Jan. 22, 2018. **History & philosophy of phylogenetics; the Hennig Principle: homology; synapomorphy; rooting**

Required reading: *Tree Thinking*: Chap. 2

Supplemental: B.D. Mishler. 2009. Three centuries of paradigm changes in biological classification: is the end in sight? *Taxon* 58: 61-67.

B.D. Mishler. 2014. History and theory in the development of phylogenetics in botany. In A. Hamilton (ed.), *The Evolution of Phylogenetic Systematics*, pp. 189-210. UC Press.

I. Introduction

Why classify? Why does it matter what we call things? To look at it another way, is it possible to think or communicate *without* classifications? How would we otherwise compare things? Kinds of classifications in biology: historical, functional, structural...

Below are four generally-accepted goals in classification, arranged from the most immediate and practical, to more theoretical and esoteric.

PURPOSES FOR CLASSIFICATION:

1) PRACTICALITY
(OPERATIONALITY, EASE, STABILITY)
2) INFORMATION CONTENT
(OPTIMAL SUMMARIZATION OF WHAT IS KNOWN ABOUT ENTITIES)
3) PREDICTIVITY
(OF UNKNOWN FEATURES OF ENTITIES)
4) FUNCTION IN THEORIES
("CAPTURE" ENTITIES ACTING IN, OR RESULTING FROM, NATURAL PROCESSES)

II. History

--Systematics (comparative biology) has always played a central role in the history of biology. The recognition of basic kinds of organisms, their properties and "relationships" in higher categories, was the earliest biological discipline. Developments in biology as a whole have interacted with systematics throughout. Detailed treatment of this history include Stevens, Hull, Dupuis, Donoghue & Kadereit, Mayr, Mishler.

-- Important themes in the history of systematics:

- Relative balance in importance of theory vs. data -- rationalism vs empiricism
- The role of technology -- a source of new characters
- Metaphors that people used (trees, maps, geometric shapes, etc.)
- The Great Chain of Being -- still with us after 2000 years!
- Polythetic vs. monothetic classifications
- "Weighting" of characters

There really have only been three revolutions, in the Kuhnian sense (Kuhn, 1970), in the history of systematics (see table below). Early folk taxonomies came out of prehistory and were oriented towards practicality and human uses of organisms. Organisms were grouped by their relationship with human affairs. The first scientific revolution was that provided by the ancient Greeks; as in many fields of science, they justified a new logical framework within which to view the natural world. The effect of this on systematics was nicely discussed by Hull (1988): an essentialistic approach that gripped biology for 2,000 years. In this approach taxa were viewed as defined by the possession of necessary and sufficient defining traits.

Such a view, which reached its culmination in the work of Linnaeus, became untenable as the wealth of biological diversity became known due to the explorations of the 18th and 19th centuries. It became clear that any and all characters can vary within a named group, and thus the use of defining characters became an obvious problem when a group of plants that clearly belonged together was threatened because variation was discovered in an essential character. This set the stage for the second revolution in the history of systematics, the development of the natural system (as discussed by Stevens, 2000). In this approach taxa were recognized by overall resemblance in many characters, although these characters were often chosen for their "importance" in the biology of the group in question. It is important to note that this revolution in systematics preceded the Darwinian revolution, and in fact was prime evidence for Darwin to present in favour of evolution in the Origin. As has been noted by many, the Darwinian revolution had no fundamental impact on systematics. The language systematists used became evolutionary, but their approach remained the use of over-all resemblance. This same approach was made more efficient by the advent of computerised algorithms as the numerical phenetics school developed, but no fundamental change in underlying paradigms occurred.

The Hennigian revolution was arguably the third major revolution in the history of systematics, one that finally completed the Darwinian Revolution for systematics. The paradigm shift started by Hennig (1965, 1966) was due to a careful examination of the idea of homology, one of the most important yet controversial concepts in systematics. Hennig's central ontological advance was that homologous similarities are of two kinds, those due to recent, shared-derived homologies (synapomorphies) and those due to distant, shared-primitive homologies (symplesiomorphies). Only the former are useful for reconstructing the relative order of branching events in a system that is changing by descent with modification. The general Hennigian view is that evolution can be viewed as a series of branching events, connected by lineages: prior states transform along lineages into posterior states, that can serve as markers that a lineage existed. Under most circumstances, careful study of states possessed by the terminal twigs of the tree can allow us to reconstruct past character transformations, thus detecting the existence of lineages and inference of relative branching order (more below).

<u>HISTORICAL PERIODS IN BIOLOGICAL SYSTEMATICS:</u>

1) PRE-HISTORY -- FOLK CLASSIFICATIONS
* 2) ANCIENT GREEKS THROUGH LINNAEUS-- ESSENTIALISM
* 3) NATURAL SYSTEM -- OVERALL RESEMBLANCE; "IMPORTANCE"
4) DARWIN -- EVOLUTIONARY LANGUAGE [only a superficial effect]
5) NUMERICAL PHENETICS -- COMPUTERS [only a superficial effect]
* 6) PHYLOGENETIC SYSTEMATICS (CLADISTICS) -- SYNAPOMORPHIES, MONOPHLYLY

* Argued to be the only true revolutions in the conceptual bases of systematics

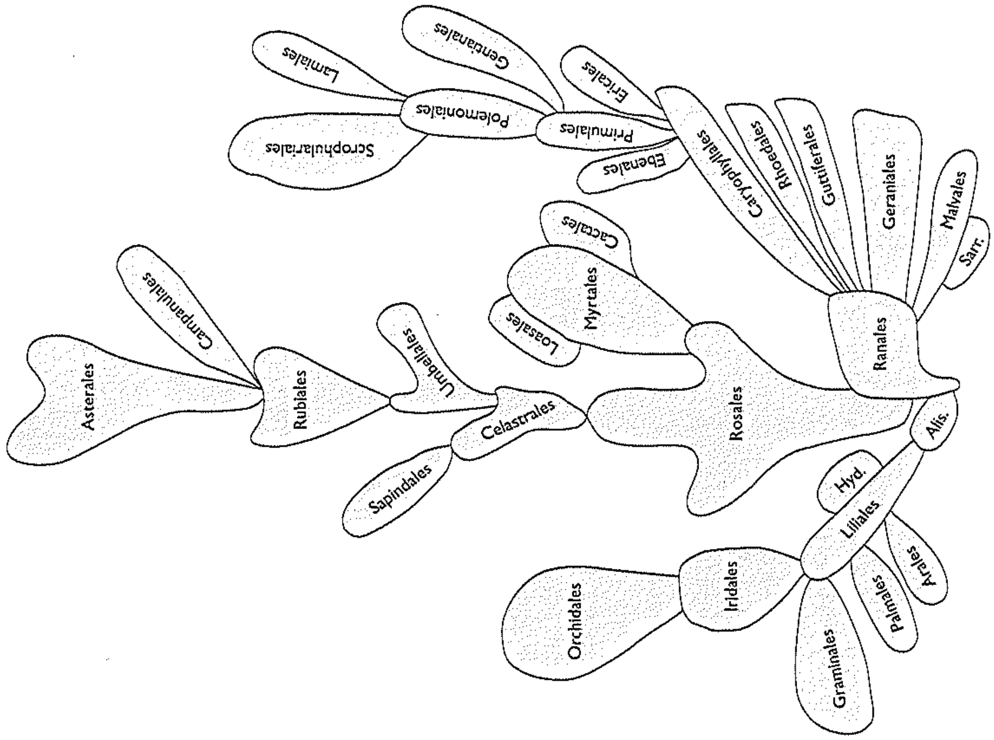


FIGURE 8.3. Bessey's cactus. *Annals of the Missouri Botanical Garden*, 2 (1915): 118.

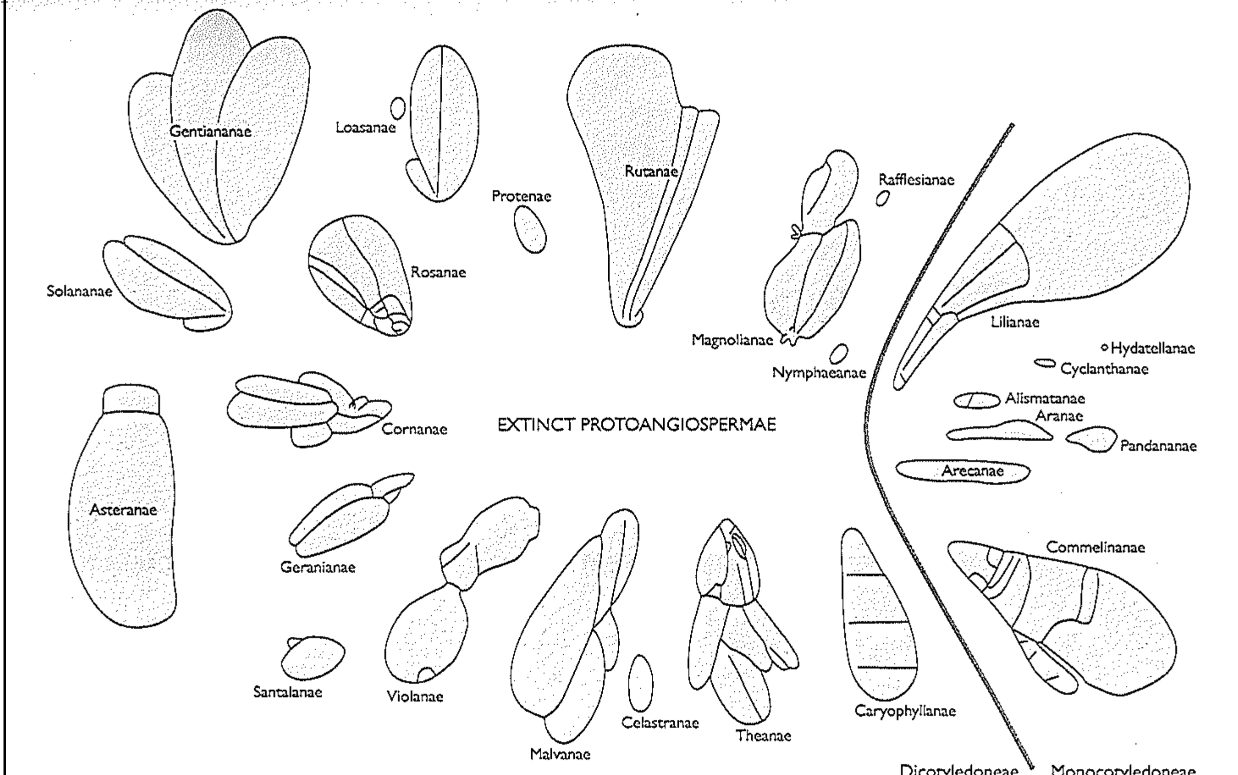


FIGURE 8.1. Phylogenetic shrub of the Angiosperms. Fig. 1, p. 249, in R. F. Thorne, "Classification and Geography of the Flowering Plants," *Botanical Review*, 58 (1992): 225–348. Springer. Used with permission.

III. Philosophy

-- Some might think philosophy has nothing to do with biology (the traditionalist's view), but that couldn't be more wrong. There are many important philosophical issues in systematics, the most important of which, for our purposes, being:

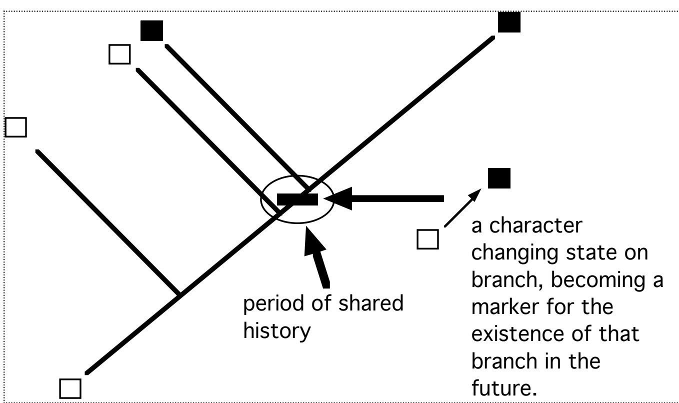
1. *Ontology* -- Background theories stating what kinds of entities exists, what are their fundamental meanings and relationships. [e.g., homologies, phylogenies, species, etc.]

2. *Epistemology* -- Background theories stating what kinds of empirical operations and methods can be used to discover the underlying ontological entities and relationships. [e.g., characters, statistics, cladistic analysis, etc.]

3. *Sociology of science* -- Motivations; patterns of teaching, cooperating, fighting; "progress" in science (Kuhn, 1970 is the classic; see Hull 1988, *Science as a Process*, for major treatment of subject in systematics). To what extent does the process of science follow the model of natural selection? What are the analogies and non-analogies? What does it matter? Plenty! The better you understand the process of science, the better you'll do at it!

IV. The Hennig Principle

The fundamental idea driving recent advances in phylogenetics is known as the <u>Hennig Principle</u>, 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 <u>homology</u> (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, <u>synapomorphies</u> due to immediate shared ancestry (i.e., a common ancestor at a specific phylogenetic level), and <u>symplesiomorphies</u> 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.

V. Homology: theory (we'll discuss *practice* in the next lecture)

Homology is 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? 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)

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