Evolution: The Darwinian Revolutions

BIOEE 2070 / HIST 2870 / STS 2871

DAY & DATE: **Wednesday 25 July 2012**
READINGS: **Goldschmidt/*Darwin's Dreampond: Drama in Lake Victoria* (all)**
Ruse/*Darwin and Design: Does Evolution Have a Purpose?* chapter 14
Lecture 6:00-7:50: **Microevolution Versus Macroevolution**
Section 8:00-9:00: **microevolution and macroevolution**

Announcements:

• Essay #2 has been graded.
You should be receiving it via reply email tomorrow or Friday.

• Essay #3 has been assigned.
You have a choice of five essay topics (just choose one), or you can write a different essay on a topic of your own choosing - just clear it with one of us.

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- **MacNeill, A. (2004) "Vertical Polygamy" Unpublished manuscript.**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

and type in the password

evolutioncp

in the dialog box indicated by “Password Protected”.

Tjis Goldschmidt and the Cichlids of Lake Victoria

Tjis Goldschmidt came to Lake Victoria with high hopes. He wanted to answer several questions:

- **How many species of furu (the local name for cichlid fish) can be distinguished?**
- **Have all of these species descended from a single common ancestor?**
- **If so, how has this adaptive radiation occurred?**
- **Has natural selection played an important role in this process?**
- **Did sexual selection play an important role in this process?**

When he first went to Lake Victoria, Goldschmidt and other scientists thought the lake (and therefore the fish species in it) was at least a few hundred thousand years old. This seemed like a relatively brief time for the evolution of such a wide diversity of cichlid fish. However, by the time he finished working there, it had become clear (based on geological evidence) that the lake was only about 12,000 years old. This discovery intensified the mystery of the apparently rapid radiation of the furu.

Here are some more questions Goldschmidt wanted to know the answer to:

- **What do the hundreds of furu species actually do?**
- **What is their role in the Lake Victoria ecosystem?**
- **How do the different species (if such they are) exploit and subdivide the ecological resources of the lake?**
- **With so many species packed into such a small area, why don't they cause each other's extinction?**

But Goldschmidt had bigger ideas: as he says on page 9, "I even supposed that the radiations [of furu species]…might serve as a model for many older groups of fish, as well as for birds and mammals." A lofty goal…but reality is something else again.

Adaptations of the Cichlid Fish Species of Lake Victoria

As described by Goldschmidt, the different species of cichlid fish (*i.e.* the "furu") of Lake Victoria can most easily be distinguished by variations in their mouthparts. These variations can be correlated with the method of feeding of the various species of cichlids, as follows (you can view photographs of very similar species of cichlids from Lake Malawi by clicking here):

- **Mud-biters** (*i.e.* bottom feeders); members of these species bite mouthfuls of bottom mud, eating the small prey animals buried in the mud.
- **Algae-scrapers**; members of these species scrape algae off of rocks on the bottom and shores of the lake.
- **Leaf choppers**; members of these species chew up leaves that have fallen into the lake.
- **Snail-crushers**; members of these species crush hard-shelled snails and other mollusks that live in the lake. They generally have very heavy crushing jaws, which are adapted to crushing the shells of snails, which in turn have very heavy shells as the result of natural selection by the furu.
- **Snail-shellers**; members of these species extract snails and other mollusks from their shells without crushing them, and consequently have very different jaws and mouthparts from the snail-crushers.
- **Zooplankton-eaters**; members of these species filter suspended zooplankton from the water, somewhat in the manner of baleen whales.
- **Insect-eaters**; members of these species eat insects (adults and larvae) which fall into the lake or live there during their larval stages.
- **Prawn-eaters**; members of these species eat the crayfish-like prawns endemic to the lake.

- **Fish-eaters; members of these species eat other (generally smaller) fish, including other cichlids.**
- **Pedophages; members of these species eat either the eggs or early immature stages of other fish, especially cichlids. Some of these species actually suck these out of the mouths of other species, where the eggs and/or immature stages are carried and protected by their parents.**
- **Cleaners; members of these species pick parasites off of the skin of other fish, including other cichlids. Like the cleaners found in tropical reefs, these furu are usually not eaten or molested by the fish they clean, suggesting that their relationships with their hosts are mutualistically beneficial.**
- **Scale-scrapers; members of these species scrape the scales off of the sides of other fish, especially other cichlids. As Goldschmidt describes later in the book, these furu are specialized into right-handed and left-handed varieties.**

There are (or were) about 400 described species of furu in Lake Victoria, with perhaps another 400-500 species yet to be described. However, many of these (between 200 and 400 species) have now been pushed to extinction by the introduction of the Nile perch, which preys on cichlids, and against which the furu have no natural defenses.

(This Nile Perch weighed 230 pounds)

Perhaps the most fundamental question Goldschmidt was attempting to answer was whether the different species of furu evolved independently in Lake Victoria (that is, independently of similar species in other African lakes), or whether they migrated to Lake Victoria from other locations. There are similar species "flocks" in other rift lakes in Africa (such as Lake Malawi), and there is good evidence that strongly suggests that the various trophic types found in each lake evolved independent from each other. This, in turn, suggests that it might be possible to construct phylogenies for the evolution of furu in Lake Victoria and other rift lakes.

However, analysis of the DNA of Lake Victoria furu indicates that these different species are so genetically homogeneous that DNA sequences cannot be used to determine their phylogenetic relationships. In other words, although these species are wildly different from each other morphologically, they are so similar to each other genetically that they cannot be distinguished as separate species on the basis of genetic evidence.

- **This is perhaps the greatest paradox of the Lake Victoria furu: that tremendous morphological diversity coexists with genetic homogeneity. This is not how the genetics of speciation is supposed to work; in fact, it's just the other way around from what the classical biological species concepts predict. So what's going on?**

One possibility is that the similarities between the various trophic types found in different rift lakes are the result of convergent evolution. In other words, the similarities between the various species in different African rift lakes could be explained by similar adaptations to similar ecological conditions, rather than by common ancestry. This process was first described by Darwin in the *Origin of Species*, in which he pointed out that convergent evolution can confound evolutionary phylogenies:

- **"On my view of characters being of real importance for classification...we can clearly understand why analogical or adaptive character, although of the utmost importance to the welfare of the being, are almost valueless to the systematist." (*Origin of Species*, 1st ed., pg 427/Wilson, pg 721)**

In essence, taxonomists can be misled to classify organisms that appear very similar into the same species, when they are not actually closely related at all. This is why Darwin proposed that taxonomists should use non-adaptive characters when classifying organisms:

- **"...no one will say that rudimentary or atrophied organs are of high physiological or vital importance, yet...organs in this condition are often of high value in classification." (*Origin of Species*, 1st ed., pg 416/Wilson, pg 714)**

Speciation in American Rat Snakes

The situation in African cichlids is similar to the convergent evolution that has occurred among the rat snakes of North America: North America rat snakes are all classified as subspecies in the same species (*Elaphe obsoleta*), based primarily on appearance. However, molecular genetic studies of these three species indicates that they are not closely genetically related. Indeed, they are more closely related to other species of snakes living nearby, but which are not classified in the same species.

Until recently, three subspecies of the single species *Elaphe obseleta* were recognized by taxonomists (click on the name to go to a webpage with photos and descriptions):

- **The black rat snake (*Elaphe obseleta obseleta*),**

- **The yellow rat snake (*Elaphe obseleta quadrivittata*), and**

- **The gray rat snake (*Elaphe obseleta spiloides*).**

These three subspecies have distinct geographic distributions: the black rat snake is found north and northwest of the Appalachians, the yellow rat snake is found in the southeast, and the gray rat snake is found in the south-central states (Louisiana, Texas, etc.)

In 1994, researchers sequenced some mitochondrial genes from these three subspecies, and determined that they are not closely genetically related. Rather than being three subspecies of the same species (*Elaphe obseleta*), they are three distinct species in their own right, corresponding roughly to the three distinct color patterns found in nature: predominantly black, predominantly yellow, and predominantly gray with lighter diamonds. However, all three species have darker color morphs in the northern parts of their ranges, an adaptation for increased absorption of solar heat (an essential adaptation to these ectothermic - "cold blooded" - animals).

The explanation for the separation of these three species is that prior to the most recent glacial period, they were one single species distributed throughout the area of the southern United States. During the most recent glacial period, this "panmictic" population was separated into three geographically isolated populations in the southern limit of the range of the original species. These three isolated populations remained genetically separate from each other long enough to become separate, non-interbreeding species, which then spread north again at the end of the last glacial period. The dark color morphs in the northern parts of the ranges of these three groups are essentially the result of convergence, not common ancestry.

Coral Snakes and Their Mimics

There are other processes that can result in unrelated organisms looking very similar. Coral snakes, which are related to the cobras of Africa and southern Asia, have a deadly poisonous bite which they use to capture their prey. Coral snakes are very distinctively colored, with rings of bright red, jet black, and bright yellow down their entire length. In the same geographical areas in which coral snakes are found, there are coral snake mimics: harmless snakes with color patterns very similar to those of coral snakes.

King snakes are a Batesian mimic of coral snakes; that is, king snakes are harmless, but look very similar to a harmful species. This kind of mimicry, first described by Henry Bates, is generally thought to require that a predator learn to recognize the harmful species. However, in the case of coral snake mimics, the harmful species (i.e. the coral snake) is almost always fatal to a predator, therefore making any learning of the appearance of the harmful species almost impossible.

Batesian Mimicry in Snakes

This problem was finally solved via a series of ingenious experiments whereby the experimenter presented various "dummies" (wooden dowels painted like coral snakes, and in other patterns using the same colors or ring patterns, but without the correct relationships) to young birds who had been raised in isolation since hatching (and therefore could not have learned which color pattern to avoid). When presented with a dowel painted with the same colors or ring patterns as a coral snake, but not in the correct relationships with each other, the young birds pecked at the dowels. However, if presented with dowels painted in the correct color and pattern as a coral snake, the young birds attempted to escape their vicinity. This outcome strongly suggests that predators have adapted to avoiding both the coral snakes and their mimics as the result of natural selection.

Mimicry, therefore, can result in unrelated species looking very similar, not as the result of convergence, but rather as the result of selection for Batesian mimics. There are other forms of mimicry that have similar effects on morphology, also confounding attempts to classify them on the basis of appearance alone. Again, this is why Darwin (and Ernst Mayr) recommended classifying organisms on the basis of non-adaptive characteristics.

Allopatric versus Sympatric Speciation Among African Cichlids

In Chapter 5 of *Darwin's Dreampond* ("A Kiss on the Hand: The Origin of Species"), Goldschmidt discusses several different models of speciation, especially allopatric speciation (*i.e.* speciation that results from geographic isolation, as first suggested by Ernst Mayr). In this chapter, Goldschmidt also discusses sympatric speciation (that is, speciation in the same geographic location). Mayr has argued that there is no such thing as true sympatric speciation: that all such cases are really just geographic speciation, which is essentially the same as allopatric speciation. This is plausible in Lake Victoria, as it is as large as Switzerland, with many geographically and ecologically distinct areas.

- **Goldschmidt originally assumed that the species flock of cichlids in Lake Victoria speciated allopatrically along geographic lines, as suggested by Mayr. However, by the end of the book, he argues for sympatric speciation, driven by sexual selection.**

In Chapter 6 ("The Dowry: Sexual Selection and Gender-related Differences"), Goldschmidt discusses the concept of sexual selection in some detail. His description suggests that he believes that sexual selection is merely a variant of natural selection, driven primarily by female choice of male mates. Sexual selection of this kind is the result of differential reproduction alone, rather than differential survival and reproduction.

- **Goldschmidt points to sexual dimorphism (different appearance and/or size of males and females) as a marker for sexual selection. He goes on to point out that the cichlids in Lake Victoria are not very sexually dimorphic. This leads him to argue that sexual selection is probably not occurring. However, sexual dimorphism can be expressed in ways other than appearance. For example, females could be choosing males that are "marked" by a particular pheromone or other chemical trace.**

In Chapter 7 ("The Niche: The Origin of Structure in Biotic Communities"), Goldschmidt points out that the evidence seems to indicate that cichlid fish tend to undergo rapid adaptive radiation (that is, they speciate very widely into many different descendent species) whenever they are introduced into new large lakes in the rift valley of Africa. This would explain the profusion and similarity of cichlid species in Lake Malawi and Lake Victoria. He further suggests that the reason for such adaptability is the unusual plasticity of the genetic coding for the structure and function of the jaws and mouthparts of cichlid fish. He also points out that this plasticity is matched by the enormous ecological variation in the available niches in the rift lakes.

So, what can we say about speciation, based on Goldschmidt's observations of the furu of Lake Victoria? Clearly, the classical model of allopatric speciation, which was the keystone of the "modern evolutionary synthesis," has lost some of its universality. Although Lake Victoria is very large, it is still a single aquatic ecosystem. Therefore, something besides pure geographical isolation must be driving the adaptive radiation of the furu. Goldschmidt implies that this "something" is a combination of microhabitat specialization, sexual selection, and the genetic plasticity of cichlids. However, it isn't entirely clear that these mechanisms are all that is needed to explain what could be renamed "Darwin's nightmare lake."

Evo-Devo and the "Engines" of Speciation and Macroevolution

The various observations noted above, plus the problems pointed out in previous lectures with the "gradualist" model of macroevolution, all suggest that a new explanation (and in particular a new mechanism) for macroevolution must be found. This "new mechanism" would necessarily have to explain the following observed patterns of macroevolutionary change (notice that none of these are easily explainable via the "modern evolutionary synthesis"):

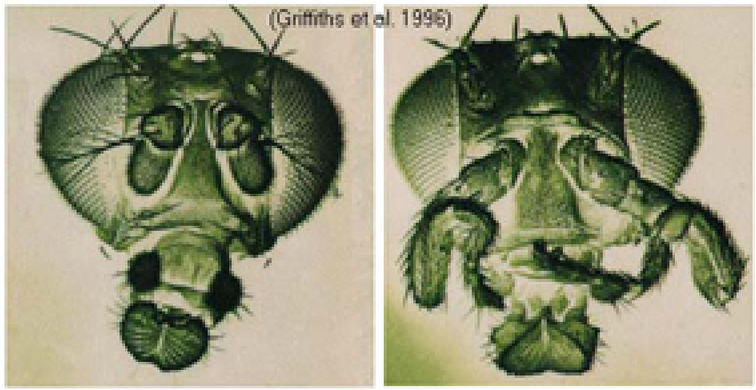
- **Relatively rapid, coordinated changes in major components of phenotypes following ecological disruption (i.e. "punctuationism")**
- **Relatively rapid adaptive radiation of apparently genetically homogeneous types following mass extinctions and/or invasion of new "adaptive zones"**
- **Relatively large changes in phenotype correlated with relatively minor changes in genotype**
- **Relatively precise convergence on specific phenotypes in similar ecological circumstances, despite apparent genetic dissimilarity**
- **Relatively precise mimicry (both Batesian and Müllerian) of specific phenotypes, despite apparent genetic dissimilarity**
- **Similar patterns of phenotypic change in widely separated groups of animals living in different environments (i.e. "parallel evolution")**

All of these observations seem to point to the same explanation: the newly emerging field of evolutionary developmental biology (often referred to as "evo-devo"). As Sean Carroll describes in his book, *Endless Forms Most Beautiful*, new discoveries in evo-devo have paved the way to explaining the various observations listed above.

One of the basic concepts of evo-devo is the "tool kit" of "master genes" found in the genomes of virtually all animals. This "tool kit" consists of a set of master control genes (called "homeotic" or "hox" genes), which are lined up within chromosomes in essentially the same linear order as the major components of the body of bilaterally symmetrical animals. These genes, of which there is a relatively small number, regulate the expression of a very large number of genes that produce the various "building blocks" of the phenotypes of animals (all the way down to genes that code for specific structural and functional proteins, out of which the phenotypes of animals are constructed).

Detailed genetic studies of these homeotic genes over the past two decades has shown that relatively small changes in such genes can have very large effects on the phenotypes that the genes regulate.

- **For example, a slight change in one homeotic gene in a fruit fly can cause the antennae on the head of the fly to be replaced by an entire leg, with all of the detailed structures found in a typical leg on the fly's thorax.**



- **Recent analyses of the genetic differences between finches with large and small beaks on the Galapagos Islands has shown that such differences are entirely the result of minute genetic changes in a single gene controlling the development of the jaw (i.e. beak) in vertebrates. Slight alterations of this homeotic gene (called bmp4) have also been implicated as the underlying cause of the extreme variations in jaw shape in African cichlid fishes.**

In other words, new discoveries in evo-devo point to a new generalization about causes in changes in phenotypes:

Slight changes in homeotic genes can produce large changes in phenotypes over relatively short periods of time

This means that new slight variations in homeotic genes can become more common in populations as the result of natural selection, producing relatively large changes in phenotypes such as those we have already discussed in relation to macroevolution. Notice that this does NOT mean that the underlying mechanism of natural selection has been replaced or shown to be ineffective. Rather, new discoveries in evo-devo point to the conclusion that natural selection at the level of homeotic regulatory genes can produce surprisingly large changes in phenotypes in relatively short periods of time, compared with the kinds of changes that were assumed to be necessary given the assumptions upon which the "modern evolutionary synthesis" was based.

This also means that evo-devo could also provide a new explanation of such long-standing problems as evolutionary convergence, parallel evolution, and mimicry. Studies of the distribution of homeotic genes have shown that they are both highly "conserved" (that is, relatively unchanging over long periods of time) and very widespread among animals (being found in similar patterns in everything from flatworms to whales). This essentially means that all bilaterally symmetric animals have access to a similar "tool kit" during development. Therefore, rather than a particular phenotypic adaptation having to evolve "from scratch" in every phylogenetic line of animals, it may be possible to produce similar (i.e. convergent or mimetic) phenotypes by selecting for the same, relatively small set of homeotic gene arrangements.

And, at the level of diverging species, evo-devo might provide a mechanism whereby natural selection can produce relatively large phenotypic differences as the result of relatively small genetic changes, thereby making allopatry unnecessary as a mechanism for producing phenotypic and genotypic divergence.

Epigenetics: Another Mechanism for Producing Phenotypic Variation

In biology, the term epigenetics refers to changes in phenotype (appearance) or gene expression caused by mechanisms other than changes in the underlying genetic material (especially the coding DNA sequence). For many years, biologists have considered that epigenetics applied only to developmental processes that occurred *within* organisms. This idea was non-controversial because it was clear that virtually all of the cells (except the sex cells) of a multicellular eukaryote are genetically identical. They begin as fertilized unicellular zygotes, which then divide multiple times via mitosis to produce all of the cells, tissues, and organs of the fully developed organism.

Mitosis produces genetically identical daughter cells, and so all of the cells of a multicellular eukaryote contain the same genetic information. The cells have different structures and functions because the genetic material is expressed differently in different cells. Development in a multicellular eukaryote therefore proceeds by the successive up- or down-regulation of the genes present in particular cells, producing different structures and functions in an organism without changing its genetic material.

All of this is non-controversial. However, new research has shown that epigenetic effects are not restricted to *intra-individual* phenotypic changes at the level of individual cells. There is increasing evidence that some significant phenotypic changes in adult organisms are *not* correlated with underlying genetic changes. Rather, some phenotypic changes in adult organisms are caused by changes in the *expression* of particular genes, rather than changes in the genes themselves. Furthermore, there is also increasing evidence that some of these purely phenotypic changes are heritable from parents to offspring (i.e. without corresponding genetic changes).

- **An example of epigenetic inheritance is the *agouti* gene/phenotype in mice. Pregnant female mice that are fed a diet rich in proteins that contain methyl groups (derived from methane and found in hydrophobic amino acids) produce offspring that express the *agouti* phenotype: they have yellowish fur, tend to be obese, and have a tendency toward certain types of cancer. Detailed genetic studies of these agouti offspring has shown that they are genetically identical to non-agouti mice. Their peculiar phenotype is the result of a change in the expression of the *agouti* gene, a change that is heritable from mothers to their offspring for many generations.**

- **Another example of heritable epigenetic phenotypic change was discovered by Marcus Pembrey and his colleagues, who observed that the paternal (but not maternal) grandsons of Swedish boys who were exposed during preadolescence to famine in the 19th century were less likely to die of cardiovascular disease. If food was plentiful then diabetes mortality in the grandchildren increased, suggesting that this was a transgenerational epigenetic inheritance. The opposite effect was observed for females -- the paternal (but not maternal) granddaughters of women who experienced famine while in the womb (and their eggs were being formed) lived shorter lives on average (click here for more).**

This kind of heritable change in the phenotypes of organisms is essentially Lamarkian inheritance, and suggests that something like Lamarkian evolution is possible, at least for those phenotypic changes that are produced by epigenetic mechanisms. Eva Jablonka and Marion Lamb devote an entire section of their new book, *Evolution in Four Dimensions*, to epigenetics and its newly recognized importance to evolution.

Epigenetic changes are completely outside the scope of the "modern evolutionary synthesis", and have therefore generated considerable controversy within the scientific community. There is widespread and growing evidence that epigenetic inheritance affects many of the phenotypic traits of living organisms, and so the "post-modern evolving synthesis" has departed significantly from the "modern synthesis" to incorporate such findings.

Summary: The Map is Not the Territory

The various observations noted above, plus the problems associated with underlying mathematical assumptions of the "modern evolutionary synthesis" pointed out in previous lectures has necessitated that evolutionary biologists begin to formulate and adopt what could be called the "post-modern evolving synthesis". Central to this new synthesis has been the recognition that the key to understanding evolution is understanding the "engines of variation". As we have seen, over the 150 year history of the scientific theory of evolution, the "variation pendulum" that swung away from Darwin toward the Mendelian geneticists, then swung back toward the neo-Darwinists during the "modern evolutionary synthesis," is swinging once again toward a mechanism grounded in evo-devo and epigenetics for the origin of species and higher taxa and the inheritance of many important phenotypic characteristics. Only time will tell if a deeper understanding these processes will make it possible for evolutionary biologists to solve the problems associated with macroevolution, but the future looks very bright!

One thing will be certain: evo-devo and epigenetics will, like all other scientific theories, be only as good as the empirical data on which it is based, and it will only last until the next set of anomalies starts nagging at the awareness of a new generation of evolutionary biologists.

..

In our next-to-last lecture, we will look at another evolutionary phenomenon that challenged the conceptual framework of the "modern evolutionary synthesis," and how new discoveries in ecological genetics and behavioral ecology have provided an explanation for what Darwin cited as the most important challenge to his theory of evolution by natural selection: the evolution of altruism and social behavior.