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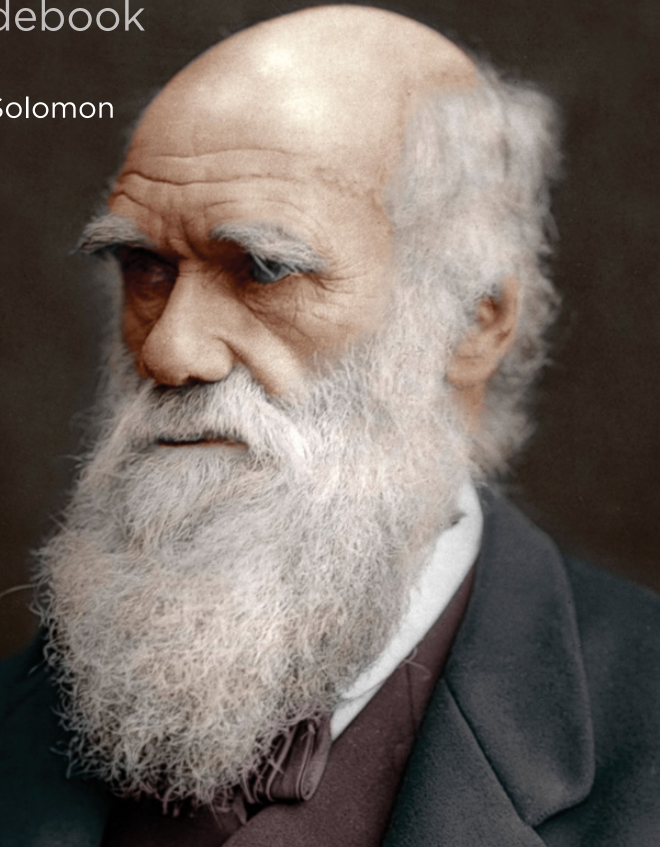
What Darwin Didn't Know

The Modern Science of Evolution

Course Guidebook

Professor Scott Solomon
Rice University



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Scott Solomon is an Associate Teaching Professor at Rice University, where he teaches ecology, evolutionary biology, and scientific communication. He received his PhD in Ecology, Evolution, and Behavior from The University of Texas at Austin, where his research examined the evolutionary origins of biodiversity in the Amazon basin. He has also worked as a visiting researcher with the Smithsonian Institution in Washington DC and with São Paulo State University in Rio Claro, Brazil.

Dr. Solomon has taught field biology courses at Rocky Mountain Biological Laboratory in Colorado and in the rainforests and coral reefs of Belize. He has also been a resident associate at Baker College, one of Rice's residential colleges, and served as a faculty fellow at Rice's Center for Teaching Excellence, where he acted as a liaison to other faculty on matters related to teaching.

Dr. Solomon's research examines the interactions between native and nonnative ants, the impacts of extreme flooding on ant communities, and the evolution of ants and their symbiotic microorganisms. He regularly lectures on science topics to the general public, including giving presentations at museums, schools, churches, and TEDx events.

Dr. Solomon's writing and photography have appeared in such publications as *Aeon*, *Nautilus*, *Slate*, and *WIRED*. He is also the author of *Future Humans: Inside the Science of Our Continuing Evolution*.

Fluent in Spanish and Portuguese, Dr. Solomon loves to travel and experience new adventures. Examples include rafting the Nile, coming face-to-face with wild mountain gorillas, fishing for piranhas and venomous lionfish, climbing Mount Kilimanjaro, swimming with hammerhead sharks, being sniffed by hyenas while camping in the Serengeti, and dining on roasted palm weevils and guinea pigs in Peru. He lives in Houston, Texas, with his wife, Catharina, and their 3 children. ●

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Darwin

What Darwin Didn’t Know

The Modern Science of Evolution

Charles Darwin’s theory of evolution by natural selection, and his related theory of sexual selection, completely changed the way biologists approach the study of life. What’s more, the implications of his theories—including the notion that all living species, including humans, are descended from a common ancestor—revolutionized our views of who we are and where we come from.

Yet there was a great deal that Darwin did *not* know, and it took more than a century before evolution was united with genetics, leading to the modern science of evolution.

The course begins where Darwin began: with a journey around the world that offered the young naturalist an extraordinary opportunity to uncover clues about how the Earth and its inhabitants have changed over time. The first lecture follows Darwin’s efforts to make sense of his observations aboard the *Beagle*—and in the decades after his return to England—examining and conducting experiments on species ranging from barnacles to pigeons and orchids, culminating in his 1859 publication of *On the Origin of Species*.

Lecture 2 demonstrates how the biggest gap in Darwin’s knowledge—the nature of heredity—was solved by Gregor Mendel’s studies on pea plants but remained largely unknown until the year 1900, long after Darwin’s death. Lectures 3 through 6 explore additional mechanisms of evolution, such as mutations, biogeography due to plate tectonics, gene flow, and genetic drift, culminating in a new foundation for evolution known as the modern synthesis.

Darwin assumed that evolution is always slow, but lectures 7 and 8 reveal evolution taking place very quickly, allowing us to see exactly how evolution happens through carefully controlled studies in the field and in the laboratory.

Darwin's theory went a long way toward explaining how changes accumulate within a species, but he had remarkably little to say about when such changes result in the evolution of a distinct new species. Lecture 9 explores modern views of what a species is and how reproductive barriers allow changes that accumulate within isolated populations to develop into new species.

Darwin assumed that all evolution is gradual, but lecture 10 traces major episodes in the history of life in which there was a relatively sudden increase in species (such as the Cambrian explosion) or a relatively sudden decrease in species (mass extinctions).

Darwin pioneered the idea that life's history resembles branches on a tree of life, so lecture 11 explores how new evidence from fossils, comparative anatomy, and DNA show many branches Darwin did not know about and a degree of tangled cross-connection he would not have suspected. Lecture 12 demonstrates how the iconic view of human evolution as a linear progression from hunched ape to upright man, popularized during Darwin's lifetime by Thomas Henry Huxley (Darwin's "bulldog"), has been replaced by a more complex, interconnected network of many humanlike species, with ours as the only survivors.

Darwin made the case that evolution is inevitable, but is it predictable? Lecture 13 reveals how often-unrelated life evolves somewhat predictably to converge on similar solutions, while lecture 14 examines how life diverges when faced with extreme conditions many scientists had assumed too inhospitable for life at all.

Topics that puzzled Darwin, with their modern resolutions, are the subjects of lectures 15, 16, and 17—from peculiar and often-counterintuitive body designs, to the coevolution of animals with flowering plants, to the paradox of ant societies with sterile workers.

Lectures 18 through 22 demonstrate how the modern science of evolution increasingly explains and affects our everyday lives—from dramatic new views on the microorganisms that live in and on our bodies, the evolution of brains and behavior, and the origins and future evolution of sex; to the reasons why our bodies break down as we age and the exploding field of evolutionary medicine. Finally, lectures 23 and 24 explore how humans are increasingly affecting the evolution of virtually every other species on the planet and what may be the evolutionary future of humans.

As a whole, the course uncovers why Darwin's ideas became so compelling to scientists—why, as Darwin put it, "there is grandeur in this view of life"—by examining the data that he and many later scientists collected to test and refine his provocative views. There were many things that Darwin didn't know, and some things that he got wrong. But perhaps the most important thing that Darwin did not know is how fully his theories would become the basis for all of modern biology and offer new ways to view the world and our place in it. ●

Lecture 1

What Darwin Knew and Why It Still Matters

When *On the Origin of Species* was published in 1859, Charles Darwin was best known as the author of a book published in 1839 about his 5-year around-the-world journey, now known as *The Voyage of the Beagle*, a scientific adventure travelogue. Contrary to popular belief, Darwin was not offered a position as the official naturalist aboard the *Beagle*; that position was already filled by Robert McCormick. Instead, the *Beagle*'s captain, Robert Fitzroy, wanted someone knowledgeable enough about geology and natural history to help make sense of the places they would visit. Darwin, who had studied botany, geology, and even something called natural theology, began the trip at the age of 22.

HMS *Beagle*

- The *Beagle* left England on December 27, 1831, with the primary objective of charting the South American coastline. Very early on, it became clear that McCormick resented the fact that Darwin was collecting specimens when, as far as Robert McCormick was concerned, that was his job. When the *Beagle* arrived in Rio de Janeiro about 3 months into the journey, McCormick boarded another ship and headed back to England.
- As Captain Fitzroy carried out his surveys, moving methodically along the coast of Brazil, Uruguay, and Argentina, Darwin spent as much time as he could ashore.

Over his 5-year journey on the *Beagle*, Darwin spent a total of 594 days on land.

- He went on extended expeditions into the interior of the continent with local gauchos, making careful notes of the peculiar animals they hunted and ate for dinner. In the cliffs along the coastline, Darwin found fossils of armadillos and giant sloths. The fact that these extinct animals resembled smaller **species** still living in the region made a deep impression on him.
- A sudden insight came to Darwin when a massive earthquake struck near where the *Beagle* was anchored along the coast of Chile.
- Darwin was fascinated by the new ideas in geology recently published by Charles Lyell, who suggested that geological features like mountains and canyons were not formed by sudden catastrophes, as previously thought. Instead, Lyell thought they were the result of processes that had repeated during long periods of time—processes that were still underway today, such as earthquakes.
- Darwin saw that the earthquake he had just experienced caused the ground to be lifted 8 or 9 feet in just a matter of minutes and realized

Contrary to popular belief, Darwin did not have a single grand epiphany while visiting the Galapagos Islands. In fact, his theory of evolution would not be fully formed until much later, when he was home in England.

that if such earthquakes happened repeatedly over a long enough period of time, they could eventually form mountains.

- Maybe the Earth was older than previously thought, perhaps many millions of years old. And as the realization deepened that the Earth itself was very old—and slowly changing—Darwin also realized that species might change in some way.
- These ideas were all percolating through Darwin's mind as the *Beagle* sailed northward along the Pacific coast of South America and arrived at the Galapagos Islands in September 1835, almost 4 years into their journey.

The Galapagos Islands

- Darwin was impressed by the animals and plants he saw on the Galapagos Islands. Specifically, he was impressed by the fact that, according to the vice-governor of the islands, it was possible to tell the giant Galapagos tortoises on each island apart by the shapes of their shells.

- Having visited several different islands within the archipelago, Darwin had seen that the islands were all quite similar to one another. He couldn't figure out why the animals on islands with similar environments would be different.

- Darwin collected specimens from each of the islands he visited, including many birds. Some of his bird specimens included the finches that would become one of the most famous symbols of the theory of **evolution**.

- When examined by an expert back in England, his collections of mockingbirds on different Galapagos Islands would turn out to each be different species. Darwin had already noted some differences among his mockingbird samples, thinking it was peculiar that these birds, like the tortoises, would differ from one island to another. After all, most of the Galapagos Islands are close enough to each other to be clearly visible.

> Darwin's visit to the Galapagos Islands was an important influence on what would become his most important contribution to science.

- After the similarities between fossil and living species he had seen in South America, what he saw in the Galapagos Islands suggested to Darwin that perhaps species were not fixed entities that came into existence through what was known then as special creation.

How Species Change

- A key moment came when Darwin was back in England in September 1838, when he read economist Thomas Malthus's *An Essay on the Principle of Population*, which showed mathematically that the rate at which the human **population** is growing is much greater than the rate at which our food supply is increasing. Malthus was concerned that this would eventually lead to a crisis in which there wouldn't be enough food for everyone alive.

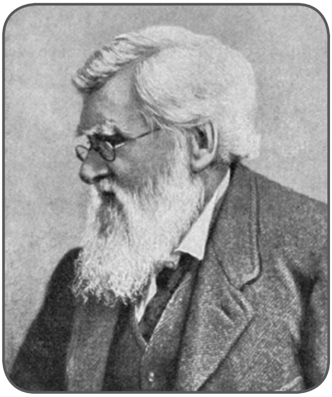
- From his observations during the *Beagle* voyage, Darwin realized that limited resources and the struggle of individuals to survive could apply to any species. If so, that meant that the individuals with traits that make them better at competing for the limited resources would have a better chance of surviving and reproducing.

- This insight was critical, because it provided a mechanism for how evolution could happen. Others before him had already suggested that species change, but so far, no one had come up with a plausible way to explain how such changes could take place.

Darwin's Delay

- Even with this breakthrough insight that species must compete for limited resources, Darwin only shared his idea with a handful of close friends—for another 21 years. The reasons for Darwin's delay in publishing his theory of evolution have long been debated.
- In the summer of 1844, 8 years after the *Beagle* returned, Darwin had just completed 5 years of editorial work on *Zoology of the Voyage of H.M.S. Beagle*, in which experts gave their assessments of the fossils, mammals, birds, fish, and reptiles collected by Darwin during the voyage.
- But later that same year, a popular book appeared called *Vestiges of the Natural History of Creation*, written by an anonymous author, stole some of Darwin's thunder. It introduced the idea that all of natural history could be regarded as a history of transmutation—what we would now call evolution. Yet the scientific evidence was very thin, leaving it open to criticism.
- What was needed was a scientist capable of marshaling appropriate evidence and offering a scientific explanation for how evolution works. And Darwin wanted to collect as much data as he could to support his theory. In fact, for 8 years, Darwin's most intense work was in his study of barnacles.
- He also studied 16 different types of pigeons to understand how **domestication** could cause physical changes to their anatomy. His interest in **artificial selection** would provide the springboard for his entire theory of **natural selection**.

- An obstacle to scientific work was his recurrent illness, the cause (or causes) of which remain somewhat mysterious. It kept Darwin from engaging directly with the scientific community, but he kept in close contact with many colleagues by mail.



Alfred Russel Wallace

- One of the many experts he corresponded with was Alfred Russel Wallace, a professional specimen collector who, much like Darwin, puzzled over the geographic distribution of plants and animals. Wallace questioned whether species had always had their current distributions or whether they had changed through time. If their geographic ranges changed through time, maybe other aspects of their biology could change through time as well.

- During his travels in Southeast Asia, Wallace exchanged several letters with Darwin and sent him some specimens. But in June of 1858, Darwin received a package from Wallace that contained a 20-page draft of a manuscript in which Wallace described a theory of “the tendency of **varieties** to depart indefinitely from the original type.”

- Wallace’s theory was essentially the same as that which Darwin had been patiently developing over the last few decades: evolution by natural selection.

- The basic idea was actually quite simple. **Variation** clearly exists among individuals of a species. Darwin had seen it through his studies on barnacles and pigeons, and Wallace had seen it through his commercial collections.

- Both Darwin and Wallace had realized that some of the differences among individuals of a species affect that individual’s chances of surviving and reproducing. And because offspring tend to resemble their parents, that means that the characteristics that make an individual more likely to survive and reproduce will become more common in later generations.

- Wallace's manuscript prompted Darwin to act. And in 1859, Darwin finally published a complete explanation of the theory of evolution by natural selection in his *On the Origin of Species*.

Alfred Russel Wallace had no idea that Darwin had been working independently on the exact same idea: evolution by natural selection. The fact that Wallace mailed his manuscript to Darwin, of all people, goes down as one of the most incredible coincidences in the history of science.

Sexual Selection

- His 1871 book, *The Descent of Man, and Selection in Relation to Sex*, not only applied his theory of evolution to include humans, but it also added a new mechanism: **sexual selection**. Darwin used the example of a peacock's tail as an example of a trait that couldn't be easily explained by natural selection because it didn't help with survival. But it could evolve if it led to greater mating success.

- Together, *On the Origin of Species* and *The Descent of Man* provided one continuous argument in favor of evolution. Most scientists have come to agree about the fact of evolution ever since. But Darwin's explanation for how evolution takes place, by means of natural and sexual selection, did not attain the same degree of scientific consensus for almost another century.

- During those decades, scientists were most keenly aware of all the things Darwin did *not* know about how life changes over time, setting off research programs in all directions. It took roughly another 100 years after Darwin's death for his theory of evolution by natural selection to fully mature into a robust scientific discipline.

We now have evidence for evolution that was completely unavailable to Darwin.

- **Transitional fossils.** The few fossils known in Darwin's lifetime had only begun to hint at the history of life.
- **Plate tectonics.** Understanding how land masses have moved makes it possible to understand evolution.
- **"Unintelligent" design.** Examples from many species provide some of the strongest evidence for a history of descent with modification rather than special creation.
- **Natural selection in real time.** Wild species have been documented in the act of experiencing evolution by natural selection.
- **Universal genetic code.** Darwin suggested that all of life might have evolved from a common ancestor, but we now know that every known type of life uses the same DNA code inherited from a single ancestor.

Such advances have made Darwin's views look even more prescient and essentially correct now than could have been realized in his time.

Readings

Arts & Humanities Research Council, Darwin Online, http://darwin-online.org.uk/.

Browne, *Darwin*'s Origin of Species.

Darwin, *The Origin of Species*.

Quammen, *The Reluctant Mr. Darwin*.

Raby, *Alfred Russel Wallace*.

Questions

What was it about the fossils Darwin discovered along the coast in Argentina that provided an early clue about evolution?

In what ways did Darwin’s visit to the Galapagos Islands influence the development of his theory of evolution?

What is natural selection, and what role does it play in Darwin’s theory of evolution?

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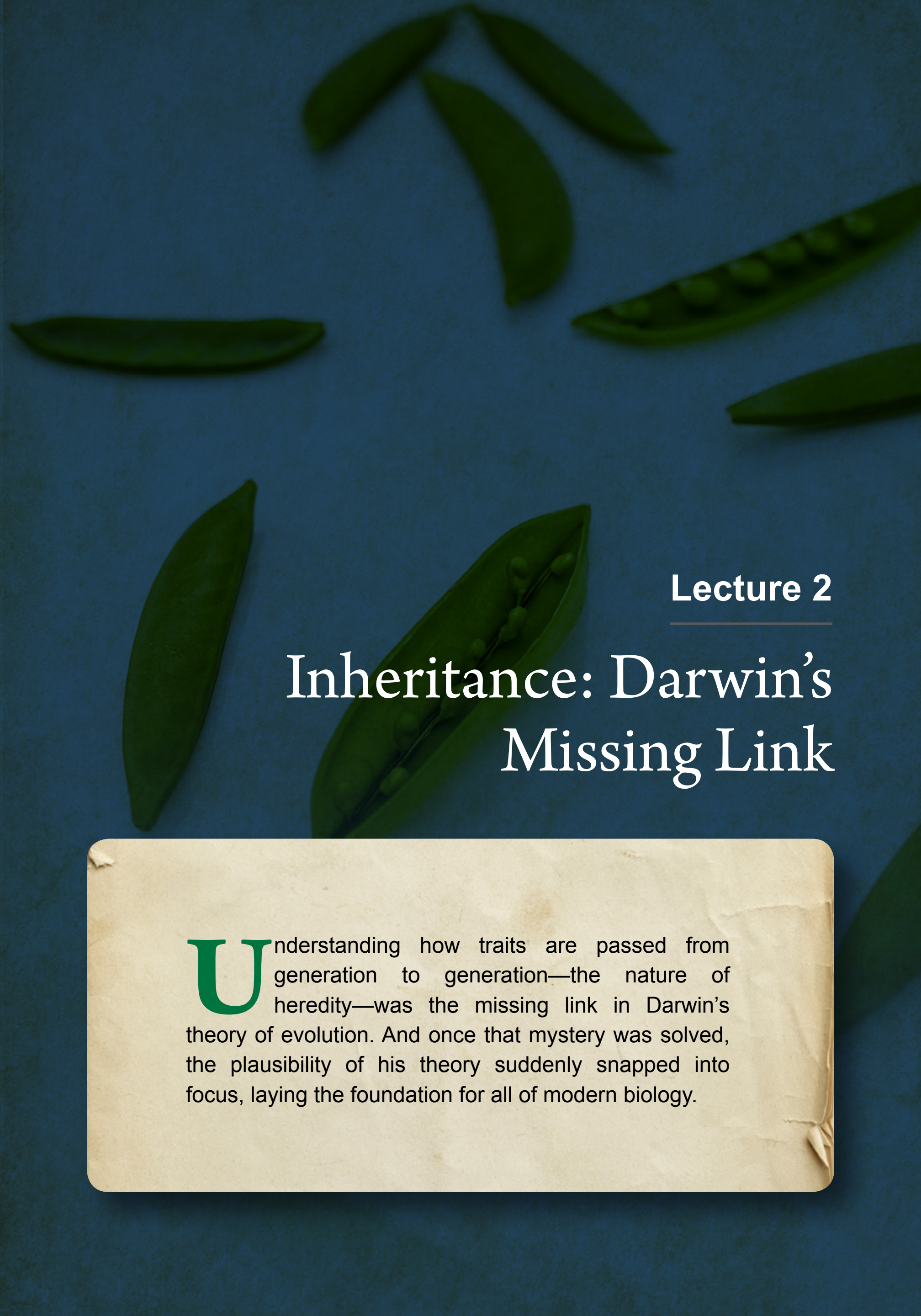
Answers can be found on **page 228**



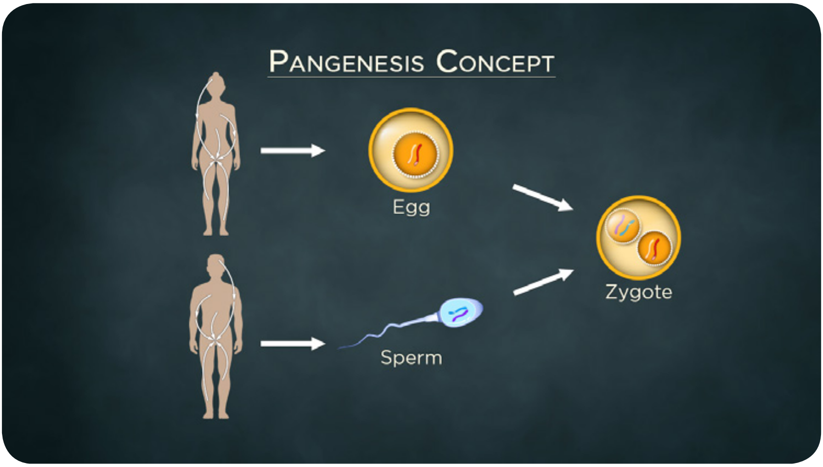
Lecture 2

Inheritance: Darwin's Missing Link

Understanding how traits are passed from generation to generation—the nature of heredity—was the missing link in Darwin's theory of evolution. And once that mystery was solved, the plausibility of his theory suddenly snapped into focus, laying the foundation for all of modern biology.

Lamarck

- In *The Variation of Animals and Plants under Domestication*, Darwin proposed an idea for how heredity works. Unfortunately, his idea was wrong. It had 3 fundamental flaws.
    - Darwin imagined a new kind of small particle he called gemmules, supposedly produced by cells all over the body and then traveling to the sex cells. Darwin suggested that when a sperm fertilizes an egg, gemmules from each parent also come together from all over the body to give offspring a full mixture of all bodily traits from both the mother and father. He called this pangenesis.

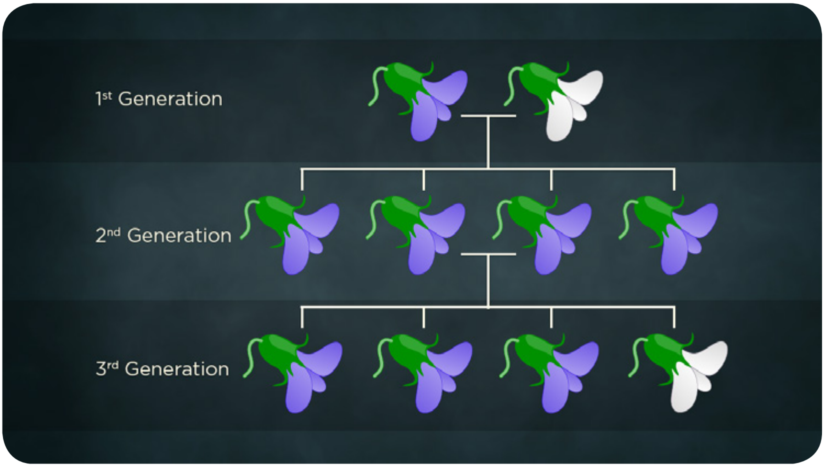


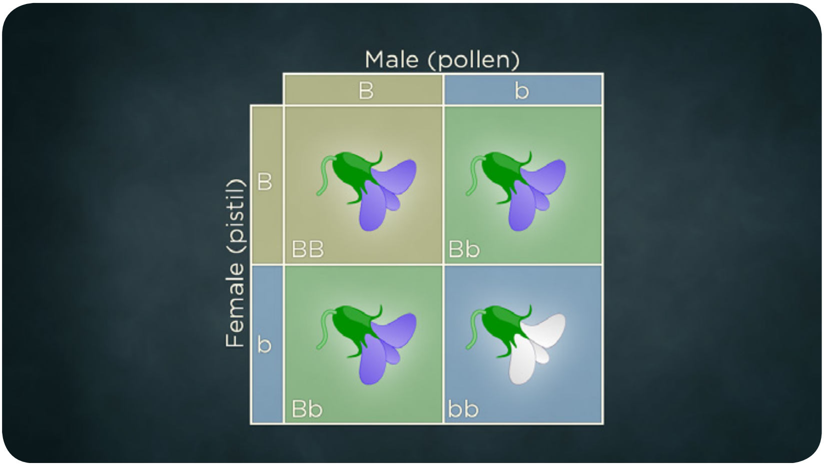
    - Darwin assumed that the traits of each parent would always blend together, like different colors of paint.
    - Darwin imagined that that gemmules bringing information from around the body at the time of reproduction would include traits acquired during an individual's lifetime.
- Darwin's ideas that gemmules and pangenesis are responsible for heredity were new, but they were heavily influenced by the work of French biologist Jean-Baptiste Lamarck, who had published a theory

of evolution 50 years before Darwin. In Lamarck's view, organisms not only pass on the traits they use in their lifetimes, but the more an individual uses a particular trait, the more that trait is passed on.

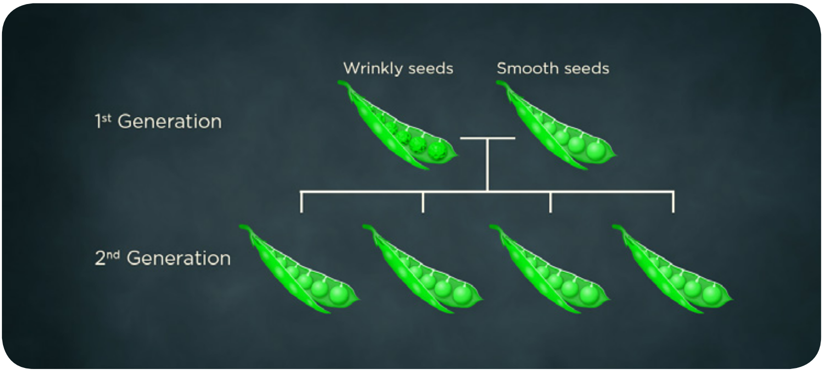
Mendel

- The breakthrough study that would provide an alternative to Darwin's ideas on heredity while vindicating his ideas on evolution was done by Gregor Mendel, an Augustinian monk. His approach to understanding heredity involved crossbreeding different varieties of pea plants.
- He found that crossing purple-flowered pea plants with white-flowered pea plants does not give you pink-colored pea plants. Instead, he got only purple-flowered plants. But when he took the hybrid offspring of the purple and white-flowered plants and crossed the hybrids with one another, Mendel found that some individuals in the next generation had white flowers. This was a surprise, because the white flowers had disappeared in one generation and then reappeared in the next.
- But it was the ratio of the plants with different flower colors that really caught Mendel's attention. Out of 929 pea plants in the second





generation, 3/4 were purple and 1/4 were white, for an overall ratio of 3 to 1. Repeating the experiment, Mendel found that the proportions were always about the same. Remarkably, he found about the same ratio when he crossed other traits of pea plants, such as smooth versus wrinkly seeds.



- Mendel realized that the heredity of traits in pea plants acted in a predictable manner. But contrary to what Darwin and many others assumed at the time, the traits in Mendel's experiments did not blend together.

- What's more, there was something about certain traits, such as purple flowers, that made them more likely to be inherited by later generations than other traits, such as white flowers. Mendel called these traits dominant and recessive.

- To describe how each parent contributes, Mendel said that each individual must have 2 elements that work together to determine the trait. We now use the word **alleles** to describe these elements: One allele comes from the mother and one comes from the father.

- Because purple is dominant over white, if an individual pea plant has 1 purple allele and 1 white allele, its flowers will be purple. Only if it has 2 white alleles will its flowers be white.

- Mendel also noticed that some traits changed together in lockstep. For example, the color (or absence of color) in the seed coat corresponded to color (or absence of color) in flowers and to the connection between the stem and leaf. In modern terms, we would say that a single **gene** is controlling more than one trait.

- In 1866, Mendel published the results of his experiments in a research journal and sent copies to scientists around Europe. It's not known whether Mendel sent a copy of his paper to Darwin, but even if he read it, the importance of Mendel's findings were apparently not obvious to Darwin. Mendel's findings weren't obvious to anyone else, either. It was too easy to come up with apparent counterexamples, which fall into 4 groups:

    - Many plants can reproduce asexually.

    - Mendel's simple scheme for pea plants did not explain cases where blending does occur, what later came to be called incomplete dominance of one allele over the other.

    - We now know there can be codominance by both alleles in a gene.

Modern quantitative genetics builds so-called non-Mendelian models, where a single polygenic trait, such as height or intelligence, might be controlled by dozens, or even hundreds, of genes.

  - Mendel did not consider polygenic traits, which are traits that are controlled by more than one gene.

- In 1900, 3 scientists separately rediscovered Mendel's paper. After 35 years of neglect, the scientific world was finally recognizing the importance of Mendel's hybridization experiments.

- As the relevance of Mendel's work on heredity began to be appreciated, this helped solve a major objection to Darwin's theory of evolution by natural selection: Whereas Darwin's mechanism of natural selection leads to differences, the blending theory of heredity had implied that organisms become more similar to one another.

- Mendel's work offered a different mechanism for heredity that does not involve blending. A pea plant with wrinkly seeds and a pea plant with smooth seeds will produce hybrid offspring that have smooth seeds, not semiwrinkly seeds or some other intermediate trait.

- Mendel's idea that some traits are dominant over others allows natural selection to work as a mechanism of evolution: There is now a way to explain why variation can persist from generation to generation.

- But Mendel's work didn't clarify how genes function. So, the search was on to uncover what genes actually were and how they worked.

Morgan

- One of the major breakthroughs was proof that each gene is located on a specific **chromosome**, a higher-level structure of genes found within the **nucleus** of just about every cell in your body. This discovery was made by Thomas Hunt Morgan, who had begun working with fruit flies about 5 years after the rediscovery of Mendel's work.

- Fruit flies were ideal subjects for studying genetics because they reproduce quickly; have a lot of variation in traits that are easy to spot, such as having red eyes versus white eyes; and have just 4 pairs of chromosomes, making them simpler to study.

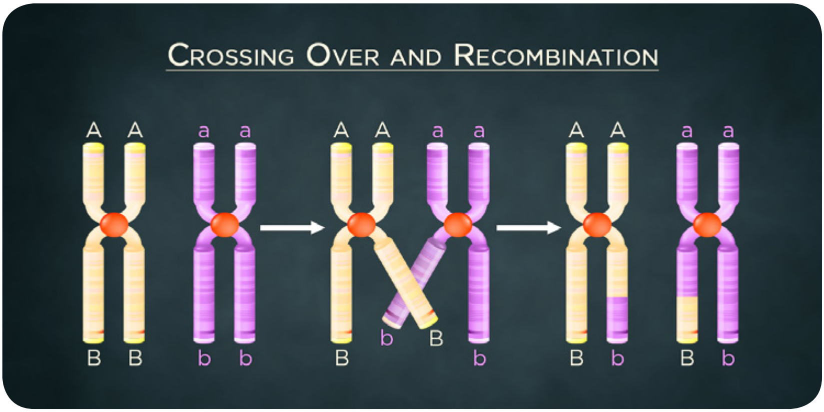
- Morgan's team also found that some of the traits of fruit flies tend to be associated with other traits. For example, flies with the male sex chromosome were more likely to have recessive white eyes than females. Morgan realized that single genes alone cannot explain the observed patterns of inheritance; these associations happen because the genes for those traits are "packaged" together by being located on the same chromosome.

- Every individual fruit fly or human has 2 copies of each chromosome: one from their mother and the other from their father. Humans have 23 pairs of chromosomes, or 46 chromosomes in total. Fruit flies only have 4 pairs of chromosomes, or 8 in total.

In humans, chromosome 1—the largest chromosome—has about 2000 genes, including a gene that influences brain size and a gene responsible for glaucoma.

- Because chromosomes come in pairs, every individual has 2 copies of each gene—one on each chromosome. The father and mother alleles passed down for any particular gene might be identical on both chromosomes or might be different. To get there, only one copy of each chromosome is needed for gametes, such as sperm and eggs, because the gamete from one parent will pair up with a gamete from the other parent to create a new individual.

- In the process of making gametes, known as meiosis, the chromosomes within a cell line up with their identical pairs. Next, the chromosomes become intertwined, exchanging chunks between



pairs through a process known as **recombination**. Because of recombination, the resulting chromosomes can contain combinations of alleles not seen in either parent. This process is one of the ways that variation is generated—a key ingredient for natural selection.

- Morgan's students also noticed that recombination is more likely to cause some genes to recombine than others, and in some cases, 2 genes never recombined. In 1911, one of Morgan's undergraduate students, Alfred Sturtevant, took the data on how often genes recombined and used them to create a map of approximately where on a fruit fly chromosome each of the genes must be located. Gene mapping led to an important advance in the study of evolution.

The ability to map genes for visible traits on chromosomes was a first step toward mapping the entire fruit fly genome in 1999, a rough draft of the human genome in 2000, and a more complete version of the human genome 3 years later.

Dobzhansky

- Ukrainian biologist Theodosius Dobzhansky discovered lots of natural variation in *Drosophila pseudoobscura*, a close relative of the fruit fly species Morgan studied. Dobzhansky used the recombination mapping technique to determine where on each chromosome the genes for each trait were located.

- Dobzhansky discovered that 2 different varieties of the same species of fly could exist in a particular area. Intriguingly, he found that the varieties differed in the order in which the genes occurred on a chromosome: One variety had genes in a particular order while another had the reverse order. Dobzhansky figured this difference must have been the result of a **mutation** in which the section of the chromosome containing these genes got inverted.

- Darwin had emphasized the importance of variation for natural selection, and now Dobzhansky was seeing evidence for variation at the genetic level.

- Dobzhansky's observation also led to an experiment in which he demonstrated that natural selection could act through differences in temperature to cause one variety to become more common than another.

- The basic ingredients for combining Mendelian genetics with Darwinian evolution were finally being combined into a coherent theory. In 1937, Dobzhansky published *Genetics and the Origin of Species*, which explained evolution in terms of genes and alleles. There were 3 main points:
    - An organism's traits can be traced to alleles, the alternative versions of each gene passed from one generation to the next.
    - In a population of organisms, the variation in traits reflects variation in alleles.
    - Natural selection occurs when some organisms leave more offspring than others, passing on more of their alleles to the next generation.
- Natural selection was acting like a filter, or sieve, that controlled which traits can pass from one generation to the next. The alleles for those traits become more common in the next generation. As Dobzhansky saw it, which alleles become more or less common was what defined evolution.

In 1930, British statistician Ronald Fisher detailed his mathematical approach to genetics and evolution in *The Genetical Theory of Natural Selection*, which was among the most important publications to connect Mendel's work to Darwin's.

- Along with the work of Sewall Wright and J. B. S. Haldane, Ronald Fisher established that studying how genes change through space and time—a field that became known as population genetics—was a key to understanding evolution.
- Dobzhansky, Fisher, Wright, and Haldane lay the foundation for others to further connect genetics and evolution through the 1940s and 1950s in what came to be known as the **modern synthesis**, which remains the cornerstone of the modern science of evolution.

The following are the most important points of the modern synthesis:

- Genes, located on chromosomes, are the basis of heritable traits.
- Genes are passed intact from parents to their offspring.
- Mutation and recombination are random processes that create new genetic diversity.
- Genetic traits that are beneficial become more common over generations through natural selection.

The many things Darwin did not know are based on, or at least presume, this genetic view of evolution, as outlined by the modern synthesis.

Readings

Mukherjee, *The Gene*.

National Institutes of Health, Genetics Home Reference, https://ghr.nlm.nih.gov/.

Zimmer, "Can a Parent's Life Experience Change the Genes a Child Inherits?"

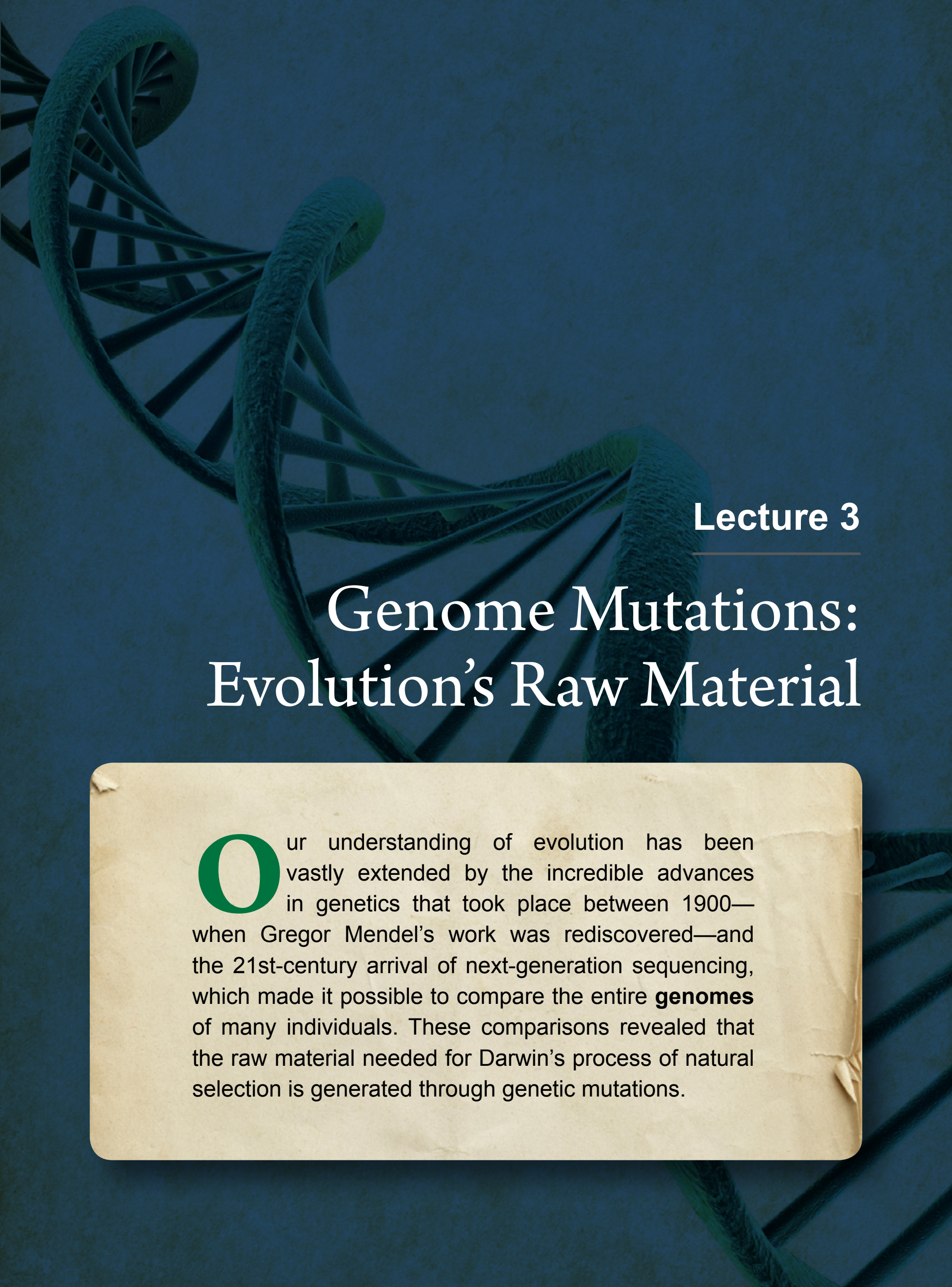
Zimmer, *She Has Her Mother's Laugh*.

Questions

What was Darwin's theory of heredity, and how was it wrong?

Can nonhereditary traits evolve through natural selection?

Answers can be found on **page 229**



Lecture 3

Genome Mutations: Evolution's Raw Material

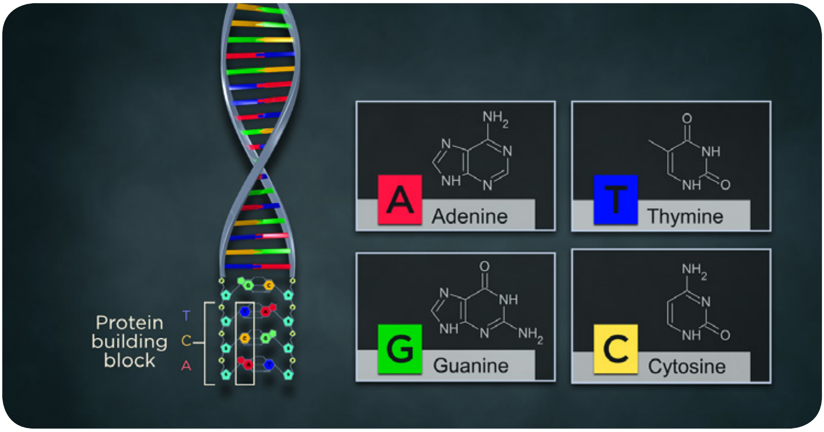
Our understanding of evolution has been vastly extended by the incredible advances in genetics that took place between 1900—when Gregor Mendel's work was rediscovered—and the 21st-century arrival of next-generation sequencing, which made it possible to compare the entire **genomes** of many individuals. These comparisons revealed that the raw material needed for Darwin's process of natural selection is generated through genetic mutations.

James Watson and Francis Crick are often credited for figuring out the structure of DNA. But a vital clue was provided by Rosalind Franklin, who was trying to determine the structure of DNA using a photography technique called x-ray diffraction, or x-ray crystallography.

After seeing one of Franklin's images, Watson and Crick worked out the structure of DNA using a physical model. This was the famous double helix.

DNA and Genes

- The ultimate basis for genes and heredity is a chemical called deoxyribonucleic acid (**DNA**), which contains 4 bases—adenine (A), thymine (T), cytosine (C), and guanine (G)—that are strung together in a sequence. The sequence of DNA bases forms a code for how to make **proteins**. Each protein that a cell needs is coded by a particular sequence of DNA called a gene.



- A lot of what Darwin didn't know about organisms and about evolution has come from the ability to decipher the genetic code of different organisms.
- Your genome, the instruction manual that created you, is a new combination based on copies made from each of your parents'

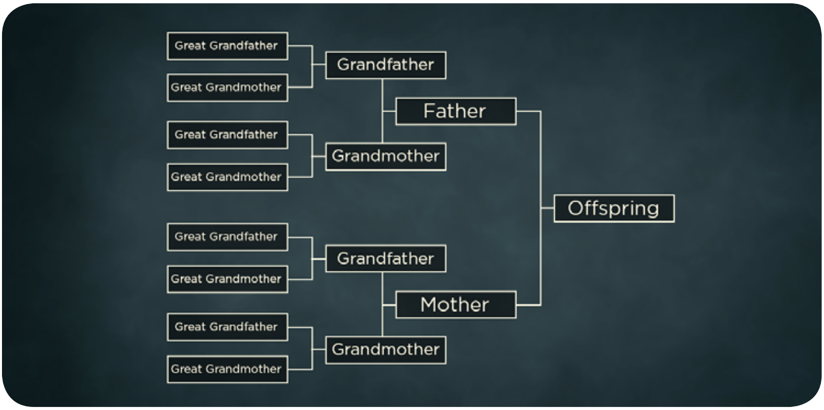
The DNA bases are a type of chemical alphabet, and all the words are 3 letters long. Three DNA bases together in a sequence form a code that is used by the cell to create the building blocks for another type of molecule: a protein.

To make a protein, the information stored in DNA is first transcribed into a very similar molecule, called ribonucleic acid (**RNA**), which then travels outside the nucleus to a particular structure in the cytoplasm of the cell. The 3-letter code of the RNA specifies a particular type of amino acid, and amino acids form the building blocks of proteins.

In general, a particular protein is coded by a stretch of DNA, and that stretch of DNA is what we call a gene.

genomes. Comparing the DNA of different individuals of the same species gives us a way to figure out what makes each individual unique. Your parents' genomes were made by combining copies of their parents' genomes, and so on back through your family tree.

Incredibly, you can trace your genome back to the first human and beyond that, in principle, to the first primate, the first mammal, the first vertebrate, the first animal, the first multicellular creature—all the way back to the first living individual.



Genetic Mutations

- Because a genome is based on information passed from parent to offspring in an unbroken chain that stretches back to the origin of life, we can think of each genome as an historical document. But like all historical documents that combine information from previous historical documents and get repeatedly copied, there are occasional copying errors. Indeed, every time DNA gets copied, there is a chance that a mistake will be made. Those mistakes are called mutations.

- There are many ways to make mistakes when copying DNA. Some mutations are minor, such as having a C where there is supposed to be a G. Sometimes an entire stretch of DNA bases can get copied incorrectly. In other cases, the correct DNA bases are copied but in the reverse order.

- Most mutations either create problems or don't really have any effect. Many mutations, especially those that involve big changes, lead to death. If they happen in a sperm or egg cell that creates an embryo, the embryo most likely won't survive.

- Many other mutations don't really have any effect, either positive or negative. Changing a DNA base that is not part of a protein-coding gene—which turns out to be the majority of the DNA that makes up chromosomes—might not cause any harm nor any good.

- Even some changes within genes can happen without any consequence. That's because the 3-letter DNA base code has 64 different possibilities (4 × 4 × 4), but those 64 possibilities specify only 20 different amino acids. The DNA code for amino acids is redundant because more than one 3-letter sequence codes for the same amino acid.

- Most mutations are harmful or neutral. But on occasion, a mutation can result in a change that is actually helpful. If an individual with a helpful mutation reproduces, then the mutation will be passed on. And if it is helpful in a way that leads to a slightly longer life—and, most importantly, more surviving babies—then the mutation will become more common in later generations.

- So, mutation provides the source of variations. And once there is variation, any differences in offspring will sort the variation, like a sieve. The new varieties that are harmful don't pass through as often to later generations, while the helpful varieties are more likely to pass through.

- Darwin saw how the sieve worked; it was the basis for his theory of natural selection. What he didn't know was where variation comes from. Now we know that mutations are the explanation for new variation that Darwin merely asserted must exist.

Sanger Sequencing

- To find mutations, we can compare the genomes of living species and look for differences. The harmful mutations are less likely to be passed on, so any differences we find will usually be the result of mutations that were either beneficial or neutral.

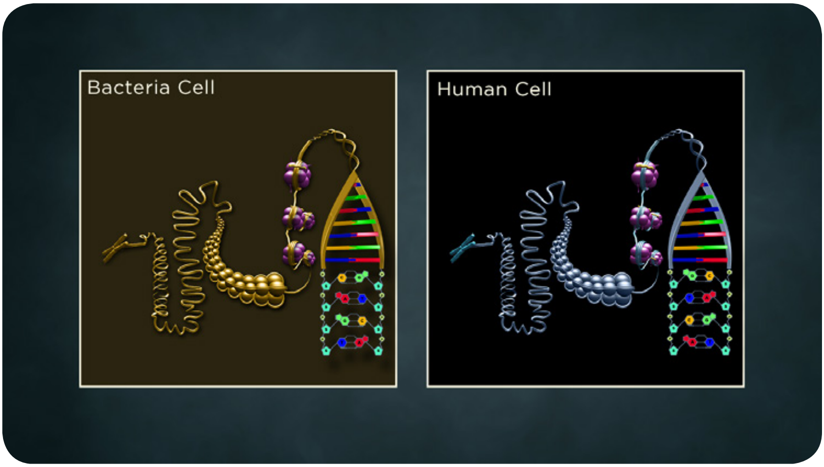
- Comparing genomes gives us a way to look back at the history of life and figure out when particular mutations happened, what change or changes they caused, and how those mutations spread across generations. In other words, comparing genomes shows us how evolution works.

- But to compare genomes, we first need to be able to read them. The technology that is used to read the sequence of DNA bases in a genome has changed rapidly over the last several decades.

- A DNA-sequencing technique called Sanger sequencing was developed in the 1970s by British biochemist Frederick Sanger. The method was cumbersome, but it worked. It was built on the principle that one strain of bacteria could be transformed into another strain by incorporating its genes.

- It turned out that bacteria could incorporate the genes from any

Darwin had suggested that all species can trace their history back to a single common ancestor, and the fact that every living organism uses the same DNA instructions to write its instruction manual offers some of the strongest evidence in favor of shared evolution for all of life.



organism, because at a chemical level, DNA is DNA. The only difference between the DNA of a bacterium and the DNA of a human is the sequence of A's, T's, G's, and C's and the way it's all packaged together into chromosomes.

- Because DNA is the same regardless of what species it comes from, we can take a piece of one organism's DNA and insert it into another species' genome. This is helpful for studying individual genes because in the context of an entire genome, a single gene is like a needle in a haystack. To determine the sequence of any one gene, it can be helpful to first make a lot of copies of the gene.

- Let's say we want to know something about a particular gene in a species of plant. We can essentially cut the gene out of that part of the plant's genome and paste the gene into a living bacterium. One thing bacteria are very good at is making a lot of copies of themselves very quickly.

- *E. coli* reproduce by making identical copies of themselves about every 20 minutes—which equates to 72 generations per day. In just a few days, a few *E. coli* cells that had a snippet of the plant's genome pasted into them will have made enough copies that a large amount of the DNA can be isolated, purified, and analyzed.

- This copying process was later automated using a technique called polymerase chain reaction (PCR). The beauty of the PCR technique is that rather than copying the whole genome, you can hone in on a particular part of it and just make copies of that section.

- Just add all the necessary ingredients—the whole genome of the species of interest, a whole bunch of the individual DNA bases (the A's, T's, G's, and C's), and a few other chemicals that are normally found within a cell—and use a machine to adjust the temperature up and down at just the right moment, and that one particular part of the genome will be repeatedly duplicated.

- Once there are a lot of copies, Sanger sequencing can be used to identify the sequence of bases. An automated version of the Sanger sequencing technique was developed in the late 1990s, making it possible to process more than 1000 samples, each about 850 DNA bases long, in just a day. That's how the first detailed draft of a human genome was completed in the year 2000—exactly 100 years after Mendel's paper on heredity was rediscovered.

The human genome has about 20,000 to 22,000 protein-coding genes made up of approximately 3 billion DNA base pairs. Stretched out in a line, a single copy of the human genome is about 6 feet long.

Amazingly, all of that information is wound up together, along with some proteins, into 46 tiny packages called chromosomes that fit inside the nucleus of a cell.

Next-Generation Sequencing

- The total cost of the Human Genome Project was about $2.7 billion. But by 2017, the cost of sequencing a whole genome dropped to less than $1000. The cost reduction was largely due to the development of even newer DNA sequencing methods known as next-generation sequencing.

- Next-generation sequencing techniques work in different ways but generally involve breaking the genome into small fragments, also known as shotgun sequencing. Each of the fragments is sequenced at the same time, which is why next-generation sequencing is sometimes called massively parallel sequencing. Computer programs are then used to reconstruct how each piece fits together, like an enormous puzzle.

- As genome sequencing became more affordable, it became possible to sequence the genomes of many different species. This approach has helped biologists piece together the evolutionary history of many groups of organisms whose relationships were unclear from other sources of information, such as the structure of their bodies.

- What's more, genome comparisons have revealed that the genome of any one species often contains fragments of other species' genomes. Even the human genome has pieces of DNA that closely resemble DNA from extinct relatives—such as Neanderthals.

- Humans also have DNA from apparently unrelated species, such as viruses. Genome similarities can sometimes reveal episodes of mating between closely related species and also suggest that genes can occasionally be transferred between species by other means, such as when a virus switches hosts.

- In addition to comparisons between different species, affordable genome sequencing made it feasible to compare the genomes of multiple individuals within a species. This meant that we can directly examine evolution's raw material—genetic variation—even before it passes through the sieve of natural selection.

- In the case of humans, comparing the genomes of many individuals from different human populations led to a surprising conclusion: As a species, humans are not very genetically diverse. There are fewer genetic differences between different humans than there are between, for example, different individual chimpanzees, most of which you might think look alike. By contrast, humans differ from one another in all kinds of visible ways, yet our genomes tell us that the differences we tend to notice among people do not actually reflect large underlying differences in our DNA.

Mutation rates in humans aren’t constant. They can vary depending on the age of the father as well as environmental factors, such as exposure to x-rays.

Estimating the rate at which mutations occur allows evolutionary biologists to count the number of differences in the genomes of different species, giving us a way to estimate how much time has elapsed since any 2 species shared a common ancestor.

But this idea of a **molecular clock** assumes that mutations occur at a constant rate, and even within any one species, mutations can occur at different rates in different parts of the genome.

With enough data, we can figure out the rate at which the molecular clock of different genes within different species ticks away, giving us the ability to reconstruct not only the history of how each species is related to every other species but also the timing of that history.

Readings

Kolbert, “There’s No Scientific Basis for Race.”

Mukherjee, *The Gene*.

National Human Genome Research Institute, “An Overview of the Human Genome Project,” https://www.genome.gov/12011238/an-overview-of-the-human-genome-project/.

Shreeve, *The Genome War*.

Willyard, “New Human Gene Tally Reignites Debate.”

Yong, “A New Origin Story for Dogs.”

Questions

A(n) ____ is a stretch of DNA bases that contains the information used by a cell to make a _____.

a. gene / protein

b. chromosome / genome

c. allele / zygote

d. genome / chromosome

A long piece of DNA that contains many genes, often combined with proteins, forms a structure called a(n) ____ that is copied when a cell divides.

a. gene

b. chromosome

c. allele

d. genome

Different versions of a particular gene are called ____.

a. genomes

b. genes

c. chromosomes

d. alleles

A(n) ____ is the complete set of all genes, as well as the DNA bases in between genes, that are folded into ____ and housed within a cell's nucleus.

a. allele / genes

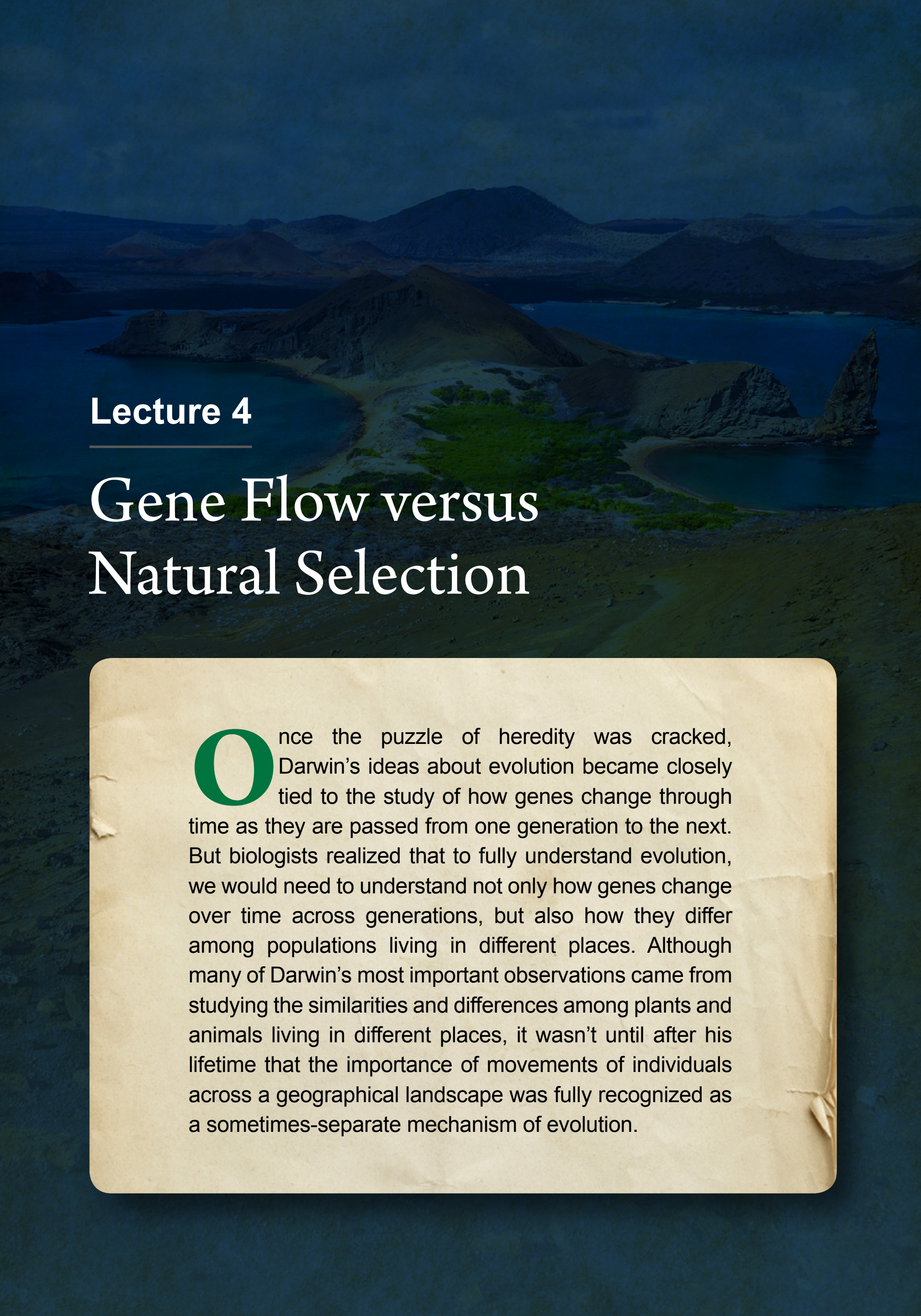
b. genome / chromosomes

c. chromosome / genomes

d. gene / alleles

Errors are often made when cells copy their genomes. Why hasn't evolution resulted in a more accurate way of copying DNA?

Answers can be found on **page 230**



Lecture 4

Gene Flow versus Natural Selection

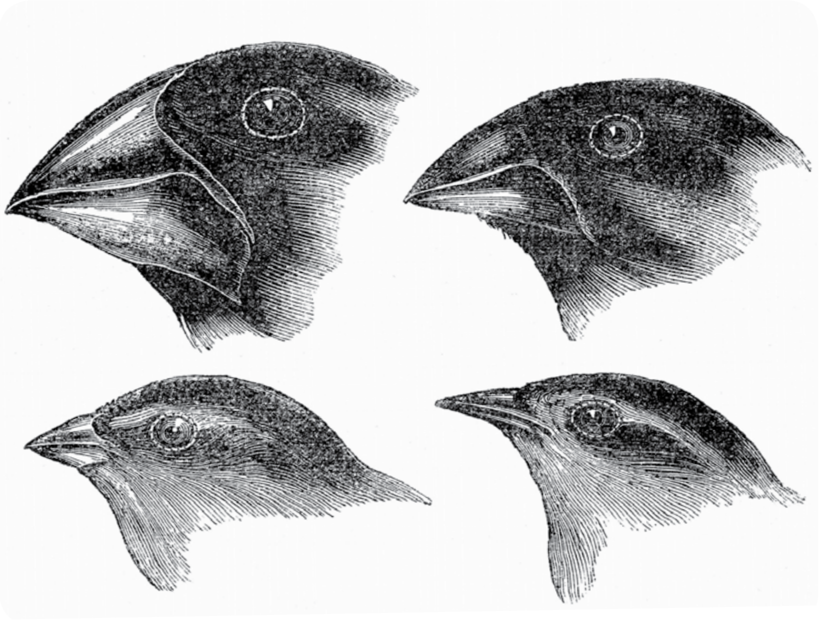
Once the puzzle of heredity was cracked, Darwin's ideas about evolution became closely tied to the study of how genes change through time as they are passed from one generation to the next. But biologists realized that to fully understand evolution, we would need to understand not only how genes change over time across generations, but also how they differ among populations living in different places. Although many of Darwin's most important observations came from studying the similarities and differences among plants and animals living in different places, it wasn't until after his lifetime that the importance of movements of individuals across a geographical landscape was fully recognized as a sometimes-separate mechanism of evolution.

Darwin's Famous Finches

- During his visit to the Galapagos Islands—and afterward, as he and others examined the specimens he collected there—Charles Darwin was deeply puzzled by what he described as the small "difference[s] between the inhabitants of the different islands." The 5 weeks he spent exploring the Galapagos Islands caused Darwin to think deeply about why species occur where they do.

- He visited 4 of the islands and was puzzled by the fact that they appeared similar, yet each had a slightly different set of inhabitants. Mockingbirds were different, and after returning to England, he would also learn that a variety of other birds he had collected were in fact all variant types of finches. Why wasn't life on each island exactly the same? And if the species on each island were different, why weren't they more different?

- Although differences in finches' beak size would eventually become clues for Darwin about how natural selection causes traits to change



over generations, it wasn't until he returned to England and gave his specimens to ornithologist John Gould that the close relationships among the species became clear.

- Gould determined that Darwin's collections of Galapagos finches represented 12 distinct species, all closely related to finches from mainland South America. That fact got Darwin thinking: Why would these islands, whose barren, volcanic environment is nothing like the lush environments in South America, nevertheless have species similar to those from South America?

- And why was life on the Galapagos so different from life on the Cape Verde islands, the first place the *Beagle* had stopped, despite both being volcanic island chains near the equator?

- This was one of many clues that led Darwin toward the development of his theory of evolution by natural selection. Visiting so many different places helped Darwin realize that distance—rather than similarity of environment—was a key factor for whether populations evolve into new species.

- When individuals of a species are able to easily interact with one another, as is generally the case for finches living together on a single small island, they will mate and produce offspring. When organisms mate, their offspring inherit a mixture of genes from both parents.

- This exchange of genes means that any differences that arise through mutation will be spread among all members of the population. That means it's difficult for mutations to lead to an evolutionary split from one species into 2. **Gene flow** through sex will keep differences from accumulating.

- In Galapagos, where there are multiple islands, the distance between them has created separation between populations. Finches living on one island may develop mutations that make them different from the finches living on another island.

- As long as enough time passes without finches from each island coming together to mate, they will eventually accumulate enough differences to become distinct species. Later, rare instances

Lake Erie is home to a species of water snake that comes in a variety of different color patterns. On the northern and southern banks, most snakes have a banded pattern, but on many of the islands in the middle of the lake, most snakes are unbanded. It turns out that the color patterns help the snakes blend into their environment and avoid being eaten.

On the islands, the snakes warm up by basking on the limestone rocks along the shoreline, where they are exposed to predators, who can more easily spot a banded snake than an unbanded one against the stark limestone. Over generations, natural selection has caused the unbanded snakes to become more common in the middle of the lake.

But why do any of the island snakes have bands if the banding pattern makes them more likely to be eaten?

The reason is that snakes from the mainland sometimes make their way out to the island. The mainland snakes are mostly banded, which gives them more camouflage on the mainland. If these banded snakes that made their way from the mainland to an island manage to avoid being eaten long enough to mate, their offspring are more likely to be banded or partially banded.

This movement of individuals and their genes from one place to another is called gene flow.

As this example shows, gene flow not only changes how common a gene is in a population, but it can also counteract natural selection.

This example also shows how natural selection can operate differently in different places. On the islands, natural selection favors one trait, whereas on the mainland, it favors a different trait. The reason is a difference in the environment: The islands are covered with limestone, but the mainland is not.

of dispersal from one island to another allowed each island to accumulate multiple species.

- Theodosius Dobzhansky, the biologist whose work with fruit flies helped him connect genetics with evolution in the 1930s, was among the first to recognize that reproductive isolation was the key to **speciation** because it allows differences to accumulate.

- Dobzhansky argued that mutation in some of the alleles in a gene of one population might not be compatible with alleles from other genes in another population. Played out over time, small incompatibilities can lead to diversification into multiple species.

- The key to making new species, then—which Darwin never realized—is preventing sex. The flip side of this idea is that populations living in different places can remain similar to one another as long as they share genes through sex.

Making Gene Flow More or Less Likely

- Natural selection causes species to become better **adapted** to the local environment by making locally beneficial traits more common. Meanwhile, gene flow counteracts selection by bringing less adaptive traits into a population and moving more adaptive traits away from a population.

- This makes it sound like natural selection and gene flow are unrelated and always work at cross purposes. But natural selection can also make it more or less likely for gene flow to happen.

- Many familiar species, such as dandelions, have evolved traits to make it easier to spread their genes to new places.

- When you blow on a dandelion, you are helping spread its seeds, which are attached to fluffy hairs that act like a parachute, allowing the seed to be carried by the wind. If the seed lands in a suitable place, it will germinate and grow into a new dandelion.

- Of course, some of the new places a seed might land won't be so great. Why leave a place that was apparently suitable enough for a dandelion to grow for a place that might be worse? Why not stay someplace that was good enough for its parent to grow? There are a few reasons:

  - Times change. The place where a dandelion is growing might be fine at the moment, but perhaps in another week it won't be so nice. By sending many seeds off in different directions, the dandelion increases the odds that at least a few seeds will end up someplace decent.

  - There are always enemies out there. If all dandelions grew in the same spot, it would be easy for animals to eat all of them, potentially wiping out an entire dandelion family. By spreading out, the dandelions make it harder for enemies to find them all.

- There are several different strategies that have evolved to help with dispersal—that is, with gene flow.

- There is dispersal by water. Coconut palm trees can be found on sandy, tropical beaches all around the world. The reason is that coconuts, which are the seeds of the coconut palm tree, are adapted for floating long distances in seawater. The part we eat is the coconut

meat, which is actually a form of stored energy that allows the coconut to last a long time before sprouting when it finally washes up on a shoreline.

- Other species have evolved ways to hitch a ride on animals. Sticker burrs, also known as grass burrs, are actually seeds from a grass that evolved to be transported by mammals by attaching to their fur.

- Another way plants evolved to encourage animals to spread their seeds is by surrounding the seeds with something delicious. Plants hide their seeds inside fruit, filling the fruit with sugar to make it more enticing. When the animal eats the fruit, the seeds are resistant to digestion, passing through the digestive tract and getting deposited when the animal defecates. This strategy not only helps the seed travel to a new location but also provides natural fertilizer to help the seed after it germinates.
- The seeds of some plants don't just get spread by animals; they are more likely to germinate after being eaten. One tree species from

Africa, *Balanites wilsoniana*, grows better when its seeds have been swallowed by elephants.

- Plants aren't the only organisms that use animals to help them spread to new locations. Aquatic snails manage to get from one lake to another by hitching a ride on the feet and legs of ducks and geese. In fact, Darwin found that such snails could cling to a duck's feet for up to 20 hours, which he estimated would give a duck enough time to fly roughly 600 miles.

- While gene flow and the ability to spread into new environments is often favored by natural selection, in some cases natural selection reduces gene flow.

- For example, natural selection often favors plants with small, lightweight seeds likely to get blown by the wind, increasing the chances that they spread even to remote islands. But once such plants become established on islands, continuing to have seeds that get blown by the wind would be much more likely to end up landing in the water and not surviving.

- A comparison of plants on islands and those on the mainland found that island plants evolved larger seeds, making them heavier and therefore less easily blown by the wind. So, natural selection may favor reduced dispersal abilities for island species, because sticking close to home will often increase the chances of survival.

Adding to the Modern Synthesis

- The relationship between gene flow and natural selection can be complex. As organisms move around from one place to another, they spread their genes, and the flow of genes between populations causes an important aspect of evolution that spreads beneficial genes and makes populations more similar to one another. In some cases, natural selection can lead to more gene flow, and in other cases, it leads to less gene flow. And gene flow can work against natural selection in cases where selection acts differently in different places.

- The understanding that gene flow can be a mechanism of evolutionary change contributed to the modern synthesis of genetics and evolution in the first half of the 20th century. The major points of the modern synthesis that we've covered so far are as follows:

  - Genes, located on chromosomes, are the basis of heritable traits.
  - Genes are passed intact from parents to their offspring.
  - Mutation and recombination are random processes that create new genetic diversity.
  - Genetic traits that are beneficial become more common over generations through natural selection.

- We can now add a 5th point:
  - Natural selection is not the only mechanism for life to evolve. The movement of individuals leads to gene flow between populations.

Gene flow has played an important role in human history. Archaeological evidence suggests that our species first evolved in Africa between 300,000 and 200,000 years ago but by 60,000 years ago had begun expanding into Asia and Europe. Eventually, waves of migrants found their way into even the most remote corners of the globe.

Genome studies are revealing that although populations in different parts of the world evolved some differences, even populations that were largely isolated from the rest of the world occasionally exchanged genes with other populations.

In fact, genome studies of extinct human relatives, such as Neanderthals, have revealed evidence for repeated instances of gene flow with our species, *Homo sapiens*. This is the reason that modern human populations living outside Africa have, on average, about 1% Neanderthal DNA in their genomes.

In other words, gene flow can be a source of variation.

Readings

Costa, *Darwin's Backyard*.

Grant and Grant, *40 Years of Evolution*.

Jobling, Hollox, Hurles, Kivisild, and Tyler-Smith, *Human Evolutionary Genetics*.

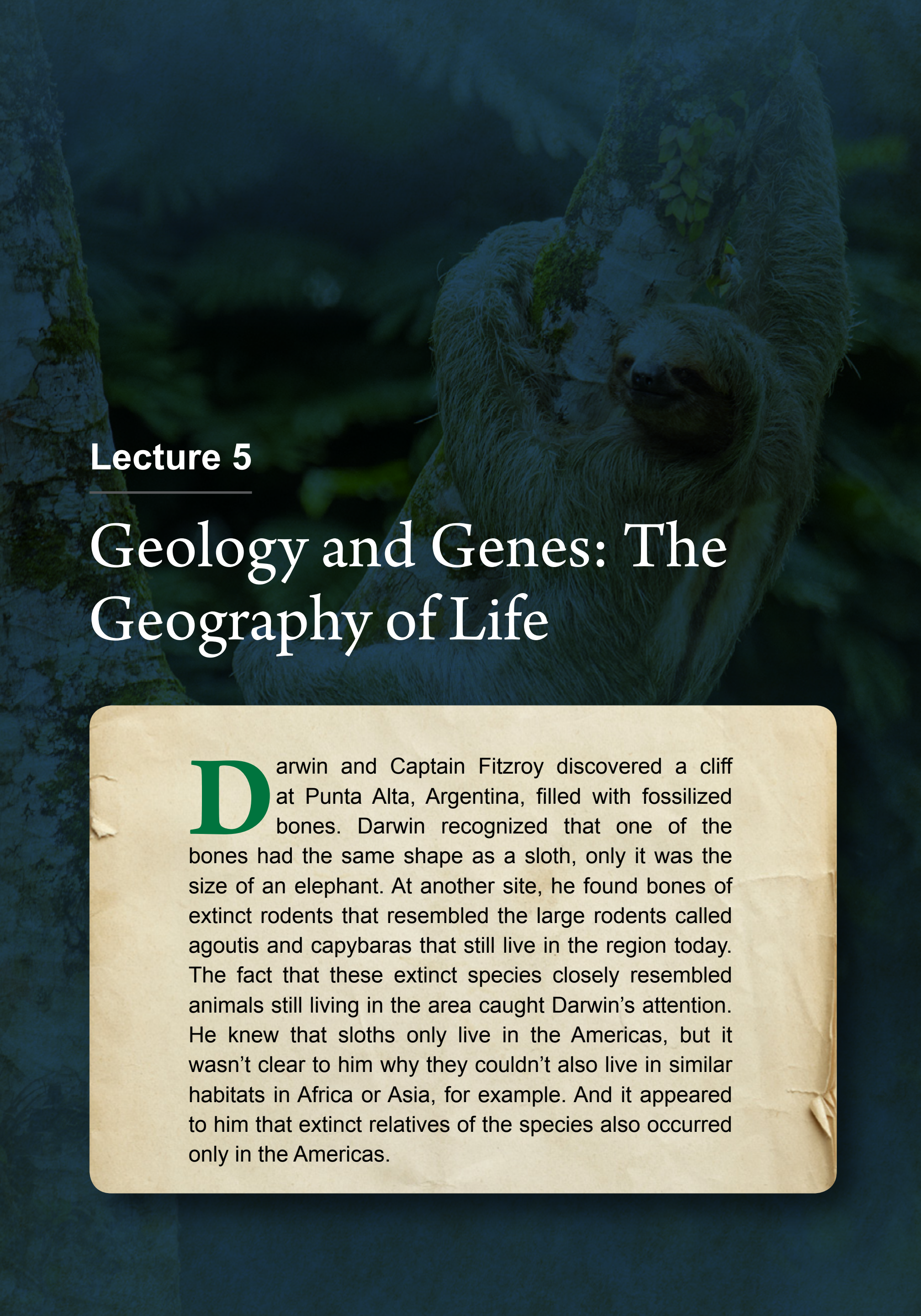
Reich, *Who We Are and How We Got Here*.

Questions

Why are archipelagoes, or other island groups, good places to study evolution?

What is dispersal? Under what circumstances would you expect natural selection to lead to organisms that are better at dispersing, and when would it lead to organisms that are poor dispersers?

Answers can be found on **page 232**



Lecture 5

Geology and Genes: The Geography of Life

Darwin and Captain Fitzroy discovered a cliff at Punta Alta, Argentina, filled with fossilized bones. Darwin recognized that one of the bones had the same shape as a sloth, only it was the size of an elephant. At another site, he found bones of extinct rodents that resembled the large rodents called agoutis and capybaras that still live in the region today. The fact that these extinct species closely resembled animals still living in the area caught Darwin's attention. He knew that sloths only live in the Americas, but it wasn't clear to him why they couldn't also live in similar habitats in Africa or Asia, for example. And it appeared to him that extinct relatives of the species also occurred only in the Americas.

Darwin's Interest in Geology

- Darwin's fossil discoveries in South America helped prime him for the observations he would later make 3000 miles away in the Galapagos Islands. These clues about the geographical distributions of living and extinct species would later be known as biogeography.

- Darwin did not know how newer geological insights, especially from the study of plate tectonics, combined with the information available from genetic studies would deepen and extend his ideas about the importance of geographical patterns in the evolution of species.

Darwin was keenly aware of the importance of geology to evolution. His interest in geology led him to his first clues about evolution, which came from fossils on the coast of Argentina, long before he ever set foot in the Galapagos Islands.

- Darwin was very concerned about proving that organisms could disperse across oceans and other apparent physical barriers. How else could he explain why some species exist in multiple regions that are separated by areas where they don't exist? Darwin supposed that a species evolving in separate locations could only achieve such a disjunct distribution if it were capable of migrating long distances.

- But with the realization that continents themselves move came the possibility that some organisms could simply raft along as the land masses slowly shifted to their new locations.

Plate Tectonics plus Genetic Studies

- Combining plate tectonics with genetic studies has helped make sense out of why organisms live where they do and how they are related to one another.

- For example, today the greatest diversity of marsupials is found in Australia. Many of them, such as koalas and red kangaroos, are found nowhere else on Earth. Yet, mysteriously, the oldest fossil marsupials aren't found in Australia; they're found on the other side of the world, in North America and China.

- A genetic analysis of living marsupial species by Maria Nilsson and colleagues found that the Australian marsupials evolved relatively recently and that marsupials lived in South America before they lived in Australia.
- Based on today's world map, it's hard to imagine how marsupials could have made their way from South America to Australia. But in the late Cretaceous period, about 70 million years ago, these land masses weren't so far apart.
- The southern landmass of Gondwana had united South America, Africa, Australia, Antarctica, Madagascar, and India in a single continent. Although pieces of Gondwana began to break away roughly 180 million years ago, when the first marsupials evolved 70 million years ago, Australia was still connected to Antarctica, which remained connected to South America.
- Fossil marsupials discovered in Antarctica provided the missing clue that helped solve the puzzle of marsupial evolution.

- The fossils found on Seymour Island, in the Antarctic Peninsula, were about 40 million years old. Comparing them with fossils found in South America, North America, China, and Australia, their similarities and ages suggest that marsupial evolution began in the Northern Hemisphere.

- The oldest marsupial fossils, found in China, are 150 million years old. By 120 million years ago, marsupials were living in North America, which was joined with Eurasia in the northern landmass called Laurasia.

- In North America, marsupials diversified into many new forms. Some of these new marsupial species traveled to South America. From there, they could make their way overland to Antarctica before moving on to Australia.

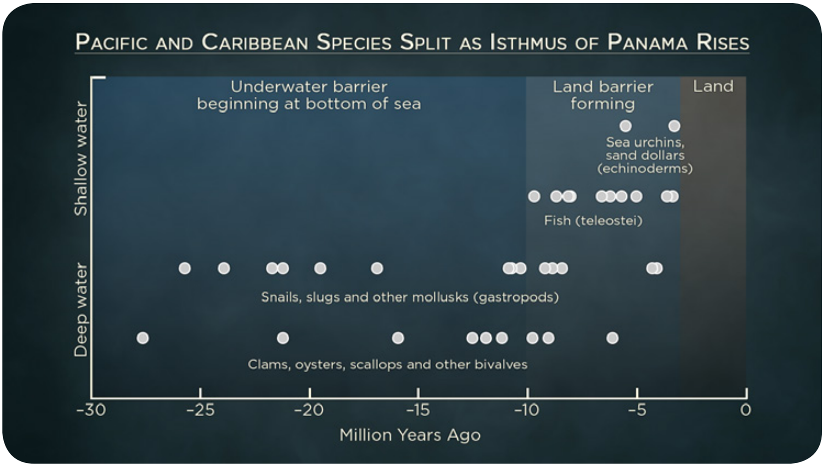
- It wasn't until 40 million years ago that Australia became isolated from all other land masses, its marsupials evolving into the many unique forms found there today.

- Meanwhile, as Antarctica drifted toward the frozen South Pole, its marsupials eventually became extinct.

- The North American marsupials went extinct, too, but for reasons that are less clear.

North and South America had been (mostly) separated since the breakup of the global supercontinent Pangea 150 million years ago, with South American species evolving separately starting about 60 million years ago. A volcanic arc had begun to form as early as 74 million years ago at the meeting place of 3 tectonic plates, but it wasn't until 3 million years ago that the land was lifted high enough, and sea levels became low enough, to form a land bridge in what is now Panama.

The formation of the Panamanian land bridge, also called the Isthmus of Panama, led to a reorganization of species known as the Great American Interchange that triggered many evolutionary changes.



Prior to the formation of the Isthmus of Panama, the Pacific Ocean and Caribbean Sea were connected, with seawater and sea creatures able to move between them. Once the isthmus was fully formed, marine organisms on one side were completely cut off from those on the other side. By preventing gene flow, this barrier allowed populations on each side to evolve independently.

Darwin had noted that based on the similarity of fish species in the eastern Pacific and the western Caribbean, these 2 bodies of water had likely once been connected before the isthmus was formed. And later geological data proved him right.

Tectonic Plates and Evolution

- The shifting of tectonic plates affects evolution in other ways, too.
- The Galapagos Islands are being continuously created anew near the boundary of 3 tectonic plates. The separation and movement of these plates interact with a hot spot in which magma rises up through the crust, creating volcanic islands.

- The oldest among the Galapagos Islands are in the southeast part of the archipelago, dating to about 3 to 4 million years ago, making the whole archipelago very young geologically. Geological dating techniques indicate that the Galapagos hot spot was forming islands at least 14 million years ago, and possibly as much as 90 million years ago.

- The collision of tectonic plates can also lead to the formation of mountain ranges that form dispersal barriers, leading to the formation of new species.

- Darwin suspected this, too, having read Charles Lyell's treatise on geology while on board the *Beagle*. In 1835, Darwin witnessed an earthquake in Chile and noticed places where the land had been lifted as much as 9 feet. He also found fossilized shells of marine creatures on an expedition into the Andes Mountains; the only logical explanation was that the shells had once been underwater but were lifted along with the surrounding rock.

- In other words, Lyell's idea that mountain chains like the Andes could be formed by gradual uplift had dramatic confirmation through events like the earthquake Darwin witnessed. We now know that Lyell's idea about uplift was correct.

- Moreover, uplift events can have especially dramatic effects on the evolution of life on Earth. In fact, the formation of the Andes—which arose from the collision of 2 tectonic plates—is responsible for creating the region that is now home to the greatest diversity of species anywhere on Earth.

- The formation of the Andes completely changed the physical geography of the continent. As the Andes rose, new habitats were created along the mountainous slopes. Some species were split into isolated populations on the west and east side of the Andes.

- To the east of the Andes stretched a vast lowland basin straddling the equator. Water from this basin once flowed west, but the rise of the Andes caused it to change direction, eventually flowing east to form what is now the Amazon River.

- These processes contributed to the evolution of many species.

Biogeographical Divisions

- Although mountain chains can be major dispersal barriers, sometimes species simply go around them.

- Imagine a species slowly expanding its range in one direction, like a slowly moving river. Suppose a mountain range blocks the flow, and the mountains are too high to go over. Perhaps the flowing river will split, with some individuals turning to the right and others turning to the left.

- If this happens very slowly, over many generations, the individuals that eventually make it all the way around to the other side might encounter those that had gone around the mountain in the other direction. But if the populations had been separated for long enough, they may have acquired some differences through the combination of mutations and natural selection. This scenario, which biologists refer to as a ring species, has happened in several places around the world.

- Geology affects evolution when mountain ranges or land bridges restrict the movement of individuals. The first person to make careful observations of these barriers was Alfred Russel Wallace, who codiscovered natural selection along with Darwin.

- On an expedition in South America, Wallace noticed that large rivers often separated species that couldn't make it across. He would later travel among the islands of Southeast Asia, where he noticed a more mysterious pattern: dramatic differences in where species could be found, but without obvious geographical barriers.

- The sea was a natural barrier for many species, but as he traveled east from mainland Southeast Asia onto the larger islands, such as Java, he found species similar to those on the mainland, including orangutans, squirrels, and woodpeckers.

- It was only when traveling from Bali to the adjacent island of Lombok that he noticed the animals became quite different. There were parrots and cockatoos and tree opossums called cuscuses—none of which could be found on Bali or anywhere else west of Lombok.

- Wallace drew a map based on his observations, with a north-south line separating Bali and other western islands, which had Asian fauna, from Lombok and other eastern islands, which had Australian fauna. It became known as Wallace's line.

- In a map published in 1876, Wallace extended his notion of different zones of animals to the entire world. He charted 6 different zones, which he called zoogeographic regions, based on differences in the types of animals that could be found in each. Biologists still use Wallace's biogeographical divisions.

- But Wallace did not know that these nearby regions were once distinct continents. Their species evolved in isolation, which is why they are so different from one another.

- That makes sense for continents, but what separates Bali from Lombok? How could 2 small islands so close together harbor such distinct forms of life?

A great many of the sites where early human fossils have been found are places that are very geologically active.

- Wallace knew that the seas separating Bali from Java were very shallow. They’re also barely more than a mile apart. He also knew that there was deeper water between Bali and Lombok. He suspected that at some time in the past, land bridges connected what are now islands to the west of his line but never extended over the line to the islands farther east. Geologists would later confirm that Wallace was correct.

The island of Flores was once home to a species of pygmy *Stegodon* elephants, only about 5 feet high. In addition, the fossilized remains of an early human species named *Homo floresiensis* were found in a cave on the island. Adults of this species stood only 3 feet 7 inches tall.

But Flores is not the only island where species have evolved to be smaller. The evolution of small body size on islands, a phenomenon called insular dwarfism, is thought to be a consequence of their isolation.

Islands—especially small, remote ones—tend to have fewer species than similar habitats on the mainland. That means less competition from other species and fewer predators. It can also mean fewer resources to sustain larger bodies.

Readings

Marshall, “Evolution by Shake, Rattle and Roll.”

McCarthy, *Here Be Dragons*.

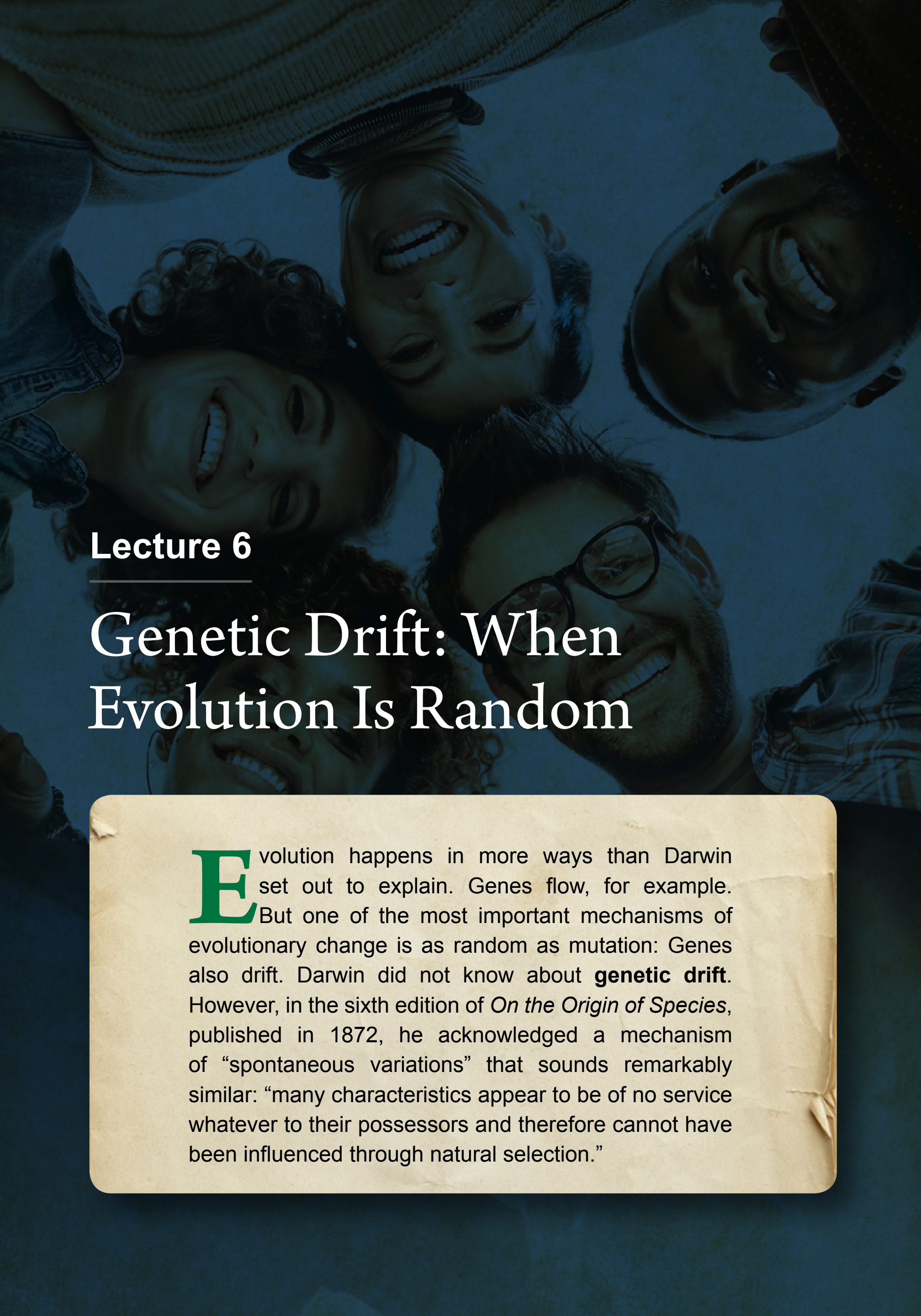
Quammen, *The Song of the Dodo*.

Questions

What did plate tectonic theory reveal about evolution that Darwin didn’t know?

How did the observations that led Alfred Russel Wallace to develop a theory of evolution by natural selection differ from those that led Darwin to develop the same theory?

Answers can be found on **page 233**



Lecture 6

Genetic Drift: When Evolution Is Random

Evolution happens in more ways than Darwin set out to explain. Genes flow, for example. But one of the most important mechanisms of evolutionary change is as random as mutation: Genes also drift. Darwin did not know about **genetic drift**. However, in the sixth edition of *On the Origin of Species*, published in 1872, he acknowledged a mechanism of "spontaneous variations" that sounds remarkably similar: "many characteristics appear to be of no service whatever to their possessors and therefore cannot have been influenced through natural selection."

A Metaphor for Genetic Drift

- Genetic drift is the random fluctuations in how common alleles are. Drift can happen in any population, but it's especially pronounced in very small populations. Any population that is suddenly reduced to a small size is likely to have a different mix of genes than the larger population had. And according to the way biologists came to understand evolution since the modern synthesis, that difference in the frequency of genes is a measure of evolution.

- The first person to recognize that genetic drift is a mechanism of evolution was American geneticist Sewall Wright. In a 1932 paper, Wright used the following metaphor to help visualize populations evolving in more than one way:

    - Imagine a landscape with hills and valleys. Pick any particular place on the landscape. This place represents the **fitness**—or ability of a population or individual to survive and pass on its genes—of a population at some point in time. The higher a place is on the landscape, the greater the fitness of the population.

- Wright used this metaphor to think about how the fitness of a population changes as different evolutionary forces act on it. Natural selection favors only the most fit individuals—those that are best at passing on their genes in the current environment—so natural selection should cause a population to move from any point on the landscape toward a higher point.

- If some of the hills are higher than others, then natural selection operating on a population that starts off near one of the lower hills will begin to climb the nearby hill until it reaches the top. The fitness of the population is now higher than it was before, but not as high as it could be if it were on top of the highest hill.

- But this is where Wright pointed out that natural selection alone could never cause a population at the top of a medium-sized hill to make it to the top of the highest hill. Going down and across a valley would mean that fitness would first have to decline before it could increase again.

- Wright knew that natural selection alone could not cause this to happen, because selection can't operate with a long-term goal in mind. Whatever traits are beneficial at a particular moment in time will be favored by natural selection, not those that would be beneficial at some point in the future if current advantages could be undone.

- But if another evolutionary force were to on occasion randomly move the population from one point to another, the chances of getting closer to the highest peak in the landscape would be better.

- Wright proposed that in very small populations, the effect of random events becomes amplified, making it possible for a population to "drift" from one point in the landscape to a point that represents equal or lower fitness. This force became known in the 1940s as genetic drift.

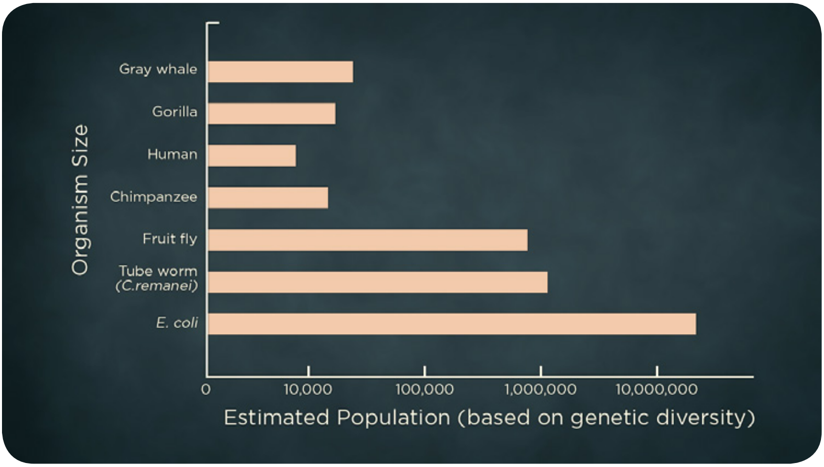
- Acting alone, genetic drift would cause a population to roam randomly around the landscape. The population might make it up a hill but just as likely might walk down into a valley.

- But what if genetic drift and natural selection could work together? Natural selection would cause the population to move up a hill, and then genetic drift might take it back down and across a valley, where that population may find itself at the base of another hill, and natural selection would push it up. In the long run, where the population ends up would depend on a specific combination of natural selection and genetic drift.

Adding More to the Modern Synthesis

- Charles Darwin did not know about genes or genetic drift. But in the sixth and final edition of *On the Origin of Species*, he admitted: "In the earlier editions of this work I underrated, as it now seems probable, the frequency and importance of modifications due to spontaneous variability."

- Darwin's grudging recognition of "spontaneous variability" played no role in his own theory. But it did foreshadow the work by 20th-century scientists like Wright on genetic drift, which became another pillar in the unification of genetics and evolution in the first half of the 20th century known as the modern synthesis.



  - Genes are the basis of heritable traits.
  - Genes are passed intact from parents to offspring.
  - Mutation and recombination are random processes that create new genetic diversity.
  - Genetic traits become more or less common over generations through natural selection.
  - The movement of individuals leads to gene flow between populations.

- Now we can add a sixth key point that defined the modern synthesis:
  - Genetic traits can become more or less common over generations through genetic drift.

- The modern synthesis did more than just link genetics and evolution; it also made both fields more quantifiable, more mathematical, more measurable.

The Hardy-Weinberg Equilibrium

- A cornerstone principle of the modern synthesis is the Hardy-Weinberg equilibrium, which showed in 1908 that the proportion of individuals in a population with different combinations of alleles could be easily calculated. Moreover, these proportions remain the same from generation to generation as long as the following equation holds true:

  $$pr = q^{2,}$$

- Where p is the number of individuals that are homozygous dominant, r is the number of individuals that are homozygous recessive, and q is the number of heterozygous individuals.
- The Hardy-Weinberg principle is an equilibrium that stays in balance only under a very strict set of assumptions, which taken together rule out any evolution:
  - All the individuals in the population must choose their mates randomly (no sexual selection).
  - All individuals must have the same number of surviving offspring (no natural selection).
  - There can be no movement from one population to another (no gene flow).
  - No new traits can ever appear (no mutations).
  - The population must be very large—infinitely large, to be exact (no genetic drift).
- Satisfy all these simple criteria and there won’t be evolution of any kind; the proportion of alleles in a population will remain the same indefinitely.
- The fact that no real population could ever meet all these assumptions is exactly the point: Real populations will always violate the assumptions of the Hardy-Weinberg equilibrium, and however they do, the proportions of alleles will change.

- In other words, evolution—often for more than one reason—is inevitable. In fact, because real populations are never infinite, we expect that genetic drift, all by itself, is always inevitable.

Effects of Genetic Drift

- Although genetic drift takes place randomly, the effect is a tendency to reduce genetic diversity within a population. But low genetic diversity is a problem, especially if the population is small. Variation is the raw material for natural selection, but without much variation, a species cannot adapt to changing conditions. Reduced diversity can be a major step toward extinction.

- To make matters worse, in small populations, there aren't a lot of options when it comes to choosing a mate, so the chances are greater that your mate may be a relative. Mating with a relative increases the odds that both individuals have a recessive allele for the same gene, in which case 1 out of every 4 of their offspring are expected to have 2 copies of the recessive allele. If the recessive allele has a harmful effect, the harmful effect will no longer be hidden.

- This is the reason why inbreeding can sometimes lead to higher rates of genetic disorders and birth defects. Biologists call this inbreeding depression.

Population Bottlenecks and Founder Events

Population bottlenecks occur during any sudden, drastic reduction in population size. Population bottlenecks are one way that small population sizes can lead to genetic drift.

Another way is when a few individuals establish a new population—for example, on an island. Such founder events lead to genetic drift because as the population grows, the genetic traits of the founders are the only traits that will be present in the population, plus any new traits that arise from mutations. Founder effects and isolation are likely to cause genetic drift any time a new population is established.

- Yet for a species that has been reduced to a small population size, there aren't many alternative mate choices, so individuals often end up mating with relatives, leading to higher levels of inbreeding depression.

- Very small populations are really in trouble. Any random accident, such as a natural disaster or a sudden food shortage, could wipe out a significant percentage of the remaining population. With an even smaller population, there's even less diversity and even worse effects from inbreeding.

- This downward spiral is called the **extinction vortex** by biologists. Once a population becomes very small, it's very difficult to escape the vortex. The most likely outcome is extinction.

The Neutral Theory of Molecular Evolution

- Genetic drift can drive alleles to be fixed (the only variant that exists for a particular gene in the whole population) or lost completely. Both outcomes lead to less diversity, and the effects are much stronger in small populations. But genetic drift can, and does, occur even in large populations.

- One of the first people to come to this conclusion was the Japanese biologist Motoo Kimura in 1968. He noted that mammals have more mutations in their genes than would be expected if natural selection were the only evolutionary force affecting them. He argued that many of the mutations in mammalian genomes don't have a positive or negative effect on an organism's ability to survive and reproduce. In other words, mutations are often neutral.

- Wherever a mutation is neutral, it won't be affected by natural selection. But every mutation will evolve by genetic drift. Because genetic drift is always operating and affects every part of the genome,

Evidence of neutral molecular evolution can be seen throughout the genomes of organisms. By comparing the genomes of different individuals within a species, we can measure how many differences exist at particular places in the genome.

Kimura suggested that genetic drift is in fact the predominant force affecting the evolution of mammalian genomes. The idea became known as the neutral theory of molecular evolution.

- Interestingly, this theory tells us that the amount of drift-related variation in a genome increases with the size of the population. So, we can use drift-related variation to estimate the size of a population just by measuring the genetic diversity at neutral sites. In fact, we can do the same thing by looking at lots of neutral sites within the genome of an individual.

Fossil evidence shows that our species, *Homo sapiens*, first evolved in Africa roughly 200,000 years ago but began expanding out of Africa sometime between 130,000 and 50,000 years ago. Archaeological data shows that humans spread through the Middle East, with some spreading west into Europe and others spreading east into Asia. Gradually, groups of intrepid pioneers reached the most distant lands, making it all the way to Australia and the Pacific Islands and across the Bering Strait to the Americas.

Human genetic diversity matches the history suggested by the archeological record. The greatest amount of genetic diversity in modern humans can be found in Africa, with lower diversity in the Middle East, Europe, and Asia and even less in Australia and North and South America.

This pattern of decreasing genetic diversity with increasing distance from Africa reflects a history of successive population bottlenecks and founder events.

Readings

Futuyma and Kirkpatrick, *Evolution*.

Quammen, *The Song of the Dodo*.

Questions

Is it possible for a species to not evolve?

Mutations and genetic drift are both random processes that contribute to evolution. In what ways are they similar, and in what ways are they different?

Which of the following is an example of gene surfing, and which is an example of genetic drift?

a. A seed washes up on the shore of an uninhabited island and grows into a tree with shaggy bark. A thousand years later, the island is filled with trees, all of which have shaggy bark.

b. As the glaciers melted at the end of the last ice age, trees began to grow in the newly exposed soil. The trees closest to the melting glaciers happened to have shaggy bark. A thousand years later, the area formerly covered by glaciers is filled with trees with shaggy bark.

Answers can be found on **page 234**

Lecture 7

Rapid Evolution within Species

Darwin considered evolutionary change to be a process that occurred very slowly. But research on a wide range of different species has shown that evolution can actually happen rather quickly—so quickly, in fact, that we can watch as it plays out in real time.

Evolution in Galapagos Finches

- Ironically, one of the best examples of rapid evolution comes from the Galapagos finches that helped inspire Darwin's ideas about slow, gradual change.

- Peter and Rosemary Grant have spent their careers conducting detailed studies of these birds. Much of their time in the field has been spent on a single small island called Daphne Major, returning there every year for more than 4 decades, beginning in 1973. The island is largely uninhabited because there is no reliable source of fresh water and no trees to provide shade from the equatorial sun.

- One advantage of working on the remote, inaccessible island of Daphne Major is that there has never been much of a human presence on the island to affect the natural processes as they play out.

- Another advantage is its small size. At just 84 acres in area, the Grants are able to capture every finch on the island and thus have tracked the entire population from year to year. And by taking blood samples, they could determine how all of the birds are related. They also recorded many different body measurements of each bird, from the depth of its beak to the color of its plumage.

- In 1977, the Galapagos Islands experienced a severe drought. Compared to a population of 751 medium ground finches before the drought, the Grants found that after the drought there were only 90. And when they analyzed their data, they discovered something no one had ever seen before: evidence that evolution had occurred in a wild species in just one generation.

- Prior to the drought, the medium ground finches had beaks that ranged in depth from about 8 to 11 millimeters, with an average of 9.2 millimeters. After the drought, the surviving finches had an average beak depth of 9.7 millimeters—an increase of 15%.

- Despite experiencing a population bottleneck, the change in beak depth wasn't caused by random genetic drift. Larger beaks were favored by natural selection.

- The drought also had a big impact on the plants living on Daphne Major, including one called spurge that makes small seeds that the finches like to eat. Without their favorite food during the drought, the finches were forced to try to eat the only other source of food on the island: a larger, spiky, hard seed called caltrop—which finches struggle to crack open.

- But finches with larger, deeper beaks can apply more force to the caltrop seeds and are therefore better at cracking them open. Beaks better adapted to switching to the alternative food source had a better chance of surviving.

- The Grants continued returning to Daphne Major every summer, and before long they witnessed natural selection at work again. It was particularly rainy in late 1982 to early 1983, leading to an abundance of the finches' preferred food, spurge seeds. With lots of tiny seeds to eat, big beaks became more of a liability than an asset, and the average beak depth declined by 2.5%.

- The Grants had not only shown that natural selection can cause rapid evolutionary change; they had also shown that the traits favored by natural selection can fluctuate as the environment changes.

- Since the Grants' pioneering work on Galapagos finches, many other studies have found evidence for rapid evolution. Quite a few of these studies also come from islands, such as the Hawaiian Islands and Trinidad, because their biological communities tend to be smaller and simpler than on the mainland.

Comparison of the genomes of 13 species of Galapagos finches suggests that the evolution of the entire group has happened rapidly. The common ancestor of the 13 species lived just 2 million years ago, and some finch species may have come into existence in just the last 100,000 to 300,000 years. Based on DNA data, a new species might emerge in as little as 200 years of sustained change in a single direction.

Effects of Human Actions on Species

- Thanks to us humans, rapid evolution seems to be happening more often.

- Darwin used the idea that humans can cause other species to evolve as the opening argument in *On the Origin of Species*, pointing out how effectively breeders can develop new varieties of crops, livestock, and pets.

- Pigeons were a prime example. In Darwin's day, keeping pigeons was a popular hobby. Pigeon fanciers, as they are known, had developed all kinds of different varieties through selective breeding. They differed in size and color, with some breeds having crests on their heads or elaborate crowns that resemble a lion's mane.

- Darwin kept many pigeons himself, mostly as research subjects. He made the case that all these pigeon varieties could be traced back to a wild ancestor: the rock pigeon. If so, that meant that all the differences between pigeon breeds came about since the time that people had been breeding them.

- At least one line of evidence suggests that domestication of a wild animal could happen quickly. In 1959, biologists Dmitri Belyaev and Lyudmila Trut began an experiment to see if they could breed foxes to become tame. Part of the motivation was to see if foxes could become domesticated, just as wolves had been thousands of years ago, leading to the first dogs.

- Belyaev and Trut bred only foxes that seemed the least afraid of humans and found that the calmer a fox was, the calmer its offspring tended to be. After just a few generations, they were already seeing calmer behavior on average, and a few foxes were less aggressive than any of the original foxes had been.

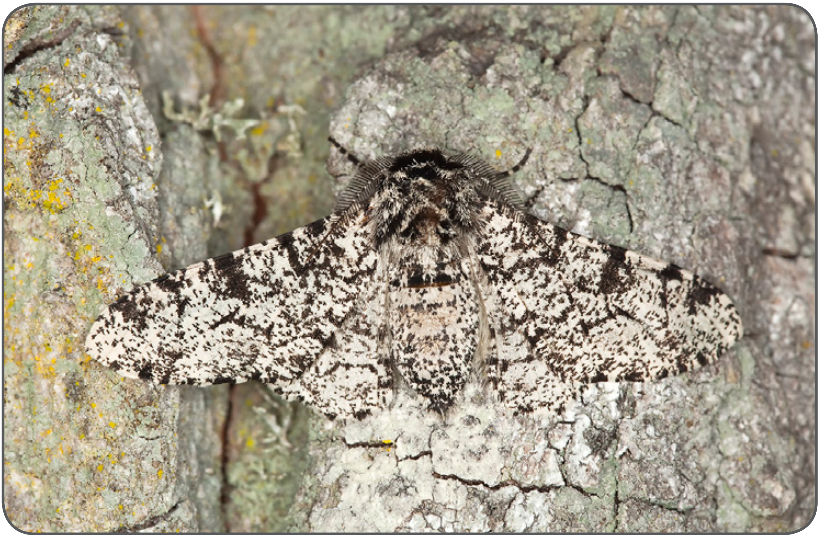
- One fox pup in the fourth generation wagged its tail when a person approached, a behavior then known only in dogs. By the sixth generation, a few of the pups were licking their caretakers' hands and rolling over on their backs to have their bellies rubbed. These doglike behaviors became more common in each subsequent generation until the vast majority of descendants behaved like dogs.

- Doglike behaviors became more common in each generation until the vast majority of descendants behaved like dogs. The foxes began to look like dogs, too. Some developed floppy ears, curly tails, and white patches of fur. As was already recognized in Darwin's time, these traits are found across a variety of domestic animals, such as pigs and rabbits. Even though these traits weren't being selected for in the foxes, they became more common as the foxes became tamer.

- Belyaev and Trut showed that foxes can be domesticated in much the same way as dogs—and in just a few decades.

- There are also examples in which rapid evolution was an unintended consequence of human actions. The peppered moth, and how it evolved in response to a change triggered by industrial pollution, is one of the earliest-studied and most famous examples.

- Peppered moths get their name from their color pattern of white with black speckles. But during the 19th century, a dark black variety of the same species appeared in England and quickly became common. By 1895, almost the entire population—about 98%—was black.



- The suspected reason for the color change was the rise in air pollution from the Industrial Revolution, which killed the lichens that grow on trees in certain parts of England and changed the trees' appearance. The pollution even turned some tree trunks black with soot. Whereas the white, speckled peppered moths had once been well camouflaged on the lichen-covered trees, the moths now stood out in stark contrast, making them easy pickings for predators, such as birds.

- The opposite was thought to be true for the dark-colored moths. Whereas they had presumably been easy prey before the pollution, the black moths were now well hidden on the dark trunks and branches—that is, until the 20th century, when electricity replaced burning coal as the engine of industry and air quality standards were introduced in the UK. As pollution levels declined, lichens returned to the trees, and the dark form of the peppered moth once again became rare.

- Scientific experiments proved that the rise and fall of the dark form of peppered moths was due to natural selection. Results showed that peppered moths are eaten by birds and that when there is no

Genome studies have pinpointed the genetic basis for the different color varieties of peppered moths to a gene called *cortex*.

Statistical analyses of the *cortex* gene pointed to a single mutation that occurred around the year 1819, just before the first black forms began appearing in insect collections.

The DNA sequence data showed a signal of recent natural selection, consistent with the evidence that the mutation responsible for the black form quickly became common and later became rare as air pollution levels rose and fell in the 19th and 20th centuries.

significant air pollution, the dark form is eaten more often than the light form.

- Another trigger for rapid evolution is the movement of people and goods around the world—because we often bring stowaways. Species that are accidentally introduced to a new place often trigger rapid evolutionary changes in the species already living there.

Soapberry bugs feed on seeds of soapberry plants using their needlelike beaks to pierce through the outside of a fruit.

Soapberry bugs native to Florida evolved beaks that were just the right length to get to the seeds inside the fruits of native soapberry plants.

But when people began planting ornamental soapberry plants from Asia in the 20th century, some of the bugs began taking advantage of this new food resource—but compared to the native plant, the introduced plant had smaller fruits, meaning the soapberry bugs didn't need such long beaks to reach the seeds.

Ecologist Scott Carroll found that the bugs evolved shorter beaks in just a few decades.

- In some cases, hunting and fishing have caused rapid evolution in the species being targeted.

- Bighorn sheep are sometimes hunted for sport and their large horns are considered valuable trophies. Because the animals with the largest horns are the most likely to be killed by trophy hunters, smaller horned individuals should be favored by natural selection. Indeed, data from a population of bighorn sheep in the Canadian Rockies showed that since 1975, the average horn size decreased.

- Commercial fishing operations are very effective at harvesting lots of large individuals. Data from populations of Atlantic cod show that from 1977 until the mid-1990s, the average size of fish was decreasing. Not only were they getting smaller, they began maturing earlier. That's because, like many fish, cod don't reproduce until they reach a certain size. Removing the larger individuals meant that those that were able to reproduce when they were younger and smaller left more offspring.

- There's a troubling irony in these last few examples. By targeting and killing the largest animals or those with the biggest horns, natural selection quickly led to a reduction in the exact thing being targeted. In the case of bighorn sheep, this might mean the trophies will become less impressive in just a few generations.

Readings

Dugatkin and Trut, *How to Tame a Fox*.

Grant and Grant, *40 Years of Evolution*.

Grant and Grant, *How and Why Species Multiply*.

Losos, *Improbable Destinies*.

Weiner, *The Beak of the Finch*.

Questions

What caused the change in beaks of the medium ground finches on the Galapagos Island of Daphne Major following the 1977 drought?

In the mountain streams of Trinidad, guppies living in the upper sections of streams—above the waterfalls—tend to have males with larger and more brightly colored spots than the guppies in lower ponds. What would you expect to happen if pike cichlids, the predators of these guppies that only live in ponds below the waterfalls, were introduced into the high ponds?

Answers can be found on **page 235**

Lecture 8

Evolution in the Lab

Experiments on animals and plants conducted in the field have the advantage of using a setting that incorporates the complexity of nature, making the experiments more realistic. But that complexity can also make it hard to control variables, as researchers try to do when conducting experiments. For that reason, experiments conducted in carefully controlled laboratory settings offer a powerful approach to complement experiments done in the field.

Darwin's Experiments

- Some of Darwin's first hints about evolution came from observations, especially those he made on his around-the-world journey aboard the *Beagle*. But he also conducted experiments, from simply throwing a marine iguana back into the sea to confirm it could swim to dangling dead ducks' feet into water to see if snails would latch on.

- However, what all Darwin's experiments lacked was an effort to observe evolution in real time. He focused on traits of living organisms, including comparisons among species, to work backward and reconstruct how evolution had played out in the past.

- Because of his assumption that evolution could only happen slowly, Darwin apparently regarded real-time experiments on evolution as impossible. However, researchers in the second half of the 20th century increasingly found that evolution could operate much faster than many biologists—including Darwin—previously thought.

- Examples of rapid adaptation opened up the possibility that an experimental approach could be used to test ideas about evolution in ways that Darwin didn't realize were possible.

Experiments with Microorganisms

- Because evolution is change that happens over generations, microorganisms—such as bacteria, yeast, and single-celled protists—are ideal experimental subjects because they reproduce quickly.

Some bacteria, such as *E. coli*, can reproduce in as little as 20 minutes

- One of the first attempts to conduct a laboratory experiment on real-time evolution was performed by William Henry Dallinger in the late 19th century. Darwin had commended Dallinger's earlier study of microorganisms, which included figuring out the maximum temperature that some bacteria could tolerate.

- In 1880, Dallinger began another experiment with microorganisms that he grew in an incubator where he could carefully control the temperature. He started his microorganisms at a comfortable temperature of 60° Fahrenheit (15.5° Celsius) but slowly increased it.

- He found that if the temperature rose too quickly, the microbes would die. But a slight increase, followed by a month at the same temperature, allowed them to adapt to the heat. Because microbes reproduce very quickly—dozens of times per day—these changes were indeed evolutionary and not the result of individuals becoming more comfortable with a gradual change.

- After 6 years, the microbes had evolved to grow at 158° Fahrenheit (70° Celsius), a temperature that would have quickly destroyed the first generation. Interestingly, Dallinger found that although the microbes could tolerate heat, they had become unable to grow at the first generation’s starting temperature.

- There’s a trade-off: Natural selection chooses those best adapted to current conditions, but previously useful traits may be sacrificed to get there.

The Long-Term Evolution Experiment

- A century later, in 1988, biologist Richard Lenski set up an experiment to understand how microbes evolve to tolerate stressful conditions. He chose *E. coli* bacteria as his research subjects, in part because they were well understood, thanks to decades of research.

- *E. coli* bacteria have become common laboratory organisms because they are easy to work with. Another advantage of *E. coli* is that, like other bacteria, they reproduce by making identical copies of themselves. An individual bacterium is just a single cell, so when bacteria reproduce, they simply make a copy of their DNA and then split themselves in half. The result is that each cell is identical.

- Lenski started his experiment with 12 identical clones of a particular strain of *E. coli* he had been growing in the lab. He transferred each into a flask containing liquid with a fairly typical mix of ingredients.

- But Lenski wanted the environment to be somewhat stressful for the bacteria so that they would be more likely to evolve in order to tolerate it. He did so by restricting their diet to sugar, in the form of glucose—and not much of it.

- Without much food, the bacteria reproduced slowly. Still, the number of bacterial cells in the flask would double with each generation. After about 6 hours, they had consumed all of the sugar, and they stopped reproducing.
- The next day, Lenski took a small sample from each flask and transferred it to a fresh one containing the same broth. Finding themselves with a source of energy once again, the bacteria could continue reproducing.
- The same procedure was repeated every day by Lenski or one of his lab members. It became known as the long-term evolution experiment.
- To figure out if the bacteria were evolving to the harsh environment, the team measured how quickly the bacteria reproduced within their flasks each day.
- After 6 years of daily transfers, corresponding to 10,000 bacterial generations, the *E. coli* in all 12 populations were growing faster than their ancestors from the first generation. After 20,000 generations, they were growing faster still.
- It was clear that the bacteria were evolving to be better able to tolerate the small amount of available food.
- Because the bacteria had all been identical at the beginning of the experiment and because bacteria reproduce by making identical clones of themselves, the only way for the *E. coli* to have become better adapted was through mutations, which happen when there is an error when copying DNA.
- Most mutations are harmful, but any beneficial mutations become more common through natural selection. Could the *E. coli* have developed beneficial mutations precisely because they were helpful?

Even after more than 68,000 generations, the *E. coli* in Lenski's long-term evolution experiment continued to get better adapted to their low-sugar environment.

Or do mutations occur randomly, regardless of whether they're helpful or not?

Research on Beneficial Mutations

- Thanks to an experiment done by Joshua and Esther Lederberg in 1952, also using *E. coli*, we know that mutations happen whether or not they are helpful.

- Most *E. coli* are susceptible to a virus called T1, although occasionally a mutation occurs that makes the bacteria resistant to the virus. If mutations happen more often when they are needed, then exposing *E. coli* to the virus should cause the resistance mutation to occur more often than in those that are not exposed to it.

- To test this idea, the Lederbergs grew identical clones of nonresistant *E. coli* on petri dishes, where they form clumps of cells called colonies. The experimenters were able to make exact replicas of the colonies on a petri dish by placing a velvet disk on its surface and then touching the disk to other petri dishes, like a stamp.

- Because the *E. coli* cells are sticky, some of them attached to the velvet and were transferred to the new petri dish. Each petri dish then had an exact copy of all the same bacteria colonies in exactly the same locations.

- Next, the Lederbergs exposed all of the bacteria on all of the petri dishes to the T1 virus. Most of the bacteria were killed by the virus, except those that had the resistance mutation.

- If the resistance mutation had occurred randomly, regardless of whether the T1 virus was around, then some of the bacteria should have had it before the virus was added. In that case, the same colonies should have survived in all of the replicas because they would all have the resistance mutation.

- But if the mutation only happened after exposure to the virus, then it shouldn't have been present before the virus was added. In that case, the bacteria that developed the mutation should be different in each replica because the mutations would have occurred after they were transferred.

- The Lederbergs found that each of the petri dishes looked pretty much the same, meaning that the resistance mutation happened before they were transferred—and therefore before exposure to the virus.

- This simple experiment helped resolve a fundamental question about the genetic basis of evolution: Beneficial mutations occur randomly, not because they are beneficial.

Understanding Apparent Paradoxes in Nature

A generalist species can eat a lot of different kinds of foods while a specialist might eat just a few. Why would evolution cause a species to be restricted in what it eats? If one type of food becomes scarce, wouldn't it be advantageous to be able to eat other things? So, why haven't all species evolved to be generalists?

One explanation for this paradox that evolutionary biologists have come up with is that evolution involves trade-offs. And experiments show that trade-offs really do exist and suggest that they can happen as a result of evolution causing one trait to improve to the detriment of another trait.

How Evolutionary Forces Interact

Selection experiments in which only fruit flies with long wings are allowed to reproduce led to flies with longer wings. But these same experiments were also able to test whether the size of the population had any effect on how quickly and effectively selection operates.

Smaller populations are more susceptible to genetic drift, in which traits become more or less common due to random chance. In selection experiments, fruit flies raised in populations with only 40 individuals still evolved longer wings, but not as much—or as quickly—as populations with 1000 individuals.

Digital Life Simulations

- More traditional approaches continue to give us new insights into the history of evolution, such as making comparisons among currently living species as well as fossils, but experiments can be a powerful addition to studies on evolution by teasing apart the details about how evolution works.

- However, even experiments using small species that reproduce quickly, such as insects and microbes, are limited by the amount of space available in the lab and by the amount of time they can be followed.

- To study evolution over very long time spans, the ideal organisms might be computer programs. Research in this area has shown that an outcome that seems very unlikely to happen randomly can be generated through the cumulative effects of simulated natural selection choosing from random mutations.

- Unfortunately, an evolutionary approach can also be used to design malicious computer programs, or malware. These programs really can act like viruses, continuing to evolve as they infect their hosts—which is part of what makes them difficult to detect and to stop. But digital evolution can also be part of the solution by evolving ways for a computer’s software to detect and defend against malware.

- Much more sophisticated programs have since been developed for biology as well, leading to a new field called digital life. In some **digital life** programs, processes akin to mutation and selection allow different programs to compete within a computer for access to the computer’s memory. Those that are effective spawn more copies of themselves, leading to evermore efficient programs.

- Researchers conducting experiments using digital life have made discoveries that would never have been possible with live organisms. Simulations have also been used to predict future evolution.

- The fact that experiments using digital life can lead to new ideas that can then be tested in living organisms makes simulations a powerful addition to evolutionary science.

What will be the future evolution of Darwin's finches in the Galapagos?

Museum records had suggested that a parasitic nest fly, *Philornis downsi*, arrived in the Galapagos during the 1960s, with the mangrove finch already facing extinction. Simulations were used to predict 2 scenarios under which the medium ground finch might be next to go extinct within 50 to 100 years, if infestations are not reduced and if the finches do not evolve greater immunity.

Readings

Costa, *Darwin's Backyard*.

Losos, *Improbable Destinies*.

Questions

Why are microorganisms like bacteria such good research subjects for studying evolution in laboratories?

What's wrong with the following statement?

> Mutations occur to help improve a species' ability to survive and reproduce.

Answers can be found on **page 237**

Lecture 9

The Many Origins of Species

Despite its title, *On the Origin of Species* focused on slow, gradual change within a species and did not fully address the question of how new species come into existence through evolution. Darwin's surprising answer to this question was that it was nothing more than a very slow process of changes, with no particular change more special than any other. He wrote, "I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety." Species were simply varieties that varied a little more.

The man known as Johnny Appleseed is legendary for planting apple trees across North America. But did you know that he may have inadvertently triggered the evolution of new species?

What makes this really surprising is that the new species weren't apples; rather, the introduction of apples led to new species of fruit flies, whose larvae eat the apples.

By 1758, Carl Linnaeus had named 12,000 species of plants and animals in his *Systema Naturae*, almost all of which came from Europe. Students and followers of Linnaeus divided up the task of extending his work and pushed that number much higher in subsequent decades. For example, the number of valid fly species alone rose during the first half of the 19th century to more than 20,000.

From Distinct Varieties to Distinct Species

- Darwin reached his point of view on the origin of new species after 8 years of categorizing barnacles—all known species and varieties of barnacles, fossils and living—a vast undertaking for a group that biologists now think have more than 1200 species.

- So, Darwin was focused on how small variations can accumulate into bigger effects, and this helped him recognize that species don't just evolve from one species into another with nothing left behind. If they did, there would only be one species alive on the planet. It would be descended from the first species on Earth, which would have gone through lots and lots of intermediate forms, eventually giving rise to the one version alive today.

- Instead, when we look around the planet, we see an almost unbelievable diversity of different types of life. The oceans, lakes, forests, deserts, and mountains are teeming with so many incredible species that even trained naturalists can become overwhelmed—and it was during Darwin's generation when the number of species first started to become overwhelming.

- What evolutionary force results in the splitting of one species into several? Darwin believed that natural selection acting on variations within a species would cause certain varieties to become more and more distinct.

- He used a hypothetical example to illustrate how he imagined this might work. He pointed out that a field planted with many different types of grass will support a greater number of individual grass plants than if a single type of grass is planted. In other words, there is a benefit to diversity.

- By the same logic, then, if a single species of grass is planted, the more variation there is among individuals, and the more individuals there will be.

- Darwin used this reasoning to suggest that variation itself will be favored by natural selection. As he put it, “in the course of many thousands of generations, the most distinct varieties of any one species of grass would always have the best chance of succeeding … thus of supplanting the less distinct varieties.”

- Darwin supposed that those “distinct varieties” could eventually become distinct species. But there was a fundamental flaw in Darwin’s thinking: Sex prevents new varieties from maintaining their distinctiveness.

What exactly is a species?

There is not a single definition of what a species is that can be applied equally to all living things. But this doesn’t prevent us from understanding how evolution creates variety. In practice, researchers take a somewhat pluralistic approach to the definition of species:

- A species is a group of individuals that share a common evolutionary history, which often results in similar appearance and similar roles in their ecosystems. For organisms that reproduce sexually, members of a species should be able to interbreed and produce fertile offspring.

How Variations Lead to Different Species

- The problem with Darwin's line of thinking is that organisms living in the same place usually exchange genes through sex. Darwin's example was grass. Suppose one variety of grass had a mutation—such as fluffy seeds, allowing the seeds to be carried farther by the wind.

- If the fluffy-seed pollen were to fertilize an ovule from nonfluffy, nonmutated grass, the offspring would likely be a grass that would not have fluffy seeds, or at least have fewer fluffy seeds.

- Based on what we now know about gene flow, any new mutation would lose its distinctiveness through sexual reproduction with other individuals lacking that mutation. This is a reason why *Homo sapiens* have not diversified into more than one species.

- This problem of variation getting drowned out by gene flow was pointed out in 1935 by Theodosius Dobzhansky, who went on to elaborate some now-classic ideas about speciation in his 1937 book *Genetics and the Origin of Species*.

- Dobzhansky's key idea was that differences can persist only if there have been barriers to gene flow. He divided those barriers into 2 categories: **prezygotic**, which prevent the formation of a zygote, or fertilized egg; and **postzygotic**, which prevent a formed zygote from developing into a living organism that is itself capable of reproduction.

- Both prezygotic and postzygotic barriers contribute to the origin of species.

- Some prezygotic barriers relate to timing. One population of periodical cicadas has a nymph stage that lasts 13 years, after which the cicadas emerge as adults in order to mate and lay eggs. Another cicada population has adults that emerge every 17 years. Because these populations have life cycles that are out of sync, they will almost never encounter one another, so they could never mate.

- Sometimes the timing differences can be seasonal. For example, a bird called the band-rumped storm-petrel has population barriers based on breeding at different times of year.

- Other types of prezygotic reproductive barriers involve finding a mate. Mating calls are one important barrier. For example, tungara frogs live in the lowland rainforests of Central America, where there are lots of other species of frogs. Female tungara frogs only respond to the calls of male tungara frogs, which are very distinctive. This prevents females from mating with males of other species, which would waste not only her time but also could risk not fertilizing her precious eggs.

- Many insects use chemical pheromones to attract mates. Species often evolve different chemical formulas in their sex pheromones to ensure that mating always involves members of the same species.

- An experiment by biologist Diane Dodd found that the diet of ancestors can contribute to which mates are preferred, suggesting that environmental factors, such as diet, can influence mating preferences.

- For flowering plants, attracting different pollinators can prevent fertilization. Two closely related species of monkeyflowers, *Mimulus lewisii* and *Mimulus cardinalis*, both live in the Sierra Nevada mountains. The first has broad, pink petals that attract bees. The second has narrow, red petals that attract hummingbirds.

- Because neither a bee nor a hummingbird is likely to visit both kinds of monkeyflower, pollen from one species is unlikely to fertilize the ovum of the other species. So, that's a prezygotic barrier.

- But even if fertilization does take place, there are also postzygotic barriers leading to speciation—and there are many more examples demonstrating this route to speciation.

- One example of a postzygotic barrier comes from *Heliconius* butterflies, also known as longwings. These beautiful butterflies have highly variable colors and patterns on their wings, which have several functions. In some species, the color patterns are used by males to recognize females of the same species. But the patterns can also be a warning to predators that a butterfly is toxic. Predators, such as birds, learn through experience that butterflies with particular wing patterns taste bad, so they avoid eating them.

- This means that the hybrid offspring of species with different wing patterns would have a wing pattern that is unfamiliar to predators—which could be dangerous. Indeed, experiments using artificial butterflies have shown that birds are more likely to attack butterflies that look like hybrids than butterflies that look like either parent. So, even if hybridization happens, the hybrids might get eaten before they can pass on their genes.

- Often, more than one reproductive barrier is acting together. In the case of the *Mimulus* monkeyflowers, researchers have determined that both prezygotic and postzygotic barriers keep these species from hybridizing in the wild.

Research has shown that speciation without physical barriers to gene flow is at least possible, though biologists don't yet know how common evolution without physical barriers might be as a way for new species to form.

The Many Species of Insects

- Biologists who work with insects depend on research collections in order to identify and classify species and to determine where species live now and in the past. Many of these research collections are housed in natural history museums.

- Behind the museums' exhibits is a vast labyrinth of specimen collections, laboratories, and other research areas. The entomology collection at the Smithsonian National Museum of Natural History in Washington DC is

The many close associations between plants and insects, combined with the tendency for insects to undergo speciation when they shift to a new host plant, helps explain why there are more species of insects than any other form of life.

one of the largest in the world, with more than 35 million specimens. These specimens represent about 300,000 insect species, and this is only about 30% of all the insect families known to science.

- Much of the work conducted by Smithsonian researchers involves adding to the collection by conducting field expeditions to collect new specimens. Having specimens pinned or preserved in alcohol and getting information entered into a computer database for as many species as possible allows researchers to piece together the evolutionary history of each group of organisms, providing insight into how speciation occurred.

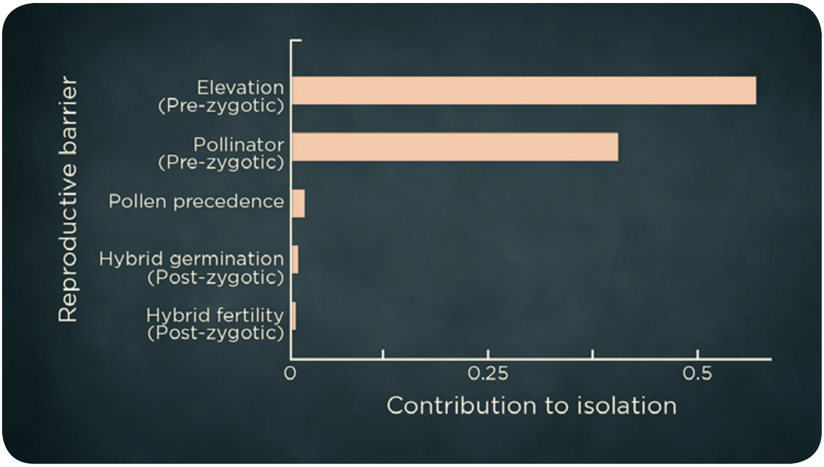
- Probably the biggest contributor of new insect species is the ability of insects to **coevolve** with plants. But then, why are there so many species of plants?

- A 2016 estimate by the Royal Botanical Gardens suggested a total of 391,000 living plant species. Part of what has helped plant species be more numerous is that plants can undergo speciation in a way that other species cannot.

- As with other sexual species, when plant cells divide, the chromosomes are normally copied and then split in half so that each daughter cell has the same number of chromosomes as the parent cell. But sometimes a mistake occurs and all the duplicated chromosomes end up in one of the daughter cells.

- This means that those cells have twice the normal number of chromosomes. If this happens, the individual with a double set of chromosomes, known as polyploid, would not be able to reproduce with an individual having the normal diploid number of chromosomes.

- For many animals, this type of reproductive isolation would mean the individual would be sterile and therefore an evolutionary dead end. But many plants are able to self-fertilize, meaning pollen from one flower could fertilize the ovum of another flower on the same plant. Moreover, even cross-fertilization can be successful in the not-so-rare case when both plants have the extra set of chromosomes. Reproductive isolation is immediate, so a new species is possible in just one generation.



- This is one example of what is known as **polyploid speciation**, which may be responsible for the origin of 80% or more of all plant species alive today. Many of our domesticated plants have speciated in part thanks to polyploid speciation, whether that means 3 sets of chromosomes, or 4 sets, or 5, or even more.

Readings

Coyne and Orr, *Speciation*.

Grant and Grant, *How and Why Species Multiply.*

Questions

How might the spread of nonnative species lead to the evolution of new species?

No single definition of species is accepted and used by all biologists. The ability to mate and produce viable, fertile offspring defines the _____ species concept, but it doesn’t apply to species like bacteria that only reproduce asexually.

a. ecological

b. morphological

c. phylogenetic

d. biological

The observable physical features of a species define the _____ species concept, but it fails to be useful for many microorganisms and can also be misleading because of convergent evolution.

a. ecological

b. morphological

c. phylogenetic

d. biological

The _____ species concept defines species as being distinct branches on an evolutionary tree reconstructed using DNA, but it doesn’t clearly distinguish species from varieties within a species.

a. ecological

b. morphological

c. phylogenetic

d. biological

The role species play in their ecosystems defines the ____ species concept, but it isn’t practical for extinct species.

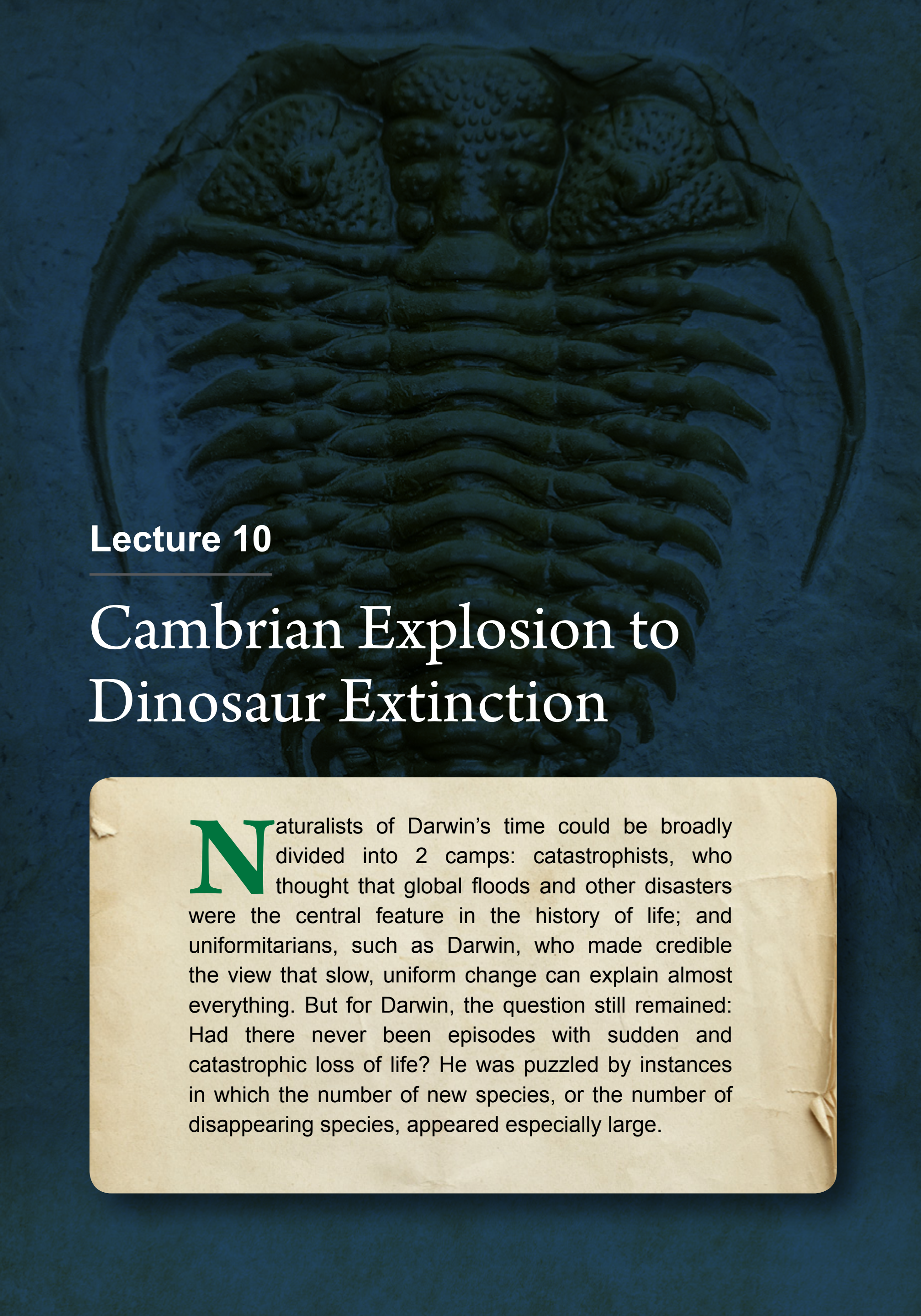
a. ecological

b. morphological

c. phylogenetic

d. biological

Answers can be found on **page 237**



Lecture 10

Cambrian Explosion to Dinosaur Extinction

Naturalists of Darwin's time could be broadly divided into 2 camps: catastrophists, who thought that global floods and other disasters were the central feature in the history of life; and uniformitarians, such as Darwin, who made credible the view that slow, uniform change can explain almost everything. But for Darwin, the question still remained: Had there never been episodes with sudden and catastrophic loss of life? He was puzzled by instances in which the number of new species, or the number of disappearing species, appeared especially large.

The Diversity of the Cambrian Period

- In 1859, when *On the Origin of Species* was published, the oldest-known fossils were from the early Cambrian period, now dated at about 540 million years old. The problem was that these early Cambrian fossils already included complex animals like trilobites, a kind of arthropod related to modern insects and crustaceans.

- In fact, Darwin considered this is a potential weakness in his theory of evolution. The sudden appearance of complex, diverse life-forms, apparently without predecessors, would later become known as the Cambrian explosion. But we now know that Darwin was correct to expect that earlier fossils would be discovered.

- The earliest fossils we now know date to 3.5 billion years ago. They are microscopic fossils of single-celled prokaryotes called cyanobacteria. Some of these very early fossils are long, thin filaments. Others formed mats called stromatolites similar to those that can still be found in shallow seas today.

- By 600 million years ago, the first multicellular organisms appear in the fossil record. They are known as the Ediacaran fauna for the site in South Australia where they were first discovered in 1946. Some look like jellyfish while others resemble ferns or kelp with quilted fronds.

- Biologists still debate the relationship of the Ediacarans to other forms of life. What we know about them is that they were anchored to the seafloor and didn't have a mouth or digestive tract. They may have absorbed nutrients directly through their bodies.

- The Ediacaran seafloor dwellers began to disappear around the time that wormlike organisms, capable of moving and burrowing into the seafloor, appear. These worms may have eaten the kelp-like Ediacarans and helped lead to their extinction.

- Virtually all of the Precambrian organisms—from the kelp-like Ediacarans to the first worms—were soft-bodied. It wasn't until the Cambrian period that harder-body predators came into existence. These newer predators exploited changes in ocean chemistry that allowed calcium in the seawater to be converted into hard body parts made of calcium carbonate. These were much more likely to be preserved in the fossil record than soft-bodied organisms.

- In other words, with the benefit of a much better fossil record, we can now see what Darwin couldn't—that what was so explosive about the Cambrian explosion was not the sudden appearance of complex, diverse life from nothing. Rather, it was a rapid increase in hard body parts, with the side effect of being preserved in the fossil record.
- But the explosive increase in the different types of large animals during the Cambrian is still amazing. Over a span of just 10 million years, from 535 to 525 million years ago, many new types of animals appeared whose body plans are still in use by their living descendants.
- Some of the most spectacular fossils from this era come from a site in the Canadian Rockies known as the Burgess Shale. The fossil animals discovered here represent an amazing diversity of body plans. Many complex organisms appear all at once.
- Where did they all come from? What could have caused this relatively sudden explosion in such diverse body plans?
- One explanation is that, for the first time, animals evolved that could eat other animals. This evolution of predators meant that any animal at risk of becoming prey needed some sort of defense. So, as the first predators evolved, there was an evolution among prey species of defense mechanisms, such as body armor.
- The first animals to make hard body parts were shelled creatures that were just a few millimeters long. They have all kinds of different shapes, from coiled to conical and even star-shaped. They likely evolved these hard body parts to protect themselves from predatory worms.
- Other species, such as trilobites, evolved not only hard shells but also sharp spines. Their body plan was so successful that trilobites became the most common group of multicellular animals in the Cambrian era.
- In response to the defenses that prey species were evolving, predators evolved more effective ways to capture prey. This, too, involved the use of hard body parts, such as claws and jaws. To capture prey, predators also developed new ways of moving around,

leading to the evolution of bodies with appendages that helped them swim or crawl along the seafloor.

- Eyes may have been among the soft body parts that began evolving even before the Cambrian. Any amount of vision would have been helpful, both for predators to find their prey and for prey to sense approaching predators. But selection pressures for better and better eyes would have been intense, leading to the evolution of increasingly more refined vision.

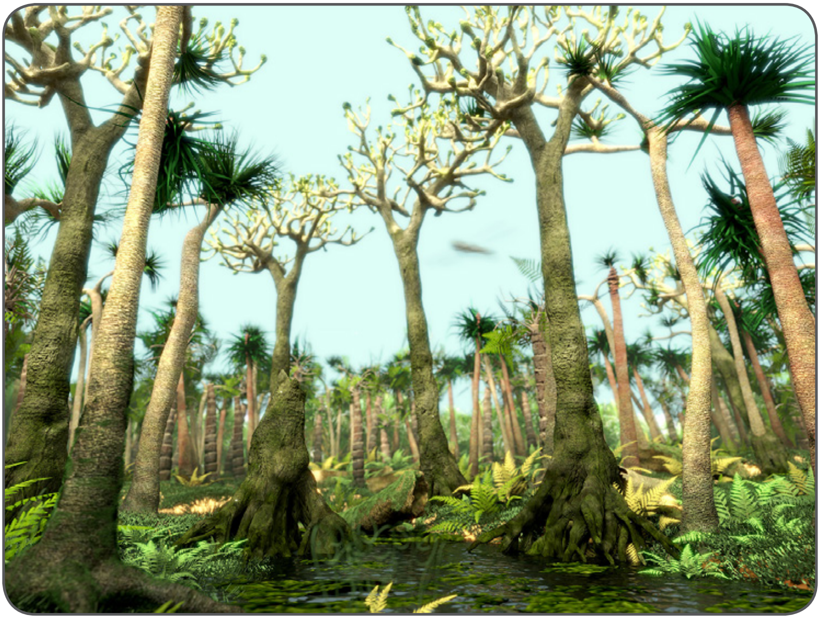
The sudden increase in diversity during the Cambrian period may have been due to the arms race between predator and prey. Prey species evolved hard body parts to protect themselves from predators, which triggered the evolution of more effective predators, causing the prey to evolve better defenses.

During this arms race, the lesser-known soft-bodied animals went extinct without a trace. Whether fast or slow, the Cambrian explosion for them was a catastrophe.

In fact, the Cambrian also ended with a major extinction event. Many of the mysterious conodonts, whose bodies were only partly hard, were among the many species to go extinct at this time. Many early trilobites species, so successful initially, had disappeared by the end of the Cambrian.

- In *Wonderful Life: The Burgess Shale and the Nature of History*, Stephen Jay Gould suggested that life during the Cambrian had been at its peak diversity, with natural selection thereafter eliminating forms of life that Earth has never seen since. Nevertheless, virtually all the diversity we take for granted was still to come.

- The first land plants appeared around 470 million years ago, turning the land's surface green for the first time. A hundred million years later, the forests of the Carboniferous period flourished in part because there was virtually nothing alive at the time that could eat them. In each case, as insects and other animals evolved that could digest plant matter, plants had to evolve defenses. Such defenses could include coevolution with unrelated species, such as microorganisms.



- The Carboniferous arms race of plants against animals is a story similar to what had played out during the Cambrian explosion. Plants evolve defenses against herbivores. Herbivores evolve new ways to eat and digest plants. Plants evolve even newer ways to protect themselves, and so on. Antagonistic relationships lead to diversity, and diversity begets more diversity.

Mass Extinctions

- During Darwin's lifetime, only a small number of fossils had been discovered—some by Darwin himself—while new fossils were being discovered all the time. He believed that a more complete fossil record would show a very long process of slow, gradual changes.

- In many ways, Darwin was right. Specifically, Darwin's explanation of how life has evolved via a process of slow changes selected by nature has proven itself repeatedly as the best explanation for adaptation. And in the years since his death, new fossil discoveries have helped biologists reconstruct the history of life on Earth, and many of these show evidence for gradual change.

- But we also now know that sudden events can trigger dramatic evolutionary changes over relatively short periods of time. Precisely because life adapts slowly (for the most part), a sudden change in physical conditions on Earth can contribute to a **mass extinction** event, which is when conditions change so rapidly that a majority of species cannot adapt.

- The fossil record of animals provides evidence of at least 5 major mass extinction events, often referred to as the "big five," in Earth's history.

    - The first occurred at the end of the Ordovician period, around 444 million years ago. About 85% of species, most of which were in the sea, became extinct. Temperatures suddenly cooled, glaciers increased, and sea levels lowered—all of which was devastating for marine life. But meanwhile, the first plants and insects to live entirely on land began to appear.

    - The second mass extinction happened during the late Devonian, 359 million years ago, when 75% of all living species became extinct, especially inhabitants of shallow-water seas, where oxygen levels plummeted. All of the larger vertebrates were wiped out.

    - The third event—the most devastating mass extinction of all—was an event that marks the end of the Permian period, around 252 million years ago. Paleontologists estimate that as many as 96% of all living species became extinct, perhaps in less than 500,000 years. Complex ecosystems do not seem to have returned to anything resembling their previous states for at least 5 million years.

    - The fourth mass extinction happened over a much longer span of about 18 million years, in 2 or 3 phases, at the end of the Triassic period, 200 million years ago. We can imagine Darwin arguing that such a period would be a fine example of "slow, gradual" change. But the overall result was that about half of all species alive became extinct, most of them animals. Meanwhile, those animals that did make it through, such as dinosaurs and pterosaurs, found themselves in an even stronger position than before.

  - The fifth, and most recent, event was so catastrophic that it led to the extinction of more than 80% of all animal species alive at the time, including most dinosaurs. The result was another major reorganization of life on Earth, with once-dominant groups, such as dinosaurs, disappearing and previously less diverse groups, such as birds and mammals, flourishing.

- Extinctions are an important part of evolution because they create opportunities for other species to evolve to fill niches in an ecosystem. Mass extinctions are especially important because

The earliest dinosaur ancestors appear in the fossil record after the third mass extinction, about 250 million years ago.

Dinosaurs came to dominate the Earth's ecosystems after the fourth mass extinction, about 200 million years ago.

Dinosaurs disappeared during the fifth mass extinction, 66 million years ago.

when many species disappear around the same time, it opens a lot of ecological niches that can be filled by new species, leading to a sudden explosion of diversity.

- Extinction and speciation are the yin and yang of evolution. Extinction reduces diversity, and speciation increases it. Together, extinction and speciation determine how many species are alive at any point in time. Both processes are always happening, but the rate at which they happen seems to fluctuate.
- Darwin simply assumed that incoming species replace outgoing species at a constant rate. But after each of the "big five" mass extinctions, it took between 5 and 10 million years for the number of animal species to return to the same levels as before the event.

Whereas the major mass extinctions of the past were caused by asteroid impacts or the eruption of supervolcanoes, we are currently in a period of increased extinction that follows the remarkable expansion of humans.

Humans have been contributing—through direct activity, such as hunting for food and sport, as well as indirect activity, such as destructing wild habitat and causing climate change—to a higher rate of extinction for large wild animals for tens of thousands of years.

Keep in mind that we don't have to have a "big six" extinction to do an enormous amount of damage. In the years since a 1982 paper first discussed the "big five" group of mass extinctions, subsequent research shows additional extinction events that don't quite reach the threshold of the "big five."

Readings

Alvarez, T. rex *and the Crater of Doom*.

Carroll, *Into the Jungle*.

Gould, *Wonderful Life*.

Kolbert, *The Sixth Extinction*.

Morris, *The Crucible of Creation*.

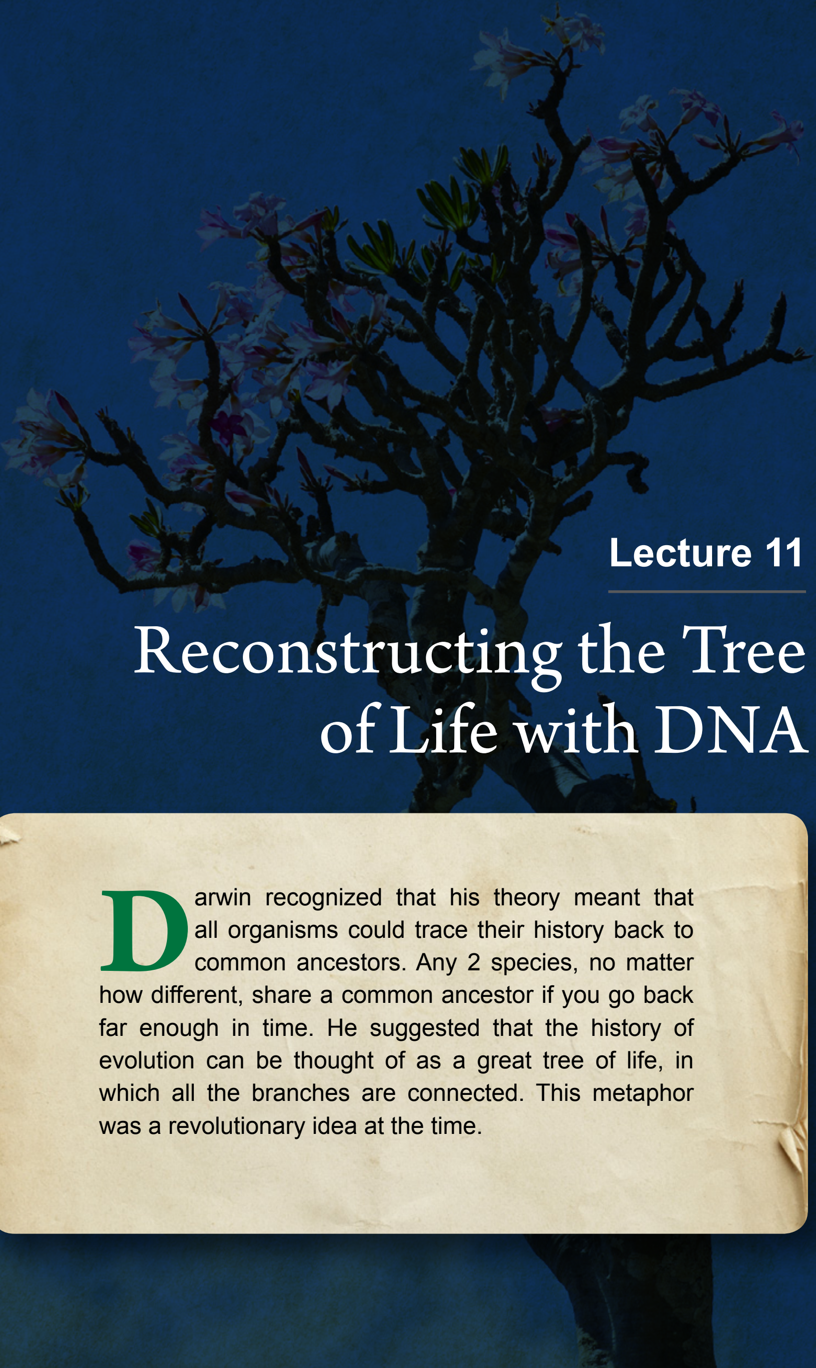
Quammen, "When Life Got Complicated."

Questions

Why has it been difficult to find fossils from before the Cambrian era began 541 million years ago?

What do mass extinctions reveal about evolution?

Answers can be found on **page 239**



Lecture 11

Reconstructing the Tree of Life with DNA

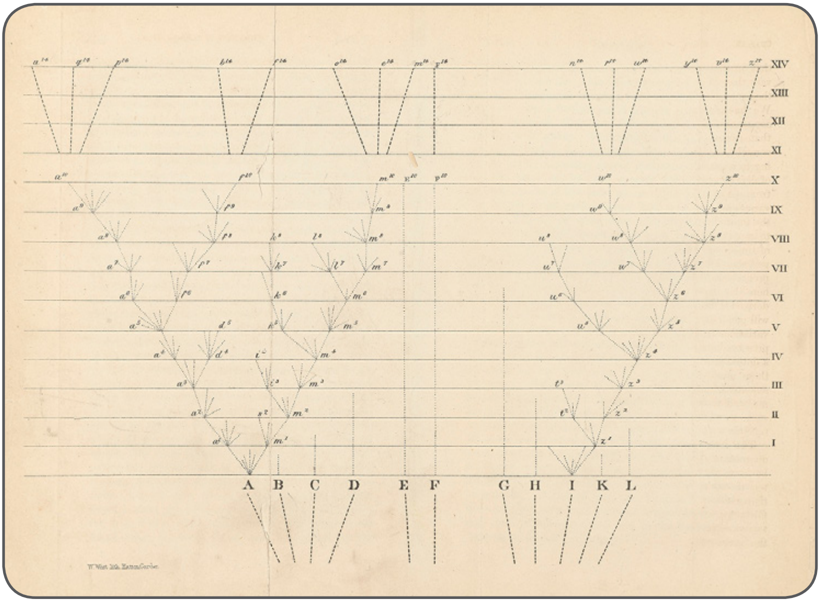
Darwin recognized that his theory meant that all organisms could trace their history back to common ancestors. Any 2 species, no matter how different, share a common ancestor if you go back far enough in time. He suggested that the history of evolution can be thought of as a great tree of life, in which all the branches are connected. This metaphor was a revolutionary idea at the time.

Early Trees of Life

- In the 18th century, Swedish botanist Carl Linnaeus created a 2-name system to name and classify each species of life: The first name described the larger group, or **genus**, in which it was categorized, while the second name was unique to each species within the genus.

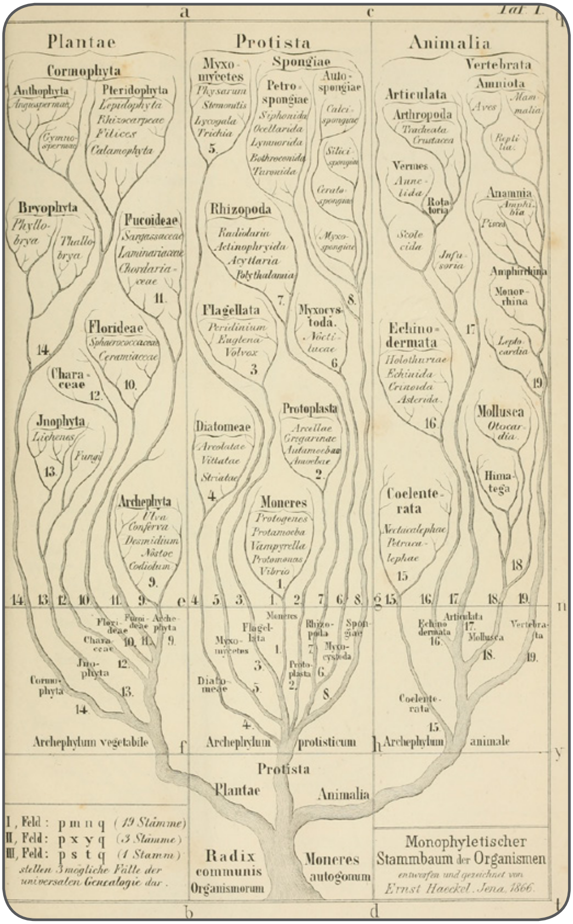
- An important aspect of Linnaeus's classification system was how it became a nested set of larger and larger categories. Just as each species was nested within a genus, he would eventually assign each genus to a particular family; families were nested within orders, orders were nested within classes, and so on. Yet this system assumed that species were fixed entities that never changed.

- Darwin's theory of evolution gave the Linnaean classification system a whole new meaning. He knew it should be possible to have a classification system based on "community of descent." In fact, the only illustration in *On the Origin of Species* was Darwin's attempt to show what a tree-of-life approach to classification could look like.



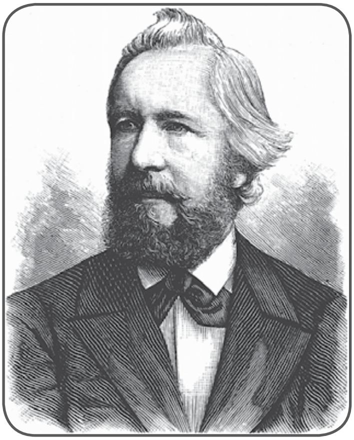
- But Darwin's tree didn't include the names of any particular species. It was more of an illustration of a general principle: that branching evolution creates groups of related organisms that resemble the relationships among family members in a genealogy.

- Drawings by Ernst Haeckel offered some of the earliest depictions of how the actual varieties of life—such as different kinds of plants and animals—might be shown on an evolutionary tree.



- Each of the tips on Haeckel's tree of life represents a species, living or extinct. Zoom in on any branch and you can see the genealogical relationships between parents and offspring. Zoom out just a little and you can see the entire history of populations.

- The branching points on the tree represent speciation events, in which populations split to become 2 distinct species. The base of the tree represents the common ancestor of all life.



Ernst Haeckel

Taken as a whole, the tree of life represents the entirety of evolution. It is a graphical representation of the history of life.

Hennig's Cladistic Approach

- Haeckel's tree of life was little more than an educated guess about the actual relationships among species. How could we figure out the real history of evolutionary relationships?

- Biologists have been working on determining these relationships ever since Darwin's lifetime. Indeed, a major goal of evolutionary biology has been to reconstruct the actual relationships that make up the tree of life—and to adjust our classification system to match it.

- A method for aligning classification with evolutionary history was developed by German biologist Willi Hennig, who suggested that any evolutionary tree, or **phylogeny**, should be reconstructed by grouping together organisms based on 2 key attributes:
    - The organisms should have traits, or characters, that are shared by all members of the group.

  - The shared trait for defining a group of organisms should be derived, meaning that the trait evolved to be different in some way than it was in the ancestral species.

- A trait that is both shared and derived is useful for reconstructing evolutionary history because it can be used to form a natural group united by a trait that evolved uniquely in that group. By the late 1950s, this kind of phylogenetic grouping, based on shared evolutionary history, began to be called a **clade.**

- What Hennig had called phylogenetic systematics also came to be known as cladistics because of its emphasis on clades. The key assumption was that organisms sharing a common ancestor more and more recently in time are expected to have more and more shared, derived characters in common.

Every organism living today—from humans to bacteria—has an evolutionary history that is just as long as that of every other living species.

- A background assumption in Hennig's approach to reconstructing evolutionary history was that simpler, or more **parsimonious**, explanations are more likely to be correct.

- Because a phylogeny is a hypothesis about the evolutionary relationships among organisms, biologists need a way to test which hypothesis is more likely to be correct. By using parsimony, a biologist might conclude that a phylogeny that infers that 6 evolutionary changes occurred is more likely to be correct than a phylogeny that infers that 8 evolutionary changes occurred.

- Hennig's application of the principle of parsimony to the grouping of organisms with shared, derived traits provided a way to reconstruct evolutionary history based on data. The greater the number of

Today, our greatest limitation in reconstructing the tree of life is simply the fact that we still know surprisingly little about all the organisms on the tree—and not just the extinct species. Biologists estimate that we know about only 20% to 50% of all living species.

shared, derived traits that a group has in common, the more support there is for that grouping.

- Evolutionary biologists began using Hennig's cladistic approach to test whether the existing classification schemes were supported by data. In some cases, the traditional category is supported by cladistic data, but in other cases, the application of Hennig's approach suggested new insights. Despite some surprises, the cladistic approach was a useful way to use data to reconstruct evolutionary history.

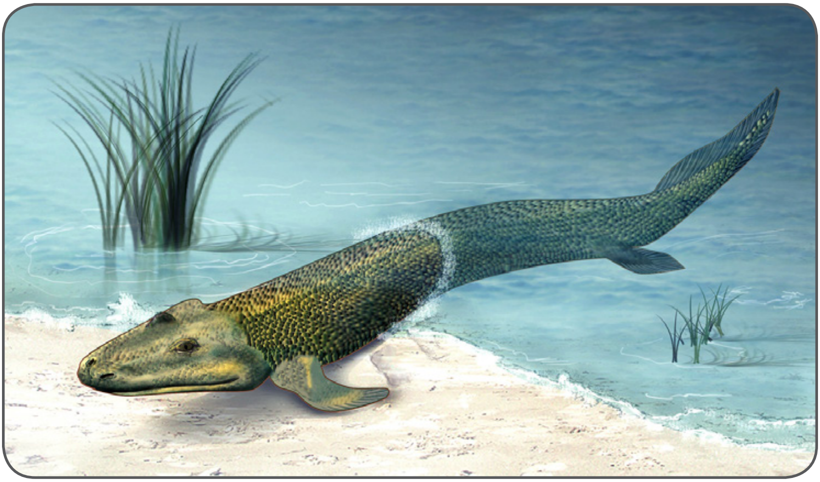
- As it was applied to a wide range of different organisms, the overall shape of the tree of life slowly came into focus. But as it did, new questions emerged. For example, it was clear that 4-legged animals evolved from fishlike ancestors, but what particular group of fish is most closely related to the 4-legged animals? Biologists have taken 2 different approaches to answer this type of question.

    - One approach is to examine currently living species and apply Hennig's method to determine which group of fish shares the greatest number of derived characters with 4-legged animals. The lobe-finned fish have fins with a bone structure that resembles the legs of land animals. This comparative approach suggests that 4-legged animals evolved from lobe-finned fish.

    - Another approach is to search for fossils of the first 4-legged animals and their closest fishlike relatives.

- Paleontologist Neil Shubin searched for the fossilized remains of some of the first fish to leave the water to walk on land. On Ellesmere Island near Greenland, he and his team found the fossilized remains of an animal in a 375-million-year-old rock. Like a fish, it had scales on its skin and fins with webbing, but like early land animals, it had eyes on the top of its head and bones inside the fins with joints that resemble the shoulders, elbows, and wrists of land animals.

- Shubin and his colleagues named their discovery *Tiktaalik*. It was a "fishbian"—a transitional form between fish and amphibian. *Tiktaalik* and its relatives help us understand exactly how, and when, the first 4-legged land animals evolved. As other transitional fossils were discovered, they helped fill in the gaps between different groups.



DNA Sequence Data

- While Hennig's cladistic approach to reconstructing evolutionary history offered many advantages, it also had some limitations.
    - Biologists began to recognize that evolutionary history is not perfectly parsimonious. We now know that some characteristics have evolved multiple times, independently. A related problem is the fact that some traits appear and are then lost in later species.
    - Another type of limitation came from relying primarily on physical characteristics to group organisms. How could we use physical characteristics alone to classify single-celled organisms like bacteria? While bacteria vary somewhat in shape—they can be spherical, rod-shaped, or spiral—this certainly does not mean that there are only 3 species of bacteria.
- The development of molecular technologies, especially DNA sequencing, offered an exciting new way to apply Hennig's method of finding the first appearance of a shared trait. Each position in the genome could be considered an independent "trait," with 4 possible states for each "trait" corresponding to each of the DNA bases: A, T, C, and G.

- The availability of DNA sequence data had 2 major impacts on efforts to reconstruct the tree of life.
    - Much more data was available. The position of every DNA base in the genome could be considered a trait in a phylogenetic analysis. Because the genomes of many organisms are measured in megabases, with 1 megabase equal to 1 million DNA bases, using genome sequences provides millions of "traits" to study for each organism—much more data for reconstructing the tree of life.
    - Biologists also developed ways to use all this data in more sophisticated ways. The only way for the DNA in an organism's genome to change from one base, such as an A, to another, such as a C, is through a mutation. And biologists have been able to work out how often these mutations occur on average in different groups of organisms. This information provides a way, through computational techniques, to determine the probability that 2 DNA sequences would evolve through mutations to differ in particular ways. These computational approaches provide an alternative to simple parsimony for distinguishing between differing phylogenies.
- A special advantage to DNA sequence data was that it could be used to understand the evolutionary relationship among organisms like bacteria, where visual traits had never been very helpful. This opened the possibility of understanding not only how individual

Darwin had hypothesized that "probably all the organic beings which have ever lived on this Earth have descended from some one primordial form," but now, for the first time, evolutionary biologists could pinpoint the first appearance of specific traits during the very early evolution of life—near the base of the tree of life.

The observation that all life shares certain key features—such as using DNA or RNA as its genetic material and the genetic code used to translate DNA into proteins—provides strong evidence for Darwin's notion that all life can be traced to a single origin.

bacteria are related to one another, but also what the structure is of the earliest branches on the tree of life.

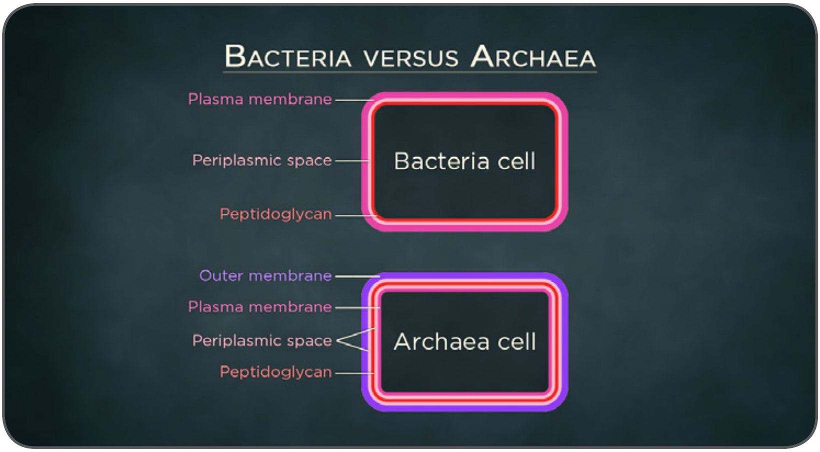
Woese's Discovery

- In 1977, microbiologist Carl Woese made the shocking discovery that **archaea**—single-celled organisms that can live in swamps and sewers—may be more closely related to humans (**eukaryotes**) than they are to bacteria.

- This means that the earliest forms of life must have been more similar to bacteria than to archaea. An early split must have occurred between bacteria and the common ancestor of archaea and eukaryotes. Only later did the archaea diverge from the eukaryotes.

- But the problem with trying to reconstruct the very early branches on the tree of life is that different genes from the same organism can have apparently conflicting evolutionary histories. The reason is that genes can sometimes be exchanged

Some studies have found that as many as 80% of the genes in bacteria and archaea have been exchanged between species at some point in their evolutionary history.



directly between distantly related species—for example, through infection by viruses—via **horizontal gene transfer**. This process poses a challenge for reconstructing the tree of life because many parts of a genome reflect a history of viral infections rather than Darwin's "community of descent."

- Attention to gene swapping suggests a tree of life that looks more like a tangled web than a branching tree.

Darwin's tree of life continues to be a useful starting point for thinking about evolutionary history in light of a vastly better fossil record than was available to Darwin. In addition, our modern tree of life shows us many things that Darwin did not know, including unexpected relationships—from the idea that birds are a subgroup of reptiles, to the closer relations of archaea with animals and plants than bacteria, to tangled relationships among distantly related organisms.

Readings

Dunn, *Every Living Thing*.

Quammen, *The Tangled Tree*.

Questions

How does our modern understanding of the tree of life differ from Darwin's?

What did the discovery of *Tiktaalik* reveal about the origin of land animals?

Answers can be found on **page 240**

Lecture 12

Human Evolution in All Directions

As revolutionary and controversial as *On the Origin of Species* was, the obvious topic it did not cover is the evolution of humans. All Darwin offered was a vague note that, eventually, "light would be thrown on the origin of man and his history." At the time of its publication in 1859, there was virtually no fossil evidence for human evolution. Yet Darwin's theory of evolution by natural selection suggested that all species could be understood in terms of "descent with modification." The logical conclusion was that humans, too, evolved from ancestors different from current-day humans.

Comparing Humans and Great Apes

Thomas Henry Huxley

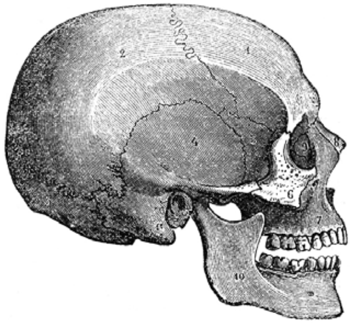
- In Thomas Henry Huxley's 1863 book, *Evidence as to Man's Place in Nature*, he pointed out the anatomical similarities between humans and great apes. Like humans, apes have forward-facing eyes and large brains for the size of their bodies and lack tails. The structure of both species' feet and hands are very similar, too, including fingernails instead of claws.

- To Huxley, these similarities suggested common ancestry between humans and great apes. But despite the similarities, it was clear that humans are different from gorillas and chimpanzees in important ways.
  - Humans walk upright on 2 legs. While chimps can walk upright for short distances, which they sometimes do when their hands are full, they aren't very good at it.
  - Even the hairiest humans have much less body hair than chimpanzees and gorillas.
  - While apes have larger brains than most mammals, the human brain is exceptionally large for our body size. And along with the difference in brain size comes dramatic differences in the cognitive abilities of humans and chimpanzees.

Thomas Henry Huxley was known as Darwin's "bulldog" for his fierce advocacy and defense of evolution through natural selection.

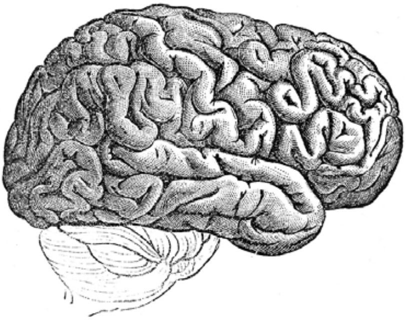
- Despite these differences, Huxley argued that humans must have once shared a common ancestor with the great apes. Yet at the time,

Compared to the brain of a chimpanzee or gorilla, the human brain is 3 times larger.

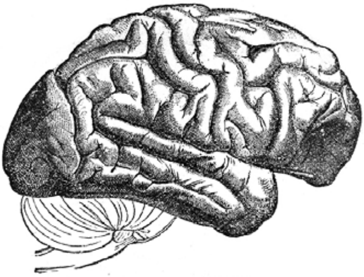


HUMAN SKULL.

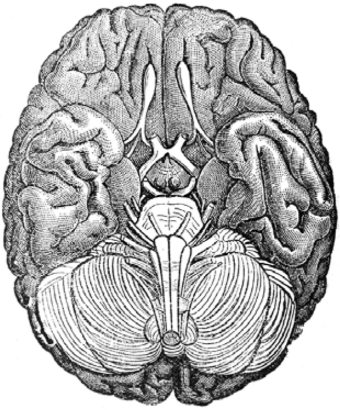
SKULL OF CHIMPANZEE.



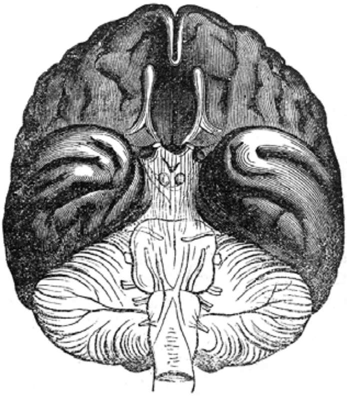
HUMAN BRAIN.



BRAIN OF CHIMPANZEE.



HUMAN BRAIN.



BRAIN OF CHIMPANZEE.

there was very little physical evidence for intermediate stages between humans and a chimp-like ancestor.

- Darwin expanded on Huxley's ideas about human evolution in his 1871 book, *The Descent of Man, and Selection in Relation to Sex*. Like Huxley, Darwin saw the similarities between humans and apes as evidence for their close evolutionary relationships. As additional evidence, Darwin pointed to early stages in development in which a human fetus has structures that are found in other animals, such as a tail.

- Darwin also acknowledged that the lack of a fossil record linking humans to apes was problematic but speculated that fossils of human ancestors would eventually be found. He even predicted that such fossils would likely come from Africa, where great ape diversity is highest.

- Darwin was right: Many fossil remains of human ancestors have since been discovered. He was also correct in his prediction that the oldest human fossils would be found in Africa.

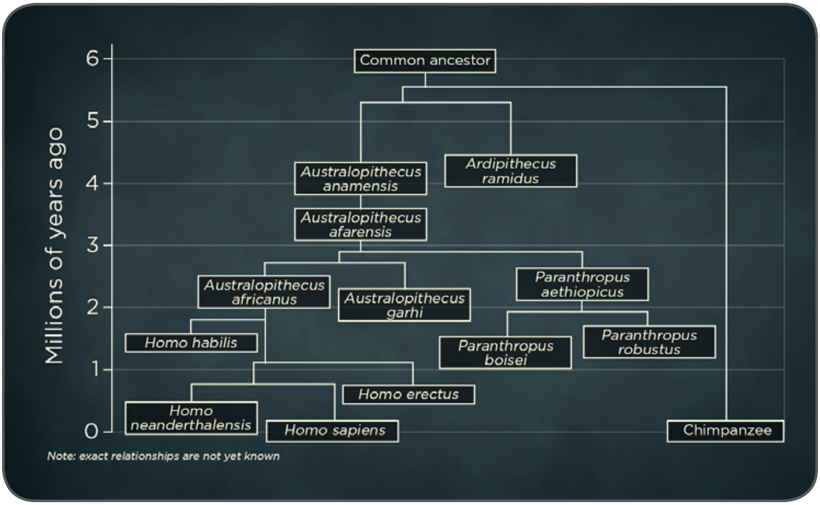
- But what Darwin did not know was just how many different types of humanlike species, or **hominins**, once existed.

- These discoveries, as well as insights gained from sequencing DNA from ancient remains, have led evolutionary biologists to leave behind the old, iconic image of human evolution, popularized by Huxley, of a linear progression from hunched ape to upright human.

- In its place, we now have enough information to draw a phylogeny, or evolutionary tree, for humans and our closest living and extinct relatives. This depiction of human evolution resembles what Darwin would have wanted—with many splits, each leading to a series of branches that represent the different species of hominins. We can think of each branch as a natural experiment in how to make a human.

- The use of DNA sequence data has provided a powerful new way to compare the genomes of humans and great apes and thereby reconstruct our own evolutionary tree.

- Our closest living relatives are chimpanzees. Next closest are gorillas and then orangutans. While the last common ancestor of all 4 lived around 10 million years ago, we shared a common ancestor with chimpanzees until as recently as 5 to 7 million years ago. Around that time, there was a speciation event that gave rise to 2 lineages: One would lead to chimpanzees while the other would be the hominins, some of whom would eventually become humans.
    - We don't know all of the characteristics of our last common ancestor with chimpanzees, but there are a series of traits that modern humans share in common with young chimpanzees, such as being largely hairless and having a higher brain-to-body ratio.
    - There wasn't a simple transition from one species of hominin to another, leading ultimately to *Homo sapiens*. Rather, the fossil evidence shows that many hominin species were alive at the same time. We don't yet know the exact relationships between each of the species, meaning that we can't trace a line of direct descent from the common ancestor we shared with chimpanzees directly to us. Yet somewhere on this tree, a transition occurred that separates animal from human.



Note: exact relationships are not yet known

The Evolutionary Tree of Hominins

- One of the oldest members of the hominin family is *Ardipithecus ramidus*, which lived about 4.4 million years ago. The fossilized remains of a skull and parts of the lower body were first discovered in Ethiopia during the early 1990s by Tim White and his colleagues. Since then, more than 100 additional specimens of this species have been discovered.

There were somewhere around 15 species of hominin that existed, depending on what source you consider and which species definition you favor. The fact that many of these species were alive at the same time and the same place, or at least nearby, means that many of these species likely interacted.

All of the forces of evolution—mutation, natural and sexual selection, gene flow, and genetic drift—led to repeated episodes of speciation. Each species had a different ecological niche, with its own advantages and disadvantages given its environment. Yet out of all this diversity, only one species—*Homo sapiens*—would survive.

- The overall appearance of *Ardipithecus ramidus* is more chimp-like than humanlike; its skull shows that it had a relatively small brain. But the shape of its pelvis suggests that it had begun to walk upright at least some of the time, although not as effectively as modern humans.

- One of the most famous fossil hominins was discovered by Donald Johanson and his colleagues in Hadar, Ethiopia, in 1974. Nicknamed Lucy, the fossil belonged to the species *Australopithecus afarensis*. Lucy had a skull about the same size as a chimpanzee, but her pelvis, backbone, knee, and foot clearly showed that she was capable of walking upright in much the same way as modern humans. The discovery of Lucy and others of her species made it clear that walking upright evolved before the evolution of a larger brain.

- By 2 million years ago, hominins had evolved to be fully bipedal, meaning they walked (and ran) on 2 feet just as well as modern humans. But they still had relatively small brains.

- *Homo erectus*, one of the first members of our genus, had a body that looked a lot like a modern human. It had a larger brain than *Australopithecus* and probably made stone tools, both of which suggest a much greater level of intelligence. *Homo erectus* is the first member of the human lineage to leave Africa, spreading as far as Southeast Asia.

The first remains of what is now recognized as *Homo erectus* were discovered by Eugène Dubois on the Indonesian island of Java in 1891.

- We are still learning how far *Homo erectus* traveled. But the shocking discovery of *Homo floresiensis* in 2003 on the Indonesian island of Flores suggests that some *Homo erectus* may have crossed the open ocean. Inside a cave, researchers discovered the remains of perhaps a dozen individuals. Despite being fully grown adults, they stood only about 3 feet, 6 inches tall. Researchers believe that they are descendants of a small group of *Homo erectus* that became stranded and evolved island dwarfism.

- This discovery was puzzling because radiometric dating of the sediments surrounding the fossil suggested it lived between 100,000 and 60,000 years ago. But the bones had an unexpected combination of features, including a relatively small brain and wrist bones that are more typical of chimpanzees and older hominin species.

- Meanwhile, back in Africa, brain size was slowly increasing until about 800,000 years ago, when it suddenly began to increase rapidly. The rapid brain size increase in hominins coincided with a period of extreme climate fluctuation, perhaps suggesting that an unstable climate meant that individuals with larger brains and greater intelligence had a survival advantage.

Hominin evolution involved radiations in all directions—geographic and anatomical—not just a single line.

Enter *Homo sapiens*

- Exactly when and where our species, *Homo sapiens*, first appeared is a source of constant debate among experts.

- A study published in 2017 described fossil skulls and jaw bones from a site in Morocco that date to approximately 315,000 years ago. The authors claimed that these fossils represent the oldest remains found yet of *Homo sapiens*. But other experts don’t agree that the Moroccan material should be considered *Homo sapiens*, noting the lack of a human chin and an overly prominent forehead.

- Fossils more widely accepted as *Homo sapiens* have been found in East Africa, including 196,000-year-old specimens from Ethiopia.

- Several additional discoveries suggest that our species lived alongside other human species. In 2013 and 2014, anthropologist Lee Berger assembled a team of experts to explore a cave in South Africa, where they found more than 1500 fossils from at least 15 individuals that they described as a new species, *Homo naledi*.

- The *Homo naledi* fossils had hands and feet that looked like modern humans, but their skulls and teeth were closer to those of early *Homo* species, like *Homo erectus*. The brain was especially small, more like that of *Australopithecus*. Radiometric dating suggested that these semihuman *Homo naledi* fossils were between 335,000 and 236,000 years old, suggesting that they were around at the same time as our species was coming into existence.

- In 2000 and 2008, pieces of intact DNA were recovered from bones found in a cave near the town of Denisova in southern Siberia. Ancient DNA expert Svante Pääbo determined that the bones represented a previously unknown group of humans, given the name Denisovans. The DNA showed that Denisovans were distinct from *Homo sapiens* and most closely related to Neanderthals.

- In 2012, by comparing the Denisovan genome with the genome of modern humans, Pääbo and his team found that modern humans have Denisovan DNA. Specifically, modern people who trace their ancestry to regions outside of Africa have as much as 5% Denisovan DNA. This means that as our ancestors spread out of Africa and encountered Denisovans, they had sex with them, resulting in babies who survived to adulthood and had children of their own.

- Additional studies by Pääbo's group showed that modern humans also have DNA from European Neanderthals. For many years, researchers assumed that Neanderthals disappeared because they were replaced by our species. But now we know that we interbred with them.

- We don't know for sure why we survived while Neanderthals and Denisovans disappeared, but we do know that the populations of many large mammals shrank about 70,000 years ago. The eruption of the Toba volcano on the Indonesian island of Sumatra sent enough ash into the atmosphere that it likely disrupted the Earth's climate for several years. Humans were among the many casualties, and we nearly became extinct.

Our evolution did not stop with the origin of our species, *Homo sapiens*. As we spread around the world, our ancestors adapted to new environments.

Some of the results of those evolutionary changes can still be seen in people living today. For example, natural selection over many generations led to a tight fit between skin pigmentation and the intensity of sunlight. Natural selection has also affected genes that help overcome the effects of living at high altitude.

Readings

Gibbons, *The First Human*.

Lieberman, *The Story of the Human Body*.

Solomon, *Future Humans*.

Stringer, *Lone Survivors*.

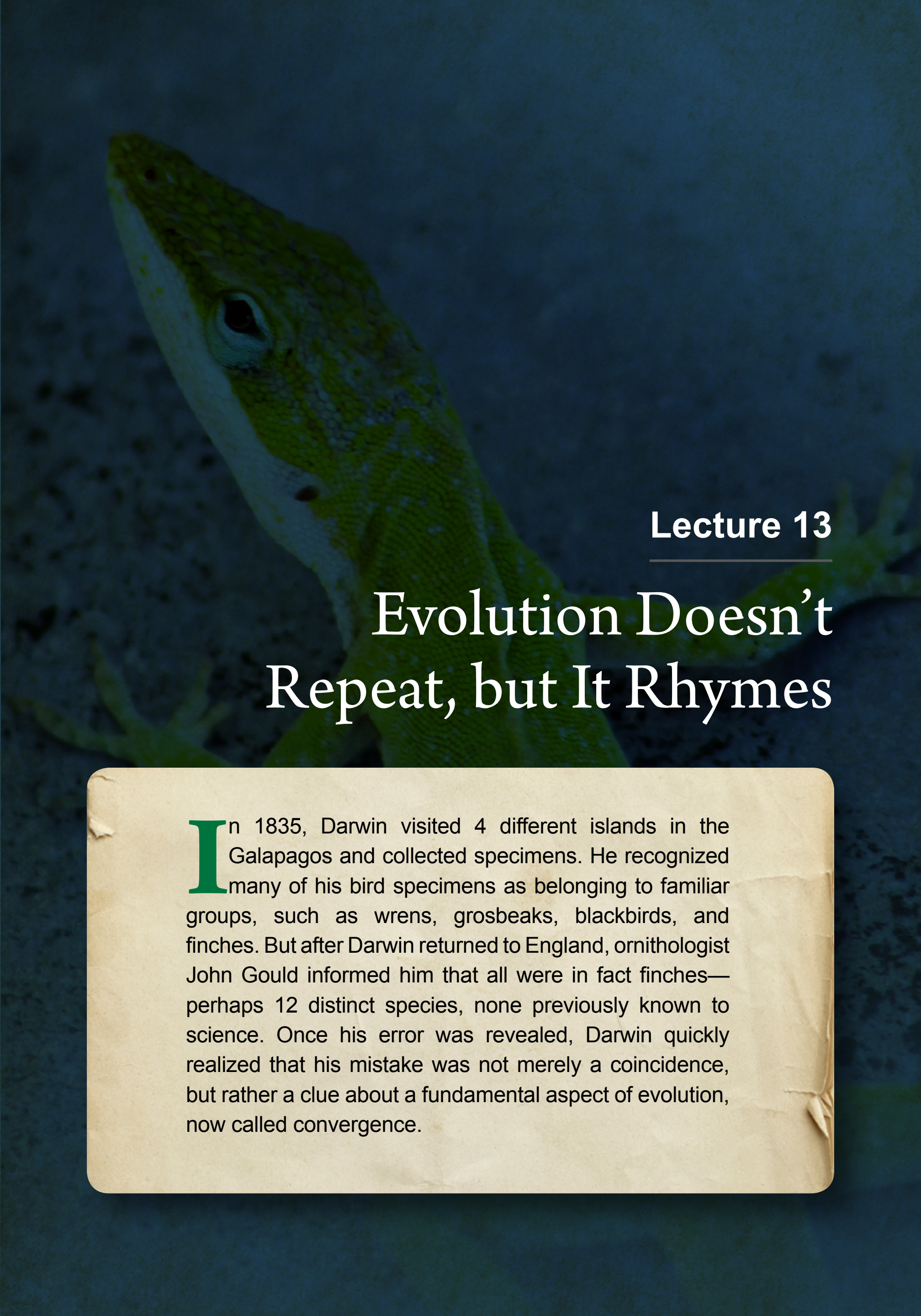
Walter, *Thumbs, Toes, and Tears*.

Questions

How has the old, iconic depiction of human evolution as a progression from a hunched-over ape to an upright human been updated in light of recent discoveries?

What did the discovery of about a dozen individuals of *Homo floresiensis* (“hobbits”) on the Indonesian island of Flores in 2003 reveal about human evolution?

Answers can be found on **page 241**



Lecture 13

Evolution Doesn’t Repeat, but It Rhymes

In 1835, Darwin visited 4 different islands in the Galapagos and collected specimens. He recognized many of his bird specimens as belonging to familiar groups, such as wrens, grosbeaks, blackbirds, and finches. But after Darwin returned to England, ornithologist John Gould informed him that all were in fact finches—perhaps 12 distinct species, none previously known to science. Once his error was revealed, Darwin quickly realized that his mistake was not merely a coincidence, but rather a clue about a fundamental aspect of evolution, now called convergence.

Convergent Evolution

- Convergent evolution occurs when natural selection causes different species to evolve in similar ways.

- Some of the Galapagos finches evolved to look like grosbeaks because both grosbeaks and certain Galapagos finches eat seeds and evolved thick beaks to crack them open. Warblers and wrens tend to eat small insects and evolved narrow beaks for extracting them from crevices, just as the ancestors of what came to be called warbler finches in the Galapagos did.

- As Darwin noted in *On the Origin of Species*, natural selection operating in similar ways in different species often leads to very similar outcomes. After explaining in the book that similarities between organisms can be used to classify them based on common ancestry, he was quick to caution others that organisms that look alike are not always close relatives.

- Whales look a lot like fish, Darwin pointed out, yet we know that whales are mammals because they have hair and produce milk. The fact that both whales and fish have streamlined bodies propelled by fins is a result of natural selection favoring streamlined bodies and finlike appendages in the ancestors of each group.

- Streamlined bodies evolved separately in the ancestors of seals, of manatees, of dolphins, and of penguins; combined with fish and whales, that makes 6 different lineages that each evolved a similar body shape—a strong example of evolution converging on a similar outcome from multiple directions.

- Darwin understood what convergent evolution is and how it works, yet he missed perhaps its most profound implications: The fact that natural selection under similar conditions produces similar outcomes suggests that evolution can be predictable.

- Darwin’s failure to see the deeper importance of convergent evolution for predicting evolution is understandable. It was not

As Mark Twain supposedly once said, “History doesn’t repeat itself, but it rhymes.” Evolution is much the same.

appreciated until the 20th century how widespread convergence is, and only in the 21st century have we begun to make systematic and powerful predictions using that information.

- Yet as the tree of life is being assembled by evolutionary biologists, more and more examples of convergent evolution are coming to light.

Studying Lizards in the Caribbean Islands

- In Jamaica, small lizards called anoles that live high up in the trees tend to have shorter legs than those that live on the ground or on tree trunks. To figure out why, biologist Jonathan Losos conducted a series of experiments and found that Jamaican anoles with long legs are always faster and can jump farther, but they tend to fall more often when climbing on narrow branches.

- These results matched his observations of the lizards' natural behaviors: Ground-dwelling anoles tend to run fast when hunting or escaping from enemies, while tree-dwelling species are ambush predators and rely on camouflage to avoid being eaten.

- It was easy to see how natural selection would have favored different leg lengths for anoles living in different parts of the habitat. But natural selection didn't stop at just dividing the ground- and tree-dwelling anoles. Among the tree-dwellers, several subcategories exist, each differing in particular ways.
    - The largest species, Garman's anole, lives high up in the canopy and has enlarged toe pads that help these lizards stay attached to nearly any surface.
    - Another species, Graham's anole, also lives high up in the trees but is small and still has large toe pads.
    - Yet another species, the Jamaican twig anole, which lives on twigs, is well camouflaged and has the shortest legs.
- When Losos visited other large islands in the Caribbean, such as Puerto Rico, Hispaniola, and Cuba, he found what at first appeared to be the same species as in Jamaica occupying each island. But after sequencing the DNA of lizards from each island, the results showed that, on each island, evolution independently resulted in lizards that look remarkably like those that occupy the same habitat on other islands.
- Convergent evolution resulted in not just similar-looking species, but entire communities of lizards. And it happened the same way on 4 different islands: Cuba, Jamaica, Hispaniola, and Puerto Rico.
- This consistency suggested to Losos that these anoles evolve in predictable ways. If that is true, then it should be possible to conduct an experiment and predict how anoles will evolve.
- Fortunately, Thomas and Amy Schoener had already set up such an experiment in the 1970s. They had found that anoles were widespread across the Bahamas, except for on very small islands. To understand why, they set up an experiment by transplanting anoles from a large island onto smaller islands and tracking what happened to the lizards on the small islands.

- The Schoeners found that hurricanes most likely drown the lizards living on the tiniest islands, which are little more than a pile of rocks. But on islands large enough to support at least a little vegetation, the anoles did just fine.

- About a decade later, Losos visited the 14 small islands with surviving anoles from the Shoeners' experiment. Based on his studies on larger islands, he predicted that anoles living on islands with only thin branches would evolve shorter legs, because that makes it easier for them to get a grip. In contrast, he predicted that anoles living on islands with wider branches would have longer legs.

- And that is exactly what he found. Losos's follow-up on the Shoeners' experiment was the most convincing evidence yet that the outcome of evolution can be predicted.

The History of Evolution

- If evolution is predictable, does that mean that the entire history of life was bound to turn out exactly the way it did?

- Stephen Jay Gould, the well-known paleontologist and popularizer of evolutionary biology, saw the history of evolution as being much more like human history: full of unexpected twists and turns. In his 1989 book, *Wonderful Life*, he argues that if any one detail in the history of life, no matter how apparently insignificant, were to change, it could alter the course of history—and life—forever.

- According to Gould, that makes the outcome of evolution totally unpredictable. The history of life unfolded the way it did because of chance events, or contingencies, meaning that if it were to somehow happen all over again, the species alive today might never have come into existence.

"Replay the tape a million times," Gould wrote, "and I doubt that anything like *Homo sapiens* would ever evolve again."

- British paleontologist Simon Conway Morris, once Gould's hero, came to be one of his staunchest opponents. Where Gould saw contingencies and unpredictability, Conway Morris saw repetition and consistency. Conway Morris began cataloguing examples of convergent evolution—so many of them, in fact, that he came to see the history of life as almost entirely predictable.

"Rerun the tape of life as often as you like," Conway Morris wrote, paraphrasing Gould, "and the end result will be much the same."

- Which of these 2 opposing views about the role of chance in evolution is correct?

- Of course, we can't do what Gould and Conway Morris both suggested—go back in time and replay the tape of life—but thanks to some clever experiments, we can do the next-best thing.

- Richard Lenski's long-term evolution experiment on *E. coli* offers one way to experimentally rerun the tape of life, as Gould and Conway Morris put it. This experiment has used 12 initially identical populations of *E. coli* bacteria growing in laboratory flasks since 1988. Throughout that time, more than 68,000 generations of bacteria have lived, reproduced, and died and Lenksi's lab team has documented the numerous ways in which they have evolved.

- The fact that each of the 12 populations was started from the exact same bacteria—genetic clones—and have been subject to the exact same laboratory conditions makes this a great test of how predictable evolution is. If Conway Morris is correct and evolution is predictable, each population should evolve in the exact same way. But if Gould is right and chance events cause evolution to go down different paths in unpredictable ways, then the populations should evolve differently.

- Early in the experiment, it looked like mere chance was sending the populations in different directions. But with the benefit of more time, it became clear that, overall, the populations were evolving in very similar ways.

- Experiments by Lenski and colleagues suggested that even when conditions are exactly the same—including both genetically identical organisms at the beginning and identical environmental conditions over time—evolution proceeds in similar ways overall but with deviations that cannot always be replicated or predicted.

- These laboratory experiments confirm what biologists have found to be true in nature: Even organisms living in similar environments and facing similar challenges will generally evolve in similar ways. The more information we have about the tree of life, the more apparent this has become.

- So, the view that has emerged is something of a compromise between Gould's view that evolution is capricious and Conway Morris's view that it is almost predetermined. But the fact that there is any predictability at all leads to some interesting ideas.

- Some have taken the idea that life has evolved in predictable ways to suggest that humans, or something resembling humans, eventually must have evolved. Yet there are many ways in which the story of human evolution could have turned out very differently.

- If our ancestors had never encountered Neanderthals or Denisovans, would those species have survived into modern times? Or if the asteroid impact that killed the dinosaurs had not occurred, would mammals have become as diverse as they did, giving rise to primates, apes, and eventually our lineage?

- Conway Morris and other advocates of the power of convergent evolution have argued that even if humans had not evolved from apes, a humanlike species would have evolved from some other lineage.

In extension of the idea that life on Earth has evolved in somewhat predictable ways is the notion that if life exists on other planets, it might resemble life on Earth because of convergent evolution.

Extensive efforts have been made to search for intelligent forms of extraterrestrial life under the assumption that something resembling us must exist somewhere out there. The number of known and candidate exoplanets, planets orbiting stars other than our Sun, continues to grow as astronomers make new discoveries.

Readings

Gould, *Wonderful Life*.

Losos, *Improbable Destinies*.

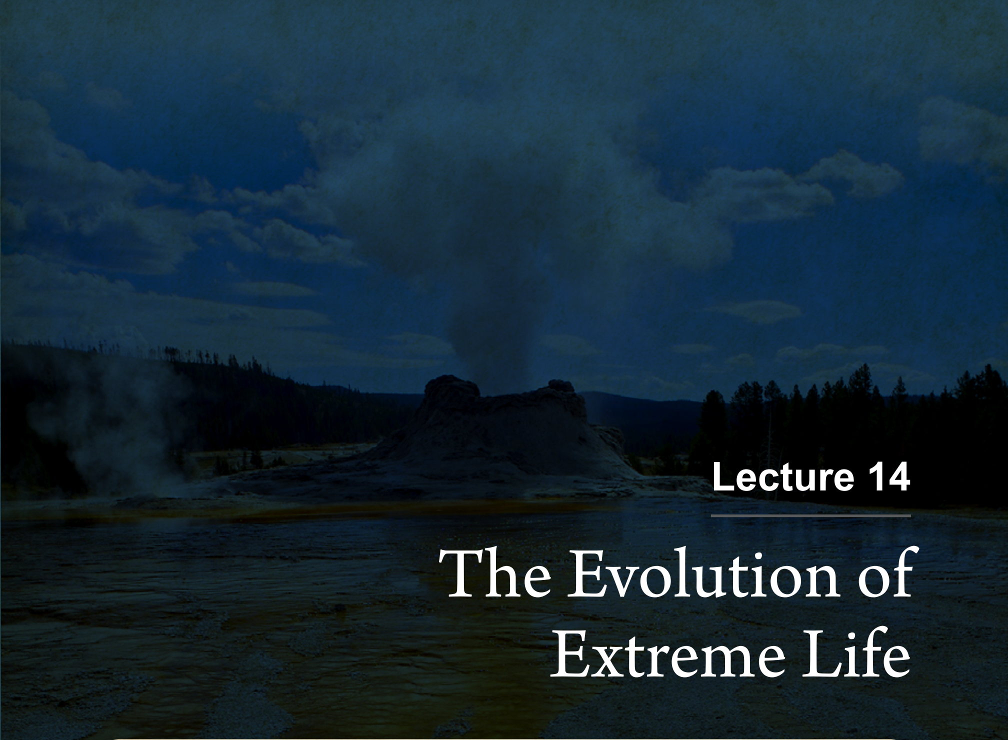
Morris, *Life’s Solution*.

Questions

How did the long-term evolutionary experiment on *E. coli* bacteria begun by biologist Richard Lenski help advance the debate about whether evolution is predictable?

What does convergent evolution suggest about the possibility of alien life?

Answers can be found on **page 242**



Lecture 14

The Evolution of Extreme Life

As was common for the time, Darwin kept collections of curios specimens that were focused primarily on the range of variation within specific categories, such as barnacles, orchids, and plant seeds. He saw these varieties as examples of the creative power of natural and sexual selection. Yet the most unusual forms of life would not be discovered until after Darwin's lifetime, so life is even more adaptable than Darwin could have known. The discovery of **extremophiles**—organisms capable of living in extreme conditions—has caused biologists to reconsider the limitations of living things on Earth. And the more we learn about how evolution has led to extreme categories of life on Earth, the wider our search for life elsewhere in the galaxy must become.

Extreme Environments of Early Life

- The discovery of archaea revealed microorganisms that resemble bacteria but with some distinctive characteristics, suggesting they are perhaps more closely related to humans than to bacteria.

- The first archaea, originally called archaebacteria, were methanogens that use carbon dioxide to access energy from hydrogen gas, producing methane as a by-product. Not only do these carbon dioxide breathers not need oxygen, but it is poisonous to them. As a result, they live in places without any oxygen, such as swamps with stagnant water, where other microbes have depleted the oxygen.

- Archaea may provide some insight into the earliest life on Earth. The early Earth's atmosphere had very little oxygen, consisting mostly of gases that were spewed out of volcanoes, such as methane, hydrogen sulfide, and carbon dioxide. The earliest life-forms therefore couldn't have depended on oxygen, and it would in fact have been poisonous to them, the way it is for methanogens today.

- It wasn't until the first microbes evolved the ability to engage in photosynthesis, which makes oxygen as a by-product, that oxygen began to accumulate in the atmosphere as an accidental consequence. This accumulation shows up in the fossil record as bands of iron oxide, or rust, about 2.5 billion years ago.

- As the Earth's atmosphere filled with oxygen, many species alive at the time were poisoned and died, leading to one of the first mass extinction events, long before any of the "big five" events.

- Among the species that survived were those that evolved to withstand living in the presence of oxygen. The rest were those that, like many archaea today, became restricted to environments where oxygen is scarce.

- So, while we consider these environments to be extreme, they are also remnants of an earlier era, when they were much more typical.

- Today, archaea are among the only forms of life capable of living in saline lakes like the Dead Sea and the Great Salt Lake. Water naturally diffuses from low to high salt concentrations through osmosis, which is why swimming in a salty lake pulls water out of your body.

- For that reason, most organisms cannot live in high-salt environments; the water in their cells and body tissues will constantly be drawn out, leading to dehydration. Pumping water back into cells against a concentration gradient requires energy, so living in high-salt environments requires a large amount of energy just to avoid drying out.

The reason salt is so useful to preserve foods, as is done in salted meats or pickling with salty water, is because most microbes can't tolerate lots of salt, so foods preserved in salt don't usually spoil.

Evolutionary Adaptations of Extremophiles

- Often, the environments where archaea and other extremophiles are found are extreme in multiple ways, such as acidic hot springs with temperatures above 80° Celsius (176° Fahrenheit) and pHs low enough to dissolve metal. To survive in such extreme conditions has required some remarkable evolutionary adaptations.

- In 1969, microbiologist Thomas Brock and an undergraduate student named Hudson Freeze reported their discovery of a bacterium called *Thermus aquaticus* they isolated from hot springs in Yellowstone National Park. After many failed attempts to culture this bacterium in the lab, they found that it had to be grown at temperatures between 70° and 75° Celsius (158° and 167° Fahrenheit). The discovery would later become a boon to the field of genetics.

- A new technique called polymerase chain reaction (PCR) was developed in 1983 by an eccentric chemist named Kary Mullis. The enzyme that cells use to copy DNA is called DNA polymerase, and the PCR technique could copy short stretches of DNA in a lab, which is a necessary first step for everything from cloning to DNA sequencing.

- But to copy DNA using PCR, it was necessary to repeatedly heat the DNA double helix to separate the 2 DNA strands so that one strand could be copied. But the temperature needed to do so—about

95° Celsius (203° Fahrenheit)—is so hot that in most organisms, the DNA polymerase enzyme will be degraded.

- A solution to this problem was described in the late 1980s. By using a version of DNA polymerase from *Thermus aquaticus*, which had evolved to be able to tolerate high temperatures, the PCR technique became much more effective and efficient.
- Thanks to the high-heat enzyme evolved by this extremophile, PCR became an essential part of the biotechnology revolution in the 1990s and 2000s. One of the new developments it enabled was the ability to search for and identify organisms based only on the DNA.
- This technique was especially useful for microorganisms like bacteria, archaea, and fungi. Before PCR, the standard techniques used to identify microorganisms involved culturing them in a flask or petri dish in a lab. A culture-based approach provides only a high-order classification of microorganisms without any way to differentiate them at the level of species, and it is inherently limited because many microorganisms simply won't grow in laboratory conditions.
- By contrast, using PCR, it became possible to take a small sample of an organism from the wild and then amplify particular sections of its genome. These genetic samples could then be compared to those

In 1977, geologists aboard the research submersible *Alvin* discovered a hydrothermal vent on the seafloor near the Galapagos Islands. This was a geological feature proposed to exist by geologists based on the theory of plate tectonics but never before seen. Even more incredibly, all around the hydrothermal vent, at a depth of about 8000 feet, were giant white clams and 8-foot-long tube worms.

These organisms were too complex to be related to the first forms of life, which were single-celled. But the fact that they could thrive in an environment that doesn't depend on sunlight for energy suggested that the first microorganisms might have evolved near deep-sea hydrothermal vents and that such environments may have been important refuges for some species during mass extinction events in which an asteroid impact or supervolcano eruption blocked much of the sunlight from hitting the Earth's surface.

taken from previously identified microorganisms in order to identify them or, if they represent a new species, determine what group they are most similar to.

- This DNA-based approach to studying genetic diversity using environmental samples is known as metagenomics. Such approaches to surveying microorganisms revealed an enormous diversity of previously unknown microbial life from boiling hot springs to pools of acid and even the deep sea. It also revealed that some of the previous classification schemes for microorganisms aren't actually a single group but are instead the result of convergent evolution.

Viruses: The Most Extreme Form of Life?

- The most extreme form of life may be viruses. In fact, biologists aren't even sure whether to consider viruses living things.

The seawater around Antarctica reaches temperatures below the freezing point of water. This is possible because of the salinity of seawater, which reduces its freezing point.

The extreme cold poses a problem for animals living in water that should freeze their tissues. Yet the seas around Antarctica are home to some of the greatest densities of fish, whales, and other marine animals.

One group of Antarctic fish, the notothenioids, have proteins in their blood that act as a natural antifreeze, binding to ice crystals and preventing them from growing. By keeping ice crystals very small, these fish can survive in waters that cause fish from other regions to freeze and die.

- If life is defined by metabolism—the ability to make and use energy for chemical reactions—and reproduction, then viruses should not be considered alive because on their own they can't do either. A virus is completely dependent on host cells for energy and to reproduce.

- Even by comparison with the simplest bacterial cells, viruses consist of very few parts. All they have is a genome made of DNA or RNA surrounded by a protein coat, or capsid. Some viruses have an additional outer membrane, or envelope.

- If this is life, it's as simple as life gets. Even the genomes of viruses are simple. Some have as few as 3 genes, which means they are coded to produce just 3 proteins.

- As a result of their simplicity, most viruses are incredibly small. Some are only 20 nanometers in diameter, which is only about the width of 10 DNA double helices lined up next to one another.

- The smallest viruses are known as **viroids** and consist of just a few hundred base pairs of RNA—an entire genome smaller than most human genes. They don't even have a capsid shell like most viruses. Viroids are taken up by host cells, mostly plants.

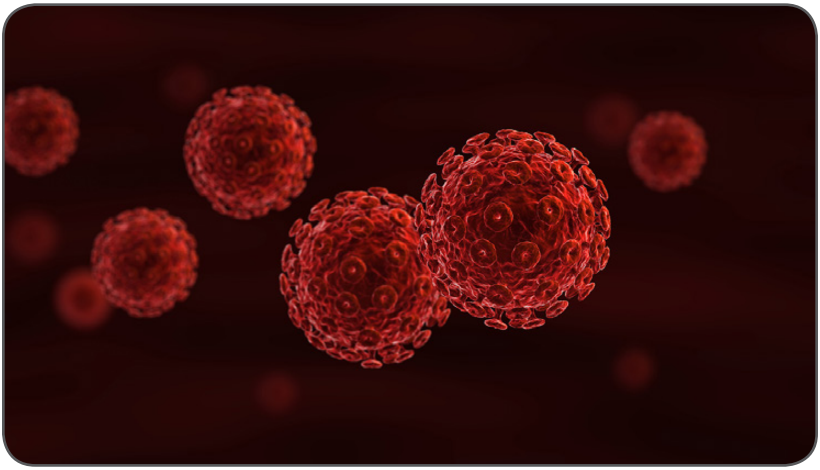
- Viruses can exist with such simplicity because they rely on other living things for many of their important functions. Some viruses, called retroviruses, can incorporate their genome into the genome of their hosts and use the host's machinery to carry out functions like making proteins.

- Viruses also reproduce by tricking their host cells into copying the viral genome. This allows most viral genomes to have evolved into genomic minimalists. One of the smallest is a virus called MS2 that infects bacteria, which has a genome that consists of only 3569 DNA bases. By comparison, the human genome has about 3 billion DNA base pairs—6 orders of magnitude larger.

- On the other hand, some viruses are as large as bacteria. Pandoraviruses live in aquatic environments and parasitize amoebas. They measure up to 1 micron in diameter, even larger than some bacteria. Along with their large physical size comes a relatively large genome consisting of as many as 2.5 million **nucleotides** comprising 2500 genes. Still, these viruses aren't capable of living without their hosts.

- In effect, viruses have outsourced many of these tasks to their host cells. Yet despite their complete reliance on host cells for survival and reproduction, viruses have been very successful, having evolved to infect all other forms of life—from bacteria to plants, fungi, and animals.

- The fact that viruses, such as influenza and HIV, evolve so quickly has made it difficult to develop effective vaccinations against them. But



Thanks to the acid produced by the cells that line the internal walls of the human stomach, it has a pH between 1.5 and 3.5—more acidic than a car battery. For many years, it was assumed that the stomach was a sterile environment because nothing was known to be capable of living in such a highly acidic environment.

But we now know that a species of bacteria, *Helicobacter pylori*, not only lives in human stomachs, but it has been with our species for at least the last 100,000 years, and probably much longer. Perhaps half of all humans have this kind of bacteria, making it one of the most widespread bacterial infections.

the fact that viruses evolve is perhaps one argument for considering them living things.

- One mystery that remains is where viruses fit into the tree of life. We don’t know whether viruses evolved multiple times independently or whether there was a single evolutionary origin of viruses that later evolved to become more diverse.
- One hypothesis is that viruses evolved from parts of dead cells, such as pieces of DNA or RNA. If that hypothesis is correct, and if viruses can be considered living things, it may be the only example we know of in which life came from a nonliving source.

What can our understanding of extreme life tell us about life elsewhere in the universe?

The search for extraterrestrial life has been motivated in part by the discovery of exoplanets—planets orbiting stars other than our Sun. Even if the chances of life evolving on any given planet are low, the sheer number of planets that are known to exist makes it likely that at least some of them are habitable.

Moreover, the discovery of extreme life on Earth shows that our definition of “habitable” must be expanded. In fact, there are few, if any, places on Earth where we haven’t found life.

- On the other hand, if viruses aren't alive, the fact that they evolve suggests that Darwin's theory applies not only to living things but also to nonliving matter. So far, we aren't aware of any other examples of nonliving things that evolve.

Readings

Carroll, *Into the Jungle*.

Quammen, *The Tangled Tree*.

Questions

How did the discovery of *Thermus aquaticus* bacteria living at temperatures around 176° Fahrenheit in the hot springs at Yellowstone National Park help change our understanding about the evolution of life on Earth?

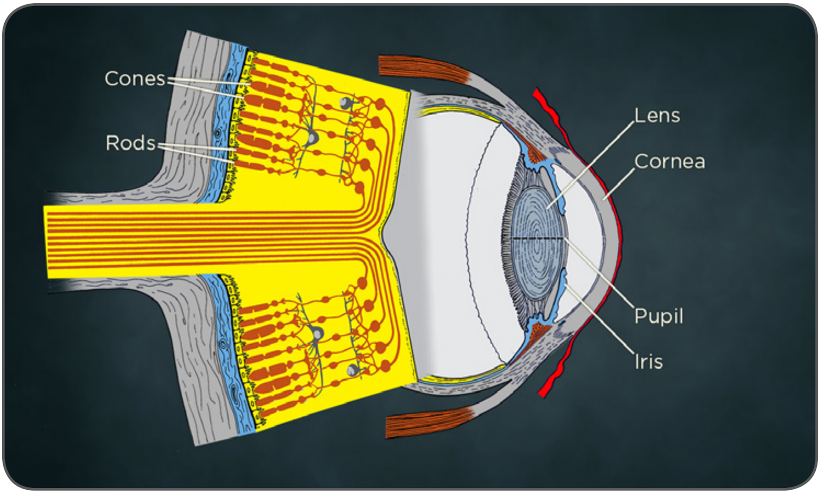
How can some fish, such as the crocodile icefish, survive in freezing water?

Answers can be found on **page 243**

Lecture 15

Imperfect Nature: Ad Hoc Body Designs

In his 1802 book, *Natural Theology*, William Paley argued that if a person were to discover a pocket watch lying on the ground, the person would recognize that the watch—with all its intricate and complex parts, all of which must work together for the watch to function—must have been designed and built by someone. The alternative, that the watch was a natural creation, would never even come to mind, Paley wrote, because it would be too far-fetched. By analogy, Paley argued that a reasonable person should also conclude that the complex, intricate components of a living organism must also have been designed by a creator. Paley's prime example was the human eye, which he compared to a telescope. Both, he argued, seem clearly designed for the purpose of vision.



How the Human Eye Works

- As light enters the eye, it passes through the cornea, the transparent outer surface, and then enters the eye through the pupil. The size of the pupil is controlled by a circular muscle, the iris. The light then continues inward, passing first through a lens and then through a clear fluid before reaching the back of the eye, the retina.
- In the retina, light must first pass through a series of nerve cells before finally reaching the specialized photoreceptor cells, the rods and cones—both of which have discs bound by a membrane that houses molecules called rhodopsin.

The human eye is one of the most famous topics in evolution.

Our eyes seem to be so perfectly suited for their purpose: to allow us to see. This apparent perfection led some people to conclude that the human eye must have been created by a divine designer.

- In the absence of light, rhodopsin has a bent shape. But when light hits the rhodopsin membrane, it straightens, changing its shape into a different configuration of the same atoms. This change in shape triggers a series of further chemical changes inside the cell, leading ultimately to the cell turning off the production of a chemical signal.

- When that chemical signal is no longer being released from the photoreceptor cell and received by an adjacent nerve cell, it causes the nerve cell to send an electrical pulse to the next nerve cell, which passes it along to yet another nerve cell, until eventually the pulse reaches the brain. This is the basis for sight.

- A human eye has about 126 million photoreceptor cells in the retina, each of which sends a signal to the brain when it detects light. Because the photoreceptors are distributed across a curved surface, the brain can form an image based on which photoreceptors are being activated at a particular time. Because some photoreceptors, called cones, are only sensitive to particular wavelengths of light, the activation of these photoreceptors allows us to perceive colors.

- Paley went on to point out that the eye of a fish is slightly different from the human eye, with a rounder lens that helps it see better underwater. The observation that each species has intricate aspects of its anatomy that appear to be perfectly suited for their environments was, at least to Paley, evidence for the existence of a divine creator.

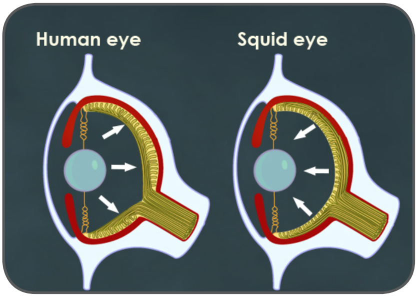
- Though he had been impressed by Paley's logic, Darwin would ultimately offer a more nuanced alternative. In Darwin's view, adaptation—the match between an organism and its environment, and the intricate complexity of an organ like the eye—could be better understood as a result of many generations of natural selection.

- Darwin recognized that it was difficult to imagine the entire sequence of adaptations leading to a complex organ like the eye. But he proceeded to describe how a simple eye, consisting of little more than a few light-sensitive cells, could be beneficial and how slight modifications on such an organ would be favored by natural selection.

- Darwin responded to criticism of his theory by pointing out how (what we would call) convergent evolution has led to animals with eyes that appear similar to ours but with key differences.

- For example, some mollusks, such as the squid, have eyes that appear very similar to the human eye. Both have a lens that focuses light on photoreceptor cells located at the back of the eye, which are connected to nerve cells that relay visual information to the brain.

- But, as Darwin noted, there are some differences. For example, a squid focuses its eye by moving its lens forward and backward. By contrast, we and other vertebrate animals focus our eyes by changing the shape of the lens.
- So far, Darwin might appear to agree with Paley that each is specifically and perfectly adapted. But other differences suggest that each organism is not perfectly designed.
- In particular, unlike the vertebrate eye, a squid's eye has photoreceptor cells that are turned the opposite direction, pointed toward the incoming light.
- In other words, the squid eye has the sensible design of facing toward the light while our eyes suffer from a critical design flaw: The photoreceptors in the human retina are facing backward, pointing away from the light. This means that photoreceptors connect to the optic nerve cells on the inside of the eye. To reach the brain, the human optic nerve must first pass through the retina.
- It's as if you had a TV or computer monitor with a signal cable coming right through the center of your monitor. Obviously, that part of the screen wouldn't be able to display any images.



- Likewise, in the human eye, at the place where the optic nerve crosses the retina, there cannot be any photoreceptor cells, so our eyes have a blind spot.
- By contrast, in a squid's eye, with its forward-facing photoreceptor cells, the optic nerve is behind the eye, so squids don't have a blind spot.
- Darwin pointed out these differences as evidence that each eye had evolved independently. But that still sounds like Paley's argument

for perfect design. What Darwin overlooked, or possibly preferred not to mention, was later recognized as one of the most convincing arguments in favor of his theory.

- The fact that many species, including humans, have aspects of our anatomy and physiology that are less than perfectly designed suggests that we are a product of a long series of modifications—perhaps wonderful in their own way, but without any overall plan for perfection. The organisms and adaptations that are passed on to later generations are simply good enough under the circumstances.

The Evolution of Eyes

- The first “eyes” weren’t really eyes at all. They were just cells, or parts of cells, that could detect the presence or absence of light. Even the simplest, earliest light-detecting abilities would have provided an advantage to organisms that use sunlight to make energy through photosynthesis. Being able to detect light made it possible for such organisms to aim for the light and maximize energy production.

- Some living organisms still have such primitive light-detection abilities, including *Euglena*, a genus of single-celled protists with a simple photoreceptor that can detect light.

- Once organisms evolved simple photoreceptors, mutations occurred in some organisms that duplicated the photoreceptors, resulting in a field of photoreceptors, spread over a particular area. This would have been advantageous because it would improve the organism’s ability to distinguish light from dark. Importantly, having many photoreceptors also allows the direction of light to be determined based on which photoreceptors are being stimulated.

- Taking it one step further, the ability to determine the direction of light was enhanced in some organisms by mutations that caused the field of photoreceptors to become curved inward, like a cup. This cup shape causes light coming from the right side of the body, for example, to stimulate cells on the left wall of the cup but not the right wall.

- A slight change from a cup-shaped eye led to a major improvement in visual ability. Restricting the opening of the cup to just a tiny hole allows only a very small beam of light to pass through to the photoreceptor cells inside. That not only provides more precision when determining the direction that light is coming from, just like a pinhole camera, but it also causes an image to form on the photoreceptors inside the pit.

- The image formed by a pinhole camera is upside down, but that image can be recorded by film placed in the back of the camera. A pinhole eye works the same way: The image is formed upside down on the photoreceptor cells in the back of the eye, but the

An example of an organism that still has cup-shaped eyespots is a flatworm known as a planarian. Planarians don't engage in photosynthesis, so they don't need to move toward light, but being able to hide can help planarians avoid being eaten by predators and being in a dark place makes it easier to hide. So, planarians probably evolved cup-shaped eyespots to hide from their enemies.

photoreceptors can send signals to the brain, where the image is processed and corrected. In other words, organisms that evolved a pinhole-type eye were the first to "see" the world around them.

- Although pinhole-type eyes can form images, the visual abilities of animals that have this type of eye are limited.
    - The image can't be focused unless the animal moves closer to or farther away from what it's looking at.
    - Opening the eye allows more light to enter the eye, which can be helpful in the dim light of the deep sea or at night, but it also makes the image blurrier.

The chambered nautilus is an example of a living organism with a pinhole-type eye. These mollusks are related to squid and are scavengers and predators. Their ability to form rudimentary images is thought to help them locate food and avoid being eaten by other predators.

Flounders have flat bodies that allow them to lie hidden on the seafloor. Some bury themselves under the sediment, with only their eyes peeking out. Flounders are ambush predators, camouflaged so that their prey, typically other fish, won't see them until it's too late.

Having both eyes facing upward certainly makes sense given the flounder's lifestyle. But what makes flounders look so odd is that their eyes don't start off on the same side of their head—because they evolved from fish that were not bottom-dwellers and had eyes on either side of their heads.

The flounder's peculiar anatomy is a result of descent with modification of a developmental pathway. The ancestors of flounders evolved for a lifestyle of living in the open water, and their flounder descendants had to modify this pathway for life on the seafloor.

- Both of these problems were solved by the first animals to evolve an eye with a lens, a piece of transparent material that bends light. The lens focuses the image on the photoreceptor cells inside the eye. A major advantage of having an eye with a lens is that the lens can be adjusted to change the eye's focus.

- Mollusks like squid adjust the focus in their eyes by moving the lens forward or backward, the same way a camera focuses its lens. The human eye works differently. Like all vertebrate animals, we focus by changing the shape of the lenses in our eyes. If the lens is flattened, light from more distant objects becomes focused on our photoreceptor cells. If the lens becomes more rounded, we can focus on objects that are closer.

- The fact that the photoreceptor cells that make up our retinas are facing away from the light, creating a blind spot where the optic nerve passes through the retina, didn't prevent our ancestors from surviving and reproducing. The fact that a more elegant design for an eye was possible didn't matter; the vertebrate eye was good enough, so it was passed from generation to generation.

- In fact, despite this design flaw, which all vertebrates inherited from our common ancestor, some vertebrates, such as eagles, have exceptionally good vision.

From our imperfect eyes to the bizarre faces of flounders, the apparently ad hoc body designs of humans and other species are now understood as strong evidence in support of a history of evolution by natural selection.

While Darwin was aware of a few examples of the peculiar anatomy of humans and other animals, he never bothered to present such facts as a distinct category of evidence—though he would be delighted to see how much more we've learned. And the more we learn, the clearer it becomes that natural selection acts much more like a tinkerer than an engineer.

Readings

Coyne, *Why Evolution Is True*.

Dawkins, *The Blind Watchmaker*.

Gould, *The Panda's Thumb*.

Lents, *Human Errors*.

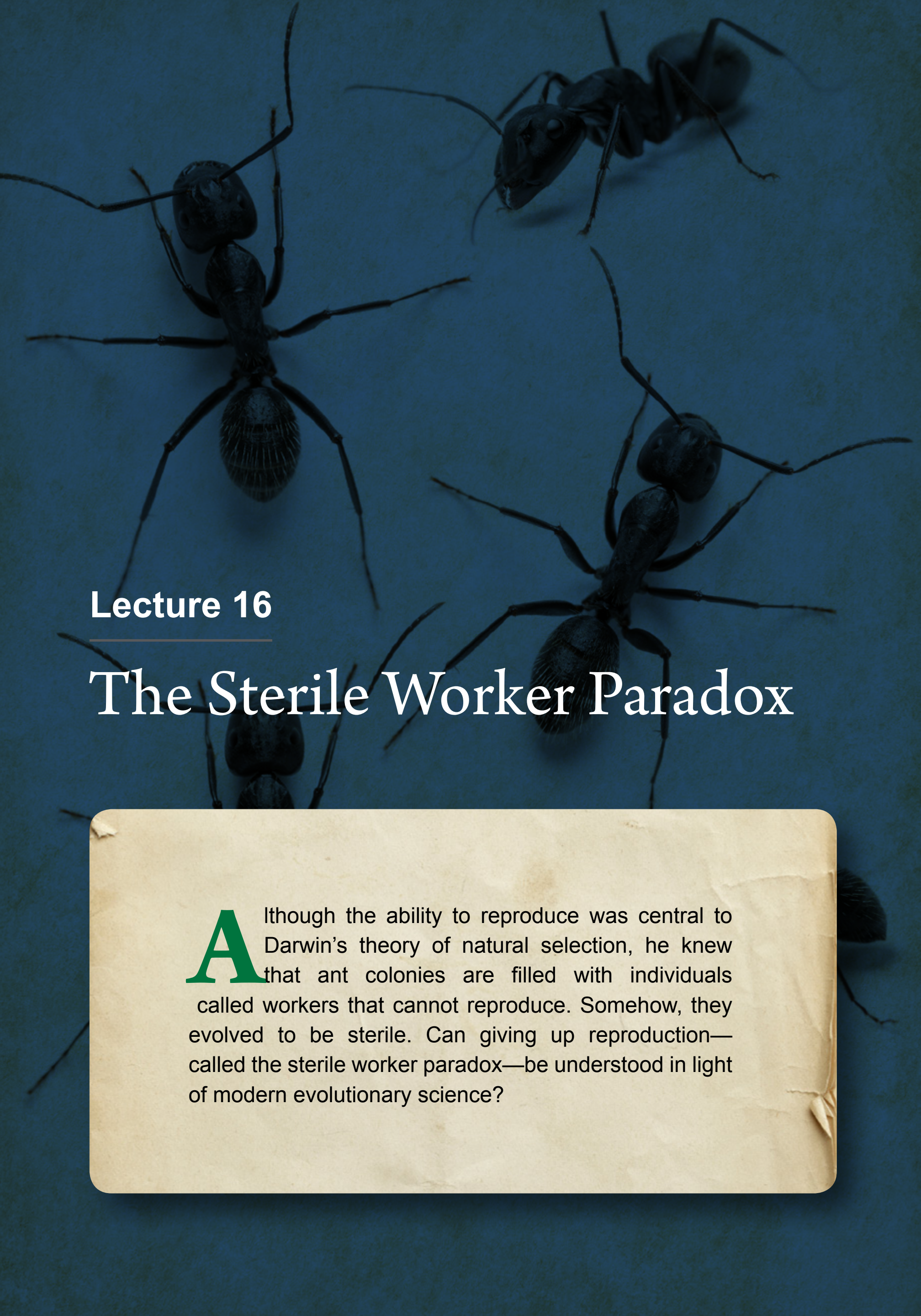
Shubin, *Your Inner Fish*.

Questions

In what ways do the eyes of a squid seem better designed for vision than human eyes?

Some living organisms, such as the chambered nautilus, have eyes that resemble earlier stages in the evolution of more complex eyes like ours. Does this mean that these organisms will eventually evolve more complex eyes?

Answers can be found on **page 244**



Lecture 16

The Sterile Worker Paradox

Although the ability to reproduce was central to Darwin's theory of natural selection, he knew that ant colonies are filled with individuals called workers that cannot reproduce. Somehow, they evolved to be sterile. Can giving up reproduction—called the sterile worker paradox—be understood in light of modern evolutionary science?

The Evolution of Eusociality

- The division of labor with long-lived queens reproducing and shorter-lived sterile workers dividing up all the other tasks, is called **eusociality**, and it makes for incredibly efficient societies. It works so well, in fact, that species that evolved this lifestyle—including ants, bees, termites, and others—have become some of the most dominant organisms on the planet.

- The first animals to evolve eusociality were probably the termites, about 150 million years ago.

- The unique ability of some termite species to eat wood may provide a clue as to why and how they evolved a social lifestyle. Termites cannot actually digest wood on their own. Instead, they have **symbiotic** bacteria and protozoans that live in their digestive tracts to break down the tough lignin and cellulose.

- But termites are not born with these symbiotic microbes; each generation passes along the microbes as part of the feeding process. Immature termites cannot feed themselves, so older termites will regurgitate into their mouths, providing them not only with food but also with beneficial gut microbes.

- In fact, as it grows, a termite must shed its exoskeleton. But the lining of the gut forms a part of that exoskeleton, and when the gut lining is shed, the microbes inside the gut are lost, too. So, termites must also get new gut microbes from each other as they age. Sharing food is one way. But beneficial gut microbes are also shared between individuals by feeding on anal secretions of nestmates.

- This reliance on sharing food and symbiotic microbes with one another is far from universal. Termites descended from a cockroach-like ancestor, but cockroaches don't share food. Yet some wood-eating cockroaches actually do share microbes because of an unusual readiness to eat one another's feces.

- This form of microbe sharing may help explain how the first termite societies evolved from nonsocial ancestors, especially because wood-eating cockroaches and termites have similar types of protozoans in their guts that help them break down cellulose.

- Unlike most cockroaches, wood-eating cockroaches live as families, with parents caring for their offspring and passing on microbes that digest wood. So, over time, there may have been an advantage to cockroach females who don’t just lay eggs and die, but instead live on while their offspring are also alive.

- Having 2 or more generations alive at the same time may be a critical first step toward evolving the more complex societies with sterile workers that characterize eusociality. Biologists refer to this as overlapping generations.

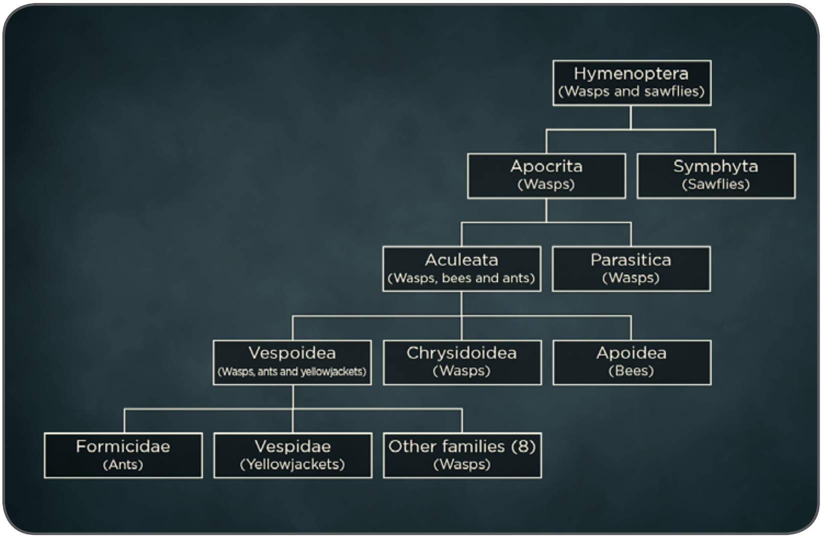
- In some eusocial species, the queens live long lives, doing little more than laying eggs for most of her life. Despite being so focused on reproduction, she will mate on just one occasion, after which she will establish her new nest and lay the eggs that will develop into the first batch of workers. As soon as they emerge as adults, they will get to work—finding food, expanding the nest, and helping to rear additional workers. The evolution of overlapping generations, with queens and their offspring alive at the same time, seems to be one step toward the evolution of eusociality.

Eusociality with Sterile Workers

- Although many animals protect themselves from predators by living in groups, from schools of fish to herds of wildebeests, eusocial species with sterile workers evolved on only a few branches on the tree of life. There are no eusocial birds, reptiles, amphibians, or fish. Only 2 mammal species are eusocial, both of which are rodents called mole rats, and the only marine species known to be eusocial are several species of snapping shrimp.

Amazingly, we now know that eusocial species with sterile workers evolved separately at least 15 times over the history of life on Earth. It happened once in the ancestor of termites, again in the ancestor of ants, several times among wasps and bees, and a few times in other groups. Each of the 15 separate eusocial species diversified, giving rise to the thousands of eusocial species alive today.

- The vast majority of eusocial species belong to a group of insects called Hymenoptera, which includes ants, bees, and wasps. Evidence for the earliest Hymenoptera ancestors comes from 280 million years ago, but the first-known eusocial species do not appear in the fossil record until ant ancestors about 110 million years ago.
- Half the biomass, or collective weight, of all insects is estimated to come from ants alone. There are about 14,000 species of ants alive today, and all of them are eusocial. This suggests that the eusocial lifestyle evolved once in the common ancestor of all ants.
- We know that the common ancestor of all ants lived about 110 million years ago, so the eusocial lifestyle of ants must be at least 110 million years old, and it has been inherited by each new ant species as it evolved.
- The Hymenoptera family tree confirms that ants are a specialized group of wasps. As eusociality evolved in female wasps and bees, a needlelike organ on their abdomens for laying eggs, called an ovipositor, became a stinger that could deliver venom instead of eggs.



- Honeybees evolved barbed stingers, causing them to get stuck in their enemy's skin. This allows for more venom to be pumped into the wound, making it more painful and therefore a more effective defense weapon. But it also causes the stinger and the attached venom sack to break off when the bee flies away, eventually killing the bee.

- Why would a bee sacrifice itself? Even if it protects the nest, why would natural selection favor one individual dying to protect another?

Kin Selection

- Biologist William D. Hamilton attempted to solve this puzzle in 1964 with a hypothesis suggesting that altruistic, or self-sacrificial, behavior could evolve in situations where an individual is incurring a personal cost to help a close relative. After all, close relatives share many copies of the same genes. Natural selection acts to pass our genes from one generation to the next, but perhaps it doesn't matter who does the passing.

- Hamilton called his theory kin selection. In a way, kin selection was an extension of Darwin's theory of natural selection acting on individuals to natural selection acting on families.

- Hamilton suggested that kin selection could explain not only why a worker honeybee could evolve a self-destructive, barbed stinger—but perhaps also the sterile worker paradox. After all, giving up reproduction is another form of altruism.

- Hamilton's kin selection theory suggested that even though a worker ant or bee might not have any of its own offspring, copies of its genes can still be passed to subsequent generations by its siblings, nieces, and nephews if they reproduce.

- Hamilton suggested that eusociality might be especially common in ants, bees, and wasps because of their unique sex determination system. Unlike in humans, every egg that is fertilized by a sperm in ants, bees, and wasps develops into a female. Unfertilized eggs, which would not survive in most other species, become males.

- Sisters are more closely related to each other than is typically the case in other species; they share on average 75% of their genes with their sisters. In ants, bees, and wasps, all the workers are sisters. This means that a worker is more closely related to the other sibling-workers in the colony than they would be to their own offspring, who would share just 50% of their genes.

- Based on the logic of kin selection, then, the best strategy for passing on copies of a worker's genes is to have more sisters. And the only way to have more sisters is to help the queen by doing all the other work in the colony so she can focus on laying eggs.

- At first it seemed like the sterile worker paradox had been solved by extending Darwin's theory to include kin selection. But as researchers discovered new examples of eusocial species, such as aphids and snapping shrimp, it became clear that not all of them had the same peculiar sex determination system as the ants, bees, and wasps.

- What's more, in some insect societies, the workers are not full siblings. In some, such as fire ants, there can be multiple queens. In others, such as leafcutter ants, the queens mate with multiple males.

In either case, having more than one mother or more than one father means that the workers are not full siblings and are therefore less closely related to one another.

- So, Hamilton's hypothesis about relatedness was neither necessary nor sufficient to explain the evolution of all eusocial species.

There is one thing that all eusocial species, at least those we know about, have in common: All of them live inside some sort of communal nest structure that can be defended.

Communal living may be a key step in the evolution of eusociality. By sharing the same living quarters, it's in everyone's best interest to protect the nest from enemies and disease.

How did evolution get from species in which a female builds a simple nest to raise her young, to shared nests that are better defended from enemies, and even to helpers giving up reproduction altogether, making them sterile workers?

Harvard biologist Edward O. Wilson has suggested that natural selection can act on 2 levels: on individuals and on groups.

For eusocial insect societies, rather than thinking of each worker ant or bee as an individual, maybe we should think of the entire colony as a complex organism—a superorganism, in which individual worker ants or bees are more like individual cells, each with its own task to perform so that the organism can function as a whole.

Preadaptations to Evolving Sociality

- If the eusocial lifestyle has been so successful, then why haven't other organisms evolved to be eusocial? Why is eusociality limited almost exclusively to invertebrates and mostly to just a few groups of insects?

- Part of the answer may be that some aspects of an organism's biology might make it more likely to evolve a eusocial lifestyle. In other words, some species might be predisposed, or preadapted, to evolving eusociality.

- Living inside a communal nest might be one such preadaptation. Having a sex determination system that makes sisters more closely related to one another—as is the case for all ants, bees, and wasps—might be another. Monogamy may be important as well. Having to share beneficial gut microbes, like termites do, could be yet another factor.
- Once an organism has one or more of these preadaptations, having overlapping generations becomes more advantageous. With different generations around, why not divide up all the different tasks that need to be performed? Then, it's just one more evolutionary step before you have division of labor that includes sterile workers.
- But what about cockroaches? They evolved from a common ancestor with termites but stayed on a nonsocial path. Why didn't all cockroaches evolve toward sociality?

Human societies have a complex division of labor, and studies suggest that fertility rates are declining. Are our descendants headed toward a point-of-no-return eusocial structure?

Edward O. Wilson, among the foremost experts on eusociality, tried to extend this concept to include humans as "loosely eusocial." His argument was not that we are headed toward a society supported by sterile workers, but that we evolved much more brain-intensive methods of generating social cooperation that made us "dominant among land vertebrates."

Wilson argues that 2-level selection explains why humans have evolved to be simultaneously selfish as individuals yet altruistic in groups. For Wilson, it's an iron law that "selfish individuals beat altruistic individuals, but altruistic groups beat groups of selfish individuals."

It's a provocative analogy to explain why humans and social insects are the dominant animals on our planet, but human altruism and cooperation are not the same as eusocial cooperation. It's a case of convergent evolution: Vastly different starting points nonetheless converge, in different ways, on features valuable for social complexity.

- Having a lot of sterile workers is reproductively expensive, and having sharp divisions of labor requires a big colony. Also, cramming many individuals all together into a single enormous nest can make it easier for predators to attack or for disease to spread and wipe out many individuals at once.

- Eusociality may be a strategy that works well for many species, but natural selection can't always lead to ideal outcomes. The best selection can do is sort between the different versions of what's alive at a particular time and make the best-adapted versions more common. If conditions change, as they often do, a different version might be favored for a while.

- Intriguingly, although some primitively eusocial bees have gone back to being solitary, all ants and termites have remained fully eusocial. This suggests that there may be a point of no return in the evolution of this complex lifestyle. So, sterility can be not just a dead end for the workers, but an irreversible path for the species as a whole.

Readings

Hölldobler and Wilson, *The Superorganism*.

Wilson, *The Social Conquest of Earth*.

Questions

Why did Darwin think that ants might undermine his theory of evolution by natural selection?

When might natural selection act at the level of entire groups rather than just on individuals?

Answers can be found on **page 245**

Lecture 17

Coevolution: Peace Accords and Arms Races

Darwin knew that many orchids have tubes called nectaries with sugary nectar inside to encourage pollinators to visit in exchange for their services in transferring pollen from one flower to another. But in the Christmas star orchid from Madagascar, the nectary was about a foot long, much longer than any that he had examined so far. In 1862, Darwin published his complete work on orchids, offering a specific prediction about the sucking mouthpart of the pollinating insect: "...in Madagascar there must be moths with proboscises capable of extension to a length of between ten and eleven inches." To Darwin, the interactions between a moth's mouthparts (the proboscis) and orchid tubes had everything to do with evolution. He saw their matching up as a result of natural selection.

Coevolution

- Orchids benefit from having insects transfer pollen from one flower to another, but if every insect that visited a Christmas star orchid also visited flowers from other species, then some of its pollen might get wasted. By restricting access to only one type of insect, the orchids could avoid wasting precious pollen.

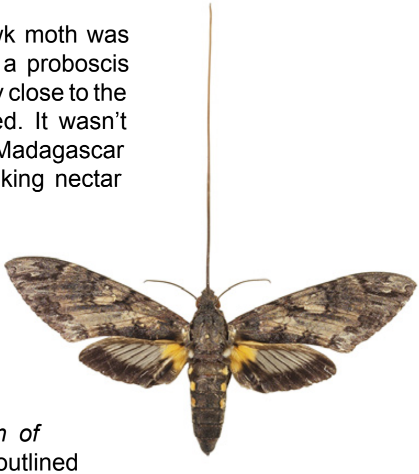
- Darwin suggested that as the orchid evolved a slightly longer nectary, the moths that drink from it would benefit from having a slightly longer proboscis. Over generations, both the orchid's nectary and the moth's proboscis grew longer and longer, each becoming more dependent on one another.

- In 1867, Alfred Russel Wallace published a supportive article with illustrations of his best guess about what to look for.

- Darwin would not live to see it, but his moth prediction turned out to be correct.

- In 1903, an especially large hawk moth was discovered in Madagascar, with a proboscis measuring 11.8 inches long—very close to the dimensions Darwin had predicted. It wasn't until 1992 that a biologist in Madagascar actually observed this moth drinking nectar with its long proboscis from a Christmas star orchid.

- The notion that species evolve in response to one another has become known (since the 1960s) as coevolution. But the basic idea is much older: In *On the Origin of Species*, Darwin had already outlined the basic idea from observing honeybee mouthparts and the shape of clover flowers, which later led to his famous prediction about the existence of a long-tongued moth.



- Another example of coevolution between plants and insects that Darwin did know about involves the yucca plant. Much like the Christmas star orchid, yucca plants can only be pollinated by a particular type of moth, called a yucca moth.

- Female yucca moths collect pollen from yucca flowers, forming a pollen ball. Then, the females lay their eggs into the ovary of a different flower and use the pollen from the pollen ball to fertilize the second flower's ovaries. The moth's eggs will develop into larvae that emerge and eat the seeds that formed as a result of the pollen fertilizing the ovaries. It's as if the moths are leaving their offspring in a nursery complete with a buffet.

- Clearly, this is a nice arrangement for the moths. But the yucca plants also benefit, because pollination by the moths creates more seeds than the caterpillars can possibly eat. This has led to the yucca plants evolving to be completely dependent on yucca moths for pollination, and in turn, the moths are completely dependent on the yucca plants for their reproduction.

- The coevolution between yuccas and yucca moths has led to adaptations in each partner. While most moths have a long, straw-like proboscis that they use for sipping nectar, female yucca moths evolved mouthparts that resemble tentacles that are used for collecting pollen and forming it into a pollen ball.

- Yucca flowers evolved to have anthers (where pollen is produced) and stamens (where pollen is deposited) that are widely separated. In many insect-pollinated flowers, insects drinking nectar from a flower pick up pollen from an anther of one flower and then inadvertently deposit the pollen on the stamen of another flower. But yucca plants only become fertilized when a yucca moth deliberately deposits

The yucca and yucca moth are an example of coevolution because as one species evolved, the other evolved, too. Coevolution is like a dance: When one partner moves, the other must move in a corresponding way.

pollen from her pollen ball on the stamen of a flower where she has laid her eggs.

Antagonistic Coevolution

- These examples involve species that seem to get along, as if they worked out an **evolutionary peace accord**. But Darwin recognized that natural selection will not lead just to partners that evolve to help each other out.

- Even the example of yucca plants and yucca moths involves cheaters. Some yucca moths lay their eggs in the ovaries of yucca flowers but don't deposit pollen on the flower's stamen to fertilize it. Phylogenetic studies show 2 species of yucca moths known to be cheaters that evolved from more cooperative ancestors. Biologists refer to coevolution among outright enemies as antagonistic coevolution.

In antagonistic coevolution, the interaction between species is less like a dance and more like a fight. But even fighting is still like dancing in the sense that each partner must still respond to the other.

- Some orchids have evolved to seduce insects, tricking them into becoming pollinators with the promise of sex. Orchids in the genus *Ophrys* have flowers that look and smell like the females of particular species of bees. Enticed males visit these flowers and are so convinced by what seem like pheromones from a female bee that they vigorously copulate with the flower. Meanwhile, pollen from the orchid gets deposited on the bee's head.

- These male bees often get fooled by additional sexually deceptive orchids. In attempting to fertilize what they think is another female bee, they instead deliver the pollen from the first orchid, fertilizing the flower instead.

- A study comparing the extent to which the male bees engaged in pseudocopulation with sexually deceptive orchids found that the more sexualized the encounter, the greater the success of fertilization for the orchids. This suggests that orchids that more accurately mimic female bees stand to benefit.

- Some evidence suggests that this deception could be costly for the bees because male bees waste sperm by mating with orchids, making less sperm available for mating with actual female bees. Interestingly, though, this cost to the bees may be advantageous to the orchids.
- The reason has to do with the sex determination system of bees and wasps. Because male bees and wasps develop from unfertilized eggs, wasting sperm by mating with flowers doesn't mean that female bees can't reproduce; even without sperm, female bees can still lay unfertilized eggs that develop into males.
- If sexually deceptive orchids succeed in tricking lots of male bees into depositing sperm (and pollen) into their flowers, it could cause female bees to lay more unfertilized eggs than fertilized eggs. That would lead to even more males in the population, which is a good thing for the orchids because the males are the only ones that pollinate the deceptive orchids.
- Furthermore, having more males than females in a population of bees means that there is more competition among male bees for access to female mates. That can cause the male bees to become less discriminating in their choices of female mates, which plays right into the orchid's strategy of sexual deception.
- Consistent with this pattern, most pollinators of sexually deceptive orchids are bees and wasps—insects with the sex determination system in which males develop from unfertilized eggs.
- Perhaps the clearest examples of antagonistic coevolution involve predators and their prey.
- It's easy to imagine how prey species would benefit from improving how to avoid being eaten. Thomson's gazelles can run at speeds of up to 50 miles per hour, but they are one of the preferred prey of African cheetahs, which can run 75 miles per hour.
- As cheetahs evolved greater speed over the last 2 million years, only the fastest gazelles escaped and passed on their genes to the next

generation. As gazelles became faster, cheetahs had to evolve even more speed in order to get a meal.

- The back-and-forth evolution between cheetahs and gazelles amounts to an **evolutionary arms race for speed.** One species drives the other to evolve greater and greater speed, with no apparent limit. This coevolutionary arms race is what caused cheetahs to become the fastest land animals on Earth.

Cospeciation

- Biologists Paul Ehrlich and Peter Raven suggested in 1964 that a long-term consequence of antagonistic coevolution may be an increase in the evolution of new species.
- For example, if a plant develops a mutation that enhances its defenses against caterpillars, the plant may successfully prevent caterpillars from feeding on it. Freed from being eaten, the plants with the new mutation can increase in numbers, spread to new places, and adapt to new conditions. This can lead to the evolution of new plant species.

- At the same time, the caterpillars will be under pressure to evolve a way to circumvent the plant's improved defenses. The caterpillars that are fortunate enough to acquire a mutation that allows them to feed on the improved plants will proliferate and may become a new species.

- In the rare cases when new species have arisen on both sides as a result of their coevolving interactions, this result is known as cospeciation, or parallel cladogenesis.

- In recent decades, many biologists have become more careful about the meaning of coevolution and how to define it in a strict sense. It's clear that the Christmas star orchid evolved in relation to Darwin's moth—that's why Darwin's prediction worked out so well. But what about the moth's own evolution?

- Some researchers have suggested that the moth's hovering with a long proboscis might have evolved separately, as a way of avoiding predators. Hawk moths are found in central Europe, which lacks deep flowers, suggesting that the moth might be able to appear, or survive, even when the flower is absent.

- The bigger point is that not every pair of organisms that appear perfectly coadapted now had to coevolve together to get that way. One side, or even both sides, may be the result of prior coevolution with other species, which might now be absent or extinct in the current habitat. There might also have been pressure in the past from outside predators and/or parasites that have now vanished.

- Conversely, there are relationships that may appear merely parasitic, but it turns out that evolution has sculpted unsuspected benefits for the host. Parasitic worms, for example, may be responsible for the removal of allergens, heavy metals, and other pollutants from the gut of host mammals, including humans.

Leeches, associated with the practice of bloodletting as a supposed cure-all, do cause blood to become thinner, so they may actually have been helpful in cultures that did not traditionally have access to blood-thinning medications, such as aspirin, or in reducing toxicity from excess iron.

Animals from every branch of the tree of life—including humans—have evolved complex interactions with microorganisms.

The complex community of bacteria and other microorganisms that inhabit our bodies is known as the human microbiome. Although these microbes are not strictly part of our bodies, they perform critical functions related to digestion, produce vitamins that improve our nutrition, and help protect us from infectious disease. Research has shown that as we evolved, so did the microbes that inhabit our bodies—and vice versa.

Humans have also coevolved with our enemies. Many human diseases, such as malaria, have affected our species for countless generations, prompting an evolutionary back and forth between human hosts and the microorganisms that cause our diseases.

> We now think the very possibility of the earliest complex plants and animals depended on a coevolution in which some single-celled organisms were increasingly hosted by other single-celled organisms.

Readings

Agrawal, *Monarchs and Milkweed*.

Rico-Gray and Oliveira, *The Ecology and Evolution of Ant-Plant Interactions*.

Questions

Why does evolution sometimes favor cheaters?

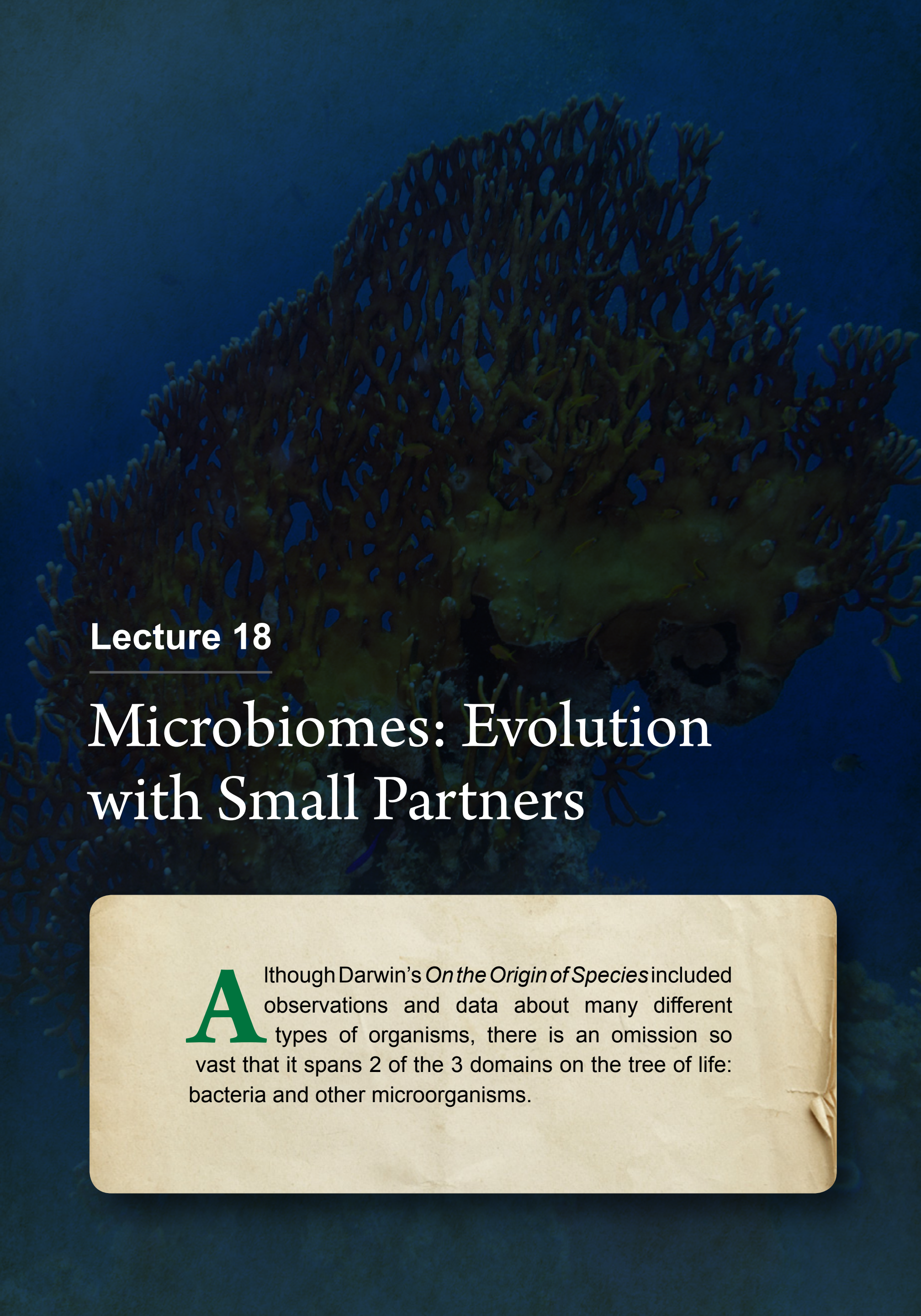
Which of the following scenarios would be most likely to lead to an evolutionary arms race?

a. An insect evolves resistance to the toxic chemical produced by a plant that it eats.

b. A bacteria produces vitamins needed by its host in exchange for a safe place to live.

c. A parasite evolves a way to manipulate its host's behavior, killing the host but helping the parasite find a new host.

Answers can be found on **page 246**



Lecture 18

Microbiomes: Evolution with Small Partners

Although Darwin's *On the Origin of Species* included observations and data about many different types of organisms, there is an omission so vast that it spans 2 of the 3 domains on the tree of life: bacteria and other microorganisms.

Microbial Partnerships

Microbes were first observed by a Dutch businessman named Antonie van Leeuwenhoek.

Not all microorganisms cause disease. In fact, fewer than 1% of the microorganisms we know of cause human diseases. And many microorganisms are actually beneficial to the lives of other organisms.

- The first person to recognize that microorganisms engage in partnerships with other organisms was Simon Schwendener, a Swiss botanist born 20 years after Darwin. Schwendener had been studying lichens, organisms considered at the time to be relatives of algae and moss.
- In the 1860s, Schwendener proposed that a lichen was not a single organism, but rather consisted of 2 different types of organisms: The structure of a lichen is made up of a type of fungus wrapped around microscopic algae. This “dual hypothesis” wasn’t widely accepted until the middle of the 20th century.
- Biologists began to realize that lichens were not really individual organisms at all. You couldn’t separate the fungus from the algae and still have a lichen; a lichen only exists when both partners participate, each contributing something to the mutual benefit of the other.
- The fungi provide structural support and nutrients, which are shared with the algae. The algae, through photosynthesis, provide energy in the form of carbohydrates that are shared with the fungi.
- It wasn’t until 2016 that biologists discovered that all lichens also contain a third partner: a yeast, a type of fungus that grows as a single cell instead of a threadlike filament.
- As Schwendener’s basic idea about lichens gained support, the intimate relationship of fungus with algae opened the minds of biologists to the possibility that other complex organisms might have evolved microbial partnerships.
- Many photosynthetic land plants depend on fungi, and evidence suggests that this relationship may have begun with the first land

plants more than 400 million years ago. In fact, the ability of plants to colonize land may have depended on the relationship they evolved with fungi to help them acquire water and nutrients from soil.

- That dependence continues today. The roots of many plants, far from being self-sufficient, are now known to have fungi growing in and around them, usually in a symbiotic way. The fungi contribute to the uptake of water and nutrients by extending the surface area for absorption out from the roots and into the soil. In exchange, the fungi get protection and energy from sugars.

- These fungi came to be known as **mycorrhizae** and are now recognized as essential for the survival of plants ranging from grasses to oak trees.

- Animals also depend on microorganisms. For example, termites that can digest wood depend on the metabolic capabilities of microorganisms living inside their guts, including bacteria, archaea, protists, and fungi.

Some insects, including a group of termites, evolved to use fungi as an external digestive system. In each case, comparing the evolutionary tree of the insects and that of their fungi reveals patterns of coevolution with occasional switches between groups.

Endosymbiosis

- As a graduate student, Lynn Margulis was intrigued by a peculiar observation: that DNA can be found in the cytoplasm of cells, the fluid-filled area outside the nucleus. She knew that the genomes of eukaryotic cells are contained within the nucleus, so why would there be DNA outside the nucleus?

- Margulis's colleagues had found DNA inside the chloroplasts of single-celled protists called *Euglena*. Chloroplasts are a type of **organelle**, structures that float around inside the cytoplasm and perform specialized tasks.

- Plants and algae also have chloroplasts in their cells that contain the chlorophyll pigment that makes them green and allows photosynthesis to take place. DNA turned up in the chloroplasts of these other organisms, too.

- What's more, the chloroplasts had certain similarities to cyanobacteria—free-living, single-celled bacteria. Both chloroplasts and cyanobacteria have ribosomes, structures in the cytoplasm where proteins are made; are surrounded by a double membrane; and engage in photosynthesis using similar chemical machinery.

- In 1924, a Russian biologist named Boris Kozo-Polyansky published a book suggesting that complex forms of life may be the result of once-separate life-forms coming together and fusing into a completely new type of organism. He called this process **symbiogenesis**—the creation of new life from organisms that are living together.

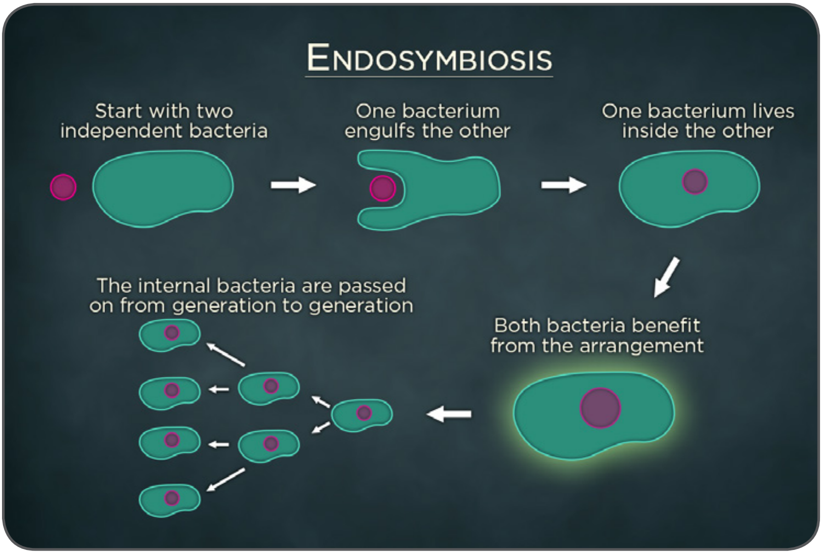
- Although Kozo-Polyansky's ideas did not become widely known, Margulis was arriving at a similar idea: Perhaps chloroplasts were once free-living cyanobacteria that somehow fused with another type of life to create a more complex cell with organelles capable of photosynthesis.

- Mitochondria, the organelles responsible for making energy, also have their own ribosomes and double membranes. They even have their own genomes, which are circular, just like the genomes of bacteria.

- To test her idea that organelles were once free-living bacteria, Margulis collaborated with Carl Woese to compare the ribosomal

RNA from mitochondria to the ribosomal RNA within the nucleus of the same cell and then compare both of these to the ribosomal RNA of free-living bacteria. Just as Margulis had predicted, the ribosomal RNA from mitochondria was more similar to that of free-living bacteria than it was to the ribosomal RNA within its own nucleus.

- These results showed that evolution doesn't just involve the splitting of 1 population into 2, as Darwin had suggested. It can also involve new forms of life being generated from the fusing together of 2 independent, distantly related organisms.
- This theory for the origin of organelles became known as **endosymbiosis** and is now widely accepted by biologists. But the implications of this theory are still causing us to rethink evolution and what it means to be an individual organism.



- After all, we can't live without the organelles inside each of our cells. They are a part of us just as much as any other component of our bodies. Just as lichens can't exist without both fungi and algae, we are all really hybrid organisms.

- Margulis was one of the first to recognize the importance of endosymbiosis and extend it to all complex organisms. She argued that any living thing more complex than a bacterium is really a type of chimera—a composite organism made up of multiple different types of once-independent living things with distinct genetic lineages.

- This explains why we can do separate studies of our mitochondrial DNA: because mitochondria were once distinct organisms that retained their own genetic signatures, even after being absorbed inside the cell.

The more carefully we look at the interactions between microbes and other hosts, the more we realize how much these interactions have shaped evolutionary history. In fact, some studies suggest that microbes may even contribute to the formation of new species.

The Human Microbiome

- As complex organisms, humans, too, are hosts to millions of microscopic organisms. Most of the microbes that live in our bodies are not harmful, and many of them are essential to our health and well-being. They help us digest our food, produce vitamins, and help protect us from infectious diseases.

By some estimates, the human body may be home to as many as 10 times more of the tiny microbial cells than the larger-sized human cells. Although these microbes occupy many parts of our bodies, the vast majority live in our gut.

If we could gather all the microbes from different parts of our body, they would collectively weigh between 2 and 6 pounds. By comparison, the average human brain only weighs about 2.5 to 3 pounds.

- Every person has a unique **microbiome**. These differences come about because we acquire our microbiomes from our environment, including the people we interact with, the food we eat, and the places we visit. Babies acquire much of their microbiome from their parents, especially from their mothers, during the birth process and by breastfeeding. Yet a host's genome influences its microbiome, too.

- A person's microbiome is unique enough that an individual can be identified by his or her microbiome alone. Yet there are enough similarities between the microbiomes of different individuals to distinguish the microbiome of humans from that of other species. And the differences follow a pattern that suggests a common evolutionary history.

Identical twins tend to have very similar microbiomes—more similar even than fraternal twins, who have different genomes but often share very similar environments.

- Studies comparing the composition of the human gut microbiome to that of our closest relatives, the great apes, suggest that as we evolved, our microbial partners have changed, too. Among the apes, the more closely related a host species is, the more similar its gut microbiome is.

Humans and chimpanzees, being each other's closest relatives, have gut microbiomes that are more similar to each other than to the gut microbiomes of other apes, such as gorillas or orangutans.

- The evolutionary histories of some individual bacteria also match the pattern of speciation among humans and the great apes, suggesting a pattern of coevolution between bacteria and their hosts—including our ancestors. This suggests that the microbes in our bodies are not a random collection of species we pick up from our environment, but a community of particular microbes that have been with us for millions of years.

- But that's changing quickly. For some bacterial species, there has been a rapid decline in prevalence from one generation to the next as a result of improvements in sanitation and access to clean water, the use of antibiotics, and the rise of Cesarean sections during childbirth. This decline reflects a more general trend of decreasing human microbiome diversity in industrialized and urban environments.

- What does the decrease in human microbiome diversity mean for our future? Natural experiments like coral bleaching, in which corals lose their symbiotic algae when water temperatures rise, highlight the importance of maintaining a healthy microbiome. Most corals that become bleached are at risk of dying.

Holobionts

- The intimate roles that microorganisms play in the lives of their hosts have caused some biologists to argue that perhaps we may be missing something fundamental about evolution by focusing only on the distinction between a host and its microbiome.

- In the 1990s, some biologists began using the term **holobiont** to describe the union of 2 (or more) symbionts: any multicellular host organism together with its microbial entourage. In this view, a complex organism like a coral isn't just an animal that has some algal cells living in its tissues. Rather, what we commonly call "coral" is in fact an assemblage of an animal plus the algae, bacteria, viruses, and other microbes that are consistently found inside coral tissues.

- In fact, inside corals, some bacteria even have viruses called bacteriophages, adding yet another layer of complexity, sometimes called the virome.

- Altogether, the virome, the microbiome, and the macrobiome define each holobiont.

- The holobiont concept has created quite a stir among evolutionary biologists. After all, Darwin considered individuals as the fundamental units of evolution. Now we are considering whether a holobiont, which represents a higher order of biological organization than individuals, should take the place of individual plants and animals in Darwin's theory.

- And in terms of the modern synthesis of evolution with genetics, the idea that genes may be the most fundamental unit of evolution also begins to look different.

- Which genes, or which combinations of genes, should be considered the fundamental unit of evolution? As we expand from individual genomes to the study of larger genetic ensembles (sometimes called hologenomes), the fundamental unit of evolutionary genetics may also expand to include the microbiome.

Readings

Blaser, *Missing Microbes*.

Dunn, *The Wild Life of Our Bodies*.

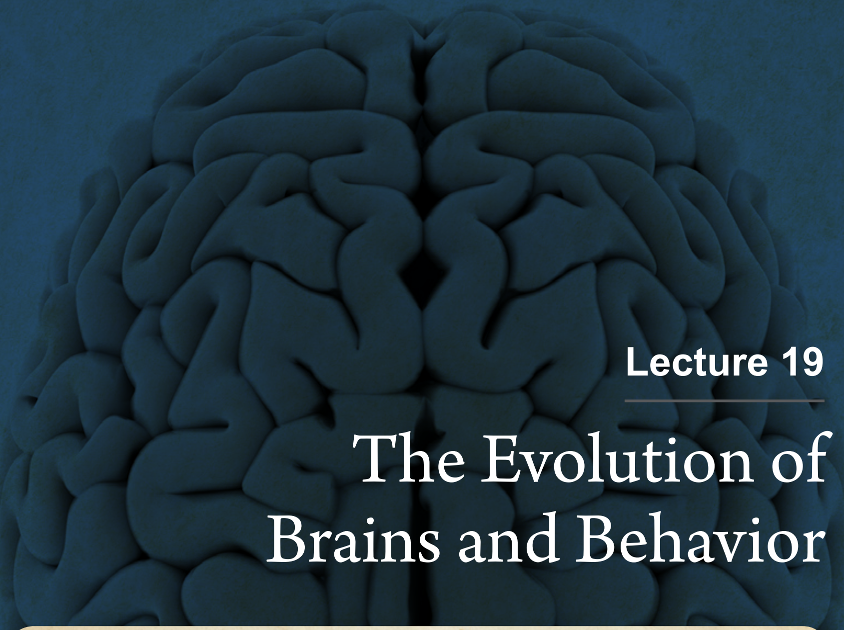
Yong, *I Contain Multitudes*.

Questions

What clues led Lynn Margulis to the theory, called endosymbiosis, that eukaryotic cells of all plants and animals evolved through the fusion of previously independent organisms?

Why do aphids die if they are given antibiotics?

Answers can be found on **page 247**



Lecture 19

The Evolution of Brains and Behavior

In 1871, Darwin's thoughts on brains and behavior came together in *The Descent of Man*, in which he pointed out shared features between humans and other mammals. He suggested that the obvious difference in mental powers was related to the larger brain size of humans. Then, he generalized, saying that ants have larger "cerebral ganglia" than other insects, resulting in greater intelligence. But the absolute size of the brain is only one factor that affects intelligence; the relative size of an animal's brain compared to the size of its body is a better indicator of its intelligence. And Darwin realized this. In 1872, he published his thoughts on the similarities of human and animal behavior in *The Expression of the Emotions in Man and Animals*.

Blue whales have a brain that is 5 times larger than a human brain but a body that is 2000 times larger than a human body.

The Study of Behavior

- Darwin suggests that emotions are generated by the nervous system. A central argument in *The Expression of the Emotions* is that all humans express emotions like grief, surprise, and anger in similar ways—evidence that the human brain and nervous system evolved in the common ancestor of humans.

- Amazingly, we can see evidence for the evolution of some of the earliest nervous systems in the behavior of some of the first animals on Earth, captured in trace fossils—impressions or marks that indirectly give us information about an organism—from the Ediacaran and Cambrian eras.

Some of the earliest trace fossils preserve marks made by primitive animals as they grazed on microbes living in mats on the seafloor. These earliest trace fossils have paths that cross the surface in one direction, suggesting the animal was consuming microbes as it ate, but not altering its direction based on any external cues.

Later trace fossils have paths with more complexity, including turns, spirals, and digging down into the sediment. Paleontologists interpret these paths as evidence that the animals had evolved a way to detect something in the environment—perhaps how abundant a food source was—and adjust their route accordingly.

Trace fossils from even later show multiple overlapping paths that each take sharp turns. These fossils from the Cambrian era may be evidence of some of the first predators chasing their prey.

- The study of behavior became more rigorous and systematic in the 1930s due largely to the work of 3 biologists: Nikolaas Tinbergen, Konrad Lorenz, and Karl von Frisch. They showed that behaviors could be studied with the same types of scientific approaches as other traits of organisms, such as their anatomy, and that behaviors were characteristics of species that have a genetic basis, implying that they can evolve.

- Tinbergen conducted a series of experiments on herring gull chicks that showed that the red spot on a gull's beak is an important signal that the chicks use to recognize their parents and that they engage in begging behavior when they see it. He proposed that to fully understand any behavior, biologists must consider 4 different questions. For example, to understand why herring gulls respond to artificial birds with a red dot on their beaks, biologists should ask the following questions:
    - What physiological mechanism in the bird's body is functioning when a herring gull chick is begging? This could involve studying the visual abilities of the chick, the part of the brain that is activated when it sees the red dot, or how nerves carry a message from the bird's brain to the muscles around its beak, causing it to open its mouth.
    - Is the behavior instinctual, or is it learned from other birds? Because herring gull chicks perform begging behaviors from the moment they hatch, this behavior appears to be instinctual.
    - How does the behavior affect the chick's ability to survive or reproduce? By encouraging the chick's parents to feed it, the begging behavior likely enhances its chances of survival.
    - How has the behavior evolved? By comparing the responses of herring gulls and their closest relatives to artificial birds with red spots, researchers could determine whether this behavior evolved uniquely in herring gulls or whether it has a longer evolutionary history.

Genetic Changes

- Major advances in the study of behavior has come with the development of tools in genetics and genomics.
- In some places, 2 mound-like fire ant nests are right next to another. How can this be, given that ants from different nests usually fight to

the death? The reason for the lack of aggression in some fire ants involves a genetic mutation that changed their behavior.

- Most ants defend the territories around the nests, and if an ant from another nest is found within their territory, they will attack it. Ants can use cuticular hydrocarbons, chemical cues within their exoskeletons, to tell whether another ant is a nestmate that belongs to the same colony or whether it belongs to another colony. The ability to tell nestmates from non-nestmates allows worker ants that encounter one another outside their nest to decide whether or not to fight.
- But in some fire ants, a type of mutation called an inversion caused a portion of one of their chromosomes to be backward. One of the genes within the inverted region of the chromosome is involved in nestmate recognition using cuticular hydrocarbons.
- If a queen happens to have the inverted version of the chromosome, then she and all of her offspring—the workers in the colony—lose the ability to tell whether or not another individual ant smells like it belongs in the colony. That means they can't tell a nestmate from an interloper from a neighboring nest.
- The result is that worker and queen ants with the inversion mutation effectively become pacifists; they simply treat all fire ants as if they were nestmates. The alternative—treating every ant they meet as an enemy—would presumably be self-destructive and would be eliminated by natural selection.
- But being pacifists has become advantageous for fire ants, contributing to their success in spreading across much of the southeastern United States. One consequence of being pacifists is that queens can now set up new nests within the same neighborhood, rather than colonies attacking one another. That means that within a given area, there might be a lot more fire ant nests than you would expect if the ants were territorial.
- And unlike most ants, who have only one queen per colony, fire ants with the mutation allow multiple new queens to join their nests. That makes it harder to kill the entire colony because to do so you have to kill all the queens.

- Despite the sophistication of their group behaviors, supported by the larger "cerebral ganglia" Darwin noted, individual ants are not all that intelligent.

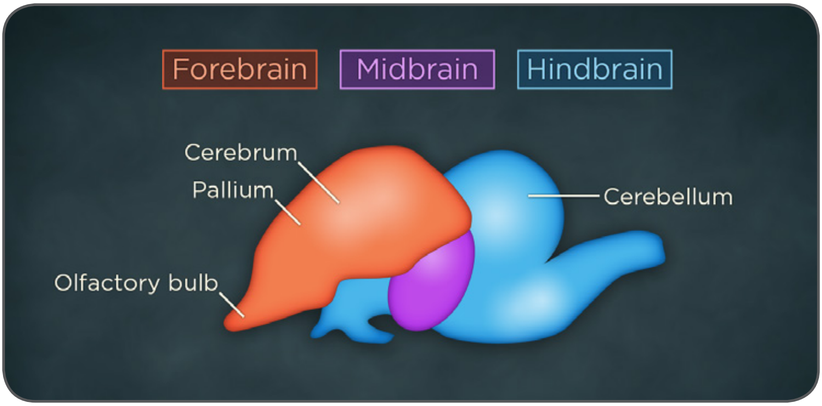
Crows from the South Pacific islands of New Caledonia are among the most intelligent of all known animals. Because much of their diet consists of insects that live inside tree cavities, they evolved the ability to make and use tools to pry out the bugs from their hiding places.

While birds may not be as intelligent as humans, the observations of New Caledonian crows show that they are capable of quite sophisticated reasoning.

To understand how birds can be capable of such complex behavior, let's consider a bird's brain.

Like all vertebrates, a bird's brain has 3 main sections: the forebrain, midbrain, and hindbrain. Much like in humans and other primates, the forebrain, including the cerebrum, is enlarged in some birds, such as crows. But whereas humans have a greatly expanded outer part of the cerebrum called the cerebral cortex, in crows a different structure is expanded: the pallium.

This is yet another example of convergent evolution, in which the ability to engage in complex reasoning evolved in primates through the expansion of the cerebral cortex and in birds through the expansion of the pallium.



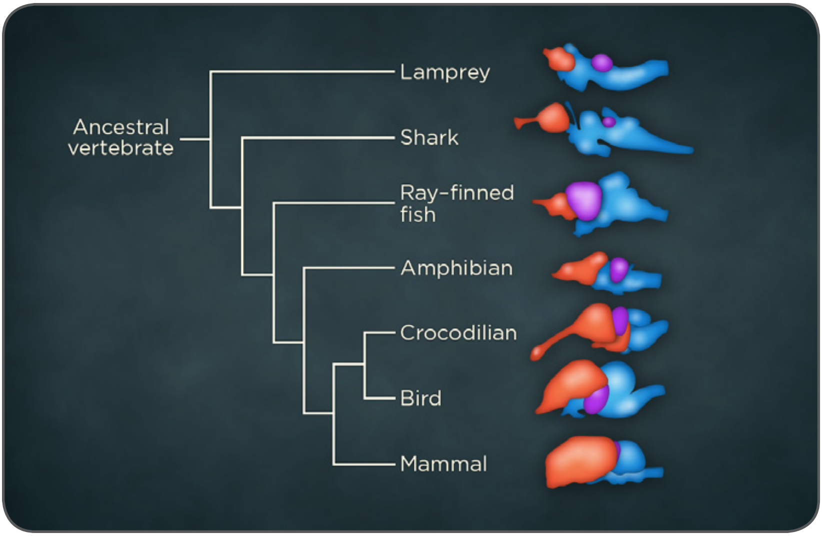
Brian Comparisons

- Comparing the brains of other species with our brains provides insight into how other organisms perceive the world. In general, the larger a particular part of a brain is, the more important the function is that it controls.

- For example, in vertebrates, a strip of the parietal lobe called the primary somatosensory cortex is dedicated to the perception of touch from different parts of the body. If something touches your finger or your cheek, a different part of the somatosensory cortex becomes activated. In essence, it’s a map of the body within the brain.

- But the map is not to scale. Some large parts of the body, such as a leg, may have only a very small section of the somatosensory cortex dedicated to them, while smaller areas, such as the face, might make up a relatively large part of the somatosensory cortex.

- As each species evolved, the somatosensory cortex became modified in several ways. These changes have included its overall size, how many distinct domains it has (each of which is dedicated to a different part of the body), and the relative size of each domain.



- Examining the somatosensory cortex of different animals gives us some insight into how these species perceive the world by reconstructing how their brains evolved. One way to visualize these changes is to consider how different an animal would look if the size of each part of its somatosensory cortex were proportional to the size of the corresponding part of the body.

- Just like in other species, the largest parts of the somatosensory cortex in humans correspond to the most sensitive parts of our bodies—in particular, the mouth and hands. And if we make our body parts proportional to the size of the corresponding region in the somatosensory cortex, we would have enormous hands, fingers, and lips (the most sensitive parts of our body) attached to tiny arms and legs (the parts least sensitive to touch).

- But the sense of touch is just one of the ways that organisms perceive the world; there are many ways that animals have evolved to do so. And in each case, natural selection has resulted in changes in both sensory organs and corresponding parts of the brain.

Brain Size and Communication

- As communication abilities increase, more complex forms of coordinated behavior become possible as well.

- Consider the social insects, such as ants, termites, and bees, which can communicate using chemical cues like pheromones or visual cues like the waggle dance of honeybees. Although individual ants or bees aren't all that intelligent, by working together, they can accomplish sophisticated tasks, such as the construction of elaborate nests, in which the flow of oxygen and carbon dioxide are carefully balanced.

- Many animals can learn from sounds, but relatively few can learn to produce new sounds for communication. This is called vocal learning. Interestingly, this ability to "talk" evolved in at least 5 different groups of mammals and 3 groups of birds. The birds are parrots, songbirds, and hummingbirds. The mammals are bats, whales and dolphins, seals and sea lions, elephants, and humans.

- What caused the human brain to become 3 times larger than that of a chimpanzee, our closest living relative? Much of the difference in brain size is due to humans having a much larger neocortex, which is the part of the outermost portion of the brain known as the cerebral cortex and is involved in higher-order functions, including many of the muscles involved in control of the voice as well as conscious thought.
- In humans, the neocortex makes up most of the cerebral cortex, with just a thin layer beneath it. While most mammals have an enlarged neocortex, it is especially large in humans. In fact, the human neocortex is roughly 3 times larger than the neocortex of a chimpanzee.

Perhaps the most remarkable ability of humans is language. Along with creative thinking, language would have been important for working together to solve problems.

While many other species have complex communication abilities, nothing we know about comes close to the ability of humans to communicate to one another using both oral and symbolic representation, or writing.

Interestingly, there isn't a single part of the brain dedicated to language; there are at least 4 different regions, including a part of your temporal lobe known as Wernicke's area and a part of your frontal lobe known as Broca's area.

Both of these areas are present in the chimpanzee brain. Studies suggest that these areas of the brain are used in a similar way in chimps as they are in humans, which means that the common ancestor we shared with chimps 5 to 7 million years ago likely used the same areas of its brain for communication.

- Large brains are linked to greater intelligence. Being able to think creatively to solve problems is thought to have been one of the distinct advantages that our species had over other species of hominins and may help explain why we survived while the others became extinct.

Readings

Darwin, *The Expression of the Emotions in Man and Animals*.

Sapolsky, *Behave*.

Questions

Suppose you are watching a bird perched on a branch that suddenly flies straight down toward the ground and then abruptly pulls up, snatching an insect out of the air before it returns to the branch. How might you begin to analyze this behavior using Tinbergen's 4 questions?

1. What is the physiological cause of the behavior?
2. Is it instinctual or learned?
3. What is its effect on survival and/or reproduction?
4. Has the behavior evolved uniquely in one species, or does it have a longer and broader evolutionary history?

How do the parts of the human brain that control language provide a clue about how language evolved in our ancestors?

Answers can be found on **page 248**

Lecture 20

The Evolution of Sex and Parenting

After publishing *On the Origin of Species*, Darwin realized that his theory of evolution by natural selection couldn’t explain certain differences between sexes, such as why a male peacock has elaborate tail feathers while the females of the species, called peahens, have modest feathers. Darwin reasoned that a peacock’s tail would be more of a hindrance than an asset when it comes to escaping from predators. Over the next decade, he developed a complementary theory that explained how traits that seemed counterproductive for survival could have evolved. In 1871, he published *The Descent of Man, and Selection in Relation to Sex*, in which he theorized that traits related to sex can be selected, too, via the process of sexual selection. According to Darwin, the tail of a peacock gives a peahen information she can use when choosing a mate so that her offspring inherit his high-quality traits.

Sexual Selection

- Darwin didn't know about the nature of genetics, but he understood the importance of inherited traits: A male with beneficial qualities will have offspring who share the same beneficial qualities. Over generations, the preference by females for such traits would mean that males who have them would pass more of their genes to the next generation.

- Over many generations, those traits would become much more common—not because they make it more likely for an individual to survive, but because they improve his odds of reproducing. After all, reproduction is the key to evolution.

- Although Darwin's theory of natural selection is sometimes paraphrased as "survival of the fittest," this phrase can be misleading. Survival only matters to evolution because you can't reproduce when you're dead.

The term "survival of the fittest" was coined by Darwin's contemporary Herbert Spencer. Darwin only began using it in the 5th edition of *On the Origin of Species*, after Alfred Russel Wallace asked him to.

- Sexual selection helps explain all kinds of peculiar phenomena, such as why males of many species sing to attract mates, even though singing makes them more conspicuous to predators.

- For example, male tungara frogs in Panama have a distinctive call that they use to attract females. Female tungara frogs like males that make a simple whine, but they especially like males that add a low, rumbly chuck. Males that call using both a whine and a chuck have the greatest mating success, so sexual selection has made this trait more common. The trouble is that

the chuck sends sound waves out into the water around the frog, making it easier for predators to find them.

- Traits like the tungara frog's rumbly chuck would not necessarily be favored by natural selection: His chances of survival decrease because the chuck call makes it more likely for him to be eaten. But traits that improve an individual's mating success will become more common in later generations anyway.

Differences in mating success are what drive evolution through sexual selection. Males that mate with many females are more likely to pass on many copies of their genes to subsequent generations.

Because the bright coloration, dancing ability, and bower construction skills of male bowerbirds are at least partly determined by their genes, generations of choosy females have selected for males that, on average, are good performers.

Conversely, species where sexual selection is weaker tend to have males and females that more closely resemble one another and, interestingly, show a greater tendency toward monogamy. Examples include gray wolves and most parrots.

- Together, Darwin's theories of natural and sexual selection have helped solve many mysteries about sex and reproduction. For example, why are males often the ones competing for mates and females are typically the ones doing the choosing?
- Darwin reasoned that these tendencies were a consequence of the one universal difference between males and females: the size of their sex cells.
- By definition, eggs are the larger sex cell. They contain not only the nucleus, where the genome is located, but also the cytoplasm, with all its specialized

In his 1930 book, *The Genetical Theory of Natural Selection*, Ronald Fisher argued that sexual selection could lead to a coevolutionary arms race between males and females, which could explain the extreme differences between some males and females, like the peacock and peahen.

organelles. Sperm, on the other hand, are always smaller. A sperm cell has a nucleus but little else, other than a tail to propel it as it searches for an egg to fertilize.

- By being larger, eggs represent a greater investment of energy and materials. Females typically produce many fewer eggs than the number of sperm produced by males. And because fertilization requires just one egg and one sperm, the investment made by each sex to produce a single offspring is unequal. According to Darwin, this unequal investment could explain why females of many species spend more time and energy caring for their offspring than males.

It might be easy to suppose that Darwin's views, which seem to assume stereotypical gender roles, were influenced by the social beliefs of Victorian England. While that may be true, the notion that female choices have so much influence over evolution did not reflect the dominant views of the day.

Sexual Reproduction

- Something Darwin did not know about sex is that not all sexually reproducing species have just 2 sexes. In fact, many algae and fungi and most single-celled eukaryotes that reproduce sexually have sex cells that are similar in size. Without a significant size difference, they can't be categorized as male or female.
- Rather, genetic differences between different types of sex cells cause some combinations of sex cells to be compatible but not others. In species with similarly sized sex cells, these different types of sex cells that affect compatibility are referred to as mating types.
- Most often, there are only 2 mating types, called positive and negative. But some species of fungi have hundreds of mating types—or hundreds of different sexes.
- Interestingly, having similarly sized sex cells appears to be the ancestral condition for all living species that have 2 sexes. The complex, multicellular organisms with unequally sized sex

cells—including all animals and plants—evolved multiple times independently from single-celled eukaryotic ancestors with similarly sized sex cells.

Why did different-sized sex cells evolve, and why did it always result in exactly 2 sexes and not more?

The reason seems to be that once size differences evolve, there are 2 alternative strategies that work equally well: Either invest in quality, producing larger sex cells but fewer of them, or invest in quantity, which requires making smaller sex cells. In other words, the same explanation Darwin offered for why the sexes tend to behave differently when it comes to reproduction and parenting seems to also explain why 2 sex systems evolved in the first place.

- A question that Darwin couldn’t answer at all is this: Among species that do reproduce sexually, what determines whether an individual offspring becomes male or female?
- Sex in humans is determined by sex chromosomes: Males have both an X and a Y chromosome while females have 2 X chromosomes. The X chromosome is larger and has many important genes. The Y chromosome is tiny and has many fewer genes, but several of them are important for males, including the genes needed to trigger male development.
- While that’s true for humans (and other mammals), it isn’t the case for all species with separate sexes.
    - In birds, the XY system of mammals is replaced by a system called ZW, in which the males have 2 identical, larger sex chromosomes, called Z, while individuals that inherit 2 different sex chromosomes, Z and W, develop as females.
    - In some species, such as alligators, sex is determined not by chromosomes but by the temperature that the embryo experiences as it develops inside the egg.

  - In ants, bees, and wasps, every egg that is fertilized by a sperm develops into a female, but an unfertilized egg can develop into a male. This means that every female has both a mother and a father, but males don't have fathers.
  - Some species can change sex as they age. For example, clownfish begin life as a male. They live in groups in which there is only ever one female. If she dies, one of the males will become female.
  - Other species, including many plants, are hermaphroditic: A single individual can make both male and female sex cells at the same time.

- The timing and frequency of reproduction is now understood as the result of a trade-off between the benefits of reproducing all at once versus spreading reproduction over more than one episode. For example, annual plants that reproduce only once during their single year of life may reproduce 2 to 5 times as much as perennial plants that have to devote more resources to surviving another year.

- A related factor is the degree of risk that an individual might not survive to reproduce in the future. Lower chances for survival seem to be why a few small mammals evolved a life cycle in which they reproduce only once.

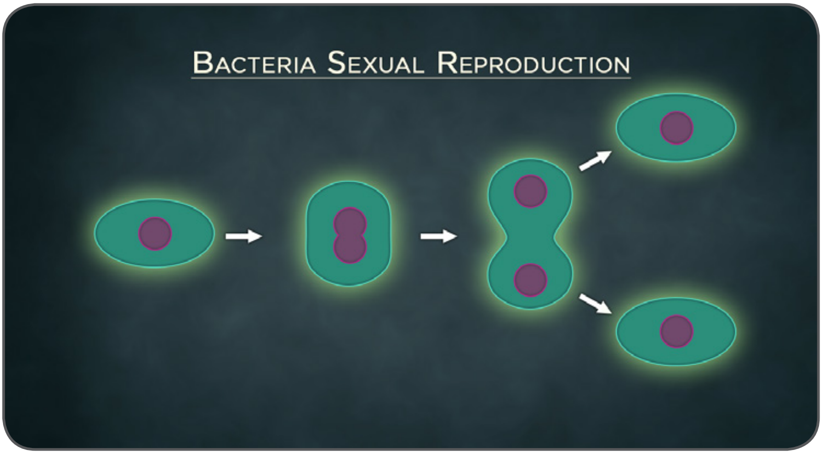
- There are mouse-sized marsupials living in highly predictable seasonal environments where males have evolved to breed once before dying in the least favorable season of the year. By contrast, similarly small marsupials found in rainforests, which lack strong seasonal differences, or in very unpredictable environments follow the typical mammal strategy of caring for young and surviving to reproduce again.

- A few species of fish and other organisms invest in long life before a single instance of sexual reproduction. Pacific salmon are a famous example of one-time reproduction, where the method of reproduction is also unusual for vertebrates: Females carry a few thousand eggs outside their body and dig a nest hole for the eggs, which are fertilized externally.

Why do males of some species help raise their offspring while males of other species don't?

Males that spend significant amounts of time and energy raising offspring that are not their own lose opportunities to pass their genes to the next generation. The possibility that a male might be raising another male's offspring has caused evolution to favor strategies that involve less doting fathers.

- Many species, such as bacteria, reproduce asexually simply by making identical copies of themselves. Asexual reproduction is fast, efficient, and ensures that all of an individual's genes are passed to the next generation. It also avoids the dangers of sex, such as attracting a predator instead of a mate or contracting a sexually transmitted infection. So why go through the hassle of searching for a mate and discarding 50% of your genetic material?



- The answer seems to be that, despite the many drawbacks, sexual reproduction provides 2 major advantages:
    - Recombination is the reshuffling of genes that happens during the formation of sperm and egg cells, and without it, harmful

    mutations can build up in a species' genome. Over time, even only slightly harmful mutations can have increasingly detrimental effects, especially in small populations more affected by genetic drift.

  - Mixing genes among individuals, as happens with sexual reproduction, increases the amount of genetic variation in a population. Because genetic variation is the raw material for natural selection, sex makes species better able to adapt to changing conditions.

- Sex is costly and dangerous, yet for most species it seems to be worth it. A 2018 survey of field research on the evolution of sex found that the mechanism favoring sexual over asexual reproduction differed across the tree of life, from plants to snails to insects. Many of the expected advantages of sex, including enhanced genetic diversity, were supported by at least some of the field studies included in the review.

- But this review found a less commonly considered reason why sexual reproduction might be favored over asexual reproduction: In 17 of 83 cases examined, sexual and asexual species living in the same place occupied different ecological niches, or roles in their environment. Species that occupy different niches aren't in competition with one another, which is good for both species, so perhaps in some cases species have evolved sexual or asexual reproduction as a way to minimize competition with other species in their area.

Readings

Emlen, *Animal Weapons*.

Ryan, *A Taste for the Beautiful*.

Questions

Why did Darwin write to a friend that “the sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick”?

Asexual reproduction, in which an individual makes an identical copy of itself, is faster and less risky than sexual reproduction and passes on all of an individual’s genes. So why does sexual reproduction exist?

Answers can be found on **page 250**

Lecture 21

The Evolution of Aging and Death

Darwin's theory seems to suggest that natural selection should always favor the evolution of longer life spans. After all, it would seem that the longer an individual is alive, the more opportunities it has to reproduce and pass on its genes. How, then, can evolution explain why some species live shorter lives than others? Why hasn't evolution led to all animals living indefinitely long? It was Alfred Russel Wallace—not Darwin—who tackled the evolution of aging and death.

Theories of Aging and Death

- In the 1860s, Alfred Russel Wallace suggested that death is a mechanism for allowing the next generation to thrive, noting that older individuals are draining resources by competing with their own offspring.

- In 1882, an expansion on this notion was published by German biologist August Weismann, whose theory was that evolution favored species with programmed death as a way to ensure the survival of later generations.

- Programmed cell death, known as apoptosis, is a normal and helpful aspect of life. For example, cells die off early in life that would otherwise cause webbing between our fingers. Yet the programmed death theory couldn't explain why individuals that happened to live longer and continued to reproduce wouldn't be favored—that is, any mutation that interfered with programmed cell death should quickly spread.

- In the 20th century, population biologists like Ronald Fisher and J. B. S. Haldane argued that the strength of natural selection declines with age. But few significant advances were made on the evolution of aging and death until 1952, when biologist Peter Medawar published *An Unsolved Problem of Biology*, in which he made a distinction between simply getting older—chronological aging—and the way the bodies of humans and other organisms break down with time, which he called **senescence**.

- Medawar rejected the notion that senescence could be explained as nature's way of ensuring the survival of younger generations. Instead, he suggested that natural selection has a weaker effect on organisms the longer they live, allowing harmful mutations to accumulate that act later in life.

- After all, there is always a chance that something will kill you. You might be eaten by a predator, contract a deadly disease, or have a bad accident. The world is a dangerous place.

- Suppose that the chance that something will kill you at any point in time is always the same. The longer you're alive, the greater the chances are that one of those tragedies will have struck, ending your life. Random events make it unlikely that any individual would live forever.

One grove of bristlecone pines in California consists of some of the oldest trees in the world. One of them is estimated to be more than 5000 years old.

Bristlecone pines survive so long by sacrificing more and more of themselves whenever they are damaged by erosion or fire. Never a very tall tree, a very old bristlecone will typically have bark that is not only very gnarled, but also mostly dead—often only a small patch of the whole tree is still alive.

- Based on the assumption that random events eventually bring death, Medawar reasoned that organisms are better off reproducing before the chances of death by one of these extrinsic factors become too high. He suggested that natural selection has led to each species timing its reproduction to maximize the chances of passing its genes to the next generation. Species that reproduce early in life do so because the chances aren't great that they'll have opportunities to reproduce later.

- Medawar built his argument on the observation made by Fisher and Haldane: The strength of natural selection declines with age. But Medawar's insight was to suggest that any gene that has an effect on an organism later in life—specifically after it has successfully reproduced—could not be affected by natural selection.

- Because later-in-life changes don't affect reproductive output as much, or at all, Medawar said that genes affecting organisms later in life, well after maturity has been reached, are operating in what he and Haldane referred to as the shadow of natural selection. It's as if these late-acting genes are immune to natural selection because regardless of what affect these genes have on the individual, they can't influence future generations.

- Thus, Medawar suggested, mutations that cause the body to break down later in life can accumulate with impunity. This idea for why organisms experience senescence is known as the mutation accumulation theory.

- One prediction Medawar's theory makes is that most individuals of a species should be able to successfully reproduce early in life but that reproduction later in life will be more variable. In other words, some individuals may have success reproducing as they age, but others will not, due to the accumulation of mutations that interfere with reproduction.

- Medawar's mutation accumulation theory was expanded on by biologist George C. Williams in 1957. Building on Mendel's early observation that seed coat color and flower color change in lockstep with one another, Williams noted that a single gene can have several different effects, a phenomenon geneticists refer to as pleiotropy.

- What if the same gene could have a positive effect on survival and/or reproduction early in life and a negative effect on survival later in life? Such a gene would certainly be favored by natural selection, because, as Medawar had shown, differences in survival and reproduction early in life have a bigger influence on passing one's genes to the next generation than such differences do later in life.

- Williams called this idea **antagonistic pleiotropy**—pleiotropic because one gene is having multiple effects and antagonistic because the effects are at odds with one another. We now know that such genes exist.

How Organisms Invest Their Energy

- Another way to think about how natural selection causes aging and senescence is to consider how an organism invests its energy. Because energy is always limited, organisms must spend their energy on what is most important at a particular time.

- In the most general sense, organisms can either spend energy on growing and maintaining their bodies or on reproduction. But there are trade-offs.

- Without enough energy invested in growth and maintenance early in life, an organism is unlikely to survive long enough to reproduce. Natural selection would quickly eliminate any genes that favored such an extreme strategy.

- But the other extreme—spending too much energy on growth and maintenance without enough left for reproduction—would also be quickly eliminated by natural selection.

- What remains are intermediate strategies, in which organisms must invest some energy in growth and maintenance early in life—enough to make it likely they'll survive long enough to reproduce. And then, when the time comes, they must invest more energy in reproduction.

- Considering the trade-off in energy expenditure between maintenance and reproduction helps make sense out of the many different reproductive strategies that exist across the tree of life.

Reproductive strategies evolve because of trade-offs between investment in reproduction versus investment in continued growth and survival.

The number of offspring different organisms produce matches with the trade-off theory.

Some species, such as corals and oak trees, produce thousands of tiny offspring at a time. Intermediate in offspring size and number of offspring are many plants that produce hundreds or dozens of offspring, while most birds and mammals produce only a handful of relatively large offspring at once. At the other end of the spectrum are elephants, which have only one very large offspring at a time.

- Yet another way that biologists have come to think about how evolution leads to aging is to consider the differences that exist between the germ line—the cells that make sperm and eggs—and the cells that make up the rest of the body, called the soma.

- From the point of view of evolution, the soma is merely a vehicle for the germ cells. Having a body is a means to an end—the end being reproduction. Once reproduction has been achieved, the soma is essentially disposable.

- This idea was named the disposable soma theory by biologist Tom Kirkwood, who published it in 1977. Because the soma is disposable, Kirkwood argued, the body can save energy by not investing as much energy in the repair and maintenance of somatic cells, especially after reproduction is complete. More energy should be put into repairing cells prior to reproduction, especially germ line cells.

- The disposable soma theory would seem to suggest that the only organisms that should age are multicellular organisms. After all, single-celled organisms like bacteria don't have separate somatic and germ line cells. Yet recent research on bacteria suggests that even single-celled, asexually reproducing species may experience the effects of aging.

Hydra are small, green organisms related to corals that live in fresh water. They can reproduce asexually by budding. A new hydra grows as a bud, or outgrowth, from another hydra. The bud grows until it is fully formed and then detaches. Hydra are apparently capable of doing this indefinitely without any evidence of slowing down.

Some biologists believe that hydra do not age—that they are effectively immortal.

Senescence in Humans

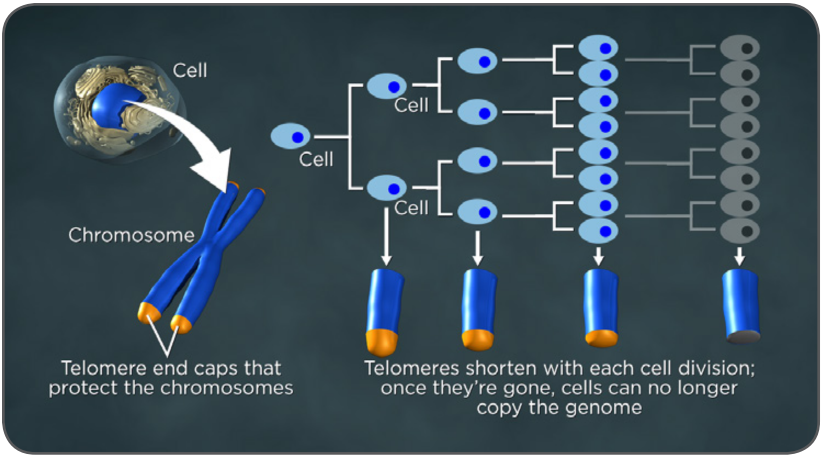
- One of the causes of senescence in humans, and many other organisms, has to do with what happens when our cells divide. The genome must be copied for every cell division so that each daughter cell gets a copy. But the process of copying the genome actually causes damage to the ends of each chromosome, called telomeres. The telomeres become shorter with each cell division, and once they are gone, the cells can no longer continue copying the genome for future cell divisions.

- However, there is an enzyme called telomerase that can limit the erosion of telomeres during cell division. Human fetuses have high levels of telomerase, as do germ cells. But most of the cells in an adult's body have lower levels of telomerase. Nevertheless, some people have more telomerase—or more effective versions of telomerase—in their body cells than other people, and those people tend to live longer.

Most human cells are capable of dividing about 50 times before the telomeres are fully eroded and cell division ceases.

- So why not treat everyone with telomerase so that we can all live longer? The reason is because high levels of telomerase are also found in cancer cells.

- Having high levels of telomerase in the cells that make sperm and eggs, and in a developing fetus, helps ensure successful reproduction. Not having much telomerase in somatic cells may be a way to minimize the chances that they develop into cancer cells.



The consequence is that our somatic cells age, but they do so in a way that gives most people enough time to reproduce before their telomeres become too short and their bodies begin to break down.

- Another aspect of human aging involves a side effect of metabolism.
- When the mitochondria inside our cells make molecules called ATP, which store energy, they also make a by-product: protons. These protons react with water to form reactive oxygen species that can damage cells in multiple ways, including causing DNA mutations.
- The more energy a cell uses, the more reactive oxygen species it generates—and the more damage it can cause. This damage can be controlled to a certain extent by antioxidants, chemicals that combine with reactive oxygen species before they can affect DNA or other parts of a cell.
- Growth and metabolism are both related to energy use. Like most multicellular organisms, humans grow until we reach reproductive maturity, at which point our growth slows down and eventually stops.
- Our metabolism slows as we age, too. Slowing down growth and metabolism as we age may have evolved as a way of minimizing cellular damage once reproductive maturity has been achieved.

Contrary to popular belief, lobsters can't live forever, but they do continue to grow throughout their entire lives. Why hasn't natural selection favored a decrease in growth once they reach reproductive maturity the way it has for most multicellular organisms?

If all humans delayed reproduction until much later in life, natural selection should favor an increased life span. But, unfortunately, any individuals who cheated by reproducing earlier in life would have an evolutionary advantage because they would tend to have more children overall, thereby preventing the evolution of longer-lived humans.

Readings

Rose, *Evolutionary Biology of Aging*.

Shostak, *The Evolution of Death*.

Questions

How does the theory of antagonistic pleiotropy, developed by biologist George C. Williams, explain why our bodies break down as we age?

An enzyme called telomerase limits the damage to chromosomes and the breakdown of the body that happen with age (each time a cell divides). So why do most cells in our body have relatively low levels of telomerase?

Answers can be found on **page 251**

Lecture 22

Evolutionary Medicine

One of the ways in which evolution is most relevant to people today involves applying evolutionary principles to research and practice of medicine. The emerging discipline of **evolutionary medicine** recognizes that the organisms that cause infectious disease are not only the product of evolution, but that they continue to evolve along with their hosts. Evolutionary medicine can help us understand why we get sick and guide us toward the treatment and prevention of sickness.

An ultimate application of evolutionary principles would be to harness evolution to benefit human health. Here, we are moving far beyond areas familiar to Darwin, whose published works didn't consider the role of evolution in disease and well-being.

The Story of HIV/AIDS

Microorganisms that cause disease are some of the fastest-evolving forms of life, with some disease-causing microorganisms passing through more than 70 generations in a single day.

- In the early 1980s in the United States, a new disease began appearing with an unusual combination of symptoms: swollen lymph nodes, pneumonia, and a rare form of skin cancer. Many of the patients who showed these symptoms soon died. By the summer of 1982, the new disease had been given a name: acquired immunodeficiency syndrome (AIDS).

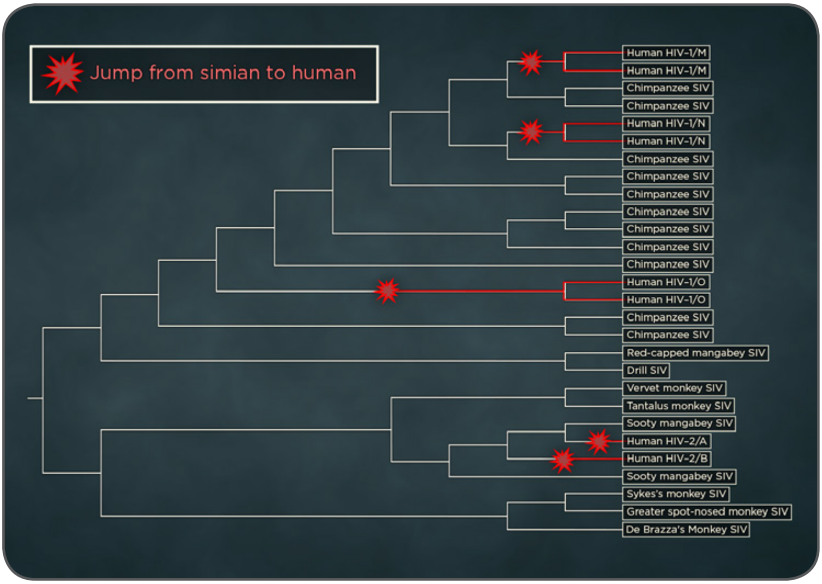
- The story of AIDS and the virus that causes it, human immunodeficiency virus (HIV), is a great example of how evolutionary biology offers insights in the fields of medicine and public health.

- The HIV virus is a so-called retrovirus that attacks the human immune system, primarily helper T cells, which play a central role in the body's defense against infectious diseases. The virus enters these cells and then makes a copy of its genome that gets incorporated into the genome of the helper T cell.

- This is a very effective way for a virus to hide because the host can't tell the difference between its own parts of the genome versus the parts that came from the virus. Meanwhile, the virus can make copies of itself using the host cell's machinery.

- Because the virus is hidden within the host's genome, the only way for the immune system to get rid of this kind of virus is to destroy any cells that have been infected. But by destroying immune cells, the host becomes more susceptible to infections from other pathogens—the hallmark of AIDS.

- The particular variety of HIV responsible for the AIDS epidemic is a strain called HIV-1. A closely related virus called simian immunodeficiency virus (SIV) affects nonhuman primates. Comparisons of the genomes of SIV with different strains of HIV-1 allowed researchers to create a phylogenetic tree depicting the evolutionary history of SIV and HIV-1.



- This analysis showed that HIV-1 evolved from a strain of SIV that infects chimpanzees. This means that some of the SIV virus switched from infecting chimps to infecting humans. Researchers used a molecular clock to estimate how long it took for the differences in the RNA genome of different HIV strains to evolve. Those studies suggest that the common ancestor of all HIV strains appeared in the early 20th century.

- Using an evolutionary approach to reconstruct the history of HIV shows us that the virus was infecting humans for more than half a century before the outbreak became more widespread in the 1980s.

- This analysis also showed that HIV-1 has become very diverse in just a short amount of time. Since it began infecting humans, HIV has evolved into 4 distinct groups (labeled M, N, O, and P), each with a slightly different envelope, or outer membrane.

- The M group is responsible for the majority of HIV infections worldwide. Moreover, a variety of subtypes have evolved within each group that differ in their genome sequence.

- We now know that HIV evolves rapidly in part because it has the extremely high mutation rate typical for an RNA virus. HIV-1 lacks the ability to proofread for transcription errors, which may occur as often as 1 out of every 1000 base pairs for every round of copying. And HIV-1 does reproduce quickly.

- The combined result of rapid copying with a rapid rate of uncorrected mutations is that HIV is evolving even as it replicates within the same host. The virus that is with the host at death from AIDS is not the same virus that caused the initial infection.

A Theory of Virulence

- The term **virulence** refers to how sick a host becomes when infected by a particular pathogen, a microorganism that causes an infectious disease. Some pathogens are not very virulent, meaning that a host could be infected by the pathogen and experience only minor symptoms, or even no symptoms, while highly virulent pathogens, such as HIV-1, can make a host very sick and can even kill it.

- Considering the evolution of pathogens has helped biologists develop a theory of virulence.

In addition to pathogenic microorganisms evolving, hosts also evolve. In fact, resistance to infectious disease is one of the ways that our species has continued to evolve into modern times.

- The life cycle of a pathogen requires that it continually finds new hosts. If it fails to do so—either because it is unable to successfully infect a new host or because its current host dies before it has the opportunity to encounter a new host—the pathogen will leave no descendants. Natural selection strongly favors any strategy that will increase the chances for a pathogen to find a new host.

- Finding a new host is easier if the current host is in close contact with other potential hosts. For humans, this means that an infected person must be around uninfected people.
- If a person feels very sick, he or she is likely to spend more time resting, making it less likely that he or she will interact with other people that could be potential hosts for the pathogen that is causing the illness. This could be a problem for the pathogen. Consider the most extreme case, in which a hypothetical pathogen caused its host to die within minutes of becoming infected.
- Pathogens make their hosts sick in different ways. In general, the faster a pathogen reproduces, the sicker its host will feel. This is certainly true for HIV, because the more copies of it there are in the body, the more immune cells that will be destroyed, making the host much more susceptible to other infections.
- A pathogen would have to reproduce extremely quickly to kill its host within minutes. If it were able to do so, the chances that the pathogen would have opportunities to infect new hosts would be extremely low because the person would not be able to interact with many other people after becoming infected. So, from the pathogen's perspective, making its host very ill very quickly is not a good evolutionary strategy.
- But what about the opposite-extreme strategy? Suppose a microbe had no negative effect on its host. Having no symptoms of illness would mean that the body's immune system may not even detect the microbe's presence. One way to do that is for the microbe to reduce its rate of reproduction so that very few copies of it are made within the host's body.
- The problem with that strategy, from the pathogen's perspective, is that it needs to have enough copies around so that at least one copy can make it to a new host. Having too few copies is not a good evolutionary strategy either.

- What this means is that most pathogens should evolve an intermediate level of virulence: Don't make the host too sick or it won't find a new host, but it has to make enough copies of itself, which will cause some sickness in the host while also making it contagious.

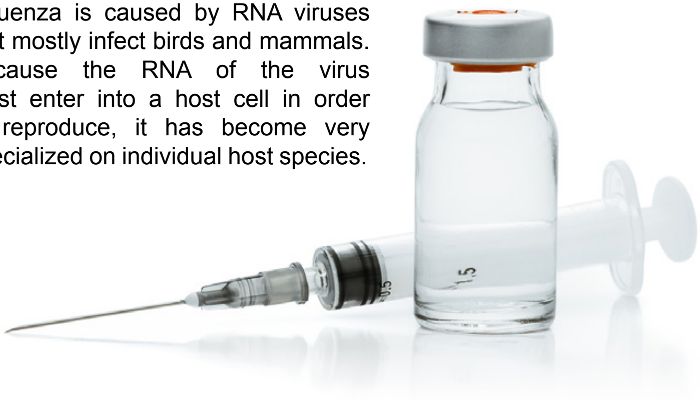
Vaccines

- Evolution also explains why it has been very difficult to develop a vaccine against HIV. Vaccines work by causing the host's immune system to develop antibodies against a specific pathogen. The antibodies recognize the pathogen and then quickly mobilize to destroy it before it can replicate, preventing a dangerous infection. Thanks to antibodies, a healthy person will not get infected by the exact same pathogen more than once.

- But if the pathogen changes enough, the antibodies won't recognize it anymore, and the immune system's response will be slower. The outer shell of the HIV virus, which is what the antibodies use to recognize it, is capable of especially rapid evolutionary change.

- Vaccines can be difficult to develop for any viruses that evolve rapidly. This is why vaccines against slow-evolving bacteria, such as tetanus, mumps, and diphtheria, are highly effective for a long period of time, while a new flu vaccine must be developed each year—and why it is never 100% effective.

- Influenza is caused by RNA viruses that mostly infect birds and mammals. Because the RNA of the virus must enter into a host cell in order to reproduce, it has become very specialized on individual host species.



Many influenza strains have evolved to be very effective at entering the host cells of birds.

- However, occasionally a mutation occurs that makes the influenza virus more capable of infecting human cells. This jump to humans tends to occur with some regularity, leading to the seasonal flu outbreaks that occur each year.
- The annual flu vaccine is made based on predictions about which mutations are most likely to occur and typically includes at least 3 different strains as a hedge against uncertainty.
- On rare occasions, mutations occur in a deadly strain of influenza infecting another species that make it capable of infecting humans.
- Epidemiologists expect influenza outbreaks to happen, and they use what we know about how influenza evolves to closely monitor humans and animals for early signs of virulent strains.

Rapid Evolution of Resistance

- Rapid evolution also makes it difficult to develop treatments for patients who have already become infected with a pathogen.
- For example, the first drug was developed to treat HIV in 1987. Called AZT, it appeared to be effective at first. But the HIV virus quickly evolved resistance to AZT, rendering it ineffective as a treatment, unless used in combination with other drugs.
- In fact, the same mutations that made HIV resistant to AZT in one patient could be found in another patient who was not in contact with the first patient but also being treated with AZT. This was a heartbreaking lesson in how convergent evolution can sometimes cause different lineages to experience changes that result in not only the same outcome, but through the exact same mechanism.
- Rapid evolution of resistance is also what makes superbugs, or bacteria that are resistant to antibiotics. When we take antibiotics to treat a bacterial infection, we are essentially conducting an evolutionary experiment in our bodies. Any bacteria that are naturally

resistant to the antibiotic will have a major advantage. They quickly become much more common within our bodies.

- To make matters worse, bacteria are especially likely to evolve antibiotic resistance when antibiotics are used inappropriately. For example, antibiotics are sometimes prescribed to treat viral infections, such as the common cold, despite the fact that antibiotics have no effect on viruses.
- Such a misuse of antibiotics allows natural selection to favor naturally occurring mutations that provide bacteria resistance to antibiotics. And because even distantly related bacteria can exchange genes, if a mutation for antibiotic resistance occurs in one type of bacteria, it will likely spread not only to that bacteria's descendants but also to other species.

Evolution can help us understand the family of diseases where mutations lead to unlimited cell growth, known as cancer.

Mutations in regulatory genes can cause problems in cell regulation and allow cells to divide indefinitely, leading to the formation of a tumor. If some individual cells are more successful at leaving descendant cells than others because of mutations in their regulatory genes, the genes for indefinite growth will become more common.

Cancer can be thought of as a product of natural selection happening within the body. Thinking of cancer as an evolutionary phenomenon can help researchers design more effective cancer treatments.

One example is adaptive therapy, in which cancer treatment drugs are administered in lower-than-normal doses. Lower doses reduce the selective advantage of cancerous cells that divide more rapidly, allowing less aggressive cells to continue competing effectively against the cells that could otherwise give rise to deadly cancers.

It has also become possible to sequence the genomes of individual cells within a person's body, including tumor cells. This allows researchers to determine what specific mutations gave rise to tumor cells and to track any changes in the tumor cells' genomes as they divide. Knowing the exact mutations that caused cells to become cancerous can also allow treatments to be used that specifically target the cancer cells.

Readings

Blaser, *Missing Microbes*.

Lieberman, *The Story of the Human Body*.

Quammen, *Spillover*.

Stearns and Medzhitov, *Evolutionary Medicine*.

Zuk, *Paleofantasy*.

Questions

How can evolution help explain why some diseases are deadlier than others?

How can conditions like diabetes and the type of anemia known as alpha-thalassemia be understood as mismatch diseases?

Answers can be found on **page 252**

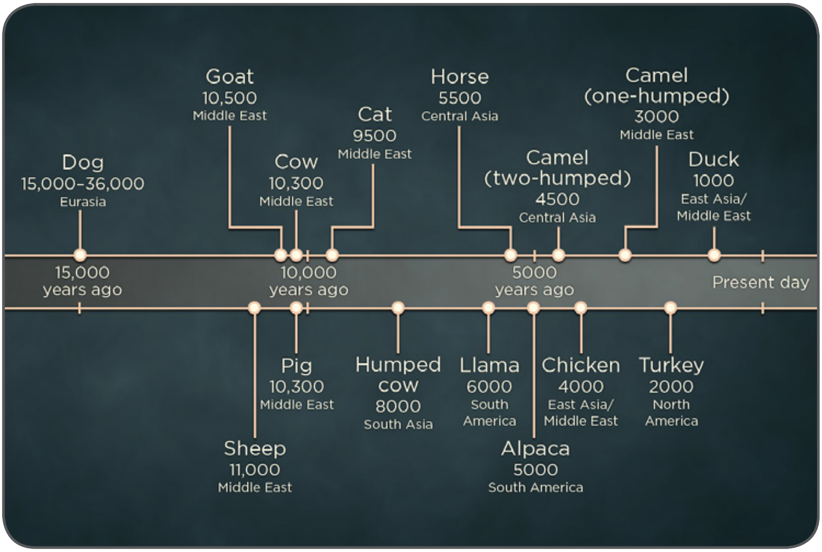
Lecture 23

Gene Editing and Directed Evolution

Given how much we have learned about evolution since Darwin's lifetime, can we (safely) use this knowledge to take evolution into our own hands? Even without always realizing it, people have been directing the evolution of other species for at least the last 10,000 years. In fact, Darwin began *On the Origin of Species* by describing the ways in which the cultivation of plants and breeding of animals has changed "our domestic productions" in dramatic ways, whether to serve our needs or satisfy our whims. Darwin called this artificial selection to show how it is analogous to the process of natural selection.

Artificial Selection

- Genetic evidence now allows us to date the onset of humans domesticating other species with increasing precision. Wolves looking perhaps somewhat like domesticated dogs may have shared caves with ice age humans as early as 36,000 years ago, and they definitely followed nomadic humans around for millennia, especially after the ice age ended roughly 12,000 years ago.
- Next, domestic versions of sheep, goats, and pigs began to appear (in that order) perhaps 11,000 to 10,000 years ago. Wildcats scavenging near human settlements began resembling the bodies of domesticated cats perhaps 9500 years ago, while their behavior became more domestic thousands of years later, beginning in ancient Egypt.



- Cattle began to be artificially selected from larger animals called aurochs and European bison between 8000 and 6000 years ago. Horses in Asia were being herded, bridled, and milked as early as 5500 years ago, while selection in the Americas began to create llamas and alpacas between 6000 and 4000 years ago.

- Chickens were selected from jungle birds at least 4000 years ago, though researchers have identified the genes of modern chickens in bones that are more than 10,000 years old. Domestication of ducks and turkeys began later, perhaps 2000 years ago. Even some insects, such as honeybees, have been domesticated, meaning that they are easier to keep and are somewhat dependent on humans.

- Artificial selection of plants tells another big piece of this story. In Mesoamerica, people began cultivating a wild plant called teosinte around 8700 years ago. We now know it as corn. Like many crop plants, artificial selection enhanced the size of the edible portion of the plant—the seeds, in the case of corn. In some species, the same wild plant was artificially selected to enhance different parts, resulting in crops that we now don't even realize come from the same species.

Did you know that broccoli, brussels sprouts, cabbage, cauliflower, kale, and kohlrabi—6 vegetables—are all just modified versions of a single species of wild mustard plant called *Brassica oleracea*?

- This has been a feature of our approach to artificial selection: We many not modify a large number of species, but those we do tend to get a lot of modifications. Of the roughly half a million plant species on Earth, humans have domesticated, or partly domesticated, perhaps only about 500 species, which would be only 0.1% of all plants and animals.

- But our intense, narrowly focused efforts at artificial selection on a relatively small number of species are increasingly displacing natural selection. For example, wild aurochs made cattle possible, but the aurochs themselves have gone extinct.

- And while humanity has historically focused on modifying the evolution of a relatively small number of plants and animals, the reach of artificial selection may be about to expand. We are starting to understand the genetic basis of a suite of traits often associated with domestication, and with greater understanding of the genetics of domestication comes the possibility of controlling evolution evermore precisely by deliberately altering genes.

A 2018 study estimated that the total biomass of our domesticated livestock (led by cattle and pigs) is 14 times the biomass of all undomesticated mammals remaining in the natural world.

Genetic Manipulation

- The earliest approaches to manipulating genes involved using mutagens—chemicals or radiation that cause mutations. Hermann Muller used x-rays in the 1920s to induce mutations that led to physical abnormalities in fruit flies, allowing him to observe how those abnormalities were inherited.

- But bombarding genes with mutagens was very crude. Researchers couldn't predict where in the genome a mutation would occur. And most of the mutations would be harmful, disrupting genes that perform essential functions and often leading to death before the mutations could even be observed.

- But in the 1970s, a new method, called **recombinant DNA**, was developed that made it possible to change an organism's genome in a much more precise way. The basic idea was to extract DNA from one organism and then recombine the extracted DNA in a different organism. Theoretically, the idea seemed plausible because DNA base pairs are chemically identical across all organisms.

- We also know of natural examples of genetic material crossing a species barrier. For example, bacteria readily exchange genes that confer resistance to antibiotics. Indeed, biologists have come to realize that the exchange of genes between different species is a fairly common occurrence.
- Aside from some differences in how DNA is packaged within a cell, the only differences between the DNA of different organisms is the sequence of DNA bases (the A's, T's, G's, and C's). The only question was how to actually combine DNA from different sources.
- In 1972, biochemist Paul Berg became the first person to find a way to successfully combine the DNA from 2 different organisms. He copied a short piece of DNA from a bacterial virus, called lambda, into a monkey virus, known as SV40.
- To do this, he used a chemical called a restriction enzyme that recognizes a particular sequence of DNA bases and makes a cut within the sequence. The SV40 genome is circular, and once this circular genome was cut, the lambda gene could be pasted into it, widening the circle.
- But widening the circle of the SV40 monkey virus was not the ultimate goal. The brilliance of modifying SV40's genome is that SV40 is a retrovirus, which inserts copies of its genome into the host's genome when it infects cells. In other words, by placing particular genes into the SV40 virus, those genes could then be spliced, or inserted into, the genome of any other species.
- The following year, in 1973, Herbert Boyer and Stanley Cohen inserted genes from one species of bacteria into another species of bacteria. They found that the foreign genes persisted within subsequent generations as the bacteria divided. Then, they inserted genes from a frog into a species of bacteria and found that even frog genes could become a permanent addition to the bacteria's genome—and not just for one generation.

- These experiments showed that genes could be added to bacteria in a way that was heritable. This was the first step needed to direct the evolution of another organism. The next step was manipulating the genomes of more complex multicellular organisms.

- In the 1980s, a breakthrough occurred when researchers developed techniques for growing embryonic stem cells from mice. Embryonic stem cells are cells from the earliest stage of development—the embryo—that can divide indefinitely and can develop into any type of cell within the body. That means that under the right conditions, an embryonic stem cell can turn into a brain cell, a heart cell, a skin cell, or even an egg or a sperm cell—which allows a trait to be passed across generations.

- Suddenly, it became possible to use retroviruses like SV40 to insert genes into the genomes of embryonic stem cells, which could develop into sperm or eggs that carry the modified gene, which could form a new transgenic individual in which every cell in the body had the modified gene.

- In the 1990s, retrovirus insertions began to be used to create all sorts of transgenic organisms. The technique worked well on mice, and they were among the most commonly used for such experiments. Transgenic mice could be used in research, for example, by inserting a human gene for epilepsy into a mouse to investigate the causes of seizures.

- But creating transgenic individuals also opened the possibility of directing the evolution of many types of organisms by manipulating their genomes in ways that would be inherited by all of their descendants. In the natural world, this would require 2 separate steps: mutation and natural selection. But genetic engineering was making it possible to select and mutate in a single step.

- Yet the technology in the 1990s and early 2000s still required copying a piece of DNA from one organism and pasting into another. It wasn't yet possible to manipulate a genome in more precise ways—for example, by changing one DNA base into another.

- But just such a technology was developed in 2012 by biologists Jennifer Doudna and Emmanuelle Charpentier. The technology

The idea of making heritable changes to a human genome raises many ethical concerns. First, the technique must be safe. But even when the technology works as precisely as hoped, many genes affect multiple processes in the body, so we also need to be sure that altering the targeted gene won't cause any collateral damage.

Another concern is that once the technology is used to treat diseases, it will also start to be used for other, less life-threatening purposes. It would be possible to edit the genomes of babies to control such traits as sex, skin color, hair color, and eye color.

The idea that we could control our own genes would mean that we could take human evolution into our own hands. And any attempt to direct human evolution, no matter how well intentioned, will undoubtedly be forced to reckon with the history of forced sterilizations and genocide in the 20th century performed in the name of eugenics.

is based on a 2-part system that evolved in bacteria as a way of defending themselves against viruses. The first part is called clustered regularly interspaced short palindromic repeats (CRISPR), which is a piece of RNA that searches for a particular sequence of DNA bases found in a virus's genome. The second part of the technology is a CRISPR-associated enzyme called Cas9, whose job is to cut the viral DNA at precisely the point recognized by CRISPR.

- Bacteria using the **CRISPR-Cas9** system had a big advantage: They could recognize a specific virus based on its gene sequence and then chop up its genome before the virus could do any harm. It's like a laser-guided missile that bacteria use to target attacking viruses.

- Doudna and Charpentier discovered that the CRISPR-Cas9 system could be reprogrammed to seek out any stretch of DNA in the genome of any organism—not just viruses that attack bacteria.

- And, most importantly, when Cas9 makes a cut in an organism's genome, the organism will attempt to repair the cut. To do so, it will remove the DNA base at the location of the cut and replace it with a new DNA base that will seal the cut and repair the damage. But the DNA base that is used for the repair doesn't have to be the same base that was there before. If a different base is added instead, the result is an alteration to the genome consisting of just a single DNA base change.

- The development of CRISPR-Cas9 made it possible for the first time to make precise edits to the DNA sequence of any species. The precise edits of CRISPR-Cas9 can simply alter or remove a single gene identified as problematic.

- Editing the genes of crop species can provide improved crop yields or resistance to diseases. In addition, genetic diversity can be increased, allowing more raw material for artificial selection. **Gene editing** also offers the possibility of modifying certain crops to add or remove particular traits.

- The CRISPR gene editing approach could be used for diseases with a genetic basis, including sickle cell disease, breast cancer, child leukemia, and hemophilia. For people with such diseases, performing what amounts to genomic surgery by editing their genomes could save their lives. But if an adult's genome with such a disease is altered, the repair won't be passed on to his or her children—unless the sperm or egg cells are also edited, otherwise known as germ line genetic engineering.

Cells in the human immune system have been edited using CRISPR to target cancer cells. The hope is that we might eventually be able to recognize cancer cells and destroy them before they can form dangerous tumors. And if that's possible, then it might be even more efficient to edit germ line cells so that the preventative benefits are passed to the next generation.

Readings

Comfort, *The Science of Human Perfection*.

Doudna and Sternberg, *A Crack in Creation*.

Questions

Do you think genetically directed evolution is different than the types of artificial selection humans have engaged in for many centuries to develop our domesticated plants and animals?

Efforts are underway to control the spread of diseases like malaria with evolutionary applications like gene drives. How might such efforts be counteracted by evolution acting in other ways?

Answers can be found on **page 253**

Lecture 24

The Future of Human Evolution

The science of evolution is not just a historical science, allowing us to reconstruct the past and present. Evolution is also an ongoing process, a way to understand how all species will continue to change. In other words, evolution gives us a way to make predictions about the future—including our own future.

Evolutionary Change

- The evolution from nonhumans to humans was rapid and dramatic. Since we split with the common ancestor we shared with chimpanzees between 5 and 7 million years ago, our ancestors went from walking on 4 legs to walking upright. And, more significantly, we developed large brains capable of complex thought and sophisticated language.

- Will this rapid rate of change continue? If we are continuing to evolve, our descendants might not be as obviously different 5 million years in the future as we are today from our ancestors 5 million years in the past. The trend toward larger and larger brains stopped about 10,000 years ago, and modern brains are actually smaller than those of Neanderthals.

- How could evolution be happening without obvious physical changes?

- One hypothesis suggests that all species constantly evolve just to maintain their defenses in the arms race against infectious diseases and other parasites. Species can even evolve in one direction for a while but then reverse direction, like Galapagos finches whose beak sizes change as food availability fluctuates. The net result of many fluctuations could end up being pretty much the same many generations in the future.

Darwin said that evolution is inevitable, but he never claimed that the changes had to be obvious. We know of examples of other organisms that survived for millions of years without much visible change to their body structure, including horseshoe crabs, crocodiles, and sharks.

- Moreover, in many regions of the world, infectious diseases are no longer the primary causes of death. As a result, those infectious diseases may no longer be causing natural selection to favor disease resistance, unlike in the past.

- The observation that diseases aren't causing natural selection in some modern human populations has prompted a minority of well-known scientists—including Ernst Mayr, Stephen Jay Gould, and Sir David Attenborough—to go so far as to claim that human evolution is basically over.

- Their argument is that our evolution stops with the advance of modern civilization. After all, more and more of us live in carefully constructed environments that separate us from the natural environment. We grow our foods at industrial scales and shop at supermarkets where local availability and seasonal cycles have become almost meaningless. We treat genetic and infectious diseases with medicine and can have surgery to repair birth defects or injuries.

When Darwin published his theory, only about 50% of all British children survived to adulthood. By contrast, today in the UK 99% survive.

Culture

- But has our culture really replaced natural selection as the driving force affecting humans today?

- For many biologists, culture is simply another part of the natural environment, much as it is for other highly social species, such as ants. Ants evolved advanced social organization, with complex artificial environments, 100 million years ago. But that didn't stop ant evolution.

- In fact, it's been only after the creation of complex artificial environments that ants went on to evolve such diverse body shapes and sizes, diets, and nesting habits, resulting in more than 15,000 species of ants alive today. And while we have not evolved into many different species, social insects have a 100-million-year head start on us.

- Thinking of culture as part of the environment makes it easier to recognize that natural selection operates on transmissible culture in humans just as it does in any other species.

- Moreover, the culture we transmit is a highly changeable feature of our environment. Think about how quickly fashions change. You could say that—for fashion and other aspects of culture—"mutations" are high, "heritability" is low, and there is a great deal of "horizontal transfer" between individuals. This suggests that fashion can evolve, but it may not evolve in a particular direction for long because it can change at a pace that is much faster than a single human generation.

Gene Flow

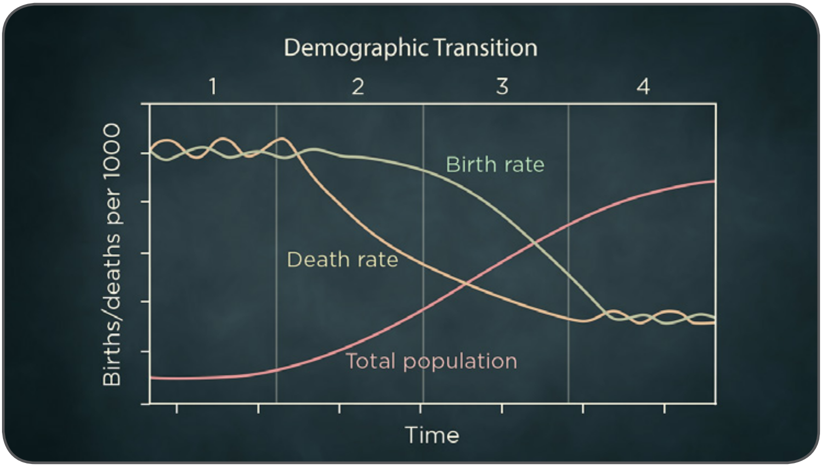
- One difference between human societies and insect societies is that a single, largely intermixing species of humans already occupies all landmasses on Earth. Despite their 100-million-year head start on us, no single group of ants or other social insects ever expanded to occupy the entire globe on their own.
- Moreover, having a global range is only part of the human story. Other species migrate over long distances, but they aren't global in the same way that humans are. Biologists use the term "panmictic" to refer to a large population that freely interbreeds.
- Perhaps the best comparison for our modern, interbreeding human population is bacteria. Like modern humans, bacteria move around the planet exchanging genes—and they do it even more than we do. And although bacteria reproduce asexually by budding, bacteria do exchange genes by swapping pieces of DNA.
- Compared to bacteria, humans are not yet a panmictic species. We are still more likely to reproduce with people who live near us, but our global transportation networks and high rates of population movements have been pushing us more in the direction of becoming as panmictic as bacteria.
- What does the movement of people—and our genes—around the world mean for our evolution? Global transportation allows us to rapidly move infectious diseases like viruses. As long as we have fast, global transportation, new infectious diseases will be a threat to human health.

Natural Selection

- How has our rapid economic development influenced natural selection in recent and modern human populations?

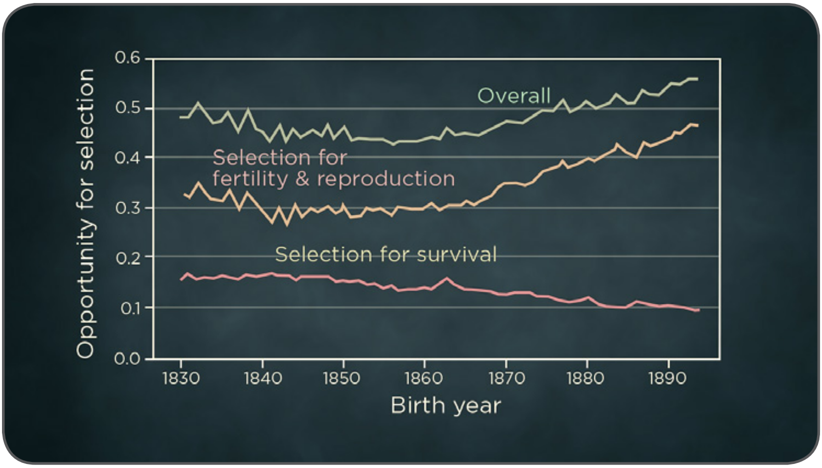
- An obvious result of better access to clean water, abundant food, and modern health care is declining death rates due especially to lower infant and child mortality rates. But a less intuitive consequence of economic development is that lower death rates tend to be followed by lower birth rates and even greater parental investment per child.

- The decline in both death rates and birth rates is known as the **demographic transition**, and it has important consequences for how humans are continuing to evolve.



- Much of the United States experienced a demographic transition beginning in the 1800s. Population records show that during the 1800s, most individuals increasingly survived into old age.

- Yet, even as average birth rates declined, there was still variation in family sizes. Even though there was less opportunity for natural selection to act on traits related to survival, selection could still affect traits related to fertility. How long people lived was becoming more similar (most lived into old age), but people still differed in how many children they had. In fact, the differences in family size meant that the opportunity for selection to affect fertility increased throughout the 1800s.



- Even after the demographic transition, there has been an evolutionary change in the timing of reproduction, but it's not toward later reproduction—it's toward earlier reproduction. Natural selection has been shown to favor an earlier start to reproduction in some populations of people.

Mutations

- Population bottlenecks deep in our human past gave us our current low levels of human genetic diversity, but that is quickly changing.
- Our global population is approaching 8 billion, with about 130 million babies born worldwide each year. On average, each baby has about 60 new mutations in its genes. These mutations contribute to the diversity of the human gene pool and represent the raw material for natural selection to shape our evolutionary future.
- In addition, there is a trend toward older fathers in many regions that will increase human genetic diversity more and more rapidly. That's because fathers of any age contribute more mutations to their children than mothers, and older fathers contribute more mutations to their children than younger fathers.

- In short, the total supply of human mutations—the raw material for human evolution—is in the process of exploding in number.

- Meanwhile, gene flow is increasing with the rapid movement of people around the globe. Populations today that were once widely separated now have many more opportunities to exchange genes through sex and reproduction.

- Gene flow makes populations more similar to one another, so one consequence of the high rates of gene flow in modern human populations is that some of the differences that once existed between human populations may start to disappear. For example, people of the future may increasingly have similar skin, hair, and eye colors.

- But more importantly, gene flow can spread helpful mutations much faster to other populations than would have previously been possible. This could mean, for example, that a mutation that provides natural protection against a particular infectious disease could spread in just a few generations to the regions where that disease is most common.

Coevolution

- Of course, organisms that cause disease will continue to evolve, too. Global travel patterns are creating more opportunities for infectious diseases to quickly shift hosts. Based on our understanding of virulence, we expect that some infectious diseases will evolve to make us sicker. Increased virulence won't necessarily decrease their odds of finding a new host (think about how easy it is to catch a bug from someone sitting near you on an airplane).

- If our diseases get worse, perhaps we will just keep evolving new defenses, leading to an intensified evolutionary arms race. But keep in mind that microorganisms can evolve a lot faster than we can. That's a sobering thought: We may be helping our diseases evolve against us.

- But remember that we also have microorganisms on our side. Our microbiome consists of millions of bacteria and other microbes, some of which evolved along with us and can help keep us healthy. Those microbes will keep evolving, too, and it's in our best interest to ensure that the helpful ones continue to have a home in and on our bodies.

- Maintaining beneficial microorganisms that can promote health is a good reason to use antibiotics responsibly. But it would be even better to develop more ways to eliminate only those microorganisms that cause disease without also harming the beneficial members of our microbiome.

Sexual Selection

- Many human populations have undergone a demographic transition, leading to more opportunities for selection to operate on traits related to reproduction. What does this help us say about the future of human sexual selection?

- Traits related to reproduction are becoming more relevant to our evolution than traits related to survival. In other words, to consider our future evolution, we need to think a lot more about sex and reproduction.

- Humans are somewhat sexually dimorphic: On average, men tend to be taller and more muscular and have more facial hair than women. This suggests that sexual selection has operated on our species in the past.

- Sexual selection is still operating today, but now sexual selection can be separated from reproduction, both by the use of birth control to prevent pregnancy and by technologies that promote pregnancy without sex and births that don't rely on the birth canal.

Darwin suggested that mate choice can be a powerful mechanism of evolution, leading to traits like the elaborate tails of peacocks that can't otherwise be easily explained.

Technology

- How far might our dependence on technology go? Some futurists believe that humans will eventually merge with our technologies, leading to the creation of so-called transhumans. But even if we get to the point where we become intimately dependent on technology for survival, that would probably not fundamentally alter our evolution.

- One of the major insights from the modern synthesis was the recognition that only heritable traits can evolve. With the partial and short-term exceptions of **epigenetics** and culture, heritability requires being encoded in our genes.
- As long as our technology has to be freshly implanted, embedded, or inserted into our bodies with each new generation, it can’t evolve in the same way as living species. Unless we find a way to encode our technology into our DNA, technology will merely affect our evolution by the impacts it has on survival and reproduction.
- We might evolve in response to our technologies, like we do in response to other aspects of our cultural environment, such as diet. We may even be able to train more and more of our digital technology with evolutionary algorithms, similar to how we already write digital life simulations or computer viruses that mutate. But the technology itself won’t be part of our biological evolution.

It seems fitting that Darwin’s theory of evolution not only tells us about our past but may also help us navigate the future of life. After all, since the modern synthesis in the middle of the 20th century, evolution has become the central framework that unites all other subfields of biology.

You might say that what Darwin didn’t know is how much his ideas would become a framework for ongoing curiosity about all of life.

Readings

Kaku, *The Future of Humanity*.

Richerson and Boyd, *Not by Genes Alone*.

Solomon, *Future Humans*.

Questions

How can natural selection and culture affect one another?

Why is human genetic diversity relatively low, and what factors are contributing to the rise in our genetic diversity?

Answers can be found on **page 254**

Questions and Answers

Lecture 1

What was it about the fossils Darwin discovered along the coast in Argentina that provided an early clue about evolution?

> **Answer:** The fossils of giant ground sloths and glyptodonts that Darwin found near Punta Alta, Argentina, resembled armadillos and sloths still living in the region. The fact that extinct species existed in the same geographical region as what appeared to be living relatives—but were not known to exist in other regions—suggested to Darwin that modern species came about through "descent with modification" and that where species live today is determined in part by where their ancestors lived.

In what ways did Darwin's visit to the Galapagos Islands influence the development of his theory of evolution?

> **Answer:** Darwin's visit to the Galapagos Islands brought surprising similarities and differences to his attention that helped him develop his idea for how species change and diversify through time. The similarities he noticed between animals—such as land iguanas and marine iguanas—and species he had seen on mainland South America suggested shared ancestry. The small, yet noticeable, differences Darwin observed across the different islands in Galapagos made him wonder why the tortoises and mockingbirds from each island were not either more different or more similar. After returning to England, Darwin learned that the finches he collected represented a group of related

species, providing additional evidence that being isolated on islands helped populations accumulate differences through natural selection.

What is natural selection, and what role does it play in Darwin's theory of evolution?

Natural selection, which Darwin suggested is the primary mechanism of evolution, occurs when heritable changes become more or less common over generations. Darwin developed this theory based on observations and experiments. He noted first that there are differences among individuals of any particular species. Second, although Darwin didn't know how, he was aware that some of the traits of individuals are somehow inherited by offspring from their parents. Third, Darwin observed that some of the heritable traits of organisms make them better at surviving and reproducing. Darwin concluded that the heritable traits that make an individual better at surviving and reproducing will become more common in future generations.

Lecture 2

What was it about the fossils Darwin discovered along the coast in Argentina that provided an early clue about evolution?

Answer: Darwin's pangenesis theory assumed that acquired traits are heritable and that parents' traits blend together in their offspring. Part of Darwin's pangenesis theory proposed that tiny particles, which he called gemmules, are made by the cells of the body and that they contain essential information about the body's current state. Darwin suggested that the gemmules travel from all over the body to the sex cells, where information is transmitted to the embryo that forms during conception. We now know that gemmules do not exist and that the information is actually coded by the DNA in the genome, a copy of which is contained in the nucleus of each cell. DNA from each parent does not blend together and does not change during an individual's lifetime, so traits acquired during a parent's lifetime aren't heritable.

Can nonhereditary traits evolve through natural selection?

> **Answer:** No. Darwin recognized that only heritable traits could evolve through natural selection. For a trait to evolve through natural selection, it must affect survival and reproduction and be heritable. Nonhereditary traits won't continue to be beneficial for more than one generation because being nonhereditary means the traits won't be present in later generations. The modern synthesis that united Darwin's theory of evolution by natural selection with Mendel's observations of heredity clarified that traits encoded by genes (which were later discovered to be determined by the sequence of DNA bases in the genome) evolve when they become more or less common within a population.

Lecture 3

A(n) ____ is a stretch of DNA bases that contains the information used by a cell to make a _____.

a. gene / protein

b. chromosome / genome

c. allele / zygote

d. genome / chromosome

A long piece of DNA that contains many genes, often combined with proteins, forms a structure called a(n) ____ that is copied when a cell divides.

a. gene

b. chromosome

c. allele

d. genome

Different versions of a particular gene are called ____.

a. genomes

b. genes

c. chromosomes

d. alleles

A(n) ____ is the complete set of all genes, as well as the DNA bases in between genes, that are folded into ____ and housed within a cell's nucleus.

a. allele / genes

b. genome / chromosomes

c. chromosome / genomes

d. gene / alleles

Answers: highlighted above

Errors are often made when cells copy their genomes. Why hasn't evolution resulted in a more accurate way of copying DNA?

Answer: Mutations occur when there is an error made when a cell copies DNA, which happens every time a cell divides. Mutations are the ultimate source of new variation within a species, and variation is the raw material for natural selection, which acts like a sieve, allowing only the varieties that are well suited for the current environment to pass through. Without the variation that comes from mutations, organisms would not be able to adapt to changing conditions and would more likely go extinct.

Lecture 4

Why are archipelagoes, or other island groups, good places to study evolution?

> **Answer:** Archipelagoes like the Galapagos Islands and the Hawaiian Islands are especially likely to promote the evolution of new species because populations can be separated long enough for differences to accumulate through mutation, natural selection, sexual selection, and genetic drift. Without geographic barriers like the water that separates islands, such differences would be erased by gene flow, the spread of genes between populations through sex. Islands also tend to have fewer numbers of individuals and species than continents, making it easier for small numbers to have a bigger effect—and making it easier for biologists to define and study a distinct population.

What is dispersal? Under what circumstances would you expect natural selection to lead to organisms that are better at dispersing, and when would it lead to organisms that are poor dispersers?

> **Answer:** Dispersal is the movement of individuals (i.e., by walking, climbing, crawling, flying, etc.) or their gametes (i.e., sperm, eggs, or seeds). Natural selection promotes better dispersal abilities—as in the case of dandelions, which evolved fluffy seeds that can be carried by the wind—under circumstances in which it would be risky to stay in the same place for too long. Examples include when specialized parasites or predators are present, because they can more easily attack many individuals that are close together. Natural selection can favor a decrease in dispersal ability—such as the loss of functional wings in the flightless cormorant—when organisms are surrounded by inhospitable terrain, such as on an isolated island, making dispersal dangerous.

Lecture 5

What did plate tectonic theory reveal about evolution that Darwin didn't know?

> **Answer:** The movement of continents can explain how species achieved their current geographic distributions. Darwin recognized that closely related species often live in widely separated places, like the cypress species that live in North America and Europe. Plate tectonics showed that the continents were not always so widely separated, suggesting that species separated by an ocean barrier didn't necessarily have to disperse across that barrier because their ancestors were once closer together. In some cases, the splitting of the continents promoted the divergence of populations into distinct species, a process known as vicariance.

How did the observations that led Alfred Russel Wallace to develop a theory of evolution by natural selection differ from those that led Darwin to develop the same theory?

> **Answer:** Wallace's observations were primarily about the geographic differences among varieties of the same species and between species. Because he was collecting specimens that could be sold in England, he took note of exactly where valuable species lived. These observations led Wallace to the idea that species did not always live where they currently live, suggesting that perhaps they have changed in other ways, too. Darwin's observations also included notes on where different species occur, but he didn't collect as many examples of the same species as Wallace did, so he wasn't as aware of geographical differences within species. However, Darwin's observations also included fossils and experiments, which gave him insight into how powerful natural selection can be and its effect over long periods of time.

Lecture 6

Is it possible for a species to not evolve?

> **Answer:** No. A cornerstone in the modern science of evolution is a model for how populations change through time, known as the Hardy-Weinberg equilibrium. According to this model, the traits in a population will stay the same through time—that is, they will not evolve—under a set of strict criteria: All individuals must choose their mates randomly (no sexual selection), no individuals can move from one population to another (no gene flow), all individuals must have the same number of surviving offspring (no natural selection), no new traits can appear due to errors in copying DNA (no mutations), and the population must be infinitely large (no genetic drift). Because these assumptions are so strict, even unrealistic, biologists assume that all real populations will experience evolution because one or more of the assumptions of the Hardy-Weinberg equilibrium will always be violated.

Mutations and genetic drift are both random processes that contribute to evolution. In what ways are they similar, and in what ways are they different?

> **Answer:** They are similar in that both mutations and genetic drift are random, but mutations occur in individuals while genetic drift is a property of populations. Mutations happen any time an error is made in copying an organism's genome. That process is random, although some types of mutations are more common because some mutations are more likely to occur than others. Likewise, some mutations are more likely than others to disrupt important functions, leading to death early in development, meaning that such mutations are rarely seen in living organisms. Genetic drift is also random. Mutations become more or less common through genetic drift, but the chances that genetic drift causes a mutation to disappear from a population or become fixed depends on how common the mutation is. For example, a mutation that is present in 10% of the population has a 10% chance of becoming fixed through genetic drift—and a 90% chance of being lost.

Which of the following is an example of gene surfing, and which is an example of genetic drift?

> A seed washes up on the shore of an uninhabited island and grows into a tree with shaggy bark. A thousand years later, the island is filled with trees, all of which have shaggy bark.

As the glaciers melted at the end of the last ice age, trees began to grow in the newly exposed soil. The trees closest to the melting glaciers happened to have shaggy bark. A thousand years later, the area formerly covered by glaciers is filled with trees with shaggy bark.

> **Answer:** Both (a) and (b) involve genetic drift, but only (b) involves gene surfing. Genetic drift is the random increase or decrease in how common an allele is. In (a), the shaggy bark allele became more common because it happened to be present in the individual that founded a new population. Gene surfing is a special case of genetic drift in which the alleles for a trait become more common because they are present in a population that is growing because it is expanding into new territory. In (b), the alleles for shaggy bark happened to be present in the trees at the edge of the range where glaciers were melting, and the trees expanded their range as new habitat opened up. Shaggy bark became common there, not because it was beneficial, but simply because it was present in a growing population. The shaggy bark allele can be thought of as surfing because it was carried along with the expanding wave of trees as they moved across the landscape.

Lecture 7

What caused the change in beaks of the medium ground finches on the Galapagos Island of Daphne Major following the 1977 drought?

> **Answer:** A change in the type of food available made some beaks more useful than others. Peter and Rosemary Grant documented

natural selection operating in real time among the medium ground finches of the Galapagos island of Daphne Major. Because the island is small, the Grants could measure every bird on the island each year. After the drought, in 1978, the average beak depth had increased 15% compared to the year before. The reason for the increase was that the drought killed the spurge plants that were the medium ground finch's preferred food. What was left was a plant called caltrop, with tougher seeds, which required more force to open and eat. The finches with deeper beaks were better able to open the caltrop seeds, making deeper-beaked finches more likely to survive and reproduce. Because offspring inherit their beak depth from their parents, the next generation of medium ground finches tended to have deeper beaks than the generation that lived before the drought.

In the mountain streams of Trinidad, guppies living in the upper sections of streams—above the waterfalls—tend to have males with larger and more brightly colored spots than the guppies in lower ponds. What would you expect to happen if pike cichlids, the predators of these guppies that only live in ponds below the waterfalls, were introduced into the high ponds?

Answer: There would be fewer guppies, and beginning in the next generation, males would evolve to have fewer and less brightly colored spots. Experiments by John Endler showed that the spot patterns on male Trinidadian guppies evolve in response to the presence or absence of predators like pike cichlids. Introducing predators to high streams would likely cause the males to evolve to have fewer and less brightly colored spots, because such males would be less likely to be eaten.

Lecture 8

Why are microorganisms like bacteria such good research subjects for studying evolution in laboratories?

> **Answer:** Many microorganisms reproduce quickly, meaning they have very short generation times (e.g., *E. coli* bacteria can reproduce every 20 minutes). What's more, because microorganisms are very small, it is possible to set up experiments with lots of individuals, which gives researchers the ability to look for rare events, such as mutations, and to create many replicates of the experiments, increasing their reliability. Lastly, bacteria can be frozen and reanimated, allowing researchers to create a frozen fossil record that can later be brought back to life and used for additional experiments.

What's wrong with the following statement?

Mutations occur to help improve a species' ability to survive and reproduce.

> **Answer:** Mutations occur randomly, not in response to an organism's needs. This was the point demonstrated by the experiment performed by Joshua and Esther Lederberg, which showed that bacteria survived being exposed to a virus only if they already had a particular mutation. That means that the mutation didn't occur because it was needed, but that some individuals just happened to already have the mutation and those that did were more likely to survive than those that didn't.

Lecture 9

How might the spread of nonnative species lead to the evolution of new species?

> **Answer:** The spread of nonnative species leads to the evolution of new species by introducing new hosts for insects, which can evolve new species to specialize on the new host. In North America,

> *Rhagoletis* fruit flies began laying their eggs in apples after apples were introduced from Europe. This allowed differences to accumulate in flies using apples versus flies that used native fruits, leading to the formation of new species. Moreover, a type of parasitic wasp that lays its eggs inside the bodies of fruit fly larvae developing inside different types of fruit have also diverged! Many other nonnative species have been spread around the world and may be leading to opportunities for new species to evolve by switching hosts.

No single definition of species is accepted and used by all biologists. The ability to mate and produce viable, fertile offspring defines the ____ species concept, but it doesn't apply to species like bacteria that only reproduce asexually.

a. ecological

b. morphological

c. phylogenetic

[✓ d. biological]

The observable physical features of a species define the ____species concept, but it fails to be useful for many microorganisms and can also be misleading because of convergent evolution.

a. ecological

[✓ b. morphological]

c. phylogenetic

d. biological

The ____ species concept defines species as being distinct branches on an evolutionary tree reconstructed using DNA, but it doesn't clearly distinguish species from varieties within a species.

a. ecological

b. morphological

c. phylogenetic

d. biological

The role species play in their ecosystems defines the ____ species concept, but it isn't practical for extinct species.

a. ecological

b. morphological

c. phylogenetic

d. biological

Answers: highlighted above

Lecture 10

Why has it been difficult to find fossils from before the Cambrian era began 541 million years ago?

> **Answer:** It has been difficult to find such fossils because the organisms that lived before the Cambrian era were small and soft-bodied, making them less likely to be preserved and discovered. Darwin was concerned that the earliest-known fossils, from the Cambrian, were complex organisms, while his theory predicted that the first forms of

life were simple. Since his lifetime, fossils have been found that go back as far as 3.5 billion years ago. These early fossils are indeed simple, single-celled organisms, just as Darwin suspected.

What do mass extinctions reveal about evolution?

Answer: Mass extinctions reveal that evolution doesn't always occur gradually, as Darwin assumed. Mass extinctions show us that even species that were once widespread and dominant—such as trilobites and dinosaurs—can be completely eliminated by sudden, catastrophic events, such as the eruption of a supervolcano or a massive asteroid impact. We have also learned that it can take many millions of years for ecosystems to recover from mass extinctions and that the forms of life that follow mass extinctions are often quite different from what came before.

Lecture 11

How does our modern understanding of the tree of life differ from Darwin's?

Answer:

1. Biologists now use DNA sequence data to reconstruct the tree of life, which has revealed some surprising relationships, such as the fact that chimpanzees and bonobos are closer to humans than they are to gorillas.

2. There are many more species known today than were known in Darwin's lifetime, including some categories of life (e.g., archaea) that were unknown to Darwin.

3. Comparing DNA among organisms has revealed instances in which distantly related organisms have exchanged genes, leading

to tangled relationships, especially among the microorganisms near the base of the tree of life.

What did the discovery of *Tiktaalik* reveal about the origin of land animals?

> **Answer:** *Tiktaalik* confirmed predictions that a species with characteristics intermediate between those of fish and amphibians would be found in a place that had once been the coast of a shallow lake (375 million years ago). *Tiktaalik* had many transitional features: scaly skin and webbed fins like a fish, but a bone structure that resembles the shoulders, elbows, and wrists of amphibians like salamanders. The discovery of *Tiktaalik* is a great example of how the modern science of evolution makes specific predictions that can be tested by data—in this case, a fossil!

Lecture 12

How has the old, iconic depiction of human evolution as a progression from a hunched-over ape to an upright human been updated in light of recent discoveries?

> **Answer:** We now know that Thomas Henry Huxley's simple, linear progression from ape to human does not accurately reflect the complexities of how humans evolved. Rather than evolving from an ape that is still alive today, both humans and chimpanzees split from a common ancestor 5 to 7 million years ago. There were many such splits; fossil discoveries show that there were once many different hominin species, some of which lived at the same time. Likewise, DNA from modern and ancient humans suggests that our species originated in Africa and then expanded into other regions, mating with closely related hominins, such as Neanderthals and Denisovans, when they encountered them. Our species, *Homo sapiens*, is the only living representative of a once-diverse group of humanlike species.

What did the discovery of about a dozen individuals of *Homo floresiensis* ("hobbits") on the Indonesian island of Flores in 2003 reveal about human evolution?

Answer:

1. Hominins were more diverse than previously thought.

2. Hominins follow the same evolutionary trends as other species; in this case, a population isolated on an island evolved a smaller body size. The "hobbits" lived as recently as 100,000 to 60,000 years ago, yet they had features that were more similar to much older hominin species, such as a small brain for the size of its body. The discovery was also surprising because the location of the island where they were found suggests that to get there, they must have crossed the open ocean—something more primitive hominins were not thought to be capable of doing. A particularly striking example of hominins following the same trend as other species was the short stature of *Homo floresiensis*—adults were only about 3 feet and 6 inches tall. Their small size indicates that they may have shrunk after their ancestors (presumed to be the much taller species, *Homo erectus*) arrived there. This suggests that humanlike species are subject to the same evolutionary processes that have given rise to small-bodied elephants, foxes, etc., on islands around the world.

Lecture 13

How did the long-term evolutionary experiment on *E. coli* bacteria begun by biologist Richard Lenski help advance the debate about whether evolution is predictable?

Answer: The long-term evolution experiment showed that in a broad sense, the evolution of *E. coli* bacteria follows repeatable trends but that the precise outcome of evolution of individual populations cannot be predicted. A series of mutations in 1 of 12 replicate populations in the experiment led to an unexpected outcome: the sudden ability of some bacteria to digest the chemical citrate in the presence of oxygen. To determine how repeatable this event was, researchers in Lenski's lab reanimated frozen samples of the ancestors of that population of bacteria, as well as the ancestors of the other 11 populations, and repeated the experiment. They found that the same mutations did occur, but not in every case, suggesting that when conditions are identical, evolution can proceed in similar ways but that a specific outcome cannot always be predicted.

What does convergent evolution suggest about the possibility of alien life?

Answer: Convergent evolution occurs when distantly related species—such as opossums and squirrels—evolve in similar ways, leading to very similar outcomes (e.g., sugar gliders in Australia and flying squirrels in North America). We now know of so many examples of convergent evolution that some biologists have argued that evolution can only proceed in a limited number of possible ways. If the same thing is true for life elsewhere in the galaxy, then alien life may resemble species that live on Earth because it would have evolved in similar ways.

Lecture 14

How did the discovery of *Thermus aquaticus* bacteria living at temperatures around 176° Fahrenheit in the hot springs at Yellowstone National Park help change our understanding about the evolution of life on Earth?

Answer: In addition to showing that it was possible for life to exist in such an extreme environment, the discovery of *Thermus aquaticus* helped start a revolution in molecular biology. That's because a technique known as polymerase chain reaction (PCR) was developed to copy DNA, but it needed an enzyme that would not break down at the high temperatures necessary for the technique to work. Because *Thermus aquaticus* was adapted to live at similarly hot temperatures, it could provide the enzyme needed to make PCR both effective and efficient. PCR, in turn, made it possible to discover additional types of microorganisms—especially other so-called extremophiles—that were previously unknown in part because they will not grow in ordinary laboratory conditions.

How can some fish, such as the crocodile icefish, survive in freezing water?

Answer: Some fish—such as notothenoids, including the crocodile icefish—thrive in such frigid waters around Antarctica by having no red blood cells, making their blood very thin. This allows their blood to be pumped through their veins even when the temperature is very low, which would make normal blood thick and therefore slow-moving. They also have proteins that act as natural antifreeze by binding to small ice crystals and preventing the ice crystals from growing.

Lecture 15

In what ways do the eyes of a squid seem better designed for vision than human eyes?

Answer: In humans and all other vertebrates, the photoreceptor cells in the retina are pointed backward, away from the light. This orientation means that the optic nerve must begin inside the eye and pass through the retina to reach the brain. The place where it passes through the retina creates a blind spot because there are no photoreceptors. In contrast, a squid's eye has photoreceptors pointed toward the light and the optic nerve is behind the retina, so there is no blind spot. Both the human eye and the squid's eye are very sophisticated, but the fact that the squid eye avoids the blind spot problem of the human eye is an example of how evolution doesn't always lead to perfection.

Some living organisms, such as the chambered nautilus, have eyes that resemble earlier stages in the evolution of more complex eyes like ours. Does this mean that these organisms will eventually evolve more complex eyes?

> **Answer:** These organisms will not necessarily evolve more complex eyes. Although the eyes in the ancestors of mammals went through a stage in which they were simpler, resembling the pinhole eyes of the chambered nautilus, that does not mean that the eye of the chambered nautilus will ever become more complex (although that is possible). The bottom line is that evolution doesn't always do the same thing in different species. Here, that might be because there isn't selection favoring a better eye in the chambered nautilus (the simpler eye is good enough for what it needs). Or perhaps selection would favor an eye with a lens for the chambered nautilus, but there simply hasn't been a mutation in the nautilus genes capable of making a primitive lens, so selection doesn't have that trait available.

Lecture 16

Why did Darwin think that ants might undermine his theory of evolution by natural selection?

> **Answer:** Darwin knew that worker ants cannot reproduce, while his theory was based on the assumption that species evolve to maximize the number of living, fertile offspring they leave behind. So, it seemed impossible for sterility to evolve through natural selection. We now know that sterile workers (including worker ants as well as worker bees, wasps, etc.) can evolve because they are helping close relatives—their mother (the queen) and their sisters (the other workers). Because related individuals share many of the same genes, helping close family members ensures that copies of those genes get passed on to the next generation. Societies with sterile workers have evolved more than a dozen times, including in termites, mole rats, and snapping shrimp. In all cases, the workers live with close family

members in a communal nest, which may have been an important first step in the evolution of these complex societies.

When might natural selection act at the level of entire groups rather than just on individuals?

> **Answer:** Group selection might operate whenever individuals are members of a superorganism. Many species of ants, as well as some bees and termites, live in complex societies where members have specialized tasks. The division of labor in these colonies resembles the body of a complex organism, such as a human body, with specialized organs and cells. Because the colony acts as a unit in which only some members reproduce, the ability of all members to survive and pass on copies of their genes is dependent on the heritable traits of the colony.

Lecture 17

Why does evolution sometimes favor cheaters?

> **Answer:** The reason evolution sometimes favor cheaters is because cheating can be a successful strategy for passing genes to the next generation. An example is yucca moths that lay their eggs where their larvae can eat yucca seeds but without pollinating the yucca flower. This strategy is successful because the cheater moths reproduce without expending energy on collecting pollen. But it only works when the yucca flowers are pollinated by other moths.

Which of the following scenarios would be most likely to lead to an evolutionary arms race?

a. An insect evolves resistance to the toxic chemical produced by a plant that it eats.

b. A bacteria produces vitamins needed by its host in exchange for a safe place to live.

c. A parasite evolves a way to manipulate its host's behavior, killing the host but helping the parasite find a new host.

Answer: Both (a) and (c) would likely lead to an evolutionary arms race. In scenario (a), the plant producing the toxic chemical benefits from making the chemical even more toxic because that makes it less likely to be eaten, while the insect benefits from continuing to evolve resistance to the increasingly toxic chemical so that it can feed and survive. In scenario (c), the parasite benefits by manipulating its host's behavior because that makes it more likely to complete its life cycle by finding a new host. Yet the host will benefit if it can avoid being infected by the parasite or evolve a way to prevent the parasite from manipulating it because that leads to death. Scenario (b) would not be likely to lead to an evolutionary arms race because both the bacteria and its host benefit from the interaction.

Lecture 18

What clues led Lynn Margulis to the theory, called endosymbiosis, that eukaryotic cells of all plants and animals evolved through the fusion of previously independent organisms?

Answer:

1. Whereas a eukaryotic organism's primary genome is located inside the nucleus, DNA could also be found in the fluid-filled area outside the nucleus, called the cytoplasm.

2. Some of the organelles in cells, such as chloroplasts (in plants) and mitochondria (in animals), have similarities to free-living bacteria and cyanobacteria: They are encapsulated by a double membrane, have structures called ribosomes where proteins are made, and have circular DNA. Lynn Margulis and biologist Carl Woese discovered that the RNA from ribosomes in organelles such as chloroplasts and mitochondria is more similar to the RNA

from free-living bacteria than to the RNA from the nucleus of the same cell as the organelle.

Why do aphids die if they are given antibiotics?

Answer: Antibiotics kill bacteria, including a species called *Buchnera* that aphids depend on to produce essential nitrogen. Aphids evolved a symbiotic relationship with the bacteria, which live inside the cytoplasm of some cells and, in exchange, produce nitrogen in a form that can be used by their aphid hosts. Conversely, the bacteria have become so dependent on their aphid hosts that their genomes have lost many of the genes needed for survival on their own.

Lecture 19

Suppose you are watching a bird perched on a branch that suddenly flies straight down toward the ground and then abruptly pulls up, snatching an insect out of the air before it returns to the branch. How might you begin to analyze this behavior using Tinbergen's 4 questions?

1. What is the physiological cause of the behavior?
2. Is it instinctual or learned?
3. What is its effect on survival and/or reproduction?
4. Has the behavior evolved uniquely in one species, or does it have a longer and broader evolutionary history?

Answer:

1. When the bird sees a flying insect beneath it, this may cause the brain to send a signal to the muscles in the wings that causes it to fly down and then up.

2. This might be an instinctual response to a moving insect, but does the young bird have opportunities to learn from observing other birds perform this behavior? Does this species of bird have an enlarged pallium associated with greater capacity for social learning and more complex problem solving?

3. Here, catching an insect to eat seems clearly beneficial for the bird's survival, although it could also help with reproductive success if performance of the dive is attractive to potential mates or if it feeds the insect to its young chicks.

4. If the closest-living relatives of the species of bird performing the behavior do the same thing, then it's likely to have evolved in the common ancestor of all the species that perform it. But if the behavior is found only in that species, then it must have evolved uniquely in that species.

How do the parts of the human brain that control language provide a clue about how language evolved in our ancestors?

Answer: Separate brain areas for different aspects of language suggest that the different components of language evolved separately. Wernicke's area, in the temporal lobe, processes spoken language. The visual cortex, in the occipital lobe, controls your ability to read written language. The act of forming words that you will speak takes place in one part of the frontal lobe, while the act of actually speaking those words is controlled by another part of the frontal lobe, called Broca's area. The fact that each of these areas is distinct suggests that they each evolved separately. Moreover, some brain structures used in language were present in the common ancestor we share with chimpanzees. Chimpanzee brains have many of the same structures, including both Broca's area and Wernicke's area, which are activated when chimpanzees use gestures to ask for food. This suggests that these parts of the brain were already present in the common ancestor we shared with chimpanzees 5 to 7 million years ago.

Lecture 20

Why did Darwin write to a friend that "the sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick"?

> **Answer:** Darwin assumed that the long, elaborate tail feathers of a peacock would make it more vulnerable to predators, so he initially couldn't understand how such a trait wouldn't be eliminated by natural selection. Darwin reconciled the peacock's tail with his views when he developed a second theory, called sexual selection, which stated that traits related specifically to reproductive success could also become more common over generations. We now know that females, called peahens, use several features of a male peacock's tail—including the number of eyespots; the color, brightness, and contrast of the eyespots; and the vibrations produced by shaking the tail feathers—to evaluate the quality of that peacock's genes, which helps the females ensure that their offspring will survive and be successful in their own efforts to reproduce.

Asexual reproduction, in which an individual makes an identical copy of itself, is faster and less risky than sexual reproduction and passes on all of an individual's genes. So why does sexual reproduction exist?

> **Answer:** There are benefits to sexual reproduction. Sexual selection provides variation, and variation is needed for adaptation through natural selection. Populations without variation, or with very little variation, are less able to adapt to changing conditions. Sexual reproduction also mixes the genes of different organisms, increasing the amount of variation in a population's gene pool. Asexual reproduction also has downsides. For example, harmful mutations can accumulate in asexual organisms without the recombination that takes place when genes are reshuffled during the formation of sex cells.

Lecture 21

How does the theory of antagonistic pleiotropy, developed by biologist George C. Williams, explain why our bodies break down as we age?

> **Answer:** This theory suggests that natural selection favors genes that help us early in life but make us sick as we age. A single gene having multiple effects is called pleiotropy, and according to the theory of antagonistic pleiotropy, natural selection can favor any mutation that improves the chances of survival and/or reproduction early in life while also decreasing the chances of survival and/or reproduction later in life. Genes that affect survival before an individual reproduces are strongly affected by natural selection, but genes that affect survival after an individual reproduces are weakly affected by natural selection—or not affected at all. Such mutations are expected to accumulate in the genomes of all organisms because the mutations improve the chances of passing on one's genes, even though they come at the cost of causing the body to break down following reproduction.

An enzyme called telomerase limits the damage to chromosomes and the breakdown of the body that happen with age (each time a cell divides). So why do most cells in our body have relatively low levels of telomerase?

> **Answer:** Telomerase is found in high levels in cancer cells, which can divide indefinitely, giving rise to a tumor. Telomerase is found in high levels in the cells of human fetuses and in the cells that make sperm and eggs, where cell division is rapid, but in lower levels in most adult cells because of the risk that the slow-dividing adult cells could become cancerous.

Lecture 22

How can evolution help explain why some diseases are deadlier than others?

> **Answer:** The organisms that cause infectious disease evolve to maximize their chances of finding a new host, which sometimes involves sacrificing the current host. Pathogens must find new hosts to complete their life cycle and pass on their genes. If the pathogen reproduces quickly inside a host, a side effect of having many copies of the pathogen inside its body is that the host may quickly become incapacitated or might quickly die. In that case, the host may have very few encounters with other potential hosts, but any encounters it does have will be more likely to result in another host becoming infected. On the other hand, if the pathogen reproduces slowly, the host may be less affected and may be more likely to interact with other potential hosts, giving the pathogen more opportunities to infect new hosts (but each encounter is less likely to result in a successful host shift).

How can conditions like diabetes and the type of anemia known as alpha-thalassemia be understood as mismatch diseases?

> **Answer:** Such diseases had helpful side effects under the circumstances in which our ancestors lived but not in the modern world. Alpha-thalassemia, a form of anemia in which the red blood cells are unusually small, evolved because it makes the red blood cells less suitable for the parasite that causes malaria. That provided an advantage for people living in areas where malaria was common, and the survival advantage outweighed the quality-of-life cost that came from having anemia. For people living today in regions without malaria, there is a mismatch between the environment in which the condition evolved and the environment of people living with the condition today. Likewise, type 2 diabetes has become common today in part because many people have access to many more calorie-dense carbohydrates than their hunter-gatherer ancestors. Natural selection favored traits in our ancestors that allowed them to consume carbohydrates when they

were available and to store extra energy in the form of fat. Such traits would have conferred a survival advantage for hunter-gatherers but today make it more likely to develop obesity and diabetes.

Lecture 23

Do you think genetically directed evolution is different than the types of artificial selection humans have engaged in for many centuries to develop our domesticated plants and animals?

Answer: It's a difficult but important question. Artificial selection works the same way as natural selection. The only difference is that in artificial selection, people decide which varieties will pass on their genes, whereas in natural selection, the genes that become more common are those that naturally result in better chances of survival and/or reproduction. As we develop genetic technology to direct the evolution of other species—as well as our own evolution—we will be forced to consider what changes we are comfortable making and what changes are unacceptable. Ethical and safety considerations will be very important if we choose to edit our own genomes in heritable ways, as these changes will influence not only living people but also future generations. The trade-offs, side effects, and other changes that took place in our crops and domesticated animals over the last several thousand years may give us some insight into the ways that gene editing could alter our bodies and behavior, albeit on a much more accelerated time line for gene editing.

Efforts are underway to control the spread of diseases like malaria with evolutionary applications like gene drives. How might such efforts be counteracted by evolution acting in other ways?

Answer: Evolution could favor mutations that counteract a change intended by humans. Gene drives work by humans causing a trait to spread more rapidly through a population than would occur naturally.

That might be helpful to humans if, for example, the change makes a mosquito a less suitable host for pathogens that cause human disease. But it also means that any mutation in the pathogen that counteracts the change will be very beneficial to the pathogen, meaning that it will be strongly favored by natural selection.

Lecture 24

How can natural selection and culture affect one another?

Answer: Natural selection and culture can act together or in opposition. Culture acts much like natural selection in that it can be heritable (i.e., through learning) and affects survival and reproduction (e.g., through differences in wealth, education, or access to healthcare). An example of culture and natural selection at odds is in the timing of reproduction among modern women. In many human populations, natural selection favors women that begin having children earlier in life (because they tend to have more children over the span of their lives than women who begin having children later in life) despite a cultural trend toward older first-time mothers in the United States, parts of Western Europe, and elsewhere in order to focus on their education and careers.

Why is human genetic diversity relatively low, and what factors are contributing to the rise in our genetic diversity?

Answer: Human genetic diversity has been low because there have been times when the total population was small, while diversity has increased with greater population size and life expectancy. Humans experienced a series of population bottlenecks that substantially reduced the number of living individuals. Some of the bottlenecks were due to founder events as the first *Homo sapiens* expanded out of Africa, spreading out across the globe in a series of waves that each consisted of a small group of founders. In addition, our species may have experienced at least one global bottleneck, possibly caused by the eruption of the Toba volcano in Indonesia about 70,000 years ago (though research published in 2018 did not confirm the global winter expected from such a large eruption). On the other hand, the increase in human genetic diversity is due to

1. exponential population growth over the last several centuries (reaching 7 billion in 2011) and

2. a rising number of mutations per baby, because of the trend in many populations toward older fathers, who contribute more mutations to their children on average than younger fathers do.

Understanding human genetic diversity in the past and in modern times is a fast-changing area of active research.

Timeline for the Modern Science of Evolution

Charles Darwin and His Contemporaries

1809 Feb. 12	Charles Darwin is born in Shrewsbury, UK.
1831 Dec.	Darwin begins his voyage on the *Beagle*.
1832 Sept.	Darwin discovers fossils of large extinct organisms that resemble smaller living organisms.
1835 April	Darwin gains a deep impression of geological time while in the Andes and following an earthquake in Chile.
1835 Sept.–Oct.	Darwin visits the Galapagos Islands, where he collects birds and other specimens and makes notes about the similarities between the island and mainland fauna and about differences among fauna of apparently similar islands.
1836 Oct.	The *Beagle* returns to England, and Darwin begins arranging his scientific collections and journal entries.
1837 July	Darwin begins his first notebook about the transmutation of species.
1838 Sept.–Oct.	Darwin reads Thomas Malthus on the struggle for existence in *An Essay on the Principle of Population*.

1838–1843	Darwin edits and oversees the 5-volume publication of the *Zoology of the Voyage of the H.M.S. Beagle*, with 5 experts assessing Darwin's collected specimens from the voyage.
1839 Jan. 29	Darwin marries Emma Wedgewood, his cousin.
1839	Darwin's *The Voyage of the Beagle* is published. (Before 1905, this work was known as *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle round the World*.)
1842	Darwin's *The Structure and Distribution of Coral Reefs* is published, and he writes his first unpublished compilation of evidence toward his eventual theory of natural selection.
1844 July	Darwin completes an unpublished 230-page essay on species.
1844 Oct.	*Vestiges of the Natural History of Creation*, published anonymously by Robert Chambers, popularizes the idea of the transmutation of species.
1846–1854	Darwin writes and publishes 4 monographs, 2 on living barnacles (*Living Cirripedia*) and 2 on fossil barnacles (*Fossil Cirripedia*).
1858	Darwin and Alfred Russel Wallace publish papers simultaneously, introducing their theories together.
1859 Nov.	The first edition of Darwin's *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* is published.

1862	Darwin’s *Fertilisation of Orchids* (also known as *The Various Contrivances by which Orchids Are Fertilised by Insects*) predicts coevolution of a long-mouthed moth capable of pollinating Christmas star orchids.
1864	Influenced by Darwin’s ideas, Herbert Spencer’s *The Principles of Biology* popularizes the phrase “survival of the fittest,” an expression Wallace later (1866) recommends to Darwin.
1865	Gregor Mendel’s “Experiments in Plant Hybridization” is published; it goes largely unnoticed for 35 years.
1868	Darwin’s *The Variation of Animals and Plants under Domestication* is published, containing his mistaken theory of heredity by pangenesis.
1869	The revised fifth edition of *On the Origin of Species* becomes the first edition to use the phrase “survival of the fittest.”
1871	Darwin’s *The Descent of Man, and Selection in Relation to Sex* is published.
1872 Feb.	The sixth and final edition of *The Origin of Species*—the first edition to use the word “evolution,” to include a chapter VII addressing “Miscellaneous Objections,” and to omit “On” from the book title—is published.
1872	Darwin publishes separately *The Expression of the Emotions in Man and Animals* (one of the first books to include photographs), which he had originally conceived as part of *The Descent of Man*. A revised second edition was published by his son, Francis Darwin, in 1890.

1876	Darwin's "Recollections of the Development of My Mind and Character," later published after his death as *The Autobiography of Charles Darwin*.
1881	Darwin's book about worms—*The Formation of Vegetable Mould through the Action of Worms, with Observations on Their Habits*—is published.
1882 April 19	Charles Darwin dies at the age of 73.

Fossil Discoveries, Heredity, and Genes

1891	The first early fossil of an early hominin, known as Java man and later recognized as *Homo erectus*, is discovered by Eugène Dubois in Indonesia.
1900	Mendel's work is rediscovered by Hugo de Vries, Carl Correns, and William Bateson.
1907	The first law allowing sterilization is passed in the US based on the now-debunked concept of eugenics.
1910	Thomas Hunt Morgan discovers that genetic material is found on chromosomes.
1924	J. B. S. Haldane publishes a series of papers using mathematical models to describe how evolution works within populations.
1927	Hermann Muller discovers that x-rays can cause mutation.

The Modern Synthesis of Genetics with Darwinian Evolution

1930	Fisher's *The Genetical Theory of Natural Selection* connects Mendel's work to Darwin's.
1932	Sewall Wright introduces the idea of an adaptive landscape to explain the concept of genetic drift and why organisms are not perfectly adapted to their environments.
1937	The publication of Theodosius Dobzhansky's *Genetics and the Origin of Species* explains evolution in terms of genes and alleles.
1942	Ernst Mayr's *Systematics and the Origin of Species* defines species based on their ability to successfully reproduce.
1942	Julian Huxley's *Evolution: The Modern Synthesis* gives an influential summary of the modern synthesis.
1949	Anthony Allison shows that natural selection is continuing to act in humans by promoting alleles for sickle cell in regions where malaria is common.

Modern Synthesis Expanded: The Molecular Revolution, New Branches on the Tree of Life, and Fast Evolution

1953	James Watson and Francis Crick determine that the structure of DNA is a double helix, launching the era of molecular biology that provides new tools for understanding evolution.
1964	William Hamilton extends natural selection to include selection on relatives.

1968	Motoo Kimura argues that genetic drift is the dominant evolutionary force affecting DNA.
1973	Herbert Boyer and Stanley Cohen lay the foundation for directed evolution by inserting genes from one type of bacteria into another type of bacteria.
1974	The first fossil of *Australopithecus afarensis*, nicknamed Lucy, is discovered.
1975	Edward O. Wilson publishes *Sociobiology: The New Synthesis*, explaining social behavior in humans and other species as a result of evolution.
1977	Carl Woese discovers that Archaea represent a third domain of life.
1978	Peter and Rosemary Grant document changes in the beaks of Galapagos finches, showing that natural selection can act rapidly in wild populations.
1983	A technique known as PCR (polymerase chain reaction) is developed that allows DNA to be copied many times in a lab, allowing researchers to compare the genes of different species and determine their evolutionary history.
1987	The first drug is developed to treat HIV infection, but the virus quickly evolves resistance.
1988	Richard Lenski begins his long-term evolution experiment using 12 identical clones of *E. coli* bacteria.

1989	Stephen Jay Gould's *Wonderful Life: The Burgess Shale and the Nature of History* argues that the fossil record from the Cambrian explosion suggests that evolution is inherently unpredictable.
1990	The first gene therapy is performed in a human.
1992	A hawk moth with a long proboscis is observed drinking nectar from a Christmas star orchid, confirming a prediction made by Darwin 130 years earlier.

The Genomic Era

2001	The first draft of a human genome is published, marking the beginning of the genomic era, in which large amounts of DNA can be used for many purposes, including reconstructing evolutionary history.
2003	The Human Genome Project is completed, providing the first detailed look at the full set of genes that make up a human.
2007	Next-generation sequencing technologies are developed, making it faster and easier to compare the genomes of individuals and species, allowing more complete and accurate insights into the history of evolution.
2010	The first Neanderthal genome is sequenced.
2012	CRISPR genome editing technology, developed by Jennifer Doudna and Emmanuelle Charpentier, pioneers a way to direct evolution by making precise edits to any organism's genome.

Glossary

adaptation: The fit between an organism and its environment that comes about as a result of natural selection.

adaptive landscape: A metaphor for how populations evolve in a hypothetical landscape consisting of hills and valleys, where the tops of the hills represent the greatest adaptation and evolutionary fitness. See also **adaptation**, **natural selection**, **genetic drift**.

allele: A version of a gene that differs in its sequence of DNA bases in a way that changes the protein it codes for in some way. White and purple are alleles for a gene that controls the color of pea plant flowers in Mendel's hybridization experiments.

antagonistic pleiotropy: The theory that seeks to explain the evolution of aging and senescence as the outcome of one or more genes that have a beneficial effect early in the lifetime of an individual but a negative effect on the individual later in life, particularly after the individual has reproduced one or more times.

archaea: One of 3 major divisions of life. First discovered by Carl Woese in 1977, archaea are single-celled organisms that resemble bacteria but are in fact more closely related to eukaryotes, including plants, fungi, and humans.

artificial selection: The way in which humans selectively breed plants and animals to change their characteristics over generations—for example, in agriculture. Darwin distinguished between artificial selection and the analogous mechanism of natural selection. (L1)

chromosome: A physical unit made of DNA and proteins that consists of many genes. The number of chromosomes in an organism's genome varies by species; humans have 23 pairs of chromosomes that together comprise the entire genome.

clade: A group of organisms that share one or more unique traits because they are descended from a common ancestor.

coevolution: Evolutionary change, cooperative or antagonistic, in 2 or more species that occurs as a result of a biological interaction between the species. (L9) See also **evolutionary arms race**, **evolutionary peace accord**.

convergent evolution: A process, partly predictable, in which species not closely related evolve independently through natural selection yet end up being similar in one or more ways; also called parallel evolution.

CRISPR-Cas9: A pair of molecules that evolved in bacteria as a defense against viruses; can be used in a laboratory to precisely edit an organism's genome. See also **gene editing**.

cultural evolution: A process in which changes occur in a population due to socially transmitted behaviors; occurs not just in humans, but also other primates, whales, and some birds.

demographic transition: A decline in death rates followed by a decline in birth rates that accompanies economic improvement, leading to changes in the strength and direction of natural and sexual selection.

digital life: Refers to the use of computer programs that are designed to evolve like living organisms through mutation and natural selection. Digital life can be used as a way to study the process of evolution in real organisms or as a way of developing computer programs to solve challenging problems that could not otherwise be easily developed by human programmers.

DNA: Short for deoxyribonucleic acid; the molecule that contains the genetic code for most organisms on Earth (some viruses have an RNA genome).

domestication: Most commonly used to describe the process by which plants or animals become dependent on humans for survival and/or reproduction through generations of artificial selection. Examples of domestication by nonhumans include fungi that have been domesticated by ants.

endosymbiosis: The process by which eukaryotic organelles such as mitochondria were formed through the fusing together of 2 previously independent, distantly related organisms. See also **symbiogenesis**.

epigenetics: A recently discovered process in which traits can be passed from one generation to the next without being encoded in the DNA sequence of an organism's genome—for example, by attaching a chemical called a methyl group to the DNA to control which genes are turned on or off.

eukaryote: Organisms with complex cells that include a nucleus and organelles such as mitochondria; includes all plants, fungi, and animals (including humans). See **endosymbiosis**.

eusociality: A form of social organization that includes sterile workers and is found in ants, bees, wasps, and few other groups.

evolution: Change in living organisms that takes place over generations. Following the modern synthesis, evolution came to be defined as a change in the frequency of alleles in a population from one generation to the next. See also **selection**, **gene flow**, **genetic drift**, **mutation**.

evolutionary arms race: A process of coevolution in which 2 or more interacting species evolve greater and greater weapons or defenses in response to one another. Examples include predators and their prey and parasites and their hosts. See also **coevolution**, **evolutionary peace accord**.

evolutionary medicine: The use of evolutionary principles to better understand the causes of disease and to design treatments that will be effective in the face of ongoing evolution by both disease-causing microorganisms and their human hosts.

evolutionary peace accord: Refers to an outcome of coevolution in which 2 or more interacting species benefit from one another. See also **coevolution**, **evolutionary arms race**.

extinction vortex: A phenomenon in which a species that is reduced to a small number of individuals loses genetic diversity through genetic drift, making it less able to adapt to changing conditions and more likely to become inbred. This further decreases its population size and diversity, resulting in a downward spiral that often eventually leads to the extinction of the species.

extremophile: An organism capable of living in extreme conditions, such as very high or low temperature, salinity, or pH.

fitness: The ability of an organism to successfully pass on its genes to subsequent generations. See also **natural selection**.

gene: A sequence of DNA bases that codes for a particular protein.

gene drive: A form of gene editing that causes both alleles of a gene to be passed from a parent to its offspring rather than just one. This causes a modified gene to spread through a population faster than it would naturally.

gene editing: A technique in which the sequence of DNA bases in an organism's genome is intentionally altered. Editing the genes of reproductive cells (eggs or sperm) makes such changes heritable, leading to evolutionary changes. See also **CRISPR-Cas9**.

gene flow: The movement of genes from one population to another as a result of dispersal; recognized as one of the mechanisms of evolution since the modern synthesis.

gene surfing: A form of genetic drift in which an allele becomes more common in a population along the edge of its range because the population is growing as it spreads into new territories.

genetic drift: Random change in how common an allele is within a population; first recognized by Sewall Wright as a mechanism of evolutionary change that tends to reduce genetic diversity because an allele will randomly either be lost from a population or become fixed, meaning that it is present in all individuals. Genetic drift can happen in any population but is more pronounced in smaller populations.

genome: The complete set of all genes of a species. The field of genomics is the study of genetic similarities and differences among individuals or species incorporating all, or nearly all, of their DNA.

genus: A unit of classification for living things developed by Carl Linnaeus and still in use today; species are nested within a genus, and genera (the plural form of genus) are nested within families.

holobiont: The union of 2 or more organisms living symbiotically—for example, a host and its microbiome considered as a single collective entity.

hominins: The group of species that includes humans and extinct relatives that share a common ancestor more recently than the common ancestor shared with chimpanzees and bonobos.

horizontal gene transfer: The exchange of genetic material between distantly related organisms, creating a challenge for reconstructing evolutionary history using just a single gene or small number of genes.

iridium: A chemical element that is rare on Earth but more common elsewhere in the solar system. A layer rich in iridium was found by Walter Alvarez in deposits that date to the end of the Cretaceous period approximately 65 million years ago, prompting the theory that an asteroid impact caused the mass extinction event that killed most dinosaurs and many other species.

mass extinction: A period in which a significantly high percentage of living species becomes extinct worldwide.

microbiome: The community of microorganisms—including bacteria, archaea, fungi, and viruses—that live in and on the bodies of host organisms such as animals, plants, or humans. See also **holobiont**, **symbiosis**.

mismatch disease: A condition that results from a mismatch between the environment of an organism's ancestors and its current environment.

modern synthesis: The unification of Darwin's theory of evolution by natural selection with Mendel's theory of genetic inheritance that took place between 1900 and the 1950s, giving rise to the modern science of evolution.

molecular clock: The practice of determining how long ago 2 individuals, 2 species, or other groupings of organisms shared a common ancestor based on the estimated rates at which mutations occurred in the DNA sequences of each.

morphology: The visible form of an organism. This was the primary and traditional basis for classification until supplemented, and sometimes supplanted, by more detailed information from phylogeny.

mutation: Any change to the DNA sequence of an organism. Mutations occur naturally based on errors made when cells copy their genomes prior to dividing; became recognized during the modern synthesis as the ultimate source of variation among individuals, which is necessary for natural selection.

mycorrhizae: A type of mutually beneficial interaction between fungi and plants.

natural selection: The mechanism of evolution proposed by Darwin in 1859 and, since the modern synthesis, widely recognized as the only way that evolution can result in adaptation. See also **adaptation**.

nucleotide: A single DNA base (adenine, thymine, guanine, cytosine); a single letter of the genetic code.

nucleus: The part of a eukaryotic cell in which the genome is housed. See also **chromosome**, **DNA**, **genome**.

organelle: A structure within the cytoplasm of a cell that serves a particular function, such as the mitochondria (which produce energy) or ribosomes (which translate RNA into proteins).

parsimony: An assumption that simpler explanations are more likely to be correct; one of several ways that alternative reconstructions of evolutionary relationships among organisms can be compared. See also **clade**, **phylogeny**.

persistence hunting: A technique that involves chasing prey for a sustained period of time so as to cause it to overheat; may have been used by early hominins, helping explain the evolution of upright posture, loss of body hair, and increase in sweat glands.

phylogeny: A graphical representation of the hypothesized evolutionary history of a group of organisms in which nodes represent speciation events among ancestral species and tips represent living species; also known as a phylogenetic tree, evolutionary tree, or cladogram.

polyploid speciation: A process by which a new species comes into existence as a result of a mutation in which one or more chromosomes in the genome of an organism is duplicated.

population: A group of individuals of a particular species that occurs in a particular place and time. Since the modern synthesis, evolution has been recognized as a process of changes at the level of populations that takes place over generations.

postzygotic barrier: Something that prevents gene flow between 2 populations or species by limiting the survival and/or reproductive abilities of hybrid individuals. The evolutionary causes for new species are often divided into prezygotic and postzygotic barriers. See also **prezygotic barrier**.

prezygotic barrier: Something that prevents gene flow between 2 populations or species by preventing the formation of a zygote, or embryo. The evolutionary causes for new species are often divided into prezygotic and postzygotic barriers. See also **postzygotic barrier.**

protein: A type of biological molecule made up of amino acids that is coded for by DNA base pairs in genes. Proteins perform many vital functions inside and outside of cells. See also **gene**.

recombinant DNA: A technique in which DNA from one organism is incorporated into the genome of another organism.

recombination: A process in which DNA is rearranged during the production of sperm or egg cells that can result in different DNA sequences and/or combinations of genes in the offspring than is found in either parent; one of the sources of variation that is sorted by natural selection.

Red Queen hypothesis: Suggests that organisms must constantly evolve in order to keep up with the evolution of their enemies, rivals, and environment. This hypothesis is one proposed explanation for the evolution of sexual reproduction because sex leads to greater variation through recombination, providing more raw material for natural selection. See also **recombination**.

rhizobia: A type of bacteria that convert nitrogen in the atmosphere into forms that can be used by plants or animals.

RNA: Short for ribonucleic acid; a molecule that serves various functions inside cells and comprises the genome of some viruses. A particular type of RNA called messenger RNA (mRNA) acts as an intermediate step in the production of proteins by genes; ribosomal RNA (rRNA) makes up part of the structure of ribosomes, where mRNA is translated into proteins. See also **DNA**, **protein**.

selection: The mechanism to explain evolution proposed by Darwin; widely recognized as the only way that evolution can result in adaptation. See also **natural selection**, **sexual selection**, **artificial selection**.

senescence: The process by which an organism's physical structures and physiological processes deteriorate as it ages. See also **antagonistic pleiotropy**.

sexual selection: A mechanism of evolution proposed by Darwin in 1871 that acts by favoring traits that promote reproductive success but not necessarily survival. See also **selection**, **natural selection**.

speciation: The process of becoming a distinct species; also known as cladogenesis. See also **prezygotic barrier**, **postzygotic barrier**, **polyploid speciation**, **species**.

species: The fundamental unit of biological classification in the modern taxonomic classification scheme for living things. A species can be defined biologically (based on reproductive barriers), morphologically (based on appearance and structure), phylogenetically (based on shared evolutionary history), ecologically (based on role in an ecosystem), or through a pluralistic combination. See also **speciation**, **variation**.

symbiogenesis: The creation of a new form of life from organisms that are living together. See also **endosymbiosis**, **symbiosis**, **speciation**.

symbiosis: An intimate association between 2 or more species; can be mutually beneficial or mutually harmful or can benefit one species at the expense of the other. See also **endosymbiosis**, **microbiome**.

variation: The degree of difference within a given species of plants or animals (also known as intraspecific variation) or between species. The increasing record of observed variation was one of the lines of evidence that convinced Darwin and Alfred Russel Wallace about the reality of evolution. Compare with **speciation**.

variety: A subcategory, often informal or semiformal, for subdividing a species based on variation within that species. The terms "variety" and "subspecies" have been used in different ways at different points in time and have fallen substantially out of use in modern evolutionary biology. See **species**.

viroid: An entity that consists of just a small genome circle of RNA that is capable of reproducing by infecting plants; even simpler than a virus.

virulence: The extent to which a microorganism negatively affects the health of its host. See also **evolutionary arms race**.

Bibliography

Some of the best writing in all of science has been devoted to evolution, a tradition dating back to the excellent example set by Charles Darwin. A nearly complete compendium of Darwin's published work as well as many of the letters he wrote to colleagues, friends, and family members can be found on the Darwin Online website: http://darwin-online.org.uk/.

Darwin's best-known, and most important, publications are the 2 books that together outline his theory of evolution:

Darwin, Charles. *The Origin of Species*. 150th anniversary ed. New York: Signet Classics, 2003.

Darwin, Charles. *The Descent of Man, and Selection in Relation to Sex*. Princeton, NJ: Princeton University Press, 1981.

There are many wonderful Darwin biographies. These are 2 of the most approachable for the nonspecialist:

Browne, Janet. *Darwin's* Origin of Species. New York: Atlantic Monthly Press, 2007.

Quammen, David. *The Reluctant Mr. Darwin*. New York: W. W. Norton, 2006.

There is an extensive literature on the modern science of evolution. Here are a few that are especially recommended as an overview of the field:

National Geographic, February 2009. https://www.nationalgeographic.com/magazine/2009/02/.

Quammen, David. *The Tangled Tree: A Radical New History of Life*. New York: HarperCollins, 2018.

University of California, Berkeley. Understanding Evolution. https://evolution.berkeley.edu/evolibrary/home.php.

Zimmer, Carl. *Evolution: The Triumph of an Idea*. New York: HarperCollins, 2001.

Intended primarily for students enrolled in a college-level course on evolution, the following textbooks provide a more detailed overview of evolutionary biology and are richly illustrated:

Futuyma, Doug, and Mark Kirkpatrick. *Evolution*. 4th ed. Sunderland, MA: Sinauer Associates, 2017.

Zimmer, Carl, and Douglas Emlen. *Evolution: Making Sense of Life*. New York: W. H. Freeman, 2013.

These are 2 books that do a great job of summarizing the extensive evidence in support of the modern theory of evolution:

Coyne, Jerry. *Why Evolution Is True*. New York: Viking, 2009.

Dawkins, Richard. *The Greatest Show on Earth: The Evidence for Evolution*. New York: Free Press, 2009.

Genetics and evolution have been deeply intertwined since the early 20th century. The following titles provide an excellent and approachable overview of genetics:

Mukherjee, Siddhartha. *The Gene: An Intimate History*. New York: Simon & Schuster, 2017.

National Human Genome Research Institute. "All about the Human Genome Project (HGP)." https://www.genome.gov/10001772/all-about-the--human-genome-project-hgp/.

Zimmer, Carl. *She Has Her Mother's Laugh: The Powers, Perversions, and Potential of Heredity*. New York: Penguin, 2018.

Darwin was an avid reader, beginning during his journey aboard the *Beagle*. Almost half a century later, he wrote in his *Autobiography*, "To my mind there are no advantages and many disadvantages in lectures compared with reading."

Agrawal, Anurag. *Monarchs and Milkweed: A Migrating Butterfly, a Poisonous Plant, and Their Remarkable Story of Coevolution*. Princeton, NJ: Princeton University Press, 2017. A well-illustrated introduction to a great example of coevolution between a plant and an insect.

Alvarez, Walter. T. rex *and the Crater of Doom*. Princeton, NJ: Princeton University Press, 1997. An overview of the quest to understand what caused the extinction of the dinosaurs 65 million years ago, written by one of the scientists involved in the quest.

Arts & Humanities Research Council. Darwin Online. http://darwin-online.org.uk/. This website provides a thorough online compendium of Darwin's life and work, which also includes letters and more; includes complete text for all editions of *On the Origin of Species* and other works.

Blaser, Martin J. *Missing Microbes: How the Overuse of Antibiotics Is Fueling Our Modern Plagues*. New York: Henry Holt, 2014. In this book, which should be a must-read for everyone, a leading biomedical researcher makes a compelling case that our overuse use of antibiotics is having many negative consequences for health and well-being, including being responsible for the rise in conditions from obesity to allergies and more.

Browne, Janet. *Darwin's* Origin of Species. New York: Atlantic Monthly Press, 2007. Browne has written extensively about Darwin, including a 2-volume biography, but this book provides an approachable overview of Darwin's life, how he developed his theory of evolution, and the impact of its publication.

Carroll, Sean M. *Into the Jungle: Great Adventures in the Search for Evolution*. New York: Pearson, 2008. A brief, easily approachable collection of stories about 19th- and 20th-century expeditions that led to key insights in the modern science of evolution.

Comfort, Nathaniel. *The Science of Human Perfection: How Genes Became the Heart of American Medicine*. New Haven, CT: Yale University Press, 2012. A science historian traces the history of genetics and eugenics and the legacy of eugenics in modern medicine.

Costa, James T. *Darwin's Backyard: How Small Experiments Led to a Big Theory*. New York: W. W. Norton, 2017. This fun book describes the many experiments that Darwin conducted at his home, Down House. In addition to showing how these experiments helped him develop and support his theory of evolution by natural selection, the book includes instructions for how to conduct similar experiments in your own home.

Coyne, Jerry. *Why Evolution Is True*. New York: Viking, 2009. This book, by a leading evolutionary biologist, compiles the evidence available in support of the modern theory of evolution, including the evidence from the imperfect designs of the bodies of humans and other species.

Coyne, Jerry, and Allen Orr. *Speciation*. Oxford: Oxford University Press, 2004. A detailed overview of the studies on the evolutionary process that gives rise to new species; intended primarily for students and researchers in evolutionary biology.

Darwin, Charles. *The Expression of the Emotions in Man and Animals*. London: John Murray, 1872. Darwin applies his theory of evolution to understand human behavior, laying the foundation for the modern discipline of evolutionary psychology. Available free online http://darwin-online.org.uk/content/frameset?itemID=F1142&viewtype=text&pageseq=1 or consider the corrected edition from Oxford University Press (2009), edited by psychologist Paul Ekman.

———. *The Origin of Species*. 150th anniversary ed. New York: Signet Classics, 2003. By far the most famous of Darwin's publications, this is where he explained his theory in detail and offered evidence to support it. This edition includes an introduction by Julian Huxley, one of the architects of the modern synthesis that combined Darwin's ideas with the emerging science of genetics in the 20th century to lay the foundation for the modern science of evolution.

Dawkins, Richard. *The Blind Watchmaker: Why the Evidence of Evolution Reveals a Universe without Design*. New York: W. W. Norton, 1986. One of the staunchest defenders of evolutionary biology makes a compelling case against William Paley's argument, which had impressed Darwin, that the complexity of the human body suggests it was designed by a creator.

Doudna, Jennifer A., and Samuel H. Sternberg. *A Crack in Creation: Gene Editing and the Unthinkable Power to Control Evolution*. Boston: Houghton Mifflin Harcourt, 2017. Cowritten by one of the pioneers of the gene editing tool CRISPR, this book describes the discovery of this new technology and explores the ways in which it may be used to take evolution into our own hands.

Dugatkin, L. E., and L. Trut. *How to Tame a Fox (And Build a Dog): Visionary Scientists and a Siberian Tale of Jump-Started Evolution*. Chicago: University of Chicago Press, 2017. A narrative account of a fascinating experiment on the domestication of foxes reveals how quickly artificial selection can operate—and how it can lead to unintended consequences.

Dunn, Rob. *Every Living Thing: Man's Obsessive Quest to Catalog Life, from Nanobacteria to New Monkeys*. New York: HarperCollins, 2009. An ant biologist and science writer recounts the history of humanity's efforts to document, classify, and categorize living things.

———. *The Wild Life of Our Bodies: Predators, Parasites, and Partners That Shape Who We Are Today*. New York: Harper, 2011. A narrative account of the organisms that live in and on our bodies, written by a biologist and science writer.

Emlen, Douglas. *Animal Weapons: The Evolution of Battle*. New York: Macmillan, 2014. This book is an accessible overview of one aspect of sexual selection—namely, how competition for access to mates can lead to the evolution of weapons like antlers and horns.

Futuyma, Doug, and Mark Kirkpatrick. *Evolution*. 4th ed. Sunderland, MA: Sinauer Associates, 2017. The authoritative textbook on evolutionary biology used in college courses around the world; intended primarily for students and researchers.

Gibbons, Ann. *The First Human: The Race to Discover Our Earliest Ancestors*. New York: Doubleday, 2006. This book provides a great overview of the history and personalities in the field of paleoanthropology.

Gould, Stephen Jay. *The Panda's Thumb: More Reflections in Natural History*. New York: W. W. Norton, 1980. A collection of essays by the prolific paleontologist and writer, each of which provides insight into the evidence for evolution, such as how the false thumbs of giant pandas and red pandas demonstrate that evolution works more like a tinkerer than an engineer.

———. *Wonderful Life: The Burgess Shale and the Nature of History*. New York: W. W. Norton, 1990. Gould's classic about the Cambrian explosion in which he makes the argument that the history of life is dependent on contingency, arguing that if we could "replay the tape of life," evolution would have proceeded very differently if certain key events had happened differently.

Grant, Peter R., and B. Rosemary Grant. *40 Years of Evolution: Darwin's Finches on Daphne Major Island*. Princeton, NJ: Princeton University Press, 2014. A retrospective, first-person account of the life's work of 2 great evolutionary biologists who have spent their careers studying finches in the Galapagos Islands. The Grants' work on Galapagos finches is one of the best examples of how natural selection operates in the wild.

———. *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton, NJ: Princeton University Press, 2011. The Grants apply what they have learned in their lifelong study of Galapagos finches to the general question that Darwin attempted to answer: What drives the evolution of new species?

Hölldobler, Bert, and E. O. Wilson. *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*. New York: W. W. Norton, 2008. A masterful overview of the biology of social insects by 2 of the world's leading authorities on the topic.

Jobling, Mark A., Ed Hollox, Matthew Hurles, Toomas Kivisild, and Chris Tyler-Smith. *Human Evolutionary Genetics*. 2nd ed. New York: Garland Science, 2014. This textbook provides a detailed introduction of the study of human genetics and its application to the study of human evolution, including the methods used by researchers to detect gene flow from DNA sequence data; intended primarily for students and researchers in the fields of genetics and evolutionary biology.

Kaku, Michio. *The Future of Humanity: Terraforming Mars, Interstellar Travel, Immortality, and Our Destiny beyond Earth*. New York: Doubleday, 2018. A physicist considers how leaving Earth will affect humans many generations in the future.

Kolbert, Elizabeth. "There's No Scientific Basis for Race—It's a Made-Up Label." *National Geographic*, April 2018. https://www.nationalgeographic.com/magazine/2018/04/race-genetics-science-africa/. A Pulitzer Prize–winning author reviews what genome data reveals about human history. Key insights include how genetic information can be used to trace a person's genealogy and that human populations grouped by DNA do not correspond to traditional racial categories.

———. *The Sixth Extinction: An Unnatural History*. New York: Henry Holt, 2014. This Pulitzer Prize–winning book provides a readable overview of the history of mass extinctions and makes the case that we are on the verge of another such event—this time caused by humans.

Lents, Nathan H. *Human Errors: A Panorama of Our Glitches, from Pointless Bones to Broken Genes*. Boston: Houghton Mifflin Harcourt, 2018. An overview of the many ways in which the human body seems imperfectly designed but which make sense in the context of our evolutionary history.

Lieberman, Daniel E. *The Story of the Human Body: Evolution, Health, and Disease*. New York: Pantheon, 2013. A Harvard biologist describes how our evolutionary history can be seen in our bodies, including his theory that bipedalism evolved as an adaptation to chase down prey and how many modern disorders can be understood as a mismatch between the environments of our ancestors and our modern environments.

Losos, J. B. *Improbable Destinies: Fate, Chance, and the Future of Evolution*. New York: Riverhead Books, 2017. Is evolution predictable? Maybe it's more predictable than we used to suspect. A leading evolutionary biologist provides a very readable tour through many examples of observations and experiments showing the widespread relevance of convergent evolution and the (partial) repeatability of evolution.

Marshall, Michael. “Evolution by Shake, Rattle and Roll.” *New Scientist*, November 10, 2010. https://www.newscientist.com/article/mg20827864-000-human-evolution-was-shaped-by-plate-tectonics/. This article provides an overview of research suggesting the intriguing idea that human evolution may have been driven in part by geologically active areas prone to earthquakes and volcanic eruptions.

McCarthy, Dennis. *Here Be Dragons: How the Study of Animal and Plant Distributions Revolutionized Our Views of Life and Earth*. Oxford: Oxford, 2011. A fun, accessible overview of the history of biogeography—the science that links geography to biology and evolution.

Morris, Simon Conway. *Life’s Solution: Inevitable Humans in a Lonely Universe*. Cambridge: Cambridge University Press, 2004. In this book, the author rebuts Stephen Jay Gould’s argument that evolutionary history is heavily influenced by contingencies by offering many examples of convergent evolution.

———. *The Crucible of Creation: The Burgess Shale and the Rise of Animals*. Oxford: Oxford University Press, 1998. Written as a response and critique of Stephen Jay Gould’s *Wonderful Life*, Conway Morris—who was a key figure in *Wonderful Life*—argues for a different interpretation of the fossils from the Cambrian explosion with implications for the history of life on Earth.

Mukherjee, Siddhartha. *The Gene: An Intimate History*. New York: Simon & Schuster, 2017. This book provides a wonderful history of genetics that reads more like a novel than a textbook. The author interweaves the personal lives of key scientists—from Darwin and his contemporaries to 21st-century genomics researchers—with personal anecdotes to make this a very readable overview of what we know about genetics and why it matters for our everyday lives.

National Human Genome Research Institute. "An Overview of the Human Genome Project." https://www.genome.gov/12011238/an-overview-of-the-human-genome-project/. Provides a brief, accessible overview of the US government's massive effort to sequence the first human genome; includes some basic information about some of the techniques used in this effort, such as PCR and DNA sequencing.

National Institutes of Health. Genetics Home Reference. https://ghr.nlm.nih.gov/. Provides an overview of basic information about genetics and genomics as well as information about genetic disorders and health conditions.

Quammen, David. *Spillover: Animal Infections and the Next Human Pandemic*. New York: W. W. Norton, 2012. The author traces the history and evolution of infectious diseases like HIV and Ebola that switched from infecting animal hosts to infecting humans.

———. *The Reluctant Mr. Darwin*. New York: W. W. Norton, 2006. A brief, readable biography of Darwin, focused on his life after returning to England from his voyage on the *Beagle*. The author focuses on why it took Darwin more than 20 years to publish his revolutionary theory of evolution by natural selection.

———. *The Song of the Dodo: Island Biogeography in an Age of Extinction*. New York: Scribner, 1996. The author masterfully ties together science, biography, and adventure travel writing to describe how field biologists are using information about how geography influences ecology and evolution to understand the modern extinction crisis.

———. *The Tangled Tree: A Radical New History of Life*. New York: HarperCollins, 2018. In his characteristic blend of biography, science history, and travelogue, the author tells the story of how our understanding of the evolutionary relationships among living things has itself evolved. A major theme is the story of how the discovery of archaea transformed our understanding of the evolution of life on Earth.

———. "When Life Got Complicated." *National Geographic*, March 2018. https://www.nationalgeographic.com/magazine/2018/03/brief-history-life-evolution-fossils-biology/. A visually rich overview of the fossils from the Cambrian explosion and the controversy over their interpretation.

Raby, Peter. *Alfred Russel Wallace: A Life*. Princeton, NJ: Princeton University Press, 2001. Engaging biography of the explorer and naturalist who independently discovered the theory of evolution that Darwin called natural selection.

Reich, David. *Who We Are and How We Got Here: Ancient DNA and the New Science of the Human Past*. New York: Pantheon, 2018. Written by one of the leaders in research on using DNA extracted from ancient human remains to reconstruct human history, this accessible book highlights the importance of migrations and gene flow in the past as well as today.

Richerson, Peter J., and Robert Boyd. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press, 2006. An accessible overview of the many ways in which human culture has contributed to our biological evolution.

Rico-Gray, Victor, and Paulo S. Oliveira. *The Ecology and Evolution of Ant-Plant Interactions*. Chicago: University of Chicago Press, 2007. Written primarily for students and researchers, this book provides a detailed overview of the many complex ways in which ants and plants have coevolved.

Rose, Michael R. *Evolutionary Biology of Aging*. Oxford: Oxford University Press, 1994. Pioneering but also authoritative synthesis of the now-established field to understand aging in terms of evolution.

Ryan, Michael. *A Taste for the Beautiful: The Evolution of Attraction*. Princeton, NJ: Princeton University Press, 2018. This book nicely summarizes the other way that sexual selection causes evolution, brought about by female preferences in their mates.

Sapolsky, Robert M. *Behave: The Biology of Humans at Our Best and Our Worst*. New York: Penguin, 2018. A great guide to how far we have come in our understanding of the biological basis for why people behave the way they do.

Shostak, Stanley. *The Evolution of Death: Why We Are Living Longer*. New York: SUNY Press, 2006. A biologist's speculative look at demographic trends, death, and longevity through an engagement with ideas from the science of evolution.

Shreeve, James. *The Genome War: How Craig Venter Tried to Capture the Code of Life and Save the World*. New York: Ballantine Books, 2007. This account of the race between private industry and the US government to sequence the first human genome reads like a thriller.

Shubin, Neil. *Your Inner Fish: A Journey into the 3.5 Billion-Year History of the Human Body*. New York: Pantheon, 2008. The author's account of how we can understand the human body by comparing our anatomy to that of fish and other animals includes many examples of how our bodies only make sense in the light of their evolutionary origins.

Solomon, Scott. *Future Humans: Inside the Science of Our Continuing Evolution*. New Haven, CT: Yale University Press, 2016. Written by the presenter of this course, this book takes the reader on a journey around the world to see how we know that humans are continuing to evolve and explores the ways in which our evolution may continue in the future.

Stearns, Stephen C., and R. Medzhitov. *Evolutionary Medicine*. Sunderland, MA: Sinauer Associates, 2016. This slim textbook is intended primarily for college and medical students but is written in a clear, straightforward manner and includes enough background information to make it accessible to a broader audience interested in learning the basics about how evolution can inform the study and practice of medicine.

Stringer, Chris. *Lone Survivors: How We Came to Be the Only Humans on Earth*. New York: Times Books, 2012. Written by a leading paleoanthropologist, this book describes how we know that many types of hominins once existed and attempts to explain why only *Homo sapiens* survived.

Walter, Chip. *Thumbs, Toes, and Tears: And Other Traits That Make Us Human*. New York: Walker & Company, 2006. A popular book that is better and broader than its title, this book brings together connections from across the evolution of human anatomy and behavior, from walking to grasping, talking, and beyond.

Weiner, Jonathan. *The Beak of the Finch: A Story of Evolution in Our Time*. New York: Vintage, 1995. A narrative account of the study of Galapagos finches by Peter and Rosemary Grant, one of the best examples of natural selection in a natural population.

Willyard, Cassandra. "New Human Gene Tally Reignites Debate." *Nature*, June 19, 2018. https://www.nature.com/articles/d41586-018-05462-w?WT.ec_id=NATURE-20180621&utm_source=nature_etoc&utm_medium=email&utm_campaign=20180621&spMailingID=56851658&spUserID=MzUzMjkxMDY5MwS2&spJobID=1422975329&spReportId=MTQyMjk3NTMyOQS2. An overview of the debate among scientists about how many genes are in the human genome.

Wilson, E. O. *The Social Conquest of Earth*. New York: Liveright, 2012. Written by one of the foremost experts on ants and the evolution of sociality, this book argues that the evolution of social organization in animals and humans can explain why species with complex societies are so abundant.

Yong, Ed. "A New Origin Story for Dogs: The First Domesticated Animals May Have Been Tamed Twice." *The Atlantic*, June 2, 2016. https://www.theatlantic.com/science/archive/2016/06/the-origin-of-dogs/484976/. This article describes how research using DNA has been used to reconstruct dog evolution from wolves.

———. *I Contain Multitudes: The Microbes within Us and a Grander View of Life*. New York: Ecco, 2016. A science writer's masterful account of the microbiome of humans and other species and how understanding the interactions between hosts and microbes changes our understanding of how complex life works and how it evolved.

Zimmer, Carl. "Can a Parent's Life Experience Change the Genes a Child Inherits? Inside the Controversial World of Epigenetics Research." *The Atlantic*, June 21, 2018. https://www.theatlantic.com/science/archive/2018/06/mothers-laugh-excerpt/562478/. This excerpt from *She Has Her Mother's Laugh*, Zimmer's book on heredity, explores what researchers are beginning to learn about epigenetic inheritance, or heredity that is not encoded in the sequence of DNA that makes up a genome.

———. *She Has Her Mother's Laugh: The Powers, Perversions, and Potential of Heredity*. New York: Penguin, 2018. This history of heredity goes beyond genetics to consider how epigenetics and the possibility of gene editing may affect our species moving forward. This book is just as readable as Mukherjee's (*The Gene*) and includes a greater emphasis on how heredity relates to evolution.

Zuk, Marlene. *Paleofantasy: What Evolution Really Tells Us about Sex, Diet, and How We Live*. New York: W. W. Norton, 2013. A very readable overview of how evolutionary principles are often misunderstood when applied to our modern lives, including what we eat, what we wear, and how we raise our children.

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