# Evolution: The Darwinian Revolutions

## BIOEE 2070 / HIST 2870 / STS 2871

**DAY & DATE:** **Monday 9 July 2012**

**READINGS:**
- **Jenkin, F. (1867) Review of the Origin of Species. *The North British Review* (June 1867), volume 46, pages 277 to 318**
- **MacNeill/*Evolution: The Darwinian Revolutions* chapters 8 & 9**
- **Provine, W. (1971) *The Origins of Theoretical Population Genetics*. University of Chicago Press, chapter 5, pages 130 to 178**
- **Ruse/*Darwin and Design: Does Evolution Have a Purpose?* chapter 7**

**Lecture 6:00-7:50:** **Genetics and Evolution**

**Section 8:00-9:00:** **Discussion of genetics and evolution**

## Announcements:

### • Essay #1 is due TODAY!

**If you have not already done so, please save your essay as a MicroSoft Word .doc or .pdf and send it to me or your TA as an email attachment *tonight!* It would also be a good idea to copy the entire essay and paste it into the body of the email, just in case. We will grade your essays and return them to you as soon as possible, with comments and a letter grade.**

### • Essay #2 has been assigned today. It is due on Monday 23 July 2012 at 6:00 PM.

**You can pick up a paper copy in class, or download one from the course website at:**

**http://evolution.freehostia.com/essay-questions**

### • Some of the readings for this section of the course are available at the course website:

**Behe, M. (1998) Intelligent design as an alternative explanation for the existence of biomolecular machines (unpublished manuscript)**

**Dobzhansky, T. (1973) Nothing in biology makes sense except in the light of evolution. *American Biology Teacher*, March 1973, volume 35 pages 125 to 129**

**Kaviar, B. (2003) A history of the eugenics movement at Cornell. 2003 Tallman Prize winner. (unpublished manuscript)**

**Mayr, E. (1982) *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, chapters 12 and 13**

**Provine, W. (1971) *The Origins of Theoretical Population Genetics*, chapter 5**

**Look for them in the "Course Packets" section of the course website at:**

**http://evolution.freehostia.com/course-packet/**

**The password for the course packets is:**

**evolutioncp**

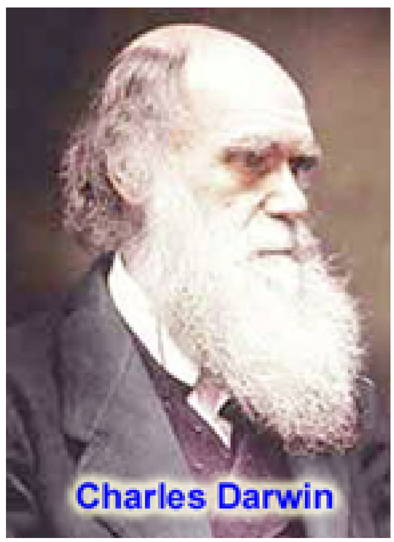
# Evolution After Darwin

**In your first essay, you wrote about the concept of adaptation and its relationship to the theory of evolution by natural selection. We have already discussed how the concept of purpose is generally not included in scientific explanations, including the evolutionary explanation for the adaptations of living organisms.**

**However, many of you noticed that Darwin didn't explicitly write about purpose (or the lack of it) in the *Origin of Species*. Instead, he constructed his argument in such a way that purpose was not necessary, and was therefore not mentioned. The implication therefore, is that since it isn't necessary for a scientific explanation of the phenomena under investigation, then it is not included in such an explanation.**

**This leaves open the question of whether purpose exists in nature. It also leaves open the question of how scientists can describe complex natural processes without reference to purpose. It's time to examine both of these questions in more detail.**

## Natural Selection: A Brief Review




**First, recall that Darwin described natural selection as the outcome of the interaction of four main processes, including:**

- **Variety among the members of populations: These variations need not be extreme, as illustrated by the relatively large changes that animal and plant breeders have accomplished, using relatively slight differences in physical appearance and behavior.**
- **Heredity: The distinct variations noted above must be heritable from parents to offspring.**
- **Fecundity: Living organisms have a tendency to produce more offspring than can possibly survive. Among those individuals that do survive, those that also reproduce pass on to their offspring whatever characteristics made it possible for them to survive and reproduce.**
- **Demography: Non-Random, Unequal Survival and Reproduction: S urvival and reproduction are almost never random. Instead, individuals survive and successfully reproduce because of their characteristics. It is these characteristics that form the basis for evolutionary adaptations.**

## The Problem Of Variation

**Darwin began the presentation of his views on variation with this statement:**

- **"Our ignorance of the laws of variation is profound." (*Origin of Species*, 1st ed., pg 167/Wilson, pg 557)**

**Neither Darwin nor any of his contemporaries (that he knew of) had a coherent theory of heredity or variation. However, this was not an insuperable obstacle to Darwin. Instead of giving up his argument, he simply accepted as a given that many important traits of animals and plants *are* heritable (pointing again to the observable facts of inheritance in domesticated animals and plants). He also proposed that, although he had no explanation of how they arose, variations among the members of a species do indeed occur, and can provide the raw material for natural selection.**

**This tactic on Darwin's part was largely successful…for a while. His assertion that the huge diversity of living forms and their exquisite adaptations had evolved by "descent, with modification" was largely accepted by his scientific contemporaries. However, his assertion that natural selection was the mechanism by which this process had occurred was not nearly as widely accepted.**

**There were two reasons for this lack of acceptance:**

- **Many of Darwin's contemporaries believed in Lamark's assertion that acquired characteristics could be inherited through use and disuse. This process directly contradicts the blind and purposeless process of natural selection, and therefore "holds the door open" for purpose in evolution.**

- **The consensus among naturalists was that inheritance worked by "blending" the characteristics of parents, which would cause any incipient adaptations to be diluted out of existence.**

**This second objection to Darwin's mechanism of natural selection was almost fatal to his theory. For example, in an influential review of the *Origin*, written in 1867 by Fleeming Jenkin (a very well-respected English engineer and designer of the first trans-Atlantic telegraph cable), Jenkin pointed out that blending inheritance would eliminate variation within a few generations.**


**"However slow the rate of variation might be, even though it were only one part in a thousand per twenty or two thousand generations, yet if it were constant or erratic we might believe that, in untold time, it would lead to untold distance; but if in every case we find that deviation from an average individual can be rapidly effected at first, and that the rate of deviation steadily diminishes till it reaches an almost imperceptible amount, then we are as much entitled to assume a limit to the possible deviation as we are to the progress of a cannon-ball from a knowledge of the law of diminution in its speed. This limit to the variation of species seems to be established for all cases of man's selection." (Jenkin, 1867)**

**Remember that the variations that provide the raw material for natural selection must be "real" – that is, they must have significant effects on survival and reproduction, and they must persist from one generation to the next.**

**However, if all traits were blended from generation to generation, all of the distinctiveness of each variation would be lost and the population would remain essentially unchanged. This was what most naturalists of Darwin's time believed. Darwin got around this objection by proposing that large numbers of new variations (*i.e.* mutations) occur with each new generation. He called these "continuous variations," and eventually proposed a theory of genetic inheritance, which he called *pangenesis*, to explain how this could happen:**

- **In his book, *The Variation of Animals and Plants Under Domestication* (written in 1868, nine years after the first edition of the *Origin of Species*) Darwin proposed that all of the traits of organisms produced "particles" of inheritance, which he called "pangenes". According to Darwin, these pangenes could travel from the anatomical locations of the traits to the sex cells, where they could be passed on to the organism's offspring.**

The problem with Darwin's line of reasoning was that neither of these assertions matched what naturalists observed. The amount of variation that appeared with each generation, while significant, was not sufficient to explain why such variations would not eventually disappear as they were blended with other traits. Furthermore, Darwin's "pangenes" could not be detected, only inferred, nor could their observable effects be separated from the effects predicted by the theory of blending inheritance (not to mention that they would produce a form of inheritance indistinguishable from Lamarck's inheritance of acquired characteristics). Several experiments by Darwin's contemporaries produced results that contradicted Darwin's theory, and consequently it was not widely accepted, even by his closest colleagues.

Consequently, although most naturalists believed that descent with modification had occurred, they did not believe that it had occurred by natural selection.

## Mendelian Genetics

- "It requires indeed some courage to undertake a labour of such far-reaching extent; this appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms." –Gregor Mendel, *Experiments in Plant Hybridization* (1865)

At about the same time that Darwin was working out his ideas on natural selection and evolution, Gregor Mendel was working out a revolutionary new theory of genetics. Mendel was born in 1822 in Moravia, a province of the Austro-Hungarian Empire (now part of the Czech Republic). Because he was a peasant's son, Mendel was expected to return to the family farm after finishing his education. However, Mendel was not satisfied with all that he had learned. College, instead of answering his questions, instilled in him an insatiable curiosity about nature.

Gregor Mendel

Mendel had read Darwin's work but he did not believe Darwin's explanation of how characteristics of organisms are blended and passed on from generation to generation. Instead, Mendel observed that some offspring of some organisms had traits that were similar to only one parent, rather than being intermediate between both. He explained this phenomenon by assuming that heredity was determined by tiny, concrete bodies that were passed from the parents to the offspring via the reproductive cells. This would explain how some traits could remain unblended in the next generation.

Such thinking stemmed from Mendel's physics training. In physics, all of nature is considered to be subject to laws based on the existence of small particles of matter. The goal of a physicist is to learn about the laws that determine the behavior of the particles. An investigator can sometimes work out these laws through careful experimentation. Mendel believed that these same methods could be used to study inheritance in living things.

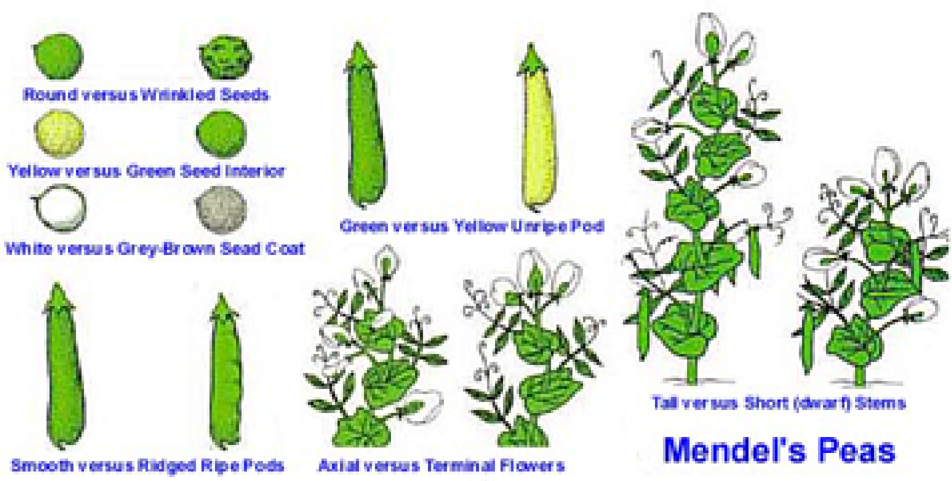
In his paper, "*Experiments in Plant Hybridization*" (*"Versuche über Pflanzen-hybriden"*), published in 1865, Mendel tells how he used the garden pea plant to study the laws of heredity. His techniques differed from those of other investigators in three ways: (1) Mendel looked at one trait at a time; (2) He followed this trait from generation to generation over eight years; and (3) He used larger numbers of organisms in his studies. At the end of his experiments, he had carefully observed over 12,000 plants.

## Particulate Inheritance

In his most famous set of experiments, Mendel studied 22 varieties of pea plants of the same species (*Pisum sativum*). He studied a total of seven different traits, each with two alternative forms:

- seed shape—which can be round (smooth) or wrinkled
- seed color—yellow or green
- seed coat color—white or greyish brown
- ripe pod shape—smooth or ridged
- unripe pod color—green or yellow
- flower position on the stem—along the sides or at the end
- stem height—either tall or short

Contrary to the account described in virtually all introductory biology textbooks, Mendel did *not* study the color of pea flowers – purple versus white – in his most famous set of experiments.




Mendel always began with plants that were true-breeding; that is, the forms of each trait were passed from parent to offspring without significant changes. Mendel then performed a series of controlled fertilizations, which geneticists call crosses. Some of these crosses were self-crosses—fertilization of a plant using its own pollen. Other crosses were cross-fertilizations—fertilization of a plant using pollen from another plant. In each cross-fertilization experiment, Mendel placed pollen from specific individual plants on the egg-containing parts of specific individual plants.

**Let's look at his results for the trait, seed shape, and its distribution from one generation to the next. Mendel took pollen from plants that produced round seeds and fertilized the flowers of plants that produced wrinkled seeds. He also did the reciprocal cross, taking pollen from plants that produced wrinkled seeds and fertilizing the flowers of plants that produced round seeds. The original true-breeding plants constitute the parental generation (abbreviated P). The offspring obtained from a cross are called the first filial generation (abbreviated $F_1$). All of the $F_1$ seeds obtained from this cross were round regardless of which plant provided the egg and which plant provided the pollen.**

**In the next growing season, Mendel planted the round seeds obtained from the first cross. He then allowed the plants produced from these $F_1$ seeds to self-fertilize, producing the second filial generation (abbreviated $F_2$). In this $F_2$ generation he obtained 5,474 plants that yielded round seeds and 1,850 plants that yielded wrinkled seeds. In his other experiments investigating the inheritance of the other six traits, he recorded similar proportions in the $F_2$ generation. All of the $F_2$ offspring were distributed in approximately a 3 : 1 ratio.**

## Dominance and Recessiveness

**Clearly, the two forms of these traits did not blend with each other. Mendel concluded that discrete units of heredity are transferred from parent to offspring. Among the offspring of the first cross (the $F_1$ generation) only one form of each trait showed up; the alternative form seemed to be lost. However, in the $F_2$ generation, the seemingly lost form showed up again. Mendel explained this result by saying that the lost form of each trait was actually latent or cancelled by the expressed form. He called the prevailing form of a trait "dominant" and the latent form of a trait "recessive".**

**Mendel's definitions of dominance and recessiveness are sometimes called**

- **Mendel's Law of Dominance: dominant traits mask the appearance of recessive traits whenever dominant and recessive traits are combined in one individual.**

## Genes and Alleles

**Mendel did not use a specific term to describe the "particles" of inheritance upon which he based his theory. The term "gene" was coined in 1909 by Danish botanist Wilhelm Johannsen to describe these fundamental physical and functional units of heredity.**

**In this example, the gene for seed shape has two different forms. One form produces round seeds; the other form produces wrinkled seeds. Different gene forms that produce different forms of a trait are called alleles (from the Greek *allos* for "other"). In this example, the allele that codes for round seeds is dominant to the the allele that codes for wrinkled seeds.**

## Genotype Versus Phenotype

**Like Mendel, geneticists often observe an organism's phenotype, the physical appearance of an organism that is the result of the way in which its genes are expressed (from the Greek *phainein* for "to appear" and *tupos* for "impression"). Phenotypes are stated in descriptive terms. For example, the phenotype of one of Mendel's pea plant could include tall stems and round, yellow seeds.**

**Mendel could only infer the pea plants' genotype, the underlying set of alleles that produces the organism's phenotype (from the Greek *genes* for "born" and *tupos* for "impression"). An organism's genotype consists of all of its alleles, which may or may not be reflected in its phenotype. The effects of dominant alleles are usually expressed in the phenotype; the effects of recessive alleles are expressed only when no dominant alleles for that trait are present. When analyzing genotypes, geneticists represent alleles by letters. A dominant allele is usually symbolized by a capital letter, whereas a recessive allele is symbolized by a lowercase letter.**

## Homozygous and Heterozygous

**Most large organisms, including nearly all plants, have two sets of genetic material, one set received from each parent during fertilization. Therefore, such organisms can have two alleles for each gene. If the two alleles are the same (whether dominant or recessive), then the organism is homozygous for that gene (from the Greek *homos* for "same" and *zugoun* for "to join"). If the two alleles are different, then the organism is heterozygous, and the dominant allele determines the phenotypic expression of that gene (from the Greek *heteros* for "different" and *zugoun* for "to join").**

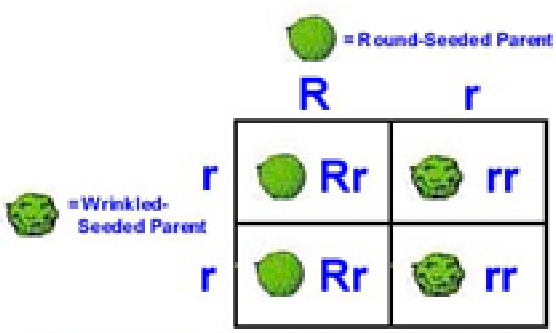
**Mendel observed that dominant and recessive forms of a trait did not become blended. Instead, the recessive form of the trait reappeared in an unaltered form in the $F_2$ generation. Based on this observation,**

- **Mendel formulated his Law of Segregation, which states that the different forms of a trait remain separate and unblended from generation to generation.**

## Punnett Squares

**A shorthand technique for predicting the outcomes of genetic crosses, developed by the English geneticist [Reginald Crundall Punnett], is the Punnett square method. In this method, the genotype of the gametes of one parent is listed down the left side of a square (the Punnett square), and the genotype of the gametes of the other parent is listed across the top of the square. The genotypes of the zygotes that could result from the combining of these gametes are indicated within the Punnett square.**

**For example, a cross between a heterozygous round-seeded pea plant and a homozygous wrinkled-seeded pea plant would be diagrammed like this:**




Punnett Square Showing a Cross of a Heterozygous Round-Seeded Pea with a Homozygous Wrinkled-Seeded Pea

**For his experiments, Mendel chose plants that, from experience, he knew would breed true and produce offspring with regular patterns (now called Mendelian patterns) of inheritance. Because his first major work was done with garden peas, which exhibit simple patterns of inheritance, he could clearly and convincingly validate his hypothesis concerning the units of heredity. Mendel was so convinced of the validity of his conclusions that his subsequent work with other plants, some of which failed to support his hypothesis, did not discourage him.**

**Mendel persisted in his own studies, although his contemporaries believed in a completely different theory of inheritance. Understanding how inheritance works and seeing that it can be explained by a few simple laws was sufficient for him. Mendel was a deeply religious man who believed in the importance of doing good for others. His genetics studies benefited the monastery and the surrounding community. He developed many different varieties of fruits and vegetables and, in his later years, studied the science of weather patterns. Based on his meteorological research, Mendel was able to predict the weather for the village farmers.**

**Late in his life, Mendel's time was mostly spent fighting political battles for the monastery and peasants of his village. In his lifetime, Mendel witnessed a complete change in his homeland. In his later years, the focus was no longer on agricultural advances but on political advances. The rise of the Hapsburg dynasty and the consolidation of the Austro-Hungarian Empire forced different values on the people. The days of intellectual freedom, when a monk could study agriculture in a monastery garden without interference by the government, were drawing to a close. Shortly before his death in 1884, Mendel said to a future abbot of the monastery:**

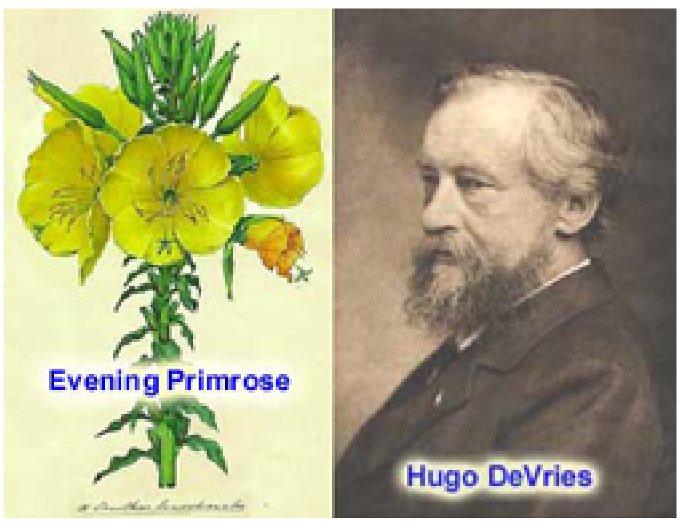
- **"Though I have suffered some bitter moments in my life, I must thankfully admit that most of it has been pleasant and good. My scientific work has brought me a great deal of satisfaction, and I am convinced that it will not be long before the whole world acknowledges it."**

## Evolution Via Mutation

**Mendel's belief that his work would eventually be recognized was not mistaken. In 1900, only fourteen years after his death, his work was simultaneously rediscovered by three different geneticists – Carl Correns, Erich Tschermak, and Hugo de Vries – working in three different countries. They realized that Mendel's particulate theory of inheritance fit patterns of inheritance they were observing.**

**It is interesting to speculate what Darwin would have thought had he known about Mendel's work. Genes that did not blend in each generation were the answer to Darwin's dilemma, and could have put him onto the right track as early as 1866, the year Mendel's most important paper was published. A copy of the journal containing Mendel's paper was found in Darwin's library at Down House, but it had not been opened or read.**

**There is an even deeper irony: the rediscovery of Mendel's work led geneticists to reject natural selection as the mechanism for evolution, in favor of mutations. Hugo de Vries, one of the rediscoverers of Mendel's work, proposed that "mutations" (*i.e.* changes in the phenotype of an organism, occurring in just one generation) were the primary "engine" of evolutionary change. De Vries did his pioneering work in genetics using the evening primrose (*Oenothera lamarckiana*), which is known for having sudden, large mutations in its overall phenotype.**




**De Vries argued that these kinds of mutations were the basis for the changes in phenotype to which Darwin referred in the *Origin of Species*, and that therefore natural selection was neither necessary nor likely as a cause of evolutionary change.**

**This mutational theory of evolution was accepted by most of the prominent geneticists at the turn of the century, and led to public testimonials that "Darwinism was dead."**