

## "PRINCIPLES OF PHYLOGENETICS: ECOLOGY AND EVOLUTION"

*Integrative Biology 200B*  
University of California, Berkeley

Spring 2007  
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Jan. 16, 2007. **The Hennig Principle, Synapomorphy, Homology, Homoplasy**

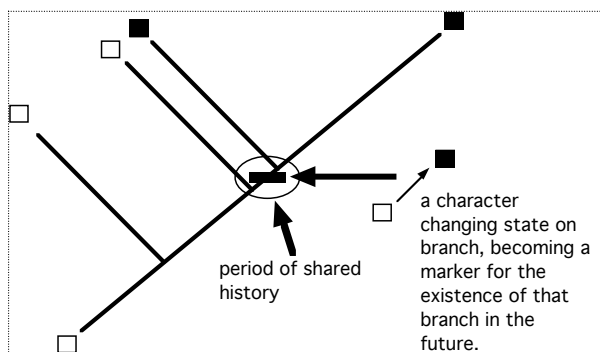
The purpose of the lectures and handouts in the first two weeks of the course is to get you up to speed on phylogenetic principles, with an emphasis on how phylogenetic trees are reconstructed. These principles apply generally to all characters, morphological or molecular (or ecological, behavioral, or physiological, for that matter). For more details on this "tree-building" half of Phylogenetics, may we recommend IB 200A, taught in the spring of even years.

### I. Introduction

Genealogical relationships themselves are invisible, so how can we know them? Is there an objective, logically sound method by which one can reconstruct the tree of life? Recent advances in theories and methods for phylogenetic reconstruction, along with copious new data from the molecular level, have made possible a new scientific understanding of the relationships of organisms. This understanding of relationships has led in turn to improved taxonomic classifications as well as the subject matter of this class: comparative methods for testing biogeographic, ecological, behavioral, and other functional hypotheses.

### II. The Hennig Principle

The fundamental idea driving recent advances in phylogenetics is known as the Hennig Principle, and is as elegant and fundamental in its way as was Darwin's principle of natural selection. It is indeed simple, yet profound in its implications. It is based on the idea of homology, one of the most important concepts in systematics, but also one of the most controversial. What does it mean to say that two organisms share the same characteristic? The modern concept is based on evidence for historical continuity of information; homology would then be defined as *a feature shared by two organisms because of descent from a common ancestor that had that feature* (more on homology below).



Hennig's seminal contribution was to note that in a system evolving via descent with modification and splitting of lineages, characters that changed state along a particular lineage can serve to indicate the prior existence of that lineage, even after further splitting occurs. The "Hennig Principle" follows from this: homologous similarities among organisms come in two basic kinds, synapomorphies due to immediate shared ancestry (i.e., a common ancestor at a specific phylogenetic level), and symplesiomorphies due to more distant ancestry (see figure on next page). Only the former are useful for reconstructing the relative order of branching events in phylogeny -- "special similarities" (synapomorphies) are the key to reconstructing truly natural relationships of organisms, rather than overall similarity (which is an incoherent mixture of synapomorphy, symplesiomorphy, and non-homology).

Classifications are applied to the resulting branching diagram (cladogram). A corollary of the Hennig Principle is that classification should reflect reconstructed branching order; only

monophyletic groups should be formally named. A strictly monophyletic group is one that *contains all and only descendents of a common ancestor*. A paraphyletic group is one that excludes some of the descendents of the common ancestor. Again, we will return to deal with the ramifications of this approach to classification next week and throughout the course.

This elegant correspondence between synapomorphy, homology, and monophyly is the basis of the cladistic revolution in systematics.

### III. Homology

*Theory.* A very important concept in biology; refers to a historical continuity of information from ancestor to decendent (not identity!!). There are thus two types of homology that we are concerned with here: phylogenetic homology, which is the same character state in two different lineages at one time-slice (i.e., synapomorphy); and transformational homology, which is the relationship through time in one lineage between character states (i.e., the relationship between an apomorphy and its plesiomorphy). Specific hypotheses of transformational homology among character states are called transformation series.

#### A. Types of homology

- Iterative Homology (within one organism), e.g., Serial Homology or Paralogy in molecular data
- Phylogenetic Homology (between organisms)
  - Taxic (= synapomorphy)
  - Transformational (plesiomorphy -> apomorphy)

#### B. How do we recognize homology?

- Remane's criteria (detailed similarity in position and quality of resemblance)
- Congruence test (a recently formulated, explicitly phylogenetic criterion)

*Empirics.* This concept is clear in theory, but how do we recognize homology? The best early codification of recognition criteria was that of Remane (Wiley, 1981): detailed similarity in position, quality of resemblance, and continuance through intermediate forms. Also, an important contribution of cladists has been the explicit formulation of a phylogenetic criterion: **\*\* a hypothesis of taxic homology of necessity is also a hypothesis for the existence of a monophyletic group \*\***

Therefore, congruence among all postulated homologies provides a test of any single character in question, which is the central epistemological advance of the cladistic approach. Individual hypotheses of putative homology are built up on a character-by-character basis, then a congruence test (using a *parsimony* principle, more next week) is applied to distinguish homologies (i.e., those apparent homologies that are congruent with other characters) from homoplasies (i.e., apparent homologies that are not congruent with the plurality of characters).

Is this circular? A digression is needed here into general concerns in the philosophy of science; reciprocal illumination.

### IV. Homoplasy

Homoplasy can have various sources: "uncaused" (i.e., simple mistakes in gathering, interpreting, or compiling data, random matches between taxa, etc.) or "caused" (i.e., convergent evolution, reticulate evolutions, lineage sorting, developmental canalization, etc.). Homoplasy is viewed in systematics as an impediment to getting the correct phylogeny, but keep in mind that it can be studied in its own right. In fact, we'll see that much of the subject matter of this class is the study of homoplasy and its causes!