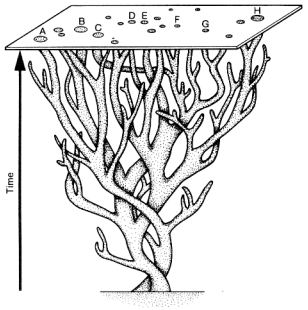
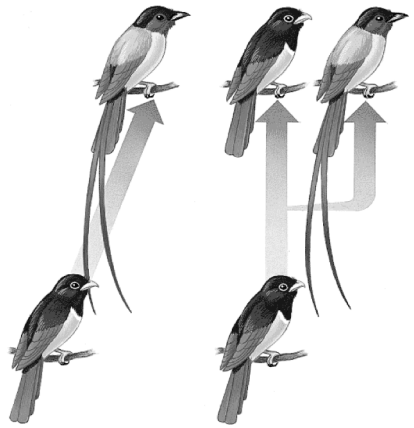
The Linnean system

- Kingdom — Animalia
- Phylum — Chordata
- Class — Mammalia
- Order — Primata
- Family — Hominidae
- Genus — Homo
- Species — sapiens

The branching history of life





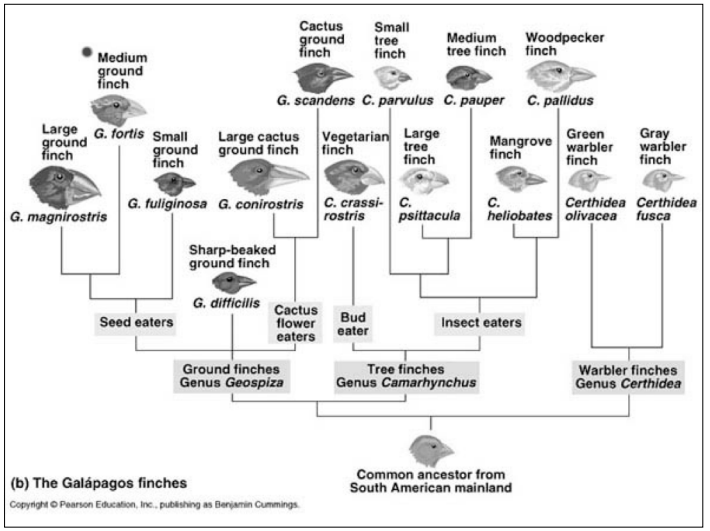
(a) Anagenesis (b) Cladogenesis

When combined: spatial subdivision, limited dispersal and migration, natural selection, and genetic drift are largely responsible for one of the most important processes in evolution

Speciation: the divergence of an ancestral species into two separate species lineages

Results over time from several factors, including:

- spatial subdivision
- limited dispersal and migration
- genetic drift
- natural selection



Adaptive radiation:

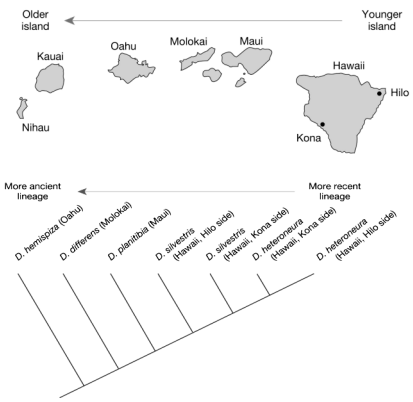
Species diversification resulting from multiple similar adaptations that allow new species to take advantage of new lifestyles

feeds on flower nectar

feeds on insects under bark

Galapagos Islands "Darwin's" Finches

Geographic Speciation of Hawaiian *Drosophila*

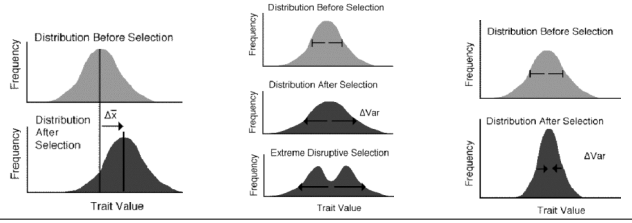


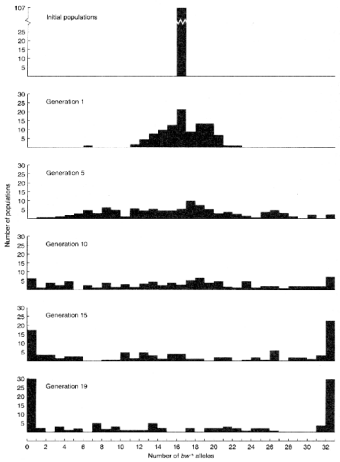
Speciation may be influenced by:

Directional Selection (left) occurs when selection favors one extreme trait value over the other extreme. This typically results in a change in the mean value of the trait under selection.

Disruptive Selection (center) occurs when selection favors the extreme trait values over the intermediate trait values. In this case the variance increases as the population is divided into two distinct groups. Disruptive selection plays an important role in speciation.

Stabilizing Selection (right) occurs when selection favors the intermediate trait value over the extreme values. Populations under this type of selection typically experience a decrease in the amount of genetic variation for the trait under selection.

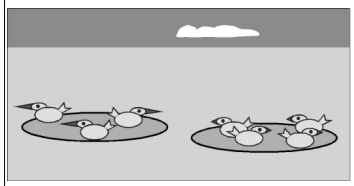




Drift causes differentiation of populations, and can also influence speciation

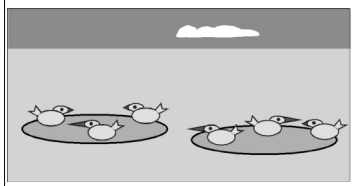
Stochastic (random) changes in allele frequencies happen independently in each population

The roles of migration and selection



m << *s*

- Selection much stronger than migration
- Populations different, reflecting pattern of selection



s << *m*

- Migration much stronger than selection
- Genetic differences will be erased by migration

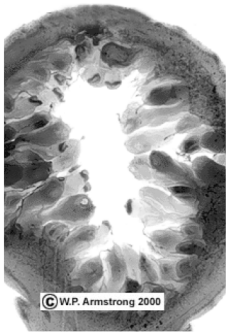
Sexual selection can influence speciation

Tungara frogs in Panama make two kinds of mating calls. Females strongly prefer calls that contain a "chuck" element

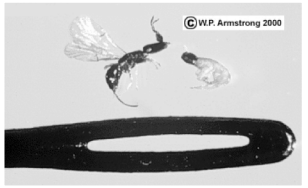
Whine

Whine + Chuck

Highly specialized relationships between species can be closely tied to the speciation histories of both

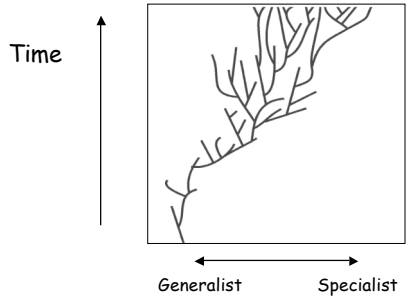


Cross section of a fig



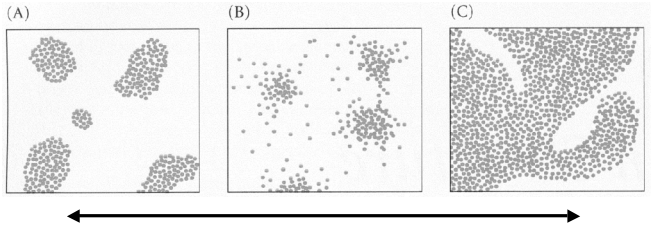
Female and male fig wasps

Species diversification often associated with increasing specialization (e.g. diet)



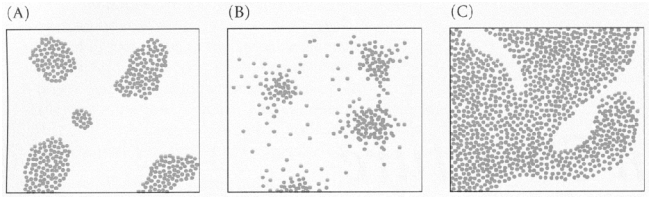
Diet

Degree of population subdivision can influence the speciation process



Continuum of population fragmentation

Population subdivision

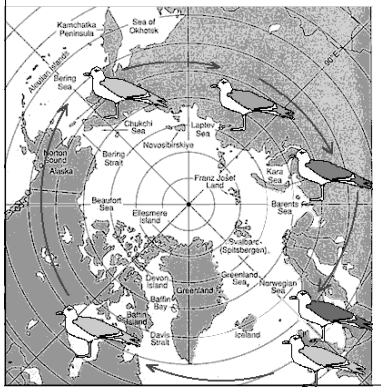


- Spatial subdivision and limited dispersal increase the effects of drift
- And decrease the effects of gene flow

Squirrels of the Grand Canyon

Herring Gulls and Lesser Black-Backed Gulls

Britain has both species, which do not interbreed but are the extreme ends of a circumpolar distribution of interbreeding gull types.



Herring gull, *Larus argentatus*

Lesser black-backed gull, *Larus fuscus*

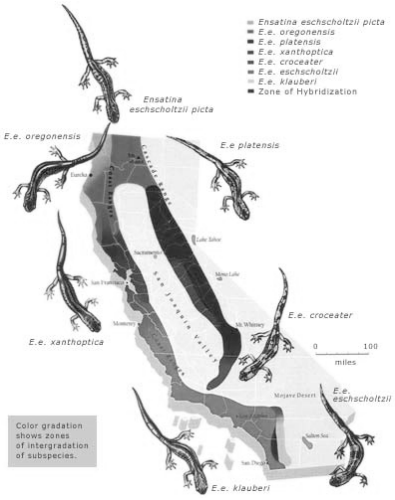
Ensatina Salamanders of California

The salamanders originated in the northern U.S., and gradually dispersed through California to the South

Populations spread along the sides of the San Joaquin Valley, but not in the valley

Salamanders can interbreed with those from populations to the north or the south...

But salamanders at the two ends of the "ring" cannot interbreed!



How species evolve from other species: the short answer

- Speciation is the outcome of isolation and divergence.
  - Isolation is created by reductions in gene flow.
  - Divergence is created when mutation, genetic drift, and selection act on populations separately.

Evolutionary biologists have a pretty good understanding of how speciation events occur…

A more frustrating problem can be defining the word "species" in biological terms

Etymology of the word "species": kind, or form

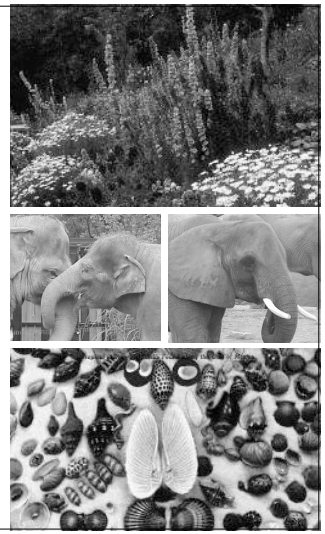
Chemistry uses the word too, to mean a specific type of atomic nucleus, atom, ion, or molecule.

What are species?

We know that natural variation exists among individuals of the same "kind"…

But clearly, there are different "kinds" of organisms in the world. We refer to them as species.

- How should we define "species"?
- How do humans recognize them?
- How do they recognize each other?
- How did they originate?



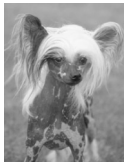
Phenetic or **Morphological** Species Concept:

"Species are the least inclusive groups of organisms that share (some arbitrary amount) of observable similarity".

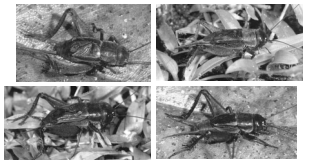
Zebra: *Equus burchelli*

Horse: *Equus caballus*

"Zebroid"*: Equus* ???



Dog: *Canis familiaris*

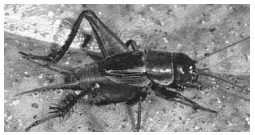


Four different species of *Gryllus* (crickets): *G. ovisopsis, G. rubens, G. firmus, G. fultoni*

Reproductive or **Biological** Species Concept:

"A species is a group of organisms that, for one reason or another, only produce viable and fertile offspring by mating amongst themselves."

Zebroid:
not usually fertile



Dogs and crickets: degree of phenotypic variation within the species does not matter.

Why, then, do "species" reproduce only amongst themselves?

Reproductive ***isolating mechanisms*** **:** barriers to gene flow

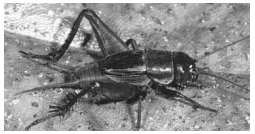
Reproductive Isolating Mechanisms : (barriers to gene flow)

- Geographic isolation : separation in **space**
- Temporal or seasonal isolation : separation in **time**
- Ecological isolation : separation by differences in **habitat**
- Mate choice : separation by differences in **mating signals**
- Mechanical isolation : mating not possible because **it just doesn't fit.**
- Gamete incompatibility : egg and sperm **do not recognize** each other
- Developmental isolation : embryo **fails to develop** to birth
- Inferior hybrids : offspring **nonviable**, **sterile**, or **selected against**

Reproductive or **Biological** Species Concept:

"A species is a group of organisms that, for one reason or another, only produce viable and fertile offspring by mating amongst themselves."

Zebroid: not fertile



Dogs and crickets: degree of phenotypic variation within the species does not matter.

What is wrong with the biological (reproductive) species concept?

- It does not account for asexually reproducing organisms
  - Bacteria, Archaea, and plenty of Eukaryotes
- Barriers in space and time prohibit some matings within a "species"
  - European and North American wolves (*Canis lupus*) are the same species
  - Is your cat the same species as one that has already died, or isn't born yet?
- Even within a biological species, reproductive barriers can exist!
  - "Ring species" (like California salamanders, or circumpolar gulls)
  - Distant individuals in a large continuous population

Evolutionary or Phylogenetic Species Concept

"A species is the smallest distinct lineage that evolves separately from other lineages, and whose members share a common ancestor"

A definition like this is objective, and doesn't depend on phenotypic similarities or interbreeding potential. However, it is nearly impossible to apply in the real world unless one has detailed historical information about the species : for example, fossils and/or a phylogeny.

Does it really have to be this complicated?

Table 23.1

Almost 150 years since Darwin published the *Origin*, and the field of biology still has no species concept that can be applied universally to all forms of life.

Maybe there isn't one.

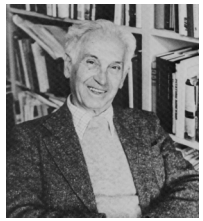
TABLE 23.1 A Summary of Species Concepts

Species Concept	Criterion for Recognizing Species	Advantages	Disadvantages
Biological	Reproductive isolation between populations (they don't breed and produce viable offspring)	Reproductive isolation = evolutionary independence	Not applicable to asexual or fossil species; difficult to assess if populations do not overlap geographically
Morphospecies	Populations are morphologically distinct	Widely applicable	Subjective (researchers often disagree about how much morphological distinction = speciation)
Phylogenetic	Smallest monophyletic group on evolutionary tree	Widely applicable; based on testable criteria	Few well-estimated phylogenies are currently available

Are species even real? Do they even exist?

How can it be that there are obviously different kinds of organisms in this world, but yet, biologists have never been able to agree on criteria (a species definition) that can define what a "kind" is? Is it possible that species are merely artificial constructs of the human, pattern-seeking mind?

Ernst Mayr's focus on species, both their nature and their origins, appears to have derived from his experiences in the South Pacific. When he went to New Guinea, there was a popular school of thinking known as the nominalist school of philosophy that held that species did not, in reality, exist. They were merely arbitrary categories, little more than names.

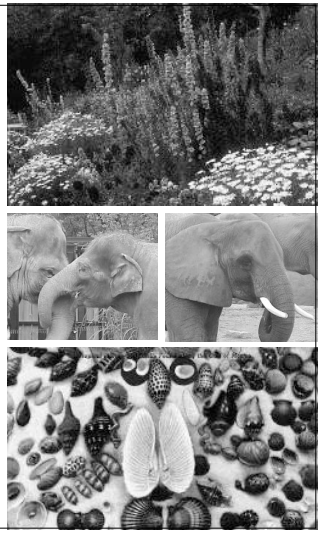


"But I discovered that the very same aggregations or groupings of individuals that the trained zoologist called separate species were called species by the New Guinea natives," Dr. Mayr said. "I collected 137 species of birds. The natives had 136 names for these birds - they confused only two of them. The coincidence of what Western scientists called species and what the natives called species was so total that I realized the species was a very real thing in nature."

Clearly, there are different "kinds" of organisms in the world.

So, what is a "kind" ?

A "snapshot" of a single evolutionary trajectory…

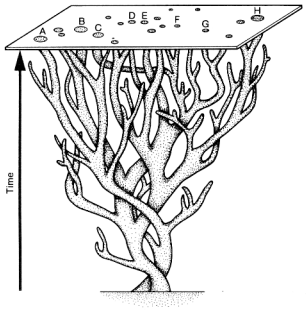


Dr. Jost's Favorite Species Concept
(similar to one known as the "Universal" Species Concept):

"Species are not static entities, but dynamic systems that exist through time. Because of shared history, species often (but not always) exhibit properties such as phenotypic similarity, genetic similarity, evolutionary independence, and reproductive isolation from other species. However, these phenomena are merely the products of a dynamic system, and not its defining or diagnostic properties."

(got all that?)

We can only experience species as "snapshots" in time



<u>Another way to think about it</u>:

"Species are the cross-sections of branches on the tree of life."

What would it look like if we could zoom in on the branches of a phylogenetic tree?

Reticulate genealogy

How does reticulate genealogy (within a species) become **divergent genealogy**?

or in other words,

How does speciation occur?