CHAPTER 22
DESCENT WITH MODIFICATION: A DARWINIAN VIEW OF LIFE

Introduction

- On November 24, 1959, Charles Darwin published *On the Origin of Species by Means of Natural Selection*.
- Darwin's book drew a cohesive picture of life by connecting what had once seemed a bewildering array of unrelated facts.
- Darwin made two points in *The Origin of Species*:
  - Today's organisms descended from ancestral species.
  - **Natural selection** provided a mechanism for evolutionary change in populations.

A. Historical Context for Evolutionary Theory

1. Western culture resisted evolutionary views of life

- *The Origin of Species* challenged a worldview that had been accepted for centuries.
- The key classical Greek philosophers who influenced Western culture, Plato and Aristotle, opposed any concept of evolution.
  - Plato believed in two worlds: one real world that is ideal and perfect and an illusory world of imperfection that we perceive through our senses.
  - Aristotle believed that all living forms could be arranged on a ladder (*scala naturae*) of increasing complexity with every rung taken with perfect, permanent species.
- The Old Testament account of creation fortified the idea that species were individually designed and did not evolve.
- In the 1700s, the dominant philosophy, **natural theology**, was dedicated to studying the adaptations of organisms as evidence that the Creator had designed each species for a purpose.
- At this time, Carolus Linnaeus, a Swedish botanist, developed **taxonomy**, a system for naming species and grouping species into a hierarchy of increasingly complex categories.
- Darwin's views were influenced by **fossils**, the relics or impressions of organisms from the past, mineralized in **sedimentary rocks**.
  - Sedimentary rocks form when mud and sand settle to the bottom of seas, lakes, and marshes.
  - New layers of sediment cover older ones, creating layers of rock called strata.
  - Fossils within layers show that a succession of organisms have populated Earth throughout time.
- **Paleontology**, the study of fossils, was largely developed by Georges Cuvier, a French anatomist.
- In particular, Cuvier documented the succession of fossil species in the Paris Basin.
  - Cuvier recognized that extinction had been a common occurrence in the history of life.
  - Instead of evolution, Cuvier advocated **catastrophism**, that boundaries between strata were due to local flood or drought that destroyed the species then present.
  - Later, this area would be repopulated by species immigrating from other unaffected areas.

2. Theories of geologic gradualism helped clear the path for evolutionary biologists

- In contrast to Cuvier's catastrophism, James Hutton, a Scottish geologist, proposed that the diversity of landforms (e.g., canyons) could be explained by mechanisms *currently* operating.
    - Hutton proposed a theory of **gradualism**, that profound change results from slow, continuous processes.
- Later, Charles Lyell proposed a theory of **uniformitarianism**, that geological processes had not changed throughout Earth's history.
- Hutton's and Lyell's observations and theories had a strong influence on Darwin.
    - First, if geologic changes result from slow, continuous processes, rather than sudden events, then the Earth must be far older than the 6,000 years assigned by theologians from biblical inference.
    - Second, slow and subtle processes persisting for long periods of time can add up to substantial change.

3. Lamarck placed fossils in an evolutionary context

- In 1809, Jean Baptiste Lamarck published a theory of evolution based on his observations of fossil invertebrates in the Natural History Museum of Paris.
    - Lamarck thought that he saw what appeared to be several lines of descent in the collected fossils and current species.
    - Each was a chronological series of older to younger fossils leading to a modern species.
- Central to Lamarck's mechanism of evolution were the concepts of use and disuse of parts and of inheritance of acquired characteristics.
    - The former proposed that body parts used extensively to cope with the environment became larger and stronger, while those not used deteriorated.
    - The latter proposed that modifications acquired during the life of an organism could be passed to offspring.
    - A classic example of these is the long neck of the giraffe in which individuals could acquire longer necks by reaching for leaves on higher branches and would pass this characteristic to their offspring.
- Lamarck's theory was a visionary attempt to explain both the fossil record and the current diversity of life through its recognition of the great age of Earth and adaptation of organisms to the environment.
- However, there is no evidence that acquired characteristics can be inherited.
    - Acquired traits (e.g., bigger biceps) do not change the genes transmitted by gametes to offspring.

B. The Darwinian Revolution

- Charles Darwin (1809-1882) was born in western England.
- While Darwin had a consuming interest in nature as a boy, his father sent him to the University of Edinburgh to study medicine.
- Darwin left Edinburgh without a degree and enrolled at Christ College at Cambridge University with the intent of becoming a clergyman.
    - At that time, most naturalists and scientists belonged to the clergy and viewed the world in the context of natural theology.
- Darwin received his degree in 1831.

- After graduation Darwin was recommended to be the conversation companion to Captain Robert FitzRoy, who was preparing the survey ship *Beagle* for a voyage around the world.
- FitzRoy chose Darwin because of his education, and because he was of the same social class, and close in age to the captain.

1. Field research helped Darwin frame his view of life

- The main mission of the five-year voyage of the *Beagle* was to chart poorly known stretches of the South American coastline.
- Darwin had the freedom to explore extensively on shore while the crew surveyed the coast.
- He collected thousands of specimens of the exotic and diverse flora and fauna of South America.
    - Darwin explored the Brazilian jungles, the grasslands of the Argentine pampas, the desolation of Tiera del Fuego, and the heights of the Andes.
- Darwin noted that the plants and animals of South America were very distinct from those of Europe.
    - Organisms from temperate regions of South America were more similar to those from the tropics of South America than to those from temperate regions of Europe.
    - Further, South American fossils more closely resembled modern species from that continent than those from Europe.
- The origin of the fauna of the Galapagos, 900 km west of the South American coast, especially puzzled Darwin.
    - On further study after his voyage, Darwin noted that while most of the animal species on the Galapagos lived nowhere else, they resembled species living on the South American mainland.
    - It seemed that the islands had been colonized by plants and animals from the mainland that had subsequently diversified on the different islands.
- While on the *Beagle*, Darwin read Lyell's *Principles of Geology*.
    - Lyell's ideas and his observations on the voyage led Darwin to doubt the church's position that the Earth was static and only a few thousand years old.
    - Instead, he was coming to the conclusion that the Earth was very old and constantly changing.
- After his return to Great Britain in 1836, Darwin began to perceive that the origin of new species and adaptation of species to the environment were closely related processes.
    - For example, clear differences in the beaks among the 13 types of finches that Darwin collected in the Galapagos are adaptations to the foods available on their home islands.
- By the early 1840s Darwin had developed the major features of his theory of natural selection as the mechanism for evolution.
- In 1844, he wrote a long essay on the origin of species and natural selection, but he was reluctant to publish his theory and continued to compile evidence to support his theory.
- In June 1858, Alfred Wallace, a young naturalist working in the East Indies, sent Darwin a manuscript containing a theory of natural selection essentially identical to Darwin's.

- Later that year, both Wallace's paper and extracts of Darwin's essay were presented to the Linnaean Society of London.
- Darwin quickly finished *The Origin of Species* and published it the next year.

- While both Darwin and Wallace developed similar ideas independently, the essence of evolution by natural selection is attributed to Darwin because he developed and supported the theory of natural selection earlier and much more extensively.

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

- Darwinism has a dual meaning.
- It refers to evolution as the explanation for life's unity and diversity.
- It also refers to the Darwinian concept of natural selection as the cause of adaptive evolution.
- Central to Darwin's view of the evolution of life is **descent with modification**.
    - In descent with modification, all present day organisms are related through descent from unknown ancestors in the past.
    - Descendents of these ancestors accumulated diverse modifications, or adaptations, that fit them to specific ways of life and habitats.
- Viewed from the perspective of descent with modification, the history of life is like a tree with multiple branches from a common trunk.
- Closely related species, the twigs of the tree, shared the same line of descent until their recent divergence from a common ancestor.
- This evolutionary tree of the elephant family is based on evidence from fossils.
- The other major point that Darwin pioneered is a unique mechanism of evolution - the theory of natural selection.
- Ernst Mayr, an evolutionary biologist, has dissected the logic of Darwin's theory into three inferences based on five observations.
    - These observations include tremendous fecundity, stable populations sizes, limited environmental resources, variation among individuals, and heritability of some of this variation.
    - 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 the individuals of a population, with only a fraction of the 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 individuals.
        - Those individuals whose inherited characteristics best fit them 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.
- Darwin's main ideas can be summarized in three points.

- *Natural selection is differential success in reproduction* (unequal ability of individuals to survive and reproduce*).*
- *Natural selection occurs through an interaction between the environment and the variability inherent among the individual organisms making up a population.*
- *The product of natural selection is the adaptation of populations of organisms to their environment.*

- For example, these related species of insects called mantids have diverse shapes and colors that evolved in different environments.
- Darwin's views on "overreproduction" were heavily influenced by an essay on human population by Thomas Malthus in 1798.
  - Malthus contended that much human suffering — disease, famine, homelessness, war — was the inescapable consequence of the potential for human populations to increase faster than food supplies and other resources.
- The capacity to overproduce seems to be a characteristic of all species, with only a small fraction of eggs developing to leave offspring of their own.
- In each generation, environmental factors filter heritable variations, favoring some over others.
  - Differential reproduction - whereby organisms with traits favored by the environment produce more offspring than do organisms without those traits - results in the favored traits being disproportionately represented in the next generation.
  - This increasing frequency of the favored traits in a population is **evolution**.
- Darwin's views on the role of environmental factors in the screening of heritable variation were heavily influenced by **artificial selection**.
  - Humans have modified a variety of domesticated plants and animals over many generations by selecting individuals with the desired traits as breeding stock.
- The Darwinian view of life has two main features.
  - 1) The diverse forms of life have arisen by descent with modification from ancestral species.
  - 2) The mechanism of modification has been natural selection working over enormous tracts of time.
- If artificial selection can achieve such major changes in a relatively short time, then natural selection should be capable of major modifications of species over hundreds or thousands of generations.
- Darwin envisioned the diversity of life as evolving by a gradual accumulation of minute changes through the actions of natural selection operating over vast spans of time.
- While natural selection involves interactions between individual organisms and their environment, it is not individuals, but populations that evolve.
- Populations are defined as a group of interbreeding individuals of a single species that share a common geographic area.
- Evolution is measured as the change in relative proportions of heritable variation in a population over a succession of generations.
- Natural selection can only amplify or diminish heritable variations, not variations that an individual acquires during its life, even if these variations are adaptive.
- Also, natural selection is situational.
  - Environmental factors vary in space and time.

- Therefore, adaptations for one set of environmental conditions may be useless or even detrimental under other circumstances.

3. Examples of natural selection provide evidence of evolution

- The evolution of resistance to insecticides in hundreds of insect species is a classic example of natural selection in action.
- Insecticides are poisons that kill insects that are pests in crops, swamps, backyards, and homes.
- The results of an application of a new insecticide are typically encouraging, killing 99% of the insects.
- However, the effectiveness of the insecticide becomes less effective in subsequent applications.
- The few survivors from the early applications of the insecticide are those insects with genes that enable them to resist the chemical attack.
- Only these resistant individuals reproduce, passing on their resistance to their offspring.
- In each generation the percentage of insecticide-resistant individuals increases.
- In general, natural selection operates not to create variation, but to edit existing variation.
    - For example, resistant insects are favored and non-resistant individuals are not when insecticides are applied.
- Natural selection favors those characteristics in a variable population that fit the current, local environment.
- While researchers have developed many drugs to combat the human immunodeficiency virus (HIV), drug-resistant strains evolve rapidly in the HIV population infecting each patient.
- The evolution of drug resistance or pesticide resistance differ only in speed, not in basic mechanism, from other cases of natural selection.
- For patients treated with the drug 3TC, which interferes with genome replication in HIV, 3TC-resistant strains become 100% of the population of HIV in just a few weeks.

4. Other evidence of evolution pervades biology

- In addition to those cases in which we can observe evolution directly, we see evidence of evolution by natural selection in the much grander changes in biological diversity documented by the fossil record.
- Evidence that the diversity of life is a product of evolution pervades every research field of biology.
- As biology progresses, new discoveries, including the revelations of molecular biology, continue to validate the Darwinian view of life.
- In descent with modification, new species descend from ancestral species by the accumulation of modifications as populations adapt to new environments.
- The novel features that characterize a new species are not entirely new, but are altered versions of ancestral features.
- Similarity in characteristics resulting from common ancestry is known as **homology**.
- Descent with modification is indeed evident in anatomical similarities between species grouped in the same taxonomic category.
- For example, the forelimbs of human, cats, whales, and bats share the same skeletal elements, but different functions because they diverged
from the ancestral tetrapod forelimb.
    - They are **homologous structures**.

- Comparative anatomy confirms that evolution is a remodeling process —an alteration of existing structures.
    - Historical constraints on this retrofitting are evident in anatomical imperfections.
    - For example, the back and knee problems of bipedal humans are an unsurprising outcome of adapting structures originally evolved to support four-legged mammals.
- Some of the most interesting homologous structures are **vestigial organs**, structures that have marginal, if any, importance to a current organism, but which had important functions in ancestors.
    - For example, the skeletons of some snakes and of fossil whales retain vestiges of the pelvis and leg bones of walking ancestors.
- Sometimes, homologies that are not obvious in adult organisms become evident when we look at embryonic development.
    - For example, all vertebrate embryos have structures called pharyngeal pouches in their throat at some stage in their development.
    - These embryonic structures develop into very different, but still homologous, adult structures, such as the gills of fish or the Eustacean tubes that connect the middle ear with the throat in mammals.
- The concept of homology also applies at the molecular level (molecular homology) and allows links between organisms that have no macroscopic anatomy in common (e.g., plants and animals).
    - For example, all species of life have the same basic genetic machinery of RNA and DNA and the genetic code is essentially universal.
    - Evidently, the language of the genetic code has been passed along through all the branches of the tree of life ever since the code's inception in an early life-form.
- Homologies mirror the taxonomic hierarchy of the tree of life.
- Some homologies, such as the genetic code, are shared by all life because they date to the deep ancestral past.
- Other homologies that evolved more recently are shared only by smaller branches of the tree of life.
    - For example, only tetrapods (amphibians, reptiles, birds, and mammals) share the same five-digit limb structure.
- This hierarchical pattern of homology is exactly what we would expect if life evolved and diversified from a common ancestor, but not what we would see if each species arose separately.
- If hierarchies of homology reflect evolutionary history, then we should expect to find similar patterns whether we are comparing molecules, bones, or any other characteristics.
- The new tools of molecular biology have generally corroborated rather than contradicted evolutionary trees based on comparative anatomy and other methods.
- Evolutionary relationships among species are documented in their DNA and proteins—in their genes and gene products.
- If two species have libraries of genes and proteins with sequences that match closely, the sequences have probably been copied from a common ancestor.
    - For example, the number of amino acid differences between human hemoglobin and that of other vertebrates show the same patterns of evolutionary relationships that researchers find based on other proteins or other types of data.
- The geographical distribution of species—**biogeography**—first suggested evolution to Darwin.
    - Species tend to be more closely related to other species from the same area than to other species with the same way of life, but living in different areas.

    - For example, even though some marsupial mammals (those that complete their development in an external pouch) of Australia have look-alikes among the eutherian mammals (those that complete their development in the uterus) that live on other continents, all the marsupial mammals are still more closely related to each other than they are to any eutherian mammal.
    - For example, while the sugar glider and flying squirrel have adapted to the same mode of life, they are not closely related.
    - Instead, the sugar glider from Australia is more closely related to other marsupial mammals from Australia than to the flying squirrel, a placental mammal from North America.
- The resemblance between them is an example of convergent evolution.
- Island and island archipelagos have provided strong evidence of evolution.
- Often islands have many species of plants and animals that are **endemic**, or found nowhere else in the world.
- As Darwin observed when he reassessed his collections from the *Beagle's* voyage, these endemic species are typically related more closely to species living on the nearest mainland (despite different environments) than those from other island groups.
- In island chains, or archipelagos, individual islands may have different, but related, species—the first mainland invaders reached one island and then evolved into several new species as they colonized other islands in the archipelago.
    - Several well-investigated examples of this phenomenon include the diversification of finches on the Galapagos Islands and fruit flies (*Drosophila*) on the Hawaiian Archipelago.
    - All of the 500 or so endemic species of *Drosophila* in the Hawaiian archipelago descended from a common ancestor that reached Kauai over 5 million years ago.
- The succession of fossil forms is compatible with what is known from other types of evidence about the major branches of descent in the tree of life.
- For example, fossil fishes predate all other vertebrates, with amphibians next, followed by reptiles, then mammals and birds.
- This is consistent with the history of vertebrate descent as revealed by many other types of evidence.
- In contrast, the idea that all species were individually created at about the same time predicts that all vertebrate classes would make their first appearance in the fossil record in rocks of the same age.
- This is not what paleontologists actually observe.
- The Darwinian view of life also predicts that evolutionary transitions should leave signs in the fossil record.
- For example, a series of fossils documents the changes in skull shape and size that occurred as mammals evolved from reptiles.
- Recent discoveries include fossilized whales that link these aquatic mammals to their terrestrial ancestors.

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

- Arguments by individuals dismissing the Darwinian view as "just a theory" suffer from two flaws.
- First, it fails to separate Darwin's two claims: that modern species evolved from ancestral forms and that natural selection is the main mechanism for this evolution.
- The conclusion that life has evolved is supported by an abundance of historical evidence.

- To biologists, Darwin's theory of evolution is natural selection—the mechanism that Darwin proposed to explain the historical facts of evolution documented by fossils, biogeography, and other types of evidence.
- The "just a theory" arguments concerns only Darwin's second point, his theory of natural selection.
- Herein lies the second flaw, as the term *theory* in colloquial use is closer to the concept of a "hypothesis" in science.
- In science, a theory is more comprehensive than a hypothesis.
- A theory, such as Newton's theory of gravitation or Darwin's theory of natural selection, accounts for many facts and attempts to explain a great variety of phenomena.
- Natural selection is widely accepted in science because its predictions have withstood thorough, continual testing by experiments and observations.
- However, science is not static and arguments exist among evolutionary biologists concerning whether natural selection alone accounts for the history of life as observed in the fossil record.
- The study of evolution is livelier than ever, but these questions of how life evolves in no way imply that most biologists consider evolution itself to be "just a theory."
- By attributing the diversity of life to natural causes rather than to supernatural creation, Darwin gave biology a sound, scientific basis.
- As Darwin said,"There is grandeur in this view of life."