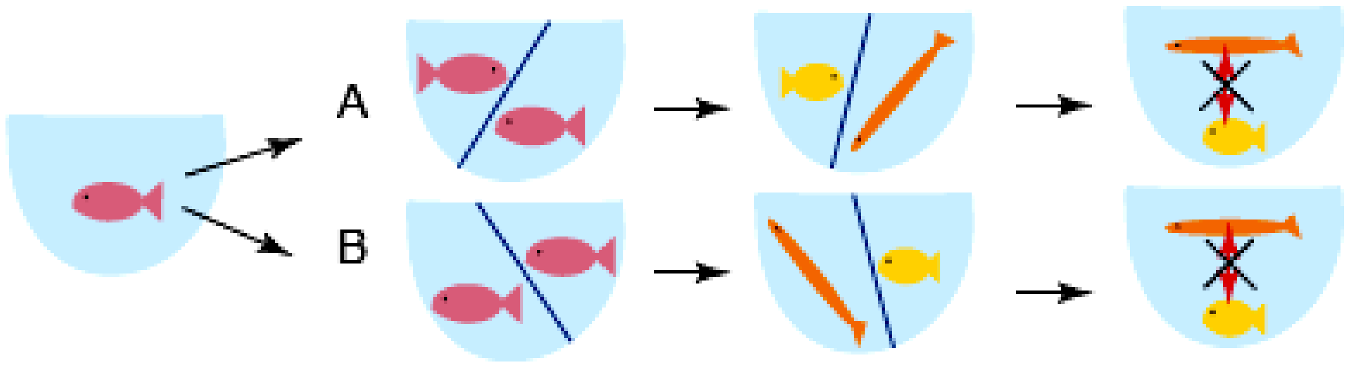
Cameroon: Barombi Mbo (4,2 km^2) – 11 species, Bermin (0,6 km^2) – 9 cichlid species, monophyletic origin, absolute isolation, ancestor – <u>10 000</u> years

Barombi Mbo



Bermin

Paralel speciation



habitat shift

role of natural selection

role of sexual selection (cichlids)