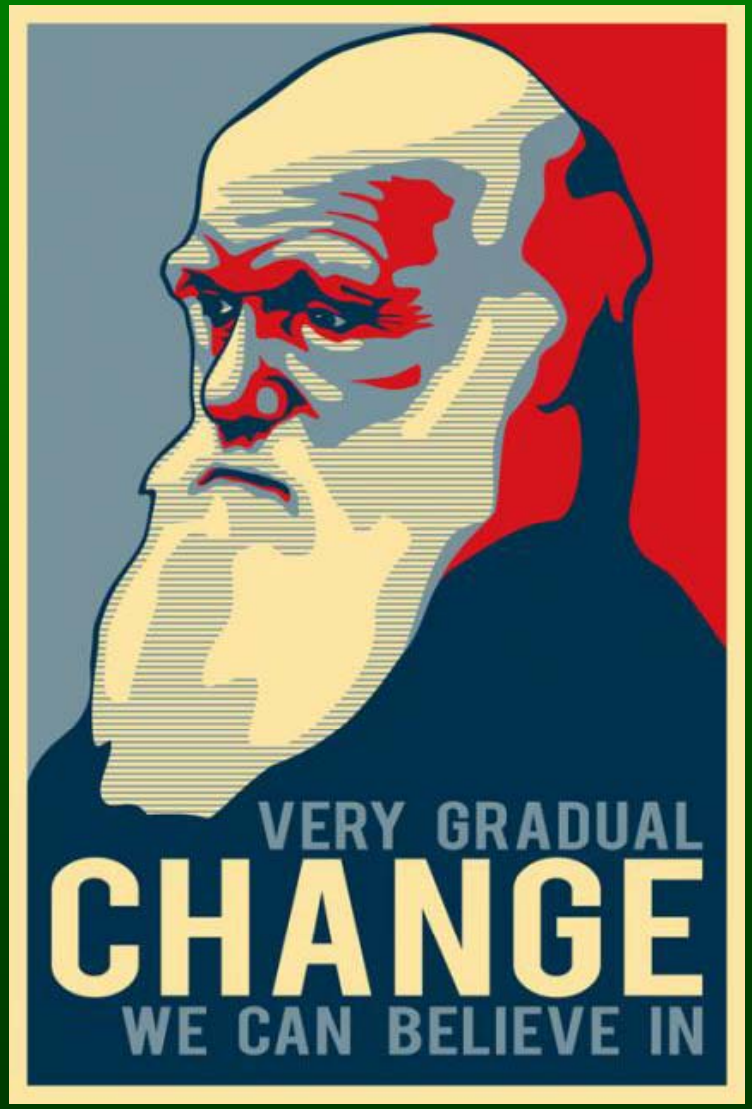
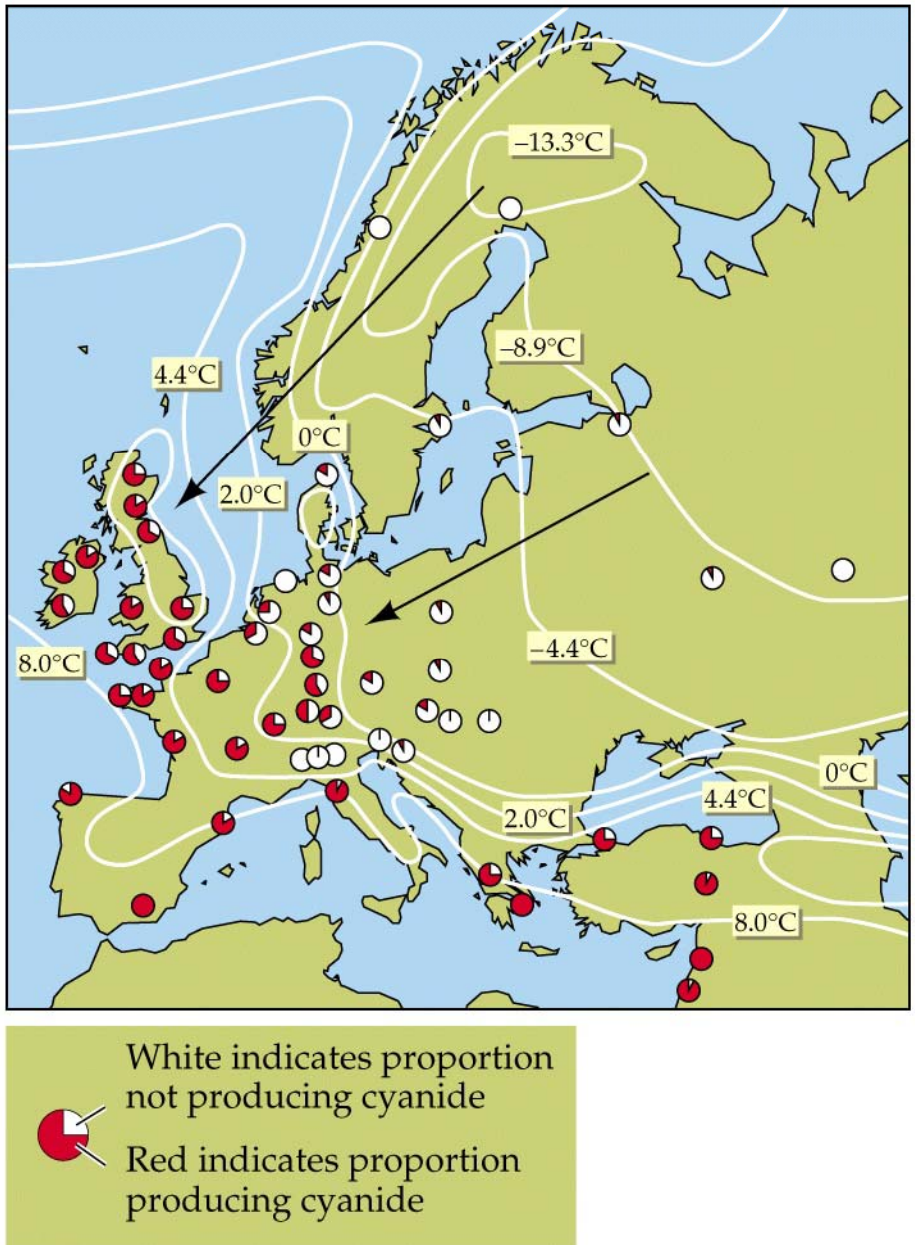
Mechanisms of Speciation



Some species show little geographic variation...

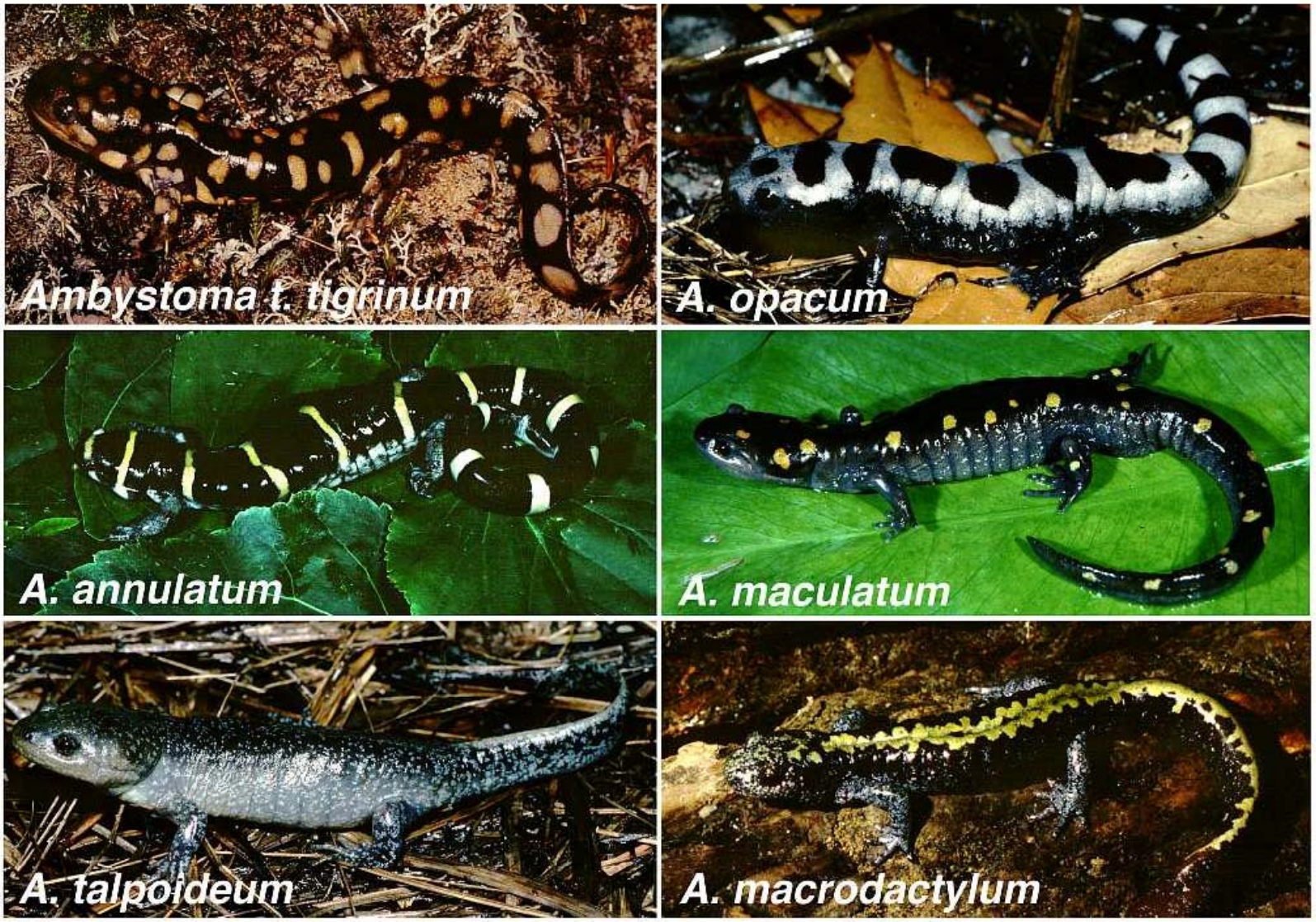
…while others vary quite a bit.

Geographic variation may be gradual...



Geographic Variation in Poisonous Clovers.

… 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.

Speciation involves barriers to reproduction

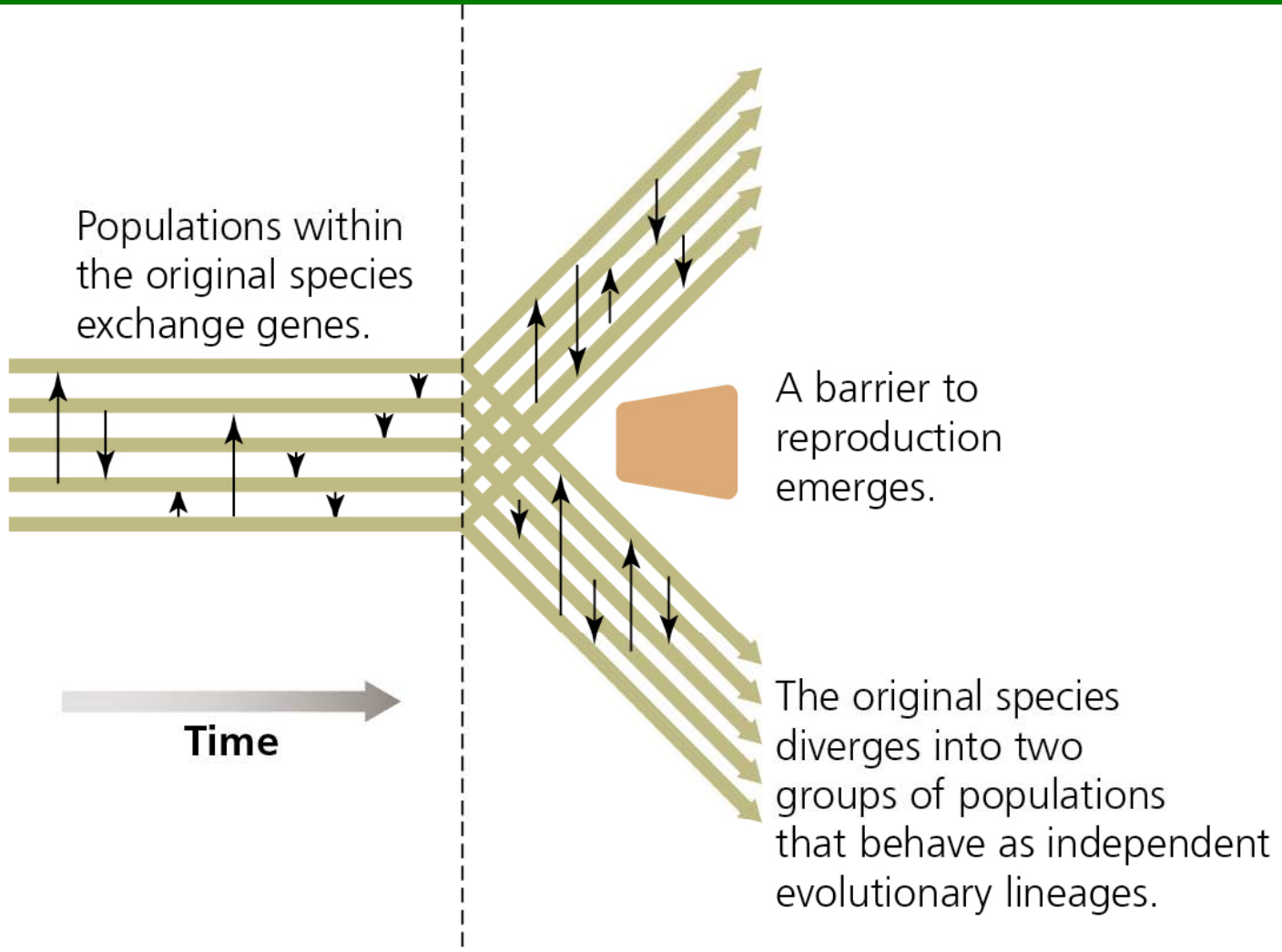


TABLE 15.1 *Some species concepts*

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 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.

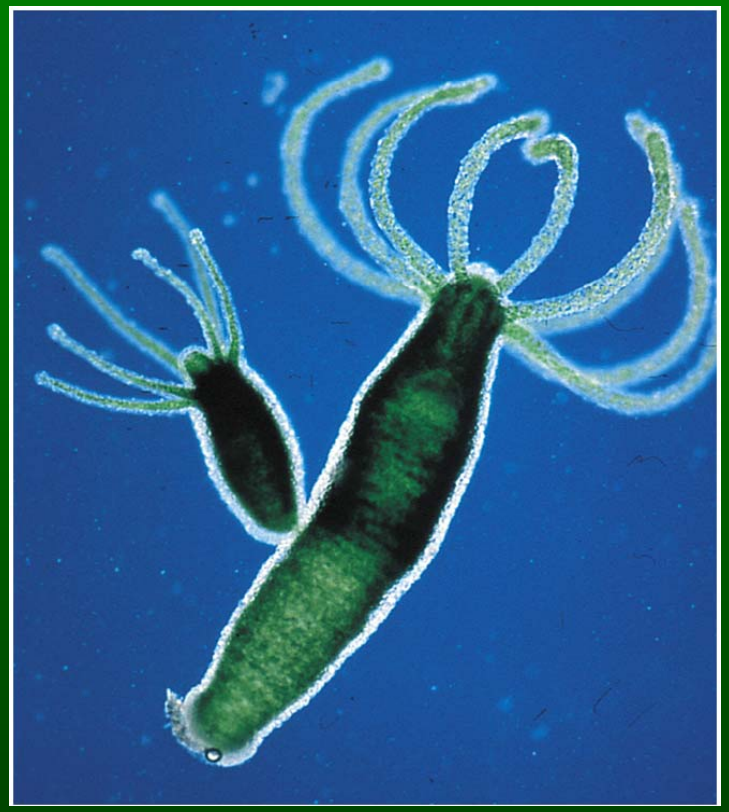
Biological Species Concept (BSC)

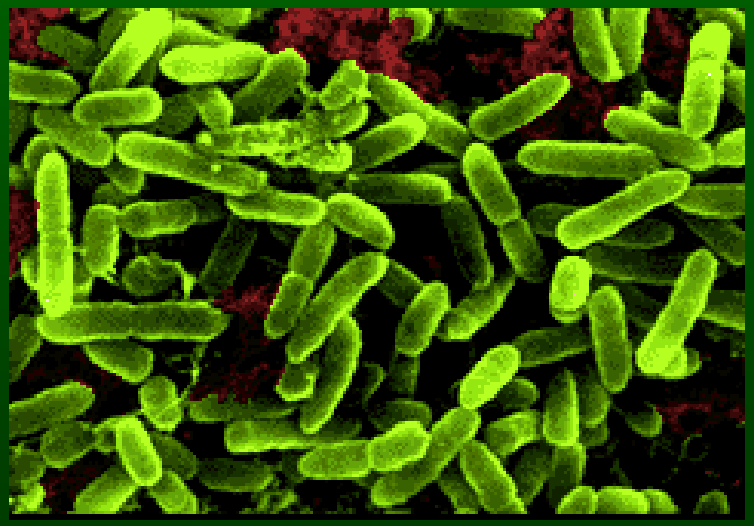
- **Species are groups of actually or potentially interbreeding individuals that are reproductively isolated from other such groups (Mayr).**
- **Used by the Endangered Species Act (for better or worse).**
- **What about non-overlapping pop's, fossil record, & microbes?**

Difficulties with the Biological Species Concept

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

Asexual reproduction

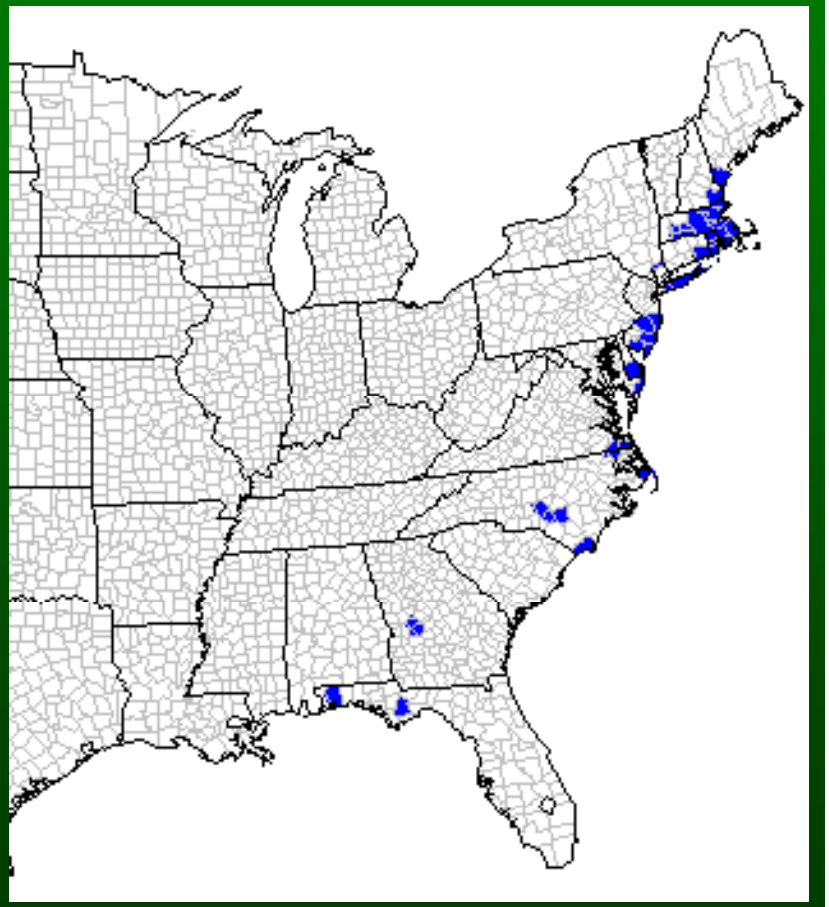




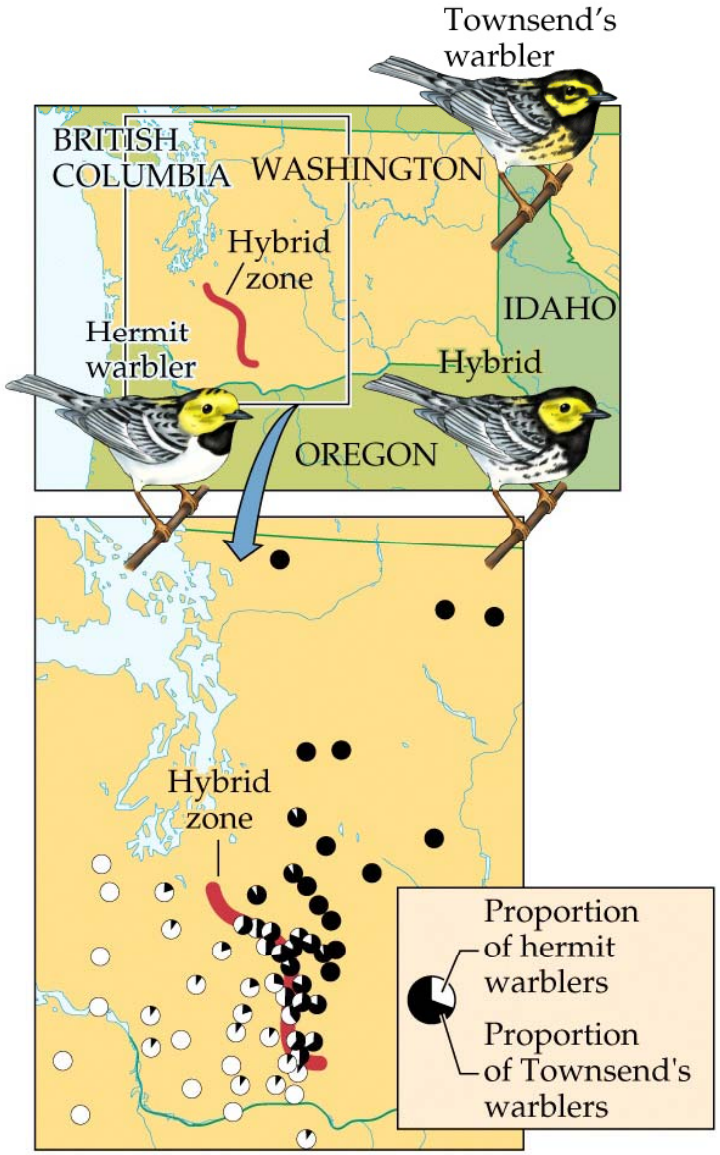

Callophrys hesseli


Callophrys hesseli underside

Many geographically isolated populations

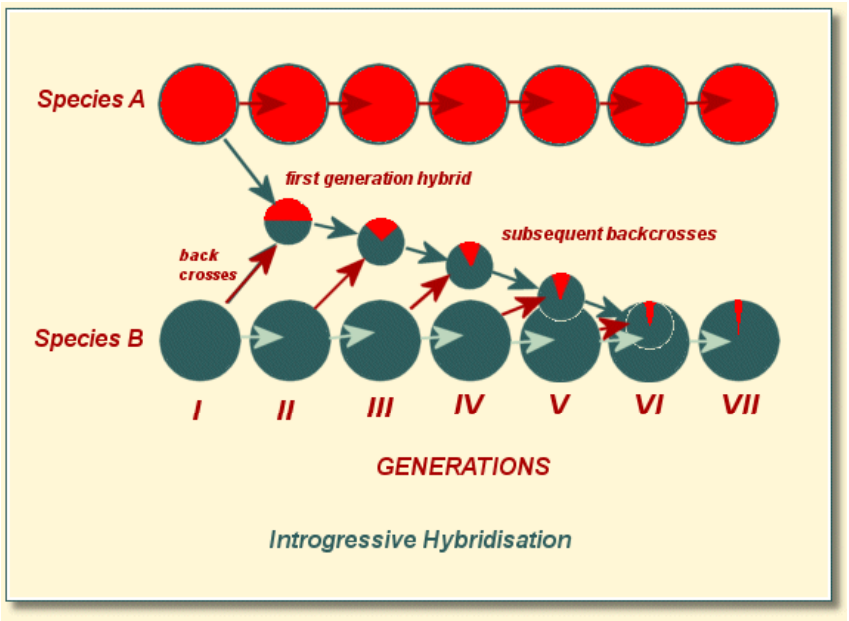


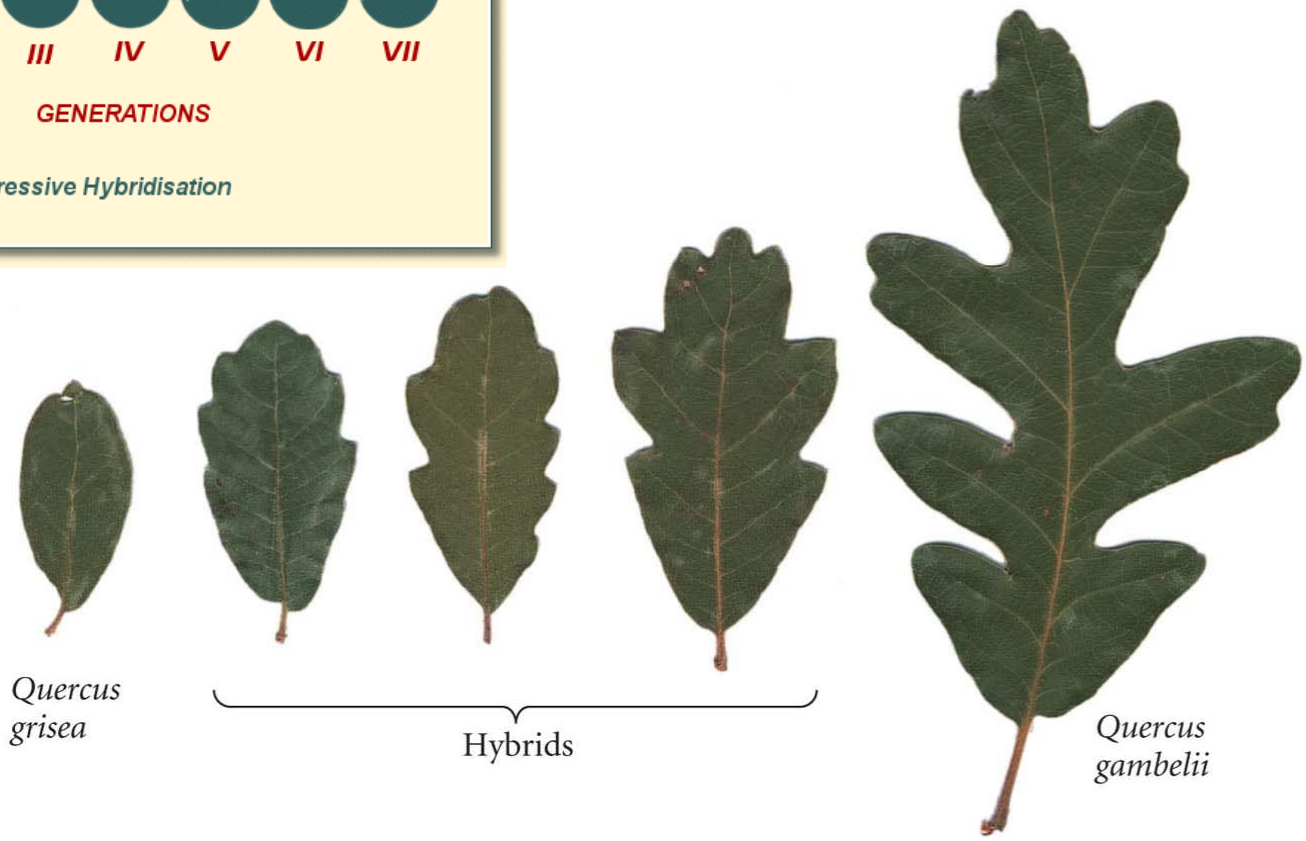
Hybridization and Introgression



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

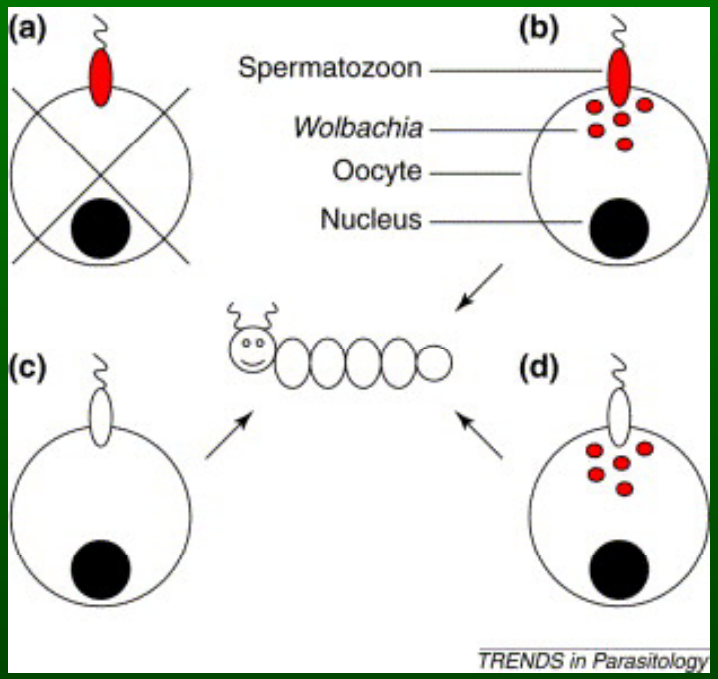
Hybridization and Introgression





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 (CI) is a phenomenon that results in sperm and eggs being unable to form viable offspring.

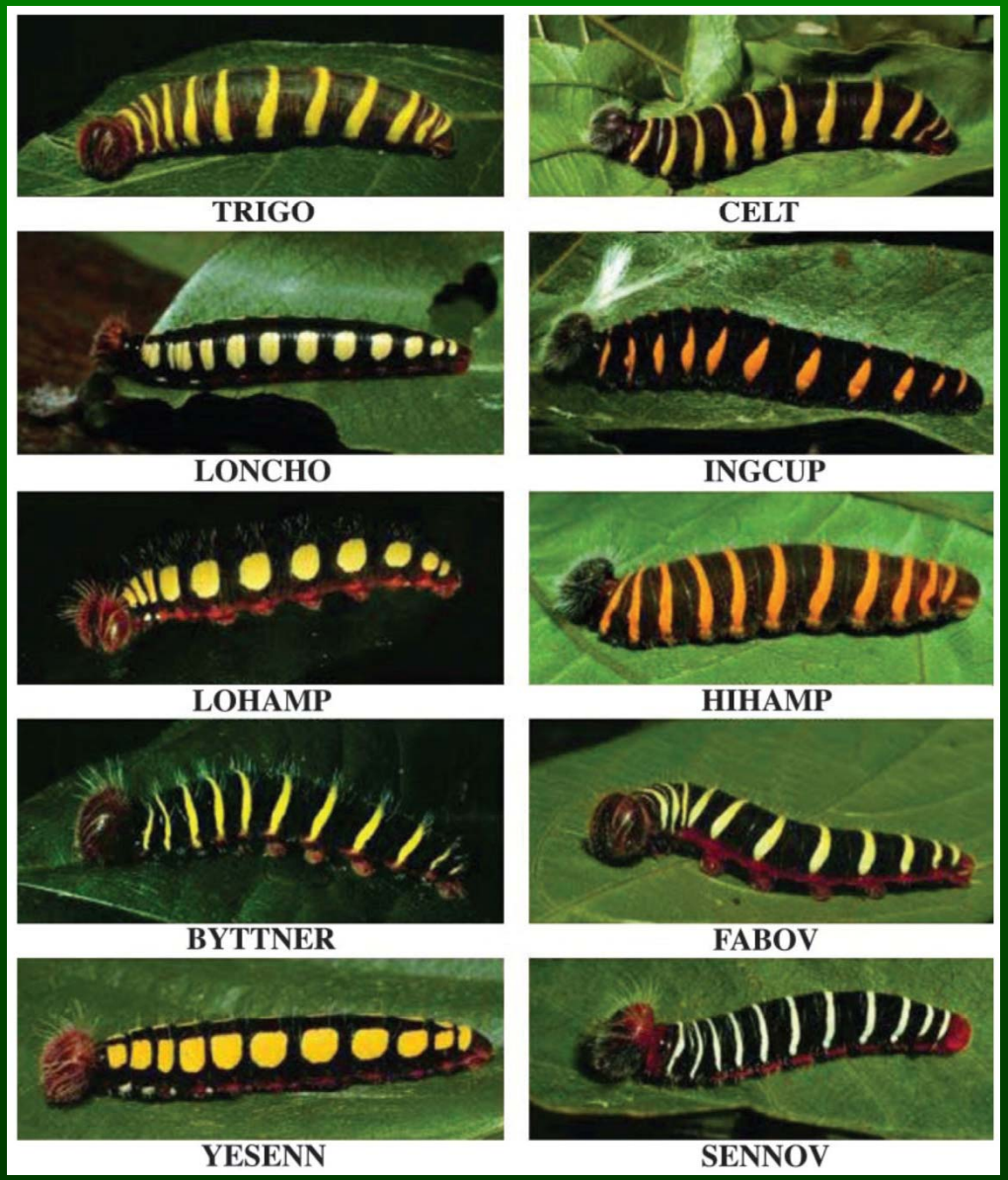
Phylogenetic Species Concept (PSC)

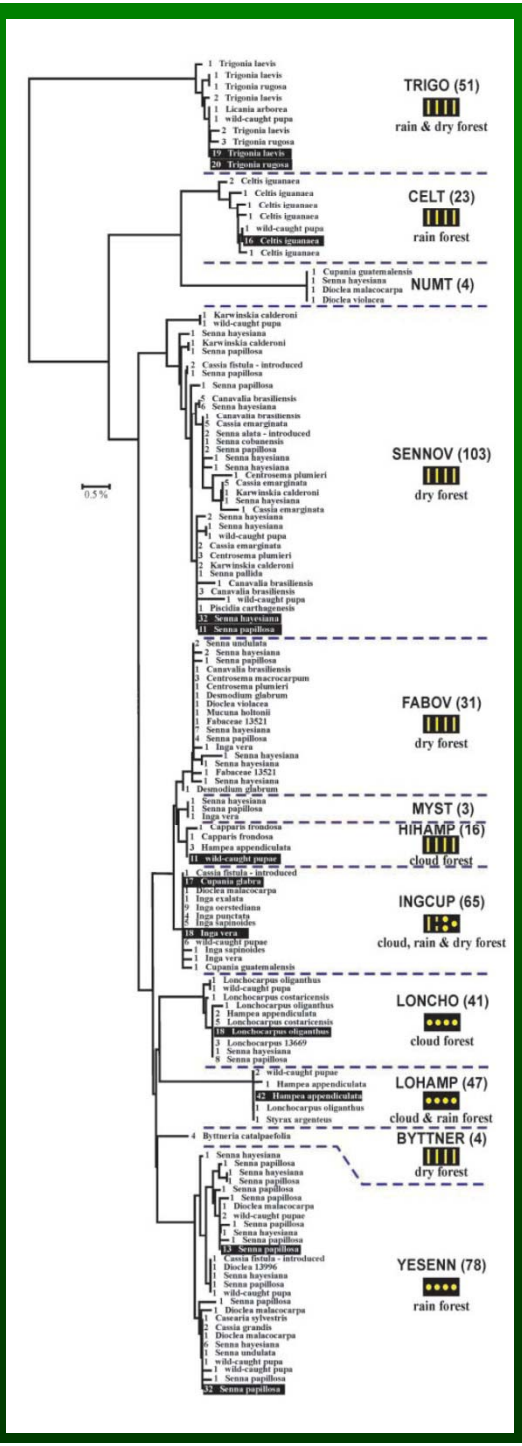
- **The smallest aggregation of populations or lineages diagnosable by a unique combination of character states (Nixon & Wheeler).**
- **Monophyletic groups derived from a single common ancestor.**
- **Not standardized, which traits are most important?**

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.*



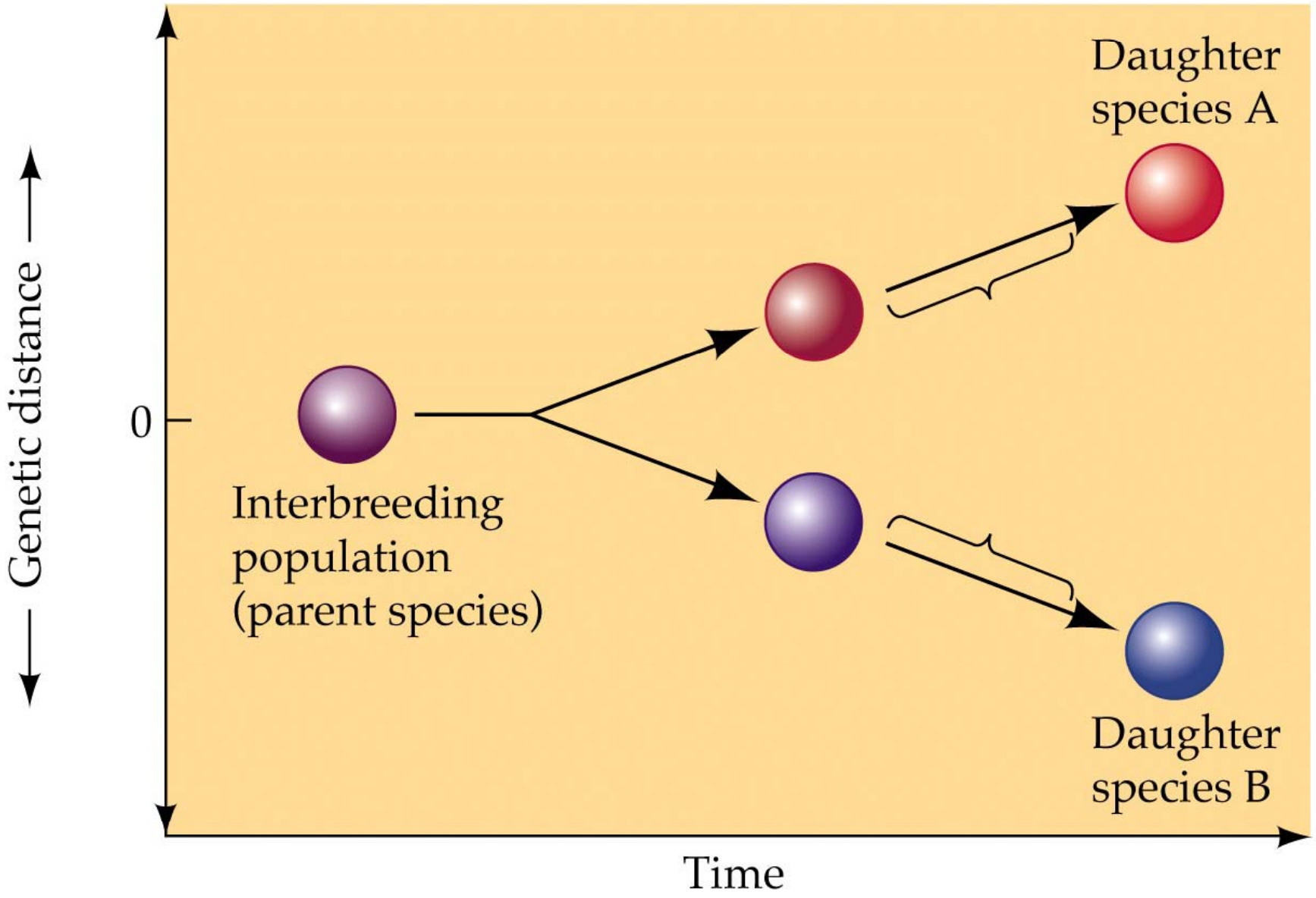


Diagnosing Species in Practice

- 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


Genetic distance
0
Interbreeding
population
(parent species)
Daughter
species A
Daughter
species B
Time

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.

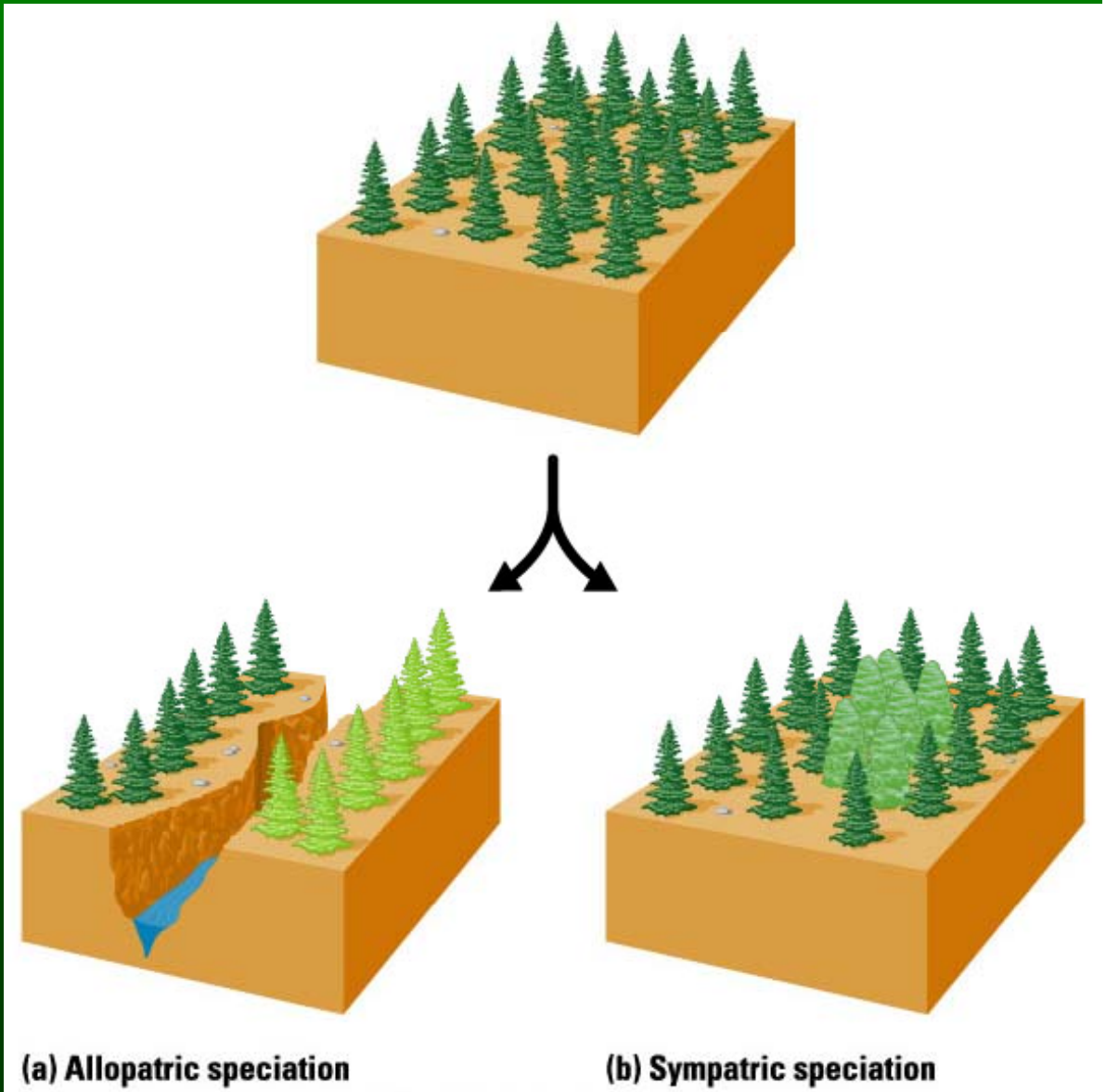
Intrinsic vs. extrinsic barriers

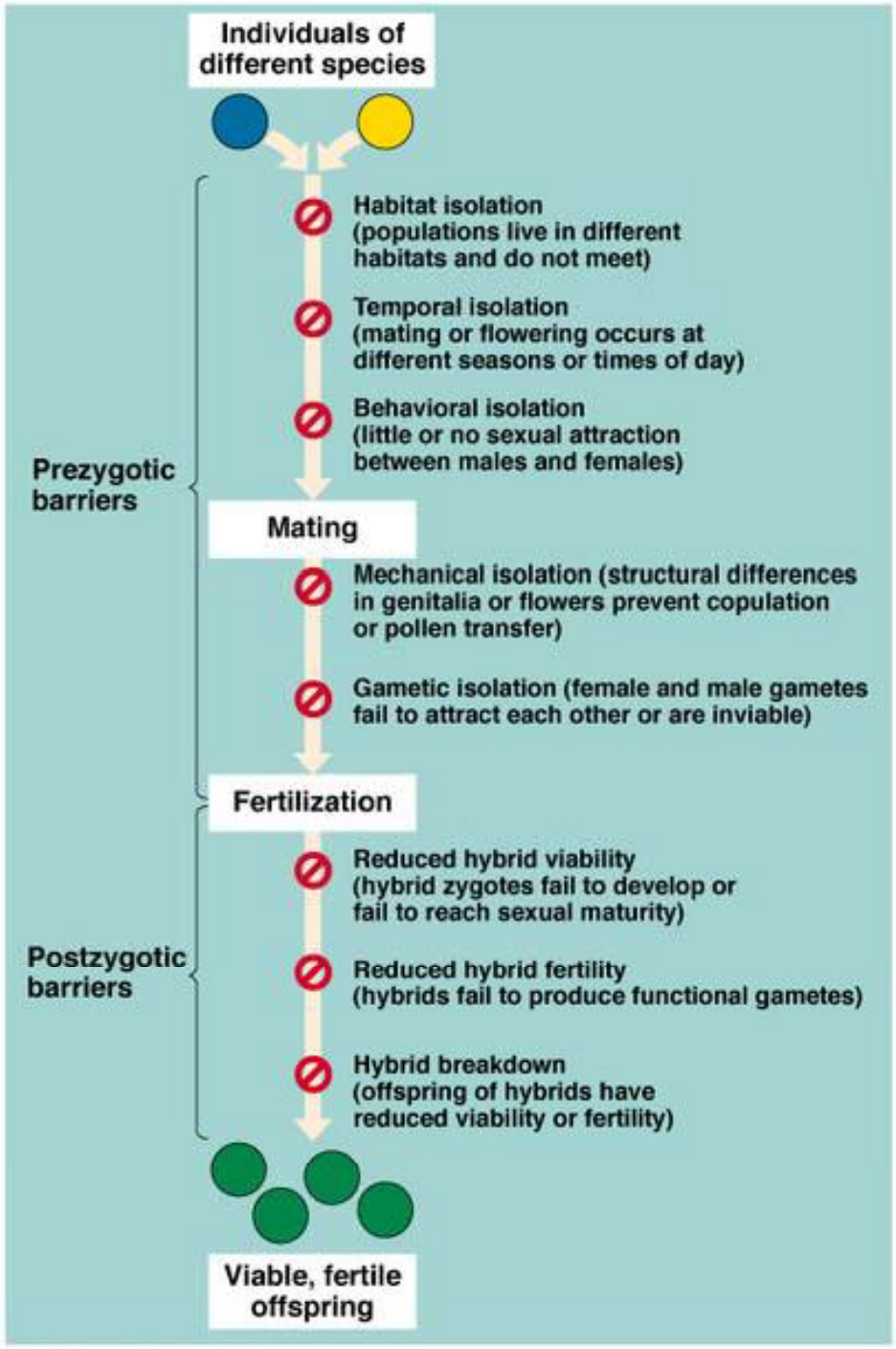
(Rem: Density vs. Weight example)

Reproductive Isolation May Occur With or Without Geographic Isolation

Allopatric speciation occurs when geographic isolation creates a reproductive barrier (an extrinsic mechanism).

Sympatric speciation occurs when a reproductive barrier is created by something other than geographic isolation (intrinsic mechanisms).





→ **aka Spatial isolation**

→ **aka Assortative mating**

→ **Hybrid low viability**

→ **Hybrid infertility**

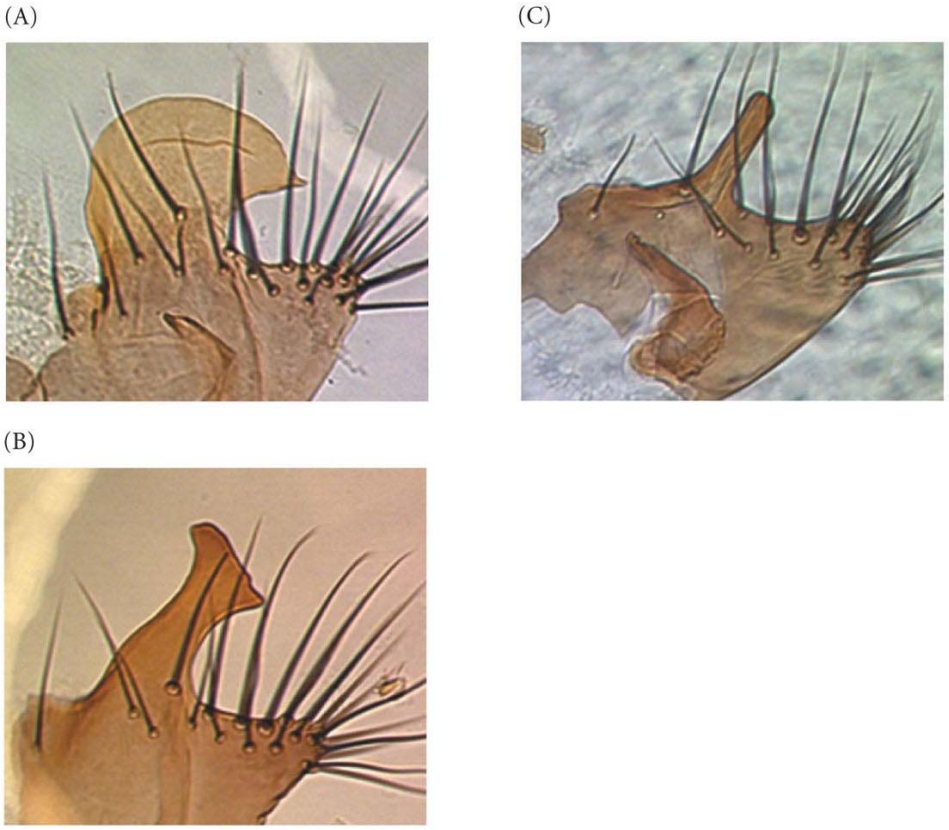
→ **Hybrid zygote abnormality**

Prezygotic Barrier: Temporal Isolation

Western Spotted Skunk
• breeds in late summer

Eastern Spotted Skunk
• breeds in late winter

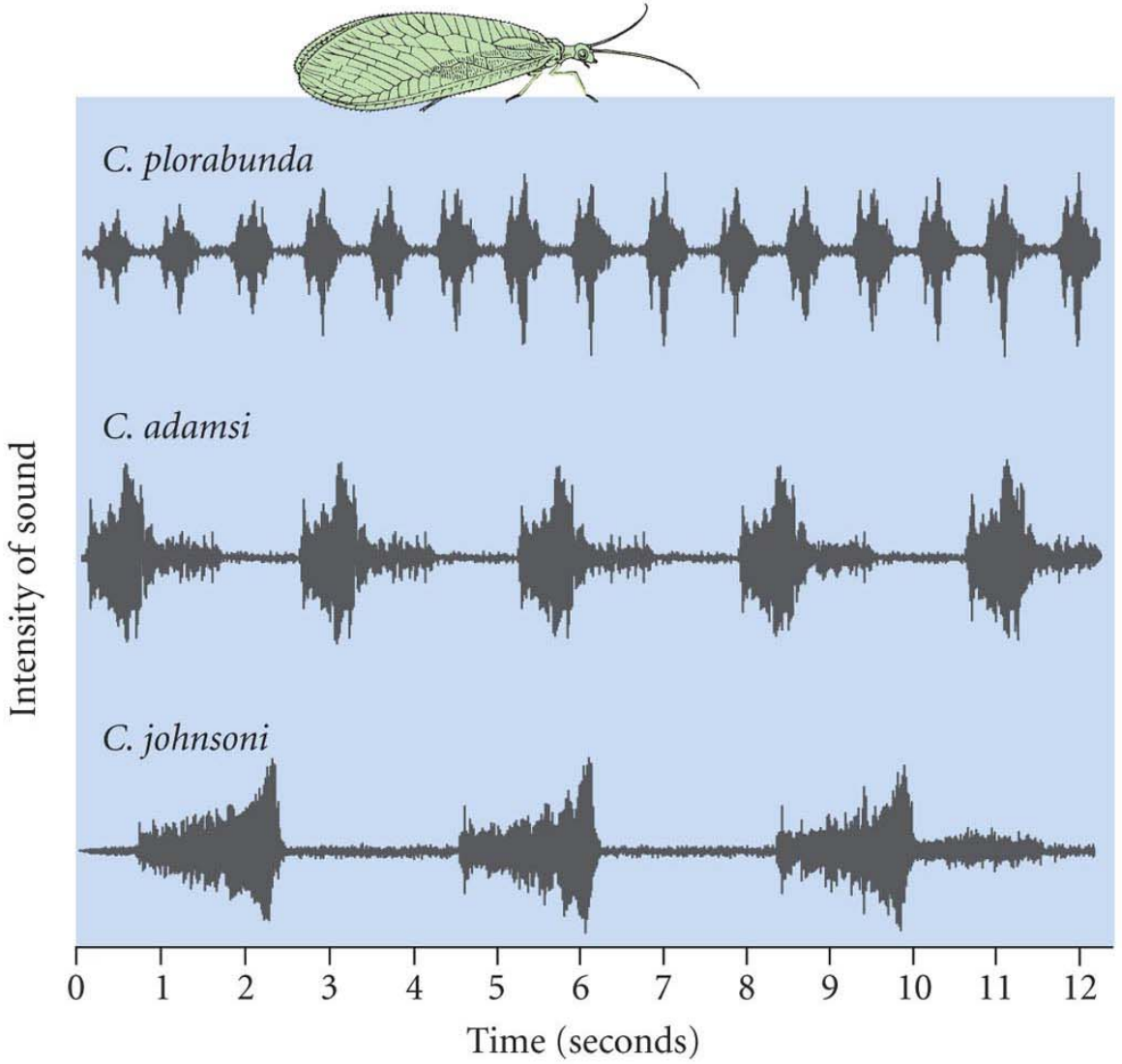
Prezygotic Barrier: Mechanical Isolation



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

Prezygotic Barrier: Gametic Isolation

Prezygotic Barrier: Behavioral Isolation



Behavioral Isolation Mechanisms

Courtship rituals, like these, are critical for mating within a species, but ineffective for attracting members of other species.

Postzygotic Barrier: Hybrid Infertility

Horse

Donkey

Mule

PRE-ZYGOTIC BARRIERS

Temporal Isolation
(frogs in ponds)

Ecological Isolation
(lion and tiger)

Behavioural Isolation
(cricket mating song)

Mechanical Isolation
(bush baby genitals)

POST-ZYGOTIC BARRIERS

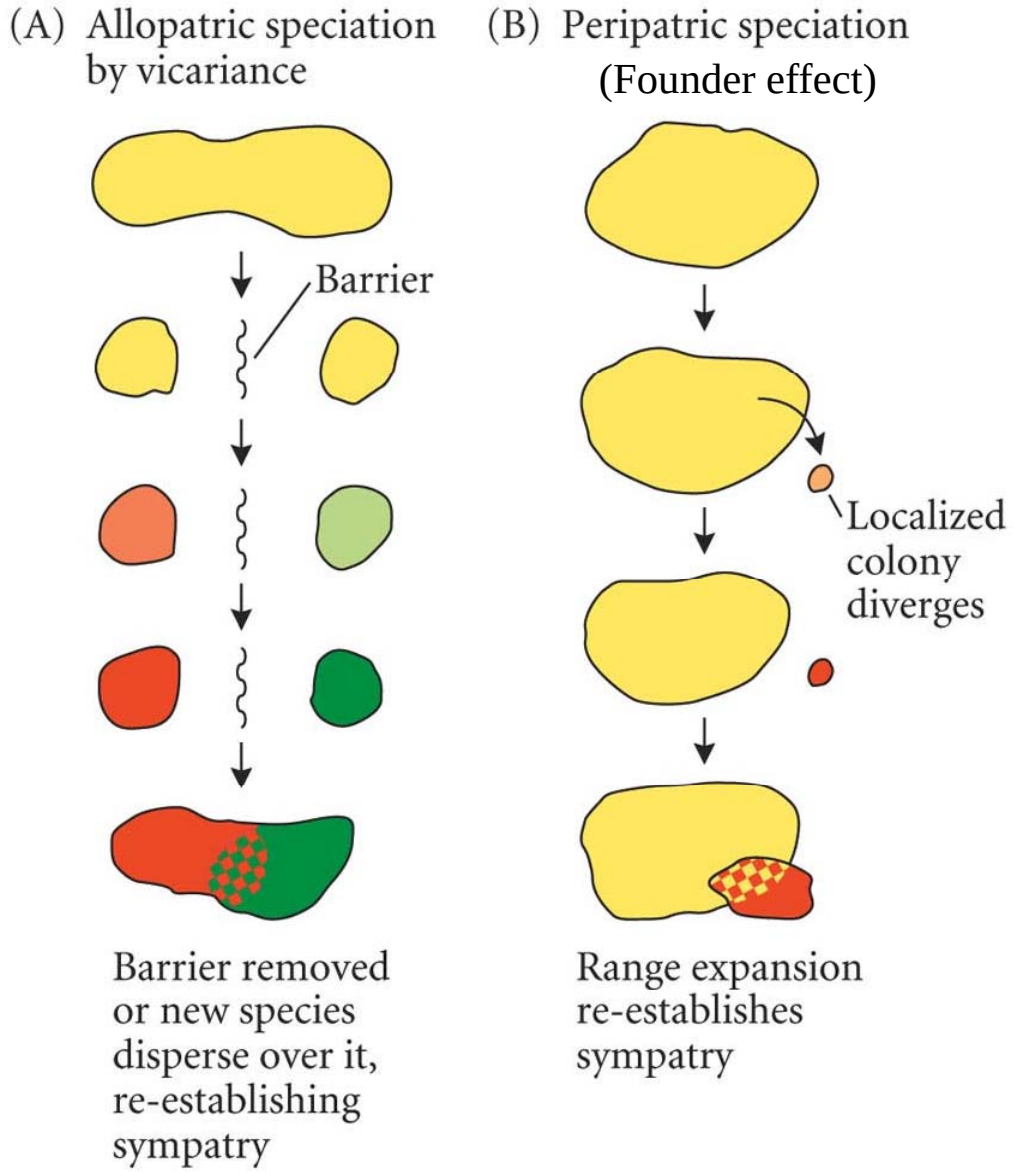
Hybrid Inviability
(*Rana* frogs)

Hybrid Infertility
(mules / asses)

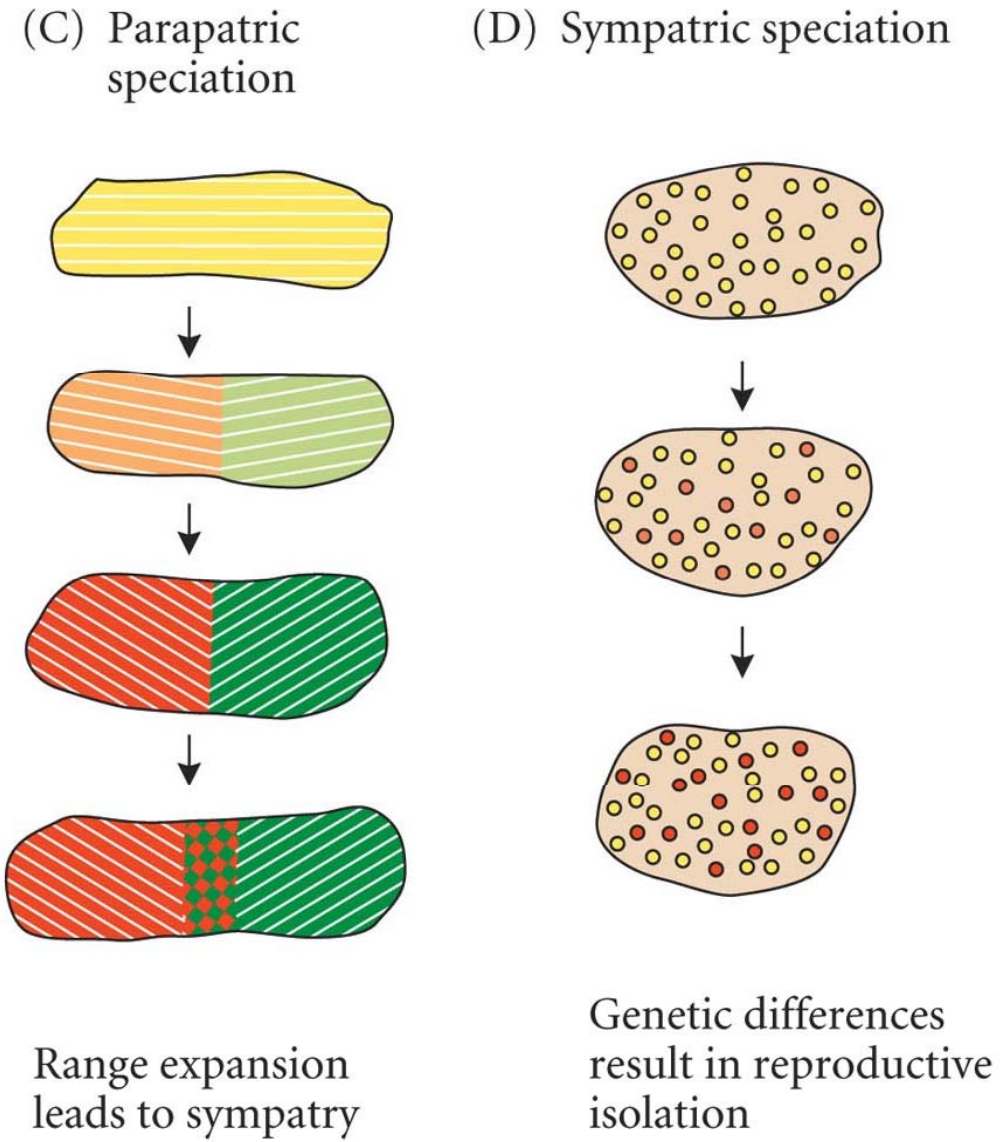
Hybrid Breakdown
(copepod offspring)

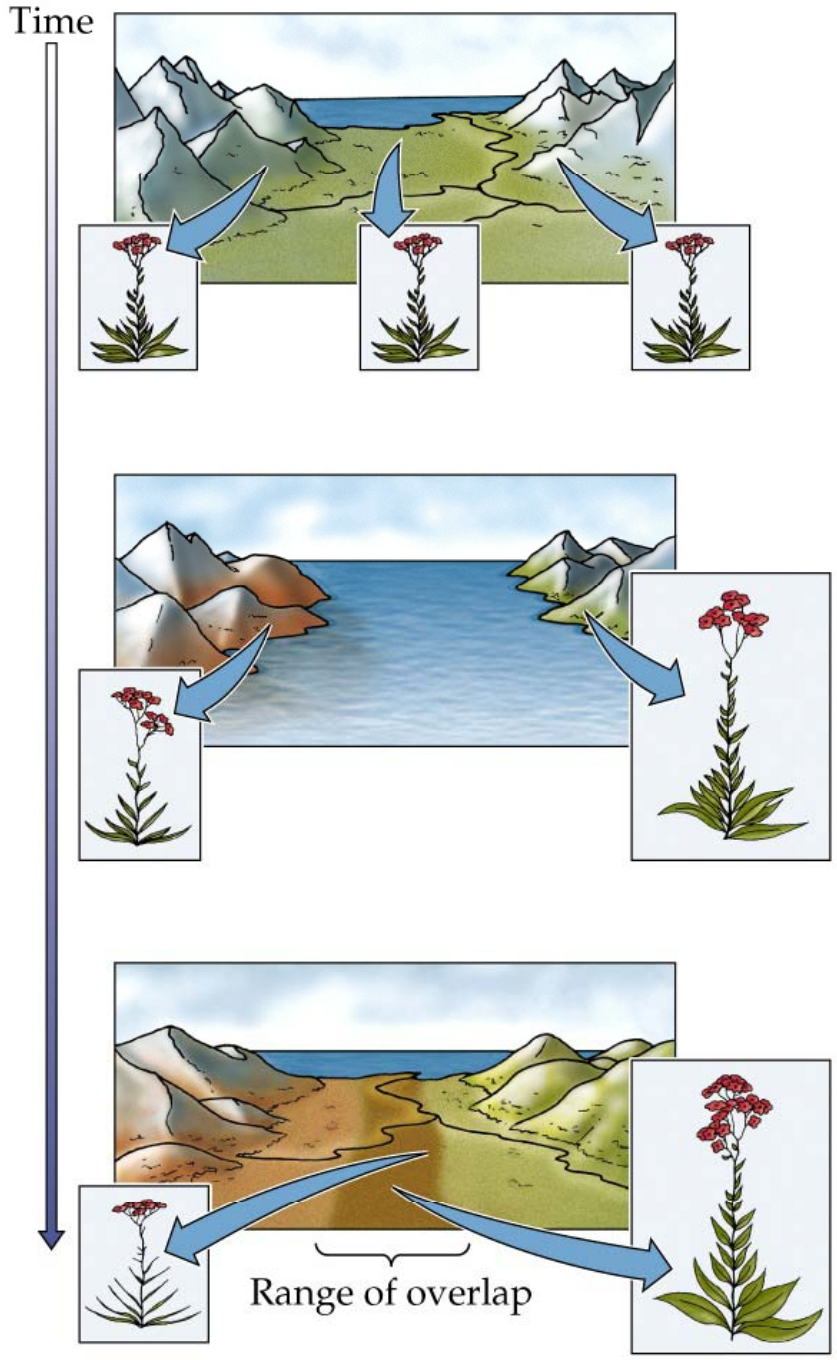
Pre-zygotic Isolating Mechanisms		**Example**
Temporal Isolation	Occurs when two species mate or flower at different times of the year	Different frog species live in the same pond but breed at different times
Ecological Isolation	Occurs when two species inhabit similar regions, but occupy different habitats	Lions and tigers occupy different habitats and do not interbreed (usually)
Behavioural Isolation	Occurs when two species respond to different specific courtship patterns	Some crickets are morphologically identical but only respond to species-specific mating songs
Mechanical Isolation	Occurs when genital differences prevent copulation (animals) or when flowers are pollinated by different animals (plants)	Bush babies have distinctly shaped genitalia that will only fit other members from the same species
Post-zygotic Isolating Mechanisms		**Example**
Hybrid Inviability	Hybrids are produced but fail to develop to reproductive maturity	Frogs of the genus *Rana* can form hybrid tadpoles which die before adulthood
Hybrid Infertility	Hybrids fail to produce functional gametes	Mules are the sterile hybrids of a male donkey and a female horse
Hybrid Breakdown	The F1 hybrids are fertile but the F2 generation fail to develop or are infertile	The offspring of hybrid copepods have a reduced potential for survival or reproduction

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



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





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.

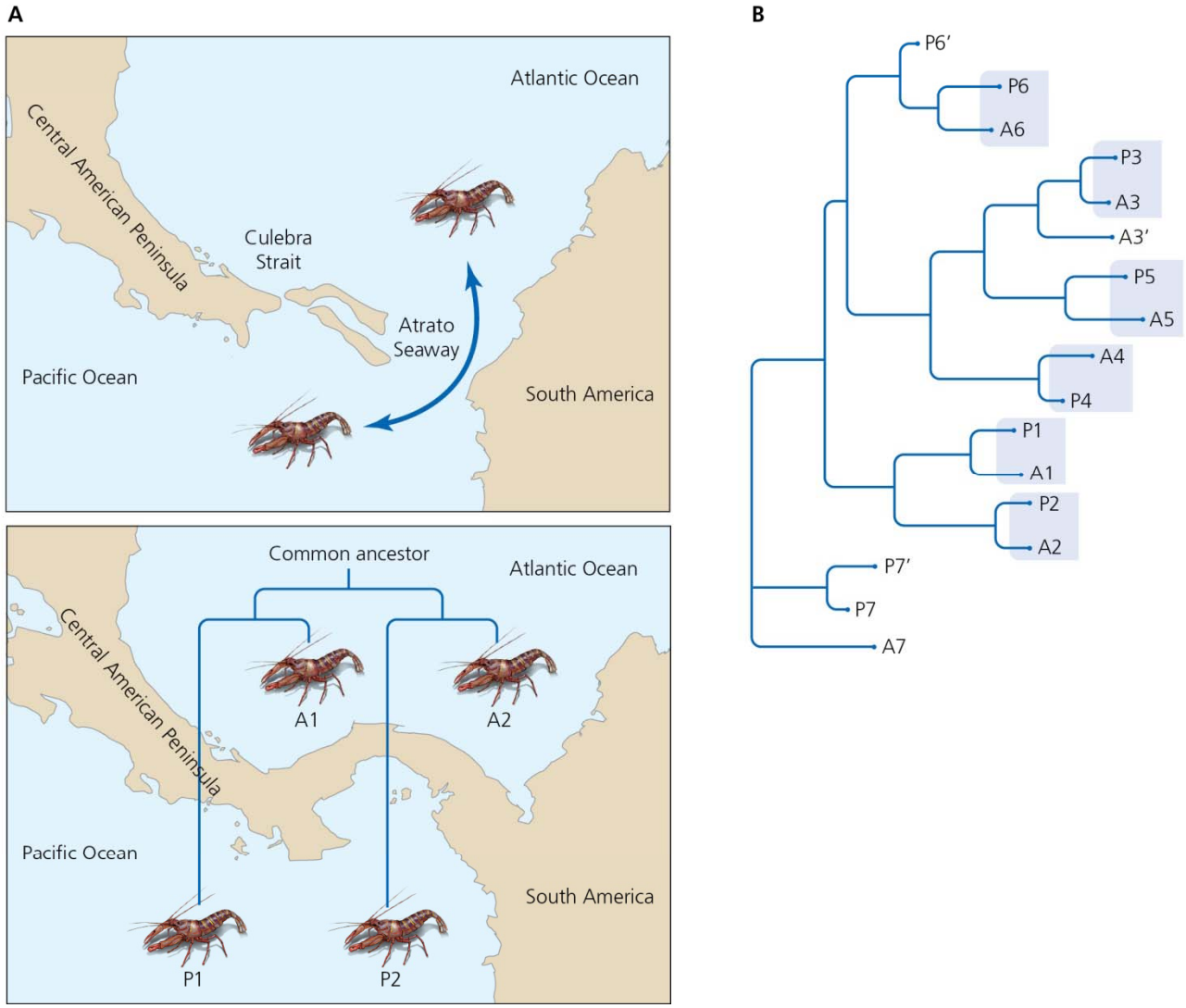
Parapatric Speciation –

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

Allopatric Speciation: Vicariance

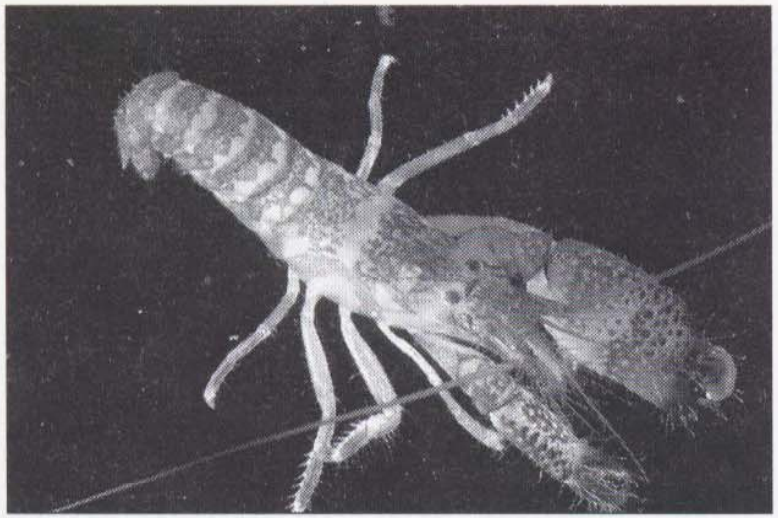
The Isthmus of Panama formed from 15 Mya to 3 Mya.

Phylogenetic signature of allopatric speciation

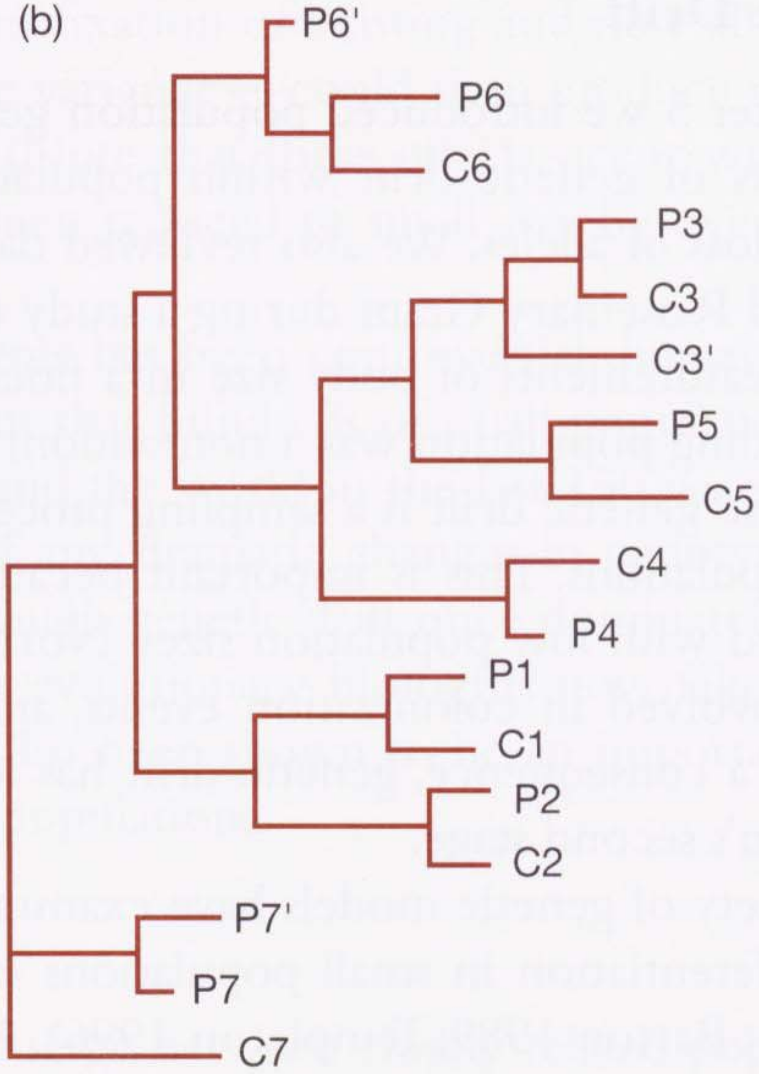


Speciation in snapping shrimp across the Isthmus of Panama

(a)



(b)

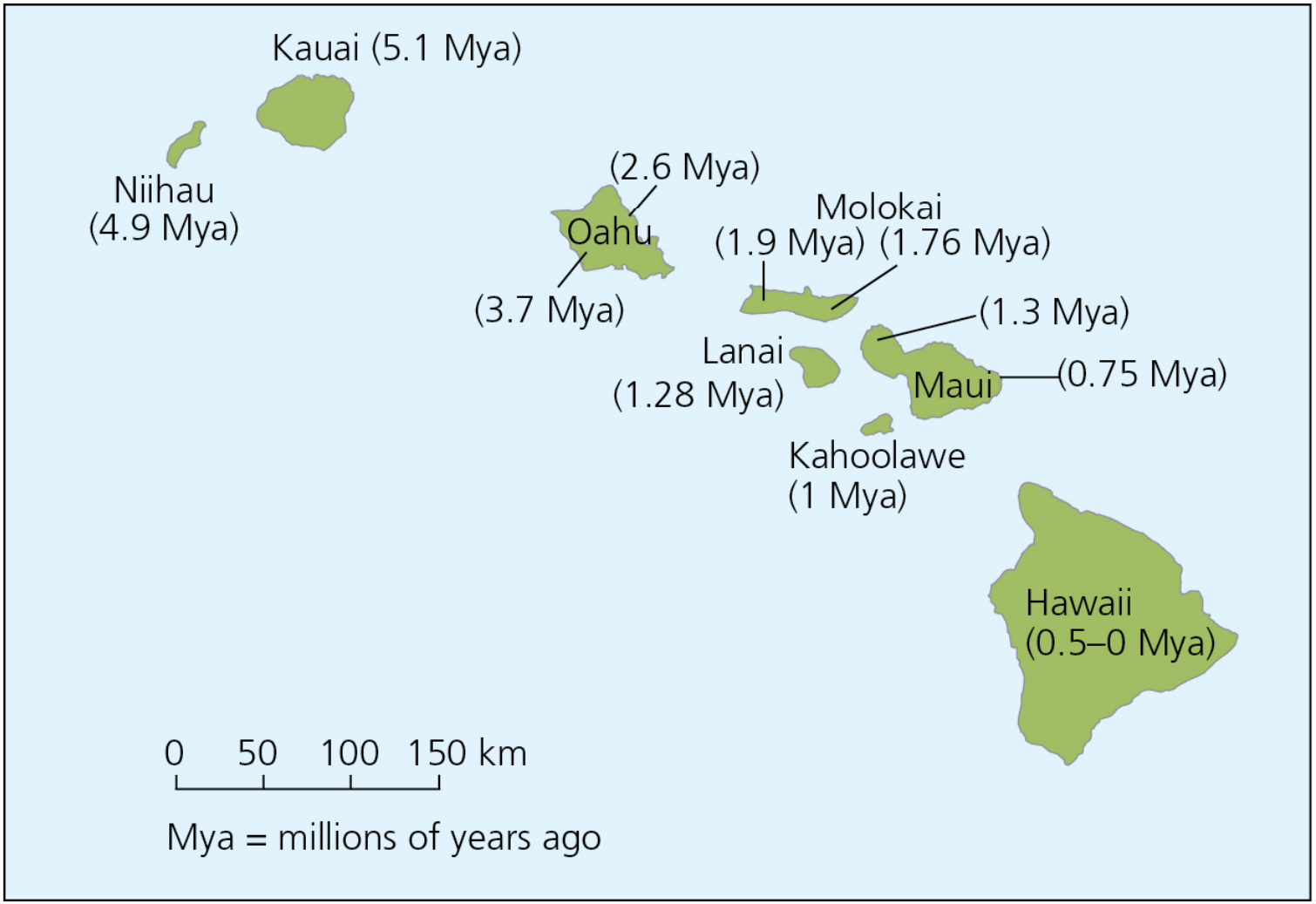


7 morphospecies w/o repro

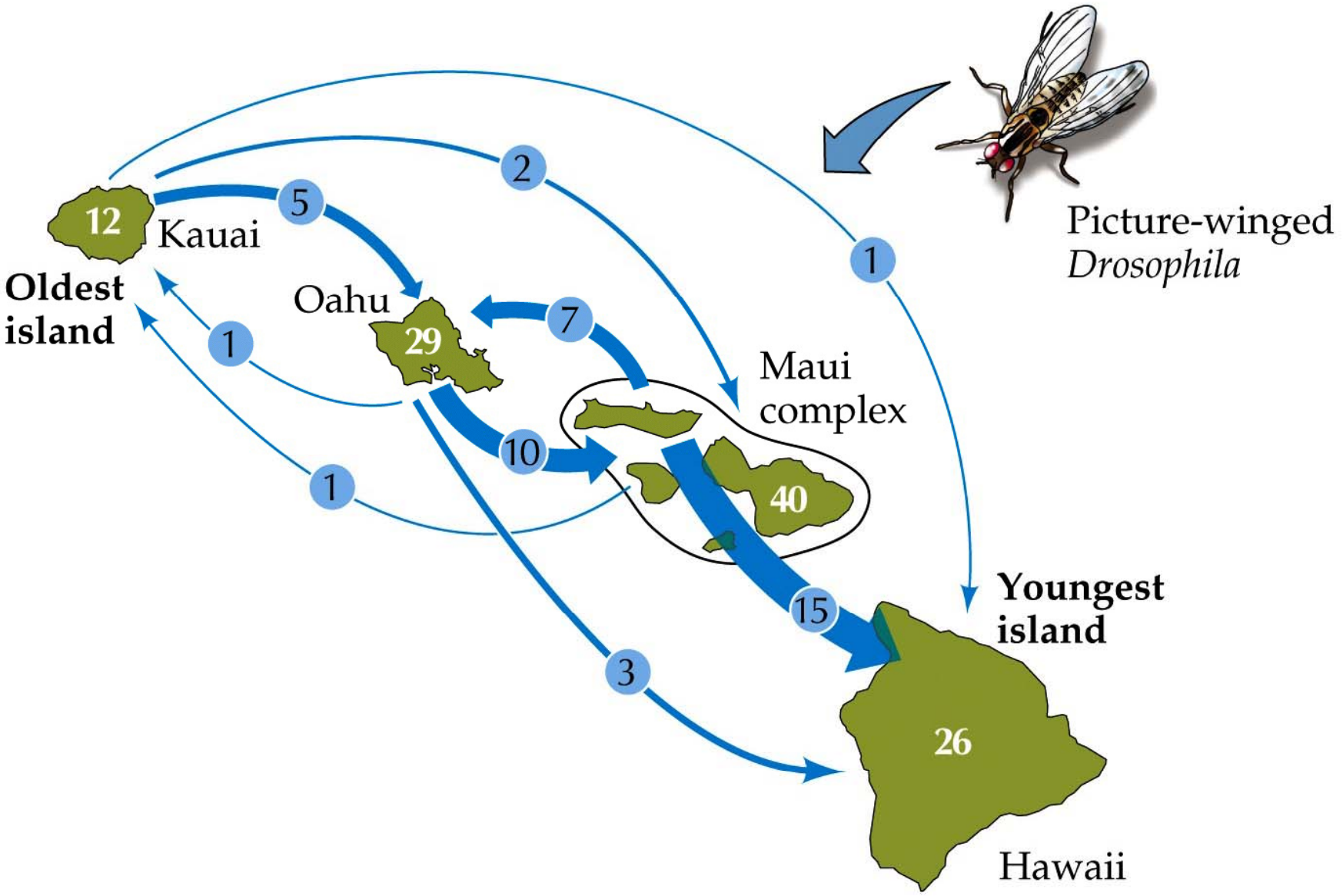
Closest clades show “Final Break” at ~3 Mya

(‘) = cryptic species

Islands provide opportunity for allopatric speciation



Allopatric speciation is common in island archipelagoes via Dispersal & Colonization



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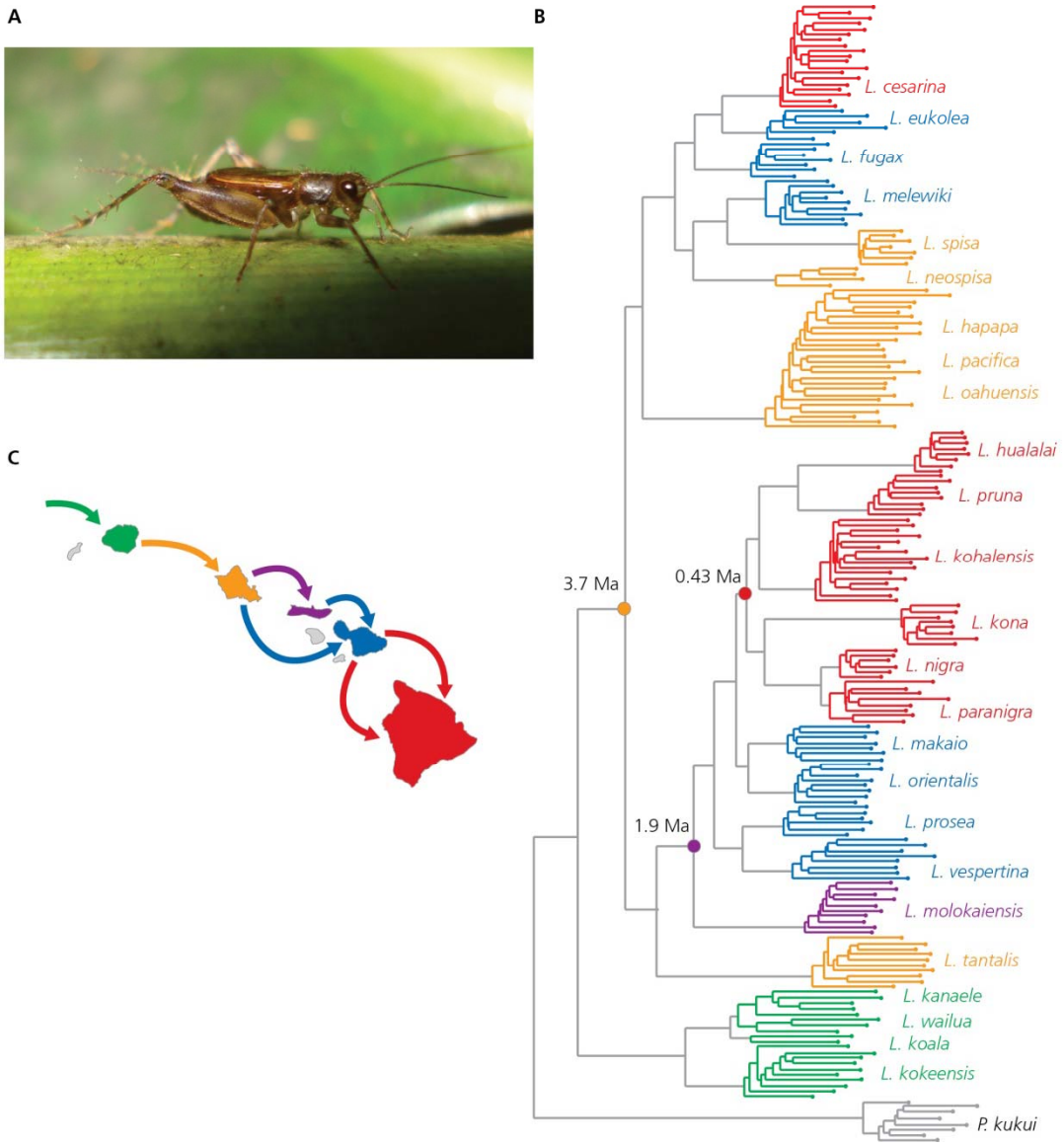


Reproductive Isolation

Byproduct (Mayr) vs. Reinforcement (Dobzhansky)

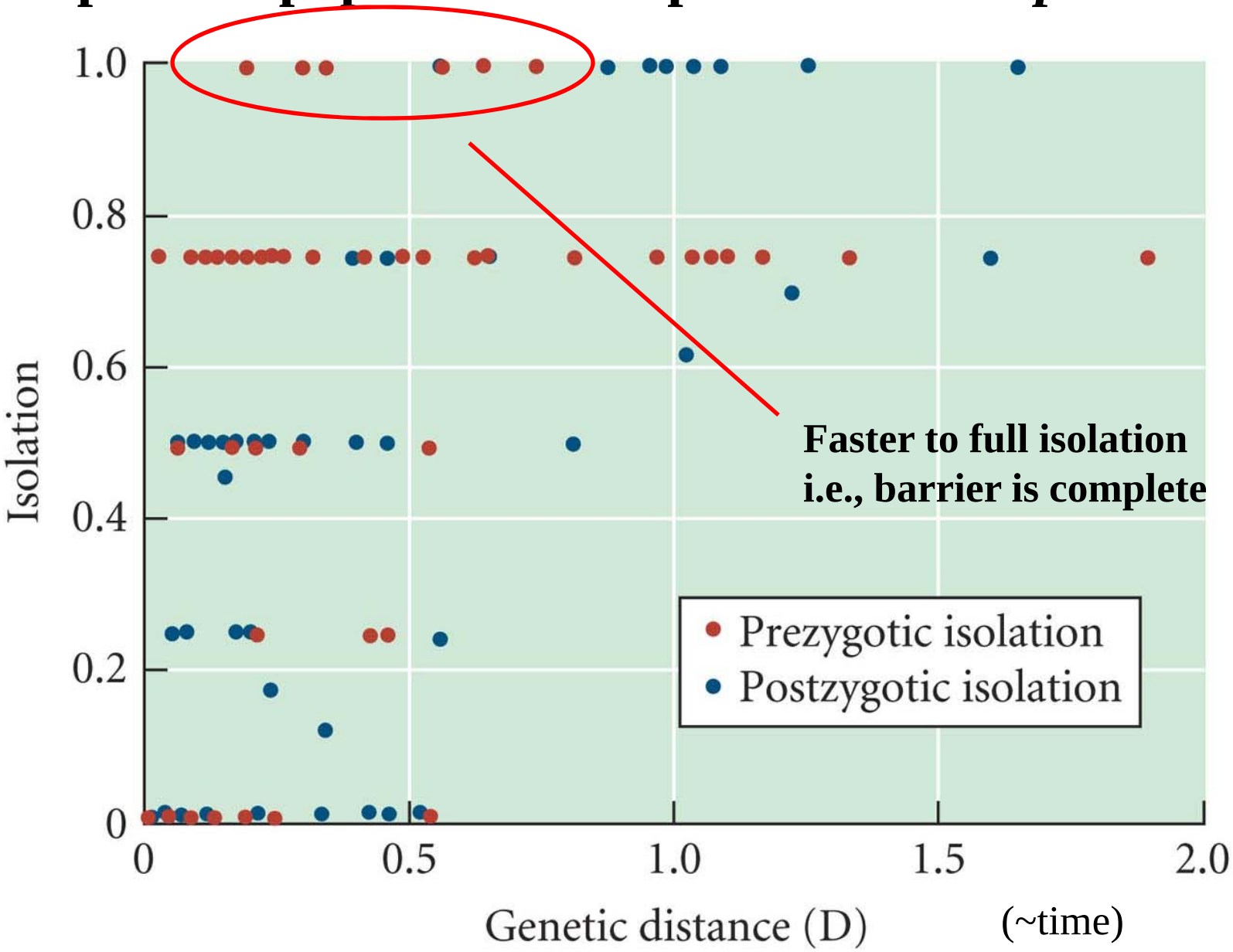
Reinforcement – type of selection that leads to assortative mating and prezygotic isolation.

Reproductive isolation revisited:

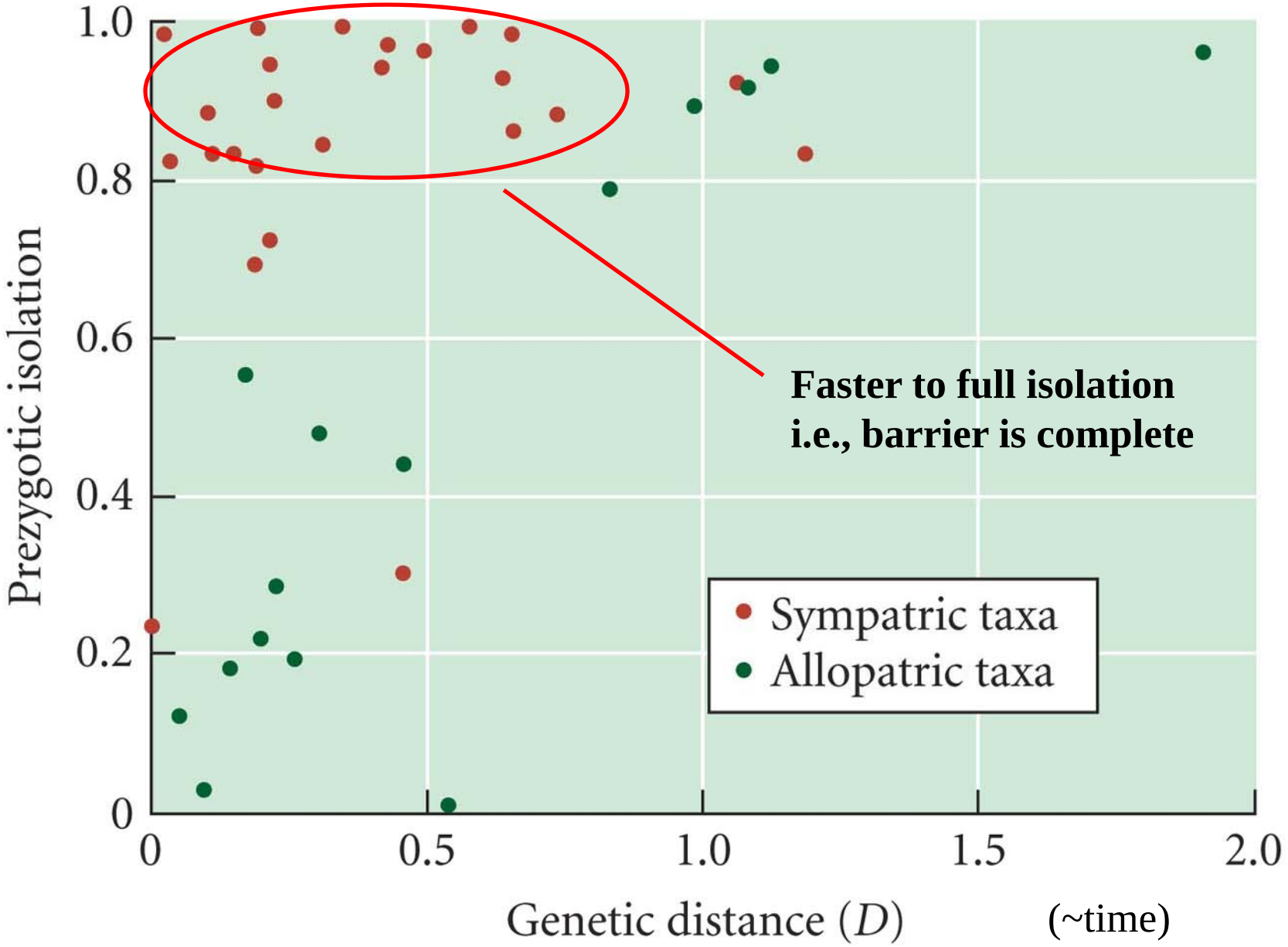
- **Both prezygotic and postzygotic barriers increase gradually over time for either model.**

- **Reinforcement speeds up prezygotic barriers in sympatric sister species through assortative mating.**

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

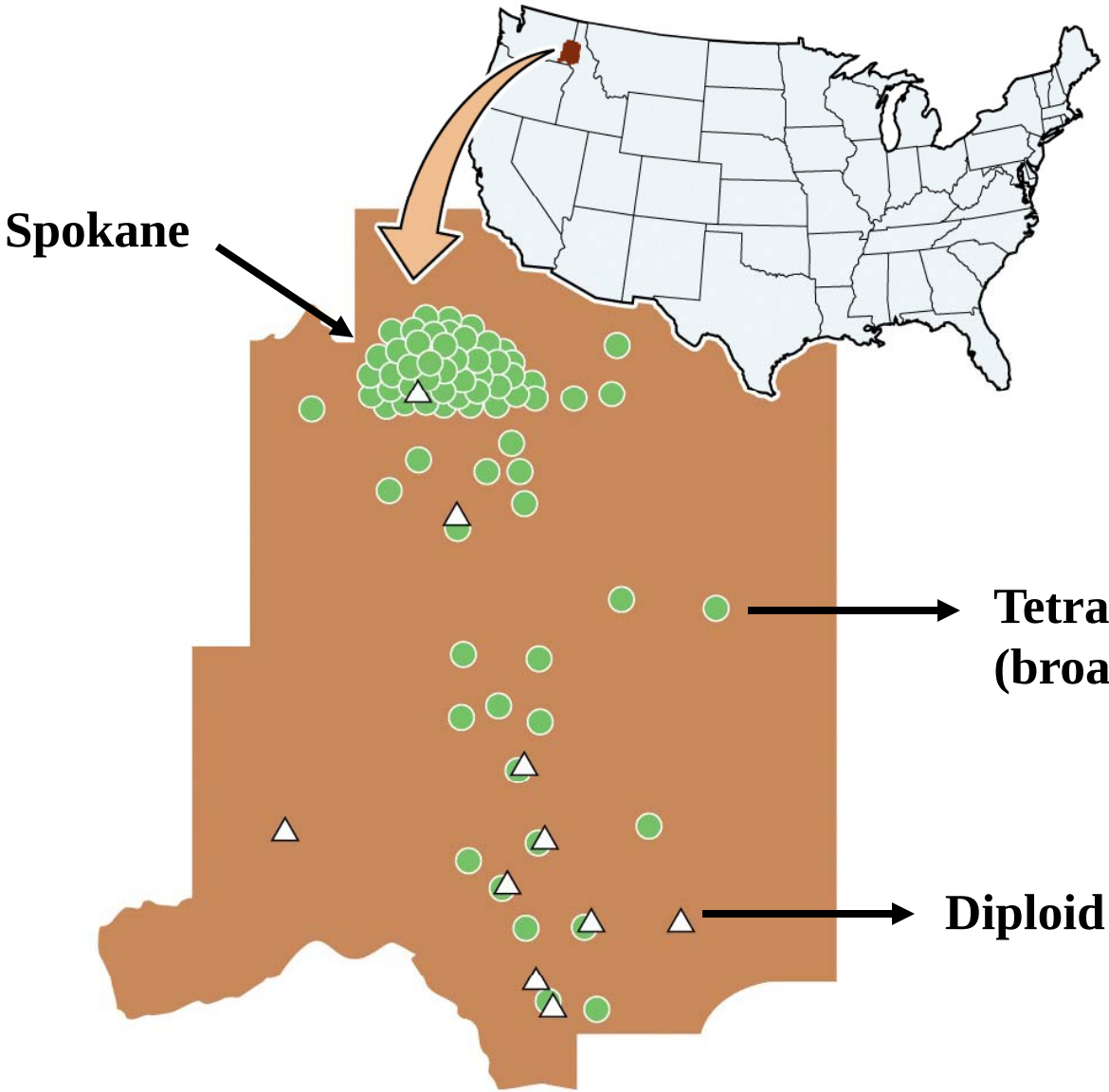


Level of prezygotic isolation between allopatric and sympatric pairs of Drosophila populations



(~time)

Sympatric speciation via hybridization

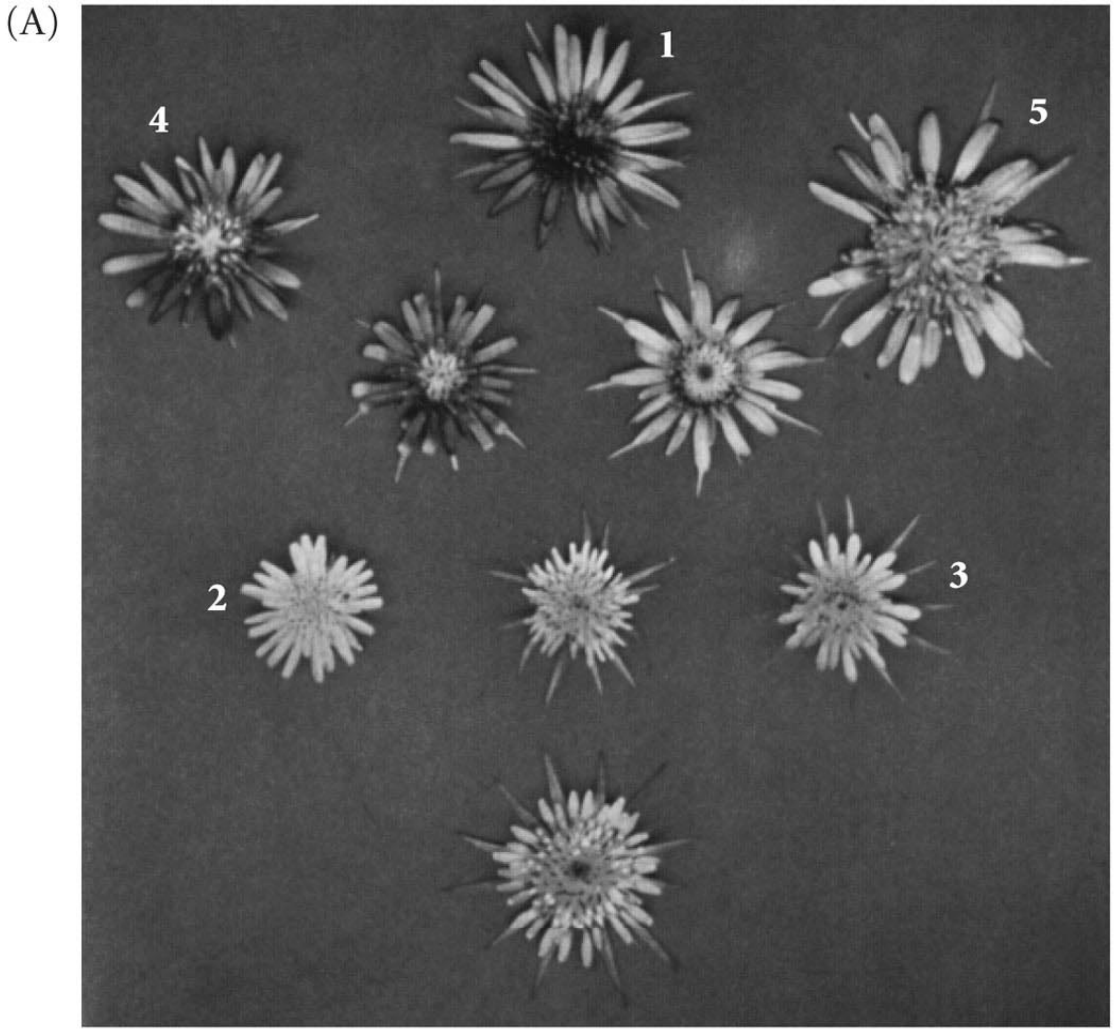


Sunflower speciation (allopolyploidy)

Tetraploid hybrid species (broader range than parentals)

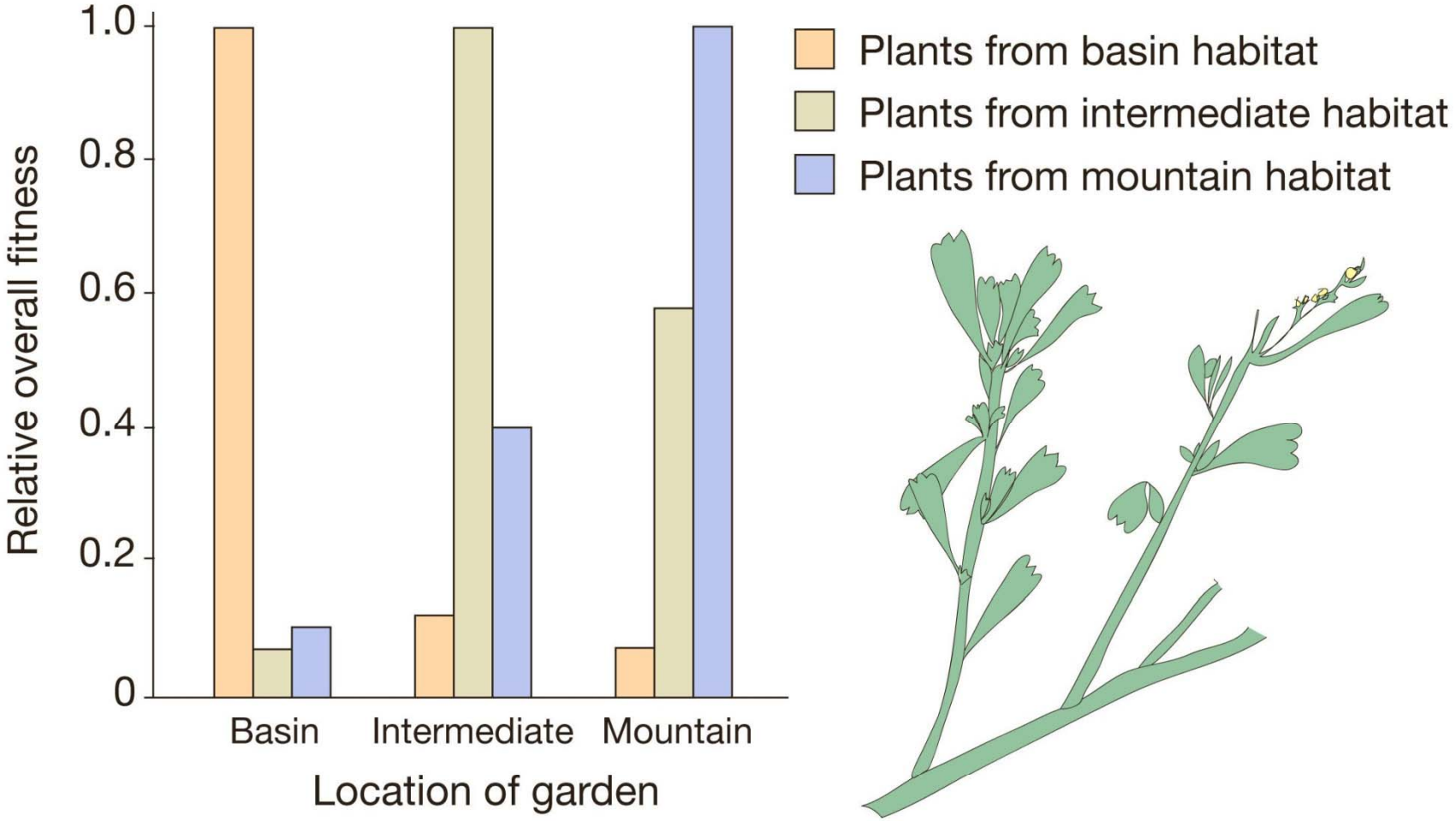
Diploid parental species

Sympatric speciation via hybridization



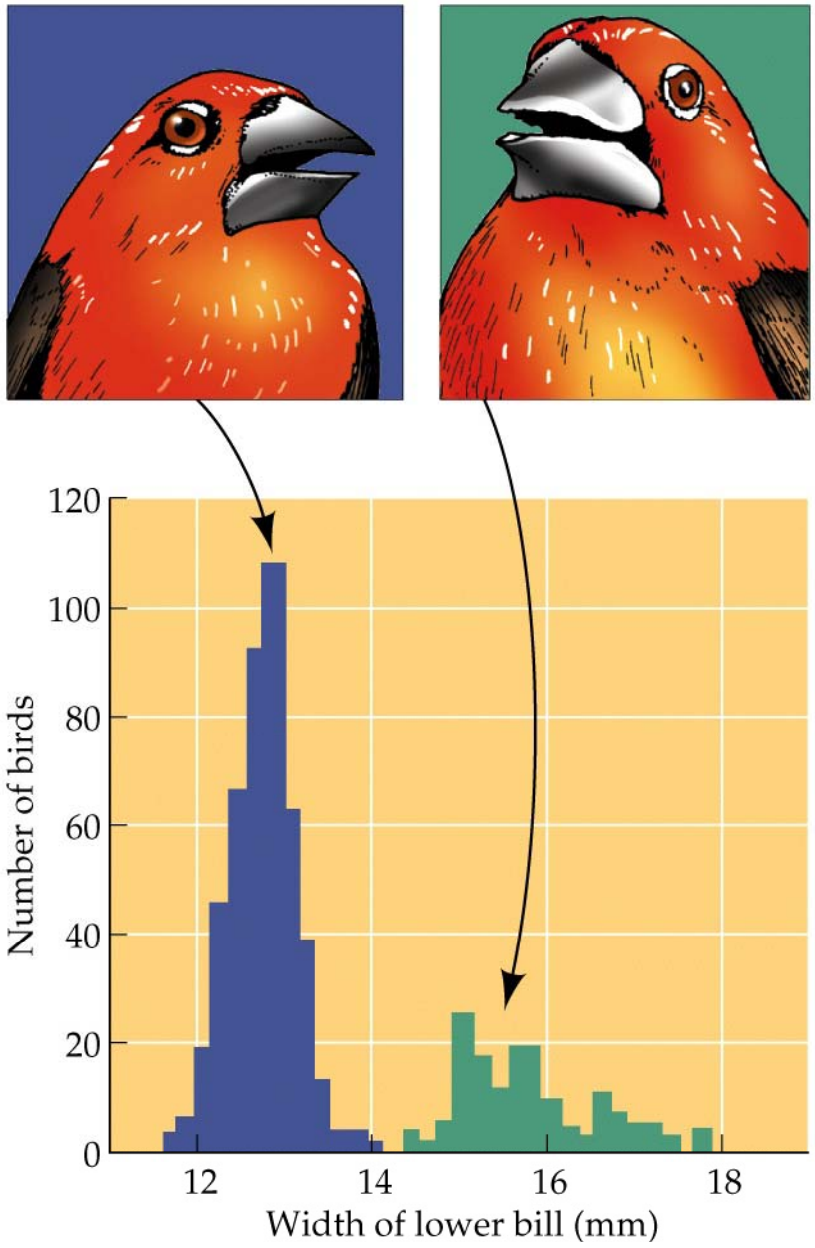
Goatsbeards
(*Tragopogon*)

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



Rem: Parapatric Model

Sagebrush

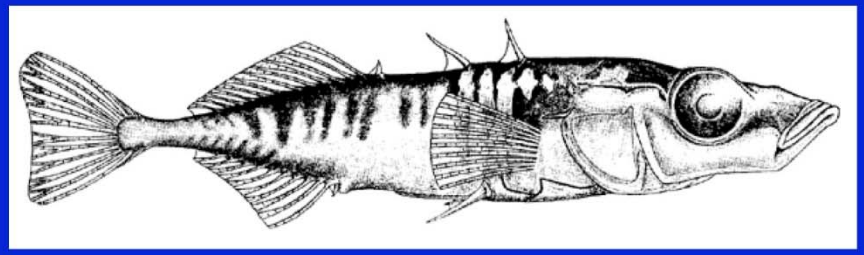


Black-bellied Seedcrackers (*Pyrenestes*)

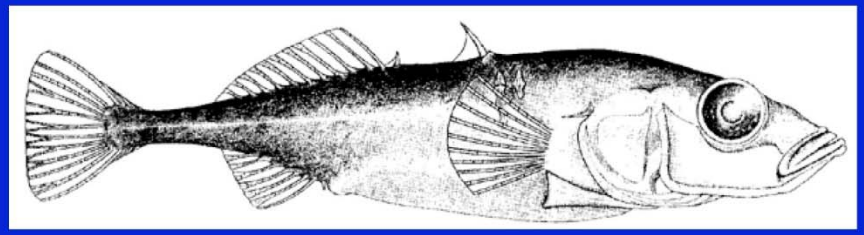
- Live in marshes in W. Africa
- Eat seeds, primarily of two plant species
- One seed type is small, the other type is large
- Bill dimorphism reflects the effects of **disruptive selection**

Leads to Assortative Mating and Sympatric Speciation.

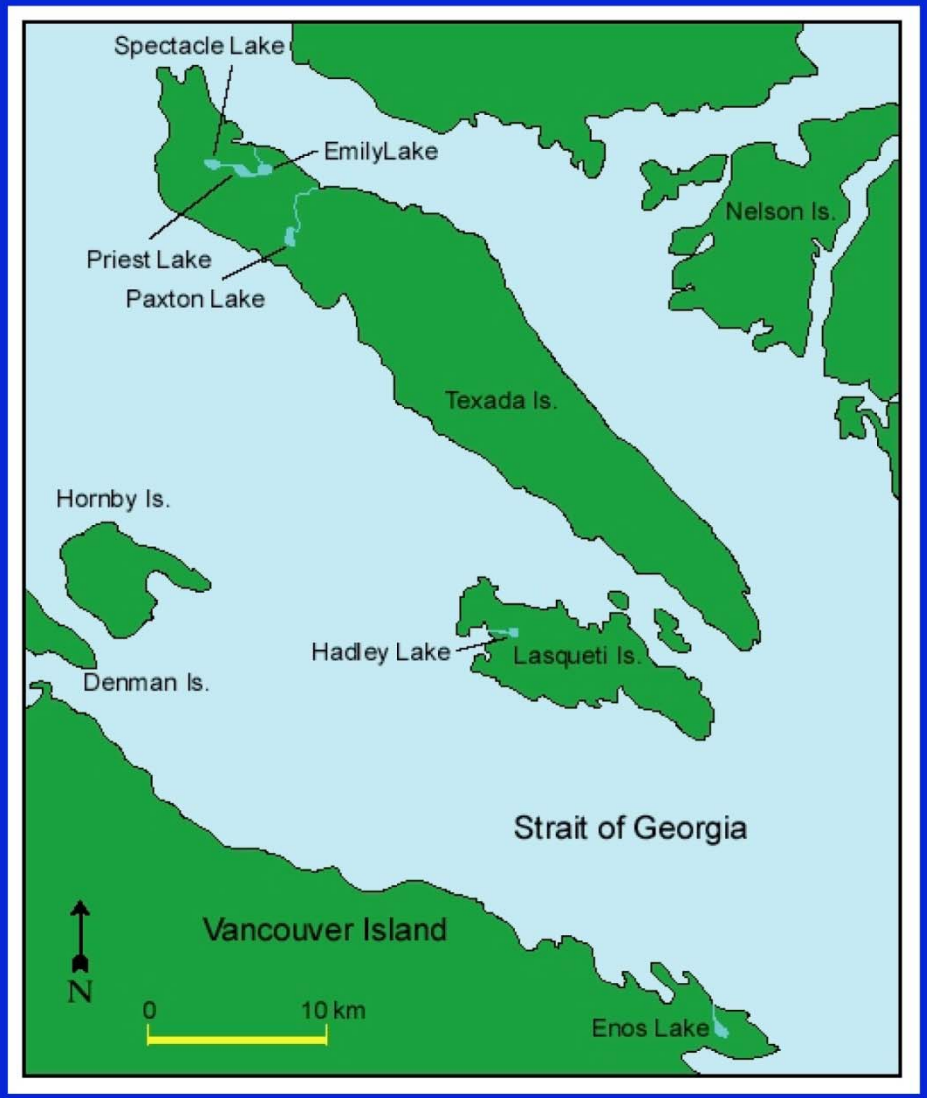
Sympatric speciation via ecological niche polymorphism



Limnetic male



Benthic male



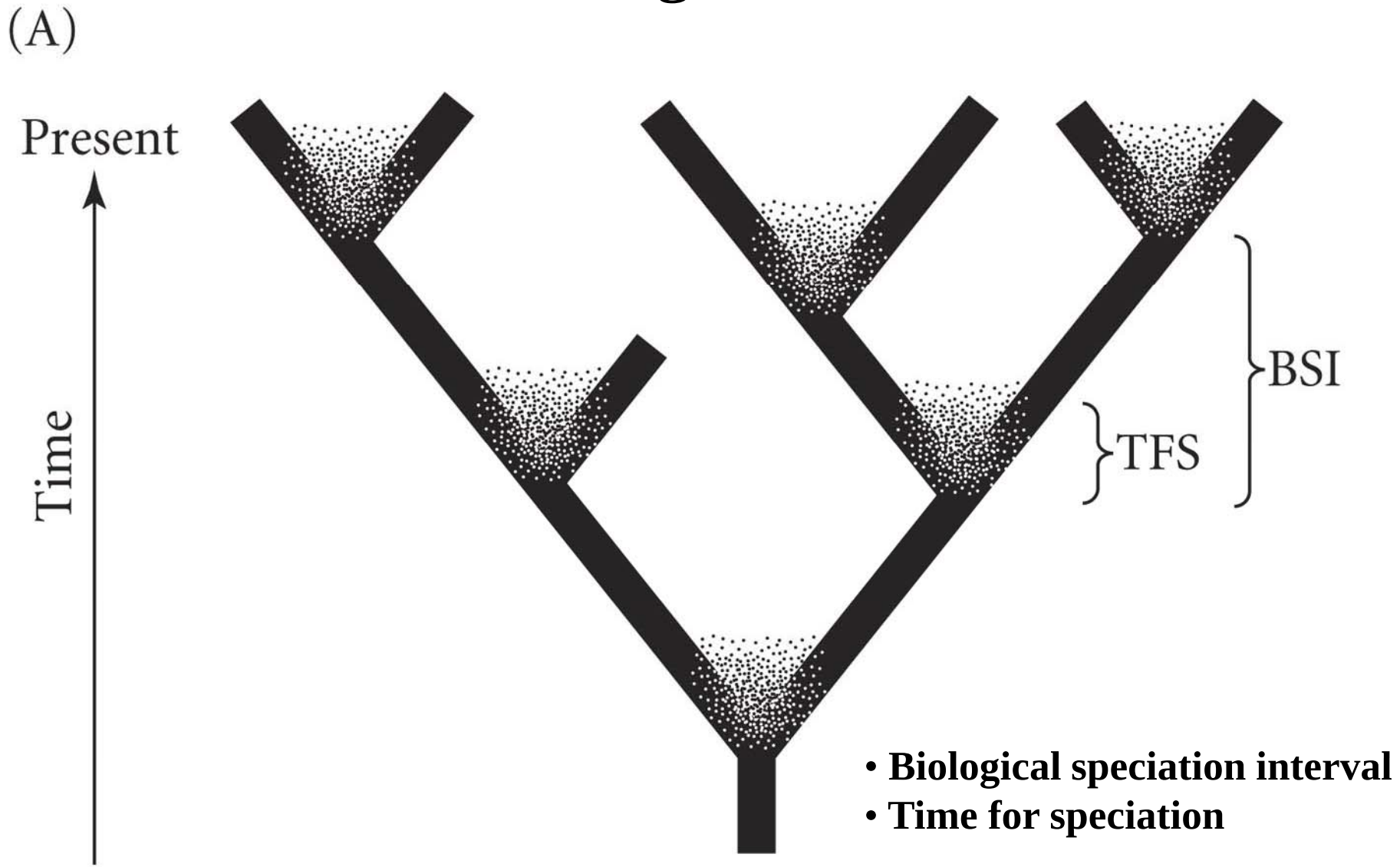
Speciation Rates

Generalists, like the horseshoe crab, tend to remain as stable species.

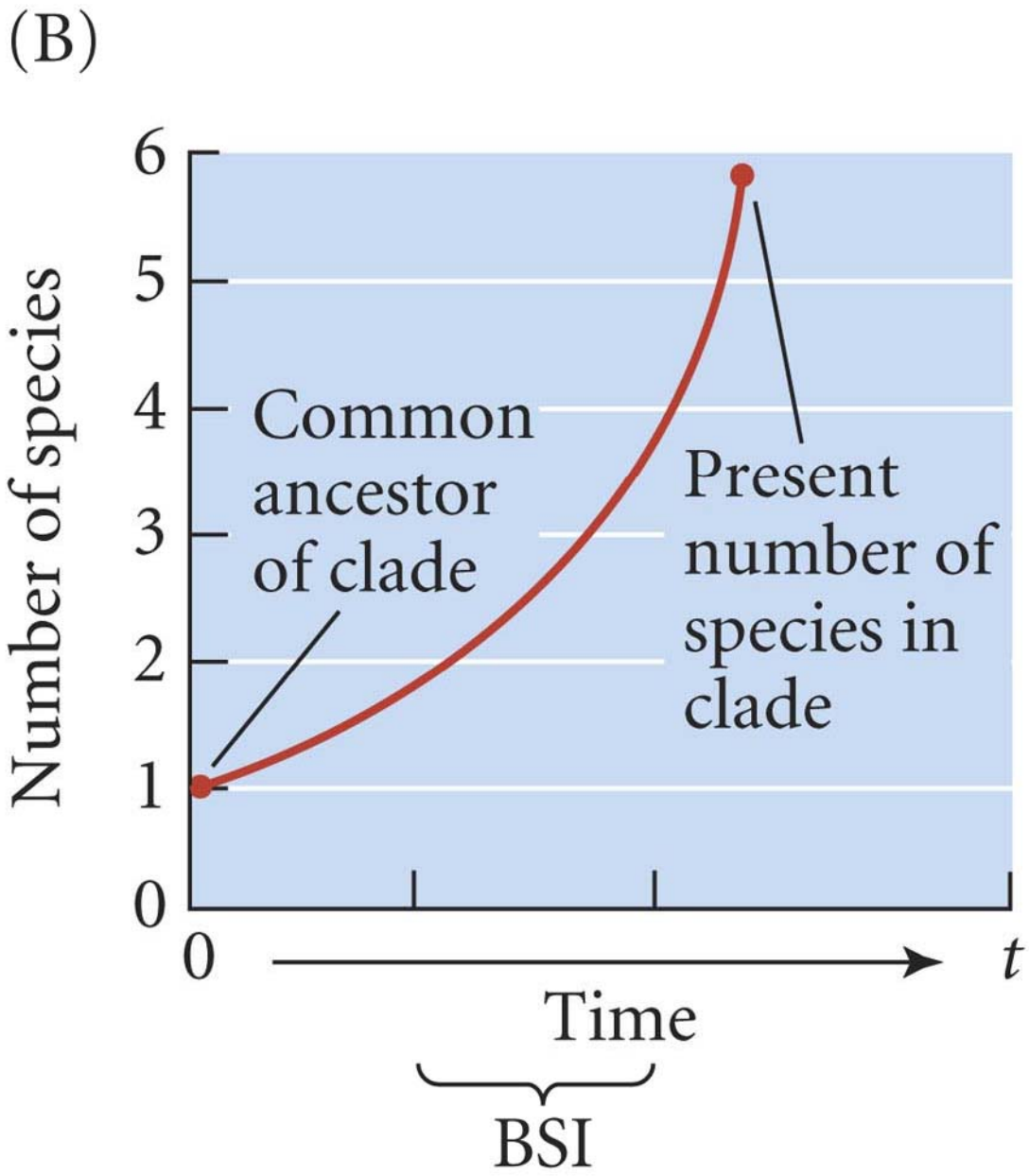
Specialists, like the Galapagos finch, tend to be unstable as species.

Speciation also becomes rapid when, as occurred with Galapagos finches, new niches become available.

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

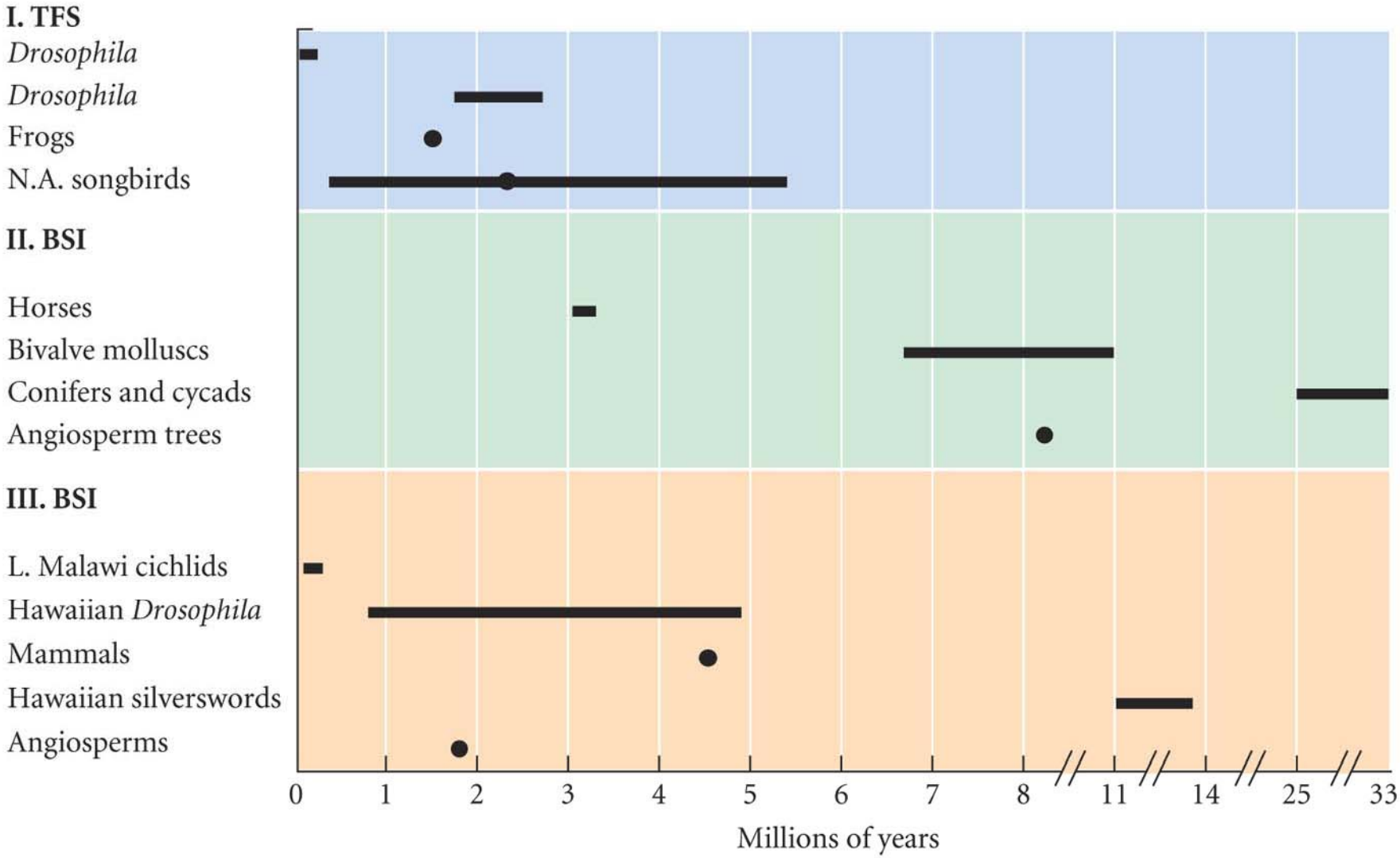


- **Biological speciation interval**
- **Time for speciation**



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

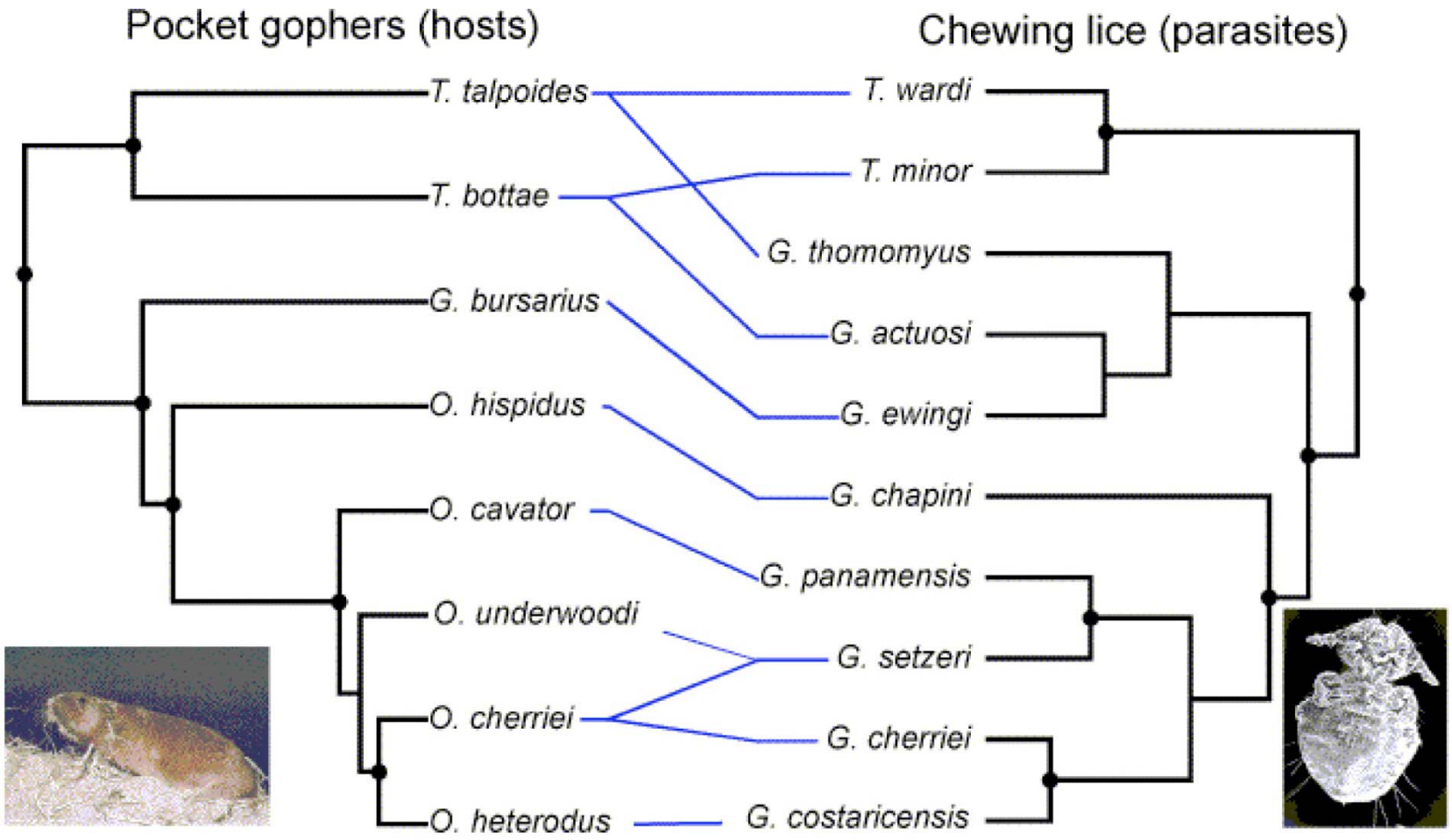
Estimates of time required for the speciation process in various groups of organisms



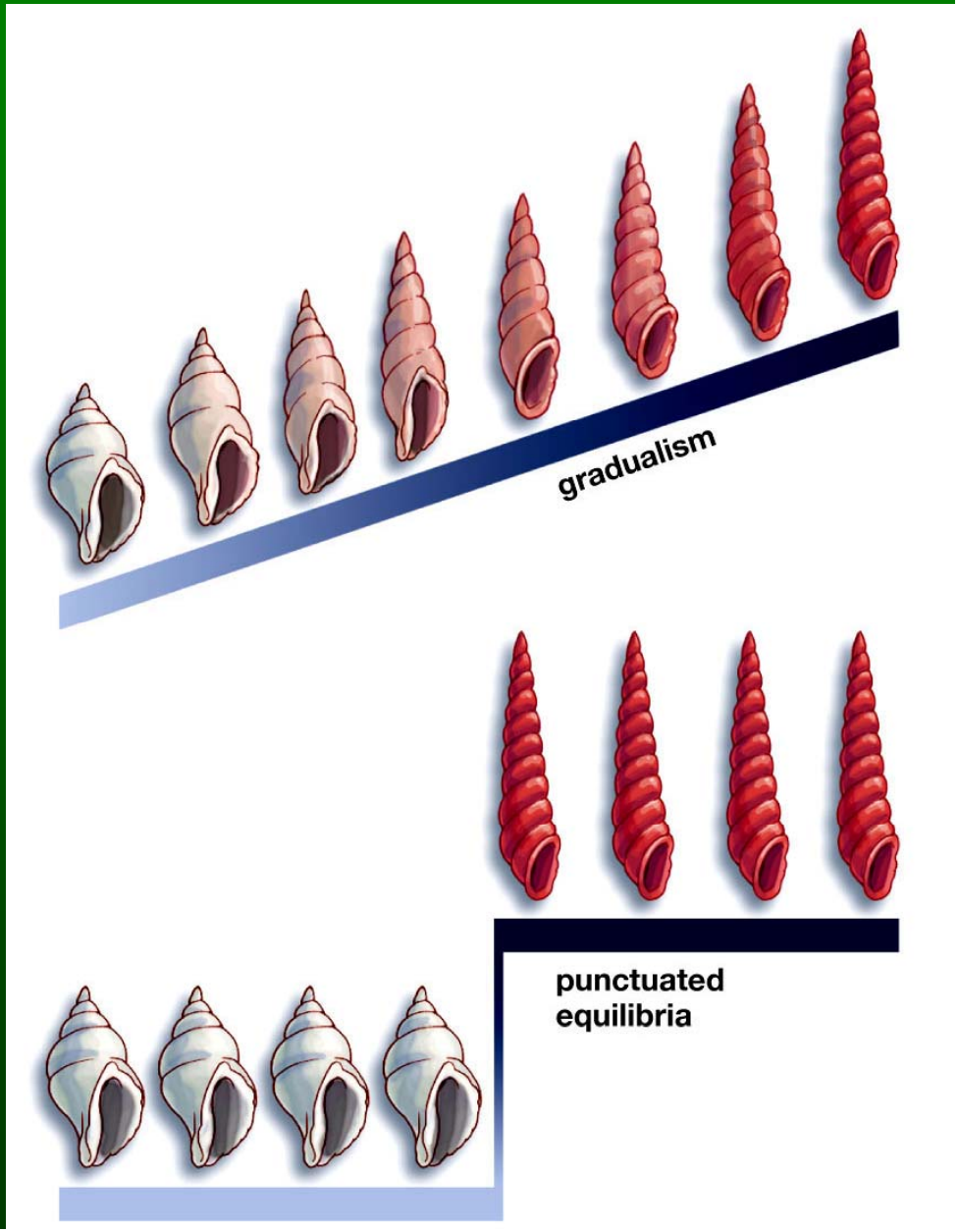
Factors promoting rapid speciation

- Many species (e.g. beetles)
- Opportunities for geographic isolation
- Limited mobility
- Short generation times
- Sexual selection
- Cytoplasmic Incompatibility (CI)
- Allopolyploidy
- Ecological specialization

Ecological Specialization

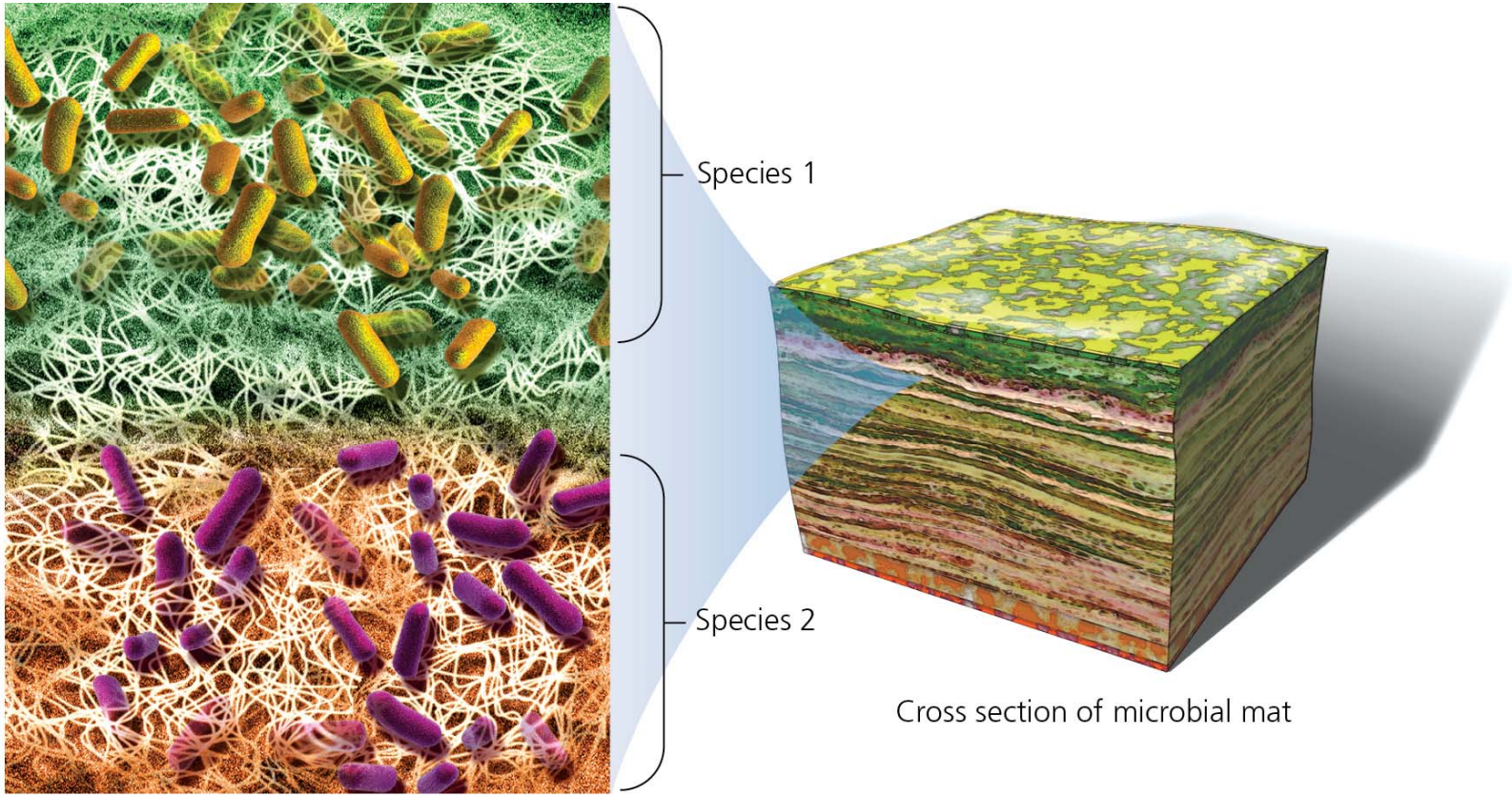


Speciation Dynamics - Gradualism or Punctuated Equilibrium?



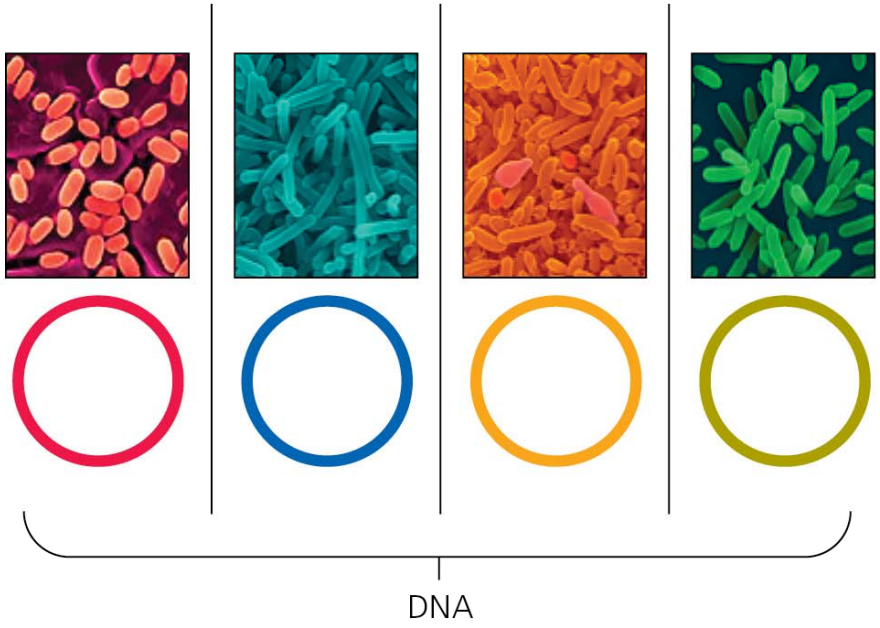
Punctuated equilibrium appears to be a more accurate view of speciation dynamics.

Bacterial species often defined by specific adaptations: Ecotypes

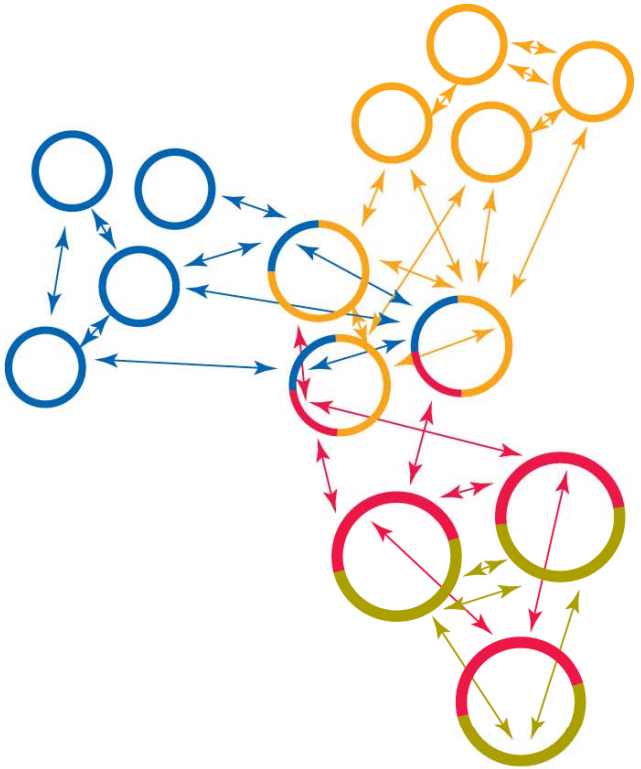


Horizontal gene transfer makes classification difficult

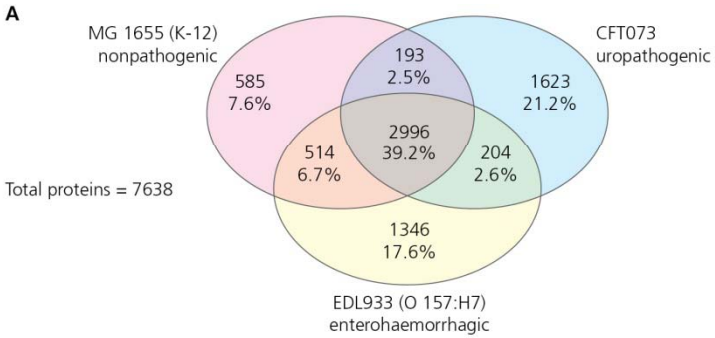
Instead of being neatly divided by species barriers ...

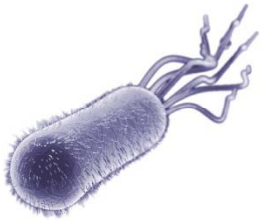


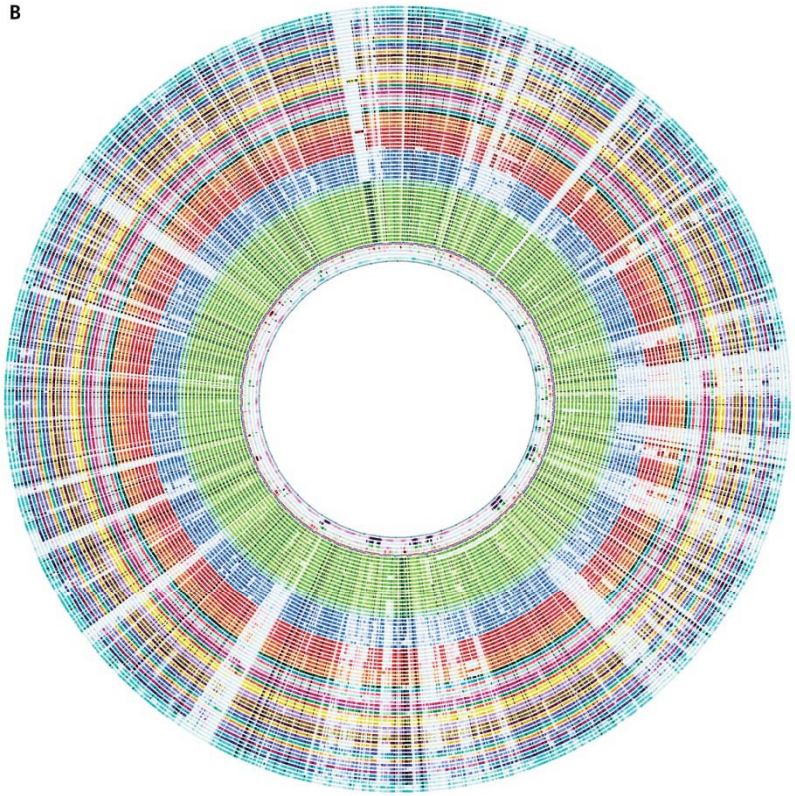
...the genomes of microbes have been mixed together by horizontal gene transfer.



Horizontal gene transfer in *E. coli*



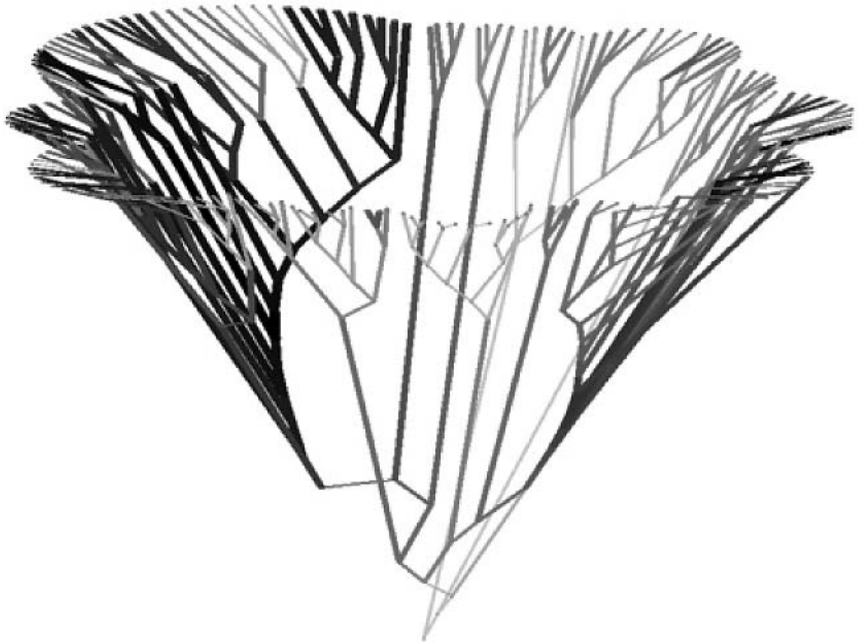




Core genome includes 993 genes (i.e., 6%)

Pan-genome includes 15,741 genes (from 61 strains)

Horizontal gene transfer is common



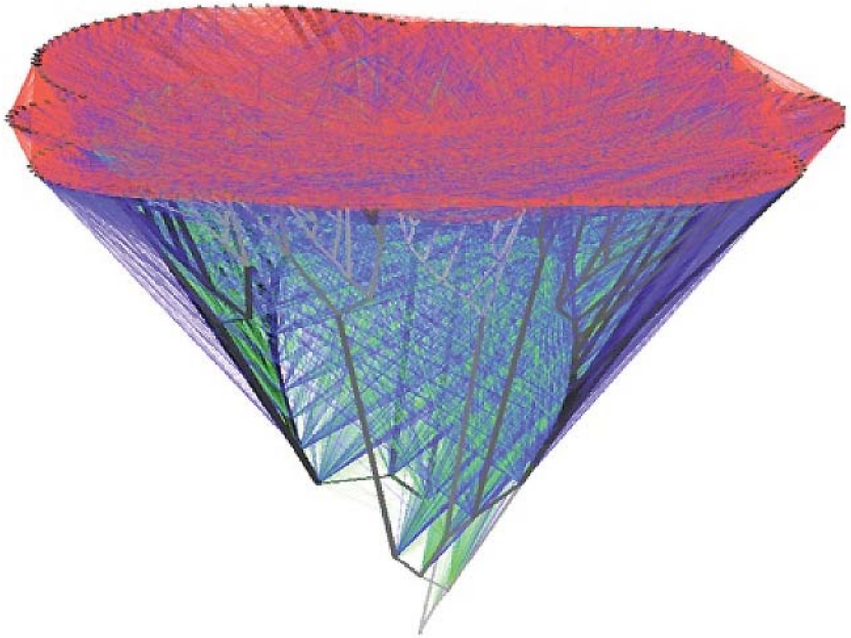


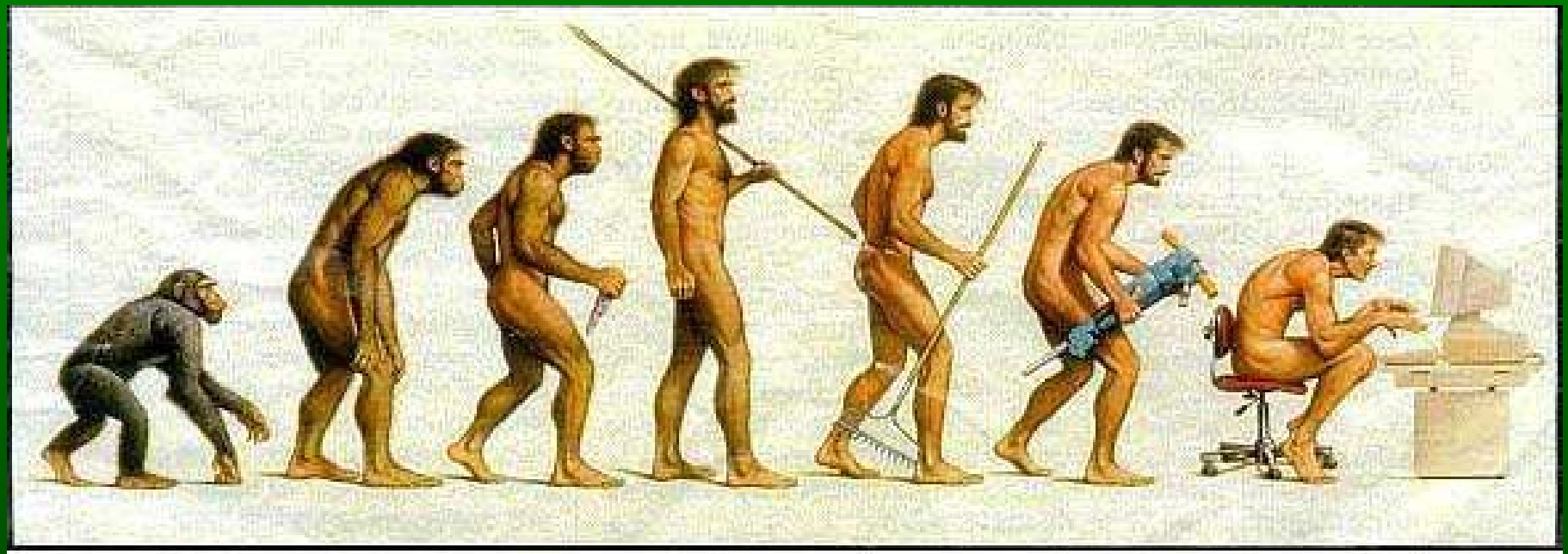
Table 17.2 Comparison of *E. coli* and its primate host species[a]

Property	*E. coli*	*Homo sapiens*	Primates
Mol % G + C	48–52	42	42[b]
16S–18S rRNA variability	>15 bases	?	<16[c]
DNA/DNA reassociation	>70%	98.6%[d]	>70%[e]

[a]Adapted from J. T. Staley, *ASM News*, 1999.
[b]Value for all primates.
[c]Mouse 18S rRNA differs from humans by 16 bases.
[d]Comparison between *Homo sapiens* and chimpanzee.
[e]Comparison between *Homo sapiens* and lemurs.

Key Concepts

- Ultimately, species concepts are human artifacts
  - Methods for recognizing species continue to improve



Somewhere, something went terribly wrong