# TOPIC Q : DIVERSITY AND EVOLUTION

## Learning Outcome

Candidates should be able to

*Core Topic 7 – Diversity and Evolution*

(a) Explain the binomial nomenclature of a species and hierarchical classification.

(b) Describe the classification of species into taxonomic groups (genus, family, order, class, phylum, kingdom) and explain various concepts of the species. (Knowledge of biological ecological, morphological, phylogenetic concepts of species is required.)

(c) Explain how species are formed with reference to geographical isolation, physiological isolation and behavioural isolation.

(d) Explain the relationship between classification and phylogeny. (Evolutionary relationships between organisms should be reflected in systematic classification.) Classification is the organisation of species according to particular characteristics. Classification may not take into consideration evolutionary relationship between the species. Phylogeny is the organisation of species according to particular characteristics which takes into consideration the evolutionary relationship between the species.

(e) Explain why variation is important in selection.

(f) Explain, with examples, how environmental factors act as forces of natural selection.

(g) Explain how natural selection may bring about evolution.

(h) Explain why the population is the smallest unit that can evolve.

(i) Explain how homology (anatomical, embryological and molecular) supports Darwin’s theory of natural selection (with emphasis on descent with modification).

(j) Explain how biogeography and the fossil record support evolutionary deductions based on homologies.

(k) Explain the importance of the use of genome sequences in reconstructing phylogenetic relationships and state the advantages of molecular (nucleotide and amino acid sequences) methods in classifying organisms.

(l) Explain how genetic variation (including recessive alleles) may be preserved in a natural population.

(m) Briefly describe the neutral theory of molecular evolution in terms of mutations producing new molecular variants which are selectively neutral. (Knowledge of genetic drift and molecular clock is required.)

Use the knowledge gained in these sections in new situations or to solve related problems.

## Content Outline

1. Introduction
2. Classification of Organisms
   (a) Hierarchical classification
   (b) Binomial nomenclature
   (c) Phylogeny
   (d) Molecular methods of classification
3. The Various Concepts of Species
   (a) Biological concept of species
   (b) Ecological concept of species
   (c) Morphological concept of species
   (d) Phylogenetic concept of species
4. Natural Selection and Evolution
   (a) Darwin's Theory of Evolution via Natural Selection
   (b) Forces of natural selection
   (c) Isolation mechanisms for speciation
   (d) The Neo-Darwinian revolution
5. Evidence of Evolution
   (a) Biogeography
   (b) Fossil records
   (c) Homology
6. Preservation of Genetic Variation in Natural Populations
   (a) Diploidy
   (b) Balanced polymorphism
   (c) Neutral mutations
7. The Neutral Theory of Molecular Evolution
   (a) Genetic drift
   (b) Molecular clock

## References

1. Campbell N. A. and Reece J.B. (2008). Biology. Chapter 21-26. Eighth Edition. Pearson Education, Inc.
2. Brooker R.J. *et. al.* (2008). Biology. Chapter 23-26. First Edition. The McGraw-Hill Companies.
3. Kardong KV. (2005). An Introduction to Biological Evolution. Chapter 1, 6,-8. 1st Edition. McGraw Hill.
4. Strickberger MV. (2000). Evolution. Chapter 11-12. Third Edition. Jones & Bartlett Publishers.

## 1. Introduction

In order to make sense of the diversity of organisms, it is necessary to group similar organisms together and organize these groups in a non-overlapping hierarchical arrangement. At the lowest level of the hierarchy, the organisms in each group form a species.

There are various concepts of species that have been adopted to classify organisms with highly similar characteristics as a single species.

It is through the understanding of such diversity of organisms that we appreciate how each of these species has evolved. Charles Darwin's Theory of Evolution via Natural Selection has been widely accepted by scientists across the world.

Several pieces of evidence have been put forth to support his theory. However, his theory is still being challenged even till this day. Recent advances in molecular Biology have since supported the Neutral Theory of Molecular Evolution, which is seen as a complement to Darwin's theory.

## 2. Classification of Organisms

Systematics is the science of classification. It is defined as the study of diversity of organisms and all their comparative and evolutionary relationships. Systematists use data ranging from fossils to molecules and genes to infer evolutionary relationships.

Taxonomy is the science concerned with the identification, classification and nomenclature of organisms.

Carolus Linnaeus (1748) developed a system of classifying every known organism in his time. The system is based on creating and differentiating organisms in terms of structural similarities and differences.

With improvements in science and technology, many other similarities and differences, such as embryological and molecular relationships, are also taken into consideration.

Thus there are two ways in classifying organisms:

**(a) Hierarchical classification**

**(b) Phylogeny**

### (a) Hierarchical classification

**Classification** is the **organisation of species according to particular characteristics**. Classification **may not take into consideration evolutionary relationship between the species**.

A common type of classification is phenotypic classification:

- It is concerned with grouping individuals species into phenotypic classes based on the morphology of organisms.
- However, phenotypic similarities and evolutionary relationships do not always correspond with each other due to:
  - complex relationship between phenotype to genotype
  - occurrences of convergent evolution
  - variations between lineages in rates and modes of phenotypic evolutionary change

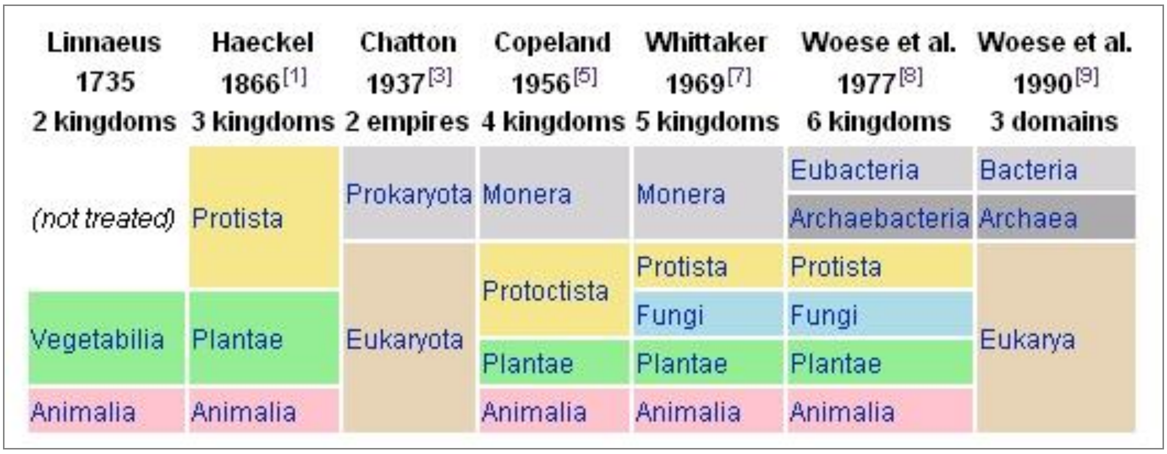
**Hierarchical classification** refers **the grouping of organisms into levels of increasingly inclusive categories**.

**A category in any rank unites groups in the level below it, based on shared characteristics**.

There are several variations to the classification of life. Among them are:

- The two-empire system, with top-level groupings of Prokaryota (or Monera) and Eukaryota empires.
- The five-kingdom system with top-level groupings of Protista, Monera, Fungi, Plantae, and Animalia.
- The most recent three-domain system, introduced by Carl Woese in 1990, with top-level groupings of Archaea, Eubacteria, and Eukaryota domains.

**Table of the different classification systems**



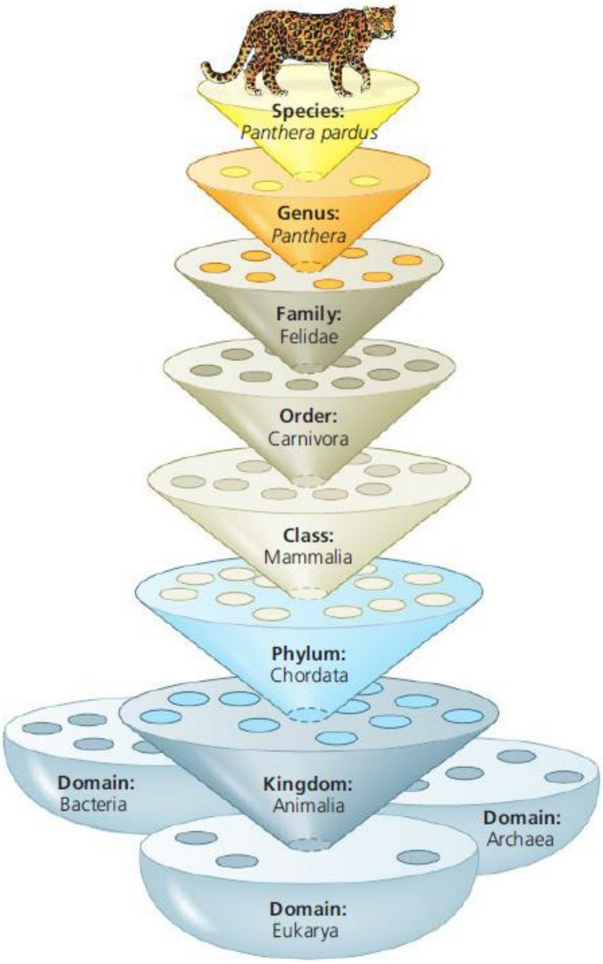
| Linnaeus<br>1735<br>2 kingdoms | Haeckel<br>1866[1]<br>3 kingdoms | Chatton<br>1937[3]<br>2 empires | Copeland<br>1956[5]<br>4 kingdoms | Whittaker<br>1969[7]<br>5 kingdoms | Woese et al.<br>1977[8]<br>6 kingdoms | Woese et al.<br>1990[9]<br>3 domains |
|---|---|---|---|---|---|---|
| *(not treated)* | Protista | Prokaryota | Monera | Monera | Eubacteria | Bacteria |
| | | | | | Archaebacteria | Archaea |
| | | Eukaryota | Protoctista | Protista | Protista | Eukarya |
| Vegetabilia | Plantae | | | Fungi | Fungi | |
| | | | Plantae | Plantae | Plantae | |
| Animalia | Animalia | | Animalia | Animalia | Animalia | |

In the three-domain / Linnaean system of classification, there is a hierarchy of designation, of which the **genera** and **species** denominations are at the bottom. This system, places related genera in the same **family**, families into **order**, orders into **class**, classes into **phylum**, phyla into **kingdom**, and more recently, kingdoms into **domain**.

The named taxonomic unit at any level of the hierarchy is called a **taxon** (plural, **taxa**).

Domain
Kingdom
Phylum
Class
Order
Family
Genus
Species

Fun mnemonics to help you remember the hierarchy:
**D**ear **K**ing **P**hilip **C**ame **O**ver **F**or **G**ood **S**oup



**Linnaean classification**

At each level, or rank, species are placed in groups within more inclusive groups.

Examples of hierarchical classification:

| | Humans | Cabbage |
|---|---|---|
| **Domain** | Eukarya | Eukarya |
| **Kingdom** | Animalia | Plantae |
| **Phylum** | Chordata | Tracheophyta |
| **Class** | Mammalia | Angiospermae |
| **Order** | Primates | Dicotylodonae |
| **Family** | Hominidae | Brassicaceae |
| **Genus** | *Homo* | *Brassica* |
| **Species** | *sapiens* | *oleracea* |

Higher levels of classification are usually defined by particular characters chosen by taxonomists. However, characters that are useful for classifying one group of organisms may not be appropriate for other organisms. For this reason, the larger categories often are not comparable between lineages; that is, an order of snails does not exhibit the same degree of morphological or genetic diversity as an order of mammals. Furthermore, the placement of species into orders, classes, and so on, **<u>does not necessarily reflect evolutionary history</u>**.

### (b) Binomial nomenclature

Developed by Carolus Linnaeus, **<u>binomial nomenclature</u>** is a standard convention used for naming species.

As the word 'binomial' suggests, the scientific name of each organism is actually the combination of **two** parts: **<u>the genus and the species</u>**, to which the organism belongs, and it is latinised.

The genus is typically capitalized, while the species is not; both are typeset in italics, e.g. *Homo sapiens*. If handwritten, the genus and species must be underlined, i.e. <u>Homo sapiens</u>.

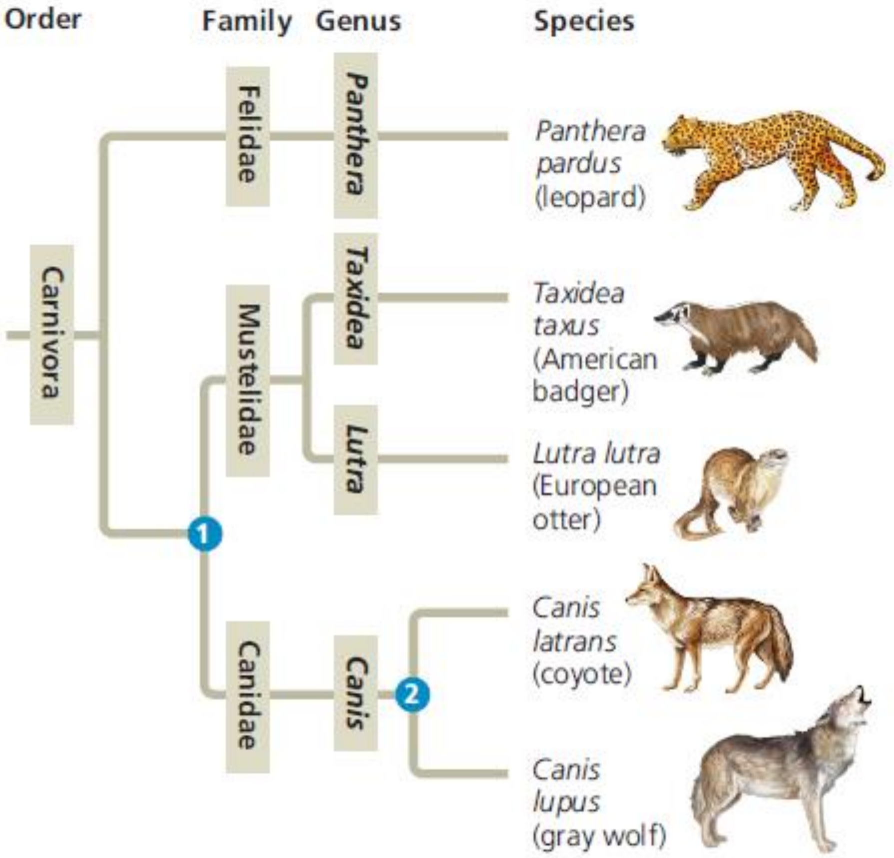
The value of this system lies chiefly in the fact that, although a given species may be named differently in different languages, the scientific name will always be the same. Ideally, scientists can **<u>meaningfully and unambiguously refer to a species</u>** when describing their work to other scientists.

Nomenclature intends to keep names stable, but quite often this is not true: an organism may have several names, reflecting different rank and position in taxonomy, depending on opinion and new findings based on molecular phylogeny. Nomenclature must acknowledge the achievement of scientists who were first to name a taxon.

## (c) Phylogeny

Unlike classification which may not take into consideration evolutionary relationship between the species, **phylogeny** is the **organisation of species according to particular characteristics which takes into consideration the evolutionary relationship between the species**.

Systematists use data ranging from fossils to molecules and genes to infer evolutionary relationships **Phylogenetic trees** are used to depict hypotheses about evolutionary relationships.



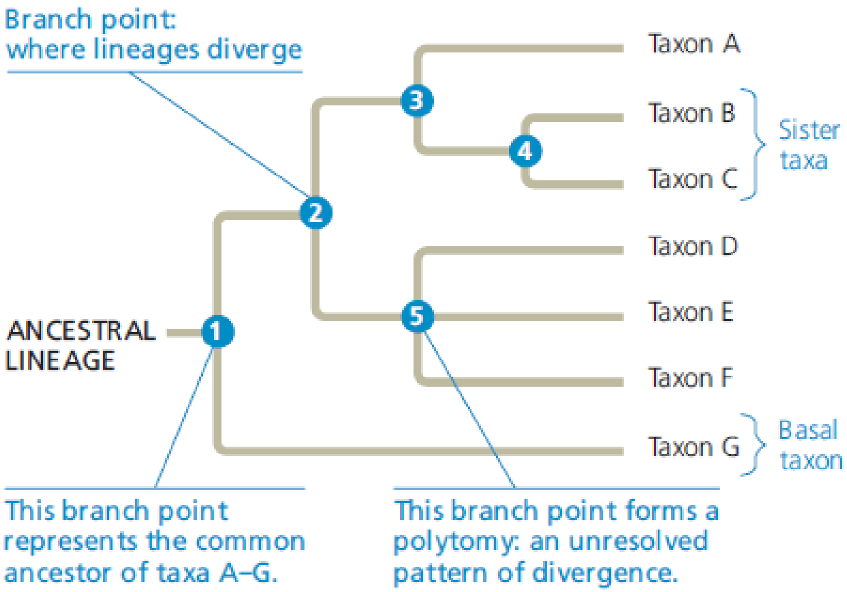
**Relationship between Classification and Phylogeny**

The branching of the trees reflects the hierarchical classification of groups nested within more inclusive groups. Hierarchical classification is reflected in the progressively fine branching of phylogenetic trees. This tree traces possible evolutionary relationships between some of the taxa within the order Carnivora, itself a branch of the class Mammalia.

Sometimes, however, taxonomists have placed a species within a genus (or other group) to which it is not most closely related. One reason for misclassification might be that over the course of evolution, a species has lost a key feature shared by its close relatives. If DNA or other new evidence indicates that such a mistake has occurred, the organism may be reclassified to accurately reflect its evolutionary history.

A phylogenetic tree is often constructed from a series of dichotomies (2-way branch points).

**Each branch point represents the divergence of two species from a common ancestor**.



**How to read a phylogenetic tree**

Branch point ③ represents the common ancestor of taxa A, B, and C. The position of branch point ④ to the right of ③ indicates that taxa B and C diverged after their shared lineage split from that of taxon A. taxa B and C are sister taxa, groups of organisms that share an immediate common ancestor (branch point ④)

### What We Can and Cannot Learn from Phylogenetic Trees

**(i)** Phylogenetic trees are intended to show **patterns of descent**, not phenotypic similarity.

For example, even though crocodiles are more closely related to birds than to lizards, they look more like lizards because morphology has changed dramatically in the bird lineage.

**(ii)** The sequence of branching in a tree **does not necessarily indicate the actual (absolute) ages** of the particular species.

Generally, unless given specific information about what the branch lengths in a phylogenetic tree mean for example, that they are proportional to time we should interpret the diagram solely in terms of patterns of descent. No assumptions should be made about when particular species evolved or how much change occurred in each lineage.

**(iii)** A taxon on a phylogenetic tree should not be assumed to be evolved from the taxon next to it.

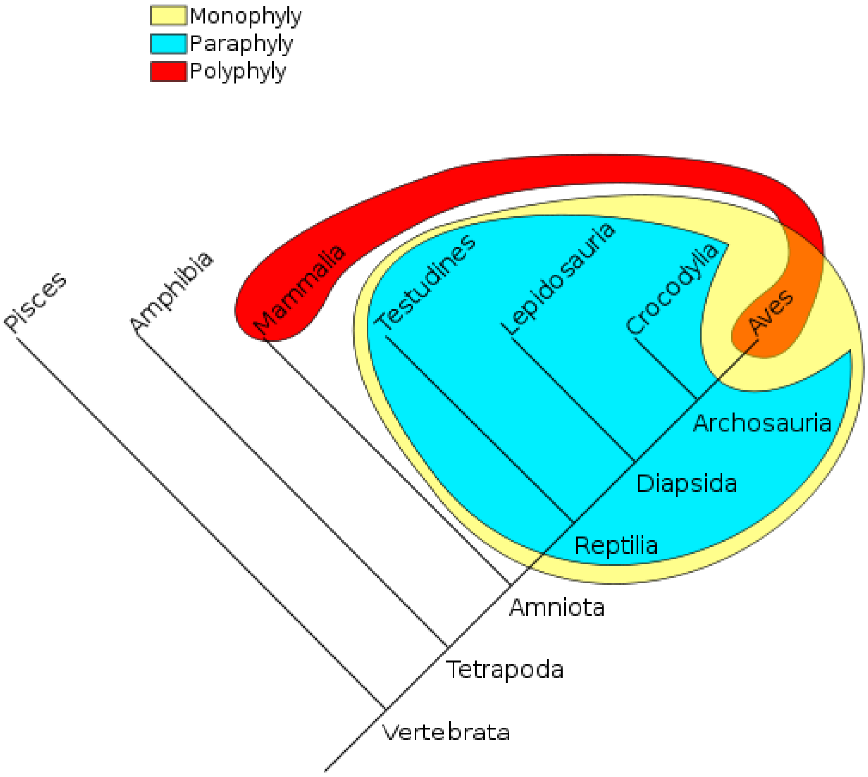
For example, taxon D did not evolve from taxon E. We can infer only that the lineage leading to D and the lineage leading to E both evolved from the common ancestor ⑤.

There are some terms that describe the nature of a grouping in phylogenetic trees.

For instance, all birds and reptiles are believed to have descended from a single common ancestor, so this taxonomic grouping (yellow in the diagram below) is called **monophyletic**. A monophyletic taxon is also known as a **clade**.

"Modern reptile" (cyan in the diagram) is a grouping that contains a common ancestor, but does not contain all descendents of that ancestor (Aves / birds are excluded). This is an example of a **paraphyletic** group.

A grouping such as warm-blooded animals would include only mammals and birds (red / orange in the diagram) and is called **polyphyletic** because the members of this grouping do not include the most recent common ancestor.



Thus, a phylogenetic tree is based on a hypothesis of the order in which evolutionary events are assumed to have occurred.

**Cladistics** is the current method of choice to infer phylogenetic trees. It is the mode of classification based principally on grouping taxa by their shared possession of similar characteristics that derived from their ancestors.

## (d) Molecular methods of classification

The use of molecular information rather than the exclusive reliance on morphological information is used nowadays to overcome some of the usual phylogenetic problems.

On molecular level, information is obtained through nucleotide (DNA or RNA) sequence comparison, as well as by comparing sequences of amino acids (and their three-dimensional structure) of particular proteins between different species.

The advantages of molecular methods in classification are as follows:

1. Evolutionary changes between species can be **compared via similarities or differences in nucleotide or amino acid sequences** even though they may **differ vastly in terms of morphology**.
2. **Degree of divergence between different species** can be **quantitatively measured by comparison of nucleotide or amino acid sequences**.
3. Molecular comparisons **transcend barriers among organisms whose relationships cannot be evaluated by traditional experimental techniques, e.g. selective breeding**. (x.f. Biological Concept of Species)

There are a number of ways to obtain nucleic acid phylogenies, they include:

### (i) Direct comparison of DNA sequences

- Technology now exists to **sequence short DNA sequences** efficiently.
- cDNA (i.e. gene sequences without introns) is usually used as a source for gene sequencing. This method allows scientists to obtain the DNA sequence of a segment of a particular gene **for comparison between species**.
- Softwares (e.g. CLUSTALW) are available online to compare these sequences between species and **deduce the level of homology** (i.e. similarity) (usually stated as a percentage).

- Advantage:
  - Comparisons of direct molecular sequences **allow evolutionary rates to be estimated more quantitatively**.
  - **Relatively quick and inexpensive**.

- Disadvantages:
  - Alignment between the sequences can sometimes be difficult if two species have diverged significantly.
  - Relatively large quantity of purified DNA is needed for the procedure. However, Polymerase Chain Reaction (PCR) can be employed to amplify the DNA for sequencing.

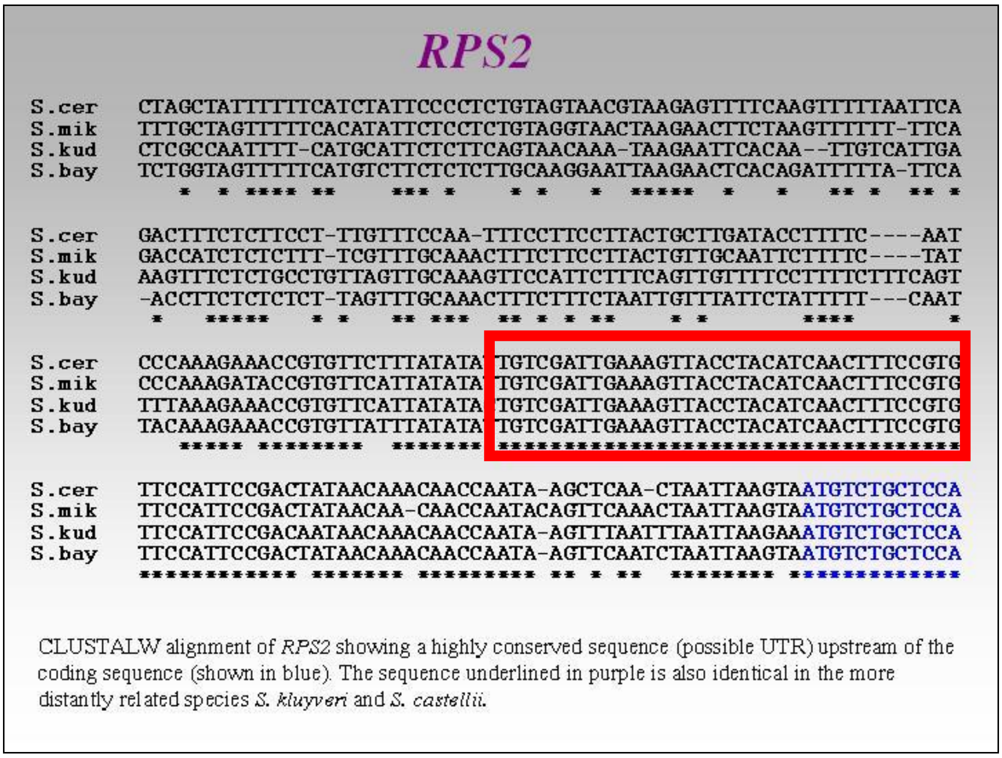
**Conserved and Consensus Sequences**

Scientists can compare the DNA sequences of various species using software which align these sequences parallel to one another.

The **more similar** the sequences of two species are, the **more closely related** those species are in their evolutionary history.

If the sequences from different species are aligned with each other, and each has exactly the same sequence of nucleotides, we say that the sequence is invariant and is a **conserved sequence**.

If, however, there is some variation in the sequence, but certain nucleotides are present at high frequencies, we refer to those nucleotides as making up a **consensus sequence**.



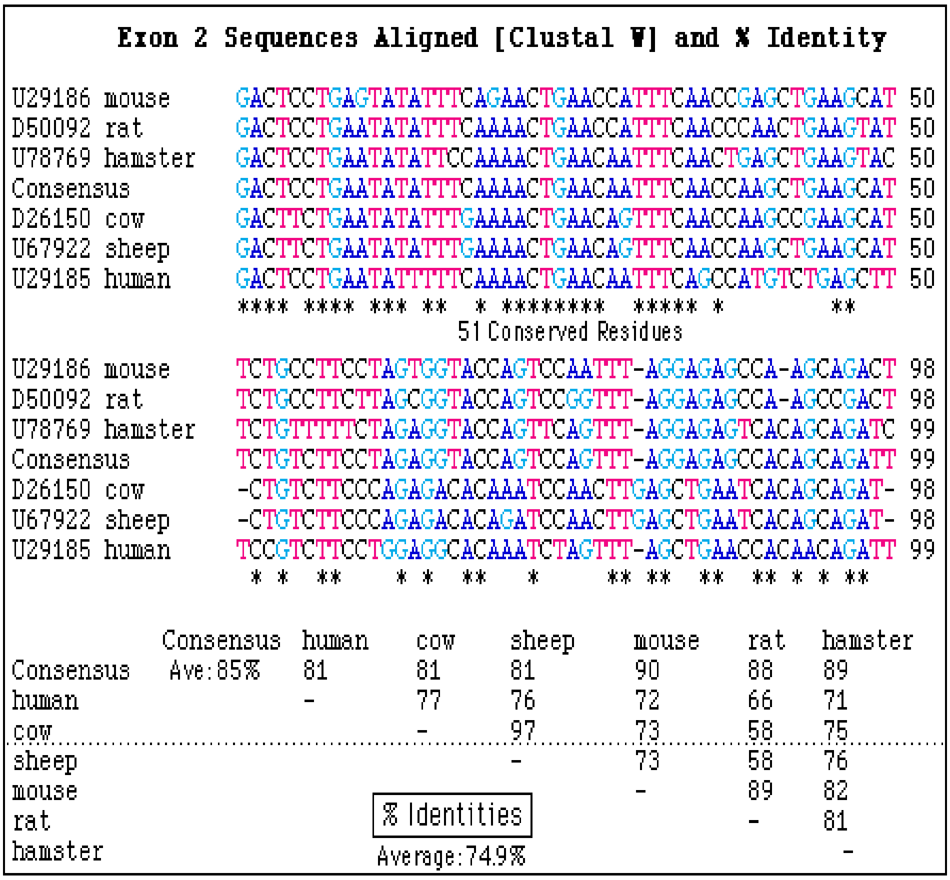
*RPS2*

```
S.cer    CTAGCTATTTTTTCATCTATTCCCCTCTGTAGTAACGTAAGAGTTTTCAAGTTTTTAATTCA
S.mik    TTTGCTAGTTTTTCACATATTCTCCTCTGTAGGTAACTAAGAACTTCTAAGTTTTTT-TTCA
S.kud    CTCGCCAATTTT-CATGCATTCTCTTCAGTAACAAA-TAAGAATTCACAA--TTGTCATTGA
S.bay    TCTGGTAGTTTTTCATGTCTTCTCTCTTGCAAGGAATTAAGAACTCACAGATTTTTA-TTCA
            *  * **** **    *** *    * *   *  *****  *   *   ** *  ** *

S.cer    GACTTTCTCTTCCT-TTGTTTCCAA-TTTCCTTCCTTACTGCTTGATACCTTTTC----AAT
S.mik    GACCATCTCTCTTT-TCGTTTGCAAACTTTCTTCCTTACTGTTGCAATTCTTTTC----TAT
S.kud    AAGTTTCTCTGCCTGTTAGTTGCAAAGTTCCATTCTTTCAGTTGTTTTCCTTTTCTTTCAGT
S.bay    -ACCTTCTCTCTCT-TAGTTTGCAAACTTTCTTTCTAATTGTTTATTCTATTTTT---CAAT
          *   *****   * *   ** ***  ** * * **    * *       ****       *

S.cer    CCCAAAGAAACCGTGTTCTTTATATA TGTCGATTGAAAGTTACCTACATCAACTTTCCGTG
S.mik    CCCAAAGATACCGTGTTCATTATATA TGTCGATTGAAAGTTACCTACATCAACTTTCCGTG
S.kud    TTTAAAGAAACCGTGTTCATTATATA TGTCGATTGAAAGTTACCTACATCAACTTTCCGTG
S.bay    TACAAAGAAACCGTGTTATTTATATA TGTCGATTGAAAGTTACCTACATCAACTTTCCGTG
            ***** ********  *******  ***********************************

S.cer    TTCCATTCCGACTATAACAAACAACCAATA-AGCTCAA-CTAATTAAGTAATGTCTGCTCCA
S.mik    TTCCATTCCGACTATAACAA-CAACCAATACAGTTCAAACTAATTAAGTAATGTCTGCTCCA
S.kud    TTCCATTCCGACAATAACAAACAACCAATA-AGTTTAATTTAATTAAGAAATGTCTGCTCCA
S.bay    TTCCATTCCGACTATAACAAACAACCAATA-AGTTCAATCTAATTAAGTAATGTCTGCTCCA
         ************ ******* ********* ** * **  ******** *************
```

CLUSTALW alignment of *RPS2* showing a highly conserved sequence (possible UTR) upstream of the coding sequence (shown in blue). The sequence underlined in purple is also identical in the more distantly related species *S. kluyveri* and *S. castellii.*

Conserved sequence (in box) in the RPS2 gene across four different species

*(Adapted from http://www.genetics.wustl.edu/saccharomycesgenomes/website12.jpg on 1/1/ 07)*



**Exon 2 Sequences Aligned [Clustal W] and % Identity**

```
U29186 mouse    GACTCCTGAGTATATTTCAGAACTGAACCATTTCAACCGAGCTGAAGCAT 50
D50092 rat      GACTCCTGAATATATTTCAAAACTGAACCATTTCAACCCAACTGAAGTAT 50
U78769 hamster  GACTCCTGAATATATTCCAAAACTGAACAATTTCAACTGAGCTGAAGTAC 50
Consensus       GACTCCTGAATATATTTCAAAACTGAACAATTTCAACCAAGCTGAAGCAT 50
D26150 cow      GACTTCTGAATATATTTGAAAACTGAACAGTTTCAACCAAGCCGAAGCAT 50
U67922 sheep    GACTTCTGAATATATTTGAAAACTGAACAGTTTCAACCAAGCTGAAGCAT 50
U29185 human    GACTCCTGAATATTTTTCAAAACTGAACAATTTCAGCCATGTCTGAGCTT 50
                **** **** *** **  * ********  ***** *         **
                              51 Conserved Residues

U29186 mouse    TCTGCCTTCCTAGTGGTACCAGTCCAATTT-AGGAGAGCCA-AGCAGACT 98
D50092 rat      TCTGCCTTCTTAGCGGTACCAGTCCGGTTT-AGGAGAGCCA-AGCCGACT 98
U78769 hamster  TCTGTTTTTCTAGAGGTACCAGTTCAGTTT-AGGAGAGTCACAGCAGATC 99
Consensus       TCTGTCTTCCTAGAGGTACCAGTCCAGTTT-AGGAGAGCCACAGCAGATT 99
D26150 cow      -CTGTCTTCCCAGAGACACAAATCCAACTTGAGCTGAATCACAGCAGAT- 98
U67922 sheep    -CTGTCTTCCCAGAGACACAGATCCAACTTGAGCTGAATCACAGCAGAT- 98
U29185 human    TCCGTCTTCCTGGAGGCACAAATCTAGTTT-AGCTGAACCACAACAGATT 99
                 * *  **    * *  **   *     ** **  **  ** * * **
```

| | Consensus | human | cow | sheep | mouse | rat | hamster |
|---|---|---|---|---|---|---|---|
| Consensus | Ave:85% | 81 | 81 | 81 | 90 | 88 | 89 |
| human | | - | 77 | 76 | 72 | 66 | 71 |
| cow | | | - | 97 | 73 | 58 | 75 |
| sheep | | | | - | 73 | 58 | 76 |
| mouse | | | | | - | 89 | 82 |
| rat | | | | | | - | 81 |
| hamster | | | | | | | - |

% Identities

Average:74.9%

Consensus sequence in exon 2 of the prion gene across six species

*(Adapted from [http://www.mad-cow.org/exon2.gif on 1/1/07](http://www.mad-cow.org/exon2.gif))*

Based the analysis above (using the computer software 'Clustal W' for alignment), we can observe that:

1. There is a 77% homology in the consensus sequence between human and cow for the prion gene.
2. The prion gene from the sheep and cow share the **<u>highest homology</u>** (97%) for the consensus sequence.

Advancement in technology also completed the sequencing of entire genomes of organisms. Comparing genomes of closely related species sheds light on more recent evolutionary events, whereas comparing genomes of distantly related species helps us understand ancient evolutionary history.

### (ii) Comparison of mitochondrial DNA sequences

- The mitochondrial DNA is **inherited only from the maternal parent to its offspring**. This is because the mitochondria found in an offspring were derived from the mitchondria present in the mother's ovum.
- **Mitochondrial Eve** is the name given by researchers to the woman who is defined as the matrilineal (i.e. lineage is traced through the mother and maternal ancestors) most recent common ancestor (MRCA) for all currently living humans.
- Passed down from mother to offspring, her mitochondrial DNA (mtDNA) is now found in all living humans: every mtDNA in every living person is derived from hers. She is believed to have lived about 170,000 years ago, or roughly 8,000 generations ago.

- Advantages:
  - **Direct phylogeny via the maternal lineage can be deduced** as the **sequence is not confounded by genetic recombination** (as compared to genetic recombination that occurs in nuclear DNA via crossing over, independent assortment and random fusion of gametes).
  - **mtDNA also mutates at a higher rate compared to nuclear DNA**, so it gives researchers a **more useful, magnified view of diversity and phylogeny**.
  - Since **mtDNA mutation is found to occur at a consistent rate**, the **time taken for the divergence of species from their ancestors can be calculated**.
  - The **molecular clock** is **a technique in molecular evolution that relates the time that two species diverged to the number of molecular differences measured between the species' DNA sequences**.

### (iii) DNA-DNA hybridisation

- Estimates the ease and accuracy by which homologous strands of DNA from two different species can form a double helix.
- DNA extracted from each species are dissociated into single strands and then allowed to re-anneal with the single strands of another species to form double strand hybrids by incubating them at appropriate temperatures.
- The hybrids are then allowed to dissociate into single strand and the melting temperature noted. The more different the strands are, the more easily they dissociate. This is because there is less complementarity, thus the bonds between the strands are weaker.
- Various experiments have shown that for each 1% difference in nucleotide composition between the two species, the thermal stability of the hybrid DNA molecule lowers by about 1$^{o}$C. The temperatures at which a single-stranded DNA of one species gets dissociated from that of another species reflects the amount of similarity between sequences, as well as the degree of genetic similarity between organisms.
- Advantages:
  - Allows an estimate of overall divergence in DNA sequences between species.
- Disadvantages:
  - Through yielding a single hybridization value, a wide variety of sequence information is lumped together, thus the estimation of divergence between the species lack precision.

There are also a number of ways to study phylogeny using amino acid sequence and proteins. They include:

**(i) Direct comparison of amino acid sequences**

- **Amino acids in proteins are sequenced** by biochemical methods and **compared against the same proteins in different species**.
- Measuring divergence in sequences of proteins commonly found in various species is used as a method of estimating evolutionary divergence. Examples include globins and cytochrome c.
- Advantages:
  - Comparisons of direct molecular sequences **allow evolutionary rates to be estimated more quantitatively**.
  - **Relatively quick and inexpensive**.
- Disadvantages:
  - Underestimates degree of evolutionary change because of the redundancy of the genetic code. Silent mutations will not be detected because these mutations do not result in a change to the amino acid sequence of a protein. They may occur in the non-coding region or within an exon in a manner that does not alter the final amino acid sequence.

**(ii) Measurement of immunological distance**

- Measures the amount of the precipitation between antibodies and their proteins (antigens), in response to injection of antigens from a related species. Antibodies are proteins produced by lymphoid tissues in response to the presence of foreign materials, i.e. antigens.
- The **higher** the precipitation between antibody and its protein, the **more closely related** are the two species.
- Advantage:
  - High specificity of antigen-binding sites of antibodies allows binding of antigens of very closely related species.
- Disadvantages:
  - Antigen-antibody reactions are complex reactions involving a number of genes. Intensity of response does not necessarily relate to time of evolutionary divergence.

## 3. The Various Concepts of Species

Species is a taxonomic concept used in Biology to refer to a population of organisms that are in some important ways similar. The idea of species has a long history.

After thousands of years of use, the concept remains central to biology and a host of related fields, and yet also remains at times ill-defined and controversial. There are several lines of thought in the definition of species*:*

### (a) Biological concept of species

The **Biological Species Concept** defines a species as **a group of populations** whose members have the **potential to interbreed in nature** and produce **viable, fertile offspring** but do not produce viable, fertile offspring with members of other such groups.

- This is generally the most common and useful concept of species for scientists working with living examples of the higher taxa, like mammals, fish, and birds.
- Members of a biological species are are defined in terms of **reproductive compatibility**.
- Gene flow is the transfer of alleles between populations. Gene flow occurs between the different populations of a species and the ongoing exchange of alleles tends to hold the populations together genetically.
- The formation of a new species hinges on **reproductive isolation** – the existence of **biological factors / barriers** that impede members of two species from producing viable, fertile offspring. Such barriers **block gene flow** between the species and limit the formation of hybrids.
- E.g. it is possible to mate a horse with a donkey and produce an offspring (i.e. mule). However they are still considered as different species for two reasons:
  - ➢ Horses and donkeys do not normally interbreed in nature
  - ➢ The offspring, i.e. mule, is non-fertile.
- Limitations:
  - ➢ **Does not apply to organisms that reproduce asexually** all or most of the time, e.g. prokaryotes.
  - ➢ **Does not apply to organisms that are extinct**.
  - ➢ **Overemphasizes on gene flow and downplays the role of natural selection**, as natural selection can cause many pairs of species that are morphological and ecologically distinct, to remain distinct and yet have gene flow between them.

### (b) Ecological concept of species

The **Ecological Species Concept** defines a species in terms of its **ecological niche, i.e. the sum of how members of the species interact with the non-living and living parts of their environment**.

- E.g. two species of Galapagos finches may be similar in appearance but distinguishable based on what they feed on.
- E.g. two species of salamanders might be similar in appearance but differ in the foods they eat or in their ability to tolerate dry conditions.
- Advantages:
  - **Can accommodate asexual as well as sexual species**.
  - **Emphasizes the role of disruptive natural selection as organisms adapt to different environmental conditions**.
- Limitation:
  - **Niches are generally difficult to identify** because a niche involves the interaction between the organism and its environment (both biotic and abiotic).

### (c) Morphological concept of species

The **Morphological Species Concept** defines a species in terms of **its body shape and other structural features**.

- E.g. a chicken is distinguishable from a duck because they have differently shaped bills. Also, the chicken has clawed feet while the duck has webbed feet.
- Species have been defined in this way since well before the beginning of recorded history. Although much criticised, the concept of morphological species remains the single most widely used species concept in everyday life, and still retains an important place within the biological sciences, particularly in the case of plants.
- Advantages:
  - **Can be applied to asexual and sexual organisms**.
  - **Does not require any information on the extent of gene flow**.
  - **Easiest and fastest concept to apply in the field** because it is based only on the appearance of the organism.
- Limitation:
  - Relies on **subjective criteria** and researchers may disagree on which structural features distinguish a species.

### (d) Phylogenetic concept of species

The **Phylogenetic Species Concept** defines a species as the **smallest group of individuals that share a common ancestor, forming one branch on the tree of life**.

- At some point in the progress of such a group, members may diverge from one another. When such a divergence becomes sufficiently clear, the two populations are regarded as separate species.
- Biologists trace the phylogenetic history of species by comparing its characteristics, such as morphology or molecular sequences, with those of other organisms. Such analyses can distinguish groups of individuals that are sufficiently different to be considered separate species. The identification of species using this concept is supported by developments in molecular systematics.
- Limitation:
  - ➢ The **degree of difference required to indicate separate species may be subjective**.

## 4. Natural Selection and Evolution

### (a) Darwin's Theory of Evolution via Natural Selection

Evolution is:

- **Descent with modification**

  a phrase Darwin used in proposing that Earth's many species are descendants of ancestral species that were different from the present-day species.

- **genetic changes** that occur in **a population of organisms through time, leading to differences amongst them.**

Evolution occurs when natural selection causes changes in the relative frequencies of alleles in the gene pool. **Natural selection is a result of differential success in the reproduction of phenotypes resulting from the interaction of organisms with the environment.** Organisms less suited to an environment, perish and consequently do not pass on their genes to subsequent generations.

Darwin developed two main ideas in his book 'The Origin of Species', namely, **descent with modification**, which explains life's unity and diversity, and **natural selection**, which brings about the match between organisms and their environment:

- **Descent with modification**

  All organisms are derived from common ancestors by a process of branching. Over time, populations evolve into different species, which are related because they are **descended from a common ancestor**.

  Thus, if one goes far enough back in time, any pair of organisms has a common ancestor. This explained the similarities of organisms that were classified together (i.e. they were similar because of shared traits inherited from their common ancestor.)

  It also explained why similar species tended to occur in the same geographic region. As the descendants of that ancestral organism occupied into various habitats over millions of years, they accumulated diverse modifications, or adaptations, that fit them to specific ways of life. Change is gradual and slow, taking place **over a long time**.

- **Natural selection**

  The mechanism of evolutionary change was natural selection. This was the most important and revolutionary part of Darwin's theory.

  For natural selection to occur, two requirements are essential:

  - There must be **heritable variation** for a particular trait. E.g. beak size, colour pattern, thickness of skin, fleetness.
  - There must be **differential survival and reproduction abilities** associated with the possession of that trait.

  Unless both these requirements are met, adaptation by natural selection cannot occur.

- **Variation**

If all the organisms within a species were identical, there would be no “choice”. Evolutionary change would not occur. Therefore, no difference implies that there will be no evolution. In a population with little variation, the probability of having an allele or trait conferring advantage would decrease.

Differential survival depends on differential features. As Darwin saw, evolution needs choices. If we could recall from our previous topics, variation arises from the following:

1. **Sexual reproduction**
    (a) Crossing over during meiosis
    (b) Independent assortment during meiosis
    (c) Random fertilisation of egg by sperm

2. **Mutations**
    (a) Gene mutations
    (b) Chromosomal mutations

The essential features of Charles Darwin's theory of evolution by natural selection are:

**(a) Overproduction of offspring**

- All individuals of a population are capable of producing large numbers of offspring.
- If all the offspring survived, this would lead to a geometric increase in the size of the population.
- Many of these offspring fail to survive and reproduce.

**(b) Constancy of numbers**

- Although organisms are capable of producing large number of offspring, most populations remain relatively constant in numbers.

**(c) Variation in traits between individuals within a population**

- Individuals of a population differ from each other and these variations are a pre-requisite for evolution by natural selection.
- These variations arise spontaneously before a change in the environment. They are not formed to make the individuals better adapted as a result of the new environment.
- The environment merely selects those individuals who by chance happen to be better adapted.

**(d) Struggle for survival and survival of the fittest**

- On the basis of overproduction of offspring, constancy of numbers and variation within a population, Darwin deduced that individuals of a population are constantly **competing with one other** for **limited resources** such as food and shelter.
- Within a population, some individuals are more adapted to the existing environmental conditions than others.
- Individuals who are **better adapted** will **survive till maturity** and **produce viable offspring** as compared to others.

**(e) Like produces like**

- Individuals who can survive to maturity are likely to produce offspring who will inherit the beneficial traits (**beneficial alleles**).
- The beneficial characteristic, which gave them the edge over others in the struggle for survival, are likely to be passed on to the offspring.
- This **may eventually lead to speciation**.

**The smallest unit of evolution is a population**.

One common misconception about evolution is that individual organisms evolve during their lifetimes. Natural selection acts on individuals, but it is populations that evolve. **Individual organism cannot evolve**. But **a population can have variation in traits and thus be subjected to forces of natural selection**, and **can undergo all the changes in genotypes and phenotypes associated with evolutionary change**.

### (b) Forces of natural selection

**Example 1 (Natural selection)**

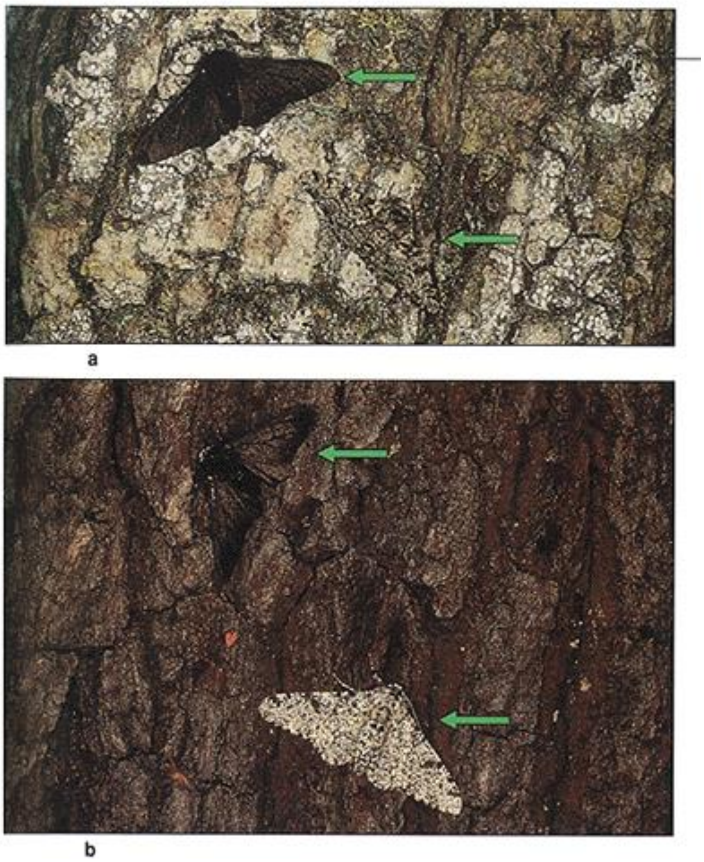
**Population: Peppered moth**

**Selection pressure: Predation**

Industrial melanism is a phenomenon that affected over 70 species of moths in England. It refers to the genetic darkening of species in response to pollutants and has been best studied in the peppered moth, *Biston betularia*. Prior to 1800, the typical moth of the species had a light pattern. Dark coloured or melanic moths were rare and were therefore collectors' items. In 1819, the first melanic morph was seen; by 1886, it was far more common, illustrating rapid evolutionary change.

During the Industrial Revolution in the 19th century, soot and other industrial wastes darkened tree trunks and killed off lichens (which were light-coloured). The light-coloured morph of the moth became rare and the dark morph became abundant. The cause of this change was thought to be selective predation by birds, which favoured camouflage coloration in the moth.

In recent years, the burning of cleaner fuels and the advent of Clean Air laws has changed the situation. Since then, with improved environmental standards, light-colored peppered moths have again become common.



**Individuals of a moth population that has undergone selection in response to changes in the environment.** Light-winged and dark-winged peppered moths (*Biston betularia)* are resting on a lichen-covered tree-trunk in (a) and on a soot-darkened tree trunk in (b).

http://www.micro.utexas.edu/courses/levin/bio304/popgen/moths.gif

**Example 2 (Evolution by natural selection)**

**Population: Galapagos finches (Darwin's finches)**

**Selection pressure: Limited food source**

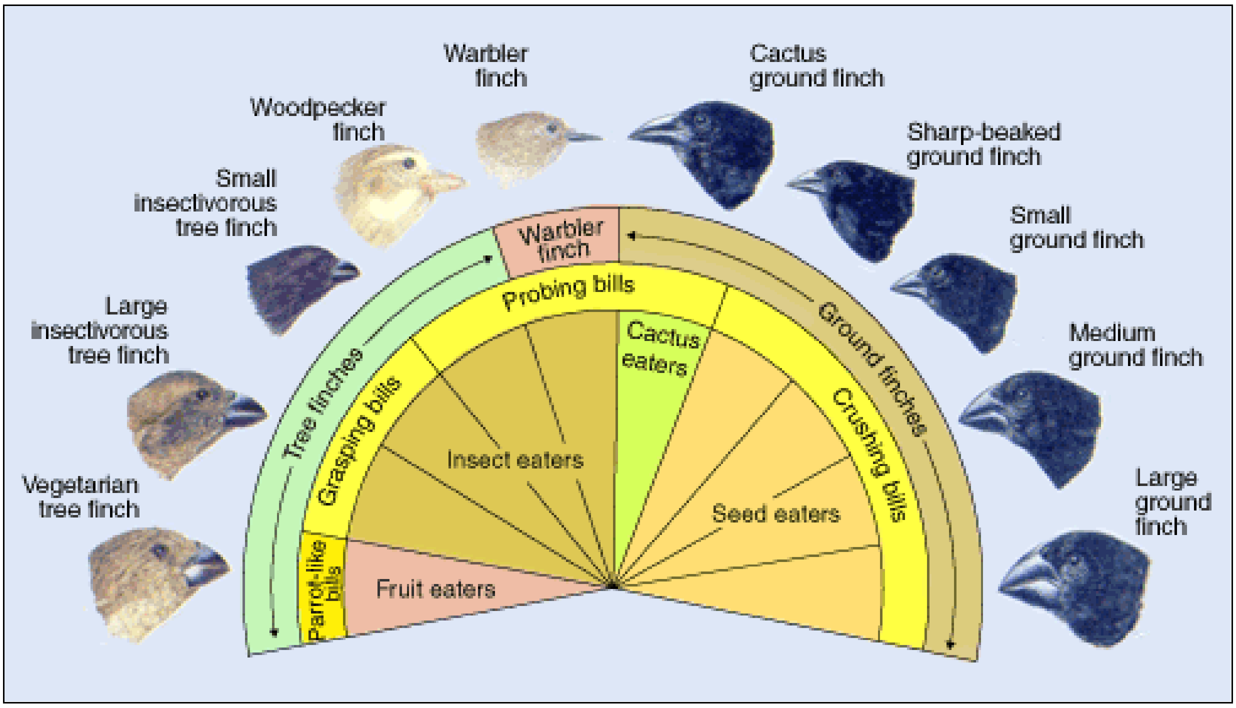
Galapagos finches are the famous example from Darwin's voyage. Each island of the Galapagos that Darwin visited had its own kind of finch (14 in all), found nowhere else in the world.

Some had large and heavy beaks adapted for eating large seeds, others for small seeds; some had parrot-like beaks for feeding on buds and fruits, and some had slender beaks for feeding on small insects. One used a thorn to probe for insect larvae in wood, like some woodpeckers do. (Six were ground-dwellers, and eight were tree finches.) This diversification into different ecological roles, or niches, is thought to be necessary to permit the coexistence of multiple species.

To Darwin, it appeared that each was slightly modified from an original colonist, probably the finch on the mainland of South America, some 600 miles to the east. It is probable that **adaptive radiation** led to the formation of so many species because other birds were few or absent, leaving empty niches to fill; and because the numerous islands of the Galapagos provided ample opportunity for geographic isolation.

**Adaptive radiation** is the **development of a variety of species from a single ancestral form.**

It is an evolutionary pattern of divergence from a common ancestral species, as a result of novel adaptations when a new habitat becomes available to the population.



**Adaptive radiation of Darwin's finches**

http://www.pbs.org/wgbh/evolution/library/01/6/images/l_016_02_l.gif

There are different types of selection. Every trait tends to vary. In a group, there will be individuals with the trait at the extremes, but most lie in between. This distribution is described as a bell-shaped curve (x.f. continuous variation).

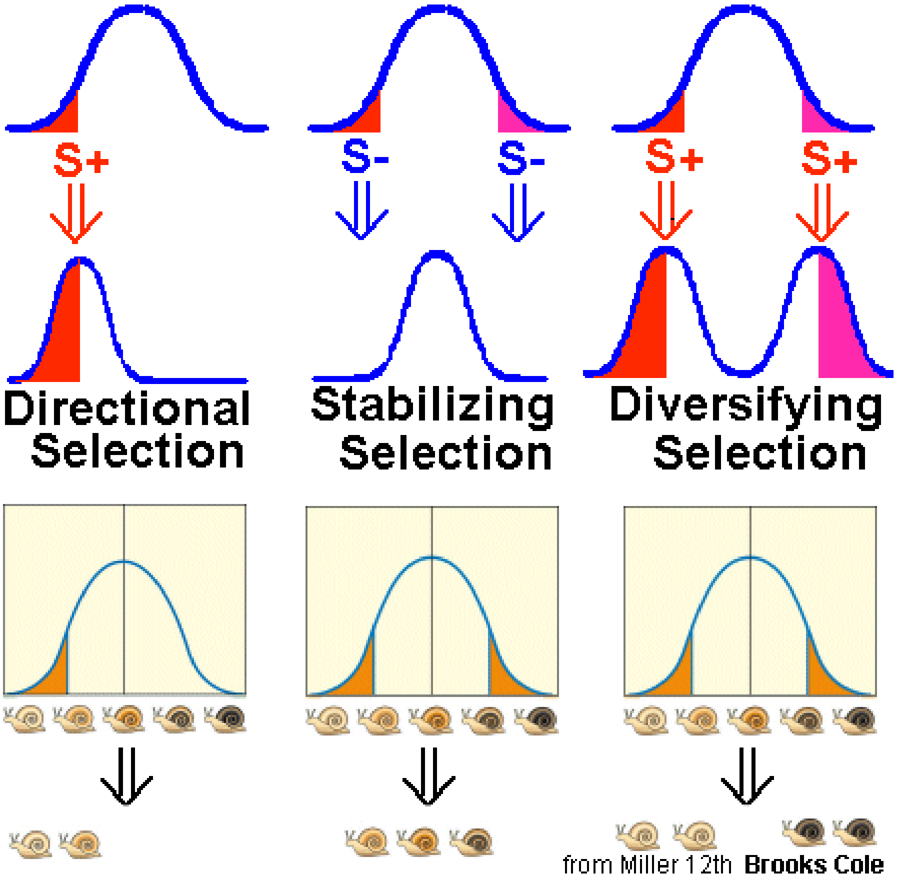
Natural selection can alter the frequency distribution of heritable traits in three ways, depending on which phenotypes in a population are favoured.

- **Directional selection**
  - When one extreme of the trait is disadvantageous, natural selection acts against it, favouring the rest of the individuals.
  - Applied generation to generation, the average of the population shifts over time, moving away from the disadvantageous extreme.
  - Such selection acts against one tail of the bell curve.
  - E.g. in artificial selection where the dairy farmer eliminates the low milk-producing cows to boost the herd and increase average milk production.

- **Stabilising selection / Normalising selection**
  - The extremes are disadvantageous and eliminated, leaving the intermediate phenotypes favoured and preserved by comparison.
  - Applied from generation to generation, variation in the trait is reduced and the population becomes more uniform.
  - E.g. in humans, infants with intermediate weight (3-4 kg) at birth enjoy the highest survival rate.

- **Disruptive selection / Diversifying selection**
  - When intermediate phenotypes are at a disadvantage, selection is disruptive.
  - Individuals with traits in the middle tend to be eliminated, dividing the population between the extremes.
  - The result is to produce mostly individuals with characters at the two extremes of the bell curve distribution.
  - This condition is referred to as **polymorphism**, meaning that in the same species, **two or more conspicuous and distinctive forms occur in abundance**.
  - E.g. a population of black-bellied seedcracker finches in Cameroon whose members display two distinctly different beak sizes.

Regardless of the mode of selection, however, the basic mechanism remains the same. Selection favours individuals whose heritable phenotypic traits provide higher reproductive success than do the traits of other individuals.



from Miller 12th **Brooks Cole**

### (c) Isolation mechanisms for speciation

There are three main isolating mechanisms which give rise to speciation, namely, **geographical isolation**, **physiological isolation** and **behavioural isolation**.

- Geographical isolation gives rise to **allopatric speciation**:
  - In **allopatric speciation**, gene flow is interrupted when a **population is divided into geographically isolated subpopulations**.
  - Geographic barrier will promote **allopatric speciation**.
  - Once geographic separation has occurred, the separated gene pools may diverge. Different mutations arise, and natural selection and genetic drift may alter allele frequencies in different ways in the separated populations. Reproductive isolation may then arise as a by-product of selection or drift having caused the populations to diverge genetically
  - For e.g., the water level in a lake may subside, resulting in two or more smaller lakes they are now home to separated populations.
  - E.g. allopatric speciation of antelope squirrels on opposite rims of the Grand Canyon. Harris's antelope squirrel (*Ammospermophilus harrisi*) inhabits the canyon's south rim while just a few kilometres away on the north rim lives the closely related white-tailed antelope squirrel (*Ammospermophilus leucurus*).

- Physiological and behavioural isolation gives rise to **sympatric speciation**:
  - In sympatric speciation, speciation occurs from **a population that lives in the same geographic area and gene flow is interrupted by reproductive barriers**.
    - **Physiological** barrier in reproduction:

      **Mating is attempted but morphological differences prevent its successful completion**.
      - E.g. the shells of two species of snails in the genus *Bradybaena* spiral in different directions: moving inward to the centre, one spirals in the counter-clockwise direction, the other in the clockwise direction. As a result, the snails' genital openings are not aligned and mating cannot be completed.
    - **Behavioural** barrier in reproduction:

      **Courtship rituals that attract mates and other behaviours unique to a species** are effective reproductive barriers, even between closely related species. Such behavioural rituals enable mate recognition – a way to identify potential mates of the same species:
      - E.g. blue-footed boobies, inhabitants of the Galapagos, mate only after a courtship display unique to their species. Part of the "script" calls for the males to high-step, a behaviour that calls the females' attention to his bright blue feet.

### (d) The Neo-Darwinian revolution

Darwin actually knew very little about genetics. The great pioneer of genetics was Gregor Mendel, whose work was contemporary with Darwin's.

Now **the theory of evolution incorporates Mendel's genetics into Darwin's framework; the combined theory was called neo-Darwinism.**

As Lynn Margulis puts it, neo-Darwinism is an attempt to reconcile Mendelian genetics, which says that organisms do not change with time, with Darwinism, which claims they do.

According to this paradigm, **evolution is driven by chance**.

**Chance mutations** affect one or a few nucleotides of DNA per occurrence.

Bigger changes come from **recombination** through **crossing over of non-sister chromatids of homologous chromosomes** and **independent assortment of bivalents**. According to the prevailing paradigm, this is the mechanism behind evolution.

## 5. Evidence of Evolution

### (a) Biogeography

**Biogeography** refers to the **geographic distribution of species**.

The geographic distribution of organisms is influenced by many factors, including **continental drift**, which is the slow movement of Earth's continents over time.

Theories of biogeography incorporate Darwin's assumption and further postulate that each **species of fauna and flora originated only once at the Centre of Origin** and from there each species diversified via natural selection, as the continents drifted apart.

An example of how biogeography supports the theory of evolution is through the study of the endemic species:

- Islands generally have many species of plants and animals that are **endemic**, which means they are **found nowhere else in the world**.
- Yet, as Darwin described in his book, **most island species are closely related to species from the nearest mainland** or a neighbouring island.
- He explained this observation by suggesting that islands are colonized by species from the nearest mainland. These colonists **eventually give rise to new species as they adapt to their new environments**.
- Such a process also explains why two islands with similar environments in different parts of the world are populated not by closely related species but rather by species that resemble those of the nearest mainland, where the environment is often quite different.

An example of how biogeography supports the theory of evolution is through the study of the distribution of marsupials across the world:

- There are two primary divisions of marsupials: American marsupials and the Australian marsupials.
- Marsupials probably evolved first in North America and reached Australia via South America and Antarctica while the continents were still joined.
- The subsequent drifting of the southern continents set Australia apart and thus marsupials on this continent evolved and diversified independently of other marsupials found on other continents.
- In Australia, marsupials diversified, and the few eutherians (placental mammals) that lived there became extinct; on other continents, most marsupials became extinct, and the eutherians diversified.

## Continental Drift and Distribution of Species

The history of Earth helps to explain the current geographical distribution of species. The drifting of continents is a major geographic factor correlated with the spatial distribution of life. The continents are not fixed, but drift about the Earth's surface. Unless two landmasses are embedded in the same plate, their positions relative to each other will change.

This is known as the continental drift theory. Plate movements rearrange geography incessantly, and there were two major periods in the history of Earth which had profound influence on the distribution of species.

About 250 million years ago (end of Paleozoic era), plate movements brought all the landmasses together into a supercontinent (that has been named Pangaea).

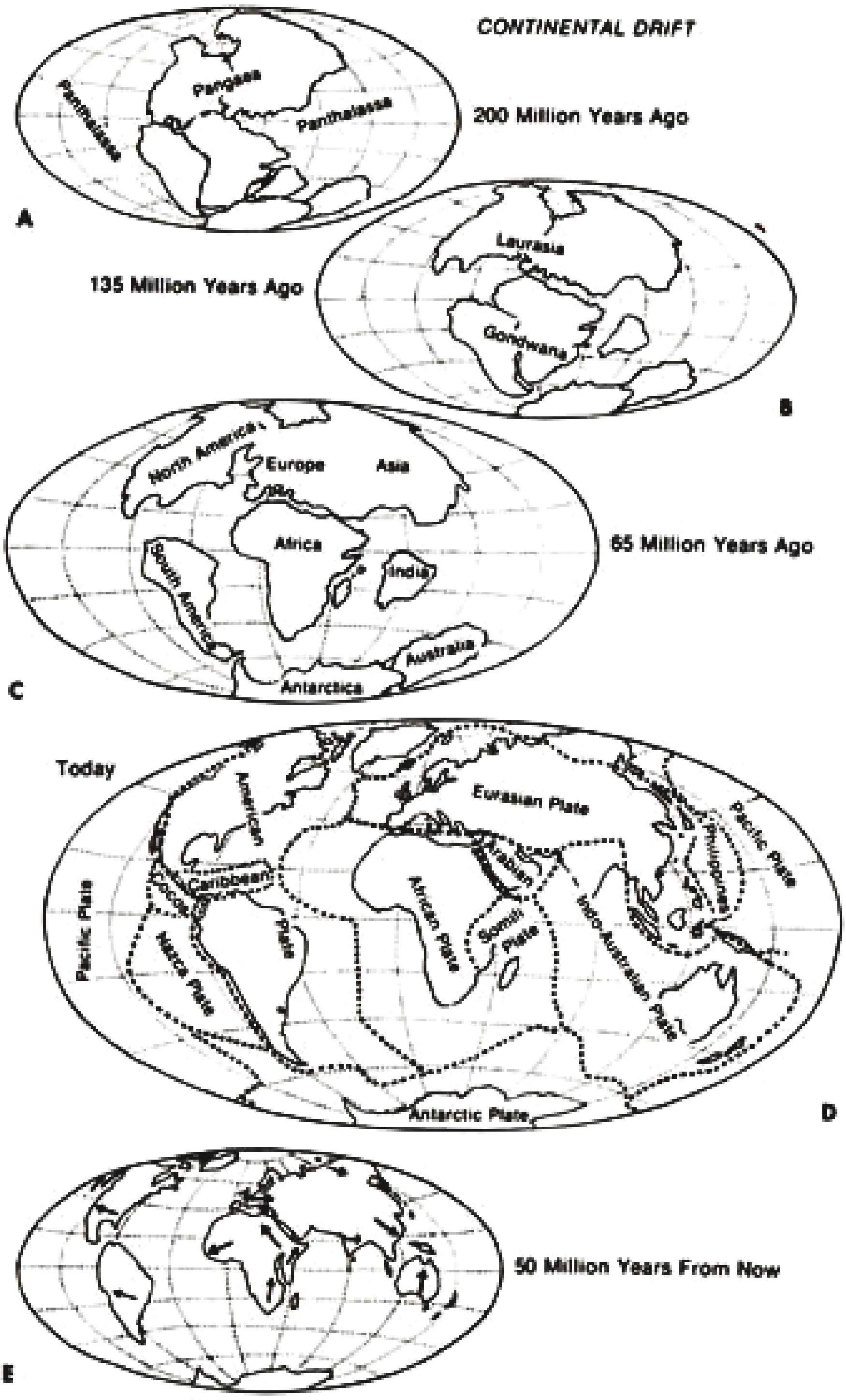
This event resulted in some major effects on life.

- Species that had been evolving in isolation come together and competed.
- As land masses united, the total amount of shoreline was reduced, ocean basins increased in depth, sea level lowered and shallow coastal seas drained.
- Formation of Pangaea destroyed a considerable amount of the marine habitat, thus affecting the survival of much marine life.
- The continental interior, which has a drier and more erratic climate than coastal regions, increased in area substantially as the land masses come together.
- The formation of Pangaea had a tremendous impact on diversity by causing extinctions and providing new opportunities for taxonomic groups that survived the crisis.

The second major event occurred about 180 million years ago, during the Mesozoic era, where Pangaea started to break up into two landmasses, namely Gondwana and Laurasia. This event also had major effects on the distribution of organisms on Earth.

- As continents drifted apart, each became a separate evolution ground, and the floras and faunas of the different biogeographic realms diverged.
- Palaeontologists have discovered matching fossils of Triassic reptiles in Ghana and Brazil. These two parts of the world, which are currently separated by 3000km of ocean, were joined together during the early Mesozoic era.

Continental drift also promotes allopatric speciation on a grand scale. When supercontinents break apart, regions that once were connected become geographically isolated.



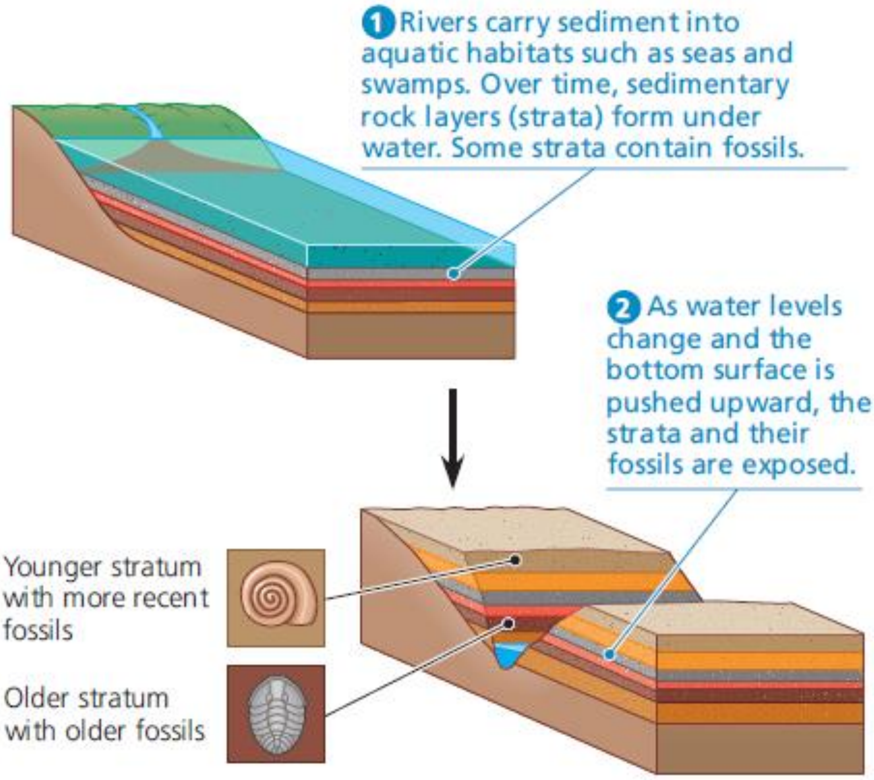
**Movement of landmass due to continental drift**

## (b) Fossil records

A second type of evidence for evolution comes from fossils.

**Fossils** are the **preserved remains or traces of animals, plants, and other organisms from the remote past**. Fossil record documents the pattern of evolution, showing that past organisms differed from present-day organisms and that many species have become extinct. Fossils show the evolutionary changes that have occurred over time in various groups of organisms.

Over longer time scales, **fossils document descent with modification, in a sequential order**. **More recent geological strata generally contain fossils of organisms that are more similar to the present organisms than do the older strata**. Thus, the homologies seen in fossil evidence does provide a strong support for evolution.



❶ Rivers carry sediment into aquatic habitats such as seas and swamps. Over time, sedimentary rock layers (strata) form under water. Some strata contain fossils.

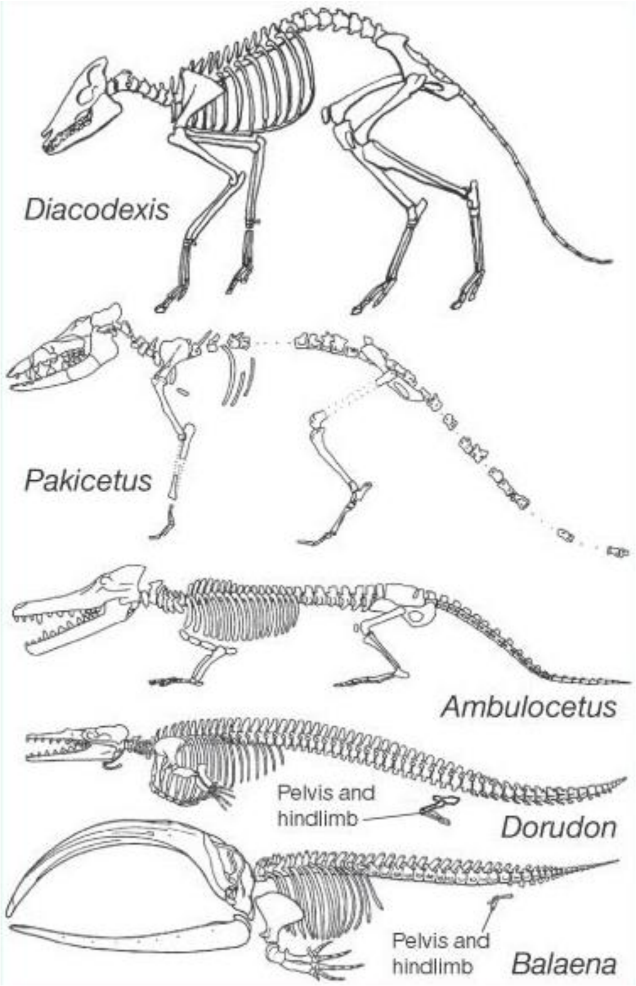
❷ As water levels change and the bottom surface is pushed upward, the strata and their fossils are exposed.

▲ **Figure 22.3 Formation of sedimentary strata with fossils.**

The order of fossils in rock strata tells us the sequence in which the fossils were laid down indicating their relative ages - it does not tell us their actual (absolute) ages. One of the most common techniques is **radiometric dating**, which is based on the decay of radioactive isotopes.

Fossil records show the emergence of simple bacteria, followed by eukaryotes and then multi-cellular organisms. Within vertebrates, fish arose first, then amphibians, then reptiles, within which arose birds and separately mammals. The fossil record holds evidence to this ordered sequence.

An example is the fossil record of early cetaceans, the mammalian order that includes whales, dolphins and porpoises. The earliest cetaceans lived 50 – 60 million years ago. The fossil record indicates that prior to that time, most mammals were terrestrial. Although scientists had long realised that whales and other cetaceans must have originated from land mammals, few fossils had been found that revealed how cetacean limb structure had changed over time, leading eventually to the loss of hind limbs and the development of flippers. In the past few decades, however, a series of remarkable fossils have been discovered in Pakistan, Egypt, and North America that document the transition from life on land to life in the sea. Each of these organisms differs from present-day mammals, and is now extinct. Collectively, these and other early fossils document the formation of new species and the origin of a major new group of mammals, the cetaceans.

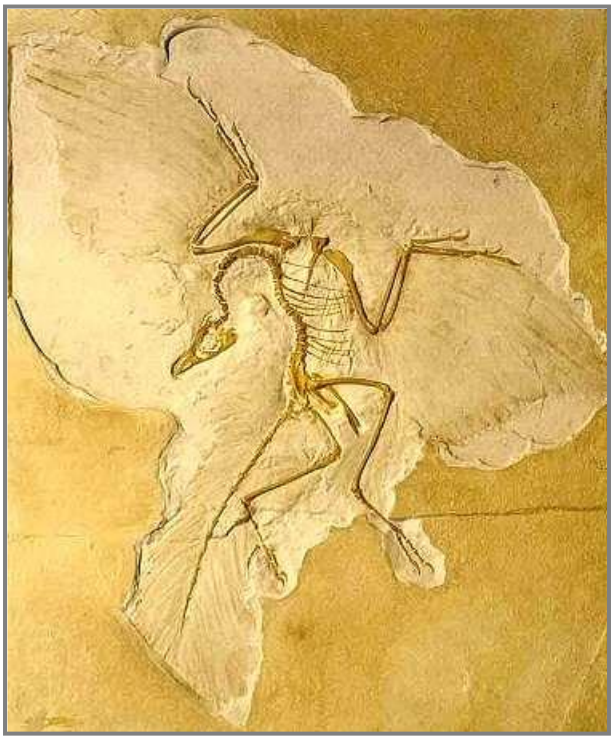


**The transition to life in the sea**

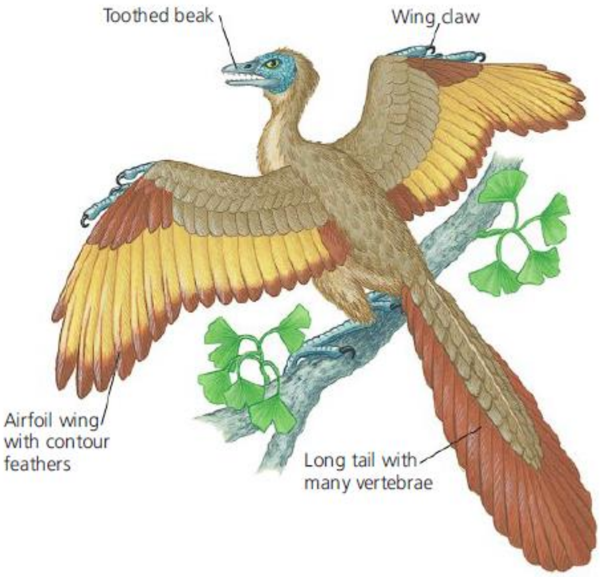
It has been hypothesized that whales and other cetaceans evolved from terrestrial organisms which were four-legged. *Pakicetus* was a terrestrial organism, while *Rhodeocetus* was predominantly aquatic and *Dorudon* was fully aquatic. *Balaena* is believed to be the most recent ancestor of whale.

(adapted from https://eapbiofield.wikispaces.com/file/view/413259aa.2.jpg)

## More Examples of Fossil Records



### Example 1: *Archaeopteryx* fossil

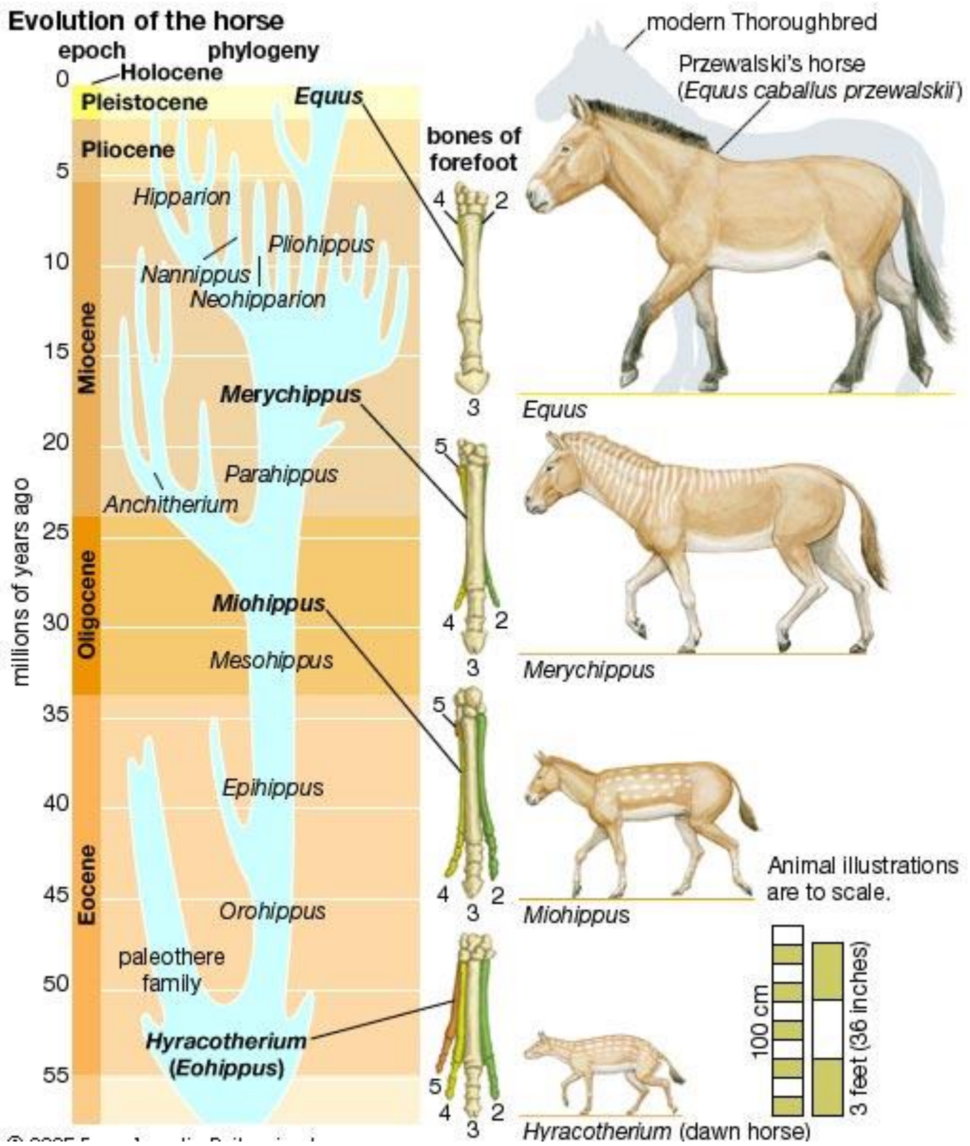


▲ Figure 34.31 **Artist's reconstruction of *Archaeopteryx*, the earliest known bird.** Fossil evidence indicates that *Archaeopteryx* was capable of powered flight but retained many characters of nonbird dinosaurs.

- Discovered in 1861 and was postulated to be the missing link between reptiles and birds.
- The fossil had a number of reptilian features such as teeth, a tail of 21 vertebrae and a number of bird-like features such as wishbone and feathers.
- It had feathered wings but retained ancestral characters such as teeth, clawed digits in its wings, and a long tail.
- Arguments were put forward to suggest that the *Archaeopteryx* is a distant 'cousin' to the lineage running from reptiles (dinosaurs) to birds.

**Example 2: Fossils of North American and European horses**

- By 1870s, paleontologists were able to provide classic examples of step-wise evolutionary tree among vertebrates.
- We now know almost all the intermediate stages between *Hyracotherium* and the modern horse *Equus*, from low-crowned to high-crowned, from browsers to grazers, from pad-footed to spring-footed and from small-brained to large-brained.
- There is a progressive trend toward **<u>larger size</u>**, **<u>reduced number of toes</u>**, and **<u>teeth modified for grazing</u>**.
- Evolutionary changes also did not go in a single direction. Horses evidently evolved adaptations for their habitats in different ways, with some individual branches maintaining fairly distinct structures until they became extinct.

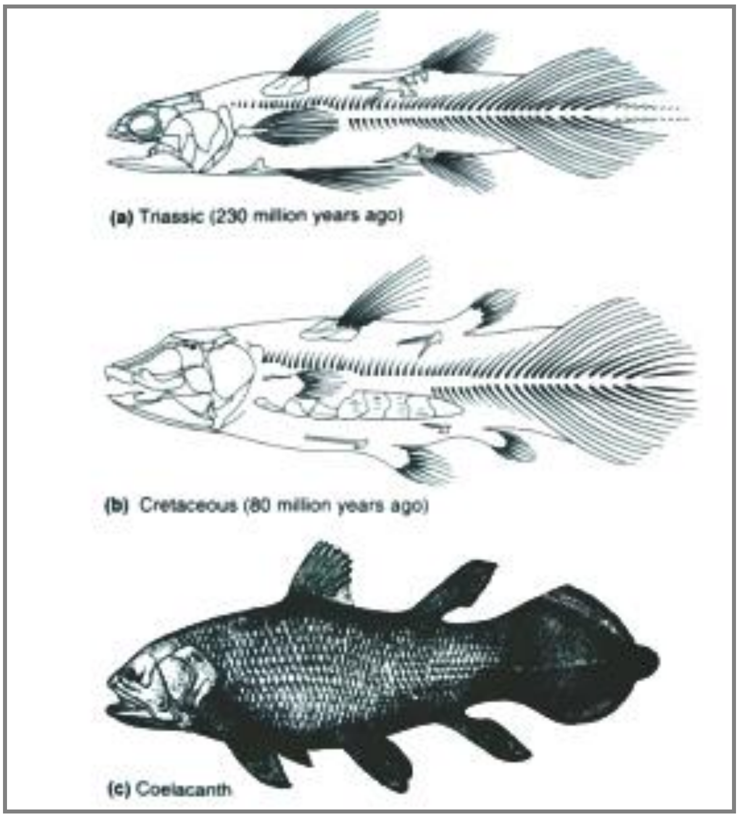


**Evolution of the horse over the past 55 million years**

The present-day Przewalski's horse is believed to be the only remaining example of wild horse, i.e., the last remaining modern horse to have evolved by natural selection. Numbered bones in the forefoot illustrations trace the gradual transition from a **<u>four-toed to a one-toed</u>** animal. (Adapted from http://concise.britannica.com/ebc/art-47479)

### Example 3: Living fossils

- Some ancient organisms may persist to modern times without further evolving morphologically. E.g. opossums, alligators, sturgeons, lungfish, horseshoe crabs, gingko trees
- Occasionally biologists discover species remarkably similar to organisms believed to have become extinct many years ago.
- E.g. coelacanths are lobe-finned fishes related to those which evolved to terrestrial vertebrates about 200 million years ago. Although fossil record of coelacanths seemed to have begun in the Devonian period (about 380 million years ago and ended 80 – 100 million years ago), fishermen have found live coelacanths (*Latimeria chalumnae*) in deep waters off the eastern coast of South Africa.



**Coelacanths of different periods**

(a) Fossil lobe-finned coelacanth (*Laugia groenlandica*) from the Lower Triassic period, about 230 million years ago.

(b) *Macropoma mantelli* from the Upper Cretaceous period, about 80 million years ago.

(c) *Latimeria chalumnae*, modern coelacanth found off the eastern coast of South Africa.

## (c) Homology

A third type of evidence for evolution comes from analyzing similarities among different organisms. Such **similarity resulting from common ancestry** is known as **homology**.

Evolution is a process of **descent with modification**, i.e. characteristics present in an ancestral organism are altered by natural selection in its descendants over time as they face different environmental conditions. As a result, related species can have characteristics with an underlying similarity even though they may have very different functions.

Homology should not be confused with ‘analogy’ or ‘homoplasy’.

- Analogy refers to features with a similar function but not common descent.
    - A forest-dwelling Australian marsupial called the sugar glider is superficially very similar to flying squirrels, which are gliding eutherians that live in North American forests. But the sugar glider has many other characteristics that make it a marsupial rather than a eutherian. Although they evolved independently from different ancestors, these two mammals have adapted to similar environments in similar ways.
- Homoplasy refers to features that simply look alike but may or may not be homologous or analogous.
    - Some insects have wings shaped like leaves. Such wings function in flight but not in photosynthesis (thus not analogous to leaves), and do not share a common ancestor (thus not homologous to leaves). However, outwardly, they have a similar appearance to leaves, thus they are homoplastic.

The Darwinian view of life predicts that different kinds of homologies – anatomical, embryological, and molecular – will fall into the same hierarchical pattern because they have all evolved during the same branching pattern of evolutionary history.

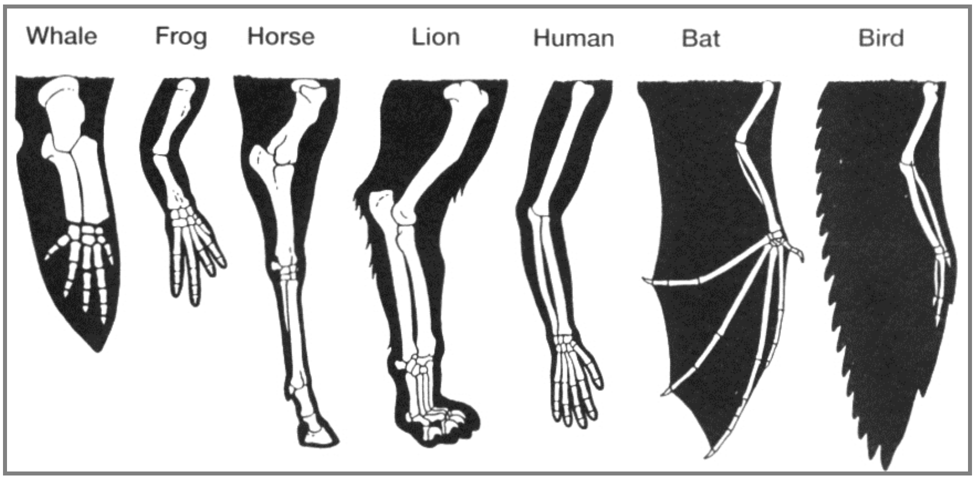
### (i) Anatomical

Comparisons of anatomical features of different organisms often provide evidence to support the theory of evolution. Much of palaeontology is based on comparative anatomy between extinct (through fossils) and existing organisms.

Comparative study of anatomical structures within a particular group of organisms often reveals that they are **based upon a common prototype** which varies with the organisms' particular environment. Since organisms are modified from ancestors, they retain the basic, underlying features of their ancestors, and **modify these features for different functions**.

Comparative anatomy also allows a **morphological series** to be constructed. The morphological series **tracks the modification to ancestral prototype through time, from one species to the next**, thus supporting Darwin's concept of descent with modification. Fossil records enable us to track these changes through time, confirming their ordered sequence of emergence based on comparative anatomy.

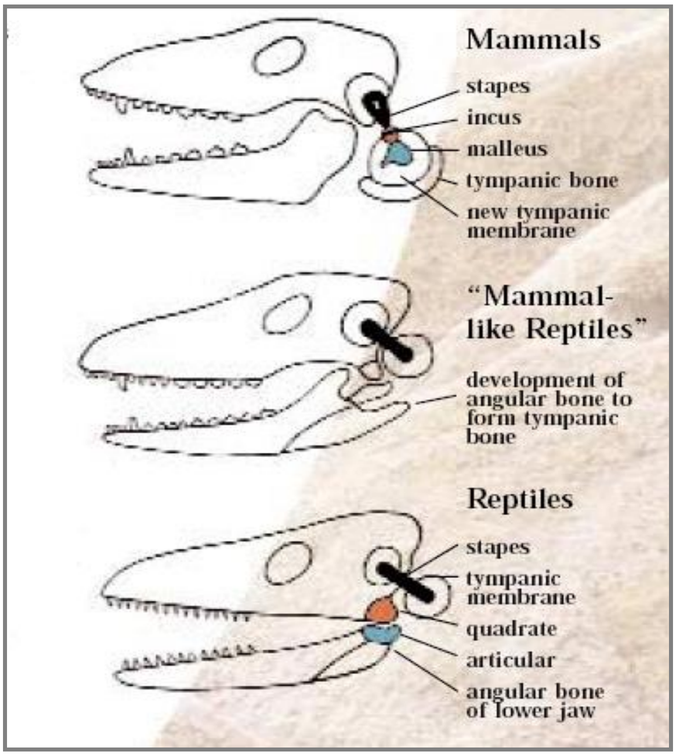
- Example 1: **Mammals** such as bats, humans, whale retain the same, underlying basic pattern of their **forelimbs**. Although suited to different functions, all possess a **humerus, forearm and wrist with digits**. They show the same arrangement of bones from the shoulder to the tips of the digits, even though these appendages have very different functions: lifting, walking, swimming, and flying. Such striking anatomical resemblances would be highly unlikely if these structures had arisen anew in each species. Rather, the underlying skeletons of the arms, forelegs, flippers, and wings of different mammals are **homologous structures** that represent variations on a structural theme that was present in their common ancestor.



**Vertebrates' forelimbs: homologous structures**

- Example 2: The vertebrate column demonstrates how, within a single phylum, an organ system seems to be based upon a prototype that is varied simply from class to class. Throughout the vertebrates, the column has become modified within each group. However, they all share a common ancestor which had the prototypic column.

- Example 3: In reptiles, the lower jaw is made up of several bones on each side and there is only one ear bone, the stapes, on each side. In mammals, the lower jaw is made up of only one bone on each side and the other jaw bones have taken on new functions in the middle ear. The reptilian articular bone becomes the malleus bone of the middle ear of mammals and the quadrate bone of the reptilian jaw becomes the incus bone of the middle ear of mammals. The angular bone is lost. This suggests that mammals evolved from reptiles.

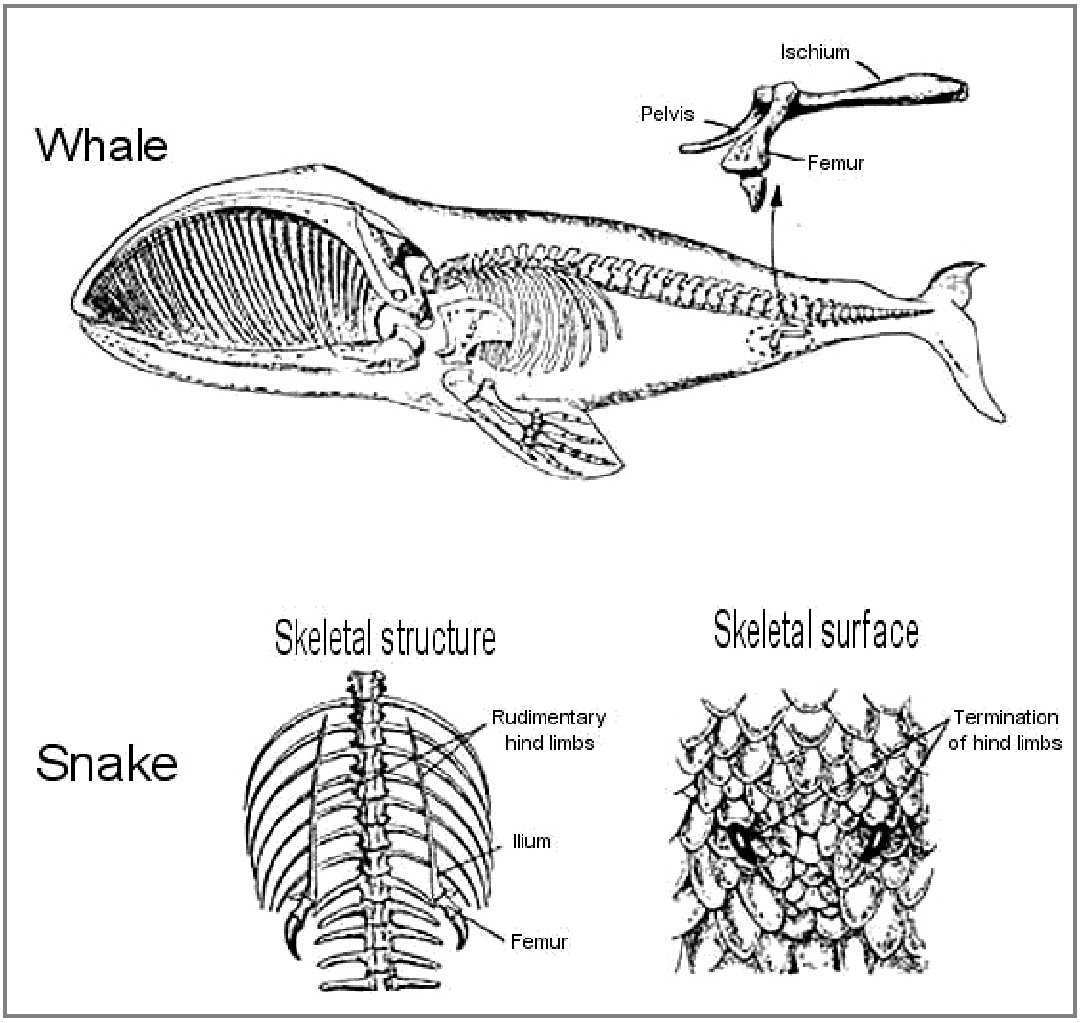


**Changes in the jaw articulation and the ear region in the evolution from reptile to mammal**

## Vestigial Structures

**<u>Vestigial structures</u>** are remnants of features that served important functions in the organism's ancestors. The study of vestigial structures also shed light on the evolutionary history of organisms as vestigial structures are evolutionary structures, reduced from a prominent role in an ancestor and passed in a reduced role to more recent descendants.

- Whales evolved from four-footed land ancestors. However, they now live exclusively in water, guided by flippers modified from the forelimbs of their ancestors. Whale hips and hind limbs are just vestiges, buried under the skin without a major function.
- Primitive snakes also possess vestigial hind limbs, leftovers of the supportive hind limbs from their lizard ancestors.
- Humans possess many vestigial structures that suggest our evolutionary link to our ancestors.
  - Humans possess an appendix, a short, blind-ended pouch that apparently lacks any significantly digestive function.
  - The amazing gripping power of the hands of human infants is also a vestigial trait. This is because other primates develop it further for the grasping of tree branches and for their infants to cling tightly to their mothers.
  - Humans possess reduced tail bones and a few tail muscles, rudimentary body hair and wisdom teeth.



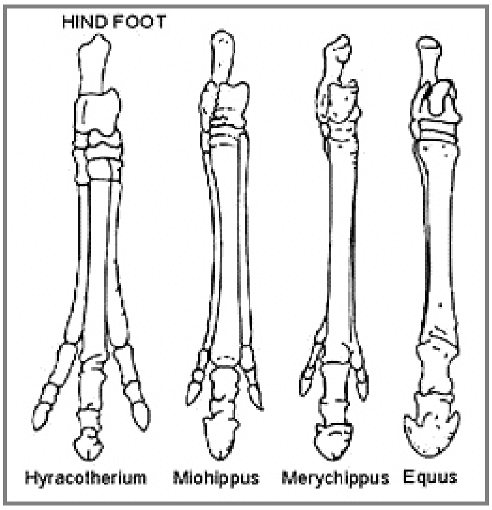
**Rudimentary hind limbs in the Greenland whale and python snake**

## Atavistic Structures

**Atavistic structures** are structures that were typical of ancestors and have disappeared for generations but occasionally appear in its descendents.

Atavism would not be expected if each species were created separately. However, if descent with modification is how evolution occurred, the sudden, occasional appearance of ancestral parts is expected. Current mistakes of genetics or embryology reactivate and express these ancestral parts because remnants of the original genetic code are inherited by current species.

- Occasionally, additional toes appear on single-toed horses. These extra toes are mal-adaptive for the fleet and efficient locomotion horses employ across open plains. However, an embryonic mistake has returned these ancient features.



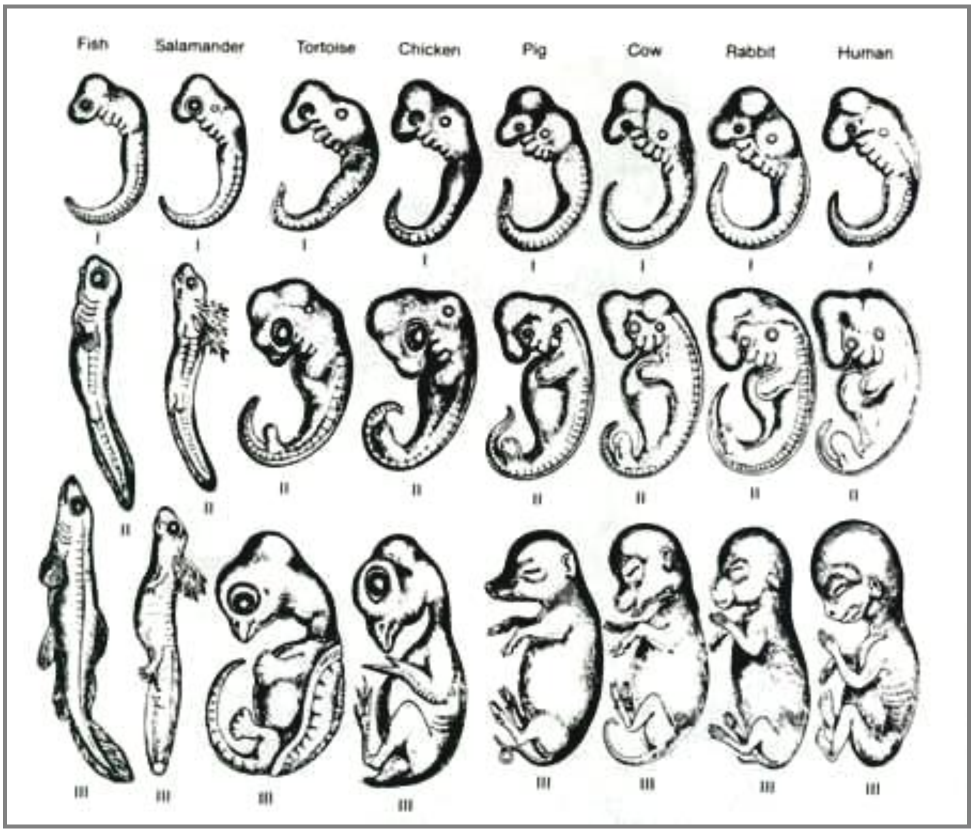
**'Lost' toes reappearing in a modern horse (*Equus*)**

### (ii) Embryological

Comparing embryological development in different species reveals additional anatomical homologies not visible in adult organisms.

For example, all vertebrate embryos have a **tail located posterior to the anus**, as well as structures called **pharyngeal pouches**. These homologous throat pouches ultimately develop into structures with very different functions, such as gills in fishes and parts of the ears and throat in humans and other mammals.

Thus homology shows that there is historical continuity between vertebrates as we find remnants of structures carried forward by evolution. Within embryology, the **remnants of ancestors persist in the embryos of descendants**.



**Embryonic retention of ancestral characteristics**

Note the persistence of gill slits in early stages of embryonic development in mammals. Also note that a tail is present early in humans but lost before birth.

(http://www.schoolhousevideo.org/Media/embryology.jpg)

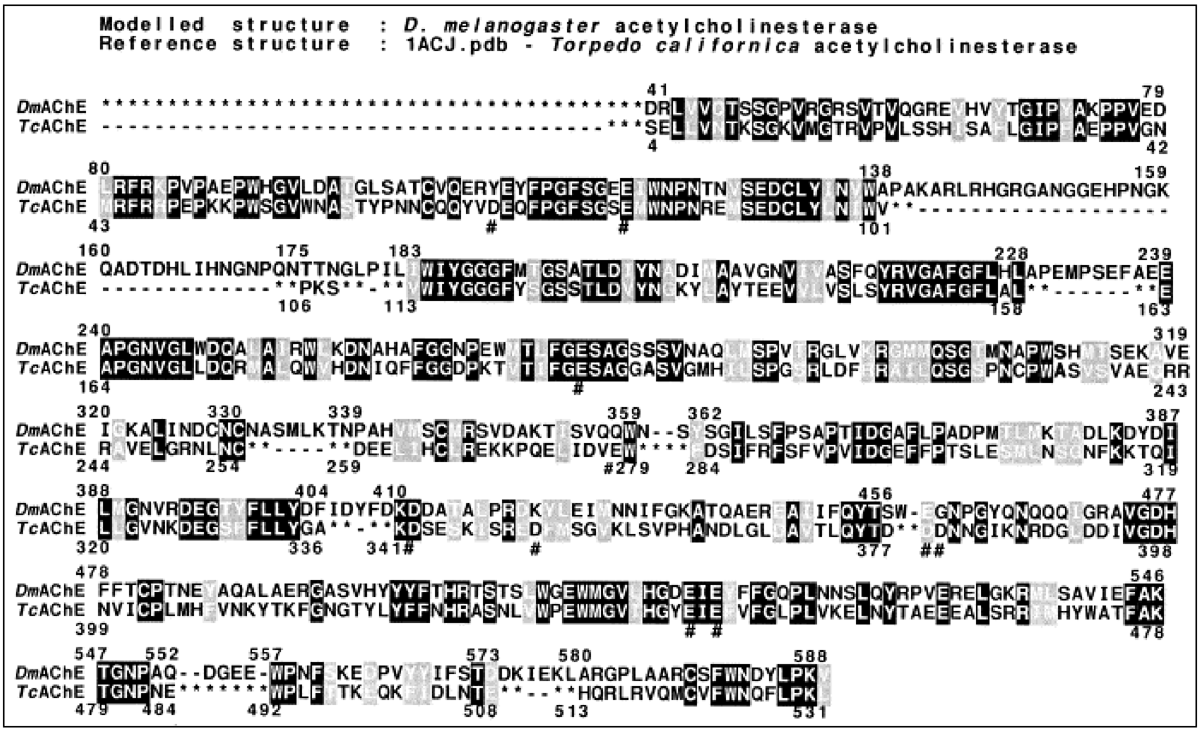
### (iii) Molecular

Biologists observe similarities among organisms at the molecular level. **All forms of life use the same genetic language of DNA and RNA**, and the **genetic code is essentially universal**.

Thus, it is **likely that all species descended from common ancestors that used this code**.

But molecular homologies go beyond a shared code. Two species that share a DNA base sequence (and also the specific protein coded for) probably have a common ancestor. For example, organisms as dissimilar as humans and bacteria share genes inherited from a very distant common ancestor. Like the forelimbs of humans and whales, these genes have often acquired different functions.

The **amino acid sequences between two related organisms will vary least as compared to their DNA sequences**. This is because DNA sequences are known to contain numerous non-coding regions and these regions may vary greatly even between two related organisms. Therefore it is more accurate to carry out amino acid sequence homology analysis rather than DNA sequence homology analysis. However, amino acid sequences of most organisms are not as readily available as their DNA sequences.

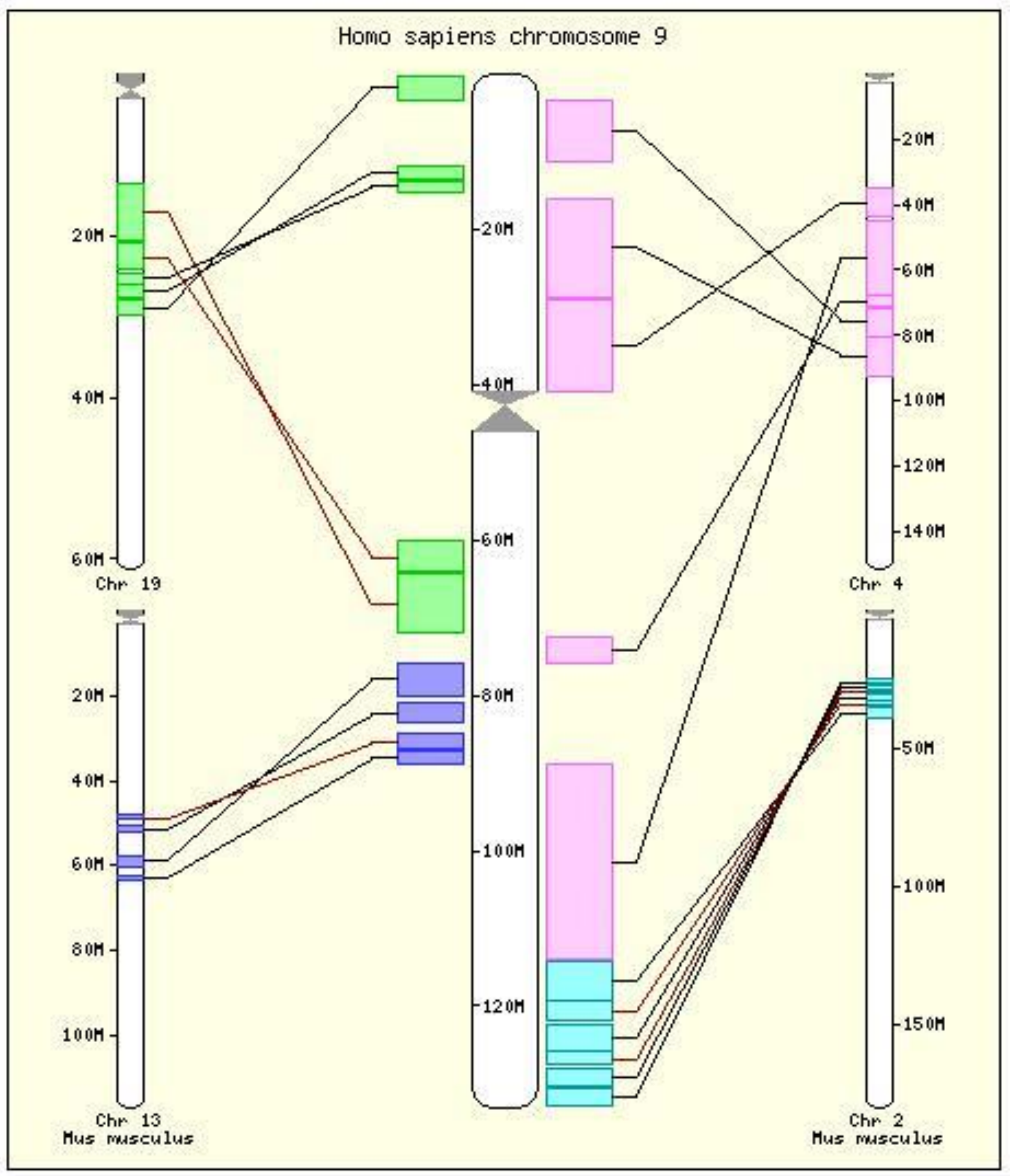


**Analysis of amino acid sequence of acetylcholinesterase from two species (*D. melanogaster* and *T. californica*) using a computer software.**

Each letter indicates a particular amino acid, for e.g. V stands for valine. Letters highlighted in black indicate exact matches between the two species.
(http://www.weizmann.ac.il/sb/faculty_pages/Sussman/papers/science_files/0_014.gif)

| Species | No. of amino acids that differ from a human haemoglobin polypeptide (Total chain length = 146 a.a.) |
|---|---|
| Human | 0 |
| Rhesus monkey | 8 |
| Mouse | 27 |
| Chicken | 45 |
| Frog | 67 |
| Lamprey | 125 |

**Molecular data and the evolutionary relationships of vertebrates**



**Synteny map showing conserved regions between human chromosome 9 and house mouse (*Mus musculus*) chromosomes 2, 4 13 and 19**

## 3. Preservation of Genetic Variation in Natural Populations

Variation is found at loci affected by selection. What prevents natural selection from reducing genetic variation at those loci by culling all unfavorable alleles?

Even though unfavourable traits are eliminated by the process of natural selection, variation within a population still remains. The tendency for natural selection to reduce variation is countered by mechanisms that preserve or restore variation.

### (a) Diploidy

- **The diploid nature of most eukaryotes hides a considerable amount of genetic variation from selection in the form of recessive alleles in heterozygotes**.
- Recessive alleles that are less favourable than their dominant counterparts, or even harmful in the present environment, can persist in a population through their propagation by **heterozygous** individuals.
- The latent variation is exposed to selection only when each parent carries the same recessive allele and combines the two copies in their zygote, i.e. homozygous recessive condition.
    - This happens only rarely if the frequency of the recessive allele is very low.
    - The rarer the recessive allele, the greater the degree of protection from natural selection.
- Heterozygote protection maintains a huge pool of alleles that may not be suitable for present conditions but could bring new benefits when the environment changes.

### (b) Balanced polymorphism

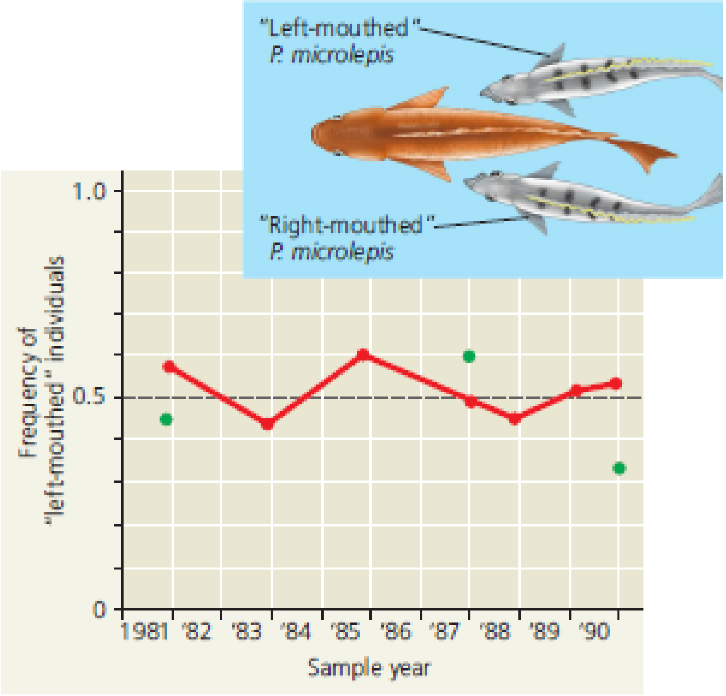
- It is the ability of **natural selection** to maintain stable frequencies of **two or more phenotypic forms in a population**.
- Natural selection preserves variation by two mechanisms, **heterozygote advantage** and **frequency-dependent selection**.

    - **Heterozygote advantage**:
        - **If individuals who are heterozygous at a particular gene locus have greater fitness than any type of homozygote, then two or more alleles will be maintained at that locus by natural selection**.
        - E.g. recessive allele in the β-globin gene locus results in sickle-cell anaemia in homozygous individuals. Heterozygotes are resistant to malaria, an advantage in tropical regions. The environment favours heterozygotes over homozygous dominant individuals who are susceptible to malaria and homozygous recessive individuals who suffer from sickle-cell anaemia.

- **Frequency-dependent selection**:
    - **The survival and reproduction of any one morph declines if that phenotypic form becomes too common in the population.**
    - The fitness of a phenotype depends on how common it is in the population.
    - E.g. the scale-eating fish (Perissodus microlepis) of Lake Tanganyika, in Africa. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. A peculiar feature of the scale-eating fish is some are left-mouthed and some are right-mouthed. Simple Mendelian inheritance determines these phenotypes, with the right-mouthed allele being dominant to the left-mouthed allele.

      Because their mouth twists to the left, left-mouthed fish always attack their prey's right flank. Similarly, right-mouthed fish always attack from the left.

      Prey species guard against attack from whatever phenotype of scale-eating fish is most common in the lake. Thus, from year to year, selection favors whichever mouth phenotype is least common. As a result, the frequency of left and right-mouthed fish oscillates over time, and balancing selection (due to frequency dependence) keeps the frequency of each phenotype close to 50%.



    - E.g. natural selection may favour non-poisonous butterflies that have the same colour pattern as poisonous butterflies. This system is called Batesian mimicry. It is a form of mimicry typified by a situation where a harmless species has evolved to imitate the warning signals of a harmful species directed at a common predator. When they are rare, birds will tend to avoid the mimics, because they will already have encountered a poisonous butterfly of the same appearance. But when the non-poisonous type becomes common, the previous encounters of birds with butterflies of their appearance are more likely to have been rewarding; the birds will not avoid eating them, and their fitness will be lower. The fitness of the mimics is negatively frequency-dependent.

### (c) Neutral mutations

- Much of the DNA variation in populations probably has little or no impact on reproductive success, and thus natural selection does not affect this DNA.
- Some of the genetic variation in populations represents neutral variation, differences in DNA sequence that do not confer a selective advantage or disadvantage.
- **Many of the nucleotide differences in non-coding sequences appear to confer no selective advantage or disadvantage** and therefore considered **neutral variation**.
- Over time, the **frequencies of alleles are not affected by natural selection** but may increase or decrease as a result of **genetic drift**.

## 7. The Neutral Theory of Molecular Evolution

During the last few decades, there is a debate among population and evolutionary geneticists, whether genetic variation in natural populations is due primarily to mutations that are favoured by natural selection or to random genetic events.

A non-neutral mutation is one that affects the phenotype of the organism and can be acted on by natural selection. A non-neutral mutation may only subtly alter the phenotype of an organism, or it may have major impact.

According to Darwin, natural selection is the agent that leads to evolutionary change in populations. It selects for the survival of the fittest and thereby promotes the establishment of beneficial alleles and the elimination of deleterious ones. Therefore, many geneticists have assumed that natural selection is the dominant force in changing the genetic composition of natural populations, thereby leading to variation.

However, Motoo Kimura proposed the **neutral theory of molecular evolution**:

- **Genetic variation observed in natural populations is due to the accumulation of neutral mutations**.
- **Neutral mutations do not affect the phenotype of the organism thus are not acted on by natural selection.** This arises due to the **degeneracy of the genetic code**.
- This theory has been called the **survival of the luckiest** and also non-Darwinian evolution to contrast it with Darwin's survival of the fittest.
- Kimura agrees with Darwin that natural selection is responsible for adaptive changes in a species during evolution.
- His main argument is that most modern variation in gene sequences in explained by neutral variation rather than adaptive variation.

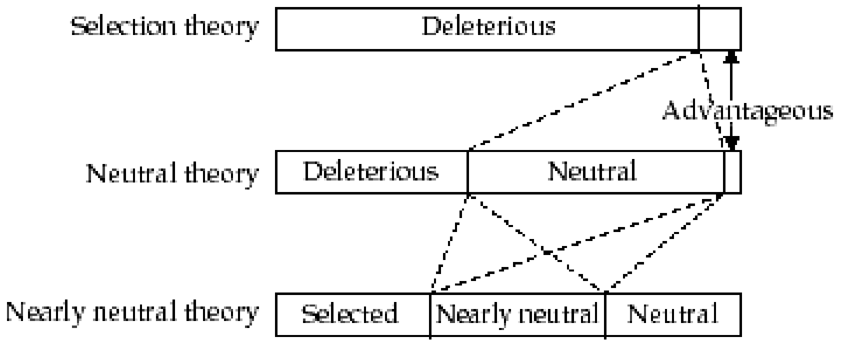


**Figure 1.1** A diagram showing the comparison between the selection, neutral, and nearly neutral theories based on the proportion of various classes of mutations.

### (a) Genetic drift

**Genetic drift** is a **process where chance events can cause allele frequencies to fluctuate unpredictably from one generation to the next, especially in small populations**.

Certain circumstances can result in genetic drift having significant impact on a population. Two examples are **founder effect** and **bottleneck effect**.

- **Founder effect**:
  - Arises when **a few individuals become isolated from a larger population, and this smaller group may establish a new population whose gene pool differs from the source population**.
  - The isolation mechanism **indiscriminately** chooses some individuals, but not others, from the source population.
  - E.g. the founder effect probably accounts for the relatively high frequency of certain inherited disorders among isolated human populations.

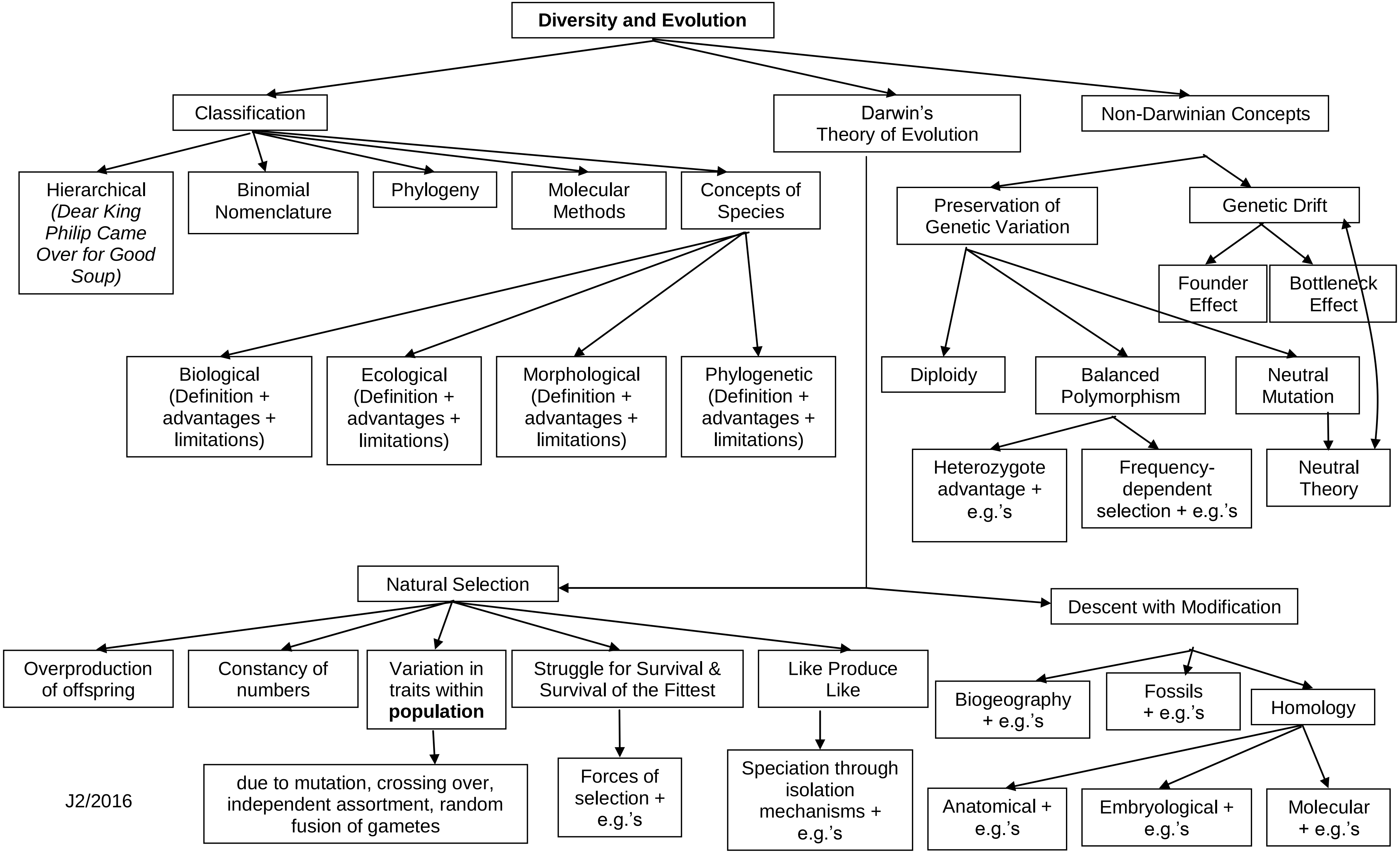
    For example, in 1814, 15 British colonists founded a settlement on Tristan da Cunha, a group of small islands in the Atlantic Ocean midway between Africa and South America. Apparently, one of the colonists carried a recessive allele for retinitis pigmentosa, a progressive form of blindness that afflicts homozygous individuals. Of the founding colonists 240 descendants on the island in the late 1960s, 4 had retinitis pigmentosa. The frequency of the allele that causes this disease is ten times higher on Tristan da Cunha than in the populations from which the founders came.

- **Bottleneck effect**:
  - Arises due to a **sudden change in the environment which may drastically reduce the size of a population**.
  - **By chance alone, certain alleles may be over-represented among the survivors, others may be under-represented, and some may be absent altogether**.
  - The sudden change in the environment can be caused by disasters like fire or flood.
  - Ongoing genetic drift is likely to have substantial effects on the gene pool until the population becomes large enough that chance events have less impact. But even if a population that has passed through a bottleneck ultimately recovers in size, it may have low levels of genetic variation for a long period of time a legacy of the genetic drift that occurred when the population was small.

## (b) Molecular clock

- A **molecular clock** is **a yardstick for measuring the absolute time of evolutionary change based on the observation that some genes and other regions of genomes appear to evolve at constant rates**.
- The assumption underlying the molecular clock is that **the number of nucleotide substitutions in genes is proportional to the time that has elapsed since the species branched from their common ancestor**.
- The molecular clock of a gene that has a reliable average rate of evolution can be **calibrated by graphing the number of genetic differences against the dates of evolutionary branch points that are known from the fossil record**.
- Limitations:
  - Some portions of the genome appear to have evolved in irregular fits and starts that are not at all clock-like.
  - Genes that seem to have reliable molecular clocks are accurate only in the statistical sense of showing a fairly smooth average rate of change. Over time, there may still be chance deviations above and below that average rate.
  - The same gene may evolve at different rates in different groups of organisms, making it necessary to calibrate and use molecular clocks with care.

Even among genes that are clock-like, the rate of the clock may vary greatly from one gene to another; some genes evolve a million times faster than others.



**Diversity and Evolution**

Classification

Darwin's Theory of Evolution

Non-Darwinian Concepts

Hierarchical *(Dear King Philip Came Over for Good Soup)*

Binomial Nomenclature

Phylogeny

Molecular Methods

Concepts of Species

Biological (Definition + advantages + limitations)

Ecological (Definition + advantages + limitations)

Morphological (Definition + advantages + limitations)

Phylogenetic (Definition + advantages + limitations)

Preservation of Genetic Variation

Genetic Drift

Founder Effect

Bottleneck Effect

Diploidy

Balanced Polymorphism

Neutral Mutation

Heterozygote advantage + e.g.'s

Frequency-dependent selection + e.g.'s

Neutral Theory

Natural Selection

Descent with Modification

Overproduction of offspring

Constancy of numbers

Variation in traits within **population**

Struggle for Survival & Survival of the Fittest

Like Produce Like

due to mutation, crossing over, independent assortment, random fusion of gametes

Forces of selection + e.g.'s

Speciation through isolation mechanisms + e.g.'s

Biogeography + e.g.'s

Fossils + e.g.'s

Homology

Anatomical + e.g.'s

Embryological + e.g.'s

Molecular + e.g.'s

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