

Evolution

Introduction

Evolution means change over a period of time. The idea that living beings may have evolved from simple compounds is a fascinating concept. Evolution is the process by which modern organisms have descended from ancient organisms. In other words, species are not constant, they change over time. The change observed so that the population is better adapted to their environment.

The study of evolution provides an insight into the investigation for nature of life, origins of life, diversity of various living beings and the similarities and differences in their structure and function.

The origin of life has different theories and these theories are uncertain. The major theories for the origin of life are:

1) Special creation

This theory is supported by most religions, civilizations. The basis of this theory is that life was created by a supernatural power at a particular time. While this theological approach concentrates on the reason behind creation of beings scientific theories concentrate on the how these beings came into existence. There is no intellectual conflict between scientific and theological theories as they are mutually exclusive realms of thought.

2) Spontaneous creation

The theory suggested that life arose from non-living matter. This theory was highly popular and coexisted with the special creation theory. Aristotle (384-322 BC) believed in this theory and said that life did not arise just from pre-existing parents but also from by spontaneous generation due to natural forces.

This theory fell from favor as more advancements in science. In 1688, Redi observed that the little worms which arise in decaying flesh were fly larvae. He supported the idea of biogenesis, which states that life can arise only from pre-existing life.

In 1765, Lazzaro Spallanzani observed that vegetables would not support growth of other life forms after intense heat treatment and sealing. Based on Spallanzani's work Louis Pasteur designed several experiments and finally disapproved the theory of spontaneous creation.

3) Cosmozoan

This theory does not suggest a mechanism for origin of life but favors the idea that life on earth has an extraterrestrial origin. In 1908, Arrhenius proposed the cosmozoan or panspermia theory. This theory assumed the existence of advanced civilization on other planets in our galaxy and life on earth and many other planets were infected from these advanced civilized planets.

4) Biochemical evolution

As per this theory, life arose as per the chemical and physical laws. In 1923, Oparin suggested that from the simple compound like nitriles, oxides, ammonia, methane many complex organic compounds were formed

gradually under the influence of electric charges, ultra-violet rays. The accumulation of the simple compounds in the oceans resulted in the production of the primeval soup from which life could have arisen.

In 1953, Stanley Miller a graduate student of Harold Urey designed an apparatus for stimulating condition prevalent on earth at the time of abiogenic evolution of organic substances. The apparatus has a spark chamber with two electrodes, a flask for boiling and a condenser. Miller used a mixture of methane ammonia, hydrogen and water. The mixture was exposed to electric discharges, following by condensation and then boiling. It was continued for 18 days. Miller was able to identify 15 amino acids, organic acid, ribose sugar and purine, adenine. Several theories were propounded to explain the evolution.

Lamarck's theory of evolution

Jean Baptiste Lamarck was a French naturalist who proposed a theory based on inheritance of acquired characteristics the offspring then adapt further, advancing evolution of the species.

He explained that the use and disuse of certain abilities led to the organism to gain or lose the ability. In support of Lamarck's theory, some of the characters indeed passed from parents to offspring like development of strong biceps muscles in blacksmith, elongated body and loss of limbs in snakes due to continuous creeping through the holes and crevices, migration of both the eyes towards the upper side in flat fishes living on the bottom of sea, lengthening of neck in the giraffe due to its continuous use in reaching to the leaves and fruits of high rise tree. This theory put more importance on need of the animal and considers it strong enough to device ways to form organs needed for adaptation.

This theory was discredited as the use or disuse of all the abilities does not cause transfer abilities to next generation (eg. healthy parents need not always have healthy children). The experiments carried out by August Weismann proved to be a major criticism against Lamarkism. He had cut off the tails of rats for about 80 generations, but tailless offsprings were never born,

Theory of Natural selection:

In June 1831, the H.M.S. Beagle set sail from England and 22 year-old Charles Darwin took up an unpaid position on this voyage. Darwin had begun his studies as a medical student, then became a divinity student at Cambridge. But neither field excited him, much to his father's disappointment. Darwin become interested in geology and spent some time studying geology informally. After three years of surveying the South American coast, the Beagle reached San Cristobal (Chatham) in September 1835. The Beagle spent 5 weeks in the Galapagos.

The voyage helped Darwin to observe the variety of differences which occurred in the same species on these different islands. Also, he observed completely different species exclusive to some islands. Thus Darwin's greatest scientific contribution was that he could provide a logical insight into how and why evolution occurred. Charles Darwin propounded the theory of Natural selection. When there are differences in organism's abilities to survive and reproduce based upon inheritable traits natural selection takes place. As per Thomas Malthus, every generation in a species, more offspring are produced than actually survive due to limited resources. Survival of

any individual is not random, and it depends on hereditary factors. Those individuals with favorable inheritable traits will survive and reproduce. Those with less favorable inheritable traits will be eliminated. This will lead to a gradual change in the entire population, favorable hereditary variations accumulating over time and the species will change.

Darwin devoted 20 years in generating evidence to support his ideas. Wallace wrote to Darwin telling him his ideas on natural selection. This geared Darwin into publishing his ideas. Thomas Wallace and Darwin agreed to publish simultaneous papers. Darwin's book, *The Origin of Species*, was an immediate sensation.

Darwin has described his views on evolution as follows:

“Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.”

There are several observed cases of Natural selection.

1. Insects resistance to insecticides

Insecticides are sprayed on crops to protect them from attack of various insects. Some insects which are resistant to the insecticides, survive the use of insecticides on crops. Thus their progeny flourishes, while the others which are susceptible will be killed by the insecticides. This is a result of genetic variability in the population of insects. Those with the beneficial genetic makeup will survive and flourish.

2. Bacterial resistance to antibiotics

Antibiotics are targeted against bacteria. Some bacteria possess the antibiotic resistance gene in their plasmid. They can survive even in the presence of antibiotics. Bacteria have the capacity to transfer the plasmid to other bacteria by transformation. Therefore all the bacteria with the plasmid having antibiotic resistance gene survive in the presence of antibiotic.

3. Increased frequency of sickle cell anemia in Africans.

The protein in red blood cells (RBCs) that transports oxygen from the lung to metabolically active tissues, like muscle, where it is needed. The discovery of haemoglobin S (HbS) by Linus Pauling and colleagues in 1949 was the first demonstration that the production of an abnormal protein could be the cause of a genetic disorder. In 1956, Vernon Ingram identified the abnormality in the amino acid sequence of the β -globin chain ($\beta 6\text{Glu} \rightarrow \text{Val}$). This abnormality resulted in the normal concave cells gaining a sickled appearance.

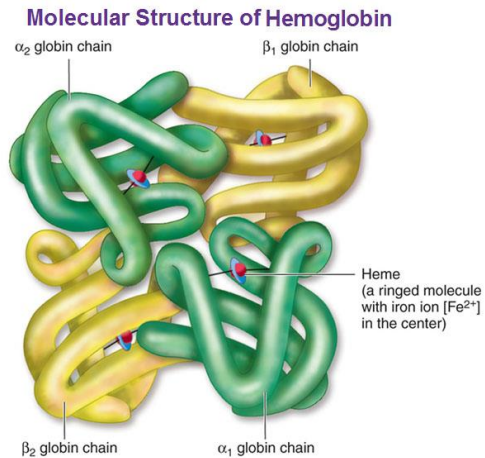


Figure 1- The structure of hemoglobin protein in the RBCs. Sickle cell anemia is produced due to mutation event in the beta chain of hemoglobin.

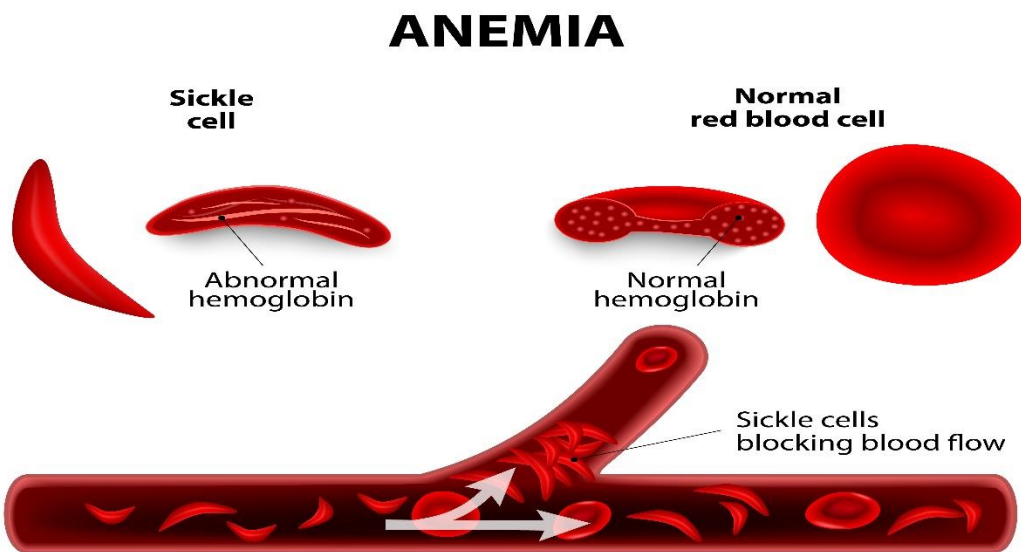


Figure 2- The abnormal cells of RBC as seen in Sickle cell Disease (SCD) compared with the normal RBCs. The sickle shape of the abnormal cells obstructs the blood flow and causes blood blockage in the thin capillaries causing extreme pain.

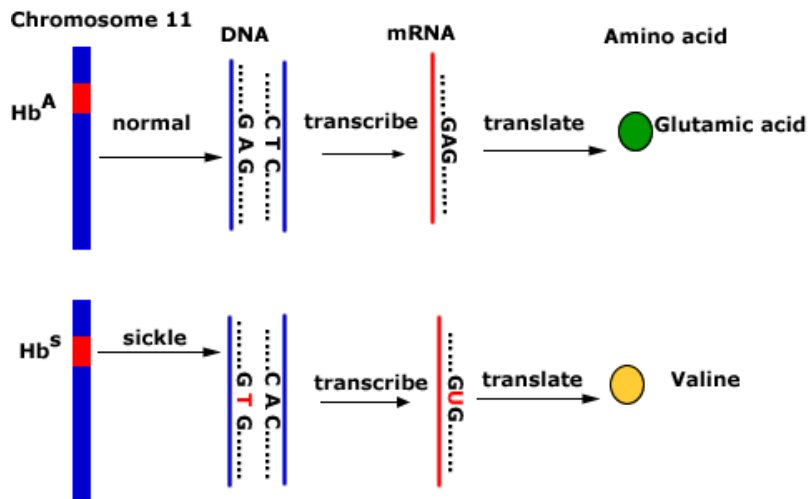


Figure 3- The gene for the beta chain of hemoglobin in normal RBCs codes for glutamic acid, which is hydrophilic in nature. The mutation in the gene coding for beta chain changes the codon on the mRNA to code for valine instead of glutamic acid. Valine is hydrophobic in nature.

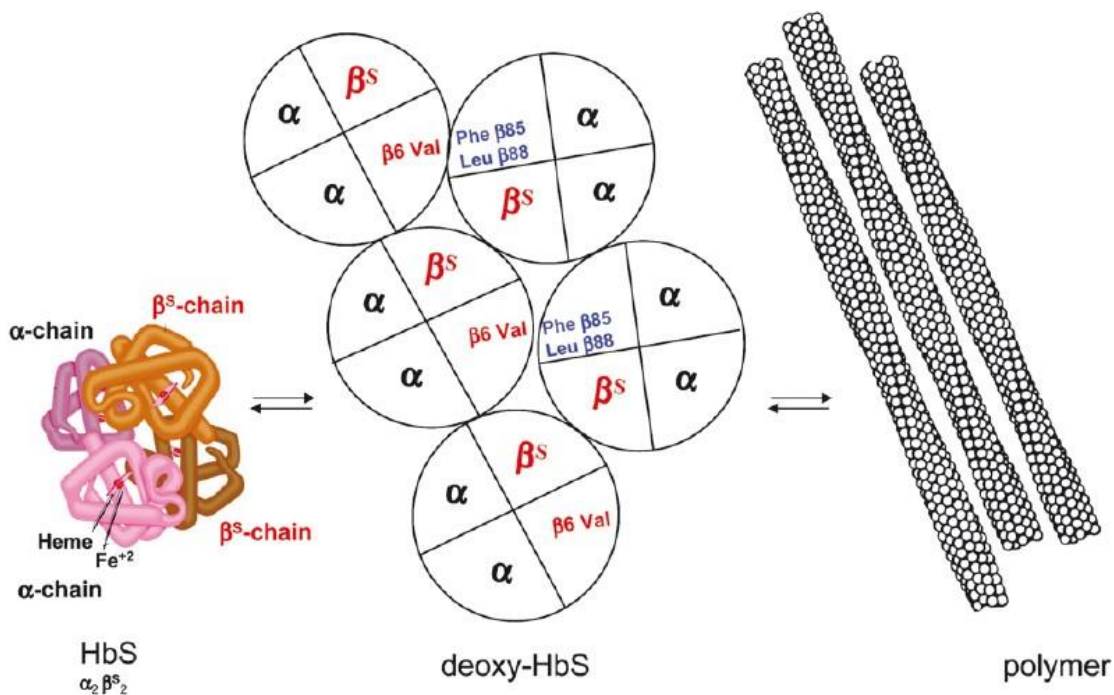


Figure 4-Basic pathophysiological mechanism of sickle cell disease: the polymerization of deoxy-HbS. The replacement of a glutamic acid by a valine residue at position 6 in the β -globin polypeptide chain characterizes the abnormal haemoglobin of SCD: HbS. The presence of hydrophobic valine in the beta chain acts as a hydrophobic pocket to which the other hydrophobic residues (phenylalanine and leucine) in the beta chain bind. At low oxygen pressure, deoxy-HbS polymerises and gets organised in long polymer fibres that deform, stiffen, and weaken the red blood cell

Inheritance of sickle cell anemia

The character of having a sickle cell is recessively inherited and follows the Mendelian pattern of inheritance for a recessive trait. The normal cell phenotype is dominant.

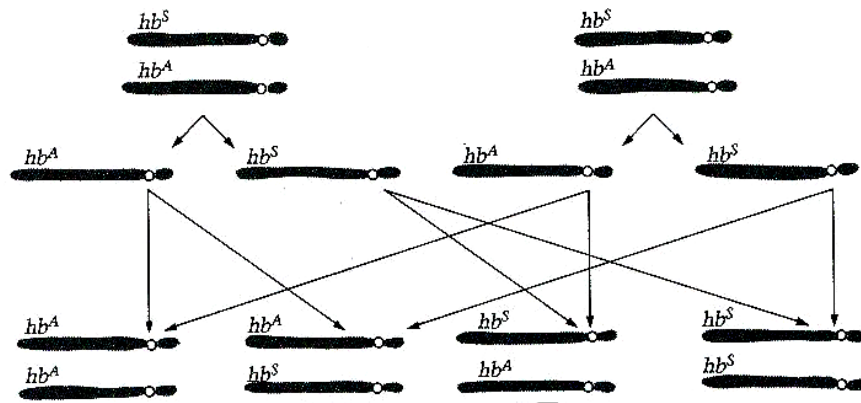


Figure 5- Inheritance of sickle cell disease. hb^A stands for normal RBC gene and hb^S stands for sickle shaped RBC gene. The recessive trait of a RBC being sickle shaped is not expressed phenotypically in a heterozygous individual. The phenotype of a sickle cell is expressed in a homozygous recessive individual. Thus the trait follows Mendelian inheritance pattern for a recessive character.

The sickle cell eventually bursts and dies. Under low oxygen conditions (high altitude or after rigorous exercise), a heterozygous individual for the sickle cell trait, RBCs start showing the sickled phenotype. These heterozygous individuals realize oxygen scarcity in their cells under such conditions as the sickling of cells reduces the oxygen carrying capacity of RBCs.

Sickle cell and resistance to malaria:

The reduced oxygen carrying capacity gives the heterozygous individual protection against malaria. Malaria pathogen completes a part of its early life cycle in the RBCs. The early stages of the malaria pathogen's development requires oxygen to complete its life cycle. Since in the heterozygous individuals the RBCs have a low capacity to carry oxygen, the malaria pathogen is not able to survive. Thus, the heterozygous and homozygous recessive individuals are protected from malaria.

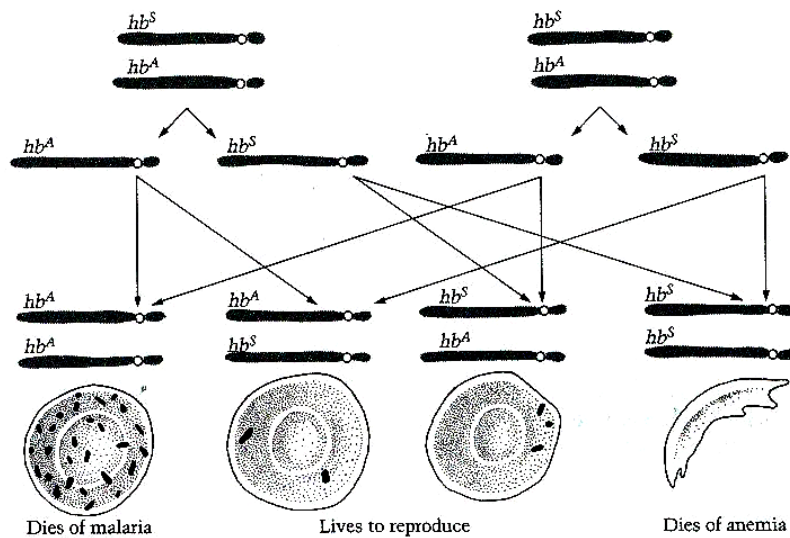


Figure 6- SCD and malaria resistance.

Evolution to protect against death by malaria:

The effect of natural selection is evident in the distribution of the sickle cell trait in areas where malaria is found to be indigenous. Thus, hinting that the process of evolution may have used the sickle cell trait as a protection against malaria, in these regions.

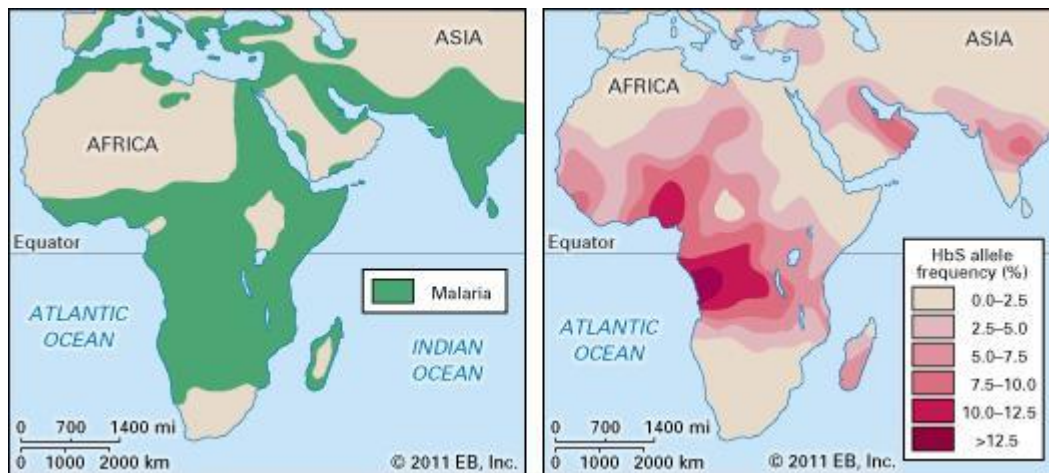


Figure 7- Geographic distribution of malaria and the appearance of sickle cell trait.

Darwin's theory of natural selection was had one major loophole. The theory could not explain the inheritance of traits from one generation to next. Existence of vestigial organs could not be explained using natural selection. Overspecialisation of some structures like antlers and tusks of elephants becomes a hindrance to these organisms. This fact that these structures that were hindrance to the organism being inherited could not be explained.

Importance of Population genetics:

Natural selection is understood on observing the changes which occur in a population rather than in an individual. Technically, evolution results from the change in gene frequencies within a population overtime. Therefore, in order to understand evolution, it would be important to describe those events that change gene frequencies in a population. Darwin could not explain how adaptive inheritable traits are passed on.

Biologists did not have a good understanding of the genetic details of how natural selection works until the field of transmission genetics was established in the early 1900s. At that time, the rediscovery of Gregor Mendel's publications paved the way for the development in the 1930s and 1940s of the field of population genetics. As the principles of evolution were integrated with the principles of modern genetics during this period, a new understanding of evolutionary biology—known as the Modern Synthesis—emerged. This was when biologists began to study mechanistic aspects of evolution as well as the broad evolutionary patterns that were so evident in nature.

There are several evidence for evolution:

1. Fossil evidence: Fossils are the preserved remains of ancient organisms. The remains of the organisms can be found in preserved form in sap, mineral replacement, in ice, or traces e.g. footprints, molds. Fossils demonstrate the existence of intermediate forms of species, thus demonstrating evolution. The given figure shows how the ancient whales spent more time immersed, hence their nostrils where at the tip of the



Figure 8- Ancient whales spent more time immersed, hence their nostrils where at the tip of the nose. Over the years, as they migrated to seas, the nostrils occupied a space higher on the skull. At present, whales can break the surface of sea because their nostrils are on the top

beginning of the skull. Over the years, as they migrated to seas, the nostrils occupied a space higher on the skull. At present, whales can break the surface of sea because their nostrils are on the top beginning of the skull.

2. Embryonic evidence: The embryonic stages of various organisms share similar features for eg. the duck and chick embryo both have presence of webbed feet (Fig. 2). The later stages of development in the chick embryo causes the death of the layer in the

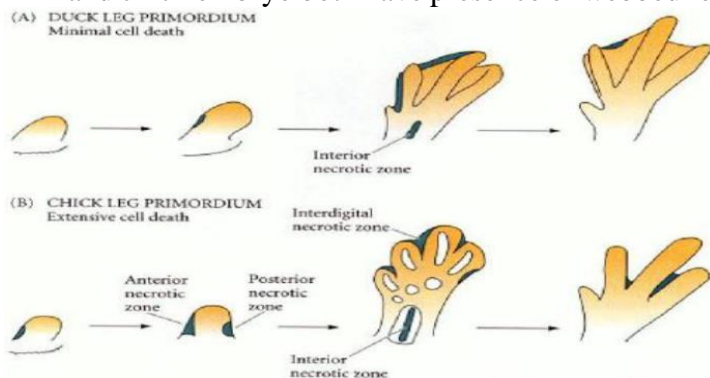


Figure 9- The embryo of duck and chick share a common structure initially. The molding of limbs in duck and chick embryo

embryo causes the death of the layer in the interdigital zone since the chick has no use of webbed feet in its habitat.

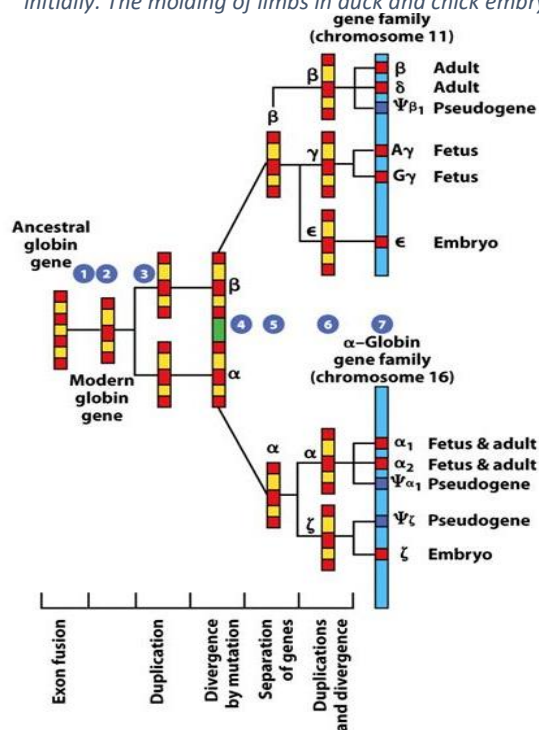


Figure 10-Evolution of globin gene

exons. (2) A primitive globin gene has one exon. (3) Duplication of the globin gene followed by (4) a mutation that produced two different genes α and β gene (5) a process of genetic rearrangement caused genes (α and β) to separate (6) & (7).

3. Genetic evidence: The DNA sequences in a gene family are usually different from one another. As long as at least one member encodes a functional protein, the other members may mutate in ways that change the functions of the proteins they encode. For evolution, the availability of multiple copies of a gene allows for selection of mutations that provide advantages under certain circumstances. If a mutated gene is useful, it may be selected for in succeeding generations. If the mutated gene is a total loss (pseudogene), the functional copy is still there to carry out its role. The presence of pseudogenes is an evidence of evolution in the gene. The gene family encoding the globins is a good example of the gene families found in vertebrates (Fig. 3). These proteins are found in hemoglobin and myoglobin (an oxygen-binding protein present in muscle). The globin genes all arose long ago from a single common ancestral gene. In adults, each hemoglobin molecule is a tetramer containing two identical α -globin subunits, two

identical β -globin subunits, and four heme pigments. During human development, different members of the globin gene cluster are expressed at different times and in different tissues. This differential gene expression has great physiological significance. Hemoglobin is a tetramer of four polypeptide units. A characteristic organization is realized while studying the globin genes from various organisms like mammal or fish, each of them contains three exons and two introns. Globin like polypeptides such as

plant leghemoglobin and the muscle protein myoglobin, reveals the presence of four exons and three introns.

Billions of years ago, when the earth was devoid of life, there was also no oxygen in the air. The first life developed about 3.8 billion years ago, the water vapor, nitrogen, methane and ammonia were used for food and energy. It is expected that the metabolic

reactions were catalyzed by metals such as iron and magnesium. With the emergence of photosynthetic organisms around 3.5 billion years ago, the atmosphere of earth was remarkably changed. Oxygen produced as a result of photosynthesis was released into the atmosphere and gradually came to be the most important constituent of atmosphere. Life forms appeared on earth utilizing this abundant oxygen on the atmosphere. The oxygen has to bind to a carrier and not supposed to react with that carrier.

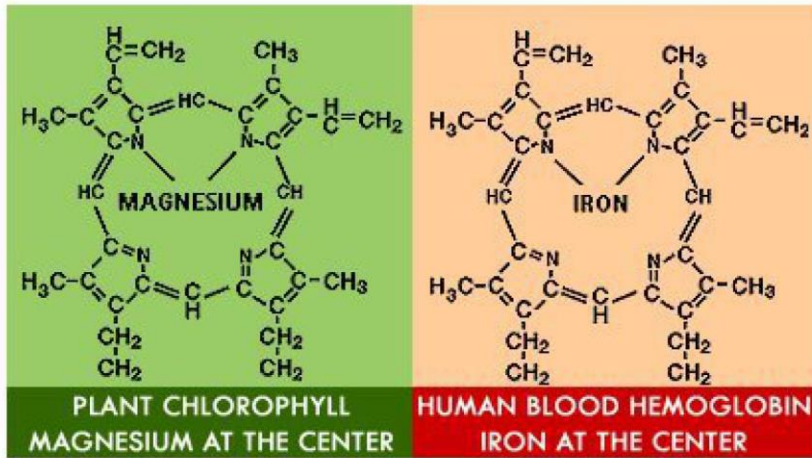


Figure 4- Comparison of Plant chlorophyll and hemoglobin structure (Image credit: <http://cascade.patch.com/groups/nicole-moseleys-blog/p/bp--hemoglobin-vs-chlorophyll>)

After binding it has to be transported to cells.

Chlorophyll, which is evolved earlier for photosynthesis, is a porphyrin ring containing magnesium. Another porphyrin ring containing iron is called heme. Heme bound to globin molecule is called hemoglobin. Hemoglobin binds to oxygen in the lungs and gives blood its red color.

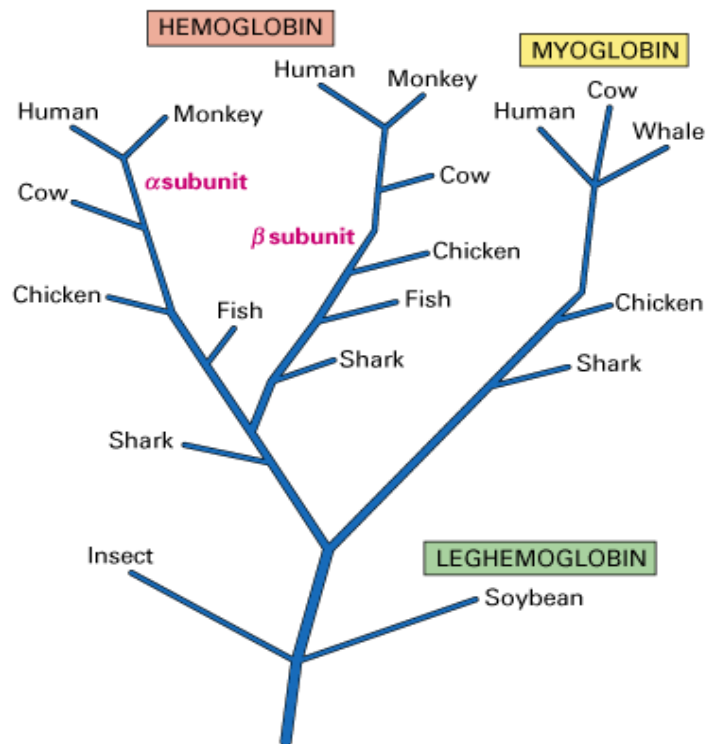
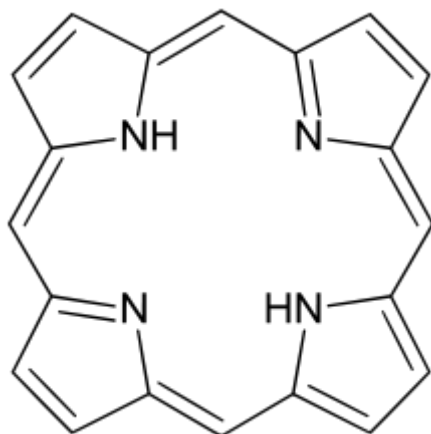


Figure 12-Phylogenetic tree showing the evolutionary history of globin protein

Myoglobin is a single polypeptide chain while vertebrate hemoglobins are tetrameric. Both are oxygen binding proteins. Leghemoglobin is also bind to oxygen, but found exclusively in root nodules of legume plants like soyabean.

We need to understand how a small change in a molecule has led to the diverse functions. For this we need to examine molecules such as haemoglobin, myoglobin, haemocyanin, leghaemoglobin and chlorophyll. All of them are modified porphyrins.



They can accommodate different metal atoms at their centers. They are very stable due to their *conjugation* (alternating single and double bonds). Nature has utilized the properties of porphyrin ring in different ways for multiple functions.

Figure 13-Porphyrin structure

Let us examine haemoglobin. As all of us know it is the oxygen carrying molecule of blood. O_2 is only marginally soluble ($< 0.0001\text{ M}$) in blood plasma at physiological pH. Hence by relying into the dissolved oxygen in the blood may not be feasible for the life systems to move on. Therefore the evolution has occurred for the better transport of oxygen molecule. Animals requires the development of a mechanism to actively transport oxygen through the system. We have about 150 g of the protein which is known as haemoglobin (Hb) per liter of the blood. This is an effective oxygen carrier that the concentration of O_2 in the blood stream reaches 0.01 M — the same concentration as air. Once the Hb- O_2 complex reaches the tissue that consumes oxygen, the O_2 molecules are transferred to another protein — **myoglobin** (Mb) — which transports oxygen through the muscle tissue.

Now let us logically examine the haemoglobin molecule. Each haemoglobin is a combination of four polypeptide chains: two alpha and two beta subunits. Each chain has an associated heme group which can bind to oxygen. Thus one Hb molecule binds with four oxygen molecules. The structure of heme group is given below.

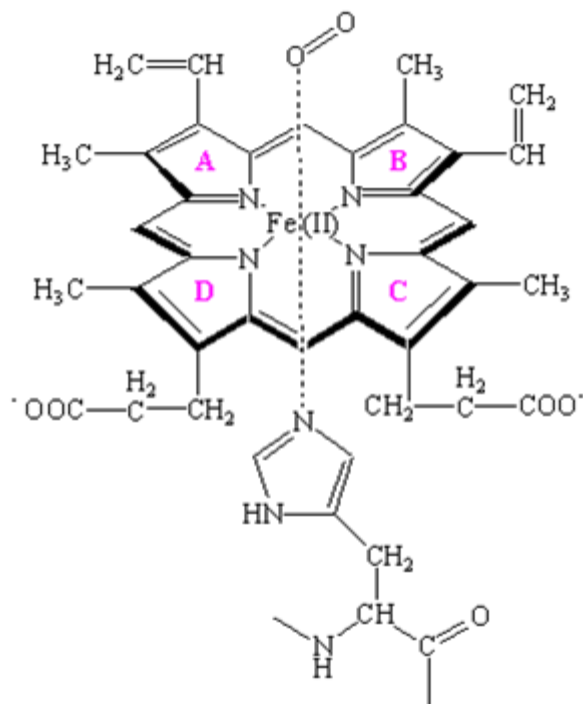


Figure 14-Myoglobin molecule

An Fe(II) atom is present at the centre of each heme. Four of the six coordination sites around this atom are occupied by nitrogen atoms from a planar **porphyrin** ring. The fifth coordination site is occupied by a nitrogen atom from a histidine side chain on one of the amino acids in the protein. The last coordination site is available to bind an O_2 molecule. Now we need to analyze why four protein parts? The distance between the iron atoms of adjacent hemes in hemoglobin is very large — between 250 and 370 nm — the act of binding an O_2 molecule at one of the four hemes in hemoglobin leads to a significant increase in the affinity for O_2 binding at the other hemes. Thus a cooperative interaction occurs that makes Hb an excellent carrier for oxygen.

The structure of myoglobin suggests that the oxygen-carrying heme group is buried inside the protein portion of this molecule (similar to Hb). This enables the pairs of hemes group from coming too close together. This is important, because these proteins need to bind O_2 reversibly and the Fe(II) heme, by itself,

cannot do this. When there is no globin to protect the heme, it reacts with oxygen to form an oxidized Fe(III) atom instead of an Fe(II)-O₂ complex.

What made the necessity of two oxygen binding molecules? Hb has four haeme group while myoglobin carries only one heme group. The affinity of Mb with oxygen is higher than the affinity of Hb with oxygen. This difference is related to its different role: whereas hemoglobin transports oxygen, myoglobin's function is to store oxygen.

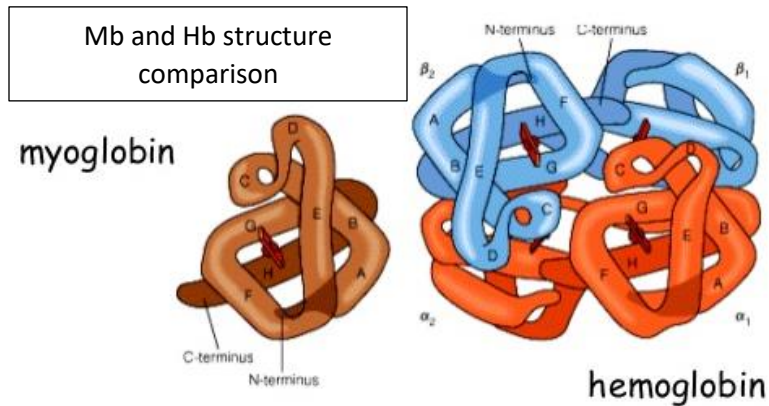


Figure 15-Mb and Hb subunits are structurally similar with 8 alpha helices and oth containing a heme group. But Mb is monomeric while Hb is heterotetramer (2 alpha and 2 beta subunits)

Being large Hb can't enter muscle tissue. Further to prevent from clotting, blood has to move. Hence Hb is not an ideal structure for delivering oxygen in muscle tissues and its storing. Since myoglobin is a storage protein, its affinity towards oxygen should not differ with its concentration. Hence evolution has favored a similar molecule, a monomeric protein which is more compact. Thus the life systems have utilized the heme group for two different functions (i) for transporting oxygen and (ii) for storing oxygen. This has achieved by combining the heme group with different proteins ie the globin part.

Also it is interesting to see, why there is a requirement of a protein part ie amino acids attached with heme group. When molecular oxygen encounters an isolated heme molecule, it rapidly converts the Fe(II) to Fe(III). The oxidized heme binds oxygen very poorly. Obviously, if this happened to the Fe(II) groups of hemoglobin and myoglobin, the proteins would be less useful as oxygen carriers. Oxidation of the heme iron is prevented by the presence of the **distal histidine** side chain, which prevents the O₂ from forming a linear Fe-O-O bond. The bond between Fe and O₂ is bent, meaning that this bond is not as strong as it might be. *Weaker oxygen binding means easier oxygen release.*

Chlorophyll

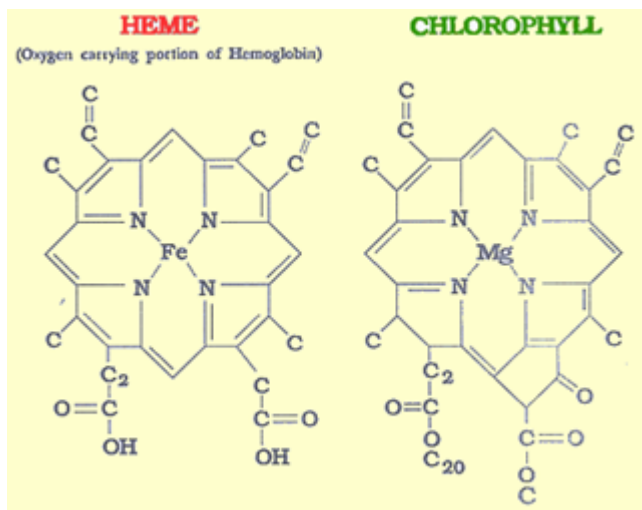


Figure 16-Structure comparison of heme and chlorophyll

Chlorophyll is the molecule that traps this 'most elusive of all powers' - and is called a photoreceptor. It is found in the chloroplasts of green plants, and is what makes green plants, green. The basic structure of a chlorophyll molecule is a porphyrin ring (similar to haeme) coordinated to a central atom. This is very similar in structure to the heme group found in hemoglobin, except that in heme the central atom is iron, whereas in chlorophyll it is magnesium.

Haemocyanin

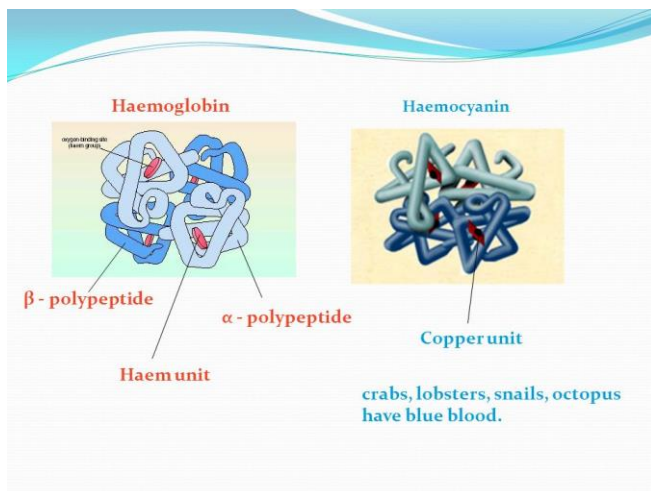
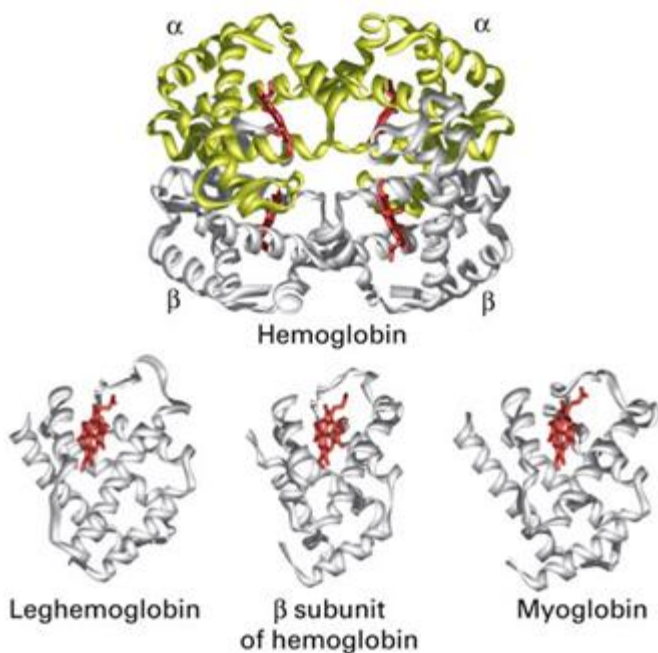


Figure 17- Structural comparison of haemoglobin and haemocyanin

Haemocyanin is another evolved compound from the porphyrin ring. Instead of Fe, haemocyanin has Cu in it. This also serves as an oxygen carrier in some animals.

Leghaemoglobin

This is the oxygen carrier found in the root nodules of legumes. It is synthesized in a symbiotic interaction with nitrogen fixing bacteria in the root nodules. Similar to haemoglobin it is red in color and carries oxygen for the growing bacteria in the root nodule.



Now it is easy for us to understand that among the molecules discussed such as haemoglobin, myoglobin, haemocyanin and leghaemoglobin, there is a similarity in the structure. Just by modifying a small part such as replacement of the central atom (Fe /Cu/Mg) of the porphyrin ring these molecules are modified (evolved) to perform diverse functions. This is nature's chemical engineering and are products of evolution.

Figure 18- Structural comparison of hemoglobin, leghemoglobin, myoglobin and beta subunit of hemoglobin

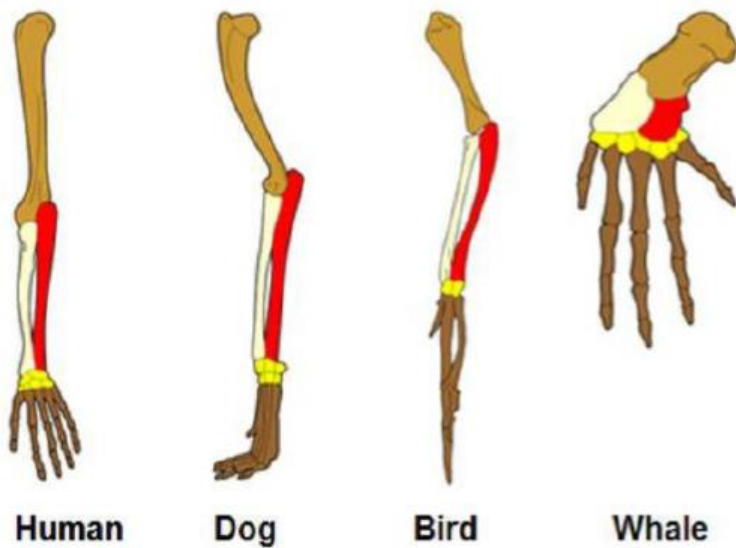


Figure 19- The forelimbs of vertebrates evolved from an ancestral pattern. Even vertebrates as dissimilar as whales and bats have the same basic arrangement of bones. The shades are based on homologous bones.

4. Form and function evidence: The **function** of a biological structure can be **inferred** from its **shape**. If we take our own bodies to illustrate, we know that ear is a canal with a funnel shaped external ear. We know that the external ear is funnel shaped for focusing sounds from the atmosphere. It is possible to explain that why many animals have more sound perception than humans based on the architecture of external ear. Vestigial organs are remains of a structure that was functional in some ancestor but is no longer functional in the organism in question. For example, humans have a tail bone (the coccyx) but no tail.

The mechanisms responsible for evolution are:

1. Mutation

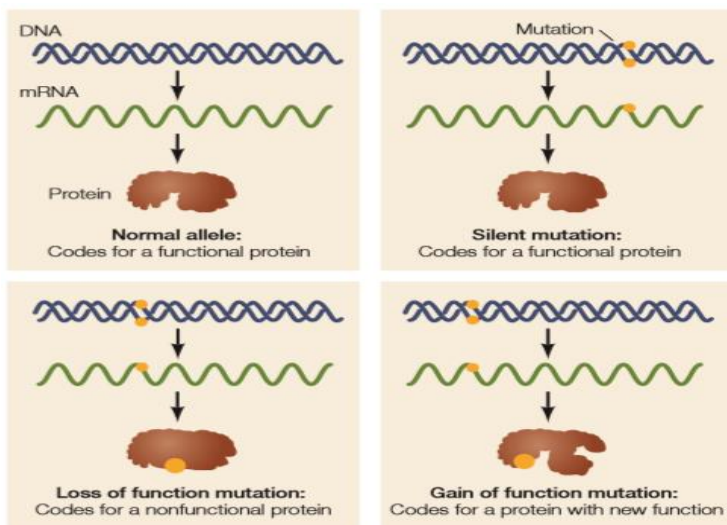


Figure 20- Mutations may or may not affect the protein phenotype. Image courtesy- Sadava et al, Life: The science of Biology, 9th edition.

of their effects on proteins and their function:

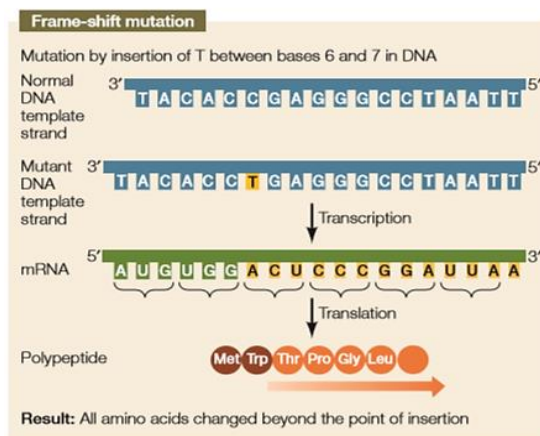
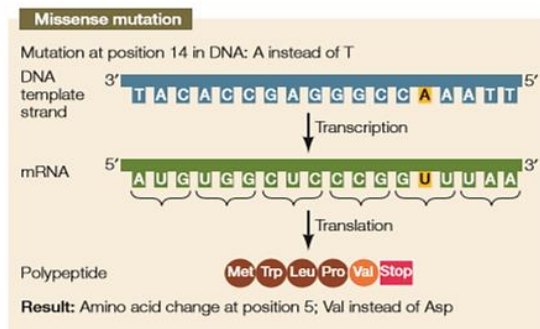
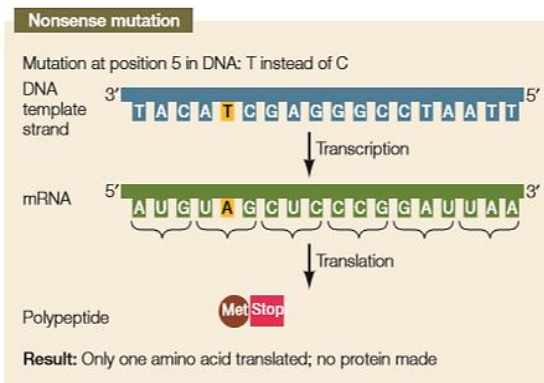
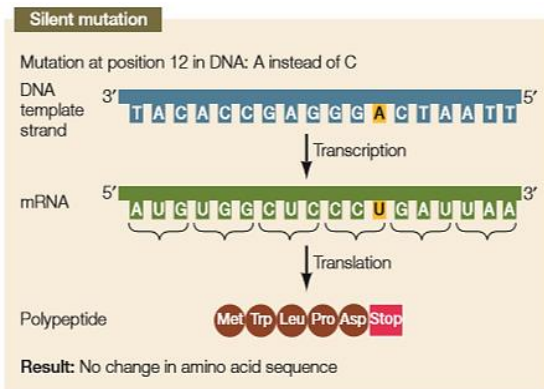
The origin of genetic variation is mutation. Accurate DNA replication, transcription, and translation all depend on the reliable pairing of complementary bases. Errors occur, though infrequently, in all three processes—least often in DNA replication. But, the consequences of DNA errors are the most severe because only they are heritable. Mutations are heritable changes in genetic information, which may occur spontaneously or may be induced.

Mutations have different phenotypic effects phenotypically, we can understand mutations in terms

All mutations are alterations in the nucleotide sequence of DNA. At the molecular level, we can divide mutations into two categories:

- **A point mutation** results from the gain, loss, or substitution of a single nucleotide. After DNA replication, the altered nucleotide becomes a mutant base pair. If a point mutation occurs within a gene (rather than in a noncoding DNA sequence), then one allele of that gene (usually dominant) becomes another allele (usually recessive).

- **Chromosomal mutations** are more extensive than point mutations. They may change the position or



orientation of a DNA segment without actually removing any genetic information, or they may cause a segment of DNA to be duplicated or irretrievably lost. Changes in single nucleotides are not the most dramatic changes that can

Figure 21- Point mutations. Image courtesy- Sadava et al, Life: The science of Biology, 9th edition.

occur in the genetic material. Whole DNA molecules can break and rejoin, grossly disrupting the sequence of genetic information. There are four types of such chromosomal mutations: deletions, duplications, inversions and translocations. These mutations can be caused by severe damage to chromosomes resulting from mutagens or by drastic errors in chromosome replication.

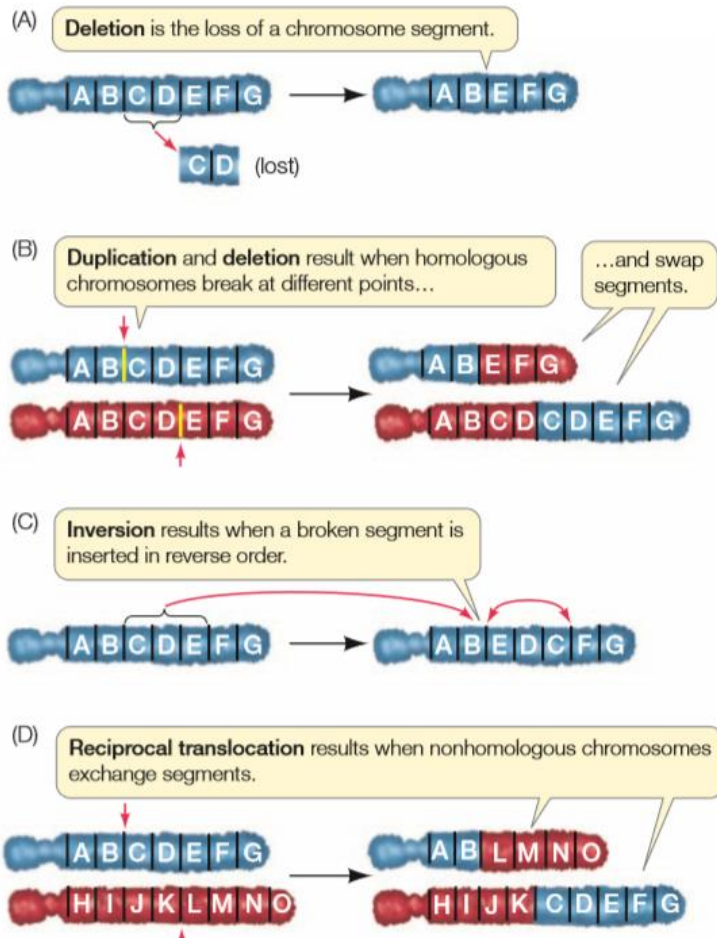


Figure 22- Chromosomal Mutations Chromosomes may break during replication, and parts of chromosomes may then rejoin incorrectly. The letters on these chromosome illustrations represent large segments of the chromosomes. Each segment may include anywhere from zero to hundreds or thousands of genes. . Image courtesy- Sadava et al, *Life: The science of Biology*, 9th edition.

Effects of mutation:

Mutations provide the scope for evolution: A mutation in somatic cells may benefit the organism immediately. Second, a mutation in germ line cells may have no immediate selective advantage to the organism but may cause a phenotypic change in offspring. If the environment changes in a later generation, that mutation may be advantageous and thus selected for under these conditions.

Germ line and somatic mutations can be harmful: Mutations in germ line cells that get carried to the next generation are often deleterious, especially if the offspring are homozygous for a harmful recessive allele. In their extreme form, such mutations produce phenotypes that are lethal. Lethal mutations can kill an organism during early development, or the organism may die before maturity and reproduction.

2. Gene flow may change allele frequencies

Frequency of appearance of an allele also depends on the migration of individuals and movements of gametes between populations. This is called as gene flow. If the arriving individuals survive and reproduce in their new location, they may add new alleles to the population's gene pool, or they may change the frequencies of alleles already present if they come from a population with different allele frequencies.

3. Genetic drift:

In small populations, random changes in allele frequencies from one generation to the next may produce large changes in allele frequencies over time. This is called as genetic drift.

During population bottlenecks, genetic variation can be reduced by genetic drift. In this case, disasters such as floods and fires can drastically reduce the size of the population, leaving by chance, individuals that are not necessarily representative of the original population. A population forced through a bottleneck is likely

to lose much of its genetic variation. Genetic drift can have similar effects when a few pioneering individuals colonize a new region. Because of its small size, the colonizing population is unlikely to have all the alleles found among members of its source population. The resulting change in genetic variation, called a founder effect, is equivalent to that in a large population reduced by a bottleneck.

4. Nonrandom mating can change genotype frequencies

Mating patterns may alter genotype frequencies if individuals in a population do not choose mates at random.

Constraints in evolution:

All life forms are constrained by various factors. For example, the growth in cell size is constrained by the stringencies of surface area-to-volume ratios. Folding of protein is limited by the bonding capacities of their constituent molecules. And the energy transfers that fuel life must operate within the laws of thermodynamics. Evolution works within the boundaries of these universal constraints.

The additional constraints which will be placed on evolution are:

1. Development process constraints evolution:

Evolutionary changes cannot start from scratch happen in this way. Current phenotypes of organisms are constrained by historical conditions and past selective pressures. The new species is formed or evolved from an existing species by incremental change. The old species is not discarded but it is changed. Thus evolution occurs from one form to another.

Metamorphosis of the tadpole larva into an adult frog is one of the most striking transformations in biology. In amphibians, metamorphosis is initiated by hormones from the tadpole, and these changes prepare an aquatic organism for a terrestrial existence.

The developmental constraints prevent the organism from producing a change which is extremely different from the ancestors.

2. Trade-offs constraint evolution

Adaptations frequently impose both fitness costs and benefits. For an adaptation to evolve, the fitness benefits it confers must exceed the fitness costs it imposes—in other words, the tradeoff must be worthwhile. For example, there are metabolic costs associated with developing and maintaining certain conspicuous features (such as antlers or horns) that males use to compete with other males for access to females. The fact that these features are common in many species suggests that the benefits derived from possessing them must outweigh the costs.

3. Short-term and long-term evolutionary outcomes sometimes differ

The short-term changes in allele frequencies within populations can be observed directly, they can be manipulated experimentally, and they demonstrate the actual processes by which evolution occurs. By themselves, however, they do not enable us to predict long-term evolutionary changes. Long-term patterns

of evolutionary change can be strongly influenced by events that occur so infrequently (a meteorite impact, for example) or so slowly (continental drift) that they are unlikely to be observed during short-term studies. The ways in which evolutionary processes act may change over time with changing environmental conditions.

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