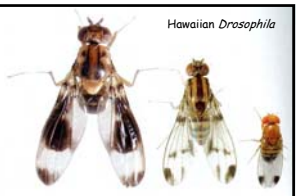
What are species, and how do they arise?



Darwin called this "the mystery of mysteries" and named his book *On the Origin of Species*. But in fact he hardly discusses the problem of getting two species out of one!

Species are real even though it can often be impossible to say with confidence whether two related populations should be considered one species or two. Biologists currently use three related species definitions or criteria.

Biological species are reproductively isolated populations; because they never or rarely exchange genes, they have independent evolutionary fates.

Phylogenetic or genealogical species are populations whose gene trees are always or predominantly monophyletic (i.e., united by exclusively shared common ancestors); for this condition to hold, there must have been little or no gene flow for many generations.

Morphological or taxonomic species are those that can be distinguished by consistent visible character differences; this criterion can be applied to fossils.

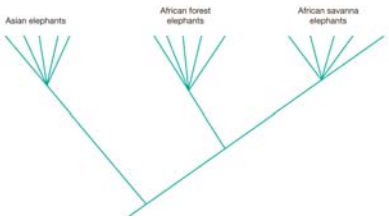
How many species of elephants are there?

Traditionally, just *two* (Asian and African).

But African elephants that live in forests differ slightly in form from elephants that live in savannas.

Recent population genetic evidence shows that forest and savanna elephants are distinct populations that have experienced little if any gene flow for some time.

Thus biologically, phylogenetically, and morphologically they are different species.



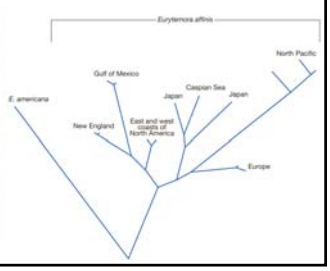
But many species are extremely "cryptic"

For example, the copepod *Eurytemora affinis* occurs in costal waters all over the world.

Carol Eunmi Lee sampled 38 populations from locations around the Northern Hemisphere.

The DNA sequences of two genes suggested that there might be ***eight*** phylogenetic species.

Lee tested this hypothesis by crossing individuals from different parts of the tree, and in most cases they did not produce fertile offspring, demonstrating that the *phylogenetic* species are also *biological* species, even though no one can tell them apart morpholgically.

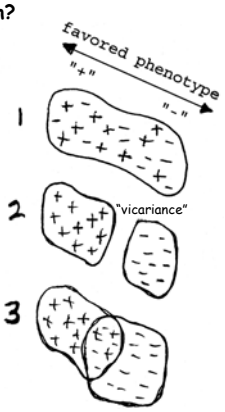


What's the mechanism of speciation?

The easiest way to get reproductive isolation is to physically divide the population.

This is the standard *allopatric* ("other country") model of speciation, which has three steps:

1. Environmental differences select for different optimum phenotypes in different parts of a species' range, but migration (gene flow) keeps the species relatively uniform genetically and phenotypically.
2. A geographic barrier to migration appears (for example, a desert or mountain range), reducing gene flow and allowing the newly isolated populations to adapt to local conditions. Thus *geographic isolation* leads to *genetic divergence*.
3. Eventually, the genetic and phenotypic divergence is sufficient to (i) prevent gene flow even if the barrier to migration is removed, and (ii) allow the two new species to coexist ecologically. Coexistence without significant gene flow proves that speciation is complete, but is not a requirement. In general, only time will tell!



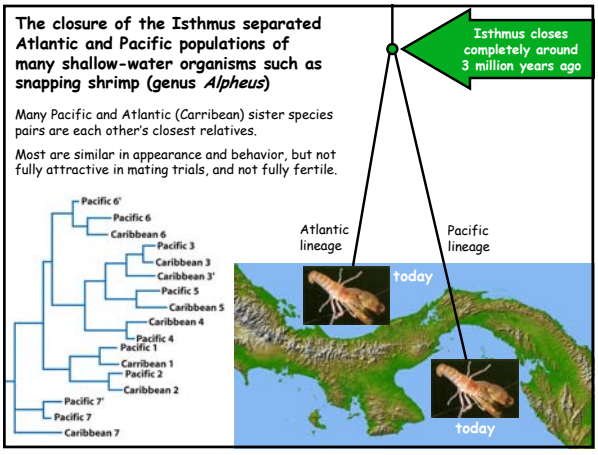
An example: The Isthmus of Panama emerged as a wrinkle in the earth's crust during the Miocene, as the South American Plate pushed into the North American Plate.

Epoch	Age Ma
Holocene	
Pleistocene	1.8
Pliocene	5.2
Miocene	23.8
Oligocene	33.5
Eocene	55.6
Paleocene	65

The closure of the Isthmus separated Atlantic and Pacific populations of many shallow-water organisms such as snapping shrimp (genus *Alpheus*)

Many Pacific and Atlantic (Carribean) sister species pairs are each other's closest relatives.

Most are similar in appearance and behavior, but not fully attractive in mating trials, and not fully fertile.

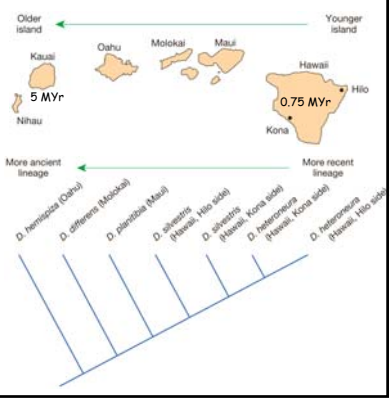


Geographic isolation may also arise through dispersal and colonization

This process is important in archipelagos such as the Hawaiian Islands, where new, initially unoccupied islands appear every million years or so at one end of the chain.

Because the ages of the Hawaiian Islands are known, it is possible to reconstruct the histories of many species groups such as these fruit flies in the genus *Drosophila*.

Note that this pattern is a remarkable "proof of evolution": the shape of the tree is predicted by the geology of the Hawaiian archipelago.



Evolutionary divergence can begin in just tens or hundreds of generations, and even *sympatrically*, when populations move into different habitats or onto different hosts.

Limnetic and benthic three-spined stickleback species have evolved *independently* in many different lakes since the last ice age ended around 15,000 years ago.

Rhagoletis pomonella (the "apple maggot") moved onto introduced apples from its native hawthorn.

Pea aphids have formed incipient species that are adapted to cultivated alfalfa and red clover.

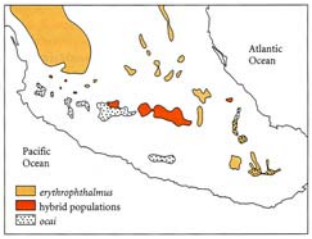
Species are "communities of genes", not metaphysical absolutes

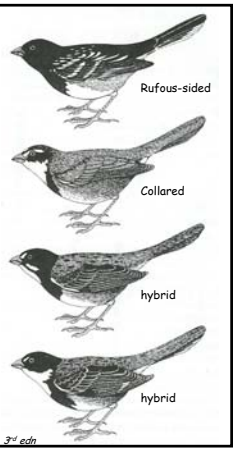
They can remain real or "good" species even if they occasionally exchange genes with other species.

These towhees hybridize in certain parts of their shared range, but not in others.

Pipilo erythrophthalmus = rufous-sided towhee

P. ocai = collared towhee

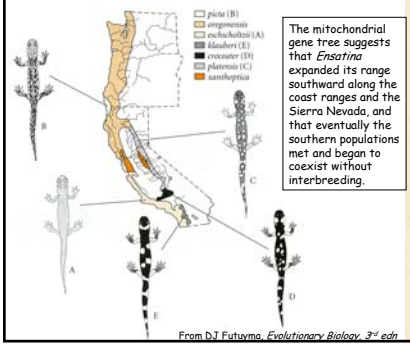




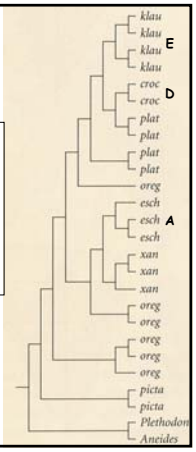
From DJ Futuyma, *Evolutionary Biology*, 3rd edn

Ring species: one or two? You make the call.

The salamander *Ensatina eschscholtzii* forms a ring of subspecies around California's Central Valley, with gene flow between adjacent populations everywhere except where the ends of the ring overlap in Southern California (A-D, A-E).



The mitochondrial gene tree suggests that *Ensatina* expanded its range southward along the coast ranges and the Sierra Nevada, and that eventually the southern populations met and began to coexist without interbreeding.



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Yogi Berra on speciation: "It ain't over 'till it's over."

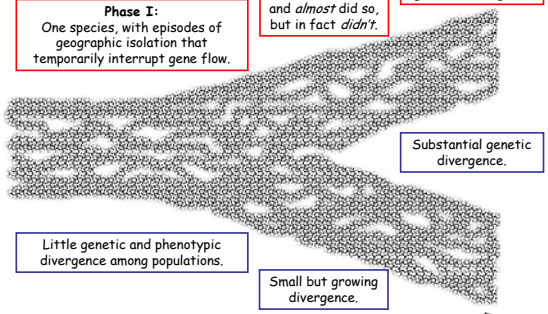
"It ain't over 'till it's over."

***When* in Phase II did they become different species?**
There's *no way to say*, even in principle!

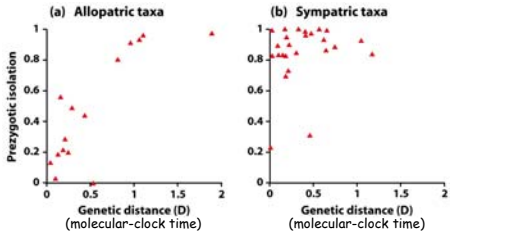
Phase I: One species, with episodes of geographic isolation that temporarily interrupt gene flow.

Phase II: *Could* have fused, and *almost* did so, but in fact *didn't*.

Phase III: Two species, never again to share genes.



And we find populations at every imaginable stage in the progression!



Drosophila species avoid each other sexually more strongly ("Prezygotic isolation"), the longer they have been separated ("Genetic distance"), if they live in *different* places ("Allopatric").

But if they live in the *same* place ("Sympatric"), then they strongly avoid each other, even if recently separated. WHY?