

"PRINCIPLES OF PHYLOGENETICS: ECOLOGY AND EVOLUTION"

*Integrative Biology 200B*  
University of California, Berkeley

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March 29, 2011. "**Speciation**" (diversification) and related issues: species revisited

## I. Species

### A. Different approaches:

- a. typological or essentialist approach (i.e., systematics through Linnaeus)
- b. phenetic, morphological, or "natural" approach
  - older botanists (Gray, Bentham, Hooker) plus many recent botanists (Cronquist, Levin, Sokal & Crovello)
  - some recent cladists (!) (Nelson & Platnick, Cracraft, Nixon & Wheeler)
- c. "biological" species concept: interbreeding groups
  - classic isolation approach (most zoologists, e.g., Mayr, Dobzhansky)
  - newer recognition approach (some zoologists, see Paterson)
- d. "evolutionary" species concept: lineages (Simpson, Wiley, De Quieroz)
- e. "ecological" species concept: niches (Van Valen)
- f. "species as individual": integrated, cohesive units with spatio-temporal boundaries (Ghiselin, Hull)
- g. "phylogenetic" species concept: basal monophyletic groups (more below)

### B. Reason for the existence of a species problem:

- a. most of the above concepts and criteria conflict in most real cases -- different concepts (and processes) "pick out" different groups in each particular case, thus the implied correspondence between different criteria relied on by the BSC (and phenetic concepts) is abundantly falsified.
- b. operationality -- how to apply various concepts in a practical sense.
- c. what causes integration/cohesion of species? -- concerns:
  - breeding relationships are often clinal and/or non-transitive (what does "potential" interbreeding mean?)
  - gene flow is often very limited or lacking (what causes the evident distinctness of many asexual species?)
  - what is a niche?
  - developmental constraints (phylogenetic inertia)?

### C. A Phylogenetic Solution:

Recognize that there is no species problem per se in systematics. Rather, there is a taxon problem. Once one has decided what taxon names are to represent in general, then species taxa should be the same kind of things -- just the least inclusive. There is an element of arbitrariness to the formal Linnaean nomenclatorial system. Evolution is real, as are organisms (physiological units), lineages (phylogenetic units), and demes (interbreeding units) for example. On the other hand, our classification systems are obviously human constructs, meant to serve certain purposes of our own: communication, data storage and retrieval, predictivity. These purposes are best served by classification systems that reflect our best understanding of natural processes of evolution, and the field of systematics in general has settled on restricting the use of formal taxonomic names to represent phylogenetically natural, monophyletic groups.

**Grouping vs. ranking.** There are two necessary parts to any species definition. The criteria by which organisms are grouped into taxa must be specified, as well as the criteria by which a taxon is ranked as a species rather than some other hierarchical level. Following the arguments given previously supporting a Hennigian phylogenetic system of classification, the **grouping** criterion that should be used is monophyly. Under this view, apomorphies are considered to be the necessary empirical evidence for unambiguous phylogenetic species, as for phylogenetic taxa at all levels.

There are difficulties applying the concept of monophyly at this level. As you consider less inclusive levels in the genealogical hierarchy there is an increasing probability that reticulating ("hybridizing") events will occur, rather than the diverging phylogenetic relationships assumed by the cladistic approach. However, the problem of reticulation is not specific to the species level; indeed reticulation can occur throughout the hierarchy of life, and so is one of more general difficulty, and one that is receiving a lot of attention in the professional literature. It is becoming clear that while a certain amount of reticulation does not preclude cladistic reconstructions of phylogeny, extensive reticulation can cause major problems (more next lecture).

Note in passing that reproductive criteria cannot be used to **group** organisms into phylogenetic species. The fundamental inappropriateness of using breeding compatibility in cladistic analysis is because the ability to interbreed (potential or actual), is a plesiomorphy by definition, thus not a phylogenetically valid grouping criterion.

The **ranking** decision should involve practical criteria such as the amount of character support for a group and may also involve biological criteria in better known organisms, including reproductive criteria, e.g., the origin of a distinctive mating system at a particular node or the acquisition of **exclusivity** (a condition in which each allele in a lineage is more closely related to another allele in the lineage than it is to an allele *outside* the lineage). This ranking decision is forced because systematists have legislatively constrained themselves to use a ranked Linnaean hierarchy. A larger issue are recent calls for reforming the Linnaean system to remove the concept of ranks. This move would keep the hierarchy of named phylogenetic groups, but remove the ranks (including species) associated with the names (more below). This move would decrease the arbitrariness of ranking decisions at the "species level," but at the moment we assume that the current Linnaean system of ranked classifications is to remain in place.

To summarize, assuming the current codes of nomenclature, a phylogenetic species concept can be defined. First, organisms should be grouped into species on the basis of evidence for monophyly, as at all taxonomic levels; breeding criteria in particular have no business being used for grouping purposes. Second, ranking criteria used to assign species rank to certain monophyletic groups must vary among different organisms, but might well include ecological criteria or presence of breeding barriers in particular cases (Mishler & Brandon 1987).

#### The Phylogenetic Species Concept:

*A species is the least inclusive taxon recognized in a formal phylogenetic classification. As with all hierarchical levels of taxa in such a classification, organisms are grouped into species because of evidence of monophyly. Taxa are ranked as species rather than at some higher level because they are the smallest monophyletic groups deemed worthy of formal recognition, because of the amount of support for their monophyly and/or their importance in biological processes operating on the lineage in question.*

Some elaboration of the term monophyly from this definition is needed. Monophyly is here defined synchronically to be: *all and only descendants of a common ancestor, existing in any one slice in time*. This ancestor was not an ancestral species, but rather a less inclusive entity such as an organism, kin group or population. The synchronic approach is necessary to avoid the time paradoxes that arise when classifying ancestors with descendants [i.e., questions like: Was your grandmother your grandmother before your parents were born?]. The evidence required for a hypothesis of monophyly is primarily corroborated patterns of synapomorphy (but possibly also including other factors, such as geography).

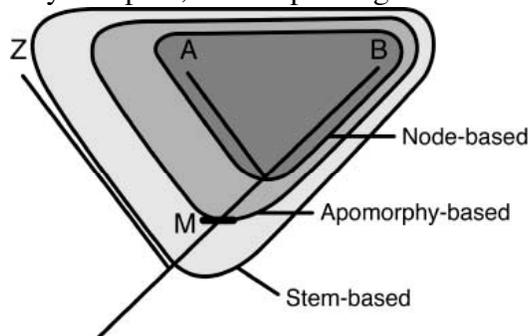
- Clade: a synchronic, monophyletic set of lineage-representatives (i.e., Hennig's semaphoronts)
  - Monophyletic: all and only descendants of a common ancestor
  - Lineage: a diachronic ancestor-descendant connection ("species" in the de Queiroz sense)
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## II. Wave of the future: phylogenetic taxonomy

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 a specially-created world-view. Perhaps the idea of fixed ranks made some sense under that view, but under an evolutionary world view they don't make sense. 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. Frivolous changes in names often occur when authors merely change the rank of a group without any change in postulated relationships. 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.

It is not completely clear at this point how exactly a new code of nomenclature should be written (see draft at: <http://www.ohiou.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, the major change would be that the Linnaean ranks should be abandoned, for efficient and accurate representation of phylogenetic relationships. Instead, names of clades should 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.



What about the species rank? The most controversial level of all, but the above arguments can be applied to the species rank just as well as to higher levels. In my opinion, this rank need to be eliminated as well. Below is how it could be done in practice; we will keep returning to this subject later in the semester, in terms of its implications.

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

- Names of clades (including the terminal level), should be hierarchically nested uninomials regarded as proper names (current usage should be followed as much as possible to retain links to the literature).
- As at all taxonomic levels, use node-based names with two or more internal type specimens.
- All the higher clades to which a taxon belongs should be regarded as part of its complete name.
- Therefore each clade has a uninomial given name, but also a set of more and more inclusive “family names”. Homonyms can thus be told apart by higher level clade names.

Recommendations:

- Don't use taxonomic ranks, including species, for comparative purposes or ecological/evolutionary inferences.
- Do use trees, branching events (represented by monophyletic taxa), and branch lengths for comparative purposes and ecological/evolutionary inferences.

### III. Diversification

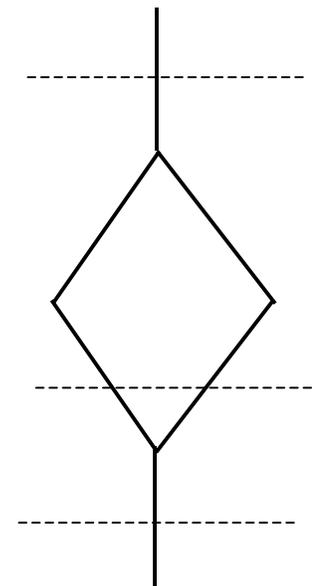
As discussed previously (3/15), there are two fundamental kinds of things in evolutionary theory (Hull, Dawkins). Both of these form nested hierarchies.

*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

Four things can happen to lineages:

1. Origin
2. Extinction
3. Divergence
4. Reticulation



For today, will focus on **divergence**, which leads to diversification of **lineages**. The total number of lineages in a clade is **diversity**.

Constraints: Why is morphospace not filled in completely?

Adaptive landscapes vs developmental landscapes

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

Reproductive isolation:

1. Prezygotic: 1) habitat isolation, 2) temporal isolation, 3) behavioral isolation, 4) mechanical isolation, 5) gametic incompatibility

Anything that prevents mating and fertilization is a prezygotic mechanism. Prezygotic mechanisms fall into two broad categories. Habitat isolation, that is, preferring different habitats, is likely to have evolved because of natural selection. In this case, reproductive isolation is a byproduct of changes occurring for other reasons. In other cases, characters associated with mating also are isolating mechanisms. Differences between lineages could evolve in order to prevent hybridization. In some cases, such as the time of mating, it is difficult to tell. Lineages could be active at different times of the day or breed at slightly different times of the year, because of food preferences or because selection favored reduced hybridization.

2. Postzygotic: 1) hybrid inviability, 2) hybrid sterility, 3) hybrid breakdown

Postzygotic barriers prevent the hybrid zygote from developing into a viable, fertile adult. Reduced viability or fertility of hybrid offspring all are known to be postzygotic isolating mechanisms. Lack of ability to survive in intermediate habits is an ecological barrier. Often differences in chromosome number or arrangement of genes on chromosomes result in genetic barriers.

Geographic modes of diversification:

1. *Allopatric*: Diversification by geographically separated populations.

Either a barrier can form, separating a single lineage into two isolated ones, or a lineage can colonize a new area. In both cases, gene flow is highly reduced. The formation of a barrier is sometimes called a vicariant event. How large a barrier has to be depends on dispersal capacity. A river may be a barrier for a snake but not a bird.

There are two important subtypes of allopatric diversification:

- I. Initial population divided into two large halves (the "dumbbell" model)
- II. Initial population divided into one large half and one small, marginal half (the peripheral isolate model)

2. *Sympatric*: Diversification between lineages with overlapping geographic ranges

In plants polyploidy can lead to immediate reproductive isolation. Chromosomal mutations in self-fertile plants can lead to instant speciation. The genus *Clarkia* provides several examples of allopolyploid and autopolyploid species. Many domesticated plants are polyploid, including oats, wheat, barley, potatoes, bananas, tobacco. It is likely that polyploid individuals were used early in the domestication of plants, both because they had unusual properties and because they were reproductively isolated from their wild relatives.

Implications for studies of "speciation":

The study of speciation involves an interplay between empirical research and concepts of species (the units of speciation). As emphasized before, the converse is true in that an understanding of processes impacting on species can influence species concepts for a group.

Studies of pattern (i.e., phylogenetic reconstructions) and process (underlying causal mechanisms) are related to each other in a reciprocal manner (Hull 1988). We must ask not just what species are and how they are to be defined, but also how they came into being and how they are maintained. General evolutionary theories about species, their origin and nature, can (and should) be examined in such a manner.

The process of studying divergence should always start with a cladogram down to as fine a level as is possible to resolve. The next step is to examine the characters changing on the branches (morphological, functional, geographic, reproductive, etc.), looking for common denominators (possible causes/constraints).

How do we study adaptive radiations in a rank-free world view?

A sampling problem: how many "basal" lineages are there?

**IV. Further reading**

B.D. Mishler and M.J. Donoghue. 1982. Species concepts: a case for pluralism. *Systematic Zoology* 31: 491-503.

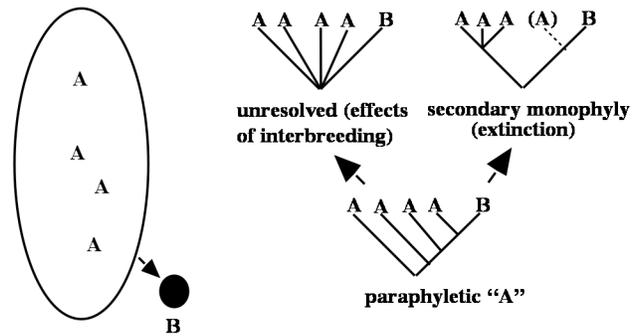
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B.D. Mishler. 2010. Species are not uniquely real biological entities. In F. Ayala and R. Arp (eds.), *Contemporary Debates in Philosophy of Biology*, pp. 110-122. Wiley-Blackwell.



"Peripatric speciation": rapid divergence of peripheral isolates