Chapter 24

The Origin of Species

Lecture Outline

Overview: That "Mystery of Mysteries"

- Charles Darwin visited the Galápagos Islands and found plants and animals that lived nowhere else in the world.
- Darwin realized that he was observing newly emerged species on these young islands.
- **Speciation**—the process by which one species splits into two or more species—is at the focal point of evolutionary theory because the appearance of new species is the source of biological diversity.
- Speciation forms a conceptual bridge between **microevolution**, changes in allele frequencies within a population, and **macroevolution**, the broad pattern of evolution over time.
    - Microevolution is the study of adaptive change in a population. Microevolutionary mechanisms include mutation, natural selection, genetic drift, and gene flow.
    - Macroevolution addresses evolutionary changes above the species levels. It deals with questions such as the appearance of evolutionary novelties (e.g., feathers and flight in birds) that can be used to define higher taxa.

Concept 24.1 The biological species concept emphasizes reproductive isolation.

- *Species* is a Latin word meaning "kind" or "appearance."
- Traditionally, morphological differences have been used to distinguish species.
- Today, differences in physiology, biochemistry, behavior, and DNA sequences are also used to differentiate species.
- In 1942, Ernst Mayr proposed the **biological species concept.**
- A species is defined as a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring but who cannot produce viable, fertile offspring with other such populations.
- A biological species is the largest set of populations in which genetic exchange is possible and that is genetically isolated from other populations.
    - Species are based on interfertility, not physical similarity.
    - Humans have considerable diversity, but we all belong to the same species because of our capacity to interbreed.
- Members of a population often resemble each other because their populations are connected by *gene flow*.
    - As a result, they share a common gene pool.

- Low levels of gene flow between widely separated populations have the potential to hold the gene pool of a species together, as long as it is not outweighed by the effects of selection or drift.

The formation of a new species hinges on the development of reproductive isolation.

- Because the distinction between biological species depends on reproductive incompatibility, the formation of a new species hinges on the development of **reproductive isolation,** the existence of biological barriers that prevent members of two species from producing viable, fertile hybrids.
    - Such barriers block gene flow, limiting the formation of interspecies **hybrids.**
- A single barrier may not block all genetic exchange between species, but a combination of several barriers can effectively isolate a species' gene pool.
    - Typically, these barriers are intrinsic to the organisms, not due to simple geographic separation.
    - Reproductive isolation prevents populations belonging to different species from interbreeding, even when their ranges overlap.
- Reproductive barriers can be categorized as prezygotic or postzygotic, depending on whether they function before or after the formation of zygotes.
- **Prezygotic barriers** block fertilization between species in one of three ways: by impeding members of different species from attempting to mate, by preventing an attempted mating from being completed successfully, or by hindering fertilization if mating is completed successfully.
- Prezygotic barriers include habitat isolation, behavioral isolation, temporal isolation, mechanical isolation, and gametic isolation.
- In **habitat isolation,** two organisms that use different habitats (even in the same geographic area) are unlikely to encounter each other to even attempt mating.
    - Two species of garter snakes in the genus *Thamnophis* occur in the same areas. Because one lives mainly in water and the other is primarily terrestrial, they rarely encounter each other.
- In **behavioral isolation,** species use unique and elaborate courtship behaviors to attract mates.
    - In many species, elaborate courtship displays identify potential mates of the correct species and synchronize gonadal maturation.
    - In the blue-footed booby, males perform a high-step dance that calls the female's attention to the male's bright blue feet.
- In **temporal isolation,** two species that breed during different times of day, different seasons, or different years cannot mix gametes.
    - The geographic ranges of the western spotted skunk and the eastern spotted skunk overlap. However, they do not interbreed because the former mates in late summer and the latter mates in late winter.
- In **mechanical isolation,** closely related species may attempt to mate but fail because they are anatomically incompatible and transfer of sperm is not possible.
    - For example, snails whose shells coil in opposite spirals cannot mate with each other.
- In **gametic isolation,** the gametes of two species do not form a zygote because of incompatibilities preventing fertilization.
    - In species with internal fertilization, the environment of the female reproductive tract may not be conducive to the survival of sperm from other species.

- For species with external fertilization, gamete recognition may rely on the presence of specific molecules on the egg's coat, which adhere only to specific molecules on sperm cells of the same species. Such a mechanism prevents fertilization between the sperm and egg of related species of sea urchin.
- A similar molecular recognition mechanism enables a flower to discriminate between pollen of the same species and pollen of a different species.

- If a sperm from one species does fertilize the ovum of another species, **postzygotic barriers** may prevent the hybrid zygote from developing into a viable, fertile adult.
- Postzygotic barriers include reduced hybrid viability, reduced hybrid fertility, and hybrid breakdown.
- In **reduced hybrid viability,** genetic incompatibility between the two species may abort the development of the hybrid at some embryonic stage or produce frail offspring.
  - Occasional hybrids form by salamanders that belong to the same genus. Most do not complete development, and those that do are frail.
- In **reduced hybrid fertility,** even if the hybrid offspring are vigorous, the hybrids may be infertile, and the hybrid cannot backbreed with either parental species.
  - This infertility may be due to problems in meiosis because of differences in chromosome number or structure.
  - For example, although a mule, the hybrid product of mating between a horse and a donkey, is a robust organism, it cannot mate (except very rarely) with either horses or donkeys.
- In **hybrid breakdown,** first-generation hybrids are viable and fertile. When first-generation hybrids mate with either parent species or with each other, however, the next generation is feeble or sterile.
  - Strains of cultivated rice have accumulated different mutant recessive alleles at two loci in the course of their divergence from a common ancestor.
  - Hybrids between them are vigorous and fertile, but plants in the next generation that carry too many of these recessive alleles are small and sterile.
  - These strains are in the process of speciating.
- Reproductive barriers can occur before mating, between mating and fertilization, or after fertilization.

The biological species concept has some major limitations.

- Although the biological species concept has had an important impact on evolutionary theory, it has limited application to species in nature.
  - For example, one cannot test the reproductive isolation of morphologically similar fossils, which must be separated into species based on morphology.
  - Even for living species, we often lack information on interbreeding needed to apply the biological species concept.
  - In addition, many species (for example, prokaryotes) reproduce asexually and are assigned to species based mainly on structural and biochemical characteristics.
  - Many bacteria transfer genes by conjugation and other processes, but this transfer is different from sexual recombination.
- The biological species concept is based only on gene flow.
- Natural selection can also maintain reproductive barriers between species.

Evolutionary biologists have proposed many alternative concepts of species.

- Although the biological species concept emphasizes the *separateness* of species due to reproductive barriers, many alternative species concepts emphasize the *unity* within a species.
- The **morphological species concept,** the oldest and still most practical, defines a species by body shape, size, and other structural features.
  - The morphological species concept has certain advantages. It can be applied to asexual and sexual species, and it can be useful even without information about the extent of gene flow.
  - However, this definition relies on subjective criteria, and researchers may disagree about which structural features identify a species.
  - In practice, scientists use the morphological species concept to distinguish most species.
- The **ecological species concept** defines a species in terms of its ecological niche, the set of environmental resources that a species uses, and its role in a biological community.
  - As an example, two species of amphibian may be similar in appearance but differ in their tolerance of desiccation. The ecological species concept emphasizes the role of disruptive natural selection as organisms adapt to different environmental conditions.
  - This concept accommodates asexual and sexual species.
- The **phylogenetic species concept** defines a species as the smallest group of individuals that shares a common ancestor and forms one branch on the tree of life.
  - Biologists compare the morphology or molecular sequences of species to those of other organisms to distinguish groups of individuals that are sufficiently different to be considered separate species.
  - The difficulty is determining the degree of difference required to indicate separate species.
- More than 20 other species concepts have also been proposed. Each species concept may be useful, depending on the situation and the types of research questions we are asking.

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

- Two general modes of speciation are distinguished by the way gene flow among populations is initially interrupted.
- In **allopatric speciation,** geographic separation of populations restricts gene flow.
- In **sympatric speciation,** speciation occurs in geographically overlapping populations when biological factors, such as chromosomal changes and nonrandom mating, reduce gene flow.

In allopatric speciation, geographic barriers can lead to the origin of species.

- Geologic processes can fragment a population into two or more isolated populations.
  - Mountain ranges, glaciers, land bridges, or splintering of lakes may divide one population into isolated groups.
- Alternatively, some individuals may colonize a new, geographically remote area and become isolated from the parent population.
  - For example, mainland organisms that colonized the Galápagos Islands were isolated from the mainland populations.
- How significant a barrier must be to limit gene exchange depends on the ability of organisms to move about.

- A geologic feature that is only a minor hindrance to one species may be an impassible barrier to another.
- The valley of the Grand Canyon is a significant barrier for the ground squirrels that have speciated on opposite sides.
- For birds that can fly across the canyon, the valley is no barrier.

- Once geographic separation is established, the separated gene pools may begin to diverge through a number of mechanisms.
  - Different mutations arise.
  - Different selective pressures in differing environments act on the two populations.
  - Genetic drift alters allele frequencies.
- A small, isolated population experiences very little gene flow. Such a population is particularly likely to have its gene pool changed substantially over a short period of time by genetic drift and natural selection.
  - For example, less than 2 million years ago, small populations of stray plants and animals from the South American mainland colonized the Galápagos Islands and gave rise to the species that now inhabit the islands.
- Many studies provide evidence of allopatric speciation.
  - For example, biogeographic and genetic data provide evidence of the divergence of two subfamilies (Mantellinae and Rhacophorinae) of frogs. The divergence began 88 million years ago, when the island of Madagascar separated from the Indian landmass.
  - There are now 100 species of Mantellinae (all on Madagascar) and 310 species of Rhacophorinae (whose diversity centers in India).
- Regions that are highly subdivided by geographic barriers tend to have more species than do regions with fewer barriers.
  - For example, a large number of bird species are found in the mountainous regions of New Guinea. Many unique plants and animals are found on the geographically isolated Hawaiian Islands.
- Field experiments provide evidence that reproductive isolation between two populations increases with distance between them.
  - Individuals from populations of dusky salamanders *(Desmognathus ochrophaeus)* were brought into the laboratory and cross-bred. The more widely separated the populations, the greater the reproductive isolation.
  - There may be little long-distance gene flow in this species. Alternatively, such gene flow may be outweighed by the effects of natural selection or genetic drift, causing the populations to diverge.

In sympatric speciation, a new species can originate in the geographic midst of the parent species.

- In **sympatric speciation**, new species arise within the range of the parent populations.
- Reproductive barriers must evolve between sympatric populations. Gene flow may be reduced by such factors as polyploidy, habitat differentiation, and sexual selection.
- In plants, sympatric speciation can result from accidents during cell division that result in extra sets of chromosomes, a mutant condition known as **polyploidy.**
- An **autopolyploid** mutant is an individual that has more than two chromosome sets, all derived from a single species.

- For example, a failure of mitosis or meiosis can double a cell's chromosome number from diploid ($2n$) to tetraploid ($4n$).
- The tetraploid can reproduce with itself (self-pollination) or with other tetraploids.
- The tetraploid cannot mate with diploids from the original population because of abnormal meiosis by the triploid hybrid offspring.
- In a single generation, autopolyploidy can generate reproductive isolation despite sympatry.

- A more common mechanism of producing polyploid individuals occurs when two different species mate to produce **allopolyploid** offspring.
  - Although the hybrids are usually sterile, they may be quite vigorous and propagate asexually.
  - In subsequent generations, various mechanisms may transform a sterile hybrid into a fertile polyploid.
  - These polyploid hybrids are fertile with each other but cannot breed with either parent species.
  - The polyploid hybrids thus represent a new biological species.
- Polyploid speciation occurs occasionally in animals, such as the gray tree frog *Hyla versicolor*.
- The origin of polyploid plant species is common. In fact, botanists estimate that more than 80% of plant species alive today descended from ancestors formed by polyploid speciation.
- Such speciation may be rapid enough that scientists have documented several such speciations in historical times.
  - For example, two new species of plants called goatsbeard *(Tragopodon)* appeared in the Pacific Northwest in the mid-1900s.
  - These species are the results of allopolyploidy events between pairs of introduced European *Tragopodon* species.
- Many plants important for agriculture are polyploid.
  - For example, wheat is an allohexaploid, with six sets of chromosomes from three different species.
  - Oats, cotton, potatoes, and tobacco are polyploid.
  - Plant geneticists now use chemicals that induce meiotic and mitotic errors to create new polyploid plants with special qualities.
    - One example is an artificial hybrid that combines the high yield of wheat with the hardiness and disease resistance of rye.
- **Habitat differentiation** may lead to sympatric speciation in animals.
- Polyploid speciation occurs in animals, but other mechanisms also contribute to sympatric speciation in animals.
- Reproductive isolation can result when genetic factors cause individuals to exploit resources not used by the parent.
  - One example is the North American maggot fly, *Rhagoletis pomonella*.
  - The fly's original habitat was native hawthorn trees.
  - About 200 years ago, some populations colonized newly introduced apple trees.

- Because apples mature more quickly than hawthorn fruit, the apple-feeding flies have been selected for more rapid development and now show temporal isolation from the hawthorn-feeding maggot flies.
- Researchers have also identified alleles that benefit only the flies that use each host plant. As a result, natural selection is acting to further limit gene flow.
- Although the two populations are still classified as subspecies, sympatric speciation is under way.

- Sympatric speciation can also be driven by **sexual selection.**
- Sympatric speciation is one mechanism that has been proposed for the explosive adaptive radiation of cichlid fishes in Lake Victoria in East Africa.
  - This vast, shallow lake has filled and dried up repeatedly due to climate changes.
  - The current lake has been home to as many as 600 species of cichlid fishes.
    - The species are genetically very similar. They likely originated within the last 100,000 years from a small number of colonist species that arrived from a lake located about 275 km away.
  - Although these species are clearly specialized for exploiting different food resources and other resources, nonrandom mating in which females select males based on a certain appearance has probably contributed, too.
  - For example, two closely related species of cichlids in the lake differ mainly in coloration. One species has a red-tinged back, while the other species has a blue-tinged back. Mate choice based on coloration appears to be the main reproductive barrier separating the gene pools of the two species.
- In summary, in allopatric speciation, a new species forms while geographically isolated from its parent population.
  - As the isolated population accumulates genetic differences due to natural selection, genetic drift, and sexual selection, reproductive isolation from the ancestral species may arise as a by-product of genetic change.
  - Such reproductive barriers can prevent breeding with the parent even if the populations reestablish contact.
- Sympatric speciation requires the emergence of some reproductive barrier that isolates a subset of the population without geographic separation from the parent population.
  - In plants, the most common mechanism of sympatric speciation is hybridization between species or errors in cell division that lead to polyploid individuals.
  - In animals, sympatric speciation may occur when a subset of the population is reproductively isolated by a switch to a new habitat or food source.
  - Sympatric speciation may also result from sexual selection.

Concept 24.3 Hybrid zones provide opportunities to study factors that cause reproductive isolation.

- When allopatric species renew contact with one another, a **hybrid zone** may form.
- A hybrid zone is a region in which members of different species meet and mate, producing hybrid offspring.
- Some hybrid zones form narrow bands.

- The hybrid zone between the yellow-bellied toad *Bombina variegata* and the fire-bellied toad *B. bombina* is 4,000 km long but less than 10 km wide.
    - Across the hybrid zone, the frequency of alleles specific to each species decreases from 100% at the edge adjacent to that species to 50% in the central portion of the zone to 0% at the far edge.
    - Toads move freely throughout the zone, but an obstacle clearly blocks gene flow between the two toad species.
    - Compared to the parent species, hybrid toads have increased rates of embryonic mortality and morphological abnormalities.
    - Because the hybrids have poor survival and reproduction, they produce few viable offspring.
- In the eastern United States, a hybrid zone exists between the ground crickets *Allonemobius fasciatus* and *Allonemobius socius*.
    - Both species are found in the Appalachian Mountains. *A. fasciatus* predominates in cool, high-elevation, and north-facing locations. *A. fasciatus* predominates in warm, low-elevation, and south-facing locations.
    - The two species are closely interspersed in many patchy hybrid zones.
    - The fitness of *Allonemobius* hybrids varies from year to year and sometimes exceeds the parental fitness.
- Apart from rapid speciation, there are three possible outcomes for hybrid zones over time.
    1. Reproductive barriers between species may be strengthened, limiting the formation of hybrids.
    2. Reproductive barriers between species may weaken, causing two species to fuse into one.
    3. A long-term, stable hybrid zone may form.
- When hybrids are less fit than members of parental species, natural selection strengthens prezygotic reproductive barriers, reducing the formation of unfit hybrids.
    - This process of **reinforcement** *strengthens* reproductive barriers, especially between sympatric species.
    - Two closely related species of European flycatcher, the pied flycatcher and the collared flycatcher, live in both sympatric and allopatric populations.
    - In sympatry, the males of the two species show very different coloration.
    - In allopatry, the males look similar enough to be attractive to females of the other species.
- When the barriers to reproduction in the hybrid zone are weak, gene flow may weaken the reproductive barriers between species.
    - The process of speciation may reverse, causing the two hybridizing species to fuse into one.
    - This may be happening among the cichlids of Lake Victoria. The increasingly murky and polluted waters of the lake have reduced the ability of females to distinguish males of their own species, reducing sexual selection and increasing the frequency and success of hybridization.
- Many hybrid zones are stable. In more than 20 years of studying the *Bombina* hybrid zone, scientists have found no evidence for reinforcement or declining numbers of hybrids.
    - Perhaps extensive gene flow from outside the narrow hybrid zone overwhelms selection for increased reproductive isolation inside the hybrid zone.
- The study of hybrid zones shows how barriers to reproduction between closely related species may change over time.

Concept 24.4 Speciation can occur rapidly or slowly and can result from changes in few or many genes.

- Biologists continue to ask fundamental questions about speciation.
  - How long does it take new species to form?
  - How many genes change when one species splits into two?

How long does it take a new species to form?

- The fossil record and molecular data provide information about the timing of speciation in specific taxa.
- In the fossil record, many species appear as new forms rather suddenly (in geologic terms), persist essentially unchanged, and then disappear from the fossil record.
  - Paleontologists Niles Eldredge and Stephen Jay Gould coined the term **punctuated equilibrium** to describe the pattern of apparent stasis punctuated by sudden change.
- Some species change more gradually, over long periods of time.
- Suppose that a species survived for 5 million years, but most of its morphological alterations occurred in the first 50,000 years of its existence—just 1% of its total lifetime.
- Because time periods as short as 50,000 years (in geologic terms) often cannot be distinguished in fossil strata, the species would seem to have appeared suddenly and then lingered with little or no change before becoming extinct.
- Even though the emergence of this species actually took tens of thousands of years, this period of change left no fossil record.
- For fossil species that show gradual change, we cannot tell when a new species forms because information about reproductive isolation does not fossilize.
  - It is likely that speciation in such groups occurs slowly, over millions of years.
- A growing number of studies suggest that speciation can take place rapidly.
  - Rapid speciation produced the wild sunflower, *Helianthus anomalus,* by hybridization of two other sunflower species.
  - The parent species and hybrid all have the same number of chromosomes ($2n = 34$).
  - In laboratory experiments creating hybrid sunflowers, the fertility of hybrids increased from 5% to 90% after four generations.
  - Researchers hypothesize that hybrids with incompatible DNA were eliminated by natural selection, while others hybrids reproduced successfully to produce chromosomes similar to those of natural *H. anomalus* populations.
- The total time between speciation events (from the start of genetic divergence to complete speciation) varies considerably.
  - A survey of data from 84 groups of plants and animals found that the interval between speciation events ranged from 4,000 years (Ugandan cichlids) to 40 million years (some beetles).
  - Overall, the time between speciation events averaged 6.5 million years and rarely took less than 500,000 years.
- These data suggest that it may take Earth's life a long time to recover from a mass extinction.

- Speciation begins only after gene flow between populations is interrupted, not after a given period of time.
- Once gene flow is interrupted, the populations must diverge genetically to the extent that they become reproductively isolated. This must occur before another event causes gene flow to resume, thus reversing the speciation process.

How many genes change when a new species forms?

- In Japanese land snails from the genus *Euhadra,* the alleles of a single gene controlling the direction of shell spirals can induce a mechanical barrier to reproduction.
  - When shells spiral in different directions, snails' genitalia cannot meet and snails cannot mate.
- Douglas Schemske and his colleagues at Michigan State University examined two species of the monkey flower *Mimulus*.
  - The two species are isolated by two prezygotic barriers: pollinator choice and partial gametic isolation.
  - The species are also isolated by three postzygotic barriers: lower success of interspecific crosses, reduced fertility, and survivorship of hybrids.
  - The two species are pollinated by bees and hummingbirds, respectively, which accounts for most of the reproductive isolation.
  - Researchers observed which pollinators visit which flowers and then investigated the genetic differences between plants.
  - Two gene loci were identified that are largely responsible for pollinator choice.
    - One locus influences flower color; the other affects the amount of nectar flowers produce.
    - By determining the attractiveness of the flowers to different pollinators, allelic diversity at these loci has led to speciation.
  - Researchers transferred the alleles between monkey flower species, reversing pollinator choice.
- A mutation at a single locus influencing pollinator preference contributes to reproductive isolation in monkey flowers.
- In other cases, speciation may be influenced by larger numbers of genes and gene interactions.
  - Hybrid sterility between two subspecies of *Drosophila pseudoobscura* results from gene interactions at two loci.
- Few or many genes can influence the evolution of reproductive isolation and speciation.
- As repeated speciation events lead to new species, differences may accumulate and become more pronounced.
- Although the changes after any speciation event may be subtle, the cumulative change over millions of speciation episodes leads to the formation of new groups of organisms that differ significantly from their ancestors.