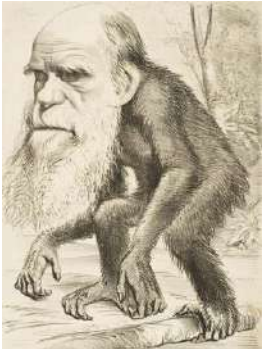
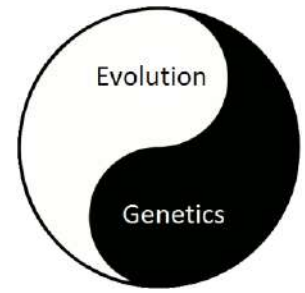


Chromosomes, Mendelism and Darwinism

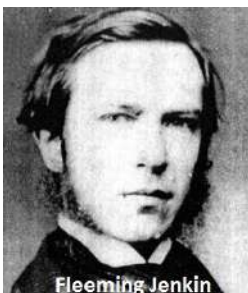
Historically and conceptually, modern Genetics and modern Evolutionary Theory are closely intertwined. Mendel and Darwin both published their masterpieces in the mid-1800s and both were promptly misunderstood, discarded and forgotten for almost half a century. Both were resurrected around the same time.



Darwin subscribed to a “blending theory” of inheritance by mistakenly believing in the inheritance of acquired characteristics including the “effects of use and disuse” That is correct; Darwin's theory of genetics, called “Pangenesis”, is no different than what textbooks today would call “Lamarckism”. Darwin shared Lamarck's belief that reproductive tissue somehow responded directly to environmental stimuli in order to generate adaptive changes in the next generation.

<http://www.literature.org/authors/darwin-charles/the-origin-of-species/chapter-05.html>

Historical irony is compounded further, upon consideration that Gregor Mendel, a (frustrated and perhaps sexually preoccupied?) celibate Catholic clergyman clearly recognized that sexual reproduction necessarily contradicted “blending inheritance”. Consider the offspring of any couple; individuals of the next generation are decidedly masculine or feminine and not intermediate. (Please – No gratuitous Michael Jackson jokes! – Let the poor man rest in peace...). Accordingly, we are supposed to believe that Mendel's new laws should have been able to rescue Darwin's theory, had Darwin only known.



True, Mendel's cerebral work was theoretical and his convoluted purple prose almost incomprehensible. But, there was little chance that Mendel's principles, predicated on the peculiarities of pea plants would have ever been acknowledged “Scientific Law” at the time. Animal genetics (human genetics in particular) appeared to follow a different and non-particulate; in other words, decidedly non-Mendelian model. The offspring of African and European

parents present a “mixed-race”, i.e. apparently “blended” phenotype. Henry Charles Fleeming Jenkin (inventor of the cable-car) “conclusively” contradicted Darwin with a decidedly racist rebuttal – so egregiously racist in fact, that modern textbooks refrain from even whispering a mention of that nasty exchange. Darwin had already conceded that “blending inheritance” contradicted Natural Selection but was unable to resolve the discrepancy.

In correspondence with Wallace, Darwin himself appreciated that a correct and proper appreciation of genetics was required to rebut Fleeming Jenkin. Here is Jenkin's rebuttal to a later edition of Darwin's Origin of Species:

... Suppose a white man to have been wrecked on an island inhabited by negroes.... Our shipwrecked hero would probably become king; he would kill a great many blacks in the struggle for existence; he would have a great many wives and children, while many of his subjects would live and die as bachelors.... Our white's qualities would certainly tend very much to preserve him to good old age, *and yet he would not suffice in any number of generations to turn his subjects' descendants white*.... In the first generation there will be some dozens of intelligent young mulattoes, much superior in average intelligence to the negroes. We might expect the throne for some generations to be occupied by a more or less yellow king; but can any one believe that the whole island will gradually acquire a white, or even a yellow population ...?

Here is a case in which a variety was introduced, with far greater advantages than any sport every heard of, advantages tending to its preservation, and yet powerless to perpetuate the new variety. – North British Review, June 1867, 46:277-318.

Darwin said that this objection gave him more trouble than any other. "Blending inheritance" indeed contradicts Natural Selection obliging Darwin to propose his alternative model of "particulate inheritance". Darwin suggested a hypothesis called Pangenesis, in which parts of the body emitted "gemmules" that accumulated via the circulatory system in the gonads by passing through the circulatory system. Heredity has something to do with "bloodlines".

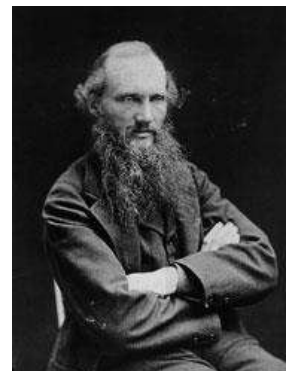


Francis Galton the great Victorian polymath (and Darwin's cousin) experimented with different lines of rabbits and determined that blood transfusions did not change their inheritance. <http://galton.org/hereditarian.html>

Of course, not all organisms have circulatory systems, so Darwin invoked other means of transport were also possible such as simple diffusion.

Modification of inherited characters as selected by natural selection would then require modification these gemmules. How were these gemmules to be modified? Darwin proposed that parental response to the environment impacted gemmules which were then passed on to the next generation. This is starting to sound a lot like what modern textbooks incorrectly call Lamarckism.

To make matters even worse, the great Lord Kelvin (in whose great honor a brand new temperature scale had been named) toppled the other pillar of Evolutionary Theory; namely "geological time". Shortly after Darwin's publication, Lord Kelvin calculated the age of Earth to be a mere 20 million to 400 million years. Our planet at some point was a molten sphere, which means it must still be relatively early in its process of cooling. Kelvin's calculations were indeed precise, but grossly inaccurate; as they failed to account for the heat generated by radioactive decay.

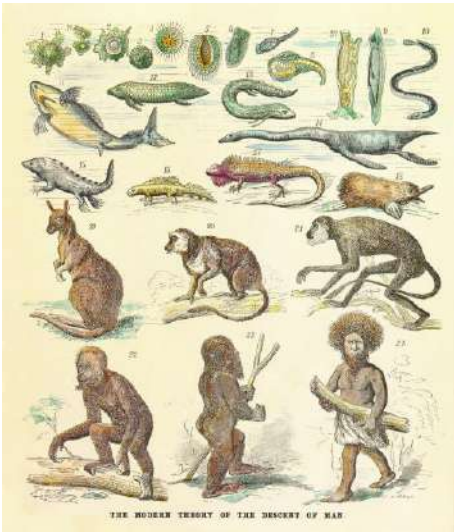


The inexorable accumulation of stable and heritable variability constituted one half of Darwin's great Theory. Natural Selection constituted the other. Darwin and his supporters knew Evolutionary Theory just had to be true. If Victorian English farmers can produce novel breeds of pigeons; then, Natural Selection can produce new species! The devil was in the details, requiring resolution by pursuing further scientific inquiry. The millstones of scientific progress sometimes grind slowly. Another fifty years were required before neo-Darwinism rose again like a phoenix.

To recap: the specious Darwin vs. Lamarck dichotomy so often misrepresented in

current textbooks is actually a vestige of a much later Neo-Darwinism vs. Neo-Lamarckism debate that arose latter in the 20th Century. Several historians, including [Stephen Jay Gould](#), have contended that modern textbooks unjustly deal Lamarck a bad rap. Lamarck still deserves credit for championing biological evolution, as opposed to biblical constancy; even if Lamarck did misconstrue genetics, not to mention getting the mechanism of evolution all wrong. Lamarck believed the inheritance of characteristics was a direct response to environment; a response acquired through effort, or will. (Remember those hungry giraffes stretching their necks.)

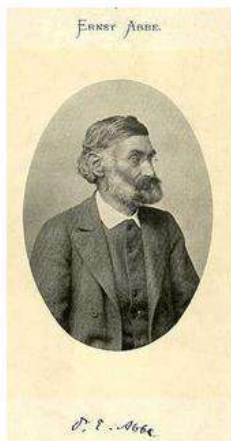




Darwin's original "Pangenesis" in many ways resembles Lamarck's version of events; Darwin also took for granted the misconceived "effects of use and disuse". Darwin however did part paths with Lamarck on one key point: Lamarck embraced metaphysics, by imagining evolution to be a goal-driven process or "teleological". Darwin, instead recognized the capricious randomness of the natural order. According to Darwin, Evolution does not correspond to some specious "vector of progress", otherwise known as the "Scala Naturae" as espoused by Lamarck, Haeckel and others.

Towards the end of the nineteenth century the discovery of chromosomes heralded the dawn of a golden era in Biology. August Weismann's uncanny intuitions recoupled genetics to evolutionary theory. Many biologists call Weismann the father of Neo-Darwinism and consider the importance of his contributions, as second only to those of Darwin.

Here is a brief recap of events that lead to Weismann's insights:



Thanks to Ernst Abbe and Karl Zeiss, advances in microscopy allowed scientists to view fine cell structure within cells. Zeiss lenses are still today considered (by many, especially self-conscious Germans) the best in the world!

In the meantime, great leaps forward had just occurred in Organic Chemistry. The characterization of aniline dyes presaged the evolution of a burgeoning dye industry in Germany: BASF, originally "Badische Anilin- und Soda-Fabrik" still remains one of the world's largest providers of chemicals. Members of the "X generation" may still recall the BASF [cassette tapes](#) often inserted into SONY's original [Walkmen](#) before the advent of digital technology. The availability of these new basophilic aniline dyes permitted the visualization of "chromosomes" (Greek for "colored bodies") as first characterized by Heinrich Wilhelm Gottfried von Waldeyer-Hartz.

The father of Cytogenetics has an easier name to remember: Walther Flemming, who first described the process he coined "mitosis". Eduard Strasburger, a great Plant physiologist, identified "nucleoplasm" and "cytoplasm". Strasburger and Flemming, are both credited with the realization that "new cell nuclei can only arise from the division of other cell nuclei". This view contradicted another great German Botanist named Matthias Schleiden (familiar to most students as the great collaborator of Schwann). Schleiden believed that cell nuclei were "cell pregnancies".

Preliminary investigations in chromosome behavior during gametogenesis were independently made by Oscar Hertwig and by Edouard van Beneden. Van Beneden parenthetically, would be appalled to be misidentified as yet another German. He was Belgian and may have been the first to add "chromatin" to the biological lexicon;

unless you subscribe to a German version of events, who credit Walther Flemming with that distinction.



August Weismann was an intellectual giant who built on the observations of his predecessors and was the first to integrate all these accomplishments into a rescue of Darwin's great idea. Weismann was the first to recognize that two cell divisions (the first "reductional" and the second "equational") were necessary to transform one diploid cell into four haploid cells if chromosome number was to be maintained from generation to generation. With a tip of the hat to his compatriot and colleague Flemming, Weismann identified cellular division during gametogenesis as "meiosis".

The Each species' chromosomes are distinguishable in number and physical appearance. At times when cell division is not imminent, chromosomes appear as a diffuse network of fine threads within the nucleus referred to as chromatin.

When cell division nears, chromatin of each chromosome condenses to form the distinguishable structures that can help characterize a species.

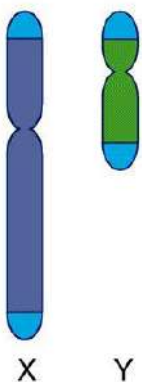
Some regions of the chromatin are dark staining and are more tightly packaged during interphase than other regions. These are called heterochromatin. Euchromatin is less densely packaged when compared to heterochromatin.

- Hetero means different.
- Eu means true.

Chromosomes, except sex chromosomes, exist in pairs in diploid organisms like humans and garden peas.

Gametes have just half the number and are called haploid.

Many plants and animals tolerate a change in the number of complete sets of chromosomes.



If there are four sets, the organism is called a tetraploid.
If eight sets, the organism is called an octoploid.

Chromosomal Theory of Heredity

Around 1910, biologists began to suspect that genes were associated with chromosomes.



Sutton



Boveri

By 1902 the chromosome movements during meiosis had been worked out, and Walter Sutton (an American) and Theodor Boveri (a German) used them to explain Mendel's laws

It was suspected that genes were composed of protein. Chromosomes are composed of protein as well as DNA. It was observed that during meiosis chromosomes behaved like Mendel's elements of inheritance.

Thomas Morgan



Thomas Morgan, a fly guy as we call people that work with *Drosophila* these days, helped prove the Chromosome Theory of Inheritance.

Morgan was an underfunded scientist working in a tiny lab. He conducted research on a broad range of topics. Interestingly, he initially doubted the importance of Mendel's research and Mendelian genetics. It was Morgan's research that proved the relationship of Differences in chromosome constitution make *drosophila* either male or female. This would constitute the so-called exception that proved Mendel's (& Sutton's) rule!

Sex chromosomes are an exception to the pair rules for diploids

Females have a pair of sex chromosomes but males have a mismatch set, an X and what is called a y. (In fact the y-chromosome looks like a small X chromosome when viewed with a microscope.)

Males of some species have an O, not a y chromosome. The O actually denotes no chromosome at all.

In humans, sperm carry either an X or a Y, not both.

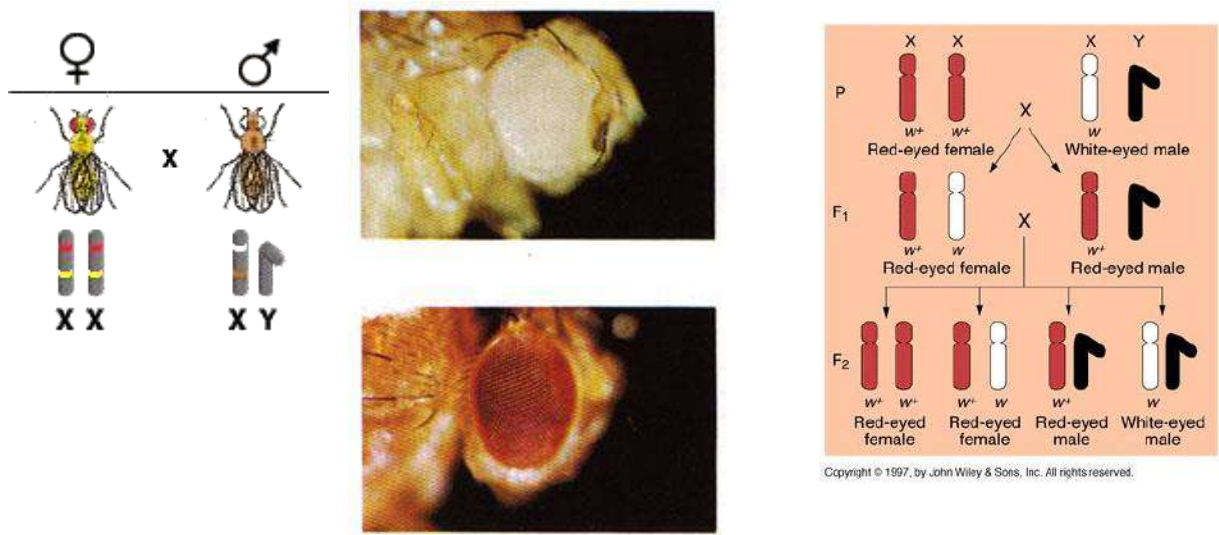
Therefore, in humans, sex is dictated by the sperm that penetrates the egg.

Too bad nobody told Henry VIII <http://www.youtube.com/watch?v=-fadCAHjN-s&hl=fr>

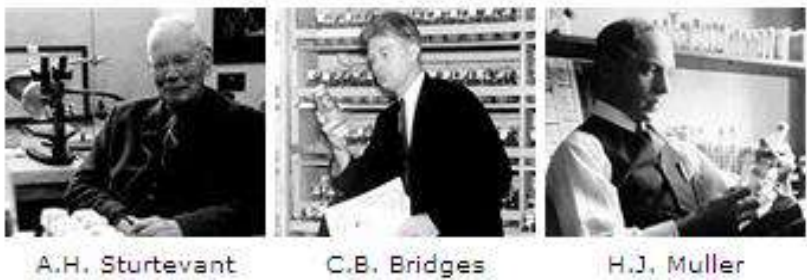
Here is another version: <http://www.youtube.com/watch?v=BpbdcI5HAYg>

In birds, honeybees and insects – things get more complicated.

Sex-linked inheritance was an important contribution to genetics.



Morgan not only changed his position on Mendel's theory, but he and his colleagues made startling discoveries, which firmly established that the genetic information resided on the chromosomes. With his students Alfred Henry Sturtevant, Calvin Blackman Bridges, and Hermann Joseph Muller, he established what is now called classical genetics.



Later, Morgan and his former students became key scientists in the development of the then new science of mutagenesis. Morgan with another important scientist even developed a means to map the locations of genes to positions on chromosomes. We shall learn this method in another section