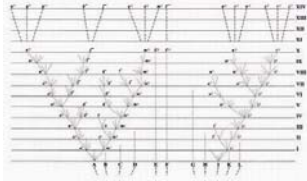




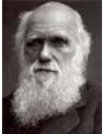
SPECIES AND SPECIATION

Two major categories of evolutionary change:

- Evolutionary change within lineages over time (anagenesis).
- Splitting of lineages over time (cladogenesis)



Darwin's only figure in
"The Origin of Species"
(1859)



MAJOR ISSUES IN SPECIATION THEORY

- **What is a species?**
- **How does speciation occur?**
 - The role of geographic isolation in divergence.
 - Do population bottlenecks facilitate changes in genetic architecture?
 - The role of natural selection in speciation.
 - Prezygotic vs. postzygotic reproductive isolation.
 - The genetic mechanisms responsible for reproductive isolation.

WHAT IS A SPECIES???

326 **Opinion** *TRENDS in Ecology & Evolution* Vol. 16 No. 7 July 2001

The mind of the species problem

Jody Hey

Box 1. Species concepts*

<ul style="list-style-type: none"> • Agamospecies Concept • Biological Species Concept* • Cladistic Species Concept • Cohesion Species Concept* • Composite Species Concept • Ecological Species Concept* • Evolutionary Significant Unit* • Evolutionary Species Concept* • Genealogical Concordance Concept • Genetic Species Concept* • Geographic Cluster Concept • Hennigian Species Concept* 	<ul style="list-style-type: none"> • Internodal Species Concept • Morphological Species Concept • Non-dimensional Species Concept • Phenetic Species Concept • Phylogenetic Species Concept (Diagnosable Version)* • Phylogenetic Species Concept (Monophyly Version) • Phylogenetic Species Concept (Diagnosable and Monophyly Version) • Polythetic Species Concept • Recognition Species Concept* 	<ul style="list-style-type: none"> • Reproductive Competition Concept* • Successional Species Concept • Taxonomic Species Concept <p><small>*References</small></p> <p style="margin-left: 20px;">• Mayr, R.L. (1960) A hierarchy of species concepts: the advancement to the rank of species problem. In: <i>Species and Evolution</i> (Ed. by Mayr, R.L.), pp. 361–424. Chapman & Hall.</p> <p><small>*Concepts that make reference to biological processes (e.g. reproduction and competition) that occur among organisms (for species) and/or between species and that contribute to a shared process of evolution within species.</small></p>
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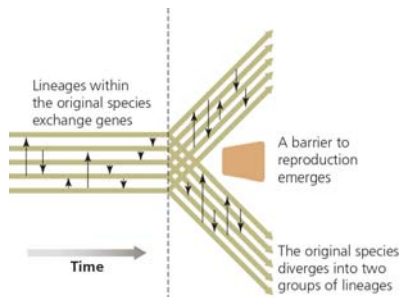
Certainly no clear line of demarcation has yet been drawn between species and sub-species – that is, the forms which...*come very near to, but do not quite arrive at, the rank of species*. ...A well-marked variety may therefore be called an *incipient species*. ...From these remarks it will be seen that I look at the term species as one arbitrarily given.

Darwin, *The Origin of Species*

SPECIATION

- The process by which one genetically-cohesive population splits into two or more reproductively-isolated populations.
- Requires the disruption of gene flow and the evolution of *reproductive isolating mechanisms* (RIMs).

Speciation involves barriers to reproduction



THE BIOLOGICAL SPECIES CONCEPT

“Species are groups of actually or potentially **interbreeding** populations that are reproductively isolated from other such groups.”

E. Mayr (1942)



PROBLEMS WITH THE BIOLOGICAL SPECIES CONCEPT

- Difficult to apply to fossils

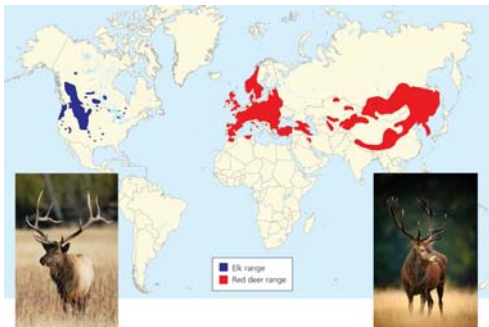


- Asexual organisms don't fit the criteria

THE DIFFICULTY OF RECOGNIZING SPECIES

- For **sympatric** species, it usually is clear -- If they do not interbreed, then they are good species.
- For **allopatric** populations, it is less clear -- It may be difficult to assess whether they are "potentially interbreeding".
- It may also be difficult to decide what constitutes reproductive isolation.
 - If individuals from different populations produce sterile hybrids, then they are certainly reproductively isolated.
 - What if they produce partially sterile hybrids?

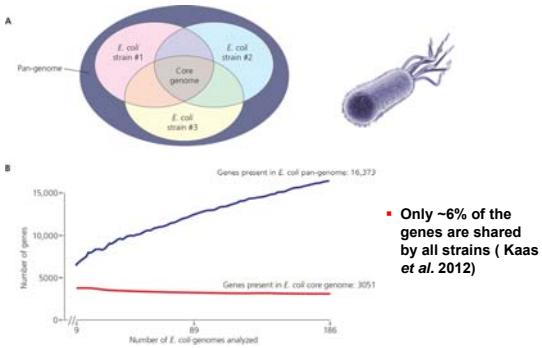
ELK AND RED DEER: TWO SPECIES?



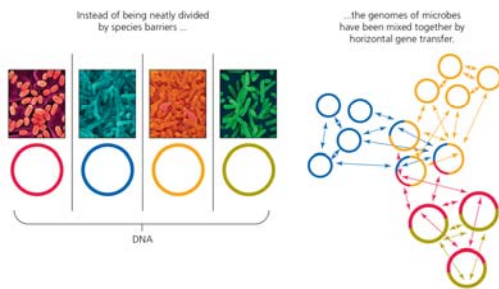
OTHER SPECIES CONCEPTS

- **PHYLOGENETIC SPECIES CONCEPT:**
smallest possible group descending from a common ancestor and diagnosable by unique, derived traits
 - The PSC can be applied to virtually any taxonomic group including microbes and can be used on fossils.
 - However, at low levels of divergence (tips of the tree) it can be decoupled from reproductive isolation

HORIZONTAL GENE TRANSFER IN *E. COLI*

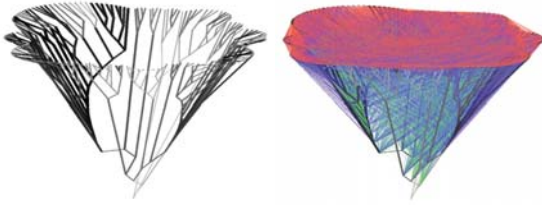


HORIZONTAL GENE TRANSFER MAKES CLASSIFICATION DIFFICULT



- From an operational standpoint microbial species are often determined by a 97% similarity cut-off. (Yikes!)

HORIZONTAL GENE TRANSFER IS COMMON IN MICROBIAL SYSTEMS



- How does this transfer of genetic material impact our views on common ancestry and phylogenetic relationships?



KEY FEATURES OF OPERATIONAL SPECIES CONCEPTS

- Reproductive cohesion within species.
- Reproductive isolation from other such groups.
- Recognition that species are dynamic evolutionary lineages, not static “types”.

U. S. ENDANGERED SPECIES ACT

- Legal Definition: Species includes: “any subspecies of fish or wildlife or plants, and any *distinct population segment* of any species of vertebrate fish or wildlife which interbreeds when mature.”
- Operational Definition: Evolutionary Significant Units (ESU):
“a population (or group of populations) that
 - 1) is reproductively isolated from other conspecific population units, and
 - 2) represents an important component in the evolutionary legacy of the species.”

OPERATIONAL SPECIES CONCEPTS PROVIDE A MEANS TO PROTECT:

- Individual populations
- Threatened portions of species ranges
- Ecologically distinct populations

Example: Separate runs of salmon



However, there are still problems...

What do we do with *Hybrid Taxa*?



Red Wolf

ENDANGERED SPECIES

Red wolves in the crosshairs

U.S. agency ponders future of innovative reintroduction as animal deaths and controversy mount



Red wolves reproduce in the wild only in North Carolina. The population is increased with pups born in captivity. A major threat to the population is hybridization with coyotes.

Wild predators and private property

Red wolf recovery area includes land held by owners opposed to reintroduction



28 SEPTEMBER 2014 • VOL. 343 ISSUE 6204

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HYBRID ZONES

- *Hybridization* refers to crosses between genetically differentiated forms.
- *Introgression* refers to the movement of genes between species (or between well-differentiated populations) mediated by backcrossing.
- Hybridization is common. Thousands of examples have been documented in animals, tens of thousands in plants.

CLOSELY RELATED SPECIES OFTEN EXHIBIT HYBRID ZONES WHEN THEY EXPERIENCE SECONDARY CONTACT

Corvus cornix



Corvus corone



Figure 16.8 Hybrid zone between the hooded crow (*Corvus corone*) and common crow (*C. cornix*) in Europe. From Mayr (1962).
