

Speciation



These are members of different species – eastern (left) and western (right) meadowlark.

Speciation

- The process by which one genetically-cohesive population splits into two or more reproductively-isolated populations.
- Requires the disruption of gene flow and the evolution of *reproductive isolating mechanisms*.

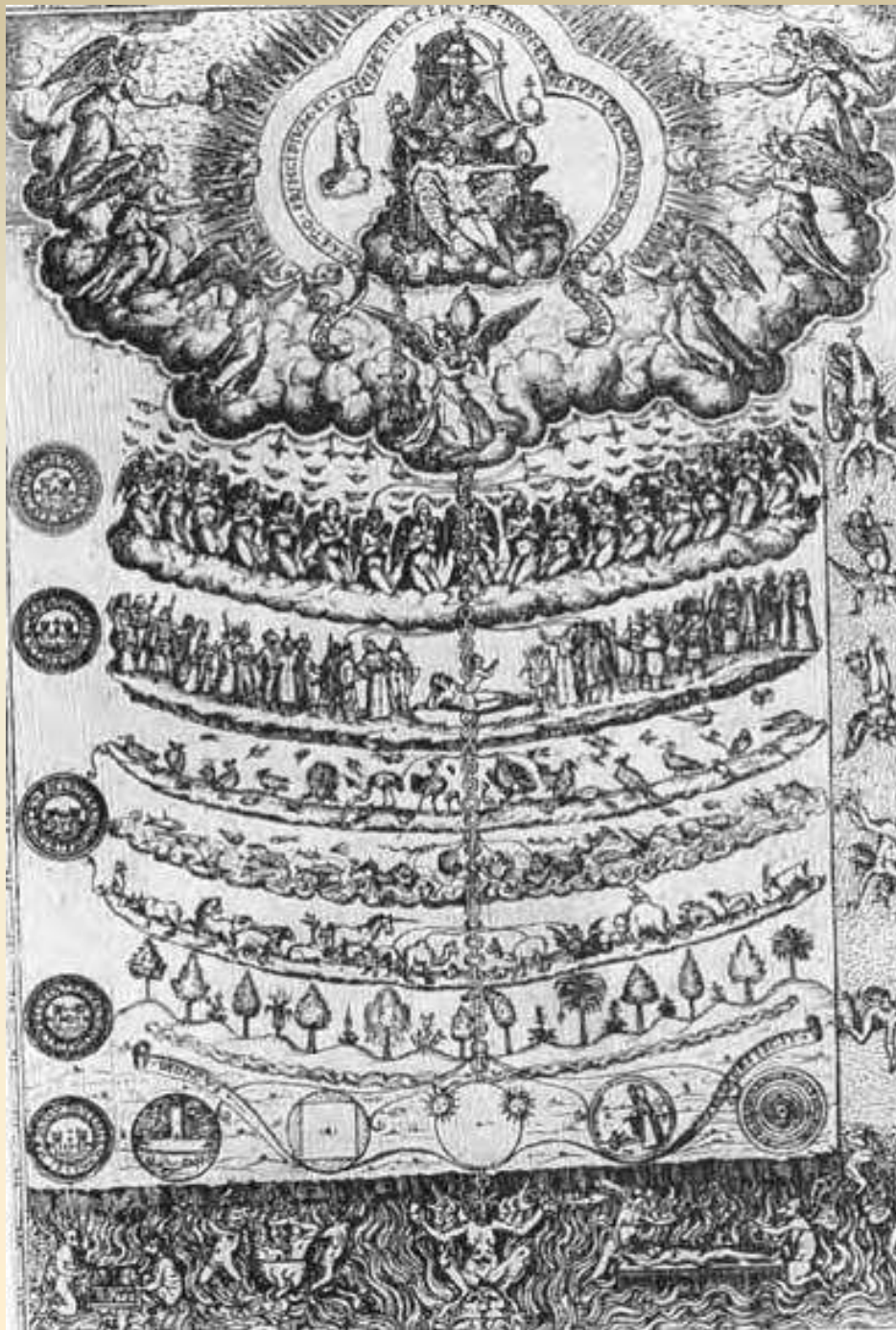


Plato (c. 427 BC – c. 347 BC)

- immensely influential classical Greek philosopher, mathematician,
- student of Socrates, teacher of Aristotle,
- writer of philosophical dialogues, and founder of the Academy in Athens.
- Along with his mentor, Socrates, and his student, Aristotle, Plato helped to lay the foundations of Western philosophy and science.

Plato's Idealism

- The observable world is no more than a shadowy reflection of underlying ideal forms.
- The ideals are true and eternal, more real than what we see with the senses.
- Triangle Example – no matter what the angles are, it remains a triangle
- Became basis for **Essentialism**, the search for eternal “ideal forms” in objects and animals.
- He had little use for observations of natural history, and his emphasis on the soul permitted, through his followers, a connection with later Christian dogma which dominated the thinking of western society up to the 17th century.

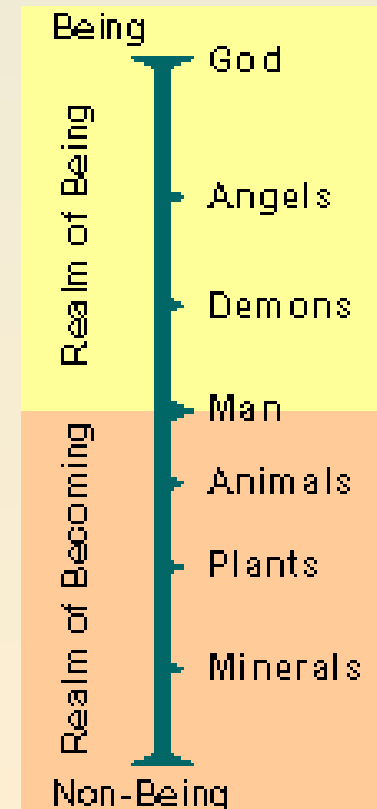


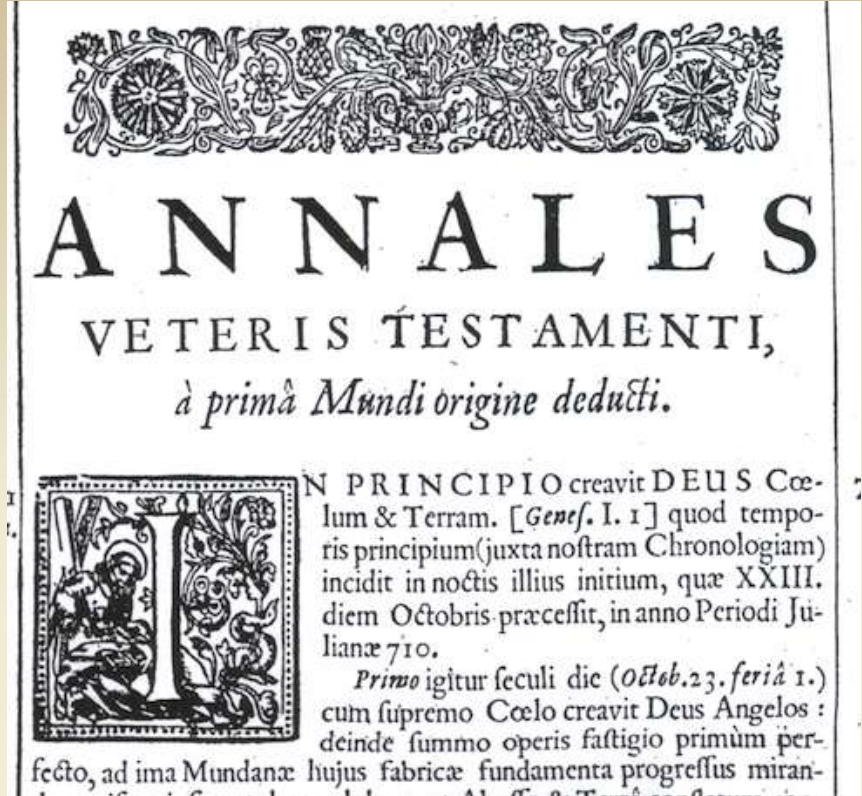
Great Chain of Being

1579, Didacus Valades,

Rhetorica Christiana

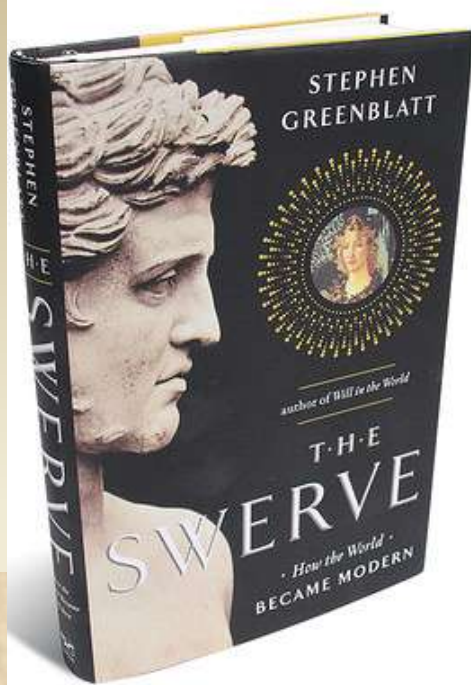
hierarchical structure of all matter and life, believed to have been decreed by God





Bishop Ussher, *Annalium pars postierior*, 1654. – following a strict interpretation of the Bible the **exact moment of Creation was calculated on Sunday, October 23, 4004 B.C.**

This was believed to be true for centuries, and may still be held as true by some.



- Renaissance humanists such as **Poggio Bracciolini** (1380-1459) sought out in Europe's monastic libraries the Latin literary, historical, and oratorical texts of Antiquity.
- Rediscovered work of Lucretius and Epicurus, offered a powerful alternative to church doctrines.
- **Epicurus**, building on the foundation laid by Democritus, believed everything is made of unchanging atoms which whirl about and collide at random. He established a well thought-out materialistic explanation of the inanimate and living world, **all things happening through natural causes.**



Thomas Jefferson Epicurean





Carolus Linnaeus

1707 - 1778

Tried to name and classify all organism

Binomial nomenclature

Species Plantarum - 1753

System of Classification

“Sexual System”

Classes - number of stamens

Orders - number of pistils

Linnaean Hierarchy

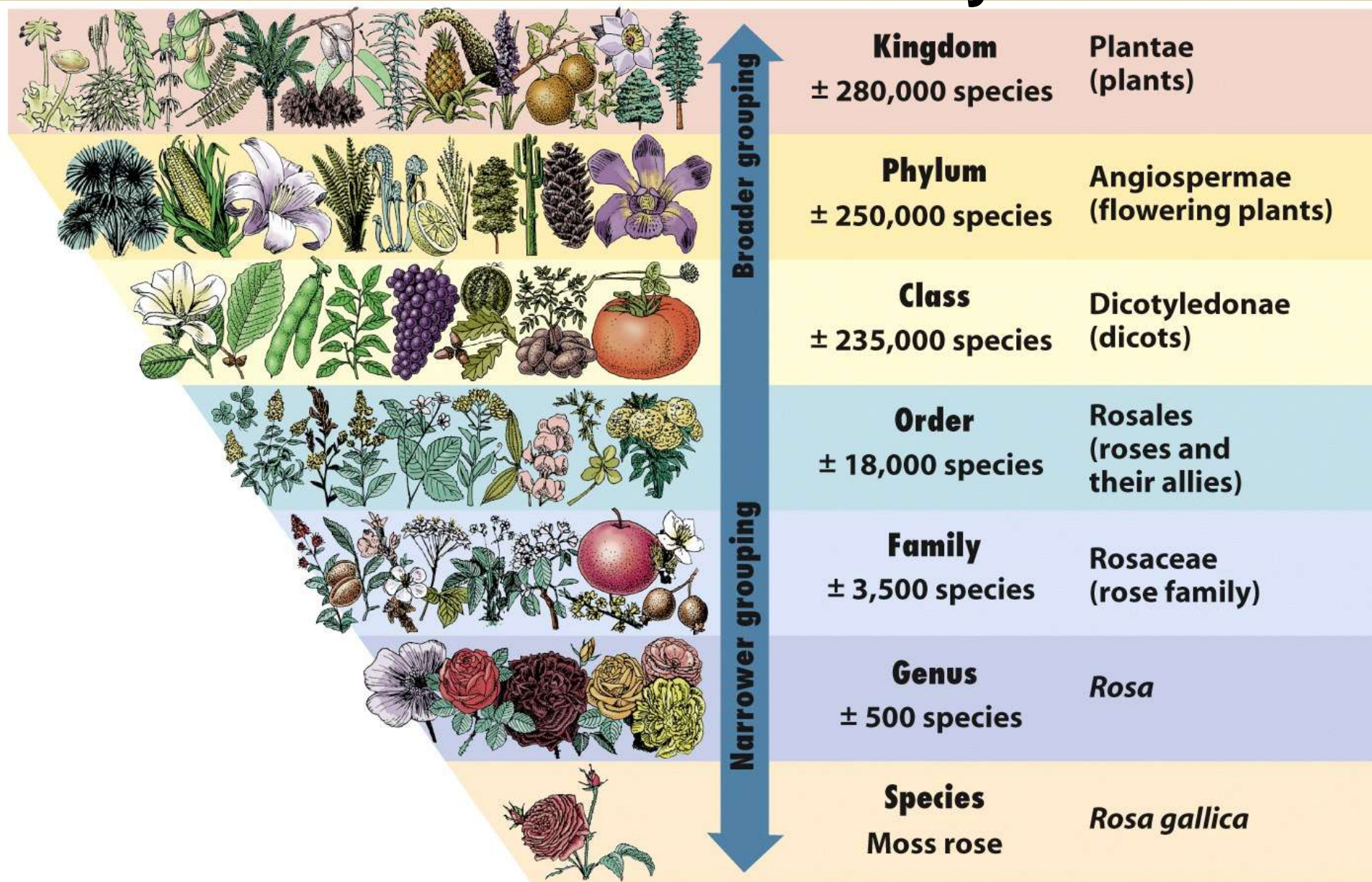
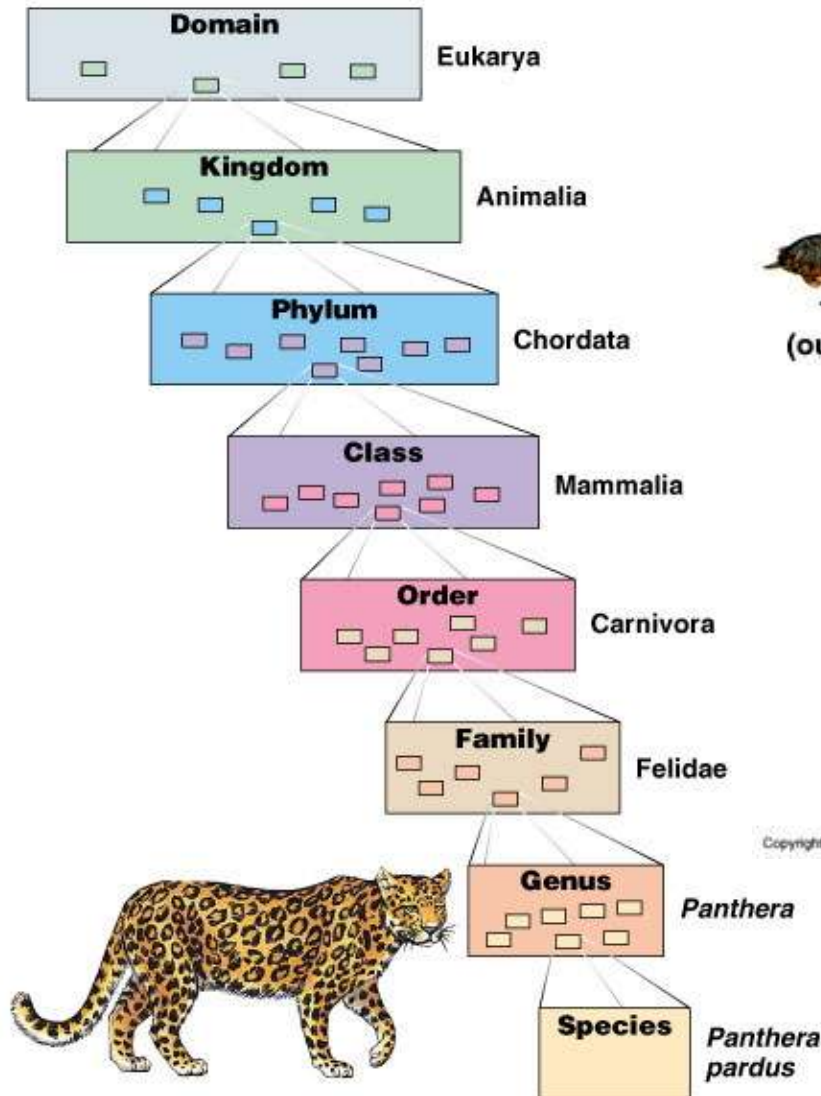


Figure 2-6 Discover Biology 3/e
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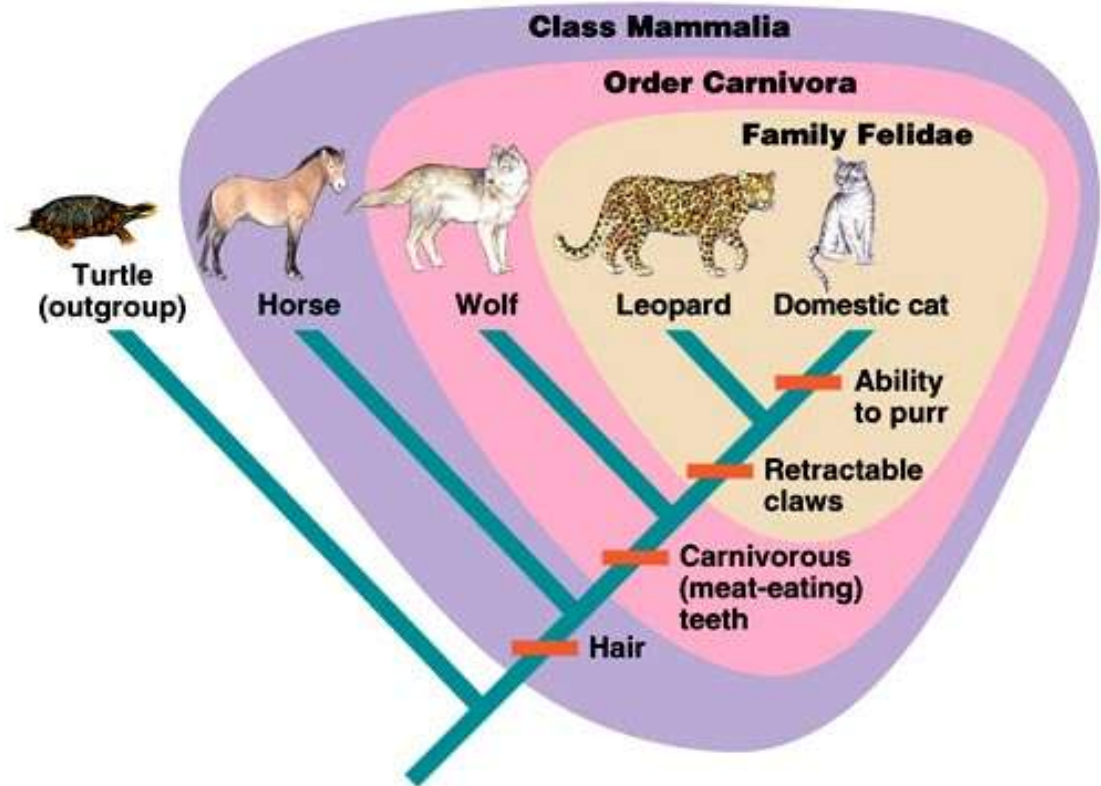
Classification

- Organisms are classified into a hierarchical classification that groups closely related organisms and progressively includes more and more organisms.
- Binomial Nomenclature. Each species can have only one scientific name. Priority of names.

Nested box-within-box hierarchy is consistent with descent from a common ancestor, used as evidence by Darwin.



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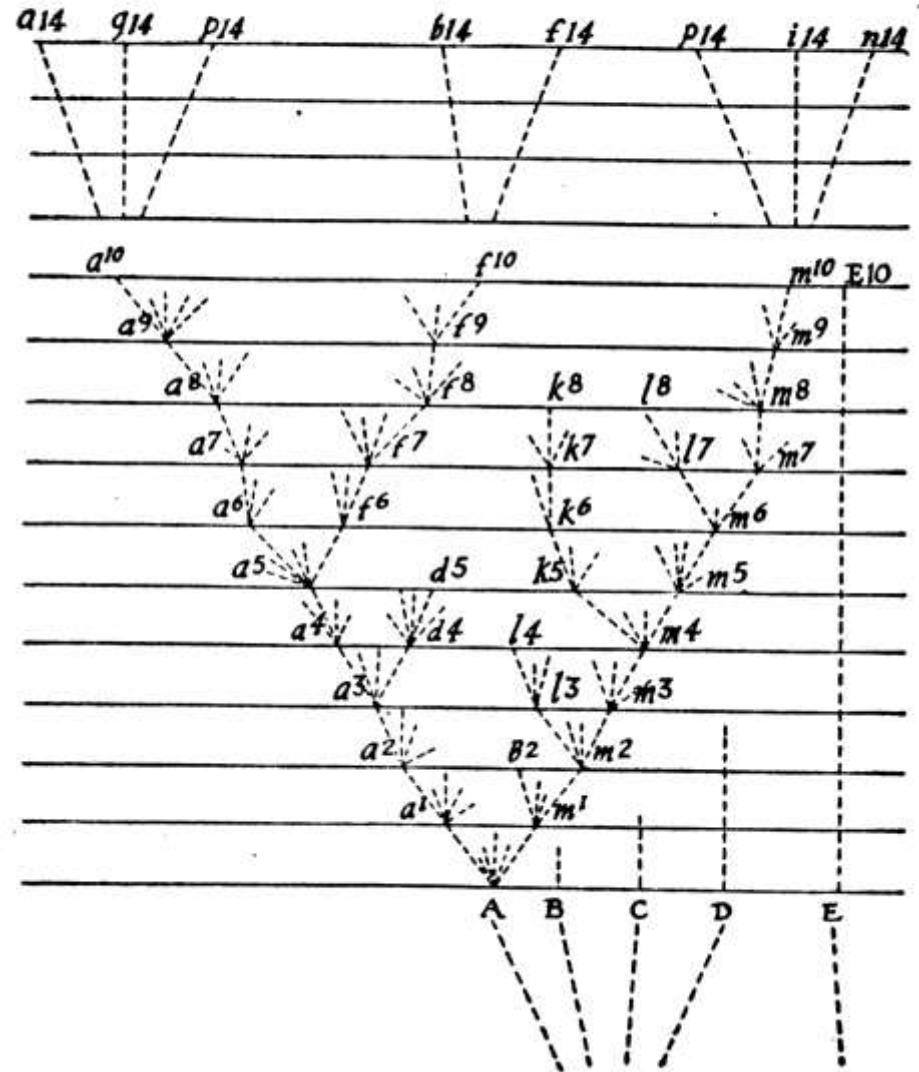
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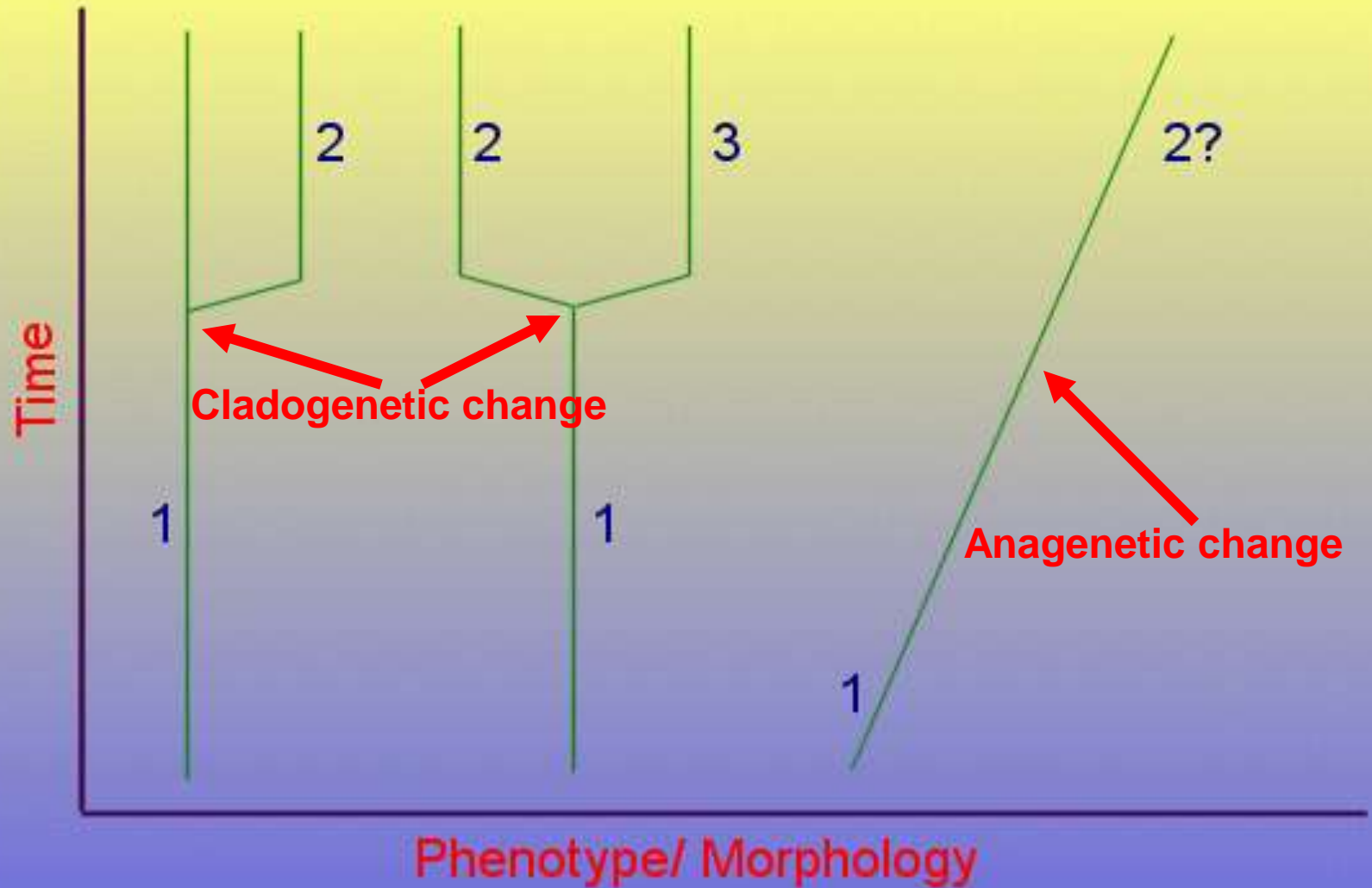


Charles Darwin 1859

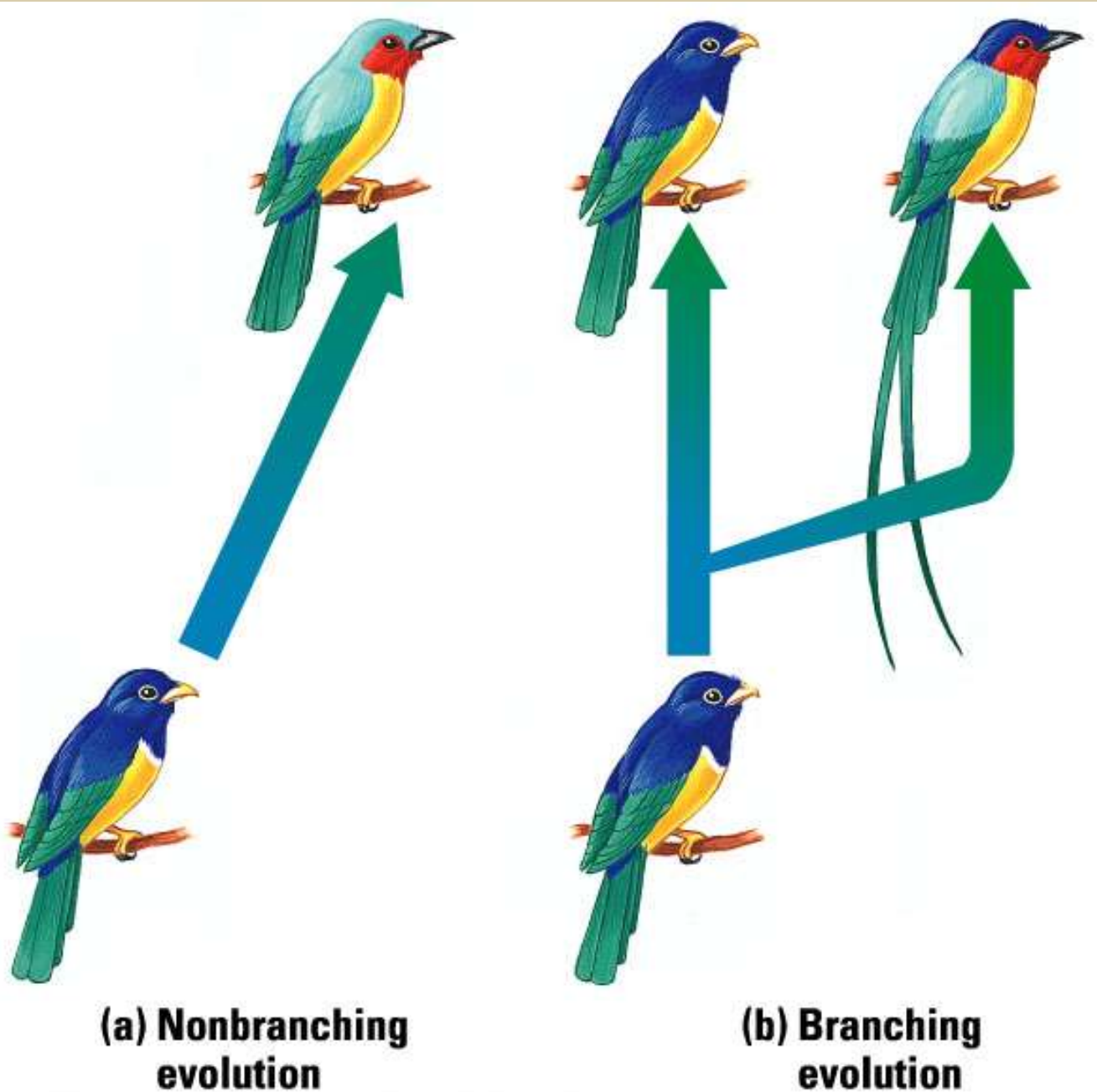
- Origin of Species by Natural Selection, or the Preservation of Favored Races in the Struggle for Life
- Descent from Common Ancestor

THE ORIGIN OF SPECIES





Two Patterns of Speciation



What is a Species?

“I look at the term species as one arbitrarily given, for the sake of convenience, to a group of organisms resembling each other.”

Charles Darwin. 1859. *The Origin of Species by Means of Natural Selection*.



What is a Species?

Certainly no clear line of demarcation has yet been drawn between species and sub-species – that is, the forms *which...come very near to, but do not quite arrive at, the rank of species*. ...A well-marked variety may therefore be called an *incipient species*. ...From these remarks it will be seen that I look at the term species as one arbitrarily given.

Darwin, *The Origin of Species*

Why do we see discrete species?

- Because intermediate forms between closely related organisms are usually selected against.
- If they were not selected against, then the two forms would merge into one as their gene pools mixed.

Species

- The species is the basic biological unit around which classifications are based.
- However, what constitutes a species can be difficult to define and there are multiple definitions of species in use today.

Species Concepts

Table 15.1 The biological species concept and some recently proposed alternatives

(Futuyma 1997)

BIOLOGICAL SPECIES CONCEPT A species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both). (Dobzhansky 1935)

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 ancestral-descendant sequence) of populations or organisms that maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. (Wiley 1978)

PHYLOGENETIC SPECIES CONCEPTS 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)

A species is the smallest monophyletic group of common ancestry. (de Queiroz and Donoghue 1990)

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)

ECOLOGICAL SPECIES CONCEPT A species is a lineage (or a closely related set of lineages) that occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range. (Van Valen 1976)

INTERNODAL SPECIES CONCEPT Individual organisms are conspecific by virtue of their common membership in a part of the genealogical network between two permanent splitting events or between a permanent split and an extinction event. (Kornet 1993)

Source: Coyne (1994).

Species Concepts

There are many difficulties associated with the definition of “species.”

Definitions that work well for some groups of organisms do not necessarily work for other organisms (**extant** versus **fossil** species).

Some species concepts take evolution into account and attempt to address problems that are associated with a species being an **evolving** rather than an **immutable** biological entity.

Morpho-species Concept

Oldest, intuitive, concept. Used by Linnaeus
Analysis of phenotypic differences.

Look for characters with discontinuous
variation.

Widely adaptable. Can be used for living or
extinct species, and in organisms that
reproduce sexually and asexually.

Problem is that it can be applied arbitrarily and
is idiosyncratic (up to individual decision).

Species are sometimes in conflict with each
other.

Morphological (or Phenetic) Species Concept (MSC):

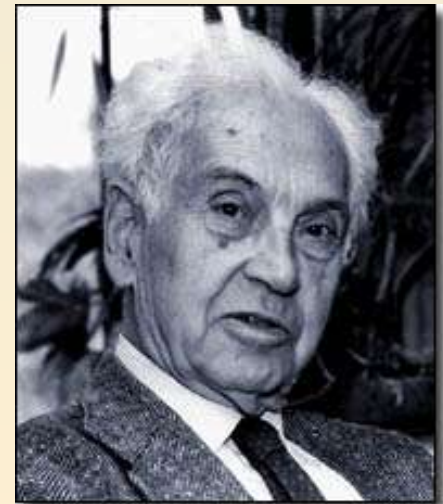
A species is a group of organisms that resemble one another and are distinct from other such sets

Biological Species Concept

“Species are groups of actually or potentially **interbreeding populations that are reproductively isolated from other such groups.”**

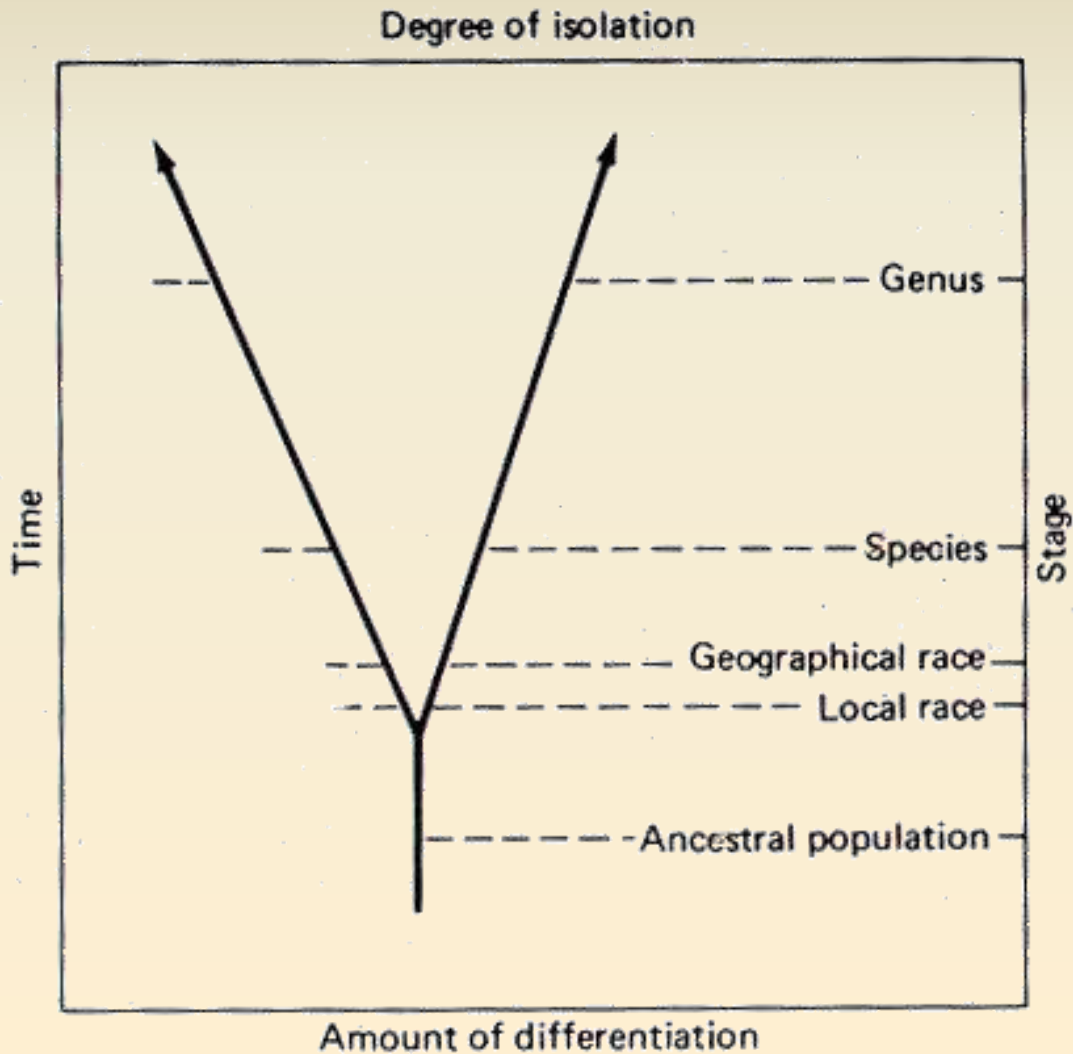
E. Mayr (1942)

Main criterion is reproduction.



Ernst Mayr

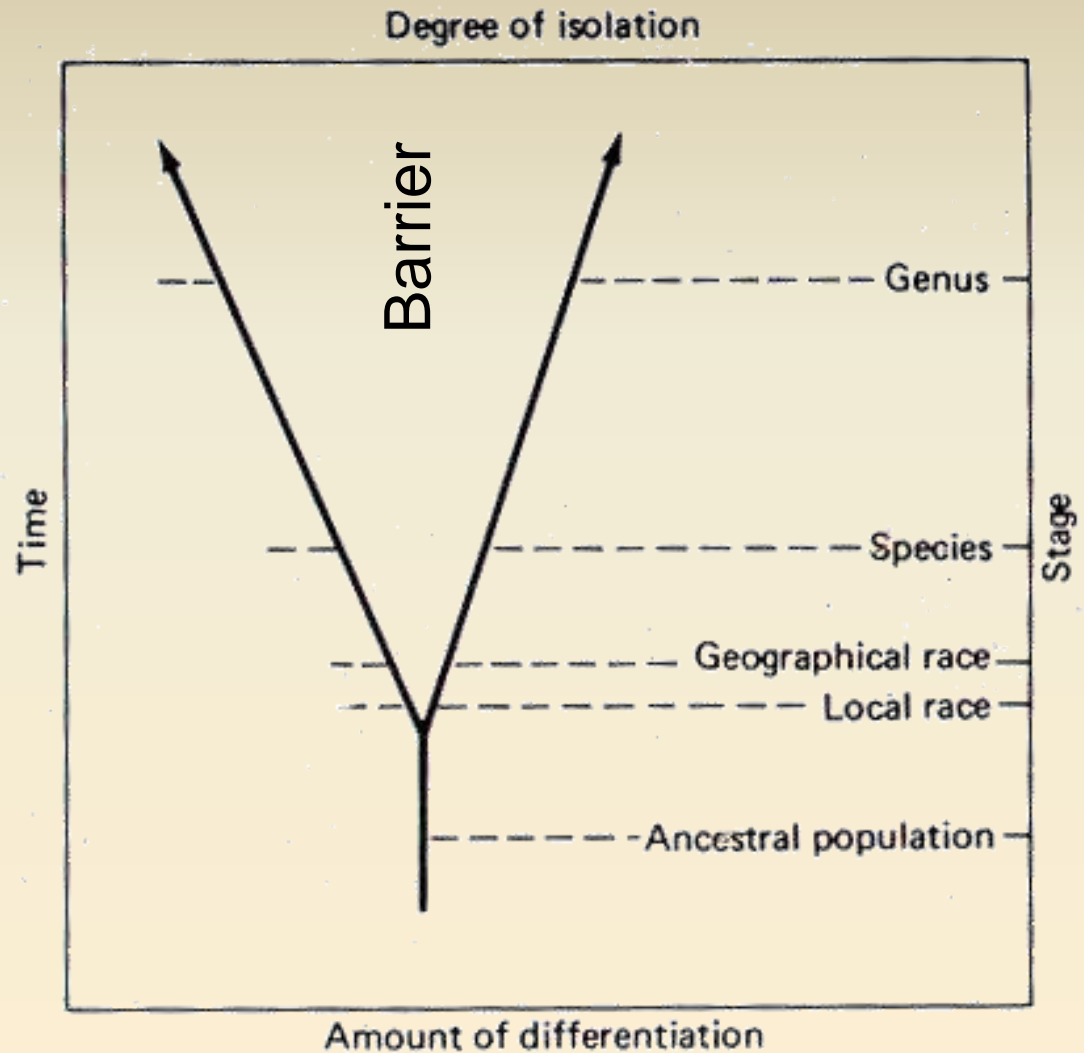
Investigated the question of how species originate ,and importance of geographical isolation



Ernst Mayr

“Every population of a species differs from all others. The degree of difference between populations of a species ranges from almost complete identity to distinctness almost of species level”

Ernst Mayr



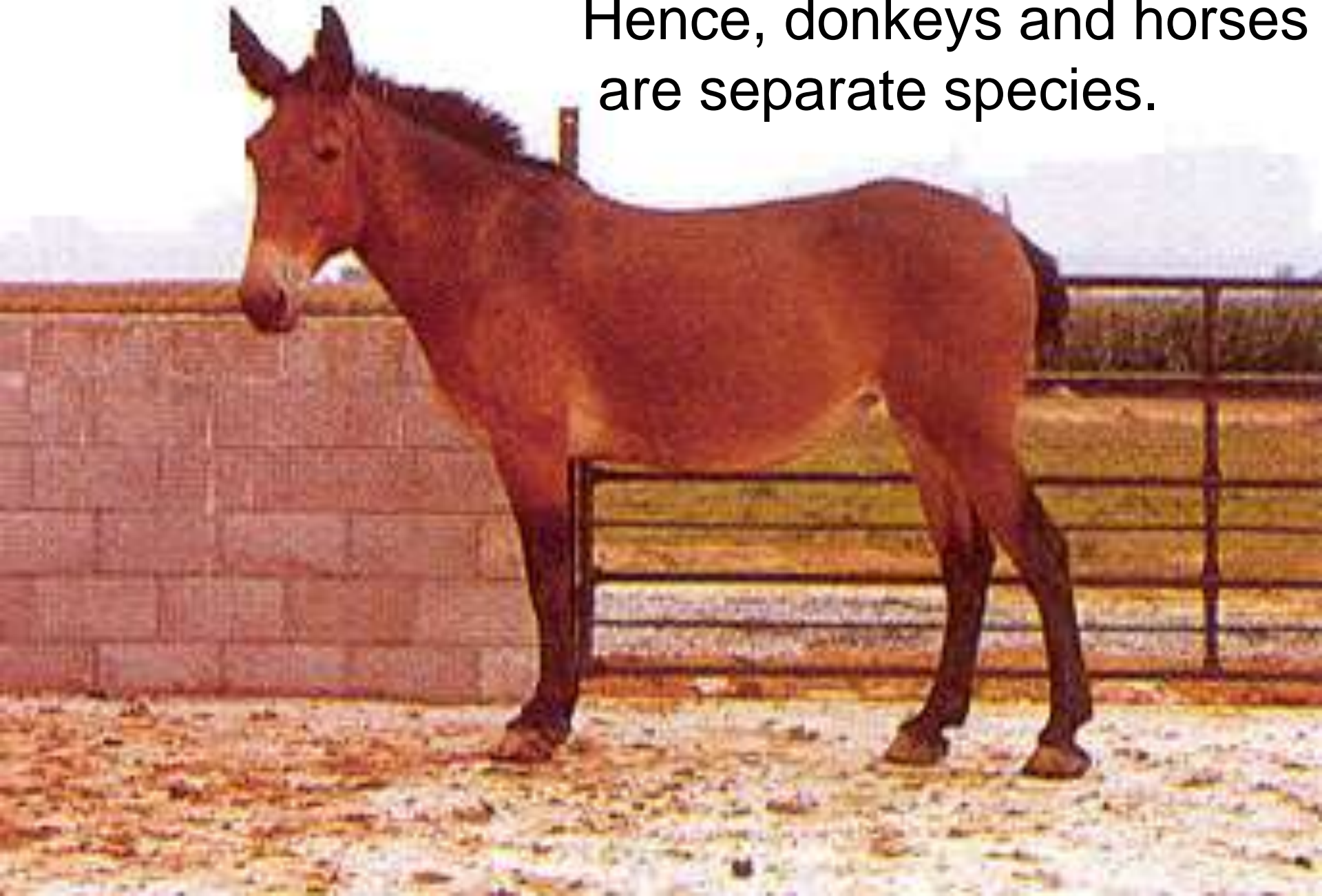
A biological concept of a species is a population or group of populations that are able to *interbreed*, under *natural conditions* to produce *fertile offspring*.

According to the BSC, speciation occurs when populations evolve **reproductive isolating mechanisms**.

A female donkey mated to a male horse produces what?



A mule (which is sterile)
Hence, donkeys and horses
are separate species.





The Western meadowlark (left) and the Eastern meadowlark (right) appear to be identical, and their ranges overlap, but their distinct songs prevent interbreeding.



**Black-capped
Chickadee**

Carolina Chickadee

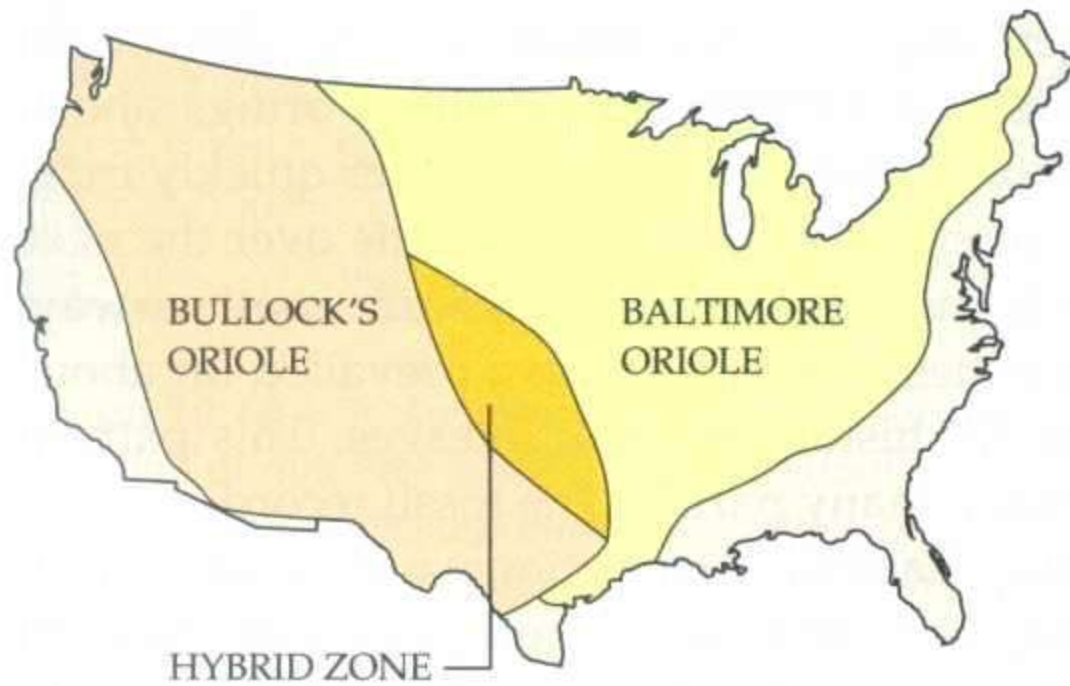




BULLOCK'S ORIOLE



BALTIMORE ORIOLE



Criticisms of the Biological Species Concept

1. It applies only to sexually reproducing species.
2. It can be difficult to determine how much reproductive separation is needed to distinguish between species. Hybridization is common
3. When ranges are nonoverlapping, reproductive isolation cannot be tested.
4. Fossils (cannot test reproduction).
5. The definition refers only to current populations and ignores the species status of ancestral populations.

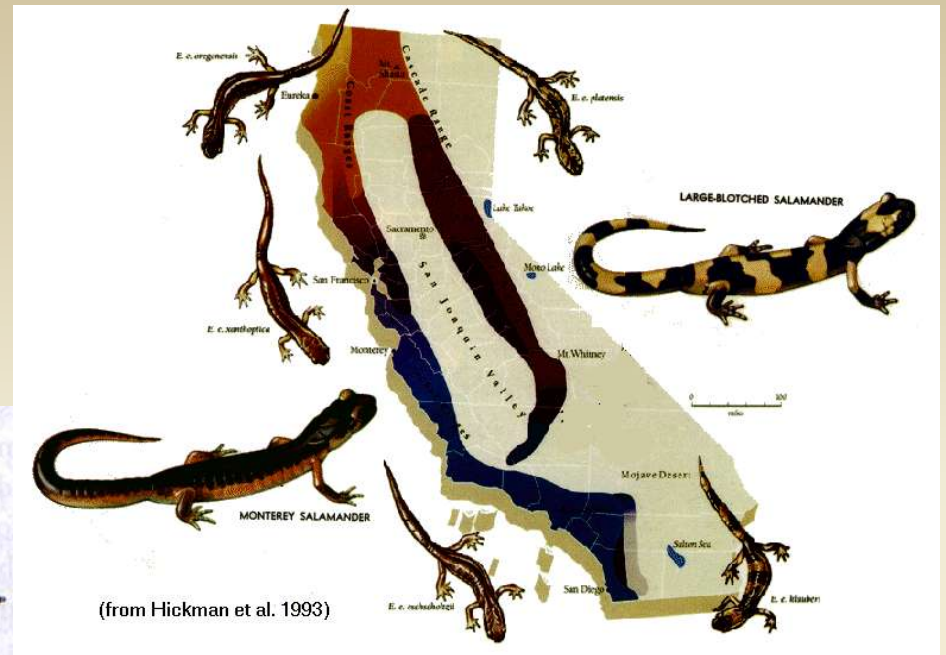
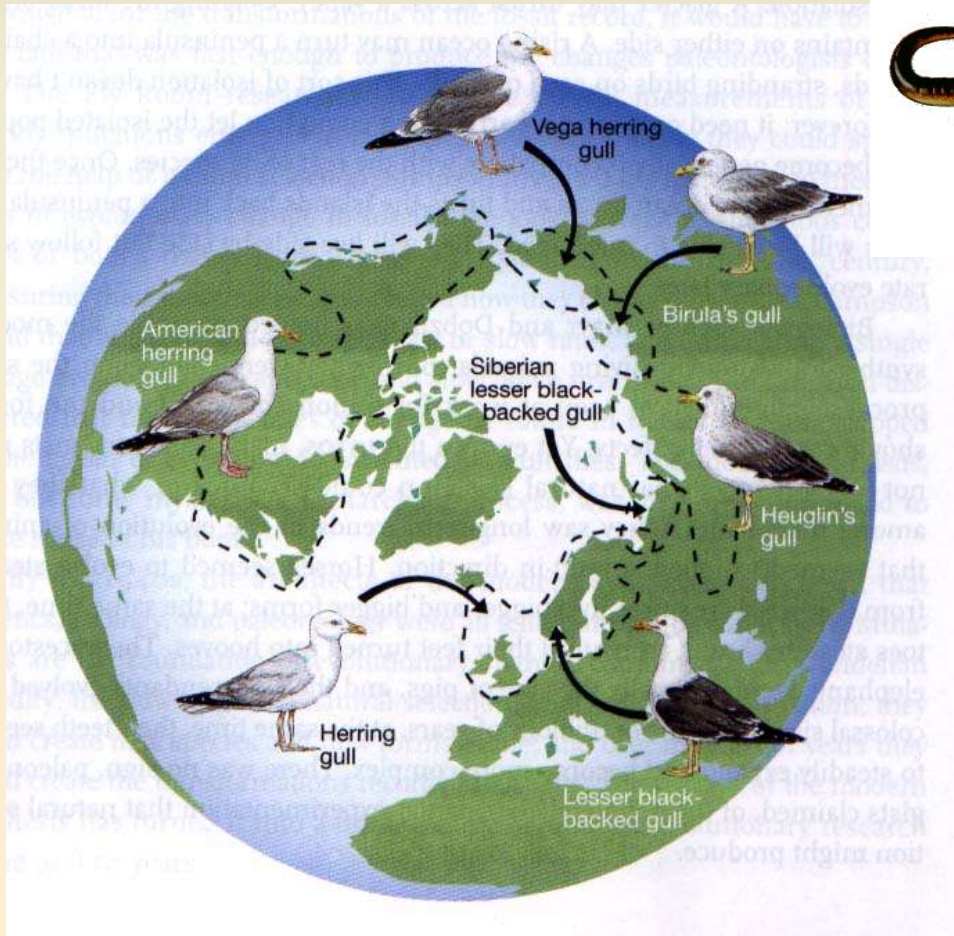
Problems with the Biological Species Concept

- Difficult to apply to fossils



- Asexual organisms don't fit the criteria

...and another
problem with the
Biological Species
Concept...



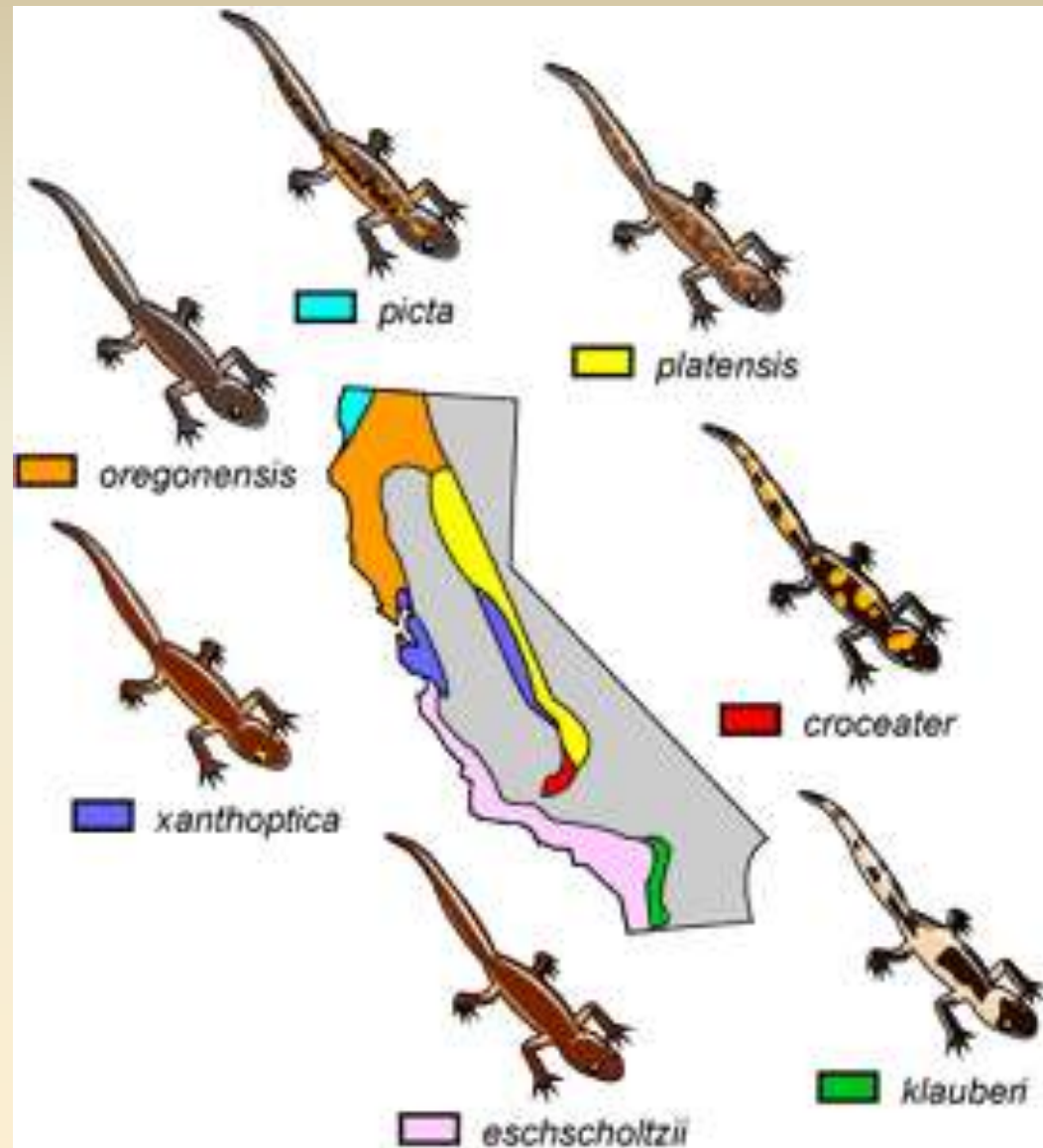
Where do you draw the line between different 'species'?

Ring species are species with a geographic distribution that forms a ring and overlaps at the ends.

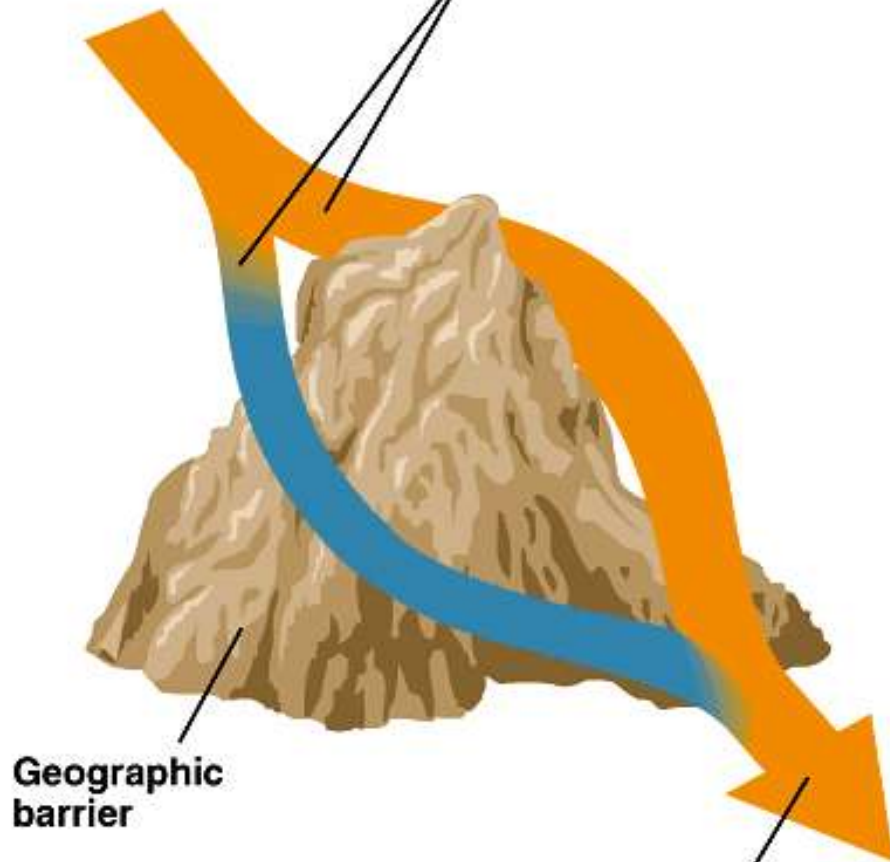
The many subspecies of *Ensatina* salamanders in California exhibit subtle morphological and genetic differences all along their range.

They all interbreed with their immediate neighbors with one exception: where the extreme ends of the range overlap in Southern California, *E. klauberi* and *E. eschscholtzii* do not interbreed.

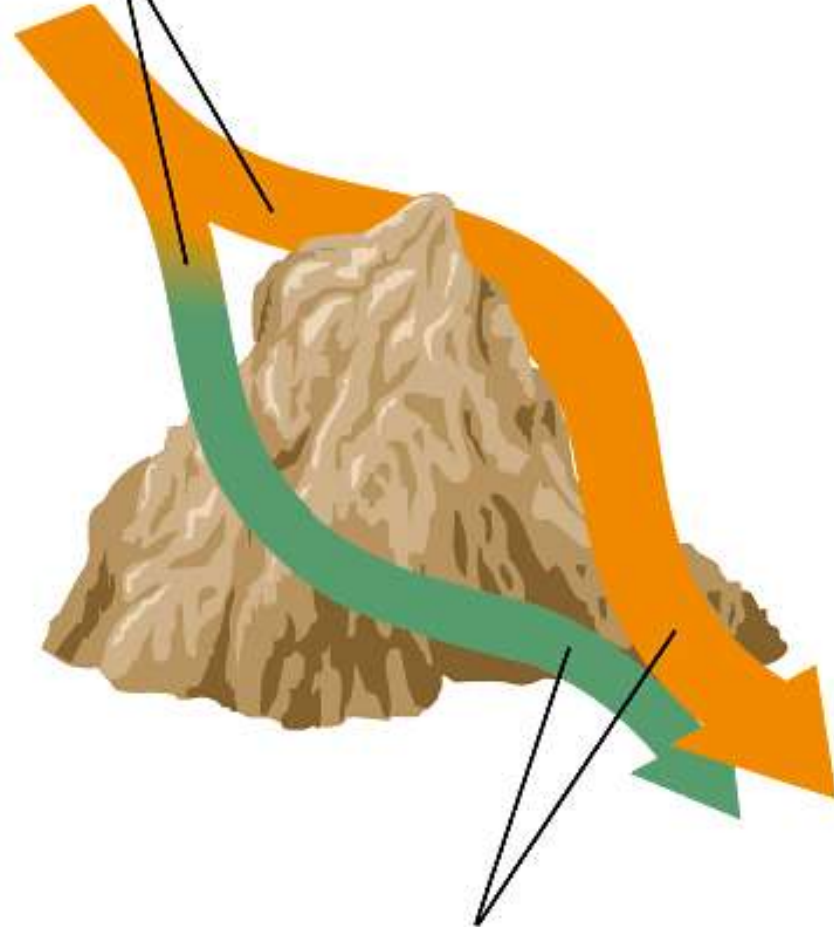
So where do we mark the point of speciation?



The populations become allopatric



**Populations become sympatric again and interbreed.
Speciation has not occurred.**



**Populations become sympatric again but do not interbreed.
Speciation has occurred.**

Platanus



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P. occidentalis
SE USA



Platanus orientalis

M03048
mbleeker@euronet.nl

P. orientalis
SW Asia



P. acerifolia

Phylogenetic Species Concept

Uses monophyly as the criterion to distinguish species.

Monophyletic Group – lineages that contain all the known descendants of a common ancestor.

Species are defined by determining a phylogeny and finding the smallest phylogenetic groups.

Traits can be used to determine species only if they have been isolated in terms of gene flow and have diverged genetically.

Populations must have been separate long enough for the trait to evolve.

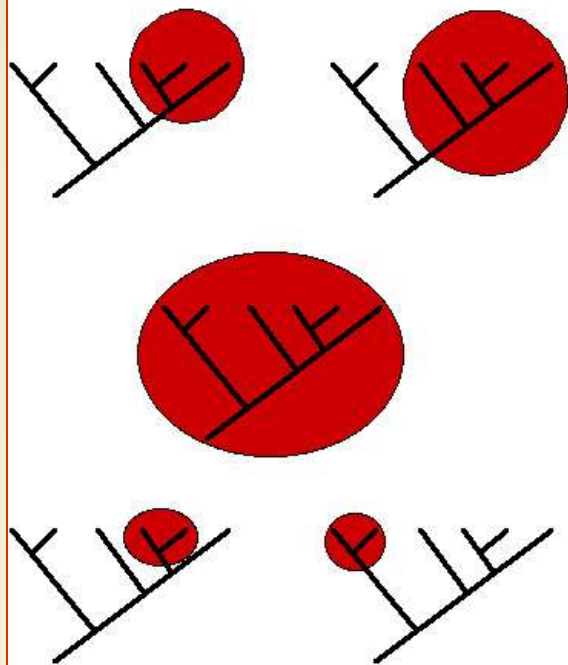
Phylogenetic Species Concept:

An irreducible cluster of organisms that is *diagnosably* distinct from other such clusters, and within which there is a parental pattern of ancestry and descent.

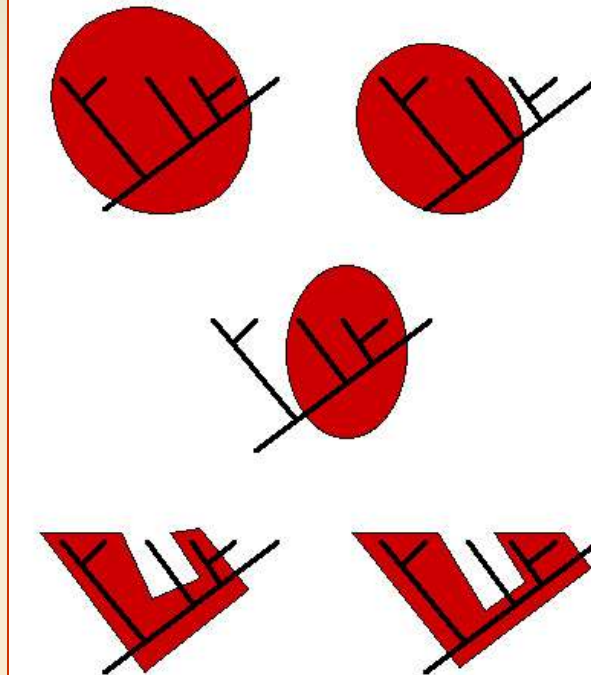
“Evolutionary Species” similar to PSC

An evolutionary species is a lineage (ancestor-descendant populations), evolving separately from other lineages.

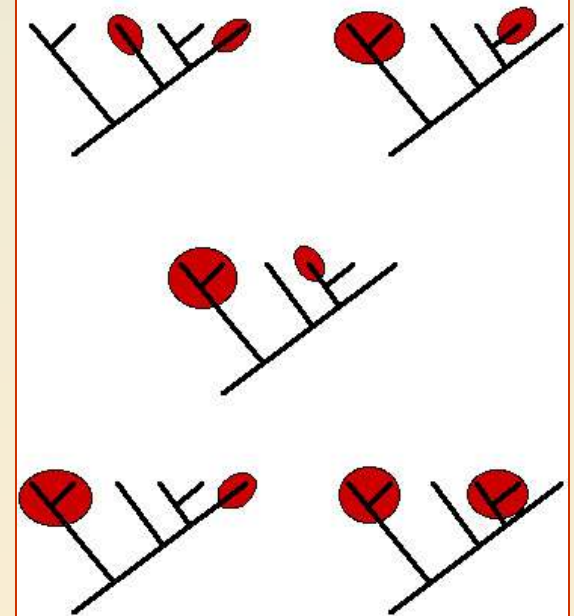
Monophyletic Groups



Paraphyletic Groups



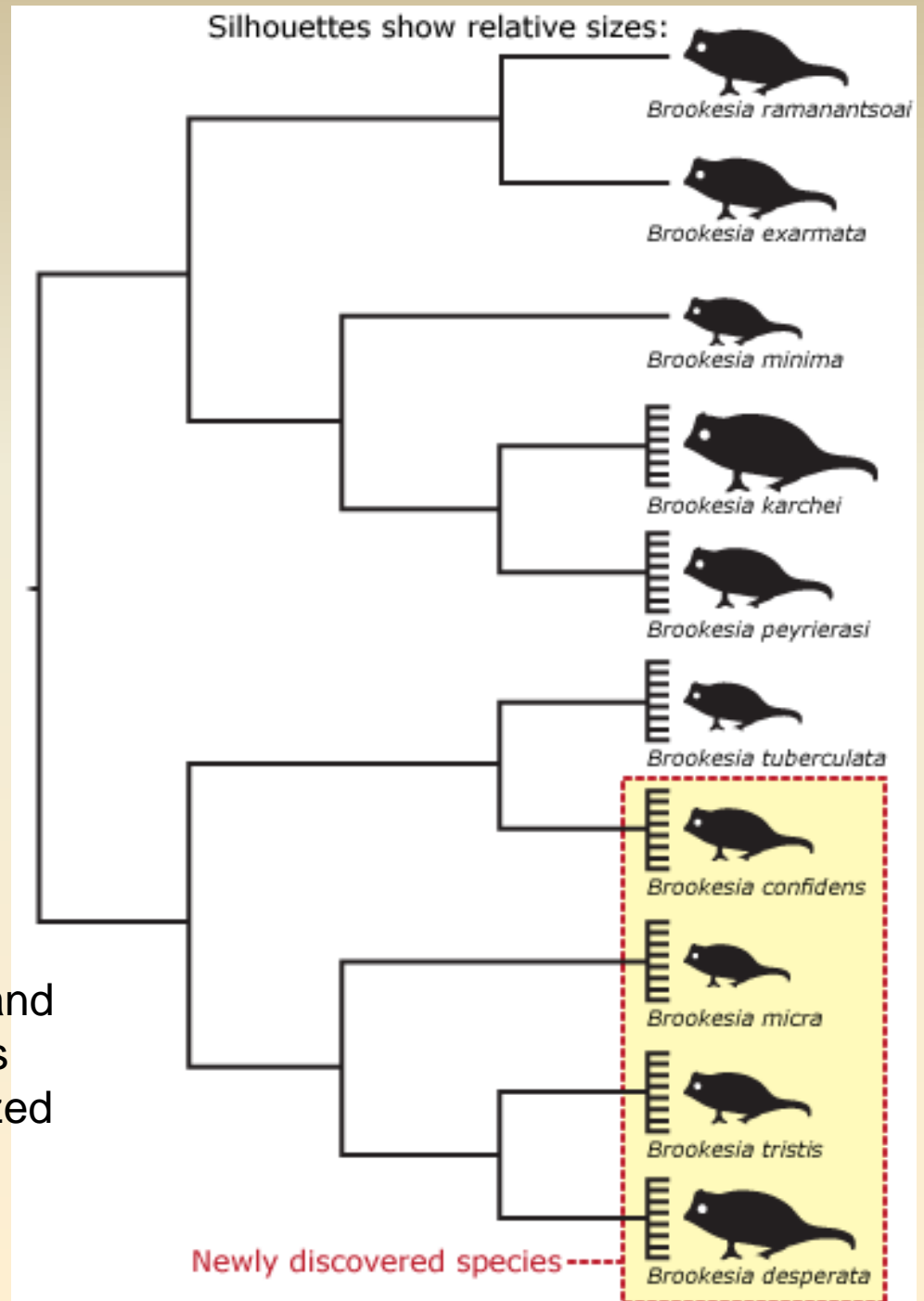
Polyphyletic Groups



Phylogenetic Species Concept

- The phylogenetic species concept emphasizes common descent and covers both sexually and asexually reproducing organisms.
- Under the PSC any population that has become separated and has undergone character evolution will be recognized as a species.

Brookesia species Chameleon Phylogeny



Glaw, F., Köhler, J., Townsend, T. M., and Vences, M. (2012). Rivaling the world's smallest reptile: discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar. *PLoS ONE*. 7: e31314

Phylogenetic Species Concept

Strengths

It contains a historical component.

It provides specific criteria that can be diagnosed in natural populations.

Testable

Sometimes reveals **Cryptic Species**

Weakness

It is somewhat vague. What exactly is meant by “irreducible cluster” and “diagnosably different”?

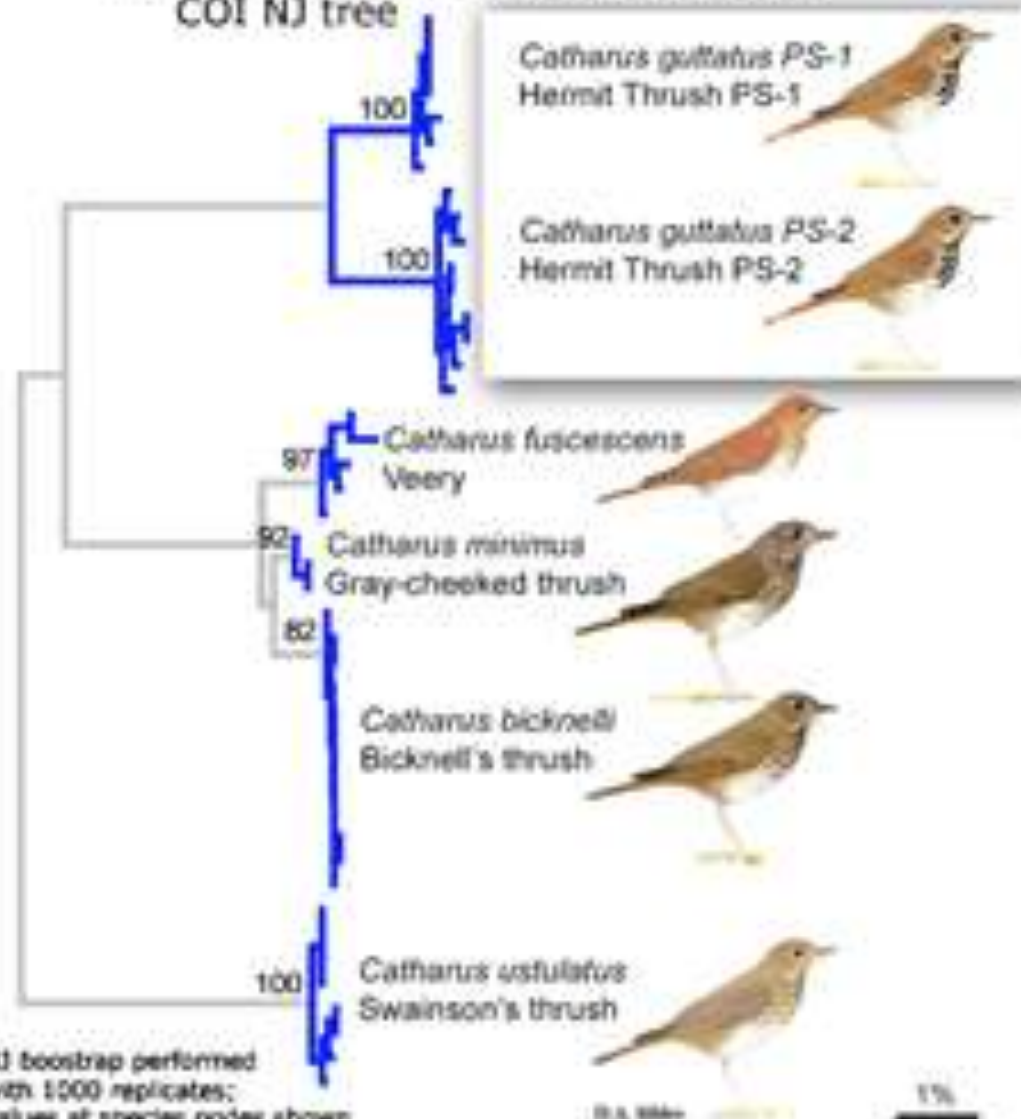
What traits do you use? Different information leads to different phylogenies

Taken literally and to the extreme, it is absurd.

COI barcodes reveal provisional new species even in well-studied groups.

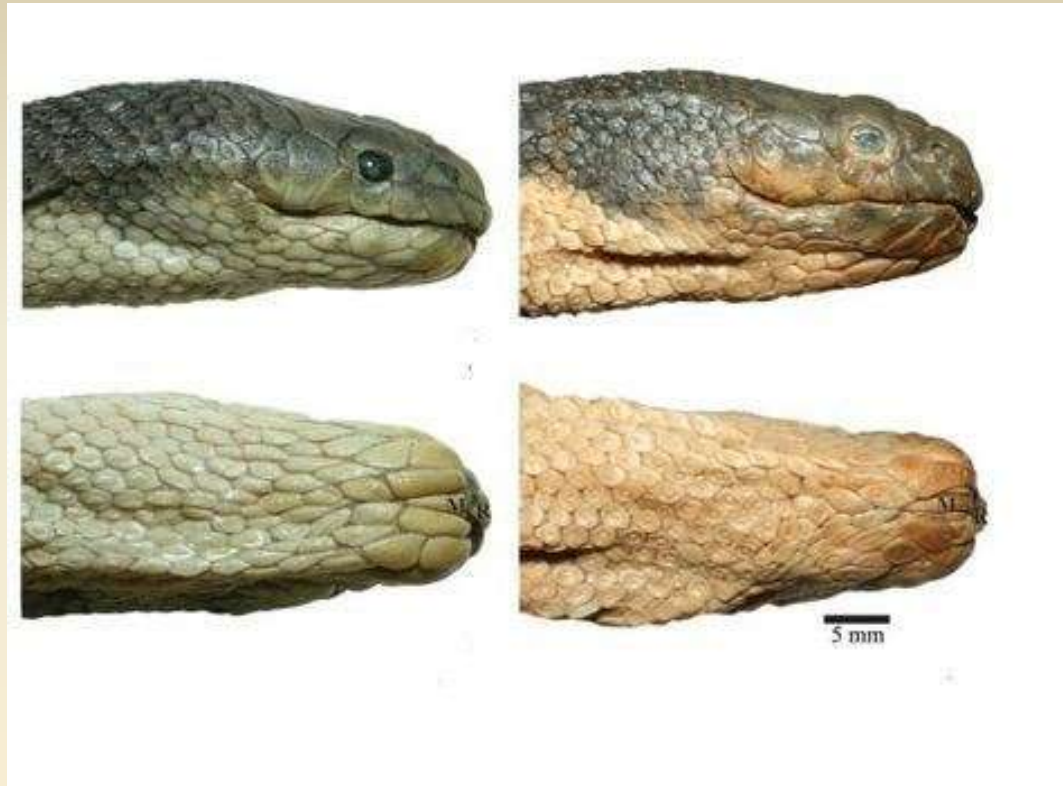
North American *Catharus* thrushes

COI NJ tree



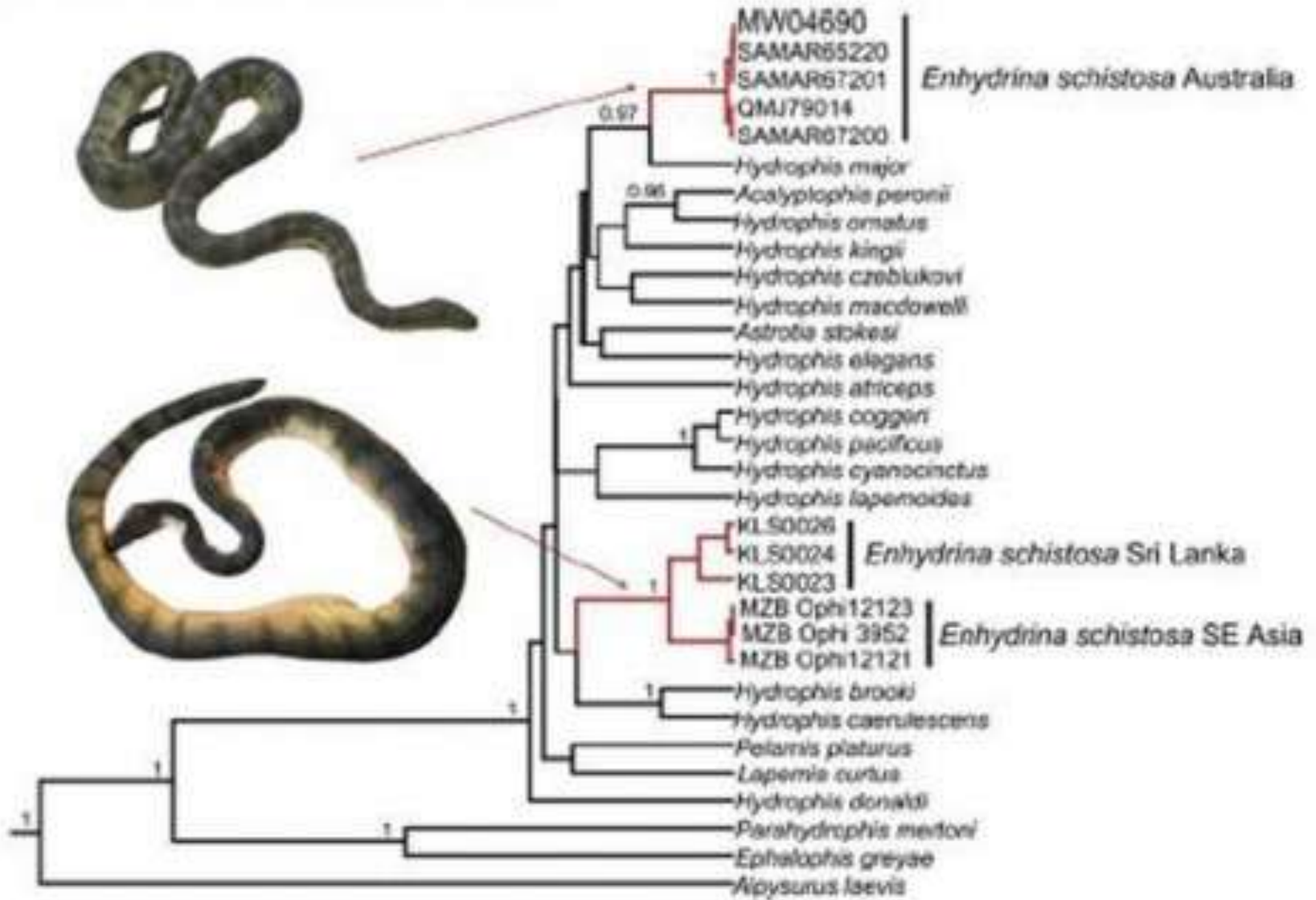
NJ bootstrap performed with 1000 replicates; values at species nodes shown

Cryptic Species – Sea Snakes



Scientists once thought that snakes in Australia and Asia were the same species, *Enhydrina schistosa*. The snakes from these regions do look similar, with beaklike mouths that have a notch between the lower jaws. However, when University of Queensland researcher Bryan Fry and colleagues tested the serpentine DNA, the results showed that they were separate species, and not even close relatives.

Cryptic Species – Sea Snakes



Bottom line:

The *Biological Species* concept is the major species concept used by modern biologists in practice.

However, an increasingly large group (of cladists) is applying the phylogenetic species concept (or a combination of PSC and BSC), particularly in regard to conservation genetics.

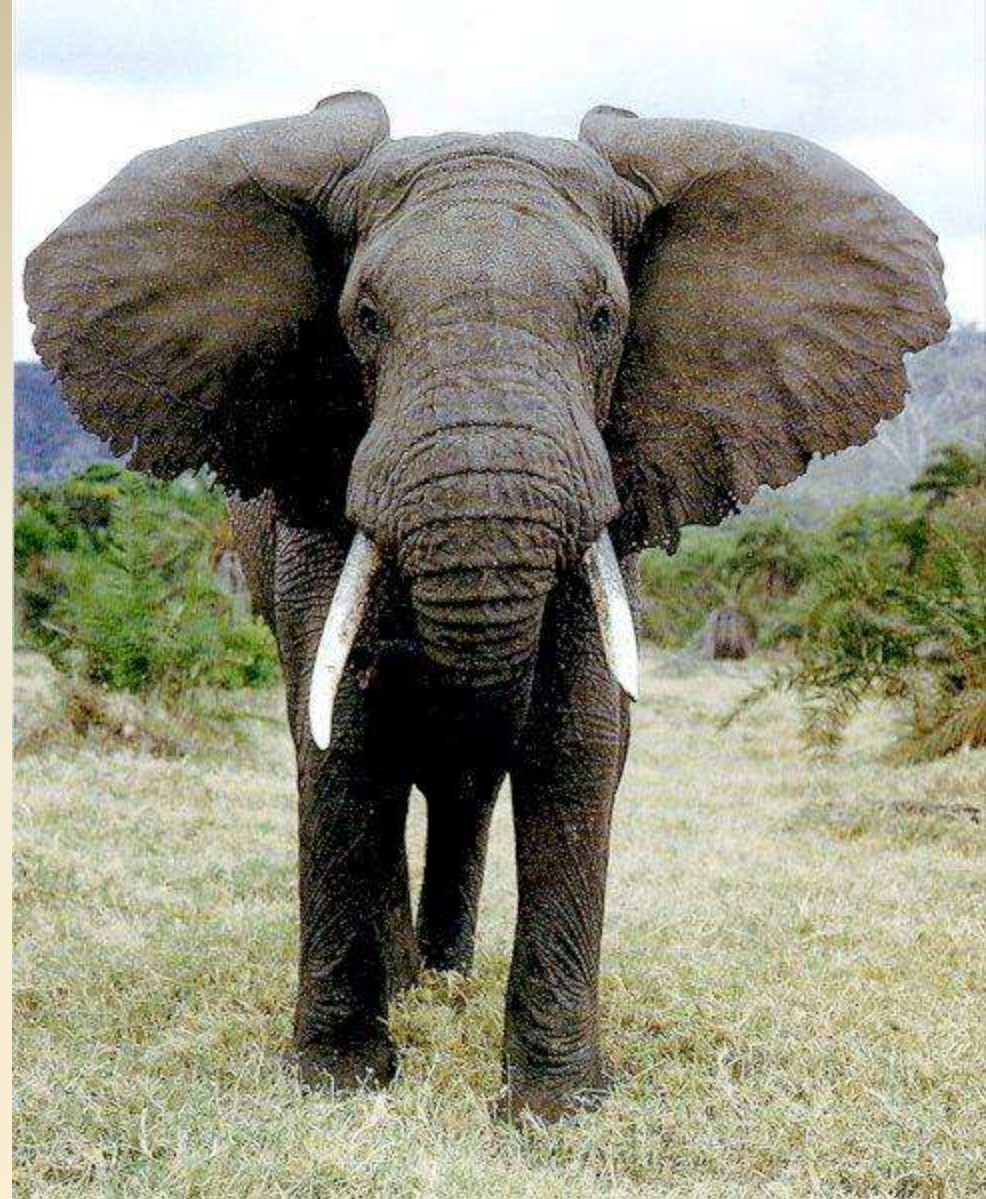
How many species of African elephants are there?

- Traditionally one species of elephant *Loxodonta africana* has been recognized in Africa (a second species *Elephas maximus* occurs in Asia).



Asian Elephant

http://en.wikipedia.org/wiki/Asian_elephant



African Elephant (Bush Elephant)

http://bioweb.uwlax.edu/bio203/s2007/shah_rach/

How many species of African elephants are there?

- However, recent morphological studies have pointed out that forest dwelling elephants in West Africa appear to differ from elephants found in Savannah habitats elsewhere on the continent (they are smaller).

Forest elephant

- Forest elephants are smaller (usually <8' at shoulder vs >10' for bush elephants), have a longer thinner mandible, straighter tusks and usually 5 front toenails and 4 rear toenails vs 4 front 3 rear of bush elephant).



http://en.wikipedia.org/wiki/File:Loxodonta_cyclotis_map.svg

African forest elephant

http://en.wikipedia.org/wiki/File:African_Forest_Elephant.jpg

How many species of African elephants are there?

- A comparison of DNA from 21 populations suggests that two phylogenetic species exist and it has been suggested by Roca et al. (2001) that forest elephants be named *Loxodonta cyclotis*.
- Whether the two populations are capable of interbreeding is unclear, but the clear genetic differences between populations suggest that conservation biologists should be attempting to conserve members of both populations.

Determining What Is and What Isn't a Distinct Species Can Have Economic Consequences

(a) Endangered species



(b) Not endangered



Northern spotted owl (left) and barred owl (right).



Key Features of Operational Species Concepts

- **Reproductive cohesion within species.**
- **Reproductive isolation from other such groups.**
- **Recognition that species are dynamic evolutionary lineages, not static “types”.**

U. S. ENDANGERED SPECIES ACT

- **Legal Definition: Species includes:** “any subspecies of fish or wildlife or plants, and any *distinct population segment* of any species of vertebrate fish or wildlife which interbreeds when mature.”
- **Operational Definition: Evolutionary Significant Units (ESU):**

“a population (or group of populations) that

 - 1) is reproductively isolated from other conspecific population units, and
 - 2) represents an important component in the evolutionary legacy of the species.”

OPERATIONAL SPECIES CONCEPTS PROVIDE A MEANS TO PROTECT:

- Individual populations
- Threatened portions of species ranges
- Ecologically distinct populations

Example: Separate runs of salmon



How Species Form

How species form

Classically, speciation has been viewed as a three stage process:

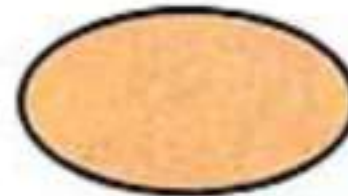
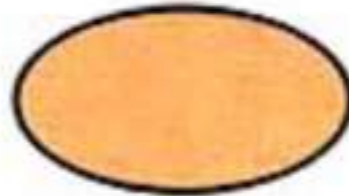
1. Isolation of populations.
2. Divergence in traits of separated populations (e.g. mating system or habitat use).
3. Reproductive isolation of populations that maintains isolation when populations come into contact again (secondary contact).

Other paths are possible

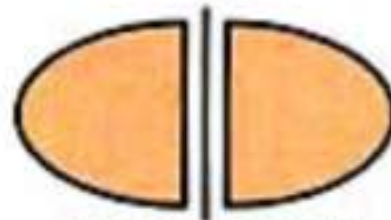
Allopatric speciation

Sympatric speciation

Original population



Initial step of speciation process

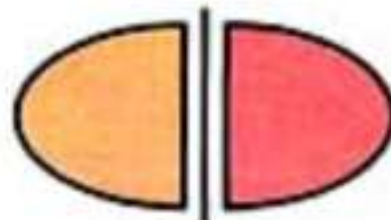


Barrier formed



Polymorphism occurs

Evolution of reproductive isolating mechanisms



In isolation



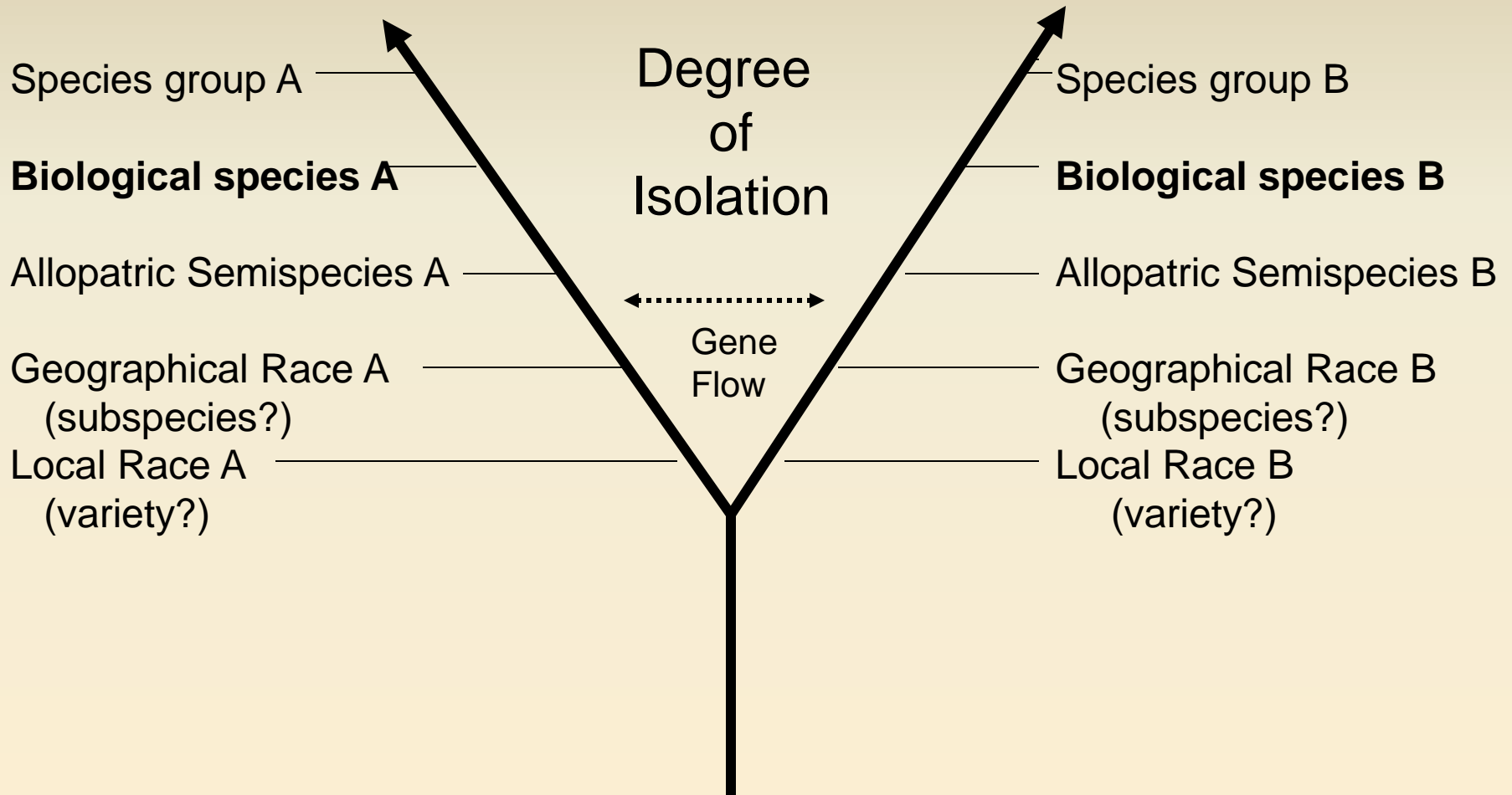
Within the population

Allopatric Speciation

- This is the essence of Ernst Mayr's allopatric model of speciation.
- A physical barrier isolates a population or populations from the rest of the species and selection favors genetic divergence of that population.

Stages in Divergence Leading to Biological Species

from V. Grant, 1981



Allopatric speciation

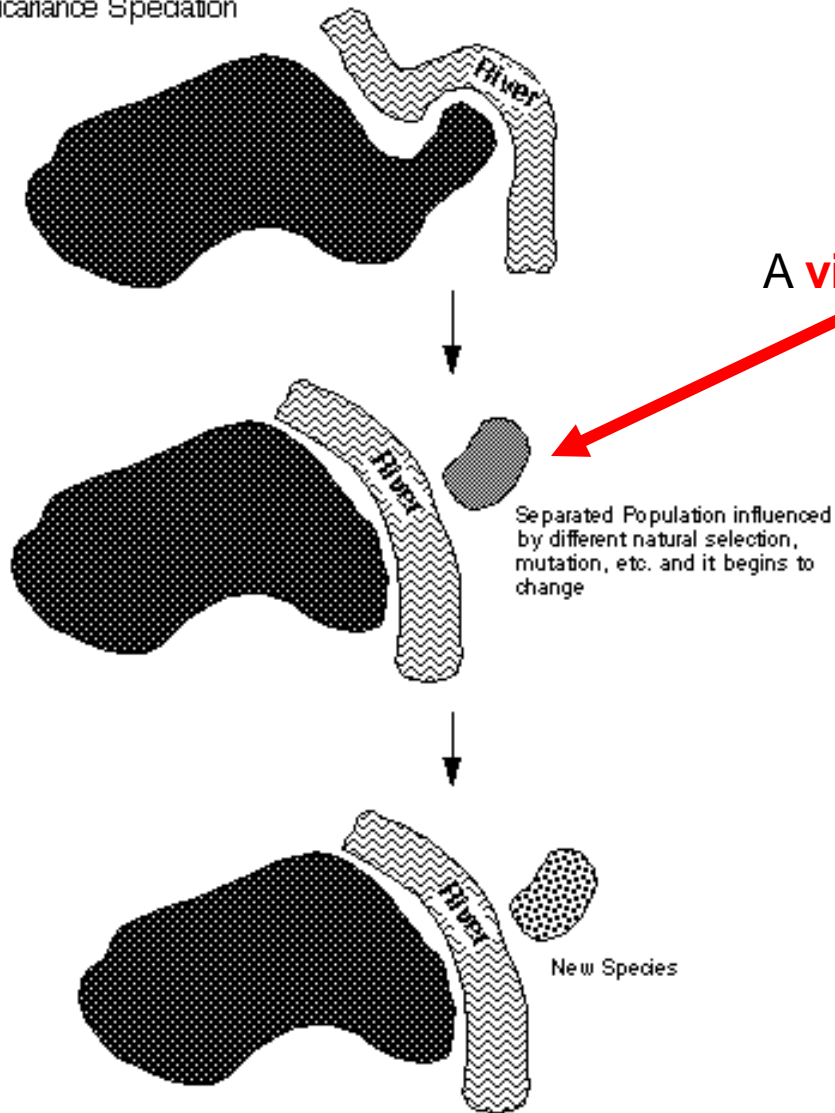
- Physical separation of populations can occur by two major means:
 - Dispersal of some individuals across a barrier.
 - Development of a new barrier that separates populations [**Vicariance**] (the vicariance event could be e.g. change in flow of a river, lava flow, development of a mountain range, habitat destruction)

Allopatric Speciation



The Kaibab squirrel (*Sciurus aberti kaibabensis*, left) became geographically isolated from the common ancestor with its closest relative, the Abert squirrel (*Sciurus aberti aberti*, right) in the North Rim of the Grand Canyon about 10,000 years ago. Since then, several distinguishing features, such as the black belly and forelimbs have gradually evolved.

Vicariance Speciation



A **vicariant** event

Allopatric Speciation

Harris' antelope squirrel



White-tailed antelope squirrel



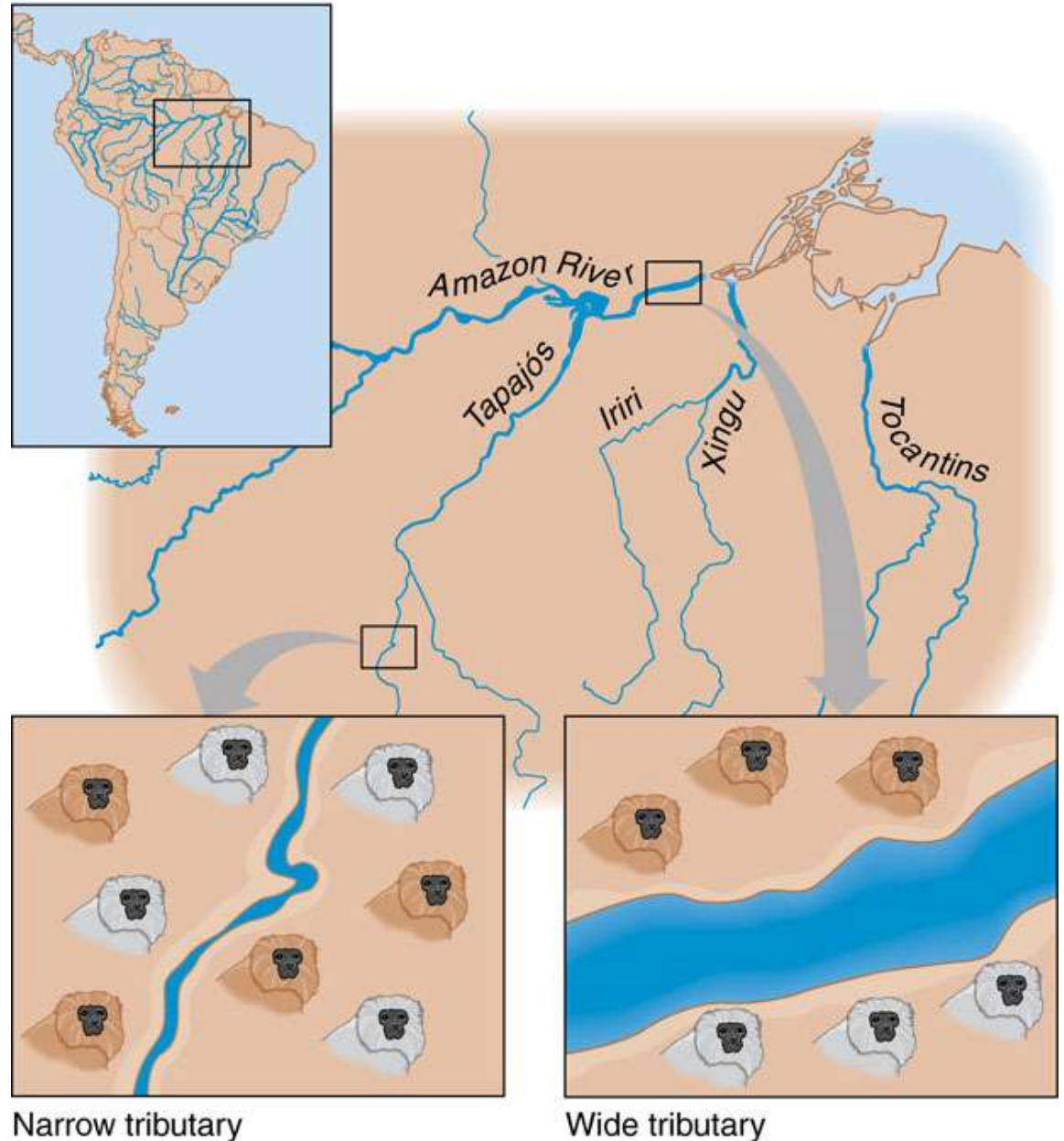
Two species of ground squirrel are postulated to have descended from a common ancestral population that was separated by formation of the Grand Canyon.



Spotted owl subspecies living in different geographic locations show some genetic and morphological differences. This observation is consistent with the idea that new species form through geographic isolation.



South America



Narrow tributary

Wide tributary

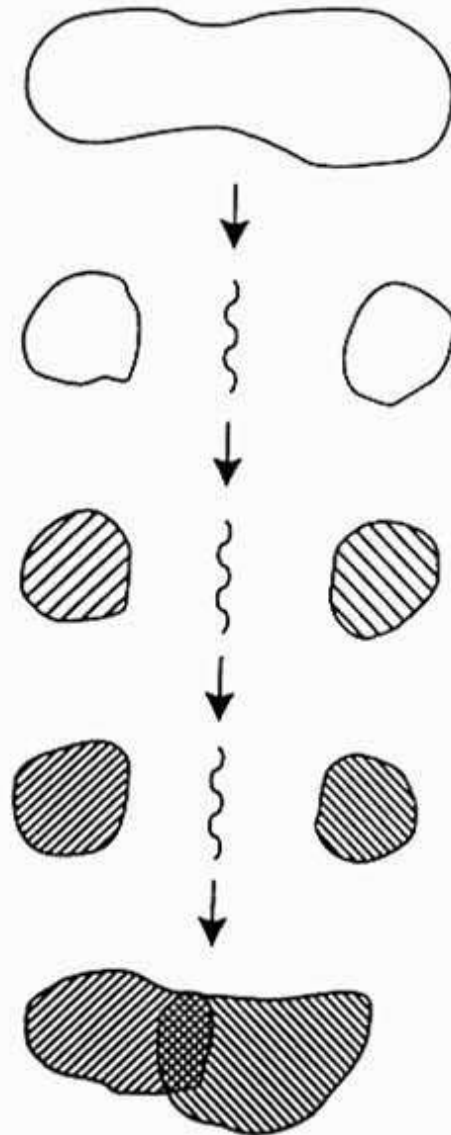
The populations of Tamarin monkeys are separated on the sides of the Amazon River.

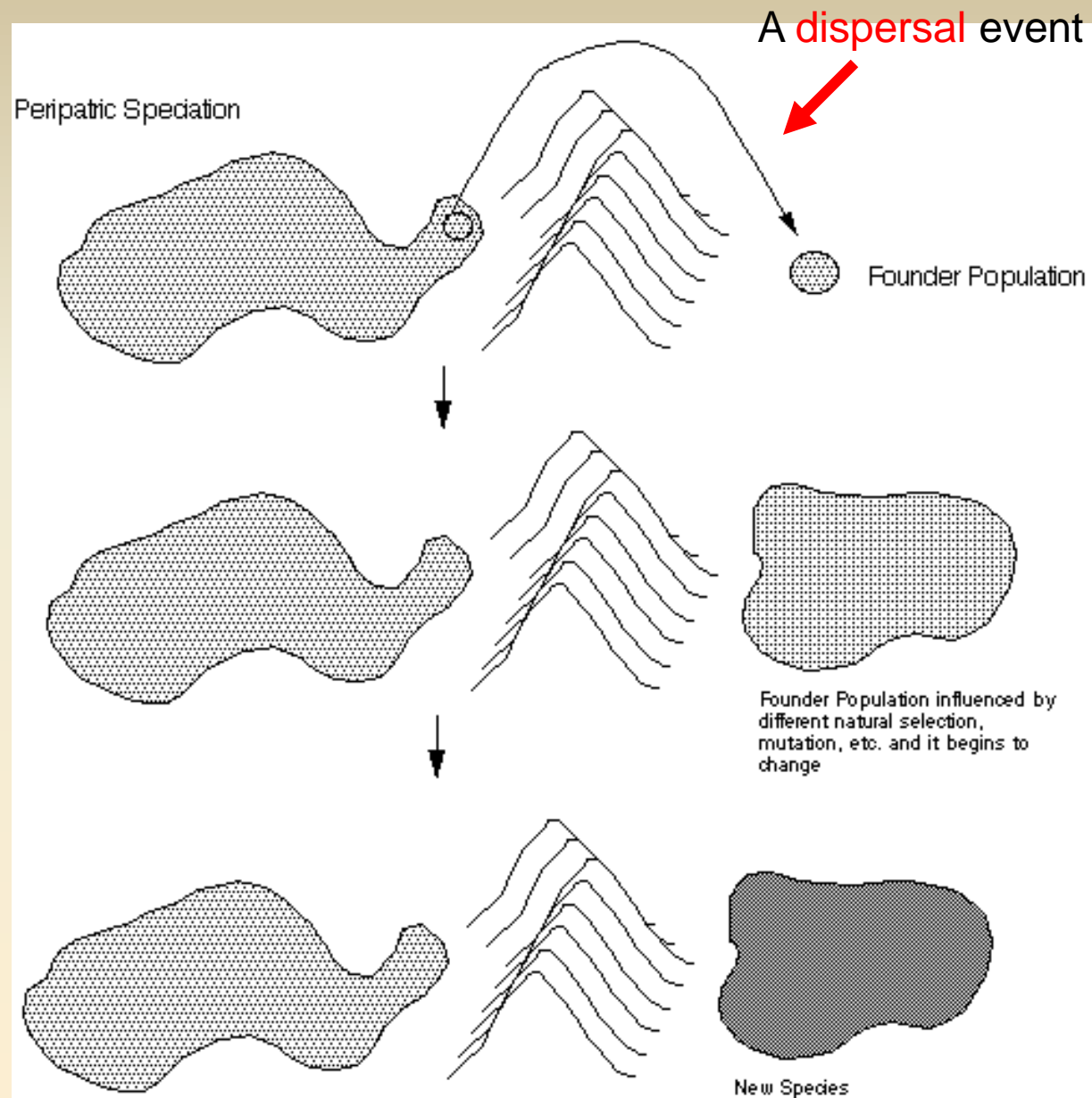
Where the river tributary is wide and individuals on opposite banks do not interbreed, the populations are diverging toward separate species.

Where the river tributary is narrow, the individuals still interbreed.

Allopatric speciation

involves the geographic separation of the parent population into two subpopulations. It can occur if a physical barrier separates the range of a population.



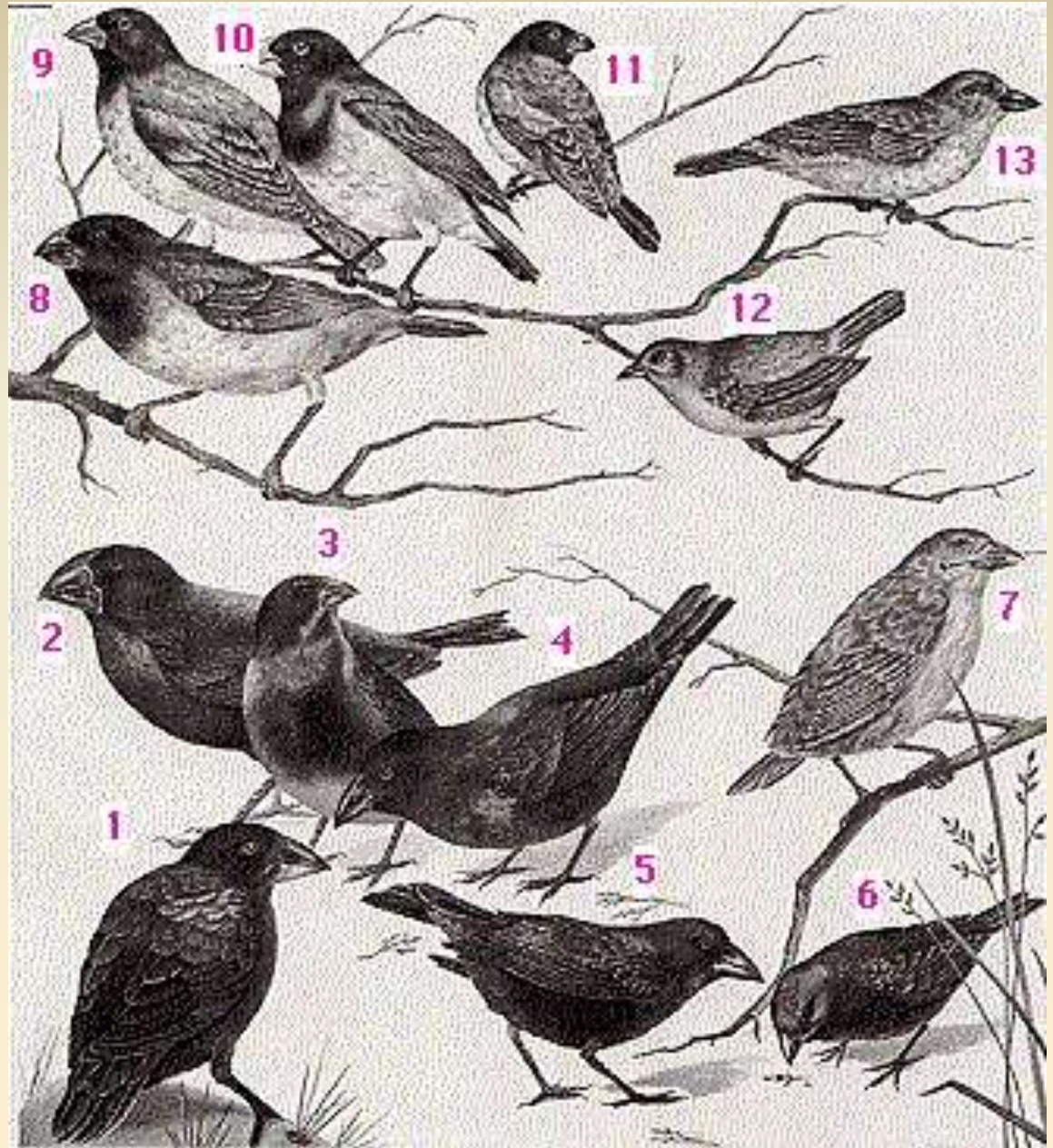


Geographic isolation through dispersal

The ancestors of Darwin's finches colonized the Galapagos Islands after dispersing from South America and speciated into the current range of species.

Similarly, the Hawaiian Islands were colonized by ancestral *Drosophila* fruit flies that appear to have speciated to produce more than 500 endemic species of *Drosophila* on the islands.

Such an event
may have led to
the development
of the thirteen
species of
Darwin's finches.



Evidence for founder hypothesis of speciation in Hawaiian Islands

- The main hypothesis for how the Hawaiian Islands became populated with a diverse variety of endemic species, most of which occur on only a single island, is the founder hypothesis.
- According to the founder hypothesis, new species are formed when a small population of individuals disperses to a new island and after being separated diverges from the ancestral form.

Evidence for founder hypothesis of speciation in Hawaiian Islands

- The Hawaiian Islands were formed by a stationary geological “hot spot” over which the continental plate drifts northwest.
- Periodically, the hot spot produces magma flows, which form islands that are then carried away on the plate and ultimately erode away. Thus the newest islands are close to the hot spot and the oldest further northwest.

Hawaiian Drosophila

D. suzukii

D. microthrix

D. nigribasis

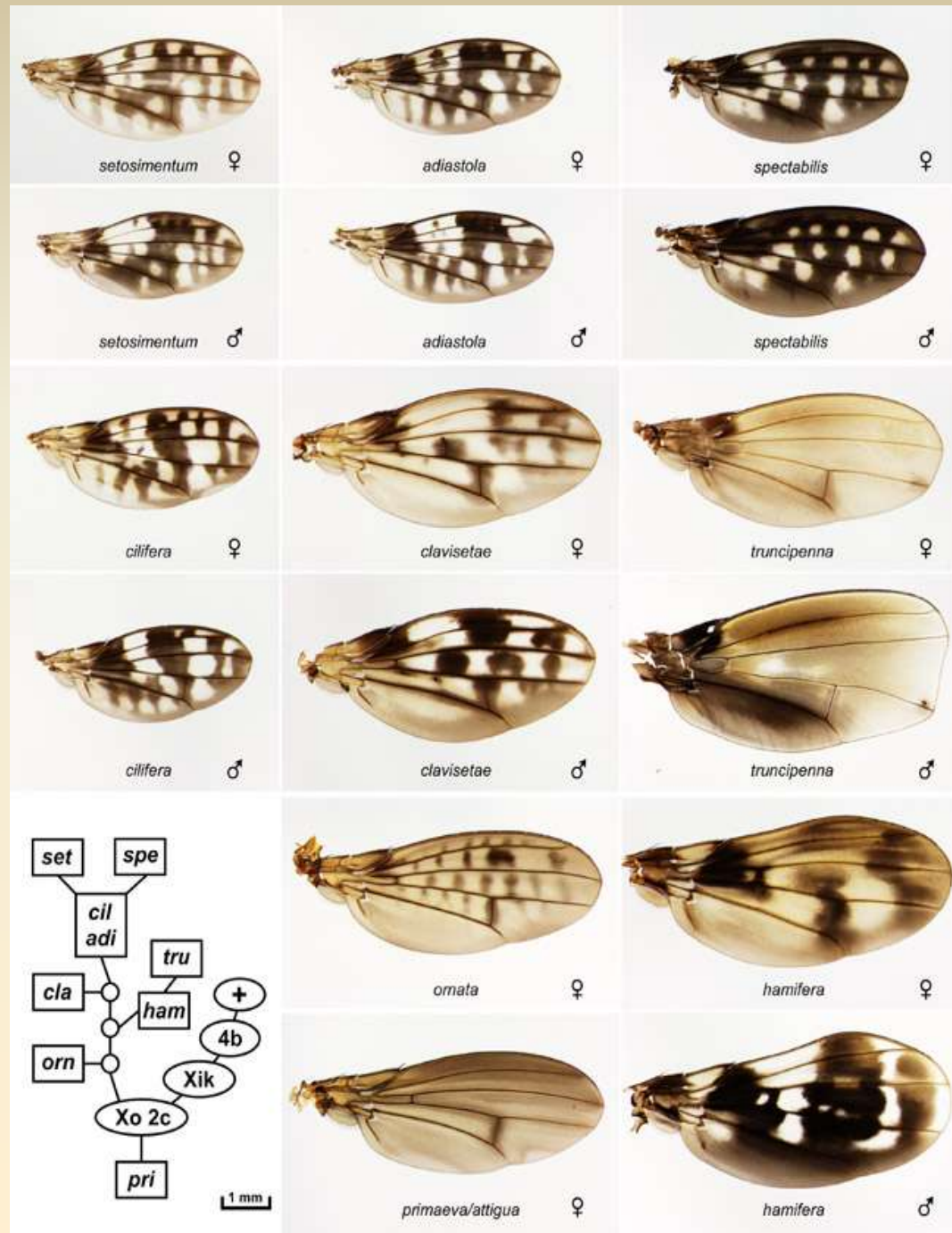
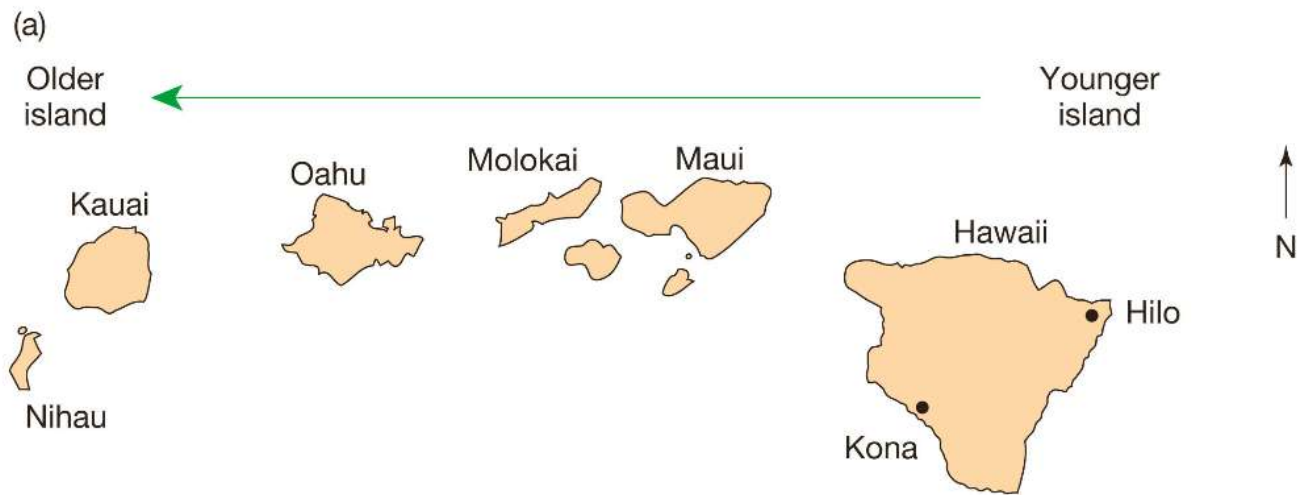
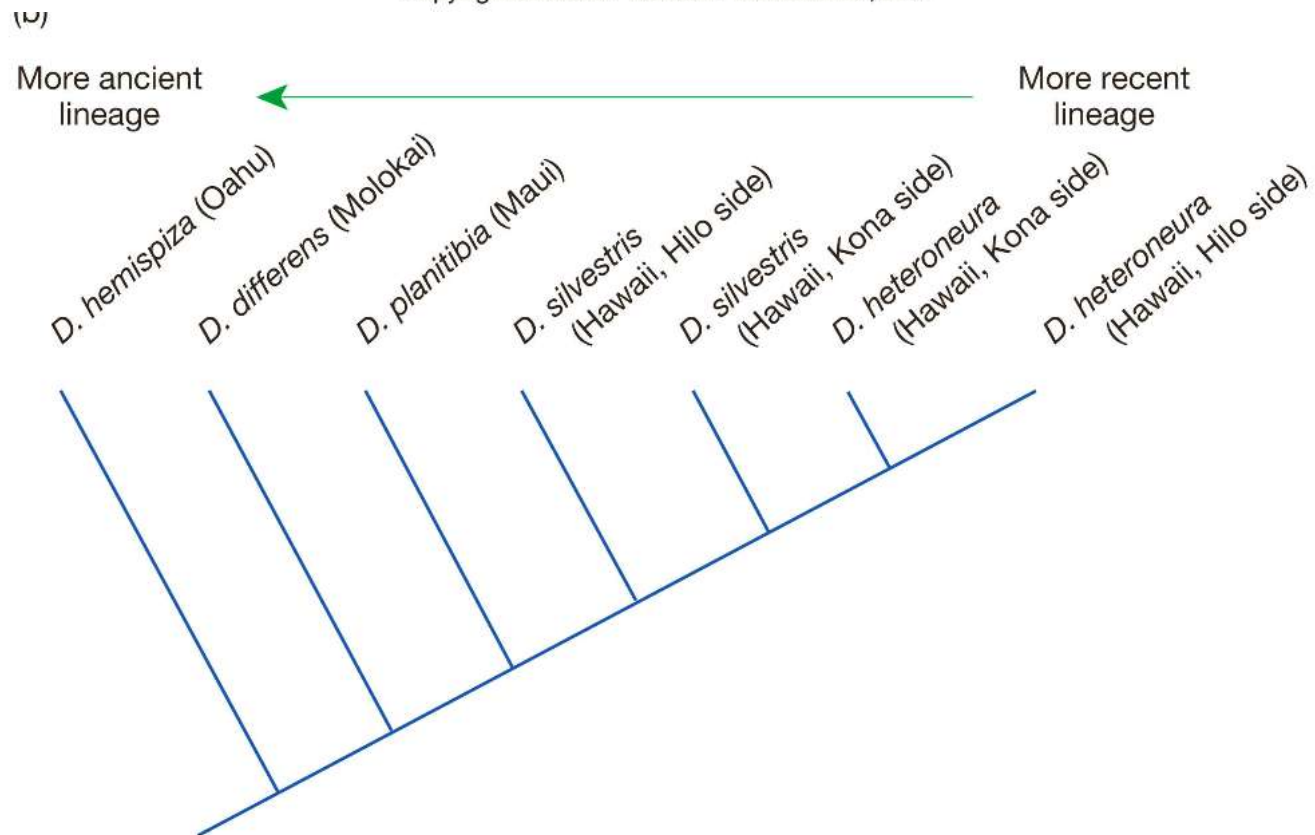


Figure 16-6 Evolutionary Analysis, 4/e
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Evidence for founder hypothesis of speciation in Hawaiian Islands

- Based on the geological information the founder hypothesis makes two predictions about the pattern of speciation that should be observed.
 - Closely related species should be found on adjacent islands and
 - Some speciation sequences should match the sequence in which islands formed.

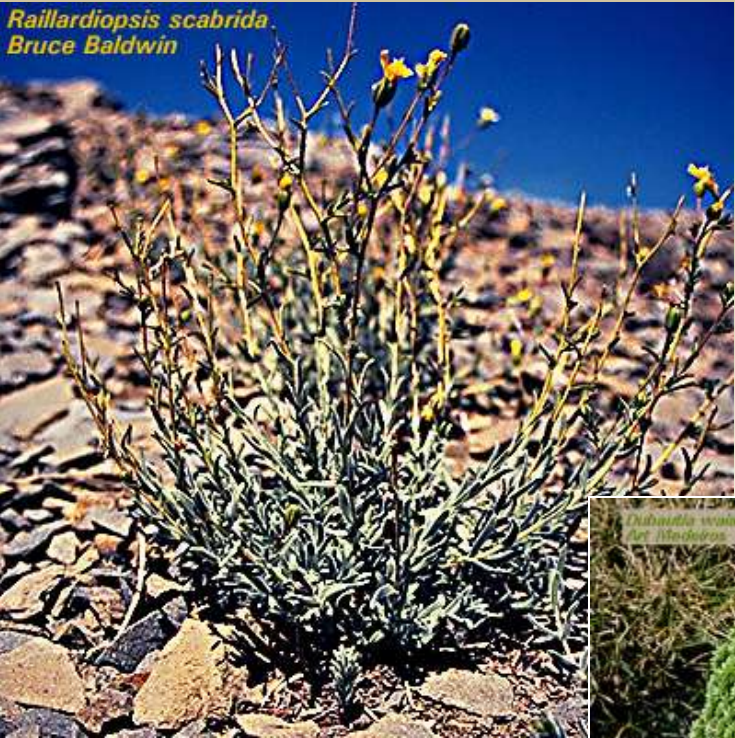
Evidence for founder hypothesis of speciation in Hawaiian Islands

- A study of mitochondrial DNA of four species of closely related *Drosophila* by DeSalle and Giddings (1986) found the predicted patterns.
- The most recent species occur on the youngest islands and several of the branching events match the order of island formation.

Adaptive Radiation

1. open habitats
2. little competition
3. radiation into new ecological niches -
4. often w/o genetic reproductive isolation
5. generally w/o much genetic divergence
- 6. can result in a “star phylogeny”

Raillardiopsis scabrata
Bruce Baldwin

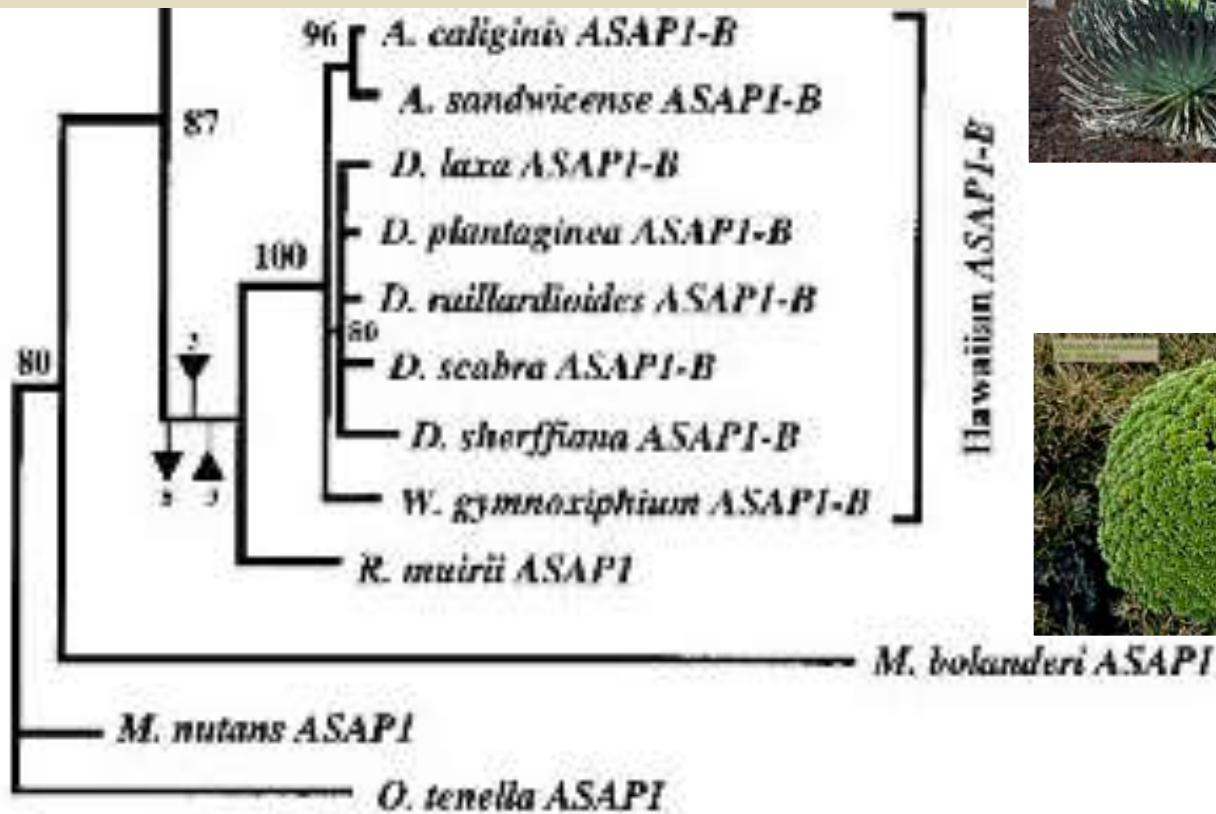


Hawaiian tarweed
adaptive radiation



Argyroxiphium sandwicense
ssp. *macrocephalum*
Gerald D. Carr





Rapid diversification, inferred from short branches & unresolved polytomy

Reproductive Isolating mechanisms

Any behavioral, structural or biochemical traits that prevent individuals of different species from reproducing successfully together

There are two types of isolating mechanisms

- prezygotic isolating mechanisms
- postzygotic isolating mechanisms.

How does reproductive isolation evolve?

Premating or prezygotic mechanisms:

- a) Ecological or habitat isolation
- b) Seasonal or temporal isolation
- c) Sexual or ethological isolation
- d) Mechanical isolation
- e) Isolation by different pollinators
- f) Gametic isolation

Postmating or zygotic mechanisms:

- a) Hybrid inviability
- b) Hybrid sterility
- c) Hybrid breakdown

REPRODUCTIVE BARRIERS BETWEEN SPECIES

PREZYGOTIC BARRIERS: Prevent mating or fertilization

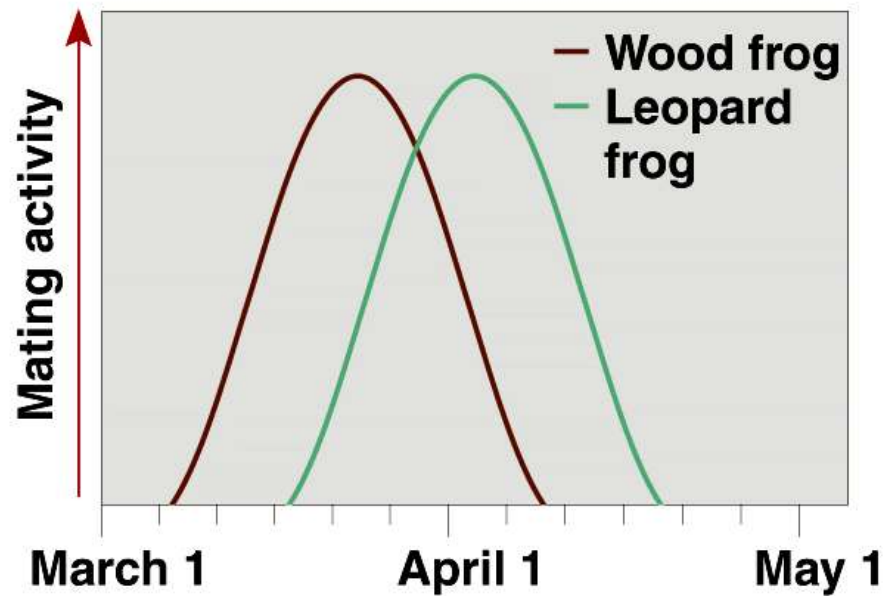
- | | |
|-----------------------|--|
| Temporal isolation: | Mating or flowering occurs at different times for different species. |
| Habitat isolation: | Species breed in different habitats. |
| Behavioral isolation: | There is little or no sexual attraction between individuals of different species. |
| Mechanical isolation: | Structural differences between species (in animal sex organs or plant flowers, for example) prevent copulation or pollen transfer. |
| Gametic isolation: | Male and/or female gametes die before uniting with gametes of other species, or the gametes fail to unite. |



Wood frog
Rana sylvatica



Northern leopard frog
Rana pipiens



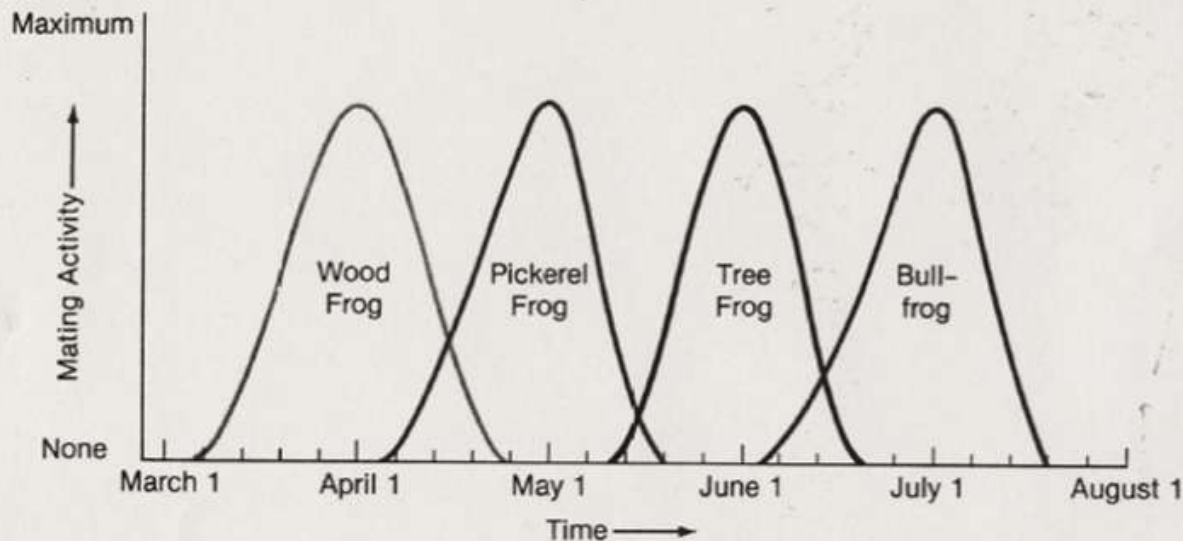


Figure 43-3 TEMPORAL ISOLATION IN BREEDING OF AMPHIBIANS.

Four kinds of frogs are seen to have maximal reproductive behavior at different times; this helps to ensure that interbreeding is reduced or absent.

In the example of frogs breeding in the North American spring and summer, the reproductive isolating mechanisms include species-specific vocalizations as well as scarcely-overlapping windows of time when each species reproduces.

Temporal isolation is when two species are found in the same area, but are incapable of mating due to different reproductive cycles for flowering or mating.

Example – Red and black sea urchins live in the same location, but **release their gametes at different times of the year.**



Ecological isolation is when species occupy separate habitats or niches and do not encounter one another to reproduce due to some geographic or ecological barrier.

Example – ground squirrel species occupy different habitats.

Woodchucks live in fields at low elevation



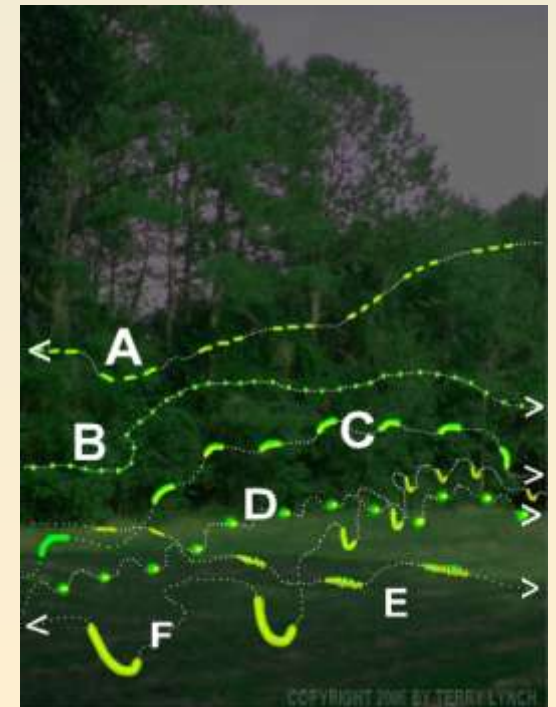
Marmots live in the Rocky Mountains at high elevations



Behavioural isolation is when distinct mating rituals by one species may prevent members of another species from recognizing or selecting a mate.

Example: male jumping spiders dance (shake their legs and wave their palps). Females of different species do not respond to the dance.

Example: Different species of fireflies do not recognize each others' mating signals, and as a result do not generally interbreed. These beetles reproduce at the same time, but a female responds only to the flashing pattern of males of her species. If she responds inappropriately, she produces less viable hybrids, which reinforces the “correct” choice.





Behavioral isolation

Even if they breed at the same time, they will not mate if they are not attracted to one another.

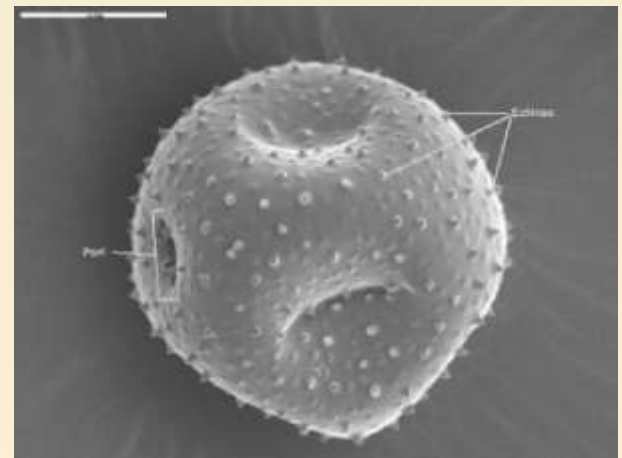
Courtship rituals, like these, are critical for mating within a species, but ineffective for attracting members of other species.



Gametic isolation – may prevent reproduction at a molecular level.

Example – in coral reefs, many species with external fertilization may release gametes simultaneously, so trillions of sperm and eggs may be in the shallow water at one time. Sperm and eggs of the same species recognize each other by molecular markers.

This can also be the reason pollen from one species will not be able to form a pollen tube if it lands on the stigma of a different species.



REPRODUCTIVE BARRIERS BETWEEN SPECIES

POSTZYGOTIC BARRIERS: Prevent the development of fertile adults

- | | |
|---------------------|---|
| Hybrid inviability: | Hybrid zygotes fail to develop, or the hybrids fail to reach sexual maturity. |
| Hybrid sterility: | Hybrids fail to produce functional gametes. |
| Hybrid breakdown: | Offspring of hybrids are weak or infertile. |



Hybrid inviability or infertility

Even if fertilization occurs successfully, the offspring may not survive, or if it survives, may not reproduce (e.g., mule).



Secondary contact and reinforcement

- **secondary contact** occurs when two formerly allopatric populations meet.

Three outcomes are possible:

1. No interbreeding occurs

- isolating mechanisms in place – speciation completed.

2. Introgression

- no isolating mechanisms in place – populations merge completely.

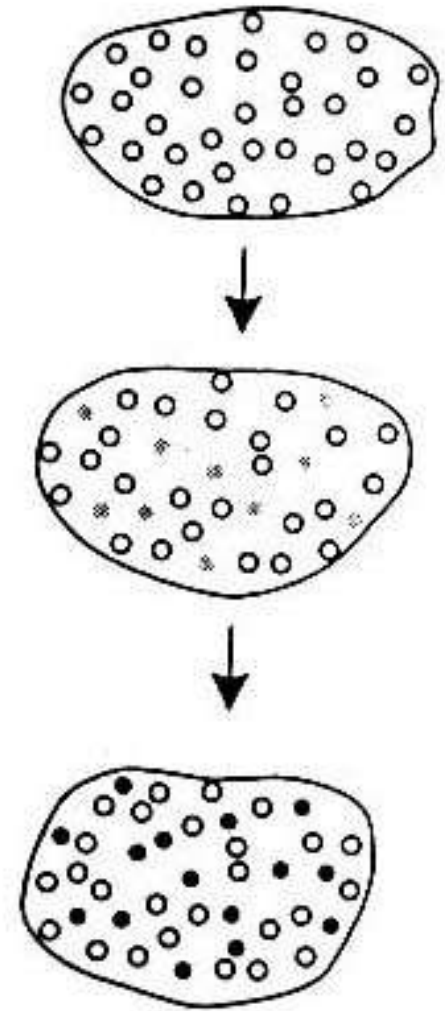
Secondary contact and reinforcement

3. Partial interbreeding occurs

- some isolating mechanisms in place – a hybrid zone forms (but hybrids are less fit).
- **reinforcement** should occur to “complete” the process by the **evolution of additional pre-zygotic barriers**.

Sympatric speciation occurs without any separation of the ancestral geographic range. Some evolutionary biologists doubt this ever happens.

In all likelihood, it can only occur after the establishment of a stable polymorphism.





(a) Allopatric speciation



(b) Sympatric speciation

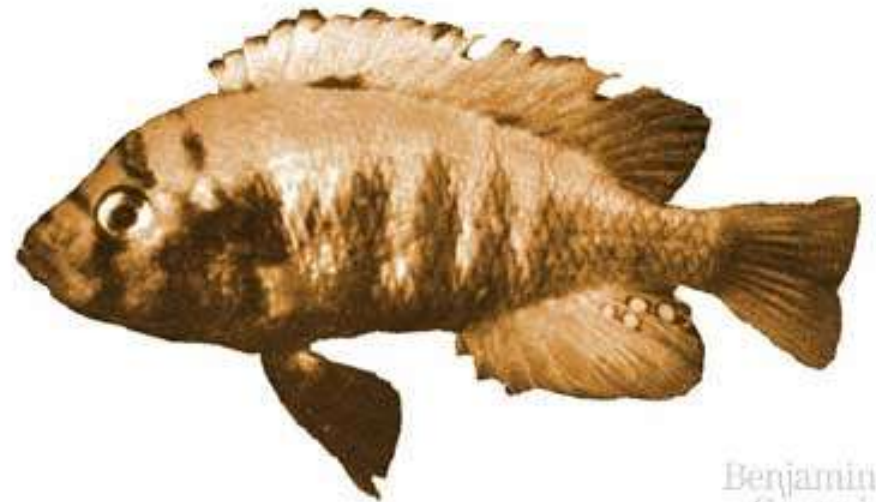
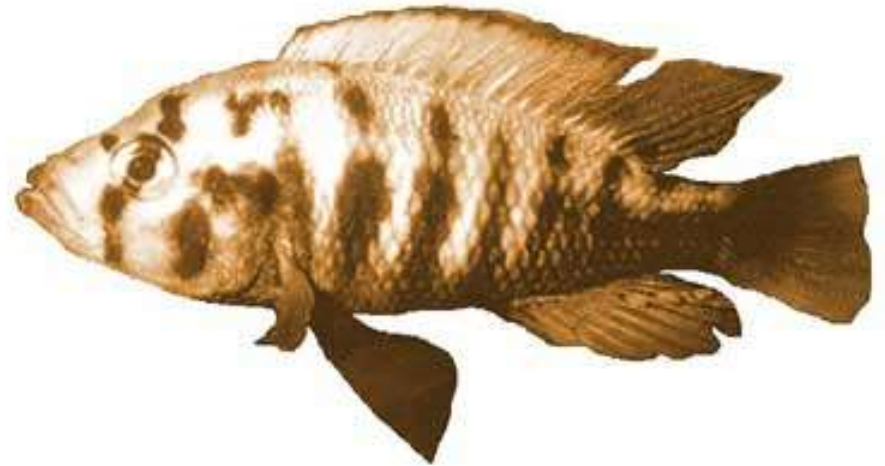
Sympatric Speciation

- Sympatric speciation happens when members of a population develop some genetic difference that prevents them from reproducing with the parent type.
- This mechanism has occurred several times in plants, where failure to reduce chromosome number results in polyploid plants that reproduce successfully only with other polyploids.
- This causes instant speciation due to non-disjunction.
- Sympatric speciation has also occurred to cichlid fish in Lake Victoria in Africa.



- Animals diverge mostly due to reproductive isolation.
- Reproductive isolation is a result of genetic factors that cause offspring to rely upon resources not used by previous generations. (Example: switch to a new food source)
- Example: Lake Victoria has 200 closely related species of Cichlids (fish) which probably all arose from one ancestor with the driving force for speciation being:

Competition for a limited resource (food) within the lake, and adaptation to new food sources. This gave rise to different species that are kept from breeding with each other by distinctive coloration pattern.



Polyploidy in plants is the only noncontroversial example of **sympatric speciation**.

21.3 Gray Tree Frogs Speciated by Intra-specific Hybridization The tetraploid *Hyla versicolor* resulted from hybridization between eastern and western populations of the diploid *H. chrysocelis*.

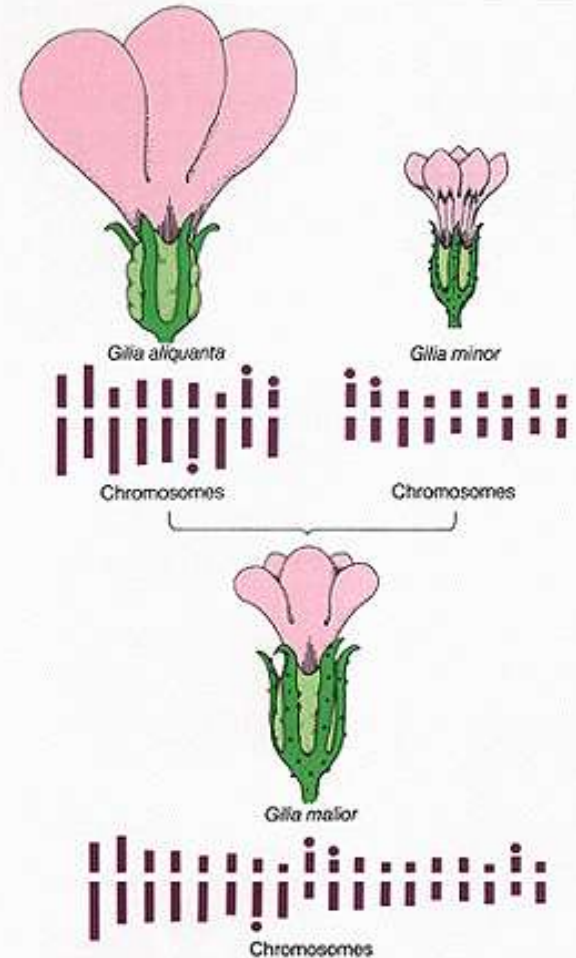
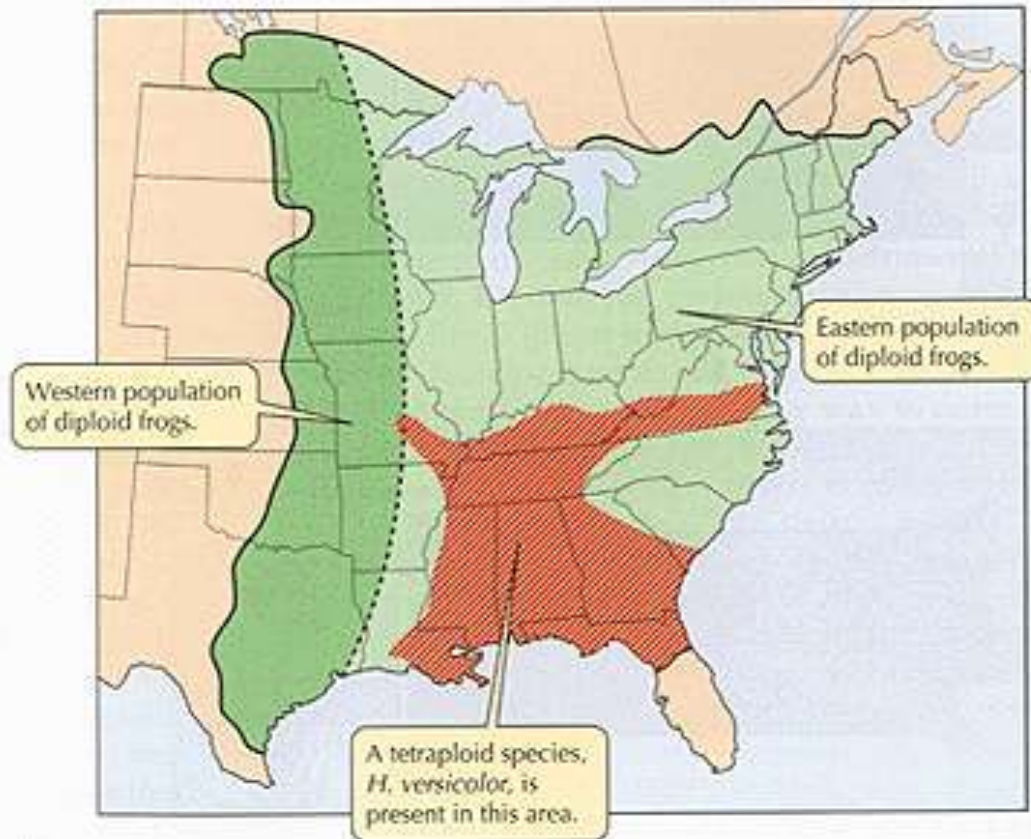
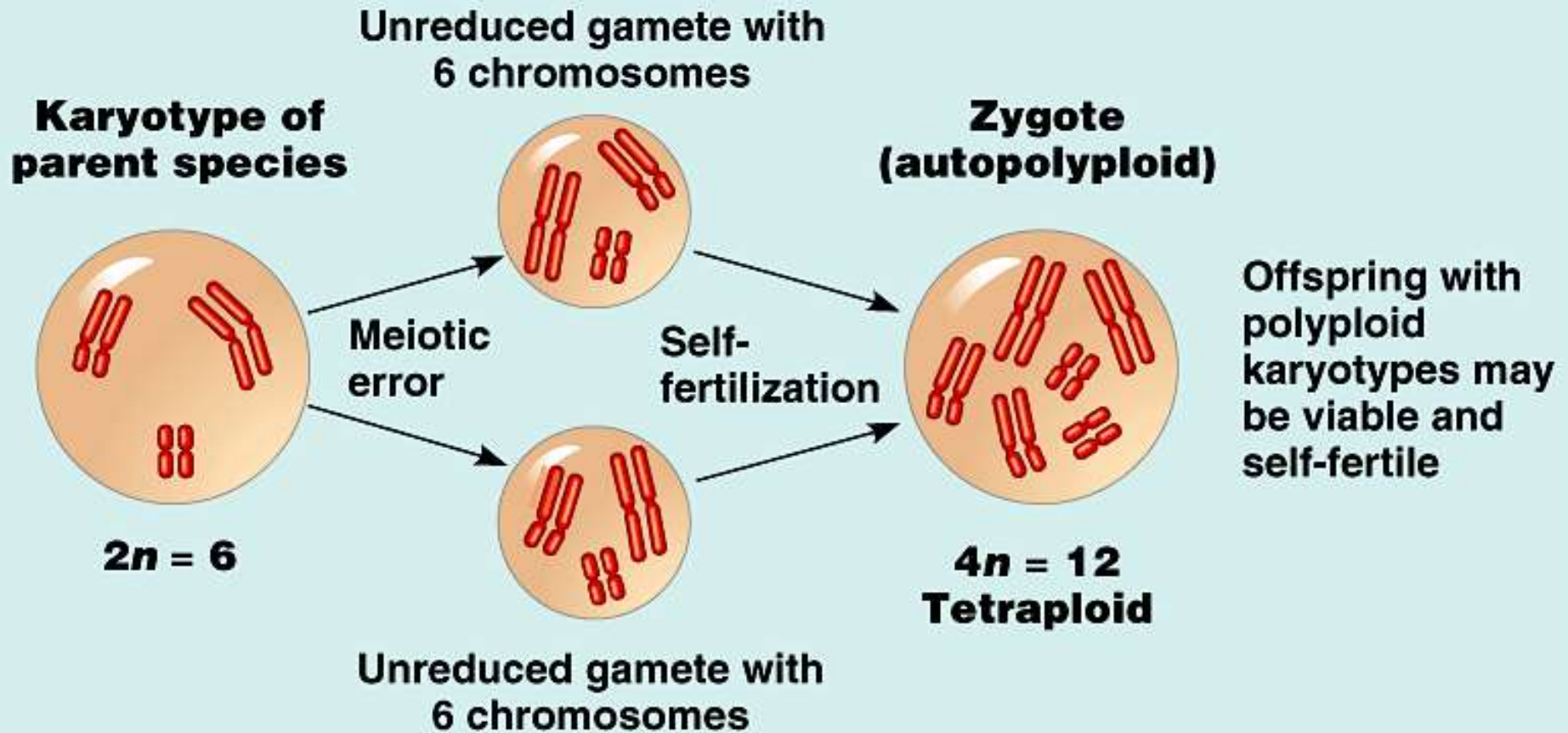


Figure 40-8 INSTANT SPECIATION: POLYPLOIDY IN *Gilia*.

Plants can form "instant species" through polyploidization, the duplication of an entire set of chromosomes. *Gilia major*, for example, occasionally undergoes allopolyploidization, the doubling of chromosomes from two parent plants of different species. The 18 chromosomes in *G. major* are no longer exact copies of the 9 from each parent species, reflecting changes in the chromosomes subsequent to the "speciation" event.

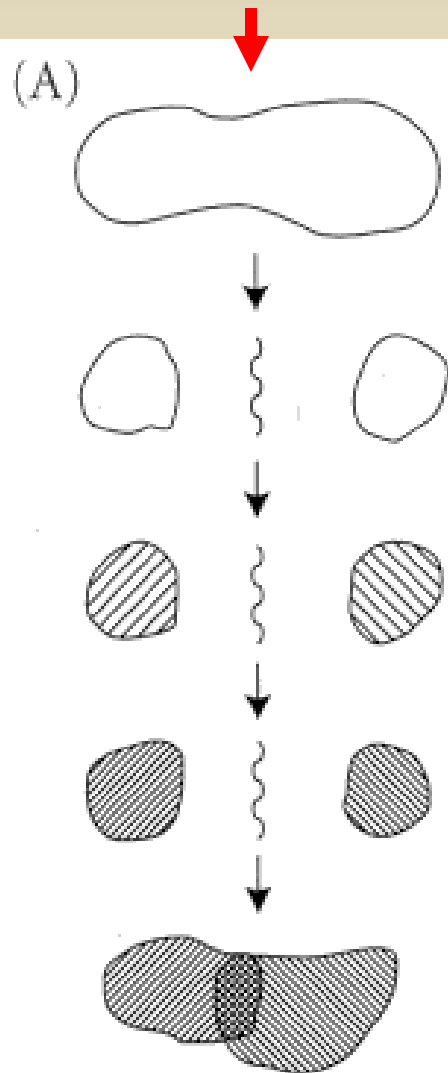


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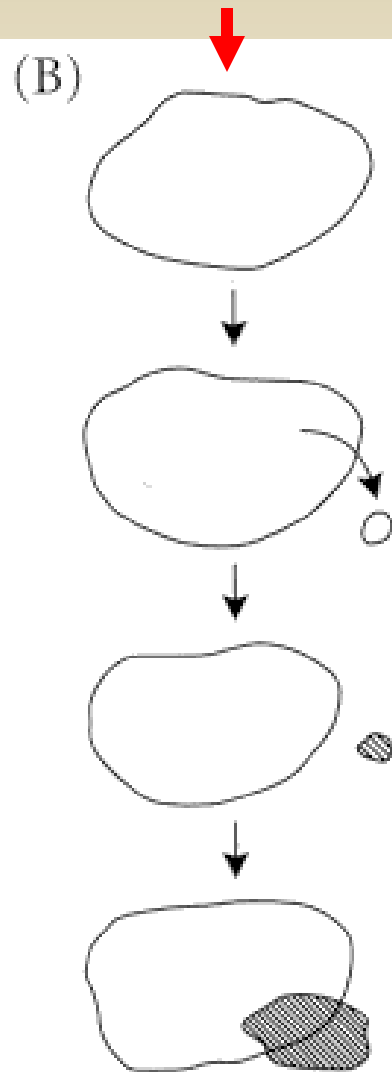
Sympatric speciation by autopolyploidy in plants.

The task of evolutionary biologists is to understand the context in which lineages split to form two distinct lineages. There are several possible speciation models, including:

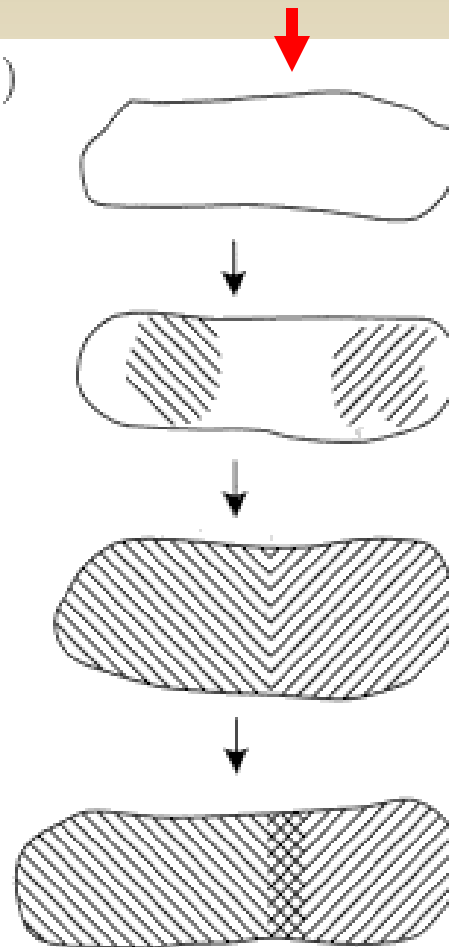
ALLOPATRIC



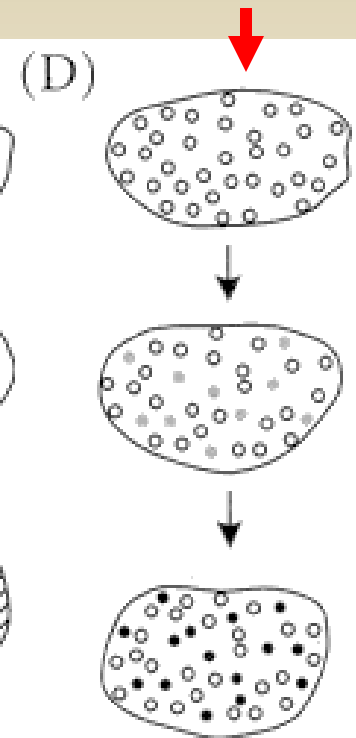
PERIPATRIC



PARAPATRIC



SYMPATRIC



(Futuyma 1997)

Modes of Speciation

Parapatric speciation

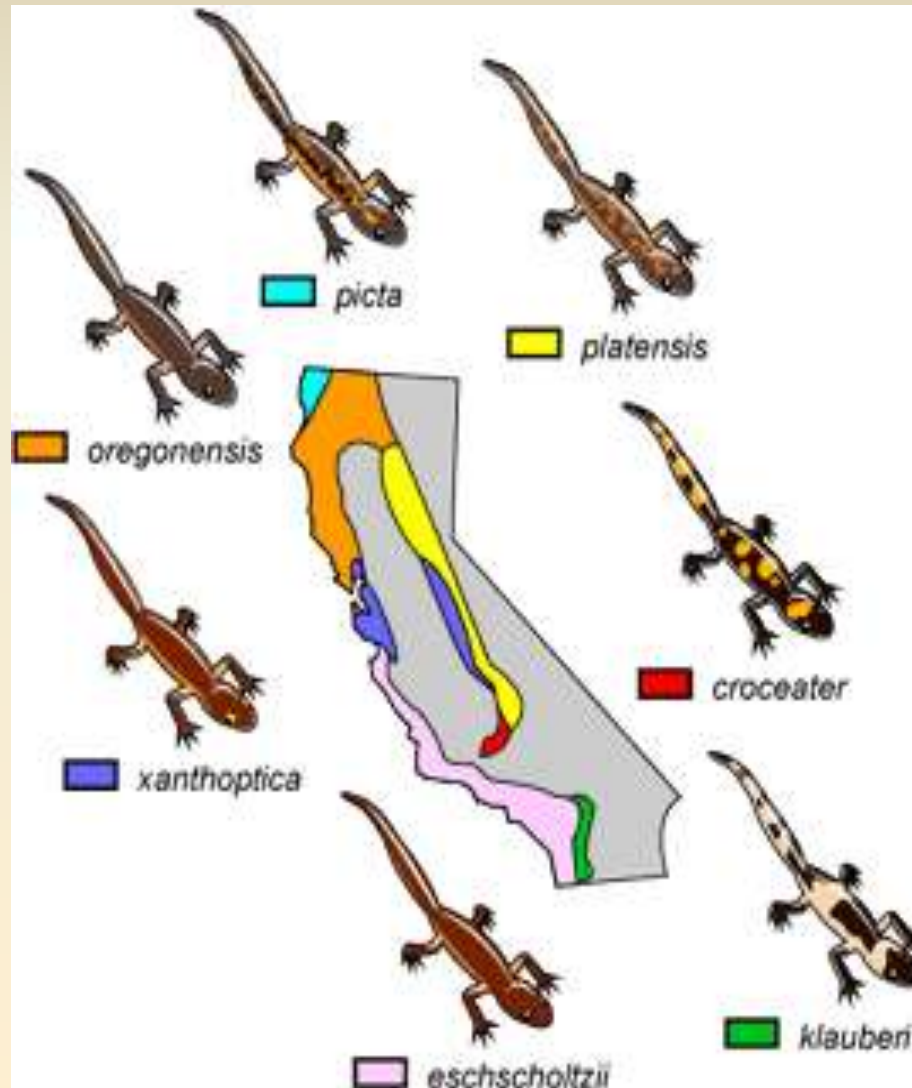
- reproductive isolation occurs without complete geographic isolation (some gene flow).

Example: ring species of salamanders (*Ensatina*) in CA

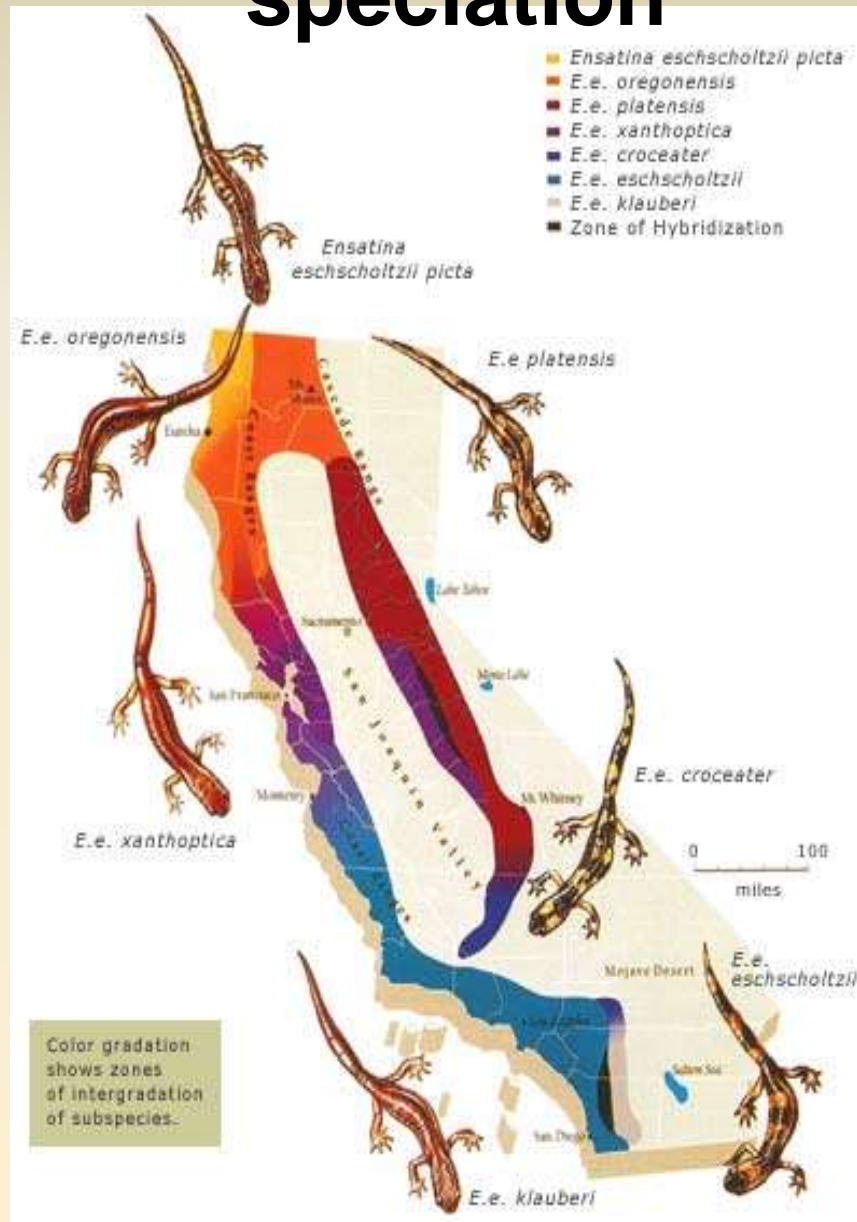
***Ensatina* salamanders**



Ring species – evidence for parapatric speciation



Ring species – evidence for parapatric speciation





BULLOCK'S ORIOLE



BALTIMORE ORIOLE



Secondary contact and reinforcement

- **secondary contact** occurs when two formerly allopatric populations meet.

Three outcomes are possible:

1. No interbreeding occurs

- isolating mechanisms in place – speciation completed.

2. Introgression – crossing and backcrossing

- no isolating mechanisms in place – populations merge completely.

Secondary contact and reinforcement

3. Partial interbreeding occurs

- some isolating mechanisms in place – a hybrid zone forms (but hybrids are less fit).
- **reinforcement** should occur to “complete” the process by the **evolution of additional pre-zygotic barriers**.

Hybridization

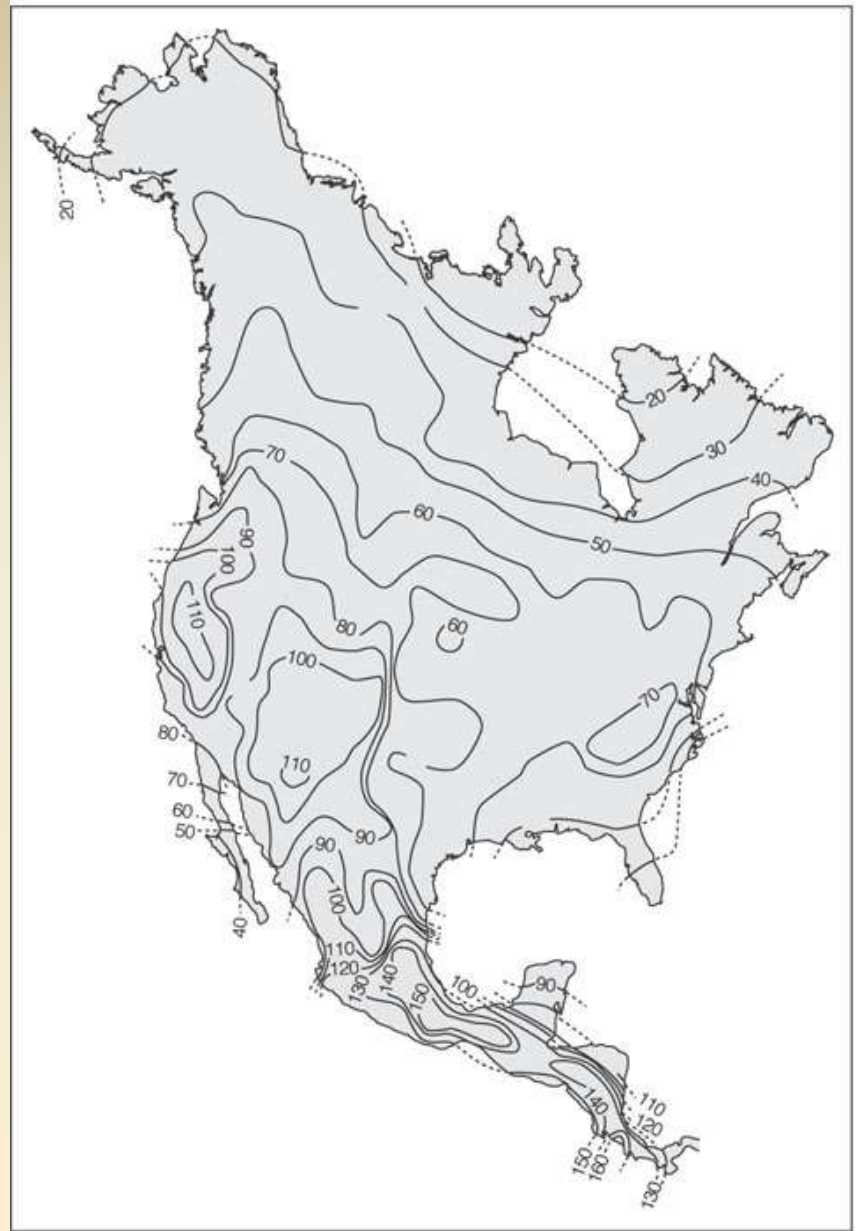
- In many cases hybrid offspring have reduced fitness and this maintains two distinct gene pools and incipient species.
- However, in some instances, hybridization appears to promote speciation, especially in plants, as some hybrids may obtain combinations of genes from parental species that enable them to occupy habitat that neither parental strain can.

Latitudinal Gradients

Within taxonomic groups, species are not distributed evenly across the planet. There are distinct gradients for many groups, with the number of species decreasing as one moves away from the equator.

A number of explanations have been suggested.

- Evolutionary Time
- Climate Stability
- Productivity
- Ecological Effects

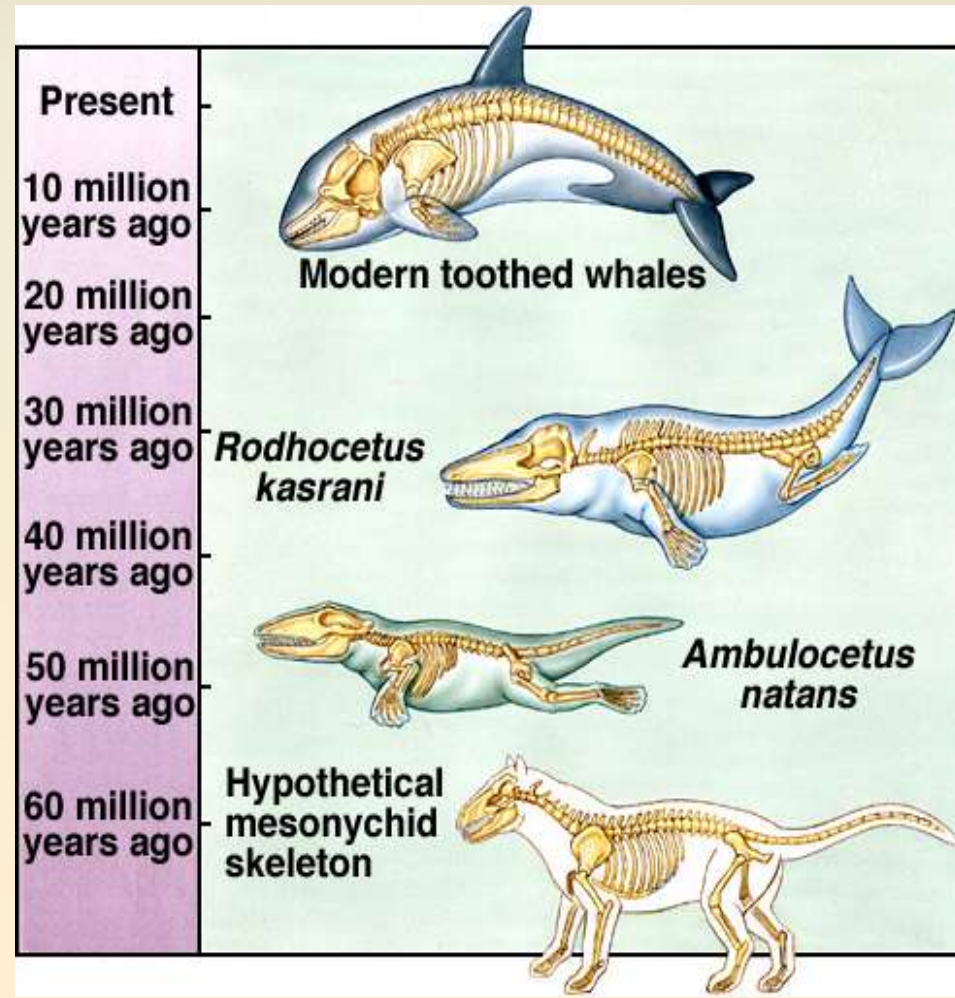


Latitudinal Gradient for Mammal Species

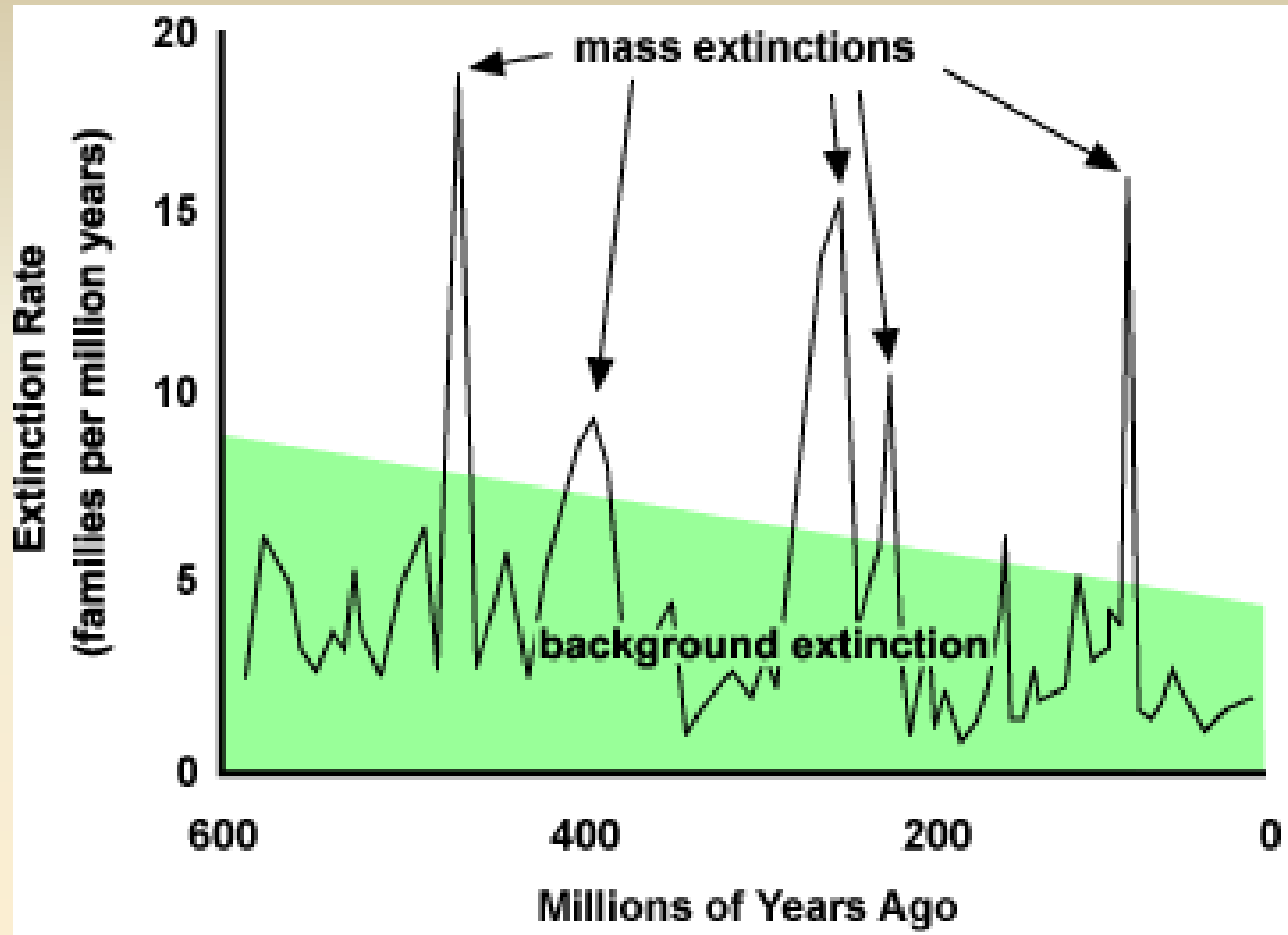
Species Come and Go

Best estimates from the fossil record indicate that greater than 99% of species that have existed are now extinct.

A typical “lifetime” for a species is about 1 million years.

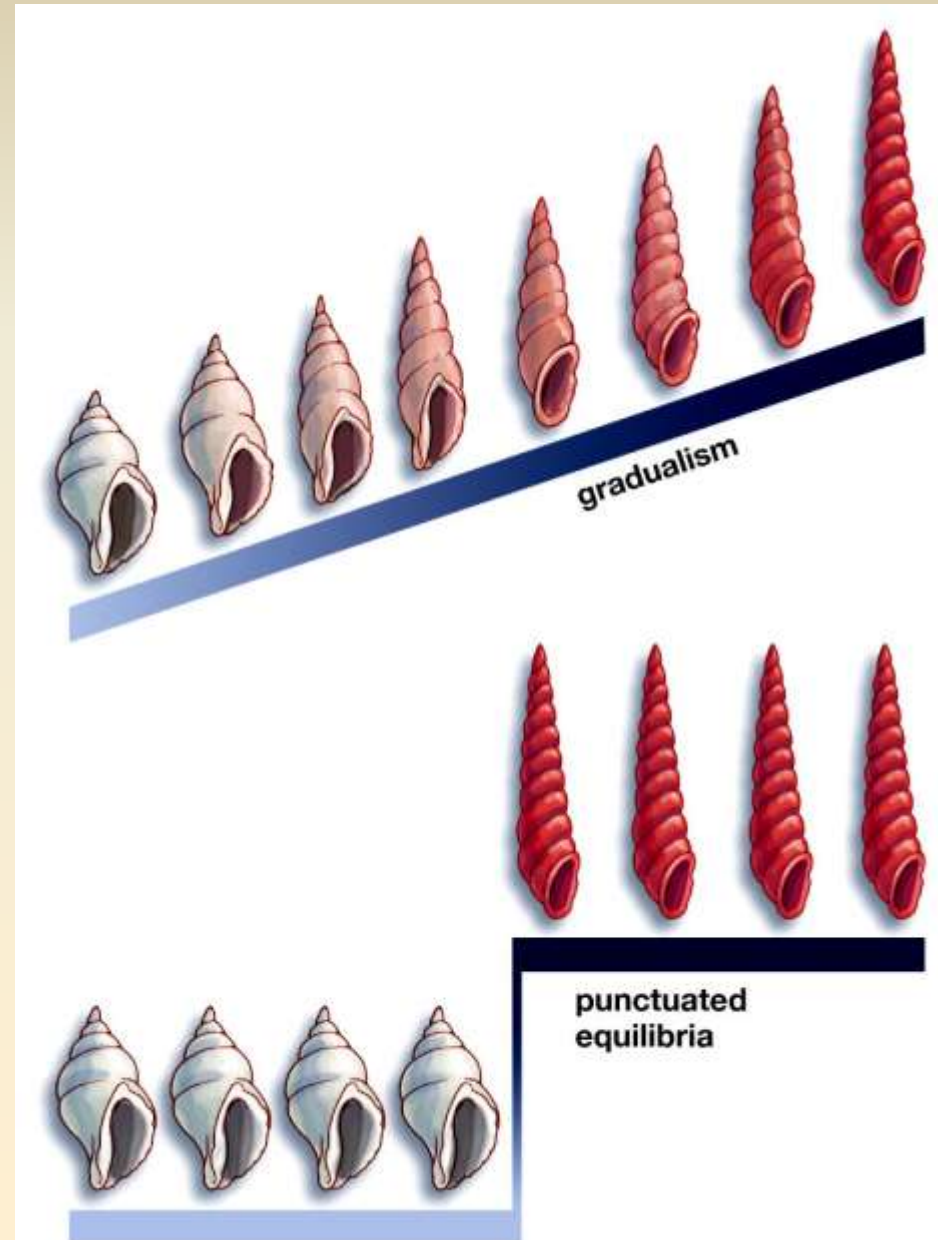


Mass Extinctions Are a Fact of Life



Speciation Dynamics - Gradualism or Punctuated Equilibrium?

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



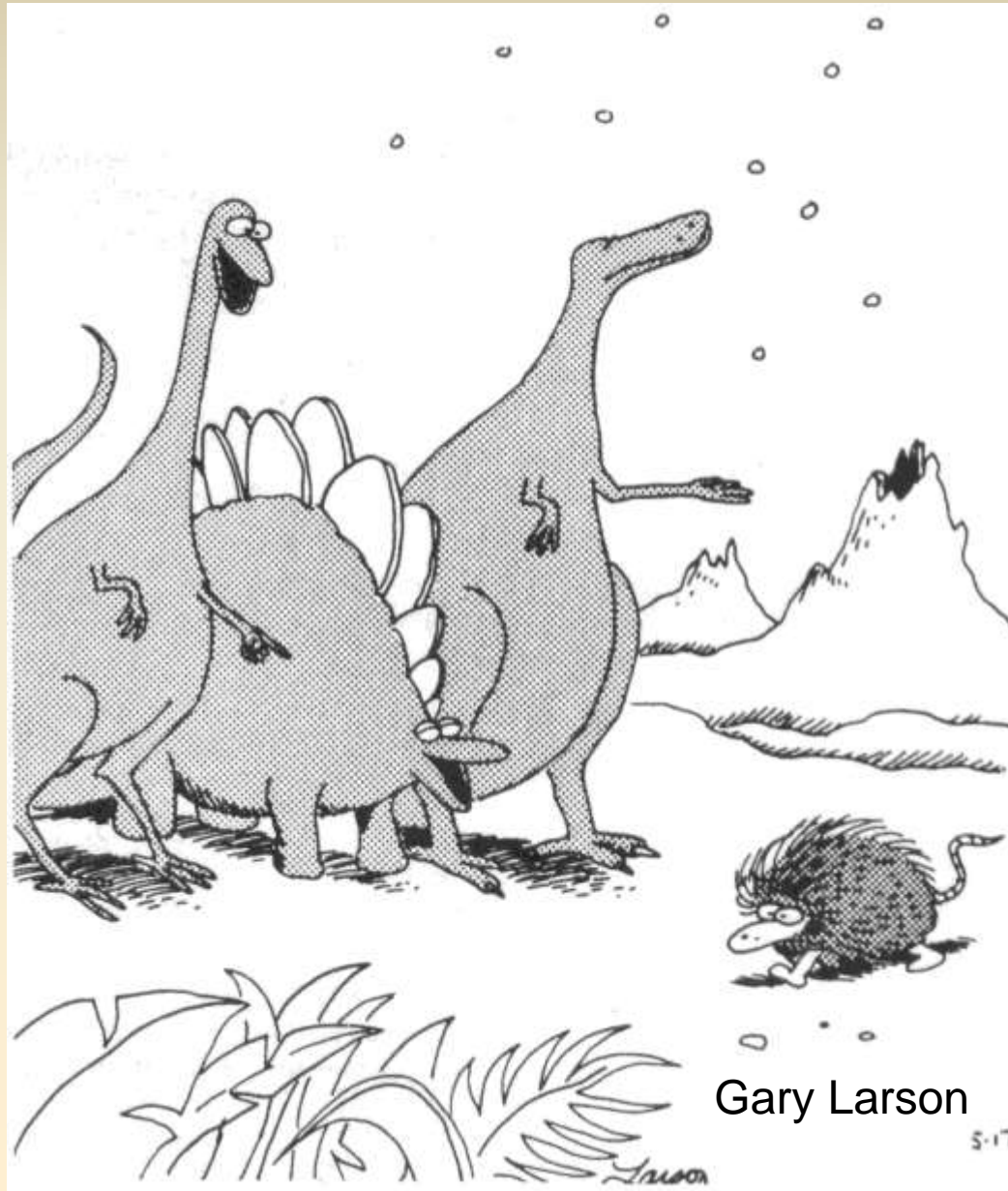
Does Evolution Create the Perfect Organism?

No, only better organisms as evolution is constrained by history and buffeted by random events.

Essentially, every organism on earth is in significant part a **sum of accidents.**



The Cretaceous/Tertiary Mass Extinction



Gary Larson

5-17

End