

Evolution spring 2008: Speciation and species concepts (second last lecture), plus last lecture (evolution and species diversity in Texas cave and spring salamanders)

NOTE: Much of what I discuss here is NOT in the text, but is derived from my research in this area (the ideas re: speciation are covered in text, but in a somewhat different way in some cases).

Species names: follow binomial form established by Linnaeus (1700s). Two parts: genus and specific epithet. For example, humans are *Homo sapiens*, where "*Homo*" is the genus, "*sapiens*" is the specific epithet, and *Homo sapiens* is the actual species name. Genus and species names are always italicized or underlined; names of higher-level taxa (families and up) aren't.

Species: many views. Most scientists agree that species are real, and are the largest units of evolution. In other words, genera, families, classes etc. don't "evolve" -- these higher-level classifications are simply ways of grouping species in convenient ways, and now nearly everyone agrees that these should reflect phylogeny (i.e., each taxonomic grouping should be a monophyletic group, an ancestor and all of its descendants).

Estimates of numbers of species on Earth range from about 10-100 million; I and lots of others think many more. Very important, because hundreds or thousands of species disappear every day/week, most of which we don't even know about.

AND -- biodiversity IS important. Not just for our pleasure, but because of the complex interactions that maintain the systems on the planet, and also because humans derive real benefits -- medicines etc. etc.

So, what is a species?

A key distinction (not really dealt with in text): there are species CONCEPTS, and then what we do in PRACTICE. A concept doesn't have to be practically applicable in all cases; we may just have to accept that we'll never (as humans) be able to recognize all species. We can only try, and apply useable criteria. Has huge implications re: conservation policies and understanding evolution in general, and remains controversial.

Some common species concepts:

1) Biological Species Concept (usually attributed to Mayr 1940's; basically proposed by Dobzhansky 1938): Species are interbreeding groups of individuals that cannot actually or potentially interbreed with members of other such groups and produce viable, fertile offspring.

ADVANTAGE: If two groups of organisms live in the same area (are sympatric) and don't interbreed and/or offspring are unsuccessful, then clearly they're different species (e.g., pine trees and oak trees, sparrows and blue jays, etc).

DISADVANTAGES:

- a) Doesn't allow for closely related forms that are geographically separated and might be able to interbreed, say, in lab, but never will in nature.
- b) Can't address asexual lineages like bacteria and parthenogens.
- c) Doesn't address lineages that have some degree of interbreeding (hybrid zones etc.) yet mostly maintain distinct identities.
- d) How infertile/inviable do "hybrid" offspring have to be, and under what conditions?
- e) Over 99.999% of widely recognized species have never been tested under this criterion and never will be, so this condition is (practically) rarely possible to test.

And many other problems. So, reproductive isolation usually inferred (assumed) indirectly by differences in morphology, genes, etc. BSC doesn't hold up well UNLESS the species are truly sympatric and are unsuccessful at interbreeding. Then there's no question that they're different species, but BSC is EXTREMELY limiting and rigorous use would result in vast underestimate of true number of species. Even those who say they use it really DON'T for the vast majority of organisms that they accept as distinct species.

2) Phylogenetic species concepts (PSC; Cracraft and others): Lots of variations. Main idea is that species are diagnosable, monophyletic groups with unique synapomorphies (shared derived character states).

ADVANTAGE: Seems like a clear-cut criterion.

DISADVANTAGES:

- a) Rarely possible to test whether features of the group are really diagnostic in the sense of being truly fixed.
- b) Allows recognition of temporary lineages (e.g., populations) with minor differences that could easily merge with others in future.
- c) From practical standpoint, would result in recognition of huge number of species (that again, may just be undersampled and/or temporary).

3) Ecological species concept (Van Valen 1970s): Species are entities that occupy distinct ecological niches.

ADVANTAGE: Tries to place species in an environmental interaction context as occupying distinct positions in nature.

DISADVANTAGES: No one agrees on what a "niche" is, it's not clear what degree of ecological separation is necessary, why can't two species share all or part of a niche, etc?

Almost never used now.

4) "Morphospecies", genetic distance, etc.

ADVANTAGE: Supposedly defined criteria for identifying fossil species, living species by some set genetic divergence, etc.

DISADVANTAGES: Not a concept at all, just operational criterion that may not reflect reality, and has no applicability across different groups.

Often used by those who DO NOT believe that species are real -- just human constructs like higher-level taxa.

5) My preferred species concept: Evolutionary Species Concept (Simpson 1960s, then modified by Wiley 1978): Species are distinct evolutionary lineages with their own unique evolutionary origins and historical fates.

ADVANTAGE: Recognizes that species are real units of evolution and that multiple criteria may be used to recognize them -- but acknowledges that we simply may not have the information to do so in all cases. Truly a concept. The most broadly applicable concept.

DISADVANTAGES:

- a) Deliberately vague in the sense of not trying to put absolute values of divergence etc. on species - so often hard to apply. Doesn't mean that species don't exist, just that we may or may not be able to detect them, and sometimes we may be wrong.
- b) Different interpretations of distinct evolutionary lineages -- what constitutes their ultimate evolutionary fate, etc? Is merging w/ another lineage OK, or did it mean that they weren't species in the first place?
- c) Requires humans to admit that they can't know or measure everything. Remember that not every CONCEPT can be put into PRACTICE in every case -- but provides a baseline for the sort of evidence that we use to identify species (give example of newly originated species with no measurable level of differentiation).

Example of applications: see notes on salamander talk below.

Some causes of speciation (NOTE: I give some examples from my own research in the lecture below, so I skip most of the examples in the text):

1) Vicariance: Generally accepted as THE main reason: physical separation due to ecological change, mountain range, river, continental drift, etc. Populations are broken up, gradually accumulate differences due to drift, selection etc. until they are no longer reproductively compatible. Conceptually -- did speciation only occur once they were "different" enough, or when they started on their own evolutionary paths? I would say the latter. In any case there is evidence from fruitflies (Coyne and Orr and others), frogs (Sasa, Chippindale, and Johnson 1998) and others that there is a point of genetic divergence at which reproductive incompatibility evolves due to accumulation of genetic differences, and it's remarkably similar across distantly related organisms. BUT again, two groups could be different species BEFORE barriers to reproduction (other than geographic separation) arise. In other words, two isolated populations might still be able to interbreed if brought together, but they never will be except artificially -- so they can still represent separate species. And -- lots of examples of organisms that are very

distinct, for which no one would argue that they're the same, yet they can interbreed successfully in captivity.

This represents ALLOPATRIC speciation: speciation due to physical separation.

2) Sympatric speciation: Organisms living in the SAME area may specialize on different microhabitats and become reproductively separated. Very controversial, but does seem to happen. Example: Schluter and colleagues: stickleback fishes in Pacific NW: recent divergence into genetically distinct lineages that specialize in living in either surface or deep lake waters; each does best in a given part of the lake and hybrids are less fit. Especially likely if some factor makes each microhabitat favorable at different times, or the in-between habitat isn't so good even though they can move through it, promoting specialization on one or the other.

3) Hybrid speciation: Hybridization may bring together allelic combinations that are better in certain habitats than those in either parent species. Then, these have an advantage and do best reproducing together. Example: sunflowers (Rieseberg).

4) Polyploidization and other chromosomal changes: already discussed; especially common in plants. Once polyploid is formed, genetically incompatible with diploid forms, and becomes new species. Almost instantaneous speciation; very well documented. So yes, scientists DO observe species forming in nature (despite the arguments of some anti-evolutionists)

5) Sexual selection: Example: Hawaiian fruitflies: If females prefer males with superior combat ability and a mutation arises in one temporarily isolated population that allows improved combat in males, females could evolve to focus on males with this feature (and genetically lose interest in males without it). So, populations diverge b/c females will only mate with the "new" types of males even if the populations come back into contact. Sexual selection has also been invoked for recent, explosive speciation in African rift lake cichlid fishes -- one of the graduate students will present on this.

ALSO: Distinguish between PREZYGOTIC reproductive isolation (before zygote is formed) -- includes isolation due to lack of physical attraction, physical incompatibility, sperm competition, and just geographic separation;

and POSTZYGOTIC isolation -- after zygote is formed: sterility, inviability, reduced fitness.

Speciation occurs and we can infer and even observe it -- but the concept of species, and the relative importance of different factors -- remains controversial even though almost everyone agrees that different species exist.

Last lecture: Evolution of Texas cave and spring salamanders (*Eurycea*) -- my research -- very brief overview

Edwards Plateau of central Texas: uplifted ancient limestone "honeycombed" with water-filled passages that fill caves and emerge as springs -- Austin and San Antonio, for example, are on the edge of the Plateau. Underlying water is the Edwards Aquifer, which is divided into various subregions.

Salamanders of the genus *Eurycea* occur in the waters of the caves and springs -- almost all populations and species are paedomorphic: keep larval amphibian form (don't metamorphose into adult -- retain gills and various morphological features but become reproductively mature) -- kind of like a tadpole maturing without transforming into a frog. Salamanders are amphibians, most closely related to frogs -- they are NOT lizards.

Until early 1990s, nearly all populations throughout Edwards Plateau were considered a single species, plus another genus of bizarre cave-dwellers southwest of Austin (*Typhlomolge*) was recognized. Morphological variation very complex: many spring forms appear very similar (especially because they maintain larval form); many cave-dwellers that probably entered caves independently took on cave-associated features like eye and pigment reduction convergently. Species boundaries were very confusing.

Then: my colleagues and I examined variation in proteins (allozyme electrophoresis), sequenced mitochondrial DNA, and looked at morphology in more detail.

Result: Extremely deep divergences among some populations/groups that correspond to geographic/hydrologic regions. For example, estimated time of divergence (based on DNA) between the groups north versus south of the Colorado River that flows through Austin is about 15 million years, even though they look very similar and occur just a few miles apart (but now we know that there are some small skeletal differences etc. and the northern species have about 13% more DNA in their nuclear genomes; we don't know if they're reproductively compatible). So, little doubt that these are distinct species under many criteria, including Evolutionary and Phylogenetic Species Concepts, although technically we haven't satisfied the BSC -- an example of the problems with the BSC.

Also: cave genus *Typhlomolge* is very distinct based on molecular and morphological data (probably diverged about 9-10 million years ago) BUT is phylogenetically nested inside what was once considered a single widespread species of *Eurycea*. So, now these cave dwellers are placed in the genus *Eurycea* although recognized as separate species.

We recognized MANY new species based on combinations of molecular data, geographic distribution, and morphology in some cases, and others remain to be formally described as new species -- for example, a new cave form found by a colleague recently in a 270 foot deep well (in a bowling alley parking lot!). There are at least 7+ very distinct species just within the Austin - San Marcos metropolitan area and nearby (probably more).

But other cave forms suspected to be distinct species turned out to be members of surface species that have taken on cave-associated features -- not yet clear whether this is genetically based or represents phenotypic plasticity (ability to develop different morphology depending on environment).

Key point: The diversity of salamander species in the Edwards Plateau region results from vicariant events that caused separation of various aquifer regions over millions of years, and allopatric speciation. In some cases, NS (or relaxation of NS) caused further morphological and behavioral differentiation -- e.g., ancient cave dwellers once placed in genus *Typhlomolge*.

Excellent example of "island" effect (recall Galapagos). Except here, these are islands of water in a dry area -- salamanders stay in the water as reproductively mature larvae, don't cross the hot, dry land. Some may superficially appear the same, but molecular data show extreme separation; others (cave vs. spring in some cases) look very different but aren't distinct based on molecular markers; and others are very distinct based on both morphology AND molecules. Overall, 17+ species now recognized when previously only about five max. were.

AND: Has major implications for conservation -- not only salamanders themselves, but other endemic (limited to one area) species that also depend on aquifer waters. AND: Humans depend on these waters too, so salamanders are an "indicator" of aquifer quality. *Eurycea sosorum*, for example, is known only from Barton Springs in downtown Austin (natural spring beloved for swimming by Austinites). Formally described as new species by Chippindale and colleagues in 1993; became the subject of huge controversy when proposed for Federally Endangered Species listing (protection like that for bald eagle, grizzly bear, etc.). Developers and others were concerned about impacts re: habitat and aquifer protection; swimmers were afraid Barton Springs would be closed off; but many in Austin embraced salamander as symbol for springs, environment and clean water.

Salamander WAS listed (eventually -- huge legal/political controversy), and some others probably will be too. But people still swim at Barton Springs, salamanders are doing well, many provisions are now in place to protect aquifer waters, and development/industrial community works closely with conservationists/scientists/government to strike a balance.

Example of how identification of unknown species and protection of biodiversity can have major -- and often positive -- effects on humans.

Scientists keep finding new species every day; race is on to protect them, and many are lost before we even know about them. Effects of loss may be complex and unpredictable. Texas salamanders: not a perfect situation, but mostly a success story so far.