SPECIES AS A UNIT OF EVOLUTION

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“a species is what a professional taxonomist says it is”

Species are vehicle of all macroevolution or keystone of evolution (Mayr, 1963)

"... I was much struck how entirely vague and arbitrary is the distinction between species and varieties" *Darwin,*1859

"The species problem is the long-standing failure of biologists to agree on how we should identify species and how we should define the word 'species'." *Hey,* 2001

- The first and basic task of a taxonomist is to sort the bewildering diversity of individuals found in nature into species.
- It is impossible to construct a classification until the several species that are to be ordered are correctly discriminated.

- Species = Latin word, meaning “kind” or “appearance”
- Linnaeus described species in terms of their morphology
- Modern taxonomists also consider genetic makeup and functional and behavioural differences when describing species

• History of defining the term “species”

- “No matter what variations occur in the individuals or the species, if they spring from the seed of one and the same plant, they are accidental variations and not such as distinguish a species permanently; one species never springs from the seed of another nor vice versa” John Ray, 1686, *Historia Plantarum*

- Natural system Linnaeus, 1753, *Species Plantarum*

- “a species is a collection of all the individuals which resemble each other more than they resemble anything else, which can by natural fecundation produce fertile individuals, and which reproduce themselves by generation, in such a manner that we may from analogy suppose them all to have sprung from one single individual” De Candole,1813, *Théorie Élémentaire de la Botanique*

- Species are the fundamental units of evolution Charles Darwin (1809–1882) *On the origin of species by means of natural selection*

The species is commonly identified as the basic unit of Linnaean hierarchy

- ‘ The species is the sum total of individuals that are united by common descent’- **vonBaer 1882**

- ‘ Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups ’ – **Mayr 1942**

  A Biological species is an inclusive Mendelian population, it is integrated by the bonds of sexual reproduction and parentage’ – **Dobzhansky 1970**

- ‘ A group of populations possessing inherited differences that prevent gene exchange with other such groups ’- **Burton 1989**

- ‘ A species is a group of interbreeding natural populations that is reproductively isolated from other such group’ – **Mayr and Ashlock 1991**

Species Concepts

1. **The Typological Species Concept** (TSC, Linnaeus) (Essentialist Species Concept)

It is based on collecting and describing a “type” specimen for a given species. Type species are groups of individuals that are morphologically similar and clearly distinguishable from individuals of other groups.

A species is a set of organisms that resemble one another and is distinct from other sets.

Species had traditionally been defined by reference to a morphological type. Usually any geographic variation among members of the group was not detected or simply ignored.

The degree of morphological difference is the main criterion of species status in this concept.

There are 4 postulates :

- species consist of similar individuals sharing the same essence
- each species is separated from all others by a sharp difference
- each species is completely constant through time
- there are strict limits to the possible variation within any one species

Cain (1954,58) termed it as ‘morphospecies’ i.e. species created by morphological similarities or dissimilarities.
The morphospecies possesses the following characters –

- It is based on morphological characters only
- It is an unchangeable entity
- It is monotypic
- It is the lowest unit of classification

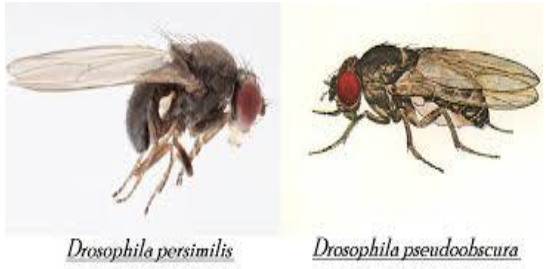
This concept was universally rejected for two reasons :

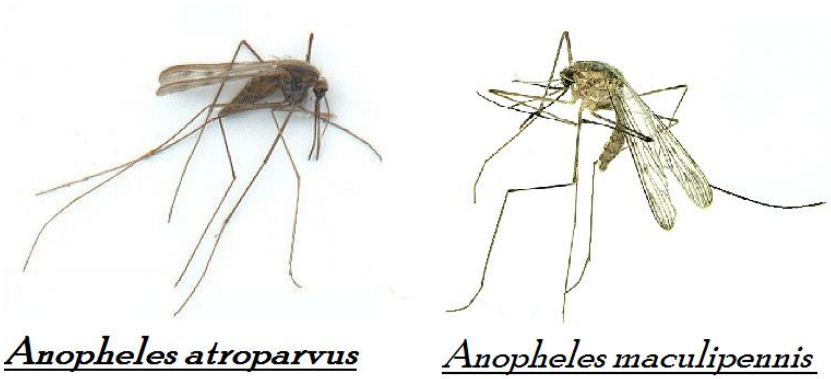
- Individuals are frequently found in nature that are clearly conspecific with other individuals in spite of their differences due to age, polymorphism and other forms of variation.

- There are species in nature – sibling species – which differ hardly at all morphologically yet are good biological species. In other words, sibling species do not show any morphological differences yet they do not breed among themselves.

SIBLING SPECIES

(i) morphologically similar, though differ genetically.
(ii) evolve more or less separately
(iii) little or no hybridisation/gene flow:





Drosophila pseudoobscura vs. *D. persimilis*: chromosomes

Anopheles mosquitoes: habitat, biting etc

2. The Nominalistic Species concept (NSC, Occam)

Nominalists deny the existence of ‘real’ universals, for them only individuals exist while species are abstractions created by people ; popular in France, 18th century (Buffon and Lamarck in their early writings) and has adherents to the present day (Mayr)

Bessey (1908) expressed :

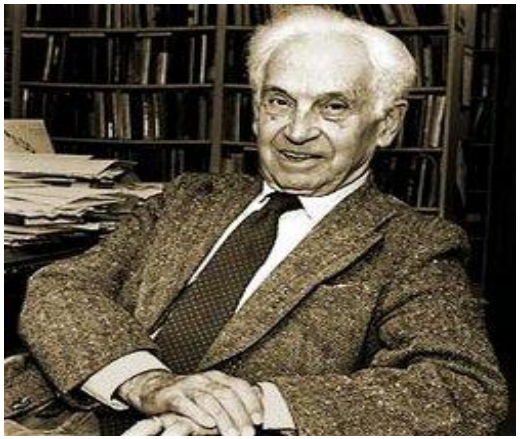
“Nature produces individuals and nothing more….species have no actual existence in nature. They are mental concepts and nothing more…species have been invented in order that we may refer to great numbers of individuals collectively.”

Remarks : Species of animals are not human constructs, nor are they types in the sense of Plato ; rather they are entities for which there is no equivalent in the realm of inanimate objects.

3.The Biological Species Concept (BSC, Dobzhansky, Mayr)

Dobzhansky (1937): species are the largest and most inclusive reproductive community of sexual and
cross-fertilizing individuals that share a common gene pool.

Mayr (1940): species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups.



- There are 3 postulates –
- Species is a genetic unit, consisting of a large, intercommunicating gene pool whereas the individual organism is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time.
- Species is an ecological unit which interacts with other species with which it shares its environment.
- Members of a species form a reproductive community where each member can identify and seek another member as a potential mate.

- Biological meaning of a species : It is a protected gene pool.

Mayr divided the BSC into the “**nondimensional**” and the “**multidimensional**” species concept:

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Nondimensional
species concept

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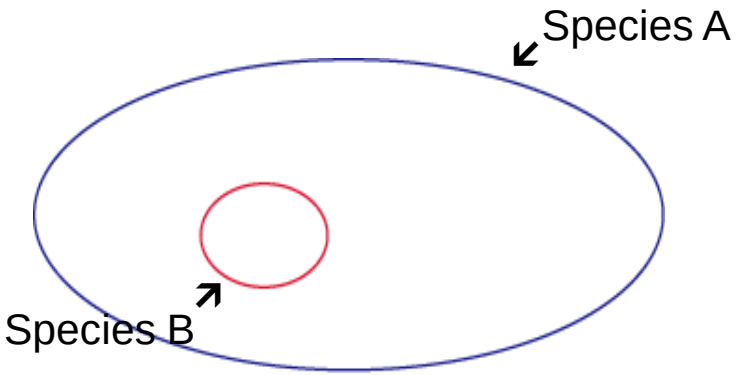
Nondimensional species concept



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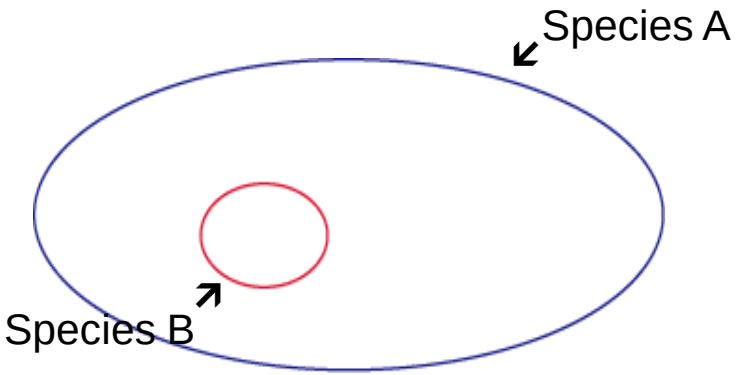
Nondimensional species concept



species **sympatric** and **synchronous**

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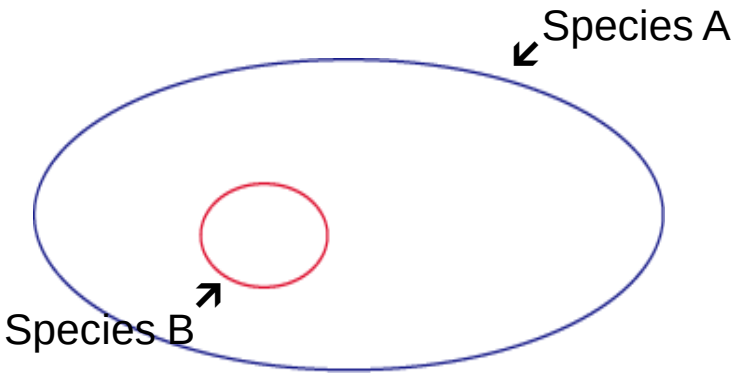

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Multidimensional species concept

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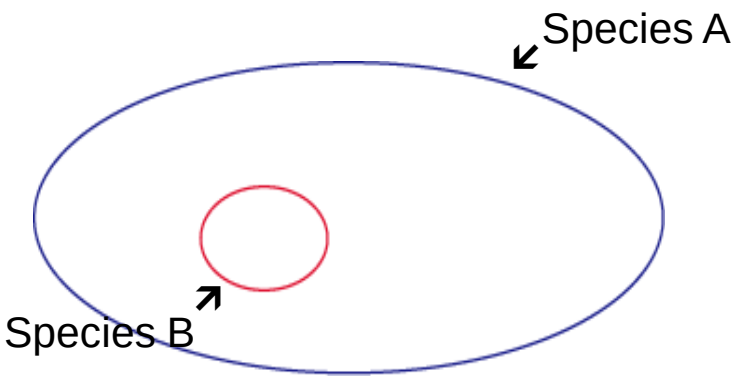

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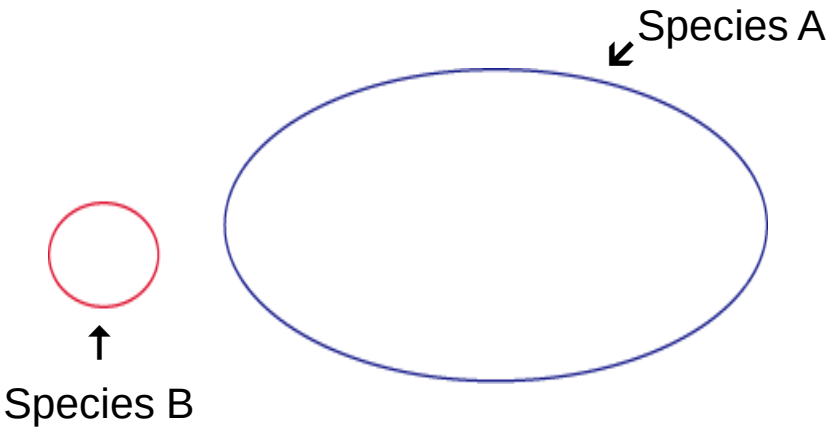
Multidimensional species concept



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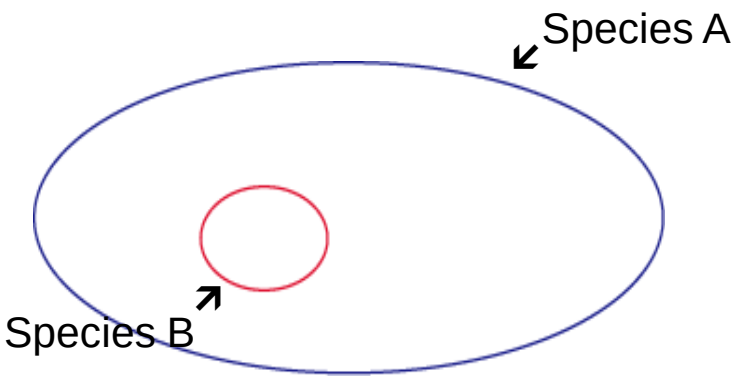
Nondimensional species concept



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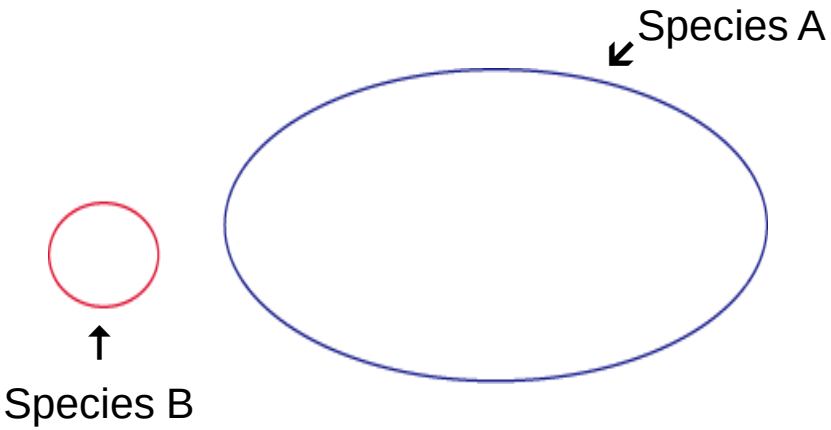


species are **allopatric** and/or **allochronous**

Types of reproductive isolation

- **A) *Pre-mating isolation* {**or ***pre-zygotic isolation*}**

  a) Ecological/seasonal isolation - mates do not meet
  b) Behavioural isolation - meet but do not attempt mating
  c) Mechanical isolation - attempts at mating do not work!

- **B) *Post-mating* {**or ***post-zygotic*} *isolation***

  d) Gametic incompatibility - gametes die before fertilization (*note:* post-mating *but* pre-zygotic)
  e) Hybrid inviability – hybrid zygotes have reduced fitness:
     - genomic factors
     - hybrids are not suited ecologically
     - reduced mating propensity of hybrids
  f) Hybrid sterility (even though may survive and mate as normal).
  g) Hybrid breakdown (Sexual selection against hybrids - disfavoured during mating.

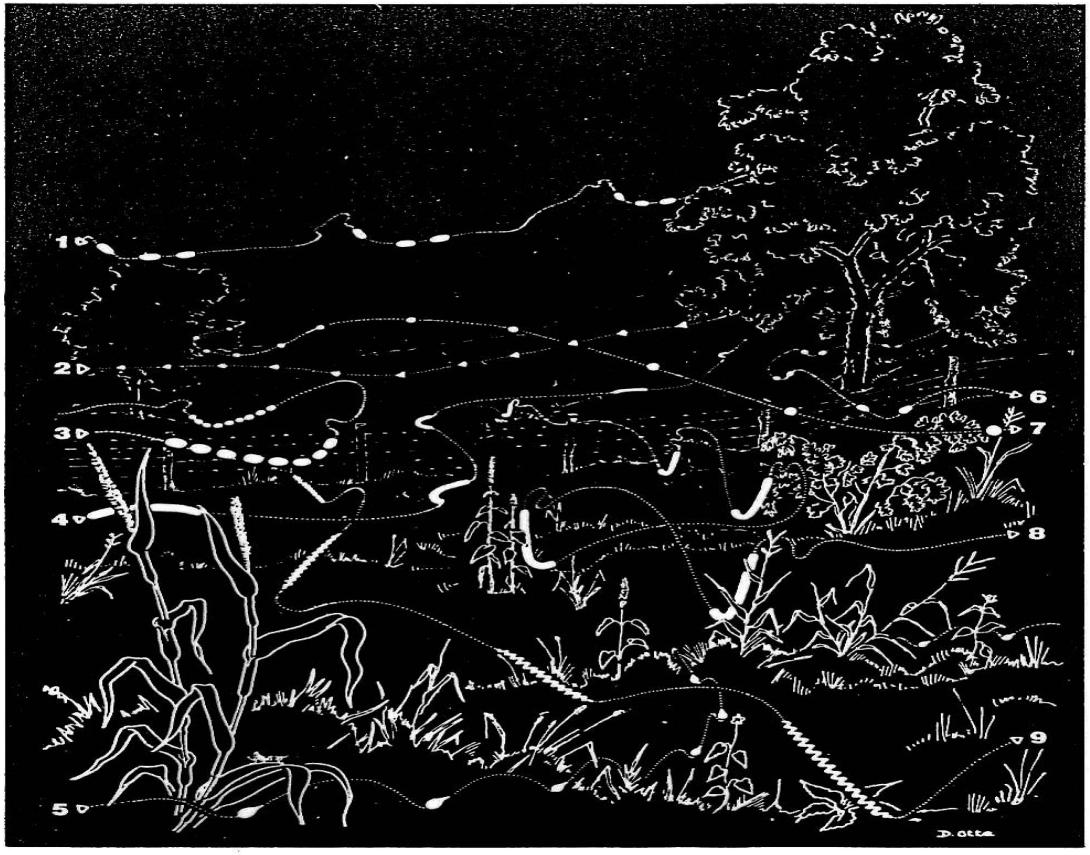
Pre-zygotic barriers

Habitat isolation:

- Two species living in different habitats may not encounter each other:
  - Two species of garter snake (*Thamnophis*) occur in the same area but one species lives in water and the other is terrestrial
  - Since they live in separate habitats, the two seldom come into contact as they are ecologically isolated

Behavioural isolation:

- Species-specific signals and elaborate behaviour to attract mates e.g different flashing patterns in fireflies in North America



Many animals recognise mates by sensing pheromones:
Female Gypsy moths emit a volatile compound to which olfactory organs of male gypsy moths are specifically tuned. Males of other moth species do not recognise this chemical as a sexual attractant

Western and Eastern meadowlarks only recognise songs of the same species

Sturnella neglecta

Sturnella magna

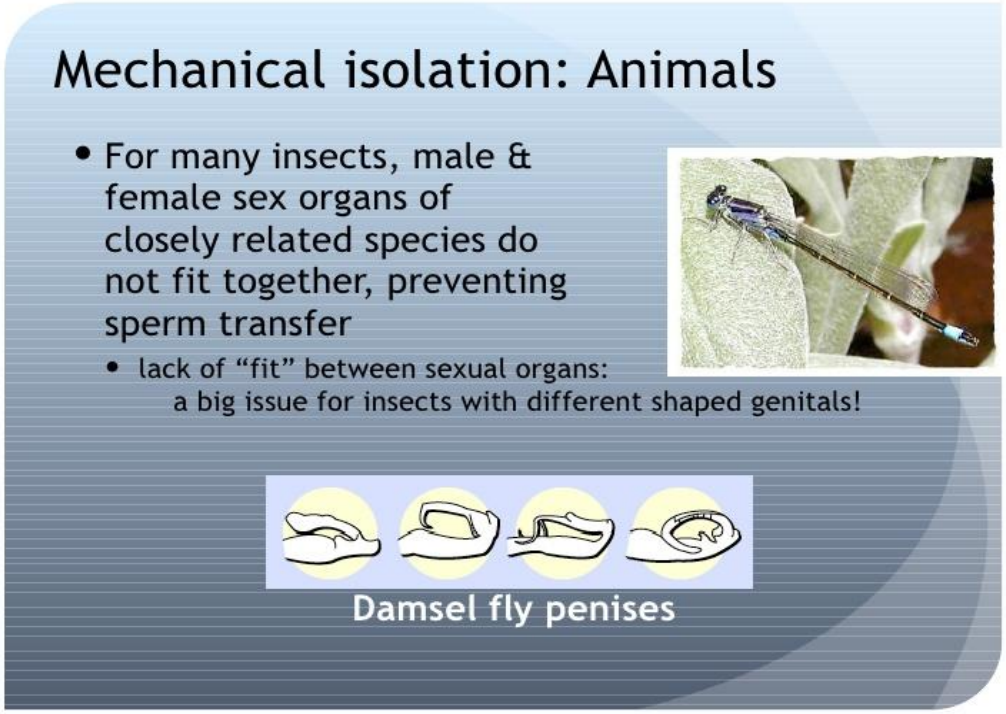
- Temporal isolation:
  - Two species that breed at different times of the day, seasons or years cannot mix gametes
  - Brown trout breed in the autumn whereas rainbow trout living in the same streams breed in the spring

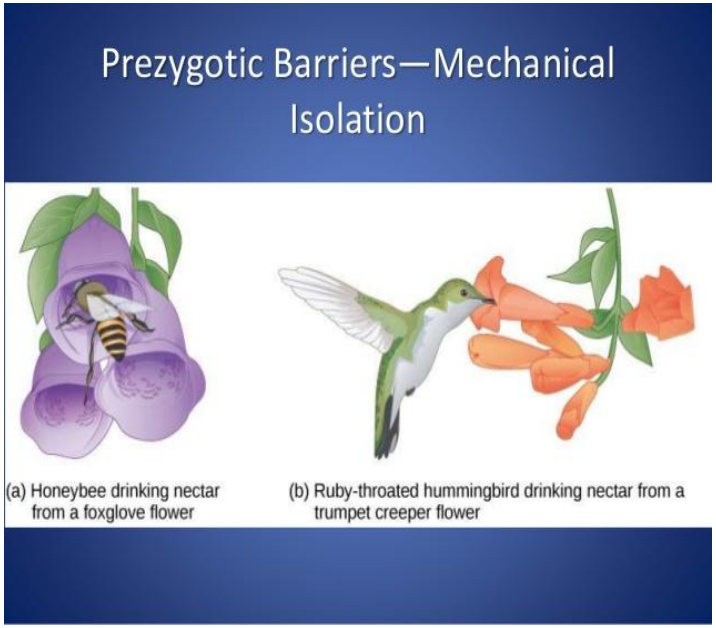
Temporal Isolation

Rainbow Trout

Brown Trout

- Mechanical isolation:
  - Anatomical incompatibility may prevent sperm transfer
  - Clasping appendages in dragonflies
  - Floral anatomy corresponding to specific pollinator





- Gametic isolation:
  - Sperm of one species may not survive internal environment of female reproductive tract in another species
  - Lack of gamete recognition in external-fertilising species

Red sea urchin

Purple sea urchin

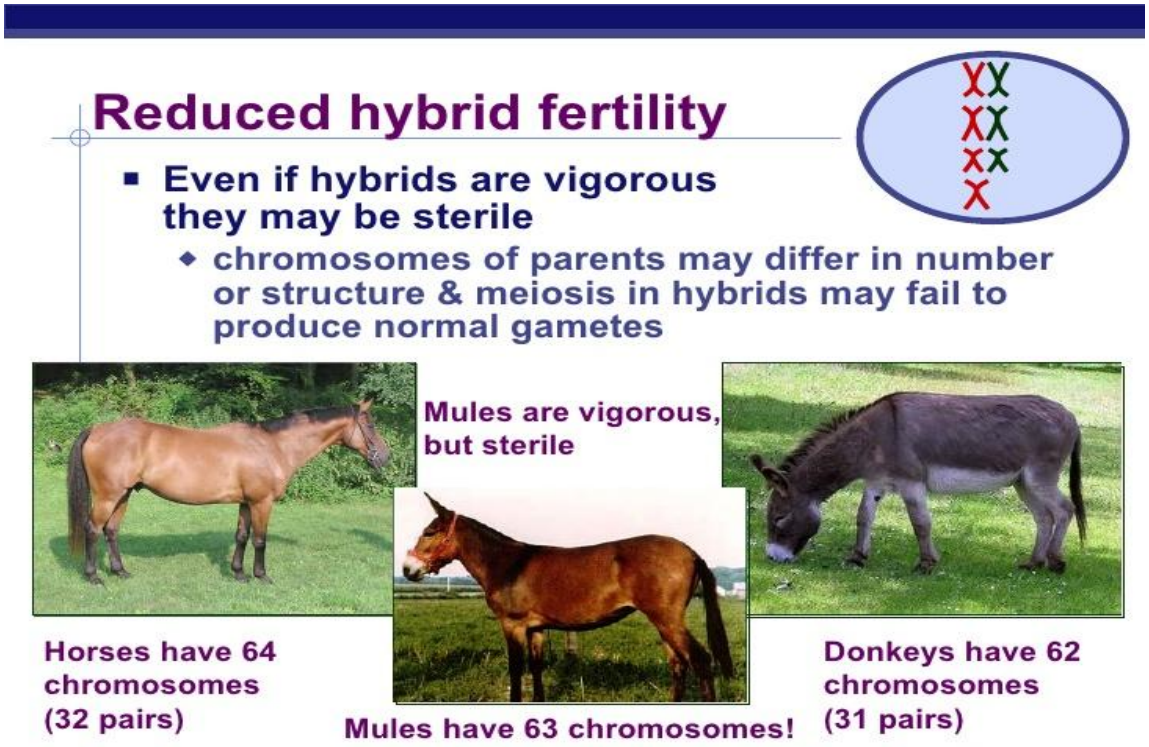
Post-zygotic barriers

- Reduced hybrid viability:
  - Genetic incompatibility may abort development at embryonic stage
  - Several species of the frog *Rana* live in the same habitats but hybrids do not complete development

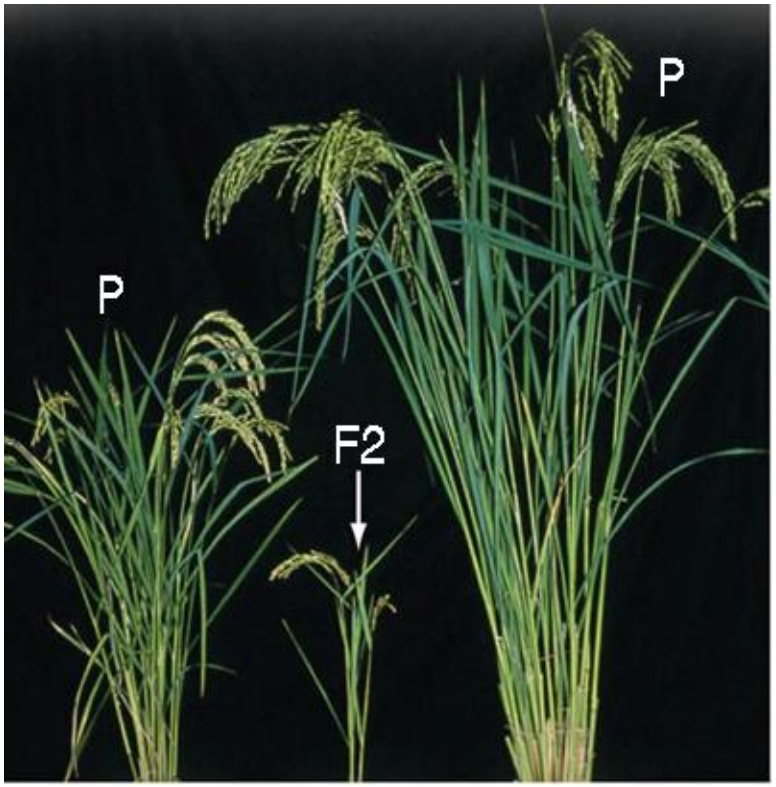
Figure 14.5a

- Reduced hybrid fertility:

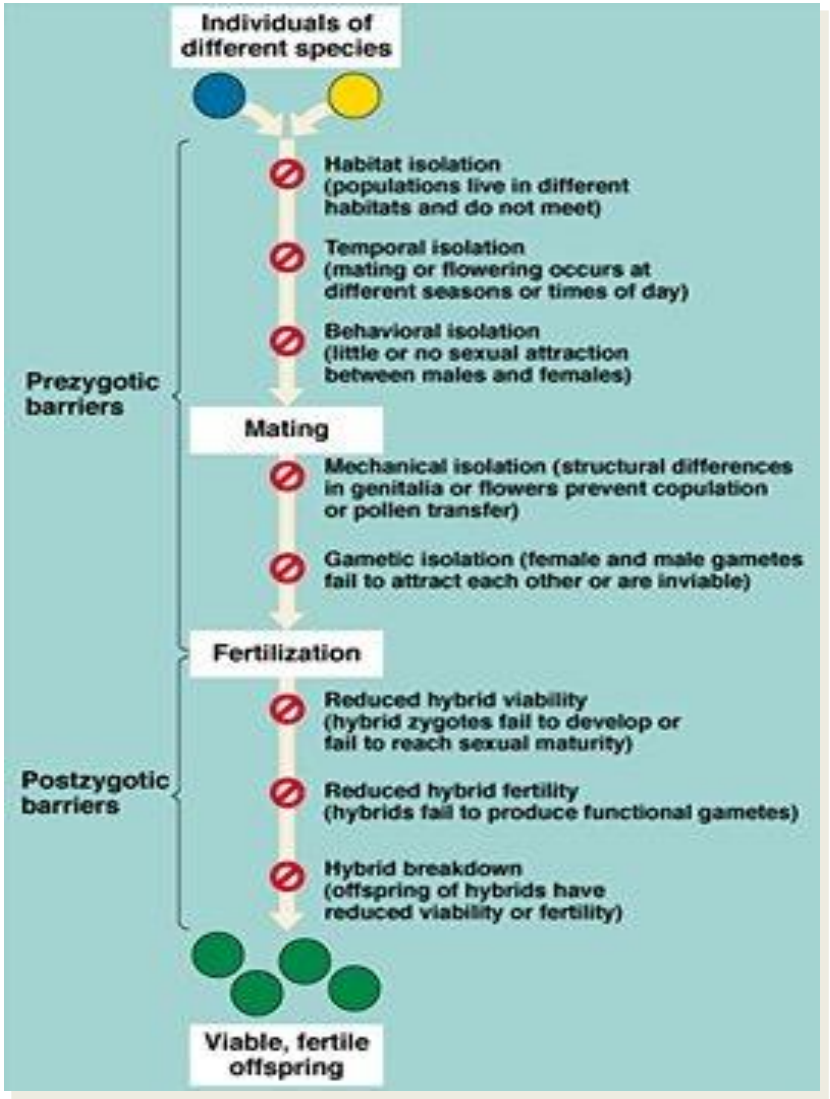
  Species mate and hybrid is viable but sterile e.g.mule
  If chromosome numbers are different, meiosis cannot produce normal gametes



- Hybrid breakdown:
  - First generation hybrids are fertile and viable but subsequent generations are weak and sterile.



Reproductive barriers – at a glance



The biological species concept is not always applicable

- Uniparental reproduction -The biological species concept cannot be applied to organisms that are completely asexual e.g. some protists and fungi, some plants (bananas), many bacteria:
  - Asexual reproduction effectively produces a series of clones
  - Asexual organisms can only be assigned to species by grouping clones with the same morphology / biochemistry
- Lack of information - Cannot be applied to extinct organisms represented only by fossils (obviously): must be classified morphologically

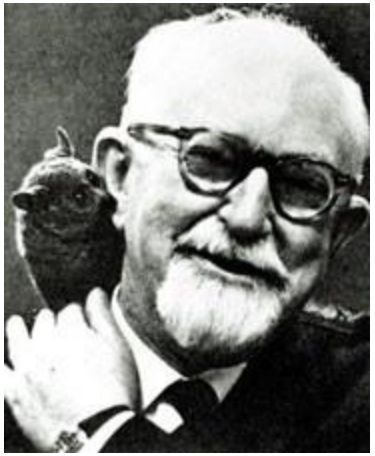
- Evolutionary intermediacy
  - Species that freely hybridize (open mating systems) with one or more other species yet maintain their evolutionary identity as species also provide a serious challenge to the validity of the biological species concept. Freely hybridizing species are known from plants, insects, and vertebrates (Templeton, 1989).
  - Acquisition of reproductive isolation without morphological differentiation
  - Acquisition of morphological differentiation without reproductive isolation

A “liger”

Hercules, the liger

A “tigon”

4. The Evolutionary Species Concept (ESC, Simpson, 1951)



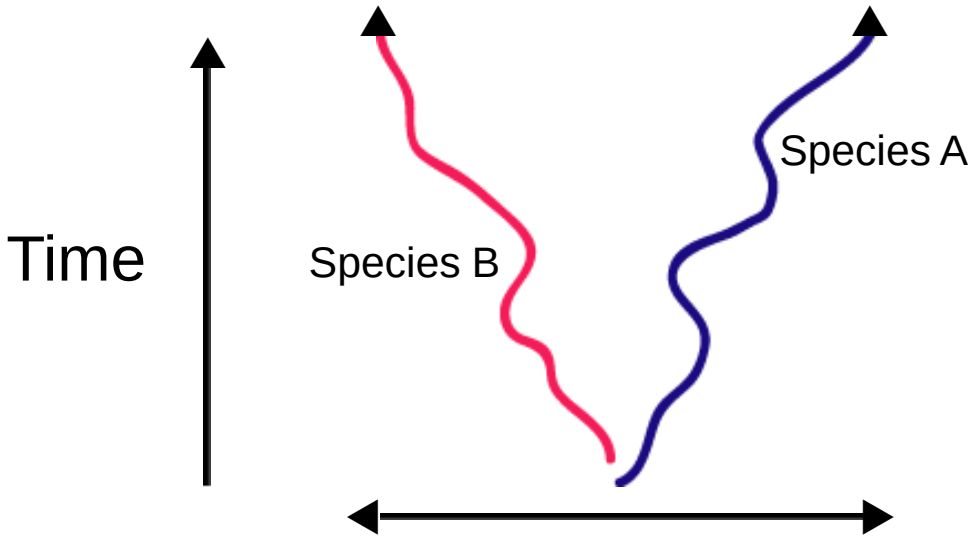
An evolutionary species is a lineage evolving separately from others with its own unitary evolutionary role and tendencies (Simpson)

A species is a single lineage of ancestor-descendant populations of organisms that maintains its identity from other such lineages (in space and time) and has its own evolutionary tendencies and historical fate (Wiley 1978)

Drawbacks :

1. Arbitrary

2. Does not provide a mechanism

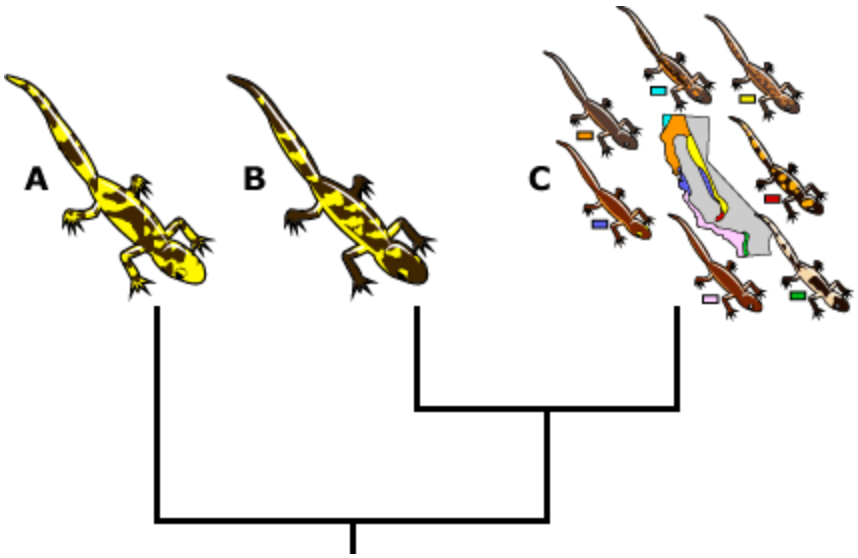


5. The Phylogenetic Species Concept (PSC, Cracraft, 1983)

Definition: the smallest diagnosable monophyletic group of populations within which there is a parental pattern of ancestry and descent.

A species is a "tip" on a phylogeny, that is, the smallest set of organisms that share an ancestor and can be distinguished from other such sets. Under this definition, a ring species is a single species that encompasses a lot of phenotypic variation.

Phylogenetic species



In this example, *Ensatina* salamander lineages A and B are separate species. Each has a common ancestor that individuals of other species do not. Even though it has diversified a lot, Lineage C is a single species, according to the phylogenetic species concept. None of the subspecies of Lineage C has a single common ancestor separate from the other subspecies.

6. The Recognition Species Concept

According to Patterson (1993), species have a specific mate recognition system (SMRS)
Species can be defined as a set of organisms with a common method of recognizing mates

7. The Cohesion Species Concept (Templeton, 1994)

A species is an evolutionary lineage that serves as the arena of action of basic micro evolutionary forces, such as gene flow (when applicable), genetic drift and natural selection

8. The Phenetic Species Concept (Ridley 1993)

A species is a set of organisms that look similar to each other and distinct from other sets.

9. The Ecological Species Concept

A species is a lineage that occupies a niche minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976).

A species is a number of related populations the members of which compete more with their own kind than with members of other species (Colinvaux 1986).

The **ecological species concept** defines a species as a set of organisms exploiting a single niche (adaptive zone)
The ESC supposes that ecological niches in nature occupy discrete zones, with gaps between them

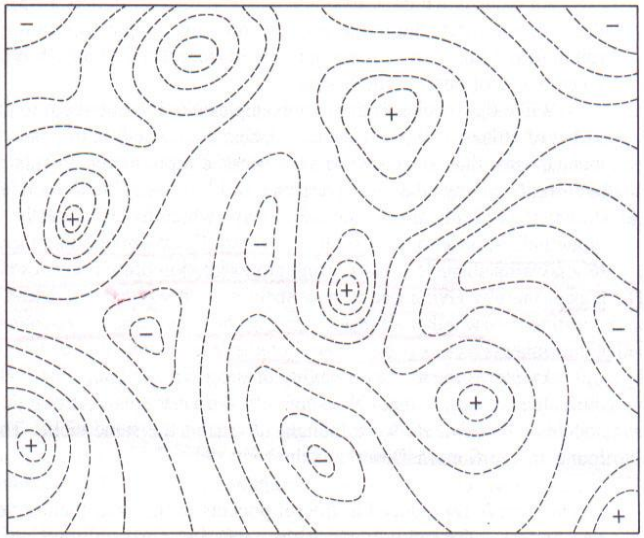
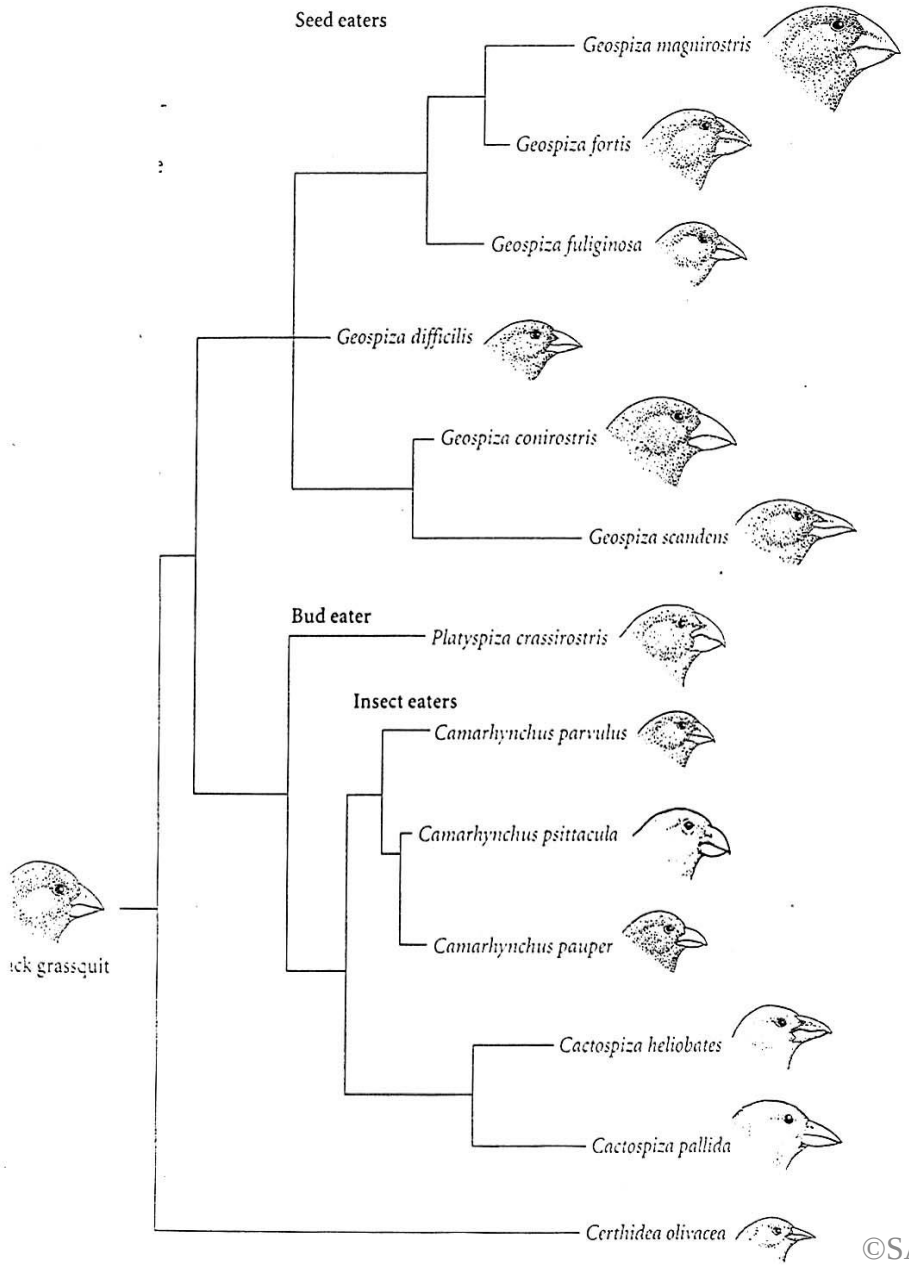


Figure 10.1 Adaptive field: *a* hypothetical two-dimensional representation of the relative fitnesses of various genotypes as determined by the environment. Peaks represent well-adapted genotypes and valleys represent poorly adapted ones. Contours depict genotypes of equal fitness. Note that peaks are not all of equal height. [From S. Wright. "The roles of mutation, inbreeding, crossbreeding, and selection in evolution," *Proceedings of the 11th International Congress of Genetics* 1:356–366 (1932).]

Darwin's finches



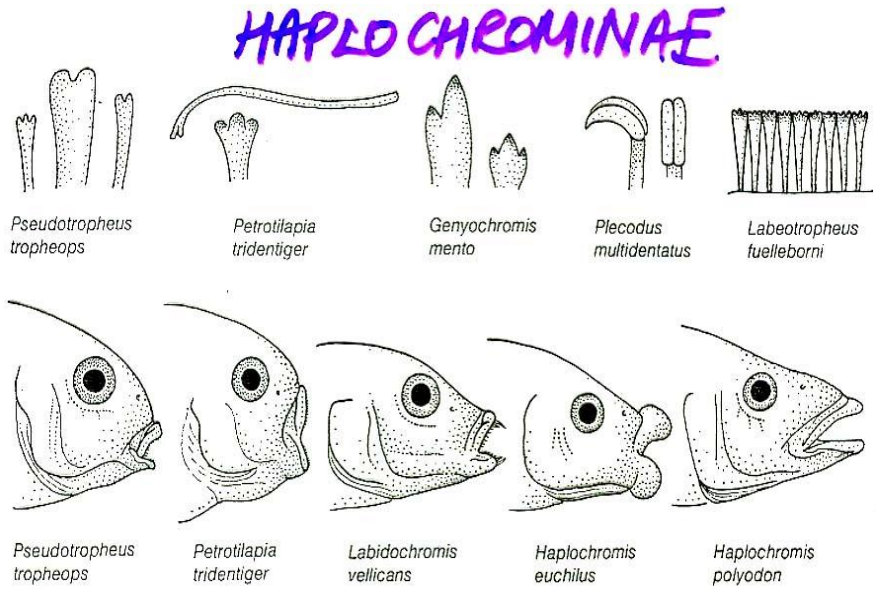


FIGURE 13
A sample of the diverse tooth forms and head shapes among the Cichlidae of the African Great Lakes. The differences in morphology are associated with differences in diet and mode of feeding. (Redrawn from Fryer 1959 and Fryer and Iles 1972, after various sources. Courtesy of the Zoological Society of London)

The cichlid fish *Cichlasoma* sp. from Cuatro Cienagas, Mexico – three morphs within the species:

- bottom living mollusc-feeder: grinding teeth
- pelagic piscivore: sharp teeth
- algae/detritivore: rounded teeth

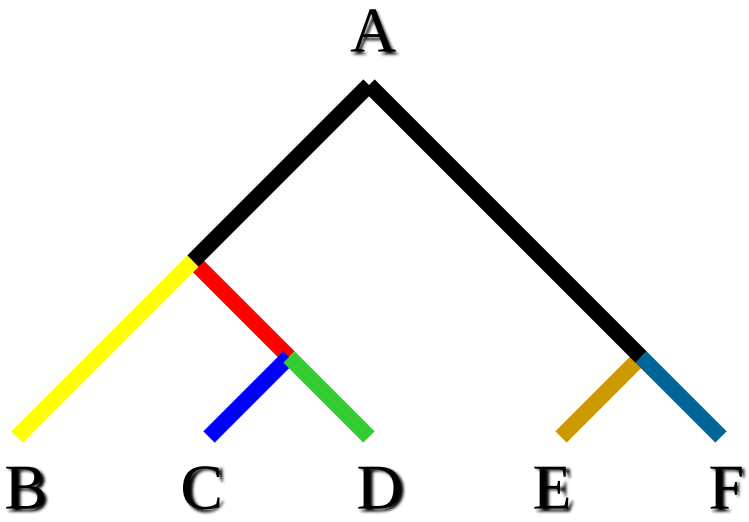
Defining Speciation

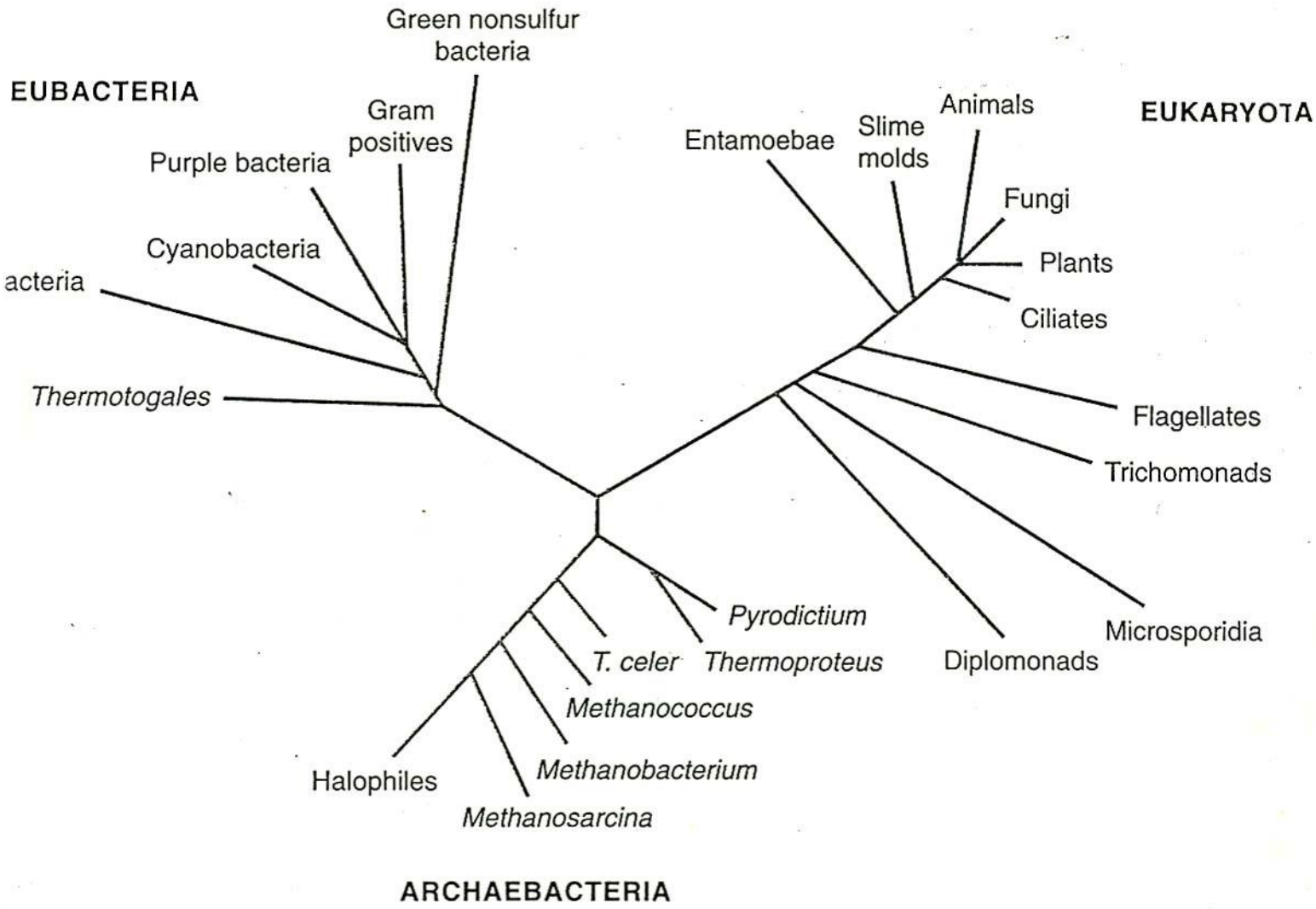
- A lineage-splitting event that produces two or more separate species.
- Speciation is a process within *evolution* that leads to the formation of new, distinct species that are reproductively isolated from one another.

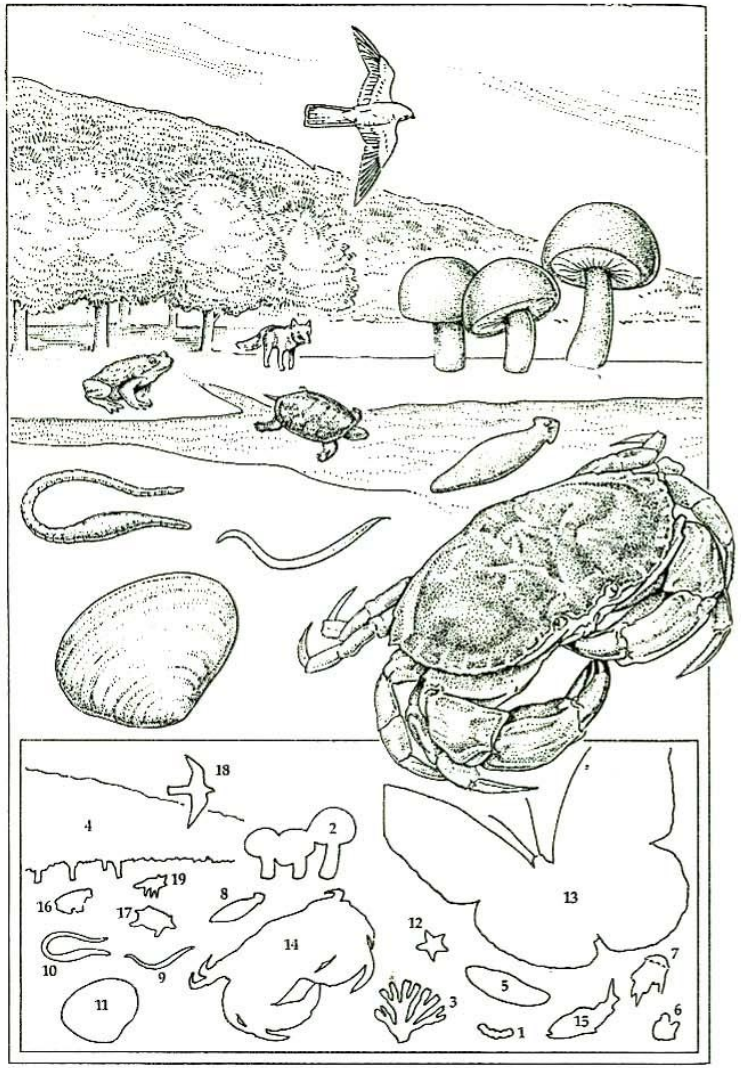
- Anagenesis (phyletic evolution)– transformation of an unbranched lineage of organisms to a different state (the new species)
- Cladogenesis (branching evolution) – budding of one or more species from a parent species that continues to exist

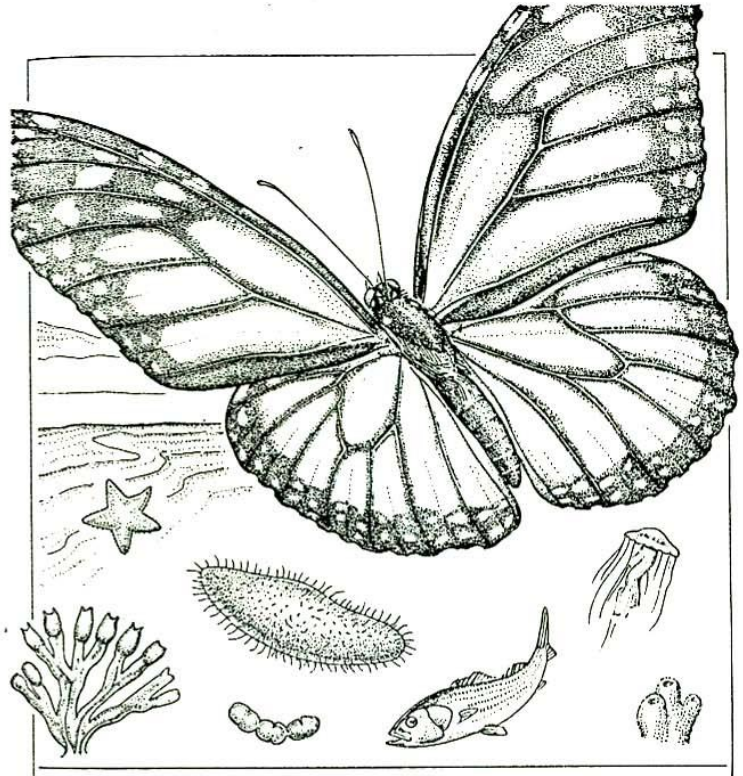
Anagenesis, or 'phyletic evolution', occurs when evolution acts to create new species, which are distinct from their ancestors, along a single lineage, through gradual changes in physical or *genetic* traits. In this instance, there is no split in the *phylogenetic tree*.

'Speciation'or *cladogenesis* arises from a splitting event, where a parent species is split into two distinct species, often as the result of geographic isolation or another driving force involving the separation of populations.




EUBACTERIA
Green nonsulfur bacteria
Gram positives
Purple bacteria
Cyanobacteria
acteria
Thermotogales
EUKARYOTA
Animals
Slime molds
Entamoebae
Fungi
Plants
Ciliates
Flagellates
Trichomonads
Microsporidia
Diplomonads
Pyrodictium
T. celer
Thermoproteus
Methanococcus
Methanobacterium
Halophiles
Methanosarcina
ARCHAEBACTERIA





The species-scape. The size of the representative organism in each group has been made to be roughly proportional to the number of species currently known to science. The code and number of species are given below. Viruses and some minor invertebrate groups have been omitted.

1. Monera (bacteria, cyanobacteria), 4,800
2. Fungi, 69,000
3. Algae, 25,900
4. Higher plants, 248,400
5. Protozoa, 30,800
6. Porifera (sponges), 5,000
7. Cnidaria and Ctenophora (corals, jellyfish, comb jellies, and relatives), 9,000
8. Platyhelminthes (flatworms), 12,200
9. Nematoda (roundworms), 12,000
10. Annelida (earthworms and relatives), 12,000
11. Mollusca (mollusks), 50,000
12. Echinodermata (starfish and relatives), 6,100
13. Insecta, 751,000
14. Noninsectan arthropods (crustaceans, spiders, etc.), 123,400
15. Fishes and lower chordates, 18,800
16. Amphibians, 4,200
17. Reptiles, 6,300
18. Birds, 9,000
19. Mammals, 4,000

From: EO Wilson 1992. The diversity of life

Further Reading

- Species concept and speciation Amal Y. Aldhebiani, *Saudi Journal of Biological Sciences,* Volume 25 Issue 3, March 2018, Pages 437-440

- Species Concepts and Species Delimitation Kevin De Queiroz *Systematic Biology*, Volume 56, Issue 6, December 2007, Pages 879–886

- FUTUYMA, DJ 1998. Evolutionary Biology. Chapter 15 pp. 447-479

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THANK YOU