

## **COUNCIL OF SCIENTIFIC AND INDUSTRIAL RESEARCH** **UNIVERSITY GRANTS COMMISSION**

LIFE SCIENCE

CODE: 03

### **UNIT 11: EVOLUTION AND BEHAVIOUR**

#### **AT A GLANCE:**

**Allele frequency:** The proportion of gene copies in a population that are a given allele; i.e., the probability of finding this allele when a gene is taken randomly from the population also called gene frequency.

**Allopatric speciation:** Speciation by genetic divergence of allopatric populations of an ancestral species; contrasted with parapatric and sympatric speciation, in which divergence occurs in parapatry or sympatry.

**Altruism:** Conferral of a benefit on other individuals at an apparent cost to the donor.

**Behavioral ecology:** The study of the evolution of behaviors, often in relation to the environment, including other members of the same species.

**Clade:** The set of species descended from a particular ancestral species.

**Cladistic:** Pertaining to branching patterns; a cladistic classification classifies organisms on the basis of the historical sequences by which they have diverged from common ancestors.

**Cladogenesis:** Branching of lineages during phylogeny.

**Cladogram:** A branching diagram depicting relationships among taxa; i.e., an estimated history of the relative sequence in which they have evolved from common ancestors.

**Carrying capacity:** The population density that can be sustained by limiting resources.

**Competitive exclusion principle:** The theoretical assertion that one of two ecologically identical species will eventually replace the other by struggle.

**Coevolution:** Severely, the joint evolution of two or more ecologically interacting species, each of which evolves in response to selection imposed by the other. Sometimes used loosely to refer to evolution of one species caused by its interaction with another, or simply to a history of joint divergence of ecologically associated species.

**Evolution:** Darwin defined it as descent with modification. It is the change in a lineage of populations between generations.

**Disruptive selection:** Selection favoring forms that deviate in either direction from the population average. Selection favors forms that are larger or smaller than average, but works against the average forms between.

**Founder effect:** The loss of genetic variation when a new colony is formed by a very small number of individuals from a larger population.

**Gene frequency:** The frequency in the population of a particular *gene* relative to other genes at its locus. Expressed as a proportion (between 0 and 1) or percentage (between 0% and 100%).

**Gene pool:** All the genes in a population at a particular time.

**Genetic drift:** Random changes in gene frequencies in a population.

**Gene flow:** The incorporation of genes into the gene pool of one population from one or more other populations.

**Hardy-Weinberg:** Pertaining to the genotype frequencies. expected at a locus under ideal equilibrium conditions in a randomly mating population.

**Hamilton's rule:** The theoretical principle that an altruistic trait can increase if the benefit to recipients, multiplied by their relationship to the altruist, exceeds the fitness cost to the altruist.

**kin selection:** A form of selection whereby alleles differ in their rate of propagation by influencing the impact of their bearers on the reproductive success of individuals (kin) who carry the same alleles by common descent.

**Lamarckism:** The theory that evolution is caused by inheritance of character changes acquired during the life of an individual due to its behavior or to environmental influences.

**Molecular clock:** The concept of a steady rate of change in DNA sequences over time, providing a basis for dating the time of divergence of lineages if the rate of change can be estimated.

**Microevolution:** A vague term, usually referring to slight, short-term evolutionary changes within species.

**Macroevolution:** The mutation of a large phenotypic effect; one that produces a phenotype well outside the range of variation previously existing in the population.

**Natural selection:** The differential survival and/or reproduction of classes of entities that differ in one or more characteristics. To constitute natural selection, the difference in survival and/or reproduction cannot be due to chance, and it must have the potential consequence of altering the proportions of the different entities. Thus natural selection is also definable as a deterministic difference in the contribution of different classes of entities to subsequent generations. Usually the differences are inherited. The entities may be alleles, genotypes or subsets of genotypes, populations, or, in the broadest sense, species.

**Parapatric:** Of two species or populations, having contiguous but non-overlapping geographic distributions.

**Phylogenetic tree:** A diagram representing the evolutionary relationships among named groups of organisms, i.e., their history of descent from common ancestors.

**Postzygotic isolation:** Reproductive isolation in which a zygote is successfully formed but then either fails to develop or develops into a sterile adult. Donkeys and horses are post zygotically isolated from each other: a male donkey and a female horse can mate to produce a mule, but the mule is sterile.

**Prezygotic isolation:** Reproductive isolation in which the two species never reach the stage of successful mating, and thus no zygote is formed. Examples would be species with different breeding seasons or courtship displays, and which therefore never recognize each other as potential mates.

**Red Queen hypothesis:** The proposition that taxa become extinct at an approximately constant rate because they fail to evolve as fast as other taxa with which they have antagonistic interactions. “Red Queen” more generally refers to averting extinction by evolving as fast as possible.

**Relatedness:** In behavioral ecology, the probability that a given individual carries the same allele as a focal individual at a given locus.

**Random mating:** A mating pattern where the probability of mating with another individual of a particular genotype (or phenotype) equals the frequency of that genotype (or phenotype) in the population.

**Stabilizing selection:** Selection that maintains the mean of a character at or near a constant intermediate value in a population.

**Sexual reproduction:** Production of offspring whose genetic constitution is a mixture of those of two potentially genetically different gametes.



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## IMPORTANT TOPICS OF THIS UNIT FOR CSIR-NET

1. NATURAL SELECTION
2. DIRECTIONAL, STABILIZING & DISRUPTIVE SELECTION
3. CONVERGENT, DIVERGENT, PARALLEL EVOLUTION AND ADAPTIVE RADIATION
4. FOUNDERS EFFECT AND BOTTLE EFFECT
5. ALLOPATRIC, PARAPATRIC AND SYMPATRIC SPECIATION
6. GENETIC DRIFT
7. PHYLOGENETIC TREE
8. GEOLOGICAL TIME SCALE
9. UREY -MILLER EXPERIMENT
10. MOLECULAR CLOCK
11. KIN SELECTION, INCLUSIVE FITNESS
12. HARDY WEINBERG EQUILIBRIUM



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### 11.1. EMERGENCE OF EVOLUTIONARY THOUGHTS:

The term *evolution* is derived from two Latin words *e=* from; *volvere* = to roll and means the act of unrolling or unfolding, *i.e.*, the principle according to which higher forms of life have gradually arisen out of lower. This term was first used by Charles Bonnet (1720–1793), extrapolating from progressive embryogenesis (in individuals) to the development of species (Calow, 1983). However, according to Savage (1969), the term evolution was first used by English philosopher Herbert Spencer.

The history of evolutionary theory is written in the life works of many persons. It remains today. A short list of early contributors follows.

- **Anaximander (611-547 BC)** proposed the theory of natural generation (Abiogenesis). It was supported by Plato, Aristotle, and Van Helmont. Father Suarez (1548-1617) was the greatest supporter of the theory of special creation.
- **Francesco Redi (1626-1698)** anticipated the theory of bio genesis. It was hypothetical by Spallanzani, Louis Pasteur.
- **George Louis Leclerc (1707-1778)** The French naturalist, also known as the Conte de Buffon, who wrote a 44 volume Natural History of all known plants and animals. He recommended evolution but presented no proof.
- **Carl Linneus (1707-1778)** A Swedish botanist known as the “Father of Taxonomy”. He reputed the system of binomial nomenclature used to name and classify organisms today. He whispered in separate creation and the fixity of species. Although he did not believe in evolution his systematic methods for classifying are used to develop phylogenetic trees.
- **George Cuvier (1769-1832)** A vertebrate zoologist. He used comparative anatomy to classify animals. Planned the Theory of Catastrophism which stated that after each worldwide catastrophe the world was repopulated by the surviving species which gave the appearance of chance over time.
- **Erasmus Darwin (1769-1802)** The grandfather of Charles Darwin, he was also a physician and naturalist. He proposed the possibility of evolution based on his studies of animal development, artificial breeding and vestigial organs.
- **James Hutton (1726- 1797)** Proposed the Uniformation Theory of Geology. According to Hutton, the earth is not static but subject to incessant cycles of erosion and uplifting. Weathered materials were deposited in layers which became sedimentary rock. This rock often contained fossils and would eventually be lifted from the sea beds to form land. It was called the uniformation theory because the forces at work were thought to always act at a uniform rate. We know that is not the case today.
- **Charles Lyell (1796-1875)** Transcribed the Principals of Geology which provided support for Hutton’s theory.



- **Alfred Wegener (1880-1930)** The German earth scientist who proposed the Theory of Continental Drift in 1915. Controversial at the time, he proposes the continents had undergone large movements over the past 300 million years. Today the science of Plate Tectonics studies the movement of the earth's crust.
- **Thomas Malthus (1766-1834)** Malthus was an English sociologist who engraved an Essay of Population in 1798. In his essay, he proposed that death and famine were inevitable because the human population tended to increase faster than the supply of food. This essay influenced Darwin greatly and was used in his formulation of the Theory of Natural Selection.

### LAMARCKISM:

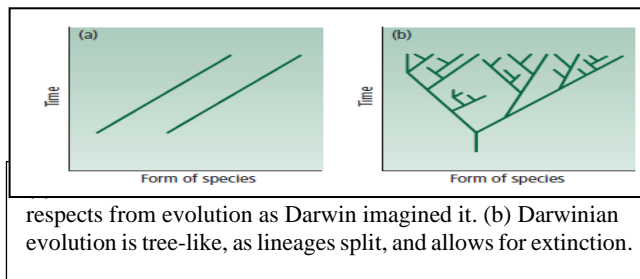
The theory of inheritance of acquired characters states that modifications which the organism acquires in adaptation to the environments which it meets during its lifetime are automatically handed down to its descendants, and so become part of heredity. This theory was propounded by a renowned French naturalist, Lamarck, shortly after the incidence of French Revolution. Lamarck spent the early part of his life as a botanist. Then at the age of 50 he turned his attention to zoology, particularly to the study of invertebrates (The terms "invertebrate" and "biology" have been coined by Lamarck). As a result of his systematic studies he became persuaded that species were not constant but rather were derived from pre-existing species. This knowledge was in totally fight with the view of the period that of fixity of species. As a result, Lamarck's views were challenged by most of the biologists of that time, particularly by Georges Cuvier. In 1809, Lamarck published Philosophie Zoologique, which included his theory explaining the changes that occur in the formation of new types. Although, his views on evolutionary mechanism are outdated now, he still occupies a very important place in the history of evolutionary thought. He was the first evolutionist to accomplish that evolution is a general fact covering all forms of life. His evolutionary ideas can be discoursed in brief as follows:

- 1. Internal forces of life tend to increase the size of the organism.** New constructions appear because of an "inner want" of the organism, *i.e.*, the internal forces of life tend to increase continuously the size of an organism and its component parts.
- 2. Direct environmental effect over living organisms.** The organs of an animal became adapted in suitable fashion in direct response to a changing environment.
- 3. Use and disuse.** The various organs became greatly improved through use or reduced to vestiges through disuse.
- 4. Inheritance of acquired characteristics.** Such physical changes, in some way, could be transferred and impressed on the germ cells to affect future generation. Thus, inheritance was observed by Lamarck simply as the direct transmission of those superficial bodily changes that arose within the lifetime of the individual owing to use or disuse (Volpe, 1985). Thus, Lamarck believed that organic changes seen in animals were resulted by the influence of environment on the gradual changes of species due to their tendency to become more and more perfect.

According to him, when an animal's environment changes, its needs change, and this leads to special demands on certain organs. Organs used more extensively would enlarge and become more efficient. Conversely, an organ or organs, no longer used, would degenerate and atrophy. He postulated that such changed characteristics (acquired traits) would be transmitted to the offspring.

### Examples of Lamarckism

1. The deer-like ancestor of giraffe lived in places (Africa) where the ground was almost invariably parched and without grass. Obligated to browse upon trees, it was continually forced to stretch upwards. This habit sustained over long periods of time by every individual of the race had resulted in the forelimbs becoming longer than the hind ones, and neck so elongated that a modern giraffe can raise his head to a height of eighteen feet without taking his forelimbs off the ground.
2. Ducks and other aquatic birds invaded waters from land in search of enough food, because food was threatened on land and these birds did not had power to fly. In water, the duck would stretch its toes apart to give more push during swimming. This new characteristic would be inherited, and the subsequent generation of duck would upon stretching their toes form a more defined web. Each generation would do the same until the webbed foot seen on ducks today was fully formed. This would then be passed on from generation to generation, essentially unchanged once the perfected state was attained.
3. Flat fishes (deep sea fishes) present at the bottom of sea where there is no sunlight, led an inactive life, lying on one side of the body. The eye of that side (lying towards bottom) migrated towards upper side and, thus, both eyes are on one side of the body.
4. The whales missing their hindlimbs as the consequence of the inherited effect of disuse.
5. The wading birds (*e.g.*, Jacana) developed its long legs through generations of sustained stretching to keep the body overhead the water level.
6. Snakes have elongated body conveyed by loss of limbs. The continuous creeping through holes and crevices made limbs continuously useless for locomotion with the result that limbs become completely lost in snakes.
7. Eyes are abridged in moles since they live underground. In cave animals also, eyes might become functionless and might even disappear.



**Criticism:**

1. The first suggestion of Lamarck suggests the tendency to increase in size. while the evolutionary trend in in certain groups of organisms may be connected with the increase in size, there are many cases, where evolution proceed not only without any increase in size but rather through a reduction in size. Several plants contradict this principle by showing such a reduction in size during their evolution.

2. The second Lamarckian principle that new organs result from new needs, is quite manifestly false. In the case of plants, Lamarck believed that the environment acted directly upon the plant, causing the production of such new characters as might adapt the plant to its environment. In the case of animals, he believed that the environment acted through the nervous systems; in other words, the desire of the animal leads to the formation of new structures. In its roughest form this would mean that the man who mused “Birds can fly, so why can’t I? should have sprouted wings and taken to the air.

3. The third Lamarckian principle that organs will develop due to use and degenerate due to disuse, may be correct as far as growth of an organ within the generation of an individual is concerned. For example, it is a normally observed fact that if muscles are put to use these would develop. However, this principle is meaningful only when it is studied in relation to the following fourth principle.

4. The fourth and final suggestion of Lamarck was that the inheritance of characters acquired during the lifetime of the individual. This principle has been tested by many biologists who have devised many types of experiments for it and have found it entirely incorrect. Certain experiments which have discredited it are the following:

- The renowned German scientist August Weismann was the first person who for the first time made a definite distinction between heritable changes and those which cannot be inherited. In 1890, he performed some experiments to test if characters may disappear due to disuse. This he did by cutting the tails (mutilation) of white mice for more than 20 generations to see if this has any effect on tail length. The measuring of tail length of the offspring of 20 successive generations, revealed that on average, the tails were not shorter. It means that, acquired character (cut tail) was not inherited.
- Castle and Phillips performed transplantation experiments to show that environment has no effect on heredity. In one of the experiments they transplanted the ovary of a black female guinea pig into the body of white female guinea pig and the recipient female was mated with a white male guinea pig. They found that all the individuals from this pair were black. This shows that the environment does not affect the heredity as has been suggested by Lamarck.
- Loeb artificially fertilized the eggs of sea urchin by certain chemical stimuli and these parthenogenetically fertilized eggs produced the generations, the members of which possessed no parthenogenesis.



## 11.2. ORIGIN OF CELLS AND UNICELLULAR EVOLUTION:

### 11.2.1. Origin of life:

Our planet and our solar system have a history of about 4.55 to 4.60 Ga (Ga = billion years). Our solar system originated long after the origin of the universe in the Big Bang about 10 to 15 billion years ago. Big Bang is a theoretical burst of thick concentrated cosmic matter that occurred 10,000-20,000 million years ago to form our creation and 100,000 galaxies. It was suggested by Abbe Lemaitre (1931). All matter formed during the Big Bang consisted of the element hydrogen. The hydrogen atoms had to undergo nuclear reactions in stars, and the stars had to explode as supernovas, before heavier elements than hydrogen (such as carbon, the main building block of life on Earth) came into existence. Our Sun did thus not originate straight at the origin of the universe.

Sun, earth and other stars are formed from Nebula (cosmic dusts and clouds of gases). Nebular hypothesis of Kant is for origin of solar system. The origin of our universe is 10-20 billion years (10,000-20,000 million years or 104 to 204 million years) old. The universe has 1 lakh million (100000 million) galaxies and 10000 million stars in the milky way.

The Sun was not as hot as it is today. The amount of solar radiation reaching the Earth was only 70-80% of that of today, because nuclear reactions in the Sun were in an earlier stage, we know that from observations on other stars.

At first there was no Moon. The chemical composition of Moon rocks and the way in which the Moon moves together with the Earth around the Sun indicate that the Moon was formed by the collision of a Mars-size asteroid with early Earth, probably at some time during the big meteor bombardment that ended about 4 billion years ago (4 Ga). The material from the core of the big asteroid was added to Earth, its mantle moved on and formed the Moon. The Moon was closer to Earth after it originated, so the tides were much more pronounced than today's tides.

The Earth's rotation rate was faster because tidal friction resulting from the presence of the Moon had not yet slowed it down. Days may have been between 8 and 14 hours long. Growth rings in Paleozoic corals shows that even as recently as 450 million years ago there were more than 400 days in a year (a year is the time that it takes the Earth to circle the Sun). Earth in the beginning was a hot spinning ball with a temperature of 5273-6273 Kelvin (5000-6000 °C). The continents were probably smaller than today's, with more ocean surface, especially more than 3 billion years ago.

The atmosphere had a very different composition. Our atmosphere at the moment contains for about 80% of dinitrogen gas (N<sub>2</sub>) and 20% oxygen gas (O<sub>2</sub>), with traces of other gases. CO<sub>2</sub> (carbon dioxide) at the moment makes up about 360 parts per million of the atmospheres (much less than 1%, which is one part per hundred). Before the industrial revolution atmospheric CO<sub>2</sub> levels were about 280 ppm.

The early Earth's atmosphere was different: there was no free oxygen gas. The primary atmosphere of the Earth, inherited from the swirling cloud of gas from our solar system formed,

would have been dominated by hydrogen gas,  $H_2$ , with ammonia,  $NH_3$ , and methane,  $CH_4$ . Atmosphere was reducing and called atmosphere I. Present atmosphere is oxidizing and is called atmosphere II and has about 21% oxygen.

Hydrogen gas is too light for a planet with the size of Earth to hold by its gravity, and the primary atmosphere would have been blown away by the violent radiation of the Sun in its so-called T-taurine stage. A secondary atmosphere would then be supplied by outgassing from the Earth's interior; either rapidly or more gradual.

This secondary atmosphere consisted of dominantly  $CO_2$  (carbon dioxide), with some  $N_2$  (dinitrogen gas),  $H_2O$  (water vapor), minor  $CO$  (carbon monoxide),  $SO_2$  (sulfur dioxide), and  $H_2S$  (hydrogen sulfide). Biopoiesis is the study of origin of life on earth. Cosmology is the study of universe (cosmos).

### 11.2.2. MAJOR EPISODES IN THE HISTORY OF LIFE

- Life originated in Archaeozoic era but first evidence of life is from Precambrian period of Proterozoic era in ocean about 3.6-4.2 billion years ago. Scientists have found isotopes of carbon in 3.8 billion year old rocks in Greenland. Oldest record of fossils is 3200-3500 (3.2 to 3.5 billion) million years old. The oldest recorded fossil is from the banded domes of calcareous sediments (Stromatolites) in Zimbabwe (Rhodesia). It is 2.9 billion years old. Age of fossils is determined either by  $^{14}C$  dating technique or by amount of lead in a rock. Fossil sign suggests that prokaryotes appeared at least 2 billion years before the oldest eukaryotes. Two distinct groups of prokaryotes, Bacteria and Archaea, diverged early, between 2 to 3 billion years ago. Photosynthetic bacteria started the production of oxygen about 2.5 billion years ago, setting the stage for aerobic life. Eukaryotes emerged some 2 billion years ago. Strong sign supports the hypothesis that eukaryotic cells evolved from a symbiotic community of prokaryotes.
- Plants, fungi, and animals arose from distinct groups of unicellular eukaryotes during the Precambrian. Plants evolved from green algae. Fungi and animals arose from different groups of heterotrophic unicells. Based on molecular sign, fungi are more closely related to animals than they are to plants. The oldest fossils of animals are those of soft-bodied invertebrates from about 700 million years ago. The basic body plans of most of the modern animal phyla probably arose in the late Precambrian. The transition from the aquatic environment to land was a pivotal point in the history of life. The first terrestrial colonization was by plants and fungi some 475 million years ago (Paleozoic); the move may have depended upon a beneficial association between the two groups. The transformation of the landscape by plants created new opportunities for all forms of life. Origin of life and evolution of life are independent processes. Origin of life is a chemical process and evolution of life is a biological process.

### 11.2.3. THEORY OF CHEMICAL EVOLUTION AND SPONTANEOUS ORIGIN OF LIFE AT MOLECULAR LEVEL

The first life was anaerobic chemoheterotrophic marine prokaryotic. First photoautotrophs were anoxygenic and anaerobic chemoautotrophs. Ribonucleotides appeared prior to deoxyribonucleotides.

Nucleic acids having power of self-duplication were the first biochemical compounds appeared in chemical evolution. It marks the commencement of life. Later on, nucleoprotein and then large lipoprotein colloidal particles called coacervates were evolved in broth (hot dilute soup) of ocean. A coacervate is a theoretical term used by Oparin & Haldane consisting of nucleoproteins, lipids and polysaccharides which grew by absorbing molecules from outside and like bacteria can split by budding.

Due to zwitterionic nature, protein molecules formed colloidal hydrophilic complex which got surrounded by water molecules. These bodies may separate from the body of the liquid in which these are suspended (aqueous phase) and form a type of suspension. Combination of such structure produces a separation of colloids from their aqueous phase (concentration). These colloid rich coacervates must be able to exchange substance with their environment and selectively concentrate compounds within them.

Fox (1957) synthesized in vitro the proteinoids (microspheres) by prolonged heating of 18-20 types of amino acids. Theory of special creation states that life was created by supernatural power in that form which has not undergone any change. It was given by Father Saurez. God has created life in six days from media prima and man was created by him on the sixth day.

Theory of catastrophism (cataclysm) was given by Cuvier, according to which after a gap of certain period (called age), the world undergoes a catastrophe (sudden calamity) to kill almost all the living organisms and then God created new generation or new life from inorganic matter. Theory of spontaneous generation (abiogenesis or autogenesis) states that living beings are formed from rain, mud, air, dung and other decaying organic matter. Van Helmont claimed to produce mice from human sweat.

Theory of biogenesis (i.e. life from life, *omnis vivum ex vivo*) was proved by Redi, Spallanzani and Pasteur autonomously. They disproved theory of spontaneous generation (abiogenesis). Francesco Redi (1668) proved that flies could not arise from putrefying meat without their eggs. Spallanzani (1767) demonstrated that putrefaction of meat is due to microbes in the air and it can be prevented by boiling and sealing the meat in air tight containers. Pasteur gave a definite proof of life arising from pre-existing life using microbes and sterilization methods.

#### 11.2.4. Naturalistic theory or chemosynthetic origin (Oparin-Haldane)

Life originated from inorganic substance through chemical processes, i.e., chemical evolution precedes biological evolution. In the 1920's, A.I. Oparin and J.B.S. Haldane individually hypothesized that the reducing atmosphere and greater UV radiation on primitive Earth favored reactions that built complex organic molecules from simple monomers as building blocks. According to this theory the first living organisms are products of a chemical evolution that occurred in four stages:

- Abiotic synthesis and accumulation of monomers, or small organic molecules, that are the building blocks for more complex molecules.
- Joining of monomers into polymers (e.g., proteins and nucleic acids).
- Formation of protobionts, named coacervates, a colloidal suspension (dewdrops) which formed from aggregates of abiotically produced molecules and later on varied chemically from their environments due to enclosure of membrane like structure and named microspheres by Sydney fox.
- Origin of heredity during or before protobiont appearance.

The origin of life was possible in Earth's ancient environment. There was little atmospheric oxygen. Lightning, volcanic activity, meteorite bombardment, and ultraviolet radiation were more intense.

##### 11.2.4.1. Stanley Miller and Harold Urey tested the Oparin/Haldane hypothesis by Experiment:

- Stanley Miller, a graduate student in biochemistry, built the apparatus shown here. He filled it with water ( $\text{H}_2\text{O}$ ), methane ( $\text{CH}_4$ ), ammonia ( $\text{NH}_3$ ) and hydrogen ( $\text{H}_2$ ) but no oxygen. He hypothesized that this mixture looks like the atmosphere of the early earth. The mixture was kept circulating by continuously boiling and then condensing the water. The gases passed through a chamber containing two electrodes with a spark passing between them. At the end of a week, Miller used paper chromatography to show that the flask now contained numerous amino acids as well as some other organic molecules.

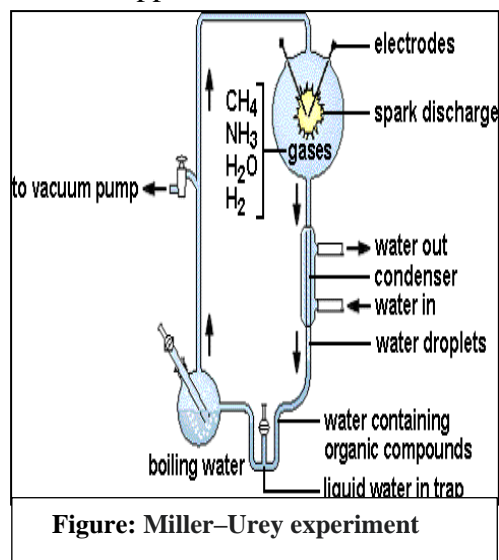


Figure: Miller-Urey experiment

- In the years since Miller's work, many variants of his procedure have been exasperated. Virtually all the small molecules that are associated with life have been formed, 17 of the 20 amino acids used in protein synthesis, and all the purines and pyrimidines used



in nucleic acid synthesis. But abiotic synthesis of ribose and thus of nucleosides has been much more difficult. One difficulty with the primeval soup theory is how polymers the basis of life itself could be gathered.

- In solution, hydrolysis of a growing polymer would soon limit the size it could reach. Abiotic synthesis produces a mixture of L and D enantiomers. Each prevents the polymerization of the other. So, for example, the presence of D amino acids inhibits the polymerization of L amino acids (the ones that make up proteins here on earth). This has led to a theory that early polymers were accumulated on solid, mineral surfaces that protected them from degradation, and in the laboratory polynucleotides and polypeptides containing about ~50 units have been synthesized on mineral (e.g., clay) surfaces.

#### 11.2.4.2. Controversy over Classical Oparin-Haldane Theory:

The orthodox theory held that life originated as a result of such actions as lightning strikes, putting energy into a strongly reducing atmosphere, which would result in the formation of many of the 'building blocks of life' as shown by the laboratory tests done by Miller. This theory in its simplest form has run into major problems, and has been practically abandoned by scientists mainly because of three lines of sign.

**A)** The atmosphere remained probably not by far as reducing as had been thought (no free  $H_2$ ,  $NH_3$ ,  $CH_4$ ), but more unbiased. The reactions to organic material, excited by electric discharge, will still take place in such an atmosphere, but at a much slower rate than in a more reducing atmosphere. At such slow rates it is very difficult to build up a rather large reservoir of organic building blocks, thus chances of getting enough bits and pieces to react to big molecules are very small, in a very dilute soup type ocean the molecules never meet in large numbers.

**B)** The time accessible for the development of the first living cells has been getting shorter and shorter, much less than the billions of years predicted. The big meteorite bombardment that also hit the moon stopped only by about 4.0 Ga. Life developed earlier would probably have been obliterated by the impacts. Organic material that carries the carbon isotope signature of having originated by photosynthesis has been dated at 3.85 Ga. The remains of not only cell like organisms, but of stromatolites, are dated at 3.5 Ga. Stromatolites are limestones secreted by the actions of photosynthesizing bacteria: not just very simple semi-life forms were around, but fairly complex bacteria that could perform the difficult reaction of photosynthesis, i.e., Eubacteria. The secretion of limestone ( $CaCO_3$ ) was probably mediated by the chemistry coupling of reactions 1 and 2







organisms use up  $\text{CO}_2$  in photosynthesis (reaction 1), they drive at the same time reaction 2 towards the right, thus causing precipitation of calcite.

### C) RNA was probably the first genetic material: An RNA Beginning?

Much more is known about how incredibly chemically complex even simple organisms (bacteria) are, and about the complexity of inheritance. All organisms alive today store and transmit hereditary information in two kinds of molecules called DNA (Deoxyribonucleic Acid, a double spiral shape) and RNA (Ribonucleic Acid, a single spiral shape). Both DNA and RNA are made up of four kinds of subunits called nucleotides. Sequences of nucleotides make up the genes, and direct the formation of proteins, on which all life depends. Proteins consist of 20 different subunits called amino acids, and the sequence of the nucleotides on DNA and RNA determines the sequence of the amino-acids in proteins. There are large parts of DNA, however, that do not code for proteins and appears to have no function ('junk DNA'). Such junk DNA occurs in Archaeobacteria and Eukaryotes, not in Eubacteria. The formation of the proteins is helped along by enzymes, which function as catalysts (catalysts support a reaction along without participating in it). We call the nucleotides and amino acids the building blocks of life; both have been found in meteorites. We have a chicken and egg problem: DNA and RNA "tell" the organism how to make proteins, but these same proteins are needed to make DNA and RNA, by acting as catalysts to form these big, complex molecules. DNA and RNA are very complex molecules and it appears to be very difficult to let these originate from simple amino acids. But there is no way in which we can get proteins to duplicate themselves.

More and more sign has become available that helps in solving the chicken and egg problem. It is now known that some molecules made of RNA, called ribozymes, can act as catalysts in modern cells. That means, that such RNA molecules could have used bits and pieces of themselves to help them to replicate, without any use of proteins. There may thus have been a 'RNA-world' in which RNA could have performed the functions of both nucleic acids (DNA, RNA) and proteins. The theory that the first proto-living things were RNA-only organisms is becoming widely accepted (and is called the theory of the RNA-world).

Several other bits of sign support this notion of an original "RNA world": Many of the cofactors that play so many roles in life are based on ribose; for example: ATP, NAD, FAD, coenzyme A, cyclic AMP, GTP. In the cell, all deoxyribonucleotides are synthesized from ribonucleotide precursors. Many bacteria control the transcription and/or translation of certain genes with RNA molecules (Link to "riboswitches"), not protein molecules.

Even so, we keep the problems of a not reducing (neutral, also not oxidizing) atmosphere, and very little time to get to the first photosynthesizing bacteria. There are two main schools of thought (with many variants), often combined in one way or another.

a) The original source material for life was not really carbon-based “life”, but some form of self-replicating crystal. We are looking at different and innovative ways in which we could have used different commonly occurring, natural compounds as some kind of template, or even as a real part of earlier organisms. The most commonly cited possible inorganic compounds are pyrite,  $\text{FeS}_2$  (positively charged surface); and clay minerals (negatively charged surface). The floating bits and pieces of ‘building blocks of life’ could have become organized in patterns using the crystals as a template, and they could have stuck first to the charged surface (the building blocks commonly have a positively and a negatively charged end). Note that crystals (regularly shaped structures) have the possibilities of carrying “information” in their irregularities (similar to the supermarket bar codes).

b) We looked in the wrong place (warm, shallow pond). Reducing circumstances may not have been average in the atmosphere, but may have occurred locally, around volcanic hot springs, and the first forms of life may have been similar to chemosynthetic bacteria. Nice extra: if life originated in rather deep water (no sunlight needed): no problems with high rate of UV-irradiation in the absence of an ozone shield (no  $\text{O}_2$ ). Additionally, many metals that are required in very small amounts because they play a role in complex organic molecules (such as chlorophyll) are present in waters streaming out of hydrothermal vents e.g., iron, nickel, manganese, magnesium, molybdenum, selenium, copper.

#### **11.2.5. Cosmozoic theory (Theory of panspermia) given by Richter (1865), Helmholtz (1884), Arrhenius (1908):**

They proposed that life reached the earth from some heavenly body through meteorites. Panspermia (primitive form of life, as suggested by Arrhenius (1908) consisted of spores and microbes existed throughout universe and produced different forms of life.

##### **The Murchison Meteorite:**

This meteorite, that fell near Murchison, Australia on 28 September 1969, turned out to contain a variety of organic molecules including: purines, pyrimidines and polyols compounds with hydroxyl groups on a backbone of 3 to 6 carbons such as glycerol and glyceric acid. Sugars are polyols. The amino acids obtained were glycine, alanine, aspartic acid, valine and were quite similar to the products formed in Miller’s experiments. The question is where these molecules simply terrestrial contaminants that got into the meteorite after it fell to earth. Some of the samples were collected on the same day it fell and subsequently handled with great care to avoid contamination. The polyols contained the isotopes carbon-13 and hydrogen-2 (deuterium) in greater amounts than found here on earth. The samples lacked certain amino acids that are found in all earthly proteins. Only L amino acids occur in earthly proteins, but

the amino acids in the meteorite contain both D and L forms (although L forms were slightly more prevalent).

### 11.2.6.THE GEOLOGIC TIME SCALE AND EVOLUTIONARY RECORD:

A notable feature of the table below is how often evolutionary changes concurred with geologic changes on the earth. But consider that changes in geology (e.g., mountain formation or lowering of the sea level) cause changes in climate, and together these alter the habitats available for life. Two types of geologic change seem to have had especially dramatic effects on life: continental drift and the impact of asteroids.

#### Some important statements:

- **Azoic Era:** Era of invisible life.
- **Archaeozoic Era:** Era of former life or era of early life.
- **Proterozoic Era:** Era of former life or Era of early life.
- **Paleozoic Era:** Era of old life or Era of ancient life.
- **Mesozoic Era:** Era of middle (life also called “age of reptiles”).
- **Coenozoic Era:** Era of recent life (also called “age of mammals, birds, insects and angiosperms”).
- **Ordovician Period:** “age of invertebrates”-and origin of amphibians.
- **Devonians Period:** “age of fishes” and of origin of amphibians.
- **Carboniferous Periods:** “age of amphibians”-and origin of reptiles. Earliest reptiles evolved in carboniferous period.
- First mammals appeared in Triassic periods.
- **Jurassic Period:** “age of Reptiles”.
- **Holocene Epoch:** “age of Man”.

### 11.3. PALEONTOLOGY AND EVOLUTIONARY HISTORY:

**11.3.1. Palaeontological evidences:** Most conclusive evidence that evolution has happened comes from the fossil record of ancient creatures. The study of ancient life is called palaeontology (Gr., *paliaos* = ancient + *onta* = existing things + *logos*= discourse). The science of palaeontology links biology with geology and is concerned with the finding, cataloguing and interpreting of fossils. A Even before the Renaissance men had exposed shells, teeth, bones, and other parts of animals buried in the ground (*i.e.*, fossils). Some of these fossils corresponded to the parts of familiar living animals, but others were strangely unlike any known form. Many of the objects (fossils) found in rocks high in the mountains, far from the sea, resembled parts of marine animals. In the fifteenth century, the versatile artist and scientist, Leonardo da Vinci (1452–1519) gave the correct explanation of these curious finds, and gradually his conclusion that they were the remains of animals that had existed at one time but

had become extinct, was accepted. This evidence of former life led to the formulation of the theory of catastrophism by the founder of palaeontology and a versatile French naturalist, Georges Cuvier(1769–1832).

The theory of catastrophism holds that a succession of catastrophes, fires and floods, have periodically destroyed all living things, followed each time by the origin of new and higher types by the acts of special creation. Cuvier was also responsible for developing the law of correlation which states that certain structures are invariably found together. Cuvier is referred to as Founder or Father of Recent Palaeontology.

**11.3.2. Branches of Palaeontology:** Palaeontology is subdivided into the following branches:

1) Paleobotany which deals with the study of plant fossils. It includes palynology which is the study of fossil spores and pollen grains.

2) Paleozoology which deals with the study of animal fossils and includes invertebrate palaeontology and vertebrate palaeontology.

3) Micropaleontology which deals with study of small microscopic fossils (microfossils) and their fragments, *e.g.*, foraminifera, fusulinids and ostracodes.

4) Paleoecology which is the study of ancient organisms and their environment.

### 11.3.3. Evidences of evolution:

#### A) Fossil evidence:

**Fossils:** Any body, body parts (traces) of animals and vegetables concealed and conserved by natural causes. Fossils are remains, traces or other direct evidence of past life forms. Most fossils form from burial of plants and animals in sediment; soft parts are more often consumed or decayed but may leave marks if buried rapidly. Most fossils are fixed in sedimentary rock, weathered particles that provide strata from lower older layers to upper newer layers.

Paleontologists study the fossil record based on boundaries between strata, where one mix of fossils gives way to another. Transitional links are intermediate between major groups. The fossil record allows us to trace the history of the modern-day horse *Equus*. The earliest fossils in this lineage is *Hyracotherium*, which was the size of a dog, with cusped low-crowned molars, four toes on each front foot, three on each hind foot-all adaptation for forest living. When forests were replaced by grasslands, the intermediates were selected for durable grinding teeth, speed, etc. with an increase in size and decrease in toes.

#### Types of fossils:

(1) **Body fossils:** hard part of organism such as shell, tooth, bone etc.*e.g.* bones of dinosaurs.

(2) **Subfossils:** Remains of animals and plants preserved in rocks less than 10,000 years *e.g.* vision in frozen ice. Sub fossils were formed after the last ice age during Holocene epoch.

(3) **Microfossils:** microscopic remains less than 0.5 mm or 1/50<sup>th</sup> inch.

(4) **Macrofossils:** Larger than 1 cm in size.

(5) **Unusual fossils:** Sudden preservation of entire organism *e.g.* Solenhofen Limestone of Southern Germany, containing fossils *Archaeopteryx*.



(6) **Coprolites:** fossils of droppings of animal faecal matter. Large coprolites of crocodiles, Dinosaurs etc.

(7) **Bioclast:** Fossils of fragments of fossils surrounded in sediments. The term is usually applied to thin sections of fossils under microscope.

(8) **Gastroliths:** These are found in abundance in the body cavities of certain reptiles.

(9) **Pseudo fossils:** Many objects of inorganic origin closely resemble the forms of organic origin and are found in sedimentary rock.

**B) The geological time table:** Geologists, as a result of their studies of the strata of sedimentary rocks in the different regions of the world, have classified geologic history into six eras. The oldest era with fossils is the Archeozoic (era of primitive life) and this is followed in turn by the Proterozoic (era of early life), the Paleozoic (era of ancient life), the Mesozoic (era of medieval life), and the Cenozoic (era of modern life). The Paleozoic, Mesozoic, and Cenozoic eras are divided into periods and the periods of the Cenozoic into epochs. There is evidence that between the different eras there were widespread geologic disturbances called revolutions which raised or lowered vast regions of the earth's surface and created or eliminated shallow inland seas. These revolutions produced great changes in the distribution of sea and land organisms and wiped out many of the previous forms of life. For instance, the Paleozoic era ended with the revolution that raised the Appalachian mountain and it is believed, killed all but 3 per cent of the forms of life existing then. The Rocky mountain revolution (which raised the Andes, Alps and Himalay as well as the Rockies) abolished most reptiles of the Mesozoic. The following table of geologic time-table shows the eras and some of their subdivisions, the approximate duration of each era, some of the important geological features, and the characteristic animals and plants.

### **C) Mass Extinctions:**

Extinction is death of all members of species in wild; mass extinctions are extinctions of many species in short time. Five mass extinctions in fossil record define end of

- (1) Ordovician
- (2) Devonian
- (3) Permian
- (4) Triassic
- (5) Cretaceous

Following extinctions, remaining groups enlarge to fill habitats vacated by extinct species. Extinction of dinosaurs at end of Cretaceous: Proposed in 1977 that Cretaceous extinction was caused by asteroid impact.

Cretaceous-Tertiary border has high level of iridium, rare in earth's crust but common in meteorites. Calculations of effects of nuclear bomb explosions ("nuclear winter") compare with worldwide climate cooling expected from large asteroid impact.

Worldwide layer of soot also defines iridium layer. Huge meteorite crater of correct age found in Caribbean Ocean and Yucatan peninsula; suspected site of impact of meteor that resulted in



dinosaur extinction, Marine animal fossil record indicates mass extinctions occur every 26 million years; corresponds to movement of solar system within Milky Way galaxy.

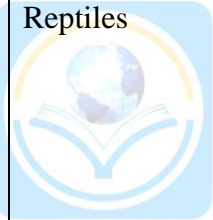
**11.3.4. The Alvarez Theory:** Louis Alvarez, his son Walter, and their colleagues proposed that a giant asteroid or comet striking the earth some 65 million years ago caused the massive die-off at the end of the Cretaceous. Presumably, the impact generated so much dust and gases that skies were darkened all over the earth, photosynthesis declined, and worldwide temperatures dropped. The outcome was that as many as 75% of all species — including all dinosaurs — became extinct.

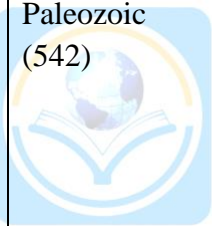
The key piece of evidence for the Alvarez hypothesis was the finding of thin deposits of clay containing the element iridium at the interface between the rocks of the Cretaceous and those of the Tertiary period (called the K-T boundary after the German word for Cretaceous). Iridium is a rare element on earth (although often discharged from volcanoes), but occurs in certain meteorites at concentrations thousands of times greater than in the earth's crust.

After languishing for many years, the Alvarez theory gained strong support from the discovery in the 90s of the remains of a huge (180 km in diameter) crater in the Yucatan Peninsula that dated to 65 million years ago. The abundance of sulfate-containing rock in the region suggests that the impact generated enormous amounts of sulfur dioxide (SO<sub>2</sub>), which later returned to earth as a bath of acid rain. A smaller crater in Iowa, formed at the same time, many have contributed to the devastation. Perhaps during this period the earth passed through a swarm of asteroids or a comet and the repeated impacts made the earth uninhabitable for so many creatures of the Mesozoic.

#### 11.3.5. The Geological Time Scale with Dates in Millions of year in bracket

Eras	periods	Epochs	Aquatic Life	Terrestrial life
Cenozoic (65) The age of Mammals	Quaternary (1.8)	Recent (0.1)		Humans in the new world
		Pleistocene (1.8)	Periodic glaciation Continental drift continues	First humans
	Tertiary (65)	Pliocene	All modern groups present	Hominids and pongids
		Miocene		Monkeys and ancestors of apes

 <p>Mesozoic (251) The Age of Reptiles</p>		Oligocene		Adaptive radiation of birds
		Eocene		Adaptive radiation of mammals
		Paleocene		
	Cretaceous (146)	Still attached: N. America & N. Europe; Australia & Antarctica	Modern bony fishes, Extinction of ammonites, plesiosaurs, ichthyosaurs	Extinction of dinosaurs, pterosaurs Rise of woody angiosperms, snakes; first placental mammals (Eutheria)
	Jurassic (200)	Africa & S. America begin to drift apart	Plesiosaurs, ichthyosaurs abundant; first diatoms Ammonites again abundant Skates, rays, and bony fishes abundant	Dinosaurs dominant; first angiosperms First mammals; Archaeopteryx; first lizards. Adaptive radiation of dinosaurs; insects abundant
	Triassic (251)	At the end Pangaea splits into Laurasia and Gondwana	First plesiosaurs, ichthyosaurs Ammonites abundant at first Rise of bony fishes	Adaptive radiation of reptiles: thecodonts, therapsids, turtles, crocodiles, first dinosaurs

 <p>Paleozoic (542)</p>	Permian (299)	Appalachian Mts. formed; periodic glaciation and arid climate	Extinction of trilobites, placoderms	Reptiles abundant: cotylosaurs, pelycosaurs. Cycads, conifers, ginkgos
	Carboniferous Periodic aridity	Pennsylvanian (320)	Ammonites, bony fishes	First reptiles Coal swamps
		Mississippian (359)	Adaptive radiation of sharks	Forests of lycopsids, sphenopsids, and seed ferns Amphibians abundant Land snails
	Devonian (416) The "Age of Fishes"	Extensive inland seas	Placoderms, cartilaginous and bony fishes. Ammonites, nautiloids Adaptive radiation of ostracoderms, erypterids	Ferns, lycopsids, and sphenopsids First gymnosperms First amphibians Arachnids (scorpions)
	Silurian (444)	Mild climate; inland seas	Nautiloids, Pilina, other mollusks	
	Ordovician (488)	Mild climate, inland seas	Trilobites abundant First jawless vertebrates	First fungi First plants (liverworts?) First millipedes?
	Cambrian (542) Periodic glaciation		Trilobites dominant. Eurypterids, crustaceans mollusks, echinoderms sponges, cnidarians, annelids, and tunicates present	No fossils of eukaryotes, but phylogenetic trees suggest that lichens, mosses, perhaps even vascular

				plants were present
Proterozoic (2500)	Ediacaran (620)		Fossils rare but evidence of several types of invertebrates	No fossils of eukaryotes, but phylogenetic trees suggest that lichens, mosses, perhaps even vascular plants were present towards the end.

### 11.3.6. Speciation:

Species is a Latin word meaning "kind" or "appearance." Indeed, we study to distinguish between different kinds of organism from differences in their appearance. Linnaeus, the ' founder of modern taxonomy, described individual species in terms of their physical form; the study of form or structure, called morphology and phenetic characters, is titled the method most often used to characterize species.

If one group of organisms reliably differ from other organisms reliably differs from other organisms, it will be defined as a separate species. The formal definition of the species will be in terms of characters that can be used to recognize members of that species. The taxonomist who describes the species will have observed specimens of it and of related species, looking for characters that are present in specimens of the species to be described, and absent from other closely related species. These are the characters used to define the species. Modern taxonomists similarly consider differences in body function, biochemistry, behaviour, and genetic makeup. Here we will discuss some commonly used species concept to describe species.

#### 11.3.6.1. Biological species concept:

The biological species concept is broadly accepted species definition was first described by evolutionary biologist Ernst Mayr in 1942. Mayr's definition is answer to the question, what factors divide biological diversity into separate forms that we identify as species?

According to this concept "species are group of population which can freely interbreed in nature and produces viable, fertile Off springs and are reproductively isolated from members of other species." The expression reproductively isolated means that members of the species do not interbreed with members of other species, because they have some characteristics that prevent interbreeding. The biological species concept is important because it places the

taxonomy of natural species within the conceptual scheme of population genetics. In terms of population genetics, a group of interbreeding organisms make up, a gene pool. In theory, the gene pool is the unit within which gene frequencies can change. In the biological species concept, gene pools become more or less identifiable as species.

The identity is imperfect, because species and populations are often subdivided. The species, in this concept, is the unit of evolution.

Organisms do not evolve but species do, and higher taxonomic groups such as phyla only evolve in so far as their constituent species are evolving.

The biological species concept clarifies why the members of a species resemble one another, and differ from other species. When two organisms breed within a species, their genes pass into their combined offspring as this process is repeated in every generation, the genes of different organisms are constantly shuffled around the species gene pool.

Dissimilar family lineages (parents, offspring grandchildren, and so on) rapidly become blurred by the transfer of genes between them). The shared gene pool gives the species its identity. By contrast, genes are not transferred to other species, and different species therefore evolve a different appearance. The movement of genes through a species by migration and interbreeding is called gene flow. According to the biological species concept, gene Flow explains why each species forms phonetic cluster.

In short, the biological species concept is based on reproductive isolation, with each species isolated by factors prevent blocking genetic mixing with other species.

#### **11.3.6.2. Limitation of the biological species concept:**

The biological species concept does not work in all circumstances. For example, it is inadequate for grouping extinct forms of life, the fossils of which must be classified according to morphology. The criterion of interbreeding is meaningless for organisms that are completely asexual in their reproduction, as are all prokaryotes, some protests, some fungi, and even some plants (such as commercial banana). Many bacteria do transfer genes on a limited scale by conjugation and other processes, but there is nothing similar to the equal contribution of genetic material from two parents that occurs in sexual reproduction. Different lineages of descent give rise to clones, which genetically" speaking, represent single individuals. Asexual organisms can be assigned to species only by the grouping of clones that have the same structural and biochemical characteristics.

There are many other species concepts with more restricted usage. One example is the phylogenetic species concept which highlights common evolutionary history. It is defined as a irreducible basal other such clusters, and within which there is a parental pattern of ancestry and descent.

Any character that distinguishes a population would define it as a species, regardless of whether it interbreeds with others or not. This species concept will lead to a classification of



organisms that can sometimes be different from biological species concept. It also applies to asexual organisms.

### 11.3.6.3. Patterns of Speciation:

Evolutionary theory must explain macroevolution, the (e.g., new species, new genera, new families). Speciation, or the origin of new species, is a central process of macroevolution because any genus, family, or higher taxon creates with a new species novel enough to be the first member of the higher taxon.

The term evolution designates a change in genotypic frequencies, which usually results in a population of individuals better adapted to the environment than their ancestors were. Speciation comes in two different forms. (a) It may be the evolution of a population over time until the current population cannot be classified as fitting to the same species as the original population. This process is known as anagenesis, or phyletic evolution (an is Latin for without, genesis is Latin for birth or creation). (b) Speciation may also be the divergence of a population into two distinct forms (species) that exist simultaneously. This branching process is known as cladogenesis.

#### A). Anagenesis (phyletic evolution):

The transformation of an unbranched ancestry of organisms, sometimes to a state different enough from the ancestral population to justify renaming it as a new species.

#### B). Cladogenesis (branching evolution):

The promising of one or more new species from a parent species that continues to exist; is more important than anagenesis in life's history, because it is more common and can promote biological diversity.

### 11.3.6.4. Reproductive isolation barriers:

Any barrier or factor that obstructs two species from producing variable, fertile hybrids. Contributes to reproductive isolation. No single barrier may be completely impenetrable to genetic exchange, but many species are genetically isolated by more than one type of barriers. Here, we are seeing only biological barriers to reproduction, which are intrinsic to the organisms. Of course, if two species are geographically segregated, they cannot conceivably interbreed, but a geographical barrier is not considered equivalent to reproductive isolation because it is not intrinsic to the organism themselves. Intrinsic reproductive barriers prevent population belonging to the different species from interbreeding even if their ranges overlap. Intrinsic reproductive barriers are actually "evolved characters" that prevents interbreeding between different species.

For instance, Courtship, is an example of reproductive barrier. if two species do not interbreed because their courtship differs, then the courtship behaviour of at least one of those species

must have undergone evolutionary change and it became a new evolved character which leads to reproductive isolation. The various types of reproductive barrier that isolate the gene pools of species can be categorized as prezygotic or postzygotic, depending on whether they function before or after the formation of zygotes, or fertilized eggs.

### A) Prezygotic Barriers:

Prezygotic barriers prevent mating between species or obstruct formation of hybrid zygotes.

- **Habitat/Ecological isolation:** Two species that live in diverse habitats within the same area may encounter each other rarely, if at all, even though they are not technically geographically isolated. For example, two species of garter snakes in the genus *Thamnophis* occur in the same areas, but one lives mainly in water and the other is primarily terrestrial. Habitat isolation also affects parasites, which are generally confined to certain plant or animal host species. Two species of parasites living on different hosts will not have a chance to mate.
- **Behavioural/Ethological isolation:** It is also commonly known as ethological isolation, it represents special indications that attract mates, as well as extravagant behavior unique to a species. It is probably the most important reproductive barrier among closely related animals. Appreciation species concept is based on this type of reproductive barrier. Male fireflies of various species signal to females of their kind by blinking their lights in particular patterns. The females respond only to signals characteristic of their own species, flashing back and attracting the males. The occurrence of different shape, coloration, habitat and the range of overlapping regions may be some of the deciding factors in behavioural isolation.



The courtship rituals are specific to a species and these courtship rituals are another form of behavioural isolation. The distinctive songs of many birds, the special mating calls of certain frogs, and the sexual displays of most animals are generally attractive only to mates of the same species. Many plants have floral displays that attract only certain insect pollinators.

- **Temporal isolation:** The time period of mating of different species are never always same; two species that breed during different times of the day, different seasons, or different years cannot mix their gametes. This differential time period of mating which prevents interbreeding between two different species is known as temporal isolation. Three species of the orchid genus *Dendrobium* living in the same rain forest does not hybridize because they flower on different days. Pollination of each species is limited to a single day because the flowers open in the morning and wither that evening.

- **Mechanical isolation:** Closely related species may attempt to mate, but cannot achieve the act or fail to achieve fertilization because their genitalia are structurally not compatible or incompatible. This type of incompatibility, long thought to be a primary isolating mechanism in animals, even such kind of barriers contribute to reproductive isolation of flowering plants that are pollinated by insects or other animals. Floral anatomy is often adapted to certain pollinators that transfer pollen only among plants of the same species.
- **Gametic isolation:** Even if the gametes of different species meet, they rarely fuse to form a zygote. For animals whose eggs are fertilized Within the female reproductive tract (internal fertilization), the sperm of one species may not be able to survive in the environment of the female reproductive tract of another species. Many aquatic animals release their gametes into the surrounding water, where the eggs are fertilized (external fertilization). Even when two closely related species release their gametes at the same time in the same place, cross specific fertilization is uncommon. Gametes recognition may be based on the presence of specific molecules on the coats around the egg, which adhere only to complementary molecules on sperm cells of the same species.

**B) Post zygotic Barriers:** If the prezygotic barriers do not obstruct the successful fertilization of the gametes belonging to different species, then postzygotic barriers prevent the hybrid zygote from developing into a viable, fertile adult.

- **Reduced Hybrid Viability or Hybrid Inviability:** When prezygotic barriers are crossed and hybrid zygotes are formed, genetic incompatibility between the two species may abort development of the hybrid at some embryonic stage. Of the numerous species of frog belonging to the genus *Rana*, some live in the same regions and habitats, where they may occasionally hybridize. But the hybrids generally do not complete their development.
- **Reduced Hybrid Fertility or Hybrid Sterility:** Even if two species mate and yield the hybrid offspring that are vigorous, reproductive isolation is intact if the hybrids are completely or largely sterile. Since the infertile hybrids cannot back breed with either parental species, genes cannot flow freely between the species. One cause of this barrier is a failure of the meiosis to produce normal gametes in the hybrid if chromosomes of the two parent species differ in number or structure. A familiar case of a sterile hybrid is the mule, a robust cross between horse and a donkey; horses and donkeys remain distinct species because, except very rarely, mules cannot back breed with either species.

- **Hybrid breakdown:** In some cases when species cross mate, the first-generation hybrids are viable and fertile, but when these hybrids mate with one another or with either parent species, offspring's of the next generation are feeble or sterile. For example, different cotton species can produce fertile hybrids (F1 generation), but breakdown occurs in the next generation (F2 generation) when offspring of the hybrids die as seeds or grow into weak and defective plants

### 11.3.7. Modes of Speciation:

The critical event for the origin of a new species is reproductive isolation. The members of a species usually differ genetically, ecologically, and in their behaviour and morphology from other species, as well as in who they will interbreed with. Some biologists favor to define species not by reproductive isolation but by other properties, such as genetic or ecological differences. Perhaps no single property can provide a universal species definition, applicable to all animals, plants, and microorganisms. However, many species do differ by being reproductively isolated, and even if the evolution of reproductive isolation is not always the crucial event in speciation, it is certainly the key event in research on speciation.

In 1889 A. R. Wallace anticipated that natural selection might indulge the creation of mating barriers among population if the hybrids were adaptively inferior. That is, genotypes that did not mate to produce inferior hybrids would be selected over genotypes that fixed. According to this theory, which Dobzhansky and others maintained, selection for reproductive isolation arises because most races and species are strongly adapted to specific environments.

Hybrids among two such highly adapted populations therefore represent a genetic dilution of their parental gene complexes that can be of great drawback in the original environments. Thus, genotypes that have incorporated prezygotic isolating mechanisms would have the advantage of not wasting their gametes in producing deleterious offspring.

There are four general methods of speciation based on different geographic conditions and how the gene flow is interrupted in the speciating populations. If new species evolves in geographic isolation from its ancestors, the process is called allopatric speciation. If the new species evolves in a geographically contiguous population, it is called parapatric speciation. If the new species evolves within the geographic range of its ancestor, it is called as sympatric speciation. If small founder populations colonize an area outside the main population range and form new species it is termed as peripatric speciation.

Reproductive isolating mechanisms are barriers to gene flow, the spread of genes between populations. These isolating mechanisms can evolve in three different customs, each of which defines a different mechanism of speciation. Usually, the mode of speciation is dictated by both the properties of the genetic systems of the organisms and stochastic (random) or accidental events. For example, vertebrates tend to have different speciation modes than phytophagous (plant-feeding) insects.



**11.3.7. 1. Allopatric and Parapatric Speciation:** The entrance of a geographic barrier, such as a river or mountain, through the range of a species physically isolates populations of the species. Physical isolation can also occur if migrants cross a particular barrier and begin a new population (founder effect). The physically isolated populations can then evolve autonomously. If reproductive isolating mechanisms consequence is a more effective barrier to hybridization. Areas in which previously isolated populations come into contact and produce hybrids are called hybrid zones. Till recently, evolutionary biologists supposed that allopatric speciation was the overall rule. Many now believe that two other modes of speciation may occur frequently in certain groups of organisms.

Parapatric speciation occurs when a population of a species that occupies a large range enters a new niche or habitat. Although no physical barrier arises, the new niche acts as a barrier to gene flow between the population in the new niche and the rest of the species. Here again, reproductive isolating mechanisms evolve to produce two species where there was only one before. Parapatric speciation is believed to have occurred often in relatively non vagile animals such as snails, flightless grasshoppers, and annual plants.

Sympatric speciation occurs when a polymorphism, which is the occurrence of alternative phenotypes in the same population, arises within an interbreeding population before a shift to a new niche. This mode of speciation may be common parasites- and phytophagous insects. For example, if a polymorphism arises within a parasitic species that allows an individual with a certain genotype to adapt to a new host, this genotype may be the forerunner of a new species. If the parasite not only feeds on the new host but also mates on the new host, a barrier to gene flow arises, although the parasite may be surrounded by other members of its species with the original genotype. Sympatric speciation can thus occur in the middle of a species range rather than at the edges.

An example of incipient sympatric speciation has been seen recently in host races of the apple maggot fly (*Rhagoletis pomonella*) in North America. This fly was found originally only on hawthorn plants. However, in the nineteenth century, it spread as a pest to newly introduced apple trees. Intact, races are now known on pear and cherry trees and on rose bushes. These races have divinified genetic; behavioral; and ecological differences from the original hawthorn-dwelling parent. Evolutionary biologists view this as an opportunity to observe sympatric speciation as it occurs.

Another form of sympatric speciation occurs when cytogenetic changes take place that result in "instantaneous speciation," These cytogenetic changes include polyploidy and translocations. For example, if polyploidy offspring cannot produce fertile hybrids with individuals from a parent population, then the polyploid is reproductively isolated.

This mechanism is abundant more common in plants because they can exist vegetative despite odd ploidy and they usually do not have chromosomal sex determining mechanisms, which are especially vulnerable to ploidy problems. The end result of cladogenesis is the divergence of a homogeneous population into two or more species.



**11.3.7. 2. Allopatric Speciation:** Speciation that occurs when the initial block to gene flow is a geographical barrier that physically isolates the population. Such occurrences include emergence of mountain ranges, movement of glaciers, formation of land bridges, subsidence of large lakes. Geographical populations often differ genetically, which includes genetic markers- associated with reproductive isolation.

One of the classic examples of cladogenesis appears in the ground finches of the Galapagos Islands. These birds are very well studied not only because they present-a striking case of speciation, but also because Darwin studies them and was strongly influenced by, them in his views. An original flock of finches -somehow reached the Galapagos Archipelago from South America, 700 miles away, and with time spread to the various islands, of the Gal4pagos Archipelago. Given the limited ability of the birds to get from island to island, allopatric speciation took place. On each island, the finch population evolved reproductive isolating mechanisms while evolving to fill certain niches not already filled on the islands. For example, in South America, no finches have evolved to be like woodpeckers because many woodpecker species already live there. But the Galapagos islands, being isolated from South America, have what is called a depauperate fauna, a fauna lacking many species found on the mainland. The islands lacked woodpeckers, and a very useful food resource for birds, insects beneath the bark of trees was going unused. Finches that could make use of this resource would be at an advantage and would thus be favored by natural selection. On one island, a finch did evolve to use this food resource. The woodpecker finch acts like a woodpecker by inserting cactus needles into holes in dead trees to extract insects.

**11.3.7. 3. Natural selection:** Natural selection is generally believed to be the prominent agent for determining the relative frequency of alleles in a population. Natural selection discriminates between phenotypes in a population with respect to their ability to produce offspring. One phenotype may better survive endemic onslaughts of parasites or predators than another, one may penetrate new habitats more effectively than another; one may mate more efficiently than other; one may even prey on the other.

The important point is that some natural situation or environmental feature selectively allows one organism to develop and to propagate more efficiently, and one genotype is thereby afforded greater representation in the population's gene pool. If this selective process continues over many generations, allelic frequencies will change suggestively and the possible will arise for evolutionary change. Additional, the natural selection process, while acting on the total phenotype, will, in fact, impact only the heritable portion of the phenotype. If a trait has a high heritability, selection can rapidly affect its frequency within a population, whereas selection will take a great deal longer to have any effect on a trait with a low heritability. Natural selection includes the following three parameters survival rate, relative fitness and the selection coefficient.

**11.3.7. 4. Genetic drift:** In small populations, there is a good chance that some individuals will fail to mate positively decently by chance for example, because of the failure to find a mate and this results in lowered per capita birth rates. This is known as the Allee effect, after ecologist W. C. Allee, who first designated it. If an individual that fails to mate possesses a rare gene, that genetic information will not be passed on to the next generation, consequential in a loss of genetic diversity from the population.

Genetic drift refers to the random change in allele frequencies attributable to this type of chance. Because the likelihood of an allele being represented in just one or a few individuals is higher in small populations as compared to large populations, small, isolated populations are particularly vulnerable to this type of reduction in genetic diversity.

**11.3.7. 5. Founder Principle:** When a insufficient individuals or a small group migrate from a main population, only a limited portion of the parental gene pool is carried away. In the small migrant group, some genes may be absent or occur in such low frequency that they may be easily lost. The unique frequency of genes that arise in population derived from small bands of colonizers or “founders”, has been called the founder effect or founder principle. This principle was proposed in 1956 by Harvard evolutionist, Ernst Mayr. The founder principle essentially accentuates the conditions or circumstances that support the operation of Sewall Wright’s genetic drift.

For example, North American Indian tribes, for the most part, lack the gene *IB* that governs type B blood. However, in Asia, the ancestral home of the American Indians, the *IB* gene is widespread. The ancestral population of Mongoloids that migrated across the Bering Strait to North America might have been very small. Accordingly, the possibility exists that none of the prehistoric immigrants happened to be blood group B. It is also likely that a few individuals of the migrant band did carry the *IB* gene but they failed to leave descendants.

**11.3.7.6. Molecular Clocks:** If macromolecules change repetitively over time, then we should expect that the structure of these molecules obtained from different organisms will be different and that the amount of differences will be an indication of the length of time since these organisms diverged from a common ancestor. It is as if a “molecular clock” were keeping time in organisms. This idea has been used to estimate the timing of divergence of various groups of organisms. However, it depends heavily on the neutral theory.

One must assume that the molecules in question (or sequences within DNA molecules) are changing randomly and constantly (and therefore not in response to selection, which would vary the rate).

One also needs to be able to calibrate molecular clocks using some reliable secondary source of information (just as we use the news services as a source of “real” time to set our watches). This could be fossil evidence indicating the actual time two groups shared a common ancestor. However, this is not always available.

These assumptions are not always happened. A basic problematic with molecular clocks is that they do not keep perfect time. Every gene (or gene product) appears to change at a rate independent of others. For example, cytochrome c and globin genes are known to evolve at different rates. Also, different organisms exhibit different rates (molecular evolution in humans is slower than other anthropoid apes, for example); and organisms in the same clade may exhibit different rates at different times.

Also, DNA from different genomes evolves at different rates (mitochondrial DNA evolves at a 10-fold higher rate than nuclear DNA; chloroplast DNA is known to change very slowly; rDNA has coding regions that are highly conserved and noncoding regions that are variable). Rates are determined directly by calibration using fossil evidence or indirectly by comparing with an out-group.

There have been many debates about rates, however, and this is one area in which phylogenies based on different techniques can differ widely. For example, consider the concept of “mitochondrial Eve”, a paleolithic female who lived 200,000 years go in Africa and from whom all present-day humans descended. This is based on an analysis of mitochondrial DNA, which is inherited exclusively through the female and modified only by mutation; it also uses a standard estimate of mutation rate of 2-4% per million years. However, the chronology and origin are disputed by paleontologists, who use fossil and cultural evidence to track human origins and consider the origin to be further back in time and to have included multiple sites in Asia, Africa and Europe.

### 11.3.8. Phylogenetic Trees:

There are two major progressions in the evolution of a higher taxon, which is a named group of organisms above the level of species. These are anagenesis, which is evolutionary change of features within a single ancestry (species), and cladogenesis, or branching of a lineage into two or more descendant lineages. Following cladogenesis, anagenesis in each of the descendant lineages results in their becoming more different from each other (divergence, or divergent evolution). A phylogeny is the history of the events by which species or other taxa have successively arisen from common ancestors.

The branching diagram that portrays this history is called a phylogenetic tree. Other kinds of evolutionary events are sometimes also represented in such diagrams, such as extinction (e.g., taxon F in Figure) and reticulation, which occurs when two lineages merge or form a hybrid descendant, so that the tree has a netlike structure.

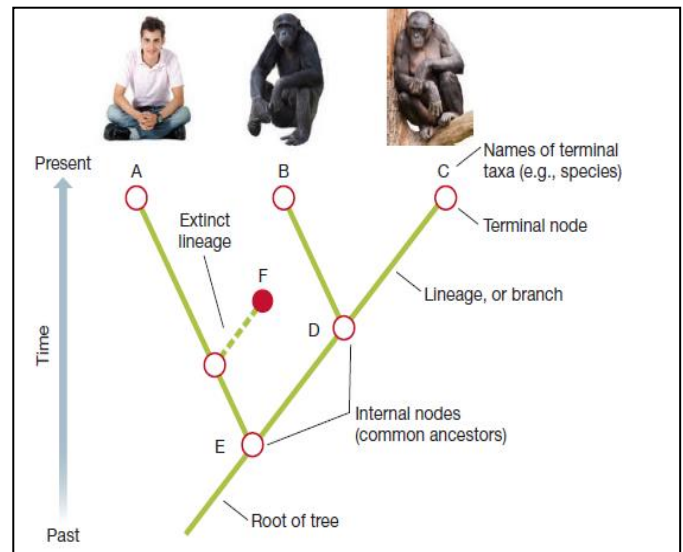


Figure: A phylogenetic tree of three taxa, human (A), chimpanzee (B), and bonobo (C), illustrating major phylogenetic terms. The time scale in most phylogenetic trees is a relative one, but the tree always implies the passage of time from the root of the tree toward the tips of the branches.

We will focus on branching trees here. The phylogenetic tree in Figure shows three living species: human (A), chimpanzee (B), and bonobo (C). (A similar tree could also represent three higher taxa, such as lizards [A], crocodiles [B], and birds [C].) Each segment in the tree is a lineage, or branch, which may split at an internal branch point or node (such as D), representing the formation of two descendant lineages (B and C) by speciation from their common ancestor.

All the descendants of any one ancestor form a clade (also called a *monophyletic group*); thus B and C form a clade that is “nested” within the larger clade A + B + C. Two clades that originate from a common ancestor are called sister groups. (If B and C are species, they are sister species.)

The tree in Figure represents the genealogical relationships among the taxa, meaning the temporal order of branching by which they have originated from the common ancestor (E in this case). The lineage leading to the most recent common ancestor (MRCA) of all the species in the phylogeny is called the root of the tree. Thus, a tree has an implicit time scale from past (at the root) to more recent time (e.g., the present). This time scale (which is often omitted from published phylogenetic diagrams) is often relative, implying only the order of branching. In some cases, however, an absolute time scale is used, and branch points are drawn to match the dates at which the branching events are thought to have occurred.

As we will see, phylogenetic trees can convey information not only about the relationships among species and their time of divergence, but also about evolutionary changes in phenotypic and genetic characteristics and geographic distributions.



The order of branching in a phylogenetic tree defines which species are more closely and which are more distantly related. Two species are more closely related to each other than to a third species if they are derived from a more recent common ancestor. By analogy, two siblings are more closely related to each other than they are to a cousin because they share more recent common ancestors (their parents) with each other than with their cousin (a grandparent).

#### 11.4. MOLECULAR EVOLUTION:

- Until recently, evolution has been measured an organismal process in as much as entire organisms were the units of natural selection and change was evident in populations only insofar as organisms in the population changed. Now it is readily apparent that evolution can take place at the molecular level, especially within DNA and RNA molecules, and that this evolution arises by processes other than selection. For this reason, it is sometimes considered non-Darwinian evolution.

**11.4.1. Evolutionary change measurable at the molecular level:** evolution has usually been studied by comparing morphological features of organisms and their fossil ancestors. In the 1960's and 1970's, it became possible to look at genetic change directly at first, gene products (enzymes, nonenzyme proteins, etc.) were analyzed using electrophoresis or immunological assay techniques later, DNA and RNA sequences were analyzed directly similarities and differences indicate evolutionary relationships.

**11.4.2. Rates of Molecular Evolution:** Early studies of genetic difference at the molecular level produced surprising results. First, the genome of most organisms is unusually diverse, with only a fraction of the genome of eukaryotes consisting of single-copy genes that code for proteins. Also, genomes are not functionally integrated; there are parasitic sequences and repetitive selfish sequences that add nothing to the fitness of the organism within which they reside. Also, there are different sequences in different organelles of the cell.

Further study of molecular variation indicated that evolutionary change occurs at this level just as it does at the phenotypic level. Though, the rates of change at the two levels are frequently different, with the rate being much higher in certain sites within genes than is seen in organisms. One of the furthestmost basic theories in evolution to have seemed since Darwin, called the neutral theory of molecular evolution, was developed to account for evolution at the molecular level. It is also controversial, although not nearly as controversial as Darwin's theory was in 1859.



### 11.4.3. Neutral Theory of Molecular Evolution:

- If there is a theory that seems to be absolutely divergent to Darwinian evolution, it is the neutral theory of molecular evolution. First planned by Kimura (1968) and elaborated further by King and Jukes (1969) and Kimura and Ohta (1971), this theory suggests that evolutionary change determinate at the molecular level can be accounted for in many cases not by selection, but by mutation and random establishment of allele frequencies in populations. It does not oppose the neo-Darwinian argument that natural selection is responsible for change at the phenotypic level; therefore, morphological, physiological and behavioral features of organisms are still assumed to arise by selection that operates on individuals. However, most of the variation we observe at the molecular level is assumed to have little effect on individuals.
- The neutral theory suggests that this arises more or less continually by mutation and becomes established in populations because of random rates of loss and fixation. Subsequently evolution at this level is more or less constant, sequence differences between species can serve as a molecular clock which can deliver information about the timing of divergence of species in a lineage.
- Preliminary tests of the theory made use of allozyme data. Briefly, this technique shows the presence/absence of various allozymes (alternative electrophoretic forms of an enzyme coded for by alternative alleles) in polymorphic populations. Although little is known about what variation in the enzymes means in terms of function, they allow one to measure allele frequencies in populations.
- More current data from DNA sequencing designate that the accumulation of large amounts of variability in noncoding DNA takes place in many organisms (apparently randomly). Even in coding regions (which are far less variable than noncoding regions), many molecular changes are apparent at sites less important in determining function. This information supports the neutral theory. However, it is apparent that molecular constraints (minimizing changes in important functional regions, for example) are influenced strongly by selection.

These limits are different for different proteins and help to explain the rapid rates of change of some molecules and slow rates of others. Consequently, it is not correct to consider the Neutral Theory and Natural Selection to be alternative and opposing views in evolution. Obviously, they are both involved and evidence for both is available, no matter which point of view (molecular or phenotypic) is taken.
- The theory makes three basic predictions concerning molecular evolution:
  - a) rates of change of genes will be constant over time;
  - b) the highest rates of change will be observed for those portions of the genome that are least subject to functional constraints, changes in which would lead to elimination by selection;

c) the maximum rate of molecular evolution is equal to the neutral mutation rate since most mutations are neutral and any advantageous mutations are so infrequent, they can have little influence on the overall rate of molecular change.

**11.4.3. 1.The first prediction:** Constant rates of molecular change is supported by molecular data (for example, rates of change of various proteins like hemoglobin and cytochrome c, which are discussed in many texts (e.g., Avers, 1989) that has been collected since Kimura first began publishing on the Neutral Theory. The uniformity of protein change with time (different rates for different proteins) suggests selection is not a particularly important factor because if it were, rates of change would vary as the selection pressure changed with environmental change (low in constant environments and high in variable environments, for example). This also indicates that the amount of structural change to proteins produced by various taxa can be used as an indicator of the amount of time since the taxa diverged (molecular clocks). However, the rate of evolution depends on the DNA sequence examined, and even when the same sequence is examined in numerous lineages, there are measurable differences in rates. For example, mitochondrial DNA sequences have evolved more slowly in turtles than in other vertebrates.

**11.4.3. 2.The second prediction:** Rates of molecular evolution will be highest in DNA positions that have the least effect on function is supported by most of the evidence we have from molecular genetics, for example: i. introns (noncoding regions of the genome) vary far more than exons (coding regions) in lineages. ii. pseudogenes (nonfunctional regions of the genome corresponding to functional regions) vary considerably more than functional genes. iii. the third position of codons varies more than the first two; substitutions at this third position are called synonymous since they do not change the amino acid coded for by the codon.

**11.4.3.3. The third prediction:** The neutral mutation rate sets the upper limit to change; positive selection for favorable mutations is negligible) is supported by the observations given above. Rates of sequence change in nonfunctional regions of a genome are much faster than those at functionally constrained regions. However, the idea that positive selection for favorable changes cannot influence molecular evolution is an extension of the theory that is not warranted in all cases. A recent test of this idea by McDonald & Kreitman (1991) compared sequence data from the alcohol dehydrogenase gene of three *Drosophila* species, individuals of which were sampled from different geographic regions. They considered differences observed between species as fixed and differences among individuals of the same species to be polymorphisms. The neutral theory predicts that the ratio of silent substitutions to replacement substitutions (which alter the amino acid sequence of a protein) should be the same at all sites even if changes at some sites are functionally constrained; therefore, the ratio of silent to replacement substitutions will be the same for both polymorphisms and fixed substitutions

(between-species differences). What they found was a much higher ratio (29%) of replacement to silent substitutions at fixed sites that distinguish species when compared with polymorphic sites (5%) which do not distinguish species. This suggests that some amino acid-replacing substitutions are adaptive and fixed not by drift but by selection operating on individuals carrying these altered genes.

This causes the frequency of these altered genes to increase more rapidly than by drift alone, and spend less time in a polymorphic state than selectively neutral silent changes. This contradicts one of the basic assumptions of the neutral theory.

The neutral theory has engendered much controversy among population geneticists, but has been of immeasurable importance for several reasons. First, it accounts for much of the variation observed within and between species at the molecular level. Second, it furnishes a null model for how molecular evolution will operate in the absence of selection not alter the function of a gene.

#### **11.4.4. Molecular Analysis**

DNA and DNA products (proteins) can be obtained from living plant and animal cells impartially easily, and then examined to determine evolutionary relationships among individuals representing various taxonomic groups. DNA can even be removed from dried plant specimens and frozen or mummified plant and animal tissues, although there is usually significant degradation and therefore loss of systematic value.

**11.4.4. 1. Protein electrophoresis:** Because proteins vary in size and have numerous charges, both positive and negative, on their surfaces, different proteins will migrate differently in a starch or acrylamide gel to which an electric field is applied. Even proteins that differ by one amino acid substitution will exhibit different positions on a gel. These are visualized using substrates specific to the enzymes of interest and stains to which the enzymatic reaction binds. Electrophoresis is used to determine the genotype of individuals in polymorphic populations. Allozyme electrophoresis identifies allozymes, forms of an enzyme coded for by different alleles at a locus. Isozyme electrophoresis is similar but isozymes are products of different loci in a single genome. This technique was more widely used before DNA isolation techniques were developed, but it is still used.

**11.4.4. 2. DNA-DNA hybridization:** This method fundamentally involves melting double-stranded DNA of two samples at high temperatures (representatives of two sibling species, for example) and then lowering temperatures to reanneal the single strands from each sample (if they come from the same organisms, they are called homoduplexes and if they come from different organisms, heteroduplexes). Reannealed homoduplexes are fairly tightly bound, and relatively high temperatures are required to melt them; however, the more unrelated the two were originally, melting of the reannealed heteroduplexes requires lower temperatures.

This technique has been used in many animal studies (including human and other hominoid groups). However, it doesn't seem to work very well with plants because little reannealing takes place.

**11.4.4. 3. Restriction Fragment Length Polymorphism (RFLP):** Basically, this method takes a molecule of nuclear DNA and cuts it at known points using various restriction enzymes that are specific for short (usually four or six) sequences of base pairs. The fragments produced by this cutting are then separated electrophoretically to produce genetic markers that can be used to compare individuals from various populations. Visualization of the fragments can be accomplished by either radioactively labeling them or staining. Direct sequencing of the fragments can also be done if they prove of systematic value.

**11.4.4. 4. Randomly Amplified Polymorphic DNA (RAPD):** This technique basically uses short synthetic oligonucleotide primers to scan a genome for small inverted repeats and then amplifies the sequence in between using PCR (polymerase chain reaction) to make many copies. Subsequently the segment of DNA being amplified is randomly located and of random length (its sequence is usually not known), the sizes (lengths) of these pieces resolved on gels frequently vary from genotype to genotype. This variation can be assessed in the same way as allozyme or RFLP data. RAPD has become especially useful in population genetics because it can generate genetic markers that are polymorphic among individuals in the same population, so "genetic individuals" can be recognized in clonal species like fungi (for example, a recent RAPD study showed that the world's largest organism was a fungus that reproduced clonally and covered many hectares of land). It has also been used to produce "genetic fingerprints" to resolve legal disputes.

RAPD is being chosen frequently over other molecular techniques now because it produces results quickly and reliably at relatively low cost.

**11.4.4. 5. Direct Sequencing of Genomes:** This involves surely determining the nucleotide sequence of a portion of a genome. Although this is more difficult, it provides relatively reliable data with which to establish phylogenetic position of related taxa. Choices of genome (or portion thereof) can affect the results obtained, but on the whole sequencing is used (generally in a cladistic analysis) to establish monophyly or polyphyly of groups, ancestral vs derived groups, etc.) when phylogenetic analysis is the object of the study. As a general rule, choices of DNA sequences to be obtained are based on the amount of evolutionary time involved in producing the variations in the group under study (extremely conserved portions of the genome are used when large amounts of time are involved and rapidly-changing portions are used when not much time has passed). In animals the mitochondrial genome (mtDNA) is frequently sequenced for comparisons of taxa from within the same order; this is because mtDNA is maternally inherited, is not subject to recombination and has numerous known orthologous genes (that is, homologies of the same gene in different taxa; as opposed to



paralogous genes, which are different versions of a gene in the same organism). In plants, the chloroplast genome (cpDNA) is frequently chosen for the same reasons.

## **11.5. The Mechanisms**

### **11.5. 1. Population Genetics:**

A population is a group of potentially interbreeding organisms of the same species occupying a certain area. Members of a population vary from one another. This variation is the raw material on which natural selection operates. There are several types of mutations, both at the gene level and the chromosome-level. Gene mutations provide new alleles, making these mutations the ultimate source of variation. A gene mutation is an alteration in the DNA nucleotide sequence, producing an alternate sequence, termed an allele.

Mutations occur at random, and can be beneficial, neutral, or harmful. Some chromosomal mutations are changes in the number of chromosomes inherited, while others are alterations in arrangement of alleles on chromosomes due to inversions and translocations.

In sexually reproducing organisms, genetic recombination is the reallocation of alleles and chromosomes. Recombination results from crossing-over during meiosis, the random segregation of chromosomes to gametes during meiotic division, and the random combination of gametes during fertilization.

The entire genotype is subject to natural selection since new combinations of alleles may have improve the reproductive success of the organism. For polygenic traits, the most favorable combination may occur when the right alleles group by recombination. Not only are variations created, they are also preserved and passed on from one generation to the next. The gene pool is the total of all the alleles in a population, in the context of gene frequencies. Neither dominance nor sexual reproduction will change allele frequencies.

Hardy-Weinberg equilibrium is a constancy of gene pool frequencies that remains across generations, and might best be found among stable populations with no natural selection or where selection is stabilizing. Microevolution is the accumulation of small changes in a gene pool over a relatively short period.

### **11.5. 2. Gene pool:**

### **11.5. 3. Hardy-Weinberg Equilibrium:**

Hardy-Weinberg Equilibrium also referred to as the Hardy-Weinberg principle, is used to compare allele frequencies in a given population over a period of time. A population of alleles must meet five rules in order to be considered “in equilibrium”.

- 1) No gene mutations may occur and therefore allele changes do not occur.
- 2) There must be no migration of individuals either into or out of the population.
- 3) Random mating must occur, meaning individuals mate by chance.
- 4) No genetic drift, a chance change in allele frequency, may occur.



5) No natural selection, a change in allele frequency due to environment, may occur.

Hardy-Weinberg Equilibrium never occurs in nature because there is always at least one rule being violated. Hardy-Weinberg Equilibrium is an ideal state that provides a baseline against which scientists measure gene evolution in a given population. The Hardy-Weinberg equations can be used for any population; the population does not need to be in equilibrium.

There are two equations necessary to solve a Hardy-Weinberg Equilibrium question:

$$P + q = 1$$

$$P^2 + 2pq + q^2 = 1$$

P = is the frequency of the dominant allele

q = is the frequency of the recessive allele

$p^2$  = is the frequency of individuals with the homozygous dominant genotype.

$2pq$  = is the frequency of individuals with the heterozygous genotype.

$q^2$  = is the frequency of individuals with the homozygous recessive genotype.

**Example:** autosomal recessive inheritance with alleles A and a, and allele frequencies p and q:

frequency of the genotypes:  $AA = p^2$  and the phenotypes [ ]:  $[A] = p^2 + 2pq$



$$Aa = 2pq$$

$$[a] = q^2$$

$$aa = q^2$$

**Example:** phenylketonuria (recessive autosomal), of which the deleterious gene has frequency of 1/10:

$$q = 1/100$$

therefore, the frequency of this disease is  $q^2 = 1/10\,000$ , and the frequency of heterozygotes is

$$2pq = 2 \times 99/100 \times 1/100 = 2/100;$$

Note that there are a lot of heterozygotes: 1/50, two hundred times more than there are individuals suffering from the condition.

For a rare disease, p is very little different from 1, and the frequency of the heterozygotes =  $2q$ .

We use these equations implicitly, in formal genetics and in the genetics of pooled populations, usually without considering whether, and under what conditions, they are applicable.

#### 11.5. 4. Genetic Equilibrium:

As shown by Hardy and Weinberg, alleles segregating in a population tend to establish an equilibrium with reference to each other. Thus, if two alleles should occur in equal proportion in a large, isolated breeding population and neither had a selective or mutational advantage over the other, they would be expected to remain in equal proportion generation after generation. This would be a special case because alleles in natural populations seldom if ever occur in equal frequency. They may, however, be expected to maintain their relative frequency, whatever it is, subject only to such factors as chance, natural selection, differential mutation rates or mutation pressure, meiotic drive and migration pressure, all of which alter the level of the allele frequencies. A genetic equilibrium is maintained through random mating.

#### 11.5.5. Factors Influencing Allele Frequency Or Deviations From Hardy-Weinberg Equilibrium:

The Hardy-Weinberg explanation of equilibrium in the allele frequency pattern of a population required three assumptions—(I) Individuals with each genotype must be as reproductively fit as those of any other genotype in the population; (II) The population must consist of a large number of individuals; and (III) Random mating must occur throughout the population. The Hardy-Weinberg theorem with its assumptions does not account for any change in allele frequency within populations. That is just what Hardy and Weinberg intended because their formula described the statics of a Mendelian population. Something more was required to formulate a mathematical explanation of change or dynamics in terms of allele frequencies. This need was filled by Fisher, Wright and J.B.S. Haldane, who provided additional theoretical models and superimposed the mechanisms for change in allele frequencies upon the Hardy-Weinberg equilibrium. Population statics was, thus, extended to become population dynamics. The shifts or changes in gene frequencies can be produced by a reduction in population size, selection, mutation, chance (genetic drift), meiotic drive and migration.

The four aspects of the Hardy-Weinberg assumptions are:

1. Demographic:
  - a. Size, mating, fertility and mortality, and migration
2. Evolutionary:
  - Mutation, selection, gene flow
3. Population structure:
  - a. Social and Cultural factors
    - i. Matings and Marriage specifications that regulate the marriage or mating type in a population.
    - ii. Non-random mating – Sexual selection of mates

4. Ecological:
  - a. Population bottle-neck events:
    - i. Pandemic: disease, earthquake etc.
    - ii. Historical: wars etc.,

A few factors and examine how these factors change or influence the gene frequency in a population and how to estimate them in empirical situation.

**11.5. 5.1. Mutation:** Mutation is an evolutionary agent and mutability is a required property of the genetic material if evolution is to occur. One can visualize several ways that mutation might bring about evolutionary changes. Mutation may be highly directed at a particular locus such that allele  $a_1$  is selectively driven to the  $a_2$  form. Alternatively, the mutation process might be random but with time the  $a_2$  form would come to predominate over  $a_1$ . Finally, mutation might simply provide a population with new alleles (new mutational “currency”) on which any and all evolutionary agents (natural selection, for example) can act.

**11.5. 5.2. Random Genetic Drift:** Random fluctuation in allele frequencies, called genetic drift, also occurs in breeding populations. The effect of genetic drift is negligible in large populations but in small breeding populations all the limited number of progeny might be of the same type with respect to certain gene pairs because of chance alone. Should this happen, fixation or homozygosity will have occurred at the locus concerned. Fixation is defined as gene frequency reaching  $p = 1.00$  or  $q = 1.00$ . Chance fluctuations may or may not lead to fixation.

**11.5. 5.3. Founder Principle:** When a few individuals or a small group migrate from a main population, only a limited portion of the parental gene pool is carried away. In the small migrant group, some genes may be absent or occur in such low frequency that they may be easily lost. The unique frequency of genes that arise in population derived from small bands of colonizers or “founders”, has been called the founder effect or founder principle. This principle was proposed in 1956 by Harvard evolutionist, Ernst Mayr. The founder principle essentially emphasizes the conditions or circumstances that support the operation of Sewall Wright’s genetic drift. For example, North American Indian tribes, for the most part, lack the gene  $I^B$  that governs type B blood. However, in Asia, the ancestral home of the American Indians, the  $I^B$  gene is widespread. The ancestral population of Mongoloids that migrated across the Bering Strait to North America might have been very small. Accordingly, the possibility exists that none of the prehistoric immigrants happened to be blood group B. It is also likely that a few individuals of the migrant band did carry the  $I^B$  gene but they failed to leave descendants. Evolutionary geneticists interpret this peculiar feature in terms of genetic drift. Most of the North American Indians possess only blood group O, or stated another way, contain only the blood allele  $i$ . With few exceptions, the North American Indian tribes have lost not only blood

group allele *IB* but also the allele that controls type A blood (*IA*). The loss of both alleles, *IA* and *IB*, by sheer chance perhaps defies credibility. Indeed, many modern students of evolution are convinced that some strong selective force led to the rapid elimination of the *IA* and *IB* genes in the American Indian populations. If this is true, it would provide an impressive example of the action of natural selection in modifying the frequencies of the genes in a population.

**11.5. 5.4. Gene Migration (Gene Flow):** Most populations are only partially isolated from other populations of same species. Usually some migration-emigration (moving out of some individuals out of a population) or immigration (entry of some members of a population into another population of same species) occurs between the populations. Immigration results in the addition of new alleles into the existing gene pool and changes the allele frequencies. Degree of changes in allele frequencies depends upon the differences between the genotypes of immigrants and native population. If there is no much genetic differences, then entry of a small number of migrants will not change the allele frequencies much. However, if the populations are genetically quite different, a small amount of immigration can result in large changes in allele frequencies. If the migrating individuals interbreed with the members of local population, called hybridization, these may bring many new alleles into the local gene pool of the host population. This is called gene migration. If the inter specific hybrids are fertile, then these may initiate a new trend in evolution which lead to formation of new species. This addition or removal of alleles when individuals enter or leave a population from another locality is called gene flow. Unrestricted gene flow decreases the differences between the gene pools and reduces the distinctiveness between different populations.

**11.5. 5.5. Natural Selection:** The process by which comparatively better adapted individuals out of a heterogeneous population are favored by the Nature over the less adapted individuals is called natural selection.

The process of natural selection operates through differential reproduction. It means that those individuals, which are best adapted to the environment, survive longer and reproduce at a higher rate and produce more offspring than those which are less adapted. So, the formers contribute proportionately greater percentage of genes to the gene pool of next generation while less adapted individuals produce fewer offspring. If differential reproduction continues for a number of generations, then the genes of those individuals which produce more offspring will become predominant in the gene pool of the population.

**A) Stabilizing Selection:**

It leads to the abolition of organisms having overspecialized characters and keeps homogenous population which is genetically constant. It favours the average or normal phenotypes, while removes the individuals with extreme expressions. In this, more individuals acquire mean character value. It diminishes variation but does not change the mean value. Its consequences very slow rate of evolution. If we draw a graphical curve of population, it is bell shaped. The

bell shaped curve narrows due to elimination of extreme variants. A real life example is that of birth weight of human babies.

- **Feature of stabilizing selection:**

- Operate in the constant or static environment.
- Retains a population genetically constant.
- Favours the average or normal phenotypes.
- Presents homozygosity in the population.
- Patterned accumulation of mutation.

### **B) Directional Selection:**

Directional selection tends to favor phenotypes at one extreme of the range of variation. Insecticide resistance is an example.

- DDT was a widely used insecticide. After a few years of extensive use, DDT lost its effectiveness on insects. Resistance to DDT is a genetic trait that the presence of DDT in the environment made into a favored trait. Only those insects resistant to DDT survived, leading over time to populations largely resistant to DDT.
- Another example is Industrial melanism in the peppered moth (*Biston betularia*). Before the Industrial Revolution in the 18th and early 19th centuries, only light colored moths were collected in light-colored woodlands in England. There was a sporadic, dark form. With the pollution caused by the burning of coal, the light colored tree trunks became darker due to soot. The once rare dark colored moths became more predominant, while the once common light colored moths became increasingly rare. The color that had the greatest contrast with the background (tree trunk) was at a disadvantage.



- Cleanup of the forest during the 1950s caused the allele frequencies of light and dark moths to reverse to pre-Industrial Revolution levels, dark moths are now rare, light moths are now common.
- The resistance of many bacterial species to antibiotics is another example of directional selection. Over 200 species show some degree of antibiotic resistance, necessitating the development and more prudent use of a new generation of antibiotic medicines.
- **Feature of directional selection:**
  - Occurs due to the change in the environment in a particular way.
  - Favours the phenotype which is non -average or extreme.
  - Alter the mean value of the trait in the population in one direction.
  - Favours buildup of those mutations that increases fitness in the changing environment.

### **C) Disruptive Selection:**

In nearly situations, individuals at both extremes of a range of phenotypes are favored over those in the middle. This is called disruptive selection. An example: The residues (tailings) of mines often contain such high concentrations of toxic metals (e.g., copper, lead) that most plants are unable to grow on them. However, some hardy species (e.g. certain grasses) are able to spread from the surrounding uncontaminated soil onto such waste heaps. These plants



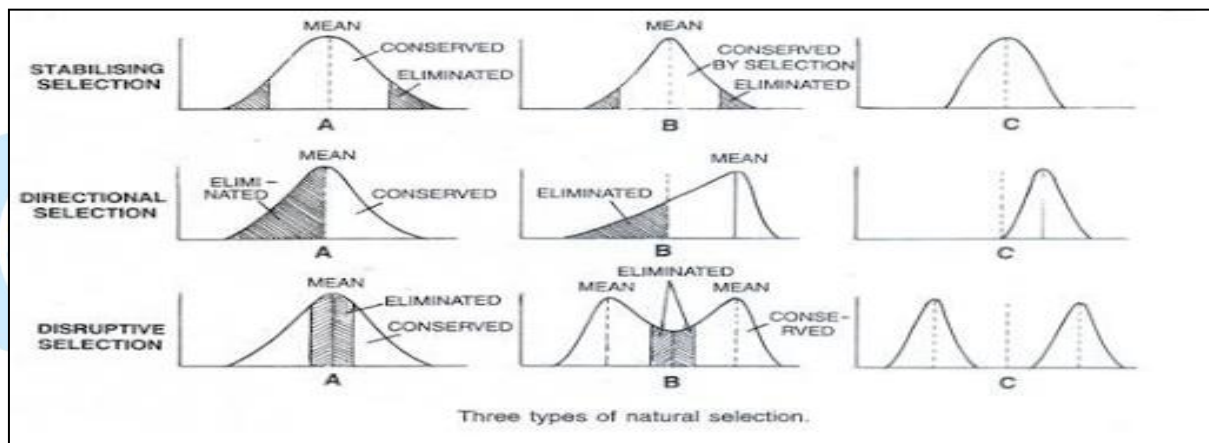
develop resistance to the toxic metals while their capability to grow on uncontaminated soil decreases. Because grasses are wind pollinated, breeding between the resistant and nonresistant populations goes on. But obviously, disruptive selection is at work.

Higher death rates of both fewer resistant plants growing on contaminated soil and more resistant plants growing on uncontaminated soil leads to increasing divergence of the populations into two subpopulations with the extreme manifestations of this trait.

The evolutionary significance of disruptive selection lies in the possibility that the gene pool may become split into two distinct gene pools. This may be a way in which new species are formed.

- **Feature of disruptive selection:**

Formerly homologous populations break up into several different adaptive forms. Stimulating values have maximum fitness and intermediate or mean values are relatively detrimental. Occurs when a population previously adapted to non-homologous environment is subjected to divergent selection pressure in different parts of its distributional area.



**Figure: Types of natural Selection**

## 11.6. Brain, Behavior and Evolution

Behavior can be defined as the way an organism responds to stimuli in its environment. These stimuli might be as simple as the odor of food. In this sense, a bacterial cell “behaves” by moving toward higher concentrations of sugar. This behavior is very simple and well-suited to the life of bacteria, allowing these organisms to live and reproduce. As animals evolved, they occupied different environments and faced diverse problems that affected their survival and reproduction. Their nervous systems and behavior concomitantly became more complex. Nervous systems perceive and process information concerning environmental stimuli and \_ trigger adaptive motor responses, which we see as patterns of behavior.

**11.6. 1.Altruism:** V. C. Wynne-Edwards published a book in 1962 entitled *Animal Dispersion in Relation to Social Behavior*. In it, he suggested that animals regulate their own population density through altruistic behavior. For example, under crowded conditions, many birds cease reproducing. The interpretation of this phenomenon was that these birds were being altruistic: Their failure to breed was for the ultimate good of the species. (Altruism means risking loss of fitness in an act that could improve the fitness of another individual.)

**11.6. 2.Cooperative behaviour:** Cooperative behaviours are acts that increase the Darwinian fitness of others. These same acts may or may not increase the Darwinian fitness of the actor, or may even decrease the fitness of the actor.

Since natural selection favours individuals who increase their own fitness (i.e., not necessarily that of other's), it is not always obvious nor easy to understand either why cooperative behavior occurs or how it might have evolved. The evolution of cooperative behavior is typically considered to result as a consequence of either

- (i) Kin selection
- (ii) Reciprocal altruism
- (iii) Group selection

**11.6. 3.Kin selection:** Kin selection is additional way of saying that it pays to help those to whom we are furthestmost closely connected. Individuals with which an individual is closely related share genetic factor including genes that code for cooperative behaviour. Increasing the Darwinian fitness of relatives therefore can serve to increase the Darwinian fitness associated with cooperative behavior.

Note that key to kin selection is the aptitude to differentiate non-relatives from relatives, either by appreciation of some kind or via correlates such as when relatively nonmobile individuals tend to be more closely related to individuals who are near to them than they are to individuals who are a greater distance from them.

Kin selection essentially is cooperative behavior among kin (relatives) resulting in greater Darwinian fitness for these relatives in comparison to groups that do not mutually cooperate; the basis of kin selection is that relatives share genes and therefore that enhancing the fitness of a relative to some degree is equivalent to enhancing ones own Darwinian fitness (and, in particular, it enhances the inclusive fitness associated with ones genes/alleles).

The most obvious form of kin selection is the caring of offspring by parents, i.e., it pays for parents to care for their offspring because their offspring share genes with them (that is, any allele that coded for not caring for otherwise helpless offspring would quickly go extinct).

#### 11.6. 4. Inclusive fitness

Inclusive fitness is the idea that the fitness associated with an individual's genes is a function not just of the Darwinian fitness of the individual, but additionally the Darwinian fitness associated with the same alleles found in relatives.

Thus, as far as your genes are concerned, your survival (and consequent reproduction) is no more important than the survival of two full siblings (i.e., brother or sister; with each you share half of your genes) or eight first cousins (with each you share 1/8 of your genes); note that we are implicitly assuming that all considered individuals have identical reproductive potentials, e.g., are of the same age and health, etc.

**11.6. 5. Coefficient of relatedness:** The coefficient of relatedness is the means by which these fractional-sharing-of-genes ideas are formalized. The coefficient of relatedness is the proportion of alleles in two individuals that are identical by decent (the calculation of which can get messy if inbreeding has occurred)

**11.6. 6. Reciprocal altruism:** Reciprocal altruism is a means by which cooperative behaviour can evolve even between non-relatives. In reciprocal altruism, one individual performs a cooperative act in the (evolutionary) hope that individual who is the recipient of the act will cooperate in return. Reciprocal altruism likely requires a means by which individuals can distinguish reciprocators from those who refuse to cooperate in return.

**11.6. 7. Group selection:** Group selection is a revenue by which cooperative behaviour might evolve, though chances are that in the real world it makes little contribution except, perhaps, in the evolution of culturally learned behaviour that is cooperative.

The basic idea is that two groups are competing either over resources or directly fighting against each other; if in one group individuals cooperate whereas in the other they do not, then the overall fitness of the cooperating group will exceed that of the non-cooperating group, thus driving the latter, along with its non-cooperative behaviour, to extinction.

For example, humans even inside large groups are very willing to put aside differences to fight against a common enemy, which is why no change of significance is ever achieved by a government except during times of crisis; the flip side of this is that individuals who selfishly benefit from the status quo can always be expected to fight, with gusto, for their benefit from the way things are).