17) Limitations of the Biological Species Concept

- The biological species concept cannot be applied to fossils or asexual organisms (including all prokaryotes)

18) Other Definitions of Species

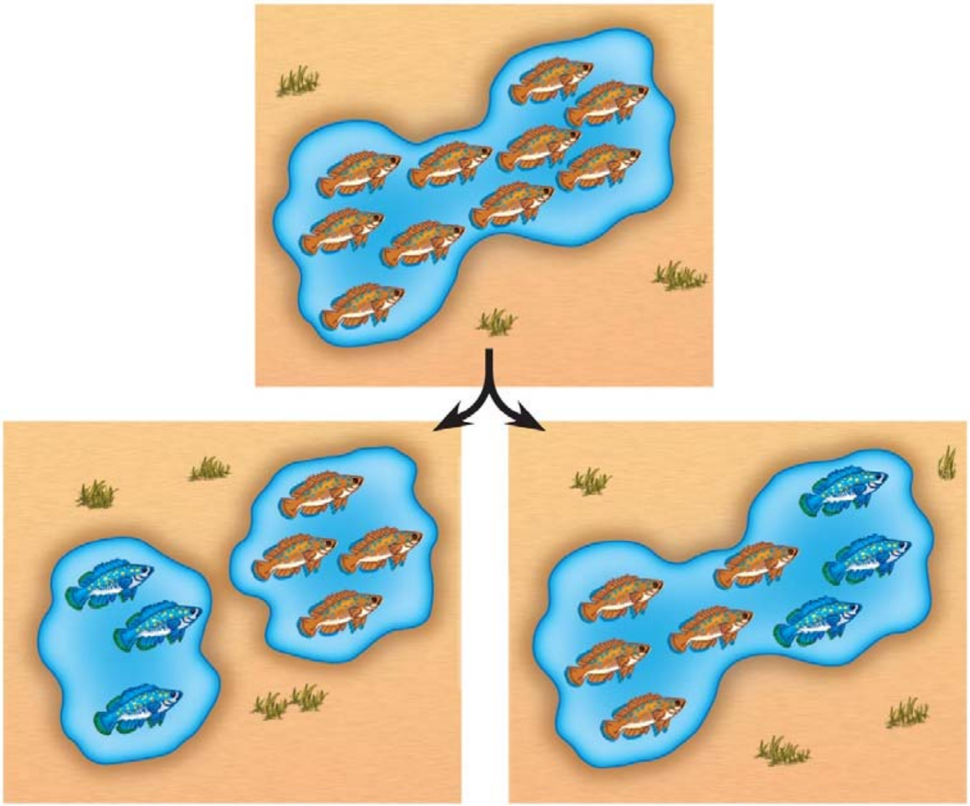
- Other species concepts emphasize the unity within a species rather than the separateness of different species
- The **morphological species concept** defines a species by structural features
  - It applies to sexual and asexual species but relies on subjective criteria

19) Other Definitions of Species—cont.

- The **ecological species concept** views a species in terms of its *ecological niche*
  - It applies to sexual and asexual species and emphasizes the role of disruptive selection
- The **phylogenetic species concept**: defines a species as the smallest group of individuals on a phylogenetic tree
  - It applies to sexual and asexual species, but it can be difficult to determine the degree of difference required for separate species

20) Speciation can take place with or without *geographic separation*

- Speciation can occur in two ways:
  - Allopatric speciation (lower left)
  - Sympatric speciation (lower right)



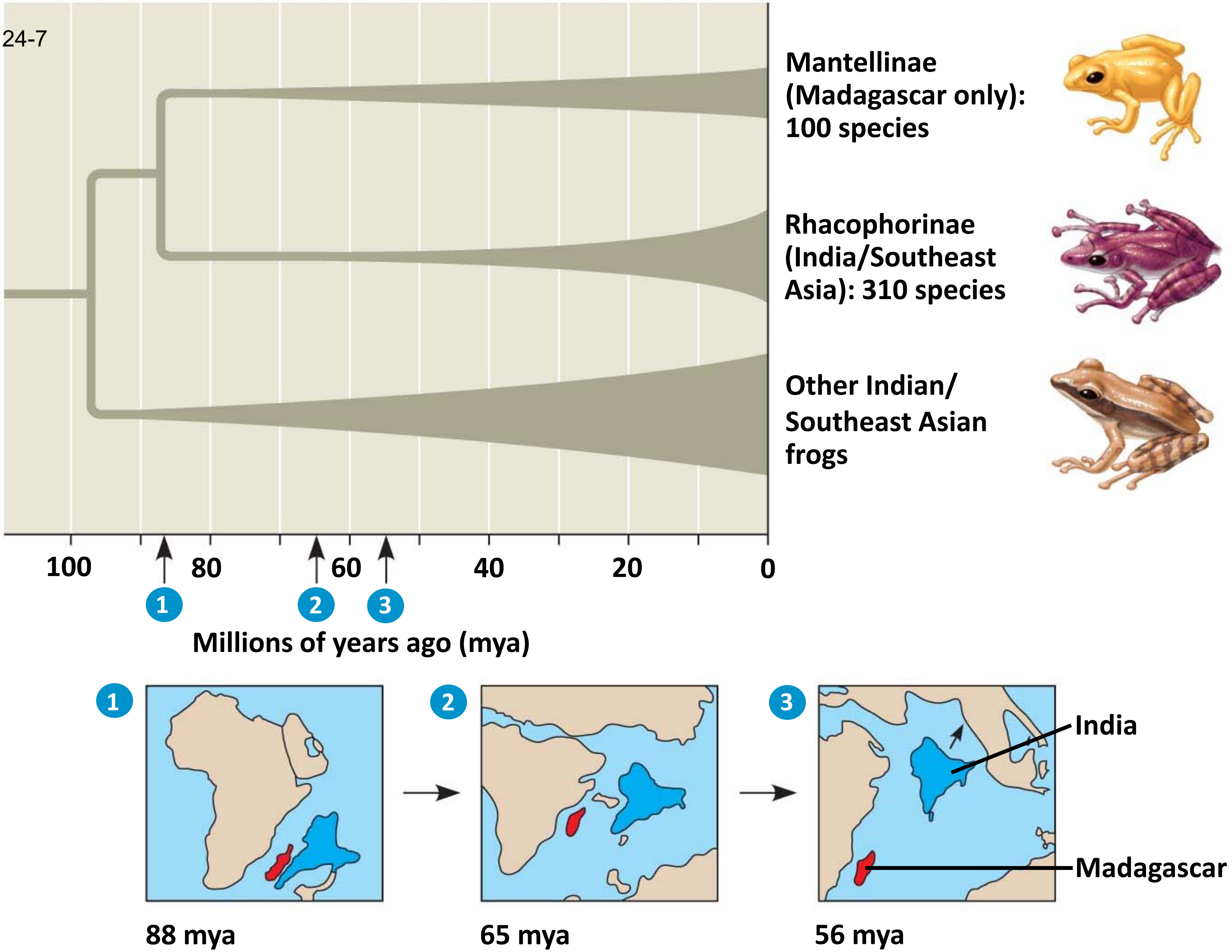
21) Allopatric (“Other Country”) Speciation

- In **allopatric speciation**, gene flow is interrupted or reduced by some “barrier” when a population is divided into geographically isolated subpopulations
- The definition of *barrier* depends on the ability of a population to disperse
- Separated populations may evolve independently through mutation, natural selection, and genetic drift
- Here, 2 sp. of antelope squirrel occupy the 2 rims of the grand Canyon—*Ammospermophilus harrisi* on the south (left) and *A. leucurus* on the north (right)

22) The following slide (Fig 24.7) shows allopatric speciation in frogs

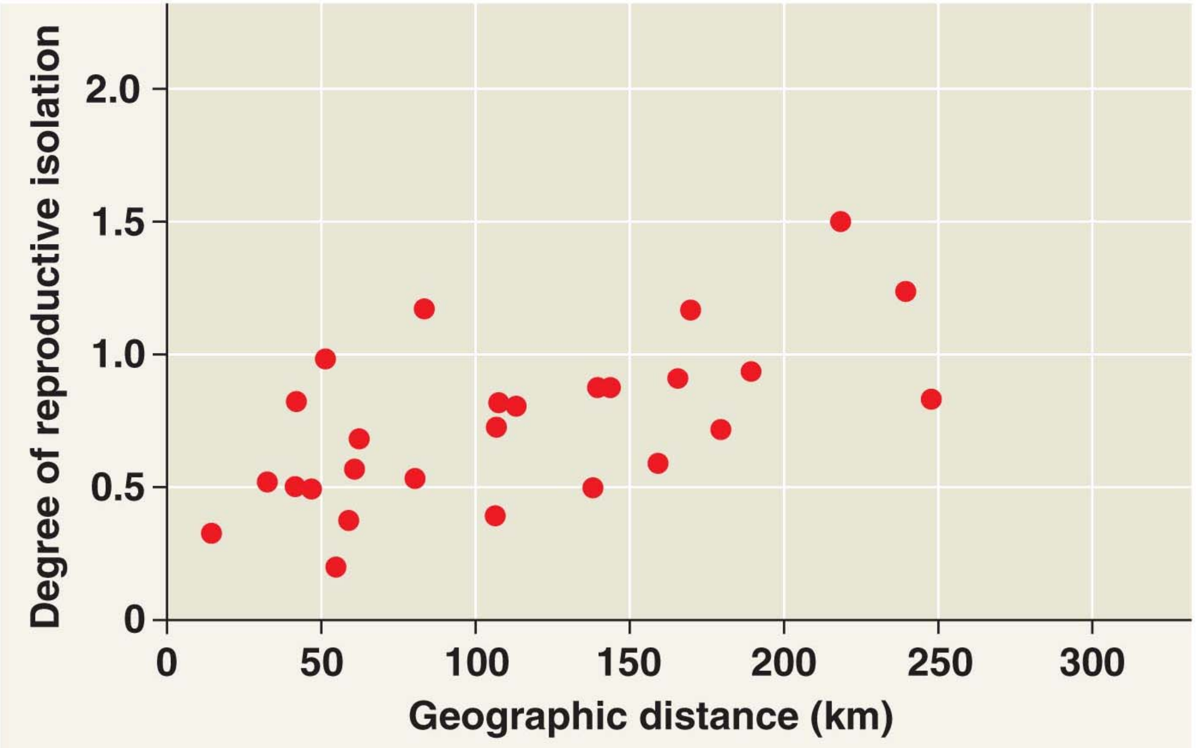
- Biogeographic & genetic data together indicate that 2 present-day subfamilies of frogs—Mantellinae & Rhacophorinae—began to diverge ~88 MYA, when Madagascar started to separate from the Indian landmass
- Apparently these 2 frog groups shared a common ancestor that lived on the Madagascar-India landmass before it began to break apart
- Following the breakup, allopatric speciation occurred within the now-separated populations, with the formation of many new species in each location

Fig. 24-7


Mantellinae
(Madagascar only):
100 species
Rhacophorinae
(India/Southeast
Asia): 310 species
Other Indian/
Southeast Asian
frogs
100
80
60
40
20
0
1
2
3
Millions of years ago (mya)
1
2
3
India
Madagascar
88 mya
65 mya
56 mya

24) Additional aspects of allopatric speciation

- Regions with many geographic barriers typically have more species than do regions with fewer barriers
- Reproductive isolation between populations generally increases as the distance between them increases

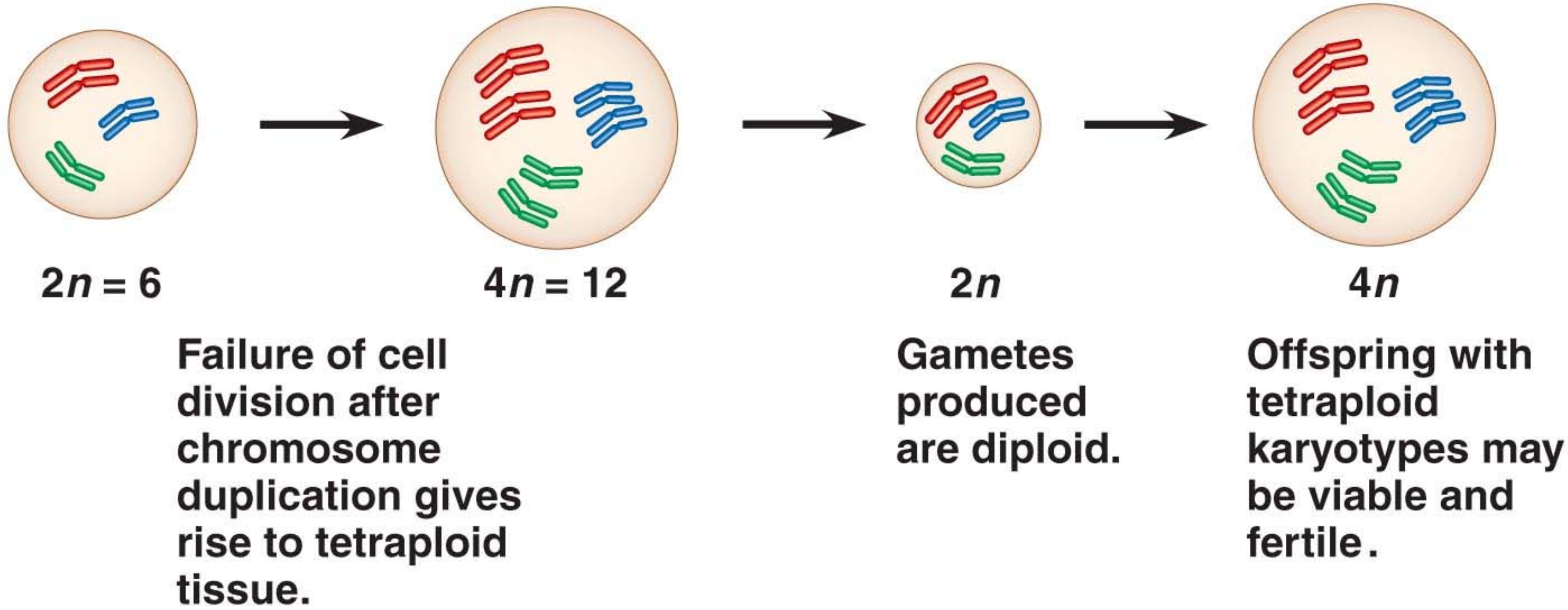


25) Sympatric ("Same Country") Speciation

- In **sympatric speciation**, speciation takes place in geographically overlapping populations
- Though less common than allopatry it can happen via
  - Polyploidy
  - Habitat differentiation
  - Sexual selection

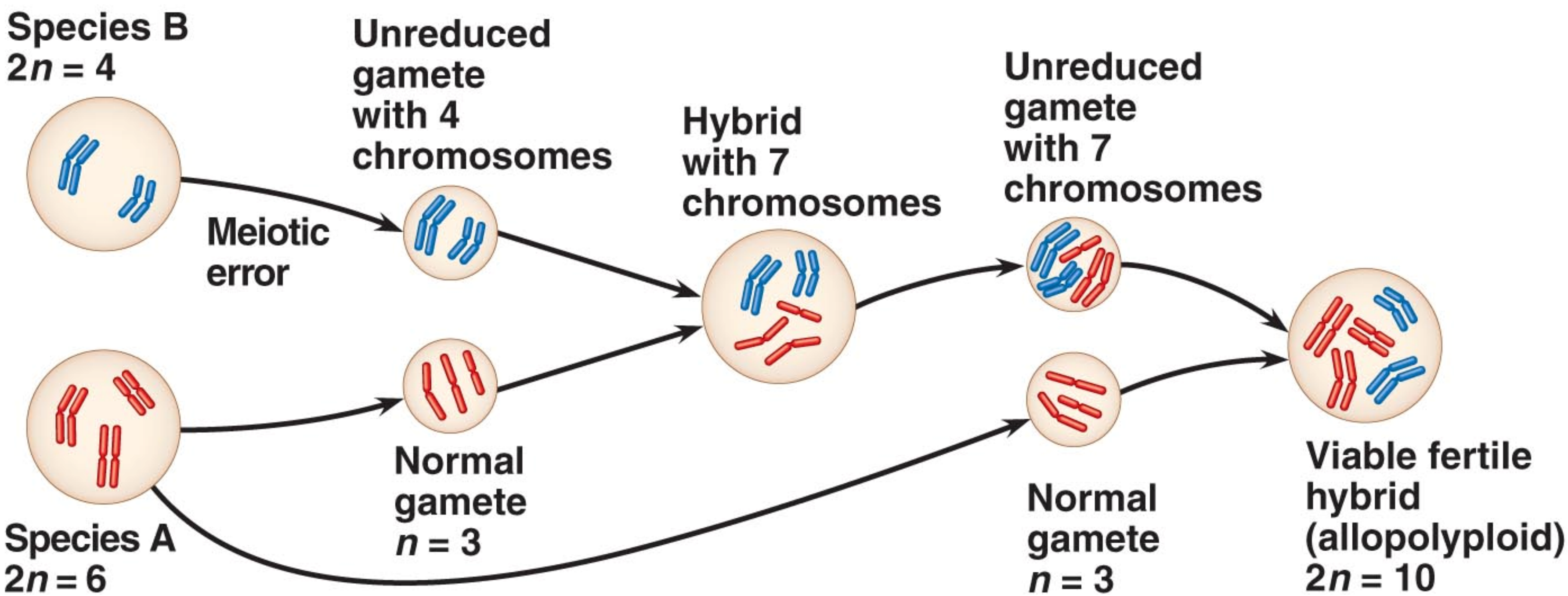
26) Polyploidy

- **Polyploidy** is the presence of extra sets of chromosomes due to accidents during cell division
- An **autopolyploid** is an individual with more than two chromosome sets, derived from one species



27) Allopolyploidy

- An **allopolyploid** is a species with multiple sets of chromosomes derived from *different* species
  - While a hybrid is often sterile, as is the one below with 7 chromosomes, it may be able to reproduce asexually
  - The new species has a diploid # = 7+3 = 10, a number that now can make gametes with an = # of chromosomes



28) Polyploidy—cont.

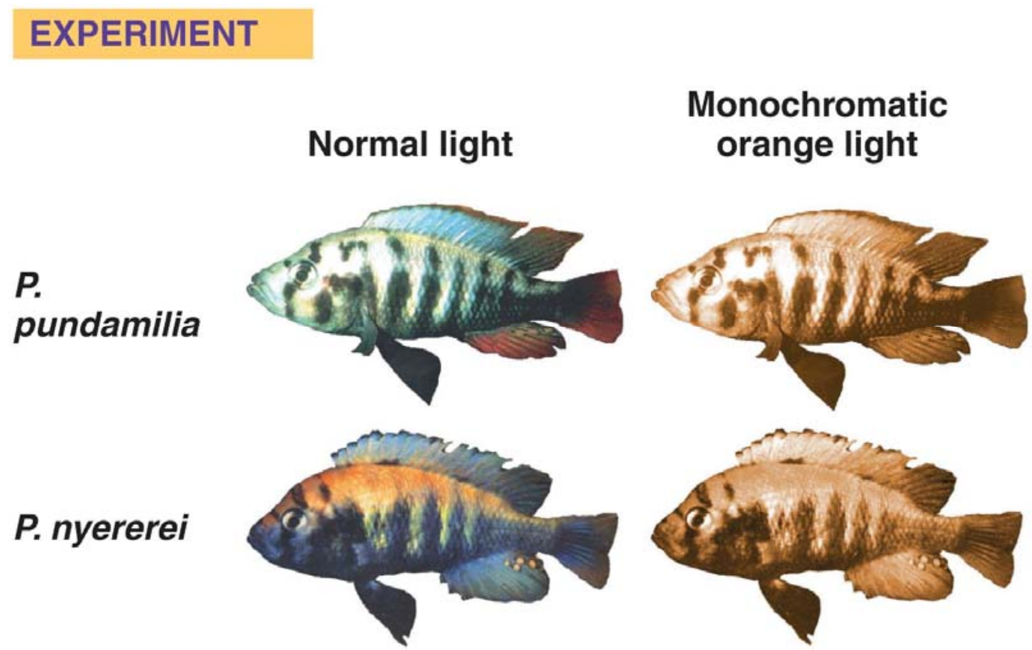
- Polyploidy is much more common in plants than in animals
- Many important crops (oats, cotton, potatoes, tobacco, and wheat) are polyploids

29) Habitat Differentiation

- Sympatric speciation can also result from the appearance of new ecological niches
- For example, the North American maggot fly can live on native hawthorn trees as well as more recently introduced apple trees

30) Sexual Selection

- Sexual selection can drive sympatric speciation
- Sexual selection for mates of different colors has likely contributed to the speciation in cichlid fish in Lake Victoria
- See Fig. 24.12



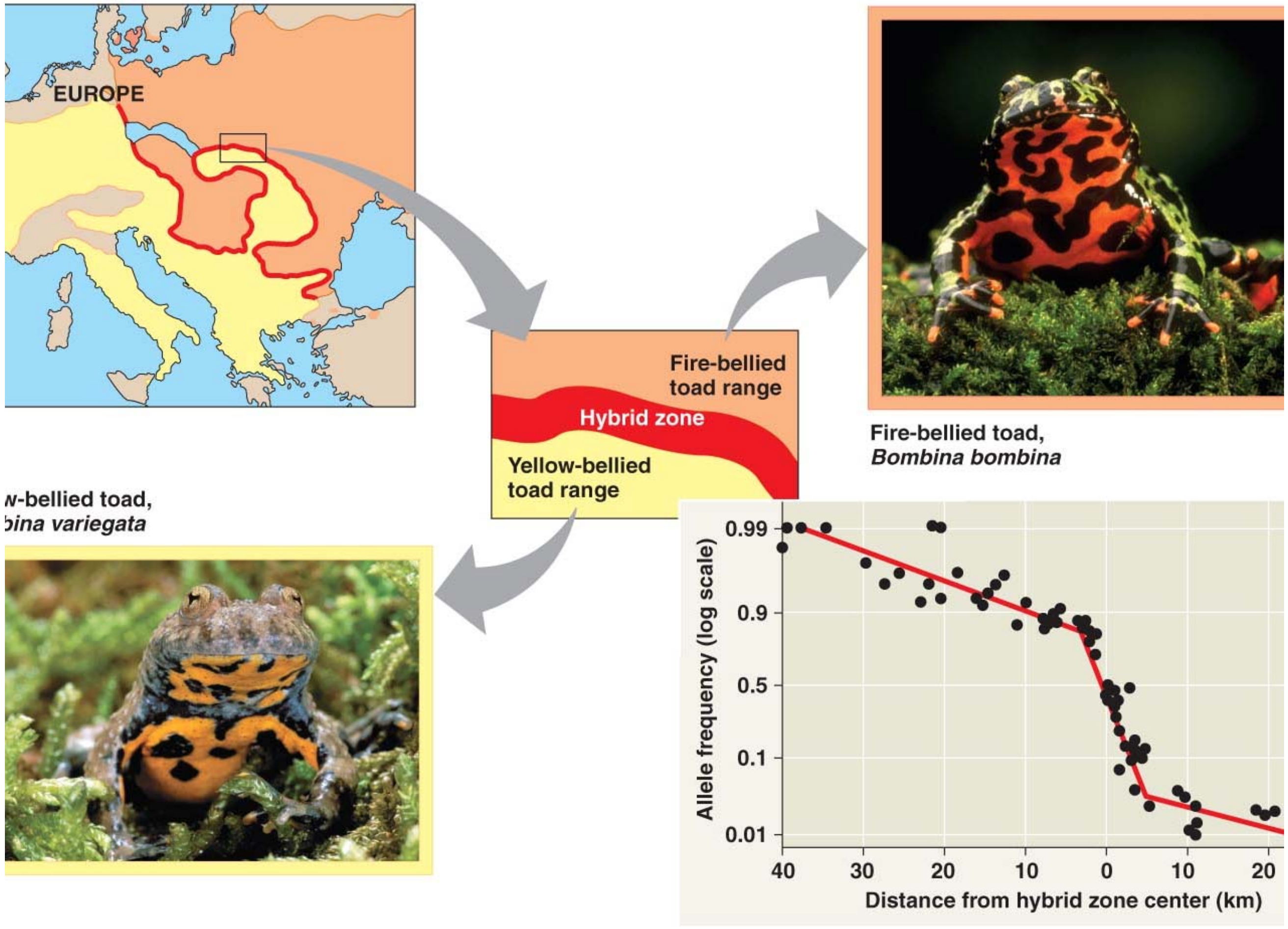
When , under artificial monochromatic light, females of these 2 recently-speciated fish can not see the difference in color between the males of their species and the other one, they select males indiscriminately, producing hybrid offspring

31) Summary review of allopatric and sympatric speciation

- In allopatric speciation:
  - geographic isolation restricts gene flow between populations
  - reproductive isolation may then arise by natural selection, genetic drift, or sexual selection in the isolated populations
  - even if contact is restored between populations, interbreeding is prevented
- In sympatric speciation:
  - a reproductive barrier isolates a subset of a population without geographic separation from the parent species
  - sympatric speciation can result from polyploidy, natural selection, or sexual selection

32) Hybrid Zones

- A **hybrid zone** is a region in which members of different, allopatric, species mate and produce hybrids
- A hybrid zone can occur in a single band where adjacent species meet—see Fig. 24.13 (next slide)
- Hybrids often have reduced fitness compared with parent species
- The distribution of hybrid zones can be more complex if parent species are found in multiple habitats within the same region

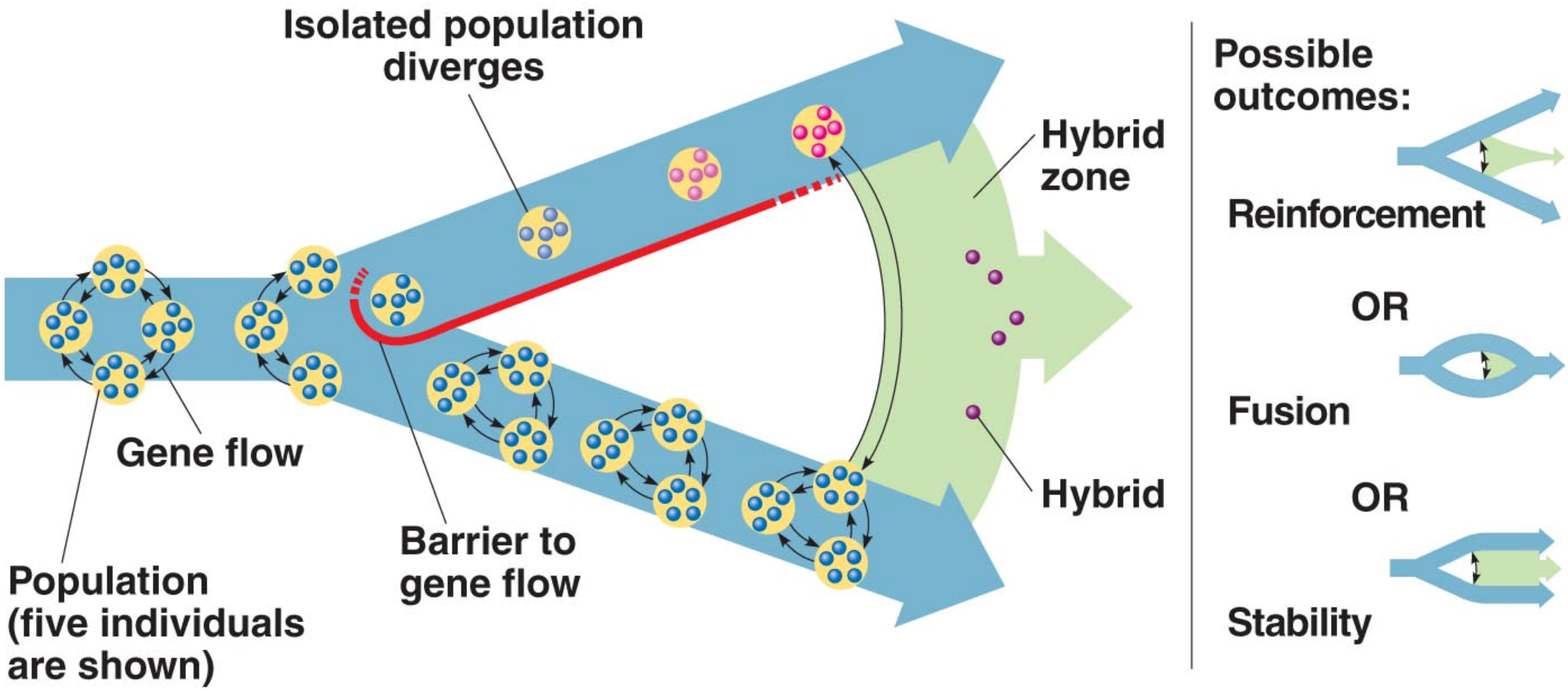


33) Case example of a Hybrid Zone in 2 European toads

Graph shows the frequency of the Yellow-bellied Toad alleles, being close to 100% within its range (yellow on map), dropping precipitously across the hybrid zone (red on map) and approaching zero in the range occupied by the Fire-bellied Toad (orange on map).

34) Outcomes, end results, of hybrid zone interactions

- When closely related species meet in a hybrid zone, the hybrids could form a new species through polyploidy; example is the goatsbeard plant (*Tragopogon*) (see text p. 496)
- If that does not happen, there are three remaining possible outcomes:
  1. Strengthening of reproductive barriers (**reinforcement**)
  2. Weakening of reproductive barriers (**fusion**)
  3. Continued formation of hybrid individuals (**stability**)



35) Possible outcomes for the hybrids in a hybrid zone

The arrows pointing to the right indicate the passage of time. Some type of barrier separates two populations of the original species, and they diverge, but hybridization between the two may still occur, with 3 possible outcomes: 1) The barrier(s) may be strengthened, thus causing hybrid formation to cease ("reinforcement"). 2) The barrier(s) may be weakened and the two populations will begin to merge again ("fusion"). Or 3), hybrids may continue to be formed in a long term stable hybrid zone—as we saw in the Fire-bellied and Yellow-bellied Toads ("stability").

36) More about the **reinforcement** possibility

- Reinforcement means the reproductive barriers are strengthened
- Occurs when hybrids are less fit than the parent species
- Consequently, over time, the rate of hybridization decreases

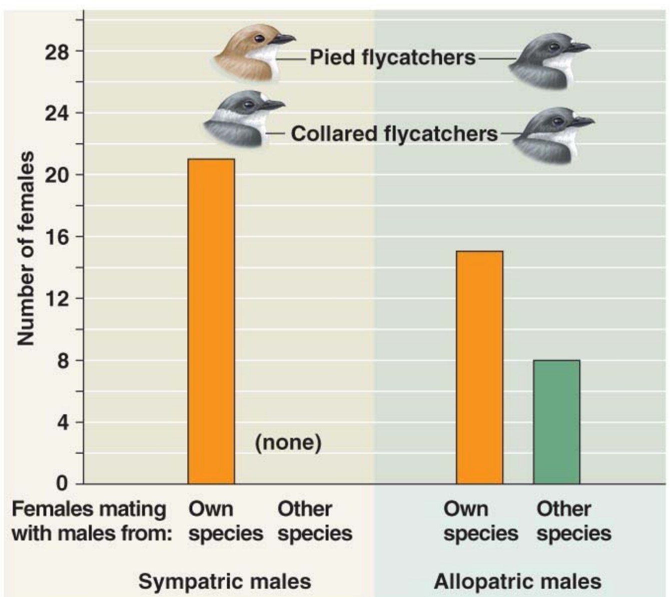
37) Different manifestations of

- Where reinforcement occurs, reproductive barriers should be stronger for sympatric than allopatric species
- Two closely-related species living together (“sympatric”) which are not forming hybrids (= “reinforcement”) ought to have powerful barriers preventing hybridization
- One example of this is shown in Fig. 24.15 (next slide)

38) Sympatric European flycatchers show a reinforced barrier to hybridization in the form of marked plumage differences

Sympatric male pied flycatcher

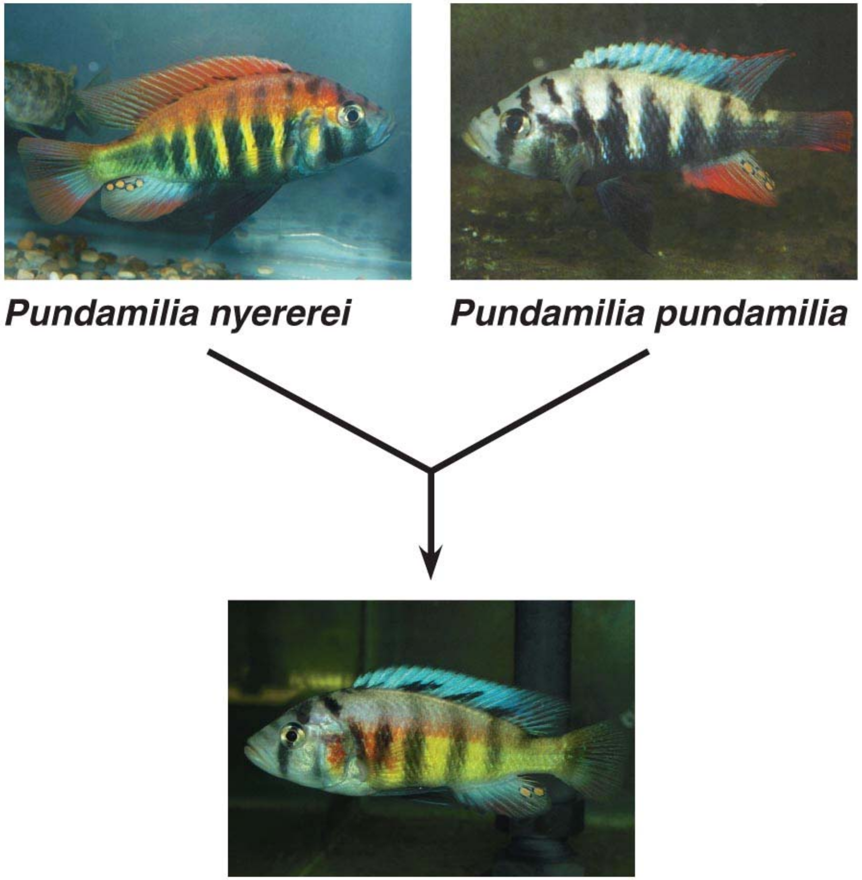
Allopatric male pied flycatcher



- These 2 species are closely related
- Where their ranges do not overlap (= allopatric), the males of both sp. look a lot alike
- Where their ranges overlap (= sympatric), the males look decidedly different, and females exhibit a 100% accurate choosing of males of their own species

39) Fusion—the weakening of reproductive barriers

- If hybrids are as fit as parents, there can be substantial gene flow between species
- If gene flow is great enough, the parent species can fuse into a single species
- In Lake Victoria, pollution-caused turbidity renders mate selection difficult and hybrids have appeared which essentially have re-merged two previously separate sp.



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

40) Stability—Continued Formation of Hybrids

- In the example of the Fire- & Yellow-bellied Toads, the hybrids are <u>less fit</u> than either parent population; any "pure" sp. toad which mates indiscriminately with the other sp. is going to produce less fit offspring, so why should there be any hybrids at all? How can *stability* prevail? Why don't we see *reinforcement* occurring?
- Possible explanation: extensive gene flow from outside the hybrid zone overwhelms selection for increased reproductive isolation inside the hybrid zone; remember the hybrid zone is very narrow
- In cases where hybrids have increased fitness (see account of ground crickets on pp. 499 & 501), local extinctions of parent species within the hybrid zone can prevent the breakdown of reproductive barriers

41) Is Speciation rapid or slow? Does it require change in just a few genes or many?

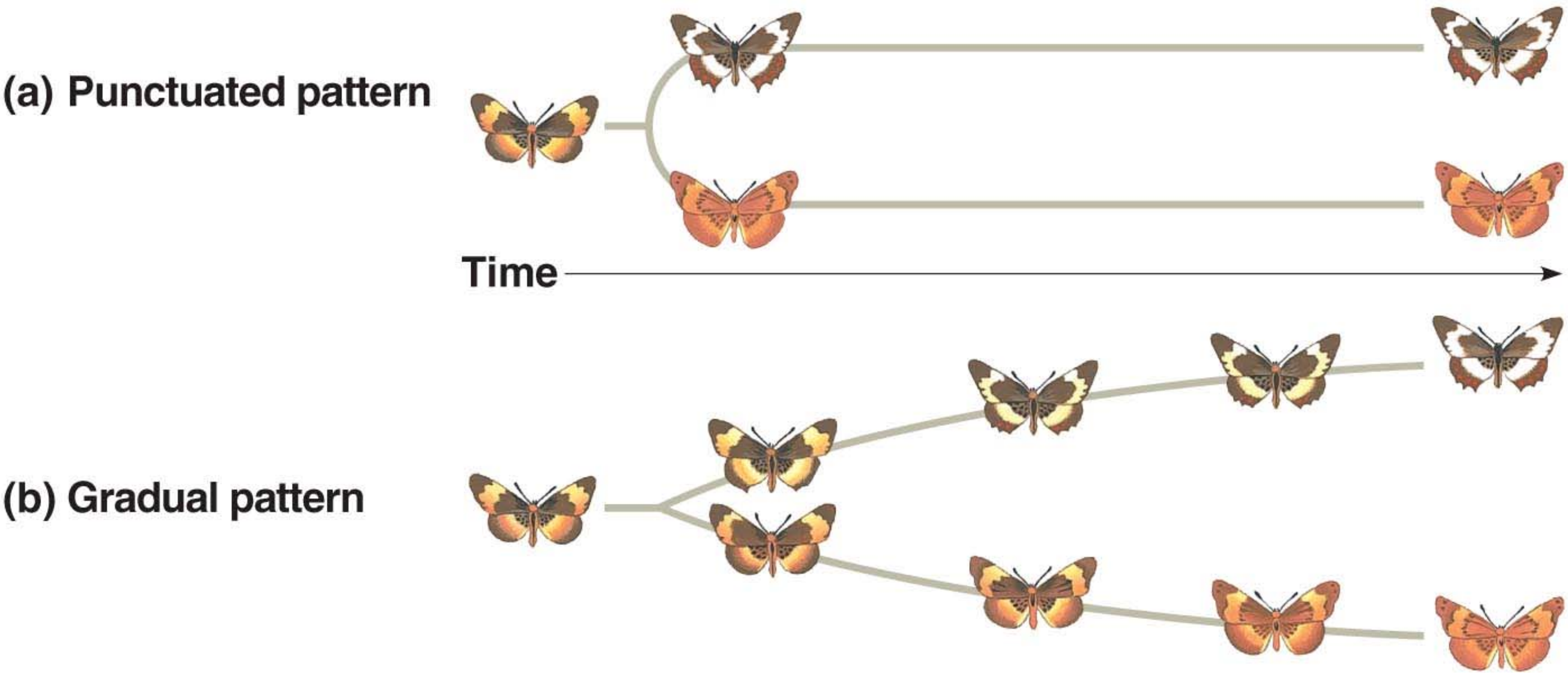
- It all depends…
- Both ends of these spectrums have been demonstrated
- Scientists are still documenting the spectrum of answers, and many questions remain concerning how long it takes for new species to form, or how many genes need to differ between species

42) The Time Course of Speciation

- Broad patterns in speciation can be studied using the fossil record, morphological data, and molecular data
- The data accumulating from these areas are converging

43) Patterns in the Fossil Record

- The fossil record includes examples of species that appear suddenly, persist essentially unchanged for some time, and then apparently disappear
- Niles Eldredge and Stephen Jay Gould coined the term **punctuated equilibrium** to describe periods of apparent stasis punctuated by sudden change
- The punctuated equilibrium model contrasts with a model of gradual change in a species' existence
- See Fig. 24.17 (next slide)



44) Two models for the tempo of evolution

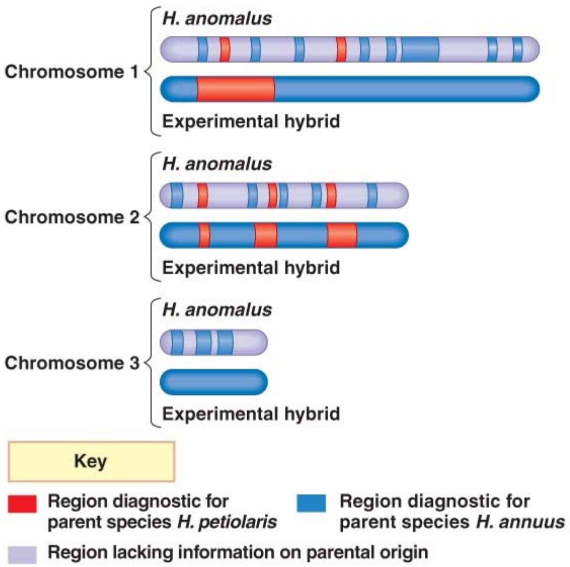
The Punctuated Equilibrium model was introduced by Eldridge and Gould.

45) Speciation Rates

- The punctuated pattern in the fossil record and evidence from lab studies suggests that speciation can be rapid
- The interval between speciation events can range from 4,000 years (some cichlids) to 40,000,000 years (some beetles), with an average of 6,500,000 years

46) The Wild Sunflower—an example of relatively rapid speciation

(a) The wild sunflower *Helianthus anomalus*



(b) The genetic composition of three chromosomes in *H. anomalus* and in experimental hybrids

- Genetic evidence indicates it is a hybrid between 2 other sunflower sp.
- Did not form by allopolyploidy, because both parent & hybrid spp have the same chromosome no.
- While early hybrids have only 5% fertility, after only 5 generations, blocks of the DNA that were incompatible failed to reproduce & were elimination by selection & the fertility rose to >90%

47) Studying the Genetics of Speciation

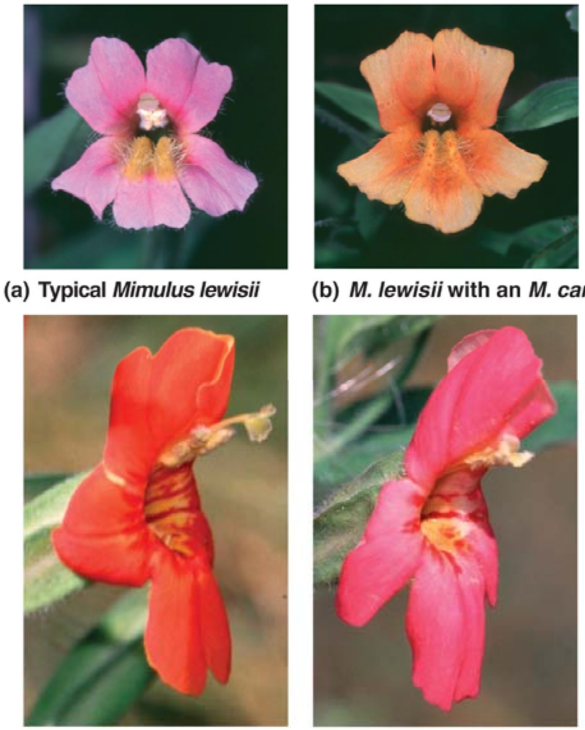
- The explosion of **genomics** is enabling researchers to identify specific genes involved in some cases of speciation
- Dr Lee Greer's lab is emerging as a significant producer of genomic research
- Depending on the species in question, speciation might require the change of only a single allele or many alleles

48) How many genes change when a new species is formed?

- In this example a change in only one gene results in reproductive isolation
- This gene controls the direction of shell spiraling; snails spiraled differently cannot align the genital openings

49) Two sp of Monkeyflower are the result of change in a relatively small number of genes

- The 2 sp are the result of prezygotic and postzygotic isolating mechanisms
- Pollinator choice accounts for most of the reproductive isolation
  - Bumblebees prefer the pink *M. lewisii*
  - Hummingbirds pollinate the red *M. cardinalis*
- It appears that 2 gene loci are involved



(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

50) Gene difference for some other species

- The separation of 2 subspecies of the fruitfly *Drosophila pseudoobscura* is the result of changes in 4 gene loci
- For two sp. of sunflower, 26 gene segemnts produce the postzygotic isolation (with an unknown number of genes)
- Summarizing, a few to many gene changes contribute to the evolution of reproductive isolation that produces new species

51) From Speciation to Macroevolution

- Macroevolution is the cumulative effect of many speciation and extinction events
- As speciation occurs again & again, such differences accumulate & become more pronounced, eventually leading to the formation of new groups of organisms that differ from their ancestors
- The next chapter deals with this story, macroevolution as evidenced by the fossil record

52) You should now be able to:

1. Define and discuss the limitations of the four species concepts
2. Describe and provide examples of prezygotic and postzygotic reproductive barriers
3. Distinguish between and provide examples of allopatric and sympatric speciation
4. Explain how polyploidy can cause reproductive isolation
5. Define the term hybrid zone and describe three outcomes for hybrid zones over time