Evolution: The Darwinian Revolutions
BIOEE 2070 / HIST 2870 / STS 2871

DAY & DATE: Monday 23 July 2012

READINGS: Eldredge & Gould (1972)/Punctuated equilibrium: An alternative to phyletic gradualism.. In Schopf, T. M. (ed) *Models in Paleobiology*, pages 82 to 115. San Francisco: Freeman (available in course packet)
Raup/*Extinction: Bad Genes or Bad Luck?* (all)
Ruse/*Darwin and Design: Does Evolution Have a Purpose?* chapter 13

Lecture 6:00-7:50: Extinction and Punctuated Equilibrium

Section 8:00-9:00: The structure of scientific revolutions

Announcements:

• **ESSAY #2 IS DUE TODAY, MONDAY 23 JULY!**

The sooner you submit it (via email, please), the sooner you will get back the graded version, with comments.

• **Essay #3 is ready for you to begin writing.**

You can pick up a copy tonight in lecture, or download a copy from the course website at:

http://evolution.freehostia.com

This time, you have a choice of five essay topics (just choose one), or you can write a third essay on a topic of your own choosing - just clear it with your TA.

ESSAY #3 IS DUE ON WEDNESDAY 1 AUGUST 2012

ABSOLUTELY NO PAPERS WILL BE ACCEPTED AFTER 1 AUGUST!

• **Some of the readings for this section of the course are available online:**

• **Cosmides & Tooby/"Evolutionary psychology: A primer"** Available at:
  http://www.psych.ucsb.edu/research/cep/primer.html

• **MacNeill, A, (2004) "The capacity for religious experience is an evolutionary adaptation for warfare."** *Evolution and Cognition*, vol 10, no 1, pp 43-60.

• **MacNeill, A. (2004) "Vertical Polygamy"** Unpublished manuscript.

Look for them online (just click the hotlinks, above) or in the "Course Packet" section of the course website at http://evolution.freehostia.com/course-packet/

The password for the course packets is:

evolutioncp

Extinction

Extinction is the death or disappearance of every member of a **species**. We have the feeling that **extinction**, while traumatic, is rare. However, it is clearly the eventual fate of virtually all **species**. According to **David Raup**, greater than 99% of all **species** that have ever existed have gone extinct. This means that less than one percent of all **species** that have ever existed are still alive today. Furthermore, many currently existing **species** are close to **extinction**.

This should put an end once and for all to the completely mistaken notion that **evolution** by **natural selection** operates "**in order to ensure the survival of the species**". This ridiculous and pointless phrase is included in nearly every newspaper and magazine article on evolution, and couldn't possibly be further from the truth. **Natural selection** pretty much ensures the **extinction**, not survival, of nearly all **species**…in the long run, anyway.

An "average" **species** persists for about four to eight million years before going extinct. An example of an extinct species is the "**elephant bird**" of **Madagascar**. It stood over ten feet tall, weighed about 1,100 pounds, and laid three-pound eggs (the equivalent of about 200 chicken eggs). Fossils indicate that it survived for almost 60 million years before going extinct. We know a fair amount about this species because it went extinct in historic times; it was driven to extinction by human hunting.

Elephant Bird

An Abbreviated Obituary

That the **elephant bird** was driven to extinction by humans is not unusual. Here is a selection of **species** that have been driven to **extinction** as the result of human activity (hunting, habitat destruction, etc.):

The **moa** of **New Zealand** went extinct in 1835. It was 13 feet tall and flightless. After surviving for 100 million years, it and nearly 15 other species of large flightless birds on the islands of **New Zealand** were hunted to extinction by the **Maori**.

The common **dodo** of **Mauritius** (in the Indian Ocean) went extinct in 1680. It was a flightless bird about the size of a turkey. The **dodo** was actually a large pigeon and unlike the turkey, it did not taste very good. It was hunted to extinction for sport, not for food.

The passenger pigeon of North America went extinct in 1914. The passenger pigeon was once the most abundant bird in the world, numbering almost a hundred billion. A single flock in 1860 was estimated at between one and two billion birds. It was driven to extinction by human market hunters in less than forty years. Here is a picture of it by Audubon, who painted it from life:

The moa and other flightless birds of New Zealand were not alone. The laughing owl of New Zealand went extinct in 1914.

Several species of macaws and parrots, large brightly colored birds of the tropics, were driven to extinction during the 19th century, along with several species of rails (large shore-dwelling birds) and the great auk, the largest flightless bird in the northern hemisphere, which went extinct in 1844. Here's a painting of it by Audubon:

Over 50 species of [Hawaiian honey creepers](#) (bright yellow birds with long, hooked bills), finches (sparrow-like birds), flightless rails, and [geese](#) were driven to extinction, almost all since the arrival of [Polynesian](#) sailors on the islands.

Extinct Hawaiian Avifauna

The [ivory-billed woodpecker](#), a close relative of our pileated woodpecker, was last seen (and assumed extinct) in 1951. An expedition to its last known habitat, organized by the Cornell Laboratory of Ornithology, failed to find conclusive evidence that there were still members of this species still alive. Here's another painting by Audubon:

Ivory-Billed Woodpecker

In addition to the birds listed above, many hundreds of species of less cuddly vertebrates have gone extinct in historic times. For example, the [Round Island](#) [boa](#) (a snake) last observed in 1975 and now considered extinct.

Round Island Boa
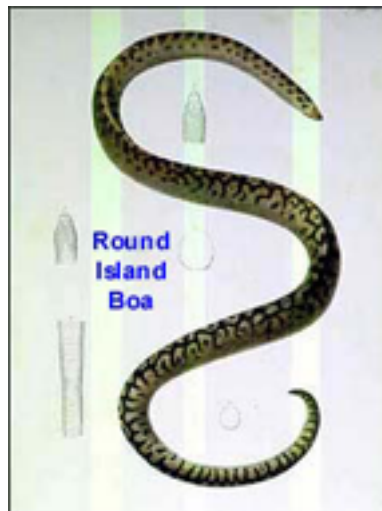
Many species of suckers (bottom-feeding freshwater fish) were mostly driven to extinction during the 19th and 20th centuries. In Lake Victoria alone, over 200 species of cichlid fish have been driven to extinction since 1960, almost all as prey of an introduced predator, the Nile perch. We will discuss the cichlid fish of Lake Victoria and their fate in more detail in a later lecture.
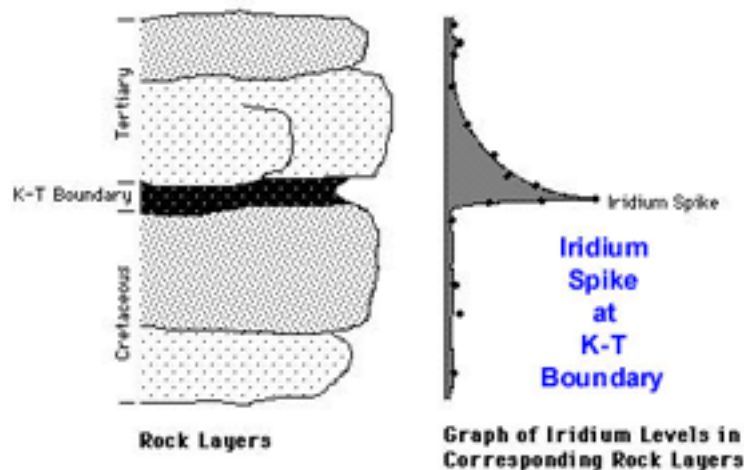
Many species of orchids, including some spectacular ones from the South American tropics, have gone extinct, either from habitat destruction or from over zealous collecting by orchid fanciers (see the movie "Adaptation" if you get a chance – it's all about the obsessions of orchid fanciers).

Suppose that 25,000 species of beetles were to go extinct tomorrow, along with 5,000 species of bees and wasps, 3,000 species of mosquitoes, 2,000 species of lice...or even 20 million of the 40+ million species of living organisms identified today. Terrible as such a thing might be to contemplate, this would be no worse than the most recent mass extinction, which was not nearly the most severe mass extinction in the history of life on Earth.

What causes extinction?

According to David Raup (*Extinction: Bad Genes or Bad Luck*), the fossil record show many examples of extinction, but it rarely indicates why such extinction has occurred. An exception to this rule is the Cretaceous-Tertiary (K-T) mass extinction event, which is clearly associated with an asteroid collision, most likely at the northern coast of the Yucatan peninsula.

The first evidence for the Cretaceous-Tertiary asteroid collision was an anomalous enrichment of iridium (a rare element) in rocks dating from the Cretaceous-Tertiary boundary.

Tertiary

K-T Boundary

Cretaceous

Rock Layers

Iridium Spike

Iridium Spike at K-T Boundary

Graph of Iridium Levels in Corresponding Rock Layers

This enrichment was puzzling to its discoverer, Walter Alvarez, who was studying iridium levels in rocks to track the rate of in-falling space dust – iridium is rare on the Earth's surface, but common in meteorites and asteroids. Louis Alvarez, Walter's father and a Nobel prize winner in physics, suggested that the anomalous iridium enrichment in the Cretaceous-Tertiary boundary rocks was evidence of a massive asteroid collision. Subsequent geological and paleontological research has largely validated his hypothesis.

The Cretaceous-Tertiary asteroid collision has been dated at 65 million years before the present, and is associated with a drastic change in the fossil record of dinosaurs. During the Mesozoic era, there was a steady extinction rate for dinosaurs, which began to accelerate during the Cretaceous Period. Dinosaur fossils completely disappear following the Cretaceous-Tertiary asteroid collision, so it appears that the collision and its ecological aftereffects caused the final mass extinction of the dinosaurs.

Not all extinctions involve mass extinction, however. The fossil record indicates that there is a pattern of "background" extinction, in which species disappear in what seems almost a random fashion, one-at-a-time. Raup discusses several factors related to extinction:

Species are temporary. The fossil record shows many examples of this. Species may last a very long time, or they may appear and disappear in a relatively short time, but eventually virtually all species go extinct. As Raup points out, over 99% of all species that have ever existed are now extinct.

- According to Raup, an average species last between four and ten million years, from first appearance in the fossil record to eventual disappearance. Some species last much longer (*e.g.* cockroaches), while others disappear much more quickly. For example, there were until recently over 600 species of cichlid fish in Lake Victoria (in Africa). Since the lake was only formed about 12,000 years ago, all of these species have evolved since then. In addition, over 200 species have appeared and then later gone extinct, all in less than 12,000 years.

Species with very small populations are easy to kill. Examples include whooping cranes, California condors, and ivory-billed woodpeckers. If a species is reduced to only a very small number of individuals, even random chance events (such as a sudden storm) can drive it to extinction.

Widespread species are usually hard to kill. However, even widespread species can be rapidly wiped out, especially if something prevents reproduction by large numbers of individuals (*i.e.* an effective "first strike").

- An example is the passenger pigeon, which was reduced from several billion to zero in about 40 years, primarily as the result of market hunting of squabs (baby pigeons).

Extinction of widespread species is favored by stresses not normally experienced by the species. In some cases, widespread success can be disastrous; if a species outgrows its environment, or if it is so widespread that diseases can easily spread from individual to individual, it can go extinct.

- For example, American chestnut trees were once very common and widespread in North America. During the early 20th century, they were exposed to an introduced disease (caused by a fungus). They are now very nearly extinct throughout most of their former range. The same kind of rapid change, leading to extinction (or near-extinction) has occurred in American elm trees, American beech trees, and several other tree species.

Simultaneous extinction of many species requires stresses that cut across ecological lines. Mass extinctions usually result from massive/rapid environmental changes (such as asteroid collisions, widespread volcanic eruptions, etc.) In addition to wiping out many species of organisms, such events also open up many ecological niches, which are then occupied by new or already existing species. Overall, most mass extinction events eventually produce more species (in their aftermath) than they extinguish.

- "The limits to the effectiveness of natural selection are most clearly revealed by the universality of extinction; more than 99 percent of all evolving lines that once existed on Earth have become extinct." - Ernst Mayr

This statement implies that natural selection is a mechanism, rather than the result of the operation of a suite of mechanisms (*i.e.* variation, inheritance, overpopulation, and non-random survival and reproduction). Raup's list of important factors in extinction doesn't really include any direct causes; upon examination, it can be seen that (like natural selection) they are all effects.

Natural Selection and Extinction

What is the relationship between natural selection and extinction? Darwin pointed out that breeders cannot select for more than one or two characters at a time. When they try to do so, the result is "extinction" – that is, the attempted breeding programs don't work. The implication for natural selection is that the same principle applies; selection for one or two characters can produce eventual changes in those characters, but selection for many characters at once usually results in extinction.

Furthermore, as Darwin and other evolutionary biologists have pointed out, natural selection cannot possibly prepare a species for the kinds of changes that cause extinction, either of the "background" type or during periods of mass extinction. This is because natural selection "fine tunes" organisms to survive and reproduce under existing conditions, but cannot anticipate changes in those conditions. Indeed, the more tightly adapted a species is to existing conditions, the more likely it is to go extinct when those conditions change.

- Consider for example the extinct cichlid fishes represented in the rocks of the New Jersey palisades. These rocks provide a record of shallow lakes and estuaries, which formed, persisted for a few hundreds of thousands of years, and then eventually filled in or dried up. The pattern of fish fossils under these conditions parallels that seen in Lake Victoria: an early proliferation of species, followed by a stabilization of species numbers (with increasing background extinction), followed by increasing extinction rates and ending in complete extinction as the lakes dried up.

This pattern would have pleased the late Stephen Jay Gould perhaps the best known American evolutionary biologist and one of the founders of the theory of punctuated equilibrium. Gould proposed that this is the standard pattern for speciation; rapid, widespread speciation in the early stages, followed by stabilization and evolutionary stasis, followed by eventual extinction and replacement by new species. In his longest and most important book, *The Structure of Evolutionary Theory*, Gould attempted to show that paleontological evidence, such as that supporting the patterns discussed above, is essential to the understanding of how evolution, and especially speciation and the origin of higher taxa, occurs. His work on the snails of Bermuda supported his theory of punctuated equilibrium and he generalized this to all of evolutionary history. More on this subject later in this lecture…

Mass Extinctions and the Evolution of New Species

We have already touched briefly on the subject of mass extinctions. Raup discusses both "background" and mass extinctions, and implies that the latter are the result of different historical processes than the former. "Background" extinctions are generally the result of random numerical fluctuations in the population sizes of species that are restricted in range and overall numbers. As described above, such species are relatively easy to kill. However, mass extinctions are much more indescriminate. The fossil record indicates that there have been at least five major mass extinctions during the past billion years, and probably many more minor mass extinctions:

Five Great Mass Extinctions
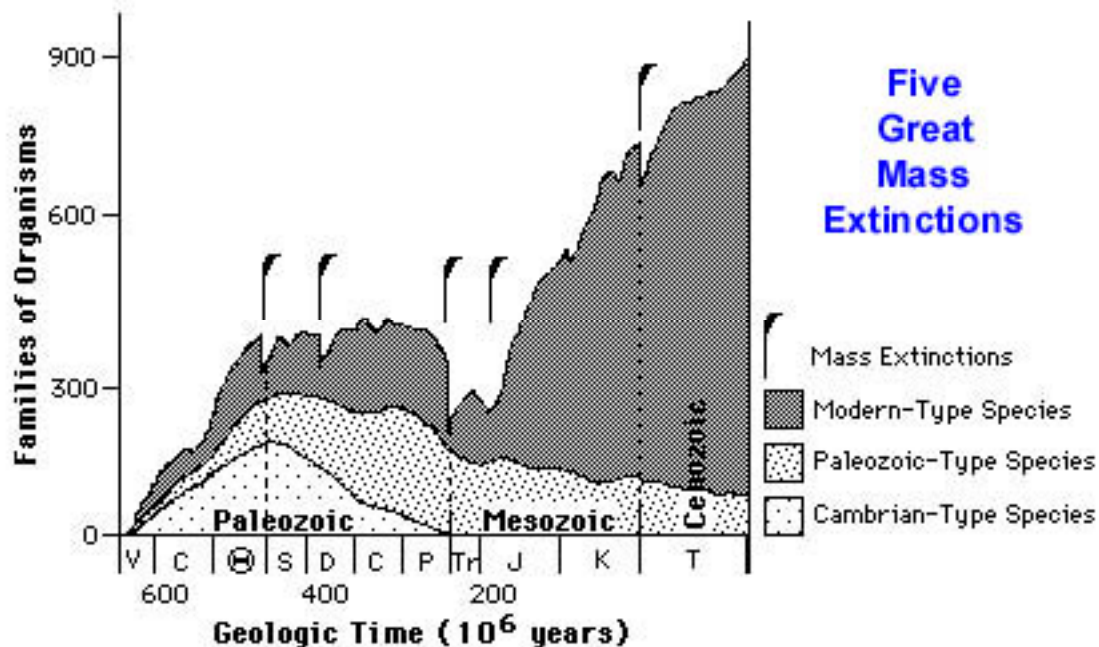
Paradoxically, however, these <u>mass extinctions</u> seem to have set the stage for subsequent periods of mass speciation (called "<u>adaptive radiation</u>").

- The <u>Permian/Triassic mass extinction</u> killed off over 95% of all species living on Earth at the time. The rocks deposited immediately after the end of the <u>Permian period</u> (about 250 million years ago) are almost entirely devoid of fossils. Then, about 15 million years later, new fossils begin to appear and proliferate.

- The <u>Cretaceous/Tertiary mass extinction</u>, which was almost certainly caused by an asteroid collision, wiped out all vertebrates larger than a turkey. This event, which was cataclysmic for the dinosaurs, allowed the mammals (including ourselves) to proliferate into more species than had existed prior to the mass extinction.

All <u>mass extinctions</u> have been followed by <u>adaptive radiations</u> of new types of organisms, with the eventual result that the <u>species diversity</u> of the Earth has increased overall. This has happened despite the fact that such <u>mass extinctions</u> have wiped out almost all of previously existing <u>species</u>. This pattern seems to be a general characteristic of the evolution of life on Earth.

Bad genes or bad luck?

David Raup asks if extinction is the result of "bad genes" or "bad luck." He concludes that in most cases, it's just "bad luck" - the species in question goes extinct because the environment in which it lives changes faster than it can adapt to the change.

- Raup's argument partly hinges on his definition of a "species." In his book, *Extinction: Bad Genes or Bad Luck?* Raup says that a <u>species</u> "...is a group of...organisms that share a common pool of genetic material" (page 14) He also says that <u>species</u> must be "...<u>reproductively isolated</u>" (page 15). Eventually, he concludes that a <u>species</u> is what a "...competent <u>taxonomist</u> says it is."

Macroevolution and Punctuated Equilibrium

One of the central tenets of the "modern evolutionary synthesis" of the first half of the 20th century was the idea that evolutionary change at all levels could be explained entirely on the basis of the standard microevolutionary mechanisms: micromutation, genetic drift, natural selection, sexual selection, and reproductive isolation. However, persistent criticism of this paradigm continued, especially among paleontologists. This process came to a head in 1972, when Niles Eldredge and Stephen Jay Gould proposed their theory of punctuated equilibrium, in a paper entitled "Punctuated equilibria: an alternative to phyletic gradualism." In it, they proposed a radical break with the modern evolutionary synthesis, asserting that macroevolution (*i.e.* the large-scale pattern of evolutionary changes in life on Earth over the past 4 billion years) is fundamentally different from microevolution.

The essential features that make up the theory of punctuated equilibrium are as follows:

Most speciation is the result of cladogenesis, rather than anagenesis. The pattern of descent with modification in an evolving line of organisms is called a phylogeny:

A Simple Phylogeny
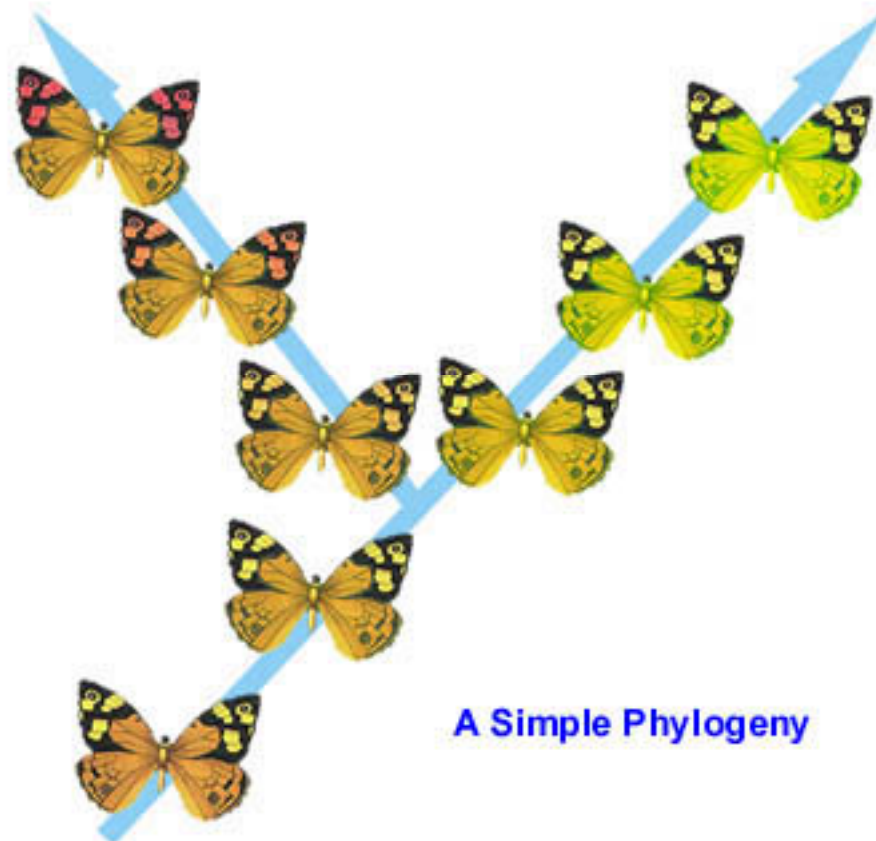
Cladogenesis is the splitting of one inter-related population of organisms into two or more reproductively isolated populations:
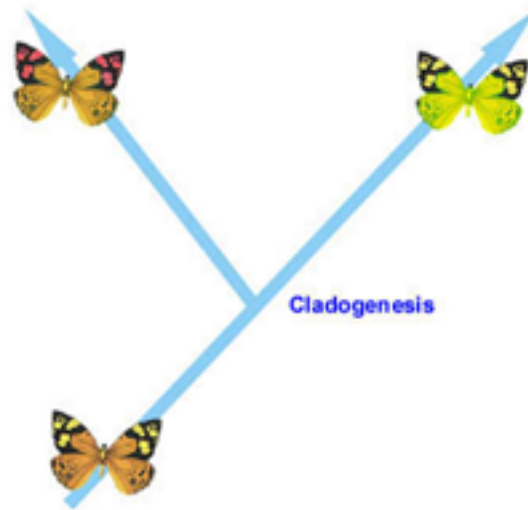

By contrast, **anagenesis** is the gradual change over time of a single phylogenetic line:

According to **Eldredge** and **Gould**, the "classical" paradigm of **gradual anagenetic change** is not supported by the **fossil record**.

Most speciation occurs via peripatric speciation (*i.e.* speciation in isolated populations at the periphery of larger, **panmictic** populations. **Eldredge** and **Gould** were inspired to this part of their theory by the earlier work of **Ernst Mayr**, who proposed that **speciation** occurs in isolated sub-populations of larger **panmictic** populations. Once the sub-population becomes **reproductively isolated** from the larger source population, the accumulation of **random genetic changes**, accentuated by **genetic drift**, **natural selection**, and **sexual selection**, cause the members of the sub-population to become reproductively incompatible with members of the original source population. **Eldredge** and **Gould** simply modify this idea to include the assertion that such isolated sub-populations split off from the main population at its geographical periphery.

Peripatric Speciation
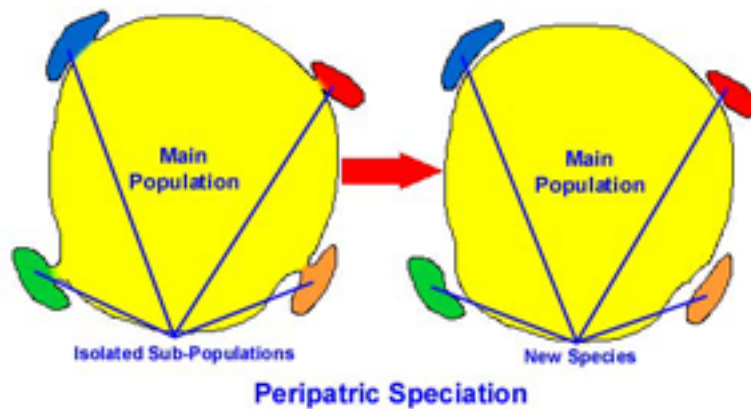
Large, widespread species usually change slowly, if at all, during their time of residence. According to the theory of punctuated equilibrium, this is because stabilizing selection operates on the large population to maintain it around a stable adaptive peak, rather than cause it to change significantly over time.

Daughter species usually develop in a geographically limited region and in a stratigraphically limited extent, which is small in relation to total residence time of the species. This was Mayr's original suggestion, inspired at least in part by Darwin's explanation for the many gaps in the fossil record. If speciation occurs in small, isolated populations over relatively brief periods of time, the chances that their remains will be fossilized is small to non-existent.

Sampling of the fossil record will reveal a pattern of most species in stasis, with abrupt appearance of newly derived species being a consequence of ecological succession and dispersion. This is simple observation: nearly all paleontologists have pointed out that this is the general pattern found in the fossil record of nearly all groups of organisms, especially animals.

Adaptive change in lineages occurs mostly during periods of speciation. Again, species in stasis are subject primarily to stabilizing selection, as the extreme members of the population are weeded out due to incompatibility with their environment. However, drastic changes in that environment can result in directional selection, caused by the removal of one extreme but the preservation of the other extreme for one or more trait.

Trends in adaptation occur mostly through the mechanism of species selection. Essentially, during periods of rapid macroevolution, selection occurs at the level of reproductively isolated groups (*i.e.* species), rather than at the level of individuals. This was perhaps the most controversial and least supported part of the theory. Proposed and supported primarily by Gould, it has lost favor even among supporters of the overall theory, and is generally not included in the theory today.

The theory of punctuated equilibrium provides paleontologists with an explanation for the patterns which they find in the fossil record. This pattern includes the characteristically abrupt appearance of new species, the relative stability of morphology in widespread species, the limited distribution of transitional fossils when those are found, the apparent differences in morphology between ancestral and daughter species, and the pattern of extinction of species.

The Problem of Paleospecies

Paleontologists like Eldredge and Gould have to recognize species from their fossil remains, and have developed the concept of "paleospecies" to do so. The term "paleospecies" makes explicit the distinction between the classification of species from fossil remains and the process of recognizing species in modern populations.

Mayr's biological species concept uses the criterion of reproductive isolation to distinguish species in modern populations. Paleontologists who pursue taxonomic endeavors (which includes most of them) have to classify their finds generally based upon morphological features. The rareness of preservation of tissues containing DNA, or even of soft tissues, limits the range of diagnostic characters that may be utilized. The paleontologist has no access to such information.

The fossil record is incomplete. This incompleteness has many contributing factors. Geological processes may cause to confusion or error, as sedimentary deposition rates may vary, erosion may erase some strata, compression may turn possible fossils into unrecognizable junk, and so forth. As Darwin first pointed out, the fossil record can be turned into the equivalent of a partially burned book, which is taken apart, pages shuffled or destroyed, and from which only a few pages are retrieved.

Also important to this process is taphonomy -- the study of how organisms come to be preserved as fossils. Here, there are further issues to be addressed. Hard parts of organisms fossilize preferentially. The conditions under which even those parts may become fossilized are fairly restricted. All this results in a heavily skewed distribution of which organisms and which parts of organisms become fossilized, and this affects which features of morphology are available for use in classification. The issue of geography enters into all this, as a consequence of the fact that living lineages occupy ecological niches, and those niches are bound to certain features of geography. For example, dry land species are notoriously unlikely to fossilize, whereas marsh or swamp-dwelling species are much more likely to fossilize.

Paleospecies, then, have to be recognized as species from morphology alone, where the available morphological characters are drawn from a skewed distribution, the pattern of fossilization is skewed, and the geographic correlates of fossilization are limited in extent.

Eldredge and Gould based their understanding of paleospecies from processes already observed in living biological species.

Most species appear to have evolved as the result of cladogenesis (the splitting of a daughter species from an ancestral species) rather than anagenesis (the gradual transformation of the entire ancestral line). This results in the multiplication of species, and without it, the diversity of the living systems that we see would be impossible.

Most species appear to have evolved via allopatric speciation of peripheral isolates, or peripatric speciation in Mayr's terminology. Peripatric speciation states that a population of an ancestral species in a geographically peripheral part of the ancestral range is modified over time until even when the ancestral and daughter populations come into contact, there is reproductive isolation. While sudden speciation by change in chromosome number is observed to occur in modern populations, this form of speciation is also known to be rare (except in plants). Sympatric speciation (the production of a daughter species within the geographic range of its parent species) likewise is held to be a very rare event seen primarily in insect and parasite lineages.

The frequency with which peripatric speciation occurs in modern lineages is rare. This rarity means that a species may produce zero, one, or perhaps a few daughter species during its entire time span of existence.

The period of transition between parent species and daughter species is short compared to the period of time a species exists as a distinct form. When a small sub-population is isolated from the rest of the population of a species, the particular set of variations in the sub-population is much smaller than that in the remainder of the population. These variations, when in conjunction with suitable features of geographic locale, climate, and resources, can lead to relatively rapid evolution of reproductive isolation from the ancestral population. This reduction in variation due to small sub-population size is known as the "founder effect".

Adaptations developed or accentuated in the new daughter species can lead to the rapid dispersal and establishment of a daughter species throughout the range of the ancestral species, or into new ranges. The ecological processes of dispersal and succession can occur very quickly compared to evolutionary processes of change.

Gene flow, genetic homeostasis, and large population size inhibit widespread ancestral populations from much directional (adaptive) change. Any adaptive change found in the ancestral population is likely to be small and unrelated to evolutionary trends.

The principle predictions that flow from Eldredge and Gould 's theory of punctuated equilibrium. are as follows:

Speciation events comprise most of the evolutionary change seen in adaptation. This is a consequence of the inhibitory effects of gene flow, genetic homeostasis, and large population sizes. The adaptations of newly speciated daughter populations are forever excluded from the ancestral population because of reproductive isolation. Furthermore, once a new species has become established, it will be subject to stabilizing selection, thereby limiting the evolution of any new adaptations following the original speciation event.

New species appear abruptly in the fossil record. The splitting of lineages as the result of allopatric speciation, followed by ecological dispersal and succession, would result in geologically abrupt appearance of the daughter species everywhere except the limited geographic area where the speciation took place. Since this critical change occurs in such a small region and in such a limited population, the probability of finding specimens which document the transition from ancestral to daughter species is very low. A population which can exploit resources untapped by current populations will grow and spread at somewhere near its theoretical intrinsic rate of increase. The cases of introduced species in modern times (the starling in North America or the Nile perch in Lake Victoria, for example) demonstrate the extreme rapidity in which a species may spread across large geographic areas.

Most species show long periods of stasis. A species may produce a few daughter species during its duration. Large interbreeding populations are unlikely to change much due to genetic homeostasis and gene flow from far-flung parts of the range (Eldredge and Gould emphasize homeostatic mechanisms over gene flow).

As noted earlier, the theory asserts "species selection" as the way in which major adaptive trends proceed. According to this viewpoint, closely related species are often likely to overlap in niche

space. Ecological processes may cause the displacement and possible extinction of certain species due to competition with other species. If adaptive change in large populations is largely inhibited, then each species represents a "hypothesis" that is "tested" in competition. This is one of the most controversial parts of the theory, and has been largely abandoned.

How to Subvert the Dominant Paradigm and Foment a Scientific Revolution

Thomas Kuhn has proposed that scientific revolutions occur suddenly, as the result of shifts in the dominant viewpoint shared by most scientists. In his most famous book, *The Structure of Scientific Revolutions,* he asserted that most of the time scientists do "normal science". That is, they make observations and perform experiments that confirm the predictions of already existing theories (which Kuhn calls "dominant paradigms.") However, while doing this, they slowly accumulate evidence that does not fit the dominant paradigm. Over time, these anomalies become more and more glaring. Eventually, a newcomer to the field (often someone relatively young and previously unknown) formulates a radically new theory that explains the anomalies and thereby extends (or sometimes even overturns) the dominant paradigm.

This is essentially what Eldredge and Gould did to the "synthetic" theory of evolution with their theory of punctuated equilibrium. Their theory could have been advanced simply upon the basis of features of geology, taphonomy, geography, and taxonomy. However, that is not how Eldredge and Gould chose to do it. Instead, they codified what they saw as an inaccurate and incorrect "picture" of the fossil record, labelled it as "phyletic gradualism", and demonstrated that their theory was to be preferred on several points.

According to Eldredge and Gould's description of the classical view, "phyletic gradualism" includes the following points:

- New species arise by the transformation of an ancestral population into its modified descendants

- This transformation is gradual and slow

- The transformation involves large numbers, usually the entire ancestral population

- The transformation occurs over all or a large part of the geographic range of the ancestral species

These statements imply several consequences, two of which seem especially important to paleontologists:

- The fossil record for the origin of a new species should consist of a long sequence of continuous, insensibly graded intermediate forms linking ancestor and descendant.

- Any breaks in a postulated phyletic sequence are due to imperfections in the geological record.

Eldredge and Gould quoted from Darwin in their 1972 paper to establish their concept of phyletic gradualism. They claim that Darwin set the task of later workers to search out evidence confirming phyletic gradualism. In doing this, they erected what is essentially a "straw man." Here is the quote from Darwin they use to justify their view:

- "Nothing can be effected, unless favourable variations occur, and variation itself is apparently always a very slow process. The process will often be greatly retarded by free intercrossing. Many will exclaim that these several causes are amply sufficient wholly to stop the action of natural selection. I do not believe so. On the other hand, I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time. I further believe, that this very slow, intermittent action of natural selection accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed." [*Origin of Species*, 1st Edition (1859), pp.108-109/Wilson, pp. 518-519]

However, a closer examination of this quote from Darwin shows that he did _not_ embrace three of the four conditions that Eldredge and Gould specified for phyletic gradualism, and the single one that Darwin did embrace is also a tenet of any theory of speciation.

- The "free intercrossing" bit is easily recognizable as a forerunner of the concept of gene flow, though Darwin was probably concerned there with blending inheritance.

- Darwin makes explicit that there is no constancy of rate implied with the comment on "intermittent action".

- Darwin also recognized that change would be more likely to occur in sub-populations. Whether Darwin meant by "of the same region" much the same thing as the modern concept of allopatric speciation is a matter of dispute.

Darwin did think that a daughter species arose from a population of the parent species. So did Eldredge and Gould. Darwin did think that the transformation would be slow, but he did not think that it would be "even". Darwin did not think that the transformation would involve large numbers, and certainly not the entire parent population. Darwin did not think that the transformation would occur across the entire ancestral range:

- "But on the view of all the species of a genus having descended from a single parent, though now distributed to the most remote points of the world, we ought to find, and I believe as a general rule we do find, that some at least of the species range very widely; for it is necessary that the unmodified parent should range widely, undergoing modification during its diffusion, and should place itself under diverse conditions favourable for the conversion of its offspring, firstly into new varieties and ultimately into new species." [*Origin of Species*, 1st Edition (1859), pg.405/Wilson, pg. 706-707]

It is difficult to extract meaning from the above without recognition that Darwin was well aware of the importance of geographical distribution in the production of new species.

- "Only a small portion of the world has been geologically explored. Only organic beings of certain classes can be preserved in a fossil condition, at least in any great number. Widely ranging species vary most, and varieties are often at first local, -- both causes rendering the discovery of intermediate links less likely. Local varieties will not spread into other and distant regions until they are considerably modified and improved; and when they do spread, if discovered in a geological formation, they will appear as if suddenly created there, and will be simply classed as new species." [*Origin of Species*, 1st Edition (1859), p.464/Wilson, pg. 744]

The above quote comes from the famous section in Chapter 12 on geographical distribution. However, Darwin makes it clear that geographic location makes a difference in the finding of intermediate forms. "Both causes" in the above could not make discovery of intermediate links less likely if Darwin expected the transformation of the entire parent population.

Were Eldredge and Gould successful in fomenting a scientific revolution and replacing the dominant paradigm? It may be too early to tell. Evolutionary biologists continue to argue vehemently over their theory, attempting to assimilate it into the "modern evolutionary synthesis." However, it seems clear in hindsight that the synthesis itself has evolved: how else to explain the ubiquitous division between microevolution and macroevolution in nearly all books and courses on evolutionary theory? While some of the more controversial assertions of the theory (such as the idea of species selection) are no longer held by many, there is general agreement that there is a legitimate distinction to be made between microevolution and macroevolution. If so, one of the bedrock principles of the "modern synthesis" has been altered beyond recognition.

Is evolution progressive?

We have already emphasized the idea that natural selection, sexual selection, and genetic drift are not purposeful processes. That is, the idea of purpose or goal-directedness is unnecessary to an evolutionary explanation for adaptation, and therefore is not included in such an explanation. Furthermore, it has been pointed out that this has led most evolutionary biologists (and indeed, most scientists) to eliminate the concept of purpose from nature altogether, restricting it to organisms with complex nervous systems capable of changing their behavior over time as the result of experience.

However, we have not yet considered another common misunderstanding of evolutionary theory: that it is necessarily progressive. Most of you will have encountered illustrations of the evolutionary history of humans that are something like the following:
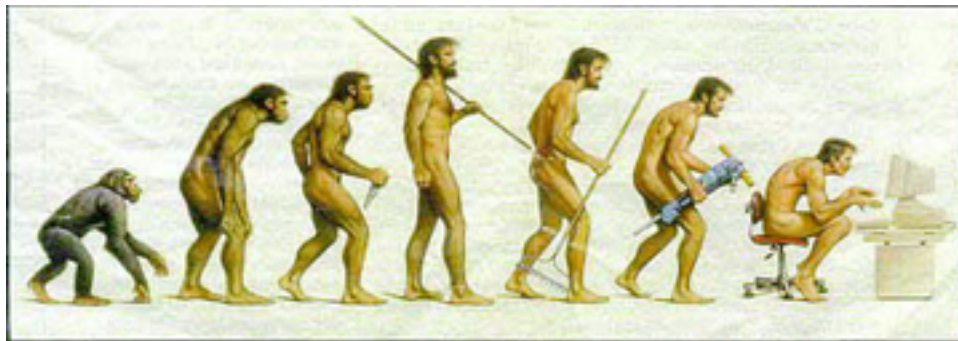
This is more than just a humorous depiction of the evolutionary past (and likely evolutionary future) of humans. It also illustrates a common view of evolution: that it is progressive. Humans have become more and more upright, intelligent, and complex, and so have virtually all other organisms.

However, it is a fundamental assumption of current evolutionary theory that, although many phylogenetic lines have resulted in organisms that are larger, more complex, and (among animals) have more complex behaviors, **such trends do *not* indicate that progress is a necessary part of evolution or of adaptation.** This idea is linked to the idea of evolution as a purposeful process, an

idea that we have already discarded as unnecessary. In the case of "progress" in evolution, many examples of *reduction* in size, complexity, and other indicators of so-called "progress" can be found, in nearly all phylogenetic lines. In particular, parasites are virtually always smaller, less complex (in both physiology and behavior), yet more specialized than their non-parasitic ancestors. Overall, therefore, it is best to state that, although there is a tendency within some phylogenetic lines for organisms to become larger and more complex, such tendencies are not an inescapable characteristic of evolution by natural selection.

In the next lecture we will consider how microevolution (natural selection, sexual selection, and genetic drift in small populations over relatively brief periods of time) differs from macroevolution (speciation and the origin of higher taxa over the long history of life on Earth), and what new discoveries in the field of evolutionary development ("evo-devo") can tell us about these differences.