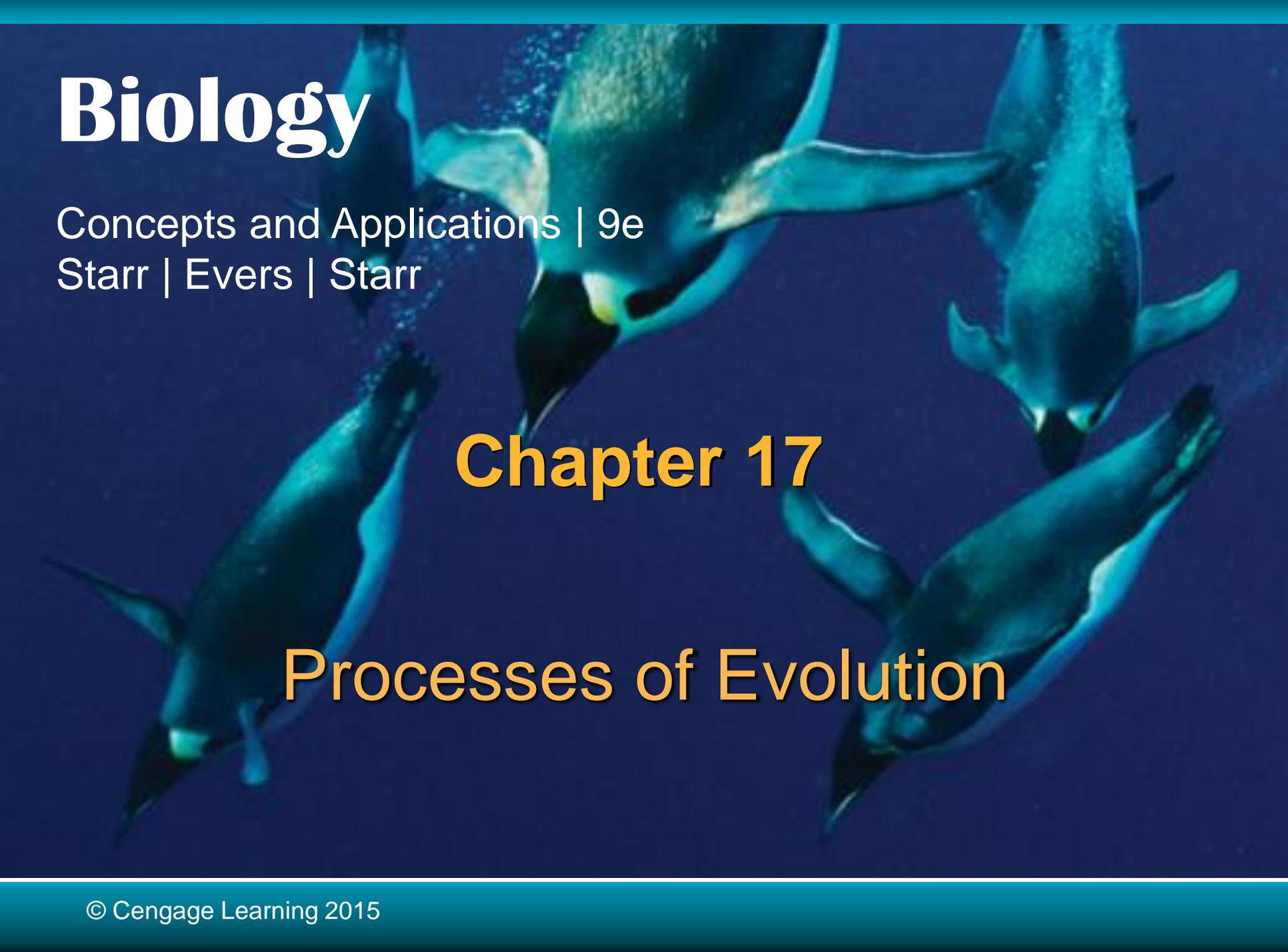


# Biology

A group of penguins is shown swimming underwater. The water is a deep blue-green color. The penguins are in various positions, some swimming towards the camera and others away. Their bodies are sleek and adapted for aquatic life. The lighting is somewhat dim, creating a serene and mysterious atmosphere.

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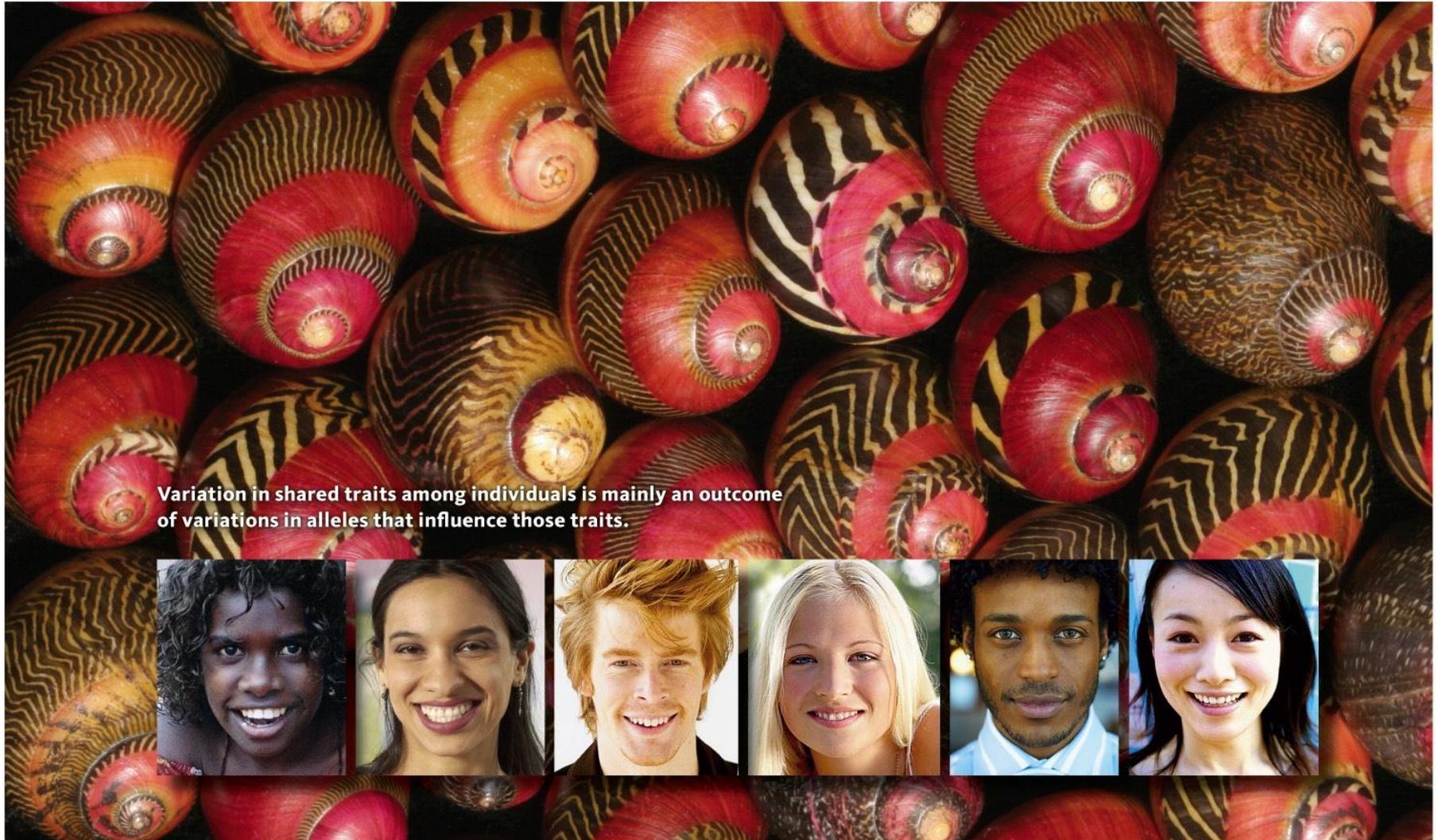
## Chapter 17

## Processes of Evolution

# 17.1 What is Microevolution?

- Individuals of a population share morphological, physiological, and behavioral traits with a heritable basis
- Variations within a population arise from different alleles of shared genes
  - Dimorphic: a trait with only two forms
  - Polymorphic: traits with more than two distinct forms

# What is Microevolution? (cont'd.)



Variation in shared traits among individuals is mainly an outcome of variations in alleles that influence those traits.

CREDITS: (1) background, © David McIntyre/Photographer's Direct; inset far left, © Roderick Hulsbergen/ <http://www.photography.euweb.nl>; all others, © JupiterImages Corporation.

# What is Microevolution? (cont'd.)

**TABLE 17.1**

## Sources of Variation in Traits Among Individuals of a Species

<b>Genetic Event</b>	<b>Effect</b>
Mutation	Source of new alleles
Crossing over at meiosis I	Introduces new combinations of alleles into chromosomes
Independent assortment at meiosis I	Mixes maternal and paternal chromosomes
Fertilization	Combines alleles from two parents
Changes in chromosome number or structure	Often dramatic changes in structure and function

# What is Microevolution? (cont'd.)

- Mutations
  - The original source for new alleles.
  - Lethal mutation
    - Mutation that drastically alters phenotype
    - Causes death
  - Neutral mutation
    - A mutation that has no effect on survival or reproduction

# What is Microevolution? (cont'd.)

- Mutations (cont'd.)
  - Occasionally, a change in the environment favors a mutation that had previously been neutral or even somewhat harmful
  - Through natural selection, a beneficial mutation tends to increase in frequency in a population over generations
  - Mutations are the source of Earth's staggering biodiversity

# What is Microevolution? (cont'd.)

- Allele frequencies
  - All alleles in a population form a gene pool
- Changes in the allele frequencies of a population are called microevolution
  - Occurs constantly by:
    - Mutation
    - Natural selection
    - Genetic drift
    - Gene flow

# 17.2 How Do We Know When A Population Is Evolving?

- Genetic equilibrium
  - A theoretical reference point
  - Occurs when the allele frequencies of a population do not change
  - Requires five conditions that are never met in nature, so natural populations are never in genetic equilibrium

# How Do We Know When A Population Is Evolving? (cont'd.)

- Five theoretical conditions of genetic equilibrium:
  1. Mutations never occur
  2. Population is infinitely large
  3. Population is isolated from all other populations of the species (no gene flow)
  4. Mating is random
  5. All individuals survive and produce the same number of offspring

# How Do We Know When A Population Is Evolving? (cont'd.)

- Hardy-Weinberg Law
  - Developed a simple formula that can be used to track whether a population of any sexually reproducing species is in a state of genetic equilibrium

# How Do We Know When A Population Is Evolving? (cont'd.)

- Consider a hypothetical gene that encodes a blue pigment in butterflies:
  - Two alleles of this gene,  $B$  and  $b$ , are codominant
  - A butterfly homozygous for the  $B$  allele ( $BB$ ) has dark-blue wings
  - A butterfly homozygous for the  $b$  allele ( $bb$ ) has white wings
  - A heterozygous butterfly ( $Bb$ ) has medium-blue wings

# How Do We Know When A Population Is Evolving? (cont'd.)

- The hypothetical gene (cont'd.)
  - At genetic equilibrium, the proportions of the wing-color genotypes are:

$$p^2(BB) + 2pq(Bb) + q^2(bb) = 1.0$$

where  $p$  and  $q$  are the frequencies of alleles  $B$  and  $b$

# How Do We Know When A Population Is Evolving? (cont'd.)

- The Hardy–Weinberg equilibrium equation
  - Defines the frequency of a dominant allele ( $B$ ) and a recessive allele ( $b$ ) for a gene that controls a particular trait in a population
  - Frequencies of  $B$  and  $b$  must add up to 1.0
    - Example: If  $B$  occupies 90% of the loci, then  $b$  must occupy the remaining 10 percent
  - No matter what the proportions:

$$p + q = 1.0$$

# How Do We Know When A Population Is Evolving? (cont'd.)

- Hardy-Weinberg (cont'd.)
  - Paired alleles assort into different gametes
  - The genotypes possible in the next generation are  $BB$ ,  $Bb$ , and  $bb$
  - The frequencies of the three genotypes add up to 1.0

$$p^2 + 2pq + q^2 = 1.0$$

# How Do We Know When A Population Is Evolving? (cont'd.)

- Hardy-Weinberg (cont'd.)
  - If 1,000 individuals each produces two gametes:
    - 490 *BB* individuals make 980 *B* gametes
    - 420 *Bb* individuals make 420 *B* and 420 *b* gametes
    - 90 *bb* individuals make 180 *b* gametes

# How Do We Know When A Population Is Evolving? (cont'd.)

- Hardy-Weinberg (cont'd.)
  - The frequency of alleles  $B$  and  $b$  among 2,000 gametes:

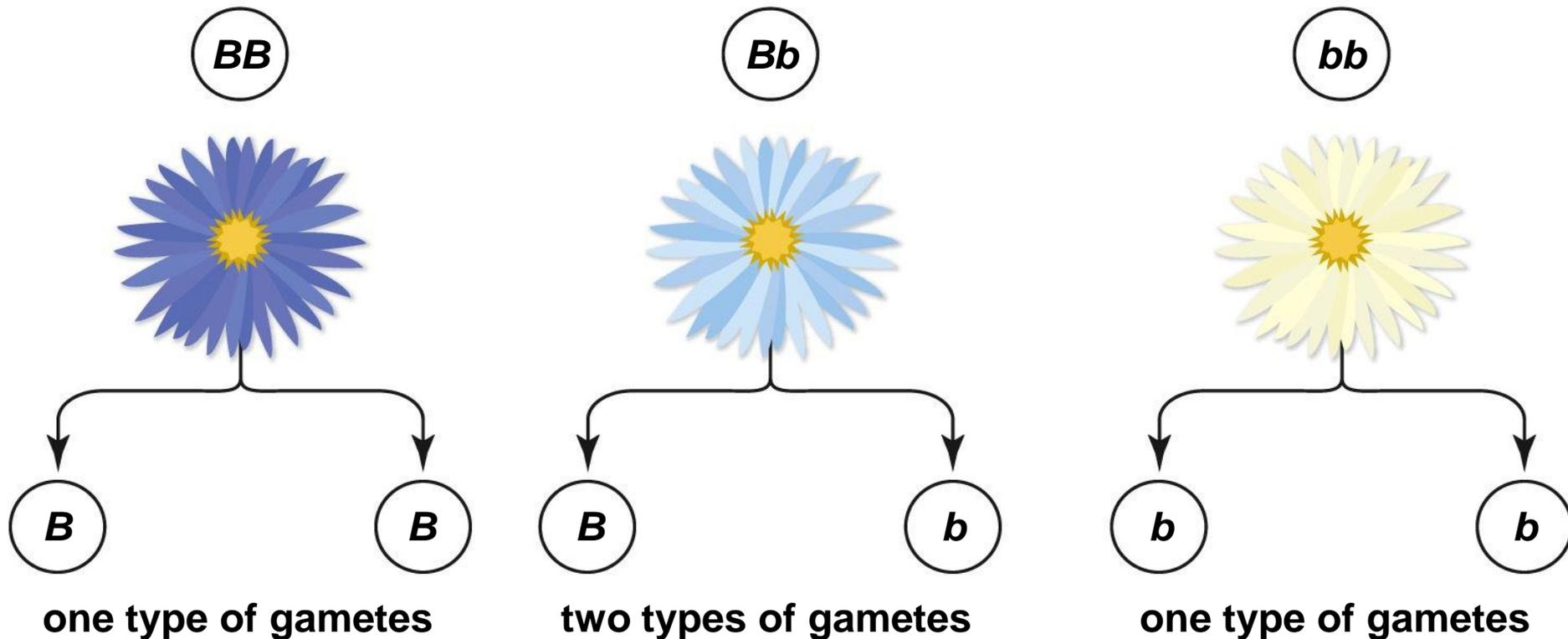
$$B (p) = (980 + 420) \div 2,000 \text{ alleles} = 1,400 \div 2,000 = 0.7$$

$$B(q) = (180 + 420) \div 2,000 \text{ alleles} = 600 \div 2,000 = 0.3$$

# How Do We Know When A Population Is Evolving? (cont'd.)

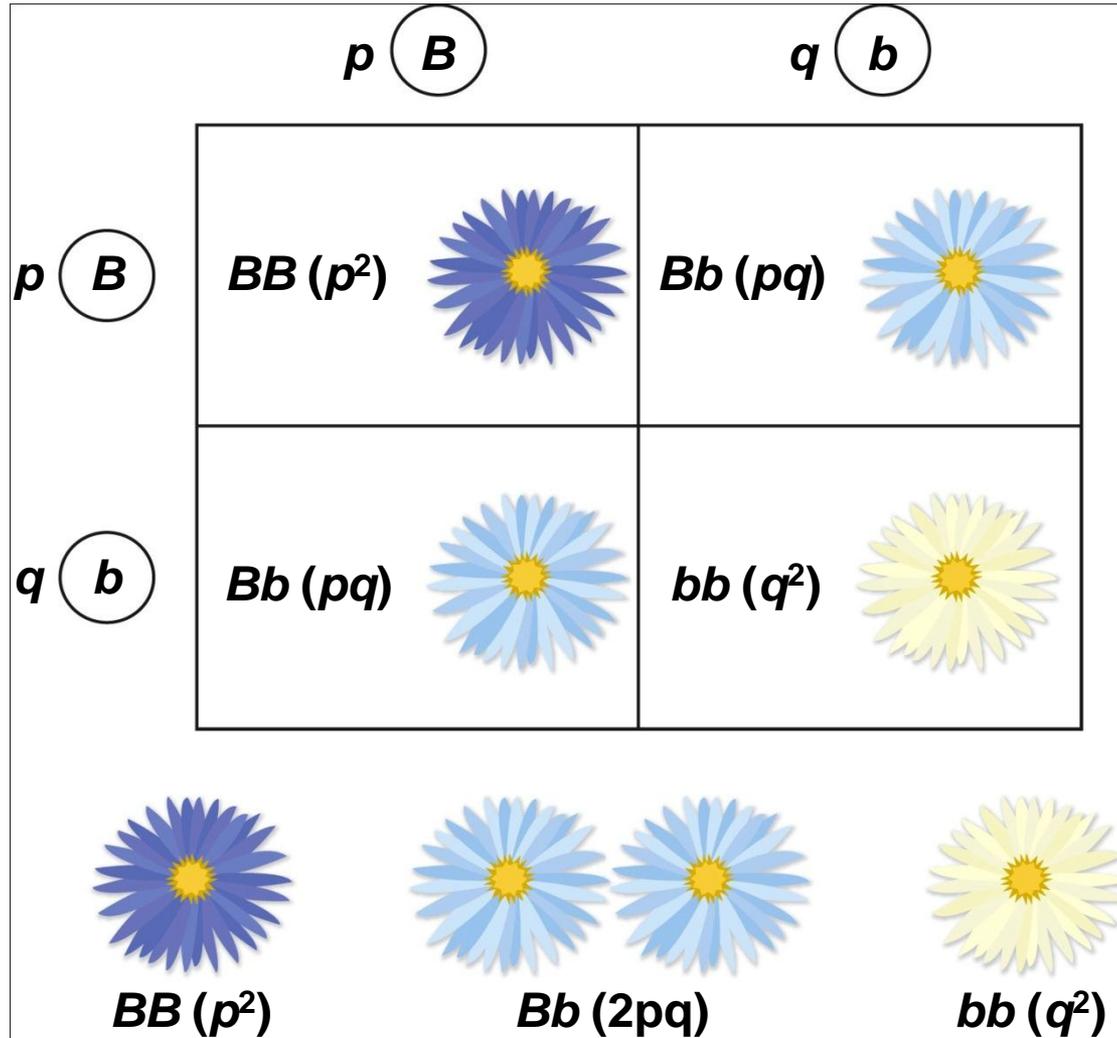
- If the population size stays constant at 1,000, there will be 490 *BB*, 420 *Bb*, and 90 *bb* individuals
- Allele frequencies for dark-blue, medium-blue, and white wings are the same as they were in the original gametes – the population is not evolving

# How Do We Know When A Population Is Evolving?(cont'd.)



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# How Do We Know When A Population Is Evolving?(cont'd.)



# How Do We Know When A Population Is Evolving?(cont'd.)

- Researchers use the Hardy–Weinberg formula to estimate the frequency of carriers of alleles that cause genetic traits and disorders
  - Example: Hereditary hemochromatosis (HH) in Ireland
    - If the frequency of the autosomal recessive allele that causes HH is  $q = 0.14$ , then  $p = 0.86$
    - The carrier frequency ( $2pq$ ) is calculated to be about 0.24

# 17.3 How Do Allele Frequencies Change?

- Different patterns of natural selection occur based on:
  - Selection pressures
  - Organisms involved
  - Three modes of natural selection

# How Do Allele Frequencies Change? (cont'd.)

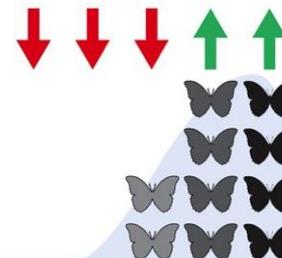
- Modes of natural selection
  - Directional selection shifts the range of variation in traits in one direction
  - Stabilizing selection favors intermediate forms of a trait
  - Disruptive selection favors forms at the extremes of a range of variation

# How Do Allele Frequencies Change? (cont'd.)

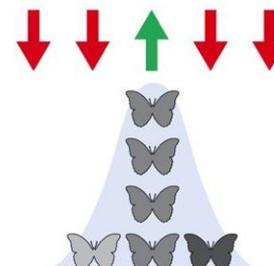
population  
before selection



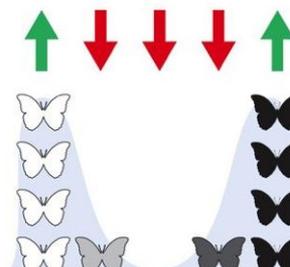
directional  
selection



stabilizing  
selection



disruptive  
selection



# 17.4 What is the Effect of Directional Selection?

- Directional selection
  - Shifts an allele's frequency in a consistent direction
  - Forms at one end of a range of phenotypic variation
  - Becomes more common over time
  - Bell-shaped curves indicate continuous variation in a butterfly wing-color trait

# ANIMATION: Directional selection

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# What is the Effect of Directional Selection? (cont'd.)

- Peppered moths
  - The peppered moth's coloration camouflages it from predatory birds
    - When the air was clean, trees were light-colored, and so were most peppered moths
    - When smoke from coal-burning factories changed the environment, predatory birds ate more white moths – selection pressure favored darker moths
    - By 1850s, dark-colored moths were more common

# What is the Effect of Directional Selection? (cont'd.)



**A**



**B**

# What is the Effect of Directional Selection? (cont'd.)

- Wafarin-resistant rats
  - Rats thrive there are people
  - Wafarin became popular in 1950s
  - Spreading poison exerts directional selection
  - Exposure caused 10 percent of urban rats to become resistant to Wafarin by 1980s

# What is the Effect of Directional Selection? (cont'd.)



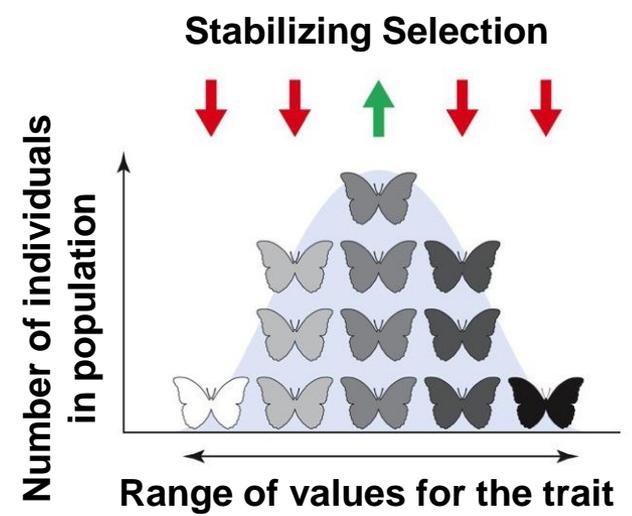
© Rollin Verlinde/Vilda.

# 17.5 What Types Of Natural Selection Favor Intermediate or Extreme Forms of Traits?

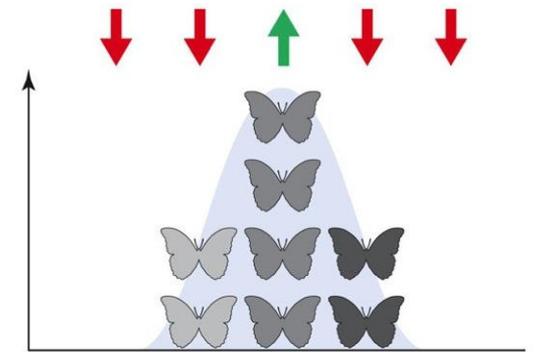
- Stabilizing selection
  - Also called balancing selection
  - Tends to preserve the midrange phenotypes in a population
  - Mode of natural selection in which intermediate forms of a trait are favored over extremes

# Intermediate or Extreme Forms of Traits (cont'd.)

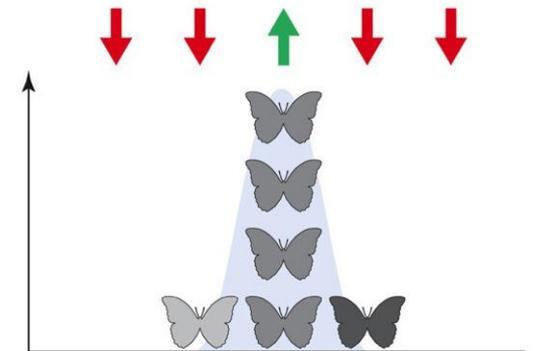
Time 1



Time 2



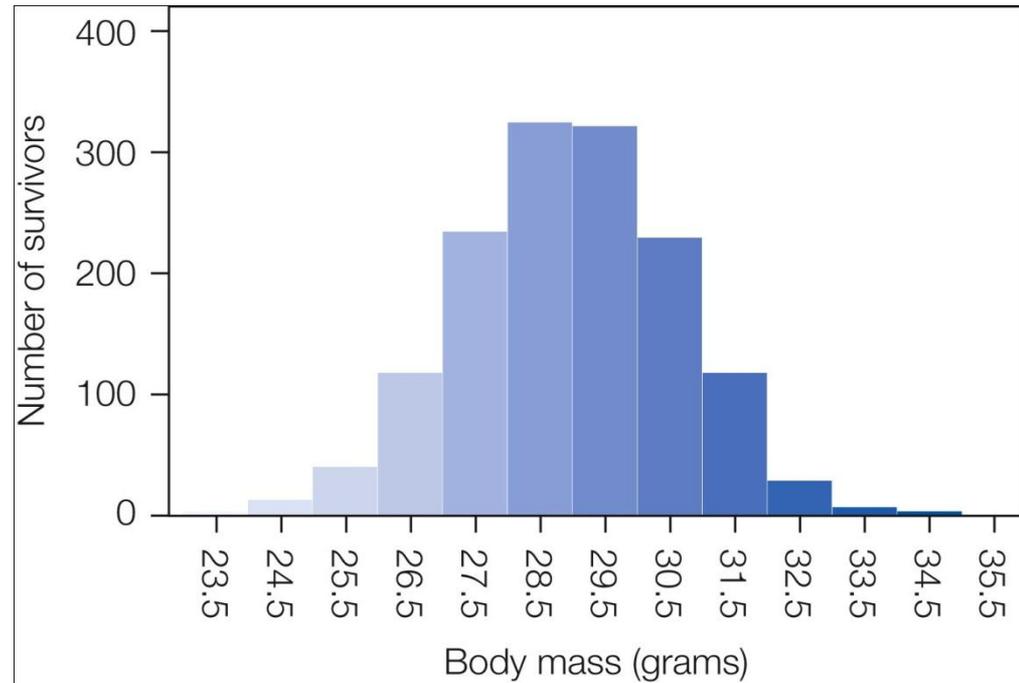
Time 3



# Intermediate or Extreme Forms of Traits (cont'd.)

- Sociable weavers
  - The body weight of sociable weavers is subject to stabilizing selection
  - Body weight is a trade-off between risks of starvation and predation
    - Leaner birds do not store enough fat to avoid starvation
    - Predators select against birds of high body weight
  - Birds of intermediate weight have the selective advantage

# Intermediate or Extreme Forms of Traits (cont'd.)



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# Intermediate or Extreme Forms of Traits (cont'd.)

- Disruptive selection
  - Mode of natural selection that favor forms of a trait at both ends of a range
  - Midrange forms are eliminated
  - Intermediate forms are selected against

# ANIMATION: Disruptive selection

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# Intermediate or Extreme Forms of Traits (cont'd.)

- African seedcrackers
  - Dimorphism in bill size results from competition for two types of food in the dry season
    - Small-billed birds are better at opening soft seeds, but large-billed birds are better at cracking hard seeds
    - Conditions favor birds with bills that are either 12 mm wide or wider than 15 mm
    - Birds with bills of intermediate size are selected against

# ANIMATION: Disruptive selection among African finches

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# 17.6 How Does Natural Selection Maintain Diversity?

- Selection pressures that operate on natural populations are complex; an allele may be adaptive in one circumstance but harmful in another
- Any mode of natural selection may maintain two or more alleles in a population

# How Does Natural Selection Maintain Diversity? (cont'd.)

- Sexual selection
  - Mode of natural selection in which some individuals of a population out-reproduce others because they are better at securing mates
  - The most adaptive forms of a trait are those that help individuals defeat same-sex rivals for mates, or are the ones most attractive to the opposite sex

# How Does Natural Selection Maintain Diversity? (cont'd.)

- Sexual dimorphism
  - Males and females are different in size or another aspect of their appearance
  - Individuals (often males) are more:
    - Colorful
    - Larger
    - More aggressive

# How Does Natural Selection Maintain Diversity? (cont'd.)



© Ingo Arndt/Nature Picture Library

# How Does Natural Selection Maintain Diversity? (cont'd.)



Bruce Beehler

# How Does Natural Selection Maintain Diversity? (cont'd.)



© Minden Pictures/SuperStock

# How Does Natural Selection Maintain Diversity? (cont'd.)

- Maintaining multiple alleles
  - Balanced polymorphism
    - Maintenance of two or more alleles for a trait at high frequency in a population as a result of natural selection against homozygotes
    - Example: the mate preferences of female *Drosophila* flies
  - Frequency-dependent selection
    - The adaptive value of a form of a trait depends on its frequency in the population

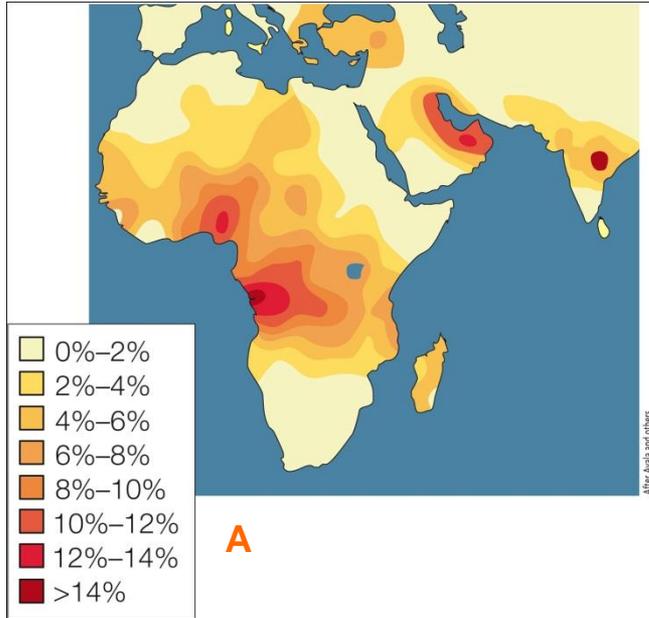
# How Does Natural Selection Maintain Diversity? (cont'd.)

- Malaria and sickle-cell anemia
  - A mutation in the normal beta globin chain of hemoglobin (*HbA*) causes sickle-cell anemia
  - Individuals homozygous for the mutated *HbS* allele often die young
  - The *HbS* allele persists at high frequencies in tropical regions of Africa because *HbA/HbS* heterozygotes are more likely to survive than *HbA/HbA* homozygotes

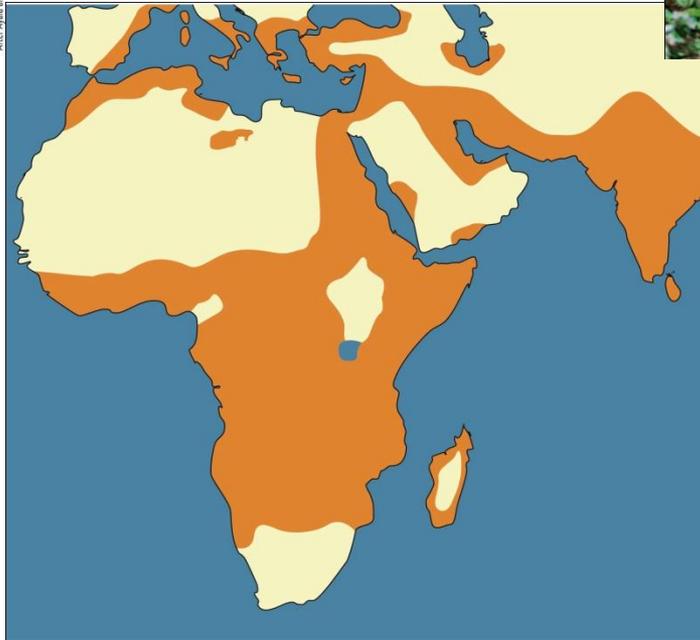
# How Does Natural Selection Maintain Diversity? (cont'd.)

- Malaria and sickle-cell anemia (cont'd.)
  - In tropical and subtropical regions mosquitoes transmit the parasitic protist, *Plasmodium*, that causes malaria
  - *HbA/HbS* heterozygotes-infected red blood cells sickle
  - The abnormal shape brings cells to attention of immune system, which destroys them and the parasites they harbor

# How Does Natural Selection Maintain Diversity? (cont'd.)



After Ayala and others



After Ayala and others



© Michael Freeman/Corbis

# 17.7 What Mechanisms Other Than Natural Selection Affect Allele Frequencies?

- Genetic drift
  - Random change in allele frequencies
  - Can lead to loss of genetic diversity by causing alleles to become *fixed*
    - An allele for which all members of a population are homozygous
    - Especially true in small populations
  - The larger the population, the smaller the impact of random changes in allele frequencies

# What Other Mechanisms Affect Allele Frequencies? (cont'd.)

- Genetic drift
  - Example: Allele X occurs at a 10% frequency
    - In a population of 10, only one person carries the allele, and if that person dies, the allele is lost
    - In a population of 100, all 10 people who carry the allele would have to die for the allele to be lost

# ANIMATION: Simulation of genetic drift

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# What Other Mechanisms Affect Allele Frequencies? (cont'd.)

- Genetic drift can be dramatic when a few individuals rebuild a population or start a new one
  - Example: Hunting reduced an elephant seal population to 20; the population is now homozygous at every gene
- Bottleneck
  - Drastic reduction in population size so severe that it reduces genetic diversity

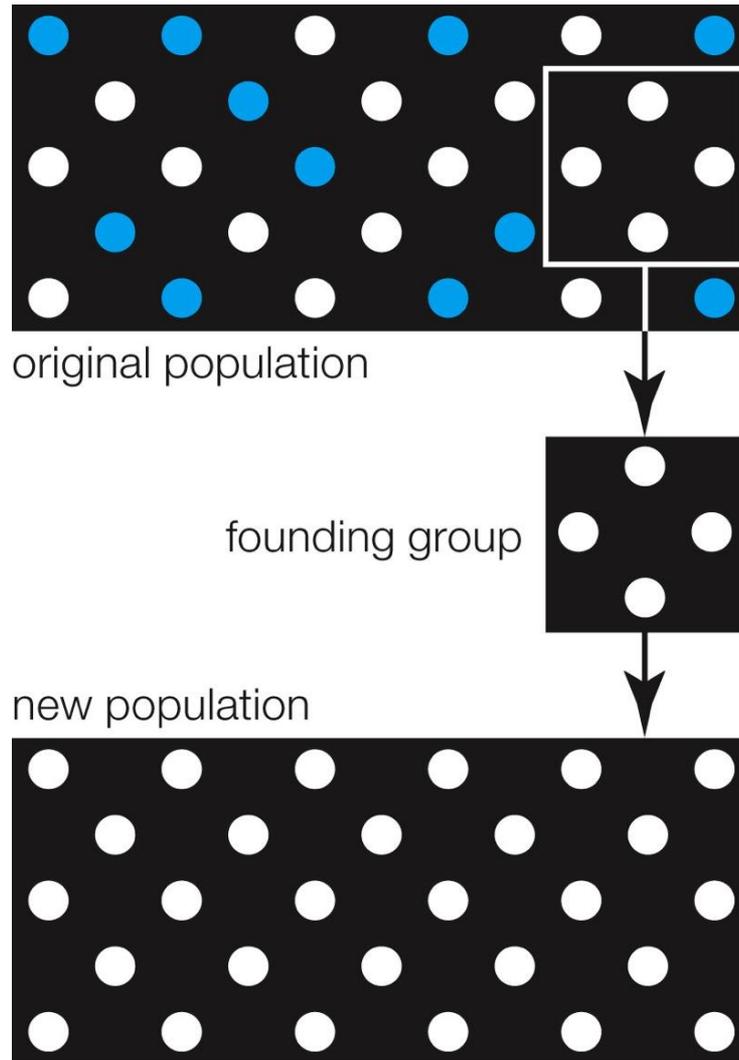
# What Other Mechanisms Affect Allele Frequencies? (cont'd.)

- Founder effect and inbreeding
  - Change in allele frequencies that occurs when a small number of individuals establish a new population

# What Other Mechanisms Affect Allele Frequencies? (cont'd.)

- Ellis-van Creveld syndrome
  - Caused by a recessive allele common in the Old Order Amish of Lancaster County, PA
  - Characterized by dwarfism, polydactyly, and heart defects

# What Other Mechanisms Affect Allele Frequencies? (cont'd.)



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# What Other Mechanisms Affect Allele Frequencies? (cont'd.)

- Gene flow: individuals, along with their alleles, move into and out of populations
  - Stabilizes allele frequencies, so it counters the effects of mutation, natural selection, and genetic drift that tend to occur within a population
  - Example: blue jays move acorns, and their alleles, among populations of oak trees that would otherwise be genetically isolated

# 17.8 How Do Species Attain and Maintain Separate Identities?

- Speciation: one of several processes by which new species arise
- Reproductive isolation
  - Absence of gene flow between populations
  - Always part of speciation

# ANIMATION: Reproductive isolating mechanisms

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# How Do Species Attain and Maintain Separate Identities? (cont'd.)

- Reproductive isolation
  - Gene flow does not occur between populations
    - Different genetic changes accumulate
    - Reinforces differences between diverging populations
    - If pollination or mating cannot occur, or if zygotes cannot form, the isolation is prezygotic
    - If hybrids form but are unfit or infertile, the isolation is postzygotic

# How Do Species Attain and Maintain Separate Identities? (cont'd.)

- Seven mechanisms of reproductive isolation
  - Temporal isolation
    - Some populations can't interbreed because the timing of their reproduction differs
  - Mechanical isolation
    - Size or shape of an individual's reproductive parts prevent it from mating with members of another population

# How Do Species Attain and Maintain Separate Identities? (cont'd.)

## – Ecological isolation

- Populations adapted to different microenvironments in the same region may be physically separated

## – Behavioral isolation

- In animals, behavioral differences can stop gene flow between related species

# How Do Species Attain and Maintain Separate Identities? (cont'd.)

## – Gamete incompatibility

- Even if gametes of different species meet, they often have molecular incompatibilities that prevent them from fusing
- Primary speciation route of animals that release free-swimming sperm in water

## – Hybrid inviability

- If genetic incompatibilities disrupt development, a hybrid embryo may die, or hybrid offspring that survive may have reduced fitness (e.g., ligers)

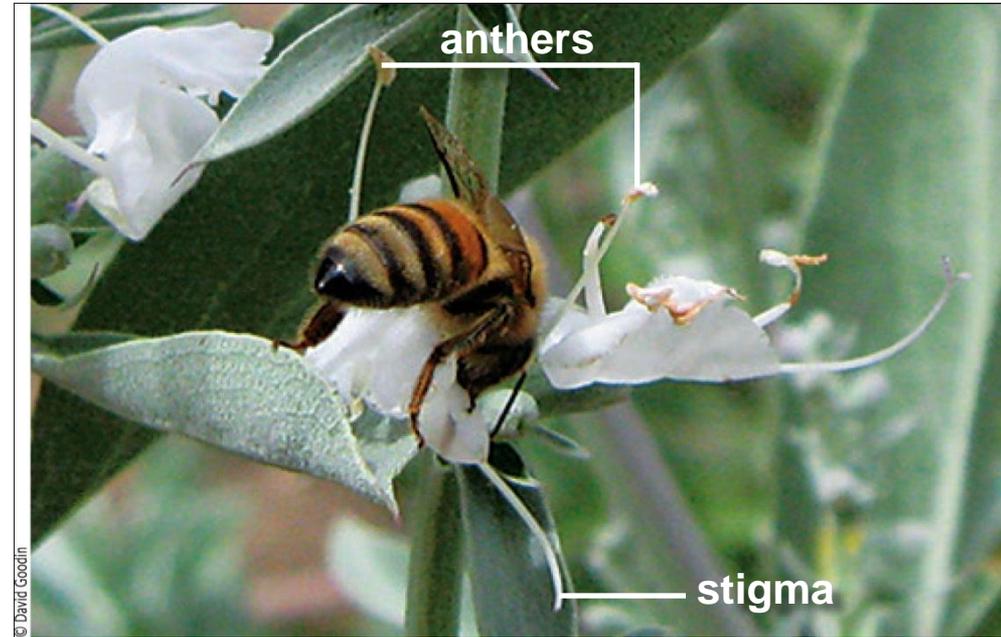
# How Do Species Attain and Maintain Separate Identities? (cont'd.)

## – Hybrid sterility

- Some interspecies crosses produce robust but sterile offspring (e.g., mules)

# How Do Species Attain and Maintain Separate Identities? (cont'd.)

A



C

B

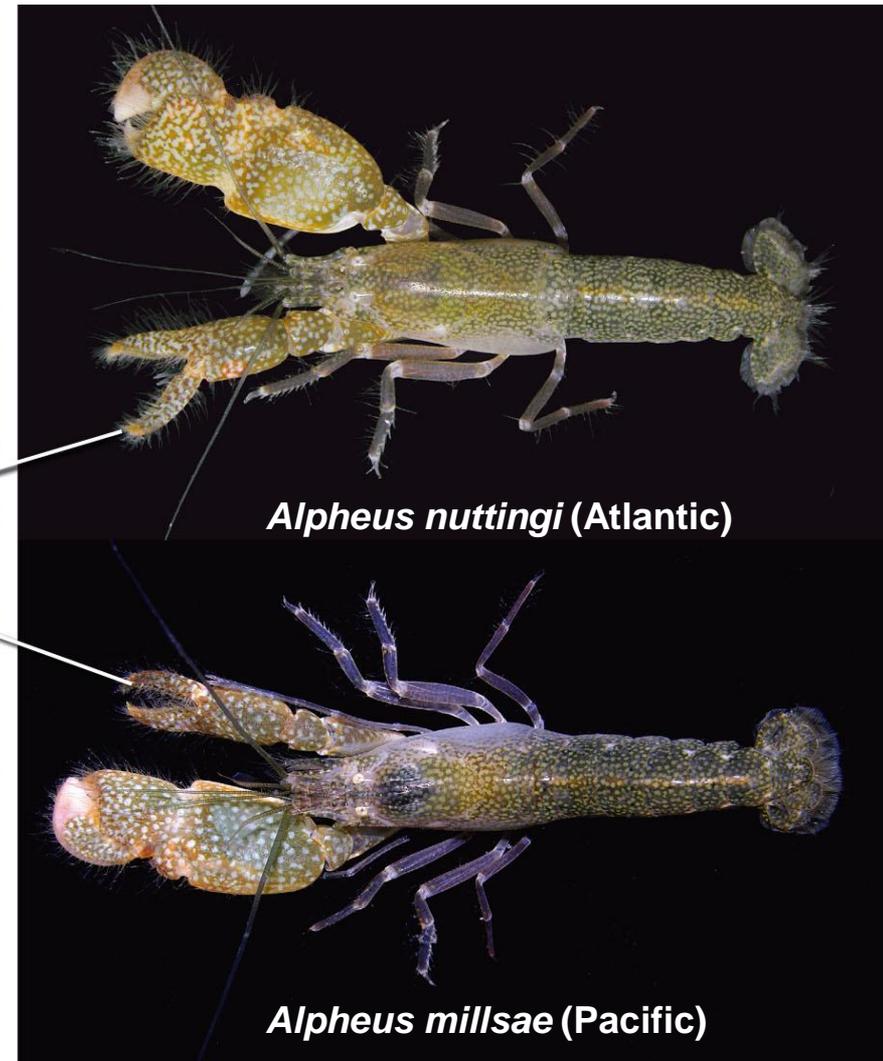
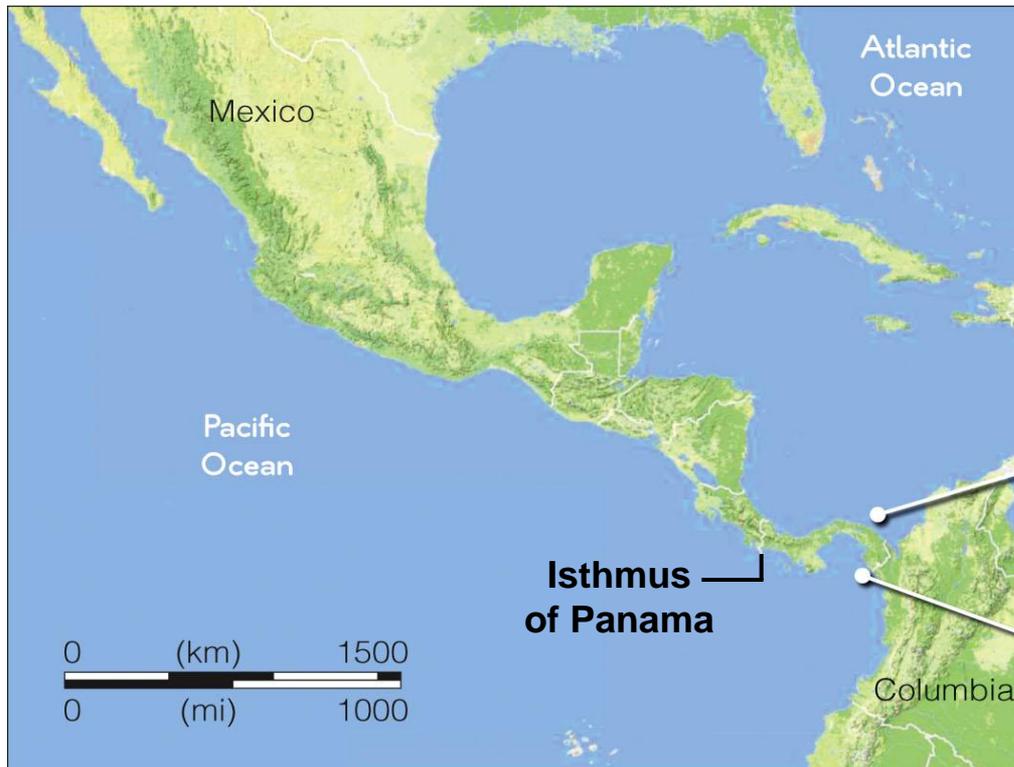
# 17.9 What is Allopatric Speciation?

- Allopatric speciation
  - Speciation pattern in which a physical barrier that separates members of a population ends gene flow between them
  - Geographic barrier arises
  - Genetic divergences then give rise to new species

# What is Allopatric Speciation? (cont'd.)

- Geographic barrier can block gene flow
  - Depends on how an organism travels
    - e.g., by swimming, walking, or flying
  - How it reproduces
    - e.g., by internal fertilization or by pollen dispersal
- Example:
  - When the Isthmus of Panama formed, it cut off gene flow among populations of aquatic organisms in the Pacific and Atlantic oceans

# What is Allopatric Speciation? (cont'd.)



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# What is Allopatric Speciation? (cont'd.)

- Speciation in archipelagos
  - Archipelagos are isolated island chains formed by volcanoes, such as the Hawaiian and Galápagos Islands
  - Archipelagos were populated by a few individuals of mainland species whose descendants diverged over time
  - Selection pressures within and between the islands can foster even more divergences

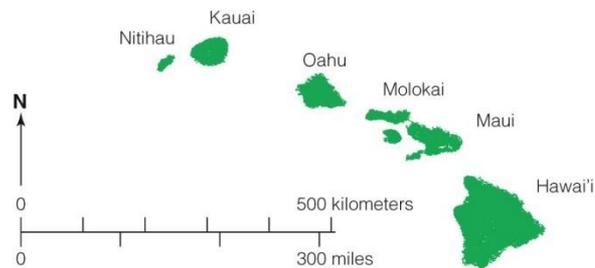
# What is Allopatric Speciation? (cont'd.)

- The first birds to colonize the Hawaiian Islands found a near absence of competitors and predators and an abundance of rich and vacant habitats, which encouraged rapid speciation
  - Honeycreepers, unique to the Hawaiian Islands, have specialized bills and behaviors adapted to feed on certain insects, seeds, fruits, nectar, or other foods

# What is Allopatric Speciation? (cont'd.)



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# 17.10 Can Speciation Occur Without a Physical Barrier to Gene Flow?

- Sympatric speciation
  - Populations sometimes speciate even without a physical barrier that bars gene flow between them
  - Can occur instantly with a change in chromosome number – many plants are polyploid (e.g., wheat)

# Can Speciation Occur Without a Physical Barrier to Gene Flow? (cont'd.)

- Examples of sympatric speciation
  - Lake Victoria cichlids (sexual selection)
    - In the same lake, female cichlids of different species visually select and mate with brightly colored males of their own species
  - Warblers around the Tibetan plateau (behavioral isolation)
    - Two populations overlap in range, but don't interbreed because they don't recognize one another's songs

# ANIMATION: Sympatric Speciation in Wheat

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# Can Speciation Occur Without a Physical Barrier to Gene Flow? (cont'd.)



Kevin Bauman, www.african-cichlid.com

# Can Speciation Occur Without a Physical Barrier to Gene Flow? (cont'd.)

- Parapatric speciation: may occur when one population extends across a broad region with diverse habitats
  - Example: Two species of velvet walking worm with overlapping habitats in Tasmania
    - Where they interbreed, their hybrids are sterile

# 17.11 What is Macroevolution?

- Macroevolution
  - Evolutionary patterns on a larger scale
- There are five patterns of macroevolution
  - Stasis
  - Exaptation
  - Mass extinction
  - Adaptive radiation
  - Coevolution

# What is Macroevolution? (cont'd.)

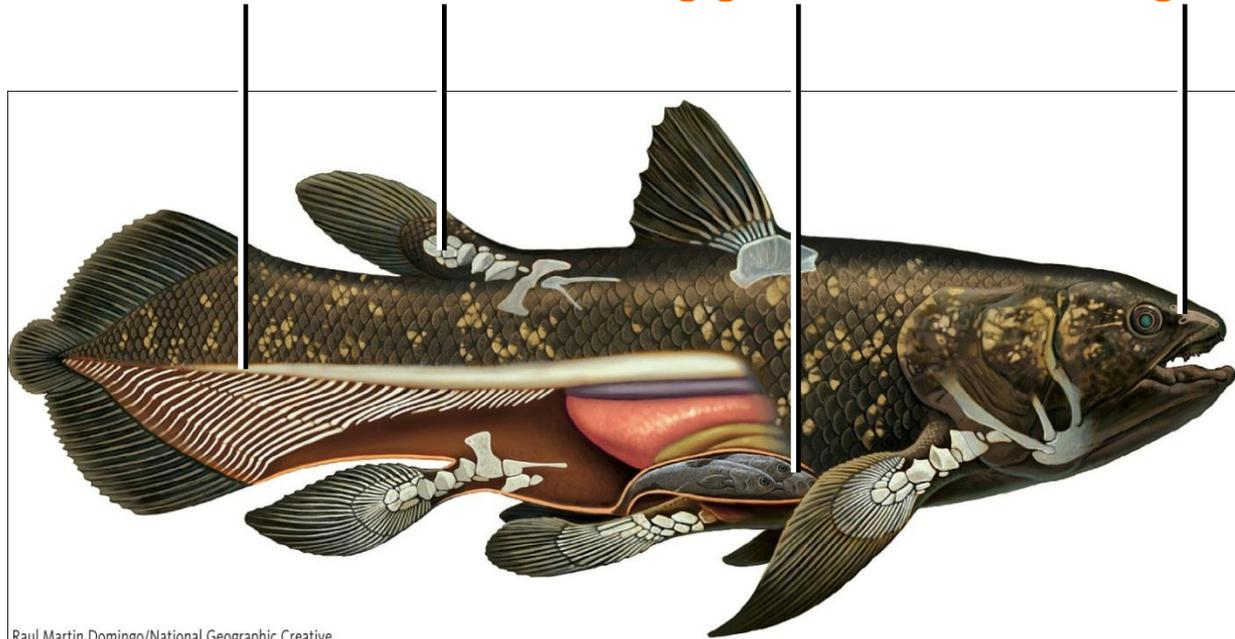
**Notochord**   **Lobed fins**   **Long gestation**   **Rostral organ**



Courtesy of The Virtual Fossil Museum, www.vfmuseum.net



© Amaz, Aelhta



Raul Martin Domingo/National Geographic Creative.

# What is Macroevolution? (cont'd.)

- Stasis
  - A lineage which persists for millions of years with little or no change
  - Example: Coelacanth
    - Ancient lobe-finned fish
    - Thought to be extinct
    - Rediscovered in 1938

# What is Macroevolution? (cont'd.)

- Exaptation
  - Adaptation of an existing structure for a completely different purpose; a major evolutionary novelty
  - Example: Feathers on modern bird used for flight evolved from feather on dinosaurs used for insulation

# What is Macroevolution? (cont'd.)

- Mass extinction
  - Extinct: refers to a species that has been permanently lost
    - Simultaneous losses of many lineages
    - 99 percent of all species that have ever lived are now extinct
  - Fossil record indicated that there have been more than 20 mass extinctions
  - Five catastrophic events in which the majority of species on Earth disappeared

# What is Macroevolution? (cont'd.)

- Adaptive radiation
  - Lineage rapidly diversifies into several new species
    - A burst of genetic divergences
  - Can occur after individuals colonize a new environment that has a variety of different habitats with few or no competitors
  - Can involve a key innovation
    - A new trait that allows its bearer to exploit a habitat more efficiently or in a novel way

# What is Macroevolution? (cont'd.)

- Coevolution
  - Joint evolution of two closely interacting species
    - Each is a selective agent for traits of the other
    - Each adapts to changes in the other
  - Over evolutionary time, two species may become so interdependent that they can no longer survive without one another
    - e.g., the large blue butterfly (*Maculinea arion*) and red ant (*Myrmica sabuleti*)

# What is Macroevolution? (cont'd.)



© Jeremy Thomas/ Natural Visions

A



© Brian Raine, www.flickr.com/people/25801055@N00.

B

# What is Macroevolution? (cont'd.)

- Evolutionary theory
  - Biologists disagree about how macroevolution occurs
  - Dramatic jumps in morphology may be the result of mutations in homeotic or other regulatory genes
  - Macroevolution may be an accumulation of many microevolutionary events, or it may be an entirely different process

# 17.12 Why Do We Study Evolutionary History?

- Instead of trying to divide the diversity of living organisms into a series of taxonomic ranks, most biologists are now focusing on evolutionary connections
- Phylogeny
  - Grouping species on the basis of their shared characters
  - Like a genealogy

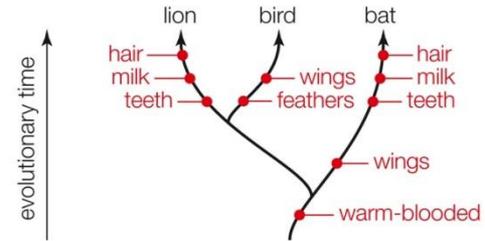
# Why Do We Study Evolutionary History? (cont'd)

**TABLE 17.2**

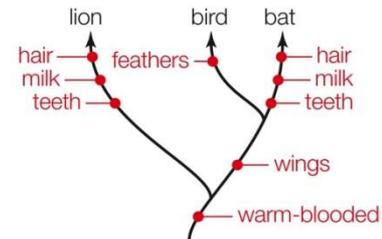
## Examples of Characters

	<b>Bird</b>	<b>Bat</b>	<b>Lion</b>
Warm-blooded	Y	Y	Y
Hair	N	Y	Y
Milk	N	Y	Y
Teeth	N	Y	Y
Wings	Y	Y	N
Feathers	Y	N	N

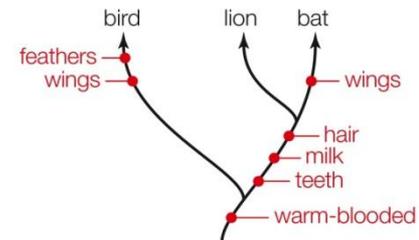
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**A** If the bird and lion are most closely related, the derived traits would have evolved ten times in total.



**B** If the bird and bat are most closely related, the derived traits would have evolved nine times in total.



**C** If the lion and bat are most closely related, the derived traits would have evolved seven times in total.

# Why Do We Study Evolutionary History? (cont'd)

- Cladistics
  - Method of determining evolutionary relationships
  - Group species into *clades* based on shared characters
  - Results in a cladogram
    - A type of evolutionary tree used to visualize evolutionary patterns

# ANIMATION: Interpreting a cladogram

Please wait, loading

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# 17.13 How Can We Use What We Learn About Evolutionary History?

- Hawaiian honeycreepers illustrate how evolution works
  - Isolation that spurred honeycreepers' adaptive radiations also ensured they had no built-in defenses against predators or diseases from the mainland
  - Specializations became hindrances when habitats suddenly changed or disappeared

# How Can We Use What We Learn About Evolutionary History? (cont'd.)



A

B

C

# 17.4 Directional Selection

- Superbad superbugs
  - Are we overutilizing antibiotics?
    - Bacterial species are able to survive after exposure to antibiotics
    - Pathogens resistant to multiple antibiotics are considered multidrug resistant (MDR) or superbugs
    - Serious and growing phenomenon in contemporary medicine

# Directional Selection (cont'd.)



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