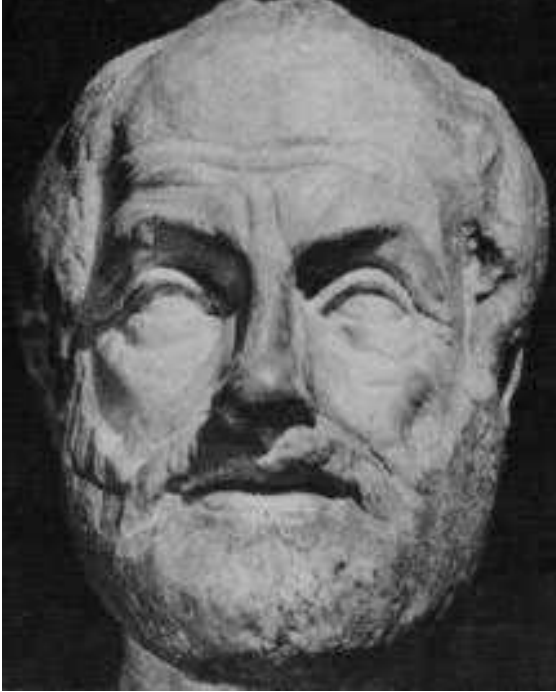

History of Evolutionary Thought



The Chain of Being

Aristotle (384-322 BC) was a Greek philosopher, who examined the natural world for evidence of a divine order. Aristotle devised a hierarchical arrangement of natural forms, termed the "Scala Naturae" or Chain of Being.

Species were arranged in a linear fashion along a scale: God, man, mammals, egg-laying animals, insects, plants, and non-living matter.

Aristotle's ideas formed the basis for the western belief in a fixity of species, each of which has a typical form.



Father of Modern Taxonomy

Carolus Linnaeus (1707-1778 AD) classified organisms following a binomial system of nomenclature, giving each species a specific and generic name [e.g. Homo sapiens (Genus species)].

Although his classification was largely based on morphology, Linnaeus recognized a fundamental difference between organisms that could interbreed (within a species) and those that could not (different species).

His classification system departed from the chain of being and reflected a nested series of relationships. The modernized Linnaean system is: Kingdom, Phylum, Class, Order, Family, Genus, Species.

Linnaeus believed in a balance of nature, within which each species had its place. Since this balance was thought to reflect a divine plan, Linnaeus originally believed that species would neither change nor go extinct.

Linnaeus later recognized that new species may occasionally arise, particularly through hybridization. One of Linnaeus' students first described a new species formed by hybridization in toadflax.





Degénération

Georges-Louis Leclerc, Comte de Buffon (1707-1788 AD) believed that the origin of life and species followed a material process, and looked to the physical and biological world for clues to this process.

In 1766, Buffon argued that the relationships among species in the Linnaean system of classification reflected common descent ("degénération"), with divergence over time.

Buffon placed great emphasis on the physical environment, which was thought to direct (somehow) the organic changes leading to a new species. The speciation process was thus caused by individual migration to new geographical locations, wherein the environment would cause changes to the organic particles.

Nevertheless, Buffon thought that the extent of divergence was limited to within a family. Each family had its own internal "mold" to which every species conformed, but species could change over time to some degree.



Organic life beneath the shoreless waves
Was born and nurs'd in ocean's pearly caves;
First forms minute, unseen by spheric glass,
Move on the mud, or pierce the watery mass;
These, as successive generations bloom,
New powers acquire and larger limbs assume;
Whence countless groups of vegetation spring,
And breathing realms of fin and feet and wing.

Erasmus Darwin
The Temple of Nature (1802)

Erasmus Darwin (1731-1802) was a leading philosopher, naturalist, and physician in 18th century Britain, who wrote one of the first treatises on evolution: *Zoonomia: Or The Laws of Organic Life* (1794-1796). He was also the grandfather of Charles Darwin.

Erasmus believed in the self-improvement of a species, through a constant effort to adapt to the environment (*transformism* or *transmutation*). He argued that life consisted of "one living filament", connecting all current forms to one common ancestor.



Inheritance of Acquired Characters

Jean-Baptiste Lamarck (1744-1829) was a French professional naturalist, who also developed a theory of transformism.

Lamarck believed in organic progression, whereby organisms would evolve through a hierarchy of more and more advanced forms. At the base of this hierarchy, "simple" organisms were constantly arising via spontaneous generation.

"Nature, in producing in succession every species of animal, and beginning with the least perfect or simplest to end her work with the most perfect, has gradually complicated their structure."

The mechanism by which organisms advanced and adapted to changing circumstances was described in Lamarck's *Philosophie zoologique* (1809):

Lamarck's "First Law":

The use or disuse of a structure would lead to its development or diminishment.

Lamarck's "Second Law":

Such acquired characters could be passed to offspring (heritable).



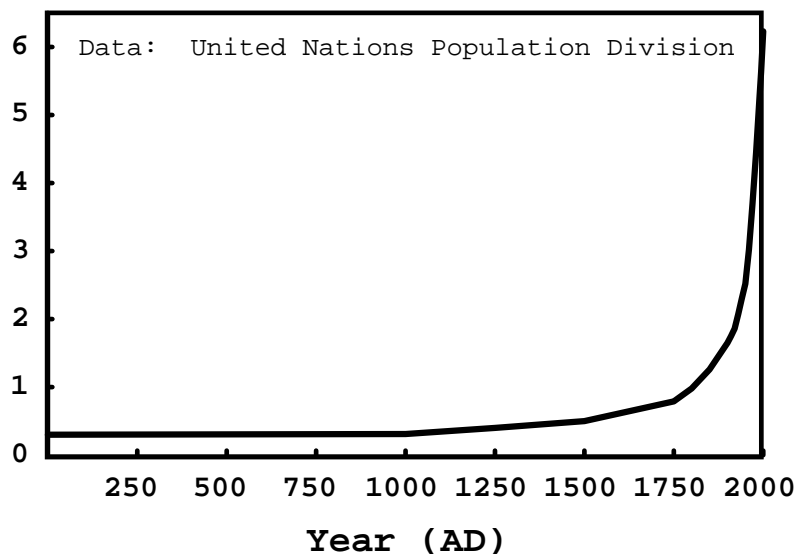
Principle of Overproduction

Thomas Malthus (1766-1834) was an English clergyman, whose writings on population growth had a strong influence on the theory of evolution by natural selection developed by Charles Darwin and Alfred Russel Wallace.

In *An Essay on the Principle of Population* (1797), Malthus observed that most organisms produce far more offspring than can possibly survive.

Even when resources are plentiful, the size of a population tends to increase geometrically until the population outstrips its food supply. This led Malthus to believe that poverty, disease, and famine was a natural and inevitable phenomenon, leading to a "struggle for existence".

**Historic World
Population Size
in Billions**





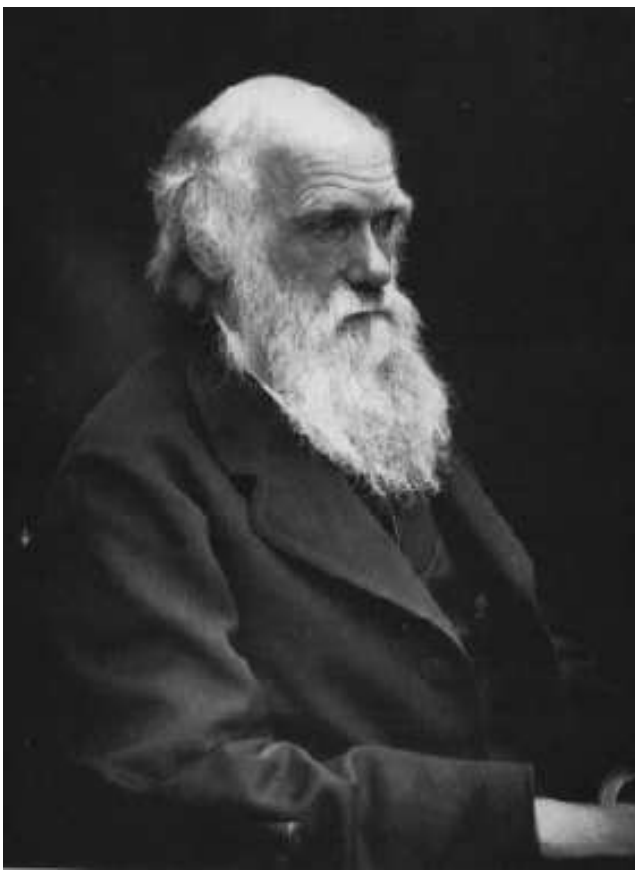
Uniformitarianism

Charles Lyell (1797-1875) was an English geologist, whose *Principles of Geology* influenced both Darwin and Wallace.

Lyell believed that the earth was constantly changing and that the processes that had molded the earth's surface could be understood from current-day geological activities.

Lyell held a "uniformitarian" view of the world, meaning that the world was subject to gradual and continuous change. Yet, there was no progress or development over time in Lyell's world-view. The earth simply remained at steady-state.

Lyell's position suggested that the world had always been (roughly) similar to its current state. In particular, Lyell believed that the species composition of the world remained unchanged, with at least some members of all classes of organisms existing throughout the history of the earth.



Evolution by Natural Selection

Charles Darwin (1809-1882) was an English naturalist, a prolific writer, and a gentleman of private means that allowed him to focus on his life's work: the development of the theory of evolution by means of natural selection.

As a young man, Darwin was enlisted as a companion and naturalist aboard the H.M.S. Beagle (1831-1836). His voyage took him around the tip of South America to New Zealand and Tasmania.



Darwin read Lyell's Principles of Geology while on board the Beagle and came to accept Lyell's view that long-term geological processes were responsible for shaping the earth's surface in a gradual manner. Indeed, Darwin successfully applied uniformitarianism to explain the development of coral reefs.

Biogeography

Perhaps the single-most important influence on Darwin's intellectual development was an appreciation, developed during the voyage, for biogeographical patterns.

Darwin noticed that two similar species (e.g. two species of rhea, a South American flightless bird) would often co-exist within a boundary zone. Within this zone, clearly neither species was superior and especially created to match the local circumstances. Instead, the species must compete with each other for survival within this territory.

Darwin also noticed that barriers, especially oceanic barriers, often led to distinctly different groups of species on different land masses. Why is the rhea of South America so different from the ostrich of Africa when the two have such similar lifestyles under such similar circumstances? Clearly, migration across oceans was limited, but why would a creator be limited by such boundaries?

It was Darwin's visit to the Galapagos islands, hundreds of miles west of South America, that would most clearly lead to Darwin's views on the origin of species. Darwin puzzled over the fact that the giant tortoises from different islands were distinct from one another -- why would there be a separate creation of such similar forms on islands so close to one another?

Darwin was also impressed by the great diversity of finch species on the islands, although Darwin had difficulty classifying the finches and thought that his collection contained a wide assortment of birds including wrens, grass-beaks, and black-bird relatives. [It later turned out that all these specimens were closely related and represented a remarkable diversification of finch species].



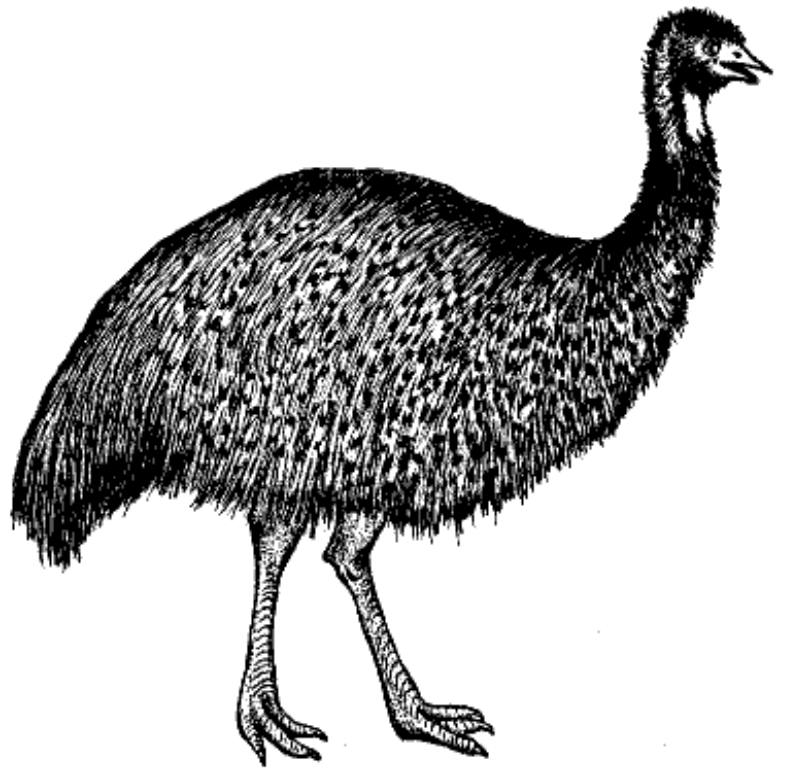
© Scott Henderson



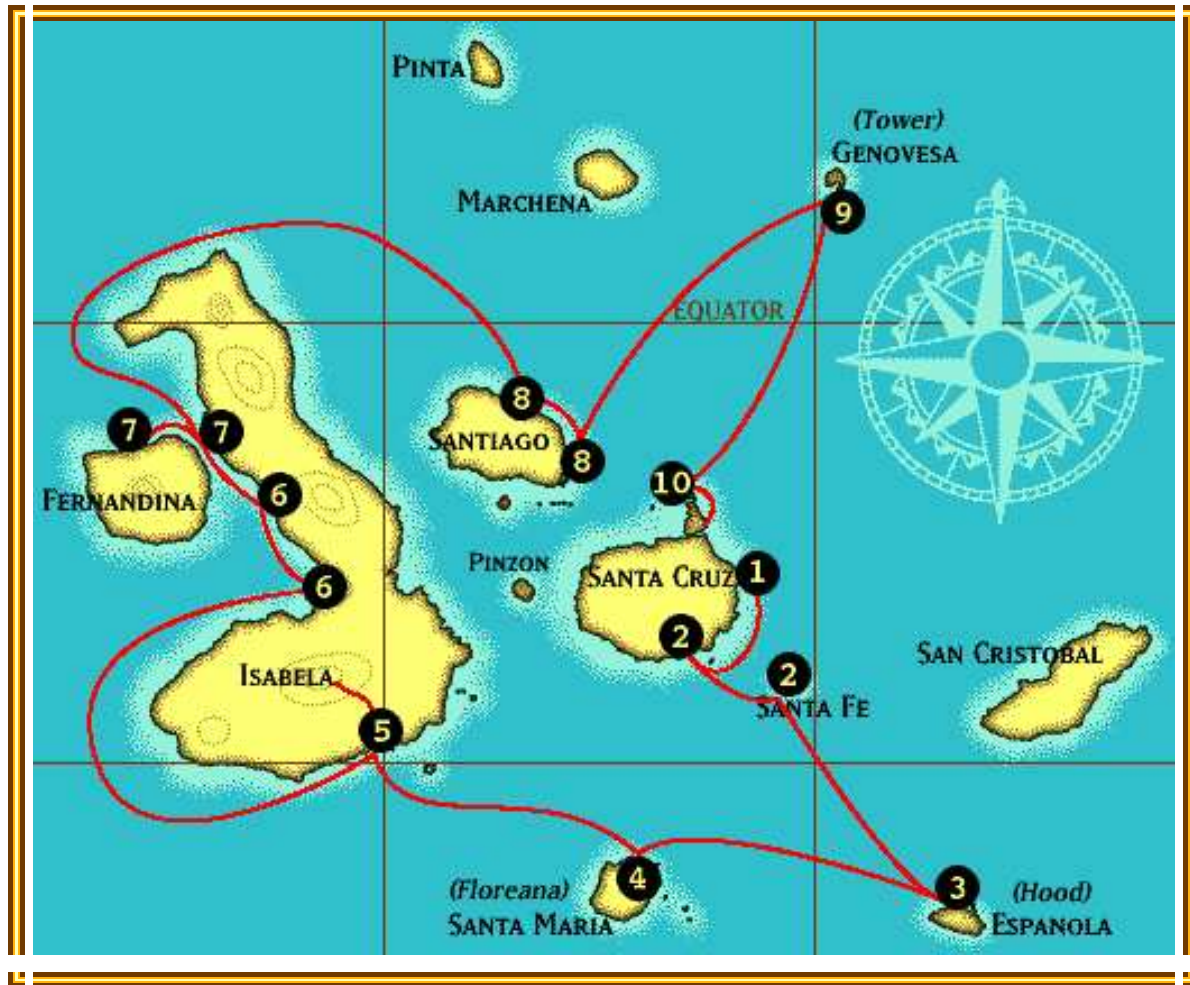
Rhea



Ostrich



Emu



Area:

Total area (sea): 45,000 square kilometers. Total land area: 7882 square kilometers

Size:

430 kilometers long, from Darwin Island in the northwest to Española in the southeast.

Islands:

13 major (above 14 square kilometers, 5 square miles); 8 smaller islands above .12 square kilometers. (.5 square miles); 40 named islets. Major islands include: Española, Fernandina, Genovesa, Isabela SouthWest/ SouthEast/ Central/ North, Marchena, Pinta, Pinzon, San Cristóbal, Santa Cruz, Santa Fé, Santa Maria, Santiago.

Darwin did recognize the differences between mockingbirds on different islands that he visited and wrote:

"When I see these Islands in sight of each other, and possessed of but a scanty stock on animals, tenanted by these birds, but slightly differing in structure and filling the same place in Nature, I must suspect they are only varieties....If there is the slightest foundation for these remarks the zoology of Archipelagoes - will be well worth examining; for such facts would undermine the stability of Species."
Darwin's Ornithological Notes (1836), p. 262 (Barlow, 1963)



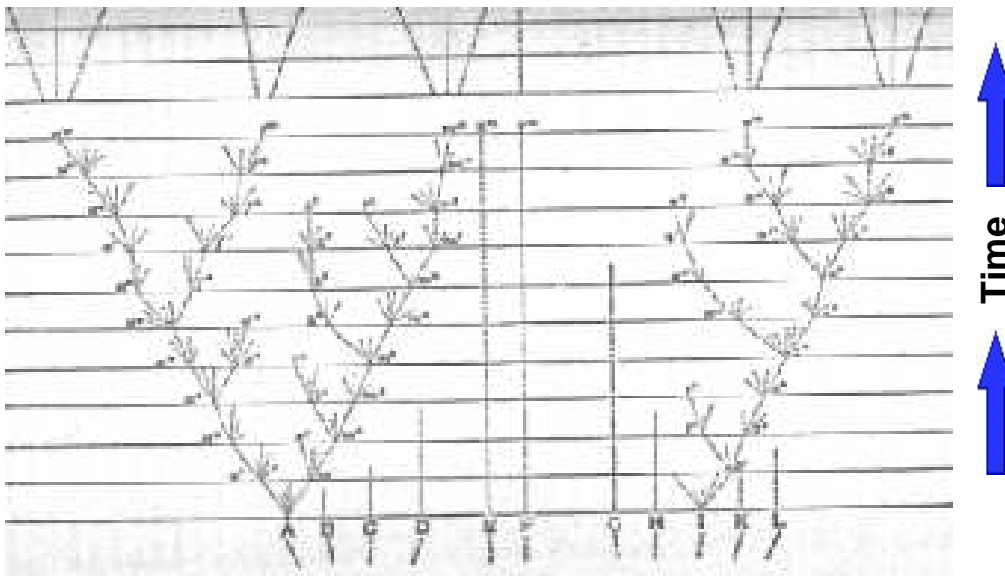
Returning to Britain, Darwin gradually developed his theory concerning natural selection. He recognized several critical facts:

- Variability exists within species
- Variant traits may be inherited [Darwin did not, however, know how.]
- From Malthus' principle of overproduction, many individuals must often die or fail to reproduce. In this "struggle for existence", variants that were slightly better suited to the environment would be more likely to survive.

It then follows logically that certain variants will be preserved over time over other variants and that populations will change over time in their composition. This is *evolution by natural selection*.

Thus, by 1838, Darwin came to believe in transmutation, which was neither directed by the will of the individual (as believed by Lamarck) nor by direct oversight of a creator.

As each population changes by natural selection, geographically isolated populations would become more and more different from one another ("divergent"). Darwin believed that this would initially lead to different varieties within a species. Eventually, with sufficient time and divergence, evolution by natural selection would also lead to new species and higher taxonomic divisions, in an ever branching process.



From: Origin of Species (Chapter 4)



Natural Selection Co-Discovered

In 1858, Alfred Russel Wallace (1823 - 1913) sent Darwin a manuscript from the Malay archipelago (Indonesia) describing Wallace's independent discovery of evolution by natural selection.

Wallace, unlike Darwin, was relatively poor and supported himself and his world-wide travels by capturing and selling specimens. Like Darwin, Wallace travelled to South America and throughout the Pacific.

Observing biodiversity and biogeography first hand was also critical to the development of Wallace's views. (QUOTE)

Charles Lyell and Joseph Hooker quickly arranged for both Darwin's and Wallace's views to be presented at the meetings of the Linnean Society in London in 1858.

The next year, Darwin published The Origin of Species by Means of Natural Selection. The depth and breadth of Darwin's book, developed over twenty years of thought and research, revolutionized science.

"At the time in question I was suffering from a sharp attack of intermittent fever... One day something brought to my recollection Malthus's "Principles of Population", which I had read about twelve years before. I thought of his clear exposition of "the positive checks to increase" - disease, accidents, war, and famine - which keep down the population of savage races to so much lower an average than that of more civilized peoples. It then occurred to me that... as animals usually breed much more rapidly than does mankind, the destruction every year from these causes must be enormous in order to keep down the numbers of each species... Vaguely thinking over the enormous and constant destruction which this implied, it occurred to me to ask the question, Why do some die and some live? And the answer was clearly, that on the whole the best fitted live. From the effects of disease the most healthy escaped; from enemies, the strongest, the swiftest, or the most cunning; from famine, the best hunters or those with the best digestion; and so on. Then it suddenly flashed upon me that this self-acting process would necessarily improve the race, because in every generation the inferior would inevitably be killed off and the superior would remain - that is, the fittest would survive."

-- Wallace (1905; My Life) describing his discovery in 1858



Mendelian Genetics

The greatest weakness in the theory of evolution by natural selection was the fact that Darwin and Wallace knew neither how variation among individuals was generated nor how it was inherited.

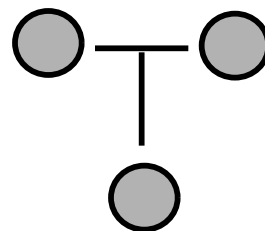
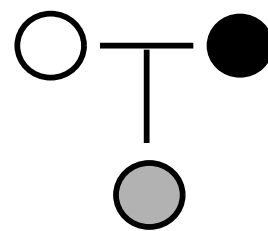
The rediscovery of Gregory Mendel's work by Carl Correns and Hugo deVries in 1900 clarified the laws of inheritance, at least for discrete characters (such as pea color).

Mendelian rules explain why offspring tend to resemble parents.

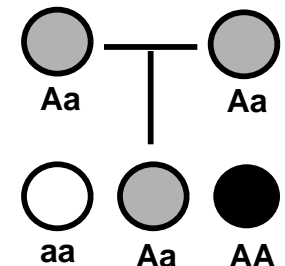
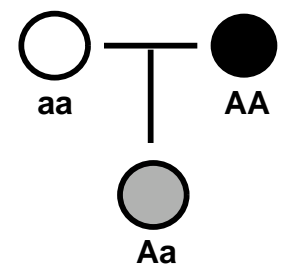
Mendelian genetics has one important characteristic: variation is not lost over time simply due to reproduction.

In contrast, with blending inheritance, offspring are the average of their parents and a diverse parental generation will be followed by a less diverse offspring generation.

Blending Inheritance



Mendelian Inheritance

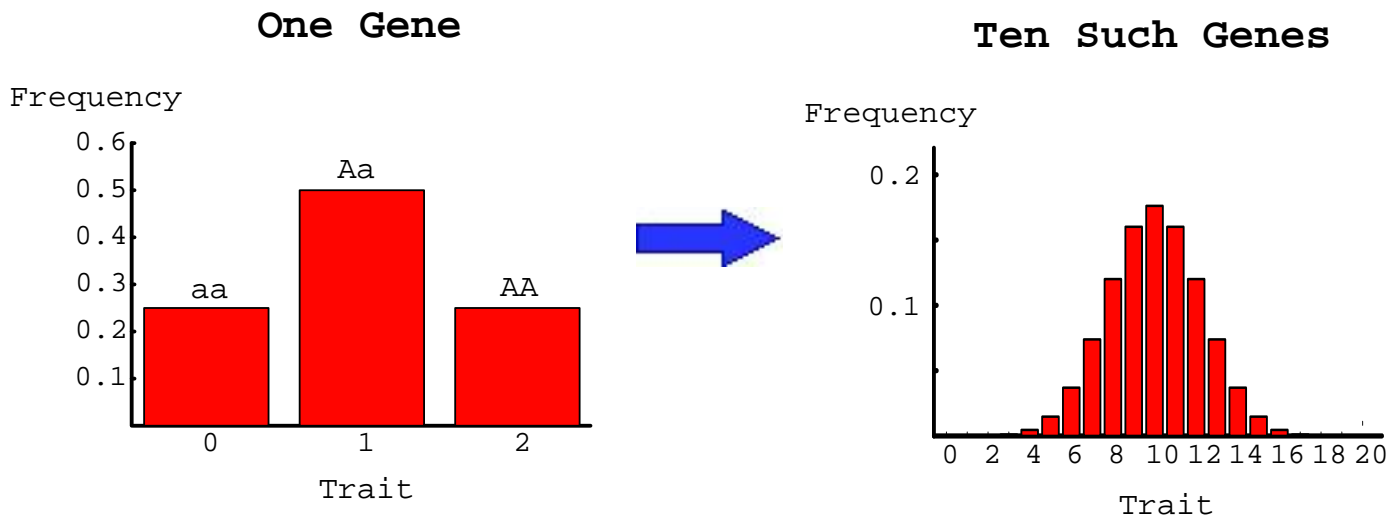


Yet, it remained unclear whether Mendel's rules applied to continuously varying traits, such as height and weight.



Uniting Mendelian and Quantitative Genetics

In 1918, Ronald Aylmer Fisher (1890-1962) demonstrated that a large number of Mendelian characters (genes) influencing the same trait would lead to a nearly continuous distribution of trait values. The frequency distribution of traits would then look approximately normal (i.e. like a bell), as is the case for traits such as height and weight.



(We'll talk more about Fisher and other important 20th century evolutionary biologists throughout the term.)