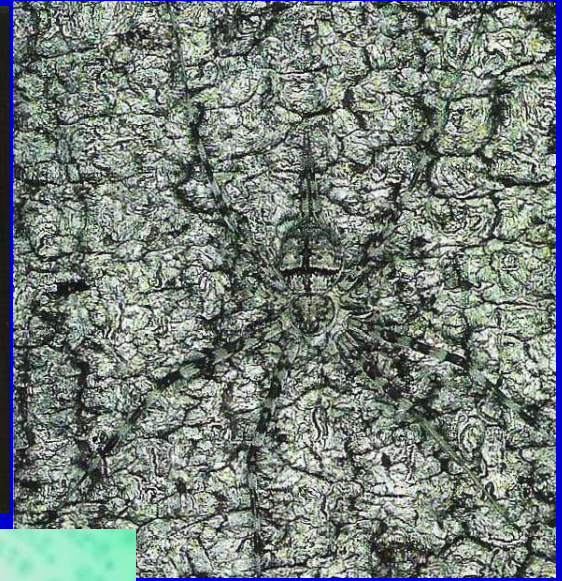
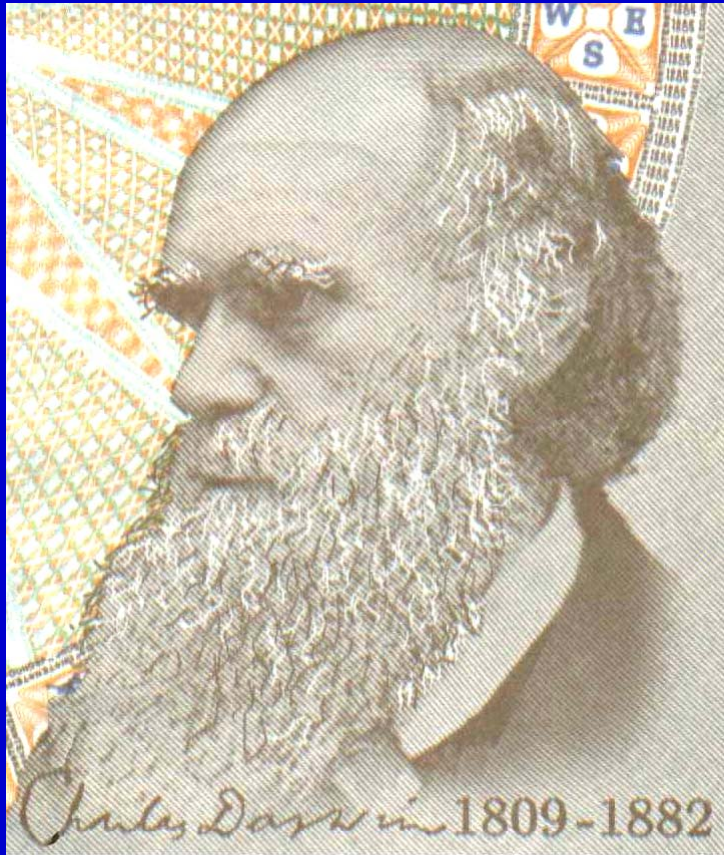


Evolutionary Biology



Evolutionary Thought before Darwin



The modern field of evolutionary biology can be traced back to Charles Darwin. There were ideas about biological change and interactions between organisms prior to Darwin that influenced his thinking. An understanding Darwin's observations, motivations, hypotheses, tests, and conclusions rests on understanding his times and the thinking of day.

Every culture has explanations for its origins:

<http://www.magictails.com/creationlinks.html>

Explanations that have a physical basis began with the Greeks:

Thales (640-546 B.C.) - the first natural explanation. All life came from water.

Xenophanes (576-480 B.C.) and Herodotus (484-425 BC) recognized fossils as the remains of living creatures, and based on the distribution of fossil marine life speculated that oceans had formerly covered some of the land.

- the first recognition of environmental change through time and change in living creatures accompanying it.

Democritus (500-404 B.C.) distinguished between organic and inorganic systems. Organic systems were derived from inorganic systems through the natural properties of inorganic systems.

Empedocles (495-435 B.C.) gave a detailed explanation of the a natural origin of life. There were 4 basic inorganic materials : **fire, air, earth, and water** and two basic forces. **love and hate.**

A proper mixture created a functional living organism.

An improper mixture resulted in reduced survival. The first example of a hypothesis of differential survival in nature.

Hippocrates (460-370 B.C.) stressed an **empirical** approach.

He stated two principles that seemed to be valid.

1. **the inheritance of acquired characters** - habits or characteristics of the parent will be passed to the offspring

2. **principle of use and disuse** - a part that is used will become more elaborate and a part that is not used will be lost

Variation was due to differences in environments and habits

Plato (427-347 B.C.) believed that the universe had general laws that could be discerned through pure thought and be described. Plato developed many ideas about the nature of the universe. One that was very influential and still survives in some form today is **ESSENTIALISM** or **IDEALISM**.

The form of an object or organism is an outward expression of its essence – an unseen underlying truth about the nature of an object

Plato thought that underlying every object's existence was its essence, or essential nature.

The variation among types of an object or types of organisms was an error, or just various degrees of imperfection from the true essential nature.

Plato also introduced the idea of an animate or living cosmos - all physical and living systems are linked together into a harmonious whole – a supernatural harmony that could only be understood through pure thought
The Platonic system replaced naturalistic explanations.

Nonnatural and natural explanations -

natural explanations depend on physical cause and effect and often make testable predictions

nonnatural explanations propose nonphysical causes and can't make predictions that can be critically tested. We can't potentially reject something that does not make predictions. Such explanations are outside the realm of science.

Aristotle (384-322 B.C.) The first great naturalist. - a student of Plato - rejected metaphysical speculation but accepted the idea that species have fixed properties.

Returned to empiricism - studying by observing - and developed the beginnings of biology: anatomy, reproductive biology and ecology of many plants and animals.

He was the first to use the gradations in form among organisms to arrange them into a ladder like scale - with man at the top of the living world - a **teleological** system.

The Great Chain of Being (*scala naturae*):

Humans

Mammals

Birds

Reptiles

Fish

Higher Invertebrates

Simple Animals

Higher Plants

Lower Plants

Inanimate matter



Early Christians readily adopted Aristotle's *scala naturae* and viewed it as the product of a perfect creation - because it was perfect it was unchanging.

During the middle ages the Arabs carried on the Greek tradition of natural explanations for biological phenomena.

The Christian church in Paris in 1209 banned any Arabic literature dealing with natural explanations.

The Age of Enlightenment - (1650-1800) - Real science began to emerge with rational and testable explanations of physical processes. Science was slow to spread into the study of life.

1600s - Francis Bacon (England) and Renee Descartes (France) suggested that natural laws surpassed Christian dogma in the understanding and explanations of natural phenomena.

They suggested that species can change through the actions of physical processes upon them.

Voltaire (1694-1778) – questioned the idea the species were fixed quantities and stressed that there was variation within species
He questioned the idea of a great chain of being with humans being the ultimate living things - this served to satisfy human egos. He saw living things as all part of a continuum of equal rank.

George Louis Leclerc - “Comte de Buffon” - 1707-1788 - studied fossils - noted changes in organisms in the fossil record and involved both improvement and degeneration of parts. Calculated from rates of sedimentation, and from the thickness of sedimentary deposits, that the earth was in excess of 160,000 years old - viewed as a heretical idea at the time. *Histoire Naturelle* (1749) - all species have an internal mold and the mold organizes the body. Similar species share a common ancestor and were modified by climate. Speculated about the inheritance of acquired characteristics. Original molds arose by spontaneous generation.

Archbishop James Ussher (1581-1656) - calculated from Biblical records that the earth was created 4004 BC, on Sunday October 23.

James Hutton (1726 - 1797) - observations of geology should be explained by processes that we observe in the present. -

“Uniformitarianism”

Uniformitarianism was later championed by Charles Lyell (1797-1875) who had an important influence on Charles Darwin

Uniformitarianism is an important part of science in general.

During the 1700s many geologists were studying fossils and noticed many forms that were apparently no longer living and many forms appeared in deep geological layers, persisted through many layers, and then disappeared.

Some, based on Christians beliefs, speculated that life had been created and destroyed many times to account for changes in the fossil record - “Catastrophism”

Erasmus Darwin (1731-1802) - Grandfather of Charles Darwin - speculated about change in species through time and the inheritance of acquired characteristics.

Carolus Linnaeus (1707-1778) - Systema Naturae (1735) - a classification of plants and animals - a hierarchical classification with species organized into genera, and into families, orders, etc. He did not believe in change or common descent. He saw all species as fixed entities.

Linnaeus's purpose was to discover the pattern in God's creation. He was a "Natural Theologian."

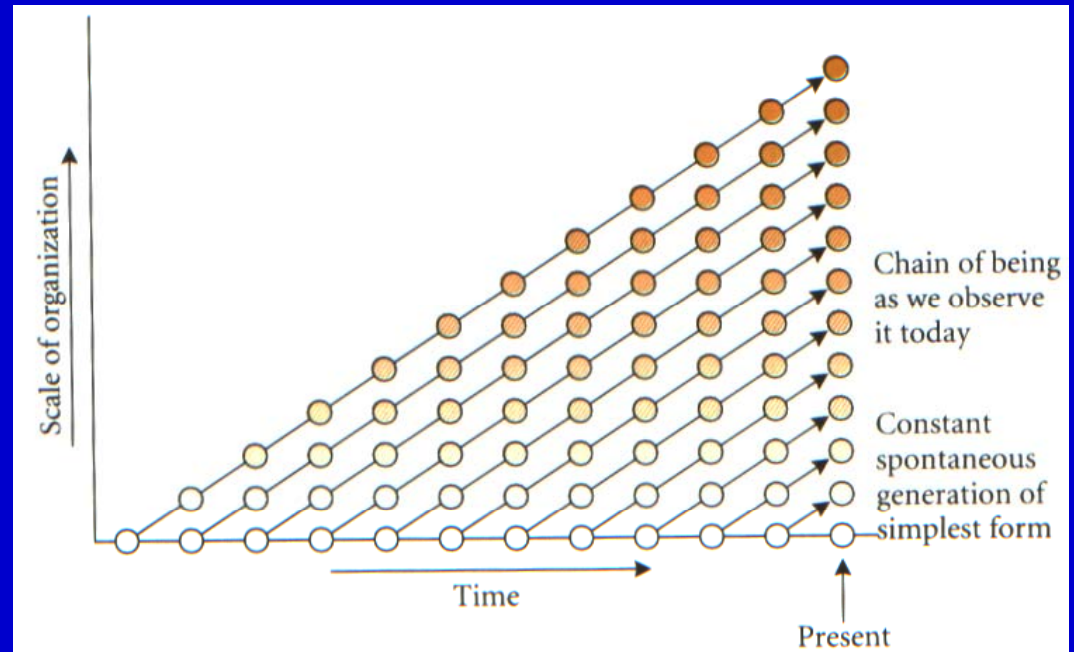
Many naturalists of the time were natural theologians.

Jean Baptiste LaMarck (1744-1829) - was interested in the apparent close fit between organisms and their environment, their **adaptations**.

questioned the idea that species were fixed – he suggested species could change in response to their environment

Restated Hippocrates inheritance of acquired characteristics and the principle of use and disuse.

He rejected Aristotle's Great Chain of Being as due to a single change of progress - He accounted for the apparent chain by successive rounds of spontaneous generation and change.



LaMarck's model did not allow for extinction of forms
Published his ideas in Philosophie Zoologique (1809).

LaMarck :

- Proposed a natural and testable hypothesis about the mechanism of evolution
- he recognized that organisms interact with their environment
- accounted for adaptations – could even account for very complex adaptations
- accounted for diversity – from the lowliest forms of life to the most advanced
- he argued that if his mechanism was correct – the world must be very old
- LaMarck also included humans in his scheme of evolution

He did not attempt to test his ideas.



LaMarck's ideas were highly criticized by many especially Georges Cuvier (1769-1832) - the greatest naturalist of his day - a natural theologian - well known for his studies of vertebrate anatomy, the father of ichthyology.

Cuvier argued that there was no evidence for change of species, and promoted the idea that species were fixed entities – created and static in form – “fixity of species” - He helped to stifle further ideas about change in living things.

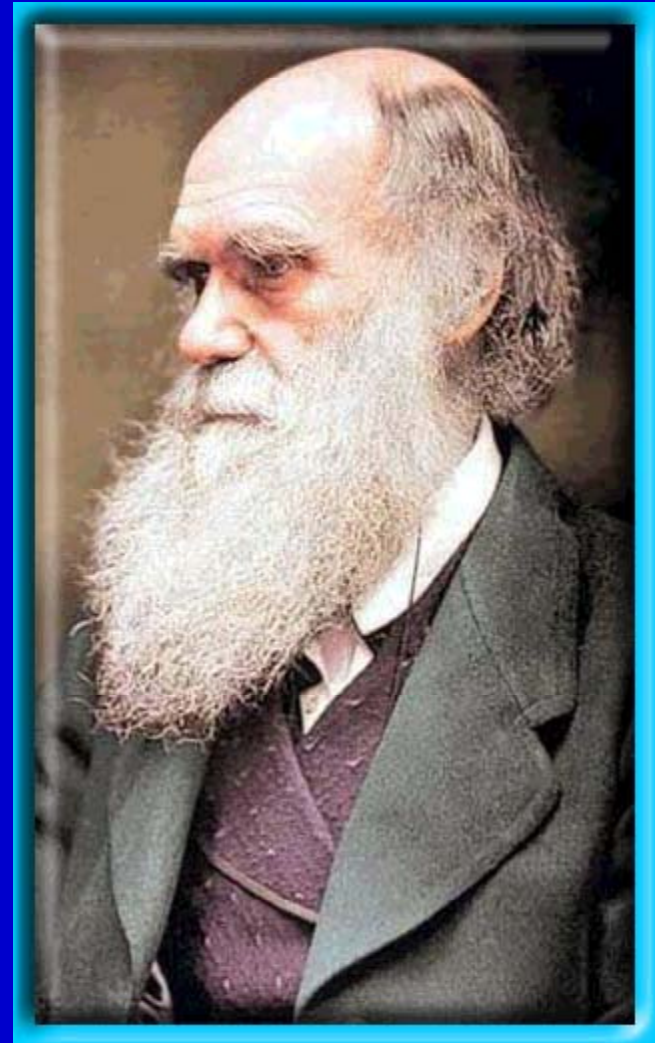
Many natural theologians contributed much to biology. However, because of the apparent age of the earth, fossil diversity, geographic variation within species, many began to revise their views of a static and unchanging living world.

Charles Darwin (1809-1882)

The son and grandson of physicians, he had an interest in natural history from childhood.

At 16, he entered Edinburgh University to study medicine, but could not stomach surgery. His second option was to study for the clergy, at Christ's College, Cambridge University.

His interests in natural history continued and he became friends with faculty members in botany (Henslow) and geology (Sedgwick).



Upon graduation (1831 - age 22) he received an invitation to become the naturalist on the H.M.S. Beagle. The Beagle expedition was to map the coastline of South America and then continue on through the Pacific, around the world. His job was to collect specimens of plants, animals, rocks, etc. to document the natural history of the lands visited. The trip was to take 2-3 years. It took 5.

- At the time, many people were actively investigating the lives of animals and plants as natural theologians.
- Geologists were documenting fossil change and stirring up doubt about the age of the earth and the literal truth of Genesis.
- Physical scientists were favoring natural explanations that were scientifically testable.
- There was discussion of change in living things through time among natural theologians but such ideas were controversial.
- The scientific method was being applied to studies of life.



Darwin spent as much time as possible on land. He had many inland trips in South America, some lasting weeks. He collected many specimens, and many were sent to England from South America before the Beagle went to the Pacific. Darwin's collections were well known before he returned to England in late 1836.

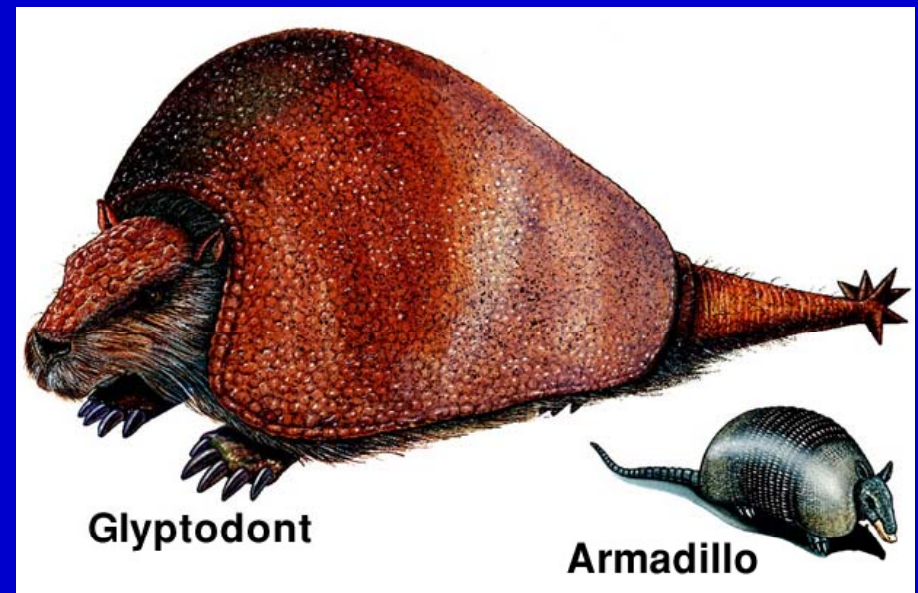
Darwin's Observations and the questions that they raised:

- Each continent had its own unique plants and animals. Even when they have similar climates the organisms are different. e.g. -Australia has marsupial mammals. South America has many placental mammals. Armadillos are found only in the new world. The only mammals in New Zealand were bats.

Why?

- Fossils found in an area are most similar to living forms in that area.

e.g. Glyptodont and Armadillo - What happened to Glyptodonts and where did Armadillos come from?



- Deeper stratigraphic layers had plants and animals that were more different from living species than were shallower stratigraphic layers. Where did those ancient forms go?



- Oceanic islands had their own unique plants and animals. Why didn't all islands have the same island species?
- Plants and animals on oceanic islands were most similar to species found on the nearest continent. Why?



- Species found in each area seemed to be well suited to the environment in which they were living - if large seeds were the only seeds available - seed eating birds had large beaks, if small seeds - small beaks - How did this come about?

His observations made him question the fixity of species.

He knew how the the uniformitarian principle was applied in geology. He wondered if there were physical explanations for his biological observations.



An ornithologist (Gould) had examined his bird specimens from the Galapagos, and told him that he had a greater variety of mockingbirds than had been previously known, each with a morphology and lifestyle previously unknown in mockingbirds.

Darwin also knew that each of the Galapagos islands had its own unique form of tortoise.

These facts caused Darwin to consider the possibility that each of the mockingbirds was descended from a single ancestor (common descent).

Evolution could explain many of the questions he had but he did not have an explanation for the cause of evolution.

Uniformitarian thinking required that he have a mechanism for past events in terms of processes that could be demonstrated in the present.

Darwin hypothesized that evolution had occurred. Species had changed through time. Armadillos were the descendants of Glyptodonts. Species evolved on each land mass independent of other land masses. Species evolved to be well suited for conditions in which they lived.

But how?

Darwin read widely in search of an answer. Two pieces of evidence lead him to an explanation of how evolution had occurred.

1. Selective breeding of plants and animals - produces new varieties that suit the whim of the human doing the selecting.
2. The extreme potential for animals and plants to multiply results in a “struggle for existence”

Thomas Malthus - a social scientist - wrote “Essay on the Principle of Population” (1798)

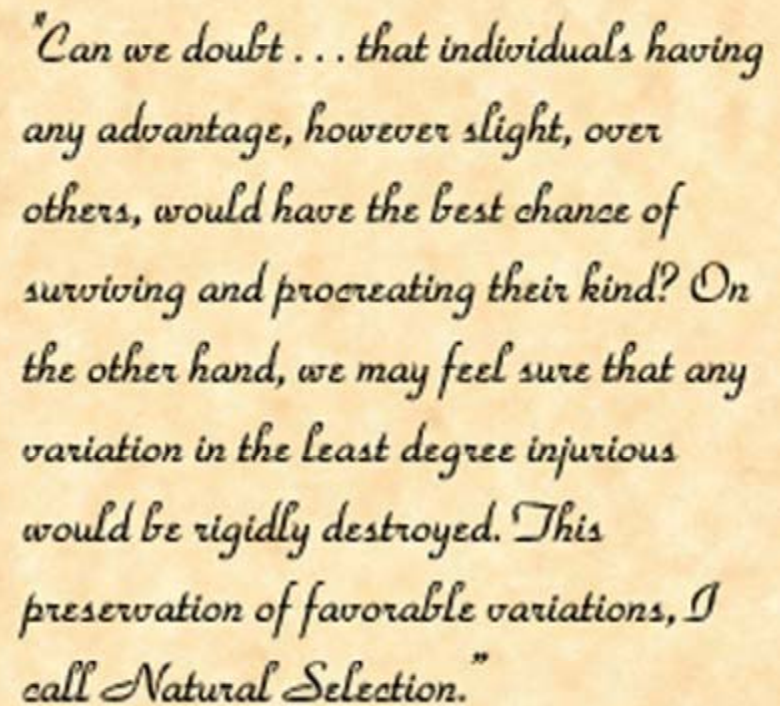
Malthus noticed that human and animal populations have the potential to grow geometrically: $2 \rightarrow 4 \rightarrow 8 \rightarrow 16 \rightarrow \text{etc.}$

And, if they do, they will eventually outstrip their food supply.

However, populations commonly remain relatively stable. Why?

Because as the birth rate increases so does the death rate. Increased population growth results in increased suffering for the members of the population.

Darwin concluded that “there is a struggle for existence” and ...



“Can we doubt . . . that individuals having any advantage, however slight, over others, would have the best chance of surviving and procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favorable variations, I call Natural Selection.”

Darwin's logic:

Fact: all species have the potential for exponential growth

Fact: most populations do not grow, in spite of producing enough offspring to grow.

Fact: when populations do grow it is seldom as rapid as possible and only for a short period of time.

Fact: the resources available to any population are relatively stable and limited.

Inference: there is a struggle for existence in populations and only a fraction of the population survives to produce the next generation

Fact: in every population there is variation (morphological, physiological, behavioral, etc)

Fact: much of the variation is heritable (can be passed from parent to offspring)

Inference: survival is not necessarily random, but could depend upon the physical attributes of individuals (natural selection is possible)

Inference: over a number of generations, the process of differential survival will result in gradual change in the population, in the direction of those better able to survive in that environment. - Adaptations - features of an organism that allow it to survive in its environment - are the product of natural selection.

Darwin's Timeline:

1831-1836 - Voyage of the Beagle

1839 - conceived idea of Natural Selection

1839 - 1841 - tested idea of evolution against known facts

1842 - wrote draft of his argument and did not publish - only revealed his thinking to his closest friends in science.

1843 - 1858 - worked on other things (barnacles, earthworms, plant growth, etc.) - published many papers

1858 - received letter from Alfred Wallace outlining Wallace's hypothesis of evolution by natural selection

1858 - presented his and Wallace's ideas to the Linnaean Society of London

1859 - published "On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life."

The Origin of Species presented the evidence for evolution and proposed that natural selection was the mechanism.

Darwin argued and presented evidence for five hypotheses:

- Evolution - change in living things had occurred.
- Common Descent - species had diverged from a common ancestor - there was a “tree of life.”
- Gradualism - species evolve gradually, in slow steps.
- Populational Speciation - species change by change in the proportion of different types in a population.
- Natural Selection - within a population, variants better suited to the environment replaced those less suited in the struggle for existence.

Darwin's evidence was diverse and thoroughly presented.

He described what was known about fossils and the fossil record.

He described what was known about the underlying morphological similarity between forms that appear very dissimilar.

He described the similarity of developmental patterns among organisms that appear very dissimilar as adults.

He described the geographic distribution of organisms - how distant landmasses shared few species in spite of similar climates.

His arguments were clear and his evidence was thorough. His book quickly convinced most biologists of his day that evolution had occurred. General scientific acceptance of natural selection as an important mechanism in evolution took several more decades.

Throughout his book, Darwin presented his attempts to find evidence against evolution and laid out the evidence that, if found, would refute his hypothesis.

“If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.”

“If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.”

Darwin lacked knowledge of genetics. Genetics as a field was just beginning - Mendel was a contemporary of Darwin. This lack of knowledge resulted in two major weaknesses in his theory.

He did not know how new variants arose. He thought the origin of variation was independent of need, but he did not have convincing evidence.

He did not know how traits were passed from parents to offspring. The common idea at the time was that the traits present in parents would blend in the offspring. Thus new variation would be quickly diluted and disappear.

Darwin's hypothesis of the mechanism of evolution differs in some important ways from LaMarck's

Darwin

species become better suited for their environment

new species are the descendants of previously existing ones

struggle for existence

variation exists - **source unknown**

differential abilities result in **differential reproduction**

mechanism of inheritance - unknown

proposed hypothesis with **critical tests** suggested and many conducted

LaMarck

species become better suited for their environment

new species are the descendants of previously existing ones

no struggle necessary

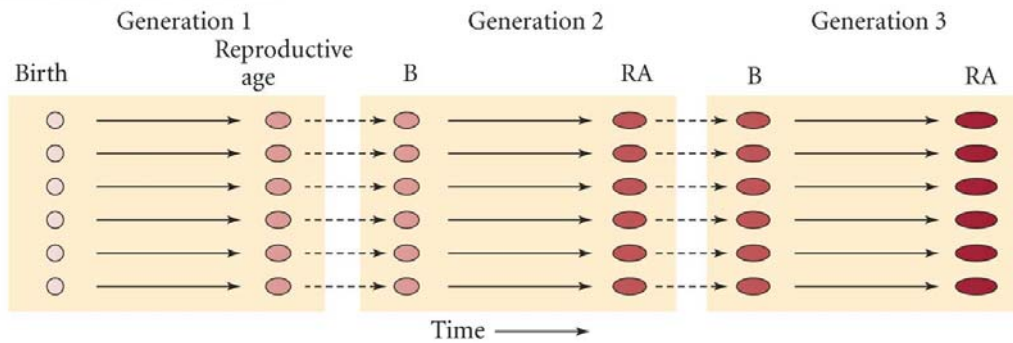
variation comes from interaction with the environment - use and disuse

no differential abilities or differential reproduction

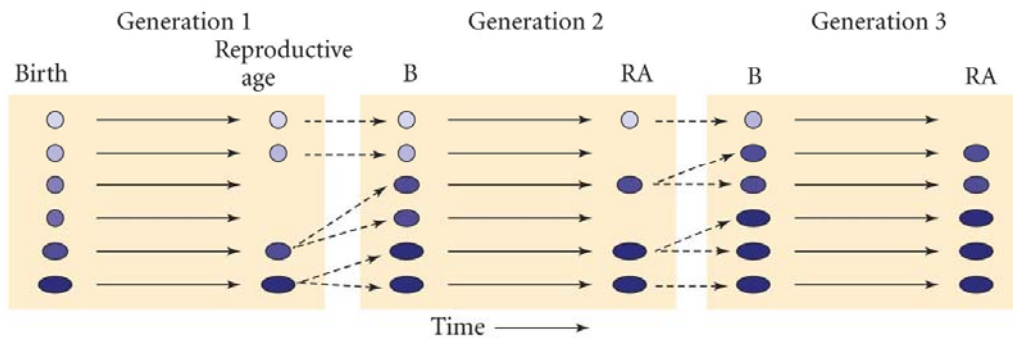
inheritance of acquired characters

proposed hypothesis without critical examination

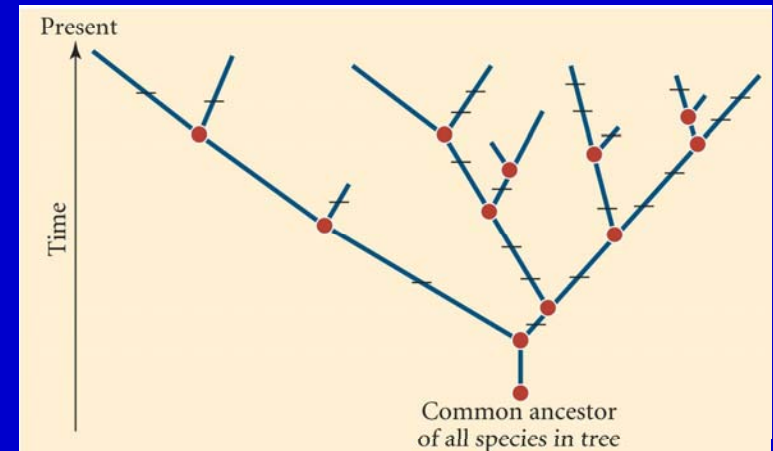
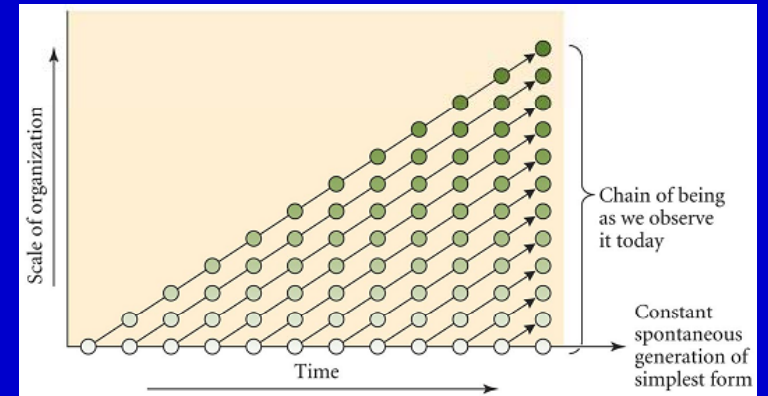
Transformational evolution



Variational evolution



EVOLUTION, Figure 1.4 © 2005 Sinauer Associates, Inc.



The Darwinian Revolution: Darwin's ideas challenged and ultimately overthrew some commonly accepted ideas of his day:

- The concept of a static living world. As in geology, the world, and the life inhabiting it, is ever-changing.
- The concept of a single creation event for all diversity. Diversity is produced by the interaction of organisms with their environment.
- The idea that life has a purpose and is progressive. Life is opportunistic and not goal-oriented. Adaptations are temporary.
- Anthropocentrism. Humans are not the purpose for, or the center of, the universe.
- Essentialism. Variation is not a deviation from a true form. It is the raw material for natural selection.

The Evolutionary Synthesis

Darwin's ideas prompted many to examine anatomy, embryology, and the fossil record in detail. By 1870, there was so much evidence that evolution had occurred that it was considered a scientific fact.

Natural selection, as the mechanism for evolution, was not accepted by most.

Several alternatives to natural selection were developed. Neo-Lamarckism, Orthogenesis, and Mutationism were the most popular.

Only after discovery of the rules of inheritance, how variation originates, and how genes behave in populations was natural selection seen as the most viable mechanism for evolution.

Neo-Larmarckism - the inheritance of acquired characteristics remained as a popular idea.

August Weissmann (1834-1914) tested and found only negative evidence for the inheritance of acquired characteristics. He pointed out that the body (soma) and the reproductive organs (germ plasm) had different roles in the life of an organism. The germ plasm was the source of gametes and there was no contribution of the soma to the production of gametes. So, modification of the soma would not have an effect on the information carried in gametes. He argued strongly for natural selection as the mechanism for evolution.

Some Neo-Larmarckian hypotheses remain in biology today. It has been demonstrated that stress induces mutation in some bacteria, but the resulting mutations do not appear to be adaptive responses to the stress (directed mutation).

Orthogenesis - many paleontologists saw clear evolutionary trends in the fossil record - increasing body size, reduction in the number of toes, decreasing thickness of shells, etc. in many different groups. Trends that seemed to persist through long expanses of time.

This led to the idea that trends were a progression to an end-point or goal. Living things were thought to contain the instructions for their own evolution and each species had a fixed evolutionary fate.

There was no way of testing such ideas because no predictions can be made. Fate is only revealed after it occurs.

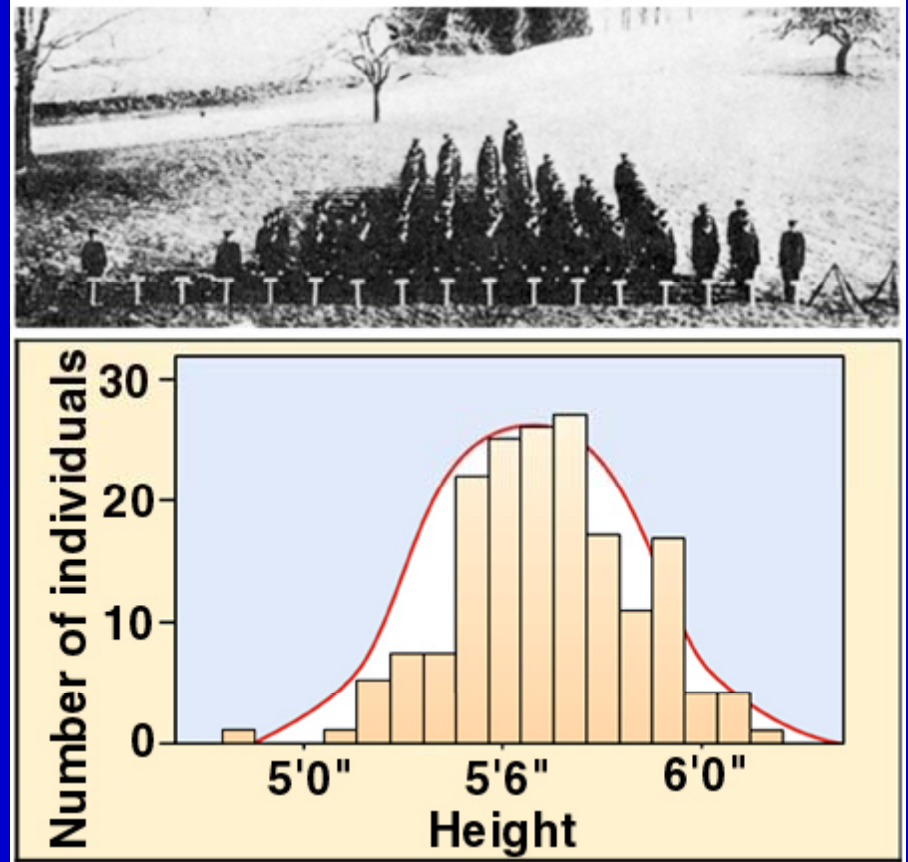
Orthogenetic ideas were abandoned when knowledge of genetics and natural selection showed that teleology was not necessary.

Mutationism - grew out of Mendelian genetics, which showed how discrete characteristics were inherited - (tall vs. dwarf, round vs. wrinkled, etc.). Because characters and their inheritance appeared discrete, the gradual evolution that Darwin had described was rejected by mutationists.

Mutations and their causes were studied by Hugo De Vries (1848-1935) and Thomas Hunt Morgan (1866-1945). Each rejected natural selection, and argued that new species arise as mutations.

Richard Goldschmidt (1878-1958) was an advocate of mutationism and is known for his idea of “hopeful monsters.” Major mutations result in large changes in body form, most of which are lethal, but some survive to produce new, and very different, types of organisms.

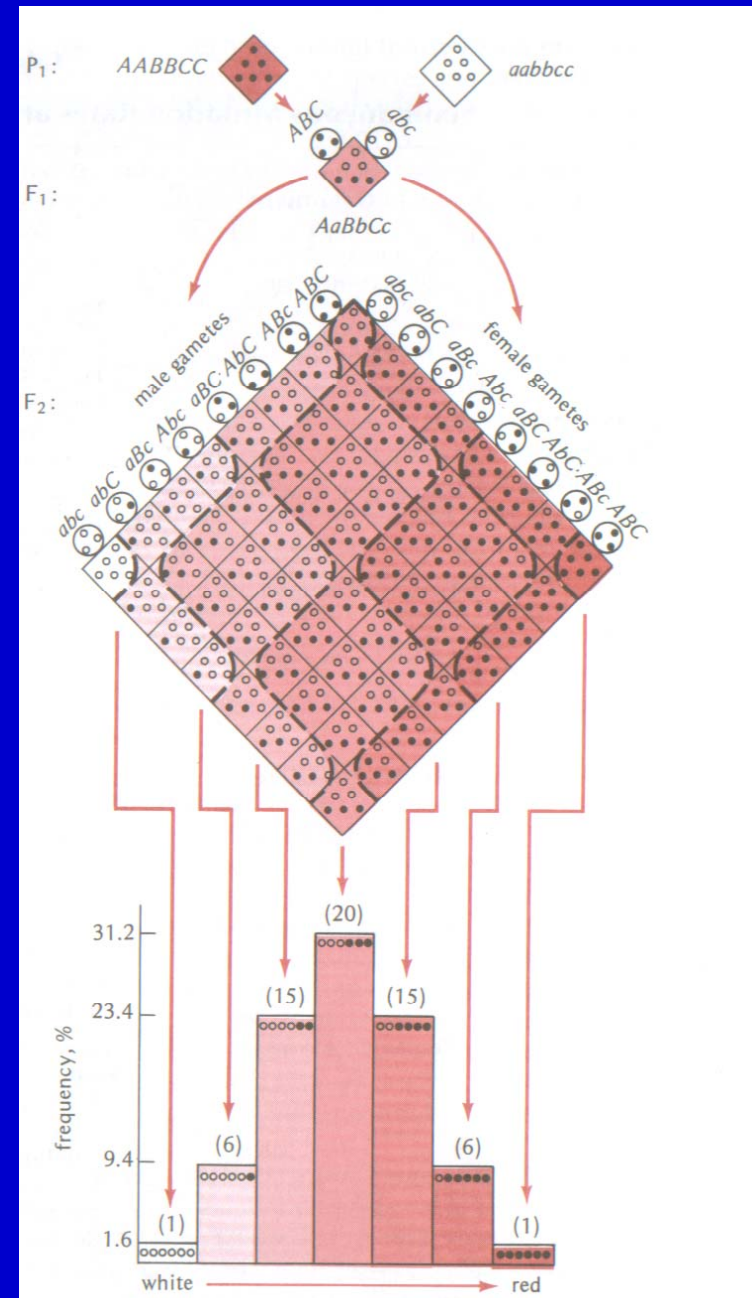
Before Mendel's laws were rediscovered, many biologists were studying continuous variation because so many traits show continuous variation. They invented mathematical tools to describe and study continuous variation. This was the beginning of statistics (normal distribution, linear regression, correlation, etc.) These biologists were called "biometricians."



Biometricians were on the right path but were sidetracked when Mendel's laws were rediscovered, because Mendel's laws seemed to apply only to discrete variation.

One of the first biometricians was Francis Galton (1822-1911), a cousin of Darwin, and a supporter of the idea of evolution by natural selection. Galton pioneered studies of heritability of behavioral characteristics and coined the phrase "nature versus nurture" to explain the relative importance of inheritance and environment in explaining human behavioral traits.

The biometrician and Mendelian viewpoints were rectified when it was shown that “quantitative traits” with continuous variation could be accounted for by polygenic inheritance. Many genes, each influencing the phenotype, and each inherited in a Mendelian fashion, produced continuous phenotypic variation.



By 1930 the pieces of the puzzle were all available, Mendelian genetics had grown to encompass polygenic systems, and the mathematics of population genetics was developed.

Mutation was not an alternative to natural selection, it was the raw material for natural selection.

Major figures:

Ronald Fisher (1890-1962) - British mathematician

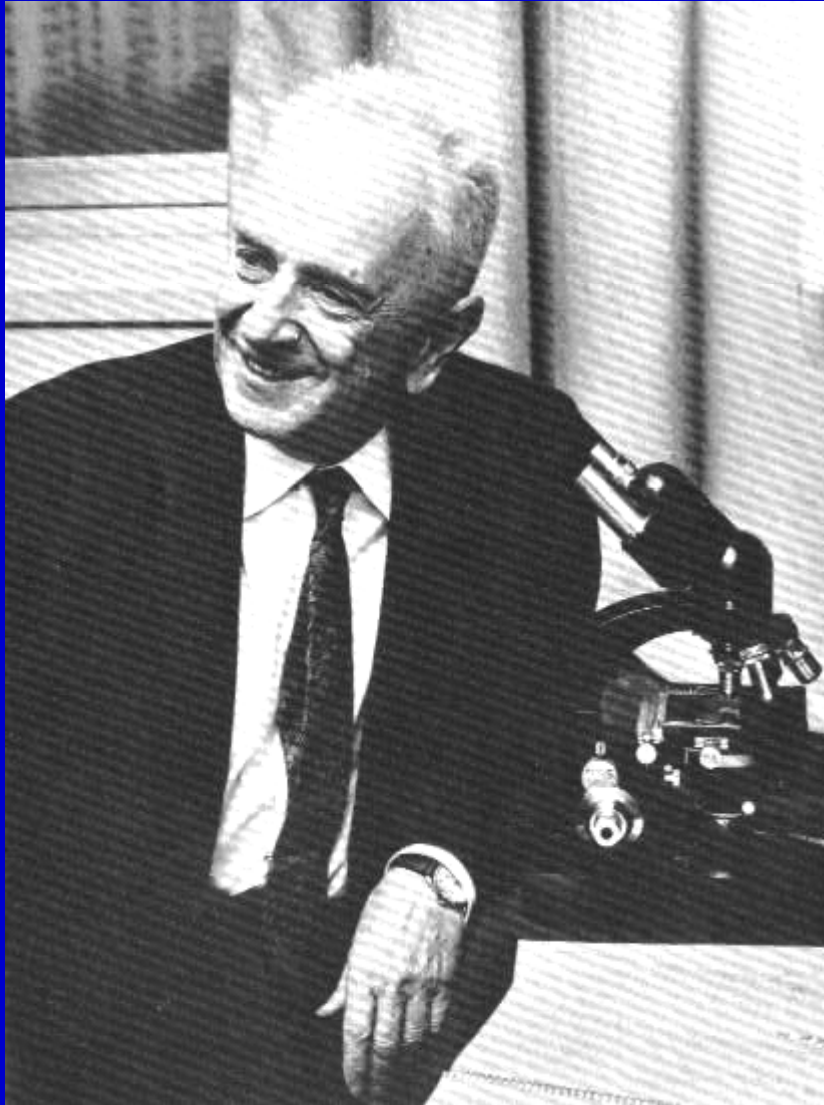
J. B. S. Haldane (1892-1964) - British biochemist and writer

Sewall Wright (1889-1988) - American biometrician, geneticist

Theodosius Dobzhansky (1900-1975) - Russian (later American) geneticist, population geneticist

Ernst Mayr (1904-2005) - American paleontologist

Julian Huxley (1887-1975) - English biologist and writer



Dobzhansky's *Genetics and Origin of Species* (1937) is seen as the central work of the evolutionary synthesis. His explanations of population genetics, genetic variation, and how natural selection worked on genetic variation led to wide acceptance of the importance of natural selection and the beginnings of the modern field of evolutionary biology.

The evolutionary synthesis combined genetics with Darwin's view of populational evolution:

1. The phenotype is a product of the genotype and environment.
2. Environmentally induced phenotypic differences are not passed to offspring, but the environment can affect expression of genes.
3. Genes are particulate, but their effects are combined in the organism. They can have discrete effects on the phenotype or through interactions with other genes produce continuous variation.
4. Genes mutate forming alternative alleles. Mutations can have large or small effects on the phenotype.

5. Environmental factors (chemicals, radiation) can cause mutation, but the mutations are not directed - they are not necessarily adaptive.
6. Evolutionary change is a population process.
7. The rate of mutation is too low to cause significant evolutionary change. Genetic drift and natural selection result in change in the proportions of alleles.
8. Slight phenotypic differences can result in differences in fitness and rapid evolutionary change.
9. Selection can produce phenotypic variation beyond the range of variation in the original population.
10. Natural populations are genetically variable.

11. Geographically discrete populations often have different allele frequencies.
12. Differences between populations, or between closely related species, usually have a genetic basis.
13. Natural selection can be demonstrated in natural populations.
14. Differences among geographically discrete populations are often adaptive.
15. Species are reproductively isolated.
16. Reproductive isolation among populations varies from slight to complete. Populations are in various stages of speciation.

17. Speciation usually occurs through geographic separation of populations.

18. Variation between species, genera, families, etc. is graded. Higher taxa appear to arise through successive accumulations of small differences.

The evolutionary synthesis also accounted for the patterns of evolution seen in the fossil record:

19. The fossil record is incomplete, but has many examples of gradual evolution of organisms very different from their ancestors. Higher taxa can develop through evolutionary time through the accumulation of small differences.

20. The fossil record is consistent with a Darwinian model of evolution. LaMarckian, orthogenetic, and mutationist ideas of evolution are not necessary, and lack evidence to support them.