March 14, 2016. **Classification III: Species concepts, speciation**

A. 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. public perception -- species *deeply* ingrained in Western thought

   d. legal issues -- endangered species legislation; conservation

   e. 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?)

   f. 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); logical division

   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 Queiroz)

   e. "ecological" species concept: niches (Van Valen)

   f. "species as individual": integrated, cohesive units with spatio-temporal boundaries (Ghiselin, Hull)

g. "phylogenetic" species concepts of various types (as noted above, some are really phenetic): lineages, homogeneous groups, basal monophyletic groups. etc. (will return to one of these below in section IV)

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 De Queiroz's General Lineage Concept) 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?)

- ecological limits; stabilizing selection; adaptive constraints. What is a niche?

- developmental constraints (phylogenetic inertia)?

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

IV. The best phylogenetic solution, if we want to keep the species rank:
    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.

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 <u>grouped</u> into species because of evidence of monophyly. Taxa are <u>ranked</u> 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 <u>monophyly</u> 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).

V. 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 (as at all levels in the Phylocode, current usage should be followed as much as possible to retain links to the literature, databases, and collections).
- 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.
- To deal with the rampant homonyms that will result from treating current species eipthets as uninomials, several proposals have been made. My preference would be to regard all the higher clades to which a taxon belongs as part of its complete name. Thereby each clade would have a uninomial given name, but also a set of more and more inclusive "family names, " thus homonyms could be told apart by higher-level clade names.
- If you must have some thing to count, use: **S**mallest **NA**med and **R**egistered **C**lades or SNARCs)

*Phylogenetic uninomial: Revolutus*
Node-based definition:
    Internal Specifier: *Syrrhopodon revolutus* Dozy & Molk. TYPE: JAVA. Herb. Émil Bescherelle. *Korthals* (isotype BM!).
    Internal Specifier: *Syrrhopodon microbolax* Müll. Hal. TYPE: MADAGASCAR, Nosy Bé. Herb. Émil Bescherelle. *Boivin* (BM!).
    Internal Specifier: MADAGASCAR. *Fisher 01.84* (UC!).
    Internal Specifier: BORNEO. *Wall 3768* (UC!).
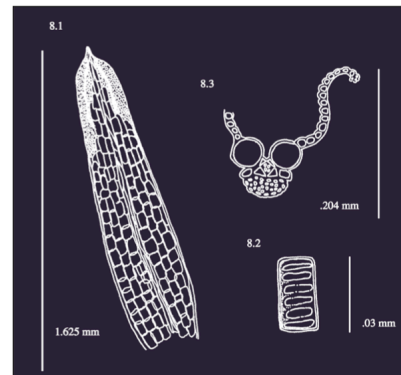
Kirsten M. Fisher -- *Systematic Botany* 2006 31:13-30. Monography and the PhyloCode: An Example from the Moss Clade *Leucophanella*

B. "Speciation" = Divergence

I. Four things can happen to lineages:

1. Origin (doesn't happen on the modern earth)
2. Extinction
3. Divergence
4. Reticulation

For today, will focus on **divergence**, which leads to **diversification** if the rate of divergence exceeds extinction. The total number of lineages in a clade at a given time is **diversity**.

    Constraints: Why is morphospace not filled in completely?

    Adaptive landscapes vs developmental landscapes
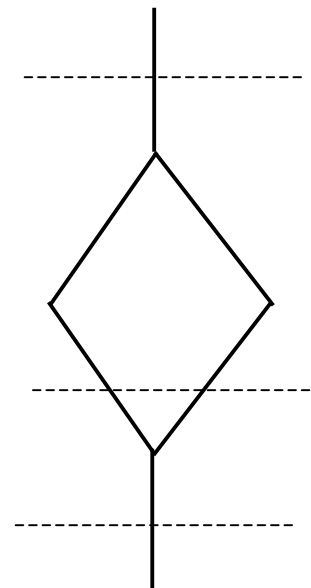
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GENERAL CLASSES OF CAUSAL FACTORS ADVANCED TO EXPLAIN
      COHESION/INTEGRATION OF "SPECIES":
            1) GENE FLOW
            2) STABILIZING SELECTION -- ECOLOGICAL CONSTRAINTS
            3) DEVELOPMENTAL CONSTRAINTS
THE NULL HYPOTHESIS: RANDOM WALK; ACCIDENTS OF HISTORY
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II. Factors affecting isolation and increased chance of divergence:

1. Prezygotic: 1) habitat isolation, 2) temporal isolation, 3) behavioral isolation, 4) mechanical isolation, 5) gametic incompatibility, 6) asexual reproduction
        Anything that prevents mating and fertilization (one type of reticulation) is a prezygotic mechanism. Prezygotic mechanisms may reflect intrinsic traits of the organisms or extrinsic factors. Habitat isolation, that is, preferring different habitats, is likely to have evolved because of natural selection. In this case, reproductive isolation might be a byproduct of changes occurring for other reasons. Lineages might 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.

III. 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 an 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.

IV. Summary: Implications for studies of "speciation" (divergence)

        If you want to retain species: 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.

        You can still study divergence without species. As above, studies of pattern (i.e., phylogenetic reconstruction) and process (underlying causal mechanisms) are related to each other in a reciprocal manner (Hull 1988). We must ask not just what clades are and how they are to be defined, but also how they came into being and how they are maintained. General evolutionary theories about clades, 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).

V. Some papers drawn on heavily for these notes:

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

B.D. Mishler and R.N. Brandon. 1987. Individuality, pluralism, and the phylogenetic species concept. *Biology and Philosophy* 2: 397-414.

B.D. Mishler and A.F. Budd. 1990. Species and evolution in clonal organisms--introduction. *Systematic Botany* 15: 79-85. [symposium on species in several asexual groups of organisms]

B.D. Mishler. 1999. Getting rid of species? In R. Wilson (ed.), *Species: New Interdisciplinary Essays*, pp. 307-315. MIT Press.

B.D. Mishler and E. Theriot. 2000a,b,c. The phylogenetic species concept sensu Mishler and Theriot: monophyly, apomorphy, and phylogenetic species concepts. Three chapters in Q.D. Wheeler & R. Meier (eds.), *Species Concepts and Phylogenetic Theory: A Debate*. Columbia U. Press.

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.

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