Meeting Life's Challenges Part 2

ORIGIN OF SPECIES

I. Main Idea

Species are distinct groups of organisms that differ in their morphology, physiology, biochemistry and DNA.

“New Species Can Emerge”

- **Darwin called the first appearance of new beings on earth the “mystery of mysteries”.**
- The origin of species or **speciation** is central to evolutionary theory because the appearance of new species is the source of biological diversity.
  - *Evolutionary theory must explain how these new species come into existence.*
- **Speciation** explains both the unity (similarities) and the diversity (differences) of living organisms.

“Speciation”

- **Speciation** is a conceptual bridge between microevolution and macroevolution.
- **Microevolution** refers to the change in allele/gene frequencies in a population over time.
- **Macroevolution** refers to the broad pattern of evolution above the species level.
    - *here small changes have accumulated to the point where large noticeable changes have occurred in groups of organisms, for example the emergence of mammals or flowering plants.*

"Biological Species Concept"

- Before we begin to explore "how" species change we ought to first understand "what" a species is.
- The **biological species concept** defines a species as a group of populations whose members can interbreed in nature and produce viable, fertile offspring-but can not produce viable, fertile offspring with members of other such groups.
  - *gene flow (transfer of alleles) between populations tends to hold populations together genetically through the ongoing exchange of alleles.*
  - *in fact, removing gene flow plays a key role in the generation of new species as we will see shortly*

"Biological Species Concept"

Similarity between different species. The eastern meadowlark (*Sturnella magna,* left) and the western meadowlark (*Sturnella neglecta,* right) have similar body shapes and colorations. Nevertheless, they are distinct biological species because their songs and other behaviors are different enough to prevent interbreeding should they meet in the wild.

Defining a species is not always easy nor intuitive.

Diversity within a species. As diverse as we may be in appearance, all humans belong to a single biological species (*Homo sapiens*), defined by our capacity to interbreed.

"Biological Species Concept"

- **Do you see any limitations in defining species this way?**
- **Yes, of course.**
  - *bacteria- they are asexual*
  - *dinosaurs- they are dead*
  - *newly discovered organism- we have not yet and maybe never will be able to test its ability to reproduce with other organisms*
- **So what do biologists do in these cases?**
- **They use other definitions of species that are suitable for the circumstances.**

"Other Species Concepts"

- **When the biological species concepts falls short biologists use other definitions of species that are suitable for the circumstances.**

- Morphological Species Concept
  - *uses cell or body structures and features*
- Ecological Species Concept
  - *defines according to the niche it fills in an ecosystem*
- Phylogentic Species Concept
  - *uses morphology and molecular sequencing*

"Reproductive Isolation"

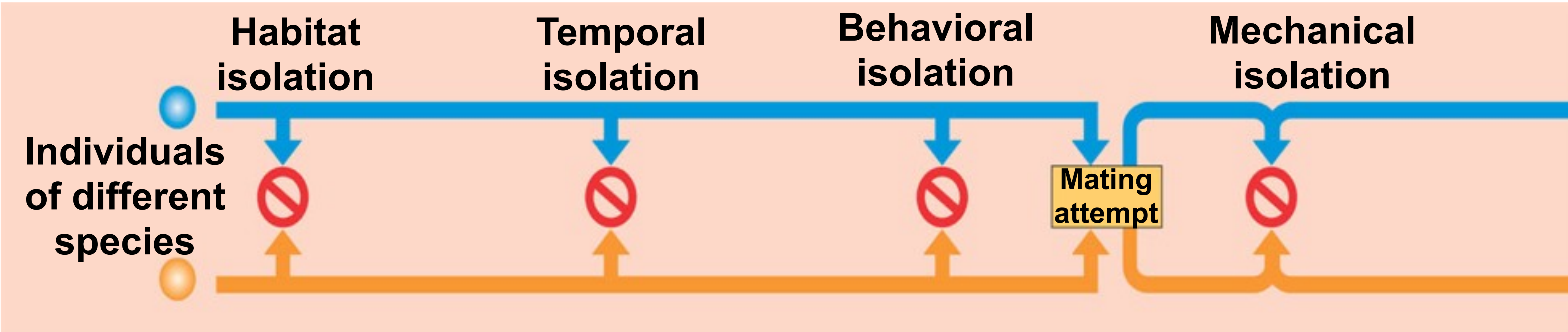
- Biological Species are defined by their reproductive compatibility, the formation of new species therefore relies on *reproductive isolation*.
- **Reproductive isolation-** existence of barriers that impede members of two species from interbreeding and producing viable, fertile offspring.
  - Such barriers block gene flow and prevent the formation of *hybrids*.
- **Hybrids-** offspring that result from interspecific matings.

“Reproductive Isolation”

- **Prezygotic Barriers-** Impede mating between species or hinder the fertilization of ova if members of different species attempt to mate
- **Postzygotic Barriers-** Often prevent the hybrid zygote from developing into a viable, fertile adult
  - *sometimes a single barrier does not prevent gene flow but a combination of barriers usually will.*

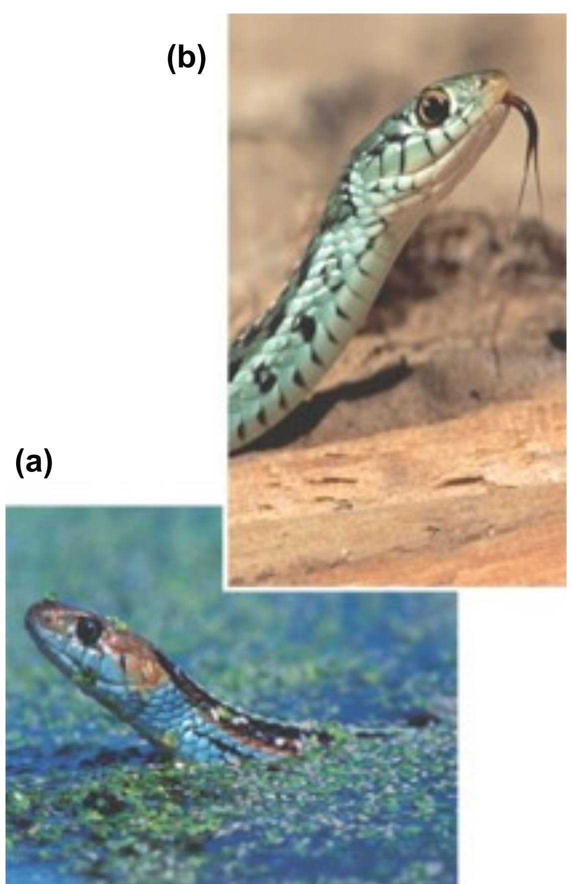
“Reproductive Isolation”

Prezygotic barriers impede mating or hinder fertilization if mating does occur



HABITAT ISOLATION

(b)



(a)

TEMPORAL ISOLATION

(d)

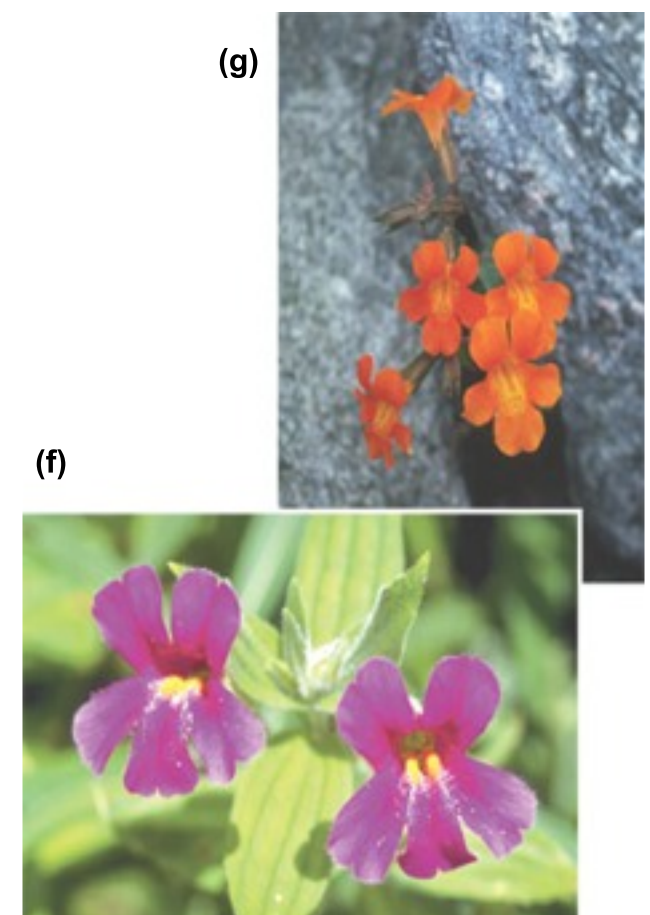
(c)

BEHAVIORAL ISOLATION

(e)

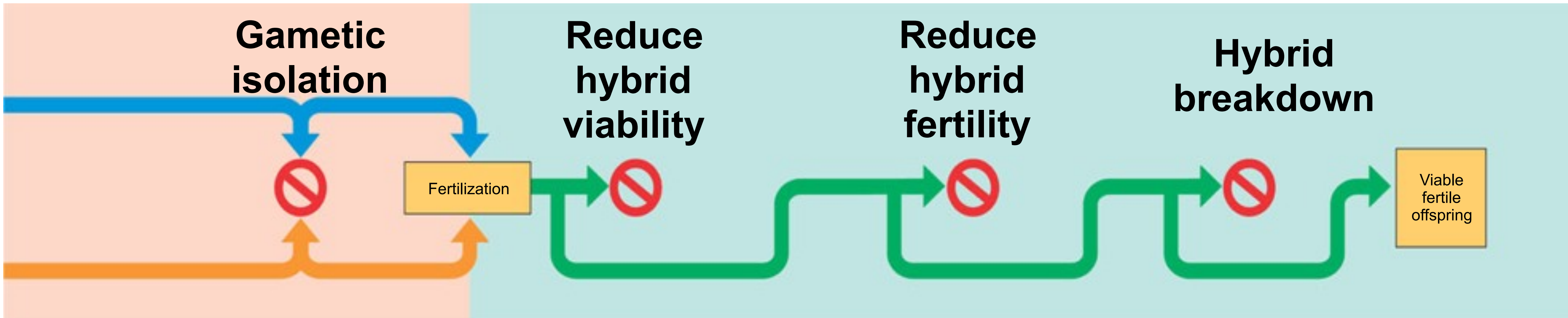
MECHANICAL ISOLATION

(g)



(f)

"Reproductive Isolation"



GAMETIC ISOLATION

REDUCED HYBRID VIABILITY

REDUCED HYBRID FERTILITY

HYBRID BREAKDOWN

(k)

(j)

(m)

(l)

(h)

(i)

ORIGIN OF SPECIES

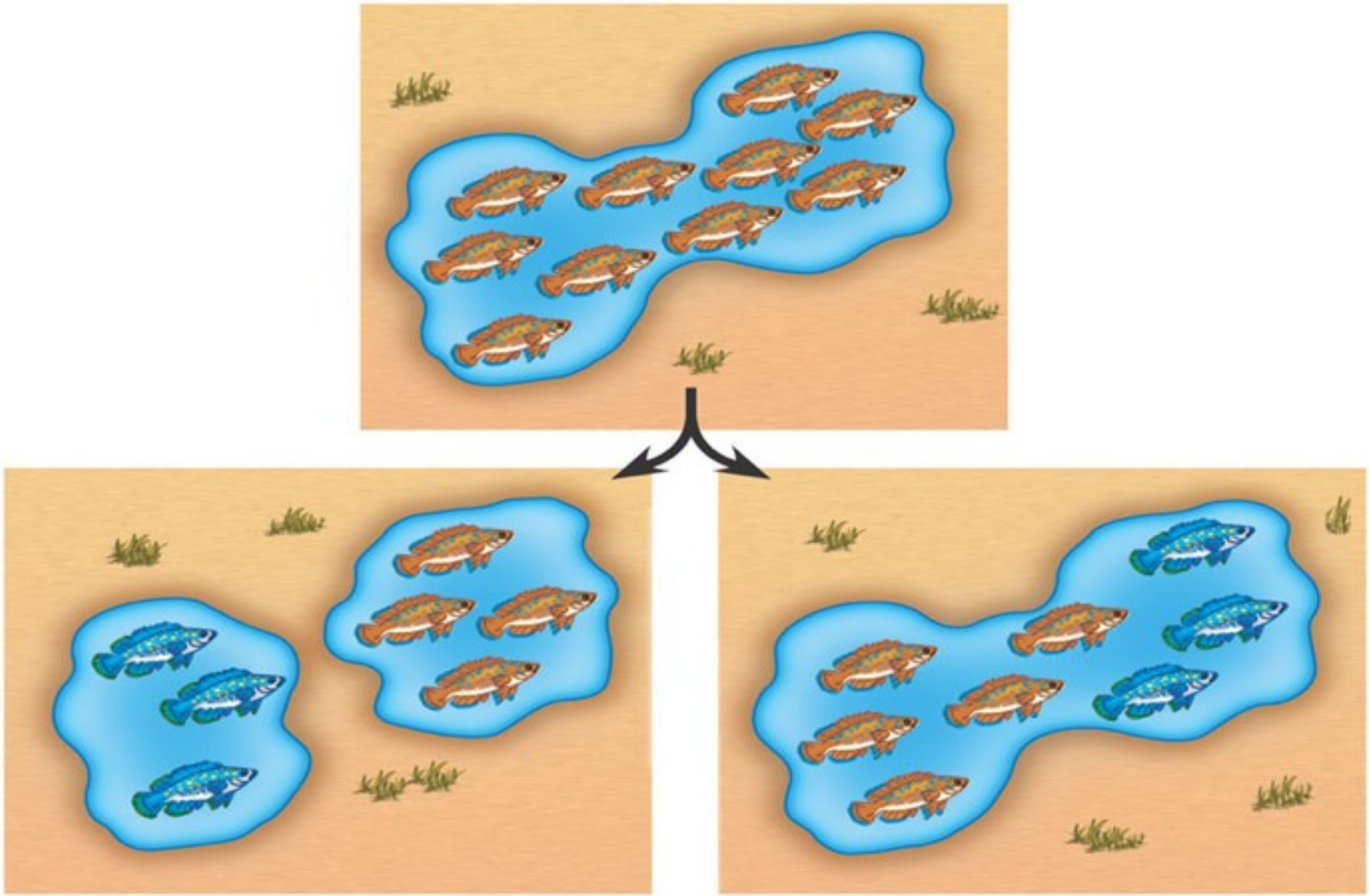
II. Main Idea

Speciation or the generation of new species from existing ones, requires and interruption of gene flow between populations of the existent species.

"Creating New Species"

- Speciation occurs in two main ways depending on how gene flow is interrupted.
- **Allopatric speciation-** gene flow is interrupted when a population is divided *geographically isolated* into two subpopulations
- **Sympatric speciation-** gene flow is interrupted not by geographical isolation but rather polyploidy, habitat differentiation or sexual selection. The population splits into subpopulations even though they remain geographically in contact.

"Creating New Species"



Allopatric speciation. A population forms a new species while geographically isolated from its parent population.

Sympatric speciation. A small population becomes a new species without geographic separation.

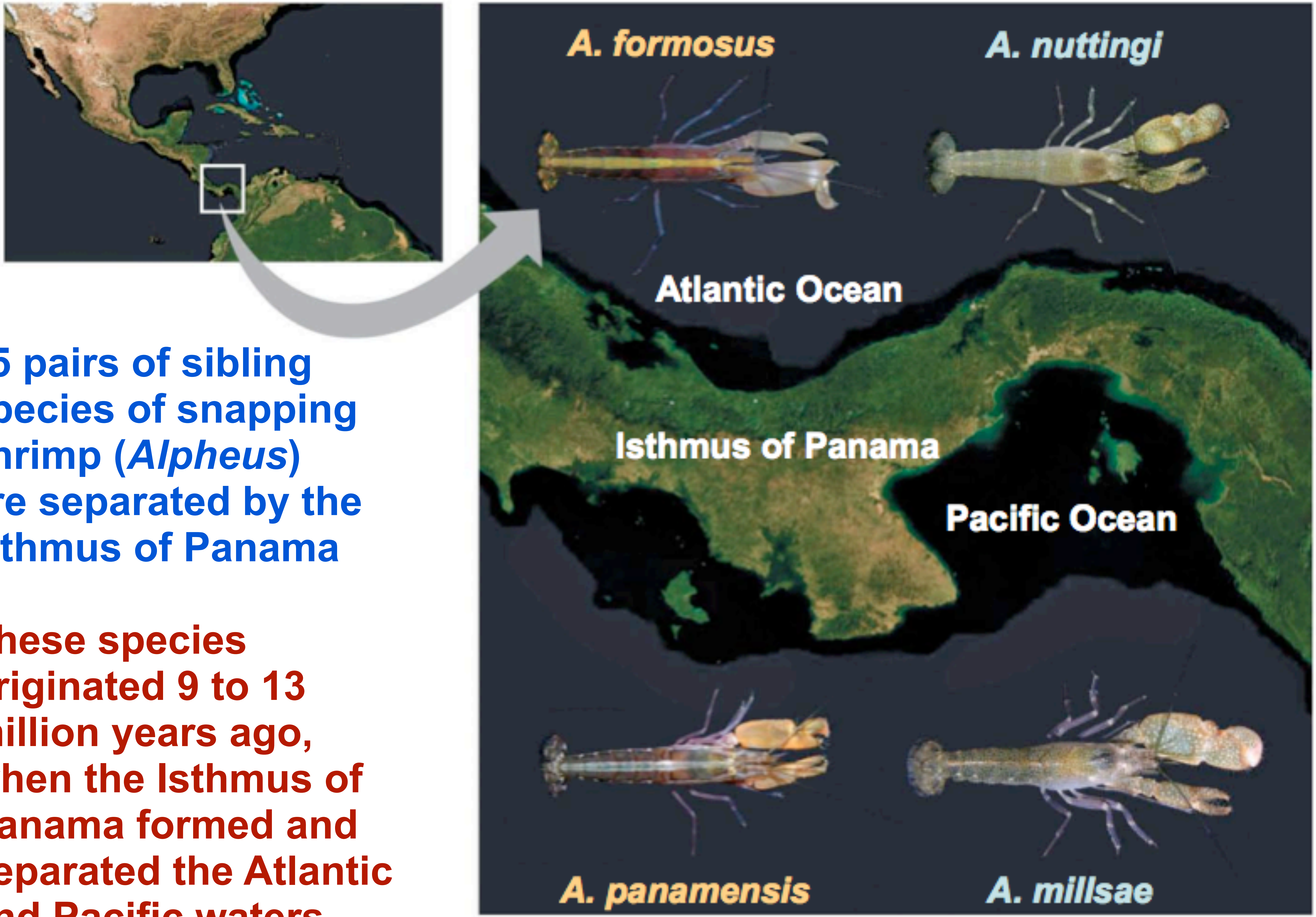
"Allopatric Speciation"

- "Physically" interrupted gene flow is the easiest and most common way to generate a new species.
- Obviously the degree of geographical isolation needed to create a new species will vary depending on the populations motility.

The grand canyon is enough to stop gene flow between chipmunks. Would it separate a population of birds? NO

“Allopatric Speciation”

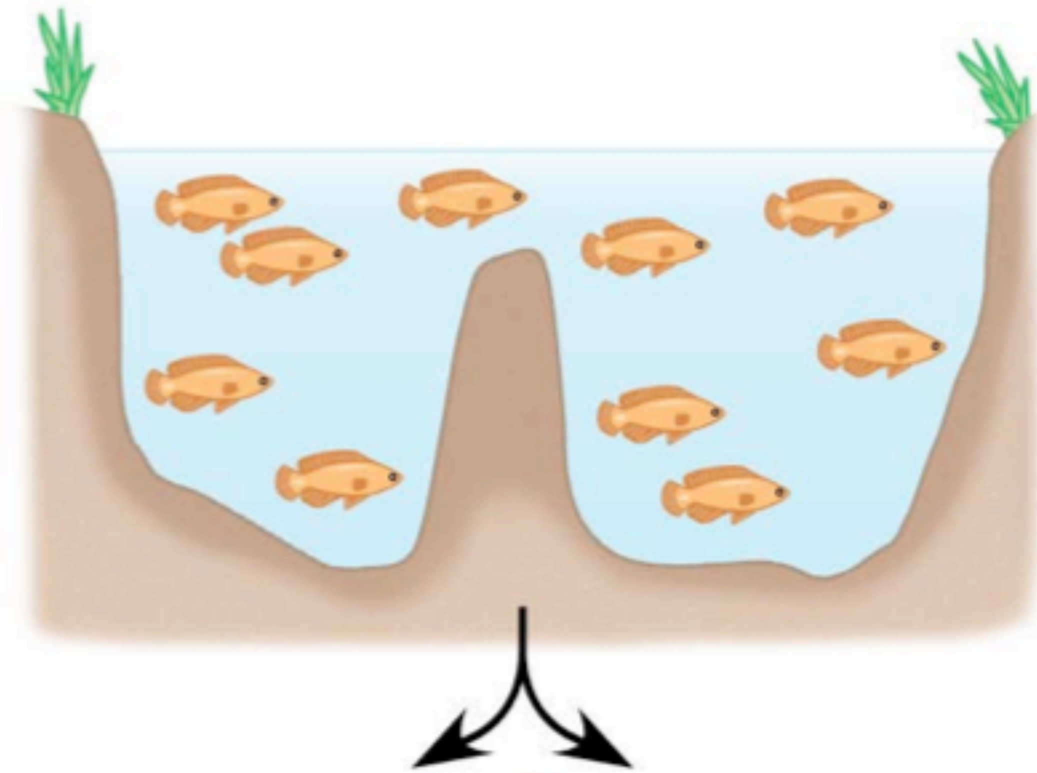
- Once gene flow is interrupted, the two separate populations may diverge.
  - different mutations
  - natural and sexual selection
  - genetic drift
- With enough time any of one or combination of these factors can dramatically change the gene pools enough that if gene flow is reestablished the members of each subpopulation are longer able to produce viable, fertile offspring.



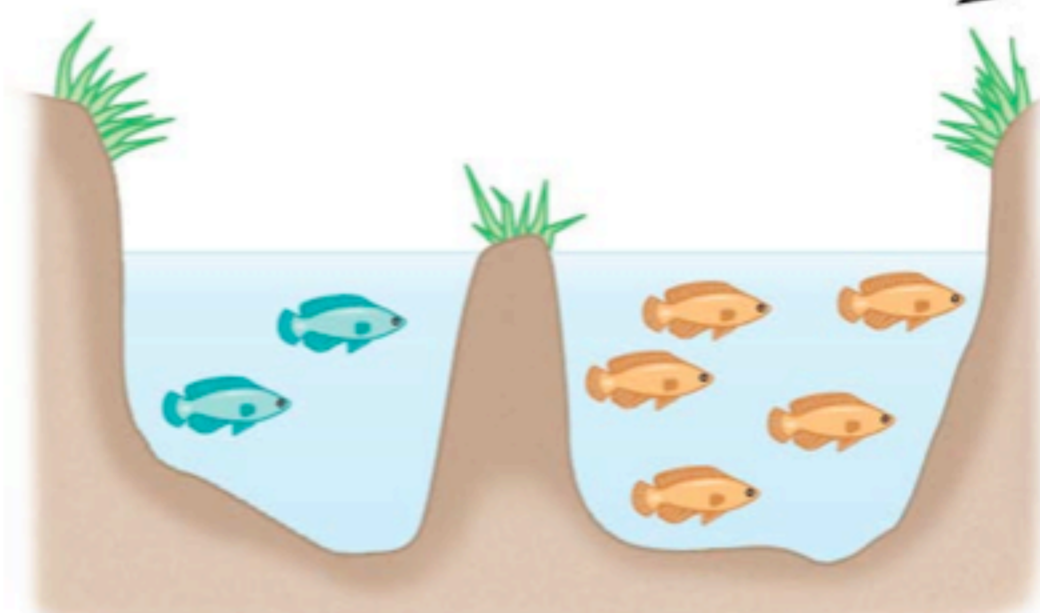
15 pairs of sibling species of snapping shrimp (*Alpheus*) are separated by the Isthmus of Panama

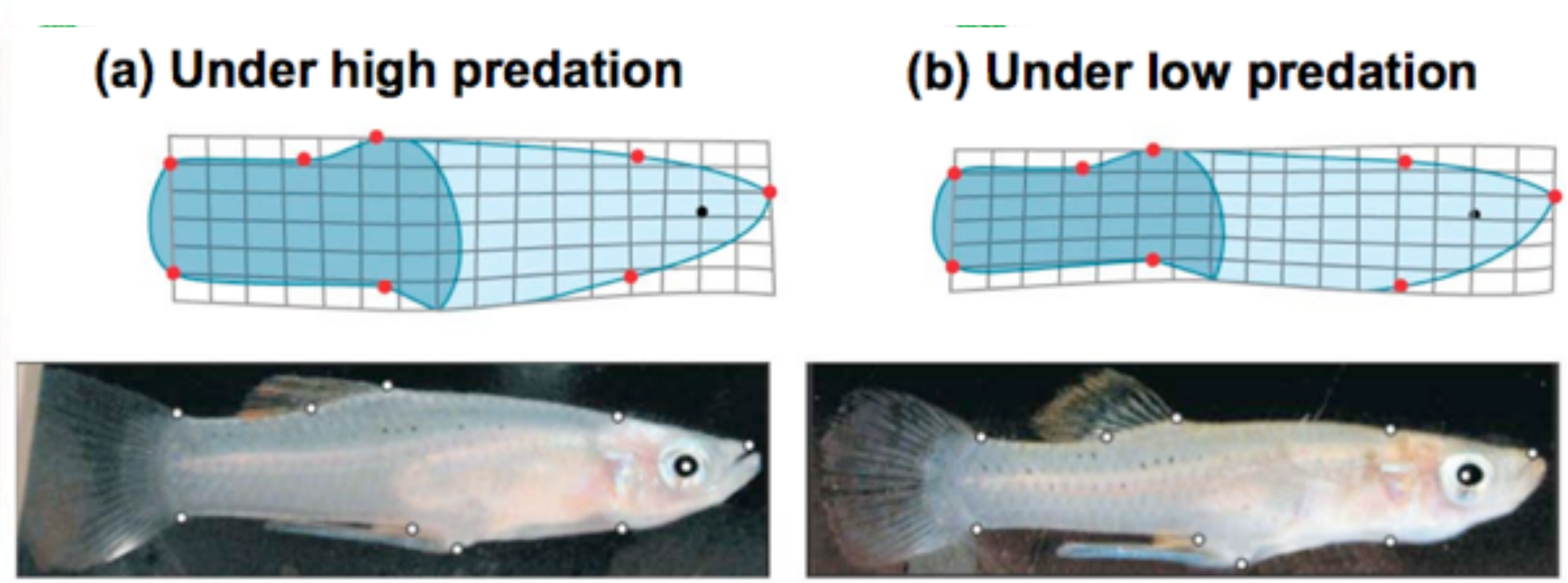
These species originated 9 to 13 million years ago, when the Isthmus of Panama formed and separated the Atlantic and Pacific waters

Evidence of Allopatric Speciation



Andros Island, Bahamas Mosquitofish (Gambusia hubbsi) colonized a series of ponds that later become isolated from each other. New ponds are all very similar except some ponds contain predatory fish while others do not.

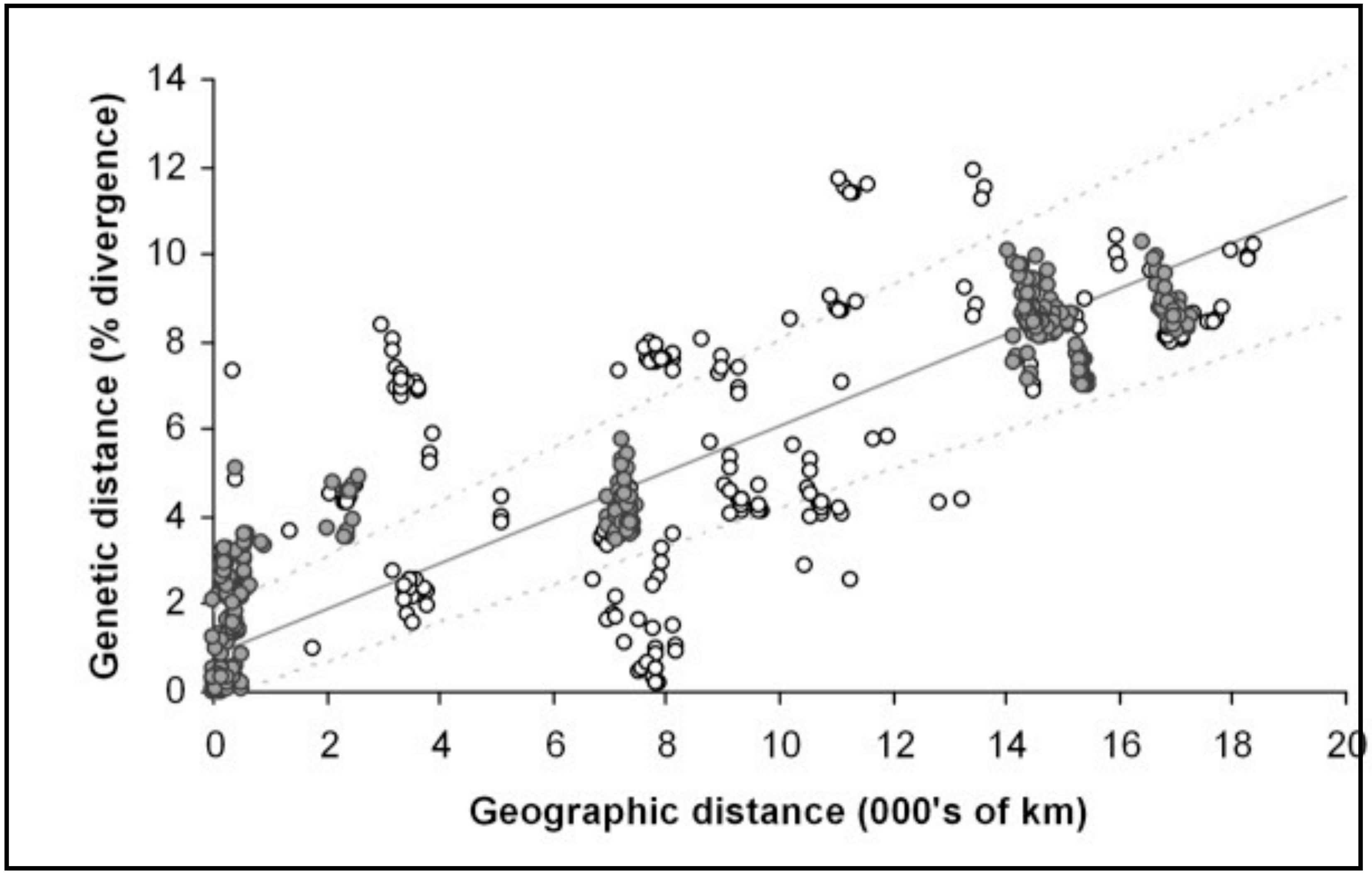




After bringing fish back together researchers found that the fish from different ponds no longer mated with one another apparently due to morphological differences or other unseen changes.

FIELD EVIDENCE: Allopatric Speciation

- Many studies, in the **FIELD** provide evidence for allopatric speciation.

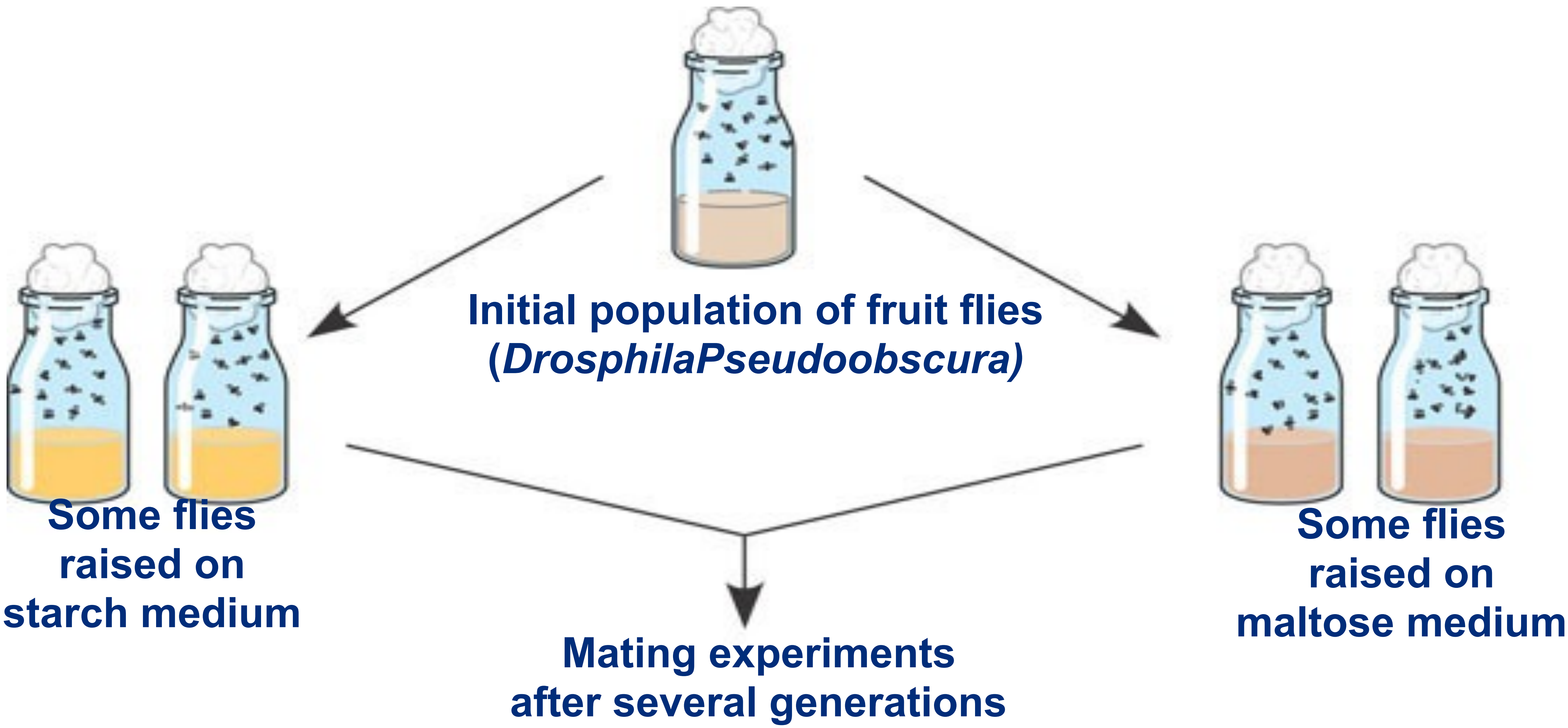


In almost all cases the *longer and farther* two populations are apart the greater the likelihood intrinsic isolation will occur.

LAB EVIDENCE: Allopatric Speciation

EXPERIMENT

Diane Dodd, of Yale University, divided a fruit-fly population, raising some populations on a starch medium and others on a maltose medium. After many generations, natural selection resulted in divergent evolution: Populations raised on starch digested starch more efficiently, while those raised on maltose digested maltose more efficiently. Dodd then put flies from the same or different populations in mating cages and measured mating frequencies.



RESULTS

When flies from "starch populations" were mixed with flies from "maltose populations,"the flies tended to mate with like partners. In the control group, flies taken from different populations that were adapted to the same medium were about as likely to mate with each other as with flies from their own populations.

Mating frequencies in experimental group

Male \ Female	Starch	Maltose
Starch	22	9
Maltose	8	20

Mating frequencies in control group

Male \ Female	Same population	Different populations
Same population	18	15
Different populations	12	15

CONCLUSION

The strong preference of "starch flies" and "maltose flies" to mate with like-adapted flies, even if they were from different populations, indicates that a reproductive barrier is forming between the divergent populations of flies. The barrier is not absolute (some mating between starch flies and maltose flies did occur) but appears to be under way after several generations of divergence resulting from the separation of these allopatric populations into different environments.

"Allopatric Speciation"

- A point of emphasis... geographical isolation by itself does not lead to reproductive isolation, reproductive isolation has to become *intrinsic* for speciation to take place.
  - females choose certain male traits
  - receptors on gametes no longer "fit"
  - organisms mate at different times of the year

think of the reproductive isolating barriers we just looked a few slides back, geographic isolation has to lead to one or more of those in order for speciation to occur

Sympatric Speciation

- In **sympatric speciation**, speciation occurs in populations that live in the same geographic area.
- Although contact between populations makes gene flow more common, none the less gene flow can be cut off between two populations that remain in close proximity.
- Sympatric Speciation relies on:
  - *Polyploidy*
  - *Habitat Differentiation*
  - *Sexual Selection*

Polyploidy

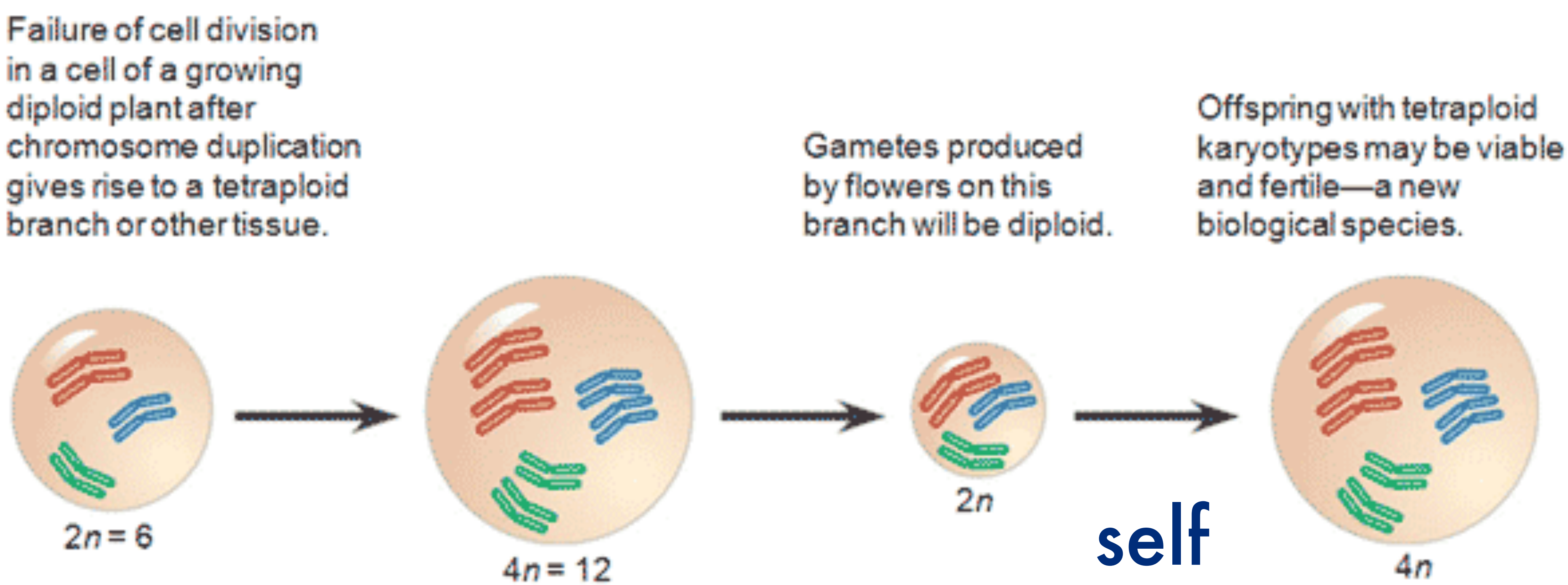
- New species arise due to a mistake in cell division that results in an extra set chromosomes, a condition called polyploidy.
- Polyploidy can happen in animals but is far more common in plants.
  - Nearly 80% of plant species today descended from ancestors that formed by polyploidy.
  - There are two distinct forms of polyploidy:
    - Autopolyploidy
    - Allopolyploidy

Autopolyploidy

- Autopolyploid species 2 or more extra sets chromosomes, derived from a single species.

One way this could happen...

mitotic error

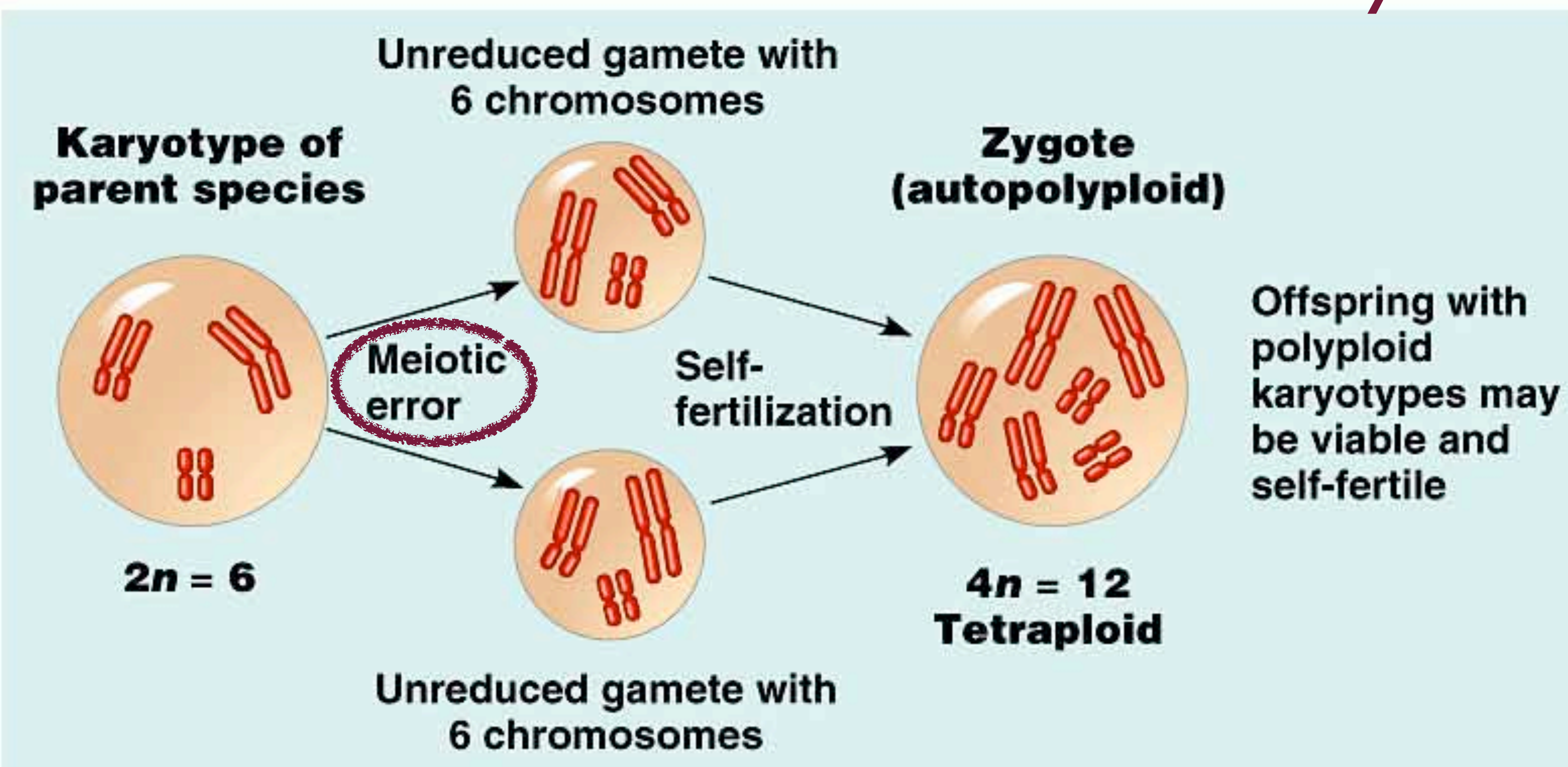


self fertilization

Autopolyploidy

- Autopolyploid species 2 or more extra sets chromosomes, derived from a single species.

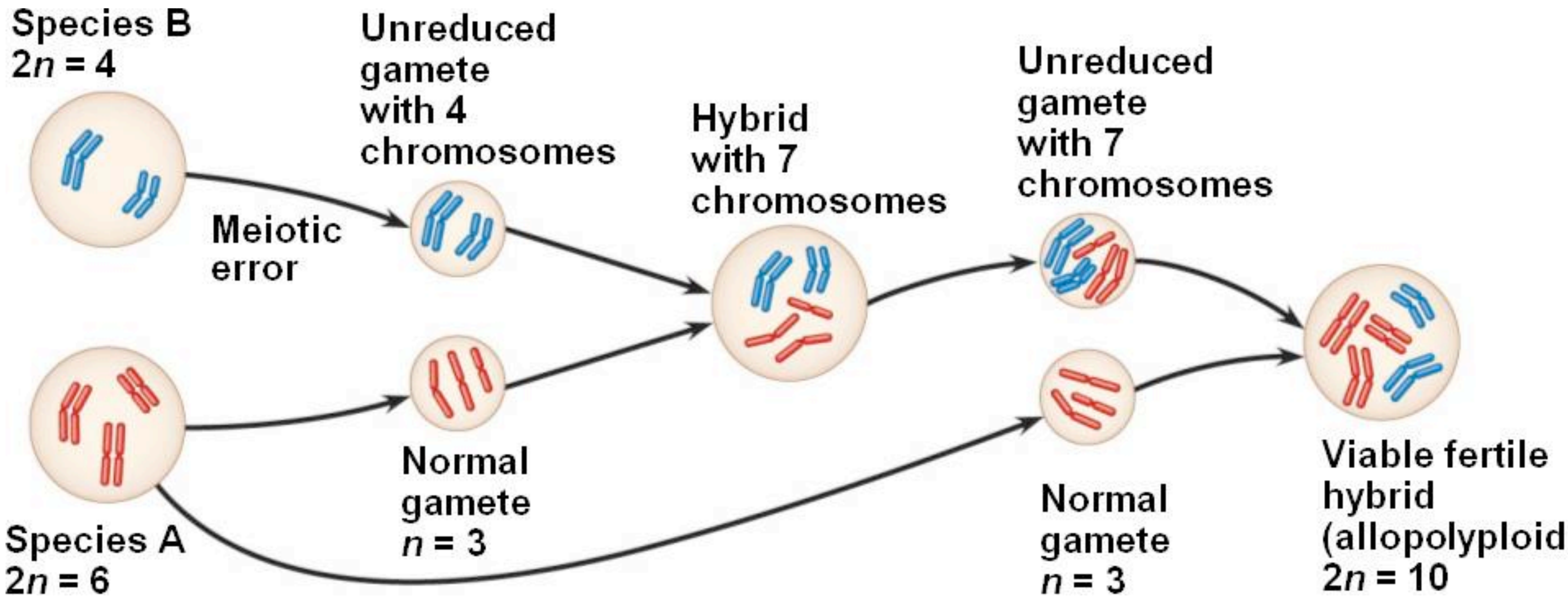
another way...



Allopolyploidy

- Two different species interbreed and produce hybrid offspring.
- Hybrids are sterile but plants can still reproduce asexually
- Mistakes in cellular division in later generations changes the sterile hybrid into a fertile polyploid called an alloploid.
- Alloploids can mate with either parent species or each other but not the hybrids, they are now a new species.
  - *Although relatively rare some important plant crops are polyploids*

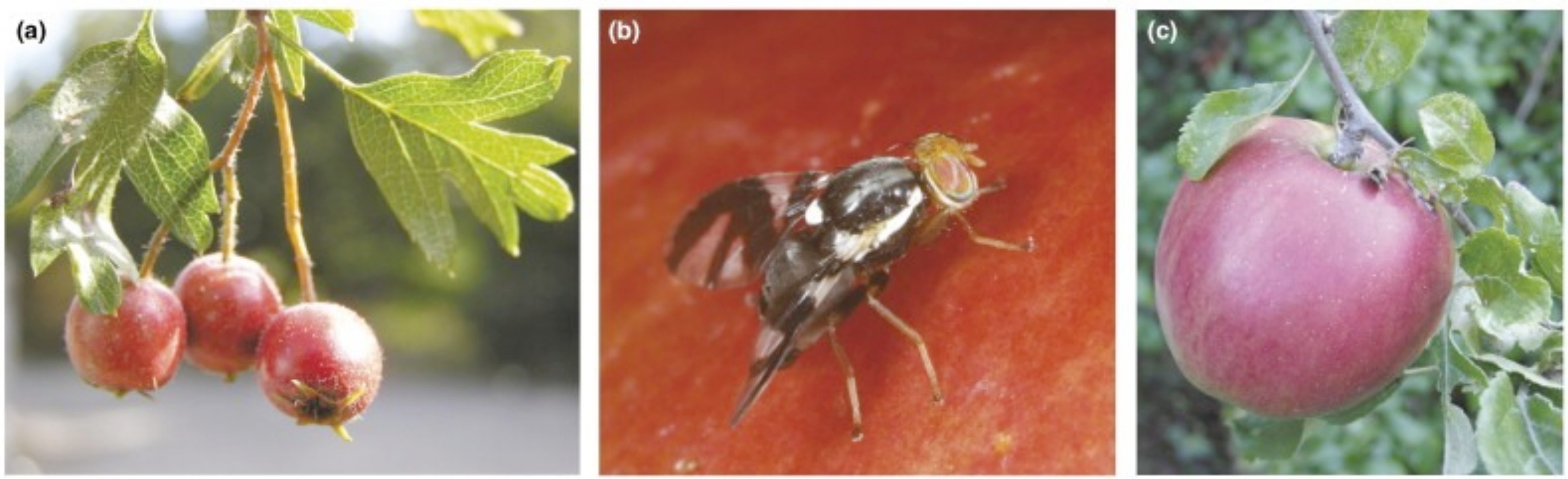
Allopolyploidy



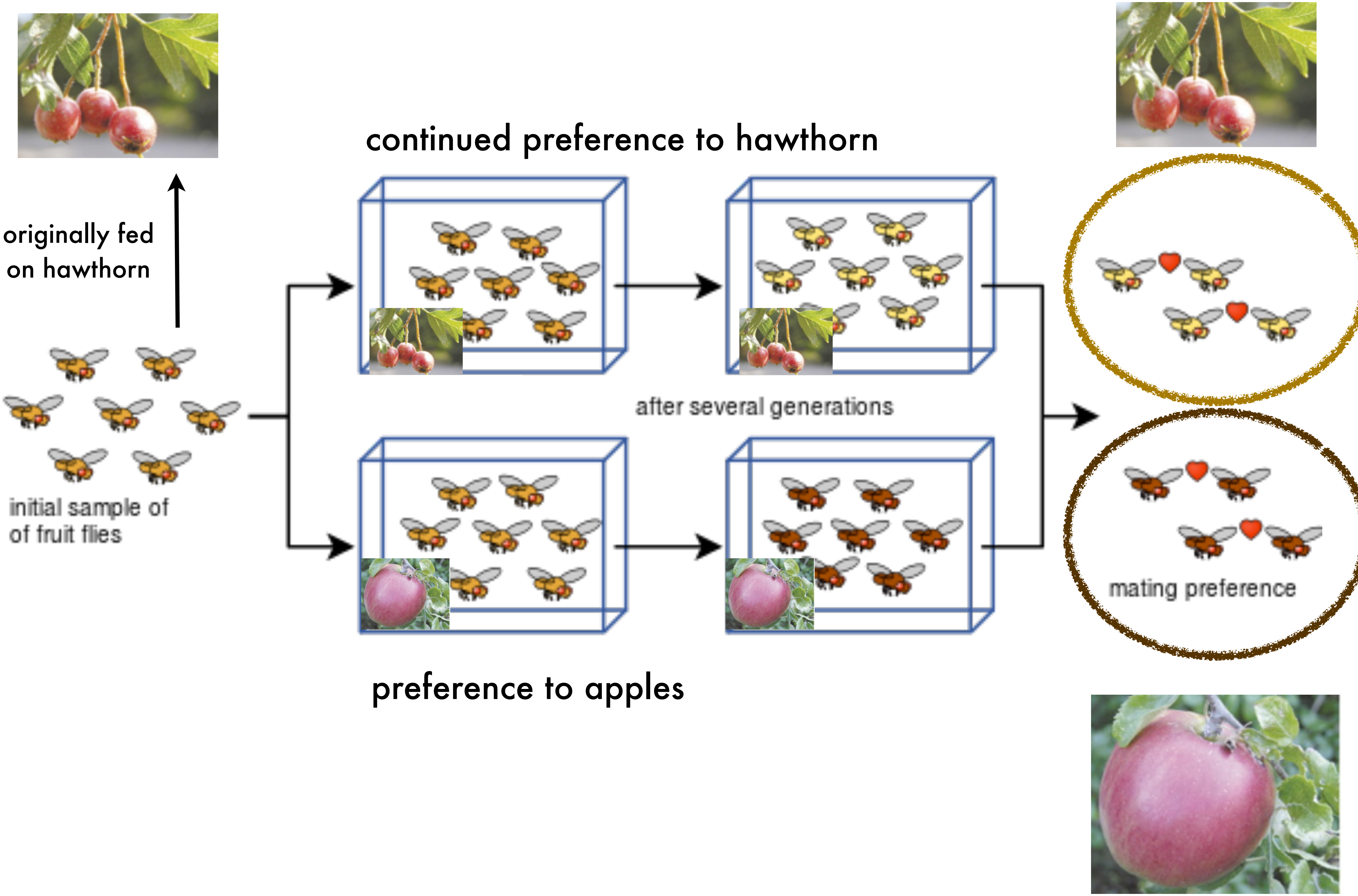
Today plant geneticists induce these errors using chemicals in the lab, researchers can intentionally produce new hybrids with a combination of desired traits found in both parent species.

Habitat Differentiation

- Sympatric speciation can also occur when a subpopulation exploits a habitat or resource not used by the parent population



Habitat Differentiation

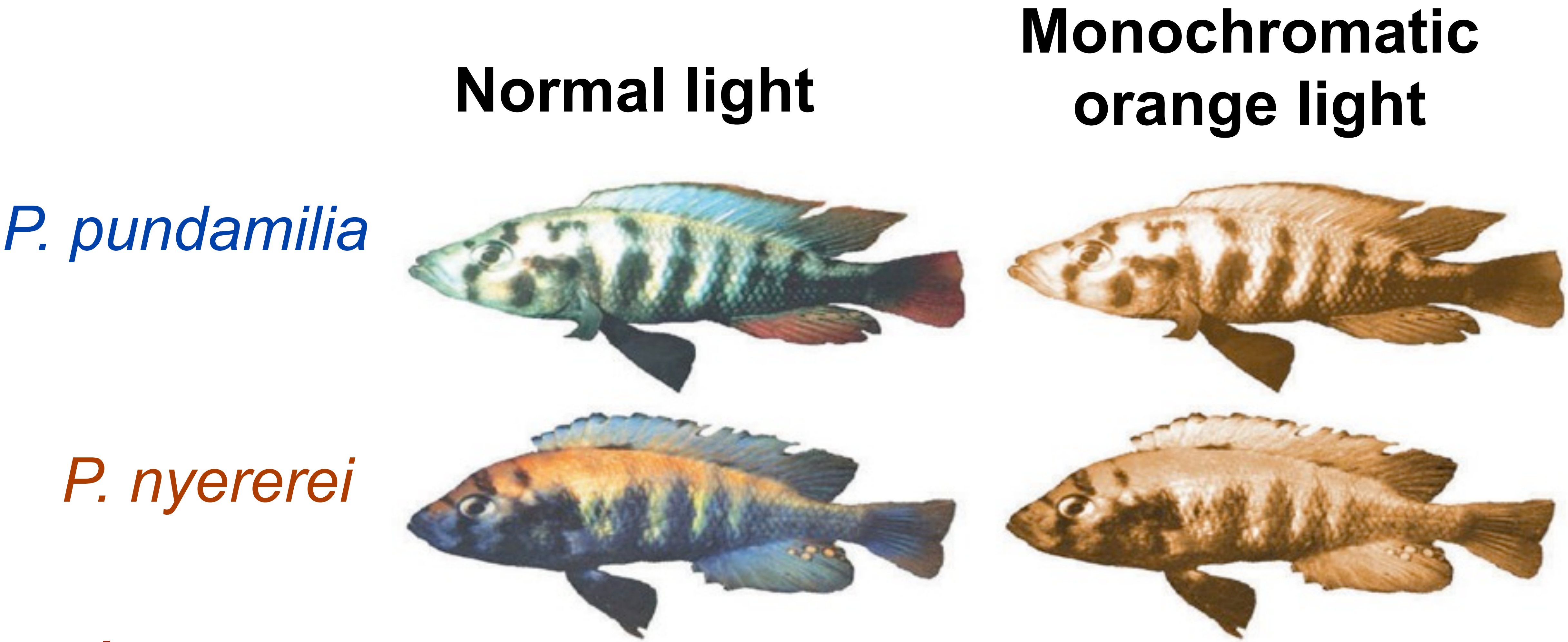


Sexual Selection

- East Africa's Lake Victoria, is home to over 600 species of cichlids.
- Genetic data suggests that these species originated from a small number of colonizing species.
- Some of these 600 species originated as a result of different food choices.
- Evidence suggests that others originated as a result of mate choice or **sexual selection**.

Experiment

Researchers from the University of Leiden placed males and females of *Pundamilia pundamilia* and *P. nyererei* together in two aquarium tanks, one with natural light and one with a monochromatic orange lamp. Under normal light, the two species are noticeably different in coloration; under monochromatic orangelight, the two species appear identical in color. The researchers then observed the mating choices of the fish in each tank.



Results

Under normal light, females of each species mated only with males of their own species. But under orange light, females of each species mated indiscriminately with males of both species. The resulting hybrids were viable and fertile.

	Normal light	Monochromatic orange light
P. pundamilia		
P. nyererei		

Conclusion

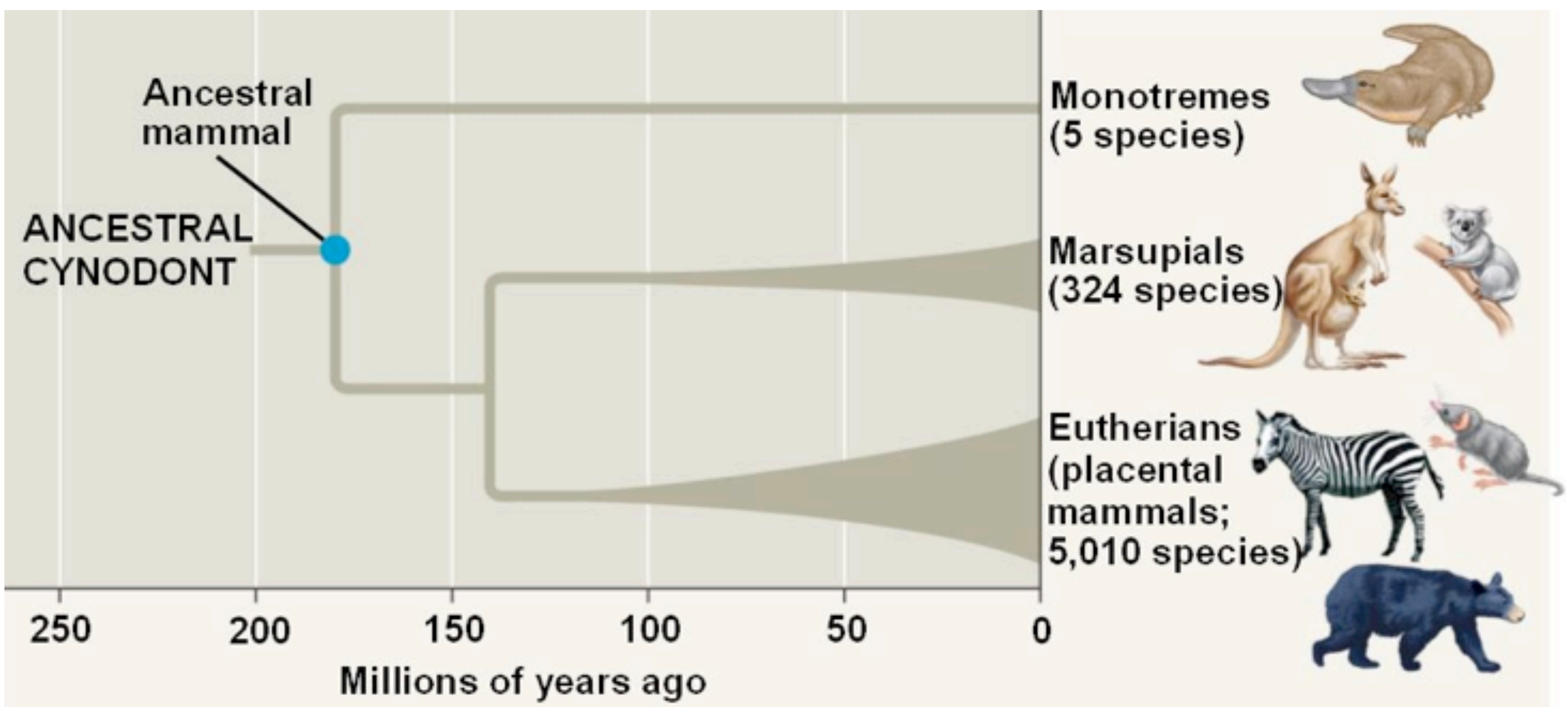
The researchers concluded that mate choice by females based on coloration is the main reproductive barrier that normally keeps the gene pools of these two species separate. Since the species can still interbreed when this prezygotic behavioral barrier is breached in the laboratory, the genetic divergence between the species is likely to be small. This suggests that speciation in nature has occurred relatively recently.

"Adaptive Radiations"

- Sometimes we see explosions of many new species all at once.
- **Adaptive Radiation**- are periods of evolutionary change in which groups of organisms form many new species whose adaptations allow them to fill different ecological niches
  - these radiations have been documented on a large worldwide scale
  - these radiations have been documented on a small regional scale

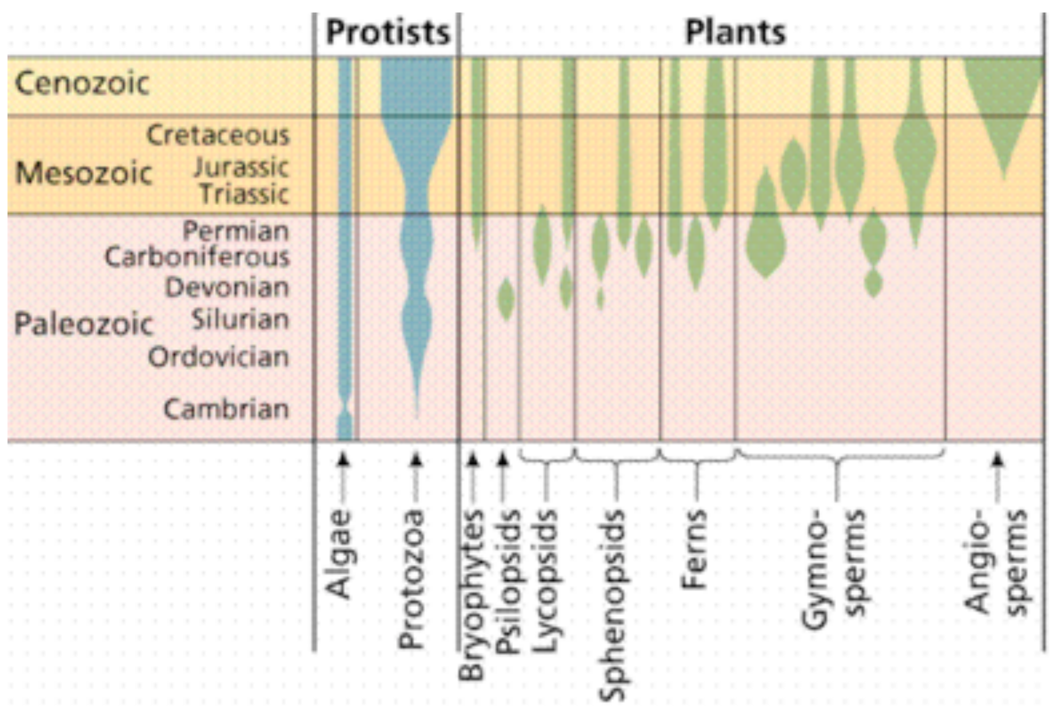
“Large, Worldwide Radiations”

- **Large scale adaptation radiations occurred after the big five mass extinctions.**
  - The number and diversity of mammals exploded after the dinosaurs went extinct.
    - *even though mammals first evolved 180 mya they lacked diversity and remained small*



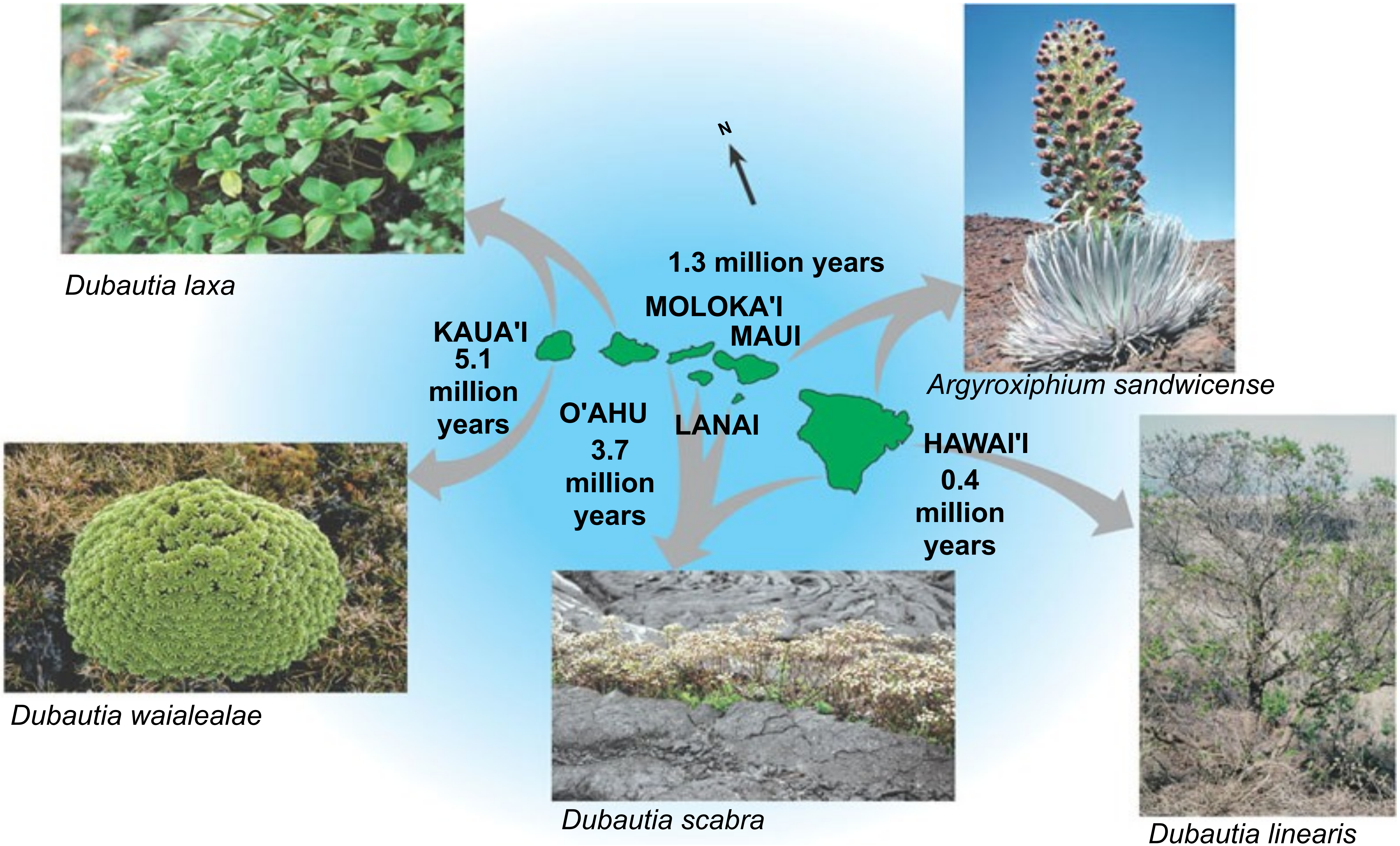
"Large, Worldwide Radiations"

- **Large scale adaptation radiations often occurred after major evolutionary innovations.**
  - Radiations followed the rise of photosynthetic prokaryotes, evolution of large predators during the cambrian explosion and the colonization of land by plants.
    - *key adaptations allowed plants to explode and diversify on land which consequently led to the explosion of insect diversity that remains today*



"Small Regional Radiations"

These plants are part the "silversword" alliance. All these plants descended from a common ancestor "tarweed" that first arrived in Kaua'i from North America nearly 5 million years ago



"Small Regional Radiations"

- **Hawaiian Archipelago**
  - Tarweed seed / spores land on the first hawaiian island Kauai ~5 mya.
    - *little competition and abundant resources*
  - tarweed spreads, adapts & diversifies across Kauai and onto Oahu the next island formed in the chain
    - *this pattern continues with each successive island formed and with varying elevations and climate on each island the tarweed diversified into numerous and very different species*

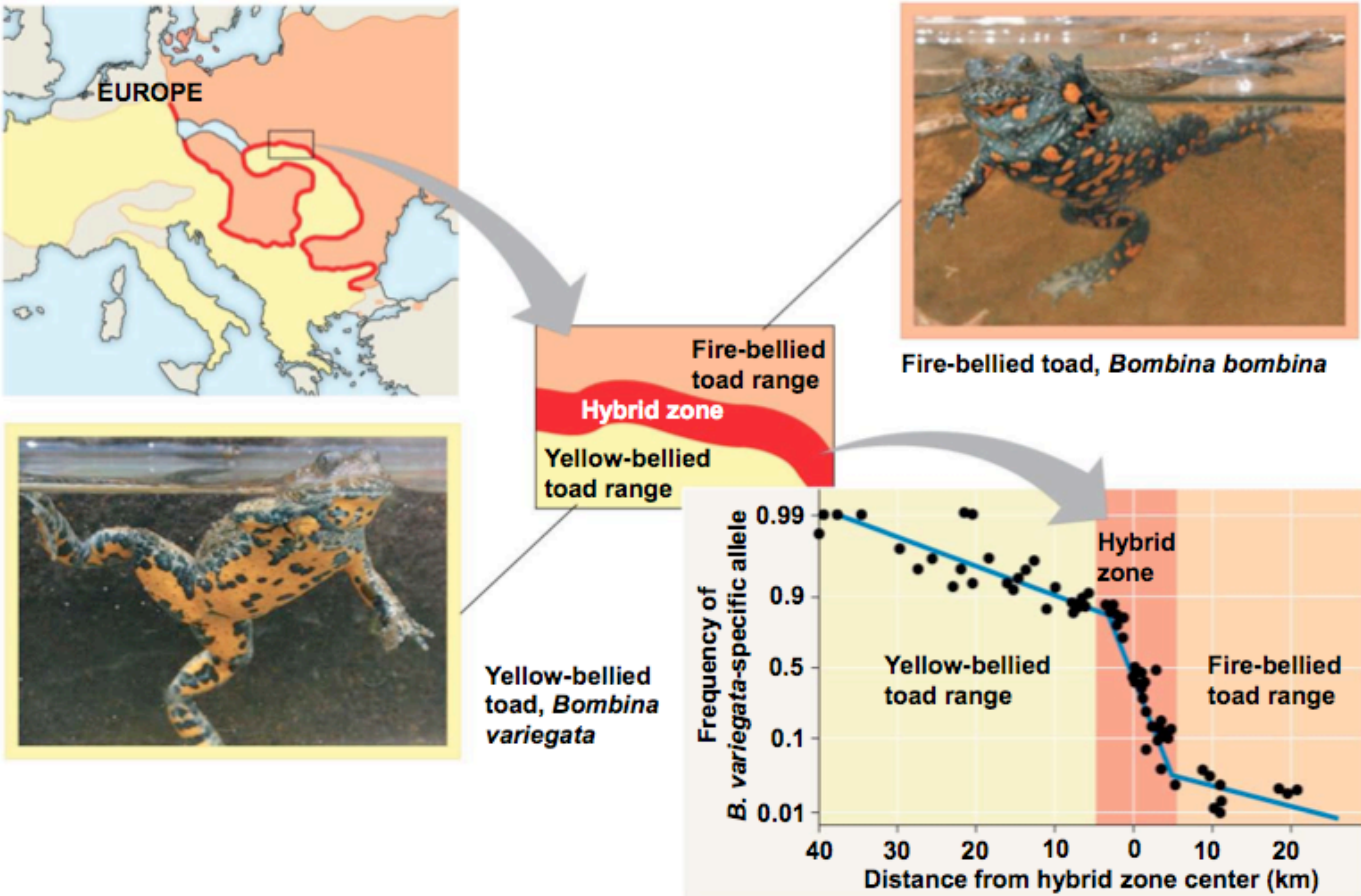
ORIGIN OF SPECIES

III. Main Idea

Hybrid zones occur when different species meet and mate, producing some offspring of mixed ancetsry.

Patterns within Hybrid Zones

- **Hybrid Zone-** a region in which members of different species meet and mate, producing *some* offspring of mixed ancestry.
- Hybrid zones can have simple or complex patterns.
- Many plant species have a complicated patterns that occur in irregular "patches" across the landscape with particular sets of conditions.
- Other hybrid zones occur as simple narrow bands like the example of on the next slide.


EUROPE
Fire-bellied toad range
Hybrid zone
Yellow-bellied toad range
Fire-bellied toad, *Bombina bombina*
Yellow-bellied toad, *Bombina variegata*
Frequency of *B. variegata*-specific allele
0.99
0.9
0.5
0.1
0.01
Hybrid zone
Yellow-bellied toad range
Fire-bellied toad range
40 30 20 10 0 10 20
Distance from hybrid zone center (km)

Patterns within Hybrid Zones

What causes this pattern of allele frequencies across a hybrid zone?

- Hybrid toads have increased embryonic mortality and morphological abnormalities.
- Since hybrids have poor survival and reproductive rates, they produce few viable offspring.
- As a result hybrid toads rarely serve a conduit that passes alleles from species to another.
- Outside the hybrid zone natural selection may be acting on different traits within the parent species keeping them genetically different.

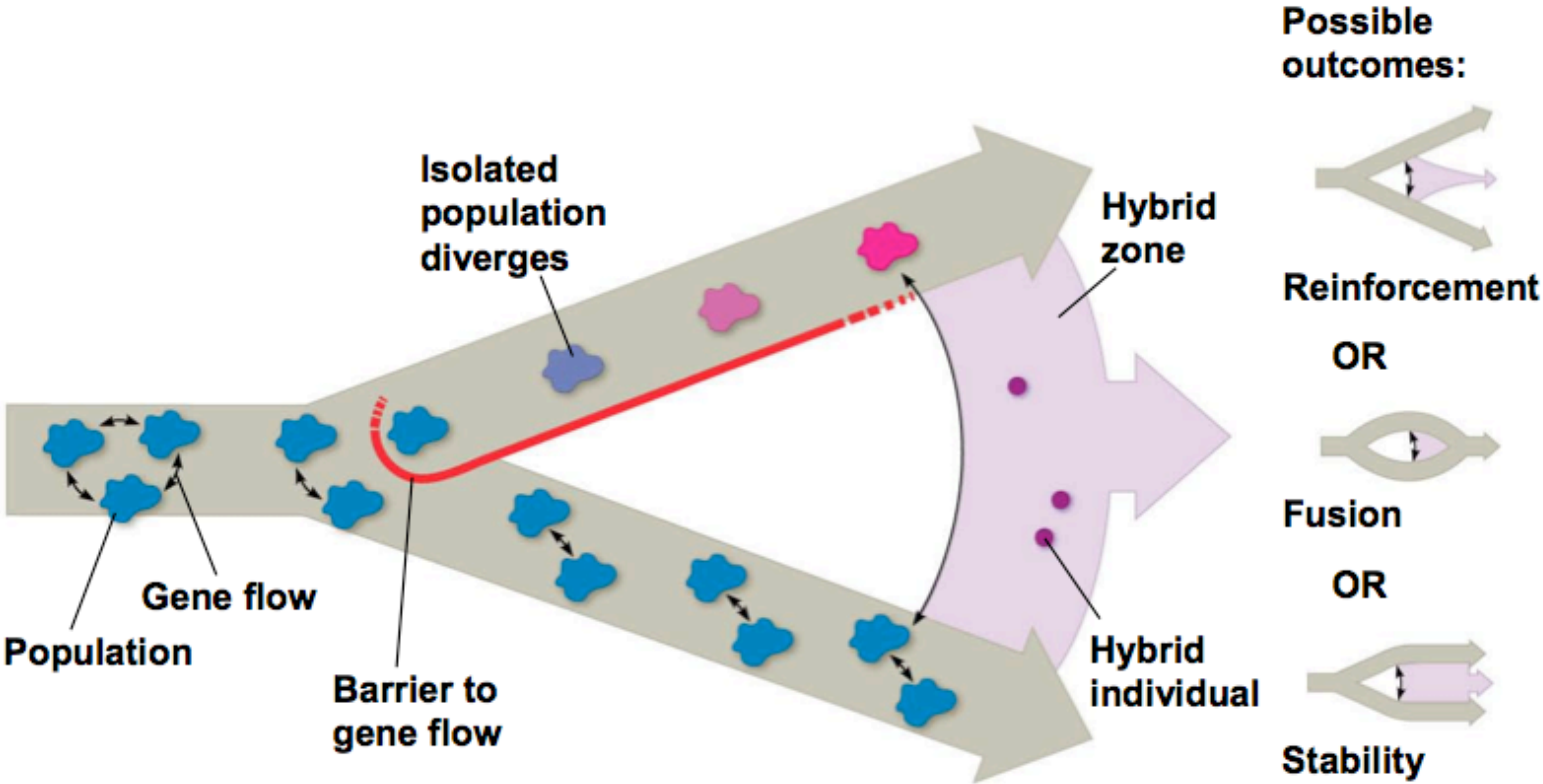
Hybrid Zones Over Time

What will become of the hybrids over time?

- Option 1: The hybrids become isolated from parent species and form their own new species.

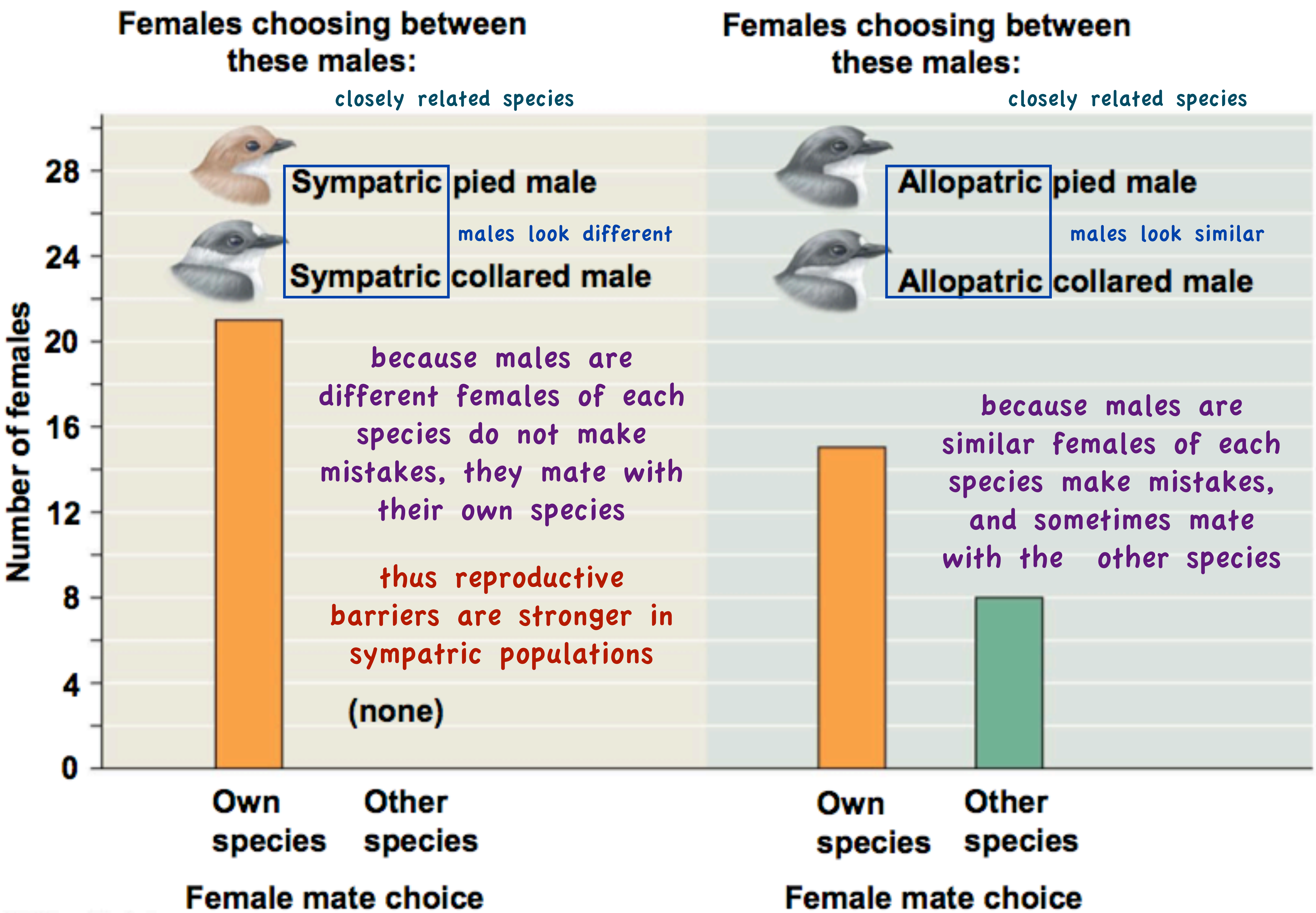
OR

- Option 2: **Reinforcement**, hybrids gradually cease to be formed.
- Option 3: **Fusion**, the hybrids bring together the two parent species and they become one.
- Option 4: **Stability**, we maintain the hybrid zone over time (no change).


Possible
outcomes:
Isolated
population
diverges
Hybrid
zone
Reinforcement
OR
Fusion
OR
Gene flow
Population
Barrier to
gene flow
Hybrid
individual
Stability

Reinforcement:
Strengthening Reproductive Barriers

- When hybrids are less fit than members of the parent species,
- we might expect natural selection to strengthen the prezygotic barriers to reproduction
- thus reducing the number of hybrids over time.
- Because this process "reinforces" reproductive barriers, it is called **reinforcement**.


Females choosing between these males:
closely related species
Sympatric pied male
males look different
Sympatric collared male
because males are different females of each species do not make mistakes, they mate with their own species
thus reproductive barriers are stronger in sympatric populations
(none)
Females choosing between these males:
closely related species
Allopatric pied male
males look similar
Allopatric collared male
because males are similar females of each species make mistakes, and sometimes mate with the other species
Number of females
0
4
8
12
16
20
24
28
Own species
Other species
Female mate choice
Own species
Other species
Female mate choice

Fusion: Weakening Reproductive Barriers

- When reproductive barriers are weak, gene flow may occur so much that the two parent populations become one.
- 200 of the 600 cichlid species have been lost over the last thirty years
  - some were naturally driven to extinction by predators like the Nile perch but many were lost as a result of fusion.

Females sexually selected males by color when water was clear

Pundamilia nyererei

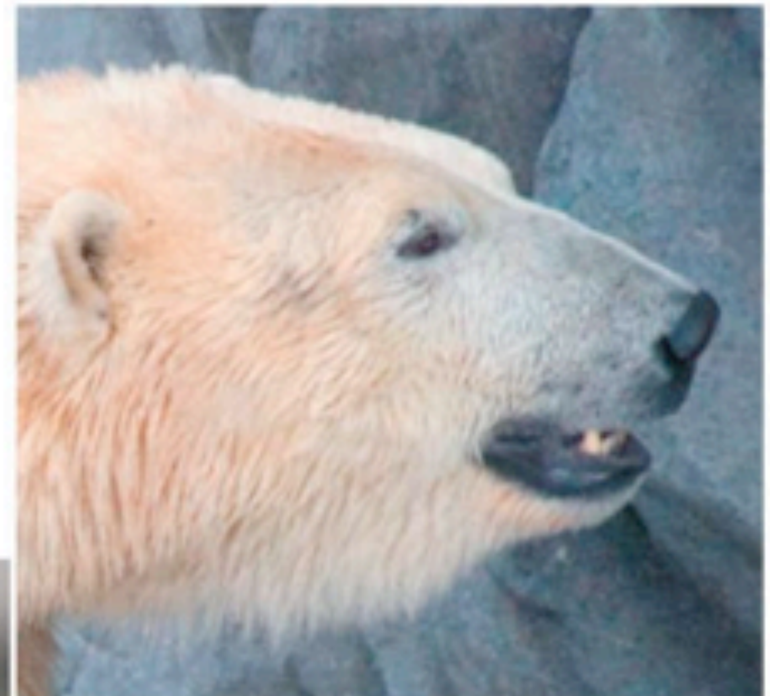
Pundamilia pundamilia

***Pundamilia* "turbid water,"**
hybrid offspring from a location with turbid water

Pollution has caused the water to become murky and females are no longer able to distinguish between color of males

Grizzly bear *(U. arctos)*

Polar bear *(U. maritimus)*



Hybrid “grolar bear”

A similar story may be happening to the polar bears at this time

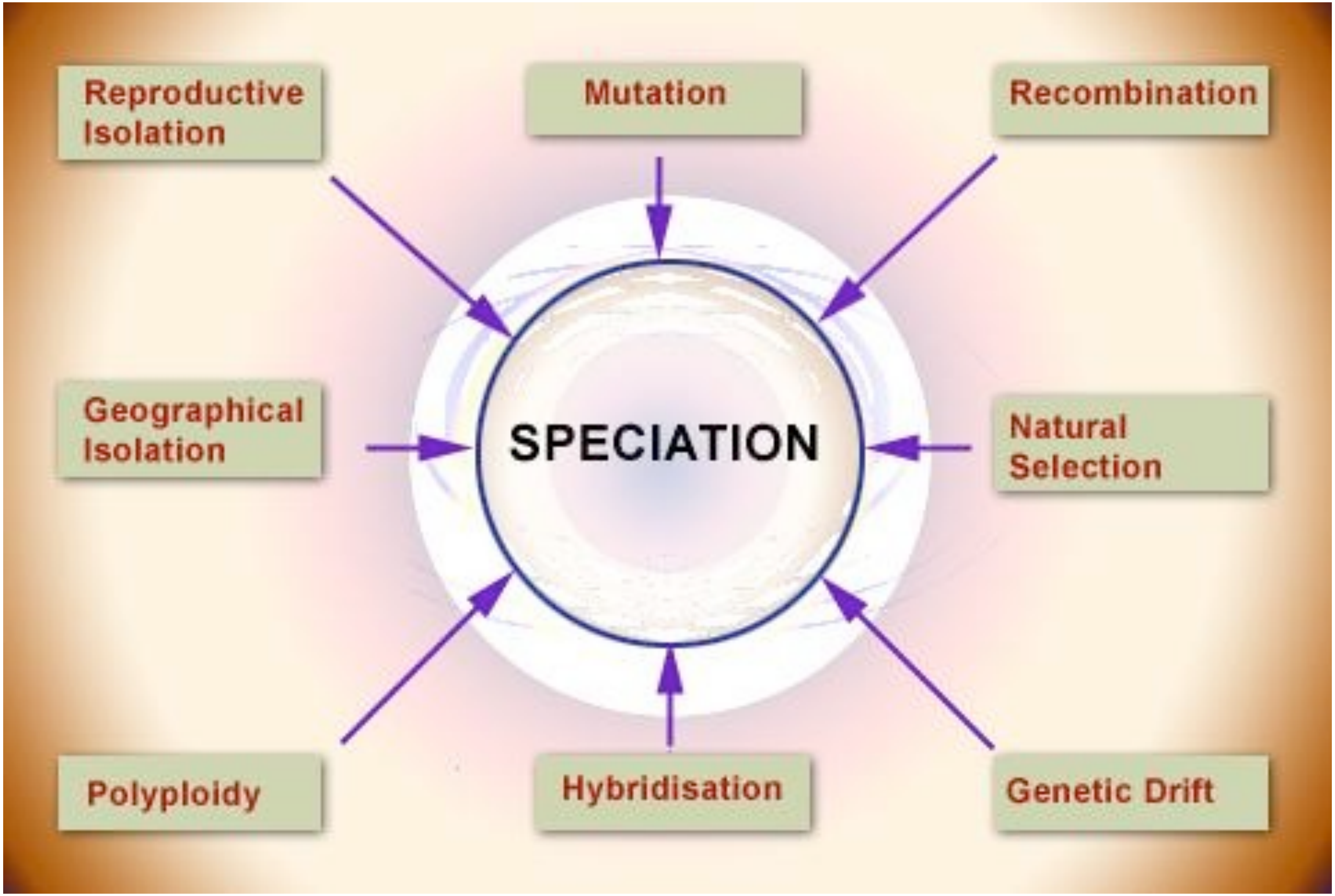
Grizzly/Polar bear hybrids have been documented (in the wild)

Can you form a hypothesis for how and why this occurring? Which species is at risk for extinction? Why?

Stability: Continuation of Hybrids

- Many hybrid zones are stable and continue to exist.
- Consider the *Bombina* toad example this hybrid zone has existed for over 20 years, likely explained by the narrow nature of the zone.
  - You see since the zone is so narrow each parent species runs into each other with such frequency that it maintains gene flow but hybrids are so poor that fusion can not take place.
  - On the other hand if the zone was wide there might be limited enough gene flow in the middle to allow reinforcement.

IN REVIEW



Reproductive Isolation
Mutation
Recombination
Geographical Isolation
SPECIATION
Natural Selection
Polyploidy
Hybridisation
Genetic Drift

ORIGIN OF SPECIES

IV. Main Idea

Speciation varies greatly in both its rate and the number of changes that are required to separate a new species from its parent population.

"The Rate of Speciation"

- The time it takes for geographical isolation to lead to reproductive isolation depends on a number a variables.
  - which genes mutate, the rate of mutations, extent of genetic drift, degree of environmental differences between the populations, generation times
- Intrinsic reproductive isolation leading to speciation may take thousands or millions of years or it may happen virtually "over night".

Patterns in the Fossil Record

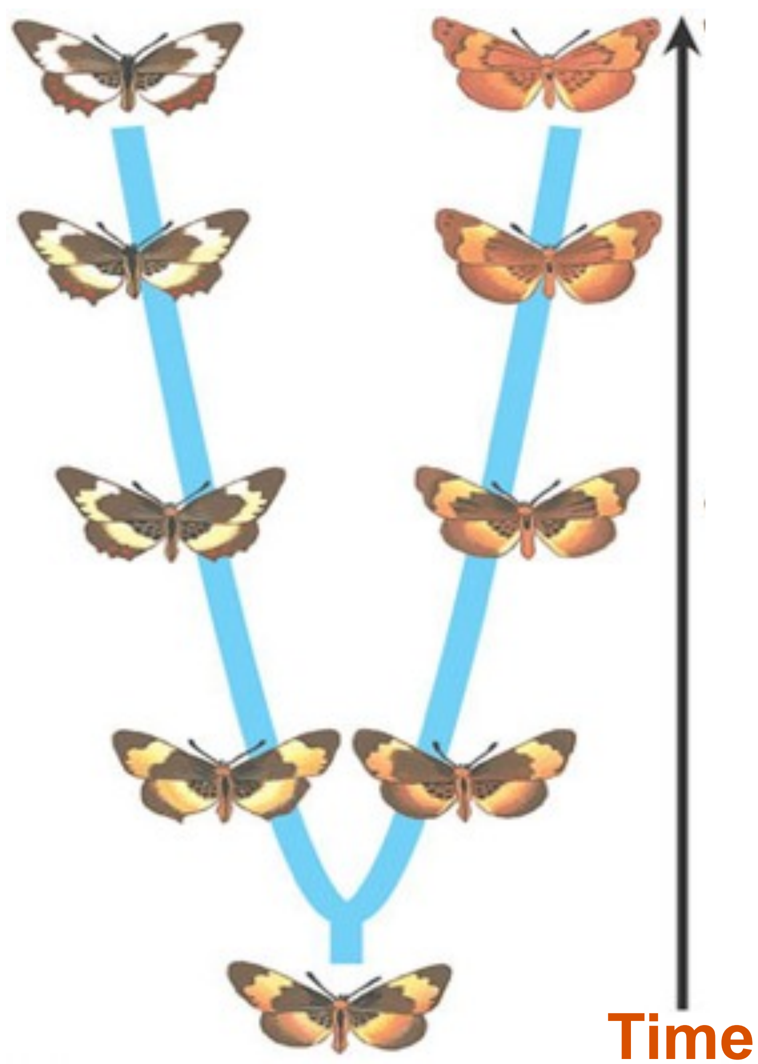
- The fossil record looks both static and dynamic.
- Some species appear in the fossil record virtually unchanged for over several strata (long time).
    - marine invertebrates
- While other species suddenly appear in the stratum, (short time)
    - ***punctuated equilibrium-Stephen Jay Gould***
- And yet others appear to gradually change over time.
    - ***gradualism-Charles Darwin***

Speciation Rates

- The fossil record and other experimental data suggest that speciation may occur relatively slowly (40 million years) or very quickly (4,000 years).
- The interval of time between speciation events includes the elapsed time from before populations of the newly formed species start to diverge + the time it takes for speciation to occur once divergence begins.
  - **On average speciation events occur at a rate of 6.5 million years and rarely less then 500,000 years.**

- Darwin described speciation as a gradual change over time.

Gradualism model. Species descended from a common ancestor gradually diverge more and more in their morphology as they acquire unique adaptations.

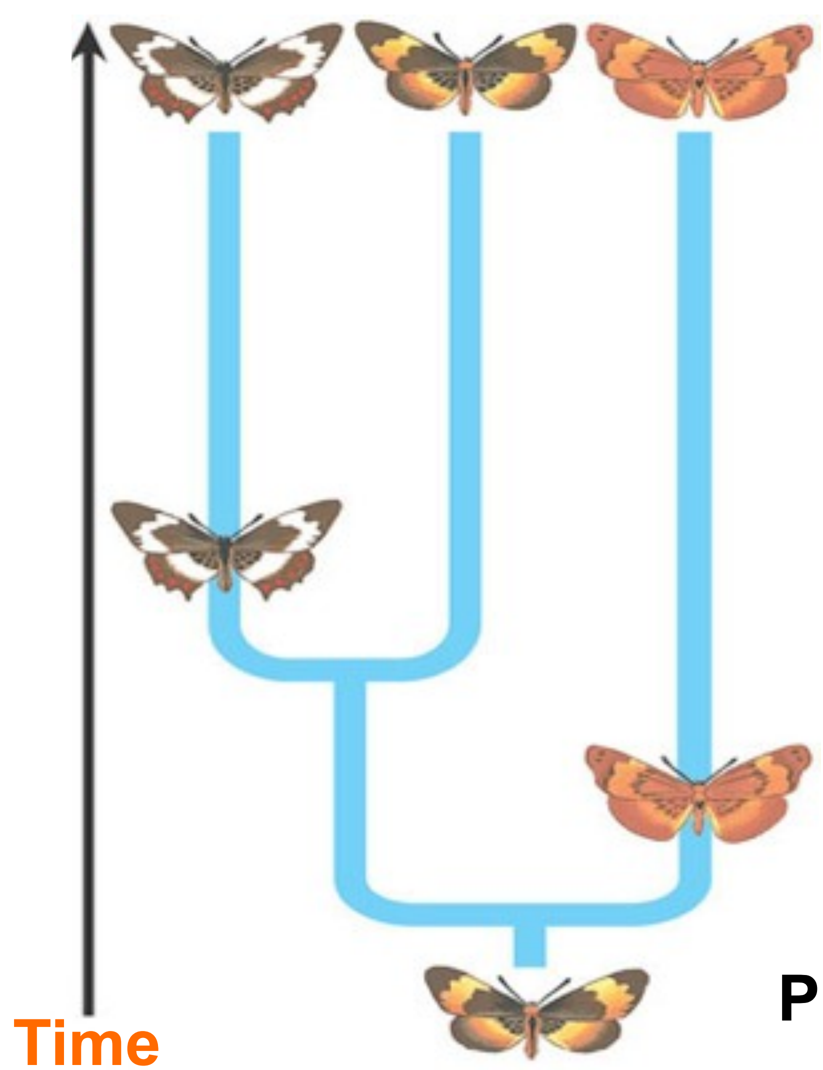


However a lot of fossil evidence looks very different from this.

- Contemporary biologists Stephen Jay Gould and Niles Eldridge proposed a different view of speciation.

Keep this in mind, say a species survives 5 million years, but the events that lead to speciation occur over 50,000 years, this is only 1% of its time on earth.

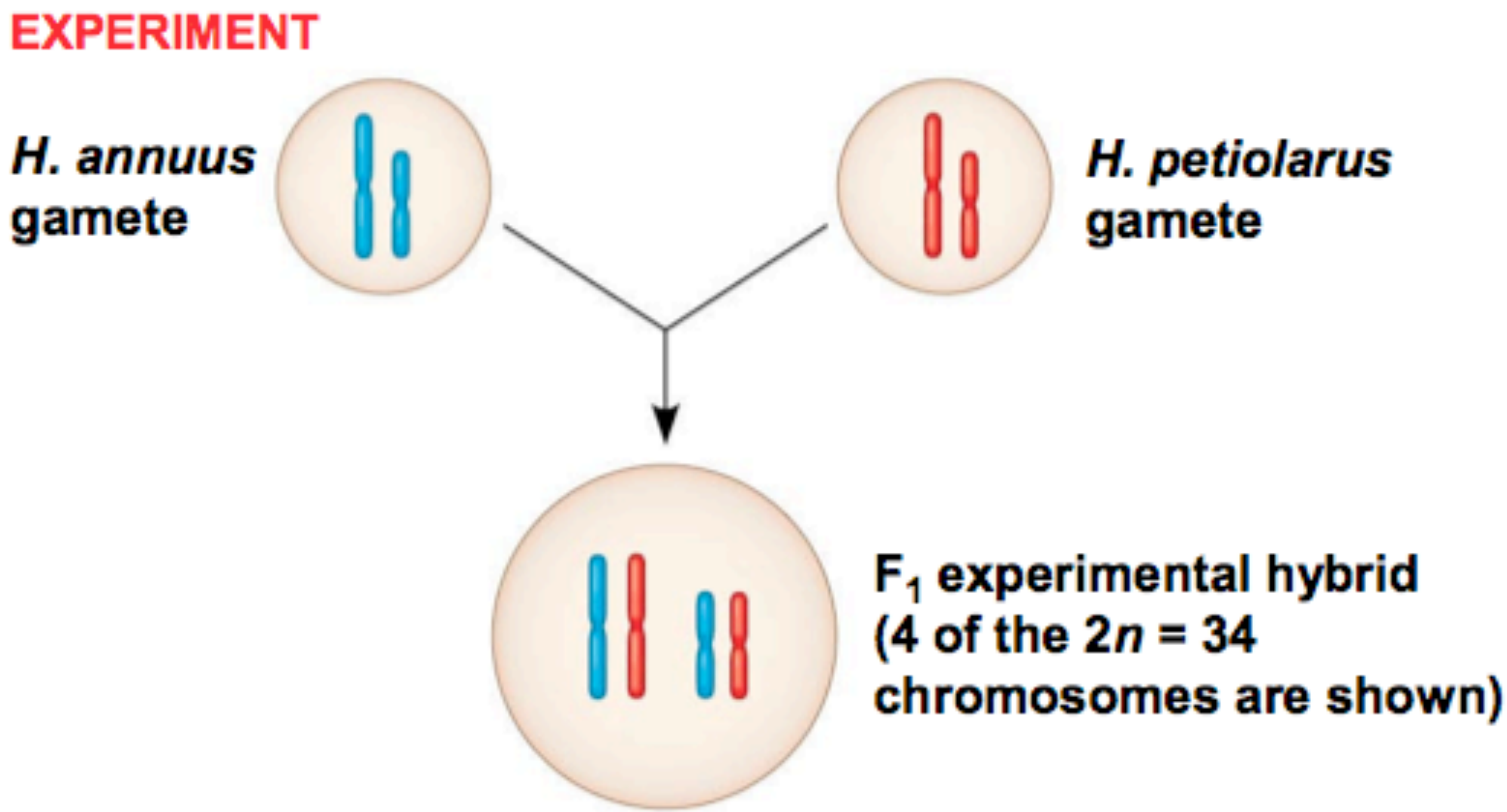
Since fossil formation is rare none of these fossil may exist only ones from the old and new species that lived for millions of years.



Many fossils appear similar for a long time, then exhibit abrupt changes in a short period of time followed by another period of stasis.

Punctuated equilibrium model.

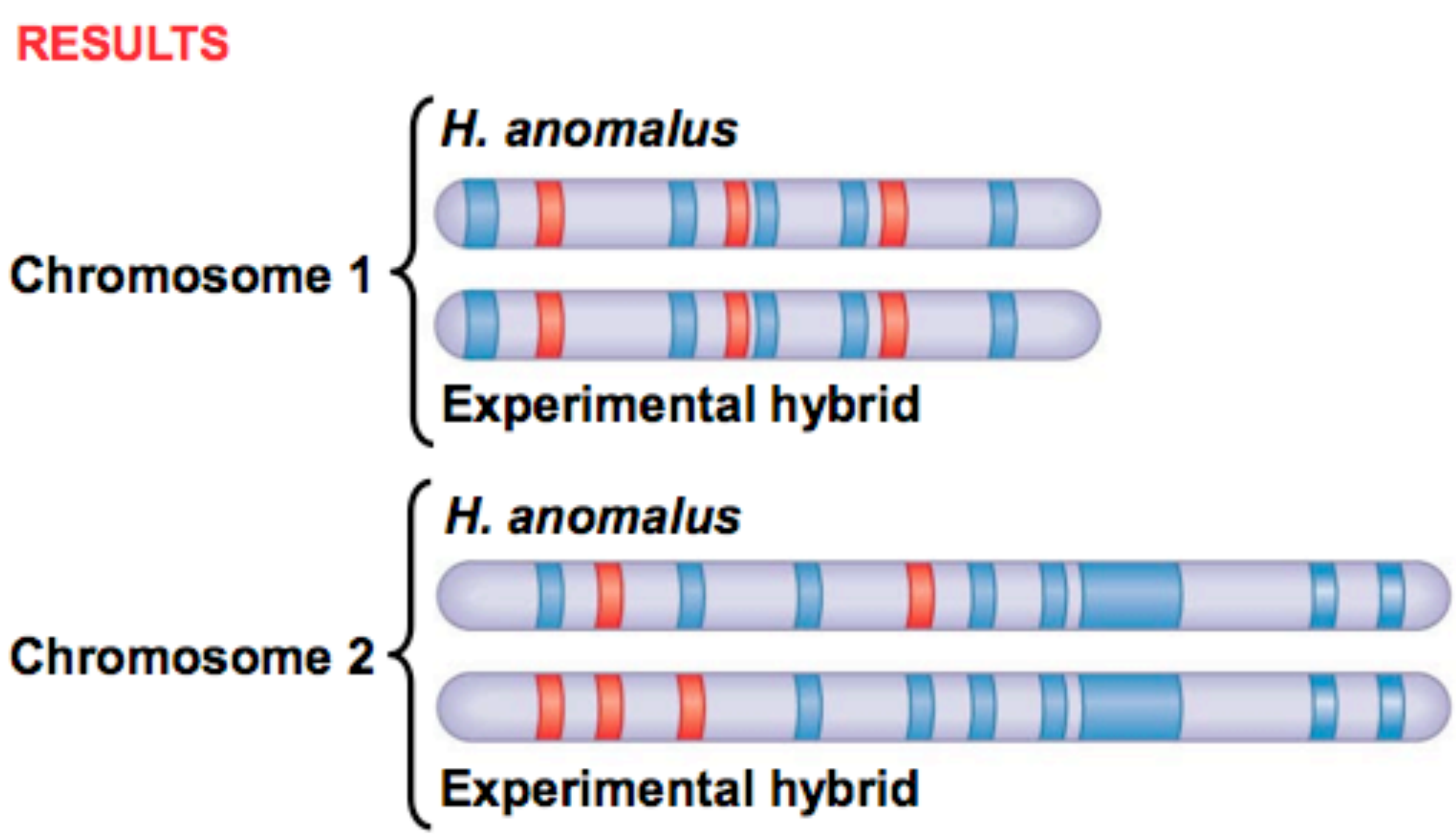
A new species changes most as it buds from a parent species and then changes little for the rest of its existence.



Indiana University, Loren Reiseberg and Colleagues crossed two parent sunflower species, *H. annus and H. petiolaris* to produce experimental hybrids in the lab (only 2 of the 17 chromosomes are shown)

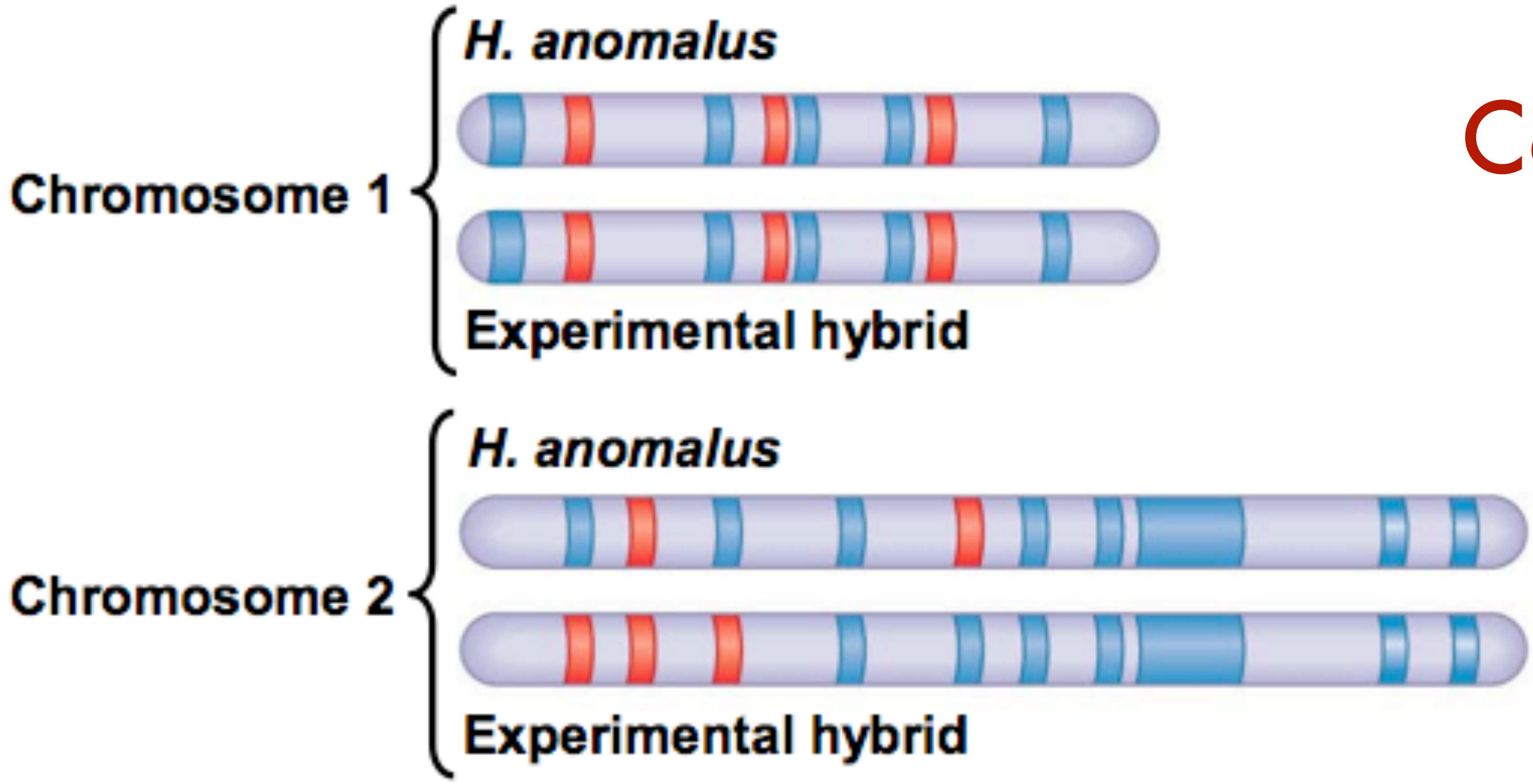
Note that in the first generation (F1), each chromosome of the experimental hybrids consisted entirely of DNA from one or the other parent species. They then tested whether the F1 and subsequent generations of experimental hybrids were fertile. They also used species-species genetic markers to compare the chromosomes in the experimental hybrids with the chromosomes in the naturally occurring hybrid *H. anomalus*

Although only 5% of the F1 experimental hybrids were fertile, after just 4 more generations the hybrid fertility rose to more than 90%. The chromosomes of individuals from this fifth hybrid generation differed from those in the F1 generation but were similar to those in the *H. anomalus* individuals from the natural populations:



Over time, the chromosomes in the population of experimental hybrids became similar to the chromosomes of *H. anomalus* individuals from the natural populations.

This suggests that the observed rise in fertility of the experimental hybrids occurred as natural selection eliminated regions of DNA from the parent species that were not compatible with one another. Overall, it appeared that the initial steps of the speciaition process occurred rapidly and could be mimicked in a laboratory experiment.



Conclusion

The Genetics of Speciation

- A fundamental question of evolutionary biology persists: How many genes change when a new species forms?
- Depending on the species in question,speciation might require the change of only a single allele or many alleles
  - For example, in Japanese *Euhadra* snails, the direction of shell spiral affects mating and is controlled by a single gene
  - In other species,speciation can be influenced by larger numbers of genes and gene interactions

- In monkey flowers (*Mimulus*), two loci affect flower color, which influences pollinator preference
- Pollination that is dominated by either hummingbirds or bees can lead to reproductive isolation of the flowers

(a) Typical *Mimulus lewisii*

(b) *M. lewisii* with an *M. cardinalis* flower-color allele

(c) Typical *Mimulus cardinalis*

(d) *M. cardinalis* with an *M. lewisii* flower-color allele

From Speciation to Macroevolution

- Speciation can begin with a few minor changes to an organism.
- Over time these changes may accumulate and become more pronounced.
- Eventually these changes may lead to new groups of organisms that vary greatly from their ancestors.
- Some groups grow in size while others go extinct.
- The cumulative effect of speciation and extinction have shaped the evolution changes documented by the fossil record.

RECALL:Evolution is Not Goal Oriented

- Whether speciation occurs slowly and gradually or whether it occurs bursts, evolution has no end point in mind.
- Evolution "tinkers" with each organism making slight modifications some of which will be beneficial and others that are not.

Overtime this "tinkering" has lead to three key features in the natural world!

1. Organisms are well suited to their environments.

2. Organisms share many characteristics.

3. Organisms are remarkably diverse.