Species

A. Importance of the species question:
   a. practicality -- need to organize diversity, communicate, give stable names to things.
   b. legal issues -- endangered species legislation; conservation priority
   c. summarize information -- predict unknown features of organisms
   d. connection to evolutionary theory -- desire to capture units functioning in natural processes

B. Some competing views of species:
   a. "typological" species concept: defining characters (i.e., systematics through Linnaeus)
   b. "phenetic" species concept: clusters of similar organisms
   c. "biological" species concept: interbreeding groups
   d. "evolutionary" species concept: lineages -- interbreeding groups through time
   e. "ecological" species concept: lineages -- occupying unitary niche
   f. "phylogenetic" species concept: basal monophyletic groups [** more below]
   g. getting rid of species all together! [** more below]

C. Why so much debate?

   The reason for the existence of a species problem is that the above concepts and criteria conflict in most real cases -- different concepts (and processes) "pick out" different groups in each particular case.

D. The problems:

   a. what causes integration/cohesion of species? -- candidates and their problems:

      Gene Flow:
      -- 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?)

      Ecological Constraints:
      - ecological role is hard to define precisely in practice (what is a niche?)

      Developmental Constraints:
      - development is exceedingly complicated, and we have little idea yet how developmental processes resist change (phylogenetic inertia?)
b. what are the spatio-temporal boundaries of species?
   - monophyly?
   - hybridization?
   - origin?
   - extinction?

E. A phylogenetic solution?
   A full discussion of phylogenetic approaches to species concepts is beyond the scope of this course (if you are interested more deeply in the theory, may I suggest IB 200A & B). A way forward for our purposes is to realize that there really is no species problem as such. 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. It must be recognized that there is an element of arbitrariness to the formal Linnaean nomenclatorial system. Evolution is real, as are lineages. 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.

   Note in passing that (despite what you may have been taught previously) 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). 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 I assume that the current Linnaean system of ranked classifications is to remain in place.

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 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 versus Lineage** (see next page for illustration). They are not the same thing -- "clade" is a synchronic concept, a snapshot of a lineage -- while a lineage is a diachronic concept, a series of replicators.

**F. A rank-free solution?**

Carrying the idea of "taxon problem" to its logical conclusion, arguably means treating species like all other taxa and getting rid of the rank of species along with all other taxonomic ranks. See Mishler (1999, Getting rid of species? In R. Wilson (ed.), *Species: New Interdisciplinary Essays*, MIT Press, posted at: http://persoon.si.edu/sbs2001/Mishler.pdf) for an essay advocating this. In brief the argument is: (1) Species must be treated as just one taxon among many; (2) All taxa should be monophyletic groups; (3) Because of problems with
instability and lack of comparability of ranks in the formal Linnaean system, we need to move to a rank-free formal classification system; (4) In such a system, not all hypothesized monophyletic groups need be named, but those that are named formally should be given unranked (but hierarchically nested) uninomials; (4) The least inclusive taxon, formally known as "species," should be treated in the same unranked manner. We do need to talk about practical implications of eliminating the rank of species for such areas as ecology, evolution, and conservation.

G. "Speciation"

This will be covered next time. For now, it is enough to say that the question of what species are is primary to the question of how they form. Given the above view of species, it is clear that "speciation" should not be regarded as a unique process, but rather a point along a spectrum of stages of divergence of lineages. As with the ranking criteria discussed above, a variety of processes can contribute to the divergence of lineages -- discontinuities in breeding patterns are only one possibility, and are not necessarily involved in any given divergence.

H. Implications for conservation biology

All "species" are not equal in a phylogenetic sense (or any other sense for that matter). As has been pointed out by a number of pioneering cladistic conservation biologists, conservation priorities can best be set by a consideration of the phylogenetic relationships among species. This is because all attributes of organisms (genetic similarities, ecological roles, morphological specializations) tend strongly to be associated with phylogeny. From the standpoint of preserving the maximum phylogenetic diversity (and its associated attributes), saving a "long-branch" species (i.e., one such as the Coast Redwood or Santa Lucia Fir with much change along the terminal branch, either due to extinction or rapid evolution) should carry a higher priority than saving a "short-branch" species (i.e., a dandelion differing in only a few minor features from near relatives). Furthermore, saving a community of 100 species of diverse
phylogenetic relationships should carry a higher priority than saving a community of 200 species belonging to only a few large genera (see the figure below for an illustration of these points). Thus, phylogenetic considerations should play a much more important role in conservation biology than they have to date.

In an ideal world all species could be preserved -- in this world of limited resources (time, money, and public goodwill) indices based on phylogeny are being developed to help us preserve the maximal genetic, morphological, chemical, and ecological diversity. The general public will be much more supportive of species preservation efforts that are carefully focused and justified in this way, rather than of uncritical, across-the-board efforts. Phylogeny reconstruction is thus not just an academic exercise, but rather the fundamental basis of a truly practical taxonomy.

Hypothetical cladogram illustrating the importance of phylogeny in setting conservation priorities. Shown is a phylogeny of 43 "species;" the branch lengths are proportional in the vertical direction to the number of evolutionary character changes along that branch. From the standpoint of preserving the maximum amount of phylogenetic diversity (and its closely associated genetic, morphological, physiological, and ecological diversity), species one would have a lower conservation priority than species two. Three groups of seven species each are also marked on the cladogram. By the same criterion, group A would have a lower conservation priority than group B. Group C, consisting of the same number of species scattered across the cladogram, would have a much higher conservation priority than either group A or B. In fact, group C would have a higher conservation priority than groups A and B taken together. Thus, the number of species in a locality is by itself a poor indicator of its priority for conservation.