

- *Species* is a latin word meaning “kind” or “appearance”
- *Difficult to clearly define*

Species concepts

Species Concept	Description	Limitation	Benefit
Typological species concept	Classification is determined by the comparison of physical characteristics with a type specimen.	Alleles produce a wide variety of features within a species.	Descriptions of type specimens provide detailed records of the physical characteristics of many organisms.

Species concepts

Species Concept	Description	Limitation	Benefit
Typological species concept	Classification is determined by the comparison of physical characteristics with a type specimen.	Alleles produce a wide variety of features within a species.	Descriptions of type specimens provide detailed records of the physical characteristics of many organisms.
Biological species concept	Classification is determined by similar characteristics and the ability to interbreed and produce fertile offspring.	Some organisms, such as wolves and dogs that are different species, interbreed occasionally. It does not account for extinct species.	The working definition applies in most cases, so it is still used frequently.

Species concepts

Species Concept	Description	Limitation	Benefit
Typological species concept	Classification is determined by the comparison of physical characteristics with a type specimen.	Alleles produce a wide variety of features within a species.	Descriptions of type specimens provide detailed records of the physical characteristics of many organisms.
Biological species concept	Classification is determined by similar characteristics and the ability to interbreed and produce fertile offspring.	Some organisms, such as wolves and dogs that are different species, interbreed occasionally. It does not account for extinct species.	The working definition applies in most cases, so it is still used frequently.
Phylogenetic species concept	Classification is determined by evolutionary history.	Evolutionary histories are not known for all species.	Accounts for extinct species and considers molecular data.

Species concepts

Table 15.1 The biological species concept and some recently proposed alternatives (Futuyma 1997)

BIOLOGICAL SPECIES CONCEPT	A species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both). (Dobzhansky 1935)
	Species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups. (Mayr 1942)
EVOLUTIONARY SPECIES CONCEPT	A species is a single lineage (an ancestral-descendant sequence) of populations or organisms that maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. (Wiley 1978)
PHYLOGENETIC SPECIES CONCEPTS	A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent. (Cracraft 1989)
	A species is the smallest monophyletic group of common ancestry. (de Queiroz and Donoghue 1990)
RECOGNITION SPECIES CONCEPT	A species is the most inclusive population of individual biparental organisms that share a common fertilization system. (Paterson 1985)
COHESION SPECIES CONCEPT	A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. (Templeton 1989)
ECOLOGICAL SPECIES CONCEPT	A species is a lineage (or a closely related set of lineages) that occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range. (Van Valen 1976)
INTERNODAL SPECIES CONCEPT	Individual organisms are conspecific by virtue of their common membership in a part of the genealogical network between two permanent splitting events or between a permanent split and an extinction event. (Kornet 1993)

Source: Coyne (1994).

Species concepts

Box 1. Species concepts^a

- 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*
- Genotypic Cluster Concept
- Hennigian Species Concept*
- 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*
- Reproductive Competition Concept*
- Successional Species Concept
- Taxonomic Species Concept

Reference

a. Mayden, R.L. (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In *Species: the Units of Biodiversity* (Claridge, M.F. et al., eds), pp. 381–424, Chapman & Hall

*Concepts that make reference to biological processes (e.g. reproduction and competition) that occur among organisms within species (and less so between species) and that contribute to a shared process of evolution within species.

Morphological concept

Species concepts

Criterion for Recognizing Species

Populations are morphologically distinct

Advantages

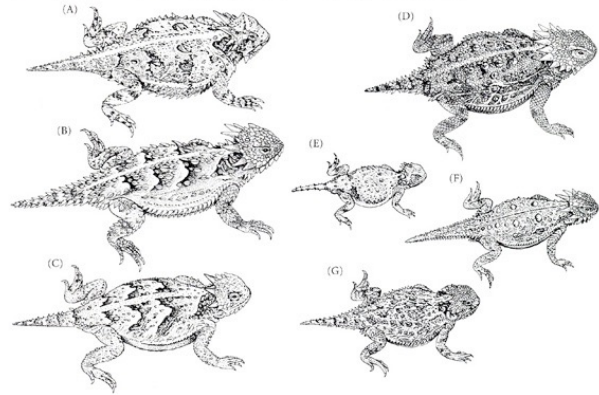
Widely applicable

Disadvantages

Subjective (researchers often disagree about how much morphological distinction = speciation)

Morphological species of horned lizards

FIGURE 15.19 An example of species distinguished by morphological characters. These seven species of horned lizards (*Phrynosoma*) from western North America can each be distinguished by several differences in the number, size, and arrangement of horns and scales, as well as body size and proportions, color pattern, and habitat. (A, *P. coronatum*; B, *P. coronatum*; C, *P. platyrhinos*; D, *P. solare*; E, *P. modestum*; F, *P. mcallii*; G, *P. douglasii*.) (After Stebbins 1954.)



from Futuyma (1998), p. 463

the familiar “taxonomic” description based on sets of distinguishing characteristics

often works but can be misleading



Different phenotypes within a single species



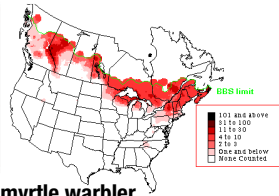
Hydrangea



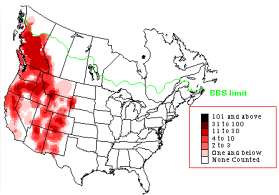
Theridion gallator

Species concepts

Different phenotypes within different species



Breeding range map of myrtle warbler (*Dendroica auduboni*)



Breeding range map of Audubon's warbler (*Dendroica coronata*)

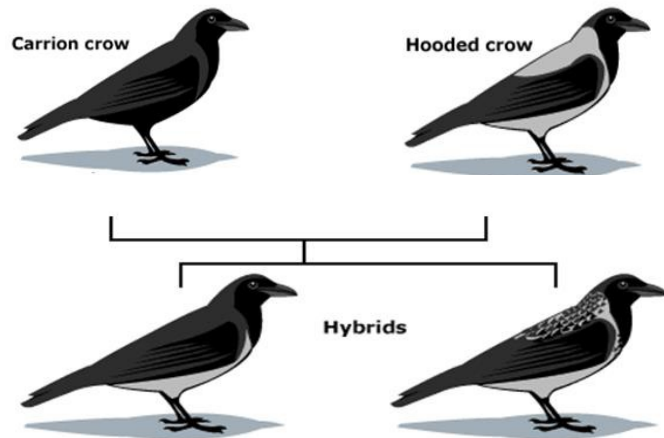
These allopatric warblers were previously classified as distinct species but they freely interbreed

Species concepts



Organisms may look different and yet be the same species

Species concepts



Should they be considered the same or separate species?

Species concepts

Different species with similar appearance

Eastern and Western Meadowlarks look identical but differ in their song

Sturnella magna

Sturnella neglecta



Different species with similar appearance



Cacti (Americas)

Euphorbia (Africa)

Some species look similar even when they are only very distantly related

=

CONVERGENT EVOLUTION



Cactaceae



Apocynaceae



Euphorbiaceae

“potentially interbreeding?”

Separate species?



Recognition Species Concept

A species is a set of organisms that can recognize each other as potential mates

Recognition species concept



Biological Species Concept (BSC)

E. Mayr

Species concepts

Criterion for Recognizing Species

Reproductive isolation between populations (they don't breed and produce viable offspring)

Advantages

Reproductive isolation = evolutionary independence

Disadvantages

Not applicable to asexual or fossil species; difficult to assess if populations do not overlap geographically

Species concepts

Biological Species Concept

- “Groups of actually or potentially interbreeding populations reproductively isolated from all other such groups.” – Ernst Mayr
- “When we understand the origin of reproductive isolation, we understand the origin of species.” – Jerry Coyne
- “... the largest and most inclusive Mendelian population ... A Mendelian population is a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool.” – Dobzhansky



Species concepts

The Biological Species Concept is the first *modern attempt* to define species, but numerous problems with this concept, on both theoretical and practical grounds

Species concepts

reproductive isolation:
an objective criterion
that is biologically
significant



Species concepts

Practical problems

- asexual species?
- allopatric species? (most borderline cases don't occur sympatrically)
- geological time?
- level of reproductive isolation?

Species concepts

Practical problems

- asexual species?
- allopatric species? (most borderline cases don't occur sympatrically)
- geological time?
- level of reproductive isolation?

Theoretical problems

reproductive compatibility is a primitive character;
reproductive isolation is derived
many cases, sister lineages are reproductively
isolated, but distantly related lineages are not

Species concepts

Practical problems

- asexual species?
- allopatric species? (most borderline cases don't occur sympatrically)
- geological time?
- level of reproductive isolation?

Theoretical problems

reproductive compatibility is a primitive character;
reproductive isolation is derived
many cases, sister lineages are reproductively
isolated, but distantly related lineages are not

The BSC doesn't apply to allopatric species, parthenogenetic species, or fossil species; highly limited (long held by ornithologists)

ALTERNATIVES

THE BIOLOGICAL SPECIES CONCEPT DOESN'T ALWAYS WORK

The biological species concept is remarkably useful when describing most plants and animals, but it doesn't work for distinguishing all life forms.

1 CLASSIFYING ASEQUAL SPECIES
Asexual reproduction does not involve interbreeding, so the concept of reproductive isolation is no longer meaningful.



2 CLASSIFYING FOSSIL SPECIES
Differences in size and shape of fossil bones cannot reveal whether there was reproductive isolation between the individuals from whom the bones came.



3 DETERMINING WHEN ONE SPECIES HAS CHANGED INTO ANOTHER
There is rarely a definitive moment marking the transition from one species to another.



4 CLASSIFYING RING SPECIES
Two non-interbreeding populations may be connected to each other by gene flow through another population, so there is no exact point where one species stops and the other begins.



5 CLASSIFYING HYBRIDIZING SPECIES
Hybridization—the interbreeding of closely related species—sometimes occurs and produces fertile offspring, suggesting that the borders between the species are not clear cut.



Evolutionary Species Concept (ESC)

Criterion for Recognizing Species

A species is a single lineage of organisms that maintains its identity from other such lineages and has its own evolutionary tendencies and historical fate (Wiley 1978)

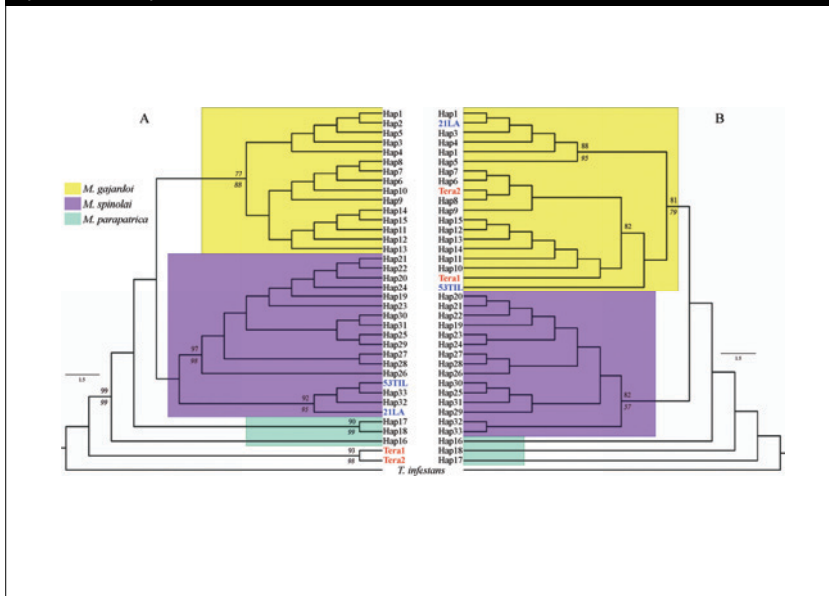
Advantages

Focus on evolutionary history, as opposed to recognition of current species, so this concept is used extensively in the fossil record

Disadvantages

Does not account for genomic hybrids, where genes have passed from one taxon to another, and the genetic make-up of individuals can be traced to different phylogenies or genealogies

Species concepts



Species concepts

Evolutionary Species Concept

- “An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies” (Simpson 1961:153).
- “A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley 1978:18).

Species concepts

- All organisms, past and present, belong to some evolutionary species
- Species must be isolated from each other to the extent that this is required to maintain their separate identities, tendencies, and fate.
- Therefore, reproductive isolation in the BSC sense is not required
- Moreover, Evolutionary species may or may not exhibit recognizable phenetic differences (# of species may be over or under-estimated, usually the latter)
- No separate, single evolutionary lineage may be subdivided into a series of ancestral and descendent species

Species concepts

ESC:benefits and Problems

- **Benefits:** clear conceptually; applies to asexual species, through time, and allopatric species
- **Problems:**
 - application (difficult to know the future),
 - asexual species (too many independent lineages)
- The Evolutionary Species Concept separates the idea of what species are from how they are recognized.
- This leads us to: **How are species recognized?**

Phylogenetic Species Concept

Species concepts

Criterion for Recognizing Species

Smallest monophyletic group on evolutionary tree

Advantages

Widely applicable; based on testable criteria

Disadvantages

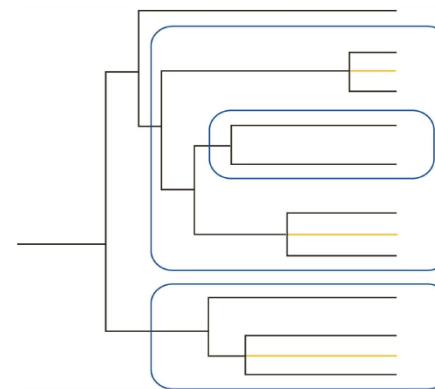
Few well-estimated phylogenies are currently available

Species concepts

- "... a population or group of populations defined by one or more apomorphous [derived] features" (Rosen 1979:277).
- "... monophyletic groups of organisms, recognized as lineages on the ... basis of ... shared, derived characters and ranked as species because of causal factors ... that maintain the lineages as the smallest important monophyletic group recognized in a formal classification" (Mishler 1985:213).

Species concepts

The phylogenetic species concept: species are monophyletic groups

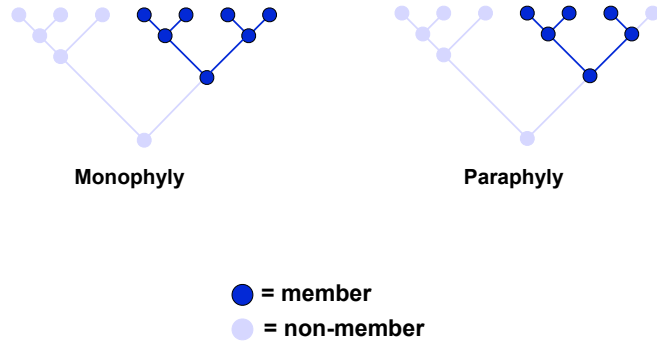


Species are defined as the smallest diagnosable monophyletic group

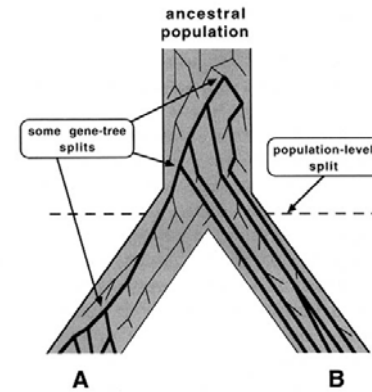
Any population that forms an independent branch on the phylogeny is recognized as a species

To be recognized as a species, populations must have been evolutionarily independent for a long enough time for diagnostic traits to emerge

Species concepts

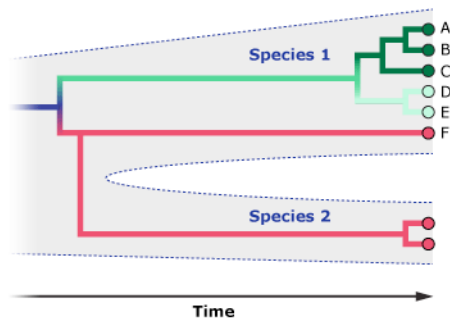


Species concepts



Fundamental distinction between a gene tree and a population tree or species tree. Note that branching events in a gene tree leading to extant individuals can either postdate (A) or predate (B) a population-level split.

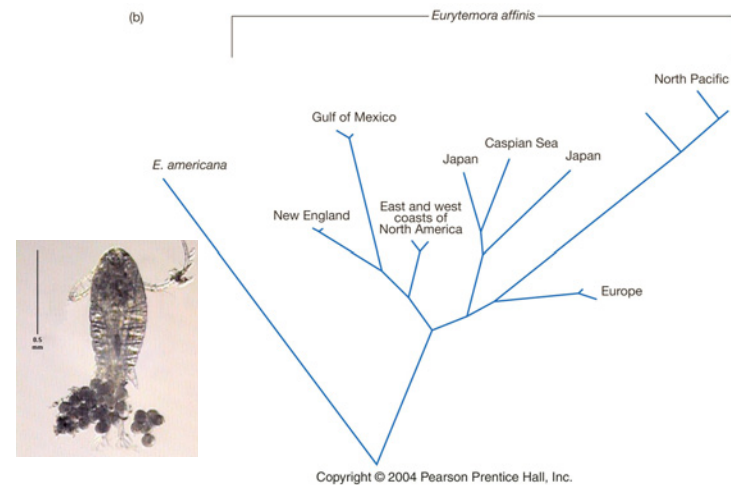
Species concepts



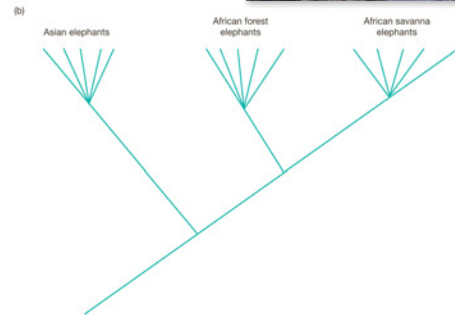
Gene version F in species 1 is more related to gene versions present in species 2 than to the other versions in species 1.

Species concepts

Application of the phylogenetic concept helped uncover cryptic species in the copepod *Eurytemora affinis*



And in African elephants



Copyright © 2004 Pearson Prentice Hall, Inc.

Common Element (General Concept of Species)

Species = segments of separately evolving metapopulation lineages

Definition of a Lineage

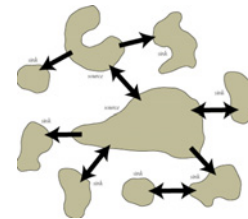
A lineage is a single, unbroken line of direct ancestry and descent.

... **A** → **B** → **C** → **D** ...

Examples of biological entities that form lineages:
genes, organelles, cells, organisms, colonies, demes, species.

Common Element (General Concept of Species)

Species = segments of separately evolving metapopulation lineages



A set of connected subpopulations
The population level is a continuum:
family group ↔ deme ↔ ... ↔ metapopulation

Ecological concept

Leigh Van Valen

Species concepts

Criterion for Recognizing Species

A species is a group of organisms that occupy the same ecological niche (Van Valen 1976).

Advantages

The ecological species concept captures the essence of the phenotype as an expression of genetics and environment

Disadvantages

Difficult to recognize, because many organisms occupy different niches due to adaptation or developmental changes

Species concepts

Summary

- Most biologists have the *same general* concept of species.
- Different species definitions are based on different properties of lineages.
- To achieve a unified concept of species, these properties should not be treated as necessary properties of species but as *lines of evidence* that enable biologists to determine whether organisms are parts of the same or different lineages (species).

Species concepts

Defining species is still complicated

Must revert to Linnaeus' system for:

- **extinct organisms**
- **asexual organisms**
- **some distinct species that can still interbreed and produce viable offspring (e.g., coyotes, wolves, and dogs)**

“Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a **barrier** of some sort.”

David Starr Jordan (1905)
Science 22: 545-562.



The mind of the species problem

