March 2, 2006: **Classification II -- Species**

I. Importance of the species problem:

a. nomenclatorial requirements (all organisms must belong to a species).

b. practicality -- need to organize diversity, summarize information, communicate, give names to things.

c. legal issues -- endangered species legislation; conservation

c. connection to evolutionary theory -- desire to have species as units functioning in process theories (but which process theories? how to connect units and theories without circularity?)

d. philosophical concerns -- need to be clear about properties of units: sets vs. individuals, universalism vs. pluralism.

II. Quasi-historical outline:

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)

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 (will return later)

III. 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)?

d. what are the spatio-temporal boundaries of species?
- monophyly?
- origin?
- extinction?

IV. 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. How do we know when we have reticulation going on? We can only detect it by doing phylogenetics.

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. This move would decrease the arbitrariness of ranking decisions at the "species level," and will probably happen some day, but for now we assume that the current Linnaean system of ranked classifications is to remain in place (more on the possibility of getting rid of species in a couple weeks).

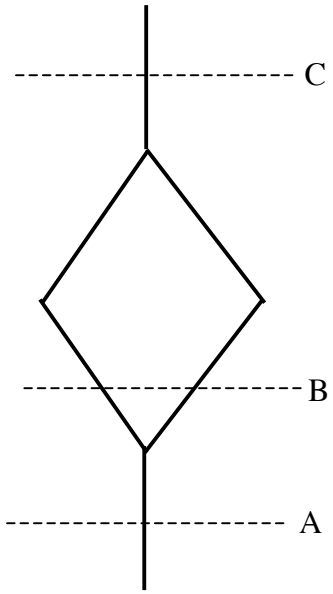
To summarize, a phylogenetic species concept can be defined based on these considerations (from B.D. Mishler and E. Theriot. 2000. In Q.D. Wheeler & R. Meier (eds.), *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press). First, organisms should be grouped into species on the 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. The grouping concept (monophyly) in this view is monistic, while the ranking concept is pluralistic.

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. Only "clades" can be monophyletic, not "lineages" (see diagram from last time). 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).

Can a group arising by hybridization be monophyletic? Given this synchronic definition it can, as long as it only arose once. In the diagram at right, in the first time-slice (A) there is one clade, then two, then one again.



Mishler, B. D. 1999. Getting rid of species? Pp.307-315 in R. Wilson (ed.), Species: new interdisciplinary essays. MIT Press.

Mishler, B. D. and E. Theriot. 2000. The phylogenetic species concept sensu Mishler and Theriot: monophyly, apomorphy, and phylogenetic species concepts. Pp.44-54, 119-132, 179-184 in Q.D. Wheeler & R. Meier (eds.), Species concepts and phylogenetic theory: a debate. Columbia University Press, NY. [three chapters]