

Chapter 24

The Origin of Species

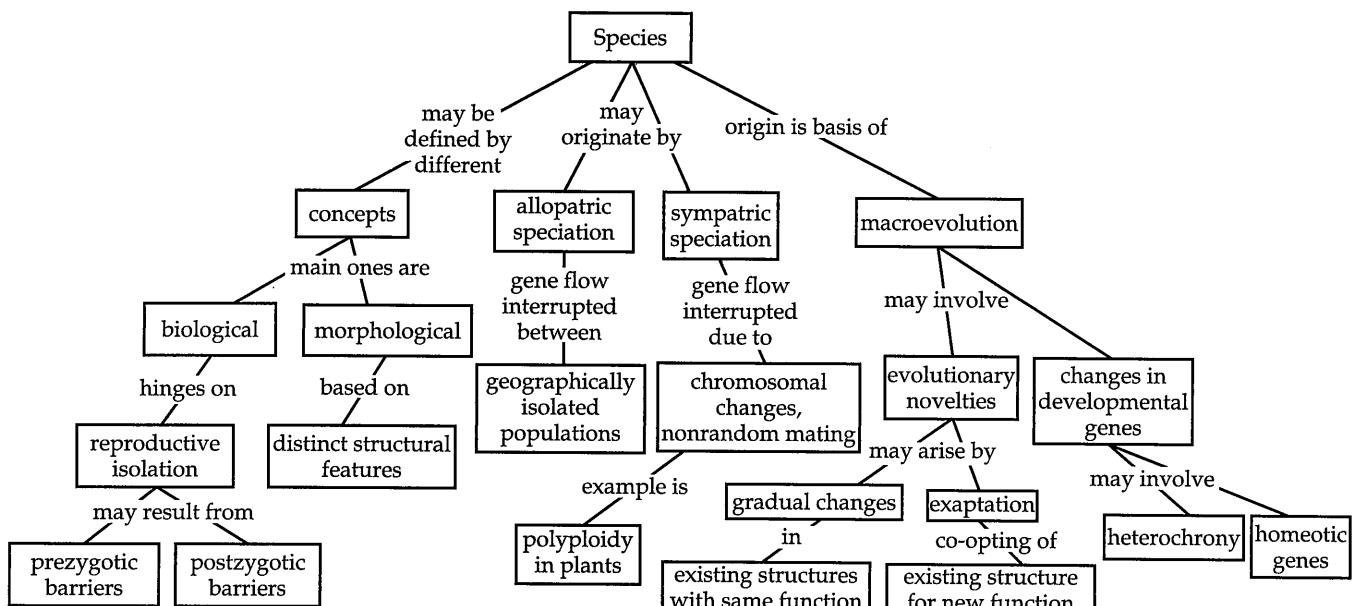
Key Concepts

24.1 The biological species concept emphasizes reproductive isolation

24.2 Speciation can take place with or without geographic separation

24.3 Macroevolutionary changes can accumulate through many speciation events

Framework



Chapter Review

Microevolution explains evolutionary changes within the gene pool of a population. **Macroevolution** considers the origin of new taxonomic groups (from species to higher taxons). The key process of macroevolution is **speciation**, the origin of a new species. Anagenesis, or phyletic evolution, involves the transformation of one species into a new species. In cladogenesis, or branching evolution, new species arise when a gene pool is split into separate pools and the parent species continues to exist. Cladogenesis is the process that increases biological diversity.

24.1 The biological species concept emphasizes reproductive isolation

Species are most often characterized by their physical form or morphology, although differences in physiology, biochemistry, behavior, and genetics also support the existence of distinct species.

The Biological Species Concept According to the **biological species concept**, developed by Ernst Mayr in 1942, a species is a population or group of populations of individuals that have the potential to interbreed in nature and produce viable, fertile offspring,

but which do not successfully interbreed with other species. The **reproductive isolation** that preserves the genetic integrity of a biological species results from barriers that prevent individuals of different species from producing viable, fertile hybrids.

Prezygotic barriers function before the formation of a zygote by preventing mating between species or successful fertilization should gametes meet. Prezygotic barriers include habitat isolation, in which two species that live in the same area occupy different habitats; temporal isolation, in which two species breed at different times; behavioral isolation, in which courtship rituals and behavioral signals are species specific; mechanical isolation, in which anatomical incompatibilities prevent mating with members of other species; and gametic isolation, in which the gametes of different species fail to fuse, due to mechanisms such as the inability of sperm to penetrate the membrane around the egg.

Should a hybrid zygote form, **postzygotic barriers** prevent it from developing into a viable, fertile adult. Postzygotic barriers include reduced hybrid viability, in which a hybrid zygote fails to survive embryonic development; reduced hybrid fertility, in which a viable hybrid individual is sterile, often due to the inability to produce normal gametes in meiosis; or hybrid breakdown, in which the hybrids are viable and fertile, but their offspring are feeble or sterile.

■ INTERACTIVE QUESTION 24.1

Name the type of reproductive barrier and whether it is pre- or postzygotic for the following examples.

Type of Barrier	Pre- or Post-	Example
a.	b.	Two species of frogs are mated in the lab and produce viable, but sterile, offspring.
c.	d.	Two species of sea urchins release gametes at the same time, but no cross fertilization occurs.
e.	f.	Two orchid species with different length nectar tubes are pollinated by different moths.
g.	h.	Two species of mayflies emerge during different weeks in spring.
i.	j.	Two species of salamanders mate and produce offspring, but the hybrid's offspring are sterile.
k.	l.	Two similar species of birds have different mating rituals.

m.	n.	Embryos of two species of mice bred in the lab usually abort.
o.	p.	Peepers breed in woodland ponds; leopard frogs breed in swamps.

The biological species concept does not work for species that are asexual, such as bacteria. Extinct species also cannot be grouped based on the criterion of interbreeding. Even for many living species, it is difficult to obtain data on whether interbreeding occurs. Alternative species concepts may be useful in various contexts.

Other Definitions of Species Most species have been identified on the basis of physical characteristics, an approach called the **morphological species concept**. The **paleontological species concept** applies to species that are known only from the fossil record. The **ecological species concept** defines species on the basis of their ecological niche, the role they play and resources they use in the specific environments in which they are found. The emphasis of the **phylogenetic species concept** is on evolutionary lineages through which each species has a unique genetic history, producing distinct physical characteristics or molecular sequences. Sibling species, which are morphologically indistinguishable, may be identified in this approach, and the existence of reproductive isolation can confirm their distinction.

■ INTERACTIVE QUESTION 24.2

Fill in the following table to review the five approaches that biologists have proposed for conceptualizing a species.

Concept	Emphasis
biological	a.
b.	anatomical differences, most commonly used
c.	unique roles in specific environments
d.	morphologically discrete fossil species
phylogenetic	e.

24.2 Speciation can take place with or without geographic separation

Allopatric ("Other Country") Speciation Allopatric speciation occurs when geographic isolation interrupts gene flow between two subpopulations. The extent of the geographic barrier necessary to maintain genetic separation depends on the ability of the organisms to disperse. Either geologic change or colonization of a new area may geographically isolate populations.

Geographic separation alone is not a reproductive barrier in the biological sense. Intrinsic reproductive barriers may arise coincidentally as allopatric populations go down separate evolutionary paths due to genetic drift and selection. Biologists may assess allopatric speciation by bringing together members of separated populations in a laboratory setting or observing situations in which individuals of the two populations interact in the wild.

Sympatric ("Same Country") Speciation In sympatric speciation, reproductive barriers prevent gene flow between overlapping populations.

Mistakes during cell division may lead to **polyploidy** in plants. An **autopolyploid** has more than two sets of chromosomes that have all come from the same species. Failures in cell division can produce tetraploids ($4n$), which can fertilize themselves or other tetraploids but cannot successfully breed with diploids from the parent population, resulting in reproductive isolation in just one generation.

Polyploid species arise more commonly through **allopolyploidy**. Interspecific hybrids may propagate asexually, but are usually sterile due to difficulties in the meiotic production of gametes. Future mitotic or meiotic mistakes can result in the production of a fertile polyploid, which cannot interbreed with either parent species.

Speciation of polyploids has been frequent and important in plant evolution. Many of our agricultural plants are polyploids, and plant geneticists now hybridize plants by inducing meiotic and mitotic errors to create new species.

■ INTERACTIVE QUESTION 24.3

- A new plant species B forms by autopolyploidy from species A, which had a chromosome number of $2n = 10$. How many chromosomes would species B have?
- If species A were to hybridize by allopolyploidy with species C ($2n = 14$) and produce a new, fertile species, D, how many chromosomes would species D have?

Sympatric speciation in animals may involve isolation within the geographic range of the parent population based on different resource usage. Nonrandom mating in a polymorphic population could also lead to sympatric speciation. In a laboratory study of two sympatric species of cichlids, mate choice based on coloration was shown to be the reproductive barrier that normally separates the two species.

■ INTERACTIVE QUESTION 24.4

- Differentiate between allopatric and sympatric speciation.
- How might reproductive barriers arise in each type of speciation?

Adaptive Radiation Adaptive radiation is the evolution of numerous, variously adapted species from a common ancestor introduced into an environment with many new ecological niches. Colonization of newly formed islands or the opening of numerous niches following mass extinctions may provide the opportunity for multiple speciation events.

■ INTERACTIVE QUESTION 24.5

What factors have contributed to the adaptive radiation of the thousands of endemic species of the Hawaiian Archipelago?

Studying the Genetics of Speciation Researchers have been able to identify genes that play a key role in speciation in some organisms. Two species of *Mimulus*, one pollinated by bees, the other by hummingbirds, have been mated in the greenhouse. The progeny of the hybrids, which have flowers that vary in color and shape, have been tested for pollinator choice. Two gene loci, which influence flower color and nectar production, have been identified as playing a key role in speciation by pollinator preference.

The Tempo of Speciation In the fossil record, new forms often appear rather suddenly, persist unchanged

for a long time, and then disappear. According to the model of evolution known as **punctuated equilibrium**, long periods of stasis are punctuated by episodes of relatively rapid speciation and change. In geologic time, the thousands of years during which a species evolves is small compared with the millions of years a successful species may exist, and this short period of divergence may not be captured in the fossil record. Proponents of the gradualism model suggest that the apparently long periods of stasis may be only in external anatomy, while changes in internal anatomy, physiology, and behavior have gone unrecorded.

■ INTERACTIVE QUESTION 24.6

Compare the gradual and punctuated equilibrium models of evolution.

24.3 Macroevolutionary changes can accumulate through many speciation events

Evolutionary Novelties Often very complex organs, such as the eyes of vertebrates and molluscs, have evolved gradually from simpler structures that served and continue to serve similar needs in ancestral species.

Evolutionary novelties may also evolve by the gradual modification of existing structures for new functions. *Exaptation* is the term for structures that evolved and functioned in one setting and were then co-opted for a new function.

■ INTERACTIVE QUESTION 24.7

Give examples of reptilian structures that were exaptations for flight in birds.

Evolution of the Genes That Control Development The combination of the fields of evolutionary and developmental biology, called “evo-devo,” explores how slight changes in developmental genes can result in major morphological differences between species.

Heterochrony is an evolutionary change in the rate or timing of development. **Allometric growth**, the dif-

fering rates of growth of various parts of the body, leads to the final shape of the organism. A minor genetic alteration that affects allometric growth can produce a very differently proportioned adult form.

Paedomorphosis is the retention in the adult of juvenile traits of ancestral organisms and can occur when genetic changes speed up the development of reproductive organs relative to the development of body form.

■ INTERACTIVE QUESTION 24.8

- Fetal skulls of humans and chimpanzees have similar shapes. The quite distinctive differences in adult skull shape results from different patterns of _____.
- A salamander species that retains its gills (a larval trait) when it is full grown and sexually mature is an example of _____.
- The shorter feet of tree-dwelling salamanders may have resulted from an evolutionary change in a regulatory gene that switches off growth of the foot sooner than in ground-dwelling salamanders. These three cases (a., b., and c.) are all examples of _____.

Changes in genes that control the spatial arrangement of body parts have also been important in macroevolution. **Homeotic genes** determine where basic body features develop. Mutations in homeotic genes called *Hox* genes, whose products provide positional information in embryos, can drastically alter body form. Duplications of the *Hox* complex of invertebrates may have been central to the evolution of vertebrates.

Evolution Is Not Goal-Oriented *Equus*, the modern horse, descended from its much smaller, browsing, multitoe ancestor, *Hyracotherium*, through a series of speciation episodes that produced many different species and diverging trends, as documented in the fossil record.

According to S. Stanley’s model of **species selection**, an evolutionary trend is analogous to a trend in a population produced by natural selection. The successful species that last the longest before extinction and generate the most new species will determine the direction of the trend. Evolutionary trends are ultimately dictated by environmental conditions; if conditions change, an evolutionary trend may end or change.

Word Roots

allo- = other; **-metron** = measure (*allometric growth*: the variation in the relative rates of growth of various parts of the body, which helps shape the organism)

ana- = up; **-genesis** = origin, birth (*anagenesis*: a pattern of evolutionary change involving the transformation of an entire population, sometimes to a state different enough from the ancestral population to justify renaming it as a separate species)

auto- = self; **poly-** = many (*autopolyploid*: a type of polyploid species resulting from one species doubling its chromosome number to become tetraploid)

clado- = branch (*cladogenesis*: a pattern of evolutionary change that produces biological diversity by budding one or more new species from a parent species that continues to exist)

hetero- = different (*heterochrony*: evolutionary changes in the timing or rate of development)

macro- = large (*macroevolution*: evolutionary change beginning with speciation, encompassing the origin of novel designs, evolutionary trends, adaptive radiation, and mass extinction)

paedo- = child (*paedomorphosis*: the retention in the adult organism of the juvenile features of its evolutionary ancestors)

post- = after (*postzygotic barrier*: any of several species-isolating mechanisms that prevent hybrids produced by two different species from developing into viable, fertile adults)

sym- = together; **-patri** = father (*sympatric speciation*: a mode of speciation occurring as a result of a radical change in the genome that produces a reproductively isolated subpopulation in the midst of its parent population)

Structure Your Knowledge

1. How are speciation and microevolution different?
2. Describe two major mechanisms through which evolutionary novelties may originate.

Test Your Knowledge

MULTIPLE CHOICE: Choose the one best answer.

1. The type of evolution that results in the greatest increase in biological diversity is
 - a. anagenesis.
 - b. cladogenesis.
 - c. phyletic evolution.

2. Which of the following is *not* a type of intrinsic reproductive isolation?
 - a. mechanical isolation
 - b. behavioral isolation
 - c. geographic isolation
 - d. gametic isolation
 - e. temporal isolation
3. Two species of frogs occasionally mate, but the offspring do not complete development. What type of barrier isolates these gene pools?
 - a. gametic isolation
 - b. prezygotic barrier
 - c. hybrid breakdown
 - d. reduced hybrid viability
 - e. reduced hybrid fertility
4. For which of the following is the biological species concept least appropriate?
 - a. plants
 - b. animals
 - c. bacteria
 - d. fossils
 - e. both c and d
5. A horse ($2n = 64$) and a donkey ($2n = 62$) can mate and produce a mule. How many chromosomes would there be in a mule's cells?

a. 31	c. 63	e. 126
b. 62	d. 64	
6. What prevents horses and donkeys from hybridizing to form a new species?
 - a. reduced hybrid fertility
 - b. reduced hybrid viability
 - c. mechanical isolation
 - d. gametic isolation
 - e. behavioral isolation
7. Which of the following species concepts identifies species based on their similarities resulting from their unique niche or role in the environment?
 - a. biological
 - b. ecological
 - c. paleontological
 - d. morphological
 - e. phylogenetic

8. Allopatric speciation is more likely to occur when an isolated population

- is large and thus has more genetic variation.
- is reintroduced to its original homeland.
- is small and exposed to different selection pressures in its new habitat.
- inhabits an island close to its parent species' mainland.
- All of the above contribute to allopatric speciation.

9. A tetraploid plant species (with four identical sets of chromosomes) is probably the result of

- allopolyploidy.
- autopolyploidy.
- hybridization and nondisjunction.
- allopatric speciation.
- a and c.

10. All of the following would help to identify sister species *except*

- genetic analysis.
- test for reproductive incompatibility.
- phylogenetic analysis.
- morphological comparisons.
- All of the above are essential to distinguishing sister species.

11. There are 28 morphologically diverse species of a group of sunflowers called silverswords found on the Hawaiian Archipelago. These species are an example of

- a geographical cline.
- adaptive radiation.
- allopolyploidy.
- the bottleneck effect.
- sympatric speciation.

12. Which of the following is descriptive of the punctuated equilibrium model?

- Long periods of stasis are punctuated by episodes of relatively rapid speciation and change.
- Microevolution is the driving force of speciation.
- Most rapid speciation events involve polyploidy in plants.
- Evolution occurs gradually as the environment gradually changes.
- In the framework of geologic time periods, speciation events occur very slowly and the equilibrium of species is punctuated by frequent extinctions.

13. A new plant species C formed from hybridization of species A ($2n = 18$) with species B ($2n = 12$) would probably produce gametes with a chromosome number of

- 12.
- 18.
- 60.
- 15.
- 30.

14. Which of the following would *not* contribute to allopatric speciation?

- geographic separation
- genetic drift
- gene flow
- different selection pressures
- founder effect

15. What is meant by the concept of species selection?

- Reproductive isolating mechanisms (both prezygotic and postzygotic) are responsible for maintaining the integrity of individual species.
- Characteristics that increase the probability of selection as a mate or success in competition for mates will be selected for and increase in frequency in a population.
- The species that last the longest and speciate the most often determine the direction of evolutionary trends.
- A new species accumulates most of its unique features as it originates and then maintains long periods of stasis in body form.
- The colonization of new and diverse habitats can lead to the adaptive radiation of numerous species.

16. Allometric growth

- results in paedomorphosis.
- results in an evolutionary trend of increasing body size.
- results from differences in the locations of expression of *Hox* genes and thus the placement of body parts.
- is usually associated with polyploidy in plants.
- is the relative differences in growth rates of different body parts.

17. The evolution of lungs from the swim bladder of ancestral fish is an example of

- heterochrony.
- paedomorphosis.
- exaptation.
- changes in homeotic gene expression.
- punctuated equilibrium.

18. Which of the following is thought to be a critical event in the evolution of vertebrates from an invertebrate ancestor?

- exaptation of body segments to vertebrae
- duplication of the *Hox* complex (homeotic genes)
- allometric growth of tail segments
- allopatric speciation
- sympatric speciation

19. A botanist identifies a new species of plant that has 32 chromosomes. It grows in the same habitat with three similar species: species A ($2n = 14$), species B ($2n = 16$), and species C ($2n = 18$). Suggest a possible speciation mechanism for the new species.

- allopatric divergence by development of a reproductive isolating mechanism
- change in a key developmental gene that causes the plants to flower at different times

c. autopolyploidy, perhaps due to a nondisjunction in the formation of gametes of species B

d. allopolyploidy, a hybrid formed from species A and C

e. Either answer c or d could account for the formation of this new plant species.

20. Which concept of species would be most useful to a field biologist identifying new species in a tropical rain forest?

- biological
- ecological
- paleontological
- morphological
- phylogenetic