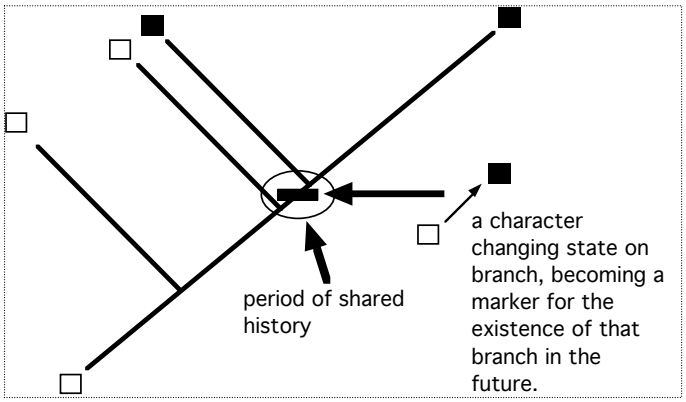
Jan. 27, 2020. **The Hennig Principle: synapomorphy; homology; homoplasy**

Required reading: *Tree Thinking*: Chap. 4, pages 90-93.

I. 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 (more on homology in the next section).



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 above). 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).

To tell synapomorphy from symplesiomorphy within a transformation series, it is necessary to have an hypothesis about which state was the prior condition, and which state(s) are posterior temporally. This is generally called *evolutionary polarity*. Some have argued that the fossil record can be used for polarization, others have argued that developmental trajectories can work for polarization. The currently preferred approach is what is called *outgroup comparison*; characters can be polarized after tree reconstruction by seeing where the tree nests in a broader phylogenetic context. This is called "rooting the tree." We will go into actual practice in lecture 5, Friday.

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 descendants of a common ancestor*. A paraphyletic group is one the excludes some of the descendants of the common ancestor. We will return to deal with the ramifications of this approach to classification throughout the course.

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

II. Homology

Homology is one of the most important concepts in biology, but also one of the most controversial. What does it mean to say that two organisms share the *same* characteristic?

A bit of history:
--classical, pre-evolutionary views (Cuvier, Owen)
--nominalistic views (many botanists, pheneticists)
--developmental views.
--evolutionary views: historical connectedness.
--synapomorphy (Patterson, Stevens)
--historical continuity of information (Van Valen, Roth)**

Ontology:
The modern concept is a hard-core historical concept -- it refers to a historical continuity of information from ancestor to descendant (not identity!!). Homology is defined as *a feature shared by two entities (e.g., organisms, genes) because of descent from a common ancestor that had that feature.* 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)

Epistemology:
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 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 quick digression into general concerns in the philosophy of science; reciprocal illumination.

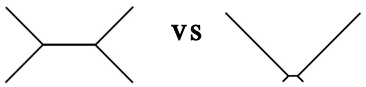
III. Homoplasy

Homoplasy is similarity *not* due to historical continuity of information, a feature shared for one of several, distinctly different kinds of non-homologous reasons. 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 sometimes viewed in systematics as an impediment to getting the correct phylogeny, but keep in mine 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!

A brief taxonomy of types of homoplasy:

1. *Error* (e.g., mistakes in reading a gel, typographic errors, mislabeled specimens).

2. *Random matching over evolutionary time.* When a character has a limited number of states, non-homologous matches can occur -- this effect can cause biased reconstructions when the probability of change is very different in different lineages (the "long branch attraction" problem).

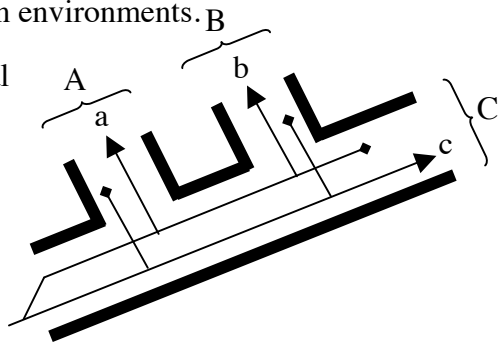


3. *Convergence*, due to natural selection in common environments.

4. *Parallelism*, perhaps due to shared developmental programs

4. *Reticulation* (e.g., hybrid speciation, introgression, horizontal gene transmission)

5. *Lineage sorting*, when different parts of the same genome have different branching histories due to differential extinction of polymorphisms.



ADDITIONAL REFERENCES

Hennig, W. 1966. *Phylogenetic systematics.* University of Illinois Press, Urbana.

Mishler, B. D. 1994. Cladistic analysis of molecular and morphological data. *American Journal of Physical Anthropology* 94: 143-156.

Mishler, B.D. 2005. The logic of the data matrix in phylogenetic analysis. In V.A. Albert (ed.), *Parsimony, Phylogeny, and Genomics*, pp. 57-70. Oxford University Press.

Rieppel, O. 2015. Homology: a philosophical and biological perspective. *Handbook of Paleoanthropology*, 295-315.

Roth, V.L. 1984. On homology. *Bioi. J. Linn. Soc.* 22:13-29.

Roth, V.L. 1988. The biological basis of homology. In *Ontogeny and Systematics* (ed. C.J. Humpries), Columbia University Press.

Roth, V.L. 1991. Homology and hierarchies: Problems solved and unresolved. *Journal of Evolutionary Biology* 4: 167-194

Patterson, C. 1982. Morphological characters and homology. pp. 21-74 in Josey, K.A. and Friday, A.E. (eds.) *Problems of Phylogenetic Reconstruction*. Academic Press.

Stevens, P.F. 1984. Homology and phylogeny: morphology and systematics. *Systematic Botany* 9: 395-409. (Part of a symposium on homology in botany)