Introduction to Evolutionary Biology

Version 2

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Evolution is the cornerstone of modern biology. It unites all the fields of biology under one theoretical umbrella. It is not a difficult concept, but very few people -- the majority of biologists included -- have a satisfactory grasp of it. One common mistake is believing that species can be arranged on an evolutionary ladder from bacteria through "lower" animals, to "higher" animals and, finally, up to man. Mistakes permeate popular science expositions of evolutionary biology. Mistakes even filter into biology journals and texts. For example, Lodish, et. al., in their cell biology text, proclaim, "It was Charles Darwin's great insight that organisms are all related in a great chain of being..." In fact, the idea of a great chain of being, which traces to Linnaeus, was overturned by Darwin's idea of common descent.

Misunderstandings about evolution are damaging to the study of evolution and biology as a whole. People who have a general interest in science are likely to dismiss evolution as a soft science after absorbing the pop science nonsense that abounds. The impression of it being a soft science is reinforced when biologists in unrelated fields speculate publicly about evolution.

This is a brief introduction to evolutionary biology. I attempt to explain basics of the theory of evolution and correct many of the misconceptions.

What is Evolution?

Evolution is a change in the gene pool of a population over time. A gene is a hereditary unit that can be passed on unaltered for many generations. The gene pool is the set of all genes in a species or population.

The English moth, *Biston betularia*, is a frequently cited example of observed evolution. [evolution: a change in the gene pool] In this moth there are two color morphs, light and dark. H. B. D. Kettlewell found that dark moths constituted less than 2% of the population prior to 1848. The frequency of the dark morph increased in the years following. By 1898, the 95% of the moths in Manchester and other highly industrialized areas were of the dark type. Their frequency was less in rural areas. The moth population changed from mostly light colored moths to mostly dark colored moths. The moths' color was primarily determined by a single gene. [gene: a hereditary unit] So, the change in frequency of dark colored moths represented a change in the gene pool. [gene pool: the set all of genes in a population] This change was, by definition, evolution.

The increase in relative abundance of the dark type was due to natural selection. The late eighteen hundreds was the time of England's industrial revolution. Soot from factories darkened the birch trees the moths landed on. Against a sooty background, birds could see the lighter colored moths better and ate more of them. As a result, more dark moths survived until reproductive age and left offspring. The greater number of offspring left by dark moths is what caused their increase in frequency. This is an example of natural selection.

Populations evolve. [evolution: a change in the gene pool] In order to understand evolution, it is necessary to view populations as a collection of individuals, each harboring a different set of traits. A single organism is never typical of an entire population unless there is no variation within that population. Individual organisms do not evolve, they retain the same genes throughout their life. When a population is evolving, the ratio of different genetic types is changing -- each individual organism within a population does not change. For example, in the previous example, the frequency of black moths increased; the moths did not turn from light to gray to dark in concert. The process of evolution can be summarized in three sentences: Genes mutate. [gene: a hereditary unit] Individuals are selected.

Populations evolve.

Evolution can be divided into microevolution and macroevolution. The kind of evolution documented above is microevolution. Larger changes, such as when a new species is formed, are called macroevolution. Some biologists feel the mechanisms of macroevolution are different from those of microevolutionary change. Others think the distinction between the two is arbitrary -- macroevolution is cumulative microevolution.

The word evolution has a variety of meanings. The fact that all organisms are linked via descent to a common ancestor is often called evolution. The theory of how the first living organisms appeared is often called evolution. This should be called abiogenesis. And frequently, people use the word evolution when they really mean natural selection -- one of the many mechanisms of evolution.

Common Misconceptions about Evolution

Evolution can occur without morphological change; and morphological change can occur without evolution. Humans are larger now than in the recent past, a result of better diet and medicine. Phenotypic changes, like this, induced solely by changes in environment do not count as evolution because they are not heritable; in other words the change is not passed on to the organism's offspring. Phenotype is the morphological, physiological, biochemical, behavioral and other properties exhibited by a living organism. An organism's phenotype is determined by its genes and its environment. Most changes due to environment are fairly subtle, for example size differences. Large scale phenotypic changes are obviously due to genetic changes, and therefore are evolution.

Evolution is not progress. Populations simply adapt to their current surroundings. They do not necessarily become better in any absolute sense over time. A trait or strategy that is successful at one time may be unsuccessful at another. Paquin and Adams demonstrated this experimentally. They founded a yeast culture and maintained it for many generations. Occasionally, a mutation would arise that allowed its bearer to reproduce better than its contemporaries. These mutant strains would crowd out the formerly dominant strains. Samples of the most successful strains from the culture were taken at a variety of times. In later competition experiments, each strain would outcompete the immediately previously dominant type in a culture. However, some earlier isolates could outcompete strains that arose late in the experiment. Competitive ability of a strain was always better than its previous type, but competitiveness in a general sense was not increasing. Any organism's success depends on the behavior of its contemporaries. For most traits or behaviors there is likely no optimal design or strategy, only contingent ones. Evolution can be like a game of paper/scissors/rock.

Organisms are not passive targets of their environment. Each species modifies its own environment. At the least, organisms remove nutrients from and add waste to their surroundings. Often, waste products benefit other species. Animal dung is fertilizer for plants. Conversely, the oxygen we breathe is a waste product of plants. Species do not simply change to fit their environment; they modify their environment to suit them as well. Beavers build a dam to create a pond suitable to sustain them and raise young. Alternately, when the environment changes, species can migrate to suitable climes or seek out microenvironments to which they are adapted.

Genetic Variation

Evolution requires genetic variation. If there were no dark moths, the population could not have evolved from mostly light to mostly dark. In order for continuing evolution there must be mechanisms to increase or create genetic variation and mechanisms to decrease it. Mutation is a change in a gene. These changes are the source of new genetic variation. Natural selection operates on this variation.

Genetic variation has two components: allelic diversity and non- random associations of alleles. Alleles are different versions of the same gene. For example, humans can have A, B or O alleles that determine one aspect of their blood type. Most animals, including humans, are diploid -- they contain two alleles for every gene at every locus, one inherited from their mother and one inherited from their father. Locus is the location of a gene on a chromosome. Humans can be AA, AB, AO, BB, BO or OO at the blood group locus. If the two alleles at a locus are the same type (for instance two A alleles) the individual would be called homozygous. An individual with two different alleles at a locus (for example, an AB individual) is called heterozygous. At any locus there can be many different alleles in a population, more alleles than any single organism can possess. For example, no single human can have an A, B and an O allele.

Considerable variation is present in natural populations. At 45 percent of loci in plants there is more than one allele

in the gene pool. [allele: alternate version of a gene (created by mutation)] Any given plant is likely to be heterozygous at about 15 percent of its loci. Levels of genetic variation in animals range from roughly 15% of loci having more than one allele (polymorphic) in birds, to over 50% of loci being polymorphic in insects. Mammals and reptiles are polymorphic at about 20% of their loci - - amphibians and fish are polymorphic at around 30% of their loci. In most populations, there are enough loci and enough different alleles that every individual, identical twins excepted, has a unique combination of alleles.

Linkage disequilibrium is a measure of association between alleles of two different genes. [allele: alternate version of a gene] If two alleles were found together in organisms more often than would be expected, the alleles are in linkage disequilibrium. If there two loci in an organism (A and B) and two alleles at each of these loci (A1, A2, B1 and B2) linkage disequilibrium (D) is calculated as D = f(A1B1) * f(A2B2) - f(A1B2) * f(A2B1) (where f(X) is the frequency of X in the population). [Loci (plural of locus): location of a gene on a chromosome] D varies between -1/4 and 1/4; the greater the deviation from zero, the greater the linkage. The sign is simply a consequence of how the alleles are numbered. Linkage disequilibrium can be the result of physical proximity of the genes. Or, it can be maintained by natural selection if some combinations of alleles work better as a team.

Natural selection maintains the linkage disequilibrium between color and pattern alleles in *Papilio memnon*. [linkage disequilibrium: association between alleles at different loci] In this moth species, there is a gene that determines wing morphology. One allele at this locus leads to a moth that has a tail; the other allele codes for a untailed moth. There is another gene that determines if the wing is brightly or darkly colored. There are thus four possible types of moths: brightly colored moths with and without tails, and dark moths with and without tails. All four can be produced when moths are brought into the lab and bred. However, only two of these types of moths are found in the wild: brightly colored moths with tails and darkly colored moths without tails. The non-random association is maintained by natural selection. Bright, tailed moths mimic the pattern of an unpalatable species. The dark morph is cryptic. The other two combinations are neither mimetic nor cryptic and are quickly eaten by birds.

Assortative mating causes a non-random distribution of alleles at a single locus. [locus: location of a gene on a chromosome] If there are two alleles (A and a) at a locus with frequencies p and q, the frequency of the three possible genotypes (AA, Aa and aa) will be p^2, 2pq and q^2, respectively. For example, if the frequency of A is 0.9 and the frequency of a is 0.1, the frequencies of AA, Aa and aa individuals are: 0.81, 0.18 and 0.01. This distribution is called the Hardy-Weinberg equilibrium.

Non-random mating results in a deviation from the Hardy-Weinberg distribution. Humans mate assortatively according to race; we are more likely to mate with someone of own race than another. In populations that mate this way, fewer heterozygotes are found than would be predicted under random mating. [heterozygote: an organism that has two different alleles at a locus] A decrease in heterozygotes can be the result of mate choice, or simply the result of population subdivision. Most organisms have a limited dispersal capability, so their mate will be chosen from the local population.

Evolution within a Lineage

In order for continuing evolution there must be mechanisms to increase or create genetic variation and mechanisms to decrease it. The mechanisms of evolution are mutation, natural selection, genetic drift, recombination and gene flow. I have grouped them into two classes -- those that decrease genetic variation and those that increase it.

Mechanisms that Decrease Genetic Variation

Natural Selection

Some types of organisms within a population leave more offspring than others. Over time, the frequency of the more prolific type will increase. The difference in reproductive capability is called natural selection. Natural selection is the only mechanism of adaptive evolution; it is defined as differential reproductive success of pre-existing classes of genetic variants in the gene pool.

The most common action of natural selection is to remove unfit variants as they arise via mutation. [natural selection: differential reproductive success of genotypes] In other words, natural selection usually prevents new alleles from increasing in frequency. This led a famous evolutionist, George Williams, to say "Evolution proceeds in

spite of natural selection."

Natural selection can maintain or deplete genetic variation depending on how it acts. When selection acts to weed out deleterious alleles, or causes an allele to sweep to fixation, it depletes genetic variation. When heterozygotes are more fit than either of the homozygotes, however, selection causes genetic variation to be maintained. [heterozygote: an organism that has two different alleles at a locus. | homozygote: an organism that has two identical alleles at a locus] This is called balancing selection. An example of this is the maintenance of sickle-cell alleles in human populations subject to malaria. Variation at a single locus determines whether red blood cells are shaped normally or sickled. If a human has two alleles for sickle-cell, he/she develops anemia -- the shape of sickle-cells precludes them carrying normal levels of oxygen. However, heterozygotes who have one copy of the sickle-cell allele, coupled with one normal allele enjoy some resistance to malaria -- the shape of sickled cells make it harder for the plasmodia (malaria causing agents) to enter the cell. Thus, individuals homozygous for the normal allele suffer more malaria than heterozygotes. Individuals homozygous for the sickle- cell are anemic. Heterozygotes have the highest fitness of these three types. Heterozygotes pass on both sickle-cell and normal alleles to the next generation. Thus, neither allele can be eliminated from the gene pool. The sickle-cell allele is at its highest frequency in regions of Africa where malaria is most pervasive.

Balancing selection is rare in natural populations. [balancing selection: selection favoring heterozygotes] Only a handful of other cases beside the sickle-cell example have been found. At one time population geneticists thought balancing selection could be a general explanation for the levels of genetic variation found in natural populations. That is no longer the case. Balancing selection is only rarely found in natural populations. And, there are theoretical reasons why natural selection cannot maintain polymorphisms at several loci via balancing selection.

Individuals are selected. The example I gave earlier was an example of evolution via natural selection. [natural selection: differential reproductive success of genotypes] Dark colored moths had a higher reproductive success because light colored moths suffered a higher predation rate. The decline of light colored alleles was caused by light colored individuals being removed from the gene pool (selected against). Individual organisms either reproduce or fail to reproduce and are hence the unit of selection. One way alleles can change in frequency is to be housed in organisms with different reproductive rates. Genes are not the unit of selection (because their success depends on the organism's other genes as well); neither are groups of organisms a unit of selection. There are some exceptions to this "rule," but it is a good generalization.

Organisms do not perform any behaviors that are for the good of their species. An individual organism competes primarily with others of it own species for its reproductive success. Natural selection favors selfish behavior because any truly altruistic act increases the recipient's reproductive success while lowering the donors. Altruists would disappear from a population as the non- altruists would reap the benefits, but not pay the costs, of altruistic acts. Many behaviors appear altruistic. Biologists, however, can demonstrate that these behaviors are only apparently altruistic. Cooperating with or helping other organisms is often the most selfish strategy for an animal. This is called reciprocal altruism. A good example of this is blood sharing in vampire bats. In these bats, those lucky enough to find a meal will often share part of it with an unsuccessful bat by regurgitating some blood into the other's mouth. Biologists have found that these bats form bonds with partners and help each other out when the other is needy. If a bat is found to be a "cheater," (he accepts blood when starving, but does not donate when his partner is) his partner will abandon him. The bats are thus not helping each other altruistically; they form pacts that are mutually beneficial.

Helping closely related organisms can appear altruistic; but this is also a selfish behavior. Reproductive success (fitness) has two components; direct fitness and indirect fitness. Direct fitness is a measure of how many alleles, on average, a genotype contributes to the subsequent generation's gene pool by reproducing. Indirect fitness is a measure of how many alleles identical to its own it helps to enter the gene pool. Direct fitness plus indirect fitness is inclusive fitness. J. B. S. Haldane once remarked he would gladly drown, if by doing so he saved two siblings or eight cousins. Each of his siblings would share one half his alleles; his cousins, one eighth. They could potentially add as many of his alleles to the gene pool as he could.

Natural selection favors traits or behaviors that increase a genotype's inclusive fitness. Closely related organisms share many of the same alleles. In diploid species, siblings share on average at least 50% of their alleles. The percentage is higher if the parents are related. So, helping close relatives to reproduce gets an organism's own alleles better represented in the gene pool. The benefit of helping relatives increases dramatically in highly inbred species. In some cases, organisms will completely forgo reproducing and only help their relatives reproduce. Ants, and other eusocial insects, have sterile castes that only serve the queen and assist her reproductive efforts. The sterile workers are reproducing by proxy.

The words selfish and altruistic have connotations in everyday use that biologists do not intend. Selfish simply

means behaving in such a way that one's own inclusive fitness is maximized; altruistic means behaving in such a way that another's fitness is increased at the expense of ones' own. Use of the words selfish and altruistic is not meant to imply that organisms consciously understand their motives.

The opportunity for natural selection to operate does not induce genetic variation to appear -- selection only distinguishes between existing variants. Variation is not possible along every imaginable axis, so all possible adaptive solutions are not open to populations. To pick a somewhat ridiculous example, a steel shelled turtle might be an improvement over regular turtles. Turtles are killed quite a bit by cars these days because when confronted with danger, they retreat into their shells -- this is not a great strategy against a two ton automobile. However, there is no variation in metal content of shells, so it would not be possible to select for a steel shelled turtle.

Here is a second example of natural selection. Geospiza fortis lives on the Galapagos islands along with fourteen other finch species. It feeds on the seeds of the plant Tribulus cistoides, specializing on the smaller seeds. Another species, G. Magnirostris, has a larger beak and specializes on the larger seeds. The health of these bird populations depends on seed production. Seed production, in turn, depends on the arrival of wet season. In 1977, there was a drought. Rainfall was well below normal and fewer seeds were produced. As the season progressed, the G. fortis population depleted the supply of small seeds. Eventually, only larger seeds remained. Most of the finches starved; the population plummeted from about twelve hundred birds to less than two hundred. Peter Grant, who had been studying these finches, noted that larger beaked birds fared better than smaller beaked ones. These larger birds had offspring with correspondingly large beaks. Thus, there was an increase in the proportion of large beaked birds in the population the next generation. To prove that the change in bill size in Geospiza fortis was an evolutionary change, Grant had to show that differences in bill size were at least partially genetically based. He did so by crossing finches of various beak sizes and showing that a finch's beak size was influenced by its parent's genes. Large beaked birds had large beaked offspring; beak size was not due to environmental differences (in parental care, for example).

Natural selection may not lead a population to have the optimal set of traits. In any population, there would be a certain combination of possible alleles that would produce the optimal set of traits (the global optimum); but there are other sets of alleles that would yield a population almost as adapted (local optima). Transition from a local optimum to the global optimum may be hindered or forbidden because the population would have to pass through less adaptive states to make the transition. Natural selection only works to bring populations to the nearest optimal point. This idea is Sewall Wright's adaptive landscape. This is one of the most influential models that shape how evolutionary biologists view evolution.

Natural selection does not have any foresight. It only allows organisms to adapt to their current environment. Structures or behaviors do not evolve for future utility. An organism adapts to its environment at each stage of its evolution. As the environment changes, new traits may be selected for. Large changes in populations are the result of cumulative natural selection. Changes are introduced into the population by mutation; the small minority of these changes that result in a greater reproductive output of their bearers are amplified in frequency by selection.

Complex traits must evolve through viable intermediates. For many traits, it initially seems unlikely that intermediates would be viable. What good is half a wing? Half a wing may be no good for flying, but it may be useful in other ways. Feathers are thought to have evolved as insulation (ever worn a down jacket?) and/or as a way to trap insects. Later, proto-birds may have learned to glide when leaping from tree to tree. Eventually, the feathers that originally served as insulation now became co-opted for use in flight. A trait's current utility is not always indicative of its past utility. It can evolve for one purpose, and be used later for another. A trait evolved for its current utility is an adaptation; one that evolved for another utility is an exaptation. An example of an exaptation is a penguin's wing. Penguins evolved from flying ancestors; now they are flightless and use their wings for swimming.

Common Misconceptions about Selection

Selection is not a force in the sense that gravity or the strong nuclear force is. However, for the sake of brevity, biologists sometimes refer to it that way. This often leads to some confusion when biologists speak of selection "pressures." This implies that the environment "pushes" a population to more adapted state. This is not the case. Selection merely favors beneficial genetic changes when they occur by chance -- it does not contribute to their appearance. The potential for selection to act may long precede the appearance of selectable genetic variation. When selection is spoken of as a force, it often seems that it is has a mind of its own; or as if it was nature personified. This most often occurs when biologists are waxing poetic about selection. This has no place in scientific discussions of evolution. Selection is not a guided or cognizant entity; it is simply an effect.

A related pitfall in discussing selection is anthropomorphizing on behalf of living things. Often conscious motives

are seemingly imputed to organisms, or even genes, when discussing evolution. This happens most frequently when discussing animal behavior. Animals are often said to perform some behavior because selection will favor it. This could more accurately worded as "animals that, due to their genetic composition, perform this behavior tend to be favored by natural selection relative to those who, due to their genetic composition, don't." Such wording is cumbersome. To avoid this, biologists often anthropomorphize. This is unfortunate because it often makes evolutionary arguments sound silly. Keep in mind this is only for convenience of expression.

The phrase "survival of the fittest" is often used synonymously with natural selection. The phrase is both incomplete and misleading. For one thing, survival is only one component of selection -- and perhaps one of the less important ones in many populations. For example, in polygynous species, a number of males survive to reproductive age, but only a few ever mate. Males may differ little in their ability to survive, but greatly in their ability to attract mates -- the difference in reproductive success stems mainly from the latter consideration. Also, the word fit is often confused with physically fit. Fitness, in an evolutionary sense, is the average reproductive output of a class of genetic variants in a gene pool. Fit does not necessarily mean biggest, fastest or strongest.

Sexual Selection

In many species, males develop prominent secondary sexual characteristics. A few oft cited examples are the peacock's tail, coloring and patterns in male birds in general, voice calls in frogs and flashes in fireflies. Many of these traits are a liability from the standpoint of survival. Any ostentatious trait or noisy, attention getting behavior will alert predators as well as potential mates. How then could natural selection favor these traits?

Natural selection can be broken down into many components, of which survival is only one. Sexual attractiveness is a very important component of selection, so much so that biologists use the term sexual selection when they talk about this subset of natural selection.

Sexual selection is natural selection operating on factors that contribute to an organism's mating success. Traits that are a liability to survival can evolve when the sexual attractiveness of a trait outweighs the liability incurred for survival. A male who lives a short time, but produces many offspring is much more successful than a long lived one that produces few. The former's genes will eventually dominate the gene pool of his species. In many species, especially polygynous species where only a few males monopolize all the females, sexual selection has caused pronounced sexual dimorphism. In these species males compete against other males for mates. The competition can be either direct or mediated by female choice. In species where females choose, males compete by displaying striking phenotypic characteristics and/or performing elaborate courtship behaviors. The females then mate with the males that most interest them, usually the ones with the most outlandish displays. There are many competing theories as to why females are attracted to these displays.

The good genes model states that the display indicates some component of male fitness. A good genes advocate would say that bright coloring in male birds indicates a lack of parasites. The females are cueing on some signal that is correlated with some other component of viability.

Selection for good genes can be seen in sticklebacks. In these fish, males have red coloration on their sides. Milinski and Bakker showed that intensity of color was correlated to both parasite load and sexual attractiveness. Females preferred redder males. The redness indicated that he was carrying fewer parasites.

Evolution can get stuck in a positive feedback loop. Another model to explain secondary sexual characteristics is called the runaway sexual selection model. R. A. Fisher proposed that females may have an innate preference for some male trait before it appears in a population. Females would then mate with male carriers when the trait appears. The offspring of these matings have the genes for both the trait and the preference for the trait. As a result, the process snowballs until natural selection brings it into check. Suppose that female birds prefer males with longer than average tail feathers. Mutant males with longer than average feathers will produce more offspring than the short feathered males. In the next generation, average tail length will increase. As the generations progress, feather length will increase because females do not prefer a specific length tail, but a longer than average tail. Eventually tail length will increase to the point were the liability to survival is matched by the sexual attractiveness of the trait and an equilibrium will be established. Note that in many exotic birds male plumage is often very showy and many species do in fact have males with greatly elongated feathers. In some cases these feathers are shed after the breeding season.

None of the above models are mutually exclusive. There are millions of sexually dimorphic species on this planet and the forms of sexual selection probably vary amongst them.

Genetic Drift

Allele frequencies can change due to chance alone. This is called genetic drift. Drift is a binomial sampling error of the gene pool. What this means is, the alleles that form the next generation's gene pool are a sample of the alleles from the current generation. When sampled from a population, the frequency of alleles differs slightly due to chance alone.

Alleles can increase or decrease in frequency due to drift. The average expected change in allele frequency is zero, since increasing or decreasing in frequency is equally probable. A small percentage of alleles may continually change frequency in a single direction for several generations just as flipping a fair coin may, on occasion, result in a string of heads or tails. A very few new mutant alleles can drift to fixation in this manner.

In small populations, the variance in the rate of change of allele frequencies is greater than in large populations. However, the overall rate of genetic drift (measured in substitutions per generation) is independent of population size. [genetic drift: a random change in allele frequencies] If the mutation rate is constant, large and small populations lose alleles to drift at the same rate. This is because large populations will have more alleles in the gene pool, but they will lose them more slowly. Smaller populations will have fewer alleles, but these will quickly cycle through. This assumes that mutation is constantly adding new alleles to the gene pool and selection is not operating on any of these alleles.

Sharp drops in population size can change allele frequencies substantially. When a population crashes, the alleles in the surviving sample may not be representative of the precrash gene pool. This change in the gene pool is called the founder effect, because small populations of organisms that invade a new territory (founders) are subject to this. Many biologists feel the genetic changes brought about by founder effects may contribute to isolated populations developing reproductive isolation from their parent populations. In sufficiently small populations, genetic drift can counteract selection. [genetic drift: a random change in allele frequencies] Mildly deleterious alleles may drift to fixation.

Wright and Fisher disagreed on the importance of drift. Fisher thought populations were sufficiently large that drift could be neglected. Wright argued that populations were often divided into smaller subpopulations. Drift could cause allele frequency differences between subpopulations if gene flow was small enough. If a subpopulation was small enough, the population could even drift through fitness valleys in the adaptive landscape. Then, the subpopulation could climb a larger fitness hill. Gene flow out of this subpopulation could contribute to the population as a whole adapting. This is Wright's Shifting Balance theory of evolution.

Both natural selection and genetic drift decrease genetic variation. If they were the only mechanisms of evolution, populations would eventually become homogeneous and further evolution would be impossible. There are, however, mechanisms that replace variation depleted by selection and drift. These are discussed below.

Mechanisms that Increase Genetic Variation

Mutation

The cellular machinery that copies DNA sometimes makes mistakes. These mistakes alter the sequence of a gene. This is called a mutation. There are many kinds of mutations. A point mutation is a mutation in which one "letter" of the genetic code is changed to another. Lengths of DNA can also be deleted or inserted in a gene; these are also mutations. Finally, genes or parts of genes can become inverted or duplicated. Typical rates of mutation are between 10^{-10} and 10^{-12} mutations per base pair of DNA per generation.

Most mutations are thought to be neutral with regards to fitness. (Kimura defines neutral as $|s| < 1/2Ne$, where s is the selective coefficient and Ne is the effective population size.) Only a small portion of the genome of eukaryotes contains coding segments. And, although some non-coding DNA is involved in gene regulation or other cellular functions, it is probable that most base changes would have no fitness consequence.

Most mutations that have any phenotypic effect are deleterious. Mutations that result in amino acid substitutions can change the shape of a protein, potentially changing or eliminating its function. This can lead to inadequacies in biochemical pathways or interfere with the process of development. Organisms are sufficiently integrated that most random changes will not produce a fitness benefit. Only a very small percentage of mutations are beneficial. The ratio of neutral to deleterious to beneficial mutations is unknown and probably varies with respect to details of the

locus in question and environment.

Mutation limits the rate of evolution. The rate of evolution can be expressed in terms of nucleotide substitutions in a lineage per generation. Substitution is the replacement of an allele by another in a population. This is a two step process: First a mutation occurs in an individual, creating a new allele. This allele subsequently increases in frequency to fixation in the population. The rate of evolution is k = 2Nvu (in diploids) where k is nucleotide substitutions, N is the effective population size, v is the rate of mutation and u is the proportion of mutants that eventually fix in the population.

Mutation need not be limiting over short time spans. The rate of evolution expressed above is given as a steady state equation; it assumes the system is at equilibrium. Given the time frames for a single mutant to fix, it is unclear if populations are ever at equilibrium. A change in environment can cause previously neutral alleles to have selective values; in the short term evolution can run on "stored" variation and thus is independent of mutation rate. Other mechanisms can also contribute selectable variation. Recombination creates new combinations of alleles (or new alleles) by joining sequences with separate microevolutionary histories within a population. Gene flow can also supply the gene pool with variants. Of course, the ultimate source of these variants is mutation.

The Fate of Mutant Alleles

Mutation creates new alleles. Each new allele enters the gene pool as a single copy amongst many. Most are lost from the gene pool, the organism carrying them fails to reproduce, or reproduces but does not pass on that particular allele. A mutant's fate is shared with the genetic background it appears in. A new allele will initially be linked to other loci in its genetic background, even loci on other chromosomes. If the allele increases in frequency in the population, initially it will be paired with other alleles at that locus -- the new allele will primarily be carried in individuals heterozygous for that locus. The chance of it being paired with itself is low until it reaches intermediate frequency. If the allele is recessive, its effect won't be seen in any individual until a homozygote is formed. The eventual fate of the allele depends on whether it is neutral, deleterious or beneficial.

Neutral alleles

Most neutral alleles are lost soon after they appear. The average time (in generations) until loss of a neutral allele is 2(Ne/N) ln(2N) where N is the effective population size (the number of individuals contributing to the next generation's gene pool) and N is the total population size. Only a small percentage of alleles fix. Fixation is the process of an allele increasing to a frequency at or near one. The probability of a neutral allele fixing in a population is equal to its frequency. For a new mutant in a diploid population, this frequency is 1/2N.

If mutations are neutral with respect to fitness, the rate of substitution (k) is equal to the rate of mutation(v). This does not mean every new mutant eventually reaches fixation. Alleles are added to the gene pool by mutation at the same rate they are lost to drift. For neutral alleles that do fix, it takes an average of 4N generations to do so. However, at equilibrium there are multiple alleles segregating in the population. In small populations, few mutations appear each generation. The ones that fix do so quickly relative to large populations. In large populations, more mutants appear over the generations. But, the ones that fix take much longer to do so. Thus, the rate of neutral evolution (in substitutions per generation) is independent of population size.

The rate of mutation determines the level of heterozygosity at a locus according to the neutral theory. Heterozygosity is simply the proportion of the population that is heterozygous. Equilibrium heterozygosity is given as H = 4Nv/[4Nv+1] (for diploid populations). H can vary from a very small number to almost one. In small populations, H is small (because the equation is approximately a very small number divided by one). In (biologically unrealistically) large populations, heterozygosity approaches one (because the equation is approximately a large number divided by itself). Directly testing this model is difficult because N and v can only be estimated for most natural populations. But, heterozygosities are believed to be too low to be described by a strictly neutral model. Solutions offered by neutralists for this discrepancy include hypothesizing that natural populations may not be at equilibrium.

At equilibrium there should be a few alleles at intermediate frequency and many at very low frequencies. This is the Ewens- Watterson distribution. New alleles enter a population every generation, most remain at low frequency until they are lost. A few drift to intermediate frequencies, a very few drift all the way to fixation. In *Drosophila pseudoobscura*, the protein Xanthine dehydrogenase (Xdh) has many variants. In a single population, Keith, et. al., found that 59 of 96 proteins were of one type, two others were represented ten and nine times and nine other types were present singly or in low numbers.

Deleterious alleles

Deleterious mutants are selected against but remain at low frequency in the gene pool. In diploids, a deleterious recessive mutant may increase in frequency due to drift. Selection cannot see it when it is masked by a dominant allele. Many disease causing alleles remain at low frequency for this reason. People who are carriers do not suffer the negative effect of the allele. Unless they mate with another carrier, the allele may simply continue to be passed on. Deleterious alleles also remain in populations at a low frequency due to a balance between recurrent mutation and selection. This is called the mutation load.

Beneficial alleles

Most new mutants are lost, even beneficial ones. Wright calculated that the probability of fixation of a beneficial allele is 2s. (This assumes a large population size, a small fitness benefit, and that heterozygotes have an intermediate fitness. A benefit of 2s yields an overall rate of evolution: k=4Nvs where v is the mutation rate to beneficial alleles) An allele that conferred a one percent increase in fitness only has a two percent chance of fixing. The probability of fixation of beneficial type of mutant is boosted by recurrent mutation. The beneficial mutant may be lost several times, but eventually it will arise and stick in a population. (Recall that even deleterious mutants recur in a population.)

Directional selection depletes genetic variation at the selected locus as the fitter allele sweeps to fixation. Sequences linked to the selected allele also increase in frequency due to hitchhiking. The lower the rate of recombination, the larger the window of sequence that hitchhikes. Begun and Aquadro compared the level of nucleotide polymorphism within and between species with the rate of recombination at a locus. Low levels of nucleotide polymorphism within species coincided with low rates of recombination. This could be explained by molecular mechanisms if recombination itself was mutagenic. In this case, recombination with also be correlated with nucleotide divergence between species. But, the level of sequence divergence did not correlate with the rate of recombination. Thus, they inferred that selection was the cause. The correlation between recombination and nucleotide polymorphism leaves the conclusion that selective sweeps occur often enough to leave an imprint on the level of genetic variation in natural populations.

One example of a beneficial mutation comes from the mosquito *Culex pipiens*. In this organism, a gene that was involved with breaking down organophosphates - common insecticide ingredients -became duplicated. Progeny of the organism with this mutation quickly swept across the worldwide mosquito population. There are numerous examples of insects developing resistance to chemicals, especially DDT which was once heavily used in this country. And, most importantly, even though "good" mutations happen much less frequently than "bad" ones, organisms with "good" mutations thrive while organisms with "bad" ones die out.

If beneficial mutants arise infrequently, the only fitness differences in a population will be due to new deleterious mutants and the deleterious recessives. Selection will simply be weeding out unfit variants. Only occasionally will a beneficial allele be sweeping through a population. The general lack of large fitness differences segregating in natural populations argues that beneficial mutants do indeed arise infrequently. However, the impact of a beneficial mutant on the level of variation at a locus can be large and lasting. It takes many generations for a locus to regain appreciable levels of heterozygosity following a selective sweep.

Recombination

Each chromosome in our sperm or egg cells is a mixture of genes from our mother and our father. Recombination can be thought of as gene shuffling. Most organisms have linear chromosomes and their genes lie at specific location (loci) along them. Bacteria have circular chromosomes. In most sexually reproducing organisms, there are two of each chromosome type in every cell. For instance in humans, every chromosome is paired, one inherited from the mother, the other inherited from the father. When an organism produces gametes, the gametes end up with only one of each chromosome per cell. Haploid gametes are produced from diploid cells by a process called meiosis.

In meiosis, homologous chromosomes line up. The DNA of the chromosome is broken on both chromosomes in several places and rejoined with the other strand. Later, the two homologous chromosomes are split into two separate cells that divide and become gametes. But, because of recombination, both of the chromosomes are a mix of alleles from the mother and father.

Recombination creates new combinations of alleles. Alleles that arose at different times and different places can be brought together. Recombination can occur not only between genes, but within genes as well. Recombination within

a gene can form a new allele. Recombination is a mechanism of evolution because it adds new alleles and combinations of alleles to the gene pool.

Gene Flow

New organisms may enter a population by migration from another population. If they mate within the population, they can bring new alleles to the local gene pool. This is called gene flow. In some closely related species, fertile hybrids can result from interspecific matings. These hybrids can vector genes from species to species.

Gene flow between more distantly related species occurs infrequently. This is called horizontal transfer. One interesting case of this involves genetic elements called P elements. Margaret Kidwell found that P elements were transferred from some species in the *Drosophila willistoni* group to *Drosophila melanogaster*. These two species of fruit flies are distantly related and hybrids do not form. Their ranges do, however, overlap. The P elements were vectored into *D. melanogaster* via a parasitic mite that targets both these species. This mite punctures the exoskeleton of the flies and feeds on the "juices". Material, including DNA, from one fly can be transferred to another when the mite feeds. Since P elements actively move in the genome (they are themselves parasites of DNA), one incorporated itself into the genome of a *melanogaster* fly and subsequently spread through the species. Laboratory stocks of *melanogaster* caught prior to the 1940's lack of P elements. All natural populations today harbor them.

Overview of Evolution within a Lineage

Evolution is a change in the gene pool of a population over time; it can occur due to several factors. Three mechanisms add new alleles to the gene pool: mutation, recombination and gene flow. Two mechanisms remove alleles, genetic drift and natural selection. Drift removes alleles randomly from the gene pool. Selection removes deleterious alleles from the gene pool. The amount of genetic variation found in a population is the balance between the actions of these mechanisms.

Natural selection can also increase the frequency of an allele. Selection that weeds out harmful alleles is called negative selection. Selection that increases the frequency of helpful alleles is called positive, or sometimes positive Darwinian, selection. A new allele can also drift to high frequency. But, since the change in frequency of an allele each generation is random, nobody speaks of positive or negative drift.

Except in rare cases of high gene flow, new alleles enter the gene pool as a single copy. Most new alleles added to the gene pool are lost almost immediately due to drift or selection; only a small percent ever reach a high frequency in the population. Even most moderately beneficial alleles are lost due to drift when they appear. But, a mutation can reappear numerous times.

The fate of any new allele depends a great deal on the organism it appears in. This allele will be linked to the other alleles near it for many generations. A mutant allele can increase in frequency simply because it is linked to a beneficial allele at a nearby locus. This can occur even if the mutant allele is deleterious, although it must not be so deleterious as to offset the benefit of the other allele. Likewise a potentially beneficial new allele can be eliminated from the gene pool because it was linked to deleterious alleles when it first arose. An allele "riding on the coat tails" of a beneficial allele is called a hitchhiker. Eventually, recombination will bring the two loci to linkage equilibrium. But, the more closely linked two alleles are, the longer the hitchhiking will last.

The effects of selection and drift are coupled. Drift is intensified as selection pressures increase. This is because increased selection (i.e. a greater difference in reproductive success among organisms in a population) reduces the effective population size, the number of individuals contributing alleles to the next generation.

Adaptation is brought about by cumulative natural selection, the repeated sifting of mutations by natural selection. Small changes, favored by selection, can be the stepping-stone to further changes. The summation of large numbers of these changes is macroevolution.

The Development of Evolutionary Theory

Biology came of age as a science when Charles Darwin published "On the Origin of Species." But, the idea of evolution wasn't new to Darwin. Lamarck published a theory of evolution in 1809. Lamarck thought that species arose continually from nonliving sources. These species were initially very primitive, but increased in complexity over time due to some inherent tendency. This type of evolution is called orthogenesis. Lamarck proposed that an organism's acclimation to the environment could be passed on to its offspring. For example, he thought proto-giraffes stretched their necks to reach higher twigs. This caused their offspring to be born with longer necks. This proposed mechanism of evolution is called the inheritance of acquired characteristics. Lamarck also believed species never went extinct, although they may change into newer forms. All three of these ideas are now known to be wrong.

Darwin's contributions include hypothesizing the pattern of common descent and proposing a mechanism for evolution -- natural selection. In Darwin's theory of natural selection, new variants arise continually within populations. A small percentage of these variants cause their bearers to produce more offspring than others. These variants thrive and supplant their less productive competitors. The effect of numerous instances of selection would lead to a species being modified over time.

Darwin's theory did not accord with older theories of genetics. In Darwin's time, biologists held to the theory of blending inheritance -- an offspring was an average of its parents. If an individual had one short parent and one tall parent, it would be of medium height. And, the offspring would pass on genes for medium sized offspring. If this was the case, new genetic variations would quickly be diluted out of a population. They could not accumulate as the theory of evolution required. We now know that the idea of blending inheritance is wrong.

Darwin didn't know that the true mode of inheritance was discovered in his lifetime. Gregor Mendel, in his experiments on hybrid peas, showed that genes from a mother and father do not blend. An offspring from a short and a tall parent may be medium sized; but it carries genes for shortness and tallness. The genes remain distinct and can be passed on to subsequent generations. Mendel mailed his paper to Darwin, but Darwin never opened it.

It was a long time until Mendel's ideas were accepted. One group of biologists, called biometricians, thought Mendel's laws only held for a few traits. Most traits, they claimed, were governed by blending inheritance. Mendel studied discrete traits. Two of the traits in his famous experiments were smooth versus wrinkled coat on peas. This trait did not vary continuously. In other words, peas are either wrinkled or smooth -- intermediates are not found. Biometricians considered these traits aberrations. They studied continuously varying traits like size and believed most traits showed blending inheritance.

Incorporating Genetics into Evolutionary Theory

The discrete genes Mendel discovered would exist at some frequency in natural populations. Biologists wondered how and if these frequencies would change. Many thought that the more common versions of genes would increase in frequency simply because they were already at high frequency.

Hardy and Weinberg independently showed that the frequency of an allele would not change over time simply due to its being rare or common. Their model had several assumptions -- that all alleles reproduced at the same rate, that the population size was very large and that alleles did not change in form. Later, R. A. Fisher showed that Mendel's laws could explain continuous traits if the expression of these traits were due to the action of many genes. After this, geneticists accepted Mendel's Laws as the basic rules of genetics. From this basis, Fisher, Sewall Wright and J. B. S.. Haldane founded the field of population genetics. Population genetics is a field of biology that attempts to measure and explain the levels of genetic variation in populations.

R. A. Fisher studied the effect of natural selection on large populations. He demonstrated that even very small selective differences amongst alleles could cause appreciable changes in allele frequencies over time. He also showed that the rate of adaptive change in a population is proportional to the amount of genetic variation present. This is called Fisher's Fundamental Theorem of Natural Selection. Although it is called the fundamental theorem, it does not hold in all cases. The rate at which natural selection brings about adaptation depends on the details of how selection is working. In some rare cases, natural selection can actually cause a decline in the mean relative fitness of

a population.

Sewall Wright was more concerned with drift. He stressed that large populations are often subdivided into many subpopulations. In his theory, genetic drift played a more important role compared to selection. Differentiation between subpopulations, followed by migration among them, could contribute to adaptations amongst populations. Wright also came up with the idea of the adaptive landscape -- an idea that remains influential to this day. Its influence remains even though P. A. P. Moran has shown that, mathematically, adaptive landscapes don't exist as Wright envisioned them. Wright extended his results of one-locus models to a two-locus case in proposing the adaptive landscape. But, unbeknownst to him, the general conclusions of the one-locus model don't extend to the two-locus case.

J. B. S. Haldane developed many of the mathematical models of natural and artificial selection. He showed that selection and mutation could oppose each other, that deleterious mutations could remain in a population due to recurrent mutation. He also demonstrated that there was a cost to natural selection, placing a limit on the amount of adaptive substitutions a population could undergo in a given time frame.

For a long time, population genetics developed as a theoretical field. But, gathering the data needed to test the theories was nearly impossible. Prior to the advent of molecular biology, estimates of genetic variability could only be inferred from levels of morphological differences in populations. Lewontin and Hubby were the first to get a good estimate of genetic variation in a population. Using the then new technique of protein electrophoresis, they showed that 30% of the loci in a population of *Drosophila pseudoobscura* were polymorphic. They also showed that it was likely that they could not detect all the variation that was present. Upon finding this level of variation, the question became -- was this maintained by natural selection, or simply the result of genetic drift? This level of variation was too high to be explained by balancing selection.

Motoo Kimura theorized that most variation found in populations was selectively equivalent (neutral). Multiple alleles at a locus differed in sequence, but their fitnesses were the same. Kimura's neutral theory described rates of evolution and levels of polymorphism solely in terms of mutation and genetic drift. The neutral theory did not deny that natural selection acted on natural populations; but it claimed that the majority of natural variation was transient polymorphisms of neutral alleles. Selection did not act frequently or strongly enough to influence rates of evolution or levels of polymorphism.

Initially, a wide variety of observations seemed to be consistent with the neutral theory. Eventually, however, several lines of evidence toppled it. There is less variation in natural populations than the neutral theory predicts. Also, there is too much variance in rates of substitutions in different lineages to be explained by mutation and drift alone. Finally, selection itself has been shown to have an impact on levels of nucleotide variation. Currently, there is no comprehensive mathematical theory of evolution that accurately predicts rates of evolution and levels of heterozygosity in natural populations.

Evolution Among Lineages

The Pattern of Macroevolution

Evolution is not progress. The popular notion that evolution can be represented as a series of improvements from simple cells, through more complex life forms, to humans (the pinnacle of evolution), can be traced to the concept of the scale of nature. This view is incorrect.

All species have descended from a common ancestor. As time went on, different lineages of organisms were modified with descent to adapt to their environments. Thus, evolution is best viewed as a branching tree or bush, with the tips of each branch representing currently living species. No living organisms today are our ancestors. Every living species is as fully modern as we are with its own unique evolutionary history. No extant species are "lower life forms," atavistic stepping stones paving the road to humanity.

A related, and common, fallacy about evolution is that humans evolved from some living species of ape. This is not the case -- humans and apes share a common ancestor. Both humans and living apes are fully modern species; the ancestor we evolved from was an ape, but it is now extinct and was not the same as present day apes (or humans for that matter). If it were not for the vanity of human beings, we would be classified as an ape. Our closest relatives are, collectively, the chimpanzee and the pygmy chimp. Our next nearest relative is the gorilla.

Evidence for Common Descent and Macroevolution

Microevolution can be studied directly. Macroevolution cannot. Macroevolution is studied by examining patterns in biological populations and groups of related organisms and inferring process from pattern. Given the observation of microevolution and the knowledge that the earth is billions of years old -- macroevolution could be postulated. But this extrapolation, in and of itself, does not provide a compelling explanation of the patterns of biological diversity we see today. Evidence for macroevolution, or common ancestry and modification with descent, comes from several other fields of study. These include: comparative biochemical and genetic studies, comparative developmental biology, patterns of biogeography, comparative morphology and anatomy and the fossil record.

Closely related species (as determined by morphologists) have similar gene sequences. Overall sequence similarity is not the whole story, however. The pattern of differences we see in closely related genomes is worth examining.

All living organisms use DNA as their genetic material, although some viruses use RNA. DNA is composed of strings of nucleotides. There are four different kinds of nucleotides: adenine (A), guanine (G), cytosine (C) and thymine (T). Genes are sequences of nucleotides that code for proteins. Within a gene, each block of three nucleotides is called a codon. Each codon designates an amino acid (the subunits of proteins).

The three letter code is the same for all organisms (with a few exceptions). There are 64 codons, but only 20 amino acids to code for; so, most amino acids are coded for by several codons. In many cases the first two nucleotides in the codon designate the amino acid. The third position can have any of the four nucleotides and not effect how the code is translated.

A gene, when in use, is transcribed into RNA -- a nucleic acid similar to DNA. (RNA, like DNA, is made up of nucleotides although t he nucleotide uracil (U) is used in place of thymine (T).) The RNA transcribed from a gene is called messenger RNA. Messenger RNA is then translated via cellular machinery called ribosomes into a string of amino acids -- a protein. Some proteins function as enzymes, catalysts that speed the chemical reactions in cells. Others are structural or involved in regulating development.

Gene sequences in closely related species are very similar. Often, the same codon specifies a given amino acid in two related species, even though alternate codons could serve functionally as well. But, some differences do exist in gene sequences. Most often, differences are in third codon positions, where changes in the DNA sequence would not disrupt the sequence of the protein.

There are other sites in the genome where nucleotide differences do not effect protein sequences. The genome of eukaryotes is loaded with 'dead genes' called pseudogenes. Pseudogenes are copies of working genes that have been inactivated by mutation. Most pseudogenes do not produce full proteins. They may be transcribed, but not translated. Or, they may be translated, but only a truncated protein is produced. Pseudogenes evolve much faster than their working counterparts. Mutations in them do not get incorporated into proteins, so they have no effect on the fitness of an organism.

Introns are sequences of DNA that interrupt a gene, but do not code for anything. The coding portions of a gene are called exons. Introns are spliced out of the messenger RNA prior to translation, so they do not contribute information needed to make the protein. They are sometimes, however, involved in regulation of the gene. Like pseudogenes, introns (in general) evolve faster than coding portions of a gene.

Nucleotide positions that can be changed without changing the sequence of a protein are called silent sites. Sites where changes result in an amino acid substitution are called replacement sites. Silent sites are expected to be more polymorphic within a population and show more differences between populations. Although both silent and replacement sites receive the same amount of mutations, natural selection only infrequently allows changes at replacement sites. Silent sites, however, are not as constrained.

Kreitman was the first demonstrate that silent sites were more variable than coding sites. Shortly after the methods of DNA sequencing were discovered, he sequenced 11 alleles of the enzyme alcohol dehydrogenase (AdH). Of the 43 polymorphic nucleotide sites he found, only one resulted in a change in the amino acid sequence of the protein.

Silent sites may not be entirely selectively neutral. Some DNA sequences are involved with regulation of genes, changes in these sites may be deleterious. Likewise, although several codons code for a single amino acid, an organism may have a preferred codon for each amino acid. This is called codon bias.

If two species shared a recent common ancestor one would expect genetic information, even information such as redundant nucleotides and the position of introns or pseudogenes, to be similar. Both species would have inherited this information from their common ancestor.

The degree of similarity in nucleotide sequence is a function of divergence time. If two populations had recently separated, few differences would have built up between them. If they separated long ago, each population would have evolved numerous differences from their common ancestor (and each other). The degree of similarity would also be a function of silent versus replacement sites. Li and Graur, in their molecular evolution text, give the rates of evolution for silent vs. replacement rates. The rates were estimated from sequence comparisons of 30 genes from humans and rodents, which diverged about 80 million years ago. Silent sites evolved at an average rate of 4.61 nucleotide substitution per 10^9 years. Replacement sites evolved much slower at an average rate of 0.85 nucleotide substitutions per 10^9 years.

Groups of related organisms are 'variations on a theme' -- the same set of bones are used to construct all vertebrates. The bones of the human hand grow out of the same tissue as the bones of a bat's wing or a whale's flipper; and, they share many identifying features such as muscle insertion points and ridges. The only difference is that they are scaled differently. Evolutionary biologists say this indicates that all mammals are modified descendants of a common ancestor which had the same set of bones.

Closely related organisms share similar developmental pathways. The differences in development are most evident at the end. As organisms evolve, their developmental pathway gets modified. An alteration near the end of a developmental pathway is less likely to be deleterious than changes in early development. Changes early on may have a cascading effect. Thus most evolutionary changes in development are expected to take place at the periphery of development, or in early aspects of development that have no later repercussions. For a change in early development to be propagated, the benefit of the early alteration must outweigh the consequences to later development.

Because they have evolved this way, organisms pass through the early stages of development that their ancestors passed through up to the point of divergence. So, an organism's development mimics its ancestors although it doesn't recreate it exactly. Development of the flatfish, Pleuronectes, illustrates this point. Early on, Pleuronectes develops a tail that comes to a point. In the next developmental stage, the top lobe of the tail is larger than the bottom lobe (as in sharks). When development is complete, the upper and lower lobes are equally sized. This developmental pattern mirrors the evolutionary transitions it has undergone.

Natural selection can modify any stage of a life cycle, so some differences are seen in early development. Thus, evolution does not always recapitulate ancestral forms -- butterflies did not evolve from ancestral caterpillars, for example. There are differences in the appearance of early vertebrate embryos. Amphibians rapidly form a ball of cells in early development. Birds, reptiles and mammals form a disk. The shape of the early embryo is a result of different yolk concentrations in the eggs. Birds' and reptiles' eggs are heavily yolked. Their eggs develop similarly to amphibians except the yolk has deformed the shape of the embryo. The ball is stretched out and lying atop the yolk. Mammals have no yolk, but still form a disk early. This is because they have descended from reptiles. Mammals lost their yolky eggs, but retained the early pattern of development. In all these vertebrates, the pattern of cell movements is similar despite superficial differences in appearance. In addition, all types quickly converge upon a primitive, fish-like stage within a few days. From there, development diverges.

Traces of an organism's ancestry sometimes remain even when an organism's development is complete. These are called vestigial structures. Many snakes have rudimentary pelvic bones retained from their walking ancestors. Vestigial does not mean useless, it means the structure is clearly a vestige of an structure inherited from ancestral organisms. Vestigial structures may acquire new functions. In humans, the appendix now houses some immune system cells.

Closely related organisms are usually found in close geographic proximity; this is especially true of organisms with limited dispersal opportunities. The mammalian fauna of Australia is often cited as an example of this; marsupial mammals fill most of the equivalent niches that placentals fill in other ecosystems. If all organisms descended from a common ancestor, species distribution across the planet would be a function of site of origination, potential for dispersal, distribution of suitable habitat, and time since origination. In the case of Australian mammals, their physical separation from sources of placentals means potential niches were filled by a marsupial radiation rather than a placental radiation or invasion.

Natural selection can only mold available genetically based variation. In addition, natural selection provides no mechanism for advance planning. If selection can only tinker with the available genetic variation, we should expect to see examples of jury-rigged design in living species. This is indeed the case. In lizards of the genus

Cnemodophorus, females reproduce parthenogenetically. Fertility in these lizards is increased when a female mounts another female and simulates copulation. These lizards evolved from sexual lizards whose hormones were aroused by sexual behavior. Now, although the sexual mode of reproduction has been lost, the means of getting aroused (and hence fertile) has been retained.

Fossils show hard structures of organisms less and less similar to modern organisms in progressively older rocks. In addition, patterns of biogeography apply to fossils as well as extant organisms. When combined with plate tectonics, fossils provide evidence of distributions and dispersals of ancient species. For example, South America had a very distinct marsupial mammalian fauna until the land bridge formed between North and South America. After that marsupials started disappearing and placentals took their place. This is commonly interpreted as the placentals wiping out the marsupials, but this may be an over simplification.

Transitional fossils between groups have been found. One of the most impressive transitional series is the ancient reptile to modern mammal transition. Mammals and reptiles differ in skeletal details, especially in their skulls. Reptilian jaws have four bones. The foremost is called the dentary. In mammals, the dentary bone is the only bone in the lower jaw. The other bones are part of the middle ear. Reptiles have a weak jaw and a mouthful of undifferentiated teeth. Their jaw is closed by three muscles: the external, posterior and internal adductor. Each reptile tooth is single cusped. Mammals have powerful jaws with differentiated teeth. Many of these teeth, such as the molars, are multi-cusped. The temporalis and masseter muscles, derived from the external adductor, close the mammalian jaw. Mammals have a secondary palate, a bony structure separating their nostril passages and throat, so most can swallow and breathe simultaneously. Reptiles lack this.

The evolution of these traits can be seen in a series of fossils. *Procynosuchus* shows an increase in size of the dentary bone and the beginnings of a palate. *Thrinaxodon* has a reduced number of incisors, a precursor to tooth differentiation. *Cynognathus* (a doglike carnivore) shows a further increase in size of the dentary bone. The other three bones are located inside the back portion of the jaw. Some teeth are multicusped and the teeth fit together tightly. *Diademodon* (a plant eater) shows a more advanced degree of occlusion (teeth fitting tightly). *Probelesodon* has developed a double joint in the jaw. The jaw could hinge off two points with the upper skull. The front hinge was probably the actual hinge while the rear hinge was an alignment guide. The forward movement of a hinge point allowed for the precursor to the modern masseter muscle to anchor further forward in the jaw. This allowed for a more powerful bite. The first true mammal was *Morgonucudon*, a rodent-like insectivore from the late Triassic. It had all the traits common to modern mammals. These species were not from a single, unbranched lineage. Each is an example from a group of organisms along the main line of mammalian ancestry.

The strongest evidence for macroevolution comes from the fact that suites of traits in biological entities fall into a nested pattern. For example, plants can be divided into two broad categories, non- vascular (ex. mosses) and vascular. Vascular plants can be divided into seedless (ex. ferns) and seeded. Vascular seeded plants can be divided into gymnosperms (ex. pines) and flowering plants (angiosperms). Angiosperms can be divided into monocots and dicots. Each of these types of plants have several characters that distinguish them from other plants. Traits are not mixed and matched in groups of organisms. For example, flowers are only seen in plants that carry several other characters that distinguish them as angiosperms. This is the expected pattern of common descent. All the species in a group will share traits they inherited from their common ancestor. But, each subgroup will have evolved unique traits of its own. Similarities bind groups together. Differences show how they are subdivided.

The real test of any scientific theory is its ability to generate testable predictions and, of course, have the predictions borne out. Evolution easily meets this criterion. In several of the above examples I stated, closely related organisms share X. If I define closely related as sharing X, this is an empty statement. It does however, provide a prediction. If two organisms share a similar anatomy, one would then predict that their gene sequences would be more similar than a morphologically distinct organism. This has been spectacularly borne out by the recent flood of gene sequences -- the correspondence to trees drawn by morphological data is very high. The discrepancies are never too great and usually confined to cases where the pattern of relationship was debated.

Mechanisms of Macroevolution

The following deals with mechanisms of evolution above the species level.

Speciation -- Increasing Biological Diversity

Speciation is the process of a single species becoming two or more species. Many biologists think speciation is key to understanding evolution. Some would argue that certain evolutionary phenomena apply only at speciation and macroevolutionary change cannot occur without speciation. Other biologists think major evolutionary change can occur without speciation. Changes between lineages are only an extension of the changes within each lineage. In general, paleontologists fall into the former category and geneticists in the latter.

Modes of Speciation

Biologists recognize two types of speciation: allopatric and sympatric speciation. The two differ in geographical distribution of the populations in question. Allopatric speciation is thought to be the most common form of speciation. It occurs when a population is split into two (or more) geographically isolated subdivisions that organisms cannot bridge. Eventually, the two populations' gene pools change independently until they could not interbreed even if they were brought back together. In other words, they have speciated.

Sympatric speciation occurs when two subpopulations become reproductively isolated without first becoming geographically isolated. Insects that live on a single host plant provide a model for sympatric speciation. If a group of insects switched host plants they would not breed with other members of their species still living on their former host plant. The two subpopulations could diverge and speciate. Agricultural records show that a strain of the apple maggot fly *Rhagolettis pomenella* began infesting apples in the 1860's. Formerly it had only infested hawthorn fruit. Feder, Chilcote and Bush have shown that two races of *Rhagolettis pomenella* have become behaviorally isolated. Allele frequencies at six loci (aconitase 2, malic enzyme, mannose phosphate isomerase, aspartate amino-transferase, NADH-diaphorase-2, and beta-hydroxy acid dehydrogenase) are diverging. Significant amounts of linkage disequilibrium have been found at these loci, indicating that they may all be hitchhiking on some allele under selection. Some biologists call sympatric speciation microallopatric speciation to emphasize that the subpopulations are still physically separate at an ecological level.

Biologists know little about the genetic mechanisms of speciation. Some think a series of small changes in each subdivision gradually lead to speciation. The founder effect could set the stage for relatively rapid speciation, a genetic revolution in Ernst Mayr's terms. Alan Templeton hypothesized that a few key genes could change and confer reproductive isolation. He called this a genetic transilience. Lynn Margulis thinks most speciation events are caused by changes in internal symbionts. Populations of organisms are very complicated. It is likely that there are many ways speciation can occur. Thus, all of the above ideas may be correct, each in different circumstances. Darwin's book was titled "The Origin of Species" despite the fact that he did not really address this question; over one hundred and fifty years later, how species originate is still largely a mystery.

Observed Speciations

Speciation has been observed. In the plant genus *Tragopogon*, two new species have evolved within the past 50-60 years. They are *T. mirus* and *T. miscellus*. The new species were formed when one diploid species fertilized a different diploid species and produced a tetraploid offspring. This tetraploid offspring could not fertilize or be fertilized by either of its two parent species types. It is reproductively isolated, the definition of a species.

Extinction -- Decreasing Biological Diversity

Ordinary Extinction

Extinction is the ultimate fate of all species. The reasons for extinction are numerous. A species can be competitively excluded by a closely related species, the habitat a species lives in can disappear and/or the organisms that the species exploits could come up with an unbeatable defense.

Some species enjoy a long tenure on the planet while others are short- lived. Some biologists believe species are programmed to go extinct in a manner analogous to organisms being destined to die. The majority, however, believe that if the environment stays fairly constant, a well adapted species could continue to survive indefinitely.

Mass Extinction

Mass extinctions shape the overall pattern of macroevolution. If you view evolution as a branching tree, it's best to picture it as one that has been severely pruned a few times in its life. The history of life on this earth includes many episodes of mass extinction in which many groups of organisms were wiped off the face of the planet. Mass extinctions are followed by periods of radiation where new species evolve to fill the empty niches left behind. It is probable that surviving a mass extinction is largely a function of luck. Thus, contingency plays a large role in patterns of macroevolution.

The largest mass extinction came at the end of the Permian, about 250 million years ago. This coincides with the formation of Pangaea II, when all the world's continents were brought together by plate tectonics. A worldwide drop in sea level also occurred at this time.

The most well-known extinction occurred at the boundary between the Cretaceous and Tertiary Periods. This called the K/T Boundary and is dated at around 65 million years ago. This extinction eradicated the dinosaurs. The K/T event was probably caused by environmental disruption brought on by a large impact of an asteroid with the earth. Following this extinction the mammalian radiation occurred. Mammals coexisted for a long time with the dinosaurs but were confined mostly to nocturnal insectivore niches. With the eradication of the dinosaurs, mammals radiated to fill the vacant niches.

Currently, human alteration of the ecosphere is causing a global mass extinction.

Punctuated Equilibrium

The theory of punctuated equilibrium is an inference about the process of macroevolution from the pattern of species documented in the fossil record. In the fossil record, transition from one species to another is usually abrupt in most geographic locales -- no transitional forms are found. In short, it appears that species remain unchanged for long stretches of time and then are quickly replaced by new species. However, if wide ranges are searched, transitional forms that bridge the gap between the two species are sometimes found in small, localized areas. For example, in Jurassic brachiopods of the genus *Kutchithyris*, *K. acutiplicata* appears below another species, *K. euryptycha*. Both species were common and covered a wide geographical area. They differ enough that some have argued they should be in a different genera. In just one small locality an approximately 1.25m sedimentary layer with these fossils is found. In the narrow (10 cm) layer that separates the two species, both species are found along with transitional forms. In other localities there is a sharp transition.

Eldredge and Gould proposed that most major morphological change occurs (relatively) quickly in small peripheral population at the time of speciation. New forms will then invade the range of their ancestral species. Thus, at most locations that fossils are found, transition from one species to another will be abrupt. This abrupt change will reflect replacement by migration however, not evolution. In order to find the transitional fossils, the area of speciation must be found.

There has been considerable confusion about the theory. Some popular accounts give the impression that abrupt changes in the fossil record are due to blindingly fast evolution; this is not a part of the theory.

Punctuated equilibrium has been presented as a hierarchical theory of evolution. Proponents of punctuated equilibrium see speciation as analogous to mutation and the replacement of one species by another as analogous to natural selection. This is called species selection. Speciation adds new species to the species pool just as mutation adds new alleles to the gene pool. Species selection favors one species over another just as natural selection can favor one allele over another. Evolutionary trends within a group would be the result of selection among species, not natural selection acting within species. This is the most controversial part of the theory. Many biologists agree with the pattern of macroevolution these paleontologists posit, but believe species selection is not even theoretically likely to occur.

Critics would argue that species selection is not analogous to natural selection and therefore evolution is not hierarchical. Also, the number of species produced over time is far less than the amount of different alleles that enter gene pools over time. So, the amount of adaptive evolution produced by species selection (if it did occur) would have to be orders of magnitude less than adaptive evolution within populations by natural selection.

Tests of punctuated equilibrium have been equivocal. It has been known for a long time that rates of evolution vary over time, that is not controversial. However, phylogenetic studies conflict as to whether there is a clear association between speciation and morphological change. In addition, there are major polymorphisms within some species. For example, bluegill sunfish have two male morphs. One is a large, long-lived, mate-protecting male; the other is a smaller, shorter-lived male who sneaks matings from females guarded by large males. The existence of within

species polymorphisms demonstrates that speciation is not a requirement for major morphological change.

A Brief History of Life

Biologists studying evolution do a variety of things: population geneticists study the process as it is occurring; systematists seek to determine relationships between species and paleontologists seek to uncover details of the unfolding of life in the past. Discerning these details is often difficult, but hypotheses can be made and tested as new evidence comes to light. This section should be viewed as the best hypothesis scientists have as to the history of the planet. The material here ranges from some issues that are fairly certain to some topics that are nothing more than informed speculation. For some points there are opposing hypotheses -- I have tried to compile a consensus picture. In general, the more remote the time, the more likely the story is incomplete or in error.

Life evolved in the sea. It stayed there for the majority of the history of earth.

The first replicating molecules were most likely RNA. RNA is a nucleic acid similar to DNA. In laboratory studies it has been shown that some RNA sequences have catalytic capabilities. Most importantly, certain RNA sequences act as polymerases -- enzymes that form strands of RNA from its monomers. This process of self replication is the crucial step in the formation of life. This is called the RNA world hypothesis.

The common ancestor of all life probably used RNA as its genetic material. This ancestor gave rise to three major lineages of life. These are: the prokaryotes ("ordinary" bacteria), archaebacteria (thermophilic, methanogenic and halophilic bacteria) and eukaryotes. Eukaryotes include protists (single celled organisms like amoebas and diatoms and a few multicellular forms such as kelp), fungi (including mushrooms and yeast), plants and animals. Eukaryotes and archaebacteria are the two most closely related of the three. The process of translation (making protein from the instructions on a messenger RNA template) is similar in these lineages, but the organization of the genome and transcription (making messenger RNA from a DNA template) is very different in prokaryotes than in eukaryotes and archaebacteria. Scientists interpret this to mean that the common ancestor was RNA based; it gave rise to two lineages that independently formed a DNA genome and hence independently evolved mechanisms to transcribe DNA into RNA.

The first cells must have been anaerobic because there was no oxygen in the atmosphere. In addition, they were probably thermophilic ("heat-loving") and fermentative. Rocks as old as 3.5 billion years old have yielded prokaryotic fossils. Specifically, some rocks from Australia called the Warrawoona series give evidence of bacterial communities organized into structures called stromatolites. Fossils like these have subsequently been found all over the world. These mats of bacteria still form today in a few locales (for example, Shark Bay Australia). Bacteria are the only life forms found in the rocks for a long, long time --eukaryotes (protists) appear about 1.5 billion years ago and fungi-like things appear about 900 million years ago (0.9 billion years ago).

Photosynthesis evolved around 3.4 billion years ago. Photosynthesis is a process that allows organisms to harness sunlight to manufacture sugar from simpler precursors. The first photosystem to evolve, PSI, uses light to convert carbon dioxide (CO_2) and hydrogen sulfide (H_2S) to glucose. This process releases sulfur as a waste product. About a billion years later, a second photosystem (PS) evolved, probably from a duplication of the first photosystem. Organisms with PSII use both photosystems in conjunction to convert carbon dioxide (CO_2) and water (H_2O) into glucose. This process releases oxygen as a waste product. Anoxygenic (or H_2S) photosynthesis, using PSI, is seen in living purple and green bacteria. Oxygenic (or H_2O) photosynthesis, using PSI and PSII, takes place in cyanobacteria. Cyanobacteria are closely related to and hence probably evolved from purple bacterial ancestors. Green bacteria are an outgroup. Since oxygenic bacteria are a lineage within a cluster of anoxygenic lineages, scientists infer that PSI evolved first. This also corroborates with geological evidence.

Green plants and algae also use both photosystems. In these organisms, photosynthesis occurs in organelles (membrane bound structures within the cell) called chloroplasts. These organelles originated as free living bacteria related to the cyanobacteria that were engulfed by ur-eukaryotes and eventually entered into an endosymbiotic relationship. This endosymbiotic theory of eukaryotic organelles was championed by Lynn Margulis. Originally controversial, this theory is now accepted. One key line of evidence in support of this idea came when the DNA inside chloroplasts was sequenced -- the gene sequences were more similar to free-living cyanobacteria sequences than to sequences from the plants the chloroplasts resided in.

After the advent of photosystem II, oxygen levels increased. Dissolved oxygen in the oceans increased as well as atmospheric oxygen. This is sometimes called the oxygen holocaust. Oxygen is a very good electron acceptor and can be very damaging to living organisms. Many bacteria are anaerobic and die almost immediately in the presence

of oxygen. Other organisms, like animals, have special ways to avoid cellular damage due to this element (and in fact require it to live.) Initially, when oxygen began building up in the environment, it was neutralized by materials already present. Iron, which existed in high concentrations in the sea was oxidized and precipitated. Evidence of this can be seen in banded iron formations from this time, layers of iron deposited on the sea floor. As one geologist put it, "the world rusted." Eventually, it grew to high enough concentrations to be dangerous to living things. In response, many species went extinct, some continued (and still continue) to thrive in anaerobic microenvironments and several lineages independently evolved oxygen respiration.

The purple bacteria evolved oxygen respiration by reversing the flow of molecules through their carbon fixing pathways and modifying their electron transport chains. Purple bacteria also enabled the eukaryotic lineage to become aerobic. Eukaryotic cells have membrane bound organelles called mitochondria that take care of respiration for the cell. These are endosymbionts like chloroplasts. Mitochondria formed this symbiotic relationship very early in eukaryotic history, all but a few groups of eukaryotic cells have mitochondria. Later, a few lineages picked up chloroplasts. Chloroplasts have multiple origins. Red algae picked up ur-chloroplasts from the cyanobacterial lineage. Green algae, the group plants evolved from, picked up different urchloroplasts from a prochlorophyte, a lineage closely related to cyanobacteria.

Animals start appearing prior to the Cambrian, about 600 million years ago. The first animals dating from just before the Cambrian were found in rocks near Adelaide, Australia. They are called the Ediacarian fauna and have subsequently been found in other locales as well. It is unclear if these forms have any surviving descendants. Some look a bit like Cnidarians (jellyfish, sea anemones and the like); others resemble annelids (earthworms). All the phyla (the second highest taxonomic category) of animals appeared around the Cambrian. The Cambrian 'explosion' may have been a result of higher oxygen concentrations enabling larger organisms with higher metabolisms to evolve. Or it might be due to the spreading of shallow seas at that time providing a variety of new niches. In any case, the radiation produced a wide variety of animals.

Some paleontologists think more animal phyla were present then than now. The animals of the Burgess shale are an example of Cambrian animal fossils. These fossils, from Canada, show a bizarre array of creatures, some which appear to have unique body plans unlike those seen in any living animals.

The extent of the Cambrian explosion is often overstated. Although quick, the Cambrian explosion is not instantaneous in geologic time. Also, there is evidence of animal life prior to the Cambrian. In addition, although all the phyla of animals came into being, these were *not* the modern forms we see today. Our own phylum (which we share with other mammals, reptiles, birds, amphibians and fish) was represented by a small, sliver-like thing called *Pikaia*. Plants were not yet present. Photosynthetic protists and algae were the bottom of the food chain. Following the Cambrian, the number of marine families leveled off at a little less than 200.

The Ordovician explosion, around 500 million years ago, followed. This 'explosion', larger than the Cambrian, introduced numerous families of the Paleozoic fauna (including crinoids, articulate brachiopods, cephalopods and corals). The Cambrian fauna, (trilobites, inarticulate brachiopods, etc.) declined slowly during this time. By the end of the Ordovician, the Cambrian fauna had mostly given way to the Paleozoic fauna and the number of marine families was just over 400. It stayed at this level until the end of the Permian period.

Plants evolved from ancient green algae over 400 million years ago. Both groups use chlorophyll a and b as photosynthetic pigments. In addition, plants and green algae are the only groups to store starch in their chloroplasts. Plants and fungi (in symbiosis) invaded the land about 400 million years ago. The first plants were moss-like and required moist environments to survive. Later, evolutionary developments such as a waxy cuticle allowed some plants to exploit more inland environments. Still mosses lack true vascular tissue to transport fluids and nutrients. This limits their size since these must diffuse through the plant. Vascular plants evolved from mosses. The first vascular land plant known is *Cooksonia*, a spiky, branching, leafless structure. At the same time, or shortly thereafter, arthropods followed plants onto the land. The first land animals known are myriapods -- centipedes and millipedes.

Vertebrates moved onto the land by the Devonian period, about 380 million years ago. *Ichthyostega*, an amphibian, is the among the first known land vertebrates. It was found in Greenland and was derived from lobe-finned fishes called Rhipidistians. Amphibians gave rise to reptiles. Reptiles had evolved scales to decrease water loss and a shelled egg permitting young to be hatched on land. Among the earliest well preserved reptiles is *Hylonomus*, from rocks in Nova Scotia.

The Permian extinction was the largest extinction in history. It happened about 250 million years ago. The last of the Cambrian Fauna went extinct. The Paleozoic fauna took a nose dive from about 300 families to about 50. It is estimated that 96% of all species (50% of all Families) met their end. Following this event, the Modern fauna,

which had been slowly expanding since the Ordovician, took over.

The Modern fauna includes fish, bivalves, gastropods and crabs. These were barely affected by the Permian extinction. The Modern fauna subsequently increased to over 600 marine families at present. The Paleozoic fauna held steady at about 100 families. A second extinction event shortly following the Permian kept animal diversity low for awhile.

During the Carboniferous (the period just prior to the Permian) and in the Permian the landscape was dominated by ferns and their relatives. After the Permian extinction, gymnosperms (ex. pines) became more abundant. Gymnosperms had evolved seeds, from seedless fern ancestors, which helped their ability to disperse. Gymnosperms also evolved pollen, encased sperm which allowed for more outcrossing.

Dinosaurs evolved from archosaur reptiles, their closest living relatives are crocodiles. One modification that may have been a key to their success was the evolution of an upright stance. Amphibians and reptiles have a splayed stance and walk with an undulating pattern because their limbs are modified from fins. Their gait is modified from the swimming movement of fish. Splay stanced animals cannot sustain continued locomotion because they cannot breathe while they move; their undulating movement compresses their chest cavity. Thus, they must stop every few steps and breath before continuing on their way. Dinosaurs evolved an upright stance similar to the upright stance mammals independently evolved. This allowed for continual locomotion. In addition, dinosaurs evolved to be warm-blooded. Warmbloodedness allows an increase in the vigor of movements in erect organisms. Splay stanced organisms would probably not benefit from warm- bloodedness. Birds evolved from sauriscian dinosaurs. Cladistically, birds are dinosaurs. The transitional fossil *Archaeopteryx* has a mixture of reptilian and avian features.

Angiosperms evolved from gymnosperms, their closest relatives are Gnetae. Two key adaptations allowed them to displace gymnosperms as the dominant fauna -- fruits and flowers. Fruits (modified plant ovaries) allow for animal-based seed dispersal and deposition with plenty of fertilizer. Flowers evolved to facilitate animal, especially insect, based pollen dispersal. Petals are modified leaves. Angiosperms currently dominate the flora of the world -- over three fourths of all living plants are angiosperms.

Insects evolved from primitive segmented arthropods. The mouth parts of insects are modified legs. Insects are closely related to annelids. Insects dominate the fauna of the world. Over half of all named species are insects. One third of this number are beetles.

The end of the Cretaceous, about 65 million years ago, is marked by a minor mass extinction. This extinction marked the demise of all the lineages of dinosaurs save the birds. Up to this point mammals were confined to nocturnal, insectivorous niches. Once the dinosaurs were out of the picture, they diversified. *Morgonucudon* , a contemporary of dinosaurs, is an example of one of the first mammals. Mammals evolved from therapsid reptiles. The finback reptile *Diametrodon* is an example of a therapsid. One of the most successful lineages of mammals is, of course, humans. Humans are neotenous apes. Neoteny is a process which leads to an organism reaching reproductive capacity in its juvenile form. The primary line of evidence for this is the similarities between young apes and adult humans. Louis Bolk compiled a list of 25 features shared between adult humans and juvenile apes, including facial morphology, high relative brain weight, absence of brow ridges and cranial crests.

The earth has been in a state of flux for 4 billion years. Across this time, the abundance of different lineages varies wildly. New lineages evolve and radiate out across the face of the planet, pushing older lineages to extinction, or relictual existence in protected refugia or suitable microhabitats. Organisms modify their environments. This can be disastrous, as in the case of the oxygen holocaust. However, environmental modification can be the impetus for further evolutionary change. Overall, diversity has increased since the beginning of life. This increase is, however, interrupted numerous times by mass extinctions. Diversity appears to have hit an all-time high just prior to the appearance of humans. As the human population has increased, biological diversity has decreased at an ever-increasing pace. The correlation is probably causal.

Scientific Standing of Evolution and its Critics

The theory of evolution and common descent were once controversial in scientific circles. This is no longer the case. Debates continue about how various aspects of evolution work. For example, all the details of patterns of relationships are not fully worked out. However, evolution and common descent are considered fact by the scientific community.

Scientific creationism is 100% crap. So-called "scientific" creationists do not base their objections on scientific reasoning or data. Their ideas are based on religious dogma, and their approach is simply to attack evolution. The types of arguments they use fall into several categories: distortions of scientific principles (the second law of thermodynamics argument), straw man versions of evolution (the "too improbable to evolve by chance" argument), dishonest selective use of data (the declining speed of light argument) appeals to emotion or wishful thinking ("I don't want to be related to an ape"), appeals to personal incredulity ("I don't see how this could have evolved"), dishonestly quoting scientists out of context (Darwin's comments on the evolution of the eye) and simply fabricating data to suit their arguments (Gish's "bullfrog proteins").

Most importantly, scientific creationists do not have a testable, scientific theory to replace evolution with. Even if evolution turned out to be wrong, it would simply be replaced by another scientific theory. Creationists do not conduct scientific experiments, nor do they seek publication in peer-reviewed scientific journals. Much of their output is "preaching to the choir."

The most persuasive creationist argument is a non-scientific one -- the appeal to fair play. "Shouldn't we present both sides of the argument?," they ask. The answer is no -- the fair thing to do is exclude scientific creationism from public school science courses. Scientists have studied and tested evolution for 150 years. There is voluminous evidence for it. Within the scientific community, there are no competing theories. Until scientific creationists formulate a scientific theory, and submit it for testing, they have no right to demand equal time in science class to present their ideas. Evolution has earned a place in the science curriculum. Creationism has not.

Science is based on an open and honest look at the data. Much of creationism is built on dishonest debating techniques and special pleading for a case the data does not support. Science belongs in science classes. Evolution is science. Creationism is not. It's that simple.

The creationist attack on public school education means that school children are denied the possibility of learning about the most powerful and elegant theory in biology. Politicians are willing to allow the scientifically ignorant, but politically strong, to wreck the educational system in exchange for votes. People interested in evolution, and science education in general, need to closely watch school board elections. Creationist "stealth" candidates have been elected in several regions. Thankfully, many have been voted out once their views became apparent.

The majority of Americans are religious, but only a minority are religious nuts. The version of religion the far right wants to impose on America is as repulsive to most mainstream Christians as it is to members of other religions, atheists and agnostics. Most informed religious people see no reason for biological facts and theories to interfere with their religious beliefs.

The Importance of Evolution in Biology

"Nothing in biology makes sense except in the light of evolution." -- Theodosius Dobzhansky

Evolution has been called the cornerstone of biology, and for good reasons. It is possible to do research in biology with little or no knowledge of evolution. Most biologists do. But, without evolution biology becomes a disparate set of fields. Evolutionary explanations pervade all fields in biology and brings them together under one theoretical umbrella.

We know from microevolutionary theory that natural selection should optimize the existing genetic variation in a population to maximize reproductive success. This provides a framework for interpreting a variety of biological traits and their relative importance. For example, a signal intended to attract a mate could be intercepted by

predators. Natural selection has caused a trade- off between attracting mates and getting preyed upon. If you assume something other than reproductive success is optimized, many things in biology would make little sense. Without the theory of evolution, life history strategies would be poorly understood.

Macroevolutionary theory also helps explain many things about how living things work. Organisms are modified over time by cumulative natural selection. The numerous examples of jury- rigged design in nature are a direct result of this. The distribution of genetically based traits across groups is explained by splitting of lineages and the continued production of new traits by mutation. The traits are restricted to the lineages they arise in.

Details of the past also hold explanatory power in biology. Plants obtain their carbon by joining carbon dioxide gas to an organic molecule within their cells. This is called carbon fixation. The enzyme that fixes carbon is RuBP carboxlyase. Plants using C3 photosynthesis lose 1/3 to 1/2 of the carbon dioxide they originally fix. RuBP carboxlyase works well in the absence of oxygen, but poorly in its presence. This is because photosynthesis evolved when there was little gaseous oxygen present. Later, when oxygen became more abundant, the efficiency of photosynthesis decreased. Photosynthetic organisms compensated by making more of the enzyme. RuBP carboxylase is the most abundant protein on the planet partially because it is one of the least efficient.

Ecosystems, species, organisms and their genes all have long histories. A complete explanation of any biological trait must have two components. First, a proximal explanation -- how does it work? And second, an ultimate explanation -- what was it modified from? For centuries humans have asked, "Why are we here?" The answer to that question lies outside the realm of science. Biologists, however, can provide an elegant answer to the question, "How did we get here?"

Some Books about Biology and Evolution

Evolutionary Biology, by Douglas Futuyma, 1986, Sinauer, Sunderland,Mass

Evolution, by Mark Ridley, 1993, Blackwell Scientific, Boston

Principles of Population Genetics, by Hartl and Clark , 1989, Sinauer,Sunderland, Mass

Introduction to Population Genetics Theory, by Crow and Kimura, 1970, Burgess Publishing Company, Edina, Minnesota

Fundamentals of Molecular Evolution, by Li and Graur, 1991, Sinauer, Sunderland, Mass

The Genetic Basis of Evolutionary Change, by Richard Lewontin, 1974, Columbia University Press, New York

The Causes of Molecular Evolution, by John Gillespie, 1991, Oxford University Press, New York

Non-Neutral Evolution, edited by Brian Golding, 1994, Chapman and Hall, Boston

The Neutral Theory of Molecular Evolution, by Motoo Kimura, 1983, Cambridge University Press, Cambridge

Natural Selection in the Wild, by John Endler, 1986, Princeton University Press, Princeton, New Jersey

Macroevolutionary Dynamics, by Niles Eldredge, 1989, McGraw- Hill, New York

History of Life, by Richard Cowen, 1990, Blackwell Scientific, Boston

The Blind Watchmaker, by Richard Dawkins, 1987, Norton, New York

Abusing Science, by Philip Kitcher, 1982, MIT, Cambridge, Mass

The Diversity of Life, by E. O. Wilson, 1992, Harvard Belknap, Cambridge, Mass.

The Origin of Species, by Charles Darwin, 1859

Descent of Man, by Charles Darwin, 1871

The Causes of Evolution, by J. B. S. Haldane, 1932 (reprinted 1990, Princeton University Press, Princeton, New Jersey)

Tempo and Mode in Evolution, by G. G. Simpson, 1944, Columbia University Press, New York

The Growth of Biological Thought, by Ernst Mayr, 1982, Harvard Belknap, Cambidge, Mass.

The Origins of Theoretical Population Genetics, by William B. Provine, 1971, University of Chicago Press, Chicago

Appendix

Part one: Geological time

	Millions of years ago
Preambrian Time	
Archean Era	4600-2500
Proterozoic Era	2500-570
Phanerozoic Time	
Paleozoic Era	
Cambrian Period	570-505
Ordovician Period	505-438
Silurian Period	438-408
Devonian Period	408-360
Carboniferous Period	360-286
Permian Period	286-245
Mesozoic Era	
Triassic Period	245-208
Jurassic Period	208-144
Cretaceous Period	144-66.4
Cenozoic Era	
Tertiary Period	
Paleocene Epoch	66.4-57.8
Eocene Epoch	57.8-38.6
Oligocene Epoch	38.6-23.7
Miocene Epoch	23.7-5.3
Pliocene Epoch	5.3-1.6
Quarternary Period	
Pleistocene Epoch	1.6-0.01
Holocene Epoch	0.01-0

Part two: Universal phylogeny