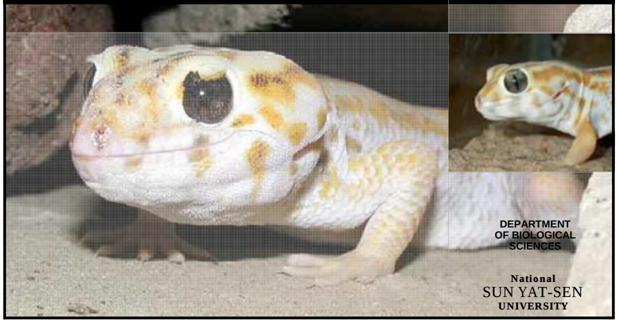
evolution & biological systematics

生物系統分類與演化學



DEPARTMENT OF BIOLOGICAL SCIENCES

National
SUN YAT-SEN
UNIVERSITY

Overview: Endless Forms Most Beautiful

- A new era of biology began in 1859 when Charles Darwin published *The Origin of Species*
- *The Origin of Species* focused biologists' attention on the great diversity of organisms

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- Darwin noted that current species are descendants of ancestral species
- **Evolution** can be defined by Darwin's phrase *descent with modification*
- Evolution can be viewed as both a pattern and a process

Fig. 22-1

Concept 22.1: The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species

- To understand why Darwin's ideas were revolutionary, we must examine them in relation to other Western ideas about Earth and its life

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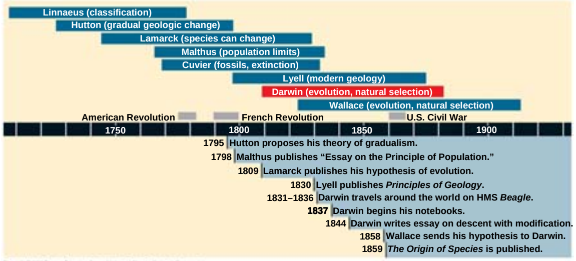
Fig. 22-2



Scala Naturae and Classification of Species

- The Greek philosopher Aristotle viewed species as fixed and arranged them on a *scala naturae*
- The Old Testament holds that species were individually designed by God and therefore perfect

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- Carolus Linnaeus interpreted organismal adaptations as evidence that the Creator had designed each species for a specific purpose
- Linnaeus was the founder of taxonomy, the branch of biology concerned with classifying organisms

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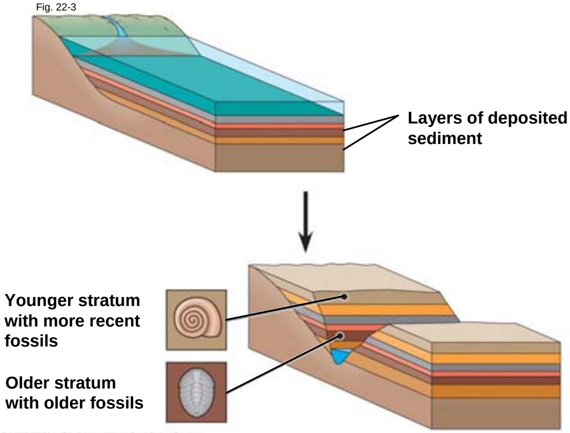
Ideas About Change over Time

- The study of **fossils** helped to lay the groundwork for Darwin’s ideas
- Fossils are remains or traces of organisms from the past, usually found in sedimentary rock, which appears in layers or **strata**

PLAY Video: Grand Canyon

Fig. 22-3



- **Paleontology**, the study of fossils, was largely developed by French scientist Georges Cuvier
- Cuvier advocated **catastrophism**, speculating that each boundary between strata represents a catastrophe

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- Geologists James Hutton and Charles Lyell perceived that changes in Earth’s surface can result from slow continuous actions still operating today
- Lyell’s principle of **uniformitarianism** states that the mechanisms of change are constant over time
- This view strongly influenced Darwin’s thinking

Lamarck's Hypothesis of Evolution

- Lamarck hypothesized that species evolve through use and disuse of body parts and the inheritance of acquired characteristics
- The mechanisms he proposed are unsupported by evidence

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modification by natural selection explains the adaptations of organisms and the unity and diversity of life

- As the 19th century dawned, it was generally believed that species had remained unchanged since their creation
- However, a few doubts about the permanence of species were beginning to arise

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Darwin's Research

- As a boy and into adulthood, Charles Darwin had a consuming interest in nature
- Darwin first studied medicine (unsuccessfully), and then theology at Cambridge University
- After graduating, he took an unpaid position as naturalist and companion to Captain Robert FitzRoy for a 5-year around the world voyage on the *Beagle*

The Voyage of the Beagle

- During his travels on the *Beagle,* Darwin collected specimens of South American plants and animals
- He observed adaptations of plants and animals that inhabited many diverse environments
- Darwin was influenced by Lyell's *Principles of Geology* and thought that the earth was more than 6000 years old

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- His interest in geographic distribution of species was kindled by a stop at the Galápagos Islands near the equator west of South America

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Fig. 22-5

PLAY Video: Galápagos Islands Overview

PLAY Video: Blue-footed Boobies Courtship Ritual

PLAY Video: Albatross Courtship Ritual

PLAY Video: Galápagos Sea Lion

PLAY Video: Soaring Hawk

PLAY Video: Galápagos Tortoises

PLAY Video: Galápagos Marine Iguana

Darwin's Focus on Adaptation

- In reassessing his observations, Darwin perceived **adaptation** to the environment and the origin of new species as closely related processes
- From studies made years after Darwin's voyage, biologists have concluded that this is indeed what happened to the Galápagos finches

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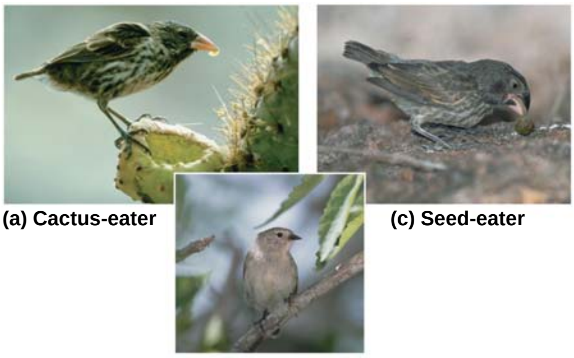
Fig. 22-6



(a) Cactus-eater

(c) Seed-eater

(b) Insect-eater

- In 1844, Darwin wrote an essay on the origin of species and **natural selection** but did not introduce his theory publicly, anticipating an uproar
- In June 1858, Darwin received a manuscript from Alfred Russell Wallace, who had developed a theory of natural selection similar to Darwin's
- Darwin quickly finished *The Origin of Species* and published it the next year

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The Origin of Species

- Darwin developed two main ideas:
  - Descent with modification explains life's unity and diversity
  - Natural selection is a cause of adaptive evolution

Descent with Modification

- Darwin never used the word *evolution* in the first edition of *The Origin of Species*
- The phrase *descent with modification* summarized Darwin's perception of the unity of life
- The phrase refers to the view that all organisms are related through descent from an ancestor that lived in the remote past

- In the Darwinian view, the history of life is like a tree with branches representing life’s diversity
- Darwin’s theory meshed well with the hierarchy of Linnaeus

Fig. 22-7

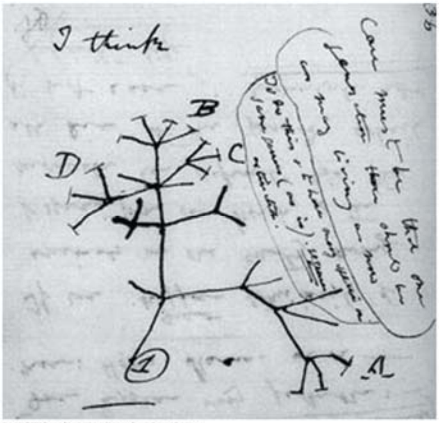


Fig. 22-8

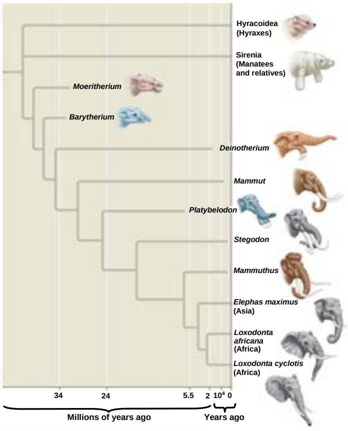
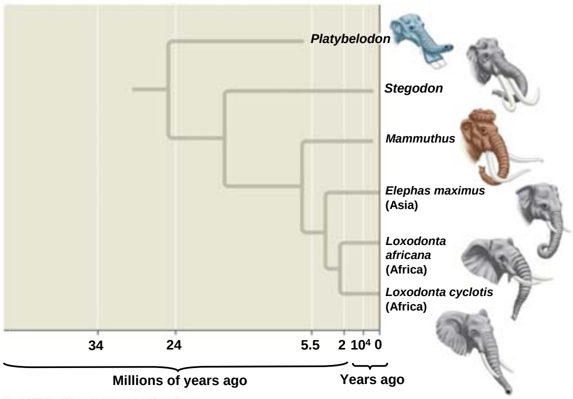


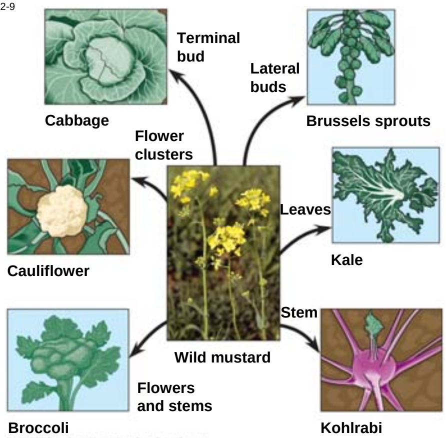
Fig. 22-8a



Artificial Selection, Natural Selection, and Adaptation

- Darwin noted that humans have modified other species by selecting and breeding individuals with desired traits, a process called **artificial selection**
- Darwin then described four observations of nature and from these drew two inferences

Fig. 22-9



- Observation #1: Members of a population often vary greatly in their traits

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Fig. 22-10

- Observation #2: Traits are inherited from parents to offspring
- Observation #3: All species are capable of producing more offspring than the environment can support

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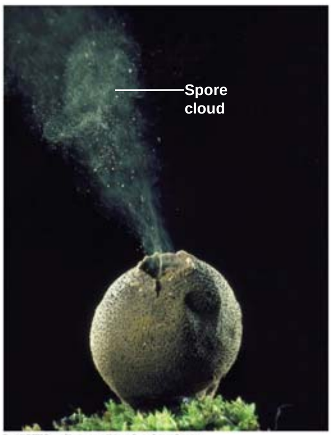
Fig. 22-11



- Observation #4: Owing to lack of food or other resources, many of these offspring do not survive

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- Inference #1: Individuals whose inherited traits give them a higher probability of surviving and reproducing in a given environment tend to leave more offspring than other individuals

- Inference #2: This unequal ability of individuals to survive and reproduce will lead to the accumulation of favorable traits in the population over generations

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- Darwin was influenced by Thomas Malthus who noted the potential for human population to increase faster than food supplies and other resources
- If some heritable traits are advantageous, these will accumulate in the population, and this will increase the frequency of individuals with adaptations
- This process explains the match between organisms and their environment

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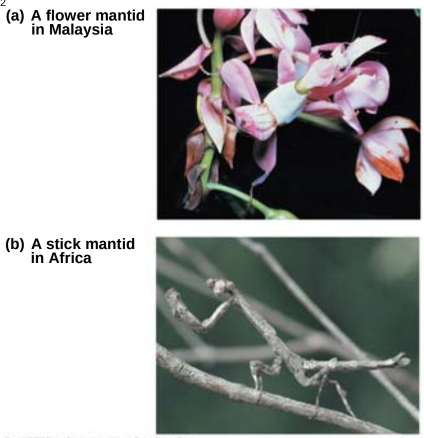
Natural Selection: A Summary

- Individuals with certain heritable characteristics survive and reproduce at a higher rate than other individuals
- Natural selection increases the adaptation of organisms to their environment over time
- If an environment changes over time, natural selection may result in adaptation to these new conditions and may give rise to new species

PLAY Video: Seahorse Camouflage

Fig. 22-12



(a) **A flower mantid in Malaysia**

(b) **A stick mantid in Africa**

- Note that individuals do not evolve; populations evolve over time
- Natural selection can only increase or decrease heritable traits in a population
- Adaptations vary with different environments

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supported by an overwhelming amount of scientific evidence

- New discoveries continue to fill the gaps identified by Darwin in *The Origin of Species*

Direct Observations of Evolutionary Change

- Two examples provide evidence for natural selection: the effect of differential predation on guppy populations and the evolution of drug-resistant HIV

Predation and Coloration in Guppies : Scientific Inquiry

- John Endler has studied the effects of predators on wild guppy populations
- Brightly colored males are more attractive to females
- However, brightly colored males are more vulnerable to predation
- Guppy populations in pools with fewer predators had more brightly colored males

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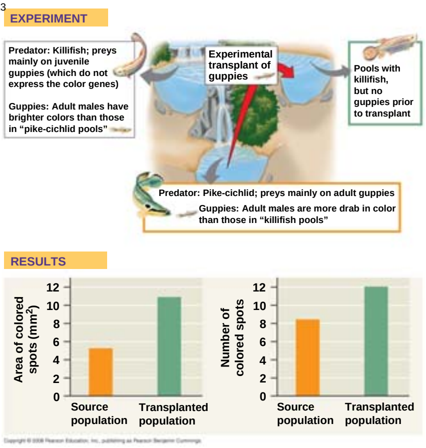
Fig. 22-13



EXPERIMENT

Predator: Killifish; preys mainly on juvenile guppies (which do not express the color genes)

Guppies: Adult males have brighter colors than those in "pike-cichlid pools"

Experimental transplant of guppies

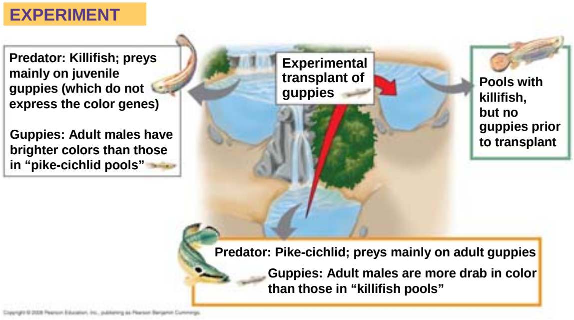
Pools with killifish, but no guppies prior to transplant

Predator: Pike-cichlid; preys mainly on adult guppies

Guppies: Adult males are more drab in color than those in "killifish pools"

RESULTS

Fig. 22-13a



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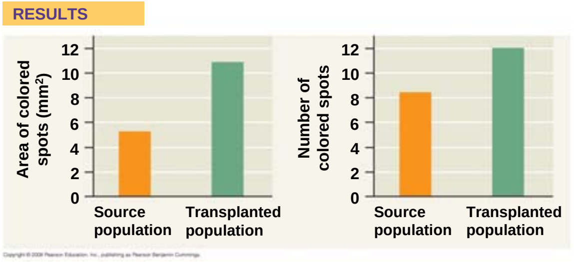
Pools with killifish, but no guppies prior to transplant

Predator: Pike-cichlid; preys mainly on adult guppies

Guppies: Adult males are more drab in color than those in "killifish pools"

Fig. 22-13b



RESULTS

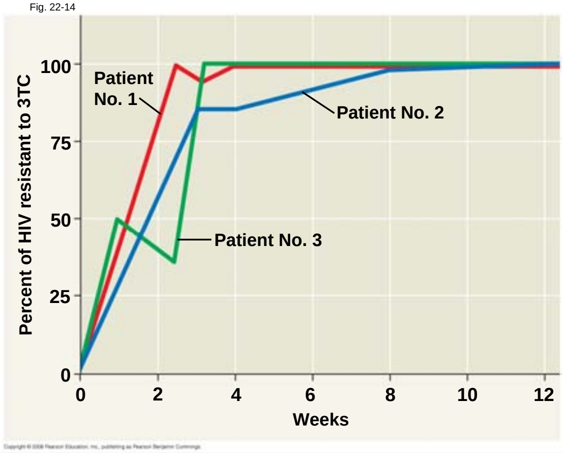
- Endler transferred brightly colored guppies (with few predators) to a pool with many predators
- As predicted, over time the population became less brightly colored
- Endler also transferred drab colored guppies (with many predators) to a pool with few predators
- As predicted, over time the population became more brightly colored

The Evolution of Drug-Resistant HIV

- The use of drugs to combat HIV selects for viruses resistant to these drugs
- HIV uses the enzyme reverse transcriptase to make a DNA version of its own RNA genome
- The drug 3TC is designed to interfere and cause errors in the manufacture of DNA from the virus

- Some individual HIV viruses have a variation that allows them to produce DNA without errors
- These viruses have a greater reproductive success and increase in number relative to the susceptible viruses
- The population of HIV viruses has therefore developed resistance to 3TC
- The ability of bacteria and viruses to evolve rapidly poses a challenge to our

Fig. 22-14

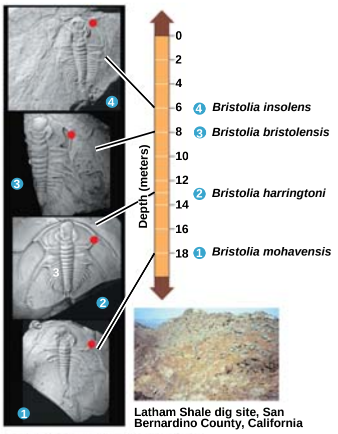


- Natural selection does not create new traits, but edits or selects for traits already present in the population
- The local environment determines which traits will be selected for or selected against in any specific population

The Fossil Record

- The fossil record provides evidence of the extinction of species, the origin of new groups, and changes within groups over time

Fig. 22-15



- The Darwinian view of life predicts that evolutionary transitions should leave signs in the fossil record
- Paleontologists have discovered fossils of many such transitional forms

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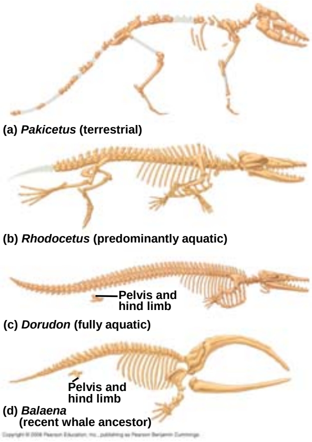
Fig. 22-16



Homology

- **Homology** is similarity resulting from common ancestry

Anatomical and Molecular Homologies

- **Homologous structures** are anatomical resemblances that represent variations on a structural theme present in a common ancestor

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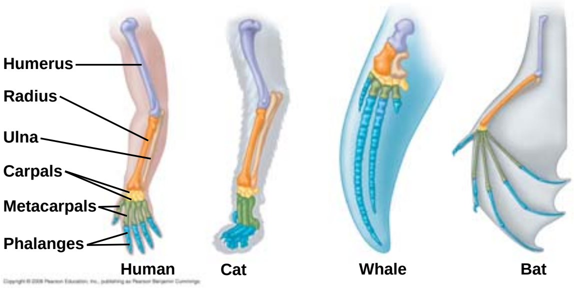
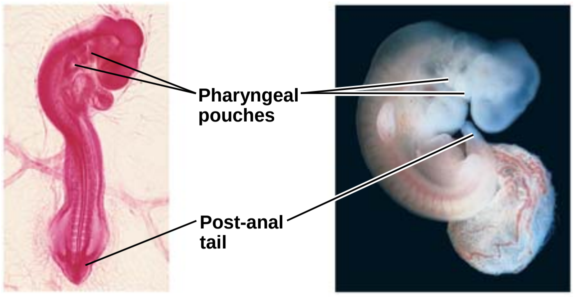
Fig. 22-17



- Comparative embryology reveals anatomical homologies not visible in adult organisms

Fig. 22-18



Chick embryo (LM)

Human embryo

- **Vestigial structures** are remnants of features that served important functions in the organism’s ancestors
- Examples of homologies at the molecular level are genes shared among organisms inherited from a common ancestor

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Homologies and “Tree Thinking”

- The Darwinian concept of an **evolutionary tree** of life can explain homologies
- Evolutionary trees are hypotheses about the relationships among different groups
- Evolutionary trees can be made using different types of data, for example, anatomical and DNA sequence data

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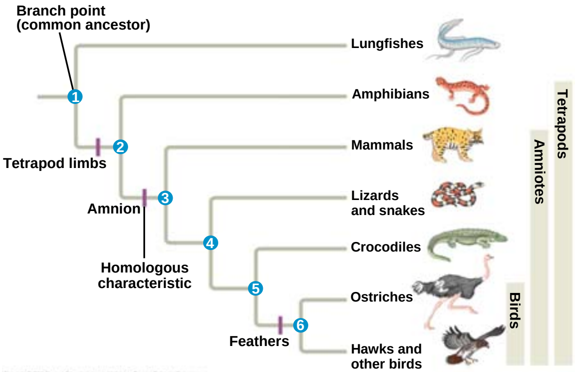
Fig. 22-19



Convergent Evolution

- **Convergent evolution** is the evolution of similar, or **analogous**, features in distantly related groups
- Analogous traits arise when groups independently adapt to similar environments in similar ways
- Convergent evolution does not provide information about ancestry

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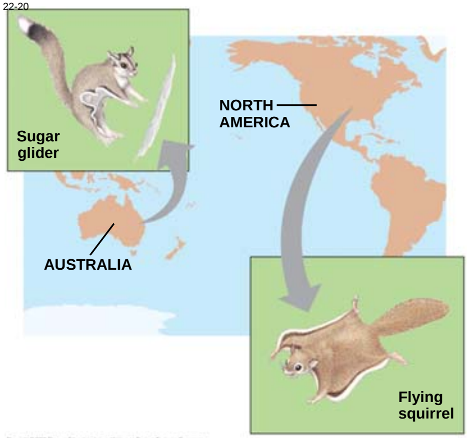
Fig. 22-20



Biogeography

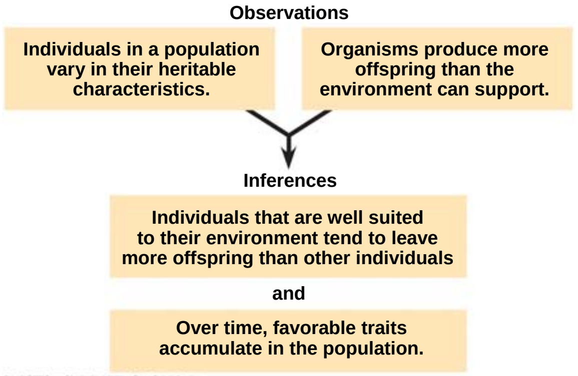
- Darwin's observations of **biogeography**, the geographic distribution of species, formed an important part of his theory of evolution
- Islands have many **endemic** species that are often closely related to species on the nearest mainland or island

- Earth's continents were formerly united in a single large continent called **Pangaea**, but have since separated by **continental drift**
- An understanding of continent movement and modern distribution of species allows us to predict when and where different groups evolved

What is Theoretical About Darwin's View of Life?

- In science, a theory accounts for many observations and data and attempts to explain and integrate a great variety of phenomena
- Darwin's theory of evolution by natural selection integrates diverse areas of biological study and stimulates many new research questions
- Ongoing research adds to our understanding of evolution

Fig. 22-UN1



Observations

Individuals in a population vary in their heritable characteristics.

Organisms produce more offspring than the environment can support.

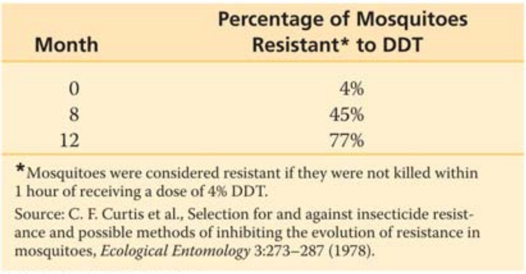
Inferences

Individuals that are well suited to their environment tend to leave more offspring than other individuals

and

Over time, favorable traits accumulate in the population.

Fig. 22-UN2

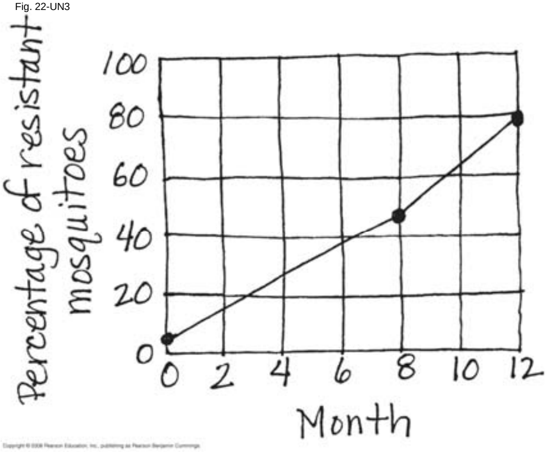


Month	Percentage of Mosquitoes Resistant* to DDT
0	4%
8	45%
12	77%

*Mosquitoes were considered resistant if they were not killed within 1 hour of receiving a dose of 4% DDT.

Source: C. F. Curtis et al., Selection for and against insecticide resistance and possible methods of inhibiting the evolution of resistance in mosquitoes, *Ecological Entomology* 3:273–287 (1978).

Fig. 22-UN3



Overview: The Smallest Unit of Evolution

- One misconception is that organisms evolve, in the Darwinian sense, during their lifetimes
- Natural selection acts on individuals, but only populations evolve
- Genetic variations in populations contribute to evolution
- **Microevolution** is a change in allele frequencies in a population over generations

Fig. 23-1

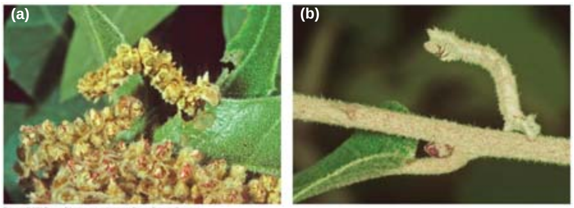
reproduction produce the genetic variation that makes evolution possible

- Two processes, mutation and sexual reproduction, produce the variation in gene pools that contributes to differences among individuals

Genetic Variation

- Variation in individual genotype leads to variation in individual phenotype
- Not all phenotypic variation is heritable
- Natural selection can only act on variation with a genetic component

Fig. 23-2



Variation Within a Population

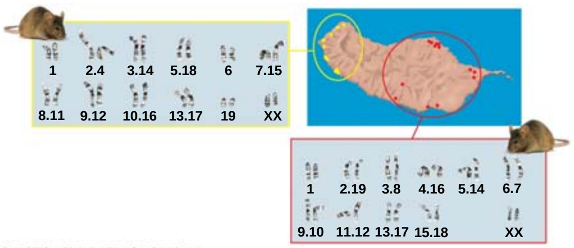
- Both discrete and quantitative characters contribute to variation within a population
- *Discrete characters* can be classified on an either-or basis
- *Quantitative characters* vary along a continuum within a population

- Population geneticists measure polymorphisms in a population by determining the amount of heterozygosity at the gene and molecular levels
- **Average heterozygosity** measures the average percent of loci that are heterozygous in a population
- Nucleotide variability is measured by comparing the DNA sequences of pairs of individuals

Variation Between Populations

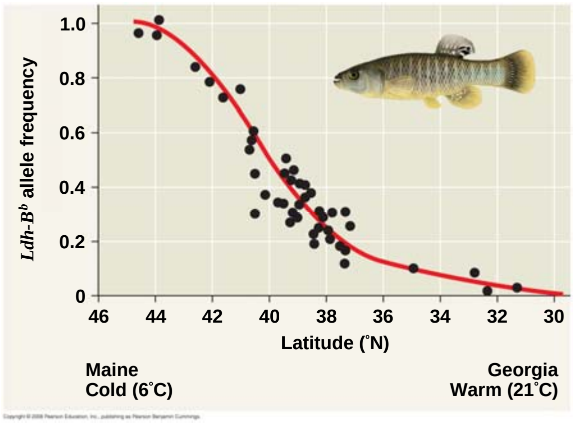
- Most species exhibit **geographic variation**, differences between gene pools of separate populations or population subgroups

Fig. 23-3



- Some examples of geographic variation occur as a **cline**, which is a graded change in a trait along a geographic axis

Fig. 23-4



Mutation

- **Mutations** are changes in the nucleotide sequence of DNA
- Mutations cause new genes and alleles to arise
- Only mutations in cells that produce gametes can be passed to offspring

PLAY Animation: Genetic Variation from Sexual Recombination

Point Mutations

- A point mutation is a change in one base in a gene

- The effects of point mutations can vary:
  - Mutations in noncoding regions of DNA are often harmless
  - Mutations in a gene might not affect protein production because of redundancy in the genetic code

- The effects of point mutations can vary:
  - Mutations that result in a change in protein production are often harmful
  - Mutations that result in a change in protein production can sometimes increase the fit between organism and environment

Mutations That Alter Gene Number or Sequence

- Chromosomal mutations that delete, disrupt, or rearrange many loci are typically harmful
- Duplication of large chromosome segments is usually harmful
- Duplication of small pieces of DNA is sometimes less harmful and increases the genome size
- Duplicated genes can take on new functions by further mutation

Mutation Rates

- Mutation rates are low in animals and plants
- The average is about one mutation in every 100,000 genes per generation
- Mutations rates are often lower in prokaryotes and higher in viruses

Sexual Reproduction

- Sexual reproduction can shuffle existing alleles into new combinations
- In organisms that reproduce sexually, recombination of alleles is more important than mutation in producing the genetic differences that make adaptation possible

Weinberg equation can be used to test whether a population is evolving

- The first step in testing whether evolution is occurring in a population is to clarify what we mean by a population

Gene Pools and Allele Frequencies

- A **population** is a localized group of individuals capable of interbreeding and producing fertile offspring
- A **gene pool** consists of all the alleles for all loci in a population
- A locus is fixed if all individuals in a population are homozygous for the same allele

Fig. 23-5

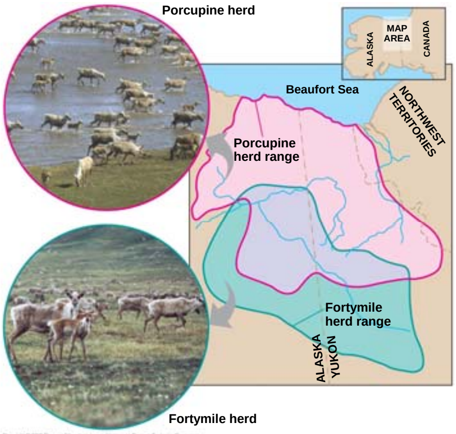
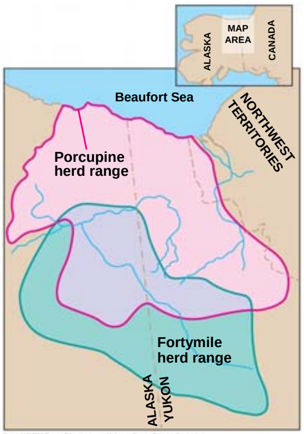


Fig. 23-5a



- The frequency of an allele in a population can be calculated
  - For diploid organisms, the total number of alleles at a locus is the total number of individuals x 2
  - The total number of dominant alleles at a locus is 2 alleles for each homozygous dominant individual plus 1 allele for each heterozygous individual; the same logic applies for recessive alleles

- By convention, if there are 2 alleles at a locus, *p* and *q* are used to represent their frequencies
- The frequency of all alleles in a population will add up to 1
  - For example, $p + q = 1$

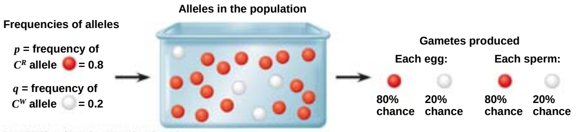
The Hardy-Weinberg Principle

- The Hardy-Weinberg principle describes a population that is not evolving
- If a population does not meet the criteria of the Hardy-Weinberg principle, it can be concluded that the population is evolving

Hardy-Weinberg Equilibrium

- The **Hardy-Weinberg principle** states that frequencies of alleles and genotypes in a population remain constant from generation to generation
- In a given population where gametes contribute to the next generation randomly, allele frequencies will not change
- Mendelian inheritance preserves genetic variation in a population

Fig. 23-6



- **Hardy-Weinberg equilibrium** describes the constant frequency of alleles in such a gene pool
- If *p* and *q* represent the relative frequencies of the only two possible alleles in a population at a particular locus, then
  - $p^2 + 2pq + q^2 = 1$
  - where p^2 and q^2 represent the frequencies of the homozygous genotypes and $2pq$ represents the frequency of the heterozygous genotype

Fig. 23-7-1

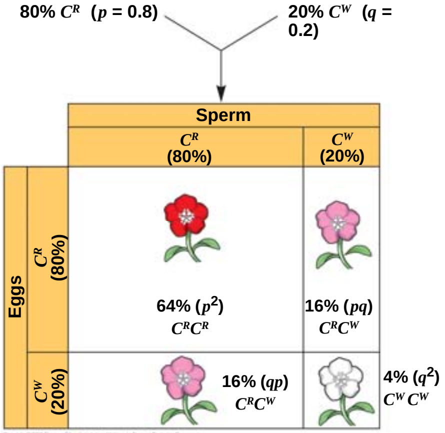


Fig. 23-7-2

64% C^RC^R, 32% C^RC^W, and 4% C^WC^W

Gametes of this generation:

64% C^R + 16% C^R = 80% C^R = 0.8 = p

4% C^W + 16% C^W = 20% C^W = 0.2 = q

Fig. 23-7-3

64% C^RC^R, 32% C^RC^W, and 4% C^WC^W

Gametes of this generation:

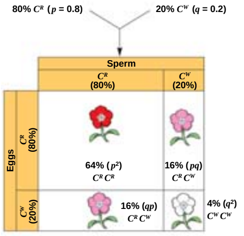
64% C^R + 16% C^R = 80% C^R = 0.8 = p

4% C^W + 16% C^W = 20% C^W = 0.2 = q

Genotypes in the next generation:

64% C^RC^R, 32% C^RC^W, and 4% C^WC^W plants

Fig. 23-7-4



64% C^RC^R, 32% C^RC^W, and 4% C^WC^W

Gametes of this generation:

64% C^R + 16% C^R = 80% C^R = 0.8 = p

4% C^W + 16% C^W = 20% C^W = 0.2 = q

Genotypes in the next generation:

64% C^RC^R, 32% C^RC^W, and 4% C^WC^W plants

Conditions for Hardy-Weinberg Equilibrium

- The Hardy-Weinberg theorem describes a hypothetical population
- In real populations, allele and genotype frequencies do change over time

- The five conditions for nonevolving populations are rarely met in nature:
  - – No mutations
  - – Random mating
  - – No natural selection
  - – Extremely large population size
  - – No gene flow

- Natural populations can evolve at some loci, while being in Hardy-Weinberg equilibrium at other loci

Applying the Hardy-Weinberg Principle

- We can assume the locus that causes phenylketonuria (PKU) is in Hardy-Weinberg equilibrium given that:
  - – The PKU gene mutation rate is low
  - – Mate selection is random with respect to whether or not an individual is a carrier for the PKU allele

- Natural selection can only act on rare homozygous individuals who do not follow dietary restrictions
- The population is large
- Migration has no effect as many other populations have similar allele frequencies

---

- The occurrence of PKU is 1 per 10,000 births
  - $q^2 = 0.0001$
  - $q = 0.01$
- The frequency of normal alleles is
  - $p = 1 – q = 1 – 0.01 = 0.99$
  - The frequency of carriers is
- The frequency of carriers is
  - $2pq = 2 \times 0.99 \times 0.01 = 0.0198$
  - or approximately 2% of the U.S. population

---

genetic drift, and gene flow can alter allele frequencies in a population

- Three major factors alter allele frequencies and bring about most evolutionary change:
  - Natural selection
  - Genetic drift
  - Gene flow

Natural Selection

- Differential success in reproduction results in certain alleles being passed to the next generation in greater proportions

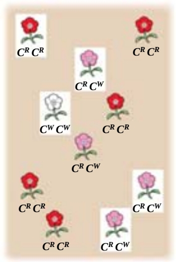
---

Genetic Drift

- The smaller a sample, the greater the chance of deviation from a predicted result
- **Genetic drift** describes how allele frequencies fluctuate unpredictably from one generation to the next
- Genetic drift tends to reduce genetic variation through losses of alleles

PLAY Animation: Causes of Evolutionary Change

Fig. 23-8-1



Generation 1

p (frequency of C^R) = 0.7

q (frequency of C^W) = 0.3

Fig. 23-8-2

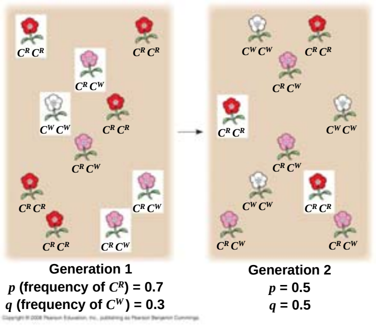
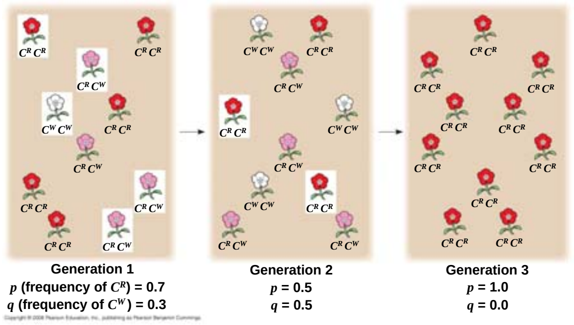


Fig. 23-8-3



The Founder Effect

- The **founder effect** occurs when a few individuals become isolated from a larger population
- Allele frequencies in the small founder population can be different from those in the larger parent population

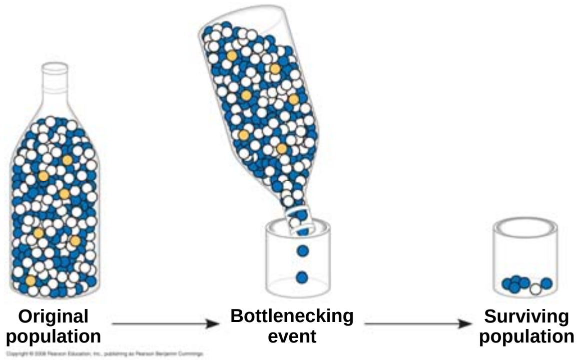
---

The Bottleneck Effect

- The **bottleneck effect** is a sudden reduction in population size due to a change in the environment
- The resulting gene pool may no longer be reflective of the original population's gene pool
- If the population remains small, it may be further affected by genetic drift

---

Fig. 23-9



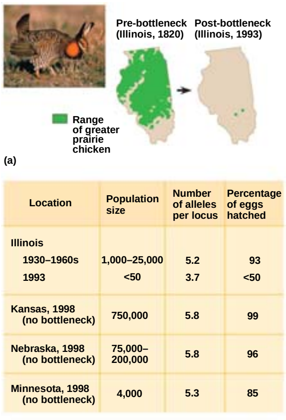
- Understanding the bottleneck effect can increase understanding of how human activity affects other species

Case Study: Impact of Genetic Drift on the Greater Prairie Chicken

- Loss of prairie habitat caused a severe reduction in the population of greater prairie chickens in Illinois
- The surviving birds had low levels of genetic variation, and only 50% of their eggs hatched

---

Fig. 23-10



Location	Population size	Number of alleles per locus	Percentage of eggs hatched
Illinois			
1930–1960s	1,000–25,000	5.2	93
1993	<50	3.7	<50
Kansas, 1998 (no bottleneck)	750,000	5.8	99
Nebraska, 1998 (no bottleneck)	75,000–200,000	5.8	96
Minnesota, 1998 (no bottleneck)	4,000	5.3	85

Fig. 23-10a

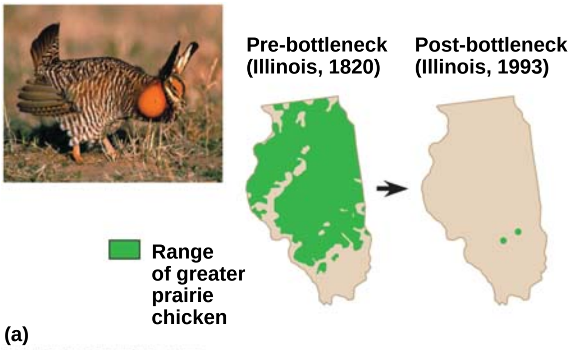
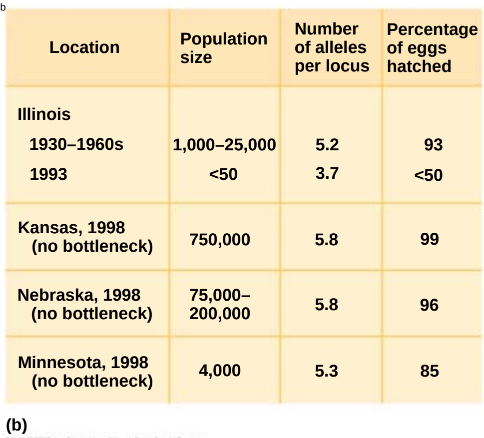


Fig. 23-10b



Location	Population size	Number of alleles per locus	Percentage of eggs hatched
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1993	<50	3.7	<50
Kansas, 1998 (no bottleneck)	750,000	5.8	99
Nebraska, 1998 (no bottleneck)	75,000–200,000	5.8	96
Minnesota, 1998 (no bottleneck)	4,000	5.3	85

(b)

- Researchers used DNA from museum specimens to compare genetic variation in the population before and after the bottleneck
- The results showed a loss of alleles at several loci
- Researchers introduced greater prairie chickens from population in other states and were successful in introducing new alleles and increasing the egg hatch rate to 90%

Effects of Genetic Drift: A Summary

1. Genetic drift is significant in small populations
2. Genetic drift causes allele frequencies to change at random
3. Genetic drift can lead to a loss of genetic variation within populations
4. Genetic drift can cause harmful alleles to become fixed

Gene Flow

- **Gene flow** consists of the movement of alleles among populations
- Alleles can be transferred through the movement of fertile individuals or gametes (for example, pollen)
- Gene flow tends to reduce differences between populations over time
- Gene flow is more likely than mutation to alter allele frequencies directly

Fig. 23-11

- Gene flow can decrease the fitness of a population
- In bent grass, alleles for copper tolerance are beneficial in populations near copper mines, but harmful to populations in other soils
- Windblown pollen moves these alleles between populations
- The movement of unfavorable alleles into a population results in a decrease in fit between organism and environment

Fig. 23-12

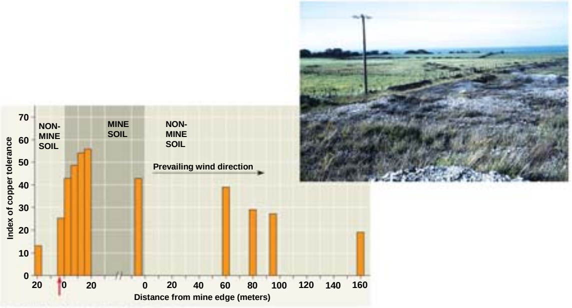


Fig. 23-12a

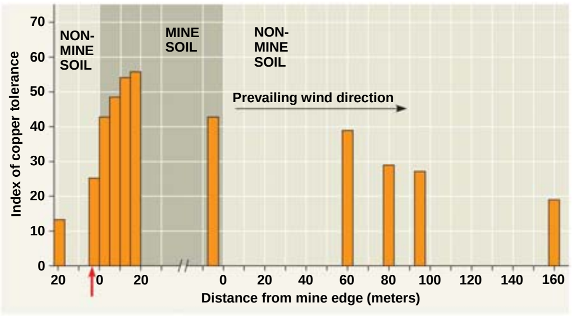


Fig. 23-12b

- Gene flow can increase the fitness of a population
- Insecticides have been used to target mosquitoes that carry West Nile virus and malaria
- Alleles have evolved in some populations that confer insecticide resistance to these mosquitoes
- The flow of insecticide resistance alleles into a population can cause an increase in fitness

---

the only mechanism that consistently causes adaptive evolution

- Only natural selection consistently results in adaptive evolution

---

A Closer Look at Natural Selection

- Natural selection brings about adaptive evolution by acting on an organism's phenotype

---

Relative Fitness

- The phrases "struggle for existence" and "survival of the fittest" are misleading as they imply direct competition among individuals
- Reproductive success is generally more subtle and depends on many factors

---

- **Relative fitness** is the contribution an individual makes to the gene pool of the next generation, relative to the contributions of other individuals
- Selection favors certain genotypes by acting on the phenotypes of certain organisms

---

Directional, Disruptive, and Stabilizing Selection

- Three modes of selection:
  - – **Directional selection** favors individuals at one end of the phenotypic range
  - – **Disruptive selection** favors individuals at both extremes of the phenotypic range
  - – **Stabilizing selection** favors intermediate variants and acts against extreme phenotypes

Fig. 23-13

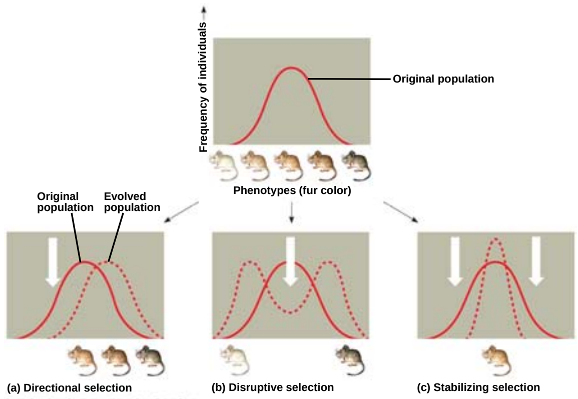


Fig. 23-13a

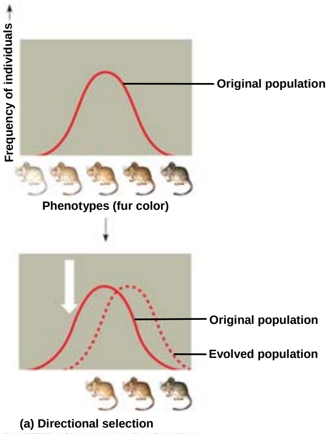


Fig. 23-13b

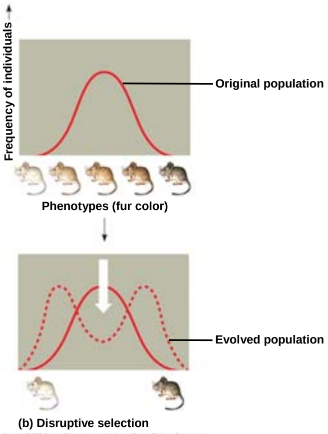
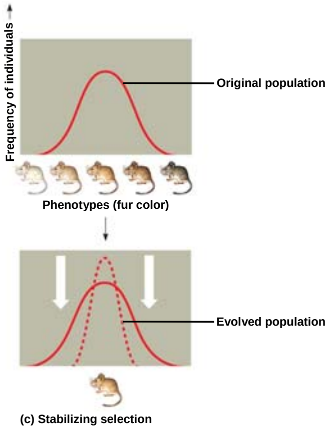


Fig. 23-13c



The Key Role of Natural Selection in Adaptive Evolution

- Natural selection increases the frequencies of alleles that enhance survival and reproduction
- Adaptive evolution occurs as the match between an organism and its environment increases

---

Fig. 23-14

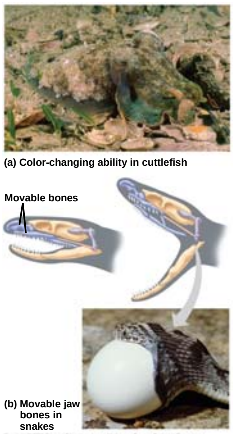
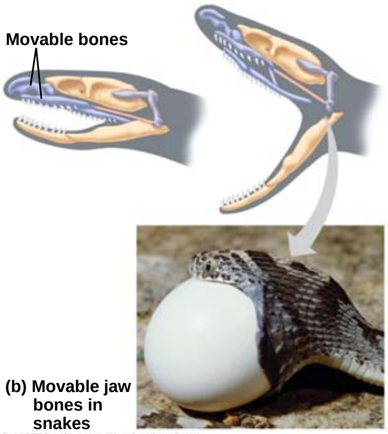


Fig. 23-14a

(a) Color-changing ability in cuttlefish

Fig. 23-14b



(b) Movable jaw bones in snakes

- Because the environment can change, adaptive evolution is a continuous process
- Genetic drift and gene flow do not consistently lead to adaptive evolution as they can increase or decrease the match between an organism and its environment

---

Sexual Selection

- **Sexual selection** is natural selection for mating success
- It can result in **sexual dimorphism**, marked differences between the sexes in secondary sexual characteristics

---

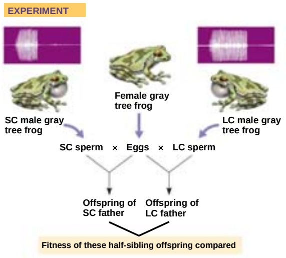
Fig. 23-15

- **Intrasexual selection** is competition among individuals of one sex (often males) for mates of the opposite sex
- **Intersexual selection**, often called mate choice, occurs when individuals of one sex (usually females) are choosy in selecting their mates
- Male showiness due to mate choice can increase a male’s chances of attracting a female, while decreasing his chances of survival

- How do female preferences evolve?
- The good genes hypothesis suggests that if a trait is related to male health, both the male trait and female preference for that trait should be selected for

---

Fig. 23-16



RESULTS

Fitness Measure	1995	1996
Larval growth	NSD	LC better
Larval survival	LC better	NSD
Time to metamorphosis	LC better (shorter)	LC better (shorter)

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

Fig. 23-16a

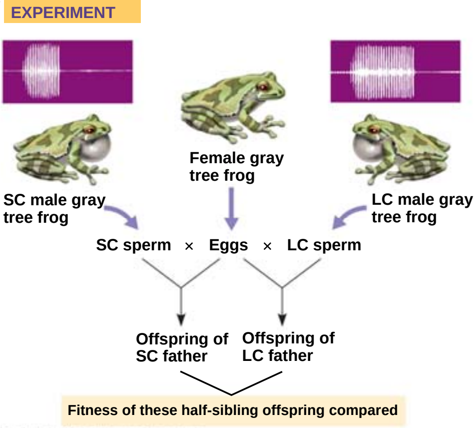


Fig. 23-16b

RESULTS

Fitness Measure	1995	1996
Larval growth	NSD	LC better
Larval survival	LC better	NSD
Time to metamorphosis	LC better (shorter)	LC better (shorter)

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

The Preservation of Genetic Variation

- Various mechanisms help to preserve genetic variation in a population

---

Diploidy

- Diploidy maintains genetic variation in the form of hidden recessive alleles

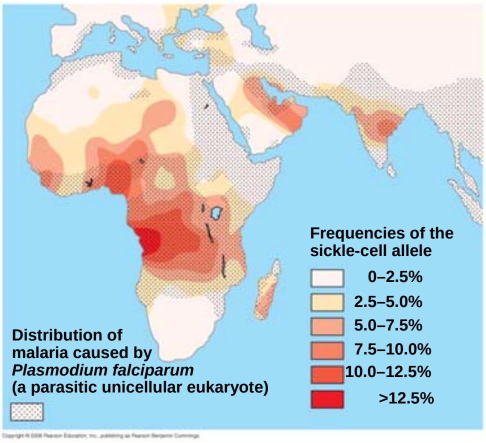
Balancing Selection

- **Balancing selection** occurs when natural selection maintains stable frequencies of two or more phenotypic forms in a population

Heterozygote Advantage

- **Heterozygote advantage** occurs when heterozygotes have a higher fitness than do both homozygotes
- Natural selection will tend to maintain two or more alleles at that locus
- The sickle-cell allele causes mutations in hemoglobin but also confers malaria resistance

Fig. 23-17



Frequency-Dependent Selection

- In **frequency-dependent selection**, the fitness of a phenotype declines if it becomes too common in the population
- Selection can favor whichever phenotype is less common in a population

Fig. 23-18

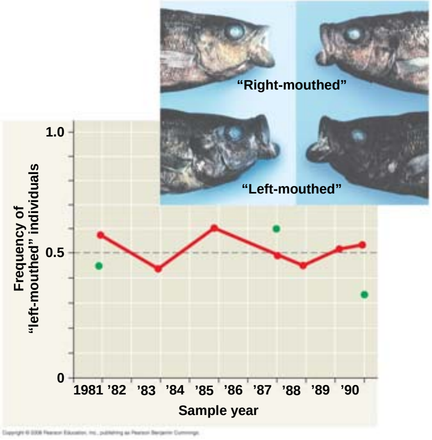


Fig. 23-18a

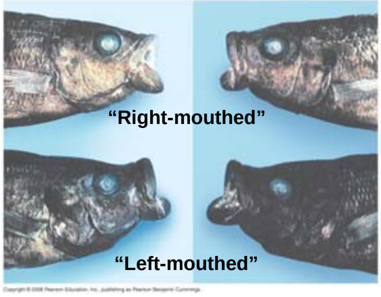
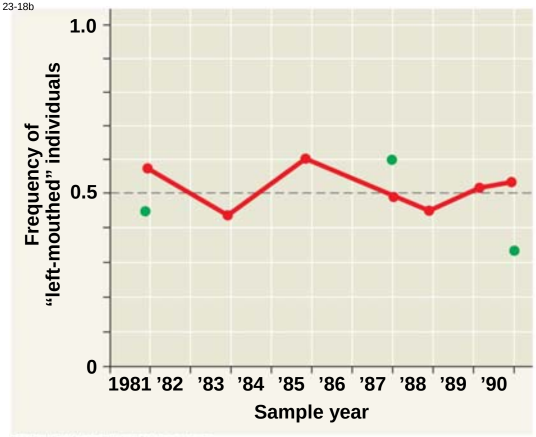


Fig. 23-18b



Neutral Variation

- **Neutral variation** is genetic variation that appears to confer no selective advantage or disadvantage
- For example,
  - Variation in noncoding regions of DNA
  - Variation in proteins that have little effect on protein function or reproductive fitness

---

Why Natural Selection Cannot Fashion Perfect Organisms

1. Selection can act only on existing variations
2. Evolution is limited by historical constraints
3. Adaptations are often compromises
4. Chance, natural selection, and the environment interact

Fig. 23-19

Fig. 23-UN1

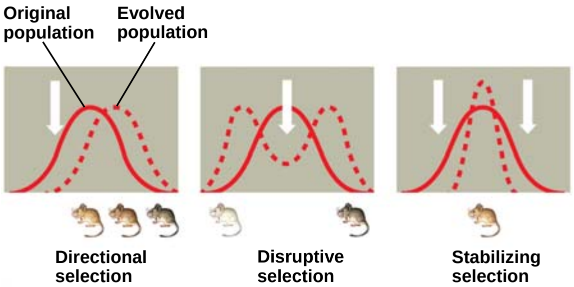
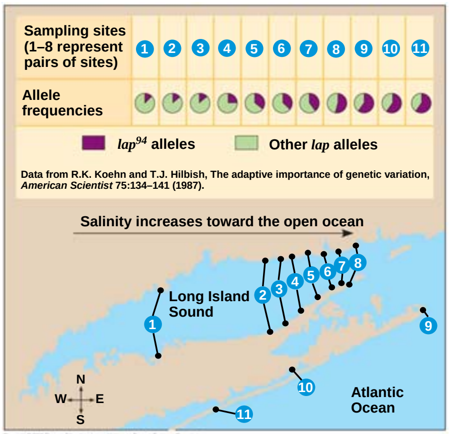
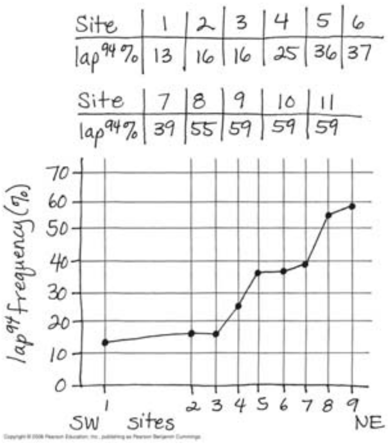


Fig. 23-UN2



Data from R.K. Koehn and T.J. Hilbish, The adaptive importance of genetic variation, *American Scientist* 75:134–141 (1987).

Fig. 23-UN3



Site	1	2	3	4	5	6
lap^{94} %	13	16	16	25	36	37

Site	7	8	9	10	11
lap^{94} %	39	55	59	59	59

Overview: That “Mystery of Mysteries”

- In the Galápagos Islands Darwin discovered plants and animals found nowhere else on Earth

PLAY Video: Galápagos Tortoise

Fig. 24-1

- **Speciation**, the origin of new species, is at the focal point of evolutionary theory
- Evolutionary theory must explain how new species originate and how populations evolve
- **Microevolution** consists of adaptations that evolve within a population, confined to one gene pool
- **Macroevolution** refers to evolutionary change above the species level

PLAY Animation: Macroevolution

Concept 24.1: The biological species concept emphasizes reproductive isolation

- *Species* is a Latin word meaning “kind” or “appearance”
- Biologists compare morphology, physiology, biochemistry, and DNA sequences when grouping organisms

The Biological Species Concept

- The **biological species concept** states that a **species** is a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring; they do not breed successfully with other populations
- Gene flow between populations holds the phenotype of a population together

Fig. 24-2

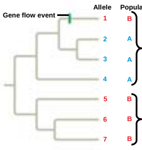
(a) Similarity between different species

(b) Diversity within a species

Fig. 24-3

EXPERIMENT

Example of a gene tree for population pair A-B



Allele 1 is more closely related to alleles 2, 3, and 4 than to alleles 5, 6, and 7.
Inference: Gene flow occurred.

Alleles 5, 6, and 7 are more closely related to one another than to alleles in population A.
Inference: No gene flow occurred.

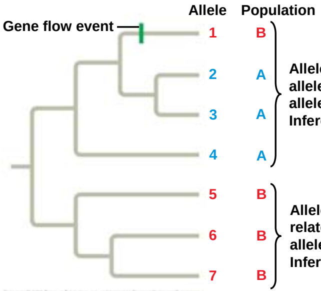
RESULTS

Pair of populations with detected gene flow	Estimated minimum number of gene flow events to account for genetic patterns	Distance between populations (km)
A-B	5	340
K-L	3	720
A-C	2–3	1,390
B-C	2	1,190
F-G	2	760
G-I	2	1,110
C-E	1–2	1,310

Fig. 24-3a

EXPERIMENT

Example of a gene tree for population pair A-B



Allele 1 is more closely related to alleles 2, 3, and 4 than to alleles 5, 6, and 7.
Inference: Gene flow occurred.

Alleles 5, 6, and 7 are more closely related to one another than to alleles in population A.
Inference: No gene flow occurred.

Fig. 24-3b

RESULTS

Pair of populations with detected gene flow	Estimated minimum number of gene flow events to account for genetic patterns	Distance between populations (km)
A-B	5	340
K-L	3	720
A-C	2–3	1,390
B-C	2	1,190
F-G	2	760
G-I	2	1,110
C-E	1–2	1,310

Fig. 24-3c

Grey-crowned babblers

Reproductive Isolation

- **Reproductive isolation** is the existence of biological factors (barriers) that impede two species from producing viable, fertile offspring
- **Hybrids** are the offspring of crosses between different species
- Reproductive isolation can be classified by whether factors act before or after fertilization

- **Prezygotic barriers** block fertilization from occurring by:
  - Impeding different species from attempting to mate
  - Preventing the successful completion of mating
  - Hindering fertilization if mating is successful

- **Habitat isolation**: Two species encounter each other rarely, or not at all, because they occupy different habitats, even though not isolated by physical barriers

---

Fig. 24-4

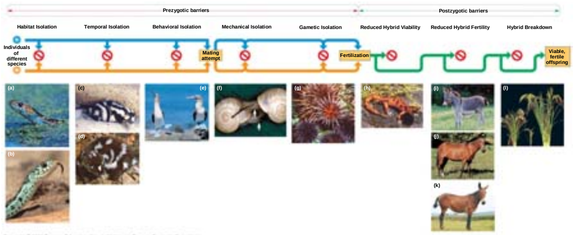


Fig. 24-4a

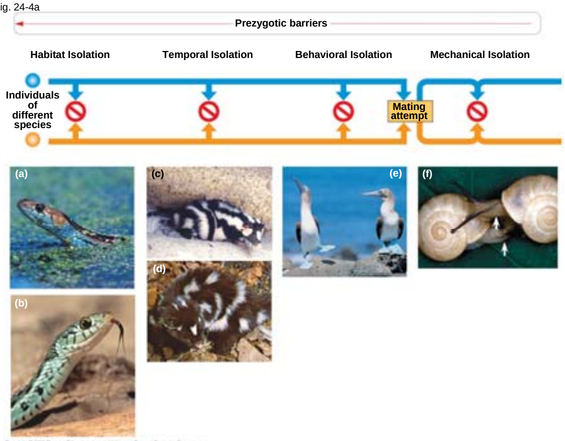


Fig. 24-4i

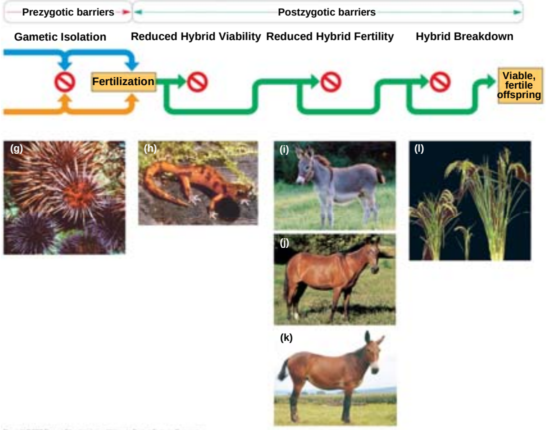


Fig. 24-4b

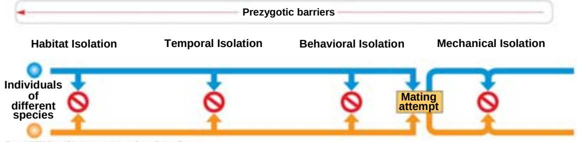


Fig. 24-4j

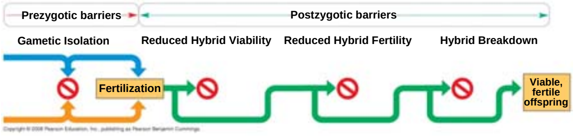


Fig. 24-4c

Water-dwelling *Thamnophis*

Fig. 24-4d

Terrestrial *Thamnophis*

- **Temporal isolation**: Species that breed at different times of the day, different seasons, or different years cannot mix their gametes

Fig. 24-4e

Eastern spotted skunk
(Spilogale putorius)

Fig. 24-4f

Western spotted skunk
(Spilogale gracilis)

- **Behavioral isolation**: Courtship rituals and other behaviors unique to a species are effective barriers

PLAY Video: Albatross Courtship Ritual

PLAY Video: Giraffe Courtship Ritual

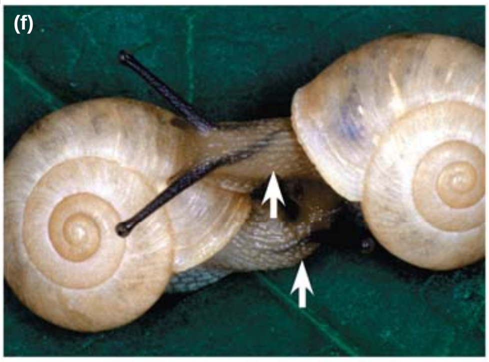
PLAY Video: Blue-footed Boobies Courtship Ritual

Fig. 24-4g

Courtship ritual of blue-footed boobies

- **Mechanical isolation**: Morphological differences can prevent successful mating

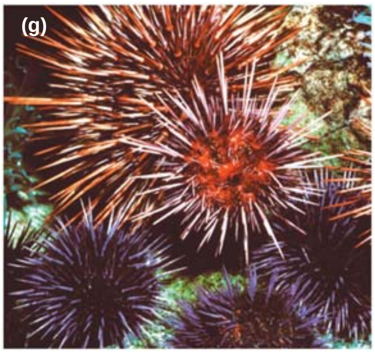
Fig. 24-4h



Bradybaena **with shells spiraling in opposite directions**

- **Gametic isolation**: Sperm of one species may not be able to fertilize eggs of another species

Fig. 24-4k



Sea urchins

- **Postzygotic barriers** prevent the hybrid zygote from developing into a viable, fertile adult:
    - – Reduced hybrid viability
    - – Reduced hybrid fertility
    - – Hybrid breakdown

- **Reduced hybrid viability**: Genes of the different parent species may interact and impair the hybrid’s development

Fig. 24-4l

Ensatina **hybrid**

- **Reduced hybrid fertility**: Even if hybrids are vigorous, they may be sterile

Fig. 24-4m

Donkey

Fig. 24-4n

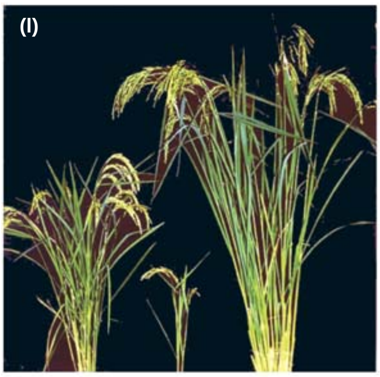
Horse

Fig. 24-4o

Mule (sterile hybrid)

- **Hybrid breakdown**: Some first-generation hybrids are fertile, but when they mate with another species or with either parent species, offspring of the next generation are feeble or sterile

Fig. 24-4p



Hybrid cultivated rice plants with stunted offspring (center)

Limitations of the Biological Species Concept

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

Other Definitions of Species

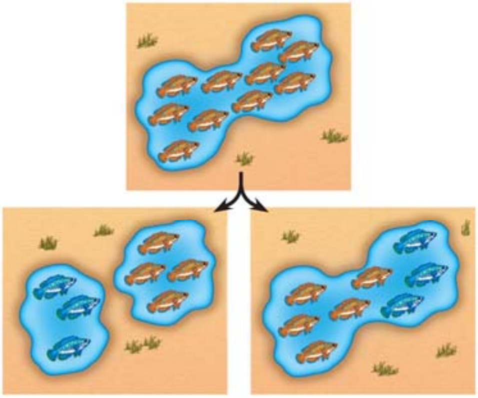
- Other species concepts emphasize the unity within a species rather than the separateness of different species
- The **morphological species concept** defines a species by structural features
  - It applies to sexual and asexual species but relies on subjective criteria

- 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

Concept 24.2: Speciation can take place with or without geographic separation

- Speciation can occur in two ways:
  - – Allopatric speciation
  - – Sympatric speciation

Fig. 24-5



(a) Allopatric speciation (b) Sympatric speciation

Allopatric ("Other Country") Speciation

- In **allopatric speciation**, gene flow is interrupted or reduced when a population is divided into geographically isolated subpopulations

The Process of Allopatric Speciation

- The definition of *barrier* depends on the ability of a population to disperse
- Separate populations may evolve independently through mutation, natural selection, and genetic drift

Fig. 24-6

Evidence of Allopatric Speciation

- Regions with many geographic barriers typically have more species than do regions with fewer barriers

Fig. 24-7

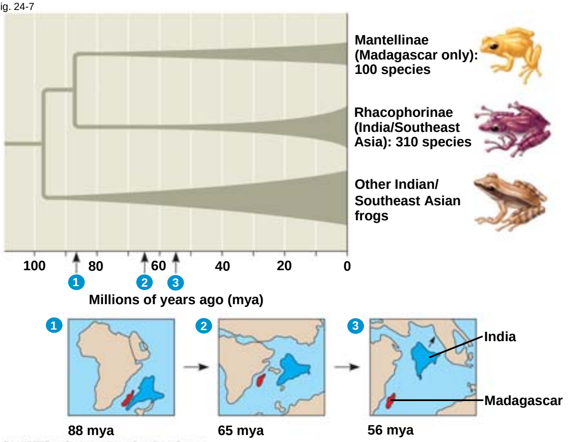


Fig. 24-7a

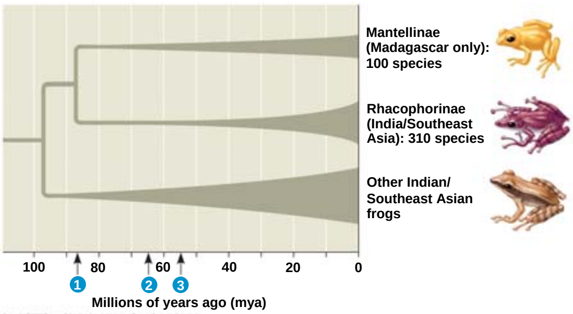
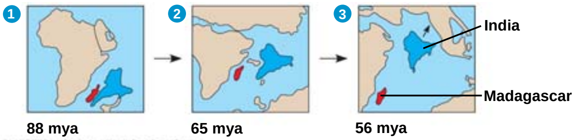
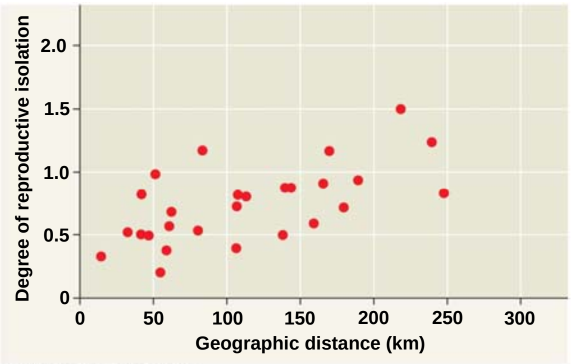


Fig. 24-7b



- Reproductive isolation between populations generally increases as the distance between them increases

Fig. 24-8



- Barriers to reproduction are intrinsic; separation itself is not a biological barrier

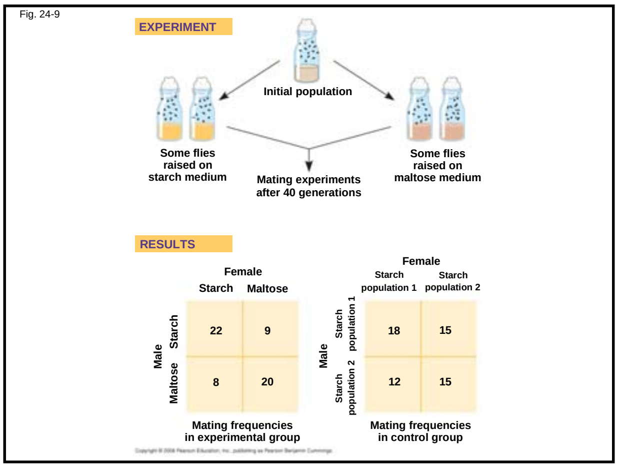


Fig. 24-9

EXPERIMENT

Initial population

Some flies raised on starch medium

Mating experiments after 40 generations

Some flies raised on maltose medium

RESULTS

		Female Starch	Female Maltose
Male	Starch	22	9
Male	Maltose	8	20

Mating frequencies in experimental group

		Female Starch population 1	Female Starch population 2
Male	Starch population 1	18	15
Male	Starch population 2	12	15

Mating frequencies in control group

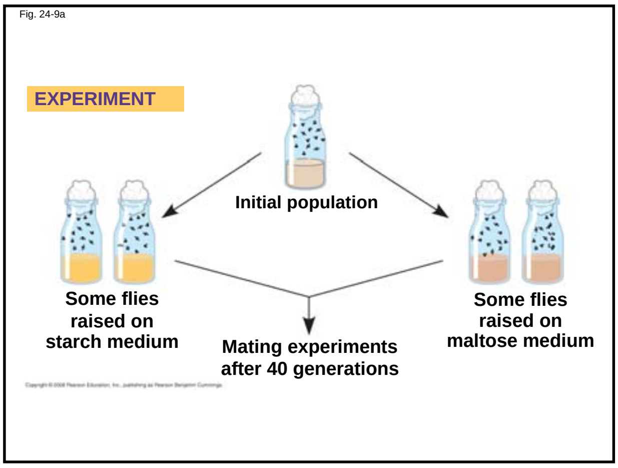


Fig. 24-9a

EXPERIMENT

Initial population

Some flies raised on starch medium

Mating experiments after 40 generations

Some flies raised on maltose medium

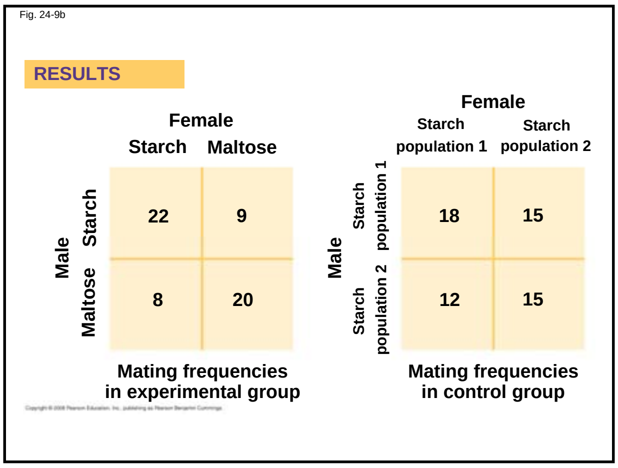


Fig. 24-9b

RESULTS

		Female Starch	Female Maltose
Male	Starch	22	9
Male	Maltose	8	20

Mating frequencies in experimental group

		Female Starch population 1	Female Starch population 2
Male	Starch population 1	18	15
Male	Starch population 2	12	15

Mating frequencies in control group

Sympatric (“Same Country”) Speciation

- In **sympatric speciation**, speciation takes place in geographically overlapping populations

---

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

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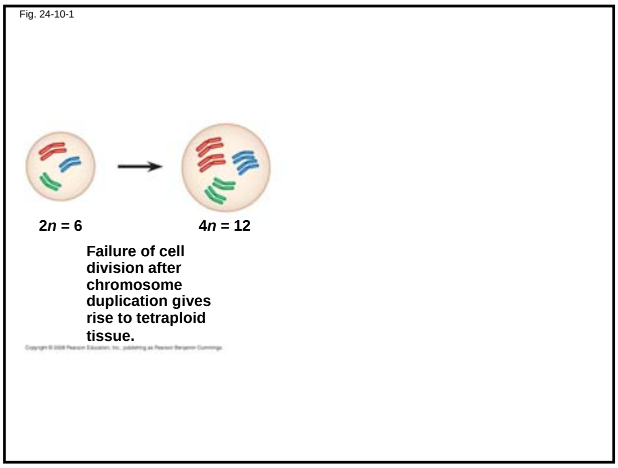


Fig. 24-10-1

$2n = 6$

$4n = 12$

Failure of cell division after chromosome duplication gives rise to tetraploid tissue.

Fig. 24-10-2

$2n = 6$

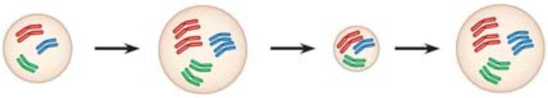
$4n = 12$

$2n$

Failure of cell division after chromosome duplication gives rise to tetraploid tissue.

Gametes produced are diploid.

Fig. 24-10-3



$2n = 6$

$4n = 12$

$2n$

$4n$

Failure of cell division after chromosome duplication gives rise to tetraploid tissue.

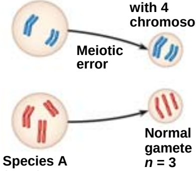
Gametes produced are diploid.

Offspring with tetraploid karyotypes may be viable and fertile.

- An **allopolyploid** is a species with multiple sets of chromosomes derived from different species

---

Fig. 24-11-1



Species B
$2n = 4$

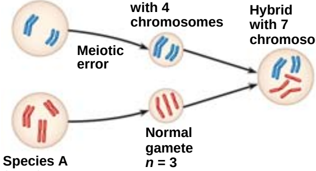
Unreduced gamete with 4 chromosomes

Meiotic error

Normal gamete
$n = 3$

Species A
$2n = 6$

Fig. 24-11-2



Species B
$2n = 4$

Unreduced gamete with 4 chromosomes

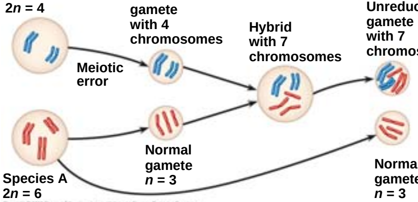
Hybrid with 7 chromosomes

Meiotic error

Normal gamete
$n = 3$

Species A
$2n = 6$

Fig. 24-11-3



Species B
$2n = 4$

Unreduced gamete with 4 chromosomes

Hybrid with 7 chromosomes

Unreduced gamete with 7 chromosomes

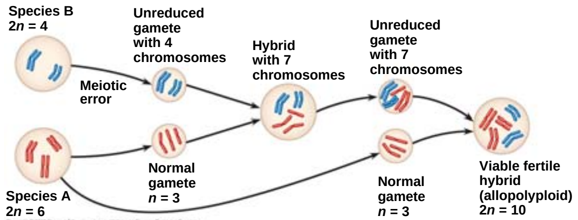
Meiotic error

Normal gamete
$n = 3$

Normal gamete
$n = 3$

Species A
$2n = 6$

Fig. 24-11-4



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

---

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

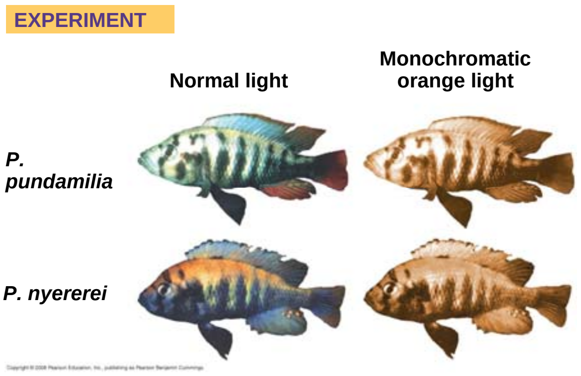
---

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

---

Fig. 24-12



Allopatric and Sympatric Speciation: *A Review*

- 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

---

provide opportunities to study factors that cause reproductive isolation

- A **hybrid zone** is a region in which members of different species mate and produce hybrids

---

Patterns Within Hybrid Zones

- A hybrid zone can occur in a single band where adjacent species meet
- 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

---

Fig. 24-13

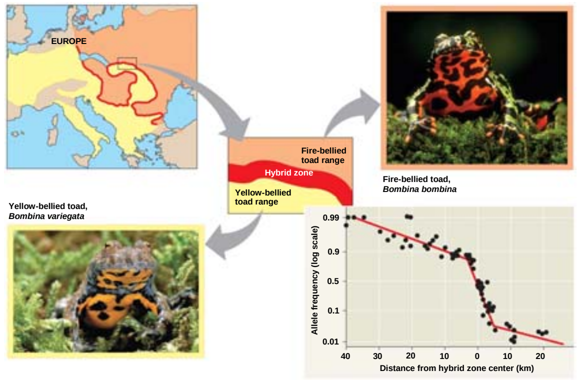


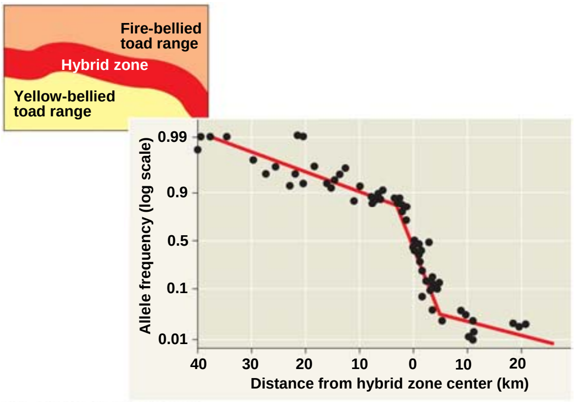
Fig. 24-13a

Yellow-bellied toad,
Bombina variegata

Fig. 24-13b

Fire-bellied toad,
Bombina bombina

Fig. 24-13c



Hybrid Zones over Time

- When closely related species meet in a hybrid zone, there are three possible outcomes:
  - Strengthening of reproductive barriers
  - Weakening of reproductive barriers
  - Continued formation of hybrid individuals

Fig. 24-14-1

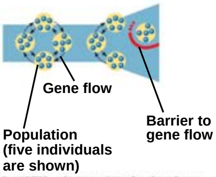


Fig. 24-14-2

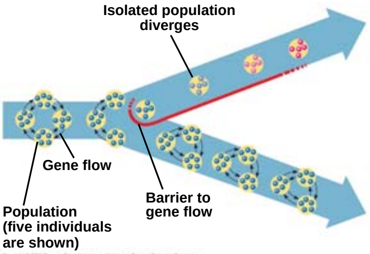


Fig. 24-14-3

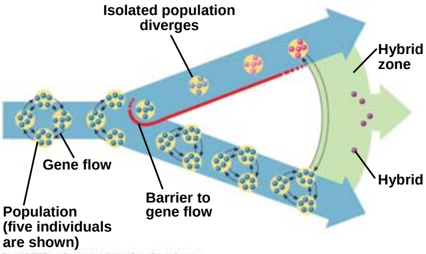
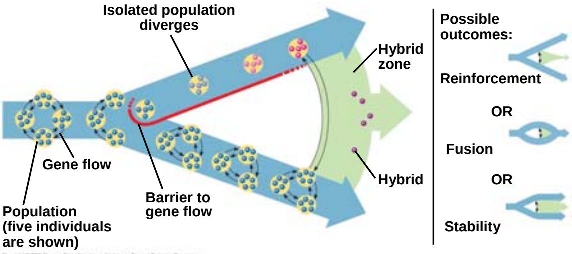


Fig. 24-14-4



Reinforcement: Strengthening Reproductive Barriers

- The **reinforcement** of barriers occurs when hybrids are less fit than the parent species
- Over time, the rate of hybridization decreases
- Where reinforcement occurs, reproductive barriers should be stronger for sympatric than allopatric species

---

Fig. 24-15

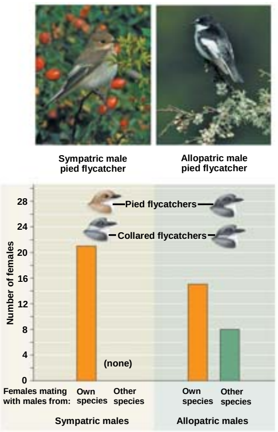
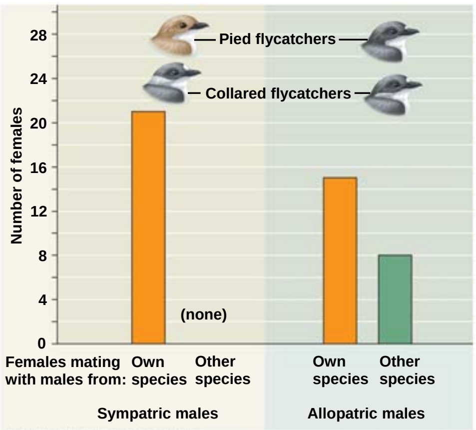


Fig. 24-15a

Sympatric male pied flycatcher

Allopatric male pied flycatcher

Fig. 24-15b

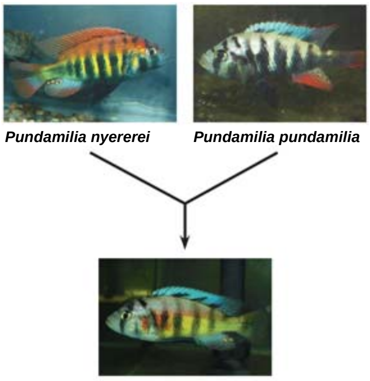


Fusion: Weakening Reproductive Barriers

- 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

---

Fig. 24-16



Pundamilia nyererei

Pundamilia pundamilia

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

Stability: Continued Formation of Hybrid Individuals

- Extensive gene flow from outside the hybrid zone can overwhelm selection for increased reproductive isolation inside the hybrid zone
- In cases where hybrids have increased fitness, local extinctions of parent species within the hybrid zone can prevent the breakdown of reproductive barriers

occur rapidly or slowly and can result from changes in few or many genes

- Many questions remain concerning how long it takes for new species to form, or how many genes need to differ between species

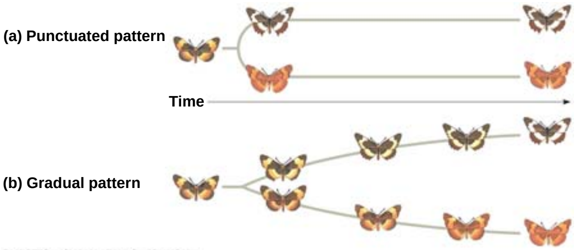
The Time Course of Speciation

- Broad patterns in speciation can be studied using the fossil record, morphological data, or molecular data

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

Fig. 24-17

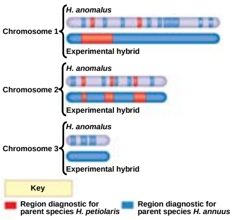


Speciation Rates

- 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

Fig. 24-18

(a) The wild sunflower *Helianthus anomalus*



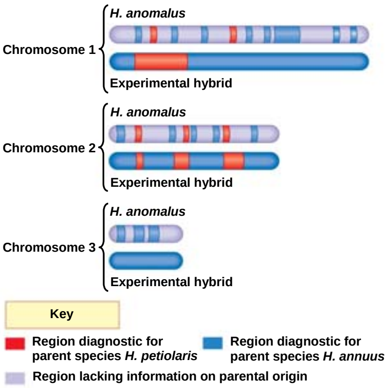
(b) The genetic composition of three chromosomes in *H. anomalus* and in experimental hybrids

---

Fig. 24-18a

(a) The wild sunflower *Helianthus anomalus*

Fig. 24-18b



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

---

Studying the Genetics of Speciation

- The explosion of genomics is enabling researchers to identify specific genes involved in some cases of speciation
- Depending on the species in question, speciation might require the change of only a single allele or many alleles

---

Fig. 24-19

Fig. 24-20

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

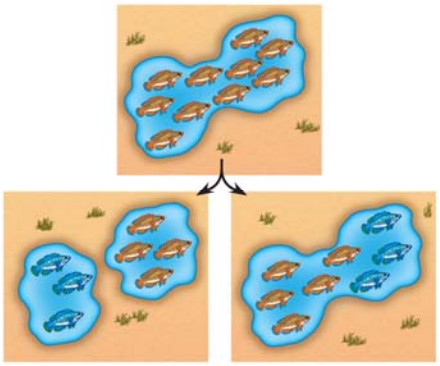
(c) Typical *Mimulus cardinalis* **(d) *M. cardinalis* with an *M. lewisii* flower-color allele**

From Speciation to Macroevolution

- Macroevolution is the cumulative effect of many speciation and extinction events

---

Fig. 24-UN1

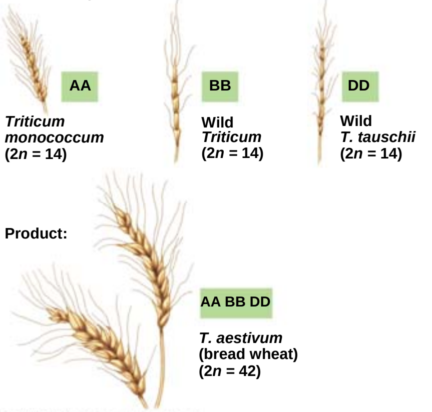


Original population

Allopatric speciation

Sympatric speciation

Fig. 24-UN2



Ancestral species:

AA

Triticum monococcum
(2*n* = 14)

BB

Wild *Triticum*
(2*n* = 14)

DD

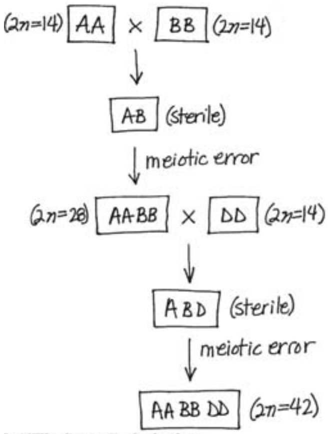
Wild *T. tauschii*
(2*n* = 14)

Product:

AA BB DD

T. aestivum
(bread wheat)
(2*n* = 42)

Fig. 24-UN3



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

Overview: Lost Worlds

- Past organisms were very different from those now alive
- The fossil record shows **macroevolutionary** changes over large time scales including
  - – The emergence of terrestrial vertebrates
  - – The origin of photosynthesis
  - – Long-term impacts of mass extinctions

Fig. 25-1

Fig 25-UN1

Cryolophosaurus

Concept 25.1: Conditions on early Earth made the origin of life possible

- Chemical and physical processes on early Earth may have produced very simple cells through a sequence of stages:
  1. Abiotic synthesis of small organic molecules
  2. Joining of these small molecules into macromolecules
  3. Packaging of molecules into “protobionts”
  4. Origin of self-replicating molecules

Synthesis of Organic Compounds on Early Earth

- Earth formed about 4.6 billion years ago, along with the rest of the solar system
- Earth’s early atmosphere likely contained water vapor and chemicals released by volcanic eruptions (nitrogen, nitrogen oxides, carbon dioxide, methane, ammonia, hydrogen, hydrogen sulfide)

- A. I. Oparin and J. B. S. Haldane hypothesized that the early atmosphere was a reducing environment
- Stanley Miller and Harold Urey conducted lab experiments that showed that the abiotic synthesis of organic molecules in a reducing atmosphere is possible

- However, the evidence is not yet convincing that the early atmosphere was in fact reducing
- Instead of forming in the atmosphere, the first organic compounds may have been synthesized near submerged volcanoes and deep-sea vents

PLAY Video: Tubeworms

PLAY Video: Hydrothermal Vent

Fig. 25-2

- Amino acids have also been found in meteorites

Abiotic Synthesis of Macromolecules

- Small organic molecules polymerize when they are concentrated on hot sand, clay, or rock

---

Protobionts

- Replication and metabolism are key properties of life
- **Protobionts** are aggregates of abiotically produced molecules surrounded by a membrane or membrane-like structure
- Protobionts exhibit simple reproduction and metabolism and maintain an internal chemical environment

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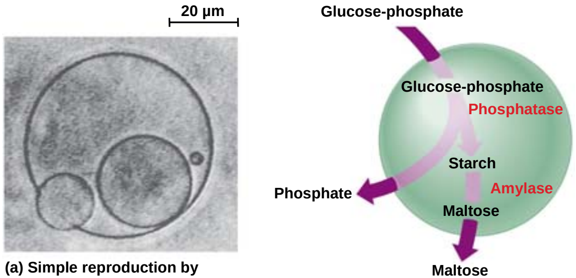
- Experiments demonstrate that protobionts could have formed spontaneously from abiotically produced organic compounds
- For example, small membrane-bounded droplets called liposomes can form when lipids or other organic molecules are added to water

---

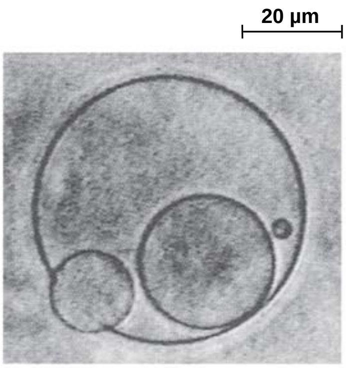
Fig. 25-3



(a) Simple reproduction by liposomes

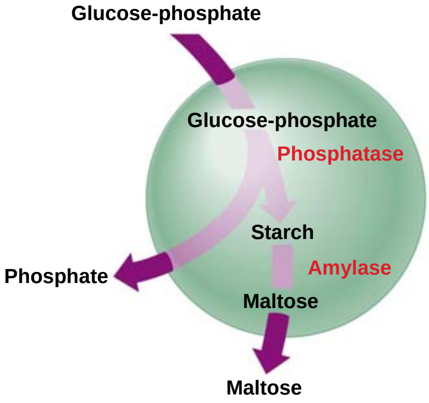
(b) Simple metabolism

Fig. 25-3a



(a) Simple reproduction by liposomes

Fig. 25-3b



(b) Simple metabolism

Self-Replicating RNA and the Dawn of Natural Selection

- The first genetic material was probably RNA, not DNA
- RNA molecules called **ribozymes** have been found to catalyze many different reactions
  - For example, ribozymes can make complementary copies of short stretches of their own sequence or other short pieces of RNA

- Early protobionts with self-replicating, catalytic RNA would have been more effective at using resources and would have increased in number through natural selection
- The early genetic material might have formed an “RNA world”

Concept 25.2: The fossil record documents the history of life

- The fossil record reveals changes in the history of life on earth

The Fossil Record

- Sedimentary rocks are deposited into layers called *strata* and are the richest source of fossils

PLAY Video: Grand Canyon

Fig. 25-4

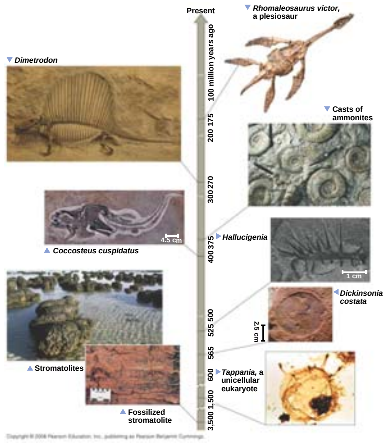


Fig. 25-4-1

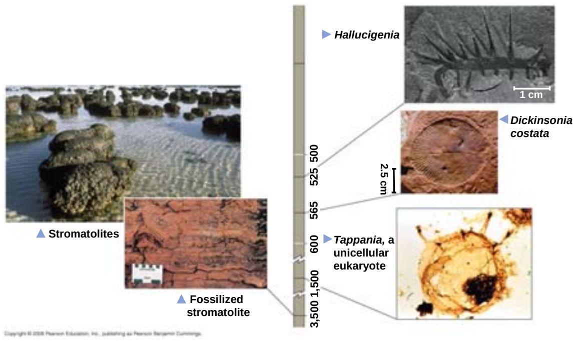
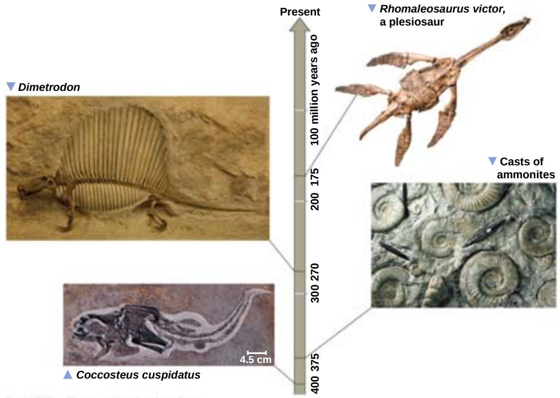


Fig. 25-4a-2



- Few individuals have fossilized, and even fewer have been discovered
- The fossil record is biased in favor of species that
  - – Existed for a long time
  - – Were abundant and widespread
  - – Had hard parts

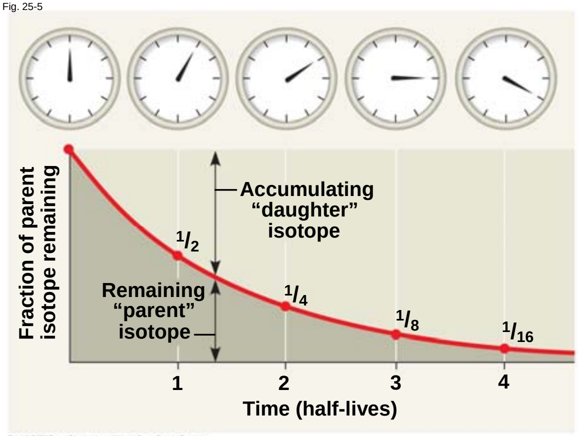
PLAY Animation: The Geologic Record

How Rocks and Fossils Are Dated

- Sedimentary strata reveal the relative ages of fossils
- The absolute ages of fossils can be determined by **radiometric dating**
- A “parent” isotope decays to a “daughter” isotope at a constant rate
- Each isotope has a known **half-life**, the time required for half the parent isotope to decay

---

Fig. 25-5



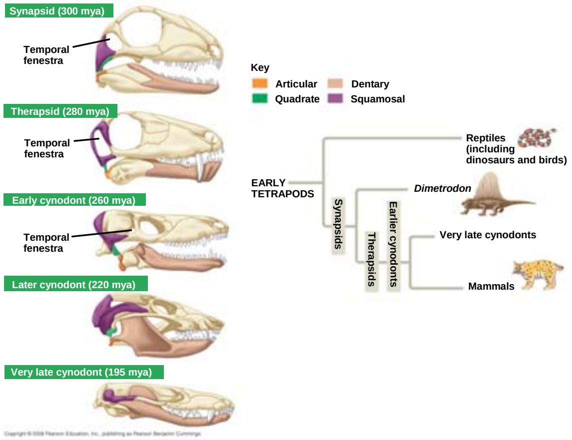
- Radiocarbon dating can be used to date fossils up to 75,000 years old
- For older fossils, some isotopes can be used to date sedimentary rock layers above and below the fossil

- The magnetism of rocks can provide dating information
- Reversals of the magnetic poles leave their record on rocks throughout the world

The Origin of New Groups of Organisms

- Mammals belong to the group of animals called *tetrapods*
- The evolution of unique mammalian features through gradual modifications can be traced from ancestral synapsids through the present

Fig. 25-6



history include the origins of single-celled and multicelled organisms and the colonization of land

- The **geologic record** is divided into the Archaean, the Proterozoic, and the Phanerozoic eons

Table 25-1

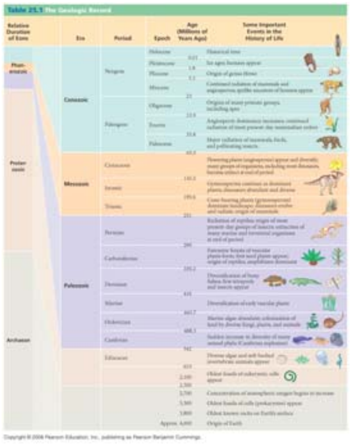
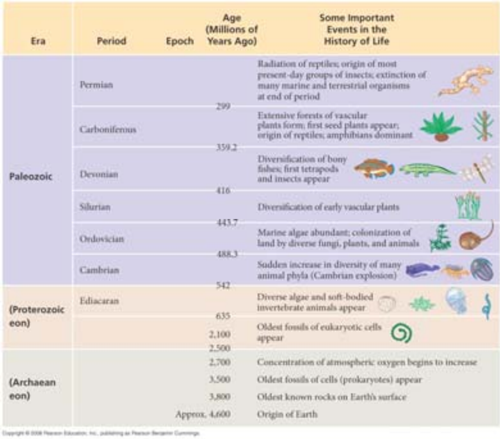
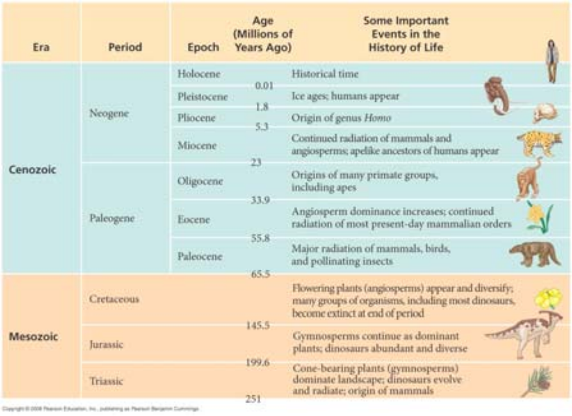


Table 25-1a



Era	Period	Epoch	Age (Millions of Years Ago)	Some Important Events in the History of Life
Paleozoic	Permian		299	Radiation of reptiles; origin of most present-day groups of insects; extinction of many marine and terrestrial organisms at end of period
	Carboniferous		359.2	Extensive forests of vascular plants form; first seed plants appear; origin of reptiles; amphibians dominant
	Devonian		416	Diversification of bony fishes; first tetrapods and insects appear
	Silurian		443.7	Diversification of early vascular plants
	Ordovician		488.3	Marine algae abundant; colonization of land by diverse fungi, plants, and animals
	Cambrian		542	Sudden increase in diversity of many animal phyla (Cambrian explosion)
(Proterozoic eon)	Ediacaran		635	Diverse algae and soft-bodied invertebrate animals appear
			2,100	Oldest fossils of eukaryotic cells appear
			2,500	
(Archaean eon)			2,700	Concentration of atmospheric oxygen begins to increase
			3,500	Oldest fossils of cells (prokaryotes) appear
			3,800	Oldest known rocks on Earth's surface
			Approx. 4,600	Origin of Earth

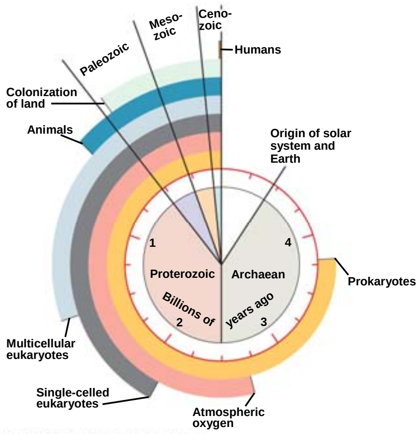
Table 25-1b



Era	Period	Epoch	Age (Millions of Years Ago)	Some Important Events in the History of Life
Cenozoic	Neogene	Holocene	0.01	Historical time
		Pleistocene	1.8	Ice ages; humans appear
		Pliocene	5.3	Origin of genus *Homo*
		Miocene	23	Continued radiation of mammals and angiosperms; apelike ancestors of humans appear
	Paleogene	Oligocene	33.9	Origins of many primate groups, including apes
		Eocene	55.8	Angiosperm dominance increases; continued radiation of most present-day mammalian orders
		Paleocene	65.5	Major radiation of mammals, birds, and pollinating insects
Mesozoic	Cretaceous		145.5	Flowering plants (angiosperms) appear and diversify; many groups of organisms, including most dinosaurs, become extinct at end of period
	Jurassic		199.6	Gymnosperms continue as dominant plants; dinosaurs abundant and diverse
	Triassic		251	Cone-bearing plants (gymnosperms) dominate landscape; dinosaurs evolve and radiate; origin of mammals

- The Phanerozoic encompasses multicellular eukaryotic life
- The Phanerozoic is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic
- Major boundaries between geological divisions correspond to extinction events in the fossil record

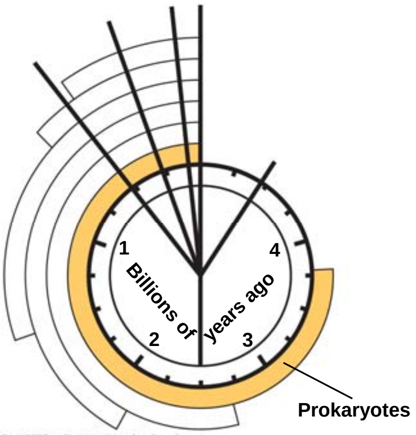
Fig. 25-7



The First Single-Celled Organisms

- The oldest known fossils are **stromatolites**, rock-like structures composed of many layers of bacteria and sediment
- Stromatolites date back 3.5 billion years ago
- Prokaryotes were Earth's sole inhabitants from 3.5 to about 2.1 billion years ago

Fig 25-UN2



Photosynthesis and the Oxygen Revolution

- Most atmospheric oxygen (O_2) is of biological origin
- O_2 produced by oxygenic photosynthesis reacted with dissolved iron and precipitated out to form banded iron formations
- The source of O_2 was likely bacteria similar to modern cyanobacteria

---

- By about 2.7 billion years ago, O_2 began accumulating in the atmosphere and rusting iron-rich terrestrial rocks
- This “oxygen revolution” from 2.7 to 2.2 billion years ago
  - Posed a challenge for life
  - Provided opportunity to gain energy from light
  - Allowed organisms to exploit new ecosystems

Fig 25-UN3

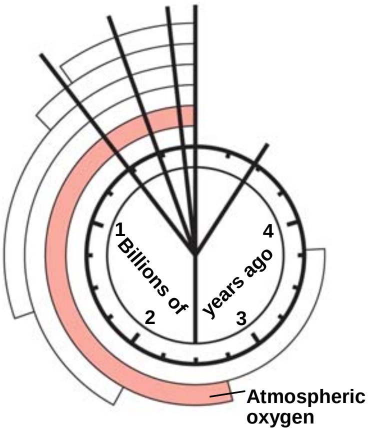
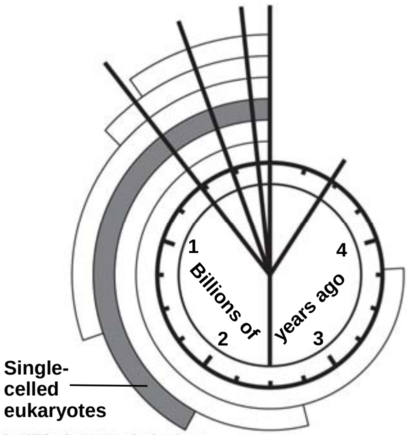


Fig. 25-8

The First Eukaryotes

- The oldest fossils of eukaryotic cells date back 2.1 billion years
- The hypothesis of **endosymbiosis** proposes that mitochondria and plastids (chloroplasts and related organelles) were formerly small prokaryotes living within larger host cells
- An *endosymbiont* is a cell that lives within a host cell

Fig 25-UN4



- The prokaryotic ancestors of mitochondria and plastids probably gained entry to the host cell as undigested prey or internal parasites
- In the process of becoming more interdependent, the host and endosymbionts would have become a single organism
- **Serial endosymbiosis** supposes that mitochondria evolved before plastids through a sequence of endosymbiotic

Fig. 25-9-1

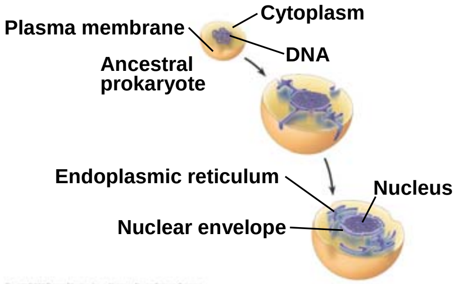


Fig. 25-9-2

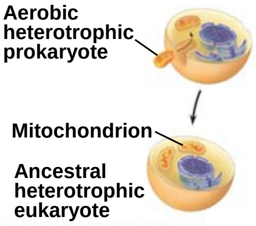


Fig. 25-9-3

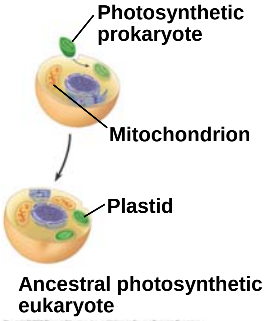
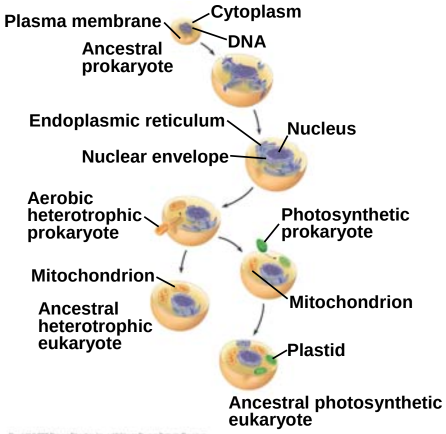


Fig. 25-9-4



- Key evidence supporting an endosymbiotic origin of mitochondria and plastids:
  - Similarities in inner membrane structures and functions
  - Division is similar in these organelles and some prokaryotes
  - These organelles transcribe and translate their own DNA
  - Their ribosomes are more similar to prokaryotic than eukaryotic ribosomes

The Origin of Multicellularity

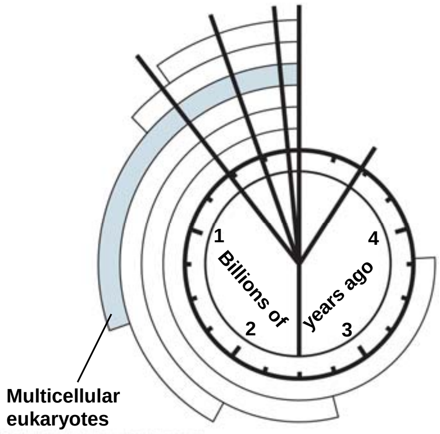
- The evolution of eukaryotic cells allowed for a greater range of unicellular forms
- A second wave of diversification occurred when multicellularity evolved and gave rise to algae, plants, fungi, and animals

The Earliest Multicellular Eukaryotes

- Comparisons of DNA sequences date the common ancestor of multicellular eukaryotes to 1.5 billion years ago
- The oldest known fossils of multicellular eukaryotes are of small algae that lived about 1.2 billion years ago

- The "snowball Earth" hypothesis suggests that periods of extreme glaciation confined life to the equatorial region or deep-sea vents from 750 to 580 million years ago
- The Ediacaran biota were an assemblage of larger and more diverse soft-bodied organisms that lived from 565 to 535 million years ago

Fig 25-UN5



The Cambrian Explosion

- The **Cambrian explosion** refers to the sudden appearance of fossils resembling modern phyla in the Cambrian period (535 to 525 million years ago)
- The Cambrian explosion provides the first evidence of predator-prey interactions

Fig 25-UN6

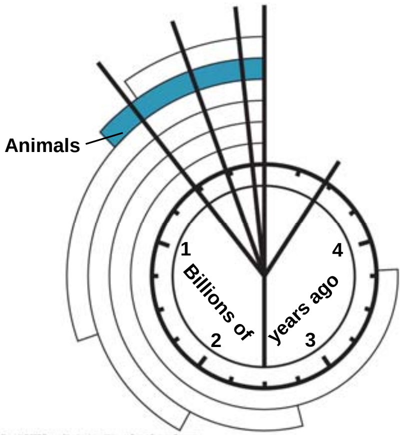
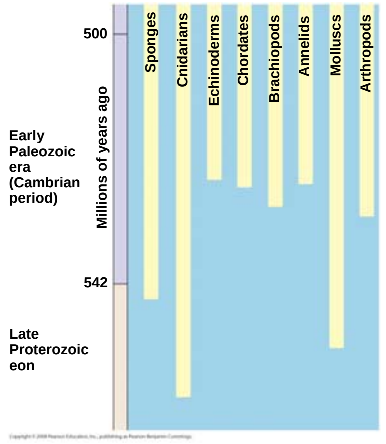
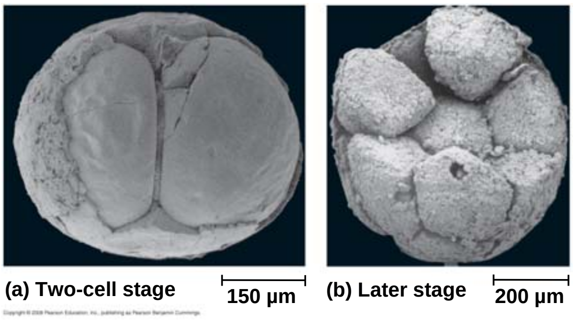


Fig. 25-10



- DNA analyses suggest that many animal phyla diverged before the Cambrian explosion, perhaps as early as 700 million to 1 billion years ago
- Fossils in China provide evidence of modern animal phyla tens of millions of years before the Cambrian explosion
- The Chinese fossils suggest that “the Cambrian explosion had a long fuse”

Fig. 25-11



(a) Two-cell stage

(b) Later stage

The Colonization of Land

- Fungi, plants, and animals began to colonize land about 500 million years ago
- Plants and fungi likely colonized land together by 420 million years ago
- Arthropods and tetrapods are the most widespread and diverse land animals
- Tetrapods evolved from lobe-finned fishes around 365 million years ago

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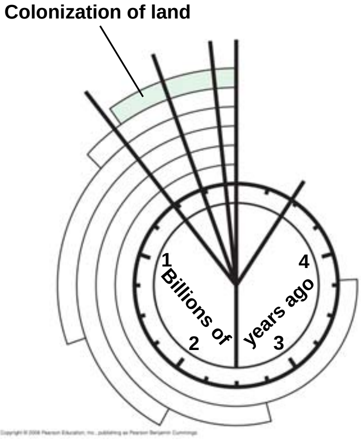
Fig 25-UN7



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dominant groups reflect continental drift, mass extinctions, and adaptive radiations

- The history of life on Earth has seen the rise and fall of many groups of organisms

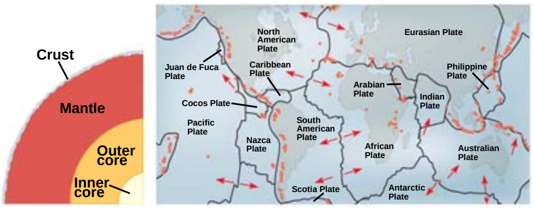
PLAY Video: Volcanic Eruption

PLAY Video: Lava Flow

Continental Drift

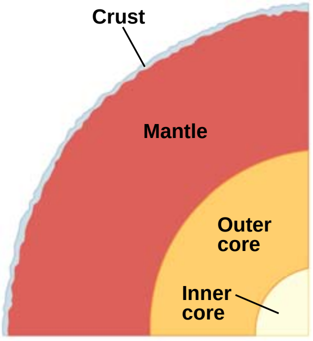
- At three points in time, the land masses of Earth have formed a supercontinent: 1.1 billion, 600 million, and 250 million years ago
- Earth's continents move slowly over the underlying hot mantle through the process of **continental drift**
- Oceanic and continental plates can collide, separate, or slide past each other
- Interactions between plates cause the

Fig. 25-12



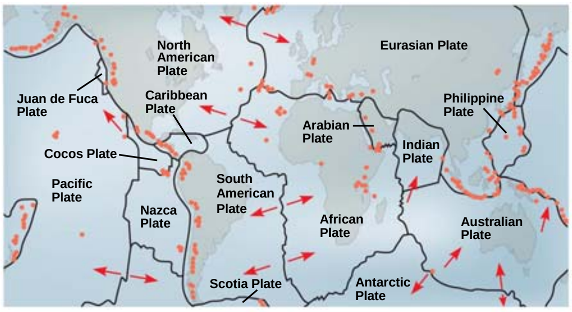
(a) Cutaway view of Earth (b) Major continental plates

Fig. 25-12a



(a) Cutaway view of Earth

Fig. 25-12b



(b) Major continental plates

Consequences of Continental Drift

- Formation of the supercontinent **Pangaea** about 250 million years ago had many effects
  - A reduction in shallow water habitat
  - A colder and drier climate inland
  - Changes in climate as continents moved toward and away from the poles
  - Changes in ocean circulation patterns leading to global cooling

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Fig. 25-13

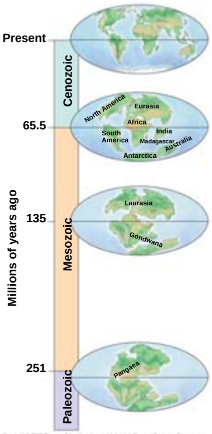


Fig. 25-13a

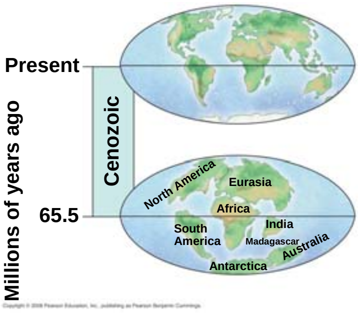
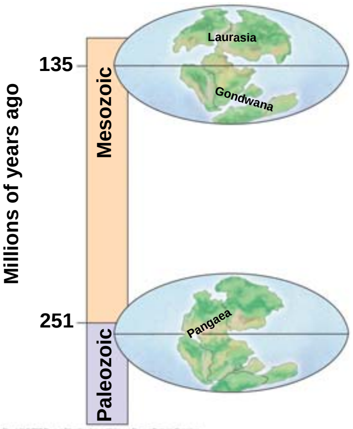


Fig. 25-13b



- The break-up of Pangaea lead to allopatric speciation
- The current distribution of fossils reflects the movement of continental drift
- For example, the similarity of fossils in parts of South America and Africa is consistent with the idea that these continents were formerly attached

---

Mass Extinctions

- The fossil record shows that most species that have ever lived are now extinct
- At times, the rate of extinction has increased dramatically and caused a **mass extinction**

The “Big Five” Mass Extinction Events

- In each of the five mass extinction events, more than 50% of Earth’s species became extinct

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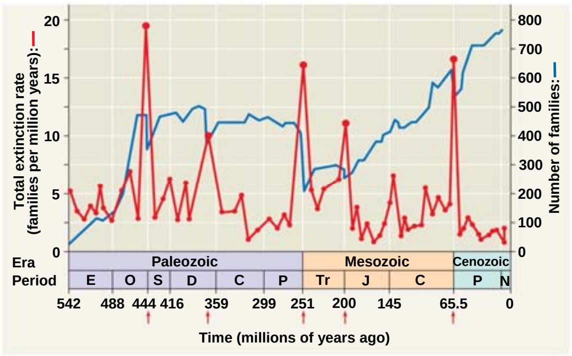
Fig. 25-14



- The Permian extinction defines the boundary between the Paleozoic and Mesozoic eras
- This mass extinction occurred in less than 5 million years and caused the extinction of about 96% of marine animal species
- This event might have been caused by volcanism, which lead to global warming, and a decrease in oceanic oxygen

---

- The Cretaceous mass extinction 65.5 million years ago separates the Mesozoic from the Cenozoic
- Organisms that went extinct include about half of all marine species and many terrestrial plants and animals, including most dinosaurs

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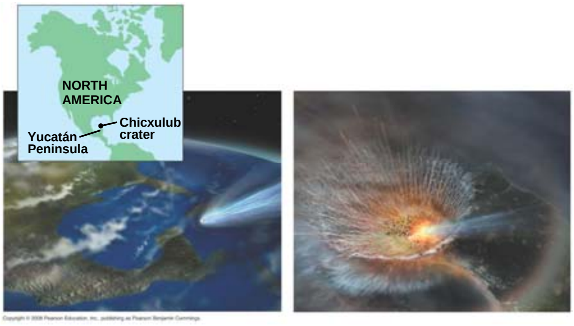
Fig. 25-15



- The presence of iridium in sedimentary rocks suggests a meteorite impact about 65 million years ago
- The Chicxulub crater off the coast of Mexico is evidence of a meteorite that dates to the same time

---

Is a Sixth Mass Extinction Under Way?

- Scientists estimate that the current rate of extinction is 100 to 1,000 times the typical background rate
- Data suggest that a sixth human-caused mass extinction is likely to occur unless dramatic action is taken

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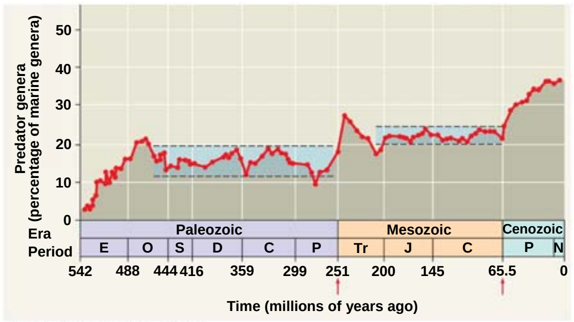
Consequences of Mass Extinctions

- Mass extinction can alter ecological communities and the niches available to organisms
- It can take from 5 to 100 million years for diversity to recover following a mass extinction
- Mass extinction can pave the way for adaptive radiations

Fig. 25-16



Adaptive Radiations

- **Adaptive radiation** is the evolution of diversely adapted species from a common ancestor upon introduction to new environmental opportunities

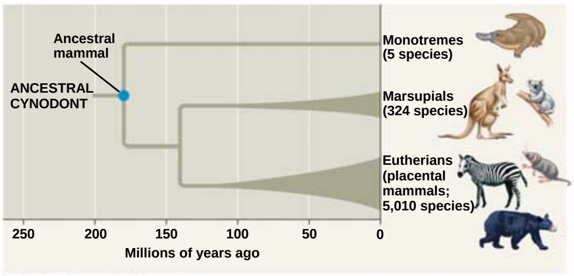
---

Worldwide Adaptive Radiations

- Mammals underwent an adaptive radiation after the extinction of terrestrial dinosaurs
- The disappearance of dinosaurs (except birds) allowed for the expansion of mammals in diversity and size
- Other notable radiations include photosynthetic prokaryotes, large predators in the Cambrian, land plants, insects, and tetrapods

---

Fig. 25-17



Regional Adaptive Radiations

- Adaptive radiations can occur when organisms colonize new environments with little competition
- The Hawaiian Islands are one of the world’s great showcases of adaptive radiation

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Fig. 25-18

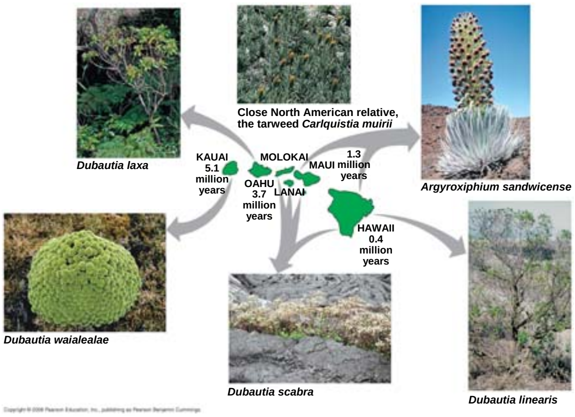

Fig. 25-18a

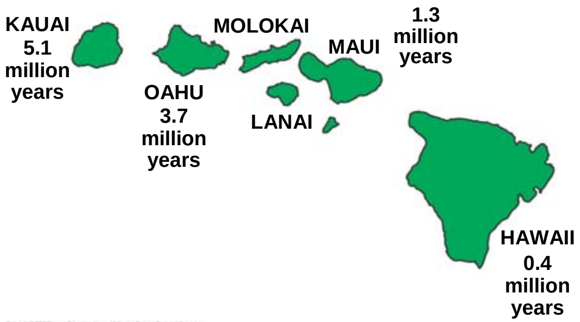

Fig. 25-18b

Close North American relative, the tarweed *Carlquistia muirii*

Fig. 25-18c

Dubautia waialealae

Fig. 25-18d

Dubautia laxa

Fig. 25-18e

Dubautia scabra

Fig. 25-18f

Argyroxiphium sandwicense

Fig. 25-18g

Dubautia linearis

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body form can result from changes in the sequences and regulation of developmental genes

- Studying genetic mechanisms of change can provide insight into large-scale evolutionary change

---

Evolutionary Effects of Development Genes

- Genes that program development control the rate, timing, and spatial pattern of changes in an organism's form as it develops into an adult

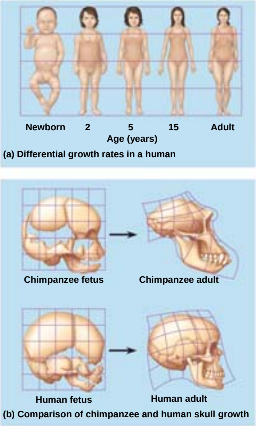
---

Changes in Rate and Timing

- **Heterochrony** is an evolutionary change in the rate or timing of developmental events
- It can have a significant impact on body shape
- The contrasting shapes of human and chimpanzee skulls are the result of small changes in relative growth rates

PLAY Animation: Allometric Growth

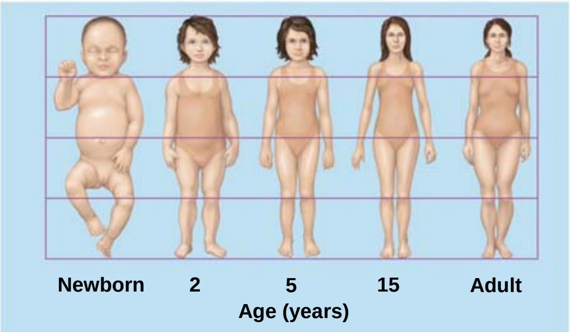
Fig. 25-19



(a) Differential growth rates in a human

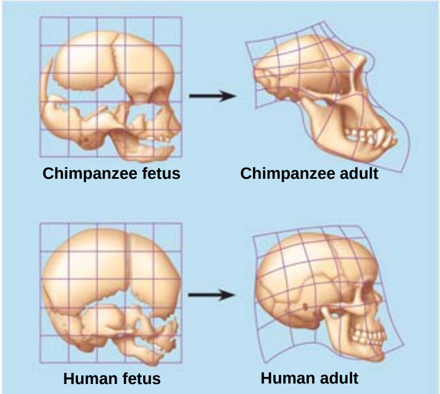
(b) Comparison of chimpanzee and human skull growth

Fig. 25-19a



(a) Differential growth rates in a human

Fig. 25-19b



(b) Comparison of chimpanzee and human skull growth

- Heterochrony can alter the timing of reproductive development relative to the development of nonreproductive organs
- In **paedomorphosis**, the rate of reproductive development accelerates compared with somatic development
- The sexually mature species may retain body features that were juvenile structures in an ancestral species

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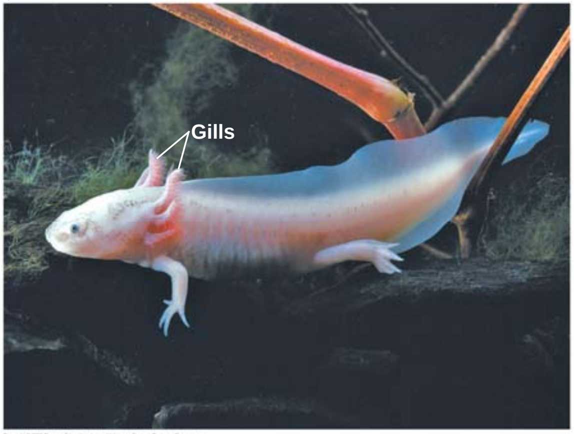
Fig. 25-20



Changes in Spatial Pattern

- Substantial evolutionary change can also result from alterations in genes that control the placement and organization of body parts
- **Homeotic genes** determine such basic features as where wings and legs will develop on a bird or how a flower’s parts are arranged

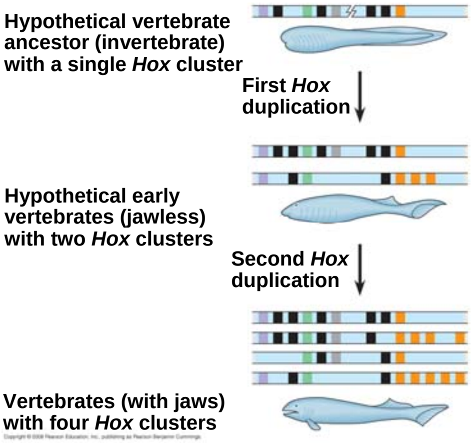
---

- *Hox* genes are a class of homeotic genes that provide positional information during development
- If *Hox* genes are expressed in the wrong location, body parts can be produced in the wrong location
- For example, in crustaceans, a swimming appendage can be produced instead of a feeding appendage

---

- Evolution of vertebrates from invertebrate animals was associated with alterations in *Hox* genes
- Two duplications of *Hox* genes have occurred in the vertebrate lineage
- These duplications may have been important in the evolution of new vertebrate characteristics

Fig. 25-21



Hypothetical vertebrate ancestor (invertebrate) with a single *Hox* cluster

First *Hox* duplication

Hypothetical early vertebrates (jawless) with two *Hox* clusters

Second *Hox* duplication

Vertebrates (with jaws) with four *Hox* clusters

The Evolution of Development

- The tremendous increase in diversity during the Cambrian explosion is a puzzle
- Developmental genes may play an especially important role
- Changes in developmental genes can result in new morphological forms

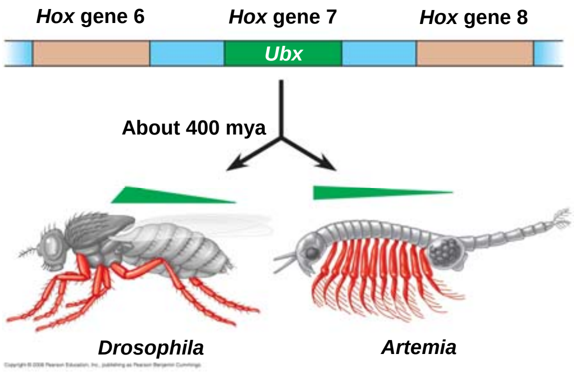
---

Changes in Genes

- New morphological forms likely come from gene duplication events that produce new developmental genes
- A possible mechanism for the evolution of six-legged insects from a many-legged crustacean ancestor has been demonstrated in lab experiments
- Specific changes in the *Ubx* gene have been identified that can “turn off” leg development

---

Fig. 25-22



***Hox* gene 6**

***Hox* gene 7**

***Hox* gene 8**

Ubx

About 400 mya

Drosophila

Artemia

Changes in Gene Regulation

- Changes in the form of organisms may be caused more often by changes in the regulation of developmental genes instead of changes in their sequence
- For example three-spine sticklebacks in lakes have fewer spines than their marine relatives
- The gene sequence remains the same, but the regulation of gene expression is different in the two groups of fish

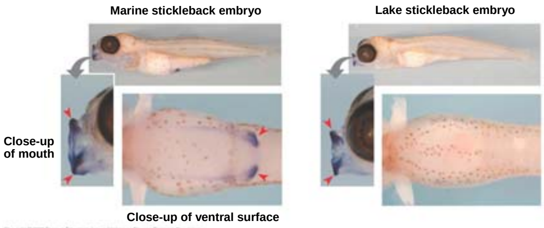
---

Fig. 25-23

RESULTS

Test of Hypothesis A: Differences in the coding sequence of the *Pitx1* gene? → **Result: No** → **The 283 amino acids of the *Pitx1* protein are identical.**

Test of Hypothesis B: Differences in the regulation of expression of *Pitx1* ? → **Result: Yes** → ***Pitx1* is expressed in the ventral spine and mouth regions of developing marine sticklebacks but only in the mouth region of developing lake stickbacks.**



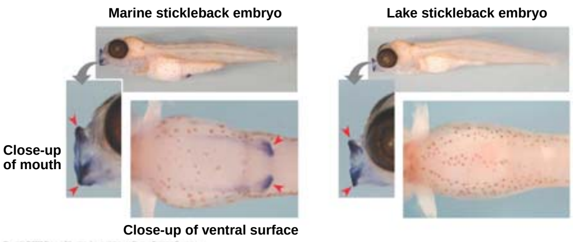
Marine stickleback embryo

Lake stickleback embryo

Close-up of mouth

Close-up of ventral surface

Fig. 25-23a



Concept 25.6: Evolution is not goal oriented

- Evolution is like tinkering—it is a process in which new forms arise by the slight modification of existing forms

---

Evolutionary Novelties

- Most novel biological structures evolve in many stages from previously existing structures
- Complex eyes have evolved from simple photosensitive cells independently many times
- Exaptations are structures that evolve in one context but become co-opted for a different function
- Natural selection can only improve a structure in the context of its current utility

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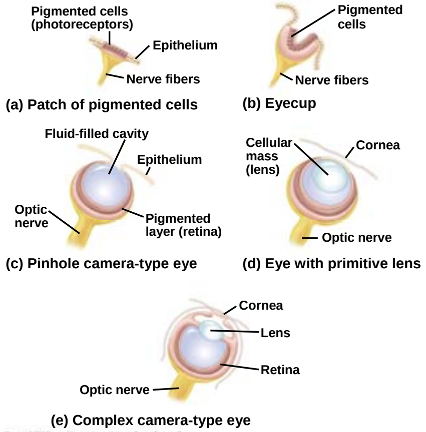
Fig. 25-24



Evolutionary Trends

- Extracting a single evolutionary progression from the fossil record can be misleading
- Apparent trends should be examined in a broader context

Fig. 25-25

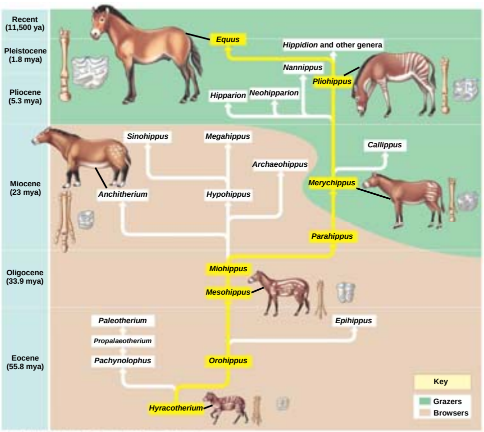


Fig. 25-25a

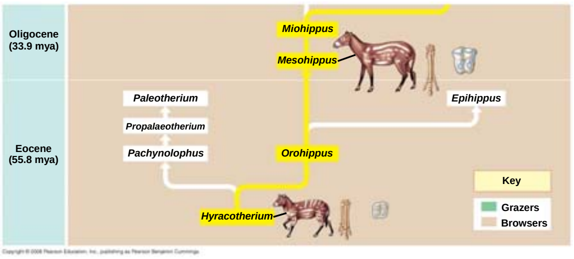
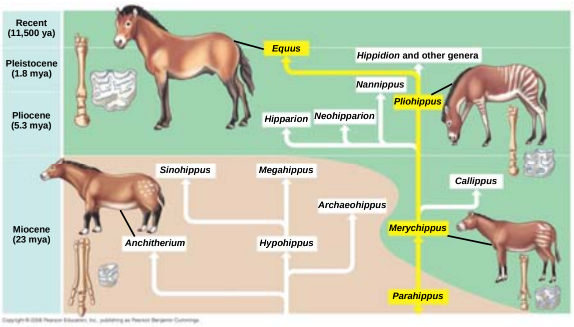


Fig. 25-25b



- According to the species selection model, trends may result when species with certain characteristics endure longer and speciate more often than those with other characteristics
- The appearance of an evolutionary trend does not imply that there is some intrinsic drive toward a particular phenotype

Fig 25-UN8

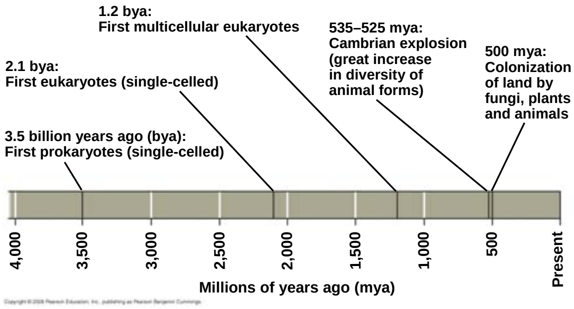


Fig 25-UN9

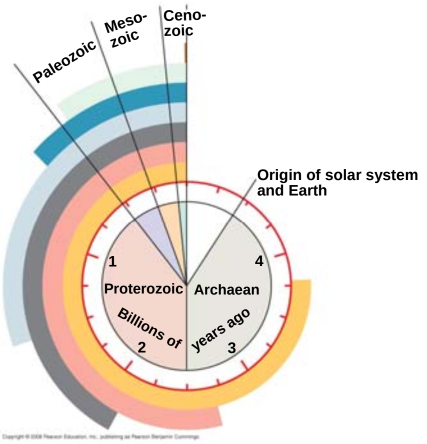


Fig 25-UN10

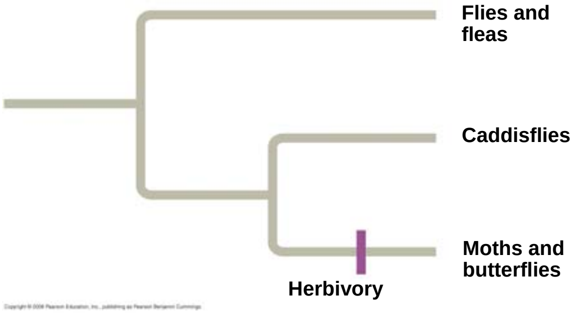
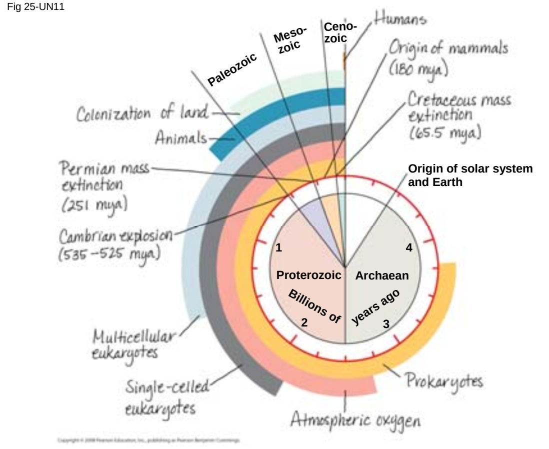


Fig 25-UN11



You should now be able to:

1. Define radiometric dating, serial endosymbiosis, Pangaea, snowball Earth, exaptation, heterochrony, and paedomorphosis
2. Describe the contributions made by Oparin, Haldane, Miller, and Urey toward understanding the origin of organic molecules
3. Explain why RNA, not DNA, was likely the first genetic material

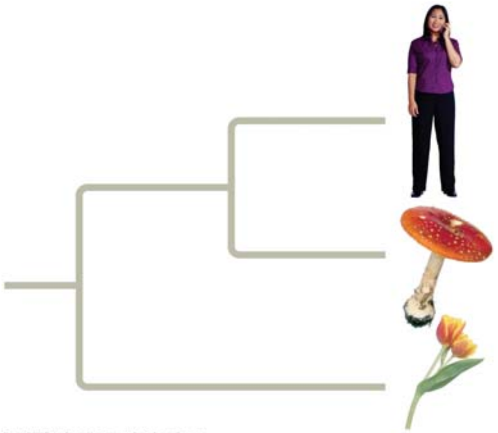
4. Describe and suggest evidence for the major events in the history of life on Earth from Earth’s origin to 2 billion years ago
5. Briefly describe the Cambrian explosion
6. Explain how continental drift led to Australia’s unique flora and fauna
7. Describe the mass extinctions that ended the Permian and Cretaceous periods

Fig. 26-1

Overview: Investigating the Tree of Life

- **Phylogeny** is the evolutionary history of a species or group of related species
- The discipline of **systematics** classifies organisms and determines their evolutionary relationships
- Systematists use fossil, molecular, and genetic data to infer evolutionary relationships

Fig. 26-2



Concept 26.1: Phylogenies show evolutionary relationships

- **Taxonomy** is the ordered division and naming of organisms

Binomial Nomenclature

- In the 18th century, Carolus Linnaeus published a system of taxonomy based on resemblances
- Two key features of his system remain useful today: two-part names for species and hierarchical classification

---

- The two-part scientific name of a species is called a **binomial**
- The first part of the name is the **genus**
- The second part, called the specific epithet, is unique for each species within the genus
- The first letter of the genus is capitalized, and the entire species name is italicized
- Both parts together name the species (not the specific epithet alone)

Hierarchical Classification

- Linnaeus introduced a system for grouping species in increasingly broad categories
- The taxonomic groups from broad to narrow are **domain**, **kingdom**, **phylum**, **class**, **order**, **family**, **genus**, and **species**
- A taxonomic unit at any level of hierarchy is called a **taxon**

Fig. 26-3

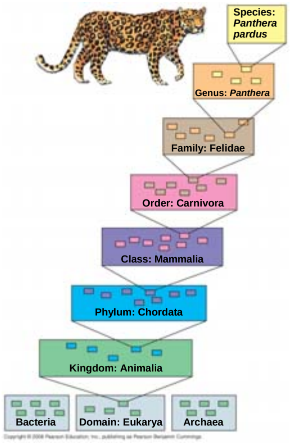


Fig. 26-3a

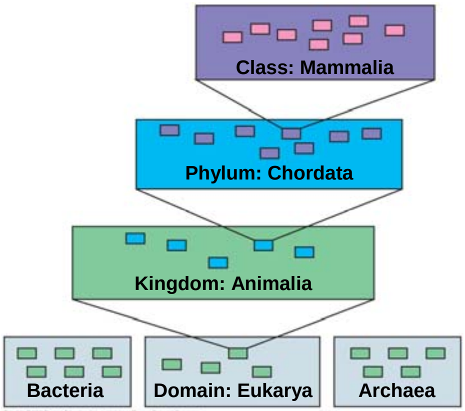
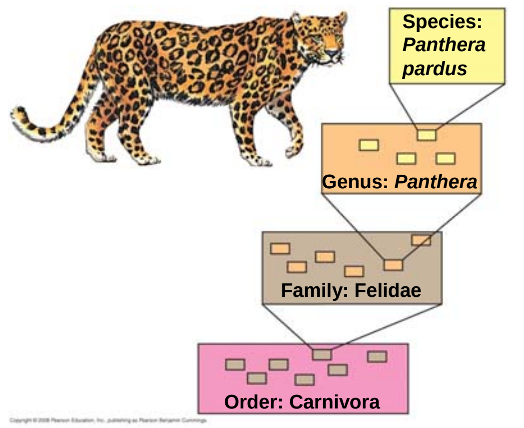


Fig. 26-3b



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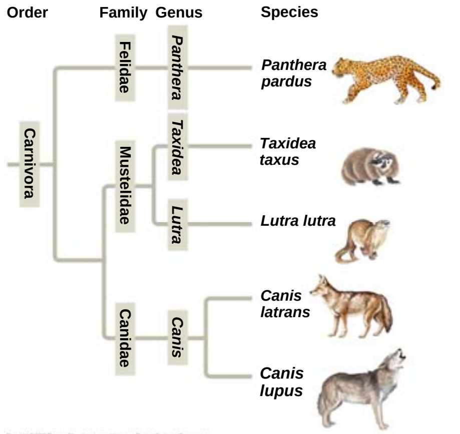
Linking Classification and Phylogeny

- Systematists depict evolutionary relationships in branching **phylogenetic trees**

Fig. 26-4



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- Linnaean classification and phylogeny can differ from each other
- Systematists have proposed the PhyloCode, which recognizes only groups that include a common ancestor and all its descendents

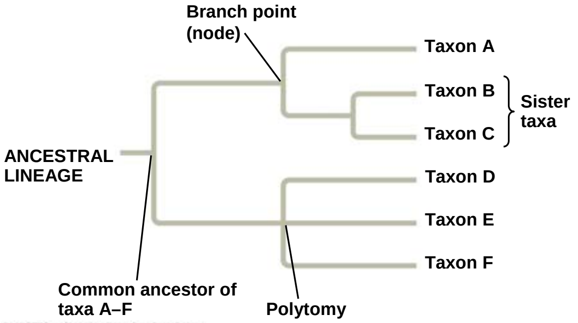
---

- A phylogenetic tree represents a hypothesis about evolutionary relationships
- Each **branch point** represents the divergence of two species
- **Sister taxa** are groups that share an immediate common ancestor

---

- A **rooted** tree includes a branch to represent the last common ancestor of all taxa in the tree
- A **polytomy** is a branch from which more than two groups emerge

Fig. 26-5



What We Can and Cannot Learn from Phylogenetic Trees

- Phylogenetic trees do show patterns of descent
- Phylogenetic trees do not indicate when species evolved or how much genetic change occurred in a lineage
- It shouldn't be assumed that a taxon evolved from the taxon next to it

---

Applying Phylogenies

- Phylogeny provides important information about similar characteristics in closely related species
- A phylogeny was used to identify the species of whale from which "whale meat" originated

---

Fig. 26-6

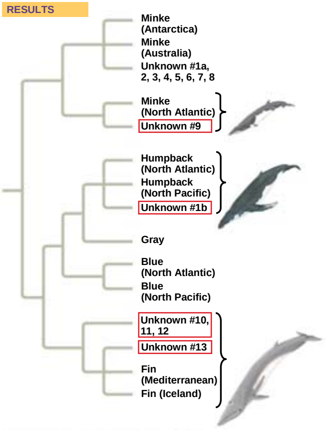


Fig. 26-6a

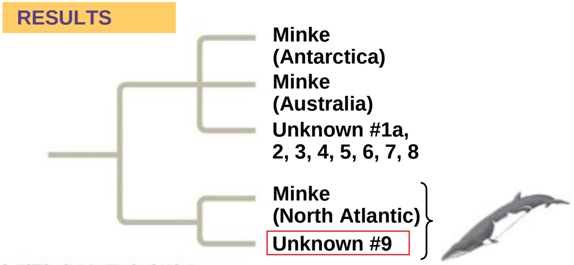


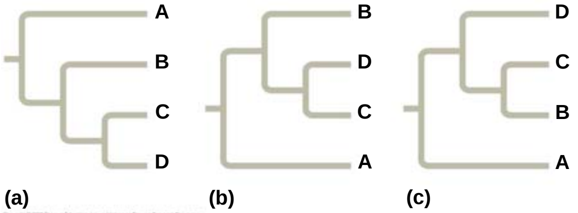
Fig. 26-6b

Fig. 26-6c

- Phylogenies of anthrax bacteria helped researchers identify the source of a particular strain of anthrax

---

Fig. 26-UN1



Concept 26.2: Phylogenies are inferred from morphological and molecular data

- To infer phylogenies, systematists gather information about morphologies, genes, and biochemistry of living organisms

---

Morphological and Molecular Homologies

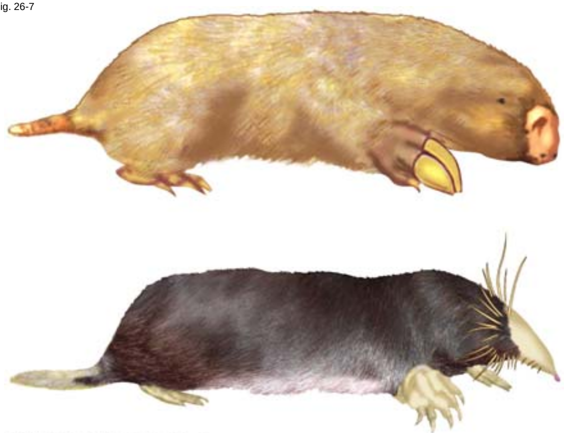
- Organisms with similar morphologies or DNA sequences are likely to be more closely related than organisms with different structures or sequences

---

Sorting Homology from Analogy

- When constructing a phylogeny, systematists need to distinguish whether a similarity is the result of homology or **analogy**
- Homology is similarity due to shared ancestry
- Analogy is similarity due to convergent evolution

Fig. 26-7



- Convergent evolution occurs when similar environmental pressures and natural selection produce similar (analogous) adaptations in organisms from different evolutionary lineages

- Bat and bird wings are homologous as forelimbs, but analogous as functional wings
- Analogous structures or molecular sequences that evolved independently are also called **homoplasies**
- Homology can be distinguished from analogy by comparing fossil evidence and the degree of complexity
- The more complex two similar structures are, the more likely it is that they are

Evaluating Molecular Homologies

- Systematists use computer programs and mathematical tools when analyzing comparable DNA segments from different organisms

Fig. 26-8

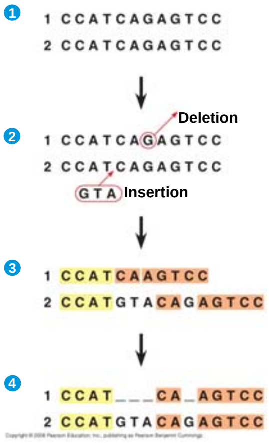


Fig. 26-8a

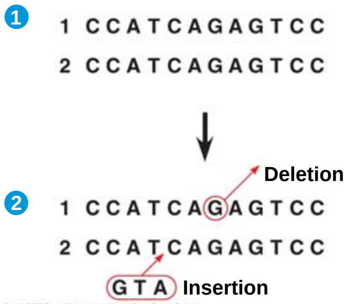
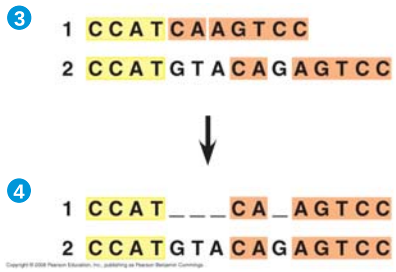


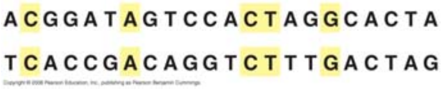
Fig. 26-8b



- It is also important to distinguish homology from analogy in molecular similarities
- Mathematical tools help to identify molecular homoplasies, or coincidences
- **Molecular systematics** uses DNA and other molecular data to determine evolutionary relationships

---

Fig. 26-9



---

are used to construct phylogenetic trees

- Once homologous characters have been identified, they can be used to infer a phylogeny

---

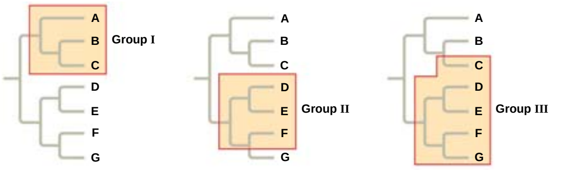
Cladistics

- **Cladistics** groups organisms by common descent
- A **clade** is a group of species that includes an ancestral species and all its descendants
- Clades can be nested in larger clades, but not all groupings of organisms qualify as clades

---

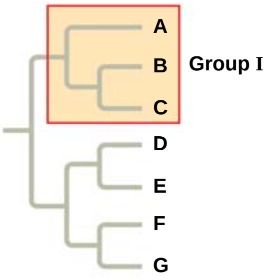
- A valid clade is **monophyletic**, signifying that it consists of the ancestor species and all its descendants

Fig. 26-10



(a) Monophyletic group (clade) (b) Paraphyletic group (c) Polyphyletic group

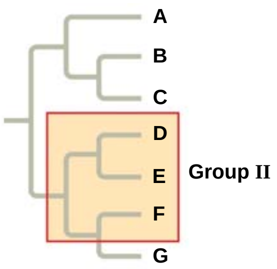
Fig. 26-10a



(a) Monophyletic group (clade)

- A **paraphyletic** grouping consists of an ancestral species and some, but not all, of the descendants

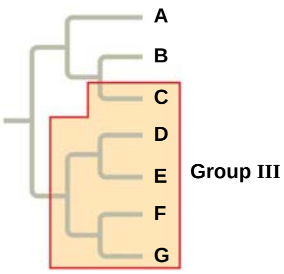
Fig. 26-10b



(b) Paraphyletic group

- A **polyphyletic** grouping consists of various species that lack a common ancestor

Fig. 26-10c



(c) Polyphyletic group

Shared Ancestral and Shared Derived Characters

- In comparison with its ancestor, an organism has both shared and different characteristics

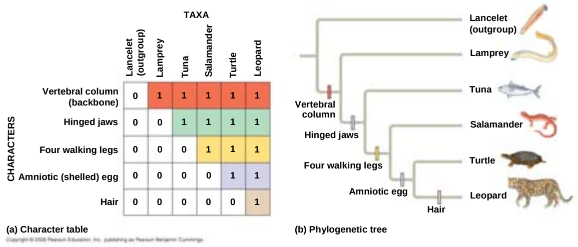
- A **shared ancestral character** is a character that originated in an ancestor of the taxon
- A **shared derived character** is an evolutionary novelty unique to a particular clade
- A character can be both ancestral and derived, depending on the context

---

Inferring Phylogenies Using Derived Characters

- When inferring evolutionary relationships, it is useful to know in which clade a shared derived character first appeared

Fig. 26-11

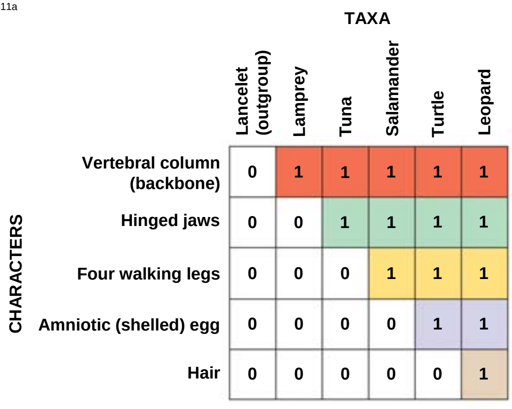


CHARACTERS	Lancelet (outgroup)	Lamprey	Tuna	Salamander	Turtle	Leopard
Vertebral column (backbone)	0	1	1	1	1	1
Hinged jaws	0	0	1	1	1	1
Four walking legs	0	0	0	1	1	1
Amniotic (shelled) egg	0	0	0	0	1	1
Hair	0	0	0	0	0	1

(a) Character table

(b) Phylogenetic tree

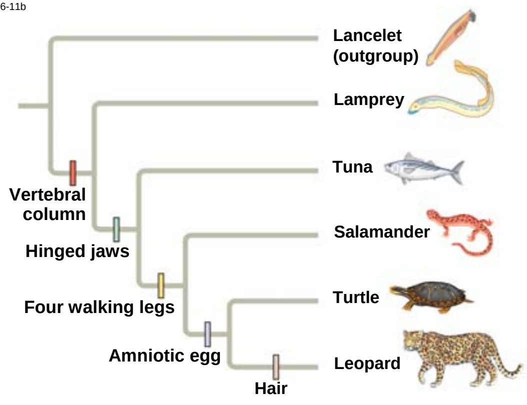
Fig. 26-11a



CHARACTERS	Lancelet (outgroup)	Lamprey	Tuna	Salamander	Turtle	Leopard
Vertebral column (backbone)	0	1	1	1	1	1
Hinged jaws	0	0	1	1	1	1
Four walking legs	0	0	0	1	1	1
Amniotic (shelled) egg	0	0	0	0	1	1
Hair	0	0	0	0	0	1

(a) Character table

Fig. 26-11b



(b) Phylogenetic tree

- An **outgroup** is a species or group of species that is closely related to the **ingroup**, the various species being studied
- Systematists compare each ingroup species with the outgroup to differentiate between shared derived and shared ancestral characteristics

---

- Homologies shared by the outgroup and ingroup are ancestral characters that predate the divergence of both groups from a common ancestor

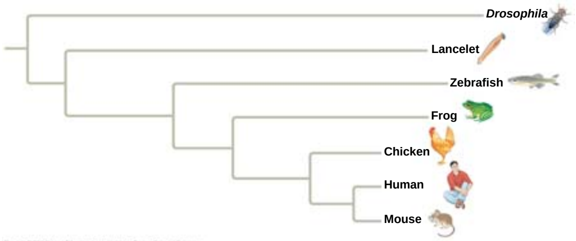
---

Phylogenetic Trees with Proportional Branch Lengths

- In some trees, the length of a branch can reflect the number of genetic changes that have taken place in a particular DNA sequence in that lineage

---

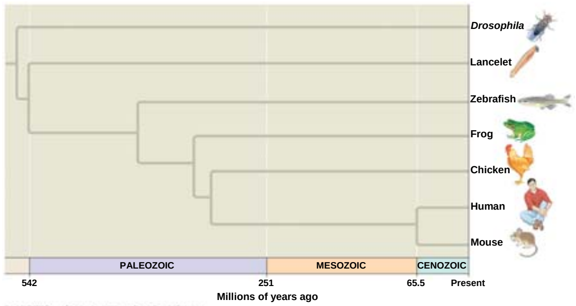
Fig. 26-12



- In other trees, branch length can represent chronological time, and branching points can be determined from the fossil record

---

Fig. 26-13



Maximum Parsimony and Maximum Likelihood

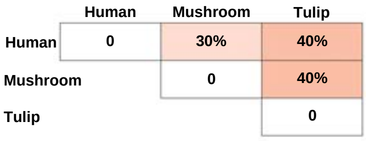
- Systematists can never be sure of finding the best tree in a large data set
- They narrow possibilities by applying the principles of maximum parsimony and maximum likelihood

---

- **Maximum parsimony** assumes that the tree that requires the fewest evolutionary events (appearances of shared derived characters) is the most likely
- The principle of **maximum likelihood** states that, given certain rules about how DNA changes over time, a tree can be found that reflects the most likely sequence of evolutionary events

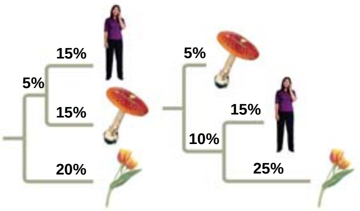
---

Fig. 26-14



	Human	Mushroom	Tulip
Human	0	30%	40%
Mushroom		0	40%
Tulip			0

(a) Percentage differences between sequences

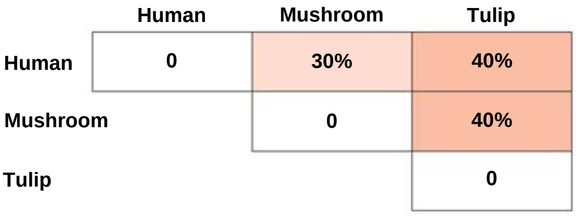


Tree 1: More likely

Tree 2: Less likely

(b) Comparison of possible trees

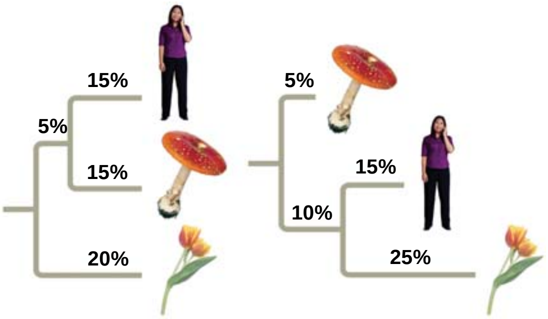
Fig. 26-14a



	Human	Mushroom	Tulip
Human	0	30%	40%
Mushroom		0	40%
Tulip			0

(a) Percentage differences between sequences

Fig. 26-14b



Tree 1: More likely

Tree 2: Less likely

(b) Comparison of possible trees

- Computer programs are used to search for trees that are parsimonious and likely

Fig. 26-15-1

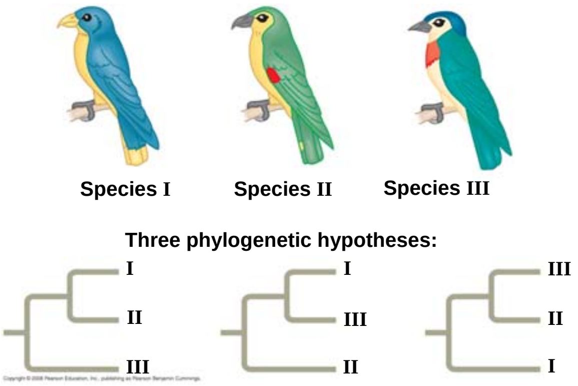


Fig. 26-15-2

Site

	1	2	3	4
Species I	C	T	A	T
Species II	C	T	T	C
Species III	A	G	A	C
Ancestral sequence	A	G	T	T

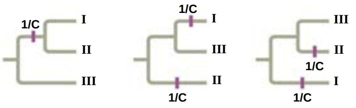


Fig. 26-15-3

Site

	1	2	3	4
Species I	C	T	A	T
Species II	C	T	T	C
Species III	A	G	A	C
Ancestral sequence	A	G	T	T

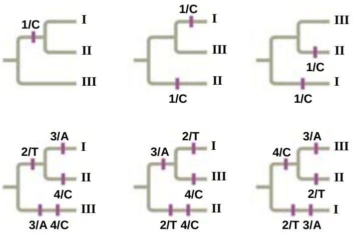
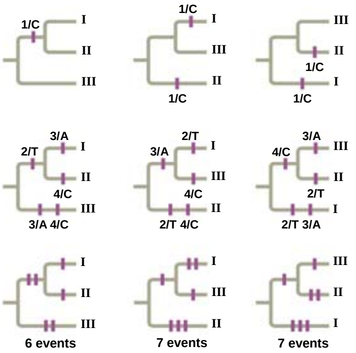


Fig. 26-15-4

Site

	1	2	3	4
Species I	C	T	A	T
Species II	C	T	T	C
Species III	A	G	A	C
Ancestral sequence	A	G	T	T

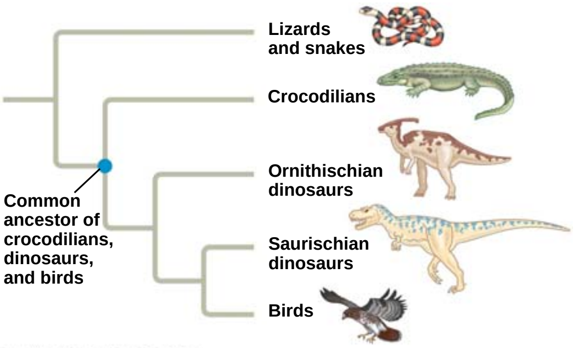


Phylogenetic Trees as Hypotheses

- The best hypotheses for phylogenetic trees fit the most data: morphological, molecular, and fossil
- **Phylogenetic bracketing** allows us to predict features of an ancestor from features of its descendents

---

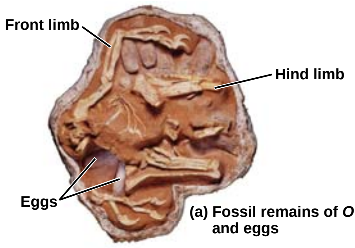
Fig. 26-16



- This has been applied to infer features of dinosaurs from their descendents: birds and crocodiles

PLAY Animation: The Geologic Record

Fig. 26-17



(a) Fossil remains of *Oviraptor* and eggs

(b) Artist's reconstruction of the dinosaur's posture

Concept 26.4: An organism's evolutionary history is documented in its genome

- Comparing nucleic acids or other molecules to infer relatedness is a valuable tool for tracing organisms' evolutionary history
- DNA that codes for rRNA changes relatively slowly and is useful for investigating branching points hundreds of millions of years ago
- mtDNA evolves rapidly and can be used to explore recent evolutionary events

---

Gene Duplications and Gene Families

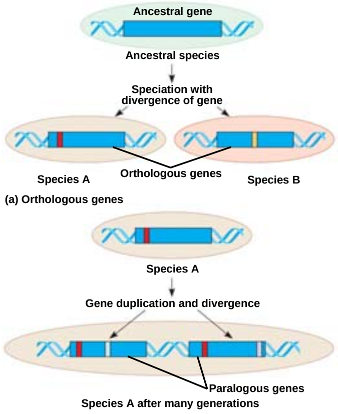
- Gene duplication increases the number of genes in the genome, providing more opportunities for evolutionary changes
- Like homologous genes, duplicated genes can be traced to a common ancestor

---

- **Orthologous genes** are found in a single copy in the genome and are homologous between species
- They can diverge only after speciation occurs

- **Paralogous genes** result from gene duplication, so are found in more than one copy in the genome
- They can diverge within the clade that carries them and often evolve new functions

Fig. 26-18



Ancestral gene

Ancestral species

Speciation with divergence of gene

Species A

Orthologous genes

Species B

(a) Orthologous genes

Species A

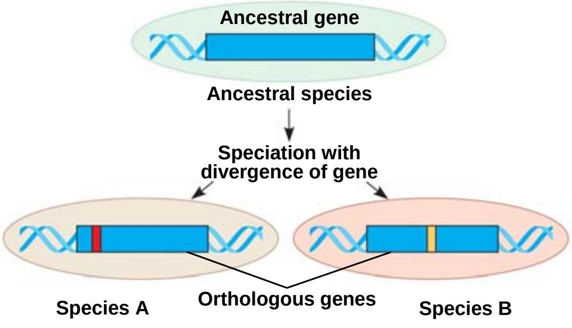
Gene duplication and divergence

Paralogous genes

Species A after many generations

(b) Paralogous genes

Fig. 26-18a



Ancestral gene

Ancestral species

Speciation with divergence of gene

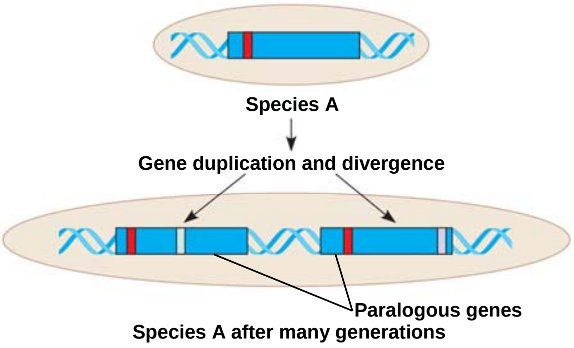
Species A

Orthologous genes

Species B

(a) Orthologous genes

Fig. 26-18b



Species A

Gene duplication and divergence

Paralogous genes

Species A after many generations

(b) Paralogous genes

Genome Evolution

- Orthologous genes are widespread and extend across many widely varied species
- Gene number and the complexity of an organism are not strongly linked
- Genes in complex organisms appear to be very versatile and each gene can perform many functions

Concept 26.5: Molecular clocks help track evolutionary time

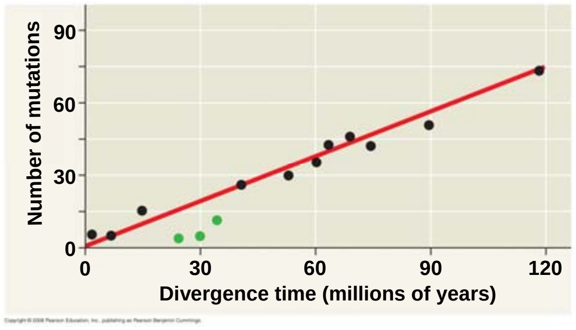
- To extend molecular phylogenies beyond the fossil record, we must make an assumption about how change occurs over time

Molecular Clocks

- A **molecular clock** uses constant rates of evolution in some genes to estimate the absolute time of evolutionary change
- In orthologous genes, nucleotide substitutions are proportional to the time since they last shared a common ancestor
- In paralogous genes, nucleotide substitutions are proportional to the time since the genes became duplicated

- Molecular clocks are calibrated against branches whose dates are known from the fossil record

Fig. 26-19



Neutral Theory

- **Neutral theory** states that much evolutionary change in genes and proteins has no effect on fitness and therefore is not influenced by Darwinian selection
- It states that the rate of molecular change in these genes and proteins should be regular like a clock

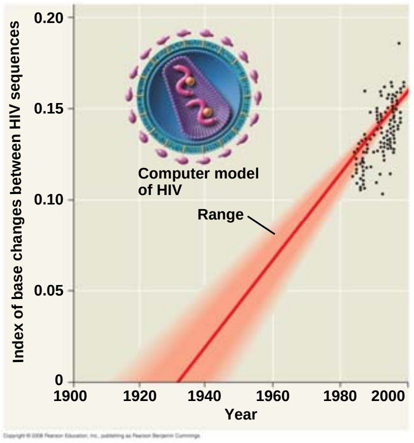
Difficulties with Molecular Clocks

- The molecular clock does not run as smoothly as neutral theory predicts
- Irregularities result from natural selection in which some DNA changes are favored over others
- Estimates of evolutionary divergences older than the fossil record have a high degree of uncertainty
- The use of multiple genes may improve estimates

Applying a Molecular Clock: The Origin of HIV

- Phylogenetic analysis shows that HIV is descended from viruses that infect chimpanzees and other primates
- Comparison of HIV samples throughout the epidemic shows that the virus evolved in a very clocklike way
- Application of a molecular clock to one strain of HIV suggests that that strain spread to humans during the 1930s

Fig. 26-20



Concept 26.6: New information continues to revise our understanding of the tree of life

- Recently, we have gained insight into the very deepest branches of the tree of life through molecular systematics

From Two Kingdoms to Three Domains

- Early taxonomists classified all species as either plants or animals
- Later, five kingdoms were recognized: Monera (prokaryotes), Protista, Plantae, Fungi, and Animalia
- More recently, the three-domain system has been adopted: Bacteria, Archaea, and Eukarya
- The three-domain system is supported by data from many sequenced genomes

Animation: Classification Schemes

Fig. 26-21

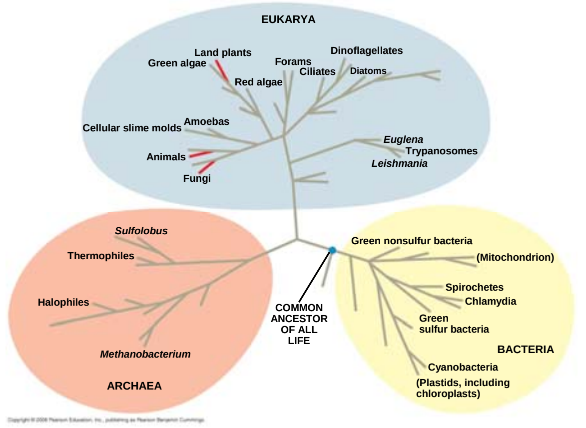


Fig. 26-21a

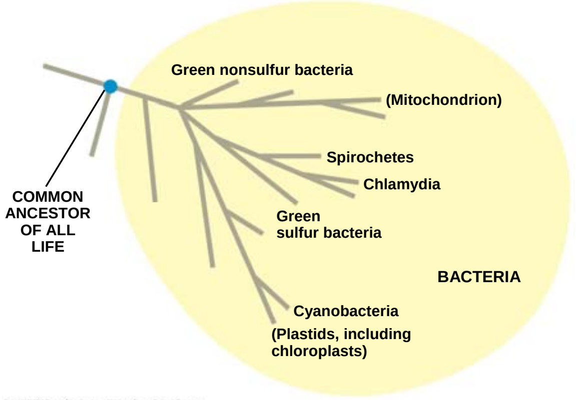


Fig. 26-21b

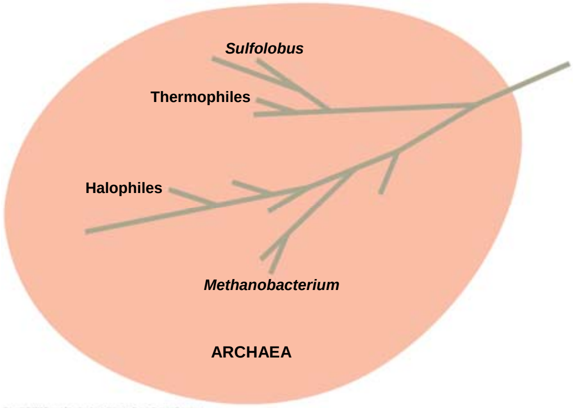
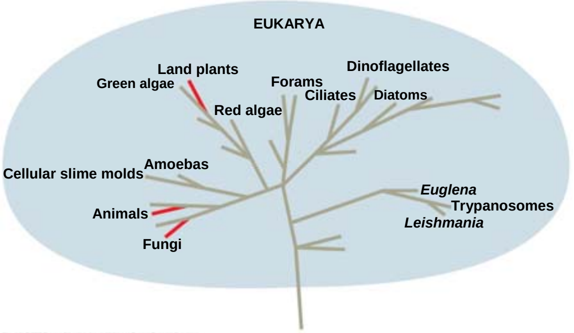


Fig. 26-21c



A Simple Tree of All Life

- The tree of life suggests that eukaryotes and archaea are more closely related to each other than to bacteria
- The tree of life is based largely on rRNA genes, as these have evolved slowly

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- There have been substantial interchanges of genes between organisms in different domains
- **Horizontal gene transfer** is the movement of genes from one genome to another
- Horizontal gene transfer complicates efforts to build a tree of life

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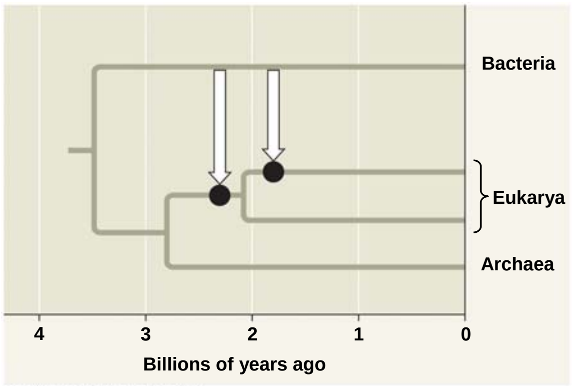
Fig. 26-22



Is the Tree of Life Really a Ring?

- Some researchers suggest that eukaryotes arose as an endosymbiosis between a bacterium and archaean
- If so, early evolutionary relationships might be better depicted by a ring of life instead of a tree of life

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Fig. 26-23

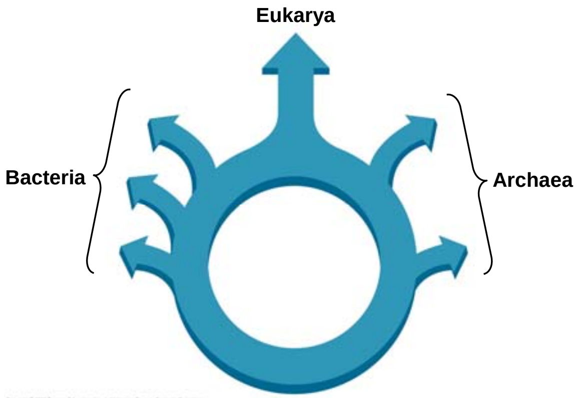


Fig. 26-UN2

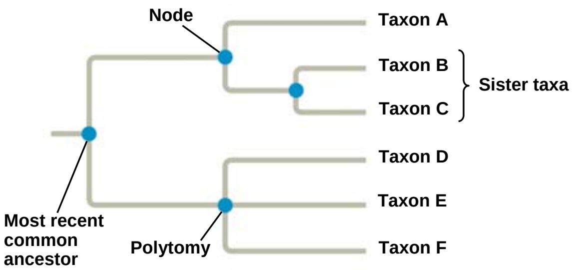


Fig. 26-UN3

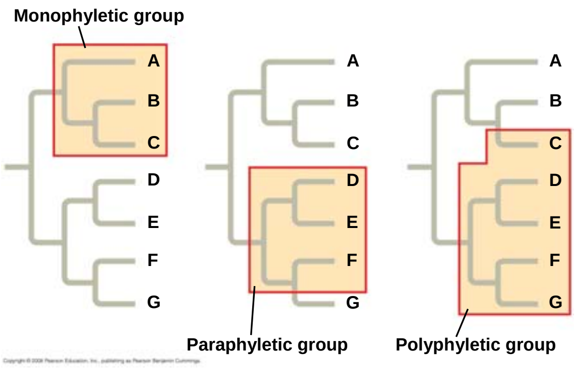


Fig. 26-UN4

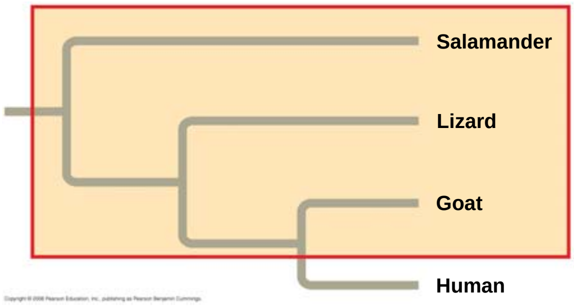
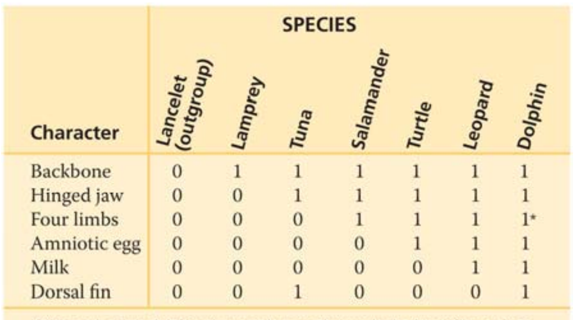


Fig. 26-UN5



Character	Lancelet (outgroup)	Lamprey	Tuna	Salamander	Turtle	Leopard	Dolphin
	SPECIES						
Backbone	0	1	1	1	1	1	1
Hinged jaw	0	0	1	1	1	1	1
Four limbs	0	0	0	1	1	1	1*
Amniotic egg	0	0	0	0	1	1	1
Milk	0	0	0	0	0	1	1
Dorsal fin	0	0	1	0	0	0	1

*Although adult dolphins have only two obvious limbs (their flippers), as embryos they have two hind-limb buds, for a total of four limbs.

Fig. 26-UN6

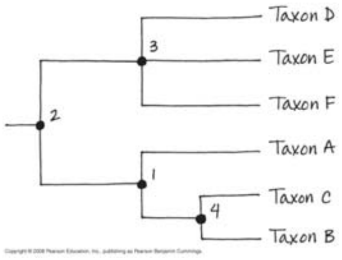


Fig. 26-UN7

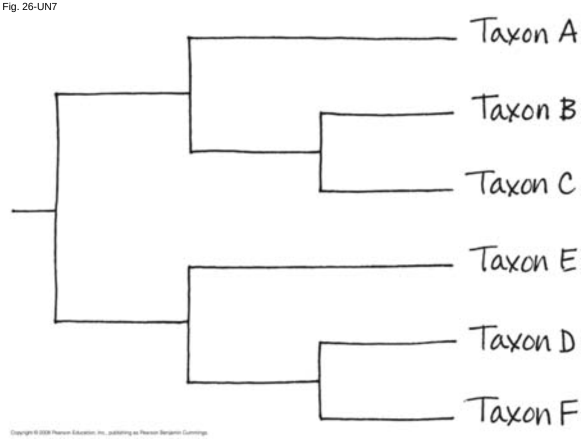


Fig. 26-UN8

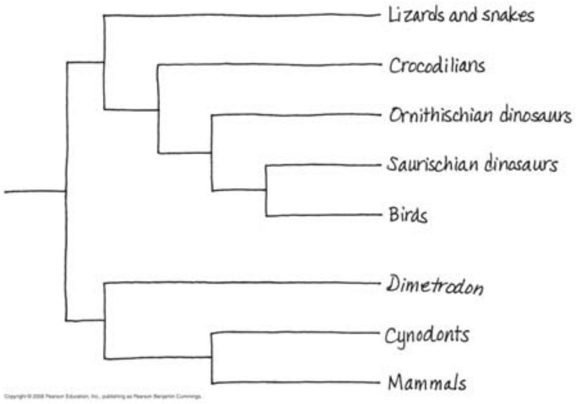


Fig. 26-UN9

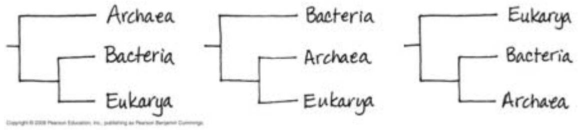


Fig. 26-UN10

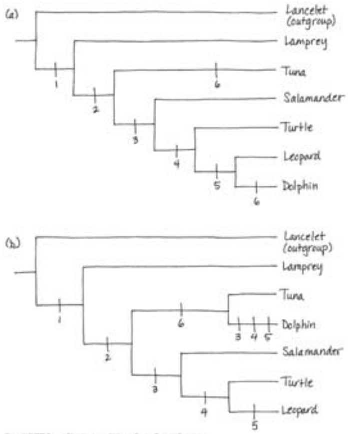


Fig. 26-UN10a

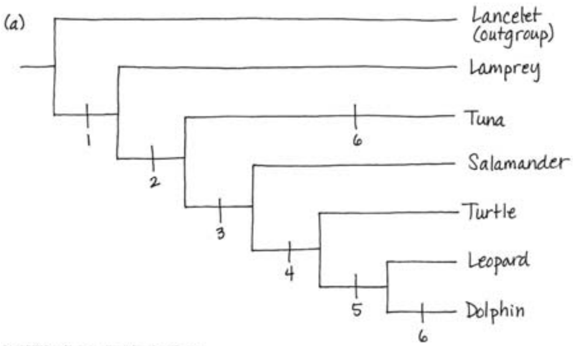


Fig. 26-UN10b