eunoia JUNIOR COLLEGE

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17-02.

Evolution 2

1. Introduction

Genetic variation is the 'raw material' by which natural selection will act on. Preserving genetic variation in a population is thus very important for evolution to occur. We will also look at how organisms are classified according to shared characteristics and how the evolutionary relationships between them are established. The concepts of homology and phylogeny will be discussed together with the various types of evidences (e.g. molecular, anatomical etc.) used to establish homologies. These evidences also serve to support Darwin's theory of evolution.

2. Learning Outcomes

(e) Explain how genetic variation (including recessive alleles) may be preserved in a natural population
(g) Explain how evidence based on homologies identified in biochemical data (molecular homologies) and the fossil record (anatomical homologies), together with biogeography, supports Darwin's theory of evolution
(i) Define biological classification as the organisation of species according to shared characteristics and describe how evolutionary relationship is established
(k) Define phylogeny as the organisation of species to show their evolutionary relationships
(l) Explain the importance of the use of genome sequences in reconstructing phylogenetic relationships and state the advantages of molecular methods, including multiple sequence alignment (nucleotide and amino acid), in classifying organisms.

Use the knowledge gained in this section in new situations or to solve related problems

3. References

Campbell, N.A. and Reece, J.B. (2008). Biology, 9th edition. Pearson.
Kenneth V Kardong, *An Introduction to Biological Evolution*, 2nd Edition.
Mark Ridley, *Evolution*, 2nd Edition.
Taylor, Green et al, *Biological Science 2*, 3rd Edition
Understanding Evolution. http://evolution.berkeley.edu/

Contents

4. Classification [LOs (i) and (k)]

Notes to self

- Biological classification or **taxonomy** is the **organisation of species** according to **shared characteristics.** It involves **naming, identification and classifying organisms**.

Nomenclature (naming)

- Common names like cat, bear etc. can be ambiguous because there are many species of each of these organisms. Scientific names however, avoid ambiguity.

1) **Each species has a 2-part** Latin name, or a **binomial name.**

e.g. Homo sapiens

Homo is genus (plural: genera).	*sapiens* is species (plural: species).
First letter is capitalized.	First letter is not capitalized.

Dicerorhinus sumatrensis,

2) When asked to name a species, you should write binomial name with both the genus and the species.
3) When handwritten, the binomial name for humans is underlined with a space in between the genus and the species, i.e. Homo sapiens

   When printed in books or journals using computers, the binomial name is *italicized* and not underlined, i.e. *Homo sapiens*

- The person who came up with the Binomial system was Carolus Linnaeus, a Swedish biologist, and physician. He first published this system in his book *Systema Naturae* in the Netherlands in 1735.

Identification

- The traditional Linnaean classification of living things looked mostly at **morphologies/physical structures.** E.g. the leaf arrangement of a plant, shape of limbs and appendages, teeth and bone arrangements etc.
- With the advent of **molecular methods**, DNA and amino acid sequence analysis, and DNA barcoding is now being used to tag and identify individual species.

Classification into taxonomic groups

- Once you can identify an organism based on certain traits mentioned above, you can **organise** them **into groups** according to **shared characteristics**.
- Closely related organisms are grouped together in the same taxon.
- A taxon consists of a group of organisms at a particular level. The assumption is that the more homologies two organisms share, the closer they must be in evolutionary distance.
- Linnaeus therefore grouped organisms into a hierarchy of **increasingly inclusive categories**. Of course during his time, he used mostly **morphological characteristics** to determine their grouping.

- E.g.: human beings

Taxon	
Domain: Eukarya	Most recently-added taxon.
Kingdom: Animalia	In Linnaean classification, this is the largest and most inclusive grouping; consists of grouping of phyla.
Phylum: Chordata	Consists of grouping of classes.
Class: Mammalia	Consists of grouping of orders
Order: Primates	Consists of grouping of families
Family: Hominidae	Consists of grouping of related genera
Genus: *Homo*	Consists of grouping of related species
Species: *sapiens*	To specify an organism, the binomial name should be used.

Dear King Phillip Came Over For Great Spaghetti

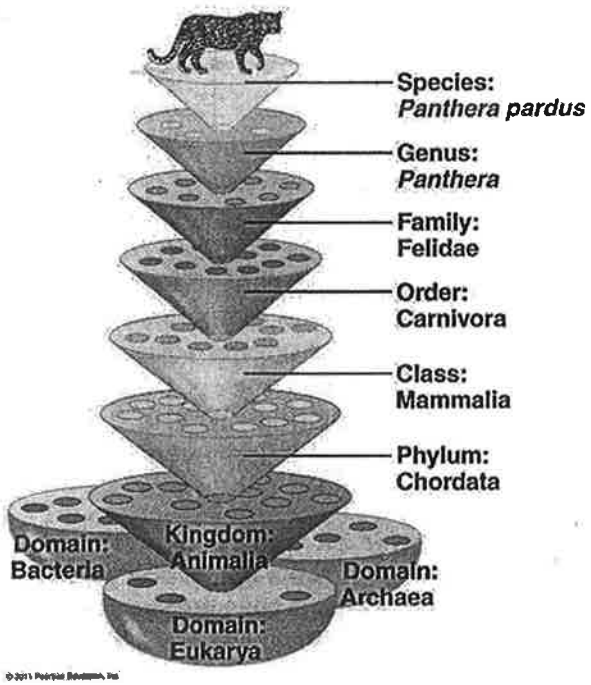


Fig. 1. Features of Linnaean classification

It is hierarchical

Species that are related are grouped into the same genus *Panthera* which in turn is grouped into a **more inclusive, larger category**, the family *Felidae* and so on.

Binomial nomenclature

Another key feature of Linnaean classification is the use of the **binomial name** to identify a species. In this case the Leopard (common name) is more precisely named *Panthera pardus* (scientific name) where the **genus name is followed by the species name.**

Advantages of Linnaean classification

1. Hierarchical classification is a systematic way of grouping organisms. A newly discovered species can be **easily categorised and named**.
2. The binomial nomenclature provides an accurate identity to each species. It is far more **precise** to identify a species using its binomial nomenclature than its common name. For example, a single species *Carica papaya* may have several common names like papaya, paw paw, depending on language and ethnicity of the person referring to it.

Disadvantages of Linnaean classification

1. Based on Linnaean classification, we **cannot infer the evolutionary relationships** between members of each category. We also **cannot tell how distantly related one species is to another** and the name **does not tell us the evolutionary history** of that species.

- In order to see where each species stands in relation to other species, we need to look at their evolutionary relationship in a phylogeny

Phylogeny

- A phylogeny is **organisation of species** to show their **evolutionary relationship**. This is usually presented in the form of a **phylogenetic tree /evolutionary tree /cladogram /phylogeny /phylogram.** (Fig. 2)
- The underlying principle of a phylogenetic tree is that species are related by descent from common ancestry. A **branch point/node** of a phylogenetic tree represents the **divergence** of two species from a **common ancestor.**

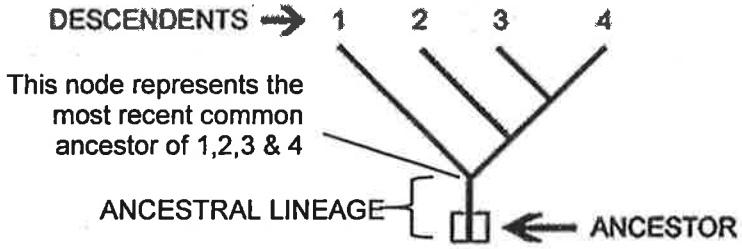


Fig. 2 shows a phylogenetic tree.
The root of the tree represents the ancestral lineage from which the descendants 1-4 arise from.

- Understanding a phylogeny is like reading a family tree. The **root** of the tree represents the ancestral lineage, and the tips of the branches represent the descendants of that ancestor. As you move from the **root to the tips**, you are moving **forward in time**.
- When a **lineage splits (i.e. a speciation event occurs)** (Fig. 3), it is represented as branching on a phylogeny. When a speciation event occurs, a single ancestral lineage or common ancestor gives rise to two (sometimes more) daughter lineages.

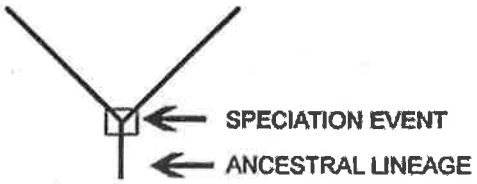


Fig. 3 shows a speciation event.
The ancestral lineage splits to give rise to two daughter lineages.

Understanding phylogenetic trees.

- Phylogenetic trees make use of **homologous characters** to group species into clades (or branches). Homologous characters have **phenotypic and genetic similarities** due to **shared ancestry**.
- Data ranging from **morphological, molecular, anatomy and fossil** records are used to infer evolutionary relationships. (We will explore these in the next section.)
- An example of a homologous character is the **pentadactyl limb**. (Fig. 4) It has a basic structure of 5 digits, and limb bones that have evolved to become different structures such as the flipper of a dolphin, the wing of a

bat and the human hand. These structures are homologous as they are **derived from a common ancestor. Modification** of the basic structure allowed for different functions and appearances.

- Note that in **homologous structures**, we look out for **shared ancestry** and not necessarily physical or functional similarities.

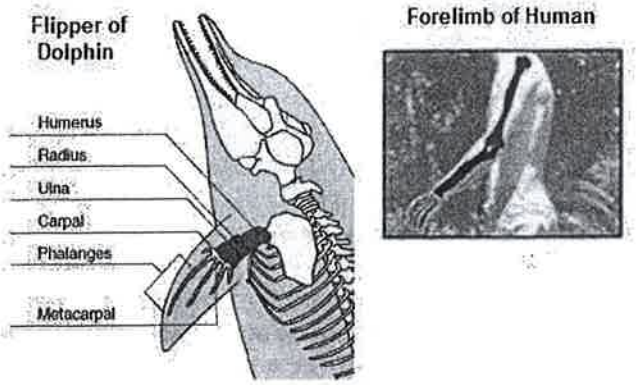


Fig. 4 Pentadactyl limb

The flipper of a dolphin is homologous to the forelimb of a person even though they may serve **different functions**,

- A common mistake in establishing evolutionary relationships is to use **analogous characters**.
- Two different species that **do not share a recent common ancestor** can **independently evolve similar traits** as a result of having to adapt to similar environments or ecological niches. This process is called **convergent evolution**.
- The pectoral fins of the shark, ichthyosaur and dolphin, superficially resemble each other. (Fig.5) The selection pressure posed by a need to swim fast in a watery media, resulted in the **structures that come from different ancestors resembling each other**. This is an example of an **analogous structure**. Closer examination of the fin reveals their **different origin** (Fig.6). The flipper of the dolphin is in fact derived from a mammalian forelimb, the pentadactyl limb, while rays of bone form the fins of a fish.
- The danger of using analogous structures is that the distinct species are wrongly placed as being closely related.

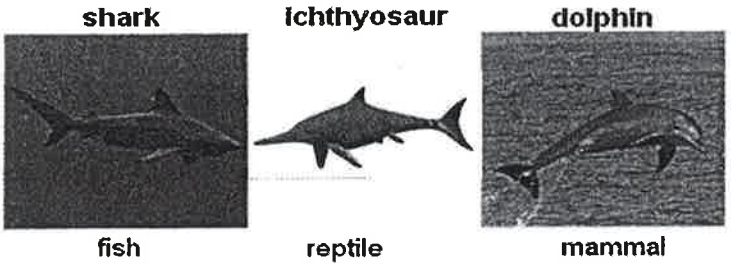


Fig. 5 Show convergent evolution. The shark is closely related to the fish, the Ichthyosaur to a reptile and a dolphin to a mammal, yet they appear outwardly similar.

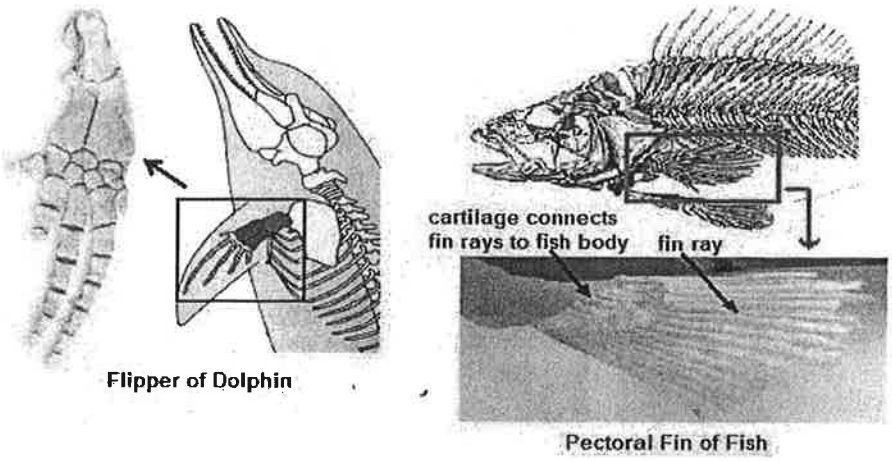


Fig.6 Analogous structures

The pectoral fin of a fish is analogous to the flipper of a dolphin (analogous structures usually have evolved to serve **similar functions** through *convergent evolution*)

- There are two kinds of **homologous characters** that are used in cladistics and these are:
  1) shared **ancestral characters** and

  2) shared **derived characters**.

- A **shared ancestral character** is a character that **originated in an ancestor** and is **shared by all its descendants**.
- A **shared derived character** is a **unique** character of the group but **not found in the ancestors.** or their ancestors' other descendents.
- All vertebrates share the **ancestral character** of having a **backbone** but members of the vertebrates **distinguish** themselves **from the common ancestor** with their **derived characters** which their descendants will possess. **Hair** is a shared derived character **unique to mammals** but is **not found in their ancestors** or their descendants like turtle, salamander, tuna, and lamprey. (Fig. 7)

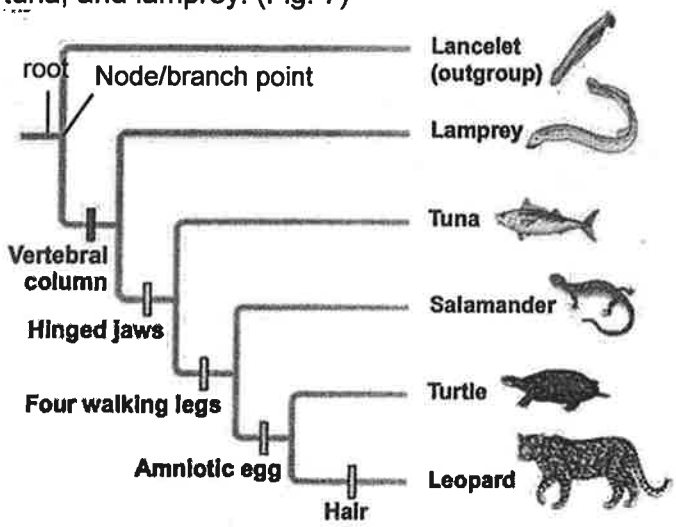


Fig. 7 Shared derived characters that are used to construct a phylogeny of vertebrates (i.e. animals with backbones. The lancelet is used as an outgroup as a reference point for the tree as it is considered an early lineage close to the vertebrates but not within it. It does not have a backbone but has a notochord which is considered a precursor to the backbone.

Phylogenetic trees reveal relatedness of species.

- Two living species are **closely related** if their **most recent common ancestor lived close to the present**, and more distantly related if their most recent common ancestor lived in the more distant past. Technically every living thing is thus related to every other, it is just a matter of degree.

Q. With reference to Fig. 7, is tuna more closely related to the lamprey or salamander? Explain your answer.
The tuna is more closely related to the salamander as it shares a more recent common ancestor with hinged jaws as compared to a more distant common ancestor with lamprey with the vertebral column.

Phylogenetic trees may reveal how long ago a species diverged from a common ancestor.

- A phylogenetic tree may show a timeline and the point **from which species have diverged** from their common ancestor. Each branch length is drawn proportional to the amount of change on that branch. Fig. 8 shows one such phylogenetic tree.

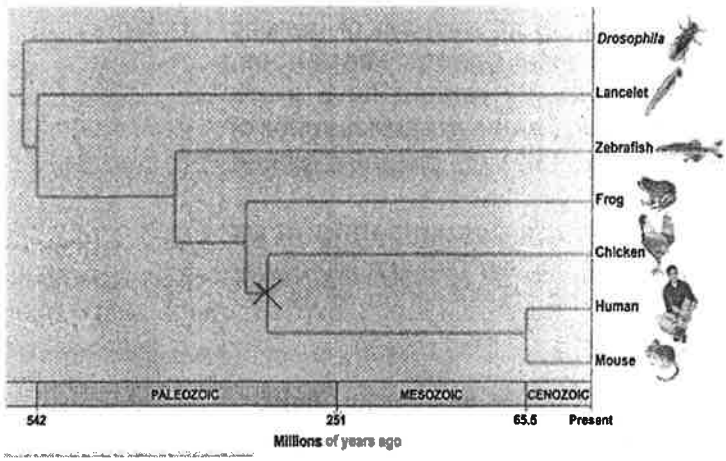


Fig. 8 The right way to read a tree.

Q: When did the common ancestor of the mouse and man started to diverge?

65.5 mya

Q: Mark with an "X" the position of the most recent common ancestor of the chicken, human and mouse.

1) Basis of molecular methods [LO (I)]

- All **known life** is based on **nucleic acids** thus studies involving any types of taxa can use DNA sequence data. Although amino acid sequences are still used today, DNA has now become by far the predominant molecule since it yields more phylogenetic information than protein. RNA molecules such as ribosomal RNA can be used, but RNA being easily degraded, are harder to handle than DNA or protein.

Q. Why does DNA yield more info than amino acid sequences?
Some mutations alter the DNA sequence but do not affect the amino acid sequences (silent mutations). some differences in DNA sequence not reflected in amino acid sequence due to the degenerate ~~genetic~~ genetic code.

- Species diverge as changes occur in nucleotide bases and subsequently amino acid sequences, with each species acquiring its own set of genetic changes. **Evolutionary changes are captured in the genetic sequences.** Thus, we would predict that **species** that are **closely related** have **more similar nucleotide sequences** in their nucleic acids and a greater number of **similar amino acid sequences** in their proteins than do distantly related species.
- Nucleotide and amino acid sequence **databases are accumulating at an increasing rate** because of recent advances in molecular biology. Molecular phylogenetics have led to extensive revision of the classification of all life-forms.

2) Advantages and importance of molecular (nucleotide and amino acid sequences) methods in classifying organisms and determining their phylogenetic relationships:

** more important points.*

1. *They can be used to compare species that are **morphologically indistinguishable** due to **convergent evolution** or are **very closely related**.
2. *On the other hand, **remotely related organisms** such as bacteria, humans and sunflower can also be compared because they have common proteins such as cytochrome c. → small size in amino acids → organism without any ~~not~~ oxidative phosphorylation without it.
3. *They are **objective**. Molecular **character states are unambiguous** as A, C, G and T are easily recognisable and cannot be confused with another whereas some morphological characters, such as those based on the shape of a structure, can be less easy to distinguish because of overlaps between different character states.
4. *They are **quantitative.** Molecular data are easily **converted to numerical form** and hence are amenable to mathematical and **statistical analysis** and hence computation. The **degree of relatedness** can be inferred and **quantified** by **calculating the nucleotide differences between species.**
5. *Changes in the nucleotide sequences accumulate over time with clockwork regularity. We can thus **estimate the time of speciation** of modern to ancient species.
6. **Some molecular differences** may **not** be **reflected as a difference in the morphological character** and hence may not be picked up by morphological analysis. e.g. a nucleotide difference in the third base of a codon, or intron.
7. While **small genetic differences**, may result in **major phenotypic differences.** In such instances, vast differences in morphology can exaggerate the evolutionary distance between two species but not in the case of molecular methods. e.g. in snakes, the loss of forelimbs and

elongation of the body, both radical changes in body form, are due to mutations in several *Hox* genes that affect the expression of body patterns and limb formation.

8. Offers **a large set of characters** to be studied relatively **quickly**. Each nucleotide position can be considered a character with 4 character states, A, C, G and T, and organisms have millions - billions of nucleotide positions. There are limited morphological characters that can be studied, e.g number of segments, number of legs, shape of thorax etc.
9. Amino acid sequences for many proteins and nucleotide sequences for a rapidly increasing number of genomes can be accessed from **electronic databases** and used for comparative study and classification. No physical specimen is required unlike in morphological analysis. Issue of accessibility to a physical specimen is no longer an issue.
10. Both **living and dead tissue may be used** so long as the DNA or protein remains intact and you do not even need an entire specimen. Depending on what morphology you are studying, you sometimes need the entire specimen or a specific part of the specimen. e.g. skull, dentition. (dental organisation) Sometimes living specimens are needed as some morphological structures that you are studying, such as the eye, are difficult to preserve. The animal may be very elusive or are endangered, further compounding the problem of obtaining specimens. However, if they left traces such as hair or shed skin behind, you can still study their DNA sequences.

3) Drawing an evolutionary tree using molecular homology

One can draw an evolutionary tree of a group of organisms using molecular data. The most common way in this day and age is to use **homologous DNA sequences or amino acid sequences.** The steps for constructing a phylogenetic tree is shown below:

Step 1

Choose a homologous gene that is **common to the groups of organisms being compared** and is **derived from a common ancestor.** Examples of such genes are cytochrome c gene and ribosomal DNA.

Step 2

Amplify and sequence the homologous gene. This involves amplifying the gene from the different organisms by PCR and then sequencing the DNA. The forward and reverse primers are designed such that they amplify homologous genes from different species. e.g. (Fig. 9) the primers below are complementary to the flanking regions of the insulin gene in the rat and human genome so they only amplify the insulin gene. In this case insulin is the homologous gene being compared.

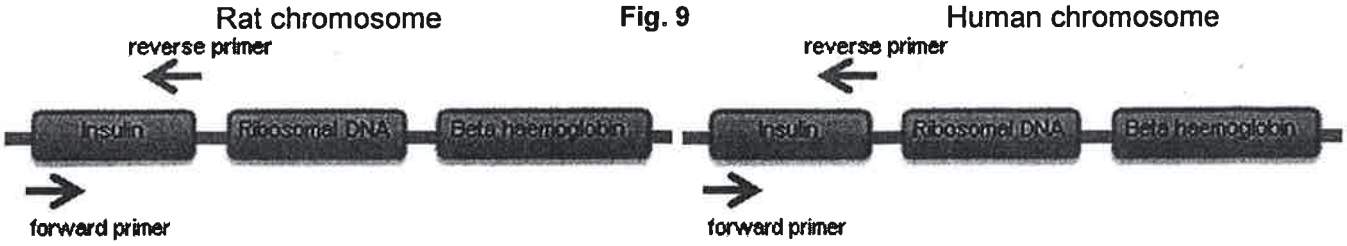


Fig. 9

Step 3

Sequence alignment. The DNA sequences are aligned and a computer programme then calculates the number of differences between the DNA sequences and converts the alignment data into a distance matrix. The alignment isn't always that straightforward like the diagram below, they usually have gaps representing deleted nucleotides (Fig. 10)

Example of a multiple alignment

Species 1	A	G	G	C	C	A	A	G	C	C	A	T	A	G	C	T	G	T	C	C
Species 2	A	G	G	C	C	A	A	G	A	C	A	T	A	C	C	T	G	A	C	C
Species 3	A	G	G	C	C	A	A	G	A	C	A	T	A	G	C	T	G	T	C	C
Species 4	A	G	G	C	A	A	A	G	A	C	A	T	A	C	C	T	G	A	C	C
					*				*					*				*		

Things to note in a multiple alignment:

1. The above alignment shows a segment of homologous genes sequenced from 4 species.
2. Each column is referred to as a nucleotide position (or amino acid position if it's an amino acid sequence alignment)
3. Conserved positions have the same nucleotides and variable positions (marked with an asterisk*) indicate a difference in the nucleotides at that position for the different species.
4. From the multiple alignments, the differences or similarities among the species can be generated and represented in a distance matrix as shown below.

Distance matrix

	1	2	3	4
1	-	0.15	0.05	0.20
2		-	0.10	0.05
3			-	0.15
4				-

The evolutionary distance in the distance matrix is expressed as the number of nucleotide differences per nucleotide site for each sequence pair. For example, sequences 1 and 2 are 20 nucleotides in length and have three differences, corresponding to an evolutionary difference of 3/20 = 0.15

Step 4

Construct the evolutionary tree. The computer programme computes the differences between each species from the alignment and generates the tree.

Q. In the space below, draw a phylogenetic tree of the 4 species based on the above matrices

- Fig. 10 shows an alignment of **haemoglobin beta chain amino acid sequences** from a variety of species. The alignment is used to calculate the molecular distances each species is from the others based on differences in the amino acid sequences. The relationships among the species are visualized in the form of a tree (phylogram) (Fig. 11). [distance matrix not shown].

Fig. 10

Phylogram

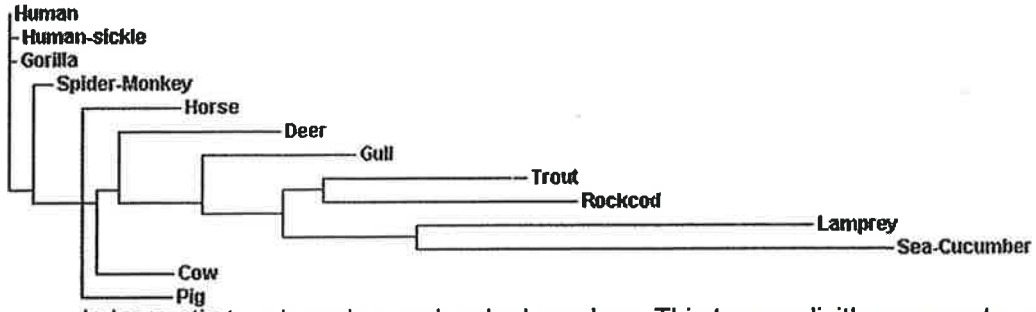


Fig. 11 shows a phylogenetic tree based on molecular homology. This tree explicitly represents number of nucleotide differences through its branch.

4) An application of molecular phylogeny (a study of mitochondrial DNA in humans)

Why use mitochondrial DNA? (you need to appreciate the advantage of using mtDNA)

- Unlike nuclear DNA, in which alleles are rearranged in the process of recombination between maternal and paternal chromosomes, there is usually **no such rearrangement of alleles in mtDNA from parent to offspring**. Thus **changes in mtDNA sequence** is **solely** due to **accumulation of mutations** over time.
- mtDNA is not highly conserved and has a **rapid mutation rate**, making it useful for studying the evolutionary relationships of organisms that are

closely related. It accumulates mutations at the rate of approximately one every 3,500 years. This is important when **comparing populations within a species** and for comparisons of **species that are closely related**. After all, there must be discernible differences for you to work out the degree of relatedness. This feature in fact works against studies involving distantly related species.

Mitochondrial Eve

- Phylogeny using the mitochondrial DNA has been used to trace the evolution of the earliest maternal line.
- Mitochondrial Eve is defined as the woman who is the **most recent common ancestor of the maternal lineage (matrilineal)** of all living humans (NOT the first woman that lived!).
- As the mother's egg contains the cytoplasm including the mitochondria, while the father's sperm contributes only the nucleus, all mitochondrial DNA (**mtDNA**) **is passed on from mother to children of both sexes.** The line can be traced back all the way to Mitochondrial Eve.
- Using **SNP markers** that are highly polymorphic, scientists could use mtDNA sequence analysis data to sort populations into more or less related groups, forming the **phylogenetic tree**.
- By looking at the **geographical region** with **greatest number of mutations which have accumulated in different branches** of this tree, as well as having the **greatest variety of lineages**, the region where Mitochondrial Eve lived can be proposed. (Fig. 12)
- This means that the **origin of our common ancestors** which were from Africa, had:
  - The **greatest variety of lineages**, L0a, L0k, L0d, L1, L2, L3, M & N
  - And the **greatest degree of nucleotide differences**. So if you compare L0a and N, you will see many differences in their mtDNA.
- This is because the common ancestor had a **longer time to accumulate** those **differences** as compared to human lineages in places like Australia.

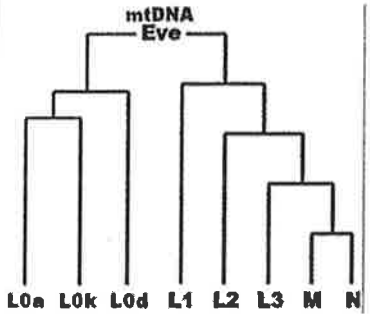
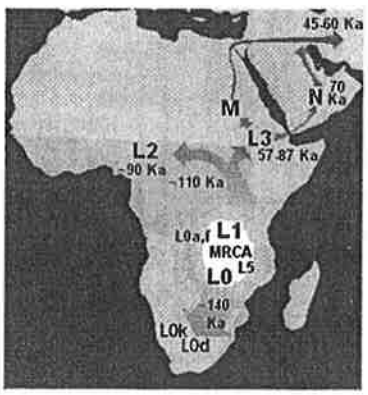


Fig. 12 "Out of Africa"

The maternal-lineage may trace back to a single female who was the most recent common ancestor, such as Mitochondrial Eve. This is done by tracing the evolution of the mitochondrial genome sequence in a phylogenetic tree. By studying the lineages throughout the world, the place that showed the greatest variety of lineages was in Africa. This must have been the origin of modern humans.



The male counterpart is the **Y-chromosomal Adam**, the most recent common ancestor of the **paternal lineage (patrilineal)** of humans. Only males inherit the Y chromosome.

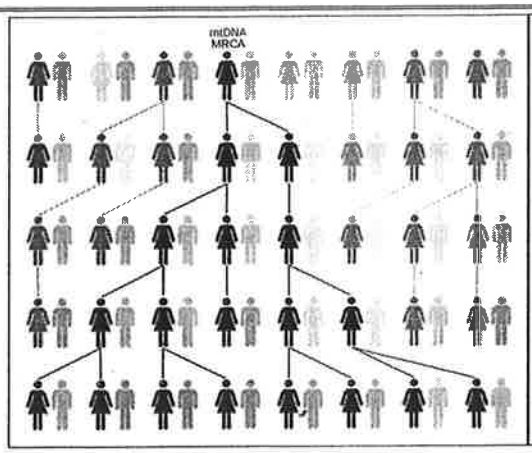


Fig. 13 Through random drift or selection the maternal-lineage will trace back to a single female who was the most recent common ancestor, such as Mitochondrial Eve. In this example, the other maternal lines became extinct.

- Of course, this Eve and Adam were not equivalent to the biblical characters and were by no means the only people alive at that time: they were simply the individuals who carried the ancestral mitochondrial DNA and Y chromosomes that gave rise to all the mitochondrial DNAs and Y chromosomes in existence today. Their contemporaries failed to produce a direct unbroken line to people living today. (Fig. 13)
- The mitochondrial DNA and Y chromosome studies appear to provide strong evidence in support of the **Out of Africa theory**. Rather than evolving in parallel throughout the world, as suggested by the **multiregional hypothesis**, Out of Africa states that *Homo sapiens* is likely to have originated in East Africa, with members of this species then moving into the rest of the Old World around 100,000 years ago, displacing the descendants of *Homo erectus* that they encountered.

Bio ✓ Hello

5. Evidence of Evolution [LO (g)]

Notes to self

Recall: **Homology** refers to similarity inherited from a **common ancestor** unlike **analogy** which refers to similarity due to **convergent evolution**.

1) Anatomical Homology

- Organisms with **anatomical homology** have **morphological structures** such as bone, organs and gross structural features that are derived from a common ancestor.
- Homologous structures represent **variations on a structural theme** that was present in their **common ancestor**. Characteristics present in an ancestral organism are may show 'modifications' in its descendants over time as they face different environmental conditions **(Descent with modification – environmental conditions select for or against the 'modifications' in the descendants which came about as a result of genetic variation in the population).**
- Hence although homologous structures are derived from a common ancestor, they **may serve different functions & may superficially look very different** but **retains a common underlying similarity**. Examples of anatomical homology are;

a) The pentadactyl (five-digit) limb of tetrapods.

- Tetrapods are the group of vertebrates with four legs. Amphibians, reptiles, birds, and mammals are tetrapods. In the case of birds and mammals like bats, the forelegs have been modified for a new function – wings for flight.
- They occupy a wide variety of environments, and use their limbs for many differing functions.

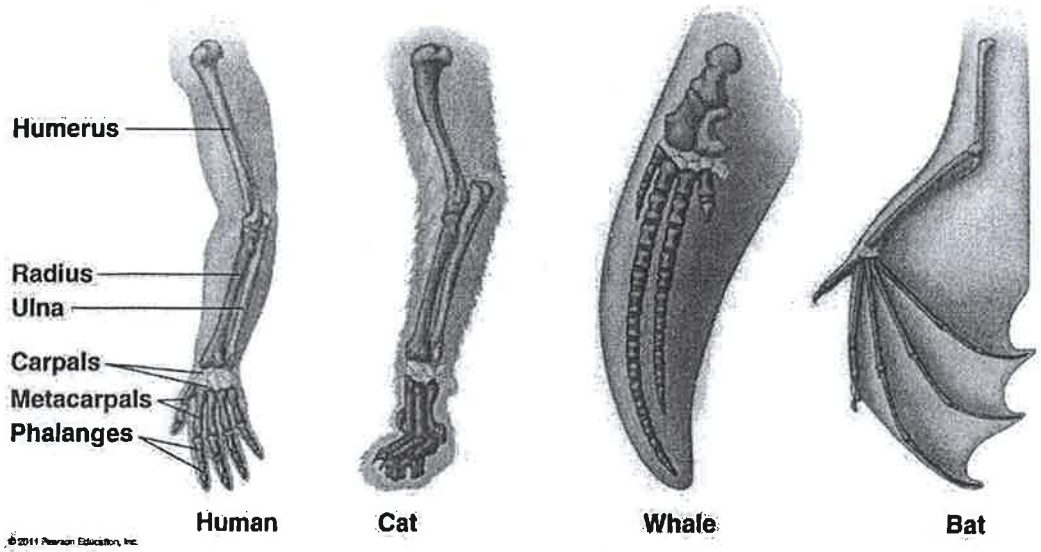


Fig. 14. Different functions but similar underlying forelimb anatomy.

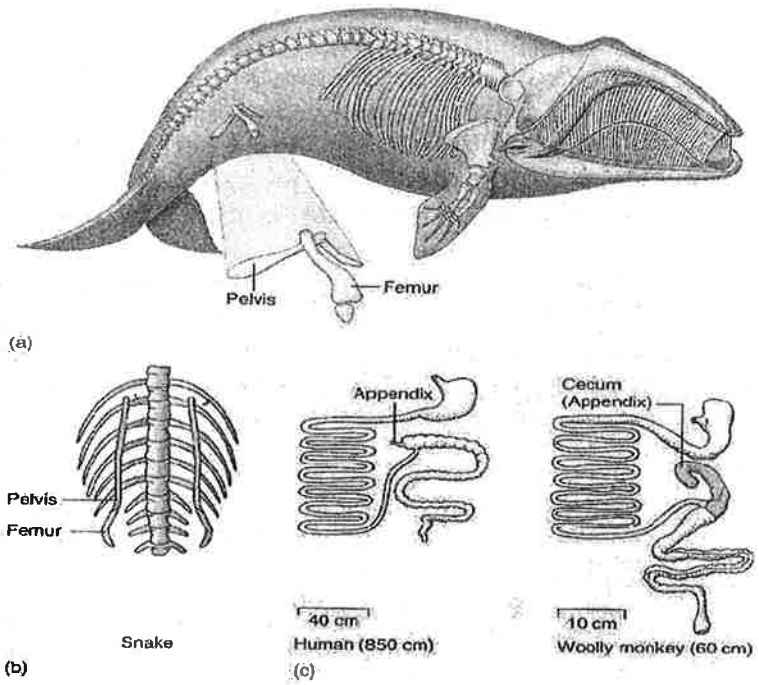
- The forelimbs of humans, cats, whales and bats show the **same arrangement of bones** from the shoulder to the tips of the digits, even though these **appendages have very different functions**: e.g. lifting, walking, swimming and flying and don't resemble each other.
- Such striking anatomical homology would be highly unlikely to have arisen from scratch in each species, i.e. without the existence of common ancestor.

- There is **no clear functional or environmental reason** to explain **why all these animals should need a five-digit**, rather than three-, seven- or more digit limb. Yet all modern tetrapods have such limbs, while fossil tetrapods that possess six-, seven-, and eight-digit limbs were found in the Devonian period but their lineage did not continue as they became extinct.
- There is however **clear functional reason** to explain the **different morphology.** An articulate hand to grasp, a hydrodynamic fin to swim and a broad flexible wing to fly.
- In this example we can clearly see evidence that **natural selection had resulted in the adaptive variations of the basic structural theme (the pentadactyl limb)** to suit their **specialised functions** and that it was a **modification of the five-digit forelimb of the common ancestor** which they all descended from.

b) Vestigial structures.

- Vestigial structures are anatomical features that **resemble structures** of their presumed **ancestors.**
- They are **typically degenerate, atrophied or rudimentary**. They may have **lost some or all of their functional roles** that they played in ancestral organisms.
- Organisms having vestigial structures **share a common ancestry** with organisms in which the structure is still functional as they are **homologous structures**.
- The existence of vestigial structures can be **attributed to changes in the environment and behaviour patterns of the organism** in question.
- In a changed environment, the **structure may no longer be beneficial** for the organism's survival, (e.g. legs for walking will not benefit a whale in water. Fig. 15) and hence the likelihood that the future offspring will **inherit the "normal" form decreases.**
- This is because all structures have a **cost** in terms of **development, maintenance, burden of weight,** and are also a **risk of disease,** (e.g. infection, cancer) thus contributing some **selective pressure** for the **removal of parts** that do not contribute to the organism's fitness.
- In other instances, the structure actually becomes **detrimental** to the organism (e.g. the eyes of a mole can become infected in a subterranean lifestyle).
- Therefore, vestigial structures are evidence that Darwin's theory of **natural selection is at work to select for reduced or degenerate structures with limited/no function**. These structures are **modified** (typically degenerated) from functional structures in the **common ancestor**.

Fig. 15 Vestigial Features
(a) Whales evolved from terrestrial ancestors with four legs. But in whales, the hips and hind-limbs are reduced to small bones with no function. (b) Snakes evolved from lizards with four legs. But in primitive snakes, the remnants of hind-limbs persist (forelimbs are absent). (c) The human appendix is a vestigial structure, reduced from the cecum of primate ancestors, which was involved in digestion of significant plant material.
Source: An Introduction to Biological Evolution. Kenneth V. Kardong 2nd Edition



2) The Fossil Record (a subset of anatomical homology)

How fossils form

- When aquatic and terrestrial organisms that are swept into the seas and swamps die, they settle to the bottom together with sediments (sand and mud) from land. Deposits pile up and compress the older sediments below into rock. Sedimentary rocks are therefore, a rich source of fossils.
- New layers of sediment cover older ones and compress them into superimposed layers of rock called **strata**. Erosion will reveal buried strata.
- Organic substances of dead organisms decay rapidly but parts rich in minerals such as shells, bones and teeth remain as fossils. Minerals in water may also seep into tissues of dead organisms and replace their organic material. These minerals subsequently crystallize forming a cast in the shape of the organism.
- There are other ways of fossilisation such as encasement in tar or amber or preservation in acidic bogs.

Fossils are relics or impressions of extinct organisms preserved in rock.

- While most fossils only preserve the resilient structures of an organism such as its bone anatomy, some well-preserved specimens actually preserve other anatomical structures such as feathers, hair, skin texture and even skin pigmentation.
- Each stratum contains its own unique group of fossil species.
- Radioactive dating techniques allow us to place these strata and fossils they bear in a chronological sequence.
- Succession of organisms is shown as you progress up the layers. Deeper strata contain older organisms that are usually simpler in morphology.

- We can see in fossils how **homologous structures have been modified through time** (descent with modification).
- As we look at many examples of fossil evidence, we will realise that as we progress forward in time, there is an **ordered sequence of progression**. Each species is preceded by a logical and related ancestor through **descent with modification.** This is compelling evidence in support for evolutionary deductions based on homologies.
- A study of fossil evidence showed that fish arose first as they appeared in the deeper strata, followed by amphibians, then reptiles and finally mammals, (Fig.16) which appeared in the upper strata.
- Fossil evidence reflects the anatomical milestones we see in evolutionary development.
- If species indeed arose spontaneously and not through descent with modification from pre-existing organisms, then that ordered sequence of progression in fossil record would not hold. Yet we find no evidence of this.

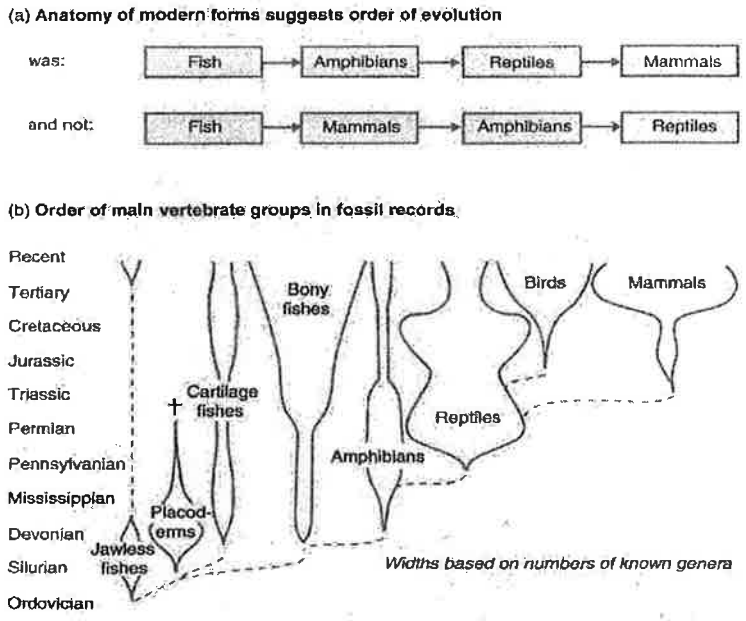


Fig. 16 (a) Anatomical analysis of modern forms indicates that amphibians and reptiles are evolutionary intermediate between fish and mammals. This order fits with (b) the geological succession of the major vertebrate groups. The width of each group indicates the diversity of the group at that time. Fossils found in the deepest strata were fishes and as we move up the layers, we begin to see amphibians, followed by reptiles and then mammals.

Example 1 - The Evolution of Horses as seen through the fossil record

- One on the best studied examples of evolutionary change is based on an **almost complete fossil record** of the horse and its ancestors.
- The earliest forms of the horse were small (the size of dogs), with short legs and broad feet. These species occurred in wooded habitats and probably browsed on leaves and herbs and escaped predators by dodging through the forest vegetation.
- The evolution to workhorses of today involved **increase in size, lengthening of limbs, toe reduction and increase in tooth size.** (Fig. 17)
- Much of the horse evolution occurred where large areas of land **changed from dense forest to open grasslands.** The increase in size and **changes in foot structure** allowed horses to **escape predators** and **travel great distances** in search of food. **Changes in horse teeth** are

consistent with a **shift in diet from tender leaves to grasses** that need more chewing.

- The *Equus* descended through a series of speciation episodes that included several adaptive radiations, not all of which led to large, one-toed, grazing horses of today. Some branches like the *Anchitherium* were dead-end branches that became extinct.
- It was only when grasslands became widespread and there was a need to escape predators that there was a **strong selection for grazers that could run faster.** This led to the only surviving genus of today, the *Equus*.

In summary:

1. The extensive fossil record for horses supports the theory of **progressive change** of **homologous structures** such as **forelimbs and teeth. (descent with modification)**
2. The **driving force** of this change is **natural selection** where there was a need to escape **predation** and a change in diet due to **changing environment**.

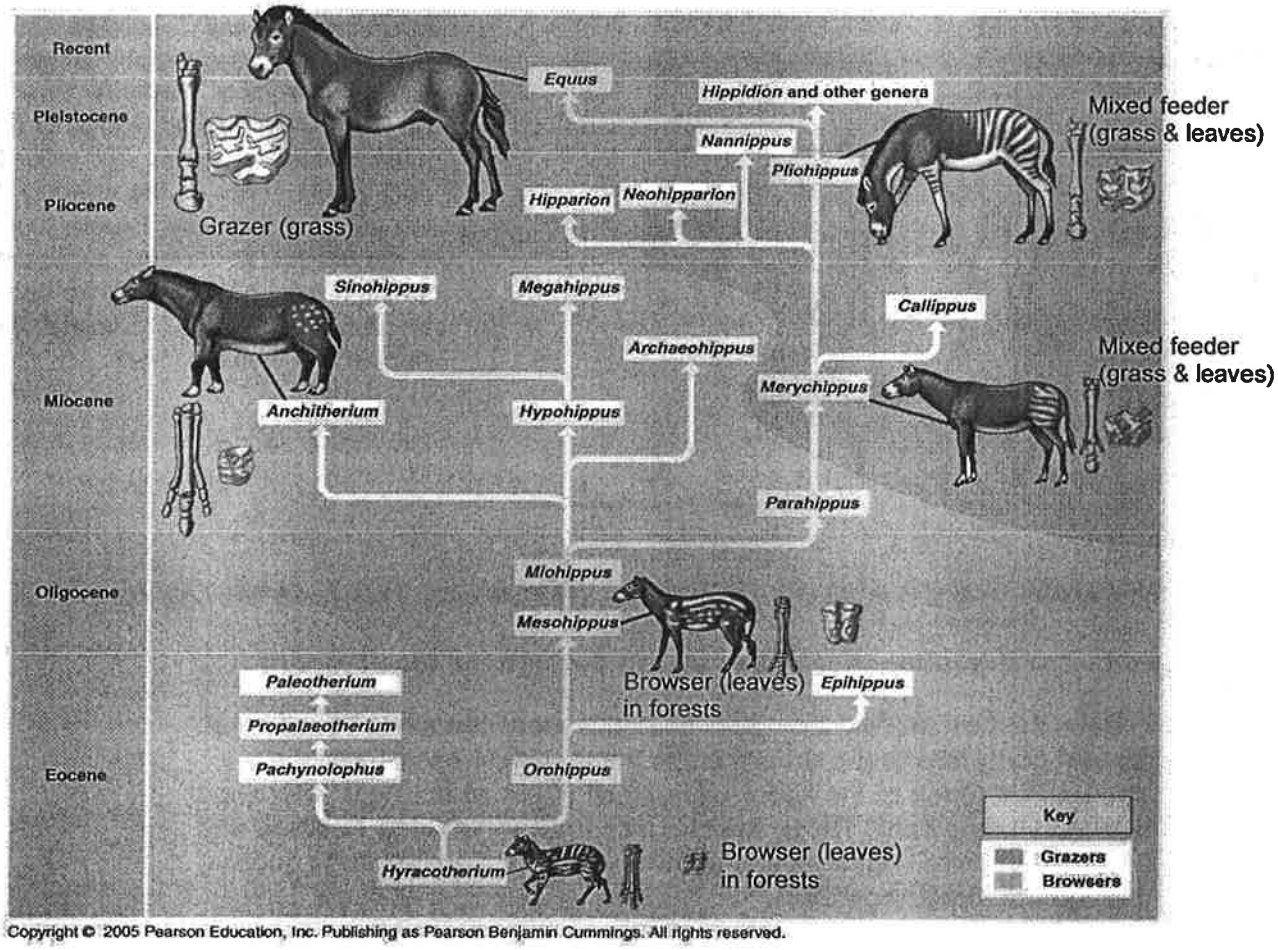


Fig. 17 Showing the forelimb bone arrangement as well as the teeth of the various horse genus

Transitional Fossils

- **Transitional fossils** are any fossilised remains of a life form that exhibits traits common to both an ancestral group and its derived descendant group.
- Unlike the largely complete fossil record of the horses, many other fossil records are incomplete for some of the following reasons.

a. You need specialised conditions for fossilisation to occur
b. Dead organisms decompose rapidly and even bones get consumed for their calcium
c. Soft-bodied organisms do not fossilise easily
d. Only a fraction of fossils have been discovered

- This lack of continuous fossils in the record, especially of transitional fossils, is a major limitation in tracing the descent of biological groups. This is especially important when the descendant group is **sharply differentiated by gross anatomy and mode of living from the ancestral group**. Such "missing" fossils are often called the "missing link."
- It is a matter of time before such "missing links" are uncovered. They support evolutionary deductions best as they **illustrate an evolutionary transition** between the two forms. They provide evidence for **descent with modification**.

Example 2 - *Archaeopteryx*

transitional fossil

- The most famous of the missing links is the oldest known bird, *Archaeopteryx* that lived 165 million years ago.
- This specimen is an **intermediate between birds and dinosaurs**.
- Features like a reptile – possession of teeth, a bony tail, link it to carnivorous dinosaurs. Thus, the *Archaeopteryx* linked birds and dinosaurs to a common ancestor.
- Features like a bird - It has feathers like a bird, bone structure that suggest that it walked on its hind legs like most birds do.
- *Archaeopteryx* reveals a pattern commonly seen in transitional fossils – it exhibits **some traits like their ancestors and others like their descendants**.

Fig. 18 shows one of the Archaeopteryx fossils. Since the 1990s many more genera of non-avian feathered dinosaurs were unearthed. In 2011, some excellent samples of preserved feathers were discovered encased in amber. Initial analysis suggests that some of these feathers were used for insulation and not flight but they could be the precursors to flight feathers.

Example 3 - *Tiktaalik roseae* the "Fishapod"

- In 2005 fossils of *Tiktaalik roseae* was discovered by Daeschler, Shubin and Jenkins.
- *Tiktaalik* illuminates the steps that led to the evolution of tetrapods. *Tiktaalik* is an example of a transitional fossil animal between fishes & tetrapods. It provides strong evidence that fish are the ancestors to modern tetrapods.

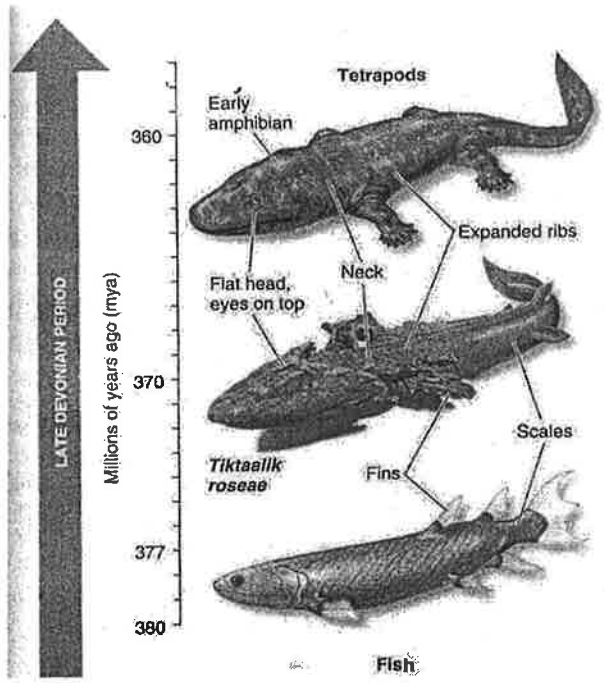


Fig. 19 Evolutionary change in the tetrapod lineage, showing a transitional form. This figure shows two early tetrapod ancestors, a Devonian fish and the transitional form *Tiktaalik roseae,* as well as one of their descendants, an early amphibian. An analysis of the fossils show that *T. roseae*, also known as a fishapod, had both fish and amphibian characteristics, so it probably was able to survive brief periods out of the water.

- It was **similar to its fish ancestors** as it had fish gills & scales.
- It was **similar to its tetrapod descendants** as it had
  1. a broad skull with eye mounted on top of its head, like a crocodile
  2. a mobile neck
  3. an interlocking rib cage suggesting it had lungs.
  4. pectoral fins which revealed the beginnings of a primitive wrist and five finger-like bones. i.e., one of the earliest records of the pentadactyl limb.

- These appendages would have allowed *T. roseae* to peek its head above shallow waters to look for prey. This would be an advantage in the marshy floodplains of the Devonian period.
- Thus, the study of fossil record allows us to see the **evolution of species through the modification of homologous structures from a common ancestor to the present descendant through a series of transitional forms.**

3) Molecular Homology

- All forms of life use the same genetic language of DNA and RNA, and the **genetic code is essentially universal.** "AAA" in DNA codes for "UUU" in mRNA, which codes for phenylalanine in organisms as diverse as shrimp, humans, bacteria and tulips.
- Thus, it is likely that all species descended from **common ancestors that used this code.** It has been maintained and transmitted through all branches of the evolutionary tree since its origin in some extremely early (and successful) organism. If organisms had indeed not descended from a common ancestor, there is no reason why they should all share the same genetic code. To date, no other code has been found in any organism.
- When scientists examined **DNA and amino acid sequences**, similarities known as **molecular homologies** can be seen even in organisms as dissimilar as humans and bacteria indicating that they shared a very distant common ancestor.
- When looking for molecular homologies, homologous genes (or their proteins) of different organisms are compared. Examples of **homologous genes** used are cytochrome c genes, ribosomal genes etc., typically genes important enough that every organism possesses them.
- Just like anatomical homologies, an **ancestral gene** would be **modified** in terms of **nucleotide sequence** over many generations. The more closely related the species, the fewer differences they have. Similarly, a higher degree of differences in nucleotide sequences would imply a more distant relationship.
- Earlier in page 8, we compared the molecular homology of DNA of various organisms and determined their relatedness. Here we will use an example using amino acid sequences.

	Short amino acid sequence within the p53 protein	Percentages of amino acids in the whole p53 protein that are identical to human p53
Human (*Homo sapiens*)	Val Pro Ser Gln Lys Thr Tyr Gln Gly Ser Tyr Gly Phe Arg Leu Gly Phe Leu His Ser Gly Thr	100
Rhesus monkey (*Macaca mulatta*)	Val Pro Ser Gln Lys Thr Tyr His Gly Ser Tyr Gly Phe Arg Leu Gly Phe Leu His Ser Gly Thr	95
Green monkey (*Cercopithecus aethiops*)	Val Pro Ser Gln Lys Thr Tyr His Gly Ser Tyr Gly Phe Arg Leu Gly Phe Leu His Ser Gly Thr	95
Rabbit (*Oryctolagus cuniculus*)	Val Pro Ser Gln Lys Thr Tyr His Gly Asn Tyr Gly Phe Arg Leu Gly Phe Leu His Ser Gly Thr	86
Dog (*Canis familiaris*)	Val Pro Ser Pro Lys Thr Tyr Pro Gly Thr Tyr Gly Phe Arg Leu Gly Phe Leu His Ser Gly Thr	80
Chicken (*Gallus gallus*)	Val Pro Ser Thr Glu Asp Tyr Gly Gly Asp Phe Asp Phe Arg Val Gly Phe Val Glu Ala Gly Thr	53
Channel catfish (*Ictalurus punctatus*)	Val Pro Val Thr Ser Asp Tyr Pro Gly Leu Leu Asn Phe Thr Leu His Phe Gln Glu Ser Ser Gly	48
European flounder (*Platichthys flesus*)	Val Pro Val Val Thr Asp Tyr Pro Gly Glu Tyr Gly Phe Gln Leu Arg Phe Gln Lys Ser Gly Thr	46
Congo puffer fish (*Tetraodon miurus*)	Val Pro Val Thr Thr Asp Tyr Pro Gly Glu Tyr Gly Phe Lys Leu Arg Phe Gln Lys Ser Gly Thr	41

Fig. 20 shows a comparison of short amino acid sequence within the p53 protein from nine different animals. This figure compares a short region of the p53 tumour suppressor protein which plays a role in preventing cancer.

Amino acids are represented by three-letter abbreviations. Certain amino acids in the sequences are identical to those in the human sequence (e.g. valine and proline in the first two positions).

The numbers in the right column indicate the percentage of amino acids within the whole p53 protein that is identical with the human p53 protein, which is 393 amino acids in length. For example, 95% of the amino acids, or 373 out of 393, are identical between the p53 sequence found in humans and that in Rhesus monkey and green monkeys.

- The sequences from the two monkeys are closest to humans, followed by the two other mammal species (rabbit and dog). The three fish sequences are least similar to the human sequence but tend to be similar to each other.

- The figure illustrates that:
  1. **Certain homologous genes are found in a diverse array of species** such as mammals, birds and fish. This suggests **common ancestry.**
  2. The **sequences of closely related species tend to be more similar to each other** than they are to distantly related species.

- Molecular homology reinforces earlier studies on evolutionary relationships based on morphological structures and fossil data.

In summary:

- **Homologies** (anatomical and molecular) provide evidence of **common ancestry** and **descent with modification** which is what Darwin's theory of natural selection suggests.
- The different types of **homology** show that they were linked to a common ancestor but **developed into different forms** as the **result of natural selection**.

4) Biogeography

- The study of the **past and present geographic distribution of organisms** is called biogeography. It supports the evolutionary deductions based on homologies.
- Plant and animal species are **discontinuously distributed** throughout the world. Elephants occur in Africa and Asia but not North or South America. Ecological factors alone cannot account for this discontinuous distribution. This was demonstrated when rabbits, that are not naturally occurring in Australia, were brought over by colonists. The rabbits thrived in their new habitat and their numbers subsequently exploded.

Evidence 1 - Biogeographic realms

- The discontinuous distribution of organisms is based on the concept of **species originating in a given area** and then **spreading (dispersing) outwards from that point. (centres of origin)** The extent of the dispersal will depend on the success of the organism, the efficiency of the dispersal mechanism and the existence of natural barriers such as oceans, mountain ranges and deserts.
- Alfred Russel Wallace and his contemporaries studied the distribution of flora and fauna in various parts of the world and based on the **distinctive assortments of fauna and flora**, **biogeographic realms** were recognised, wherein each continent today sports its defining complement of species. (Fig. 21)
- **Biogeographic realms support the evolutionary deductions** of descent from a common ancestor as the related species that evolved from a **common ancestor** are more or less **confined to their geographical area**. You don't see different elephant species in America for instance.

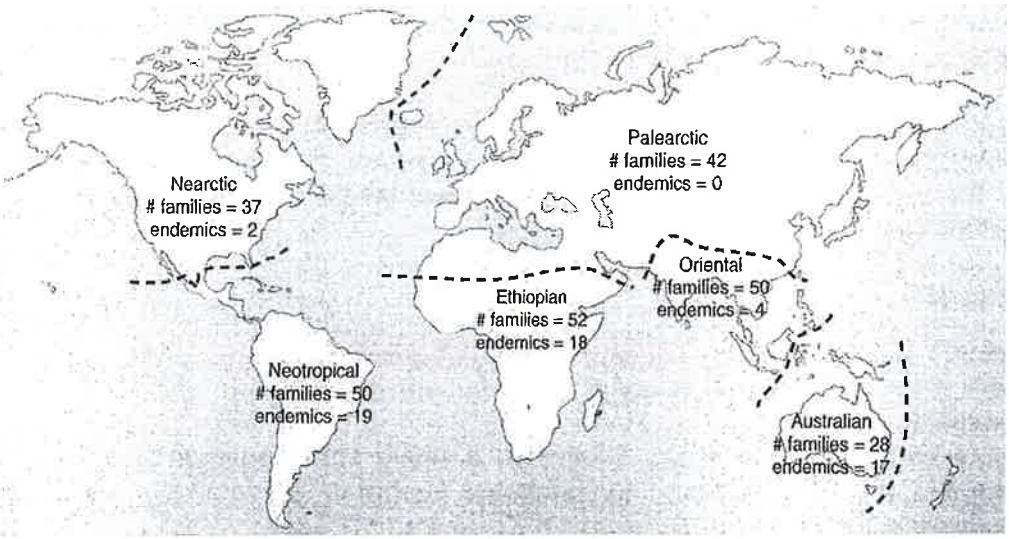


Fig. 21 Biogeographic Realms Continental land areas support characteristic assortments of plants and animals, which in turn define six biogeographic realms. The number of mammalian families is indicated, along with the number of endemic families.

Evidence 2 - Darwin's finches

- The **Galapagos Islands** are situated in the Pacific Ocean, almost 1200km west of Ecuador and form an archipelago. These islands were formed by volcanic activity which thrust them up above sea level, so that they have **never had any direct geographical links with any land mass.** Plant species must have arrived on the island by wind dispersal as seeds while birds, bats and flying insects would have fewer problems of dispersal to these islands. Animals without the ability to fly probably drifted in as passengers on floating debris.
- When Darwin arrived at the Galapagos Islands, he was drawn to the variation among the finches.
- There were **13 distinct species of finches**, with diverse adaptive features. What he found intriguing was that the **finches on Galapagos bore a similarity with the finches from the South American coast** despite the vast differences in habitats. The Galapagos Islands are dry and rocky and the nearest part of South America is humid and has a lush tropical rain forest.
- Darwin concluded that a group of **ancestral finches from the mainland colonised the islands**. Here they flourished, and the inevitable competition produced by increase in numbers, and the availability of **vacant ecological niches**, favoured occupation of niches by those organisms showing the appropriate **adaptive variations**.
- This phenomenon of **rapid diversification** into a multitude of new forms, **filling the different environmental niches**, is called **adaptive radiation.**
- Incidentally, Darwin also visited yet another group of volcanic islands, the **Cape Verde Islands, off West Africa**, that resembled the Galapagos in climate, soil and size. Yet the inhabitants are nothing like the inhabitants of Galapagos but resembled African species.
- Biogeography explains why two islands with similar environments in different parts of the world are populated not by closely related species but rather by totally different species that resemble those of the nearest mainland, the centre of origin.
- The **distribution of finches supports the evolutionary deduction** of descent with modification from a common ancestor because the finch species didn't emerge from the Galapagos islands but **came from a**

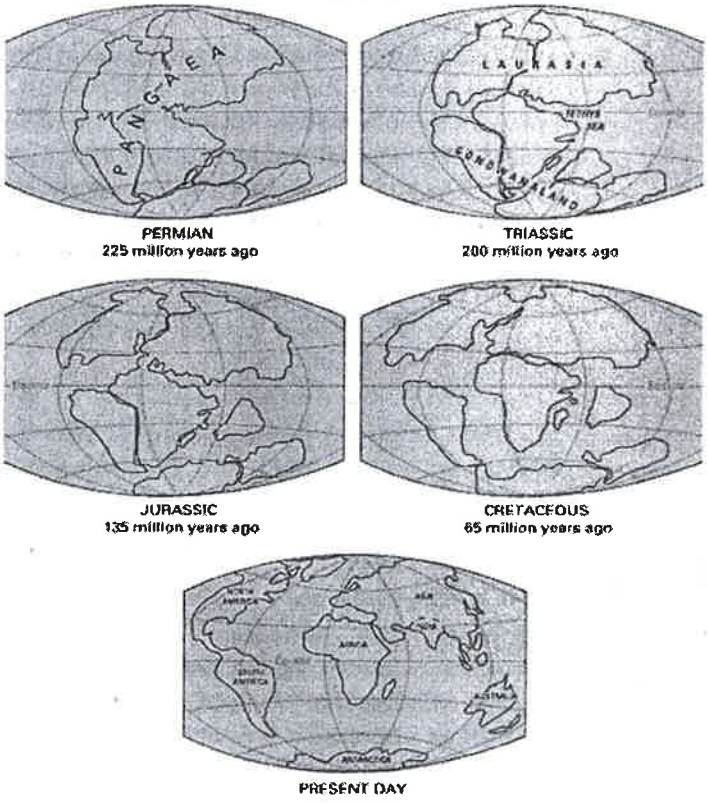
common ancestor from the mainland which then **evolved into the different species** on the archipelago.

- **However,** there are instances where **related forms are found in widely separated regions**. These **exceptional occurrences** can be **explained** by the hypothesis of **continental drift**, based on the concept of plate tectonics which we will discuss next.

Continental drift

- Continental drift is the slow movement of the Earth's continents relative to each other over time as a result of movement of plates on which the continents float.
- About 250 million years ago, Earth had a single supercontinent called Pangaea. (Fig. 22) Over time, the landmass started to split to give rise to smaller continents.
- As continents drift apart they will affect the migratory patterns and hence distribution of organisms.
- Our understanding of evolution and continental drift can be used to predict where fossils of different groups of organisms might be found. (Fig. 23)

Fig. 22 The continents have moved over the surface of the globe through geological time. The position of the main continents since the Permean period is shown in the figure on the right.



Geologists, who discovered that the movement of tectonic plates in the earth's crusts causes the migration of continents, later confirmed the continental drift hypothesis.

Many biogeographical observations can be explained by the splitting or colliding of landmasses.

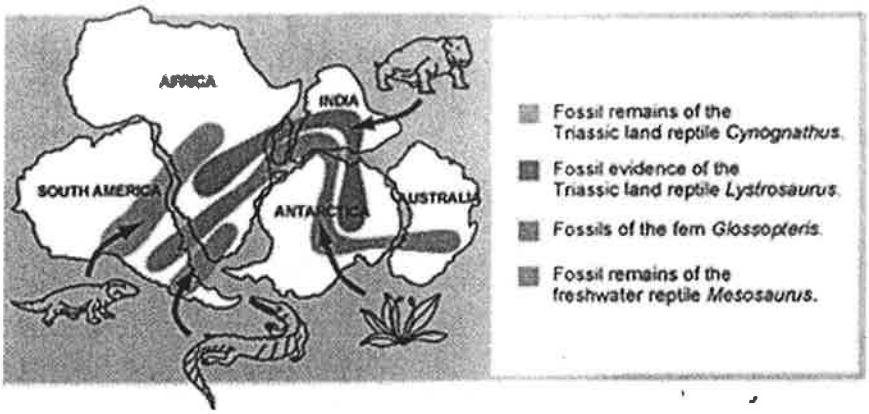
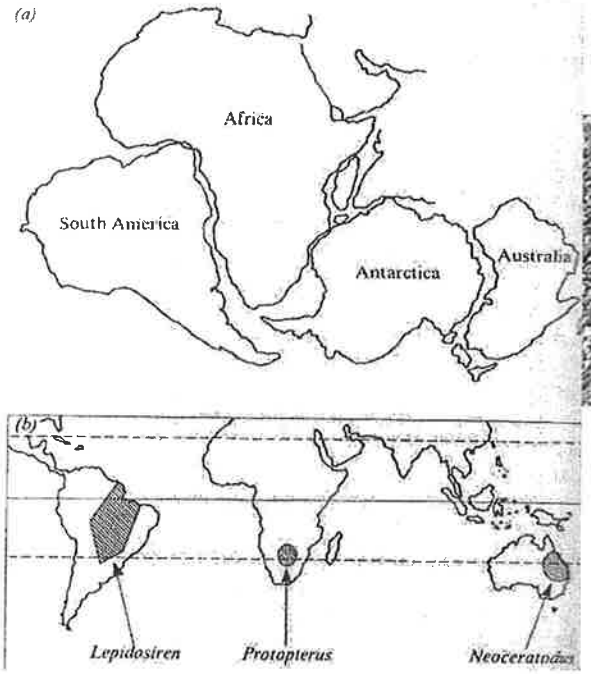


Fig. 23 Wegener, the person who in 1915 proposed the idea of continental drift found that the distributions of fossils of several organisms supported his theory that the continents were once joined together. Conversely, continental drift can be used to explain how species that spread out from one location ended up in different continents.

Evidence 3 - Lungfish distribution as explained by continental drift.



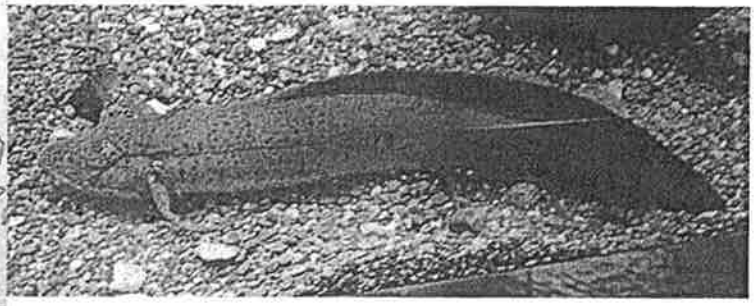


Fig. 24
a) Relative positions of South America, Africa and Australia during early stages of continental drift, indicating proximity of areas where lungfish may have originated.
b) Present distribution of species of lungfish.

- Related species are normally distributed within a region but in the case of the lungfish, they are found on different continents. How did this occur?
- *Neoceratodus* today is found only in Australia. However, fossils of this genus and other lungfish relatives have been found almost worldwide in Mesozoic strata, indicating that this group once had a much wider distribution. This being possible because the landmasses were connected in the past.
- Hence from the study of biogeography (and fossil record), it can be seen that the lungfish had a **common ancestor** that **dispersed from a centre of origin** when the continents were **still merged**. However due to **continental drift**, these ancestors of the lungfish become **geographically separated** and started to diverge and evolve through allopatric speciation.

In summary:

- To appreciate how biogeography supports the theory of evolution, you need to be able to see a **pattern in the geographical distribution of species, extinct or extant** (still existing), and **link** this pattern to an evolutionary concept such as descent from a **common ancestor**.

6. Preservation of Genetic Variation [LO (e)]

1) How genetic variation *arises* in a natural population. (A recap.)

A. Mutations (Gene mutations, chromosomal mutations)

(i) Gene mutations

- These include **substitution**, **deletion** or **addition** of a nucleotide that **changes** the **triplet code** & hence the **amino acid**. Mutations in non-coding regions such as the promoter & enhancer can result in phenotypic variation as well.

(ii) Chromosomal mutations

a) **Polyploidy** - when **more than 2 homologous sets** of chromosomes are present e.g. triploids: 3n, tetraploid: 4n.
b) **Aneuploidy** - when **a particular chromosome** is **over-represented** or **under-represented** e.g. Trisomy 21 (resulting in Down syndrome in humans)
c) **Deletion** - when a **segment of a chromosome** is **missing** e.g. a deletion in chromosome number 5 resulting in Cri-du-chat syndrome
d) **Duplication** - when an **extra segment** of a **chromosome** is **present**.
e) **Inversion** - when a chromosome segment is **detached, flipped around 180 degrees and reattached** to the rest of the chromosome
f) **Translocation** - when a segment from one chromosome is **detached & reattached to a different chromosome**. Therefore, linkage relationships are altered.

B. Meiosis

(i) Independent assortment

- **Independent assortment & separation of homologous chromosomes** during metaphase I & anaphase I respectively.
- **Independent assortment & separation of sister chromatids** during metaphase II and anaphase II respectively.

→ results in gametes with numerous combinations of maternal & paternal chromosomes.

(ii) Crossing over between non-sister chromatids of homologous chromosomes results in more allelic combinations.

C. Sexual Reproduction

- **Random fusion of gametes** adds to the variety of genotypes. Different genotypes will result in different phenotypes and these will act as raw materials for natural selection to act on.

2) How genetic variation (including recessive alleles) may be *preserved* in a natural population

- Natural selection tends to reduce genetic variation by culling unfavourable phenotypes.
- What prevents natural selection from removing unfavourable alleles (including some recessive alleles)? The tendency for directional and stabilizing selection to reduce variation is countered by mechanisms that preserve or restore it.
  A. Diploidy/ Heterozygote Protection
  B. Balancing selection
    i. Heterozygote Advantage
    ii. Frequency-dependent selection

A. Diploidy / Heterozygote Protection

- Most eukaryotes are diploid, and a considerable amount of genetic variation is hidden from selection in the form of recessive alleles. **Recessive alleles** that are **less favourable than their dominant counterparts or even harmful** in the current environment **can persist** because they are propagated in heterozygous individuals where the **dominant allele masks the effect of the recessive allele**.
- Natural selection only acts on phenotypes. Recessive alleles are exposed to natural selection only when an individual carries 2 copies of this allele (i.e. homozygous recessive).
- Heterozygote protection maintains a huge pool of alleles that might not be favoured under the present conditions but some of which **could bring new benefits when the environment changes**.

B. Balancing selection

- Balancing selection occurs when natural selection **maintains two or more alleles at a locus**. Balancing selection can arise by the heterozygotes having a selective advantage, as in the case of sickle cell anemia – heterozygote advantage. It can also arise through frequency-dependent selection, where fitness depends on how common an allele is.

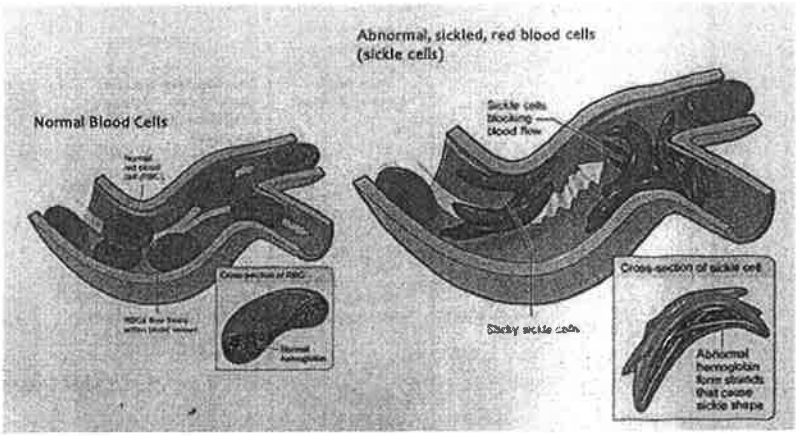
(i) Heterozygote Advantage (e.g. sickle-cell anaemia)

http://www.ornl.gov/sci/techresources/Human_Genome/posters/chromosome/hbb.shtml
http://sickle.bwh.harvard.edu/malaria_sickle.html

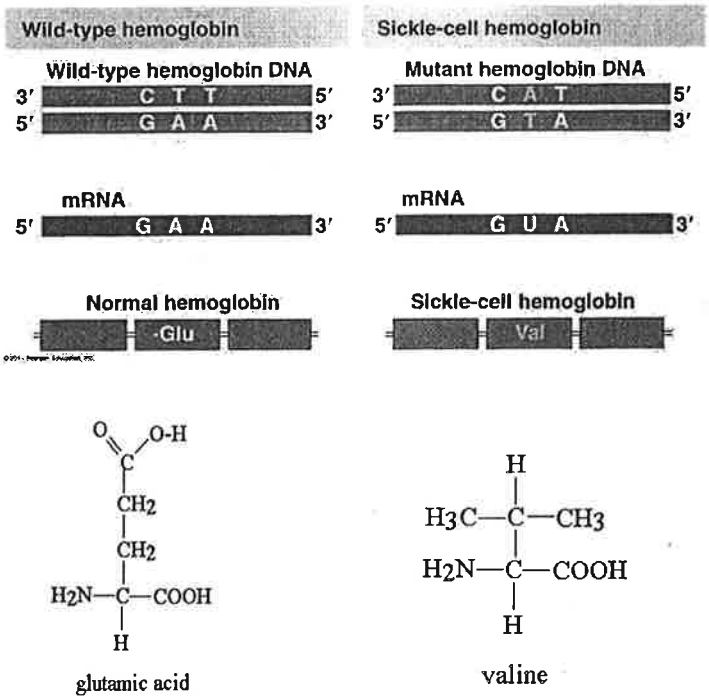
- When individuals who are **heterozygous** at a particular locus have **greater fitness than both kinds of homozygotes** (i.e., homozygous dominant and homozygous recessive), they exhibit heterozygote advantage. Heterozygote advantage is seen in sickle cell anaemia.

Fig. 25

Left: Sickled cells and normal cells. **Right:** Sickled cells can block blood flow to organs and damage them



- There are two beta globin alleles important for the inheritance of sickle cell anaemia: HbA and HbS. Individuals with two normal HbA alleles (HbAHbA) have normal haemoglobin, and therefore normal RBCs. Those with two mutant HbS alleles (HbSHbS) develop sickle cell anaemia. *Refer to previous notes for details.*



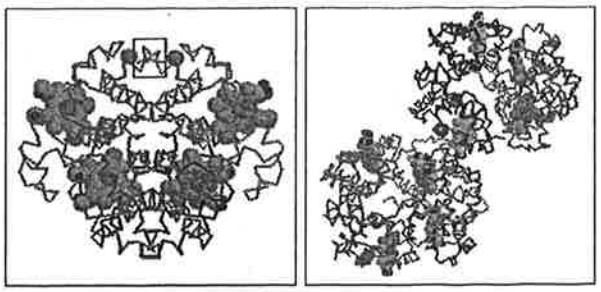


Fig. 26 Left: Mutant adult haemoglobin sequence (HbS) and normal sequence. *Note: the normal codon can also be GAG due to the degeneracy of the code.*

Top left: A normal HbA protein, the red box shows where the glutamic acid is located. **Top right:** 2 HbS protein molecules clumping The R-group of glutamic acid contains a carboxylic acid and hence makes its R-group polar while the R-group of valine contains a methyl group and hence makes its R-group non-polar and hence hydrophobic

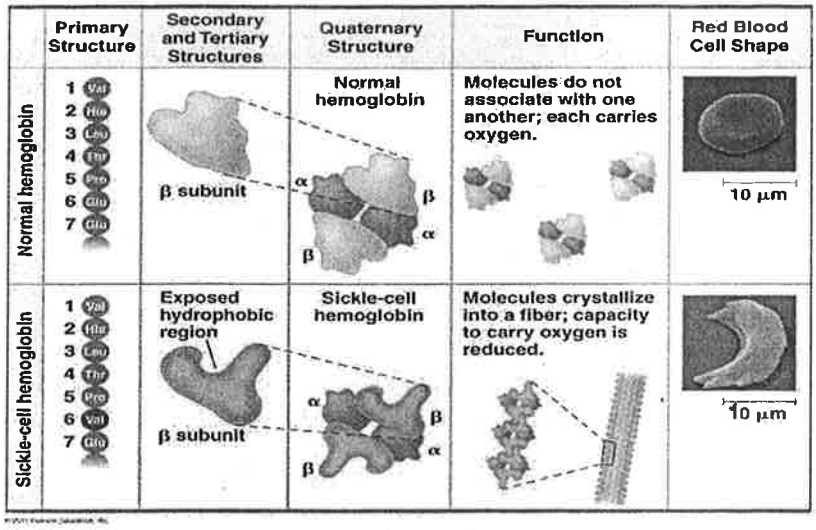


Fig. 27. Showing the formation of fibres.
The mutation results in a conformational change in the molecule such that the hydrophobic patch and groove are exposed. This conformational change makes it possible for the molecules to crystallise to form fibres as the hydrophobic patch of one molecule fits into the hydrophobic groove of another. These fibres distort the shape of the red blood cell resulting in the characteristics sickle shape

- Those who are **heterozygous** for the sickle cell allele (HbAHbS) produce both normal and abnormal haemoglobin. Heterozygous individuals are **usually healthy**, but they may suffer some symptoms of sickle cell anaemia under conditions of low blood oxygen, such as high elevation. Heterozygous (HbAHbS) individuals are said to be **"carriers"** or exhibit **sickle cell trait**.
- **Heterozygote advantage occurs in regions of endemic malaria.** Malaria is characterized by chills and fever, vomiting, and severe headaches. Anaemia and death may result. Malaria is caused by a protozoan parasite (*Plasmodium falciparum*) that is transmitted to humans by the *Anopheles* mosquito.
- The precise mechanism in which heterozygous genotype confers protection/survival advantage against malaria is unknown. A number of factors are likely involved. When malarial parasites invade the red blood cell, their metabolism lowers the oxygen tension within the red blood cells that contain defective haemoglobin causing it to sickle and be destroyed together with the parasites. The crystallization process of HbS also damages the parasites in the cell.
- In a region where malaria is prevalent, individuals with the HbAHbS genotype do not develop sickle cell anaemia and at the same time have **less chance of contracting malaria**. They are able to survive and reproduce in malaria-infected regions. Therefore, **BOTH the HbA and HbS alleles of these people remain in the population**. Thus, the HbS allele confers a survival advantage on people who have one copy of the allele, and the otherwise harmful HbS allele is therefore maintained in the population at a relatively high frequency.
- HbSHbS homozygotes have sickle cell anaemia, which usually results in early death.
- Compared to HbAHbS heterozygotes, people with the HbAHbA genotype (normal haemoglobin) have a greater risk of dying from malaria.

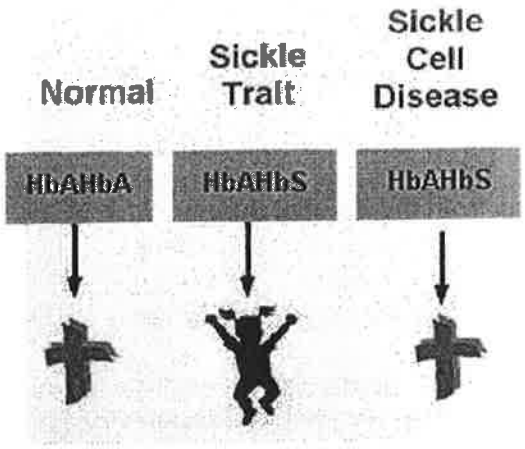


Fig. 28 Schematic representation of the effect of the sickle cell haemoglobin gene on survival in endemic malarial areas.

People with normal haemoglobin (left of the diagram) are susceptible to death from malaria.

People with sickle cell disease (right of the diagram) are susceptible to death from the complications of sickle cell disease.

People with sickle cell trait, who have one allele for HbA and one allele for HbS, have a greater chance of surviving malaria and do not suffer adverse consequences from the HbS allele.

- The frequency of the HbS allele in malaria-infected regions of Africa is 16%. The sickle cell allele is also widespread in the Mediterranean and other areas where malaria is or used to be a major threat to life. In contrast, the HbS allele frequency is only 4% in the United States, where malaria has been virtually eliminated.

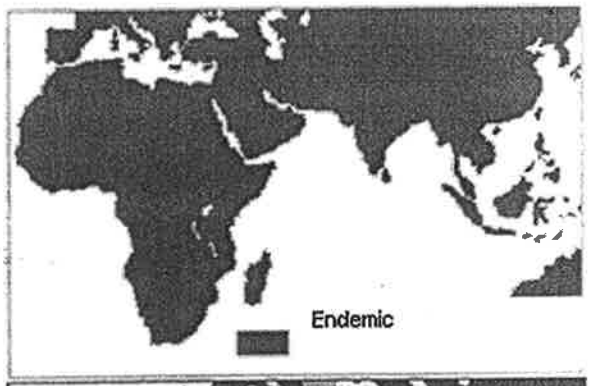


Fig. 29 showing distribution of malaria in Southern Europe, Asia and Africa.

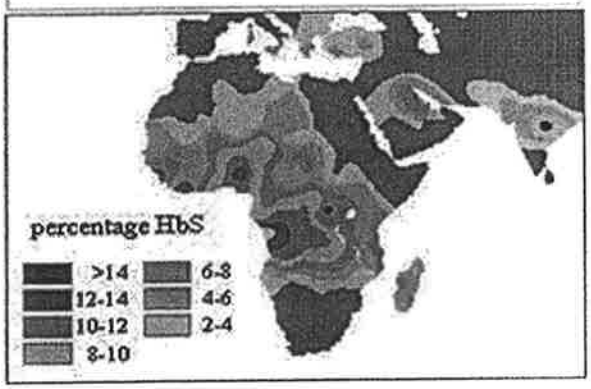


Fig. 30 showing distribution of sickle-cell allele within the same area. The darker the shaded area, the greater the percentage of people carrying the allele. Note the correlation to the map in Fig. 34

- A common misstatement is that malaria selects for sickle cell disease. This is not true. In areas where there is no endemic malaria, a person with sickle cell disease is at an extreme survival disadvantage because of the ravages of the disease process. This means that a negative selection exists for sickle cell disease. Instead we should state that **sickle cell trait (i.e., the heterozygous condition) is selected for in regions of endemic malaria**.

(ii) Frequency-dependent selection

- In frequency dependent selection, the **fitness** (hence selective advantage) of the phenotype **depends on how common it is**.
- In Lake Taganyika in Africa, the scale-eating fish (*Perissodus microlepis*) exhibits such frequency-dependent selection. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. These fish are either "left-mouthed" or "right-mouthed". The **right mouthed allele is dominant to the left-mouthed allele**. The left-mouthed fish always attacks the prey's right side because its mouth twists to the left and vice-versa for the right-mouthed fish.
- The prey guards itself against attack from whatever phenotype of scale-eating fish is most common in the lake. So from year to year, **selection favours whichever mouth phenotype is least common**. As a result, the frequency of left-mouthed and right-mouthed fish **oscillates over time** and frequency-dependent selection **keeps the frequency** of each phenotype **close to 50%.**

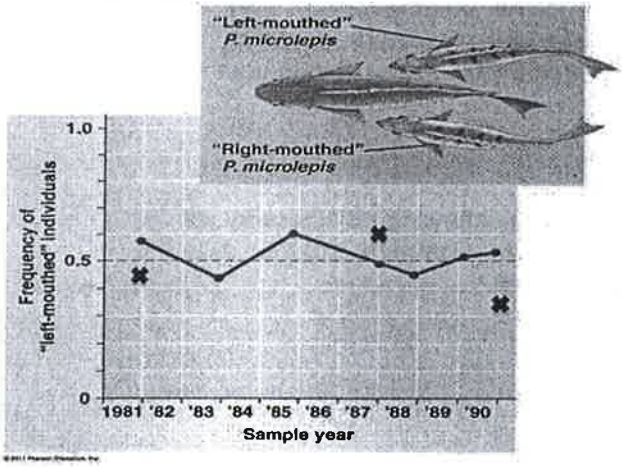


Fig. 31 Frequency dependent selection in scale-eating fish. A study by Japanese scientists show that the frequency of left-mouthed individuals rises and falls in a regular manner (as shown by the trend line). At each of the three time periods when phenotypes of breeding adults were assessed, adults that reproduced (shown by the crosses ✖) had the opposite phenotype of what was common in the population. Thus it showed that the right-mouthed individuals were favoured by selection when left-mouthed individuals were more common, and vice versa.