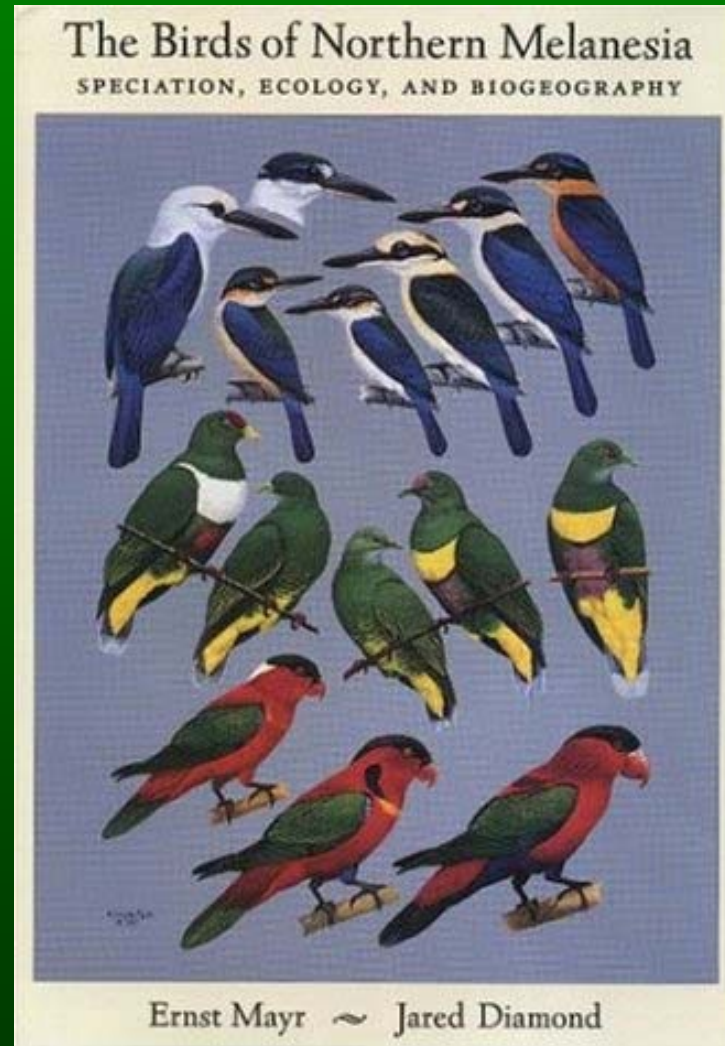


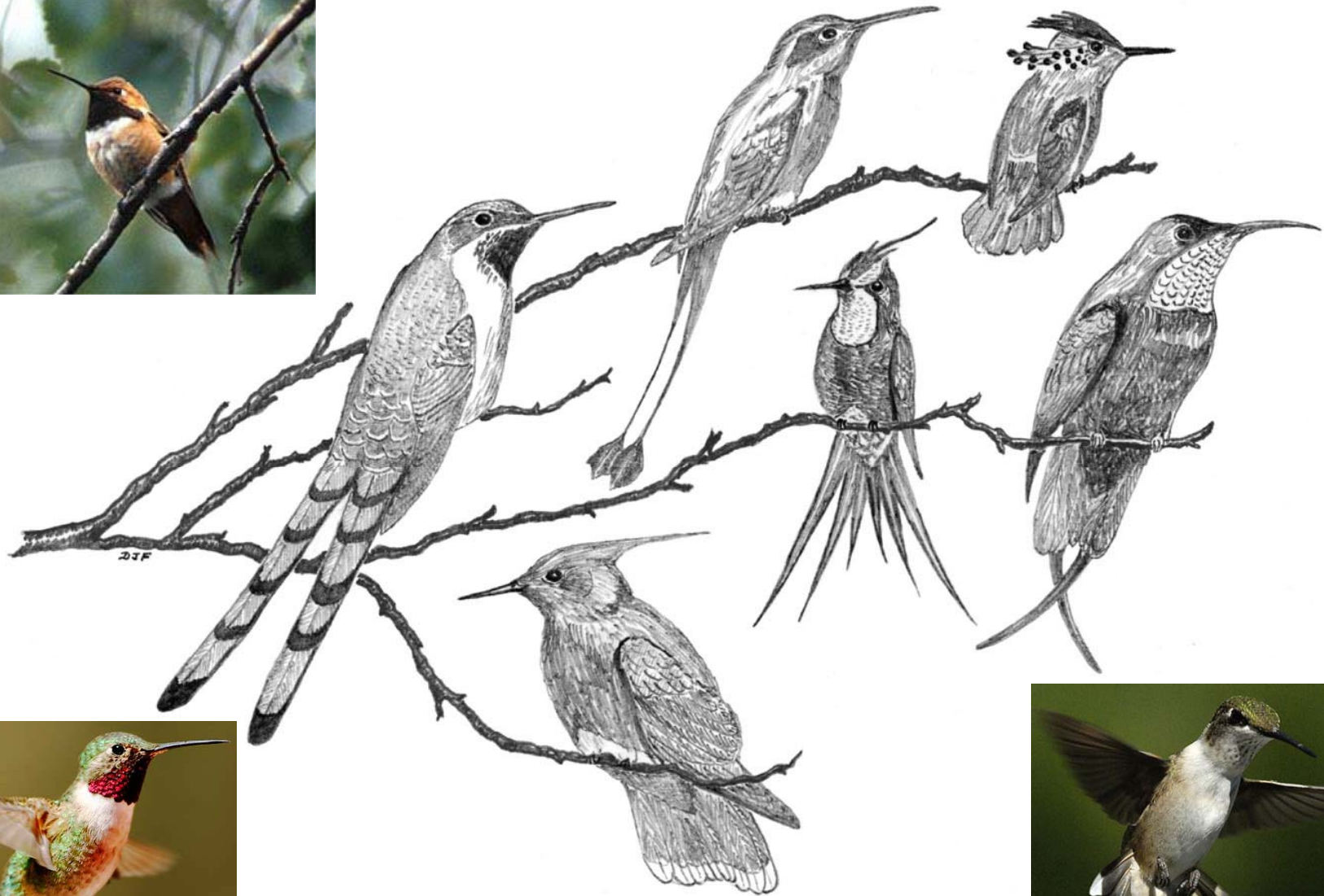
Mechanisms of Speciation



Some species show little geographic variation...



...while others vary quite a bit.



Geographic variation may be gradual...



Geographic Variation
in Poisonous Clovers.

White indicates proportion
not producing cyanide

Red indicates proportion
producing cyanide

... or abrupt.



Terrestrial adults of six species of ambystomatid salamanders.

What is a species?

Because speciation is often a gradual process,
it may be difficult to recognize boundaries
between species.

TABLE 15.1 *Some species concepts*

Biological species concept Species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1942).

Evolutionary species concept A species is a single lineage (an ancestor-descendant sequence) of populations or organisms that maintains an identity separate from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978).

Phylogenetic species concepts (1) A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent (Cracraft 1989). (2) A species is the smallest monophyletic group of common ancestry (de Queiroz and Donoghue 1990).

Genealogical species concept Species are “exclusive” groups of organisms, where an exclusive group is one whose members are all more closely related to one another than to any organism outside the group (Baum and Shaw 1995).

Recognition species concept A species is the most inclusive population of individual biparental organisms that share a common fertilization system (Paterson 1985).

Cohesion species concept A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Templeton 1989).

For All Species (Spp.) Concepts:

- Spp. consist of groups of “actual” or “potential” interbreeding pop’s.
- Spp. are a fundamental unit of evolution (bridging both macroevolution and microevolution).
- Spp. share a distinguishing characteristic, which is evolutionary independence. This occurs when microevolutionary forces (mutation, selection, migration & drift) operate on each spp. separately.
 - Forms a boundary for the spread of alleles.
 - Different spp. follow independent evolutionary trajectories.

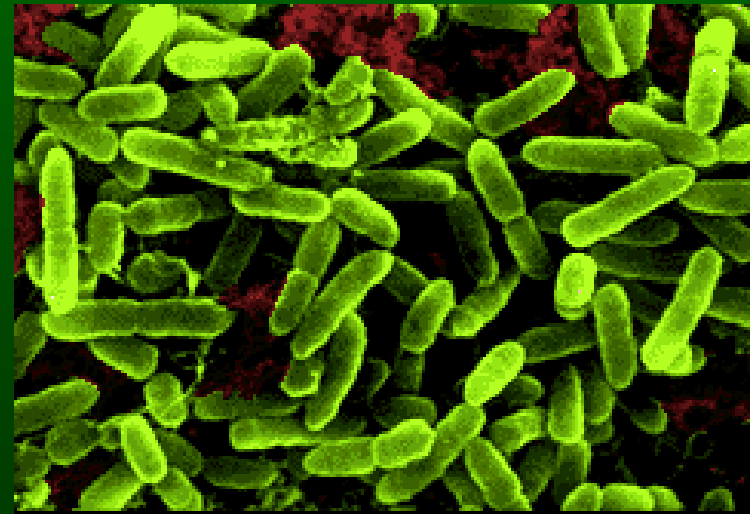
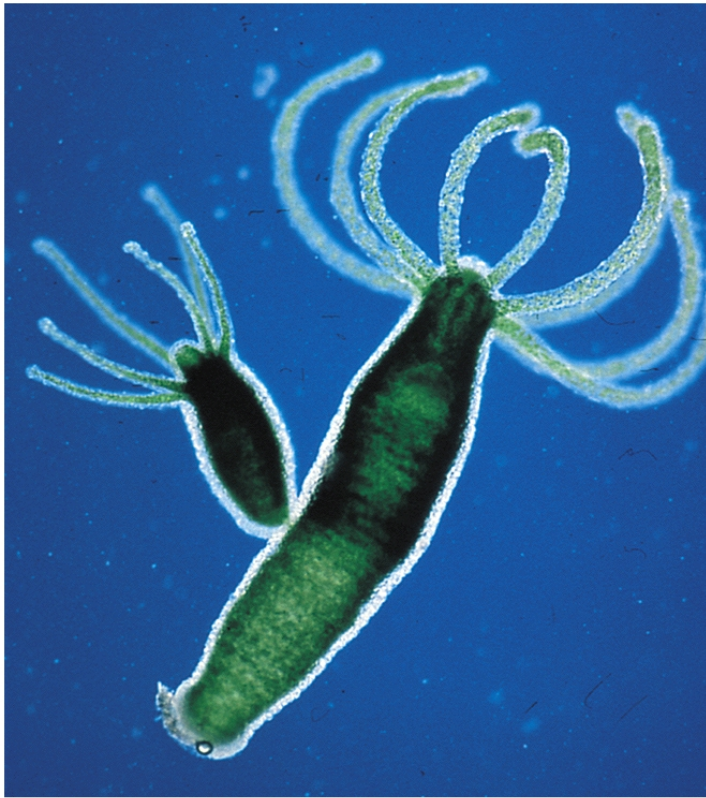
Biological Species Concept (BSC)

- Species are groups of actually or potentially interbreeding individuals that are reproductively isolated from other such groups (Mayr).
- Used by the Endangered Species Act (for better or worse).
- What about non-overlapping pop's, fossil record, & microbes?

Difficulties with the Biological Species Concept

- **Asexual reproduction**
- **Many geographically isolated populations**
- **Variation in reproductive isolation**
- **Hybridization and introgression**
- **Endosymbiont-caused isolation**

Asexual reproduction



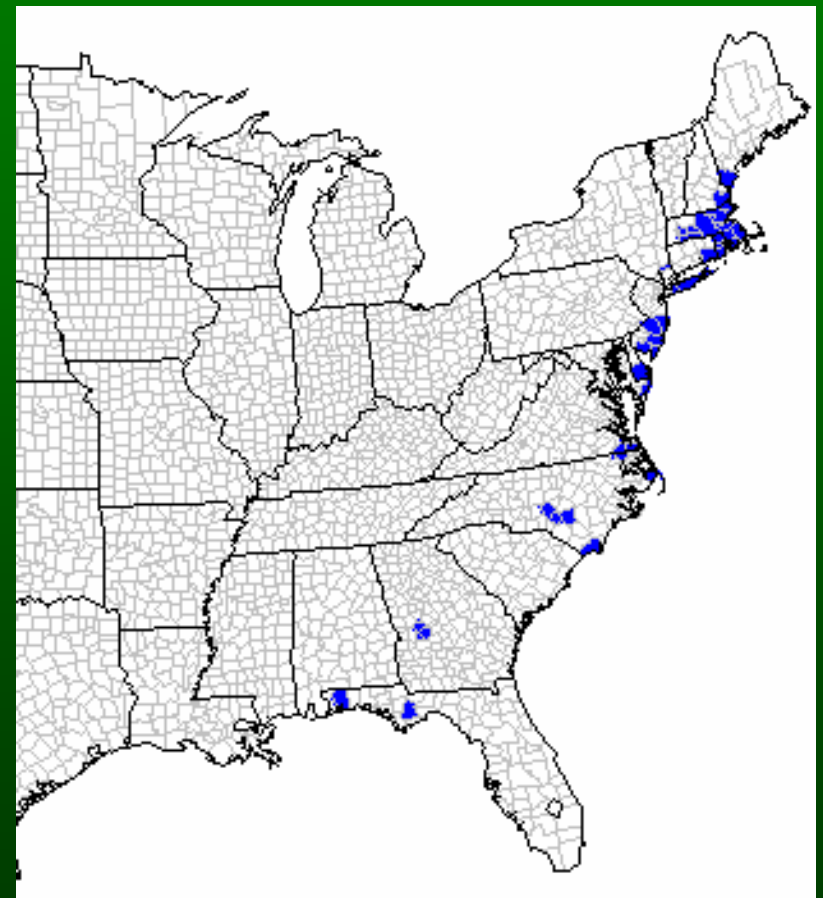
Many geographically isolated populations



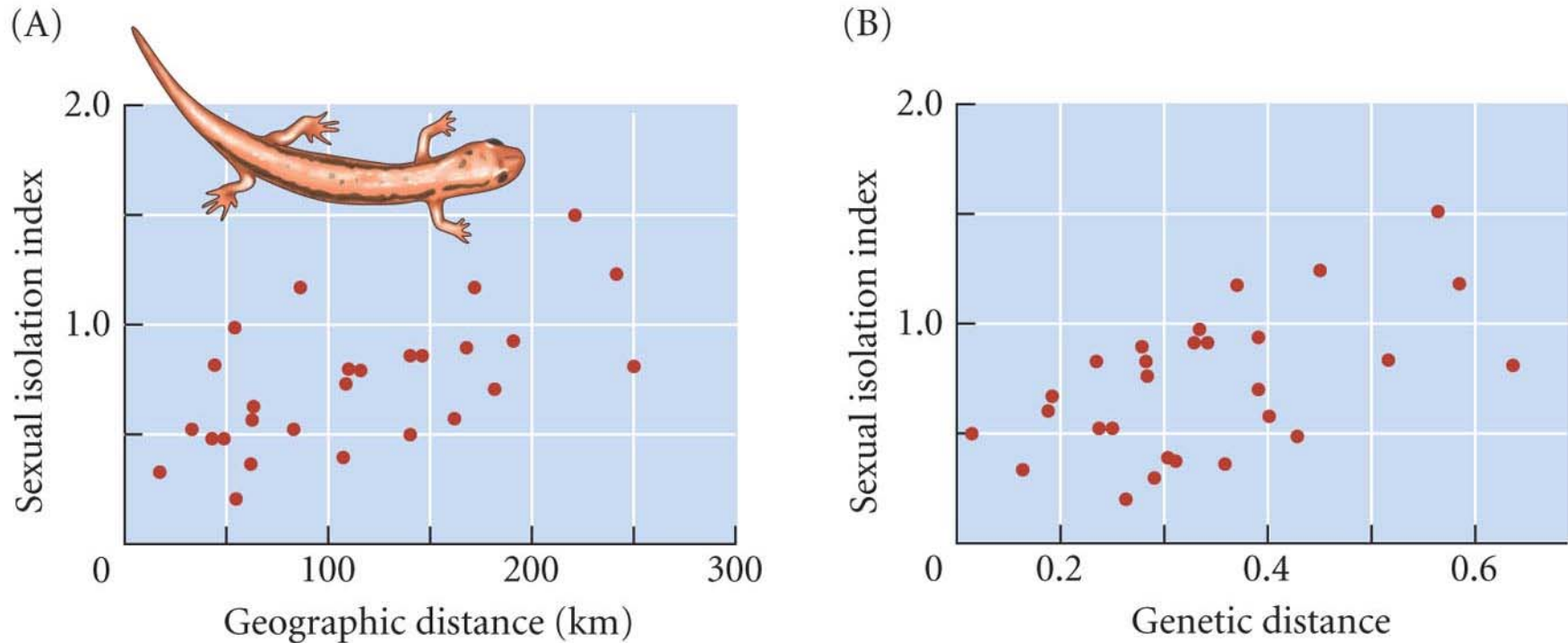
Calliphrys hesseli



Calliphrys hesseli underside

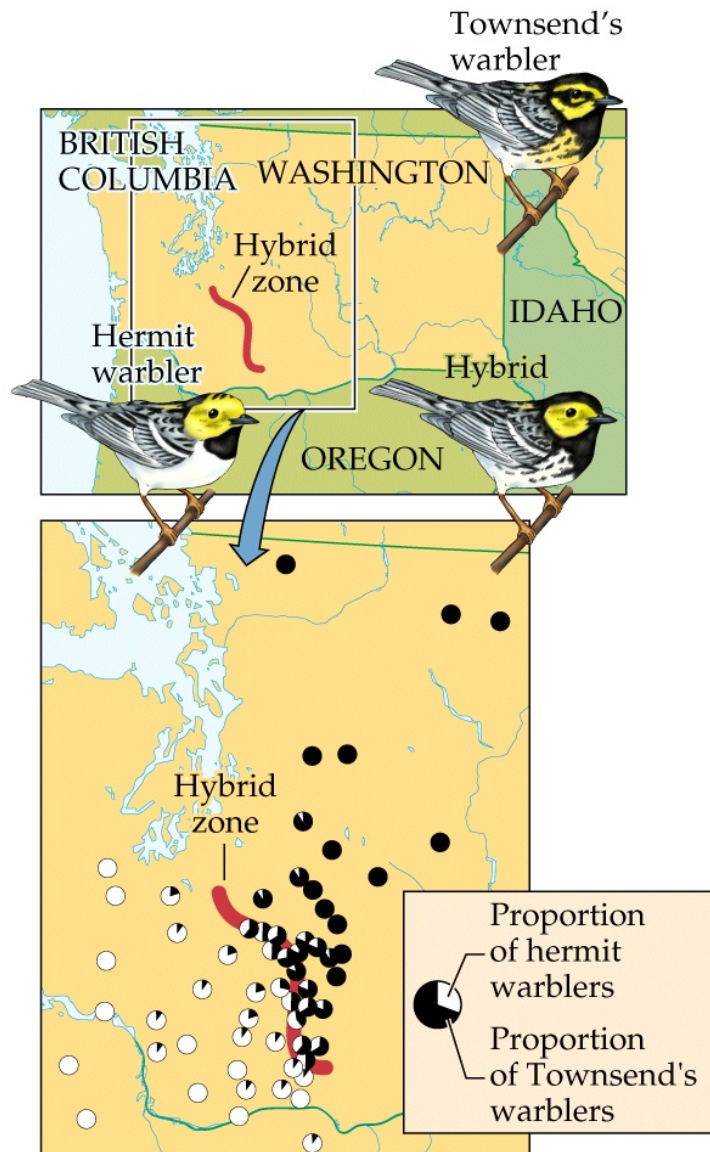


Variation in reproductive isolation



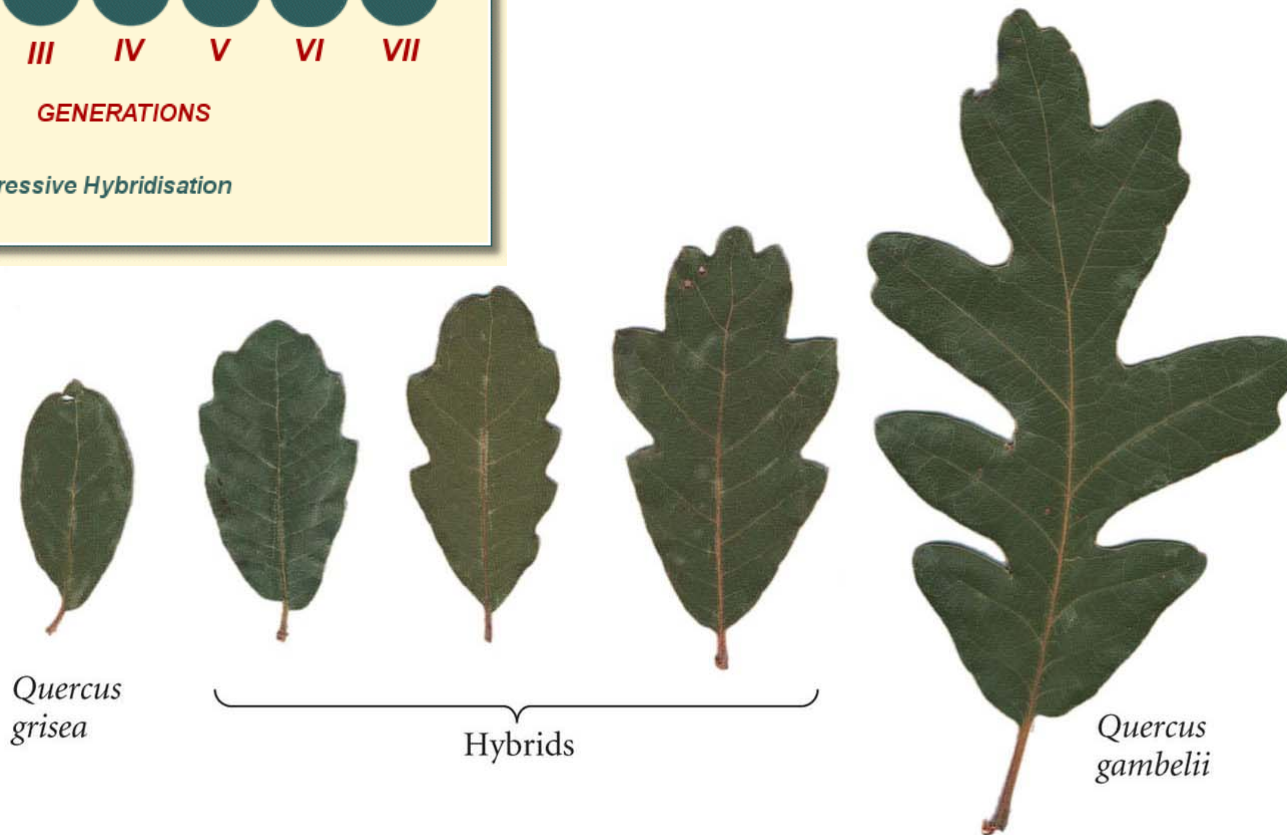
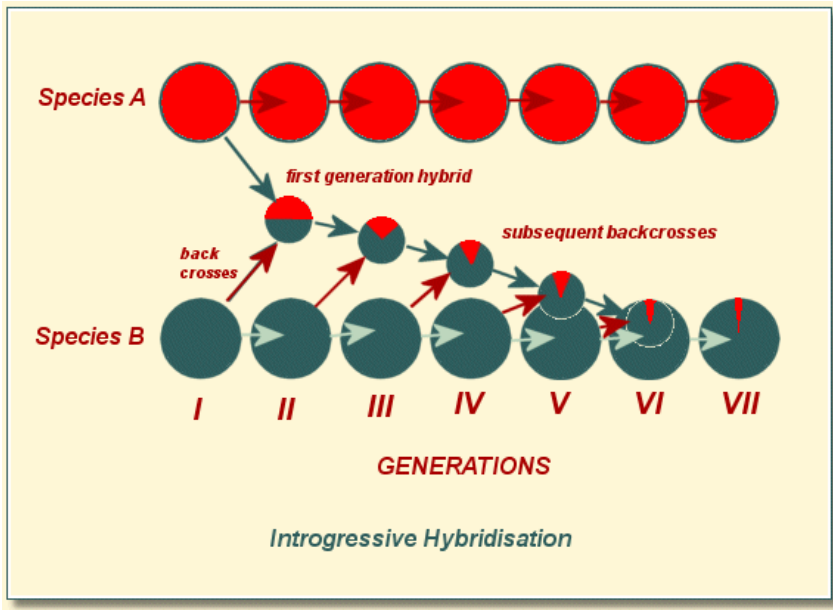
Degree of sexual isolation between populations
of *Desmognathus ochrophaeus*

Hybridization and Introgression

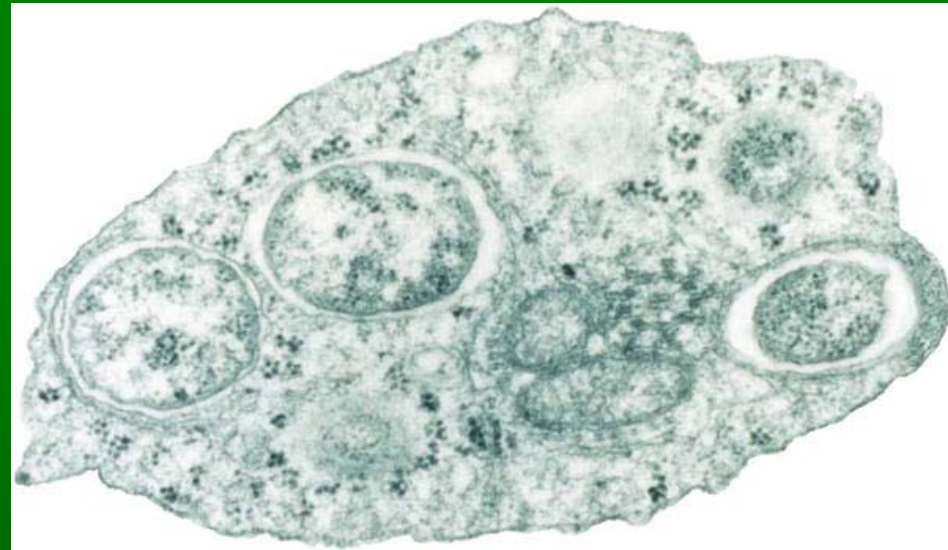


Hybrids may form if separated populations rejoin without sufficient genetic differences having accumulated.

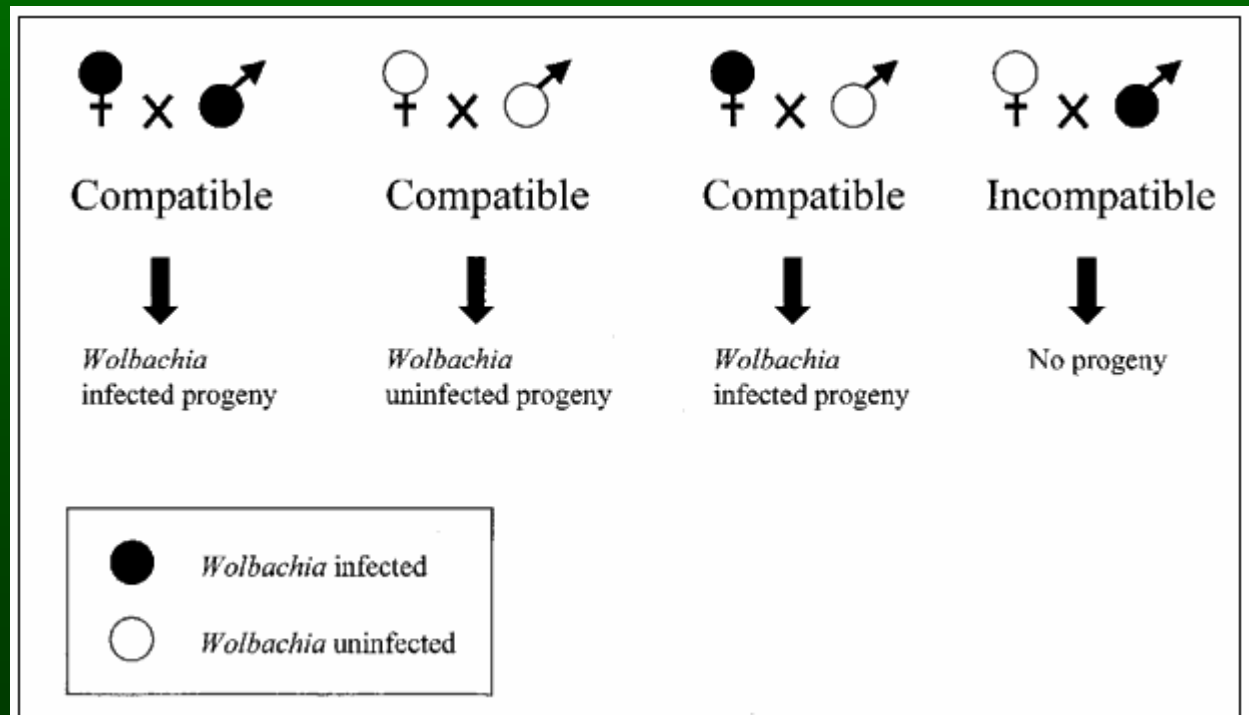
Hybridization and Introgression



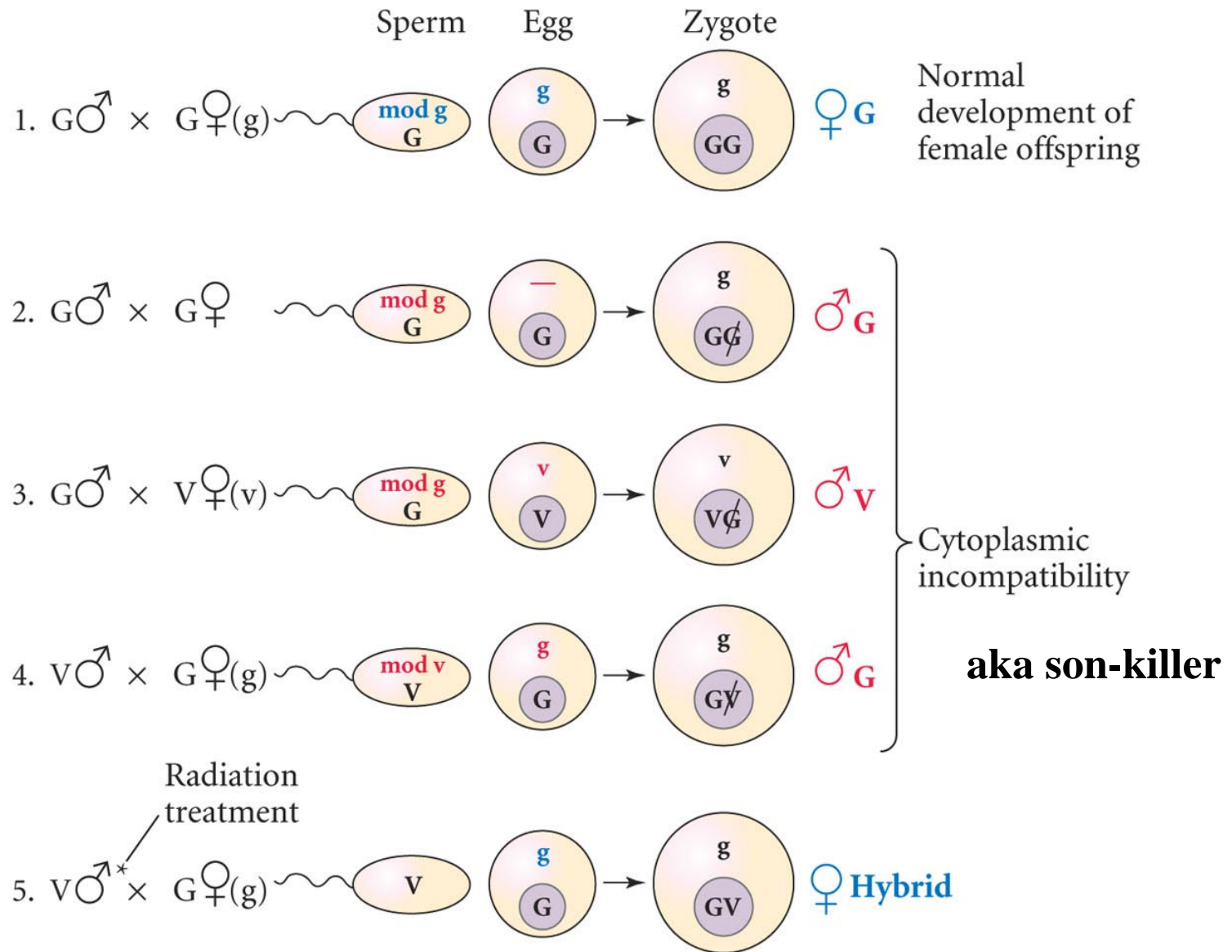
The movement of a gene from one species into the gene pool of another by backcrossing an interspecific hybrid with one of its parents.



Endosymbiont-caused isolation



Cytoplasmic incompatibility in the wasps *Nasonia vitripennis* and *N. giraulti*.



Phylogenetic Species Concept (PSC)

- **The smallest aggregation of populations or lineages diagnosable by a unique combination of character states (Nixon & Wheeler).**
- **Monophyletic groups derived from a single common ancestor.**
- **Not standardized, which traits are most important?**

Evolutionary Species Concept (ESC)

- **A single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies (Simpson).**
- **Required for fossil record analysis.**
- **Must be applied carefully and consistently, i.e., “Cryptic species”.**

10 Cryptic Species revealed in the neotropical skipper butterfly *Astraptes fulgerator*.



TRIGO



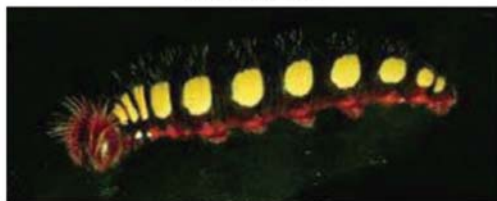
CELT



LONCHO



INGCUP



LOHAMP



HIHAMP



BYTTNER



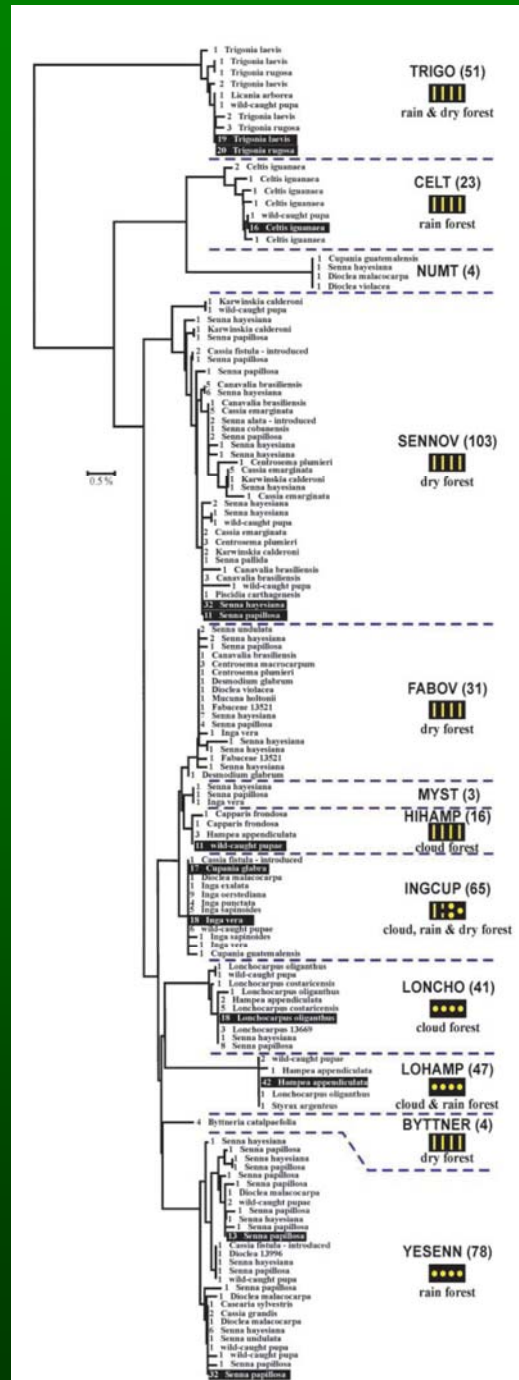
FABOV



YESENN



SENNOV

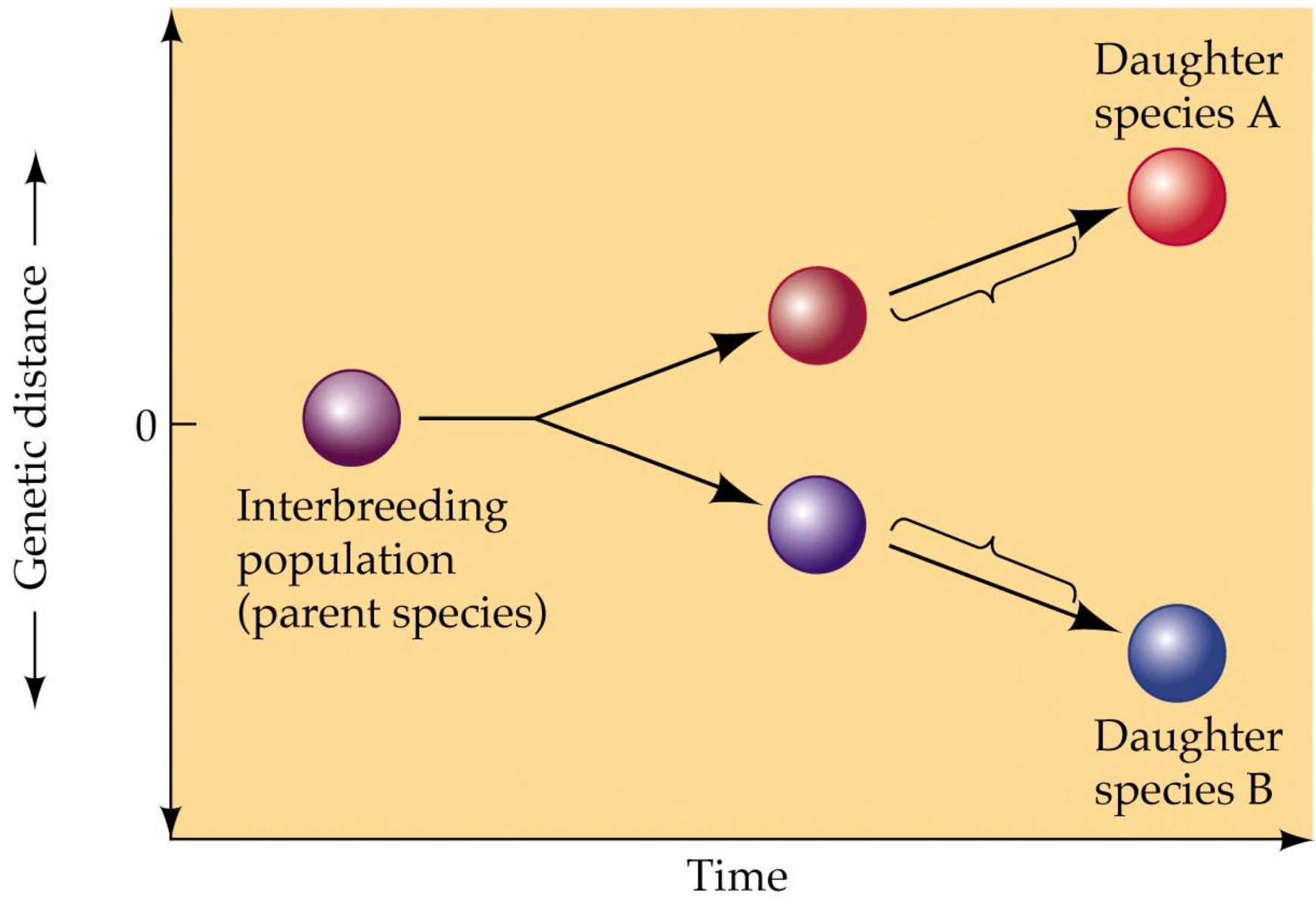


Diagnosing Species in Practice

- **Morphology**
- **Behavior**
- **Molecular data**

What is speciation?

- **Isolation:** Physical separation between pop's
 - May or may not be required!
- **Divergence:** In habitat use and/or mating tactics
 - Via Selection, Mutation, and/or Drift
- **Completion:** aka Reproductive Isolation
 - 2° Contact via Reinforcement
 - Hybridization events



Major Questions in Speciation Research

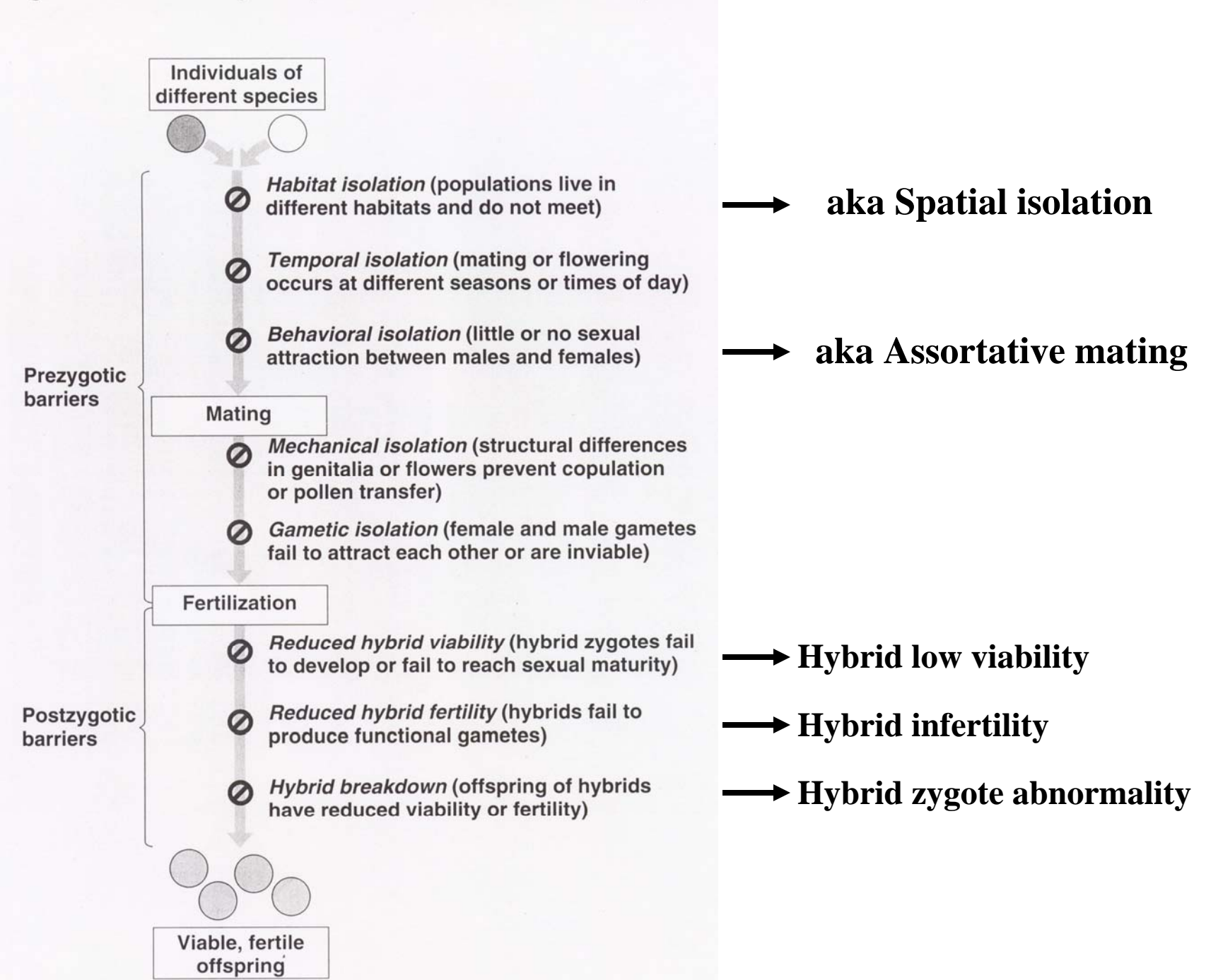
- What is the geographic context of speciation?
- What are the roles that evolutionary forces (selection, drift, gene flow) play in speciation?
- Are few genes or many involved in speciation?
- How long does speciation take?
- Why do some lineages speciate more rapidly than others?

Under the **Biological Species Concept**, the key to understanding the formation of new species lies in understanding the **evolution of reproductive barriers**.

Intrinsic vs. extrinsic barriers

(Rem: Mass vs. Weight example)

Figure 22.6 Summary of reproductive barriers between species



Prezygotic Barrier: Temporal Isolation

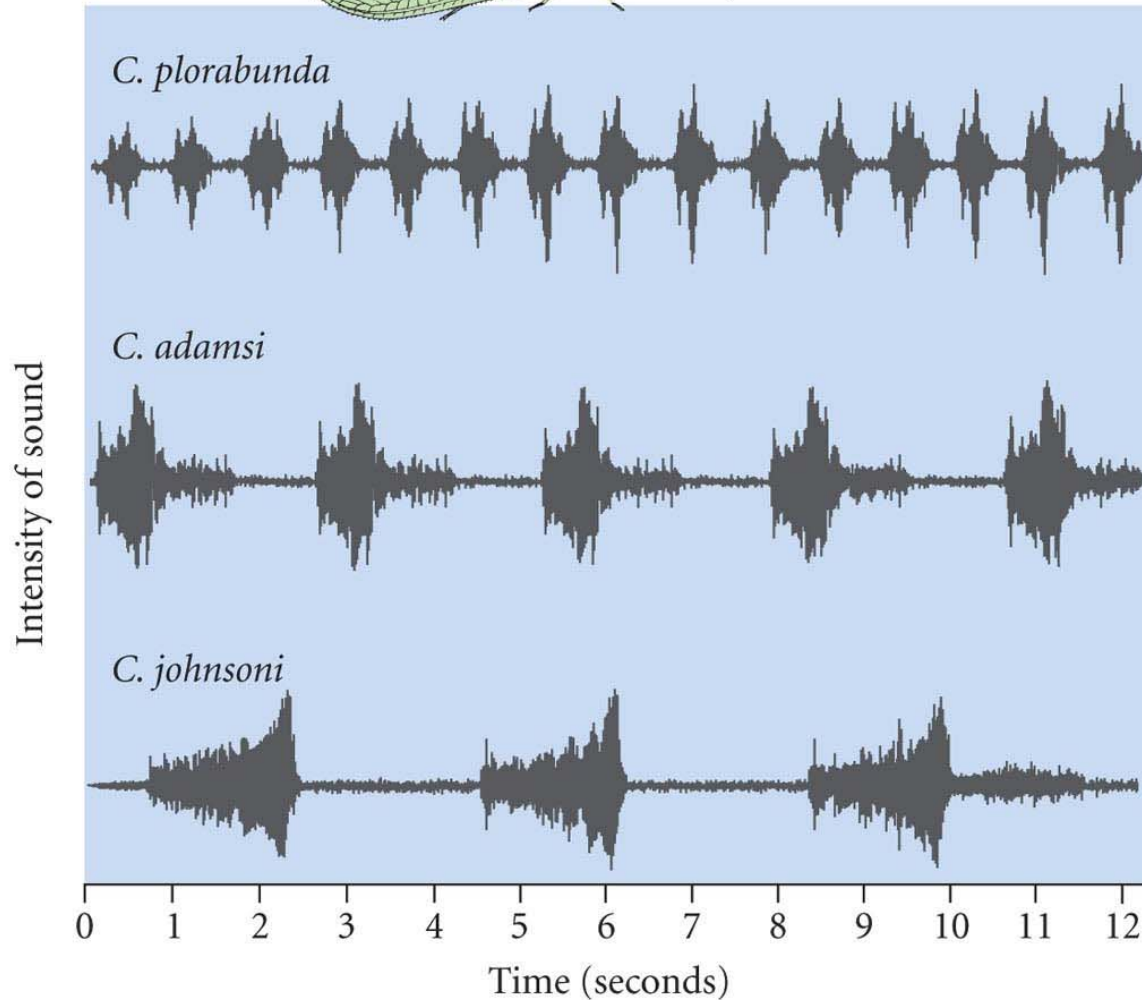
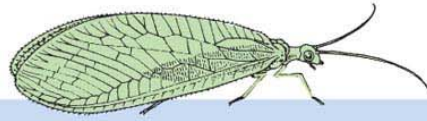


Western Spotted Skunk
• breeds in late summer



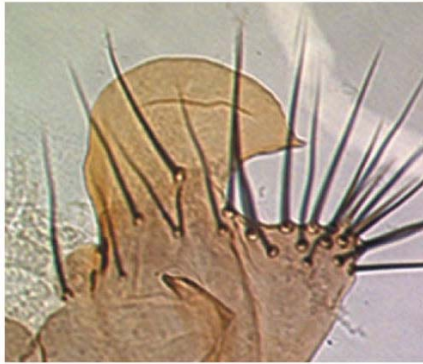
Eastern Spotted Skunk
• breeds in late winter

Prezygotic Barrier: Behavioral Isolation

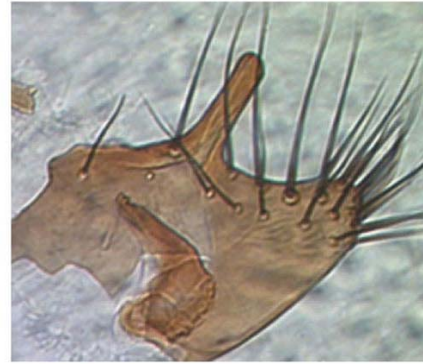


Prezygotic Barrier: Mechanical Isolation

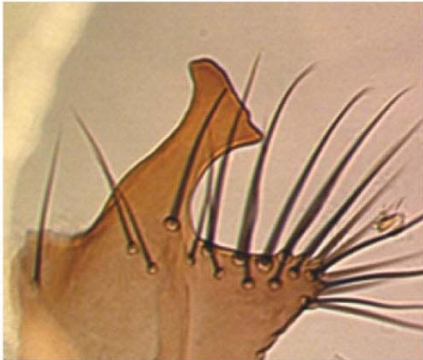
(A)



(C)



(B)



The posterior lobe of the genital arch in males of three closely related species of *Drosophila*.

Prezygotic Barrier: Gametic Isolation



Postzygotic Barrier: Hybrid Infertility



Horse



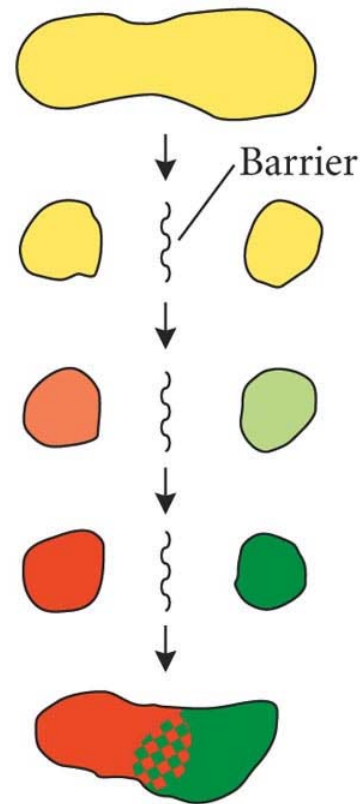
Donkey



Mule

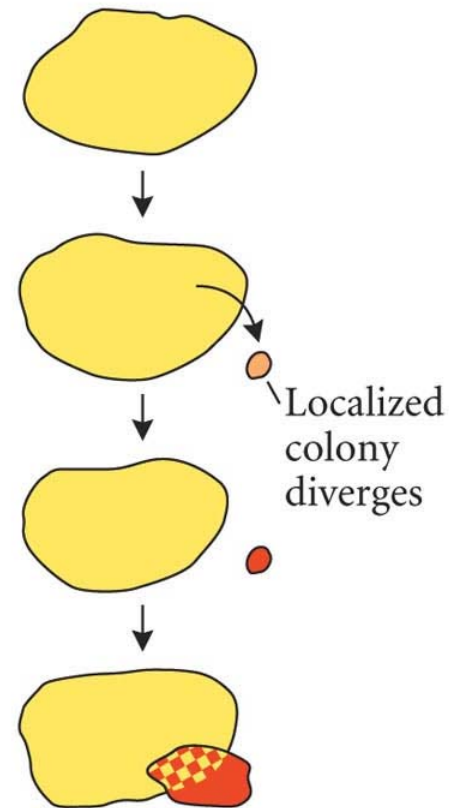
Successive stages in each of four models of speciation differing in geographic settings.

(A) Allopatric speciation by vicariance

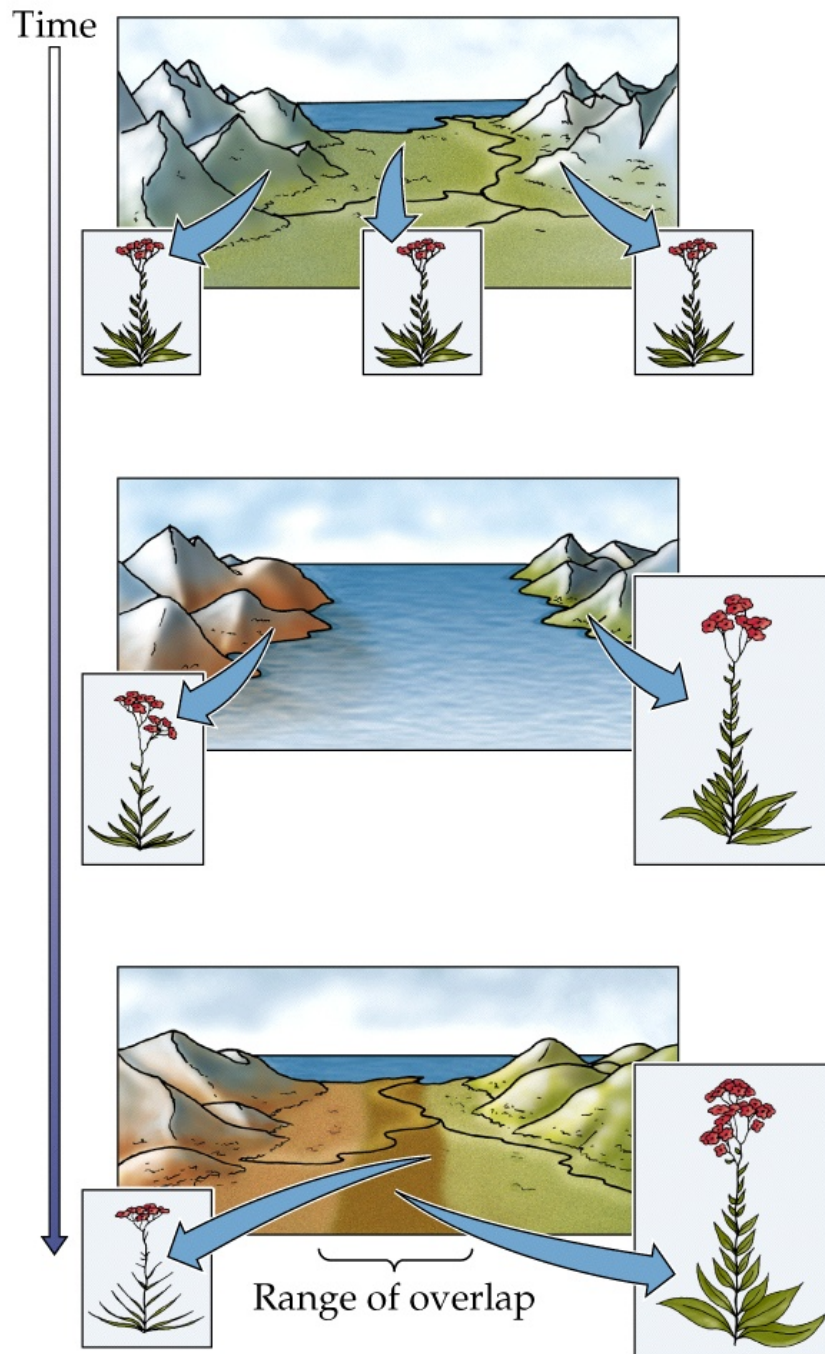


Barrier removed or new species disperse over it, re-establishing sympatry

(B) Peripatric speciation (Founder effect)



Range expansion re-establishes sympatry



Allopatric speciation –

- Geographic isolation disrupts gene flow.

Peripatric Speciation –

- Founder effect

Sympatric Speciation –

- No physical separation required.
- Polyploids especially in plants.
- Disruptive selection creates divergence in ecological traits.
- Selection for assortative mating.

Parapatric Speciation –

- Divergence along a gradient.
- Requires a hybrid zone.

Allopatric Speciation: Vicariance



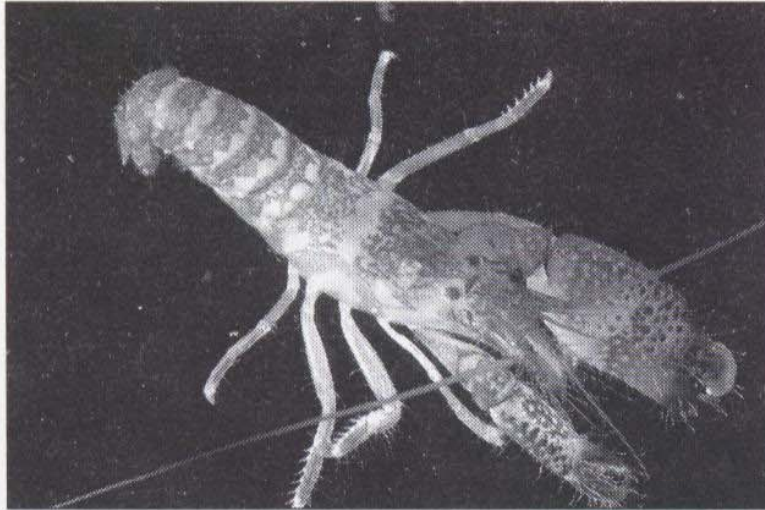
ISTHMUS OF PANAMA



The Isthmus of Panama formed from 15 Mya to 3 Mya.

Speciation in snapping shrimp across the Isthmus of Panama

(a)

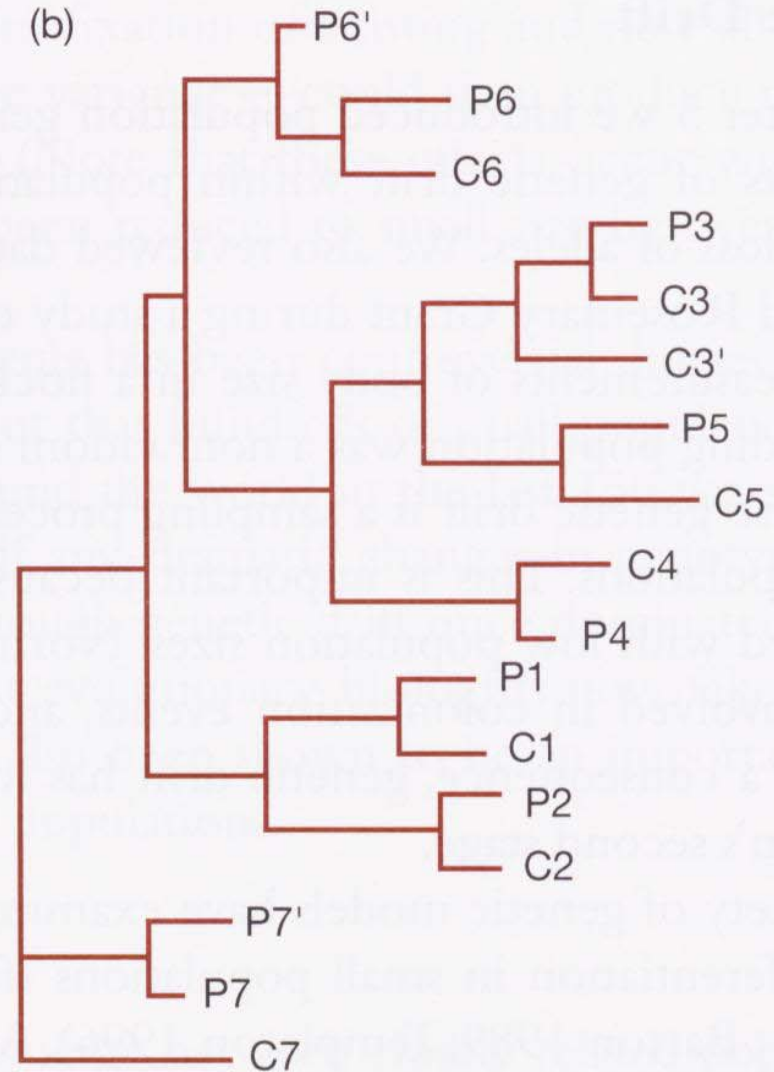


7 morphospecies w/o repro

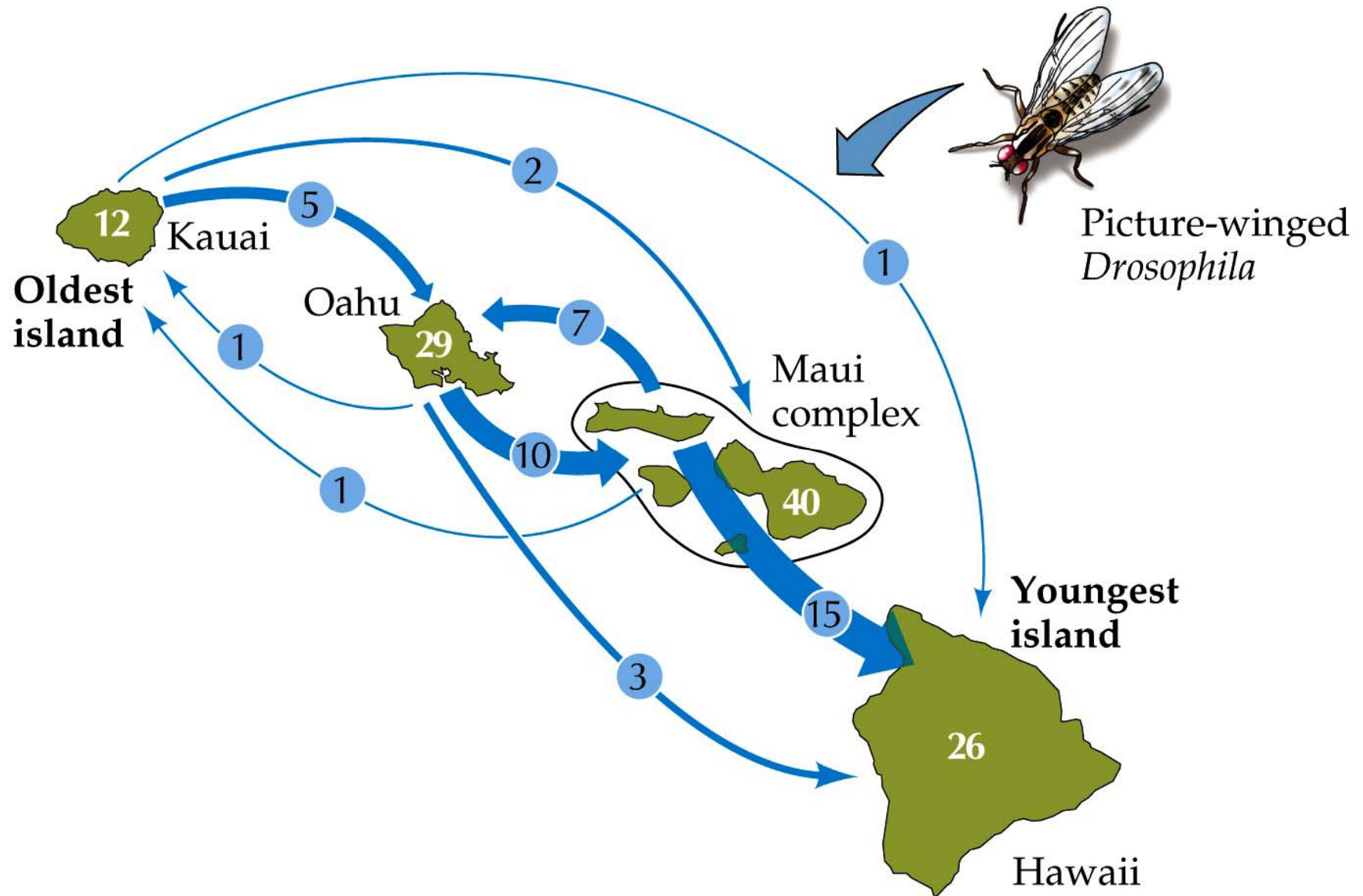
Closest clades show “Final Break” at ~3 Mya

(‘) = cryptic species

(b)

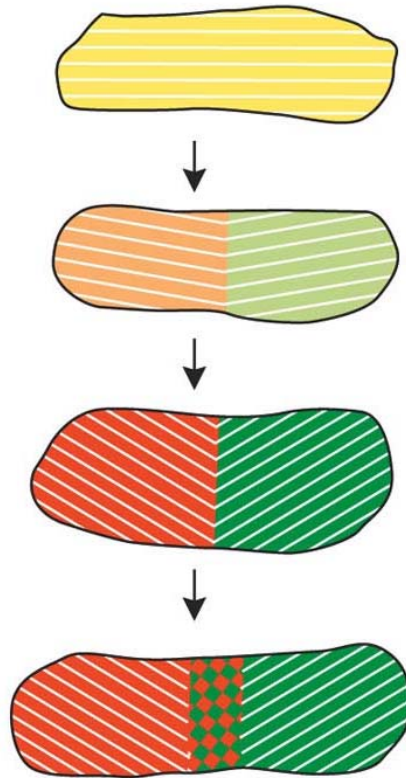


Allopatric speciation is common in island archipelagoes via Dispersal & Colonization



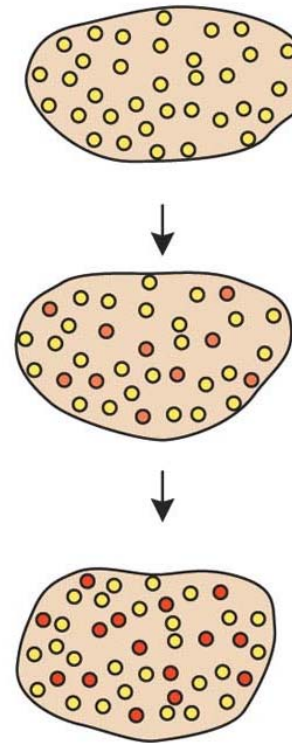
Successive stages in each of four models of speciation differing in geographic settings.

(C) Parapatric speciation



Range expansion
leads to sympatry

(D) Sympatric speciation



Genetic differences
result in reproductive
isolation

Reproductive Isolation

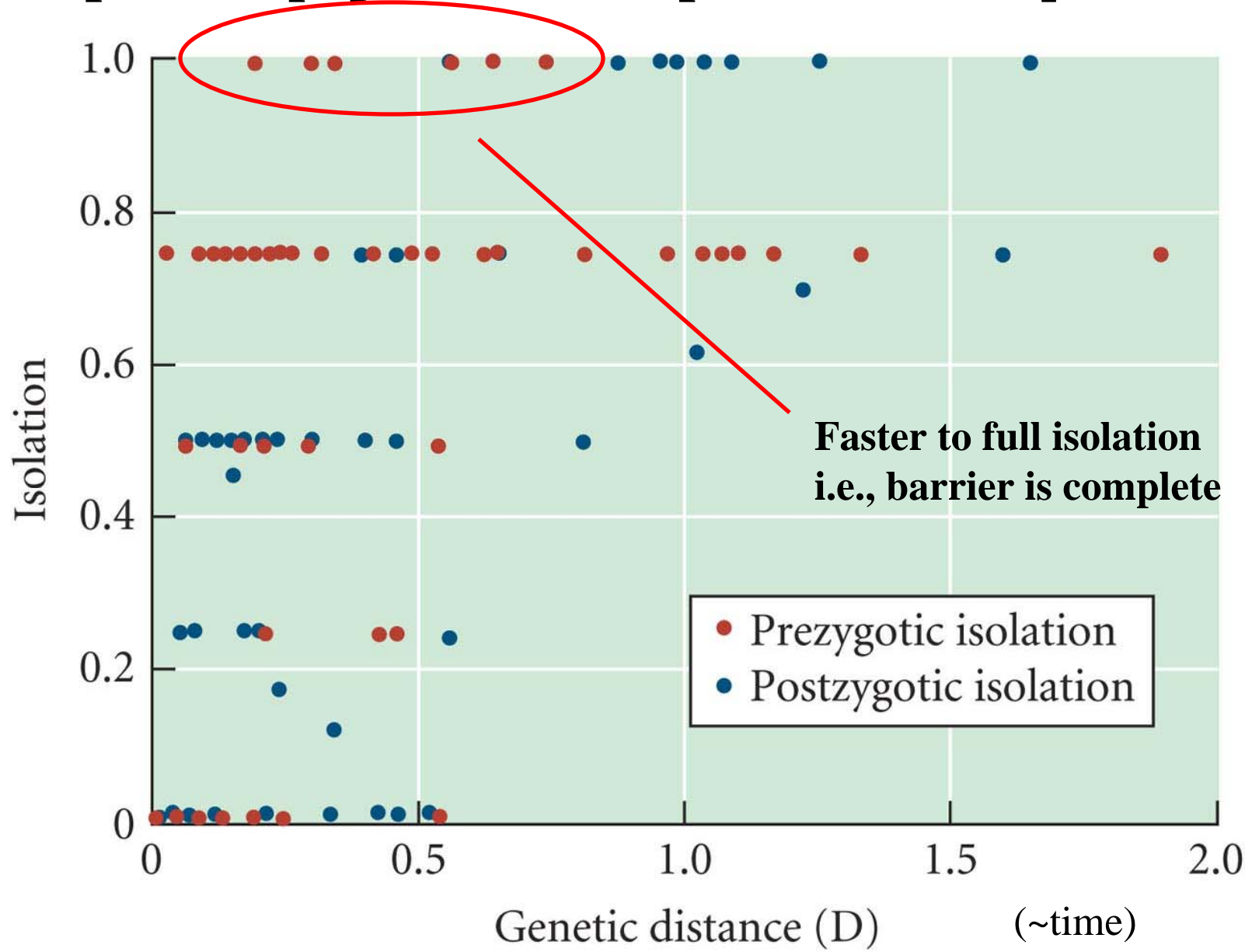
Byproduct (Mayr) vs. Reinforcement (Dobzhansky)

Reinforcement – type of selection that leads to assortative mating and prezygotic isolation.

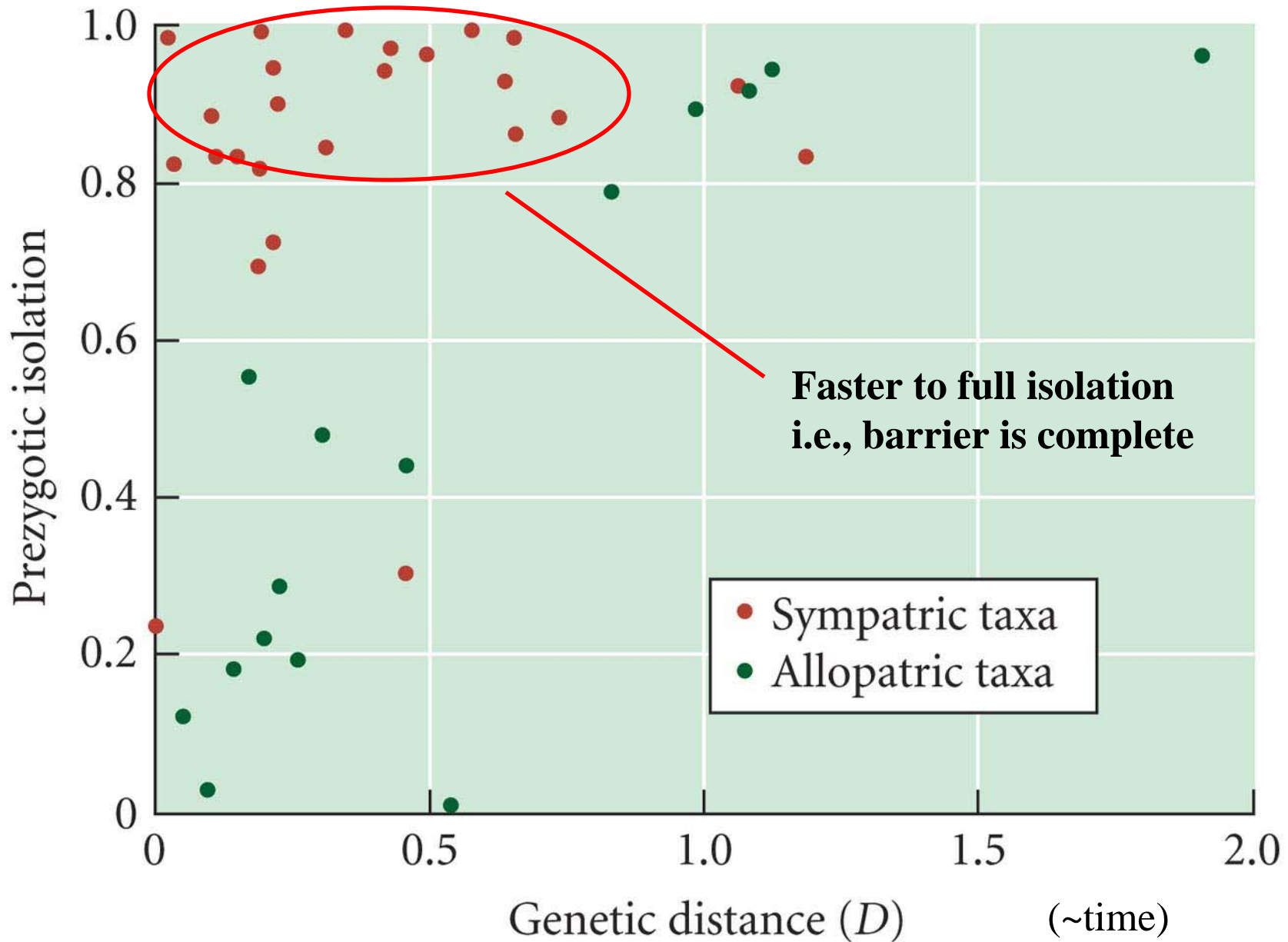
Reproductive isolation revisited:

- **Both prezygotic and postzygotic barriers increase gradually over time for either model.**
- **Reinforcement speeds up prezygotic barriers in sympatric sister species through assortative mating.**

Pre- or postzygotic reproductive isolation between pairs of populations & species of *Drosophila*

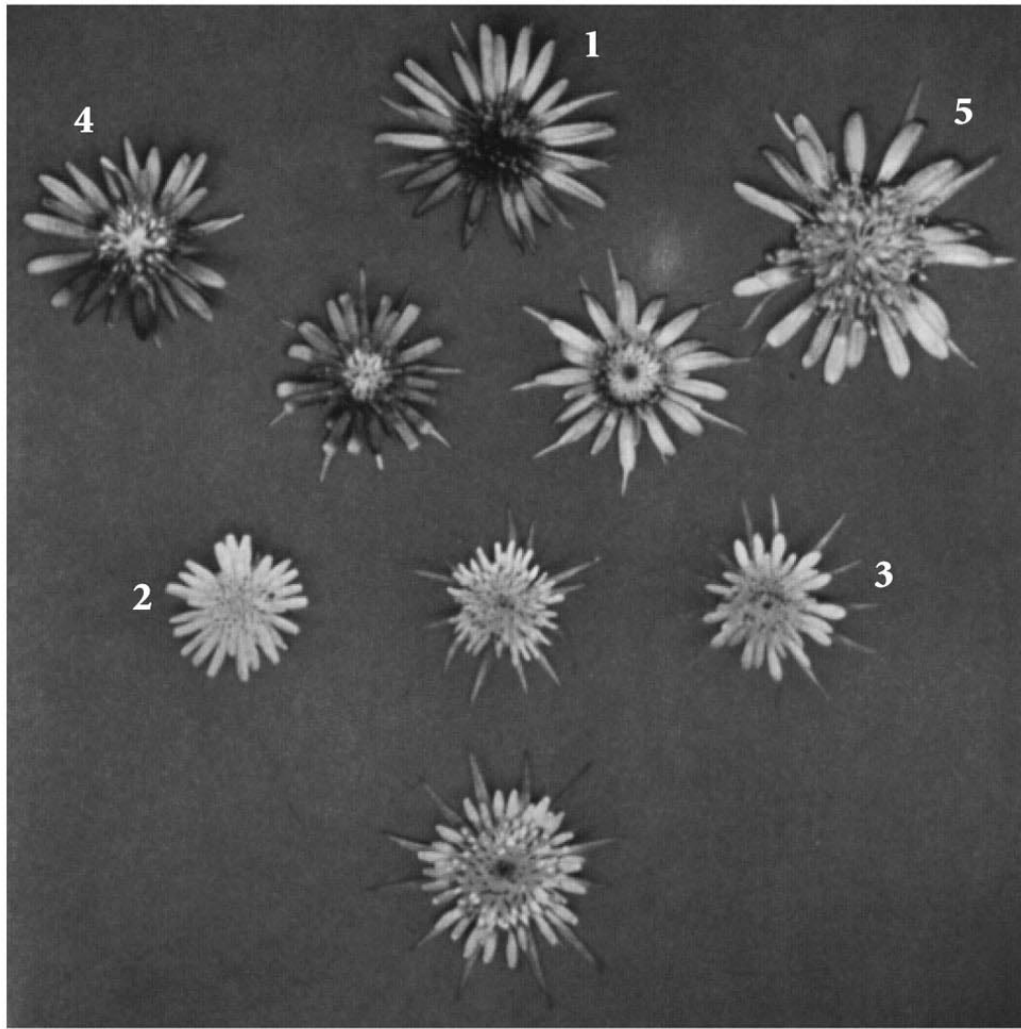


Level of prezygotic isolation between allopatric and sympatric pairs of *Drosophila* populations



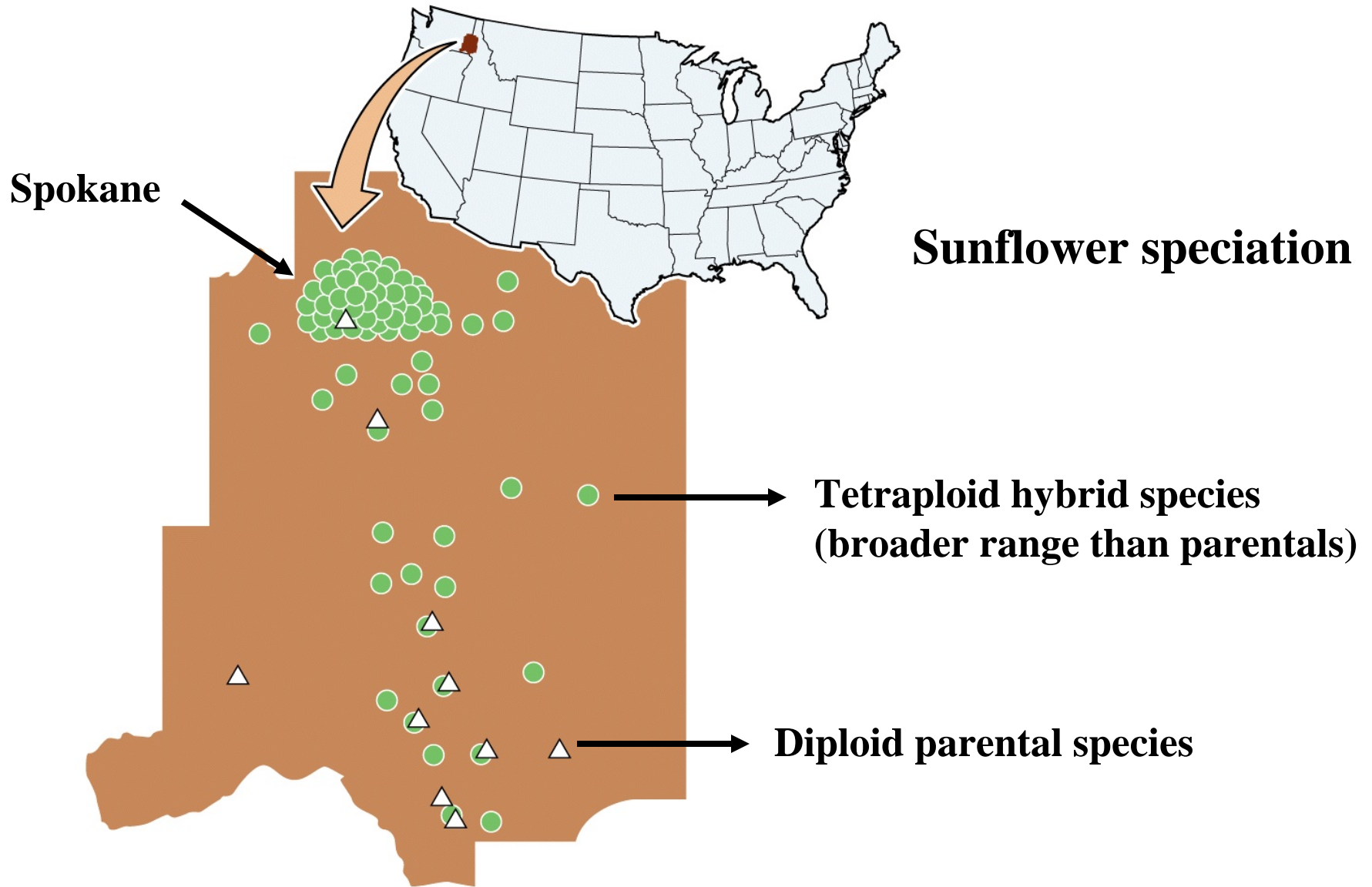
Sympatric speciation via hybridization

(A)



Goatsbeards
(Tragopogon)

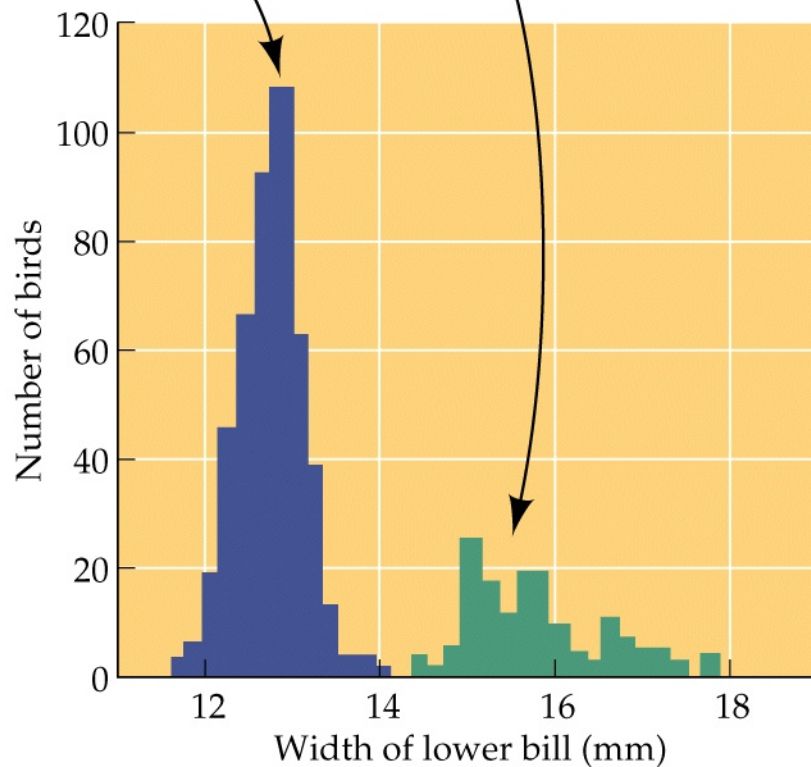
Sympatric speciation via hybridization





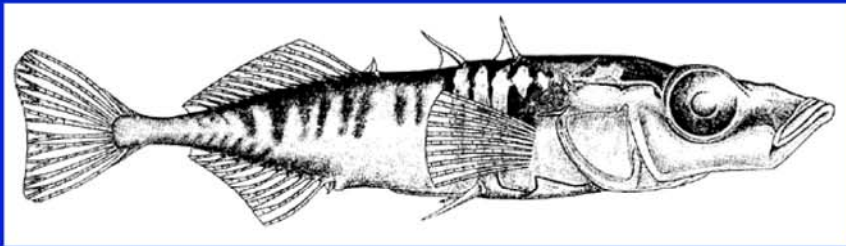
Black-bellied Seedcrackers (*Pyrenestes*)

- Live in marshes in W. Africa
- Eat seeds, primarily of two plant species
- One seed type is small, the other type is large
- Bill dimorphism reflects the effects of **disruptive selection**

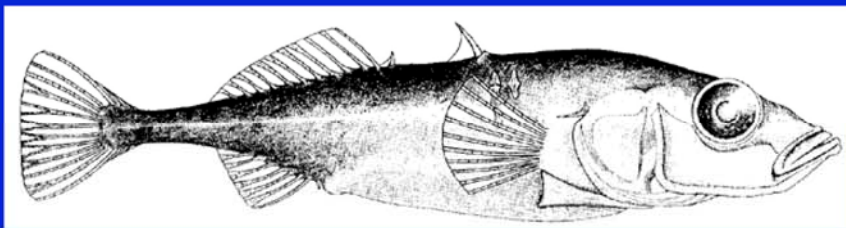


**Leads to Assortative Mating
and Sympatric Speciation.**

Sympatric speciation via ecological niche polymorphism



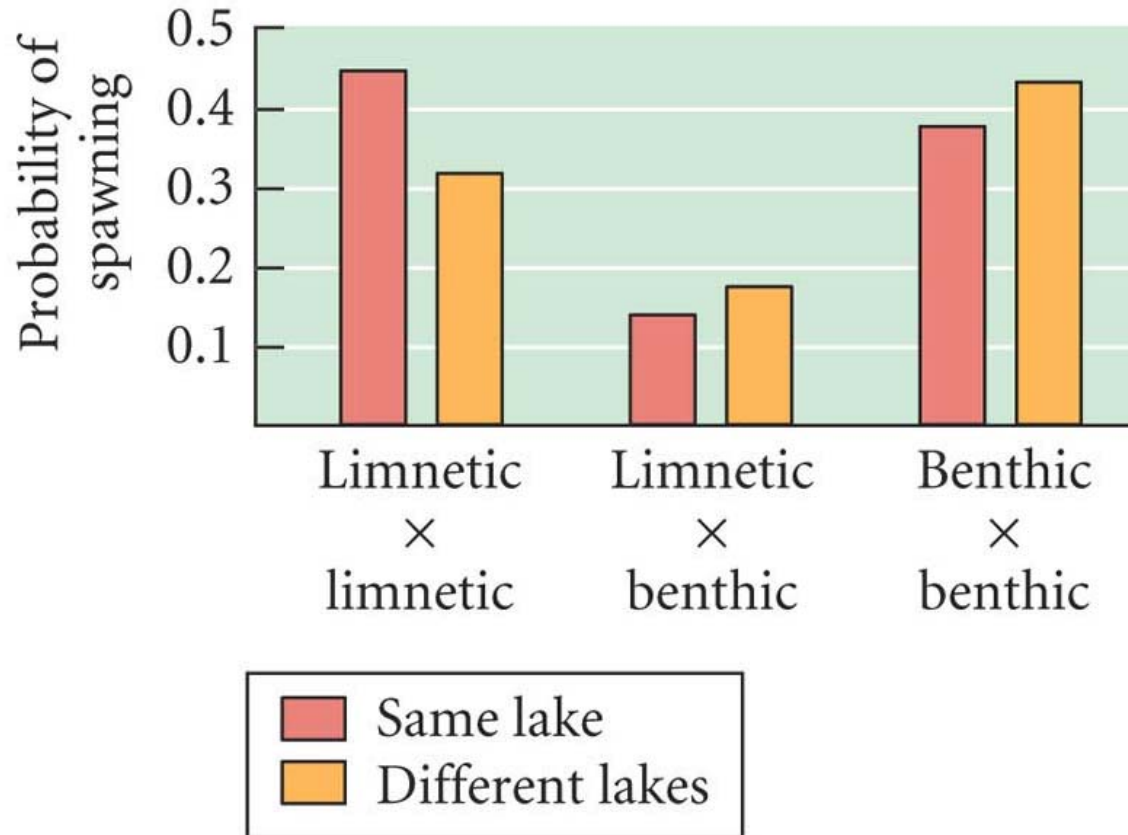
Limnetic male



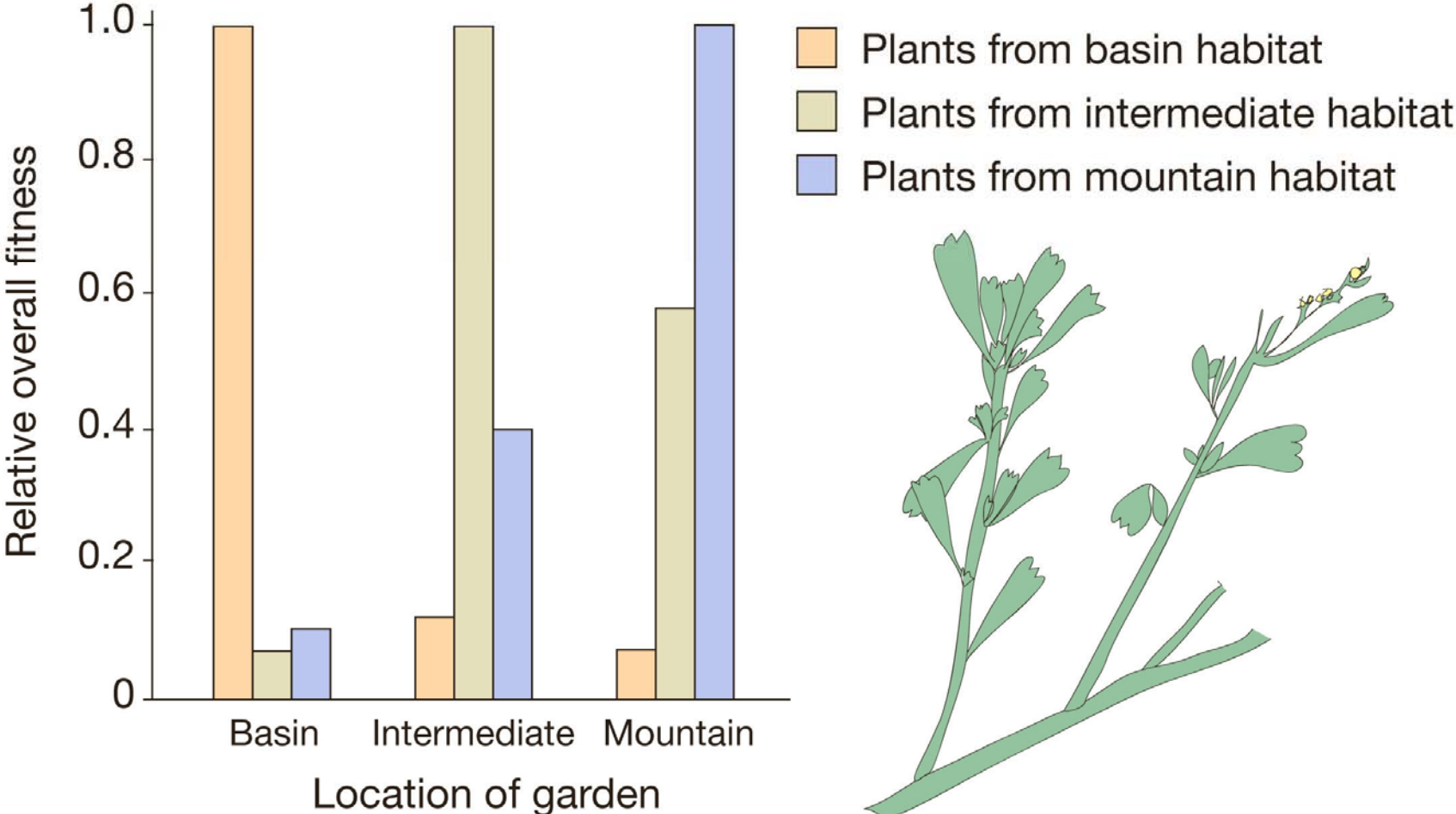
Benthic male



Sympatric speciation in the three-spined stickleback

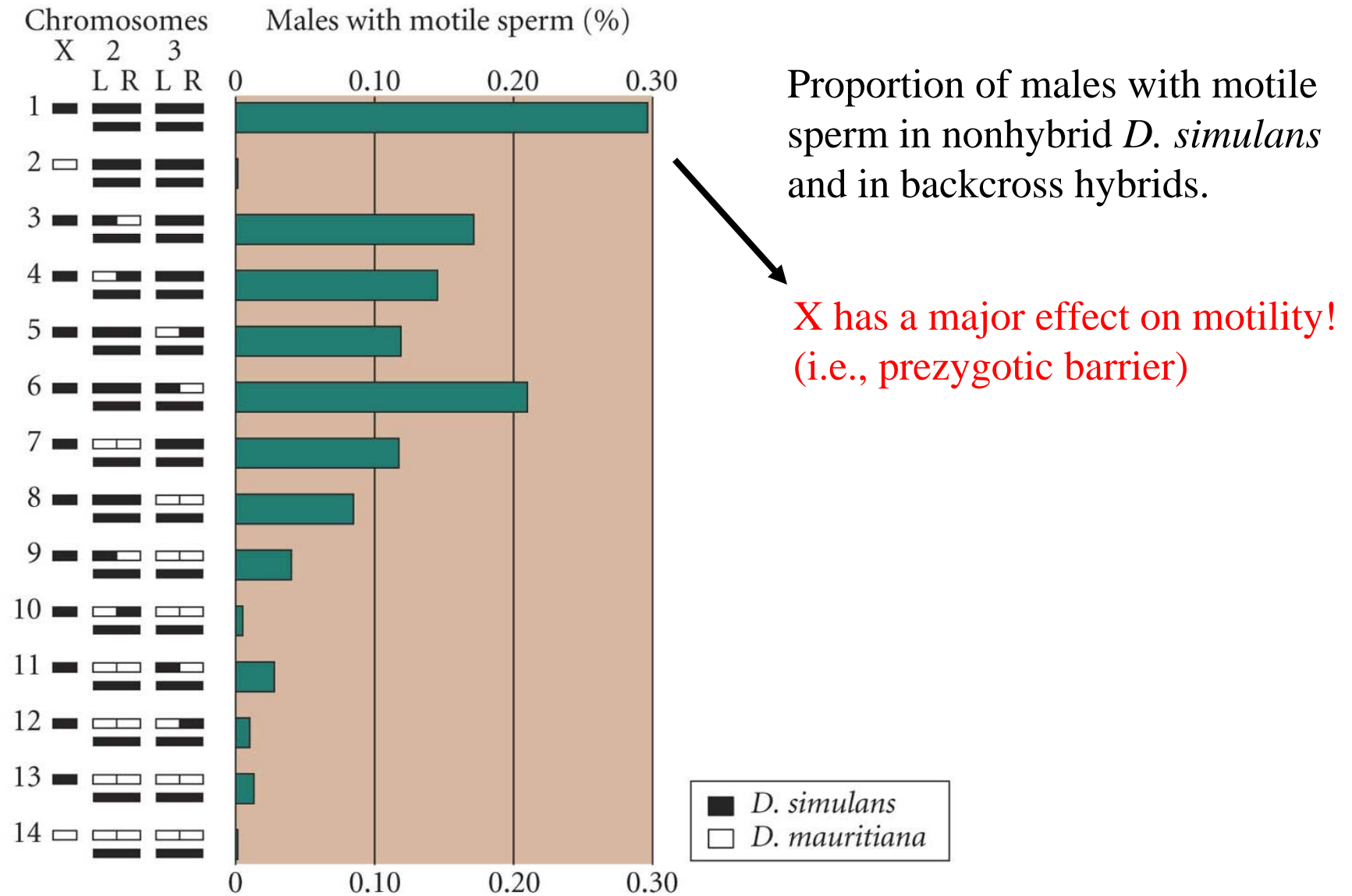


Hybridization – fitness of hybrids determines hybrid zone and eventual outcome.

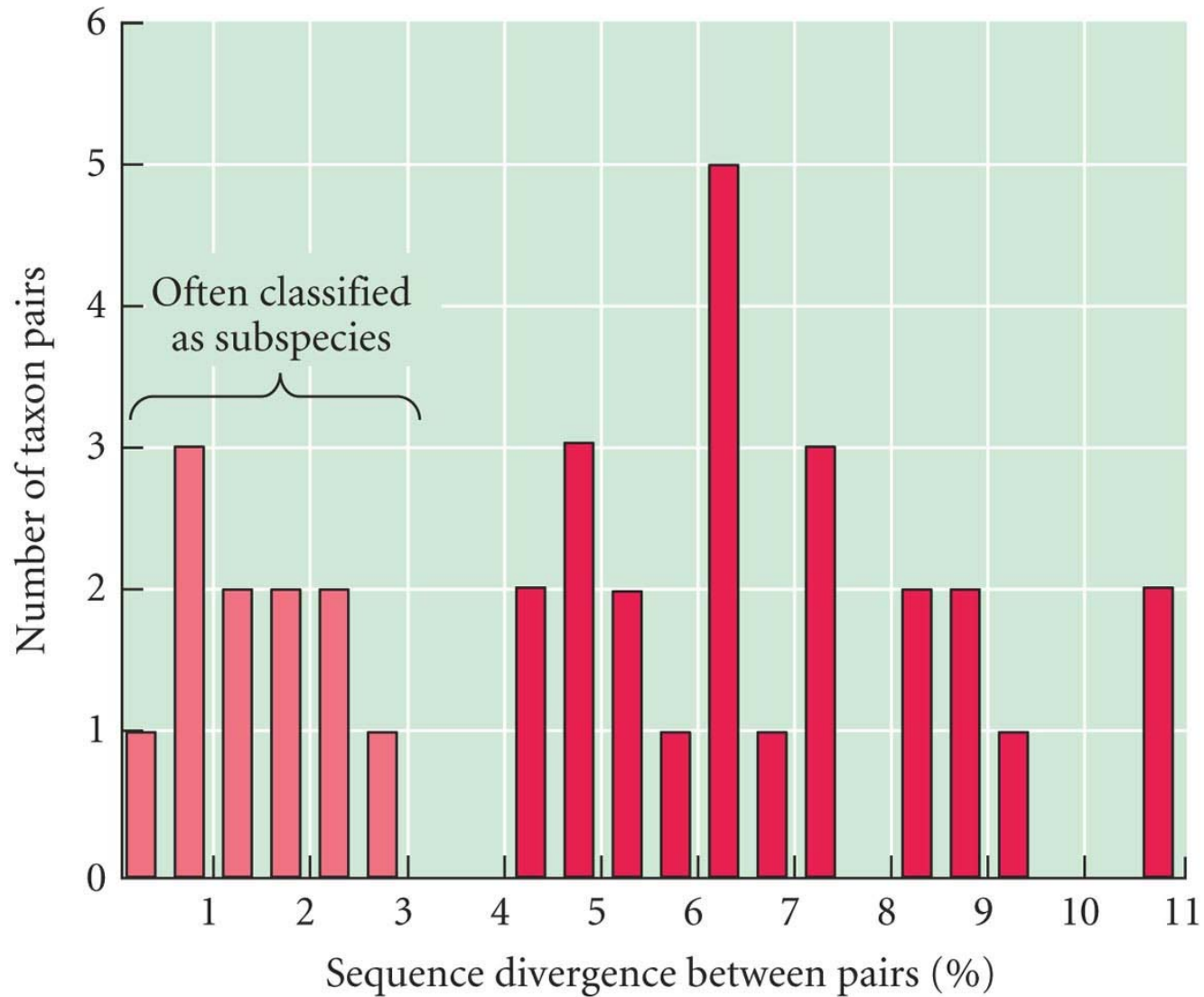


Sagebrush

How many genes are involved in speciation?

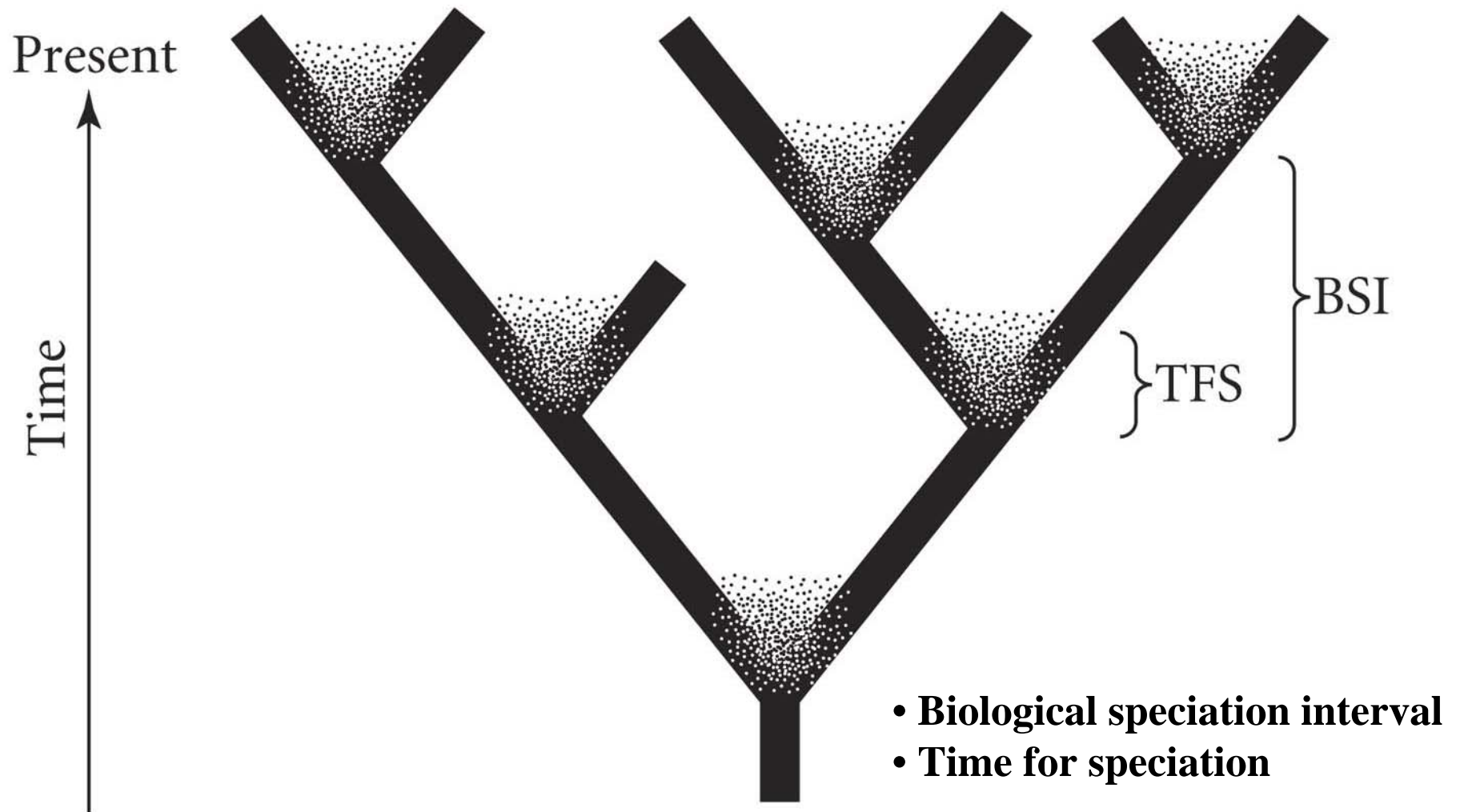


Sequence divergence of mtDNA between pairs of closely related songbirds

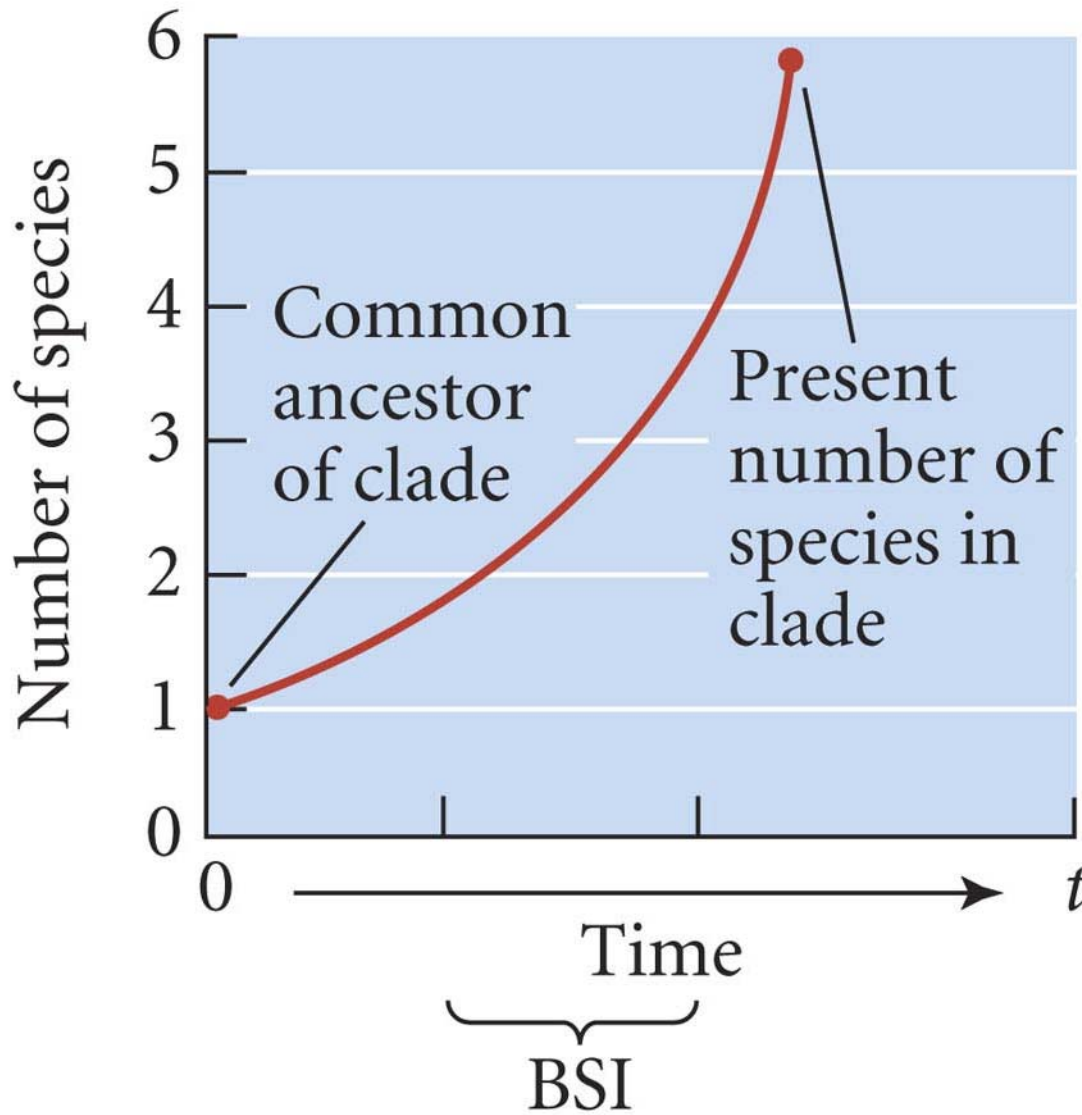


Two meanings of the “rate of speciation” ...How long does it take?

(A)



(B)



- **Must grow exponentially**
- **No extinctions**

Estimates of time required for the speciation process in various groups of organisms

I. TFS

Drosophila

Drosophila

Frogs

N.A. songbirds

II. BSI

Horses

Bivalve molluscs

Conifers and cycads

Angiosperm trees

III. BSI

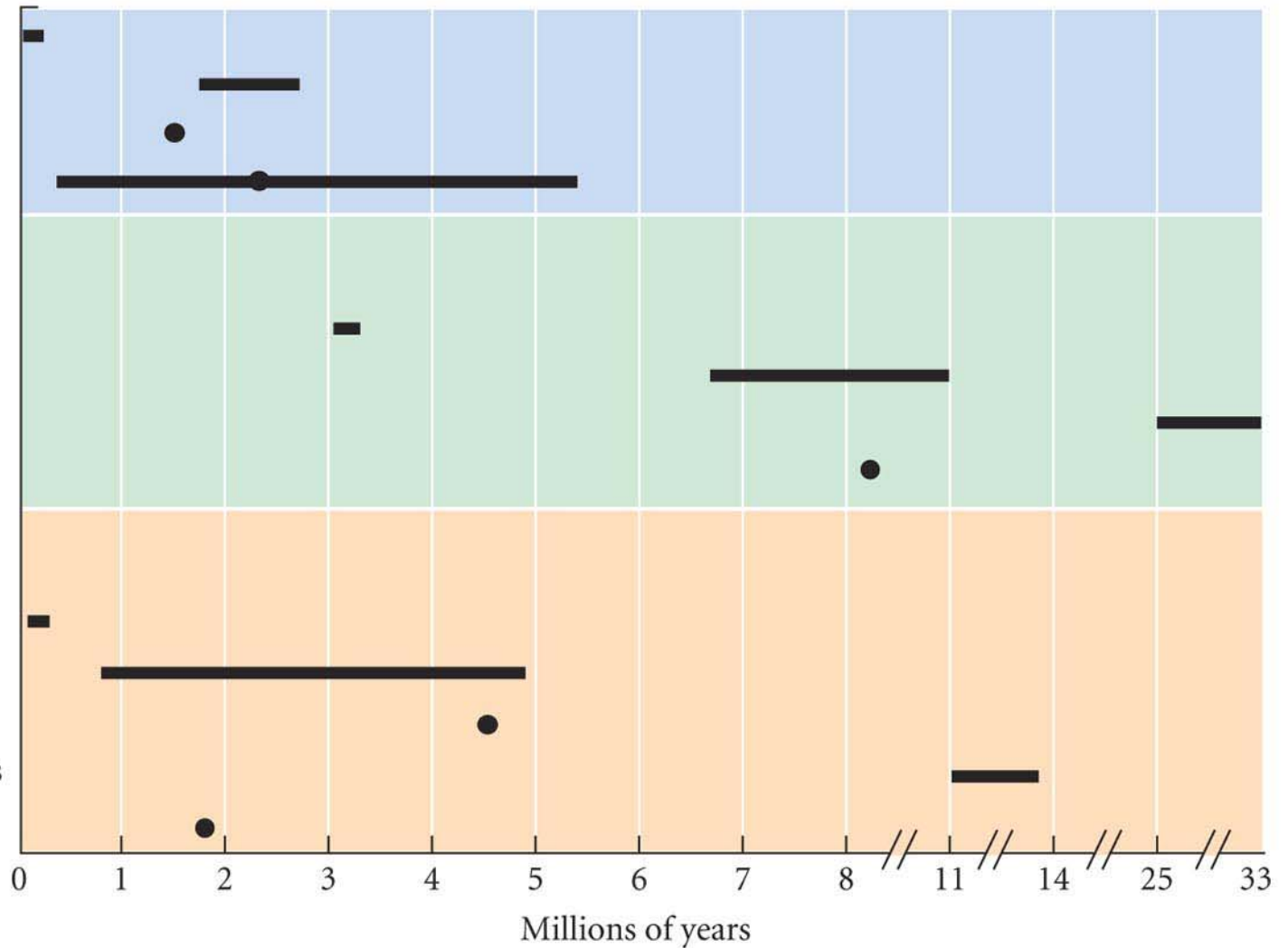
L. Malawi cichlids

Hawaiian *Drosophila*

Mammals

Hawaiian silverswords

Angiosperms



Factors promoting rapid speciation

- Many species
- Opportunities for geographic isolation
- Limited mobility
- Short generation time
- Sexual selection
- Ecological specialization

Ecological Specialization

