

CHAPTER 22

DESCENT WITH MODIFICATION: A DARWINIAN VIEW OF LIFE

OUTLINE

- I. Historical-Context for Evolutionary Theory
 - A. Western culture resisted evolutionary views of life
 - B. Theories of geological gradualism helped clear the path for evolutionary biologists
 - C. Lamarck placed fossils in an evolutionary context
- II. The Darwinian Revolution
 - A. Field research helped Darwin frame his view of life: *science as a process*
 - B. *The Origin of Species* developed two main points: the occurrence of evolution and natural selection as its mechanism
- III. Evidence of Evolution
 - A. Evidence of evolution pervades biology
 - B. What is theoretical about the Darwinian view of life?

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. State the two major points Darwin made in *The Origin of Species* concerning the Earth's biota.
2. Compare and contrast Plato's philosophy of idealism and Aristotle's *scala naturae*.
3. Describe Carolus Linnaeus' contribution to Darwin's theory of evolution.
4. Describe Georges Cuvier's contribution to paleontology.
5. Explain how Cuvier and his followers used the concept of catastrophism to oppose evolution.
6. Explain how the principle of gradualism and Charles Lyell's theory of uniformitarianism influenced Darwin's ideas about evolution.
7. Describe Jean Baptiste Lamarck's model for how adaptations evolve.
8. Describe how Charles Darwin used his observations from the voyage of the HMS *Beagle* to formulate and support his theory of evolution.
9. Describe how Alfred Russel Wallace influenced Charles Darwin.
10. Explain what Darwin meant by the principle of common descent and "descent with modification".
11. Explain what evidence convinced Darwin that species change over time.
12. State, in their own words, three inferences Darwin made from his observations, which led him to propose natural selection as mechanism for evolutionary change.
13. Explain why variation was so important to Darwin's theory.
14. Explain how Reverend Thomas Malthus' essay influenced Charles Darwin.
15. Distinguish between artificial selection and natural selection.
16. Explain why the population is the smallest unit that can evolve.

17. Using some contemporary examples, explain how natural selection results in evolutionary change.
18. Explain why the emergence of population genetics was an important turning point for evolutionary theory.
19. Describe the lines of evidence Charles Darwin used to support the principle of common descent.
20. Describe how molecular biology can be used to study the evolutionary relationships among organisms.
21. Explain the problem with the statement that Darwinism is "just a theory".
22. Distinguish between the scientific and colloquial use of the word "theory".

KEY TERMS

evolution	fossils	descent with modification	vestigial organs
natural selection	sedimentary rocks	artificial selection	ontogeny
evolutionary adaptations	paleontology	biogeography	phylogeny
natural theology	gradualism	homology	
taxonomy	uniformitarianism	homologous-structures	

LECTURE NOTES

Evolution, the unifying theme woven throughout the text and course, refers to the processes that have transformed life on earth from its earliest forms to the enormous diversity that characterizes it today.

The first convincing case for evolution was published in a book by Charles Darwin on November 24, 1859. In this book, *On the Origin of Species by Means of Natural Selection*, Darwin:

- Synthesized seemingly unrelated facts into a conceptual framework that accounts for both the unity and diversity of life.
- Discussed important biological issues about organisms, such as why there are so many kinds of organisms, their origins and relationships, similarities and differences, geographic distribution, and adaptations to their environment.
- Made two major points:
 1. Species evolved from ancestral species and were not specially created.
 2. *Natural selection* is a mechanism that could result in this evolutionary change.

I. Historical Context for Evolutionary Theory

A. Western culture resisted evolutionary views of life

The impact of Darwin's ideas partially depended upon historical and social context (see Campbell, Figure 22.1).

- Darwin's view of life contrasted sharply with the accepted viewpoint: the Earth was only a few thousand years old and was populated by unchanging life forms made by the Creator during a single week.
- Thus, *On the Origin of Species by Means of Natural Selection* not only challenged prevailing scientific views, but also challenged the roots of Western culture.

1. The scale of nature and natural theology

Many Greek philosophers believed in the gradual evolution of life. However, the two that influenced Western culture most, Plato (427 – 347 B.C.) and his student Aristotle (384 – 322 B.C.), held opinions which were inconsistent with a concept of evolution.

- Plato, whose philosophy is known as *idealism (essentialism)*, believed that there were two coexisting worlds: an ideal, eternal, real world and an illusionary imperfect world that humans perceive with their senses. To Plato,
 - ⇒ Variations in plant and animal populations were merely imperfect representatives of ideal forms; only the perfect ideal forms were real.
 - ⇒ Evolution would be counterproductive in a world where ideal organisms were already perfectly adapted to their environments.
- Aristotle questioned the Platonic philosophy of dual worlds, but his beliefs also excluded evolution.
 - ⇒ Recognizing that organisms vary from simple to complex, he believed that they could be placed on a scale of increasing complexity (*scala naturae*); on this ladder of life, each form had its allotted rung and each rung was occupied.
 - ⇒ In this view of life, species were fixed and did not evolve.
 - ⇒ The *scala naturae* view of life prevailed for over 2000 years.

The *creationist–essentialist* dogma that species were individually created and fixed became embedded in Western thought as the Old Testament account of creation from the Judeo–Christian culture fortified prejudice against evolution.

- *Natural Theology*, a philosophy that the Creator's plan could be revealed by studying nature, dominated European and American biology even as Darwinism emerged.
- For natural theologians, adaptations of organisms were evidence that the Creator had designed every species for a particular purpose.
- Natural theology's major objective was to classify species revealing God's created steps on the ladder of life.

Carolus Linnaeus (1707 – 1778), a Swedish physician and botanist, sought order in the diversity of life *ad maiorem Dei gloriam* (for the greater glory of God).

- Known as the father of *taxonomy*—the naming and classifying of organisms—he developed the system of *binomial nomenclature* still used today.
- He adopted a system for grouping species into categories and ranking the categories into a hierarchy. For example, similar species are grouped into a genus; similar genera are grouped into the same order.

Linnaeus found order in the diversity of life with his hierarchy of taxonomic categories.

- The clustering of species in taxonomic groups did not imply evolutionary relationships to Linnaeus, since he believed that species were permanent creations.
- Linnaeus, a natural theologian, developed his classification scheme only to reveal God's plan and even stated *Deus creavit, Linnaeus disposuit* ("God creates, Linnaeus arranges").

2. Cuvier, fossils, and catastrophism

Fossils = Relics or impressions of organisms from the past preserved in rock

- Most fossils are found in *sedimentary rocks*, which:
 - ⇒ Form when new layers of sand and mud settle to the bottom of seas, lakes, and marshes, covering and compressing older layers into rock (e.g. sandstone and shale)
 - ⇒ May be deposited in many layers (*strata*) in places where shorelines repeatedly advance and retreat. Later erosion can wear away the upper (younger) strata, revealing older strata which had been buried.
- The fossil record thus provides evidence that Earth has had a succession of flora and fauna (see Campbell, Figure 22.2).

The study of fossils, *paleontology*, was founded by the French anatomist Georges Cuvier (1769-1832) who:

- Realized life's history was recorded in fossil-containing strata and documented the succession of fossil species in the Paris Basin
- Noted each stratum was characterized by a unique set of fossil species and that the older (deeper) the stratum, the more dissimilar the flora and fauna from modern life forms
- Understood that extinction had been a common occurrence in the history of life since, from stratum to stratum, new species appeared and others disappeared

Even with paleontological evidence, Cuvier was an effective opponent to the evolutionists of his day.

- He reconciled the fossil evidence with his belief in the fixity of species by speculating that boundaries between fossil strata corresponded in time to catastrophic events, such as floods or droughts.
- This view of Earth's history is known as *catastrophism*.

Catastrophism = Theory that major changes in the Earth's crust are the result of catastrophic events rather than from gradual processes of change

Cuvier explained the appearance of new species in younger rock that were absent from older rock by proposing that:

- Periodic localized catastrophes resulted in mass extinctions.
- After the local flora and fauna had become extinct, the region would be repopulated by foreign species immigrating from other areas.

B. Theories of geological gradualism helped clear the path for evolutionary biologists

In the late 18th century, a new theory of geological *gradualism* gained popularity among geologists that would greatly influence Darwin.

Gradualism = Principle that profound change is the cumulative product of slow, continuous processes

- Competed with Cuvier's theory of catastrophism
- Proposed by James Hutton (1785), a Scottish geologist. He proposed that it was possible to explain the various land forms by looking at mechanisms currently operating in the world.

Example: Canyons form by erosion from rivers, and fossil-bearing sedimentary rocks form from particles eroded from the land and carried by rivers to the sea.

Charles Lyell, a leading geologist of Darwin's time, expanded Hutton's gradualism into the theory known as uniformitarianism.

Uniformitarianism = Theory that geological processes are uniform and have operated from the origin of the Earth to the present

- It was Lyell's extreme idea that geological processes are so uniform that their rates and effects must balance out through time.
- Example: Processes that build mountains are eventually balanced by the erosion of mountains.

Darwin rejected uniformitarianism, but was greatly influenced by conclusions that followed directly from the observations of Hutton and Lyell:

- The Earth must be ancient. If geological change results from slow, gradual processes rather than sudden events, then the Earth must be much older than the 6000 years indicated by many theologians on the basis of biblical inference.
- Very slow and subtle processes persisting over a great length of time can cause substantial change.

C. Lamarck placed fossils in an evolutionary context

Several 18th century naturalists suggested that life had evolved along with Earth's changes. Only Jean Baptiste Lamarck (1744-1829) developed and published (1809) a comprehensive model which attempted to explain how life evolved.

Lamarck was in charge of the invertebrate collection at the Natural History Museum in Paris, which allowed him to:

- Compare modern species to fossil forms, and in the process, identify several lines of descent composed of a chronological series of older fossils to younger fossils to modern species.
- Envision many ladders of life which organisms could climb (as opposed to Aristotle's single ladder without movement).
 - ⇒ The bottom rungs were occupied by microscopic organisms which were continually generated spontaneously from nonliving material.
 - ⇒ At the tops of the ladders were the most complex plants and animals.

Lamarck believed that evolution was driven by an innate tendency toward increasing complexity, which he equated with perfection.

- As organisms attained perfection, they became better and better adapted to their environments.
- Thus, Lamarck believed that evolution responded to organisms' *sentiments interieurs* ("felt needs").

Lamarck proposed a mechanism by which specific adaptations evolve, which included two related principles:

1. *Use and disuse*. Those body organs used extensively to cope with the environment become larger and stronger while those not used deteriorate.
2. *Inheritance of acquired characteristics*. The modifications an organism acquired during its lifetime could be passed along to its offspring.

Although his mechanism of evolution was in error, Lamarck deserves credit for proposing that:

- Evolution is the best explanation for both the fossil record and the extant diversity of life.
- The Earth is ancient.

- Adaptation to the environment is a primary product of evolution.

II. The Darwinian Revolution

At the beginning of the 19th century, natural theology still dominated the European and American intellectual climate. In 1809, the same year Lamarck published his theory of evolution, Charles Darwin was born in Shrewsbury, England.

- Though interested in nature, Charles (at 16) was sent by his physician father to the University of Edinburgh to study medicine, which he found boring and distasteful.
- He left Edinburgh without a degree and enrolled at Christ College, Cambridge University to prepare for the clergy.
 - ⇒ Nearly all naturalists and other scientists were clergymen, and a majority held to the philosophy of natural theology.
 - ⇒ Charles studied under the Reverend John Henslow, a botany professor at Cambridge, and received his B.A. degree in 1831.
 - ⇒ Professor Henslow recommended him to Captain Robert FitzRoy who was preparing the survey ship HMS *Beagle* for an around the world voyage.

A. Field research helped Darwin frame his view of life: *science as a process*

1. The voyage of the *Beagle*

The HMS *Beagle*, with Darwin aboard, sailed from England in December 1831 (see Campbell Figure 22.3).

- The voyage's mission was to chart the poorly known South American coastline.
- While the ship's crew surveyed the coast, Darwin spent most of his time ashore collecting specimens of the exotic and diverse flora and fauna.

While the ship worked its way around the continent, Darwin observed the various adaptations of plants and animals that inhabited the diverse environments of South America: Brazilian jungles, grasslands of the Argentine pampas, desolate islands of Tierra del Fuego, and the Andes Mountains. Darwin noted the following:

- The South American flora and fauna from different regions were distinct from the flora and fauna of Europe.
- Temperate species were taxonomically closer to species living in tropical regions of South America than to temperate species of Europe.
- The South American fossils he found (while differing from modern species) were distinctly South American in their resemblance to the living plants and animals of that continent.

Geographical distribution was particularly confusing in the case of the fauna of the Galapagos, recently formed volcanic islands which lie on the equator about 900 km west of South America.

- Most animal species on the Galapagos are unique to those islands, but resemble species living on the South American mainland.
- Darwin collected 13 types of finches from the Galapagos, and although they were similar, they seemed to be different species.
 - ⇒ Some were unique to individual islands
 - ⇒ Others were found on two or more islands that were close together

By the time the *Beagle* left the Galapagos, Darwin had read Lyell's *Principles of Geology*, and was influenced by Lyell's ideas.

- Darwin had begun to doubt the church's position that the Earth was static and had been created only a few thousand years before.
- When Darwin acknowledged that the Earth was ancient and constantly changing, he had taken an important step toward recognizing that life on Earth had also evolved.

2. Darwin focuses on adaptation

Darwin was not sure whether the 13 types of finches he collected on the Galapagos were different species or varieties of the same species.

- After he returned to England in 1836, an ornithologist indicated that they were actually different species.
- He reassessed observations made during the voyage and in 1837 began the first notebook on the origin of species.

Darwin perceived the origin of new species and adaptation as closely related processes; new species could arise from an ancestral population by gradually accumulating adaptations to a different environment. For example,

- Two populations of a species could be isolated in different environments and diverge as each adapted to local conditions.
- Over many generations, the two populations could become dissimilar enough to be designated separate species.
- This is apparently what happened to the Galapagos finches; their different beaks are adaptations to specific foods available on their home islands. (See Campbell, Figure 22.4)

By the early 1840s, Darwin had formed his theory of natural selection as the mechanism of adaptive evolution, but delayed publishing it.

- Reclusive and in poor health, Darwin was well known as a naturalist from the specimens and letters he had sent to Britain from the voyage on the *Beagle*.
- He frequently corresponded and met with Lyell, Henslow, and other scientists.

In 1844, Darwin wrote a long essay on the origin of species and natural selection.

- He realized the importance and subversive nature of his work, but did not publish the information because he wished to gather more evidence in support of his theory.
- Evolutionary thinking was emerging at this time, and Lyell admonished Darwin to publish on the subject before someone else published it first.

In June 1858, Darwin received a letter from Alfred Wallace, who was working as a specimen collector in the East Indies.

- Accompanying the letter was a manuscript detailing Wallace's own theory of natural selection which was almost identical to Darwin's.
- The letter asked Darwin to evaluate the theory and forward the manuscript to Lyell if it was thought worthy of publication.
- Darwin did so, although he felt that his own originality would be "smashed."
- Lyell and a colleague presented Wallace's paper along with excerpts from Darwin's unpublished 1844 essay to the Linnaean Society of London on July 1, 1858.

Darwin finished *The Origin of Species* and published it the next year.

- Darwin is considered the main author of the idea since he developed and supported natural selection much more extensively than Wallace.
- Darwin's book and its proponents quickly convinced the majority of biologists that biodiversity is a product of evolution.
- Darwin succeeded where previous evolutionists had failed not only because science was moving away from natural theology, but because he convinced his readers with logic and evidence.

B. *The Origin of Species* developed two main points: the occurrence of evolution and natural selection as its mechanism

1. Descent with modification

Darwin used the phrase "descent with modification," not evolution, in the first edition of *The Origin of Species*.

- He perceived a unity in life with all organisms related through descent from some unknown ancestral population that lived in the remote past.
- Diverse modifications (*adaptations*) accumulated over millions of years, as descendants from this common ancestor moved into various habitats.

Darwin's metaphor for the history of life was a branching tree with multiple branching from a common trunk to the tips of living twigs, symbolic of the diversity of contemporary organisms.

- At each fork or branch point is an ancestral population common to all evolutionary lines of descent branching from that fork.
- Species that are very similar share a common ancestor at a recent branch point on the phylogenetic tree.
- Less closely related organisms share a more ancient common ancestor at an earlier branch point.
- Most branches of evolution are dead ends since about 99% of all species that ever lived are extinct.

To Darwin, Linnaeus' taxonomic scheme reflected the branching genealogy of the tree of life.

- It recognized that the diversity of organisms could be ordered into "groups subordinate to groups", with organisms at the different taxonomic levels related through descent from common ancestors.
- Classification alone does not confirm the principle of common descent, but when combined with other lines of evidence, the relationships are clear.
- For example, genetic analysis of species that are thought to be closely related on the basis of anatomical features and other criteria reveals a common hereditary background.

2. Natural selection and adaptation

Darwin's book focused on the role of natural selection in adaptation (see Campbell, Figure 22.5). Ernst Mayr of Harvard University dissected the logic of Darwin's theory into three inferences based on five observations:

- *Observation 1:* All species have such great potential fertility that their population size would increase exponentially if all individuals that are born reproduced successfully.
- *Observation 2:* Populations tend to remain stable in size, except for seasonal fluctuations.

- *Observation 3:* Environmental resources are limited.
 - ***Inference 1:*** Production of more individuals than the environment can support leads to a struggle for existence among individuals of a population, with only a fraction of offspring surviving each generation.
- *Observation 4:* Individuals of a population vary extensively in their characteristics; no two individuals are exactly alike.
- *Observation 5:* Much of this variation is heritable.
 - ***Inference 2:*** Survival in the struggle for existence is not random, but depends in part on the hereditary constitution of the surviving individuals. Those individuals whose inherited characteristics fit them best to their environment are likely to leave more offspring than less fit individuals.
 - ***Inference 3:*** This unequal ability of individuals to survive and reproduce will lead to a gradual change in a population, with favorable characteristics accumulating over the generations.

Summarizing Darwin's ideas:

- Natural selection is this differential success in reproduction, and its product is adaptation of organisms to their environment.
- Natural selection occurs from the interaction between the environment and the inherent variability in a population.
- Variations in a population arise by chance, but natural selection is not a chance phenomenon, since environmental factors set definite criteria for reproductive success.

Darwin was already aware of the struggle for existence caused by overproduction, when he read an essay on human population written by the Reverend Thomas Malthus (1798).

- In this essay, Malthus held that much of human suffering was a consequence of human populations growing faster than the food supply.
- This capacity for overproduction is common to all species, and only a fraction of new individuals complete development and leave offspring of their own; the rest die or are unable to reproduce.

Variation and overproduction in populations make natural selection possible.

- On the average, the most fit individuals pass their genes on to more offspring than less fit individuals.
- This results from environmental editing, which favors some variations over others.

From his experiences with *artificial selection*, Darwin inferred that natural selection could cause substantial change in populations.

- Through the breeding of domesticated plants and animals, humans have modified species over many generations by selecting individuals with desired traits as breeding stock.
- The plants and animals we grow for food show little resemblance to their wild ancestors (see Campbell, Figure 22.6).
- Darwin reasoned that if such change could be achieved by artificial selection in a relatively short period of time, then natural selection should be capable of considerable modifications of species over hundreds of thousands of generations.

- Even if the advantages of some heritable traits over others are slight, they will accumulate in the population after many generations of natural selection eliminating less favorable variations.

Gradualism is fundamental to the Darwinian view of evolution. Darwin reasoned that:

- Life did not evolve suddenly by quantum leaps, but instead by a gradual accumulation of small changes.
- Natural selection operating in differing contexts over vast spans of time could account for the diversity of life.

Summarizing Darwin's view of evolution:

- The diverse forms of life have arisen by descent with modification from ancestral species.
- The mechanism of modification has been natural selection working gradually over long periods of time.

a. Some subtleties of natural selection

Populations are important in evolutionary theory, since a population is the smallest unit that can evolve.

Population = A group of interbreeding individuals belonging to a particular species and sharing a common geographic area

Natural selection is a consequence of interactions between individual organisms and their environment, but individuals do not evolve.

- Evolution can only be measured as change in relative proportions of variations in a population over several generations.
- Natural selection can only amplify or diminish heritable variations.
- Organisms can adapt to changes in their immediate environment and can be otherwise modified by life experiences, but these acquired characteristics cannot be inherited.
- Evolutionists must distinguish between adaptations an organism acquires during its lifetime and those inherited adaptations that evolve in a population over many generations as a result of natural selection.

Specifics of natural selection are situational.

- Environmental factors vary from area to area and from time to time.
- An adaptation under one set of conditions may be useless or detrimental in different circumstances.

b. Examples of natural selection in action

In an effort to test Darwin's hypothesis that the beaks of Galapagos finches are evolutionary adaptations to different food sources, Peter and Rosemary Grant of Princeton University have been conducting a long-term study on medium ground finches (*Geospiza fortis*) on Daphne Major, a tiny Galapagos island.

They have discovered that:

- Average beak depth (an inherited trait) oscillates with rainfall (see Campbell, Figure 22.7).
 - ⇒ In wet years, birds preferentially feed on small seeds, and average beak depth decreases.
 - ⇒ In dry years, small seeds are less plentiful, so survival depends on the finches being able to crack the less preferred larger seeds. Average beak depth increases during dry years.

- It can be inferred that the change in beak depth is an adaptive response to the relative availability of small seeds from year to year.

This study illustrates some important points about adaptive change:

- *Natural selection is situational.* What works in one environmental context may not work in another.
- *Beak evolution on Daphne Major does not result from inheritance of acquired characteristics.* The environment did not *create* beaks specialized for large or small seeds, but only acted on inherited variations already present in the population. The proportion of thicker-beaked finches increased during dry periods because, on average, thicker-beaked birds transmitted their genes to more offspring than did thinner-beaked birds.

Michael Singer and Camille Parmesan of the University of Texas, have documented rapid evolutionary adaptation in a butterfly population (Edith's checkerspot) living in a meadow near Carson City, Nevada.

- In only a decade, this butterfly population apparently adapted to changing vegetation by inherited changes in reproductive behavior.
- Females lay eggs preferentially on certain plants which provide food for the larvae after they hatch. In 1983, checkerspots laid about 80% of their eggs on a native plant, *Collinsia parviflora*.
- By 1993, the butterflies were laying about 70% of their eggs on *Plantago lanceolata*, an invading weed from surrounding cattle ranches.
- The researchers demonstrated that the switch in plant preference is genetic; daughters of butterflies that deposited eggs on *Plantago* inherited the taste for that plant, choosing it over *Collinsia* when they laid their eggs.

There are hundreds of examples of natural selection in laboratory populations of such organisms as *Drosophila*. Other examples of natural selection in action include:

- Antibiotic resistance in bacteria (see Campbell, Chapter 18)
- Body size of guppies exposed to different predators (see Campbell, Chapter 1)

III. Evidence of Evolution

A. Evidence of evolution pervades biology

Darwin used several lines of evidence to support his principle of common descent, an evolutionary change. Recent discoveries, including those from molecular biology, lend support to his evolutionary view of life.

1. Biogeography

It was biogeographical evidence that first suggested common descent to Darwin, because the biogeographical patterns he observed only made sense in the light of evolution.

Biogeography = The geographical distribution of species

Islands have many endemic species which are closely related to species on the nearest mainland or neighboring island. Some logical questions follow:

- Why are two islands with similar environments in different parts of the world not populated by closely related species, but rather by species more closely related to those from the nearest mainland even when that environment is quite different?
- Why are South American tropical animals more closely related to South American desert animals than to African tropical animals?
- Why does Australia have such a diversity of marsupial animals and very few placental animals even though the environment can easily support placentals?

2. The fossil record

Darwin was troubled by the absence of transitional fossils linking modern life to ancestral forms.

- Even though the fossil record is still incomplete, paleontologists continue to find important new fossils, and many key links are no longer missing.
- For example, fossilized whales link these aquatic mammals to their terrestrial predecessors (see Campbell, Figure 22.8).

Although still incomplete, the fossil record provides information that supports other types of evidence about the major branches of the phylogenetic tree. For example:

- Prokaryotes are placed as the ancestors of all life by evidence from cell biology, biochemistry, and molecular biology.
- Fossil evidence shows the chronological appearance of the vertebrates as being sequential with fishes first, followed by amphibians, reptiles and then birds and mammals. This sequence is also supported by many other types of evidence.

3. Comparative anatomy

Anatomical similarities among species grouped in the same taxonomic category are a reflection of their common descent.

- The skeletal components of mammalian forelimbs are a good example (see Campbell, Figure 22.9)
 - ⇒ Although the limbs are used for different functions, it is obvious that the same skeletal elements are present.
 - ⇒ It is logical that whether the forelimb is a foreleg, wing, flipper, or arm, the basic similarity is the consequence of descent from a common ancestor and that the limbs have been modified for different functions. They are homologous structures.

Homologous structures = Structures that are similar because of common ancestry

- Other evidence from comparative anatomy supports that evolution is a remodeling process in which ancestral structures that functioned in one capacity have become modified as they take on new functions.
- Some homologous structures are *vestigial organs*.

Vestigial organs = Rudimentary structures of marginal or no use to an organism

- Vestigial organs are remnants of structures that had important functions in ancestral forms but are no longer essential.
- Example: The remnants of pelvic and leg bones in snakes show descent from a walking ancestor, but have no function in the snake.

- Because it would be wasteful to continue providing blood, nutrients, and space to structures that no longer have a major function, vestigial organs serve evidence of evolution by natural selection.

4. Comparative embryology

Closely related organisms go through similar stages in their embryonic development.

- Vertebrate embryos (fishes, amphibians, reptiles, birds, mammals) go through an embryonic stage in which they possess gill slits on the sides of their throats (see Campbell, Figure 22.10).
- As development progresses, the gill slits develop into divergent structures characteristic of each vertebrate class.
- In fish, the gill slits form gills; in humans, they form the eustachian tubes that connect the middle ear with the throat.

Comparative embryology often establishes homology among structures, such as gill pouches, that become so altered in later development that their common origin is not apparent by comparing their fully developed forms.

In the late nineteenth century, embryologists developed the view that "ontogeny recapitulates phylogeny."

- This view held that the embryonic development of an individual organism (*ontogeny*) is a replay of the evolutionary history of the species (*phylogeny*).
- This is an extreme view; what does occur is a series of similar *embryonic* stages that exhibit the same characteristics, not a sequence of adult-like stages.
- Ontogeny can provide clues to phylogeny, but all stages of development may become modified over the course of evolution.

5. Molecular biology

An organism's hereditary background is reflected in its genes and their protein products.

- Siblings have greater similarity in their DNA and proteins than do two unrelated organisms of the same species.
- Likewise, two species considered to be closely related by other criteria should have a greater proportion of their DNA and proteins in common than more distantly related species.

Molecular taxonomists use a variety of modern techniques to measure the degree of similarity among DNA nucleotide sequences of different species.

- The closer two species are taxonomically, the higher the percentage of common DNA; this evidence supports common descent.
- Common descent is also supported by the fact that closely related species also have proteins of similar amino acid sequence (resulting from inherited genes).
- If two species have many genes and proteins with sequences of monomers that match closely, the sequences must have been copied from a common ancestor.

Molecular biology has also substantiated Darwin's idea that all forms of life are related to some extent through branching descent from the earliest organisms (see Campbell, Figure 22.11).

- Even taxonomically distant organisms (bacteria and mammals) have some proteins in common.
- For example, cytochrome *c* (a respiratory protein) is found in all aerobic species. Cytochrome *c* molecules of all species are very similar in structure and function, even though mutations have substituted amino acids in some areas of the protein during the course of evolution.
- Additional evidence for the unity of life is the common genetic code. This mechanism has been passed through all branches of evolution since its beginning in an early form of life.

B. What is theoretical about the Darwinian view of life?

Dismissing Darwinism as "just a theory" is flawed because:

- Darwin made *two* claims:
 1. Modern species evolved from ancestral forms.
 2. The mechanism for evolution is natural selection.
- The conclusion that species change or evolve is based on historical fact.

What, then, is theoretical about evolution?

- Theories are conceptual frameworks with great explanatory power used to interpret facts.
- That species can evolve is fact, but the *mechanism* Darwin proposed for that change—natural selection—is a theory. Darwin used this theory of natural selection to explain facts of evolution documented by fossils, biogeography, and other historical evidence.

In science, "theory" is very different from the colloquial use of the word, which comes closer to what scientists mean by a hypothesis, or educated guess.

- Unifying concepts do not become scientific theories, unless their predictions stand up to thorough and continuous testing by experiment and observation.
- Good scientists, however, do not allow theories to become dogma; many evolutionary biologists now question whether natural selection alone can account for evolutionary history observed in the fossil record.

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- Mayr, E. *The Growth of Biological Thought: Diversity, Evolution and Inheritance*. Cambridge, Massachusetts: Harvard University Press, 1982. This is an excellent reference for historical perspective and could be a useful companion to the text for supplementing lecture material on many topics.