UNIT 3 CHAPTER 12

The Forces of Evolutionary Change

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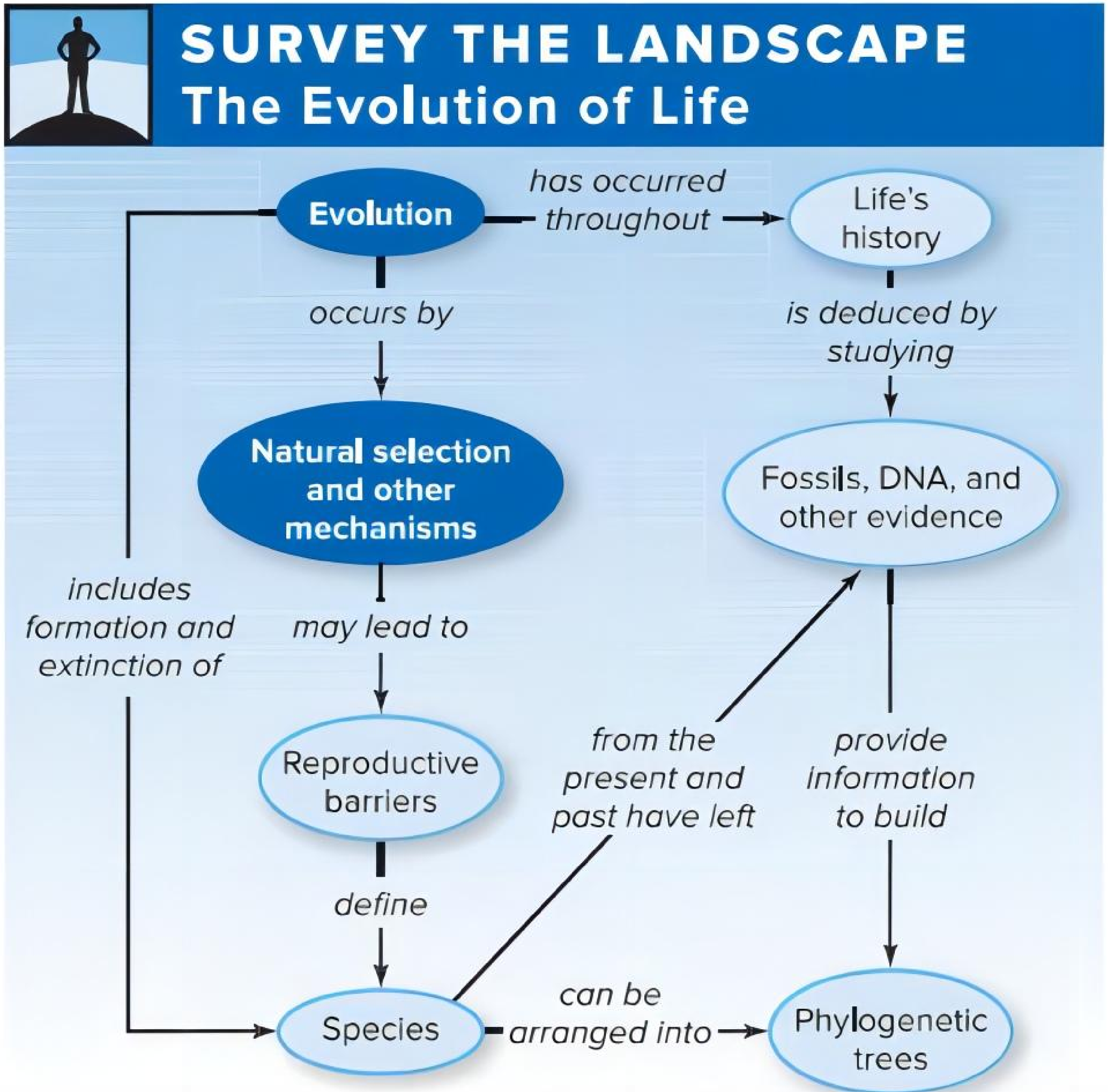
LEARNING OUTLINE (Chapter 12)

- 12.1 Evolution Acts Populations
- 12.2 Evolutionary Thought Has Evolved for Centuries
- 12.3 Natural Selection Molds Evolution
- 12.4 Evolution Is Inevitable in Real populations
- 12. 5 Natural selection can shape populations in Many ways
- 12.6 Sexual selection Directly Influences Reproductive success
- 12.7 Evolution occurs in several additional ways


SURVEY THE LANDSCAPE
The Evolution of Life
Evolution
has occurred throughout
Life's history
occurs by
is deduced by studying
Natural selection and other mechanisms
Fossils, DNA, and other evidence
includes formation and extinction of
may lead to
Reproductive barriers
from the present and past have left
provide information to build
define
Species
can be arranged into
Phylogenetic trees

12.1 Evolution Acts on Populations

- Scientific reasoning has profoundly changed thinking about the origin of species.Just 250 years ago,no one knew Earth's age.A century later,scientists learned that Earth is millions of years old(or older),but many believed that a creator made all species in their present form.Today's scientists, relying on a wide range of evidence, accept evolution as the explanation for life's diversity.

12.1 Evolution Acts on Populations

- But what is evolution? A simple definition of evolution is **descent with modification.** “Descent"implies inheritance; “modification"refers to changes in traits from generation to generation.
- Evolution has another,more specific,definition as well. A gene is a DNA sequence that encodes a protein; in part, an organism's proteins determine its traits. Moreover, each gene can have multiple versions,or alleles.We have also seen that a population consists of interbreeding members of the same species.
- Biologists say that evolution occurs in a population **when some alleles become more common, and others less common**, from one generation to the next. A more precise definition of evolution,then,is **genetic change in a population over multiple generations.**

12.1 Evolution Acts on Populations

- The allele frequencies for each gene determine the characteristics of a population. Many people in Sweden, for example,have alleles conferring blond hair and blue eyes;a population of Asians would contain many more alleles specifying darker hair and eyes.If Swedes migrate to Asia and interbreed with the locals (or vice versa), regional allele frequencies change.
- Some people use the term **microevolution** to refer to **the small, generation-by-generation changes occurring in every population or species**.This chapter describes the most common ways that such changes occur.Over long periods,these same processes give rise to what is sometimes called **macroevolution**, **which includes the appearance of new species.**Evolution does not, however, explain how life began. Chapter 15 describes what science can tell us about life's ancient origin.

12.2 Evolutionary Thought Has Evolved for Centuries

A. Many Explanations Have Been Proposed for Life's Diversity

- Geology laid the groundwork for evolutionary thought.Some peopleexplained the distribution of rock strata with the idea of catastrophism(a series of upheavals).The more gradual uniformitarianism (continual remolding of Earth's surface)became widely accepted.
- The principle of superposition states that lower rock strata are older than those above,suggesting an evolutionary sequence for fossils within them.

B.Charles Darwin's Voyage Provided a Weakh of Evidence

- During the voyage,Darwin observed the distributionof organisms in diverse habitats and their relationships to geological formations.After much thought and consideration of input from other scientists, he developed his theory of the origin of species by means of natural selection.

12.2 Evolutionary Thought Has Evolved for Centuries

C.On the Origin of Species Proposed Natural Selection as an EvolutionaryMechanism

- **Natural selection** is based on multiple observations: Individuals vary for inherited traits;many more offspring are born than survive;and life is a struggle to acquire limited resources.The environment eliminates poorly adapted individuals,so **only those with the best adaptations reproduce**.
- **Artificial selection** is based on similar requirements, except that a human breeder allows only certain individuals to reproduce.

D.Evolutionary Theory Continues to Expand

- The modern evolutionary synthesis unifies ideas about DNA,mutations,inheritance,and natural selection.

TABLE **12.1** **The Logic of Natural Selection: A Summary**

Observations of nature
1. **Genetic variation:** Within a species, no two individuals (except identical siblings) are exactly alike. Some of this variation is heritable.
2. **Limited resources:** Every habitat contains limited supplies of the resources required for survival.
3. **Overproduction of offspring:** More individuals are born than survive to reproduce.
Inferences from observations
1. **Struggle for existence:** Individuals compete for the limited resources that enable them to survive.
2. **Unequal reproductive success (natural selection):** The inherited characteristics of some individuals make them more likely to obtain resources, survive, and reproduce.
3. **Descent with modification:** Over many generations, a population's characteristics can change by natural selection, even giving rise to new species.

12.2 Evolutionary Thought Has Evolved for Centuries

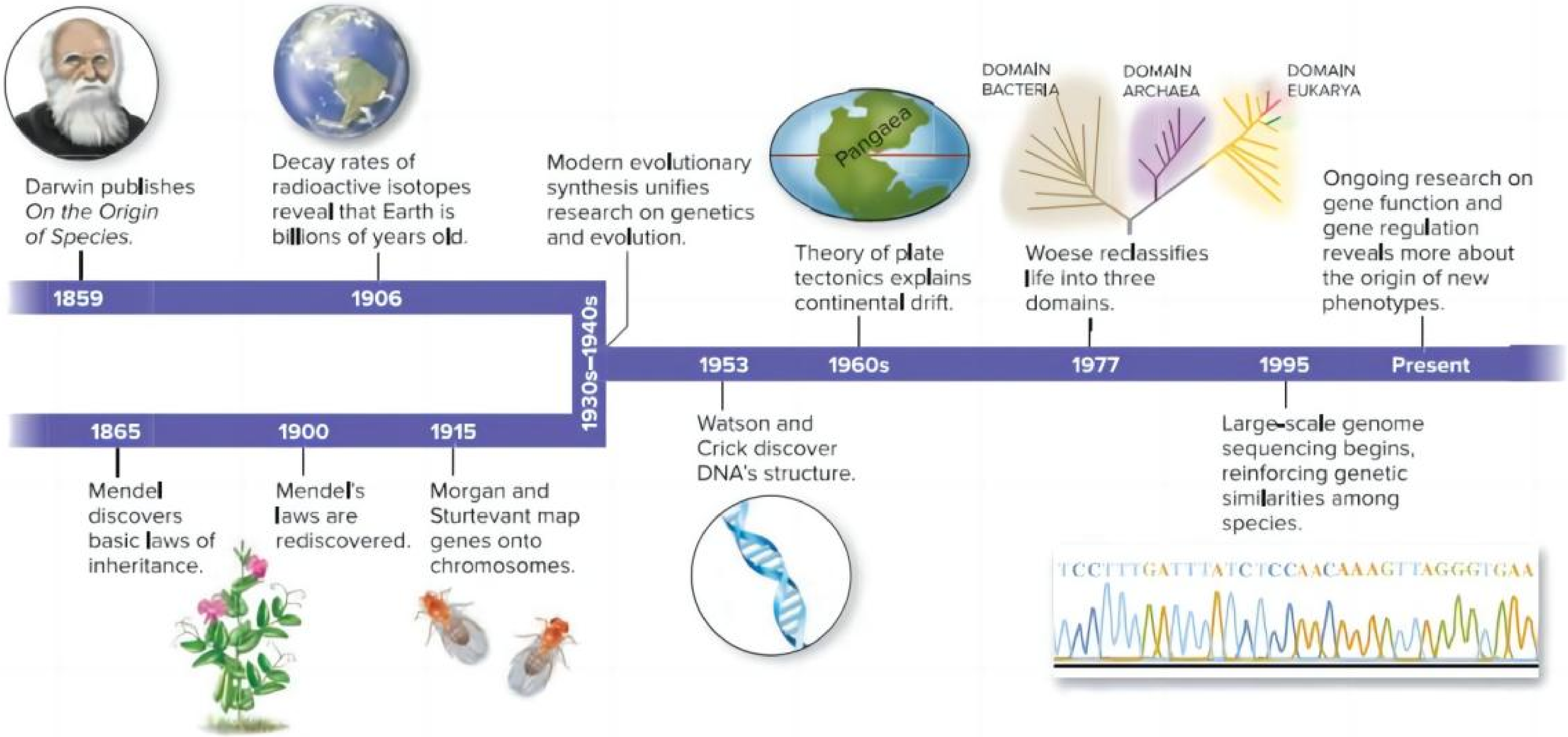


Figure 12.6 **Evolutionary Theory Since Darwin.** Charles Darwin and Gregor Mendel laid a foundation for evolutionary theory, but thousands of scientists since that time have added to our understanding of evolution.

12.3 Natural Selection Molds Evolution

- Natural selection is the most famous,and often the most important, mechanism of evolution.

A. Adaptations Enhance Reproductive Success

- As Darwin knew,organisms of the same species are different from one another,and every population produces more individuals than resources can support. Some members of any population will not survive to reproduce. **A struggle for existence is therefore inevitable.The variation inherent in each species means that some individuals in each population are better than others at obtaining nutrients and water,avoiding predators,tolerating temperature changes,attracting mates,or reproducing.**
- **Adaptations in the evolutionary sense include only those structures,behaviors,or physiological processes that are heritable and that contribute to reproductive success**.
- Natural selection requires preexisting genetic diversity. Ultimately,this diversity arises largely by chance. **Nevertheless,it is important to realize that natural selection itself is NOT a random process.** Instead,it selectively eliminates most of the individuals that are least able to compete for resources or cope with the prevailing environment.

12.3 Natural Selection Molds Evolution

B.Natural Selection Eliminates Poorly Adapted Phenotypes

- An individual's phenotype is its observable properties,most of which arise from a combination of environmental influences and the action of multiple genes. **By “weeding out” individuals with poorly adapted phenotypes, natural selection indirectly changes allele frequencies in the population.**

C.Natural Selection Does Not Have a Goal

- Several factors combine to prevent natural selection from producing all of the traits that a species might find useful.
- **First,**every genome has limited potential,imposed by its evolutionary history.
- **Second**,no population contains every allele needed to confront every possible change in the environment. If the right alleles aren't available at the right time,an environmental change may wipe out a species.
- **Third,**disasters such as floods and volcanic eruptions can indiscriminately eliminate the best allele combinations,simply by chance.
- And **finally**,natural selection cannot act on some harmful genetic traits,such as diseases that appear only after reproductive age.

12.3 Natural Selection Molds Evolution

D.What Does “Survival of the Fittest” Really Mean?

- Natural selection is often called “**the survival of the fittest**,” in an evolutionary sense,**fitness refers to an organism's genetic contribution to the next generation.**
- Fitness includes not only the total **number of offspring** produced but also the **proportion that reach reproductive age**.
- **Many adaptations contribute to an organism's overall fitness.** Being able to overcome poor weather conditions,combat parasites and other disease causing organisms,evade predators,and compete for resources enhances an organism's chances of reaching reproductive age. At that point,the ability to at tract mates affects the number of offspring an organism produces.

12.4 Evolution ls Inevitable in Real Populations

- Shifting allele frequencies in populations are the small steps of change that collectively drive evolution.Given the large number of genes in any organism and the many factors that can alter allele frequencies (including but not limited to natural selection),**evolution is not only possible but unavoidable.**

A.At Hardy-Weinberg Equilibrium,Allele Frequencies Do Not Change

- The study of population genetics relies on the intimate relationship between **allele frequencies and genotype frequencies**. Each genotype's frequency is the number of individuals with that genotype,divided by the total size of the population. For example,if 64 of the 100 individuals in a population are homozygous recessive,then the frequency of that genotype is 64/100,or 0.64.

Assumptions of the Hardy–Weinberg model

1. Natural selection does not occur.
2. Mutations do not occur.
3. The population is infinitely large.
4. Individuals mate at random.
5. Individuals do not migrate into or out of the population.

Allele frequencies: $p + q = 1$

Definition/equation	Example
p = frequency of dominant allele	p = frequency of D (dark fur) = 0.6
q = frequency of recessive allele	q = frequency of d (tan fur) = 0.4
$p + q = 1$	$0.6 + 0.4 = 1$

Genotype frequencies: $p^2 + 2pq + q^2 = 1$

Definition/equation	Example
p^2 = frequency of DD genotype	$0.6 \times 0.6 = 0.36$
$2pq$ = frequency of Dd genotype	$2 \times 0.6 \times 0.4 = 0.48$
q^2 = frequency of dd genotype	$0.4 \times 0.4 = 0.16$
$p^2 + 2pq + q^2 = 1$	$(0.6)^2 + (2 \times 0.6 \times 0.4) + (0.4)^2 = 1$

Reproduction (random mating)

Female gametes

Male gametes	D	d
D	DD $p^2 = (0.6)^2 = 0.36$	Dd $pq = (0.6)(0.4) = 0.24$
d	Dd $pq = (0.6)(0.4) = 0.24$	dd $q^2 = (0.4)^2 = 0.16$

Figure It Out

- In a species of ladybug,one gene controls whether the beetle has spots or not,with the allele conferring spots being dominant.Suppose you find a swarm consisting of 1000 ladybugs;250 of them lack spots.What are the frequencies of the dominant and recessive alleles?

Figure It Out

- A population of 100 sea stars is in Hardy-Weinberg equilibrium.The trait for long arms is completely dominant to the trait for short arms.In this population,40%of the alleles for this trait are dominant, and 60% are recessive.What is the frequency of the heterozygous genotype in this population?

Figure It Out

- Assume that 1 in 3000 Caucasian babies in the United States is born with cysticfibrosis(膀胱炎),a disease caused by a recessive allele.The value of q2 is therefore 1/3000=0.0003; q is the square root of 0.0003,or .018.Use this information to estimate the frequency of heterozygotes (symptomless carriers)in the American Caucasian population.

12.4 Evolution Is Inevitable in Real Populations

B.In Reality,Allele Frequencies Always Change

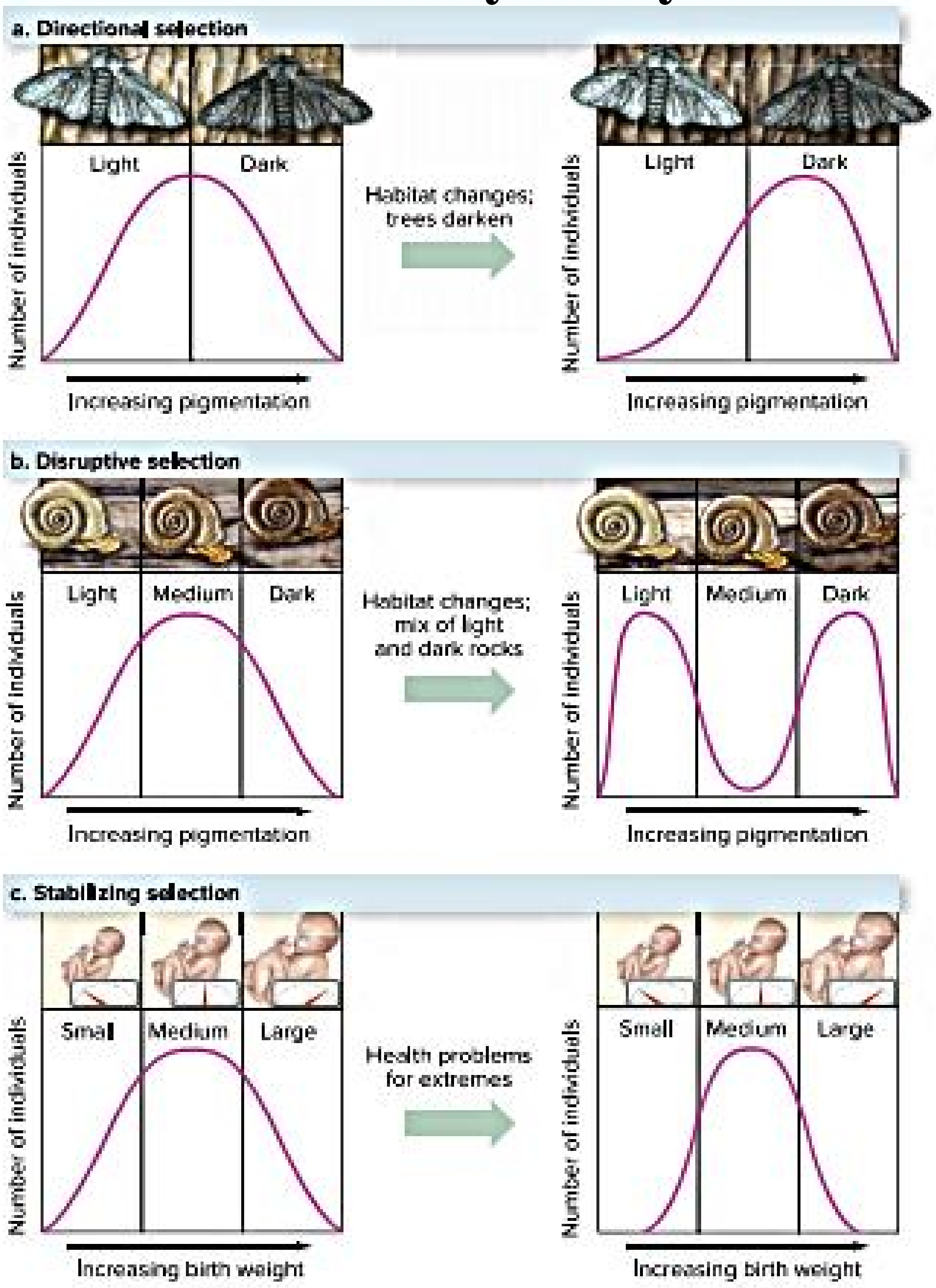
A population at Hardy-Weinberg equilibrium does not evolve.A real population, however, violates the assumptions of Hardy-Weinberg equilibrium when any of the following occurs:

- some phenotypes are better adapted to the environment than others;
- mutations introduce new alleles;
- allele frequencies change due to chance (genetic drift 基因漂变);
- individuals remain in closed groups,mating among themselves rather than with the larger population (nonrandom mating) ;
- individuals migrate among populations.

All of these events are common.But natural selection still acts to reduce the frequency of alleles that cause deadly childhood illnesses. Moreover, genetic mutations can and do occur.Some mutations happen randomly when DNA replicates. External agents,including harmful chemicals and radiation,can also cause mutations. Finally, genetic drift,nonrandom mating,and migration all happen in real populations. These forces act on populations of other species as well,so allele frequencies always change over multiple generations.

12.5 Natural Selection Can Shape Populations in Many Ways

- Of all the mechanisms by which a population can evolve,natural selection is probably the most important.Natural selection changes the genetic makeup of a population by favoring the alleles that contribute to reproductive success and selecting against those that do not.
- Natural selection,however,does not eliminate alleles directly.Instead,individuals with the"best"phenotypes are most likely to pass their alleles to the next generation;those with poorly suited phenotypes are less likely to survive long enough to reproduce. Three modes of natural selection—**directional, disruptive, and stabilizing**—are distinguished by their effects on the phenotypes in a population.



12.5 Natural Selection Can Shape Populations in Many Ways

- **In directional selection**（定向选择）,one extreme phenotype is fittest,and the environment selects against the others.A change in tree trunk color from light to dark,for example,may select for dark-winged moths and against light-winged individuals.The fittest phenotype may initially be rare,but its frequency increases over multiple generations as the environment changes.
- **In disruptive selection** (破坏选择)(sometimes called diversifying selection),two or more extreme phenotypes are fitter than the intermediate phenotype.Consider,for example,a population of marine snails that live among brown rocks encrusted with white barnacles.The white snails near the barnacles are camouflaged,and the dark brown ones on the bare rocks likewise blend in.The snails that are neither white nor dark brown are most often seen and eaten by predatory shorebirds.
- In a third form of natural selection, called **stabilizing selection**（稳定选择）(or normalizing selection),extreme phenotypes are less fit than the optimal intermediate phenotype.Human birth weight illustrates this tendency to stabilize.Very small or very large newborns are less likely to survive than babies of intermediate weight. By eliminating all but the individuals with the optimal phenotype,stabilizing selection tends to reduce the variation in a population. It is therefore most common in stable, unchanging environments.

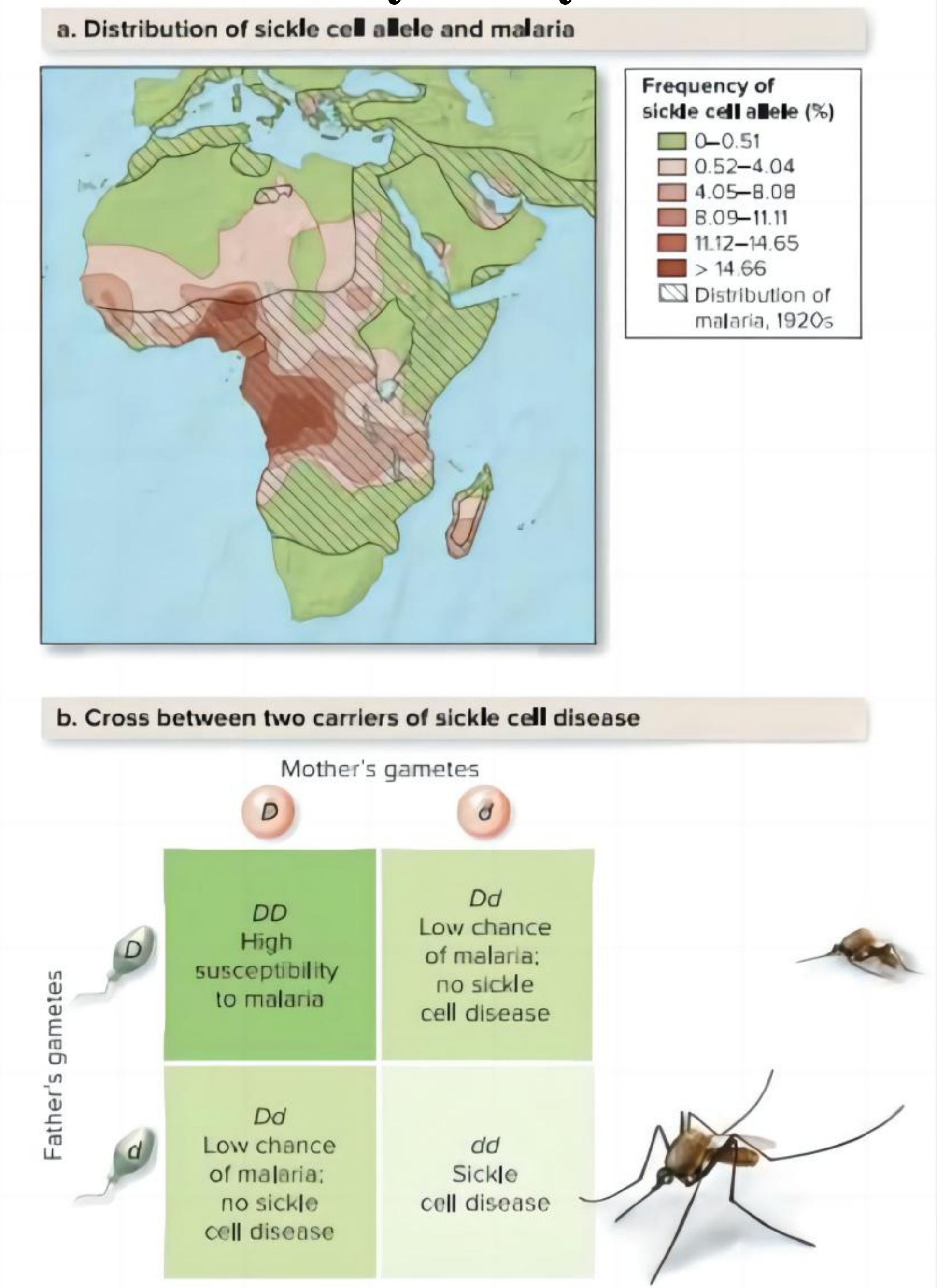
12.5 Natural Selection Can Shape Populations in Many Ways

- The best documented example of heterozygote advantage in humans is sickle cell disease.The disease-causing allele encodes an abnormal form of hemoglobin.The abnormal hemoglobin proteins do not fold properly;instead,they form chains that bend a red blood cell into a characteristic sickle shape .In a person who is homozygous recessive for the sickle cell allele,all the red blood cells are affected.Symptoms include anemia(贫血),joint pain,a swollen spleen (脾脏肿大),and frequent,severe infections;the person may not live long enough to reproduce.On the other hand,a person who is heterozygous for the sickle cell allele is only mildly affected.Some of his or her red blood cells may take abnormal shapes,but the resulting mild anemia is not usually harmful. Still,if the sickle cell allele causes such severe problems in homozygous recessive individuals,why hasn't natural selection eliminated it from the population?The answer is that heterozygotes also have a reproductive edge over people who are homozygous for the normal hemoglobin allele.
- Specifically,heterozygotesare resistant to a severe infectious disease, malaria(疟疾).When a mosquito carrying a protist called Plasmodium (疟原虫) feeds on a human with normal hemoglobin—a homozygous dominant person—the parasite enters the red blood cells.Eventually,infected blood cells burst,and the parasite travels throughout the body.The resulting bouts of fever,chills,fatigue,and nausea are severe;if damaged blood cells block blood vessels,the patient may die of organ failure.But the sick led red blood cells of an infected carrier—a heterozygote —halt the parasite's spread.

12.5 Natural Selection Can Shape Populations in Many Ways

- Not surprisingly,the sickle cell allele's frequency is highest in parts of the world where malaria is most common. In these areas,the heterozygotes remain healthiest;they are resistant to malaria,but they are not seriously ill from sickle cell disease.They therefore have more children (on average)than do people who are homozygous for either allele.

- Unfortunately, two carriers have a 25%chance of producing a child who is homozygous recessive.These children pay the evolutionary price for the genetic protection against malaria.



12.6 Sexual Selection Directly Influences Reproductive Success

- In many vertebrate species,the sexes look alike.The difference between a male and a female house cat,for example,is not immediately obvious.In some species, however, natural selection can maintain a sexual dimorphism (二相性),which is a difference in appearance between males and females. One sex may be much larger or more colorful than the other,or one sex may have distinctive structures such as horns or antlers.

- Some of these sexually dimorphic features may seem to violate natural selection. For example, female cardinals are brown and inconspicuous,but their male counterparts have vivid red feathers that make the birds much more visible to predators. Similarly,the extravagant tail of a peacock is brightly colored and makes flying difficult.How can natural selection allow for traits that apparently reduce survival?

- The answer is that a special form of natural selection is at work. Sexual selection is a type of natural selection resulting from variation in the ability to obtain mates,and it occurs in two forms.In intrasexual selection（一种性别成员之间的选择）,the members of one sex compete among themselves for access to the opposite sex .

- In intersexual selection（双性选择）,the members of one sex choose their mates from among multiple individuals of the opposite sex. If female birds of paradise prefer brightly colored males,then showy plumage directly increases a male's chance of reproducing. Because the brightest males get the most opportunities to mate, alleles that confer those feathers are common in the population.

b.

Figure 12.15 **Intrasexual Selection.** (a) Two bighorn rams butt heads in Montana. (b) Male ox beetles fight during the mating season.

a. b.

Figure 12.16 **Intersexual Selection.** (a) Male weaver birds build nests; females select their mates based on nest quality. (b) The male bird of paradise displays bright plumes that attract females.

12.6 Sexual Selection Directly Influences Reproductive Success

- Why do males usually show the greatest effects of sexual selection?In most (but not all)vertebrate species,females spend more time and energy on rearing offspring than do males.Because of this high investment in reproduction,females tend to be selective about their mates. Males are typically less choosy and must compete for access to females.
- The evolutionary origin of the males'e laborate ornaments(装饰物) remains an open question.One possibility is that long tail feathers and bright colors are costly to produce and maintain ;they are therefore indirect advertisements of good health or disease resistance. Likewise,the ability to win fights with competing males could also bean indicator of good genes.A female who chooses a high quality male will increase not only his fitness but also her own.

12.7 Evolution Occurs in Several Additional Ways

- Natural selection is responsible for adaptations that enhance survival and reproduction, but it is not the only mechanism of evolution.This section describes four more ways that a population can evolve: mutation,genetic drift,nonrandom mating,and gene flow. All occur frequently,and each can,by itself,disrupt Hardy-Weinberg equilibrium.The changes in allele frequencies that constitute evolution therefore occur nearly all the time.

A.Mutation Fuels Evolution

- A change in an organism's DNA sequence introduces a new allele to a population.The new trait may be harmful,neutral,or beneficial,depending on how the mutation affects the sequence of the encoded protein. Mutations are the raw material for evolution because genes contribute to phenotypes, and natural selection acts on phenotypes. For example,random mutations in bacterial DNA may change the shapes of key proteins in the cell's ribosomes or cell wall.Some of these mutations may mean a new phenotype—resistance to an antibiotic,for example.If exposure to antibiotics selects for that phenotype,the mutations will pass to the next generation.

12.7 Evolution Occurs in Several Additional Ways

B.Genetic Drift Occurs by Chance

- **Genetic drift** (sometimes called **sampling drift** , 采样漂变) is a change in allele frequencies that occurs purely by chance. Unlike mutation,which increases diversity, genetic drift tends to eliminate alleles from a population.
- All forms of genetic drift are rooted in sampling error,which occurs when a sample does not match the larger group from which it is drawn. Such sampling errors are most likely to affect small populations. If,by chance,none of the individuals carrying the rare allele happens to reproduce,that variant will disappear from the population. Even if some do reproduce,the allele still might not pass to the next generation. After all,the events of meiosis ensure that each allele has only a 50% chance of passing to each offspring. A rare allele can therefore vanish from a population—not because it reduces fitness but simply by chance.**Genetic drift is inevitable; that is,allele frequencies for any gene will fluctuate at random in every generation.**

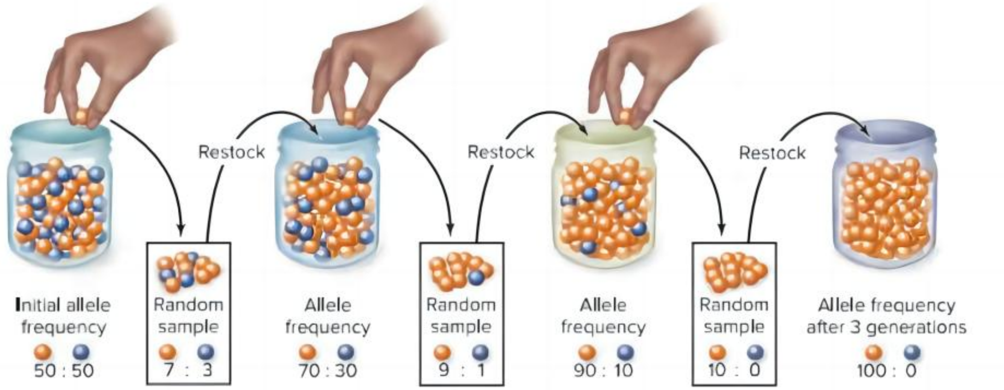
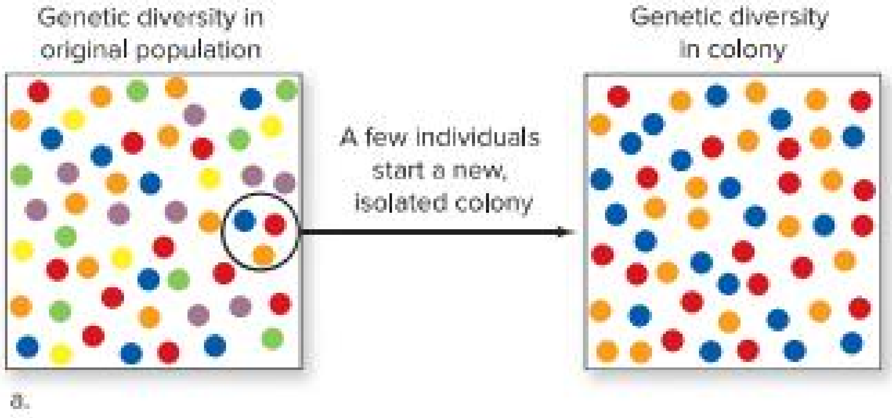


Figure 12.17 Sampling Error. Ten marbles are drawn at random from the first jar. Even though 50% of the marbles in the jar are blue, the random sample contains only 30% blue marbles. In the next "generation," 30% of the marbles are blue, but the random sample contains just one blue marble. The third sample contains no blue marbles and therefore eliminates the blue "allele" from the population, purely by chance.

12.7 Evolution Occurs in Several Additional Ways

- Hardy-Weinberg equilibrium requires populations to be very large (approaching infinity)to minimize the effects of these random changes in allele frequencies.In reality,of course,many populations are small,so genetic drift can be an important evolutionary force. Random chance can eliminate rare alleles,but genetic drift can also operate in other ways.As described below,sampling errors can occur when a small population separates from a larger one or when a large population is reduced to a very small size.
- **The Founder Effect (奠基者效应) :** One cause of genetic drift is the founder effect,which occurs when a small group of individual sleaves its home population and establishes a new,isolated settlement.The small group's random “allele sample"may not represent the allele frequencies of the original population.Some traits that were rare in the original population may therefore be more frequent in the new population.Likewise,other traits will be less common or may even disappear.

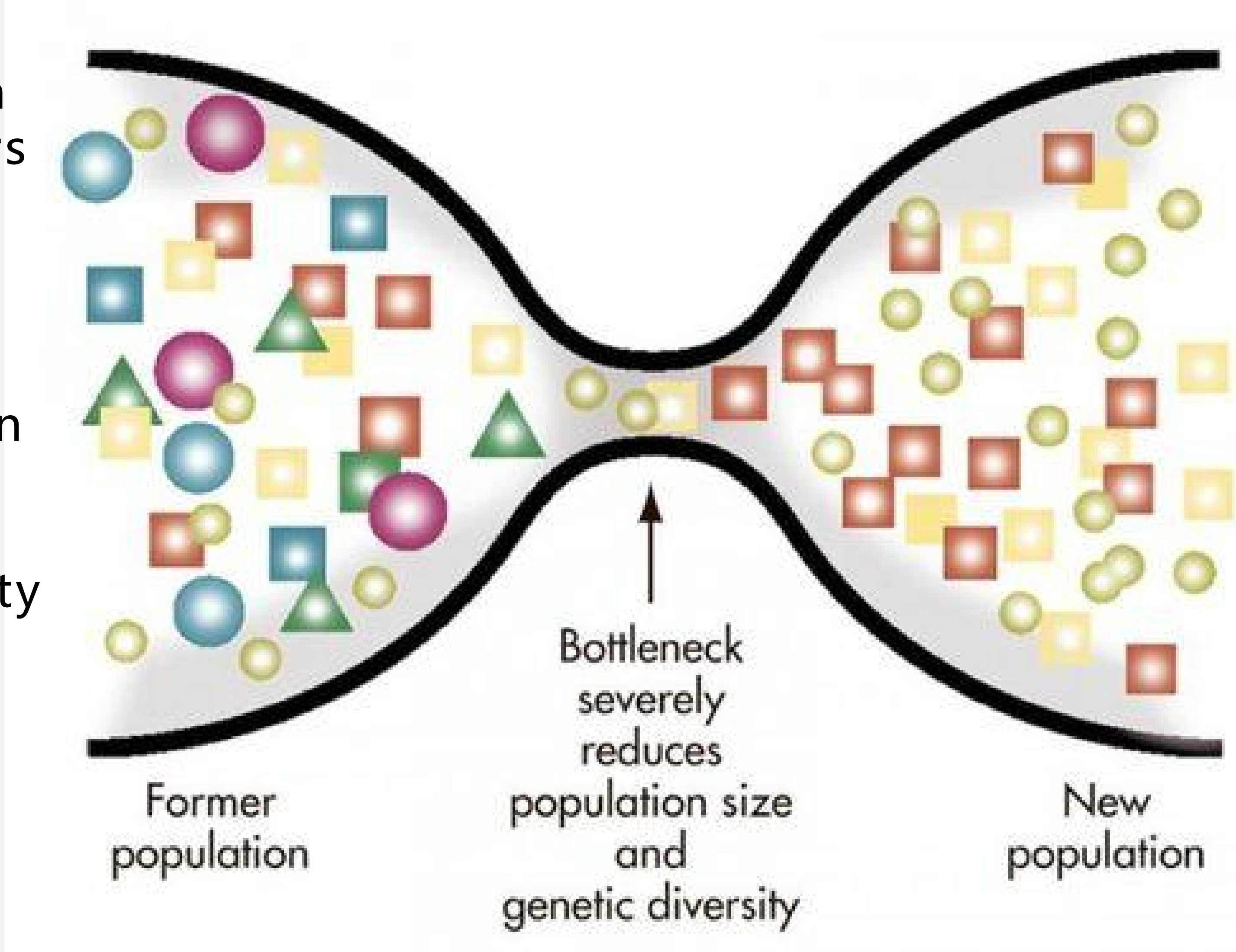
12.7 Evolution Occurs in Several Additional Ways



- The Amish people of Pennsylvania provide a famous example of the founder effect.About 200 followers of the Amish denomination immigrated to North America from Switzerland in the 1700s. One couple,who immigrated in 1744,happened to carry the recessive allele associated with Ellis-van Creveld syndrome.This allele is extremely rare in the population at large.Intermarriage among the Amish,however,has kept the disease's incidence high in this subgroup more than two centuries after the immigrants arrived.

12.7 Evolution Occurs in Several Additional Ways

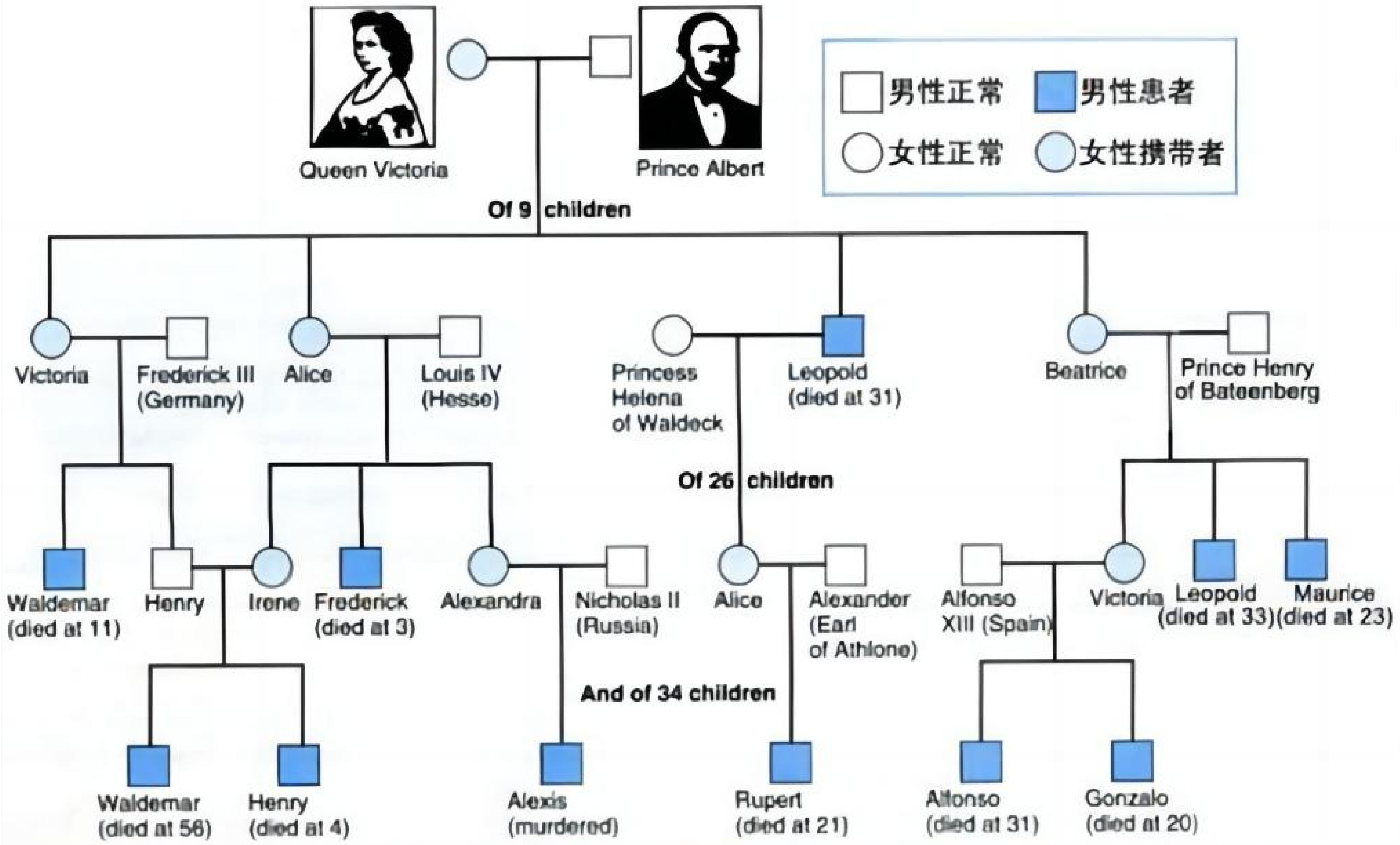
- **The Bottleneck Effect(瓶颈效应)**: Genetic drift also may result from a population bottleneck, which occurs when a population's size drops rapidly over a short period.The bottleneck randomly eliminates many alleles that were present in the larger ancestral population.Even if the few remaining individuals mate and restore the population's numbers,the loss of genetic diversity is permanent.Note that the loss of alleles is random;the bottleneck effect is therefore different from natural selection,which weeds out alleles that reduce fitness.



12.7 Evolution Occurs in Several Additional Ways

C.Nonrandom Mating Concentrates Alleles Locally

- In a population with completely random mating,every individual has an equal chance of mating with any other member of the population.Wind-pollinated plants illustrate random mating.In most species,however,mating is not random. As we have already seen, many animals exhibit some preference in mate choice,including sexual selection.Many other factors also influence mating, including geographical restrictions and physical access to the opposite sex.
- The practice of artificial selection is another way to reduce random mating. Humans select those animals or plants that have a desired trait;they then allow only those "superior"individuals to mate.The result is a wide variety of sub-populations (such as different breeds of dogs)that humans maintain by selective breeding.



欧洲皇室家族伴性遗传病——血友病遗传的简单谱系图

维多利亚女王是血友病基因的携带者，她的儿子有50%的几率得病，她的女儿有50%的几率成为携带者。这个谱系图只表现了携带有血友病基因的人。

12.7 Evolution Occurs in Several Additional Ways

D. Gene Flow Moves Alleles Between Populations

Migration (迁移) is one common way that gene flow occurs .The migrating brown rabbit in the figure will add new alleles to the population of black rabbits,increasing the local genetic diversity in its new home.But gene flow does not require the movement of entire individuals. Wind can carry a plant's pollen for miles,spreading one individual's alleles to a new population.

Over time,sustained migration has reduced the genetic differences between human populations.For example, isolated European populations once had unique allele frequencies for many genetic diseases. Geographical barriers,such as mountain ranges and large bodies of water,historically restricted migration and kept the gene pools separate. Highways,trains,and airplanes ,however,have eliminated physical barriers to migration. **Eventually,gene flow should make these regional differences disappear.**

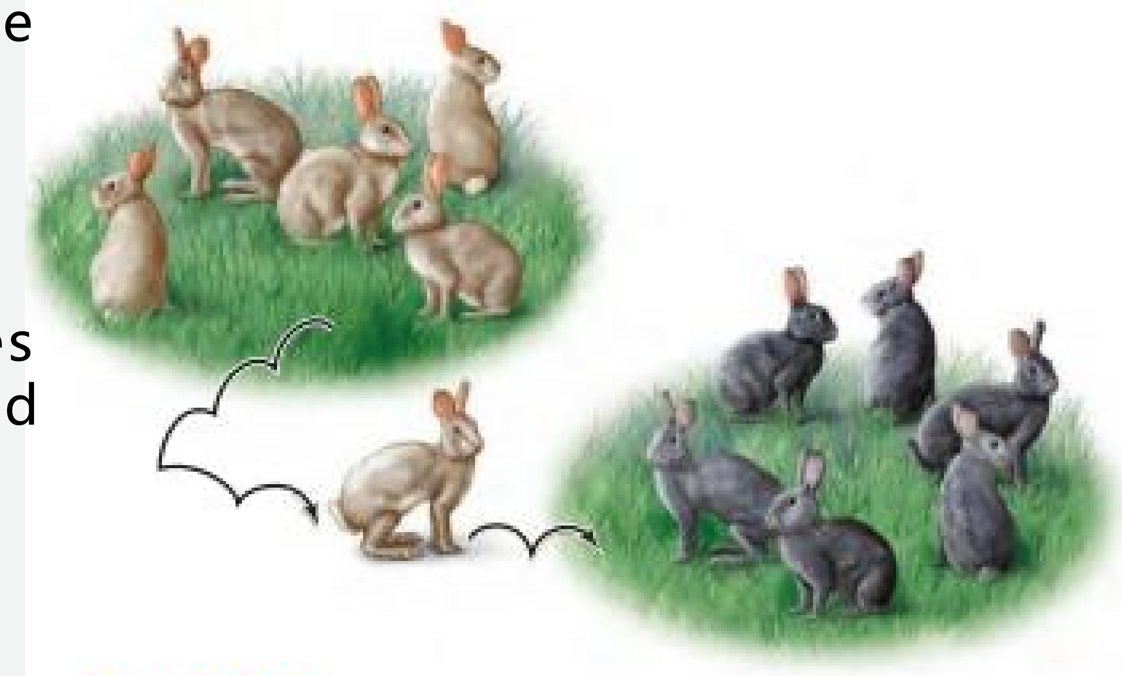


Figure 12.21 Gene Flow. A migrating animal can transfer its alleles to another population.

Thanks !