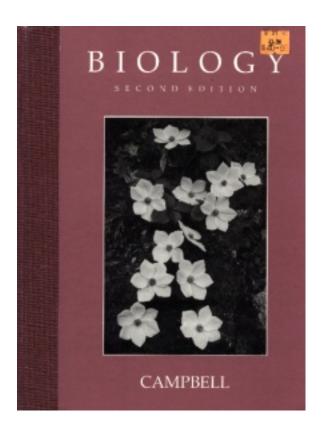
Introduction to Biological Evolution

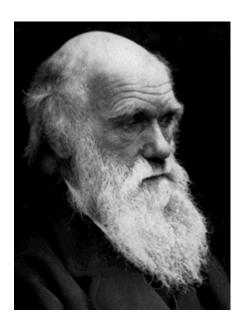
From *Biology*, 2nd Edition, by Neil Campbell, Benjamin/Cummings, 1990.



INTRODUCTION

In the broadest terms, biological **evolution** refers to the processes that have transformed life on Earth from its earliest beginnings to the diversity seen today. The idea of evolution lies at the very heart of all modern biology. It has been commented by Theodosius Dobzhansky that: "Nothing in biology makes sense, except in the light of evolution" (*The American Biology Teacher*, **35**(3), pp. 125-129). Though there is a large number of religious groups in the United States which object to "the theory of evolution," no competent scientist doubts the validity of the basic concepts of biological evolution.

Biology came of age on November 24, 1859, the day Charles Darwin (1809–1882) published *The Origin of Species by Means of Natural Selection, or The Preservation of Favored Races in the Struggle for Life.* This book presented the first convincing case for evolution and led the way in the emergence of biology from a bewildering chaos of facts into a cohesive science.



Charles Darwin (1809–1882)

Darwin addressed the sweeping issues of biology: the great diversity of organisms, their origins and relationships, their similarities and differences, their geographical distributions, and their adaptations to the surrounding environment.

The Origin of Species was truly radical, for not only did it challenge prevailing scientific views, but it also shook the deepest roots of Western culture. Darwin's view of life contrasted sharply with the conventional paradigm of an Earth only a few thousand years old (since Darwin's explanation of biological diversity would imply that the Earth is thousands or even millions of times older than this), populated by immutable (unchanging) forms of life that had been individually made by the Creator during the single week in which he formed the entire universe. Darwin's ideas subverted a world view that had been taught for centuries.

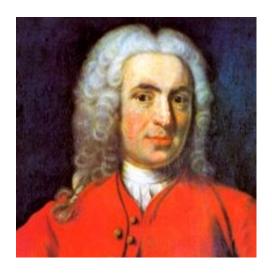
HISTORY AND ANCIENT PHILOSOPHY

Darwin was not the first to suspect that species change with time, however. A physician named Empedocles lived around 450 BCE and taught that there was once a much greater variety of living things on the Earth, but many races of beings "must have been unable to beget and continue their kind. For in the case of every species that exists, either craft or courage or speed has from the beginning of its existence protected and preserved it." Democritus (who lived at about the same time as Empedocles) thought that the simplest forms of life arose from a kind of primordial ooze [Cosmos, pp. 179-80]. But the philosophers who influenced Western culture most, Plato (427–347 BCE) and his student Aristotle (384–322 BCE), held opinions that were incompatible with any concept of biological evolution. Aristotle believed that all living forms could be arranged on a scale of increasing complexity, later called the scala naturae ("scale of nature"). There were no vacancies and no mobility along this ladder of life; each form had its allotted rung, and every rung was taken. In this view of life, which prevailed for over 2000 years, species are fixed, or permanent, and do not evolve.

Prejustice against evolution was fortified in Judeo-Christian culture by the Old Testament account of creation. The creationist dogma that species were individually designed and permanent became firmly embedded in Western thought. Even as Darwinism emerged, biology in Europe and America was dominated by natural theology, a philosophy concerned with discovering the Creator's plan by studying his works. Natural theologians saw the adaptations of organisms as evidence that the Creator had designed each and every species for a particular purpose. In fact, many die-hard creationists are today adopting the "intelligent design" ideas in attempts to introduce their religious beliefs into the American public school curriculum.

TAXONOMY AND LINNAEUS

In the eighteenth century, Carolus Linnaeus (1707-1778), a Swedish physician and botanist, sought order in the diversity of life as majoreum Dei gloriam — "for the greater glory of God." Linnaeus was the father of taxonomy, the branch of biology concerned with naming and classifying the diverse forms of life. He developed the two-part, or binomial, system of naming organisms according to genus and species. In addition, Linnaeus adopted a filing system for grouping species into a hierarchy of increasingly specialized categories (kingdom, phylum, class, order, family, genus, species). Clustering certain species under taxonomic banners implied no evolutionary kinship to Linnaeus, for he believed that species were permanent creations. Ironically, a century latter, the taxonomic system of Linnaeus would become a focal point in Darwin's argument for evolution.



Carolus Linnaeus (1707–1778)

PALEONTOLOGY AND CUVIER

Fossils are relics or impressions of organisms from the past, sealed in rock. Most fossils are found in sedimentary rocks that form from the sand and mud that settles to the bottom of seas, lakes, streams, and marshes. New layers of sediment cover older ones and compress them into rock such as sandstone and shale. Sedimentary rock can be deposited in many superimposed layers called strata. Later erosion may scrape or curve through upper (younger) strata and reveal more ancient strata that had been buried. The fossil record thus displays graphic and incontrovertible evidence that the Earth has had a succession of flora (plant life) and fauna (animal life).



Grand Canyon, Arizona (National Parks Service photo)

Paleontology, the study of fossils, was largely founded by Georges Cuvier (1769–1832), the great French anatomist. Realizing that the history of life is recorded in the strata containing fossils, he documented the succession of fossil species in the Paris Basin. He noted that each stratum is characterized by a unique suite of fossil species, and the deeper (older) the stratum, the more dissimilar the flora and fauna are from modern life.

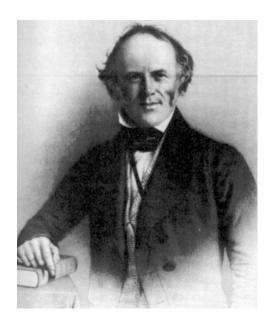


Georges Cuvier (1769–1832)

Cuvier even understood that extinction had been a common occurence in the history of life (a controversial idea at the time). From stratum to stratum, new species appear and others disappear. Yet, Cuvier was a staunch and effective opponent to the evolutionists of his day (which included Charles Darwin's grandfather, Erasmus Darwin). Cuvier speculated that the boundaries between the fossil strata corresponded in time to catastrophic events such as floods or drought that had destroyed many of the species that had lived at that location at that time. Where there were multiple strata, there had been many catastrophes. This view of Earth history is known as **catastrophism**. Although Cuvier himself left religion out of his writing, his aversion to evolution came through loud and clear. But even as Cuvier was winning his debates against advocates of evolution, a theory of Earth history that would help pave the way for Darwin was gaining popularity among geologists.

GEOLOGY AND LYELL

Competing with Cuvier's theory of catastrophism was a very different idea of how geological processes had shaped the crust of the Earth. In 1795, Scottish geologist James Hutton proposed that it was possible to explain the various land forms by looking at mechanisms currently operating in the world. For example, canyons were cut by rivers running down their lengths, and sedimentary rocks with marine fossils were built of particles that had been eroded from the land and carried by rivers to the sea. Hutton explained the state of the Earth by applying the principle of **gradualism**, which holds that profound change is the cumulative product of slow but continuous processes.



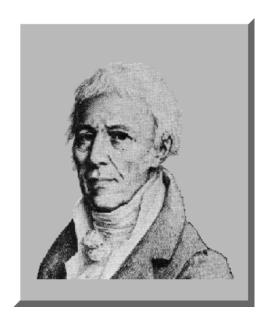
Charles Lyell (1797–1875)

The leading geologist of Darwin's era, Charles Lyell (1797–1875), embellished Hutton's gradualism into a theory known as **uniformitarianism**. The term refers to Lyell's extreme idea that geological processes are so uniform that their rates and effects must balance out through time. For example, processes that build mountains

are eventually balanced by the erosion of mountains. Darwin rejected this extreme version of uniformity in geological processes, but he was strongly influenced by two conclusions that followed directly from the observations of Hutton and Lyell. First, if geological change results from slow, continuous actions rather than sudden events, then the Earth must be very old, certainly much older than the 6000 years assigned by many theologians on the basis of biblical inference. Second, very slow and subtle processes persisting over great length of time can cause substantial change. Darwin was not the first to apply this principle of gradualism to biological evolution, however.

LAMARCK'S THEORY OF EVOLUTION

Toward the end of the eighteenth century, several naturalists suggested that life had evolved along with the Earth. But only one of Darwin's predecessors developed a comprehensive model that attempted to explain how life evolves, and that was Jean Baptiste Lamarck (1744-1829).



Jean Baptiste Lamarck (1744-1829)

Lamarck published his theory of evolution in 1809, the year Charles Darwin was born. By comparing current species to fossil forms, Lamarck could see what appeared to be several lines of descent, each a chronological series of older to younger fossils leading to a modern species.

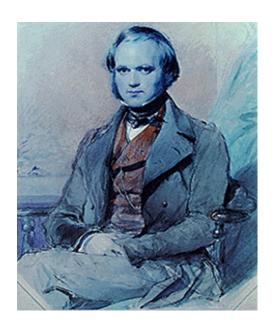
Where Aristotle saw one ladder of life, Lamarck saw many, and they were more analogous to escalators. On the ground floor were the microscopic organisms, which Lamarck believed were continually generated spontaneously from inanimate material. At the top of the evolutionary escalators were the most complex plants and animals. Evolution was driven by an innate tendency towards greater and greater

complexity, which Lamarck seemed to equate 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, or "felt needs."

Lamarck is remembered most for the mechanism he proposed to explain how specific adaptations evolve. It entails two related principles. First is use and disuse, the idea that those organs of the body used extensively to cope with the environment become larger and stronger while those organs that are not used deteriorate. Among the examples Lamarck cited was a giraffe stretching its neck to new lengths in pursuit of leaves to eat. Lamarck's second principle of adaptation is the inheritance of acquired characteristics. Lamarck believed that the modifications an organism acquires during its lifetime can be passed along to its offspring. The long neck of the giraffe, Lamarck reasoned, evolved gradually as the cumulative product of a great many generations of ancestors stretching higher and higher. There is, however, no evidence that acquired characteristics can be inherited! Giraffes who stretch their necks do not create genes for "long necks" which are transmitted by gametes to offspring. Lamarck, however, does deserve credit for his unorthodox theory, which was quite visionary in many respects: in its claim that evolution is the best explanation for both the fossil record and the current diversity of life; in its emphasis on the great age of the Earth; and in its stress on adaptation to the environment as a primary product of evolution.

CONCEPTS OF DARWINISM

In the first edition of *The Origin*, Darwin did not use the word *evolution*, referring instead to **descent with modification**.



Charles Darwin in 1840 (after returning from his trip on the Beagle)

Darwin perceived unity in life, with all organisms related through descent from some unknown prototype that lived in the remote past. As the descendants of that inaugural organism spilled into various habitats over millions of years, they accumulated diverse modifications, or adaptations, that fit them to specific ways of life. In the Darwinian view, the history of life is like a tree, with multiple branching and rebranching from a common trunk all the way to the tips of the living twigs, symbolic of the current diversity of organisms. At each fork of the evolutionary tree is an ancestor common to all lines of evolution branching from that fork. Species that are closely related, such as the domestic cat and the lion, share many characteristics because their lineage of common descent extends to the smallest branches of the tree of life. Most branches of evolution, even some major ones, are dead ends; about 99% of all species that have ever lived are extinct.

Ernst Mayr, of Harvard University has dissected the logic of Darwin's theory of natural selection into three inferences based on five facts:

- Fact 1: All species have such great potential fertility that their population size would increase exponentially if all individuals that are born would reproduce successfully.
- **Fact 2:** Most populations are normally stable in size, except for seasonal fluctuations.
- Fact 3: Natural 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.
- **Fact 4:** Individuals of a population vary extensively in their characteristics; no two individuals are exactly alike.
- **Fact 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 have 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.
- Natural selection is this differential success in reproduction, and its product is adaptation of organisms to their environment. Even if the advantages of some variations over others are slight, the favorable variations will

accumulate in the population after many generations of being disproportionately perpetuated by natural selection.

Thus, natural selection occurs through an interaction between the environment and the variability inherent in any population. Variations arise by chance mechanisms, but natural selection is *not* a chance phenomenon. Environmental factors set definite criteria for reproductive success.

A struggle for life is ensured by excessive production of new individuals. Darwin was already aware of the struggle for existence when he read an influential essay on human population that had been written by the Reverend Thomas Malthus in 1798. Malthus contended that much of human suffering — disease, famine, homelessness, and war — were inescapable consequences of the potential for the human population to grow at a much faster rate than increased supplies of food and other resources could keep pace with.



Thomas Malthus (1766–1834)

The capacity to overproduce seems to be characteristic of all species. Of the many eggs laid, young born, and seeds spread, only a tiny fraction complete their de-

velopment and leave offspring of their own. The rest are eaten, frozen, starved, diseased, unmated, or unable to reproduce for some other reason.

Variation and overproduction are the two characteristics of populations that make natural selection possible. On the average, the most fit individuals pass their genes on to more offspring than the less fit. The environment screens variations, favoring some over others. Differential reproduction results in the favored traits being proportionately represented in the next generation.

Darwin did not see life evolving abruptly by quantum leaps, but envisioned instead a gradual accumulation of minute changes. Gradualism is fundamental to the Darwinian view of evolution. We can now summarize Darwin's view of life: The diverse forms of life have arisen by descent with modification from ancestral species, and the mechanism of modification has been natural selection working continuously over enormous tracts of time.

AN EXAMPLE OF NATURAL SELECTION

The most cited and extensively documented example of natural selection in action involves the English perpered moth, Biston betularia. It is found throughout the English midlands, occurring in two varieties that differ in coloration. The form for which the peppered moth is named is light, with splotches of pigment. The other variety is uniformly dark. Peppered moths feed at night and rest during the daytime, sometimes on trees and rock encrusted with light-colored lichens. Against this background, light individuals are camouflaged, but the dark moths, being very conspicuous, are easy prey for birds. Before the Industrial Revolution, dark peppered moths were very rare, presumably becoming bird food before they could reproduce and pass the genes for darkness on to the next generation. But industrial pollution darkened the landscape of much of the countryside in the late 1800's, mainly killing lichens that covered rocks and the dark bark of trees. Against this darkened background, light moths stood out, and dark moths were concealed from birds. The frequency of dark individuals in populations of Biston began to increase. By the turn of the century, the population in the Manchester region consisted almost entirely of dark moths. This phenomenon, known as industrial melanism, occurred in hundreds of other species of moths in polluted areas.





The two variants of the English peppered math Biston betularia

The dark moths were reproductively favored because the newly visible light moths were more commonly eaten by birds and consequently left fewer offspring. In recent years, the case of the peppered moth had taken a satisfying turn, for much of the pollution has been curbed, enabling some parts of the countryside in industrial areas to return to natural hues. In those places, the light form of *Biston* has made a strong comeback.

THE MODERN SYNTHESIS

An important turning point for evolutionary theory was the birth of **population genetics**, which emphasizes the extensive genetic variation within populations and recognizes the importance of quantitative inheritance. A comprehensive theory of evolution that became known as the **modern synthesis**, or neo-Darwinism, was forged in the early 1940s, as the genetic basis of variation and natural selection was worked out. Paleontologitsts, taxonomists, and biogeographers also contributed to the modern synthesis. The modern synthesis emphasizes the importance of populations as units of evolution, the essential role of natural selection, and gradualism.

Today, nearly all biologists acknowledge that evolution is a fact. The term theory is no longer appropriate except in referring to the various models that attempt to explain how life evolves. Lamarck and Darwin had contrasting theories of evolution. Most of Darwin's ideas persist in the modern synthesis, the theory of evolution that has prevailed for the past 50 years. However, many evolutionists, including Niles Eldredge, are now changing some of the generalizations of the modern synthesis. The debate focuses on the tempo of evolution and on the relative importance of evolutionary mechanisms other than natural selection. The study of evolution is more lively and robust than ever. Still, it is important to understand that the current questions about how life evolves in no way implies any disagreement over the fact of evolution. Arguing over evolutionary theory is like arguing over different theories of gravity: We know that objects keep right on falling, even as the debate goes on.

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