March 11, 2016. Classification II: Phylogenetic taxonomy including incorporation of fossils; Phylocode

I. The argument for phylogenetic classification (review)

The debate over classification has a long and checkered history (see Hull 1988; Stevens, 1994). A conceptual upheaval in the 1970's and 80's resulted in a true scientic revolution -- Hennigian Phylogenetic Systematics. Many issues were at stake in that era, foremost of which was the nature of taxa. Are they just convenient groupings of organisms with similar features, or are they lineages, marked by homologies? A general, if not completely universal consensus has been reached, that taxa are (or at least should be) the latter (Hennig, 1966; Nelson, 1973; Farris, 1983; Sober, 1988).

A summary of the arguments for why formal taxonomic names should be used solely to represent phylogenetic groups is as follows: evolution is the single most powerful and general process underlying biological diversity. The major outcome of the evolutionary process is the production of an ever-branching phylogenetic tree, through descent with modification along the branches. This results in life being organized as a hierarchy of nested monophyletic groups. Since the most effective and natural classification systems are those that "capture" entities resulting from processes generating the things being classified, the general biological classification system should be used to reflect the tree of life.

This isn't to say that phylogeny is the only important organizing principle in biology, There are many ways of classifying organisms into a hierarchy, because of the many biological processes impinging on organisms. Many kinds of non-phylogenetic biological groupings are unquestionably useful for *special purposes* (e.g., "producers," "rain forests," "hummingbird pollinated plants," "bacteria"). However, it is generally agreed that there should be one consistent, *general-purpose*, reference system, for which the Linnaean hierarchy should be reserved. Phylogeny is the best criterion for the general purpose classification, both theoretically (the tree of life is the single universal outcome of the evolutionary process) and practically (phylogenetic relationship is the best criterion for summarizing known data about attributes of organisms and predicting unknown attributes). The other possible ways to classify can of course be used simultaneously, but should be regarded as special purpose classifications and clearly distinguished from phylogenetic formal taxa.

II. Incorporation of fossils

Fossils are best treated like any other taxa, but require some special consideration given the typical paucity of characteristics, e.g., the concept of "Form Genus." We covered additional conventions last lecture such as "incertae sedis." A couple important concepts to mention today:

- "crown group" = deepest clade incorporating all extant taxa.
- How to treat hypothesized ancestors? Would appear as 0-length terminal branches.
- Avoid saying "basal taxa" or even "early diverging taxa" -- nodes are ordered in time, for sure, but never terminal taxa -- and fossils should be treated as terminal taxa.
- The question of which terminal taxa retain the most plesiomorphic characters is an important empirical question, addressed in the previous section of the class, when we were talking about ancestral state reconstructions, but it has nothing to do with whether a clade is not very diverse, or is typically shown on the left-hand side of a dichotomy!

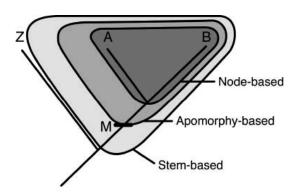
III. The argument for rank-free classification

A number of recent calls have been made for the reformation of the Linnaean hierarchy (e.g., De Queiroz & Gauthier, 1992). These authors have emphasized that the existing system is based in a non-evolutionary world-view; the roots of the Linnaean hierarchy are in a specially-created world-view. Perhaps the idea of fixed, comparable ranks made some sense under that view, but under an evolutionary world view they don't make sense. There are several problems with the current nomenclatorial system:

- 1. The current system, with its single type for a name, cannot be used to precisely name a clade. E.g., you may name a family based on a certain type specimen, and even if you were clear about what node you meant to name in your original publication, the exact phylogenetic application of your name would not be clear subsequently, after new clades are added.
- 2. There are not nearly enough ranks to name the thousands of levels of monophyletic groups in the tree of life. Therefore people are increasingly using informal rank-free names for higher-level nodes, but without any clear, formal specification of what clade is meant.
- 3. Most aspects of the current code, including priority, revolve around the ranks, which leads to instability of usage. For example, when a change in relationships is discovered, several names often need to be changed to adjust, including those of groups whose circumscription has not changed. E.g., when it was detected that the Cactaceae is nested inside of the Portulacaceae, one of these well-known family names has to be abandoned. Frivolous changes in names often occur when authors merely change the rank of a group without any change in postulated relationships.
- 4. While practicing systematists know that groups given the same rank across biology are not comparable in any way (i.e., in age, size, amount of divergence, diversity within, etc.), many users do not know this. For example, ecologists and macroevolutionists often count numbers of taxa at a particular rank as an erroneous measure of "biodiversity." The non-equivalence of ranks means that at best (to those who are knowledgeable) they are a meaningless formality and perhaps not more than a hindrance. At worst, in the hands of a user of classifications who naively assumes groups at the same rank are comparable in some way, formal ranks lead to bad science -- removing the ranks would serve the same purpose as child-proof door locks for the back seat of your car!

How exactly to write the new phylogenetic code of nomenclature is not completely clear at this point, especially as applied to species (see draft of the Phylocode and other materials at: http://www.ohio.edu/phylocode/index.html), but the

http://www.ohio.edu/phylocode/index.html), but the basics are clear. Such a new code should maintain the principle of priority (the first name for a lineage should be followed) and other aspects of the current code that promote effective communication of new names to the community. However, two major changes would be made:

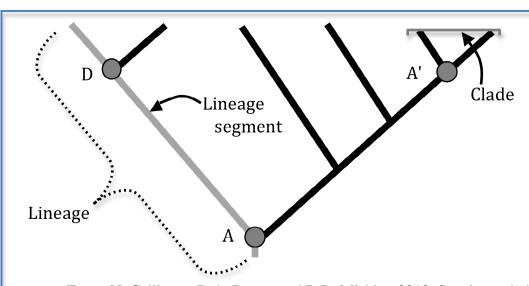


1. The Linnaean ranks would be abandoned, Instead, names of clades would be hierarchically nested uninomials regarded as proper names. A clade would retain its name regardless of where new knowledge might change its phylogenetic position, thus increasing nomenclatorial stability. Furthermore, since clade names would be presented to the community without attached ranks, users would be encouraged to look at the actual attributes of the clades they compare, thus improving research in comparative biology.

2. Two or more types (called "specifiers") would be used, for efficient and accurate representation of phylogenetic relationships. There are two types of specifiers, internal and external. Two or more of the former are used to name node-based groups. Two or more of the former and one of the latter are used to name stem-based groups. Apomorphy-based names are controversial, and really shouldn't be used.

IV. Important concepts in phylogenetic classification to revisit:

- 1. Different ways of defining monophyly: *synchronic* (i.e., " all and only descendants of a common ancestor") or *diachronic* (i.e., " an ancestor and all of its descendants"). Which is better? Should the word "species" appear in the definition of monophyly? Does that matter?
- 2. **Clade** versus **Lineage** (see figure below for illustration). They are not the same thing -- "clade" is a synchronic concept, a snapshot of a lineage at one time -- while a "lineage" is a diachronic concept, a series of replicators.



From: N. Cellinese, D.A. Baum, and B.D. Mishler. 2012. Species and phylogenetic nomenclature. Systematic Biology 61: 885-891.

The distinction between clades and lineages, showing the incompatibility of different views of species. A clade is a synchronic, monophyletic set of lineage-representatives, where monophyly is defined synchronically as "all and only descendants of a common ancestor" (represented by A' in this case). Note that the terminal-most named clade is a "species" in the sense of Mishler and Theriot (2000a, 2000b, 2000c). A lineage is a diachronic ancestor-descendant path (grey line up the left side of the tree), whereas a lineage segment is a part of a lineage that connects two nodes (A and D in this example), note that the latter is a "species" in the de Queiroz (2007) sense.

V. How could rank-free classification be applied to terminal taxa?

At the moment, the species rank is the most controversial topic among Phylocode advocates. Some (primarily zoologists) want to retain it as one fundamental rank in an otherwise rank-free system, others (primarily botanists) want to get rid of it (see Cellinese et al. 2012). Debate about removing species from the Phylocode rages at this very moment. More next time...