May 2, 2006: **Introduction to Macroevolution (diversification, reticulation, extinction)**

**1.** Two fundamental kinds of things in evolutionary theory (Hull, Dawkins):
*replicator* = things of which copies are made -- a succession of replicators forms a *lineage*
*interactor* = things that interact in a common environment such that replication is differential
Both of these form nested hierarchies!

Four things can happen to lineages:
1. Origin
2. Extinction
3. Divergence (sometimes known as "speciation")
4. Reticulation

**2.** Diversification

Constraints: Why is morphospace not filled in completely?

General classes of causal factors advanced to explain cohesion/integration of species:
1) Gene Flow
2) Stabilizing Selection -- Ecological Constraints
3) Developmental Constraints

The Null Hypothesis: Random Walk; Accidents Of History

Adaptive landscapes vs developmental landscapes

The levels of selection

Coalescence theory, the study of non-recombining gene genealogies.

**3.** Extinction (see supplementary handouts)

**4.** The shape of evolution

What is the null expectation?

Evolutionary radiations

Adaptive radiations -- concept of "key innovation"

Dating events:
1. Clock or at least approximate clock by smoothing
2. Calibration

**5.** Adaptation:
Based on the observation that organism matches environment. Darwin & many Darwinians thought that all structures must be adaptive for something. But, this has come under severe challenge in recent years. Not all structures and functions are adaptive. Some matches between organism and environment are accidental, or the causality is reverse (i.e., the structure came first,

function much later). In fact, there are very few completely worked-out examples of adaptations.

Definition of adaptation in a formal sense requires fulfillment of four different criteria:
1. **Engineering**. Structure must indeed function in hypothesized sense. Requires functional tests.
2. **Heritability**. Differences between organisms must be passed on to offspring, at least probabilistically. Requires heritability tests (parent-offspring correlations; common garden studies).
3. **Natural Selection.** Difference in fitness must occur because of differences in the hypothesized adaptation (in common environment -- see over). Requires fitness tests.
4. **Phylogeny**. Hypothesized adaptive state must have evolved in the context of the hypothesized cause. Think in terms of problem (e.g., environmental change) and solution (adaptation). Requires phylogenetic tests.

Only something that passes all these tests is a *adaptation*. If it passes tests 1-3 it could be called an *aptation*. If it then fails test 4 it could be called as *exaptation*.

**6.** Coevolution

-- can be broadly defined as congruence between two or more systems undergoing evolution by descent with modification.

-- A generalization of the phylogeny/ homology relationship (i.e., the "coevolution" of organism lineages and characters).

-- It comes in many forms:

-- Vicariance biogeography (organism/ earth coevolution), i.e., look for congruent patterns among many groups) Nelson, Platnick, Rosen.

**** evidence from other organisms is relevant to understanding the distribution of some particular group! ****

- analogies to "homology" in characters (remember?)
- number of methodologies have diversified, including consensus methods and Brooks parsimony. Big problems include how to deal with missing data and incongruence (went over last lecture).
- congruence is taken as evidence of shared history (vicariance); incongruence as evidence of separate history (dispersal). Is this a well-supported kind of inference?

-- Host/ parasite relationships

-- Community evolution (e.g., symbionts, pollinator/ plant coevolution, or other long-term ecological associations)

-- Cladistic tests of adaptational hypotheses (association between organism phylogenies, putative adaptations, and putative ecological explanations)