UNIT 1: CONCEPT OF TAXONOMY

BLOCK I: TAXONOMY

1.1 OBJECTIVES

- To define vaccines & their types
- To understand immunodiagnostics & its applications
- To describe the methods of agglutination
- To explain the principle of Complement Fixation Test
- To describe immunotherapy & its various forms

1.2 INTRODUCTION

Taxonomy, in a broad sense the science of classification, but more strictly the classification of living and extinct organisms—*i.e.*, biological classification. The term is derived from the Greek *taxis* ("arrangement") and *nomos* ("law"). Taxonomy is, therefore, the methodology and principles of systematic botany and zoology and sets up arrangements of the kinds of plants and animals in hierarchies of superior and subordinate groups. The term first proposed by the Swiss originated botanist Augustin Pyramus de Candolle in 1813 for the plant classification. He used the term in his famous book—Theory elementaire de la botanique (Elementary Theory of Botany). So taxonomy is the arrangement of the plants and animals on the basis of some laws.

Simpson (1961) has defined taxonomy as the theoretical study of classification including its bases, principles, procedures and rules. Ernst Mayer also defines taxonomy as the theory and practice of classifying organisms. So the science of classification is known as taxonomy. Kristofferson (1995) has defined taxonomy as "the practice of recognizing, naming, and ordering taxa into a system of words consistent with any kind of relationships among taxa that the investigator has discovered in nature". Popularly, classifications of living organisms arise according to need and are often superficial. Anglo-Saxon terms such as *worm* and *fish* have been used to refer, respectively, to any creeping thing—snake, earthworm, intestinal parasite, or dragon—and to any swimming or aquatic thing. Although the term *fish* is common to the names *shellfish*, *crayfish*, and *starfish*, there are more anatomical differences

between a shellfish and a starfish than there are between a bony fish and a man. Vernacular names vary widely. The American robin (*Turdus migratorius*), for example, is not the English robin (*Erithacus rubecula*), and the mountain ash (*Sorbus*) has only a superficial resemblance to a true ash.

Biologists, however, have attempted to view all living organisms with equal thoroughness and thus have devised a formal classification. A formal classification provides the basis for a relatively uniform and internationally understood nomenclature, thereby simplifying cross-referencing and retrieval of information.

The usage of the terms TAXONOMY and SYSTEMATICS with regard to biological classification varies greatly. American evolutionist Ernst Mayer has stated that "taxonomy is the theory and practice of classifying organisms" and "systematics is the science of the diversity of organisms"; the latter in such a sense, therefore, has considerable interrelations with evolution, ecology, genetics, behaviour, and comparative physiology that taxonomy need not have.

The process of taxonomy involves two distinct steps:

(i) Correct recognition and definition of the organisms and their relationships and

(ii) Application of suitable designations for the organisms and to different groups which include them.

The former is called classification which includes study of characters and grouping of individuals while the latter is termed as nomenclature.

History

People who live close to nature usually have an excellent working knowledge of the elements of the local fauna and flora important to them and also often recognize many of the larger groups of living things (e.g., fishes, birds, and mammals). Their knowledge, however, is according to need, and such people generalize only rarely.

However, some of the earliest forays into formal, but limited, classification were undertaken by the ancient Chinese and ancient Egyptians. In China a catalog of 365 species of medicinal plants became the basis of later hydrological studies. Although the catalog is attributed to the mythical Chinese emperor Shennong who lived about 2700 bce, the catalog was likely written about the beginning of the first millennium. Similarly, ancient Egyptian medical

papyri dating from 1700 to 1600 bcc provided descriptions of various medicinal plants, along with directions on how they could be used to treat illnesses and injuries.

The first great generalize in Western classification was Aristotle, who virtually invented the science of logic, of which for 2,000 years classification was a part. Greeks had constant contact with the sea and marine life, and Aristotle seems to have studied it intensively during his stay on the island of Lesbos. In his writings, he described a large number of natural groups, and, although he ranked them from simple to complex, his order was not an evolutionary one. He was far ahead of his time, however, in separating invertebrate animals into different groups and was aware that whales, dolphins, and porpoises had mammalian characters and were not fish. Lacking the microscope, he could not, of course, deal with the minute forms of life.

The Aristotelian method dominated classification until the 19th century. His scheme was, in effect, that the classification of a living thing by its nature—*i.e.*, what it really is, as against superficial resemblances—requires the examination of many specimens, the discarding of variable characters (since they must be accidental, not essential), and the establishment of constant characters. These can then be used to develop a definition that states the essence of the living thing—what makes it what it is and thus cannot be altered; the essence is, of course, immutable. The model for this procedure is to be seen in mathematics, especially geometry, which fascinated the Greeks. Mathematics seemed to them the type and exemplar of perfect knowledge, since its deductions from axioms were certain and its definitions perfect, irrespective of whether a perfect geometrical figure could ever be drawn. But the Aristotelian procedure applied to living things is not by deduction from stated and known axioms; rather, it is by induction from observed examples and thus does not lead to the immutable essence but to a lexical definition. Although it provided for centuries a procedure for attempting to define living things by careful analysis, it neglected the variation of living things. It is of interest that the few people who understood Charles Darwin's ORIGIN OF SPECIES in the mid-19th century were empiricists who did not believe in an essence of each form.

Aristotle and his pupil in botany, Theophrastus, had no notable successors for 1,400 years. In about the 12th century, botanical works necessary to medicine began to contain accurate illustrations of plants, and a few began to arrange similar plants together. Encyclopaedists also began to bring together classical wisdom and some contemporary observations. The first flowering of the Renaissance in biology produced, in 1543, Andreas Vesalius's treatise on

human anatomy and, in 1545, the first university botanic garden, founded in Padua, Italy. After this time, work in botany and zoology flourished. John Ray summarized in the late 17th century the available systematic knowledge, with useful classifications. He distinguished the monocotyledonous plants from the dicotyledonous ones in 1703, recognized the true affinities of the whales, and gave a workable definition of the species concept, which had already become the basic unit of biological classification. He tempered the Aristotelian logic of classification with empirical observation.

Levels of Taxonomy

There are three levels of taxonomy corresponding with three periods of taxonomy:

(i) Alpha taxonomy:

The level of taxonomy by which species are characterized and naming of the species is done.

(ii) Beta taxonomy:

The level of taxonomy by which the arrangement of species in their natural system of categories is made.

(iii) Gamma taxonomy:

The level of taxonomy which deals with the intra specific variations and evolutionary sequence and also a causal interpretation of organic diversity.

Mayer and Ashlock (1991) have divided the taxonomy into two levels:

(i) Micro taxonomy:

The level which deals only the problems related to species.

(ii) Macro taxonomy:

The level which deals with the problems and principles of higher taxa (from subgenus and above) only.

Mayer and Ashlock (1991) recognize three schools of macro-taxonomy such as:

(i) Phonetics (or Numerical taxonomy),

(ii) Cladistics (Phylogenetic systematics) and

(iii) Evolutionary taxonomy (or Evolutionary systematics).

(i) Phenetics (or Numerical taxonomy):

It is an attempt to classify organisms based on overall characteristics rather than on evolution from a common ancestor. Phenetics helps to draw phyletic lineage (relationship) on the basis of similarities and dissimilarities. Pheneticists do not rely upon primitive (plesiomorphic) and derived (apomorphic) characters.

(ii) Cladistics (Phylogenetic systematics):

The term cladistics refers to taxonomy by which the organisms are ranked and classified according to the "recency of common descent". The categorical status of the animal according to this theory depends upon the position of branching points on the phylogenetic tree.

Taxa based on entirely shared derived (synapomorphic) characters originated from a common ancestor. It is a method of phylogenetic analysis to identify monophyletic lineages or clades. Julian Huxley used the term 'clade' in 1958 and Cain and Harrison introduced the term 'cladistic' in 1960.

(iii) Evolutionary taxonomy (or Evolutionary systematics):

The whole concept is based on Darwinism. According to this concept each valid taxon is derived from a common ancestor but the common characteristic features of a realm of the biological world do not always include a common ancestry.

The evolutionary or Darwinian classification is a branch of biological classification in which the organisms are classified using a combination of phylogenetic relationship and overall similarity. This type of taxonomy considers taxa more important rather than single species.

Usually taxonomists agree to divide the taxonomy into two types:

(i) Classical taxonomy and

(ii) Neo-taxonomy or experimental taxonomy.

(i) Classical taxonomy:

The oldest form of taxonomy is called classical taxonomy or orthodox taxonomy. It is related to the description, naming and classification of the animals and plants based on the morphological features (related to external features including genitalia, anatomy, embryology and karyotype; etc.).

(ii) Experimental taxonomy or neo-taxonomy:

It is related to the genetically studies based on a common gene pool for a taxon and become helpful to distinguish two different taxa. Some modern procedures are applied to collect the data for morphology. The use of electron arid scanning electron microscope in different groups of invertebrates such as protozoans, helminthes, arthropods to study the fine structures that become helpful in morph taxonomy.

The closely related two current aspects in taxonomy are taken into consideration, such as:

(i) Biochemical taxonomy and

(ii) Cytological taxonomy.

(i) Biochemical taxonomy:

It deals with taxonomic characters obtained from chemical analysis of enzymes, hormones, and proteins with peptides, nucleic acids, amino acids and sugars.

The amino acid sequences of proteins become different in the different organisms and become helpful to distinguish the different species. Numerous techniques are applied to the study of constituent bio-molecules such as enzymes, hormones, nucleic acids, amino acids, etc. and help in the systematics.

To study the chemical substances, various procedures such as immunological, chromatography (paper chromatophy and column chromatography), electrophoretic method are applied in the study of systematics. The immunological data are used to distinguish two different taxa. The blood group genes are applied in the classification of pigeons and primates.

Chromatography is kind of different techniques for the separation of a complex liquid mixture such as biological fluids (e.g., amino acids, steroid, carbohydrate, etc.) that pass through a column of adsorbing material (e.g., paper, magnesia) the components of the mixtures are adsorbed in separate layers in the column.

This technique is applied in various groups of arthropods, snails and the data is very much helpful in animal systematics.

(ii) Cytotaxonomy:

It deals with taxonomic characters obtained from cytological studies. Cytotaxonomy is a branch of taxonomy dealing with the relationships and classification of organisms based on the structure, number of chromosomes. The position of the centromere is an important feature of chromosome structure which helps in taxonomic studies.

Periods of Taxonomy

(i) First period:

This period may be extended from the time of Aristotle (384-322 B.C.) to Linnaeus (1707-1778). In this period Linnaeus strongly introduced binominal nomenclature for plants and animals and followed Aristotelian and Democritus principle in classification of animals. He also first introduced the hierarchic system of classification both in plants and animals following class, order, genus and species categories.

(ii) Second period:

In this period the evolutionary classification was introduced by Charles Robert Darwin (1809-82) and variation among the organisms is the main force in evolution which was discussed extensively. Darwin published his famous book "On the Origin of Species by Means of Natural Selection" in 1859.

In his book the theory of evolution by natural selection was his own creation although based on the work of Lamarck, Cuvier (1768-1832) and Erasmus Darwin (1731-1802), the grandfather of Charles Darwin. This theory helped a lot to the systematic zoology. E. Darwin's book Zoonomia (1794) presented the laws of organic life. He suggested the struggle for existence in Zoonomia which was elaborated by Charles Darwin.

(iii) Third period:

This period includes the development of modern taxonomy which started about 1930. The study of genetics and population biology was started with typical taxonomy.

This period is remarkable with the publication of New Systematics by J. S. Huxley in 1940, intraspecific variations were studied and the science of population genetics was started in 1908 by G. H. Hardy and W. Weinberg who independently discovered a principle concerned with the frequency of genes (alleles) in a population in the light of evolutionary theory.

Concepts of Taxonomy

In 1975 Mayer and Ashlock first put forward the concept of Micro-taxonomy. Development of the debates on the species, centering mainly on the so-called biological species concept, was called micro-taxonomy or the science of species by Mayr (1982).

One of the major problems of micro-taxonomy evolves around the concept of species. A merging of different research traditions, in systematics as well as in paleontology and genetics, prompted the development of micro-taxonomy. Micro-taxonomy involves the study of concepts of species like Typological species concept, Nominalistic species concept, Biological species concept, Evolutionary species concept etc.

Micro-taxonomy deals with problems like the evolution of species, estimation of the population of species in the living world or in special groups of organisms to which any two, three or all species definitions apply.

It also deals with geographic variation, the recognition of polytypic species, the definition of subspecies and species, the taxonomic status of incipient species and the role of non-morphological characters in the delimitation of species. In any case, the biological distinction is primary and the morphological difference secondary.

Macro-taxonomy is the science of classification:

Theoretical comments ranged from a denial that supra-specific taxa were natural entities, to vague statements that a phylogenetic classification is the more natural. How do we reconstruct phylogeny? How do we represent it in a formal classification? These were the problems being dealt under macro-taxonomy. Macro-taxonomy involves study of homology, analogy, affinities, systematic status and phylogeny.

Micro-taxonomy and Macro-taxonomy are related in the sense that one is incomplete without the other. For the science of classification of species it is very important to know the science of species. Macro-taxonomy involves the establishment of equivalent basis of their features. So how is grouping (Macro-taxonomy) possible without knowing the features of the object (Micro-taxonomy). Hence one is heavily dependent on the other.

Modern Trends in Taxonomy

The term new or modern is a relative term, as what is considered new or modern today may become old systematics in the future. The new systematics introduced by Huxley in 1940 may indeed be very old systematics today. To dispel such misinterpretation of new systematics the words of Mayr (1964) is of immense help.

Mayr wrote **"**What then is the new systematics? Perhaps it is best described as a view-point, an attitude, a general philosophy. It started primarily as a rebellion against the nominalistic typological and thoroughly non-biological approach of certain, alas all too many, taxonomists of the preceding period".

The New Taxonomy, thus, is an approach of the population taxonomists that differ drastically from the simple pigeonholing of classical Linnaean taxonomy. Workers in the new systematics consider themselves biologists rather than filing clerks.

New Taxonomy is neither a special technique nor a special method but an attitude which can be applied at every taxonomic level. It deals with –

1. The utilisation of an ever-increasing number of characters and a continued depreciation of key characters — in contrast to the typological approach.

2. A ready acceptance of new tools and techniques such as —

(a) Visual analysis of sounds in insects, frogs and birds,

(b) Analysis of courtship displays and other behaviour,

(c) Utilisation of biochemical characters,

(d) Utilisation of computers.

3. A further clarification of concepts, such as

(a) Clear separation of taxon from categories,

(b) Recognition of the subspecies as a category and not as an evolutionary unit, and

(c) Clean understanding of the causes of similarities and differences between taxa.

The Linnaean system

Carolus Linnaeus, who is usually regarded as the founder of modern taxonomy and whose books are considered the beginning of modern botanical and zoological nomenclature, drew

up rules for assigning names to plants and animals and was the first to use binomial nomenclature consistently (1758). Although he introduced the standard hierarchy of class, order, genus, and species, his main success in his own day was providing workable keys, making it possible to identify plants and animals from his books. For plants he made use of the hitherto neglected smaller parts of the flower.

Linnaeus attempted a natural classification but did not get far. His concept of a natural classification was Aristotelian; i.e., it was based on Aristotle's idea of the essential features of living things and on his logic. He was less accurate than Aristotle in his classification of animals, breaking them up into mammals, birds, reptiles, fishes, insects, and worms. The first four, as he defined them, are obvious groups and generally recognized; the last two incorporate about seven of Aristotle's groups.

Frank Franklin II/AP

The standard Aristotelian definition of a form was by genus and differentia. The genus defined the general kind of thing being described, and the differentia gave its special character. A genus, for example, might be "Bird" and the species "Feeding in water," or the genus might be "Animal" and the species "Bird." The two together made up the definition, which could be used as a name. Unfortunately, when many species of a genus became known, the differentia became longer and longer. In some of his books Linnaeus printed in the margin a catch name, the name of the genus and one word from the differentia or from some former name. In this way he created the binomial, or binary, nomenclature. Thus, modern humans are HOMO SAPIENS, Neanderthals are HOMO NEANDERTHALENSIS, the gorilla is GORILLA GORILLA, and so on.

Classification since Linnaeus

Classification since Linnaeus has incorporated newly discovered information and more closely approaches a natural system. When the life history of barnacles was discovered, for example, they could no longer be associated with mollusks because it became clear that they were arthropods (jointed-legged animals such as crabs and insects). Jean-Baptiste Lamarck, an excellent taxonomist despite his misconceptions about evolution, first separated spiders and crustaceans from insects as separate classes. He also introduced the distinction, no longer accepted by all workers as wholly valid, between vertebrates—i.e., those with backbones, such as fishes, amphibians, reptiles, birds, and mammals—and invertebrates, which have no backbones. The invertebrates, defined by a feature they lack rather than by the features they

have, constitute in fact about 90 percent of the diversity of all animals. The mixed group “Infusoria,” which included all the microscopic forms that would appear when hay was let stand in water, was broken up into empirically recognized groups by the French biologist Felix Dujardin. The German biologist Ernst Haeckel proposed the term Protista in 1866 to include chiefly the unicellular plants and animals because he realized that, at the one-celled level, there could no longer be a clear distinction between plants and animals.

The process of clarifying relationships continues. Only in 1898 were agents of disease discovered (viruses) that would pass through the finest filters, and it was not until 1935 that the first completely purified virus was obtained. Primitive spore-bearing land plants (Psilophyta) from the Cambrian Period, which dates from 541 million to 485 million years ago, were discovered in Canada in 1859. The German botanist Wilhelm Hofmeister in 1851 gave the first good account of the alternation of generations in various nonflowering (cryptogamous) plants, on which many major divisions of higher plants are based. The phylum Pogonophora (beard worms) was recognized only in the 20th century.

The immediate impact of Darwinian evolution on classification was negligible for many groups of organisms and unfortunate for others. As taxonomists began to accept evolution, they recognized that what had been described as natural affinity—i.e., the more or less close similarity of forms with many of the same characters—could be explained as relationship by evolutionary descent. In groups with little or no fossil record, a change in interpretation rather than alteration of classifications was the result. Unfortunately, some authorities, believing that they could derive the group from some evolutionary principle, would proceed to reclassify it. The classification of earthworms and their allies (Oligochaeta), for example, which had been studied by using the most complex organism easily obtainable and by then arranging progressively simple forms below it, was changed after the theory of evolution appeared. The simplest oligochaete, the tiny freshwater worm AEOLOSOMA, was considered to be most primitive, and classifiers arranged progressively complex forms above it. Later, when it was realized that AEOLOSOMA might well have been secondarily simplified (i.e., evolved from a more complex form), the tendency was to start in the middle of the series and work in both directions. Biased names for the major subgroups (Archioligochaeta, Neoligochaeta) were widely accepted when in fact there was no evidence for the actual course of evolution of this and other animal groups. Groups with good fossil records suffered less from this type of reclassification because good fossil material allowed the placing of forms according to natural affinities; knowledge of the strata in which they

were found allowed the formulation of a phylogenetic tree (i.e., one based on evolutionary relationships), or dendrite (also called a dendrogram), irrespective of theory (SEE ALSOphylogeny).

The long-term impact of Darwinian evolution has been different and very important. It indicates that the basic arrangement of living things, if enough information were available, would be a phylogenetic tree rather than a set of discrete classes. Many groups are so poorly known, however, that the arrangement of organisms into a dendrite is impossible. Extensive and detailed fossil sequences—the laying out of actual specimens—must be broken up arbitrarily. Many groups, especially at the species level, show great geographical variation, so that a simple definition of species is impossible. Difficulties of classification at the species level are considerable. Many plants show reticulate (chain) evolution, in which species form and then subsequently hybridize, resulting in the formation of new species. And because many plants and animals have abandoned sexual reproduction, the usual criteria for the species—interbreeding within a pool of individuals—cannot be applied. Nothing about the viruses, moreover, seems to correspond to the species of higher organisms.

THE TAXONOMIC PROCESS

Basically, no special theory lies behind modern taxonomic methods. In effect, taxonomic methods depend on: (1) obtaining a suitable specimen (collecting, preserving and, when necessary, making special preparations); (2) comparing the specimen with the known range of variation of living things; correctly identifying the specimen if it has been described, or preparing a description showing similarities to and differences from known forms, or, if the specimen is new, naming it according to internationally recognized codes of nomenclature; (4) determining the best position for the specimen in existing classifications and determining what revision the classification may require as a consequence of the new discovery; and (5) using available evidence to suggest the course of the specimen's evolution. Prerequisite to these activities is a recognized system of ranks in classifying, recognized rules for nomenclature, and a procedure for verification, irrespective of the group being examined. A group of related organisms to which a taxonomic name is given is called a taxon (plural taxa).

Ranks

The goal of classifying is to place an organism into an already existing group or to create a new group for it, based on its resemblances to and differences from known forms. To this end, a hierarchy of categories is recognized.

For example, an ordinary flowering plant, on the basis of gross structure, is clearly one of the higher green plants—not a fungus, bacterium, or animal—and it can easily be placed in the kingdom Plantae (or Metaphyta). If the body of the plant has distinct leaves, roots, a stem, and flowers, it is placed with the other true flowering plants in the division Magnoliophyta (or Angiospermae), one subcategory of the Plantae. If it is a lily, with swordlike leaves, with the parts of the flowers in multiples of three, and with one cotyledon (the incipient leaf) in the embryo, it belongs with other lilies, tulips, palms, orchids, grasses, and sedges in a subgroup of the Magnoliophyta, which is called the class Liliatae (or Monocotyledones). In this class it is placed, rather than with orchids or grasses, in a subgroup of the Liliatae, the order Liliales.

This procedure is continued to the species level. Should the plant be different from any lily yet known, a new species is named, as well as higher taxa, if necessary. If the plant is a new species within a well-known genus, a new species name is simply added to the appropriate genus. If the plant is very different from any known monocot, it might require, even if only a single new species, the naming of a new genus, family, order, or higher taxon. There is no restriction on the number of forms in any particular group. The number of ranks that is recognized in a hierarchy is a matter of widely varying opinion. Shown in Table 1 are seven ranks that are accepted as obligatory by zoologists and botanists.

Obligatory hierarchy of ranks

	Animals	**Plants**
domain	Eukaryota	Eukaryota
kingdom	Animalia	Plantae
phylum	Chordata	Tracheophyta
class	Mammalia	Pteropsida
order	Primates	Coniferales
family	Hominidae	Pinaceae

Obligatory hierarchy of ranks

	Animals	**Plants**
genus	Homo	Pinus
species	Homo sapiens (modern human)	Pinus strobus (white pine)

In botany the term DIVISION is often used as an equivalent to the term PHYLUM of zoology. The number of ranks is expanded as necessary by using the prefixes SUB-, SUPER-, and INFRA- (e.g., subclass, superorder) and by adding other intermediate ranks, such as brigade, cohort, section, or tribe. Given in full, the zoological hierarchy for the timber wolf of the Canadian subarctic would be as follows:

Kingdom Animalia

Subkingdom Metazoa

Phylum Chordata

Subphylum Vertebrata

Superclass Tetrapoda

Class Mammalia

Subclass Theria

Infraclass Eutheria

Cohort Ferungulata

Superorder Ferae

Order Carnivora

Suborder Fissipeda

Superfamily Canoidea

Family Canidae

Subfamily Caninae

Tribe (none described for this group)

Genus CANIS

Subgenus (none described for this group)

Species CANIS LUPUS (wolf)

Subspecies CANIS LUPUS OCCIDENTALIS (northern timber wolf)

Although the name of the species is binomial (e.g., CANIS LUPUS) and that of the subspecies trinomial (C. LUPUS OCCIDENTALIS for the northern timber wolf, C. LUPUS LUPUS for the northern European wolf), all other names are single words. In zoology, convention dictates that the names of superfamilies end in -OIDEA, and the code dictates that the names of families end in -IDAE, those of subfamilies in -INAE, and those of tribes in -INI. Unfortunately, there are no widely accepted rules for other major divisions of living things, because each major group of animals and plants has its own taxonomic history and old names tend to be preserved. Apart from a few accepted endings, the names of groups of high rank are not standardized and must be memorized.

The discovery of a living coelacanth fish of the genus LATIMERIA in 1938 caused virtually no disturbance of the accepted classification, since the suborder Coelacanthi was already well known from fossils. When certain unusual worms were discovered in the depths of the oceans about 10 years later, however, it was necessary to create a new phylum, Pogonophora, for them since they showed no close affinities to any other known animals. The phylum Pogonophora, as usually classified, has one class—the animals in the phylum are relatively similar—but there are two orders, several families and genera, and more than 100 species. Both of these examples have been widely accepted by authorities in their respective areas of taxonomy and may be considered stable taxa.

It cannot be too strongly emphasized that there are no explicit taxonomic characters that define a phylum, class, order, or other rank. A feature characteristic of one phylum may vary in another phylum among closely related members of a class, order, or some lower group. The complex carbohydrate cellulose is characteristic of two kingdoms of plants, but among animals cellulose occurs only in one subphylum of one phylum. It would simplify the work of the taxonomist if characters diagnostic of phylum rank in animals were always taken from one feature, the skeleton, for example; those of class rank, from the respiratory organs; and so

on down the taxonomic hierarchy. Such a system, however, would produce an unnatural classification.

The taxonomist must first recognize natural groups and then decide on the rank that should be assigned them. Are sea squirts, for instance, so clearly linked by the structure of the extraordinary immature form (larva) to the phylum Chordata, which includes all the vertebrates, that they should be called a subphylum, or should their extremely modified adult organization be deemed more important, with the result that sea squirts might be recognized as a separate phylum, albeit clearly related to the Chordata? At present, this sort of question has no precise answer.

Some biologists believe that "numerical taxonomy," a system of quantifying characteristics of taxa and subjecting the results to multivariate analysis, may eventually produce quantitative measures of overall differences among groups and that agreement can be achieved so as to establish the maximal difference allowed each taxonomic level. Although such agreement may be possible, many difficulties exist. An order in one authority's classification may be a superorder or class in another. Most of the established classifications of the better-known groups result from a general consensus among practicing taxonomists. It follows that no complete definition of a group can be made until the group itself has been recognized, after which its common (or most usual) characters can be formally stated. As further information is obtained about the group, it is subject to taxonomic revision.

NOMENCLATURE

Communication among biologists requires a recognized nomenclature, especially for the units in most common use. The internationally accepted taxonomic nomenclature is the Linnaean system, which, although founded on Linnaeus's rules and procedures, has been greatly modified through the years. There are separate international codes of nomenclature in botany (first published in 1901), in zoology (1906), and in microbiology (bacteria and viruses, 1948). The Linnaean binomial system is not employed for viruses. There is also a code, which was established in 1953, for the nomenclature of cultivated plants, many of which are artificially produced and are unknown in the wild.

The codes, the authority for each of which stems from a corresponding international congress, differ in various details, but all include the following elements: the naming of species by two words treated as Latin; a law of priority that the first validly published and validly binomial name for a given taxon is the correct one and that any others must become

synonyms; recognition that a valid binomen can apply to only one taxon, so that a name may be used both in botany and in zoology but for only one plant taxon and one animal taxon; that if taxonomic opinion about the status of a taxon is changed, the valid name can change also; and, lastly, that the exact sense in which a name is used be determined by reference to a type. Rules are also given for the obligate categories of the hierarchy and for what constitutes valid publication of a name. Finally, recommendations are given on the process of deriving names.

Linnaeus believed that there were not more than a few thousand genera of living things, each with some clearly marked character, and that the good taxonomist could memorize them all, especially if their names were well chosen. Thus, although the naming of the species might often involve much research, the genus at least could be easily found.

At the present time, in many taxa, the species has a definite biological meaning: it is defined as a group of individuals that can breed among themselves but do not normally breed with other forms. Among microorganisms and other groups in which sexual reproduction need not occur, this criterion fails.

In botanical practice, matters more usually resemble the Linnean situation. Many sorts of chromosomal variants (individuals with different arrangements of chromosomes, or hereditary material, which prevent interbreeding) and marked ecotypes (individuals whose external form is affected by the conditions of soil, moisture, and other environmental factors), as well as other forms, that would clearly be classified as separate species by the zoologist may be lumped together unrecognized or considered subspecies by the botanist. Botanists commonly use the terms VARIETY and FORM to designate genetically controlled variants within plant populations below the subspecies level.

The use of a strictly biological species definition would enormously increase rather than reduce the number of names in use in botany. A recognized species of flowering plant may consist of several “chromosomal races”—i.e., identical in external appearance but genetically incompatible and, thus, effectively separate species. Such various forms are often identifiable only by cytological examination, which requires fresh material and extensive laboratory work. Many botanists have said that there has been so little stability in the accepted nomenclature that further upheavals would be intolerable and render identification impossible for many applied botanists who may not require such refinements. To postpone recognition of such forms, however, will probably cause upheaval in the future.

Some species of birds are widespread over the archipelagos of the southwest Pacific, where nearly every island may have a form sufficiently distinct to be given some kind of taxonomic recognition. For example, 73 races are currently recognized for the golden whistler (*Pachycephala pectoralis*). Before the realization that species could vary geographically, each island form was named as a separate species (as many of the races of P. PECTORALIS actually were). It is often believed—and often it is only belief rather than fact—that all of these now genetically isolated populations arose as local differentiations of a single stock. Thus, they are now usually classed in zoological usage as subspecies of one polytypic species. The term POLYTYPIC indicates that a separate description (and type specimen) is needed for each of the distinct populations, instead of one for the entire species. The use of a trinomial designation for each subspecies (e.g., PACHYCEPHALA PECTORALIS BOUGAINVILLEI) indicates that it is regarded as simply a local representative (in this case, on Bougainville Island in the Solomons) of a more widely distributed species. The decision on whether to consider such island forms as representatives of one species depends partly on whether, in the judgment of the taxonomist, populations from adjacent islands are sufficiently similar to allow free interbreeding.

VERIFICATION AND VALIDATION BY TYPE SPECIMENS

The determination of the exact organism designated by a particular name usually requires more than the mere reading of the description or the definition of the taxon to which the name applies. New forms, which may have become known since the description was written, may differ in characteristics not originally considered, or later workers may discover, by inspection of the original material, that the original author inadvertently confused two or more forms. No description can be guaranteed to be exhaustive for all time. Validation of the use of a name requires examination of the original specimen. It must, therefore, be unambiguously designated.

At one time authors might have taken their descriptions from a series of specimens or partly (or even wholly) from other authors' descriptions or figures, as Linnaeus often did. Much of the controversy over the validity of certain names in current use, especially those dating from the late 18th century, stems from the difficulty in determining the identity of the material used by the original authors. In modern practice, a single type specimen must be designated for a new species or subspecies name. The type should always be placed in a reliable public institution, where it can be properly cared for and made available to taxonomists. For many

microorganisms, type cultures are maintained in qualified institutions. Because of the short generation time of microorganisms, however, they may actually evolve during storage.

A complex nomenclature is applied to the different sorts of type specimens. The holotype is a single specimen designated by the original describer of the form (a species or subspecies only) and available to those who want to verify the status of other specimens. When no holotype exists, as is frequently the case, a neotype is selected and so designated by someone who subsequently revises the taxon, and the neotype occupies a position equivalent to that of the holotype. The first type validly designated has priority over all other type specimens. Paratypes are specimens used, along with the holotype, in the original designation of a new form; they must be part of the same series (i.e., collected at the same immediate locality and at the same time) as the holotype.

For a taxon above the species level, the type is a taxon of the next lower rank. For a genus, for instance, it is a species. From the level of the genus to that of the superfamily there are rules regarding the formation of a group name from the name of the type group. The genus HOMO (human beings) is the type genus of the family Hominidae, for example, and the code forbids its removal from the family Hominidae as long as the Hominidae is treated as a valid family and the name HOMO is taxonomically valid. Whatever the remainder of its contents, the family that contains the genus HOMO must be the Hominidae.

Indiscriminate collecting is of little use today, but huge areas of Earth are still poorly known biologically, at least as far as many groups are concerned, and there remain many groups for which the small number of properly collected and prepared specimens precludes any thorough taxonomic analysis. Even in well-studied groups, such as the higher vertebrates, new methods of analyzing material often necessitate special collecting. The determination of variation within species or populations may necessitate the study of more specimens than are available, even when (as is usual) the specialist can utilize material from many institutions. Usually, collecting is done to fill gaps (in geographical range, geological formations, or taxonomic categories) already brought to light by specialists reviewing the available material. The well-informed collector of living things knows where to go, what to look for, and how to spot anything especially valuable or extraordinary.

The actual techniques of collecting and preserving vary greatly from one group of organisms to another—soil protozoa, fungi, or pines are neither collected nor preserved in the same manner as birds. Some animals can be preserved only in weak alcohol, but others macerate

(decompose) in it. Certain earthworms “preserved” in weak alcohol simply flow out of their own skins when lifted out. Special methods are used after long experience to preserve characters of special value in taxonomy. Some methods make specimens difficult to observe; this is especially true of material that has to be sectioned or otherwise made into preparations suitable for microscopic observation.

After taxonomic material has been collected and preserved, its value can be lost unless it is accurately and completely labeled. Only rarely is unlabeled or insufficiently labeled material of any use. The taxonomist normally must know the locality of collection of each specimen (or lot of specimens), often the habitat (e.g., type of forest, marsh, type of seawater), the date, the name of the collector, and the original field number given to the specimen or lot. To this information is added the catalog number of the collection and the sex (if not already determined in the field and if relevant). The scientific identity of the specimen, as determined by an acknowledged specialist, is usually added to the label at the museum. Also included is the name of the specialist who identified the specimen. Later revisions of the classification and additional knowledge of the organism may result in later alterations of the scientific name, but the original labels must still be kept unaltered.

Other information may also be required. For example, the males and females of some insect groups are extremely different in appearance, and males and females of the same species may have to be identified. The capture of a pair in the wild actually in copulation gives a strong (but, surprisingly, not absolute) indication that the male and female belong to the same species; the labels of each specimen (if they are separated) indicate the specimen with which it was mating.

Evaluating taxonomic characters

Comparison of material depends to some extent on the purposes of the comparison. For mere identification, a suitable key, with attention given only to the characters in it, may be enough in well-known groups. If the form is likely to be a new one, its general position is determined by observing as many characters as possible and by comparing them with the definitions and descriptions in a natural classification. The new specimen is compared with its nearest known relatives, usually with reference to type material. Any character may be of taxonomic use. In general, taxonomists tend to work from preserved material, so that their findings can be checked. For extinct forms, of course, only preserved material (fossils) is available.

Many biochemical, physiological, or behavioral characters may be at least as good as anatomical characters for discriminating between closely related species or for suggesting relationships. There has been a tendency to discount anatomical characters, but, when they are obtainable in quantity (as for most plants and animals), they probably represent as large a sample of the effects of the organism's heredity as can be got, short of complete genetic analysis. Enthusiasts in genetics often stress that the only real basis for classification is the actual genotype of each organism—i.e., the hereditary information by which the organism is formed. It is impossible to obtain such information for extinct forms, and the time required to obtain it for most existing ones would be enormous, even if the techniques were available. An important development, however, has been the hybridization technique employing deoxyribonucleic acid (DNA), the substance by which hereditary information is coded. With this technique, it has been possible to determine similarities in parts of DNA molecules from different organisms but not the nature of their differences.

In making comparisons, resemblances resulting from convergence must be considered. Whales and bony fishes, for example, have similar body shapes for the same function—progression through water. Their internal features, however, are widely different. In this case, the convergence is evident because of the large number of characters that link whales to other mammals and not to the fishes and because the fossil record for the vertebrates provides a fair indication of the actual evolutionary sequence from primitive fishes through primitive amphibians to primitive reptiles, mammal-like reptiles, and mammals. In the absence of a good fossil record, it may be difficult or impossible to positively identify a case of convergence, yet it has been asserted that the occurrence of convergence must not be stated unless it has been "proved." To obey this assertion would be to make the method of analysis dictate in part the results achieved.

In some forms, especially internal parasites, great modification has occurred in adapting to a parasitic way of life.The parasite is unrecognizable as a close relative of the barnacles (crustaceans not far removed from the crabs themselves) without the free-swimming larval stage, which shows its affinities. Transient or inconspicuous characters may be of great importance in indicating affinities; the complete life cycle of a specimen may have to be observed before its affinities can be determined. Although such characters may be useless for identification and for definition of a natural group if only a few forms in a group show them, they may be of the utmost importance in understanding relationships. Characters are therefore weighted to some extent by the taxonomist according to their utility for different purposes.

Any characters intrinsic to the organism can be used in classification. Extrinsic characters, including the position of fossils in a geological sequence and geographical distribution of fossil and recent forms, may force the taxonomist to look more closely at the intrinsic characters.

Weighting or non-weighting (i.e., by the degree of importance) of characters has been a subject of great dispute. On the one hand, it has been pointed out that weighting is often demonstrably arbitrary and always imprecise. On the other, it has been said that if characters were actually examined without weighting, some obvious cases of extreme convergence would have to be classed with each other instead of in their proper place. A classification based on un-weighted characters is called a phenetic one (based on appearances) as opposed to a phyletic one (based on evolutionary change within a single line of descent), in which characters are weighted by their presumed importance in indicating lines of descent. The quarrel results in part from a misunderstanding of aims.

At present, the classification of living things is a rough, non-quantitative sketch of their diversity. A properly surveyed map of this diversity would advance classification enormously. If, on such a map, the diving petrels (PELECANOIDES) of the Southern Hemisphere and the little auk (PLAUTUS) of the Northern Hemisphere were closer to each other than to their own phylogenetic relatives (the other petrels, fulmars, and albatrosses; and the guillemots, terns, gulls, and shorebirds, respectively), this would show the extent of their convergence, which is certainly great, but it would not be a reason for combining them in a separate group. In recent years numerical techniques have been developed for estimating overall resemblance or phenetic distance. For these methods, it is necessary to use large numbers of characters taken from each form and, as far as possible, at random; this involves enormous labour.The mathematical techniques are not as yet wholly satisfactory, some having been borrowed from statistical analysis and applied to taxonomic problems without any consideration of whether they were designed to answer the questions asked by the taxonomist.

It is worth noting that if there were a complete fossil record for any group, then simply placing any form nearest to those most like it (which must be its immediate ancestors or descendants) would produce an arrangement in which all cases of parallelism and convergence would be revealed. Since evolution occurs by descent with modification, this arrangement would presumably reflect the greatest use of the information available about the

group and thus would also be the most useful general arrangement. For such groups, the phenetic arrangement is the phyletic one also.

Making a classification

When some idea has been obtained of the constituent forms in a group and of the similarity and dissimilarity that they bear to each other, it is necessary to fit a hierarchical system to them. As already indicated, for groups with good fossil records, a dendritic, or branching, arrangement is desired, and classification must be partly arbitrary because of lack of knowledge. If the taxonomist has two compact groups of species, those within each group agreeing closely with each other in many characters and differing sharply from members of the other group in others, there is no difficulty in classification except in ranking. If each group contains a scattering of forms, any one close to another but the most divergent members in each group less like each other than they are like certain of the other group, breaking up the groups into definite classes becomes arbitrary.

A particularly difficult case arises when these forms also occur in time series: the present-day dogs, cats, hyenas, and other carnivores differ greatly from each other, but at one time their ancestors were much alike; presumably, therefore, they came from one ancestral stock. Paleontologists trace back each taxonomic line and are inclined to carry their separations of taxonomic groups as far backward in time as possible, until the earliest members of related groups are far more like each other than each is to the rest of the later members of the group to which it is assigned. This separation of groups is extreme phyletic splitting, but cutting off a large basal group containing all the primitive members may require arbitrary breaks in the many lines of descent and will obscure the evolutionary relationships. There is no answer to this dilemma except to avoid extremes.

A similar difficulty arises when the same character complex has arisen independently in related lines. The American paleontologist George Gaylord Simpson, for example, pointed out that mammalian characters such as the single jawbone (dentary) have arisen several times in groups of the extinct mammal-like reptiles. To use Sir Julian Huxley's useful terminology, the definition of the Mammalia expresses a grade of organization (the attainment of a particular level of advancement), not a clade (a single phyletic group or line). Some taxonomists insist that in an evolutionary classification every group must be truly monophyletic—that is, spring from a single ancestral stock. Usually, this cannot be

ascertained; the fossil material is insufficient or, as with many soft-bodied forms, nonexistent. Definite convergence must not be overlooked if it can be detected.

How far groups should be split to show phyletic lines and what rank should be given each group and subgroup thus is matters for reasonable compromise. The resulting classification, if fossils are unknown, may be frankly “natural” or phenetic, as is often explicitly the case with the flowering plants and is actually the case with many animal groups. If sufficient fossils are available, the resulting classification may be consonant with what is known about the evolution of the group or with what is merely conjectured. In reality, many classifications are conjectural or tendentious, and simpler and more natural ones might be closer to the available facts.

Even when only mere fragments are dealt with, a classification of some sort may still be necessary. Large numbers of leaves, some stems, trunks or roots, many seeds, and few flowers are known as fossils and may be of interest to the evolutionist. It may be many decades before a particular sort of fossilized leaf can be associated with a particular sort of branch, let alone trunk, flower, or seed. It is customary to construct form groups (i.e., a genus or species name is assigned to the fossilized material on the basis of its structure) in order to classify fossilized remains and to give them valid binomial names. When (if ever) two or more bits of fossil material are identified as belonging to one organism, one name only is retained. This procedure is best known for plants, but one phylum of animals (the Conodonta) is made up of enigmatic structures that are obviously some part of something animal.

Current systems of classification

DIVISION OF ORGANISMS INTO KINGDOMS

As long as the only known plants were those that grew fixed in one place and all known animals moved about and took in food, the greater groups of organisms were obvious. Even in the time of Linnaeus, however, many biologists wondered about such animal groups as corals and sponges, which were fixed in position and in some ways even flowerlike.

A more serious problem of classification arose with the invention of the microscope and the discovery of microscopic forms of life. It became apparent that many of these microorganisms held both animal and plant characteristics and could not simply be classified in either kingdom. For example, EUGLENA is a unicellular organism with

chlorophyllcharacteristic of a plant, yet with such animal features as an eyespot and locomotion by means of a flagellum.

Some microorganisms are parasitic inside animals and ingest complicated materials as food, while related microorganisms obtain their nutrients through photosynthesis. It has been proposed that the unicellular forms of microorganisms be placed in a separate kingdom, the Protista. Some biologists do not find this to be a happy solution, however, as some of the "unicellular" plants occur in "colonies" of various numbers of cells and may even have specialized reproductive cells.

In the mid-20th century, biologists recognized two vastly different cell types, procaryote (prokaryote) and eucaryote (eukaryote), and based a division of the living and extinct world on these two broad categorizations. The divisions were based primarily on the absence or presence, respectively, of a membrane-bound nucleus containing the genetic material of the cell, as well as on other organizational and structural features. Many classifications of living organisms adopted such a division and further created two superkingdoms, Prokaryota and Eukaryota. Within the Prokaryota was placed the kingdom Monera (the bacteria, blue-green algae, and a recently described bacterial group called the Archaebacteria (also called Archaeobacteria). The Eukaryota comprised all other living organisms.

Viruses are far more difficult to classify. They are known only as parasites; no free-living forms have been found. They have a far simpler structure than bacteria and reproduce by injecting their hereditary material, which is either deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) but not both (as in all other living things), into cells of other organisms. In effect, viruses utilize the host's protein-synthesizing mechanism to reproduce. The individual virus particle (virion), therefore, does not grow and divide by fission as do bacteria. Some biologists have speculated that viruses are genes that have gotten out of control and become parasitic; others have denied that viruses can be considered living at all. Many are highly important disease producers in plants, animals, and bacteria.

The principal characteristic shared by bacteria and viruses is that the hereditary material is not contained within a special nuclear membrane. Such a prokaryotic condition might be postulated by evolutionists as primitive when compared with forms with a complex nucleus, as in eukaryotic organisms. Viruses as they now exist may be the simplest of living things, but it is not known how much they are modified from ancestral forms that are assumed not to

have been parasitic and that were evidently on the main line of evolution; nor is their relation to bacteria known.

Another prokaryotic group, the blue-green algae, is traditionally placed with the other algae (e.g., seaweeds) and studied more by botanists than by microbiologists. Blue-green algae may be either unicellular or filamentous, and they behave like true plants, photosynthesizing in a way that resembles green plants rather than bacteria. Many move by gliding, as do some bacteria and some true unicellular algae. They are often extremely abundant around hot springs or at the edges of muddy ponds, and, though they are resistant to harsh environments, blue-green algae are killed by many drugs (e.g., antibiotics) used against bacteria. Perhaps they are best regarded as representing a group close to the main evolutionary line that gave rise to the eukaryotic plants.

Another problem relates to the position of the fungi, a large group including such familiar forms as mushrooms, toadstools, molds, and yeasts. (Although some authorities place the true slime molds (Myxomycetes)with the fungi, others point to the many characteristics they share with the protists.) The fungi are eukaryotic, lack chlorophyll (and therefore cannot photosynthesize as do green plants), and have rigid walls to the "cells," or filaments (hyphae) that sometimes contain cellulose, as do green plants. Some fungi walls or filaments are made of chitin, the major constituent of the external skeleton of insects and other arthropods, or even of other structural compounds. A fungal "cell" usually contains many nuclei. Asexual and sexual spores are usually produced; some produce motile spores with flagella, like the spores of some algae. The sexual cycle is often very complex. Because fungi in general grow and produce "fruit" like ordinary plants, they have traditionally been included with them, but the differences between the fungi and the plants seem considerable.

The preceding considerations exemplify the difficulties inherent in producing a generally accepted classification, even at the highest levels. Since the earliest attempts at classifying the living world into two kingdoms, Plantae and Animalia, biologists have debated the relationships among all organisms. Most biologists, however, accept the fundamental differences in cell structure that separates the superkingdoms Eukaryota and Prokaryota.

The two-kingdom classification of organisms has not been a suitable alternative since the discovery of a microscopic group of organisms. One four-kingdom classification (Table) recognizes the kingdoms Virus, Monera, Plantae, and Animalia within the superkingdoms Prokaryota and Eukaryota. Separate kingdoms are not recognized for the microorganisms

(Protista) or for the fungi, which are placed in the plant kingdom. Another classification recognizes Protista (including the fungi and protozoans) rather than viruses.

The four-kingdom scheme of classification

kingdom	**members**
Virus	
Monera	bacteria, blue-green algae, archaebacteria, and prochlorophytes
Plantae	algae, slime molds, true fungi, bryophytes (mosses, liverworts, and hornworts), ferns, psilophytes, lycopodiophytes, conifers, gnetophytes, ginkgophytes, cycads, and flowering plants
Animalia	protozoans, sponges, corals, flatworms, tapeworms, arthropods, mollusks, lamp shells, annelids, bryozoans, echinoderms, hemichordates, and chordates, including the vertebrates

A classification of living organisms

Recent advances in biochemical and electron microscopic techniques, as well as in testing that investigates the genetic relatedness among species, have redefined previously established taxonomic relationships and have fortified support for a five-kingdom classification of living organisms. This alternative scheme is presented below and is used in the major biological articles. In it, the prokaryotic Monera continue to comprise the bacteria, although techniques in genetic homology have defined a new group of bacteria, the Archaebacteria, that some biologists believe may be as different from bacteria as bacteria are from other eukaryotic organisms. The eukaryotic kingdoms now include the Plantae, Animalia, Protista, and Fungi, or Mycota.

The protists are predominantly unicellular, microscopic, nonvascular organisms that do not generally form tissues. Exhibiting all modes of nutrition, protists are frequently motile organisms, primarily using flagella, cilia, or pseudopodia. The fungi, also nonvascular organisms, exhibit an osmotrophic type of heterotrophic nutrition. Although the mycelium may be complex, they also exhibit only simple tissue differentiation, if any at all. Their cell

walls usually contain chitin, and they commonly release spores during reproduction. The plants are multicellular, multitissued, autotrophic organisms with cellulose-containing cell walls. The vascular plants possess roots, stems, leaves, and complex reproductive organs. Their life cycle shows an alternation of generations between haploid (gametophyte) and diploid (sporophyte) generations. The animals are multicellular, multitissued, heterotrophic organisms whose cells are not surrounded by cell walls. Animals generally are independently motile, which has led to the development of organ and tissue systems. The monerans, the only prokaryotic kingdom in this classification scheme, is principally made up of the bacteria. They are generally free-living unicellular organisms that reproduce by fission. Their genetic material is concentrated in a non-membrane-bound nuclear area. Motility in bacteria is by a flagellar structure that is different from the eukaryotic flagellum. Most bacteria have an envelope that contains a unique cell wall, peptidoglycan, the chemical nature of which imparts a special staining property that is taxonomically significant (i.e., gram-positive, gram-negative, acid-fast).

The use of "division" by botanists and "phylum" by zoologists for equivalent categories leads to a rather awkward situation in the Protista, a group of interest to both botanists and zoologists. As used below, the terms follow prevailing usage: phylum for the primarily animal-like protozoa and division for other protistan groups that are more plantlike and of interest primarily to botanists.

The discussion above shows the difficulty involved in classification. For example, one traditional classification of the Aschelminthes, presented below and in the article aschelminth, divides the phylum Aschelminthes into five classes: Rotifera, Gastrotricha, Kinorhyncha, Nematoda, and Nematomorpha. An alternative classification elevates these classes to phyla, and still another classification establishes different relationships between the groups—phylum Gastrotricha, phylum Rotifera, phylum Nematoda (containing classes Adenophorea, Secernentea, and Nematomorpha), and phylum Introverta (containing classes Kinorhyncha, Loricifera, Priapulida, and Acanthocephala). The true relationships between these pseudocoelomates remain to be established.

1.2 SIGNIFICANCE OF TAXONOMY

Taxonomy is the science of classifying organisms. At no time there has been a greater need for taxonomists than now when the crisis facing biodiversity is escalating. Decision 11/8 of the second meeting of the Conference of Parties to the Convention on Biological Diversity (CBD) identified the lack of sufficient taxonomists as a significant impediment for implementing the decisions of the convention at national as well as international levels. Over the past half a billionyears the world lost perhaps one species per million species each yearincluding everything from mammals to plants and today the annualrate of extinction is estimated to be 1000 to 10000 times faster(Wilson,2003). This is really a matter of grave concern for all thosewho think that our biodiversity is precious and should be protected. Itis also known now that sentineling extinctions take place on manyregions of the world today and not merely a thing of the past whichhappened in that cloud forest of the Western Ecuador in 1978-1980.Besides we are quite ignorant of the real magnitude of the world's bio-diversity. The audit of biodiversity today is far short of a reality.Though opinions on the biodiversity of the world differ from 5-100million(Wilson,2003) species, a 'best guess' or mid-way on the road, places it at 14 million living species today (Cherian,2004). Amongthese fewer than 2 million species of organisms are scientifically identified and named. At the current pace of taxonomic research, it may require 5000 taxonomists to complete merely the taxonomic listing of5 million species in 25-30 years if one taxonomist can deal with 1000species. Our efforts to conserve our biodiversity will be much easier ifwe know the basic units that are species and their relationships.Taxonomy provides discovery and identification of these basic unitsand their relationships (Narendran, 2006, 2008).Taxonomy is the basis for all meaningful studies on biodiversity,pest management, medicine, bioprospecting, fisheries, quarantine,defense etc. Before initiating any kind of studies, it is absolutely essential to know the correct name of the organism on which the studies areinitiated. This is important because the correct scientific name of theorganism is a functional label, using which various pieces of information concerning that organism, including all the past work done on it,can be retrieved and stored ensuing ease of reference and stored ensuring easy reference (Narendran 2000). Taxonomy plays animportant role in pest management programmes. When natural enemies are being sought or transferred from one region to another in bio-logical control projects, the correct identification of both the pest andthe natural enemy species is of great importance (Narendran2003).History and experience have already shown that absence of taxonomic

expertise have resulted in the failure of several pest managementprogrammes resulting in tremendous loss of agricultural products as well as huge amount of money. There are several instances in the history of pest management to show that failures resulted because taxonomists were not consulted in the identification of the pest or its natural enemies before starting the pest management programmes especially biological control programmes against insect pests. Without thehelp of taxonomists biological control workers may commit severalmistakes (Schauff & LaSalle, 1998; Narendran 2001, 2003,2006). Theymay inadvertently import a species of natural enemy that may bealready present in the country of introduction. They may spend sever-al days studying the biology of a species that may have already beendone under an unpublished or published synonym of the species. Thebiological control workers may spend a lot of money and effort in ship-ping, curation, breeding etc of wrong species of natural enemies suchas hyperparasites or natural enemies that do not attack target hostspecies etc. Preservation of taxonomic collections has very greatimportance since they may prove to be of immense value in biologicalcontrol projects.

Quarantine agencies often seek help of taxonomists to determinewhether an imported plant or animal is harmful or not and based onthe advice of taxonomists, prevent the entry of harmful organisms. In these days of germ warfare, it is necessary to seek help of taxonomistsfor the identification of organisms introduced to a country by enemies. Besides these, taxonomist's help can be made use of in many otherfields such as medicine, fisheries, academic studies and many otheruseful fields. In spite of all these important aspects, taxonomy is stillnot adequately developed in the underdeveloped and developing countries like India. Taxonomy involves hard field oriented work. It needscareful observation, analytical mind and a little above average of intelligence to analyses and in weighting of a taxon to determine it at speciesor infraspecific level. In some cases several days or even months maybe necessary to arrive at a proper conclusion in determining the identity of a taxon. In several other instances wide ranging discussions andconsultations with experts working on the group or related fields arenecessary for taking a decision in the identification process. Yet thereare many workers of other fields of specialization who consider taxonomy is an out dated subject and not worthy of doing. These critics havemy optic vision that has lost sight of the whole wonderful world of unexplored fauna and flora which await discovery by taxonomists. In orderto understand taxonomy it is absolutely essential to have an impartialnon-biased mind with a curiosity to find the undiscovered fauna andflora and with strong will to undertake hard work. It is ironic to notethat often the very same people who criticize taxonomy approachestaxonomists for

prompt and urgent identification of the specimensthey want to work with. There are various subdivisions in Taxonomy and among these themost commonly used one is the Classical Taxonomy which is the con-ventional taxonomy based mainly on external morphology which isoften supported and supplemented by ethological and ecological data.Some taxonomists base their classification on greater number of characters from many sets of data in order to produce an entirely phonetic classification and this is known as Numerical Taxonomy. It is based onphenetic similarities and maximum number of characters (morpholog-ical, behavioral, karyological, etc) and each character is given equalweight. Molecular taxonomy is relatively a recent research branch oftaxonomy, invaded often by prejudiced workers of molecular biology.It includes DNA barcoding, analyses of isosymes, molecular cytogenetics and a number of other related techniques. Recently many biologists have turned their interests to DNA bar-coding technique for taxonom-ic identification. DNA bar coding is a taxonomic method which uses ashort genetic marker in the mitochondrial DNA (mtDNA) of an organ-ism so as to identify that organism as belonging to a particular species.Though molecular taxonomy has its usefulness, it has several demeritstoo. For identifying two unknown organisms, species or subspecies itwould be difficult to use this method. The main problem is the distribution of variability within and between species. Long periods of independence allow variability within groups pose a serious stumblingblock in molecular taxonomy (Narendran, 2006). DNA bar coding does not provide reliable information above species level. It is also now known that recently diverged species might not be distinguishable on the basis of DNA bar coding (CO1 sequences). One of the main differences between molecular taxonomy and classical taxonomy is that theformer uses a technique such as DNA bar coding which is nothing butan over simplification of the science of taxonomy. Classical taxonomyon the other hand has a holistic approach, treating each organism as awhole and it is not described in vacuum but in comparison with otherorganisms, objects and substances (Grimaldi and Engel, 2007). A liv-ing organism expresses its identity in the way it organizes its variousparts and how it relates to the environment. In molecular technique(DNA bar coding) an organism is nothing but a DNA sequence. Inorder to understand a living organism, it is absolutely essential to havea holistic approach establishing a relationship with it and such relationships are possible only by looking or sensing an organism as awhole and not by bar codes (Katz, 2005). This is not to state thatmolecular taxonomy is not useful and classical taxonomy is better.Genomic bar coding is definitely useful as a supplementary tool toclassical taxonomy (especially in differentiating sibling species) andnot to replace it completely. The problem, as Grimaldi and Engel(2007) point out is that high tech

descriptions (such as molecular taxonomy) are seen by some as more scientific and this view is not accept-able to many scientists who believe that all branches of science isimportant especially when classical taxonomy is still making startlingdiscoveries(for instance discovery of a new insect order recently viz.Matophasmatoidea) even now. As Ogura (1964) pointed out classicaltaxonomy will continue to reign supreme many more years to come.The article 7(a) of the convention of of Biological Diversity statesthat the countries which signed the biodiversity document, have toundertake an inventory of biological diversity in order to provide fundamental information on the distribution and abundance of biodiversity. Such data are necessary for the long-term sustainable management, use and conservation of bio diverse area. The fourth meeting onCBD held at Darwin (Australia) in 1998 stated that the various countries which participated in the meeting, affirmed the existence of a taxonomic impediment for the proper management and conservation ofworld's biodiversity. Removal of these impediments is very essentialnot only for discovering and understanding the world's biodiversitybut also for global efforts to conserve our biodiversity. The mainimpediments include shortage of man power in taxonomic work, lackof adequate funding for taxonomic research, lack of training in taxonomy from higher secondary school level, lack of library facilities fortaxonomic studies and lack of adequate taxonomic centers not only foridentification but also for giving adequate training in taxonomy besides many other impediments. There are many requirements for removing these taxonomic impediments and some of the major onesare: 1) Taxonomy (all aspects from Classical to molecular) should beincluded as a compulsory subject in the curriculum and syllabi fromhigher secondary school level to postgraduate levels.; 2) enough fundsshould be given to taxonomists or to non-governmental and govern-mental organizations and institutes for meeting the cost of publishingpapers and monographs in taxonomy) creating enough employment opportunities for taxonomists etc are some of the major requirements to be met with by the respective countries which signed the bio-diversity document. It is high time we set our priorities straight for thedevelopment of all aspects of taxonomy without being prejudiced orbiased to any any aspect of taxonomy. More and more students shouldtake up taxonomy as their carrier. "Taxonomy... is no less attractive, challengingly difficult, satisfying and productive than most sophisticated, spectacularly dramatic biological experiments currently in fashion-here is an unknown and a new world, literally at our door step, fordiscovery, exploration and conquest " (Mani, 1989).

1.4 APPLICATIONS OF TAXONOMY

Taxonomy is a hierarchical structure for the classification and/or organization of data. In content management and information architecture, taxonomy is used as a tool for organizing content.A taxonomy is an organizing principle. It is a foundation on which to base any kind of information system. It does not matter what kind of project you are involved in, it will benefit from clearly defined, concise language and terminology.A taxonomy and controlled vocabulary help to fine tune search tools, they creates a common language for sharing concepts, and it allows an efficient organization of documents and content across information sources.Taxonomy is very important in content management. It ensures that search and navigation work properly and that content is accessible and can be found via two access points: searching and browsing.

Taxonomy is organized by supertype-subtype relationships, also called generalization-specialization relationships, or less formally, parent-child relationships. Once a taxonomy tree has been created, all the items in the tree are tagged as belonging to one or more specific taxonomy categories. This process is typically referred to as "categorization", "tagging" or "profiling". Users can then browse and search within specific categories.

In such an inheritance relationship, the subtype by definition has the same properties, behaviors, and constraints as the supertype plus one or more additional properties, behaviors, or constraints. For example: a bicycle is a kind of vehicle, so any bicycle is also a vehicle, but not every vehicle is a bicycle. Therefore a subtype needs to satisfy more constraints than its supertype. Thus to be a bicycle is more constraint than to be a vehicle.

Historically used by biologists to classify plants or animals according to a set of natural relationships, in content management and information architecture, taxonomy is used as a tool for organizing content. Creating taxonomy is central to any enterprise content strategy as means of organizing content so that it could be found by either searching or browsing.

Biological taxonomy is a sub-discipline of biology, and is generally practiced by biologists known as "taxonomists", though enthusiastic naturalists are also frequently involved in the publication of new taxa.Because taxonomy aims to describe and organize life, the work conducted by taxonomists is essential for the study of biodiversity and the resulting field of conservation biology.

Biological classification is a critical component of the taxonomic process. As a result, it informs the user as to what the relatives of the taxon are hypothesized to be. Biological classification uses taxonomic ranks, including among others (in order from most inclusive to least inclusive): Domain, Kingdom, Phylum, Class, Order, Family, Genus, Species, and Strain.

Taxonomy in Biodiversity Conservation

Taxonomy usually refers to the theory and practice of describing, calling, and categorizing living things. Such work is necessary for the fundamental understanding of biodiversity and its conservation. Yet the science behind delimiting the natural world into "species" is frequently ignored, misconstrued, and even derided in some quarters.

Most people concerned about biodiversity conservation commonly utilize the term "species" without a clear understanding of what separates one species from another, and why. This is where the science of taxonomy plays an integral role. Species are differentiated from each other in a number of methods.

Although the meaning of species has been the cause of the substantial historic argument, in other words, species are organisms usually acknowledged as morphologically distinct from other groups.

Taxonomy in Biological Control

In biological control, the insect species, its possible area of origin, and, consequently, the area where promising natural enemies may be discovered, is determined. The close co-operation of taxonomists throughout pre-and post-release studies of natural opponents in target areas helps to show the native fauna present and the advancement of a biological control programmed.

Biological control programs should budget for appropriate taxonomic research studies in locations where the local fauna is inadequately known. Advising regional scientists on the proper collection, preservation, and identification of appropriate indigenous and unique species should be emphasized.

Taxonomy to Combat Invasive Alien Species

Taxonomic information is vital for firms and border authorities to find, manage, and control Invasive Alien Species (IAS). Reliable control and management steps can just be carried out

when unique species are properly and immediately determined. Misidentifications can cost money when rapid choices need to be taken.

Networking and sharing of experiences, details, and know-how can help in decreasing the costs related to IAS and lower the need for elimination programs with early detection and prevention. When elimination is required, taxonomists can provide proficiency that is central to develop the most efficient yet economic and ecologically benign eradication procedures.

Increased capacity-building (especially for developing countries) is necessary to determine, record, and display intrusions; provide existing and available lists of possible and recognized IAS; determine potential risks to neighboring countries; and to access info on taxonomy, ecology, genes, and control approaches.

It is vital that nearby nations, and all countries along a specific pathway for invasive species, can acknowledge such species and concur on their nomenclature. Baseline taxonomic details on native biota at the nationwide level is likewise important to make sure that IAS can be acknowledged and distinguished from naturally present species.

Taxonomy in Agriculture and Forestry

Recently we have faced an unpleasant problem of conserving our crops and trees from the attack of many different sorts of pests (Locusts). It is extremely important to understand the right category names of such insects prior to their proper control.

Every species has its own different niche in nature and varies from its associated types in food partiality, mating seasons, tolerance or resistance capability to numerous stimuli, predators, rivals, pathogens, and so on and all these are extremely crucial for an applied worker before applying control procedures.

All this crucial information can be quickly obtained by group screening of the insect, if the identity of the insect is sometimes known, it is also really helpful to have a regional observation of the process of triggering so much damage of the crop on getting proper identification of the insect species, it ends up being simpler to collect details about its practices which is essential for its effective control.

Taxonomy in Wildlife Management

The primary role of a taxonomist is the organization of classes of living organisms, about which scientifically helpful indicative generalizations can be made. The primary function is

to distinguish the different sorts of organisms and by explaining their characteristics through descriptions, keys, figures, and so on. Should need to provide names for each individual organism, so that the info can be recorded, saved, and reclaim when needed.

To make a set of principles based on the option and importance of characters with the ultimate objective of organizing species in the hierarchy of greater categories.

Estimate genetic and phylogenetic relationships amongst organisms.

Taxonomy in Public Health

Taxonomy plays a fantastic function in public health management. There are a variety of different kinds of diseases that are spread by many arthropods, bugs which are disease-specific. So, we must prepare the control strategy in such a way that only the target species is assaulted. This is only possible if we get the correct identification of that species. For example, some species of anopheles mosquitoes are responsible for transmitting malaria however the other species not.

Ticks are vectors of nematodes, protozoa, rickettsia, spirochetes, other bacteria, and infection that cause diseases in human beings and other animals.

Taxonomy plays a crucial role in the recognition of these interactions. The control system then used just on the target species and in this a method of cash and workforce was conserved and the loss can be stopped. This right recognition guarantees an optimum of efficient control at minimum expense.

UNIT 2: MODERN APPROACHES IN TAXONOMY

2.1 Objectives

2.2 Introduction

2.3 Chemotaxonomy

2.4 Cytotaxonomy

2.5 Neotaxonomy and Molecular Taxonomy

2.6 Summary

2.7 Terminal Questions and Answers

2.1 OBJECTIVES

The Study of Chemotaxonomy, Cytotaxonomy& Neotaxonomy and Molecular Taxonomy.

2.2 INTRODUCTION

Taxonomists now accept that, the morphological characters alone should not be considered in systematic classification of plants. The complete knowledge of taxonomy is possible with the principles of various disciplines like Cytology, Genetics, Anatomy, Physiology, Geographical Distribution, Embryology, Ecology, Palynology, Phenology, Bio-Chemistry, Numerical Taxonomy and Transplant Experiments. These have been found to be useful in solving some of the taxonomical problems by providing additional characters. It has changed the face of classification from **alpha** (classical) to **omega** (modern kind). Thus the new systematic has evolved into a better taxonomy.

2.3 CHEMOTAXONOMY

Various medicines, spices and preservatives obtained from plant have drawn the attention of Taxonomists. Study of various chemicals available in plants help to solve certain taxonomical problems. Chemotaxonomy is the scientific approach of classification of plants on the basis of their biochemical constituents. As proteins are more closely controlled by genes and less subjected to natural selection, it has been used at all hierarchical levels of classification starting from the rank of ‘variety’ up to the rank of division in plants. Proteins, amino acids, nucleic acids, peptides etc. are the most studied chemicals in chemotaxonomy.

The chemical characters can be divided into three main categories.

1. Easily visible characters like starch grains, silica etc.
2. Characters detected by chemical tests like phenolic, oil, fats, waxes etc.
3. Proteins

SIGNIFICANCE OF CHEMOTAXONOMY:

The occurrence and distribution of the various types of chemical substances present in plants prove to be of taxonomic significance. However, it should be noted that, all kinds of chemical substances present in plants do not reveal information useful to the taxonomist. Phytochemical characters of taxonomic significance have been classified into three types.

These include:

a. Primary constituents:

These include the macromolecular compounds directly taking part in metabolism and include proteins, nucleic acids, chlorophyll and polysaccharides. All chemical materials synthesized by an organism reflect the information in DNA, RNA and proteins. These latter molecules have been termed as semantides. Semantides, thus contain useful information of taxonomy and phylogeny.

b. Secondary constituents:

They include compounds lacking nitrogen and not involved directly in plant metabolism i.e., simple phenolic compounds like caffeic, benzoic and nicotinic acids and polyphenolic compounds like flavonoids, terpenes, coumarines, alkaloids and pigments of which flavonoids are most widely studied with respect to plant systematics.

c. Miscellaneous substances:

However, no suitable classification of the chemical characters and their use in taxonomy is developed so far. On the basis of their molecular weight, Jones and Luchsinger (1987) have divided the natural chemical plant products useful in taxonomy, into two major groups.

d. Micro-molecules:

They are low molecular weight compounds with a molecular weight of 1000 or less, e.g. amino acids, alkaloids, fatty acids, terpenoids, flavonoids, etc.

e. Macromolecules:

They include the high molecular weight compounds with a molecular weight of over 1,000, e.g. proteins, DNA, RNA, complex polysaccharides, etc.

2.4 CYTOTAXONOMY

Cytotaxonomy is a branch of taxonomy that uses the characteristics of cellular structures to classify organisms. In cytotaxonomy, the chromosomal configuration of an organism is the most widely used parameter to infer the relationship between two organisms. The inference of species relationships is based on the assumption that closely related species share similar characteristics in their chromosomal setup (referred to as karyotype). By analyzing the similarities and differences in the chromosomes, karyotype evolution and species evolution can be reconstructed.

The number, structure, and behavior of chromosomes is of great value in taxonomy, with chromosome number being the most widely used and quoted character. Chromosome numbers are usually determined at the metaphase stage during mitosis. Usually, the diploid chromosome number (2n) is referenced, unless dealing with a polyploidy series in which case the base number or number of chromosomes in the genome of the original haploid is quoted. Another useful taxonomic character is the position of the centromere. Meiotic behavior may show the heterozygosis of inversions. This may be constant for a taxon, offering further taxonomic evidence.

Often, cytological evidence is accompanied and strengthened by other analyses, including genomics and DNA-based phylogenies.

Cytology has contributed to tracking the evolutionary history of many organisms, especially primates and flowering plants. As example, karyotype comparisons have largely clarified the evolution of Arabidopsis thalianaand of saffron crocus, though there are many more studies that deserve highlighting.

SIGNIFICANCE OF CYTOTAXONOMY:

The role of cytotaxonomy is very important in taxonomic studies. Cytotaxonomy is more significant than physiological taxonomy because it is the comparative study of chromosomes at the molecular level. Small changes in chromosomes can be detected among the individual.

Chromosomes are constituted by the DNA, variation in the DNA leads to change in chromosome which ultimately causes variation among the individual, species, genus and everything.Cytotaxonomy is a part of taxonomic biology that deals with the classification of organisms. Cytogenetic studies represent both structural and functional homologies among taxa based on their evolutionary conservation.

A.BIOSYSTEMATICS

Biosystematics is an "Experimental, ecological and cytotaxonomy" through which life forms are studied and their relationships are defined. The term biosystematics was introduced by **Camp** and **Gilly** in 1943. Many authors feel Biosystematics is closer to Cytogenetic and Ecology and much importance given not to classification but to evolution.

B.KARYOTAXONOMY

Chromosomes are the carriers of genetic information. Increased knowledge about the chromosomes have been used for extensive biosystematics studies and resolving many taxonomic problems. Utilization of the characters and phenomena of cytology for the explanation of taxonomic problem is known as **cytotaxonomy** or **karyotaxonomy**. Thecharacters of chromosome such as number, size, morphology and behaviour during meiosis have proved to be of taxonomic value.

C. SEROTAXONOMY (IMMUNOTAXONOMY)

Systematic serology or serotaxonomy hadits origin towards the end of twentieth century with the discovery of serological reactions and development of the discipline of immunology. The classification of very similar plants by means of differences in the proteins they contain, to solve taxonomic problems is called **serotaxonomy**. **Smith** (1976) defined it as "**the study of the origins and properties of antisera**."

2.5 NEOTAXONOMY AND MOLECULAR TAXONOMY

(MOLECULAR SYSTEMATICS / MOLECULAR PHYLOGENETICS)

Molecular Taxonomy is the branch of phylogeny that analyses hereditary molecular differences, mainly in DNA sequences, to gain information and to establish genetic relationship between the members of different taxonomic categories. The advent of DNA cloning and sequencing methods have contributed immensely to the development of molecular taxonomy and population genetics over the years. These modern methods have revolutionized the field of molecular taxonomy and population genetics with improved analytical power and precision.

USES OF MOLECULAR TAXONOMY

1. Molecular taxonomy helps in establishing the relationship of different plant groups at DNA level.

2. It unlocks the treasure chest of information on evolutionary history of organisms.

NEOTAXONOMY

The aim of neo-taxonomy or systematic or biosystematics is not only to describe, identify and arrange organisms in convenient categories but also to understand their evolutionary histories and mechanisms. Earlier approaches were primarily based exclusively on observed or morphological data without considering intraspecific differences. Many of the species are thus known by single or few specimens.

Recently, however, great attention is paid to sub-groupings of the species like populations and subspecies. The old morphological species are now called biological ones, which also includes ecological, ethological genetically and other characters. All these new approaches have contributed greatly in explaining the true structure of the species and their evolutionary position and in modification of the basic system of taxonomy. However most of the new approaches need specific methods. A brief account of some of the more important current approaches is discussed in this unit. Some of these approaches are still developing and provide much excitement by generating new data and information. You should, however,

bear in mind that even today it is the morphological features which are used the most, as they are most easily observed, In addition while going rough the new approaches you will realize that data from just one approach may not be sufficient to identify organisms.

Taxonomists try as far as possible to use data from as many approaches as possible for accurate identification. Thus today taxonomy is usually called biosystematics or systematic or evolutionary taxonomy or neotaxonomy as it tends to place organisms which share a common ancestor (monophyletic ancestory) within the same group. Inference of ancestory is based upon similarity and difference among organisms. These differences and similarities are not limited to morphological traits alone. They include a wide variety of similarities and differences in behavior, embryological structures, and fine morphological details with the help of electron microscopes, biochemistry, ecology, cytogenetically data and statistical data.

NEW SYSTEMATICS (NEO-SYSTEMATICS, BIO-SYSTEMATICS)

It is a concept of systematics that considers a species to the product of evolution. It takes into consideration all the known characteristics of organisms and all the known evidence from different fields of biology. The concept of new systematics was developed by Sir Julian Huxley in 1940. Nonsystematic is also called biosystematics. Biosystematics is the science through which life forms are discovered. Identified, described, named, classified and catalogued with their diversity, life histories, living habitats, roles in an ecosystem, and spatial and geographical distributions recorded. In essence, it is biosystematics, the science that provides indispensable information to support many fields of research and beneficially applied programs. The important features are:

♦ Species are not isolated. They are related amongst themselves by common descent and differ from them due to the accumulation of different variations.

♦ The main stress is laid upon subspecies and populations instead of species. It has given rise to the concept of population systematics.

♦ Statistical data are used to determine primitiveness or advancement of species.

♦ Morphological definition of species is replaced by biological definition. Besides morphology, biosystematics or new systematics considers traits from cytology, genetics, ecology, biochemistry and physiology. This has led to the origin of many branches of systematics like: Morpho taxonomy (based on morphological traits), Cytotaxonomy (based on cytological on biochemical studies), Chemotaxonomy (based on specific chemicals like secondary metabolites), Numerical taxonomy (using statistical methods in taxonomy) and

Experimental taxonomy (based on experimental determination of genetic interrelationships and effect of environment).

♦ A large number, sometimes thousands of specimens are studied to record variations before deciding the limits of species.

♦ The basic unit in new systematics is population.

♦ The new systematics is scientific and very useful academically as well as economically.

♠ Numerical taxonomy is also called phonetic or Adansonia taxonomy (Adanson, 1763). Turril (1938) used the term Omega (ω) taxonomy for biosystematics or new systematics. His Alpha (α) taxonomy (Turril, 1938) deals with collection and identification of organisms on the basis of gross morphology, a compilation of flora and monographs. Difference between Systematics and New Systematics.

BASICS TO TAXONOMY

Classification means the ordering of organisms into groups. The branch of science that deals with the study of principles and procedures of biological classification are called taxonomy (A.P. de Candolle, 1813). Taxonomy enfolds the following fundamental elements:

♦Identification: Identification is determining the correct place in a system of classification and finding out the correct name of an organism. It is done with the help of keys. It is just like locating a title in the library on the basis of knowledge of its subject, title and name of the author. This is carried out for an organism by determining its similarity with an already known organism. Suppose there are three plants say a, b, c. All represent different species. Another plant, say d resembles b. The recognition of the plant d as identical to the already known plant b is its identification. Identification not only assigns the organisms to a particular group and locate its correct name but also provides information if the organism is new to systematics and requires giving a name.

♦ Nomenclature (L nomen: name; calare: call): It is the science of providing distinct and proper specific names to organisms as per the established universal practices and rules so that they can be easily recognised and differentiated from others.

♦ Classification: Classification is the arrangement of organisms into groups on the basis of their affinities or relationships. It involves the placing of a kind of organisms or a group of different kinds of organisms in particular categories depending upon the system of classification but in conformity with nomenclature system.

NOMENCLATURE

♠ The science of giving names to living beings is called nomenclature. Two types of names are given to the organisms, common and scientific.

COMMON OR VERNACULAR NAMES

♠ The naming of organisms has been started with the appearance of language in human civilisation. Common names are local names, which are given to the animals and plants in a particular language and region of the world by local persons. The vernacular or common names are based on some peculiarity of the organisms. They are brief and easier to pronounce and remember by the residents of an area. They give an immediate idea to the residents as to identify the organisms. Natives become familiar with the names since childhood. Even then the Vernacular names cannot be used by biologists due to the following reasons:
♦ Common names differ from region to region and language to language. An organism may have several names in a given language.

♦ A common name may have different meanings in different areas.

♦ An organism may have several names in a given language.

♦ A single common name is often given to more than one organism.
♦ There is no uniformity in common names.
♦ Certain common names are misleading and insignificant. For example silverfish (Lepisma, an arthropod), cuttlefish (Sepia, a mollusc), Jellyfish (Aurelia, a coelenterate), starfish (Asterias, an echinoderm), etc., create confusion in identifying exactly the desired organism. The common names 'kiss me quick' for Euphorbia Milli, 'widow's tear' for Tradescantia and 'love in mist' for the plant Nigella damascena are simply fantastic and also without significance.
♦ A wrong common name cannot be easily corrected.

SCIENTIFIC OR TECHNICAL NAMES

♠ Organisms must have a scientific name, which is acceptable all over the world. Such naming must be based on agreed principles and criteria.

♠ The scientific names ensure that only one name is given to an organism and description of the organism should help the other people to arrive at the same name in any part of the world. Each kind of organism, representing a species, is given a different name to distinguish it from the other. One has to ensure that such a name has not been used earlier for any other organism. The following have been the practices of providing scientific names to the organisms.

♦ Polynomial nomenclature: It was the first attempt of the scientists to provide scientific names to organisms: Before 1750 (medieval periods), scholars used to add a series of descriptive words to designate a particular species. This can be illustrated with the example of Caryophyllum. The name given was Caryophyllum saxatile folis gramineous umbellate corymbs meaning Caryophyllum growing on rocks having grasslike leaves and umbellate corymb arrangement of flowers. Such long names cannot be easily remembered. These names also varied with a selection of different characters by different taxonomists.
♦ Binomial nomenclature: The scientific names were developed by Linnaeus (Philosophia Botanica, 1751). The standard references recognised for this are Species Plantarum (1753) and tenth edition of Systema Naturae (1758).
The technical names recognised internationally are thus the ones given by Linnaeus in the 10th edition of his book Systema Naturae published in 1758. The system developed by Linnaeus is known as binomial nomenclature. Binomial nomenclature is the system of scientific naming using 'genus' as the first part and 'species' as the second part, e.g., Mangifera indica (mango), Apis mellifera (honey bee), Pisum sativum (garden pea), etc.

TRINOMIAL NOMENCLATURE:

Occasionally, three words are also used for naming an organism, especially the animals. These include generic, specific and sub-species part, for example, the modern man is called Homo sapiens sapiens. Other examples are Gorilla gorilla gorilla, Acacia ni loti ca indicia, Ascaris lumbricoides humans, Corvus splendens insolence (Burmese crow), etc.

RULES OF BINOMIAL NOMENCLATURE

♠ To provide uniformity, and to avoid confusion, 12th International Congress at Leningrad in 1975, laid down certain principles that were published in 1978 in the form of International

Code of Botanical Nomenclature (ICBN) and International Code of Zoological Nomenclature (ICZN). The names of bacteria and viruses are decided by International Code of Bacteriological Nomenclature (ICBacN or ICBN) and International Code of Viral Nomenclature (ICVN). Similarly, there is a separate International Code of Nomenclature of Cultivated Plants (ICNCP). The important rules are:

♦ A scientific name consists of two words, first genus and second species. They should not have less than three letters and more than twelve letters.

♦ A general term for the word identifying the species is the specific descriptor. In zoology, the word identifying the species is called the specific name, and in botany, the specific epithet.

♦ The generic name is always written first, which is a noun having its first letter in capital form. The generic name is always unique for a living organism.

♦ The specific name is written after the generic name, which is an adjective having its all letters in small form. A botanical specific name may begin with a capital letter if it denotes a person or a place, e.g., Pentoxylon Shanii, Tolypella Jwelli, etc. A species can be named only if it is assigned to a genus. The same specific name can be assigned to two genera but two species of the same genus cannot have the same specific name, e.g., Mangifera indica, Holoptalea indica (chilbil). It can be single or compound (e.g., Hibiscus rosa-Sinensis)

♦ The gender of the specific name follows the gender of the generic name, e.g., Mangifera indica, Tamarindus in the discus.

♦ The biological or scientific name is always printed in italics whereas it is underlined when handwritten.

♦ All taxa at ranks above species have a name composed of one word only, a “unit nominal name”.

♦ When used with a common name, the scientific name usually follows in parentheses, e.g. the house sparrow (Passer domesticus).

♦ The scientific name should generally be written in full. The exception to this is when several species from the same genus are being listed or discussed in the same paper or report; in that case the genus is written in full when it is first used, but may then be abbreviated to an initial for successive species name, e.g. Cycas revoluta, C. Rumph ii, C. circinalis, etc. In rare cases, this abbreviated form has spread to more general use; for example, the bacterium

Escherichia coli is often referred to as E. coli, and Tyrannosaurus Rex is better known simply as T. rex, these two both often appearing even where they are not part of any list of species of the same genus.

♦ The abbreviation “sp.” is used when the actual specific name cannot or need not be specified, e.g., Pinus sp. The abbreviation “spp.” (plural) indicates “several species”. These are not italicised or underlined.

♦ The two-word scientific names are generally followed by the name of the discoverer or author in scholarly texts. The author’s name can be a full or abbreviated form (i.e., Mangifera indica L., Homo sapiens Linn., Cycas circinalis Linnaeus) in the Roman script without a comma. Author’s name is not italicised.

♦ The abbreviation “cf” is used when the identification is not confirmed. For example, Corvus cf. splendens indicates a bird similar to the House Crow but not certainly identified as this species.

♦ The scientific names are derived from the Latin language as it is a dead language. When words are used from other languages, they are Latinized with the suitable ending, e.g., Mangifera indica.

♦ The name of categories higher than the rank of the genus is not printed in italic so or underlined when handwritten. Bold letters, however, can be used. e.g., Phanerogams, Spermatophyta, Mammalia, etc.

♦ No names are recognised prior to those used by Linnaeus in 1758 in the 10th edition of Systema Naturae.The names of subfamilies and families should be based on the name of the type genus e.g., family Gramineae is changed to Poaceae, Compositae is changed to Asteraceae, etc.

♦ When a species is transferred or revised, the name of the original author is retained but in parentheses, e.g., Syzygium cumin (Linn).

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♦ In case an organism has been given more than one name, the earlier legitimate one is recognized to be valid (not prior to 1.5.1753 for plants or 1.8.1758 for animals). This is called the law of priority.

UNIT 3: DIMENSION OF SPECIATION AND TAXONOMIC CHARACTERS

3.1 Objectives
3.2 Introduction
3.3 Dimension of Speciation
3.4 Mechanism of Speciation
3.5 Species Concept
3.5.1 Species
3.6 Theories of Biological Classification
3.7 Taxonomic Characters

3.1 OBJECTIVES

We will study the following point

- Taxonomic Characters
- Dimension of Speciation
- Mechanism of Speciation
- Species Concept

3.2 INTRODUCTION

Speciation is the evolutionary process by which populations evolve to become distinct species. The biologist Orator F. Cook coined the term in 1906 for cladogenesis, the splitting of lineages, as opposed to anagenesis, phyletic evolution within lineages. Charles Darwin was the first to describe the role of natural selection in speciation in his 1859 book On the Origin of Species. He also identified sexual selection as a likely mechanism, but found it problematic. There are four geographic modes of speciation in nature, based on the extent to which speciating populations are isolated from one another: allopatric, peripatric, parapatric, and sympatric. Speciation may also be induced artificially, through animal husbandry, agriculture, or laboratory experiments. Whether genetic drift is a minor or major contributor to speciation is the subject of much ongoing discussion. Rapid sympatric speciation can take place through polyploidy, such as by doubling of chromosome number; the result is progeny

which are immediately reproductively isolated from the parent population. New species can also be created through hybridization followed—if the hybrid is favoured by natural selection by reproductive isolation.

Speciation is the process of formation of a new genetically independent group of organisms, called species, through the course of evolution.

- The process of splitting of genetically homogenous population into two or more populations that undergo genetic differentiation and eventual reproductive isolation is called speciation.
- The entire course of evolution depends upon the origin of new populations (species) that have greater adaptive efficiency than their ancestors.

Speciation occurs in two ways.

1. Transformation of old species into new species over time.
2. Splitting of a single species into several, that is the multiplication of species.

Speciation occurs as a result of several factors which are:

1. **Natural selection**

- As explained by Charles Darwin, different individuals in a species might develop specific distinct characteristics which are advantageous and affect the genetic makeup of the individual.
- Under such conditions, these characteristics will be conserved, and over time, new species might be formed.
- However, in this case, the essential aspect of this factor is that speciation occurs only when a single species splits into several species resulting in the multiplication of species.

2. **Genetic drift**

- Genetic drift is the change in the allele frequencies in a population as a result of "sampling error" while selecting the alleles for the next generation from the gene pool of the current population.

- It has been, however, argued that genetic drift doesn't result in speciation and just results in evolution, that is, change from one species to another, which cannot be considered speciation.

3. **Migration**

- When a certain number of species from a population migrate from one geographical region to another, the species might accumulate characteristics which are different from that of the original population.
- Migration usually results in geographical isolation and ultimately leads to speciation.

4. **Chromosomal Mutations**

- Chromosomal mutations have the potential to serve as (or contribute to) isolating mechanisms, and the locking up and protection of a particularly favorable gene complement through a chromosomal mutation.
- These mutations, when preserved from one generation to another, might result in the formation of new species.

5. **Natural causes**

- Sometimes, natural events imposed by the environment like a river or a mountain range might cause the separation of what once a continuous population is divided into two or smaller populations.
- These events result in geographical isolation of the incipient species followed by reproductive isolation leading to speciation.

6. **Reduction of gene flow**

- Speciation might also occur in the absence of some extrinsic physical barriers.
- There might be a reduced gene flow over a broad geographical range where individuals in the Far East would have zero chance of mating with individuals in the far western end of the range.
- In addition, if there are some selective mechanisms like genetic drift at the opposite ends of the range, the gene frequencies would be altered, and speciation would be ensured.

Classically, speciation has been observed as a three-stage process:

1. Isolation of populations.
2. Divergence in traits of separated populations (e.g. mating system or habitat use).
3. Reproductive isolation of populations that maintains isolation when populations come into contact again (secondary contact).

- Recent research shows that steps one and two may take place simultaneously in the same place, and often the third step does not occur.
- The process of speciation begins with the isolation of subpopulation of a species which could either occur through physical isolation (allotropic speciation) or genetic isolation (sympatric speciation).
- Once the population is separated, a gradual accumulation of small genetic changes results in a subpopulation of a species that eventually accumulate so many changes that the subpopulations become different species.
- Over time, the subpopulation now becomes genetically independent and will continue to diverge by mutation, selection, and genetic drift.
- The genetic differentiation might cause a slight change in the mating dance or even a small change in the shape of the male genitalia or some changes in the habitat or feeding habits of the subpopulation, which results in reproductive isolation.
- Eventually, the genetic differentiation between the subpopulation becomes so high that the formation of hybrids between them would be physiologically, developmentally, or behaviorally impossible even if the modes of the separation were abolished.

TYPES OF SPECIATION/MODES OF SPECIATION

- The classification of the modes or types of speciation is based on how much the geographical separation of the original population contributes to the reduced gene flow and ultimately, the formation of new species.

The modes of speciation are:

- Allopatric speciation is the mode of speciation in which the original population is divided into two by a barrier resulting in reproductive isolation.

- The model for allopatric speciation was presented by Mayr.
- It is based on the concept that new species arise when some physical geographic barrier divides the large population of a species into two or more small populations.
- The individuals of these isolated populations cannot interbreed because of their physical isolation.
- Physical isolation might occur either due to physical barriers like vast expanses of ocean, high mountains, glaciers, deep river valleys, wide rivers or deserts, or a considerable distance due to a larger geographical range.
- Each isolated population starts to adapt to their separated environments while accumulating differences and evolving independently into new species.
- Allopatric speciation can occur even in cases in which the barrier allows some individuals to cross the barrier to mate with the members of the other groups.
- For speciation even to be considered "allopatric," gene flow between the soon-to-be species must be significantly reduced—but it doesn't have to be entirely reduced to zero.

Examples

- The classic example of allopatric speciation is that of Darwin's finches. The divergent populations of finches inhabiting the Galapagos Islands were observed to have differences in features such as body size, color, and beak length or shape. The differences resulted because of the different types of food available in various Islands.
- Another example is of Grand Canyon Squirrels which were separated during the formation of the Grand Canyon and resulted in two different species of squirrels.

PERIPATRIC SPECIATION

- Peripatric speciation is a special condition of allopatric speciation which occurs when the size of the isolated subpopulation is small.
- In this case, in addition to geographic separation, genetic drift also plays an important as genetic drift acts more quickly in small populations.
- The small isolated subpopulation might carry some rare genes which upon reaching the new geographical region become fixed over the course of a few generations as a result of genetic drift.
- As a result, the entire population of the new region ends up having these rare genes.

- Over time, new genetic characters, as well as natural selection, cause the survival of individuals which are better suited to the climate and food of the new region.
- Finally, under the influence of all these factors, new species are formed.
- However, it is very difficult to explain what role genetic drift played in the divergence of the two populations, which makes gathering evidence to support or refute this mode very challenging.

Examples

- The Australian bird PETROICA MULTICOLOUR and LONDON UNDERGROUND MOSQUITO, a variant of the mosquito CULEX PIPIENS, which entered in the London Underground in the 19th century, are the examples of Petripatric speciation.

PARAPATRIC SPECIATION

- Parapatric speciation is a mode of speciation in which there is no extrinsic barrier between the populations but, the large geographic range of the population causes the individuals to mate with the neighboring individuals than with the individuals in a different part of the geographical range.
- In this case, the population is continuous, but the population doesn't mate randomly.
- Here, the genetic variation occurs as a result of reduced gene flow within the population and varying selection pressures across the population's range.
- This occurs in population which is distributed over a large geographical range. Thus, the individuals in the far west region cannot mate with the individuals in the Far East region.
- Through a few generations, new species might be formed within the existing population.

Examples

- The grass species ANTHOXANTHUM ODORATUM where some species living near the mine have become tolerant to heavy metals; however, other plants that don't live around the mines are not tolerant.
- But because the plants are close together, they could fertilize each other and result in a new species.

SYMPATRIC SPECIATION

- Sympatric speciation is the process of the formation of new species from an original population that are not geographically isolated.
- It is based on the establishment of new populations of a species in different ecological niches and the reproductive isolation of founders of the new population from the individuals of the source population.
- Gene flow between daughter and parental population during sympatric speciation is postulated to be inhibited by intrinsic factors, such as chromosomal changes and non-random mating.
- Exploiting a new niche might automatically reduce gene flow with individuals exploiting a different niche.
- This mode of speciation is common in herbivore insects when they begin feeding and mating on a new plant or when a new plant is introduced within the geographical range of the species.
- The gene flow is then reduced between the species that specialize in a particular plant which might ultimately lead to the formation of new species.
- The selection resulting in specialization needs to be really strong for the population to diverge.
- Thus, sympatric speciation is a sporadic event in multicellular organisms or randomly mating populations.

Examples

- Sympatric speciation is observed in apple maggot flies which 200 years ago laid eggs and bred only on hawthorns but now lays eggs on both hawthorns and domestic apples.
- As a result, gene flow between parts of the population that mate on different types of fruit is reduced, and in fewer than 200 years, some genetic differences between these two groups of flies have evolved.

3.3 DIMENSION OF SPECIATION

All forms of natural speciation have taken place over the course of evolution; however, debate persists as to the relative importance of each mechanism in driving biodiversity.

One example of natural speciation is the diversity of the three-spined stickleback, a marine fish that, after the last glacial period, has undergone speciation into new freshwater colonies in isolated lakes and streams. Over an estimated 10,000 generations, the sticklebacks show structural differences that are greater than those seen between different genera of fish including variations in fins, changes in the number or size of their bony plates, variable jaw structure, and color differences.

ALLOPATRIC

Allopatric (from the ancient Greek allos, "other" + patrā, "fatherland") speciation, a population splits into two geographically isolated populations (for example, by habitat fragmentation due to geographical change such as mountain formation). The isolated populations then undergo genotypic or phenotypic divergence as: (a) they become subjected to dissimilar selective pressures; (b) they independently undergo genetic drift; (c) different mutations arise in the two populations. When the populations come back into contact, they have evolved such that they are reproductively isolated and are no longer capable of exchanging genes. Island genetics is the term associated with the tendency of small, isolated genetic pools to produce unusual traits. Examples include insular dwarfism and the radical changes among certain famous island chains, for example on Komodo. The Galápagos Islands are particularly famous for their influence on Charles Darwin. During his five weeks there he heard that Galápagos tortoises could be identified by island, and noticed that finches differed from one island to another, but it was only nine months later that he reflected that such facts could show that species were changeable. When he returned to England, his speculation on evolution deepened after experts informed him that these were separate species, not just varieties, and famously that other differing Galápagos birds were all species of finches. Though the finches were less important for Darwin, more recent research has shown the birds now known as Darwin's finches to be a classic case of adaptive evolutionary radiation.

PERIPATRIC

In peripatric speciation, a subform of allopatric speciation, new species are formed in isolated, smaller peripheral populations that are prevented from exchanging genes with the main population. It is related to the concept of a founder effect, since small populations often undergo bottlenecks. Genetic drift is often proposed to play a significant role in peripatric speciation.

Case studies include Mayr's investigation of bird fauna; the Australian bird Petroica multicolor; and reproductive isolation in populations of Drosophila subject to population bottlenecking.

In parapatric speciation, there is only partial separation of the zones of two diverging populations afforded by geography; individuals of each species may come in contact or cross habitats from time to time, but reduced fitness of the heterozygote leads to selection for behaviours or mechanisms that prevent their interbreeding. Parapatric speciation is modelled on continuous variation within a "single," connected habitat acting as a source of natural selection rather than the effects of isolation of habitats produced in peripatric and allopatric speciation.[32]

Parapatric speciation may be associated with differential landscape-dependent selection. Even if there is a gene flow between two populations, strong differential selection may impede assimilation and different species may eventually develop. Habitat differences may be more important in the development of reproductive isolation than the isolation time. Caucasian rock lizards Darevskia *rudis*, *D. valentini* and *D. portschinskii* all hybridize with each other in their hybrid zone; however, hybridization is stronger between *D. portschinskii* and *D. rudis*, which separated earlier but live in similar habitats than between *D. valentini* and two other species, which separated later but live in climatically different habitats.

Ecologists refer to parapatric and peripatric speciation in terms of ecological niches. A niche must be available in order for a new species to be successful. Ring species such as Larus gulls have been claimed to illustrate speciation in progress, though the situation may be more complex. The grass Anthoxanthum odoratum may be starting parapatric speciation in areas of mine contamination.

SYMPATRIC

Sympatric speciation is the formation of two or more descendant species from a single ancestral species all occupying the same geographic location.

Often-cited examples of sympatric speciation are found in insects that become dependent on different host plants in the same area.

The best known example of sympatric speciation is that of the cichlids of East Africa inhabiting the Rift Valley lakes, particularly Lake Victoria, Lake Malawi and Lake Tanganyika. There are over 800 described species, and according to estimates, there could be well over 1,600 species in the region. Their evolution is cited as an example of both natural and sexual selection. A 2008 study suggests that sympatric speciation has occurred in Tennessee cave salamanders. Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

Budding speciation has been proposed as a particular form of sympatric speciation, whereby small groups of individuals become progressively more isolated from the ancestral stock by breeding preferentially with one another. This type of speciation would be driven by the conjunction of various advantages of inbreeding such as the expression of advantageous recessive phenotypes, reducing the recombination load, and reducing the cost of sex.

The hawthorn fly (Rhagoletis pomonella), also known as the apple maggot fly, appears to be undergoing sympatric speciation. Different populations of hawthorn fly feed on different fruits. A distinct population emerged in North America in the 19th century sometime after apples, a non-native species, were introduced. This apple-feeding population normally feeds only on apples and not on the historically preferred fruit of hawthorns. The current hawthorn feeding population does not normally feed on apples. Some evidence, such as that six out of thirteen allozyme loci are different, that hawthorn flies mature later in the season and take longer to mature than apple flies; and that there is little evidence of interbreeding (researchers have documented a 4–6% hybridization rate) suggests that sympatric speciation is occurring.

METHODS OF SELECTION

REINFORCEMENT

Reinforcement, sometimes referred to as the Wallace effect, is the process by which natural selection increases reproductive isolation. It may occur after two populations of the same species are separated and then come back into contact. If their reproductive isolation was complete, then they will have already developed into two separate incompatible species. If their reproductive isolation is incomplete, then further mating between the populations will produce hybrids, which may or may not be fertile. If the hybrids are infertile, or fertile but less fit than their ancestors, then there will be further reproductive isolation and speciation has essentially occurred (e.g., as in horses and donkeys).

The reasoning behind this is that if the parents of the hybrid offspring each have naturally selected traits for their own certain environments, the hybrid offspring will bear traits from both, therefore would not fit either ecological niche as well as either parent. The low fitness of the hybrids would cause selection to favor assortative mating, which would control hybridization. This is sometimes called the Wallace effect after the evolutionary biologist Alfred Russel Wallace who suggested in the late 19th century that it might be an important factor in speciation. Conversely, if the hybrid offspring are more fit than their ancestors, then the populations will merge back into the same species within the area they are in contact.

Reinforcement favoring reproductive isolation is required for both parapatric and sympatric speciation. Without reinforcement, the geographic area of contact between different forms of the same species, called their "hybrid zone," will not develop into a boundary between the different species. Hybrid zones are regions where diverged populations meet and interbreed. Hybrid offspring are very common in these regions, which are usually created by diverged species coming into secondary contact. Without reinforcement, the two species would have uncontrollable inbreeding. Reinforcement may be induced in artificial selection experiments as described below.

ECOLOGICAL

Ecological selection is "the interaction of individuals with their environment during resource acquisition". Natural selection is inherently involved in the process of speciation, whereby,

"under ecological speciation, populations in different environments, or populations exploiting different resources, experience contrasting natural selection pressures on the traits that directly or indirectly bring about the evolution of reproductive isolation". Evidence for the role ecology plays in the process of speciation exists. Studies of stickleback populations support ecologically-linked speciation arising as a by-product, alongside numerous studies of parallel speciation, where isolation evolves between independent populations of species adapting to contrasting environments than between independent populations adapting to similar environments. Ecological speciation occurs with much of the evidence, "...accumulated from top-down studies of adaptation and reproductive isolation".

SEXUAL SELECTION

It is widely appreciated that sexual selection could drive speciation in many clades, independently of natural selection. However the term "speciation", in this context, tends to be used in two different, but not mutually exclusive senses. The first and most commonly used sense refers to the "birth" of new species. That is, the splitting of an existing species into two separate species, or the budding off of a new species from a parent species, both driven by a biological "fashion fad" (a preference for a feature, or features, in one or both sexes, that do not necessarily have any adaptive qualities). In the second sense, "speciation" refers to the wide-spread tendency of sexual creatures to be grouped into clearly defined species, rather than forming a continuum of phenotypes both in time and space – which would be the more obvious or logical consequence of natural selection. This was indeed recognized by Darwin as problematic, and included in his On the Origin of Species (1859), under the heading "Difficulties with the Theory". There are several suggestions as to how mate choice might play a significant role in resolving Darwin's dilemma. If speciation takes place in the absence of natural selection, it might be referred to as nonecological speciation.

ARTIFICIAL SPECIATION

New species have been created by animal husbandry, but the dates and methods of the initiation of such species are not clear. Often, the domestic counterpart of the wild ancestor can still interbreed and produce fertile offspring as in the case of domestic cattle, that can be considered the same species as several varieties of wild ox, gaur, yak, etc., or domestic sheep that can interbreed with the mouflon.

The best-documented creations of new species in the laboratory were performed in the late 1980s. William R. Rice and George W. Salt bred Drosophila melanogasterfruit flies using a maze with three different choices of habitat such as light/dark and wet/dry. Each generation was placed into the maze, and the groups of flies that came out of two of the eight exits were set apart to breed with each other in their respective groups. After thirty-five generations, the two groups and their offspring were isolated reproductively because of their strong habitat preferences: they mated only within the areas they preferred, and so did not mate with flies that preferred the other areas. The history of such attempts is described by Rice and Elen E. Hostert (1993). Diane Dodd used a laboratory experiment to show how reproductive isolation can develop in Drosophila pseudoobscura fruit flies after several generations by placing them in different media, starch- and maltose-based media.

Alternatively, these observations are consistent with the notion that sexual creatures are inherently reluctant to mate with individuals whose appearance or behavior is different from the norm. The risk that such deviations are due to heritable maladaptations is very high. Thus, if a sexual creature, unable to predict natural selection's future direction, is conditioned to produce the fittest offspring possible, it will avoid mates with unusual habits or features. Sexual creatures will then inevitably tend to group themselves into reproductively isolated species.

GENETICS

Few speciation genes have been found. They usually involve the reinforcement process of late stages of speciation. In 2008, a speciation gene causing reproductive isolation was reported. It causes hybrid sterility between related subspecies. The order of speciation of three groups from a common ancestor may be unclear or unknown; a collection of three such species is referred to as a "trichotomy."

Speciation via polyploidy

Polyploidy is a mechanism that has caused many rapid speciation events in sympatry because offspring of, for example, tetrapod x diploid matings often result in triploid sterile progeny. However, among plants, not all polyploids are reproductively isolated from their parents, and gene flow may still occur, such as through triploid hybrid x diploid matings that produce

tetraploids, or matings between meiotically unreduced gametes from diploids and gametes from tetraploids (see also hybrid speciation).

It has been suggested that many of the existing plant and most animal species have undergone an event of polyploidization in their evolutionary history. Reproduction of successful polyploid species is sometimes asexual, by parthenogenesis or apomixis, as for unknown reasons many asexual organisms are polyploid. Rare instances of polyploid mammals are known, but most often result in prenatal death.

HYBRID SPECIATION

Hybridization between two different species sometimes leads to a distinct phenotype. This phenotype can also be fitter than the parental lineage and as such natural selection may then favor these individuals. Eventually, if reproductive isolation is achieved, it may lead to a separate species. However, reproductive isolation between hybrids and their parents is particularly difficult to achieve and thus hybrid speciation is considered an extremely rare event. The Mariana mallard is thought to have arisen from hybrid speciation.

Hybridization is an important means of speciation in plants, since polyploidy (having more than two copies of each chromosome) is tolerated in plants more readily than in animals. Polyploidy is important in hybrids as it allows reproduction, with the two different sets of chromosomes each being able to pair with an identical partner during meiosis. Polyploids also have more genetic diversity, which allows them to avoid inbreeding depression in small populations.

Hybridization without change in chromosome number is called homoploid hybrid speciation. It is considered very rare but has been shown in Heliconiusbutterflies and sunflowers. Polyploid speciation, which involves changes in chromosome number, is a more common phenomenon, especially in plant species.

GENE TRANSPOSITION

Theodosius Dobzhansky, who studied fruit flies in the early days of genetic research in 1930s, speculated that parts of chromosomes that switch from one location to another might cause a species to split into two different species. He mapped out how it might be possible for sections of chromosomes to relocate themselves in a genome. Those mobile sections can

cause sterility in inter-species hybrids, which can act as a speciation pressure. In theory, his idea was sound, but scientists long debated whether it actually happened in nature. Eventually a competing theory involving the gradual accumulation of mutations was shown to occur in nature so often that geneticists largely dismissed the moving gene hypothesis. However, 2006 research shows that jumping of a gene from one chromosome to another can contribute to the birth of new species. This validates the reproductive isolation mechanism, a key component of speciation.

RATES

There is debate as to the rate at which speciation events occur over geologic time. While some evolutionary biologists claim that speciation events have remained relatively constant and gradual over time (known as "Phyletic gradualism" – see diagram), some palaeontologists such as Niles Eldredge and Stephen Jay Gould have argued that species usually remain unchanged over long stretches of time, and that speciation occurs only over relatively brief intervals, a view known as punctuated equilibrium. (See diagram, and Darwin's dilemma.)

PUNCTUATED EVOLUTION

Evolution can be extremely rapid, as shown in the creation of domesticated animals and plants in a very short geological space of time, spanning only a few tens of thousands of years. Maize (Zea mays), for instance, was created in Mexico in only a few thousand years, starting about 7,000 to 12,000 years ago. This raises the question of why the long term rate of evolution is far slower than is theoretically possible.

Evolution is imposed on species or groups. It is not planned or striven for in some Lamarckist way. The mutation on which the process depends are random events, and, except for the "silent mutations" which do not affect the functionality or appearance of the carrier, are thus usually disadvantageous, and their chance of proving to be useful in the future is vanishingly small. Therefore, while a species or group might benefit from being able to adapt to a new environment by accumulating a wide range of genetic variation, this is to the detriment of the individuals who have to carry these mutations until a small, unpredictable minority of them ultimately contributes to such an adaptation. Thus, the capability to evolve would require

group selection, a concept discredited by (for example) George C. Williams, John Maynard Smith and Richard Dawkins as selectively disadvantageous to the individual.

The resolution to Darwin's second dilemma might thus come about as follows:

If sexual individuals are disadvantaged by passing mutations on to their offspring, they will avoid mutant mates with strange or unusual characteristics. Mutations that affect the external appearance of their carriers will then rarely be passed on to the next and subsequent generations. They would therefore seldom be tested by natural selection. Evolution is, therefore, effectively halted or slowed down considerably. The only mutations that can accumulate in a population, on this punctuated equilibrium view, are ones that have no noticeable effect on the outward appearance and functionality of their bearers (i.e., they are "silent" or "neutral mutations," which can be, and are, used to trace the relatedness and age of populations and species.[15][94]) This argument implies that evolution can only occur if mutant mates cannot be avoided, as a result of a severe scarcity of potential mates. This is most likely to occur in small, isolated communities. These occur most commonly on small islands, in remote valleys, lakes, river systems, or caves, or during the aftermath of a mass extinction.[94] Under these circumstances, not only is the choice of mates severely restricted but population bottlenecks, founder effects, genetic drift and inbreeding cause rapid, random changes in the isolated population's genetic composition. Furthermore, hybridization with a related species trapped in the same isolate might introduce additional genetic changes. If an isolated population such as this survives its genetic upheavals, and subsequently expands into an unoccupied niche, or into a niche in which it has an advantage over its competitors, a new species, or subspecies, will have come in being. In geological terms, this will be an abrupt event. A resumption of avoiding mutant mates will thereafter result, once again, in evolutionary stagnation.

In apparent confirmation of this punctuated equilibrium view of evolution, the fossil record of an evolutionary progression typically consists of species that suddenly appear, and ultimately disappear, hundreds of thousands or millions of years later, without any change in external appearance. Graphically, these fossil species are represented by lines parallel with the time axis, whose lengths depict how long each of them existed. The fact that the lines remain parallel with the time axis illustrates the unchanging appearance of each of the fossil species depicted on the graph. During each species' existence new species appear at random intervals, each also lasting many hundreds of thousands of years before disappearing without a change

in appearance. The exact relatedness of these concurrent species is generally impossible to determine. This is illustrated in the diagram depicting the distribution of hominin species through time since the hominins separated from the line that led to the evolution of our closest living primate relatives, the chimpanzees.

3.4 MECHANISM OF SPECIATION

How does a single species give rise to two or more different species? This concept, called speciation, requires that a single population of organisms divide into two or more populations that no longer interbreed. Without interbreeding, there is no gene flow between the populations, and these populations may then evolve separately into distinct species. There are many definitions for what a species is, but we will begin with biologist Ernst Mayr's 1940 definition, in which he states that species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups. We will extend this to say that if two individuals of different species do mate and produce offspring, that those offspring would not be fertile.

In the accompanying animation, we examine two mechanisms of establishing a barrier to gene flow, leading to speciation. Speciation occurs when the gene pool of a population is somehow reproductively isolated from other populations of the parent species and no longer has gene flow occurred between them.

On the basis of period taken in speciation, there are two types of mechanisms of speciation:

A. Gradual speciation.

B. Instantaneous or abrupt speciation.

***A. Gradual speciation**:*

It is the gradual divergence of populations due to the accumulation of variations over a long period of time.

Gradual speciation occurs in two ways:

1. Geographic or allopatric speciation (Gr. alio = other; patria = naHve land):

When an original population becomes separated spatially because of geographic barriers, into two or more groups, these are termed as allopatric populations.

The geographical barriers (e.g. a creeping glacier, a land bridge (e.g. Isthmus of Panama) or ocean or mountain or migration of some individuals to a new habitat which is geographical isolated from original range) impose the restriction on the gene flow between populations, so that the latter become reproductively isolated.

These groups become more and more different and finally become different species, called allopatric species, e.g. Darwin's finches of Galapagos Islands are geographically isolated from related birds of South American mainland; and adaptive radiations in the Australian marsupials to form new species.

2. Sympatric speciation (Gr. sym = together; patria = native land):

It occurs within same geographical area and' within original population but two elementary species occupy different etiological or ecological niches and are reproductively isolated by the development of biological isolating barriers.

Differences between Allopatric and Sympatric speciation.

Allopatric speciation	**Sympatric speciation**
1. In this, subpopulations are separated by certain geographical barriers. 2. It occurs in different populations. 3. These are geographically isolated. 4. Darwin's finches on Galapagos islands.	1. In this, subpopulations occur in same geographical area but in different ecological nitches. 2. It occurs within original population. 3. These are ecologically or ethologically isolated. 4. Pig frog and Gopher frog occur in different habitats.

B. Abrupt of instantaneous speciation:

It is defined as the sudden development of new species which is reproductively and ecologically isolated from the parental species. This mechanism operates through individuals and thus, not a population phenomenon.

It may occur by:

1. Mutations:

Mutations are large, sudden and inheritable changes while individuals with mutations are called mutants. Mutations are called fountain head of variations as these form the main types of sources of variations.

Significance:

Such mutations can produce sibling species which are morphologically similar but ecologically and reproductively isolated. For example, the production of two sibling species of Drosophila pseudo-obscura and D. persimilis.

2. Hybridization and Polyploidy:

Hybridization involves the interbreeding of two genetically different – individuals of two same or different species to produce hybrids while polyploidy means presence of more than two sets of chromosomes.

Occasionally, the interspecific hybrids are produced naturally or artificially. Such hybrids are, however, sterile due to incompatibility between the chromosomes of two different species and their failure to pair in meiosis.

But the doubling of chromosomes may produce fertile offsprings. Doubling of chromosome number allows normal meiosis and formation of normal but diploid gametes so hybridization followed by polyploidy can lead to the formation of new species very rapidly. This results in the production of new species.

3.5 SPECIES CONCEPT

The following points highlight the four important groups of species concept. The groups are:

1. Typological Species Concept

2. Nominalist Species Concept

3. Evolutionary Species Concept

4. Biological Species Concept.

TYPOLOGICAL SPECIES CONCEPT:

This concept says that the observed diversity of the universe reflects the existence of a limited number of underlying "universals" or types. Individuals are considered to be merely expressions of the same type. When two individuals or groups of individuals have sufficiently different characters then only they should be considered as different species.

Variation results in the revealing of characters which are already present but not expressed in each species. Thus, variation according to the typological species concept is considered to be an irrelevant phenomenon.

This concept dates back 2,300 years to the philosophies of Plato and Aristotle, and was the species concept of Linnaeus and his followers. Species was supposed to be a fixed or static unit which did not change and, as such, existed permanently and forever.

Since this philosophical tradition is sometimes referred to as essentialism, the typological definition is also sometimes called the essentialist species concept. The species can be recognized by their essential natures or essential characters which are expressed in accordance with their morphology.

It is, therefore, also called the morphological species concept. Taxonomists almost unanimously accepted the essentialist species concept up to the early post-Linnaean period.

It thus includes four postulates:

(i) Species are similar individuals sharing the same essence.

(ii) Each species is separated from all others by a sharp discontinuity.

(iii) Each species is completely constant through time.

(iv) Strict limits are present to the possible variation within any one species.

Two practical reasons exist for the present universal rejection of this concept:

1. Individuals are frequently found in nature that are clearly conspecific with other individuals in spite of striking differences in structure owing to sexual dimorphism, age differences, polymorphism and other terms of individual variation. These were often described originally as different species.

For example:

(i) The male and female of river duck, the mallard, were originally placed under separate species. The males were described as Anas boscas and the females as Anas platyrhynchos.

(ii) In many groups of birds (humming bird, pea-hen etc.) females differ more from the males of their own species than from the females of other related species.

(iii) Larval stages of several chordates and invertebrates are markedly different from their parents or adult stage and, thus, were very often considered as separate species.

(iv) In case of the deep sea fishes the males are dwarf and attached to the body of the females. So they were considered as separate species.

Thus, in the above cases, they should be deprived of their separate species status, regardless of their degree of morphological differences, as soon as they are found to be numbers of the same breeding population. Different phases that belong to the same population cannot be considered as different species.

2. Sibling species differ hardly at all morphologically, yet are good biological species. Degree of difference is not the decisive criterion in the ranking of taxa as species. The typological species concept is still defended by a few writers.

In situations where there is a lack of biological information, a taxonomist may be forced to recognize a species provisionally on the basis of morphological evidences, but such species are subject to later reconsideration.

NOMINALISTIC SPECIES CONCEPT:

Nominalistic species concept is that of Occam and his followers, who believed that nature produces individuals only. Species are man's own creation and have no actual existence in nature. They are mental concepts and nothing more. Species have been invented so that we may refer to great numbers of individuals collectively. This concept was popular in France during the 18th century.

The drawbacks of this concept are:

(i) No naturalist whether a primitive native or a trained population geneticist – can agree that species are man-made, when it is an established fact that they are the products of evolution.

(ii) Nominalists misinterpreted the relation between similarity and relationship. The members of any species are not grouped together as they are similar (as claimed by these workers), rather they are similar to each other because of common heritage. It is just like when two brothers are identical twins not due to their similarity but rather due to both being derived from a single zygote.

EVOLUTIONARY SPECIES CONCEPT:

The shortcomings of Biological species concept (in uniparental organisms where interbreeding fails), had led Meglitsch (1954), Simpson (1961), Grant (1971) and other authors – particularly paleontologists – in formulating the evolutionary species concept.

Simpson (1961) defined it as "an evolutionary species is a lineage (an ancestral- descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies". Willey (1981), on the other hand, believed that each species is an internally similar part of a phylogenetic tree.

The drawbacks of this concept are:

(i) This definition is of a phyletic lineage and not of a species. It side-stepped the crucial role of why phyletic lines do not interbreed with each other.

(ii) This concept ignores the core of the species problem as to the causation and maintenance of discontinuities between contemporary species.

(iii) This concept has failed to solve the problem of how to deal with the relationship of descendant populations in a single lineage.

BIOLOGICAL SPECIES CONCEPT:

The biological species concept is also known as the Newer Species Concept, because it was accepted in the latter half of the nineteenth century after Darwin's "Origin of Species" was published (in 1859) and also due to the fact that organic evolution was established. It was after 1750 that an entirely new species concept began to emerge. But it was in 1905 that K. Jordan first clearly formulated the concept in all of its consequences. This concept combined the thoughts of the typological and nominalistic concepts by stating that the species have independent reality and are typified by the statistics of populations of individuals. It, however, differs from both by stressing the populational aspect and genetic cohesion of the species and also by pointing out that species receives its reality from the historically evolved, shared information content of its gene pool.

Thus, the members of a species show the following properties:

(i) A reproductive community:

The member of an animal species recognizes each other as potential mates and seeks each other for the purpose of reproduction.

(ii) An ecological unit:

The species members form an ecological unit which, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment.

(iii) A genetic unit:

The species consists of a large, inter-communicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time. These three properties raise the species above the typological interpretation of a "class of objects". Thus, from this theoretical species concept, the species definition which results is — A species is a group of interbreeding natural population that is reproductively isolated from other such groups. This species concept is called biological not because it deals with biological taxa, but because the definition itself is biological. It utilizes criteria that are meaningless as far as the inanimate world is concerned. Biologically, a species is a potential gene pool. It is a Mendelian population which has its own devices, that is, isolating mechanisms which protect it against harmful gene flow from other gene pools. Gene of the same gene pool forms harmonious combinations because they have become co-adopted by natural selection. Mixing the genes of two different species lead to high frequency of disharmonious gene combinations. Mechanisms that prevent this are favoured by selection. Thus, the word species in biology is a relational term. 'A' is a species in relation to 'B' and 'C' because it is reproductively isolated from them. Since evolution is a regular process, the species is an arbitrary division of the continuous and ever-changing series of individuals in nature. Therefore, species is dynamic and multidimensional in nature. The biological species concept has been able to solve the paradox caused by the conflict between the fixity of species of the naturalist and the fluidity of the species of the evolutionist. It was this conflict that made Linnaeus deny evolution and Darwin the reality of species.

The biological species concept combines the discreteness of the local species at a given time with an evolutionary potential for continuing change. The biological species concept has its importance in the fact that it is employed in the largest number of biological disciplines — ecology, physiology, behaviour biology etc. Intraspecific categories designate groupings of population's within species. Normally, the species is the lowest category used in routine taxonomy.

3.5.1 SPECIES

1. Morphological Species:

This is the traditional concept of species. It was originally introduced by Carolus Linnaeus in his Systema Naturae in 1758. According to this concept, a population group of morphologically distinct organisms constitutes a species.

The main objections to this concept are that it does not take into consideration:

(i) The range of variation in size, colour, form & weight.

(ii) The genetic diversity

(iii) The common origin of related species and

(iv) The change of species in time.

Morphological species concept does not take into account of pronounced sexual dimorphism exhibited by different organisms. For example, the males and females of river duck, the mallard, were originally placed under separate species. The males were described as Anas boschas and females as A. platyrhyechos.

In many other birds like birds of paradise, humming birds, wood warblers etc. females differ more from the males of their own species than from the females of other related species. In many deep-sea angler fishes of the family Ceratioidei, the males are much smaller in size than females, live as parasitic forms upon them. Such dwarf males, originally mistaken as separate species, attach themselves by the mouth of the female and feed up their body fluids.

Insects and lower invertebrates like rotifers, echiuroids like Bonellia exhibit more pronounced morphological differences in the two sexes. Larval stages of several vertebrates and invertebrates are so markedly different from their parents that they were very often placed in separate species.

2. GENETIC SPECIES:

According to Lotsy (1918) a species is a group of genetically identical individuals. This view was supported by some geneticists. But this definition of species is incorrect because even the

off-springs of same parents have different genetic constitution. Only identical twins are genetically similar.

3. BIOLOGICAL SPECIES:

This is the modern concept of species proposed and developed by Dobzhansky in 1937 and Mayr in 1942. According to Dobzhansky mendelian population sharing a common gene pool constitute a species. The most uptodate and convincing definition of species has been given by Mayr (1942) to his book "Systematics and the origin of species". According to him, species are the groups of actually or potentially interbreeding natural populations that are reproductively isolated from each such groups.

The general characters of animal species may be summarized as follows:

1. Each species possesses a common gene pool.

2. Each species is in a process of continually adjusting to its environment.

3. Each species fills an ecological niche not exactly utilized by another species.

4. Each species possesses a constellation of isolating mechanisms that indirectly or directly prevent exchange of genes with related species.

5. Each species has the capacity to give rise to new species.

Subspecies and varieties:

Subspecies is an aggregate of local breeding populations of a given species which has become recognizably different from another population of the same species. A subspecies usually differ from other similar breeding groups of the same species both taxonomically and with respect to certain gene pool characteristics.

The subspecies name is written immediately after species name. So the whole constitute a trinominal.

The term variety was used to describe the non-genetic variants of phenotype caused by the climatic effects. But now the term subspecies replaces the term variety.

Clines:

The term ‘cline’ was introduced by Huxley (1939). It refers to a gradient (decrease or increase) within a continuous population. The regular or continuous variations occur for genotypes (genocline) or phenotypes (phenocline).

One of the best examples of clinal gradation is exhibited by the meadow frog of North America, Rana pipens. It is found throughout the Paire grass land and includes a number of temperature adapted races, which exhibit an orderly variability and adaptability. When the population of North and South extremes is compared the differences are pronounced, yet between the two extremes, there is no break in variation.

Demes:

The term ‘Deme’ was introduced by Gilmour and Gregor in 1939. A deme is a community of potentially interbreeding individuals at a given locality which share a single gene pool. The term deme is always used with a prefix which characterizes the deme more precisely.

1. Topedeme – a group of individuals existing in a certain geographic region.

2. Ecodeme – a group of individuals associated with a specific habit

3. Phenodeme – a deme differing phenotypically from others.

4. Genodeme – a deme differing from others in genotype.

5. Plastodeme – a deme differing phenotypically from others owing to the effect of environment.

Sibling species:

Mayr (1952) has used the term sibling species for the sympatric populations that are morphologically similar if not identical, but are reproductively isolated.

Sibling species occur in almost all animal groups. But they are more common in insects. A best studied example is the genus Drosophila. Drosophila pseudoobscura and D. persimilis

are so identical in their morphology that these were described as two races of the same species (race A and race B) by Lancefield (1924).

The salivary gland chromosomes of both these differ, in the arrangement of genes and also the banding patterns. Morphological differences also exist in the sex comb, male genitalia and relative wing size. These two races of flies coexist in nature over a wide area without natural hybridization.

Artificial crosses between race A and race B produce F1 hybrids, of which only females are fertile and the males are sterile. Lancefield found that sterility is due to the differences in the Y- chromosome. In race A, Y chromosome is sub-metacentric and in race B, Y is a metacentric.

With these observations, these biological races are now established as two distinct species and are described as 'Sibling species'. In addition to morphological and chromosomal differences, these two species exhibit differences in ecological, physiological and sexual behaviors.

Monotypic and polytypic species:

Species containing only a single subspecies are called 'monotypic' while those containing more than one species are termed 'polytypic'.

3.6 THEORIES OF BIOLOGICAL CLASSIFICATION

Theories of Taxonomy

A theory of taxonomy establishes the principles that we use to recognize and to rank taxonomic groups. There are two currently popular theories of taxonomy, (1) traditional evolutionary taxonomy and (2) phylogenetic systematics (cladistics). Both are based on evolutionary principles. We will see, however, that these two theories differ on how evolutionary principles are used. These differences have important implications for how we use taxonomy to study the evolutionary process. The relationship between a taxonomic group and a phylogenetic tree or cladogram is important for both of these theories. This relationship can take one of three forms: monophyly, paraphyly, or polyphyly. A taxon is monophyletic if it includes the most recent common ancestor of the group and all descendants of that ancestor. A taxon is paraphyletic if it includes the most recent common ancestor of all members of a group and some but not all of the descendants of that ancestor. A taxon is polyphyletic if it does not include the most recent common ancestor of all members of a group; this condition requires that the group has had at least two separate evolutionary origins, usually requiring independent evolutionary acquisition of similar. Both evolutionary and cladistics taxonomy accept monophyletic groups and reject polyphyletic groups in their classifications. They differ on the acceptance of paraphyletic groups, however, and this difference has important evolutionary implications.

Traditional Evolutionary Taxonomy

Traditional evolutionary taxonomy incorporates two different evolutionary principles for recognizing and ranking higher taxa: (1) common descent and (2) amount of adaptive evolutionary change, as shown on a phylogenetic tree. Evolutionary taxa must have a single evolutionary origin, and must show unique adaptive features.
The mammalian paleontologist George Gaylord Simpson (Figure 10-5) was highly influential in developing and formalizing the procedures of evolutionary taxonomy. According to Simpson, a particular branch on the evolutionary tree is given the status of a higher taxon if it represents a distinct adaptive zone. Simpson describes an adaptive zone as “a characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is led.” By entering a new adaptive zone through a fundamental change in

organismal structure and behavior, an evolving population can use environmental resources in a completely new way. A taxon that comprises a distinct adaptive zone is termed a grade. Simpson gives the example of penguins as a distinct adaptive zone within birds. The lineage immediately ancestral to all penguins underwent fundamental changes in the form of the body and wings to permit a switch from aerial to aquatic locomotion. Aquatic birds that can fly both in the air and underwater are somewhat intermediate in habitat, morphology, and behavior between aerial and aquatic adaptive zones. Nonetheless, the obvious modifications of the wings and body of penguins for swimming represent a new grade of organization. Penguins are therefore recognized as a distinct taxon within the birds, the family Spheniscidae.

PHYLOGENETIC SYSTEMATICS/CLADISTICS

A second and stronger challenge to evolutionary taxonomy is one known as **phylogenetic systematics** or **cladistics**. As the first name implies, this approach emphasizes the criterion of common descent and, as the second name implies, it is based on the cladogram of the group being classified. This approach to taxonomy was first proposed in 1950 by the German entomologist, Willi Hennig (Figure 10-8) and therefore is sometimes called "Hennigian systematics." All taxa recognized by Hennig's cladistic system must be monophyletic. We saw how evolutionary taxonomists' recognition of the primate families Hominidae and Pongidae distorts genealogical relationships to emphasize adaptive uniqueness of the Hominidae. Because the most recent common ancestor of the paraphyletic family Pongidae is also an ancestor of the Hominidae, recognition of the Pongidae is incompatible with cladistic taxonomy. To avoid paraphyly, cladistic taxonomists have discontinued use of the traditional family Pongidae, placing chimpanzees, gorillas, and orangutans with humans in the family Hominidae. We adopt the cladistic classification in many sections.

The disagreement on the validity of paraphyletic groups may seem trivial at first, but its important consequences become clear when we discuss evolution. For example, claims that amphibians evolved from bony fish, that birds evolved from reptiles, or that humans evolved from apes may be made by an evolutionary taxonomist but are meaningless to a cladist. We simply by these statements that a descendant group (amphibians, birds, or humans) evolved from part of an ancestral group (bony fish, reptiles, and apes, respectively) to which the descendant does not belong. This usage automatically makes the ancestral group

paraphyletic, and indeed bony fish, reptiles, and apes as traditionally recognized are paraphyletic groups. How are such paraphyletic groups recognized? Do they share distinguishing features that are not shared by the descendant group?

Paraphyletic groups are usually defined in a negative manner. They are distinguished only by features absent from a particular descendant group, because any traits that they share from their common ancestry are present also in the excluded descendants (unless secondarily lost). For example, apes are those "higher" primates that are not humans. Likewise, fish are those vertebrates that lack the distinguishing characteristics of tetrapod's (amphibians and amniotes). What does it mean then to say that humans evolved from apes? To the evolutionary taxonomist, apes and humans are different adaptive zones or grades of organization; to say that humans evolved from apes states that bipedal, tailless organisms of large brain capacity evolved from arboreal, tailed organisms of smaller brain capacity. To the cladist, however, the statement that humans evolved from apes says essentially that humans evolved from something that they are not, a trivial statement that contains no useful information. To the cladist, any statement that a particular monophyletic group descends from a paraphyletic one is nothing more than a claim that the descendant group evolved from something that it is not. Extinct ancestral groups are always paraphyletic because they exclude a descendant that shares their most recent common ancestor. Although many such groups have been recognized by evolutionary taxonomists, none are recognized by cladists.

Zoologists often construct paraphyletic groups because they are interested in a terminal, monophyletic group (such as humans), and they want to ask questions about its ancestry. It is often convenient to lump together organisms whose features are considered approximately equally distant from the group of interest and to ignore their own unique features. It is significant in this regard those humans have never been placed in a paraphyletic group, whereas most other organisms have been. Apes, reptiles, fishes, and invertebrates are all terms that traditionally designate paraphyletic groups formed by combining various "side branches" that are found when human ancestry is traced backward through the tree of life. Such a taxonomy can give the erroneous impression that all of evolution is a progressive march toward humanity or, within other groups, a progressive march toward whatever species humans designate as being the most "advanced." Such thinking is a relic of preDarwinian views that there is a linear scale of nature having "primitive" creatures at the bottom and humans near the top just below angels. Darwin's theory of common descent states, however,

that evolution is a branching process with no linear scale of increasing perfection along a single branch. Nearly every branch will contain its own combination of ancestral and derived features. In cladistics, this perspective is emphasized by recognizing taxa only by their own unique properties and not grouping organisms only because they lack the unique properties found in related groups.

3.7 TAXONOMIC CHARACTERS

(i) Classical Taxonomy:

Classification of any group of organism uses selected stable characteristics which vary among the taxa. These are known as taxonomic characteristics. Classically, the bacteria have been classified on the basis of similarities in phenotypic characteristics, like morphological features, response to Gram stain, cultural characteristics, physiological biochemical properties, pathogenicity, antibiotic sensitivity, serological relationships etc. Taxonomically important morphological, cultural and physiological- biochemical characteristics are shown in Table 3.1, 2 and 3 respectively.

(ii) Molecular Taxonomy:

Approach to bacterial taxonomy has undergone drastic changes since the development of molecular biology in the second half of the twentieth century. The concept that macromolecules, like proteins and nucleic acids, could be used as an indicator of evolution of living organisms was first suggested by Zuckerkandl and Pauling in 1965.

They described these macromolecules as “molecular chronometers”, because the sequences of monomers in them have changed slowly and randomly and the number of changes in a particular macromolecule has increased linearly with geological time scale.

A comparison of the sequence of monomers of a particular macromolecule from two organisms should, therefore, give a measure of their phylogenetic relationship. If the sequences differ considerably, it indicates that the two organisms are phylogenetically distant.

This new approach has given rise to the molecular taxonomy. Although initially amino acid sequencing of proteins was used as a parameter for determination of phylogenetic relations,

nucleic acids soon replaced proteins. Among the characteristics of nucleic acids, DNA base composition, DNA homology, DNA sequencing, r-RNA sequence analysis etc. have been used for solving taxonomic problems.

The principles of some of the methods are briefly described:

(a) DNA base composition:

The first characteristic that was applied in solving taxonomic problems was the base composition of DNA. A unique feature of DNA is that the ratio of (G + C): (A + T) is more or less constant for a biological species. The ratio is conventionally expressed as G + C moles %. Organisms which are closely related, like the strains of a given species have close values of G + C moles %. In bacteria; this value varies from about 25% to 80%.

Several methods are available for experimental determination of DNA base ratio. Of these, two methods commonly employed are those by determination of melting temperature of DNA and buoyant density. The principles are described briefly.

A characteristic feature of double-stranded DNA helix is that at a high temperature the helical structure collapses producing two single strands due to dissolution of the H-bonds. This is known as melting and the temperature at which melting occurs is a character of a particular species of DNA.

Because there are three H-bonds between G and C, and two between A and T, a DNA molecule having more of G + C melts at a higher temperature. Another important characteristic of DNA is that molten or denatured DNA shows an increase in optical density at 260 nm, a phenomenon known as hyperchromicity.

This means that as the double stranded DNA is dissociated into single-stranded state, its optical density at 260 nm (OD_{260}) gradually increases and reaches a maximum when all the DNA present in a sample becomes denatured. This can be measured in an instrument called UV spectrophotometer having an arrangement for gradually raising the temperature of a DNA solution.

By plotting % increase of $OD_{26}o$ against temperature, a curve is obtained as shown in Fig. 3.4. The temperature at which 50% of maximum increase is reached is taken as the melting

temperature (T_m) of that particular species of DNA. From the melting temperature, the G + C moles % can be calculated from the relation, $T_m = 69.3 + 0.41(G + C)$ %.

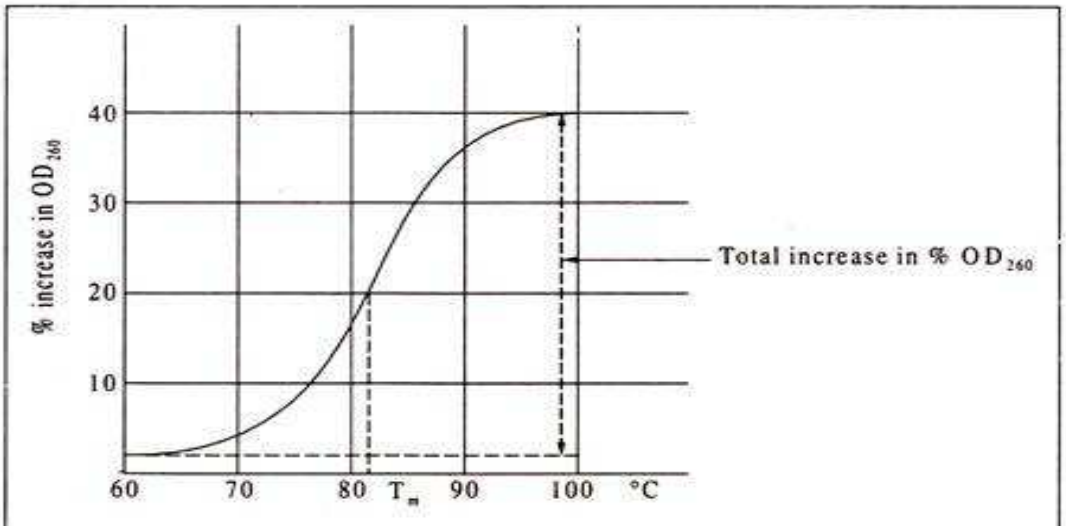


Fig. 3.4 : A melting curve of DNA showing T_m

Although G + C content of DNA is a useful taxonomic character, it alone may not indicate a close relation, because two quite unrelated organisms may have by chance close G + C content. But for two organisms resembling each other in most other phenotypic characters, a close G + C content of DNA can be taken as a reliable indication of their phylogenetic relatedness.

By analysis of G + C content of DNA of large number of bacteria, it has been found that strains within a species have more or less identical values and its variation in different species within a genus usually does not exceed by more than 10%.

It should be remembered that G + C content gives only the overall composition of DNA and gives no information about the sequence of bases in the DNA molecule. It is this sequence in a DNA segment that constitutes the specificity of a gene. So, G + C content of DNA does not give any information regarding the similarity of genes of two organisms.

Another technique of determination of G + C moles % of DNA utilizes a different property of double-stranded (ds-) DNA. The buoyant density of ds-DNA increase linearly with its G + C content. In an equilibrium density gradient, homogeneous nucleic acid accumulates as a symmetrical band, the width of which is inversely proportional to the square root of its molecular weight.

Smaller molecules having a lower molecular weight tend to diffuse more rapidly than larger molecules and, hence, have wider bands. Also, DNA samples differing in G + C content form separate bonds, because of their difference in density.

In equilibrium density gradient centrifugation using caesium chloride (CsCl), the samples of DNA, previously purified by removing proteins and RNA, are mixed thoroughly with a 6M solution of the caesium salt in a PVC (polyvinyl chloride) centrifuge tube and the mixture is subjected to high speed ultracentrifugation for a sufficiently long time to allow the formation of a density gradient.

The highest density is at the bottom of the tube and it gradually decreases upwards. The different components of the DNA sample collect in distinct bands at levels where the density of a particular component equals that of the gradient.

The fractions can be collected by puncturing the PVC tube at the bottom and their density determined. From the buoyant density of the DNA bands, their G + C moles % can be calculated from the relation, p (buoyant density) = 1.660 + 0.98 (G + C) %.

(b) Nucleic acid hybridization:

More reliable information about the similarity of the genomes of two organisms can be obtained by DNA-DNA hybridization, because formation of a heteroduplex between two single stranded DNA molecules derived from two organisms depends on the degree of complementarity of the two single strands.

A double-stranded DNA can be dissociated into single strands by application of heat. An interesting feature of single-stranded DNA is that on cooling, the strands tend to re-associate to form double-helix structure automatically. This process, known as annealing, occurs optimally when the temperature is brought to about 25°C below the melting temperature in a solution of high ionic concentration, such as 0.3M NaCl which reduces electrostatic repulsion between the DNA strands.

Various methods have been developed for quantitative determination of heteroduplex formation. One of the most commonly employed techniques involves binding of comparatively long DNA molecules of one organism to nitrocellulose filter and allowing the

bound DNA molecules to hybridize with comparatively short DNA molecules of the other organism.

For differentiating between the two species of DNA, one of them — usually the second one — is made radioactive by labeling with either ^{32}P or ^{3}H. Radioactive DNA is obtained by growing an organism in a medium containing a radioactive salt e.g. ^{32}P labeled phosphate. DNA becomes labeled and is then isolated and purified for use in hybridization.

For DNA-DNA hybridization, the longer non-radioactive single stranded DNA molecules are first allowed to bind to a nitrocellulose filter, unbound DNA is removed by washing and the filter with bound DNA is incubated with the radioactive smaller single-stranded DNA under optimal conditions of annealing.

During incubation the smaller radioactive molecules hybridize with the longer DNA molecules depending on their homology in the base sequences. Then the filter is washed to remove the unbound radioactive DNA molecules and the radioactivity of the filter is measured.

(c) Ribosomal RNA homology:

An important discovery made in 1965 revealed that in all living organisms, the DNA segments transcribing ribosomal RNA (r-cistrons or r-DNA) have changed more slowly in course of evolution than the rest of the genome. In other words, the r-cistrons are more conserved in comparison to the genes encoding proteins.

This provided an instrument for comparing the phylogenetic relationships between distantly related organisms through determination of base sequences of r-RNA or r-DNA. Among the different r-RNAs, the 16S r-RNA of prokaryotic organisms and the analogous 18S r-RNA of eukaryotes have been found to be most suitable for comparison of their sequences in taxonomic studies.

The method used in the beginning for determination of r-RNA homology was oligonucleotide cataloging. Purified r-RNA was cleaved into oligonucleotides by specific enzymes, like bacteriophage T1 RNase, separated by two-dimensional electrophoresis, further hydrolysed into smaller segments and again electrophoresed to determine their nucleotide sequences.

The sequence of one unique oligonucleotide of each organism was stored in computer. Sequences of different organisms were compared to determine their similarity. Ribosomal RNA of most of the major taxonomic group has been found to possess one or more unique sequences which are known as their oligonucleotide signature. Such signature sequences have been determined for most of the major taxonomic groups of bacteria.

One of the major impacts of r-RNA studies on taxonomy is the recognition of three major domains — the Archaea, the Eucarya including all eukaryotes, and the Bacteria. It has been claimed by Woese, Kandler and Wheelis (1990) that the three major evolutionary lines diverged from a common ancestral form.

Advances in the molecular biological techniques have now made it possible to determine nucleotide sequences of r-DNA for preparing phylogenetic trees with the help of computers. Such trees are built up by comparing the sequences of two molecules by alignment. The number of mismatches in the sequence is counted and used to calculate the evolutionary distance. The similarity between the two molecules is expressed as similarity coefficient.

A group of closely related organisms e.g. species of the same genus, will generally have a narrow range of similarity coefficients. Conversely, a wider range of similarity coefficients indicates that the organisms have branched off from each other in more remote past.

UNIT4: PROCEDURES IN TAXONOMY

4.1 Objectives

4.2 Introduction

4.3 Taxonomic procedure

4.3.1 Taxonomic collection

4.3.2 Preservation

4.3.3 Identification

4.4 International Code of Zoological Nomenclature (ICZN)

4.4.1 Principals, Application and Rules

4.4.2 Zoological Nomenclature and Formation of Scientific Names of Various Taxa

4.1 OBJECTIVES

- Study of Taxonomic procedure, Taxonomic collection, Preservation & Identification.
- Study of International Code of Zoological Nomenclature (ICZN) & Zoological Nomenclature and Formation of Scientific Names of Various Taxa

4.2 INTRODUCTION

Taxonomy, in a broad sense the science of classification, but more strictly the classification of living and extinct organisms—*i.e.*, biological classification. The term is derived from the Greek *taxis* ("arrangement") and *names* ("law"). Taxonomy is, therefore, the methodology and principles of systematic botany and zoology and sets up arrangements of the kinds of plants and animals in hierarchies of superior and subordinate groups. The term first proposed by the Swiss originated botanist Augustine Paramus de Candolle in 1813 for the plant classification. He used the term in his famous book—Theory elementaire de la botanique (Elementary Theory of Botany). So taxonomy is the arrangement of the plants and animals on the basis of some laws.

4.3 TAXONOMIC PROCEDURE

Biological collections are typically preserved plant or animal specimens along with specimen documentation such as labels and notations. TYPES OF COLLECTIONS Most biological collections are either dry collections or wet collections. They also may include collections preserved at low temperatures or microscopy collections. DRY COLLECTION Dry collections consist of those specimens that are preserved in a dry state. Some specimens can be preserved naturally (starfish) or artificially with sufficient rigidity to accommodate normal handling. Such specimens often are suitable for dry preservation. Specific characteristics. Drying may provide the best available means to preserve natural colors (for example, butterflies) or distinguishing features (such as skeletal parts or surface details). Such specimens in a dry state may have great potential for interpretation and research.

WET COLLECTIONS: Wet collections are specimens kept in a liquid preservative to prevent their deterioration. Certain biological specimens are preserved in a wet form due to: · convenience · an intent to preserve body form and soft parts for a variety of uses When color preservation is not critical and dry preservation sacrifices qualities needed for other intended uses, fluid preservation is beneficial. BIOLOGICAL LOW-TEMPERATURE COLLECTIONS Specimens are maintained at low temperatures to preserve: · soft parts for various biochemical analyses · whole organisms in a viable (able to live and grow) state. specimens preserved at low temperatures - Some algae, Protozoa (especially parasitic strains), Viruses, Cloned viral genomes, Bacteria,Bacteriophages,Plasmids · Animal tissues (dissected organs, muscles),Cell lines - Blood and blood components (whole blood, serum, plasma, antisera) - Semen,Venom - Other samples (cloned probes, isolated proteins and nucleic acids, cell suspensions) Note: The largest organisms that can be preserved in a viable state are some insects.

BIOLOGICAL MICROSCOPY COLLECTIONS: Scientists preserve certain specimens as microscope preparations to preserve whole or partial organisms for various kinds of microscopic examination & some kinds of biochemical analyses, including extraction of DNA. Specimens prepared for microscopy may be found in all biological collections, but are most common in these collections are like entomology, mycology, parasitology etc. It’s also common for microscopy collections to be ancillary to more traditional collections. Examples of such ancillary collections included histology, karyology & scales.

Value of biological collections most biological collections are highly valuable for the following reasons. Museums are only place where extinct species are preserved. Specimens of special historical value. Specimens rarely found in any collections. Many areas in world are geographically inaccessible. Material from such area is invaluable & is preserved at all costs A material is of unique value if it forms the basis of published research. It may be needed again for verification of original data or for renewed study in the light of more recent knowledge or by new techniques.

- METHODS OF COLLECTON Mist net Arctic tern caught in mist net
- Attracting Nocturnal Insects with UV Light Many insects can see ultraviolet light, which has shorter wavelengths than light visible to the human eye. For this reason, a black light will attract different insects than a regular incandescent light. . The black light can be suspended in front of a white sheet, giving flying insects a surface on which to land. You can then observe the insects on the sheet, and collect any interesting specimens by hand. A black light trap is constructed by suspending a black light over a bucket or other container, usually with a funnel inside. Insects fly to the light, fall down through the funnel into the bucket, and are then trapped inside the container. Black light traps sometimes contain a killing agent, but can also be used without one to collect live specimens.
- Malaise traps A Malaise trap is a large, tent-like structure used for trapping flies and wasps. Insects fly into the tent wall and are funneled into a collecting vessel attached to highest point.
- Insects are collected mainly by beating and sweeping beating sweeping
- Plankton net Aquatic insects and other arthropods are collected by using dip nets & plankton nets Dip net
- Trawling and dredging for collecting deep-sea animals Trawling Dredging
- Collecting net
- Aspirator
- Berlese funnel
- Floatation method Used to collect arthropods, eggs and pupae of insects from soil or matted vegetation.
- Killing bottles Cyanide bottle Killing tube POISON

- RECORDING DATA: Geographic locality Stratigraphic position (for fossils only) Date, Stage (adult male, female or immature form) Altitude or depth, Host Name of collector etc.
- Genitalia preserved in tiny glass vial along with specimen.
- Storage building should be Fireproof Dustproof Earthquake resistant Air-conditioned. Special care for type specimens Type specimens should not be allowed to be handled frequently. They should only be examined by experts. Avoid their transport as far as possible. They should be stored separately from general collection. They should be clearly labeled in distinct colours.
- Method of cataloguing is different from group to group. In higher vertebrates each specimen is given separate number and catalogued separately.In case of insects this is not done due to their large number. All specimens from one locality are catalogued together. Only type specimens are unusually catalogued. In large museums type catalogues are bound in book in which types are serially numbered. There are various ways in using filing cards of collections: Some museums have elaborate card filing system which help in easy collection of information about specimen. Some large museums place all information about each specimen on separate IBM card.
- Museum number Original field number Scientific name Locality Date Collector remarks

4.3.1 TAXONOMIC COLLECTION

Every taxonomist has to take the responsibility of curating collections. This requires a great deal of expertise, knowledge and clear understanding of the function of different collections. Preparation of Material There are certain materials which are ready for study as soon as collected from the field e.g., bird and mammal skins. There are certain insects which should never be placed in alcohol or any other liquid preservative whereas others are useless when dried. Certain invertebrates are to be preserved in alcohol of formalin before their study. Microscope slide mounts or slides of parts of organs may have tube prepared for the smaller forms. Most insects are pinned, and the wings are spread if they are taxonomically important as in butterflies, moths and some grasshoppers. Housing Research collections should be housed in fireproof and dustproof buildings. Most museums keep their collections in air-conditioned buildings. Rapid changes in temperature and humidity are harmful to museum cases and specimens. Storage cases should be built to be insect-proof. Photographs and films

should be stored in air-conditioned rooms. Cataloging the method of cataloging depends on the group of animals. All the specimens including vertebrates collected at a given locality or district or by one expedition are entered in the catalog together. This greatly facilitates in knowing the distributional data and the preparation of faunistic analyses. Cataloging is usually done after the specimens have been identified, at least up to the genus level. In groups where the collections consist of large numbers of specimens, it is customary to catalog the specimens by lots. Each lot consists of a set of specimens from a given locality or region. It is also important to note whether a lot was received as a gift or by purchase or exchange. The names of the collector and donor are always given. When museums and their collections were small, curators had maintained card-files which provided all sorts of information such as collecting station, name of the collector etc.

Maintenance of computer record should never be at the cost of work on systematic collections. Arrangement of the Collection The collection should be arranged in the same sequence as some generally adopted classification. The sequence of orders and families is usually standardized in many classes of animals. The contents of trays and cases should be clearly indicated on the outside which could serve as a check list. Where specimens are of large and unequal size, they have to be stored separately. Curating of Types the names of species are based on type specimens. Many descriptions of classical authors are equally applicable to several related species. Types are usually deposited in large collections in public or private institutions which have come to be recognized as standard repositories of types. While conducting an authoritative revision ofa given genus, a specialist should be able to see all the existing types. If many of them are in a single institution, the specialist should travel the read obtain scattered types.

Modern curators are quite liberal in lending type specimens to qualified specialists. It is recommended that the type collections should be arranged alphabetically according to the given specific name. A type collection is a reference collection rather than classification. Type specimens assume such an important role in the taxonomy of lesser-known groups that many workers believe that no individual should retain a type in his private collection after the study has been completed. Exchange of Material the selecting of material for exchanges and keeping its record is time-consuming, so the exchanges are not as popular as they used tube. Among private collectors this practice is common. Specialists doing a monograph on a certain genus or family can always borrow material from other institutions and return it after completing his work. Exchanges are not desirable in groups where series of unlimited size can be obtained and where the concerned areas are not easily accessible.

Exchanges are sometimes necessary to build up complete identification collections. Many specialists give away excess specimens as open exchanges not expecting any return. Improperly preserved or inadequately labeled specimens should be eliminated by the curator .The most efficient method for the elimination of useless material is to ask specialists to pull out such specimens while scrutinizing the material during a revision. LoansModern curators are very generous in lending specimens to qualified experts.This is due to the fact that systematic collections are the general property of science and not of a specific institution or curator. Every loan, however, involves loss of time and effort, and the borrower should refund the lender for his efforts. Research grants now include an item so as to cover the costs of postage, selecting the specimens, recording the loan, and getting the material packed for shipment. The modern curator, being essentially a research worker, must delegate these tasks to hired clerical help. A request for the loan of specimens should be as specific as possible, including a statement of the reason for the request and some indication of the length of time for which the material is needed.

The beginner may be unable to borrow certain material except through a loan to his or her institution or to the beginner's major professor. If the borrower is unable to complete the studies in the designated time, the person or institution that made the loan should be informed. The lender should never be placed in the embarrassing position of having to write and ask about the status of the study. If a specialist has agreed to identify a collection provided he or she receives certain specimens, the specialist should make sure that the terms of the agreement are well understood and should return to the lender a list of the specimens which he or she has retained. All types and unique specimens must be returned to the lender in such cases.

4.3.2 PRESERVATION

Specimens of insects and arthropods, if properly preserved and cared for, can last hundreds of years. Any given specimen carries an enormous potential to inform us about itself and the time and place of collection. Maintaining any specimen for many years carries a cost. Proper preservation ensures a high quality specimen, which increases the quality of information the specimen contains, and increases the value of the maintenance of the specimen. A good specimen takes up just as much room as a bad one. The same as five dirty, rusty, junk cars take up just as much space as five clean, shiny, perfectly restored cars.

Detailed information about general and specific types of preservation can be found within the publications recommended on the Collecting Insects page of this wiki. Below is an overview appropriate for general preservation and curation.

	Order	Adult: Temporary (Field) Preservation	Adult: Permanent Preservation	Immature Preservation	Comments *
1	**Arachnids (Spiders, Mites, Etc.)**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry
2	**Protura**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry
3	**Collembola (springtails)**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry
4	**Diplura**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry
5	**Microcoryphia (jumping bristletails)**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry
6	**Thysanura (silverfish)**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry
7	**Ephemeroptera (mayflies)**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to

					dry
8	**Odonata (dragonflies and damselflies)**	Dry, kill jar	Pinned or enveloped	Ethanol (80%)	Do not kill or preserve adult in fluid
9	**Orthoptera (grasshoppers and crickets)**	Dry, kill jar; ethanol (80%), may fade color	Pinned	Ethanol (80%)	
10	**Grylloblattodea**	Dry, kill jar; ethanol (80%)	Ethanol (80%)	Ethanol (80%)	
11	**Mantophasmatodea**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	
12	**Phasmatodea (walkingsticks)**	Dry, kill jar	Pinned	Ethanol (80%)	
13	**Mantodea (preying mantids)**	Dry, kill jar	Pinned	Ethanol (80%)	
14	**Blattodea (cockroaches)**	Dry, kill jar; ethanol (80%)	Pinned	Ethanol (80%)	
15	**Isoptera (termites)**	Ethanol (80%)	Ethanol (80%)	Ethanol (80%)	Never allow to dry

Rubbing Alcohol, also called Isopropyl Alcohol and Isopropanol is a commonly available alcohol that can be used to preserve specimens, but it is not recommended for long term storage. Specimens will become very brittle over a short period of time.

Ethanol, also called ethyl alcohol and grain alcohol is generally the best fluid for short and long term preservation of specimens. Low concentrations of alcohol (below 70%) will not properly preserve a specimen, while high concentrations (above 90%) may cause the specimen to crush under osmotic pressure. Generally 80% (160 proof) ethanol is the best to use. In a pinch, high alcohol distilled spirits, such as 100 proof vodka or rum, can be used, but only for short periods of time until replaced by proper strength ethanol.

If there is a chance that the ethanol will be significantly diluted (for example, many specimens in the same jar, specimens are large and fluid filled, etc.) it is best to replace the ethanol once after 24-48 hours. Some large immature flies, dragonflies, beetles, and caterpillars may begin to rot internally before they become sufficiently preserved if placed directly in ethanol. Two common practices used to prevent this are: 1) inject the specimen with ethanol before immersing within ethanol; 2) bring water to a boil, take it off the heat, drop the specimen in the water and leave it for 1-2 minutes, remove specimen, pat dry, place in ethanol. Replace ethanol once after 24-48 hours. Never allow specimens preserved in ethanol to dry out, unless they have been removed for pinning.

4.3.3 IDENTIFICATION

Taxonomic identification is the recognition of the identity or essential character of an organism. Taxonomists often present organized written descriptions of the characteristics of similar species so that other biologists can identify unknown organisms. These organized descriptions are referred to as taxonomic keys. A taxonomic key is often published with pictures of the species it describes. However, written descriptions are usually preferred over pictures, since pictures cannot convey the natural variation in the morphology of a species, nor the small, yet characteristic, morphological features of a species. In addition, matching an unidentified organism to one picture in a book of hundreds or thousands of pictures can be very time-consuming.

4.4 INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE (ICZN)

The International Code of Zoological Nomenclature (ICZN) is a widely accepted convention in zoology that rules the formal scientific naming of organisms treated as animals. It is also informally known as the ICZN Code, for its publisher, the International

Commission on Zoological Nomenclature (which shares the acronym "ICZN"). The rules principally regulate:

- How names are correctly established in the frame of binominal nomenclature[1]
- Which name must be used in case of name conflicts
- How scientific literature must cite names

Zoological nomenclature is independent of other systems of nomenclature, for example botanical nomenclature. This implies that animals can have the same generic names as plants.

The rules and recommendations have one fundamental aim: to provide the maximum universality and continuity in the naming of all animals, except where taxonomic judgment dictates otherwise. The code is meant to guide only the nomenclature of animals, while leaving zoologists freedom in classifying new taxa.

In other words, whether a species itself is or is not a recognized entity is a subjective decision, but what name should be applied to it is not. The code applies only to the latter. A new animal name published without adherence to the code may be deemed simply "unavailable" if it fails to meet certain criteria, or fall entirely out of the province of science (e.g., the "scientific name" for the Loch Ness Monster).

The rules in the code determine what names are valid for any taxon in the family group, genus group, and species group. It has additional (but more limited) provisions on names in higher ranks. The code recognizes no case law. Any dispute is decided first by applying the code directly, and not by reference to precedent.

The code is also retroactive or retrospective, which means that previous editions of the code, or previous other rules and conventions have no force any more today, and the nomenclatural acts published 'back in the old times' must be evaluated only under the present edition of the code.

(Adopted by the 15th International Congress of Zoology (London) and published on November 6, 1961)

The object of the code is to promote stability and universality in the scientific name of animals, and to ensure that each name is unique and distinct.

The Swedish naturalist Carl von Linne' (1707-1778), who changed his name to a binomen, Carolus Linnaeus, was the father a set of rules of nomenclature published in *Critica Botanica* (1737), *Philosophia Botanica* (1751) and in the 10th edition of *Systema Naturae* (1758). The confusion that prevailed after Linnaeus was solved in the 5th International Congress of Zoology in Berlin in 1901. The original code was, however, adopted in 1904 in the 6th International Congress of Zoology in Bern and published in 1905 in Paris as, *"Regles Internationales de la Nomenclature Zoologique."*

The most recent version (a modified version of 1961 code) was published in 1964 in parallel French and English. It was adopted by the 16th International Congress of Zoology, Washington (1963) with modifications in articles 11, 31, 39 and 60.

International Congress of Zoology is a legislative body, which adopts by voting the constitution and proposals put before it by the commission.

International Commission on Zoological Nomenclature is a judicial body elected by the International Congress of Zoology. It is protector of the code and deals with the interpretations, disputes and implementation of the **code**. Amendments have to be routed through the commission.

International Code of Zoological Nomenclature (1964) is the system of rules and recommendations authorized by the International Congress of Zoology. The object of the code is to promote stability and universality in the scientific names of animals and to ensure that each name is unique and distinct. Code does not restrict the freedom of taxonomic thought and action.

Before the present code, the following codes were prevalent in Europe and U.S.A.:

1. Strickland Code (1842) in Berlin.

2. W.H.Dall Code (1877) in USA.

3. Douville' Code (1881) in France.

Salient features of the "Code"

The 1964 code consists of a *Preamble, 86 Articles, 5 Appendices, a Glossary* and a detailed *Index*, in parallel English and French. Starting date of the code is 1st January 1758 (publication date of the10th edition of *Systema naturae).*

1. Names must either be Latin or Latinized.

2. Names of taxa higher than species should be uninominal.

3. Name of a species is binomen.

4. Name of a subspecies is a trinomen.

5. Name of a subgenus is placed in parenthesis between genus and species, e.g. *Xorides (Gonophonus) nigrus.*

6. Family name should end in DAE, e.g. Tipulidae.

7. Genus name should be a noun in nominative singular or treated as such, e.g. *Apis, Rana.*

8. Species name should be an adjective or noun in nominative singular agreeing in gender with the generic name, e.g. *Drosophila obscura, Felis tigris* etc. OR a noun standing in opposition to the generic name, e.g. *Felis leo.*

9. Zoological nomenclature is independent of other systems.

10. All names given to the species from time to time should be mentioned in synoymy.

11. Author's name is not part of the name. It's use is optional and is suffixed, e.g. *Cancer pagurus* Linnaeus.

12. **Law of priority:** The valid name is the oldest name published and available.

13. **Synonymy:** Synonyms are different names assigned to the same taxon. They should be mentioned along with the valid taxon, e.g. *Erias vitella(=Erias fabia).*

14. **Homonymy:** Homonyms are identical names in spelling for different species of the same genus and for different genera of a family. Junior homonym has to be rejected. Homonymy arises when an existing species' name is not known to the person assigning a name, or a species with identical name is transferred to the same genus.

15. **Holotype:** Single specimen on which description of the species is based. Red colored label is fixed on the specimen.

16. **Allotype:** Specimen of the opposite sex to holotype. Also carries a red label.

17. **Paratype:** All remaining specimens after the designation of holotype and allotype are assigned the status of paratypes. They carry yellow labels.

18. **Syntypes:** If no holotype is designated, all specimens that the author studied for the description of the species are called syntypes.

19. **Lectotype:** In the absence of a holotype, one specimen from syntypes can be designated as Lectotype and rest of the specimens as Paralectotypes.

20. **Neotype:** If all type-specimens are destroyed, a neotype, that fits the description very well, can be designated under exceptional circumstances.

4.4.1 PRINCIPALS, APPLICATION AND RULES

"Zoological nomenclature is the system of scientific names applied to taxonomic units of animals *(taxa)* known to occur in nature, whether living or extinct." The nomenclature should fulfill the following three basic requirements:

UNIQUENESS: The name of a taxon is like the index number of a file. It gives immediate access to all information in literature, available about a particular taxon. Every name must be unique because it is key to the entire literature. Uniqueness has been achieved by adopting *binominal nomenclature,* as proposed by Linnaeus in the X edition of *Systema Naturae* in 1758.

According to binominal nomenclature, each species name should consist of the first generic and second species name. Species name should not duplicate under any genus, e.g. *Panthera leo, Panthera tigris, Panthera pardus.* A combination of the two makes the name unique.

UNIVERSALITY: Scientific names should be known to all and be universally accepted. Vernacular names would be difficult to keep track of, and scientists will have to learn names in several languages of the world. To avoid this, zoologists have adopted by international agreement a single language, *Latin,* which is a dead language and therefore does not evolve and is acceptable to everybody.

One need not learn Latin language in order to give name. Any word in any language, if latinized by changing the ending by suffixing *–us,-a,* or *–ensis* is acceptable as valid Latin name, e.g., *japonica, indicus, chinensis.* Use of Latin is also advantageous due to the fact that most of the ancient scientific literature is written either in Latin or Greek and it would be easy to refer to the old literature if names are given in Latin.

STABILITY: Zoological names would lose their utility if they were changed frequently and arbitrarily. It would create confusion if we call an object *spoon* today and *apple* next week. *International Code of Zoological Nomenclature* has been designed to bring about stability. Taxonomists are bound to follow the rules given in the **code** before assigning names to taxa. Most of the changes in names are due to taxonomists' errors. Lot of name changing has taken place during the last 200 years. International Code of Zoological Nomenclature safeguards against frequent name changing.

4.4.2 ZOOLOGICAL NOMENCLATURE AND FORMATION OF SCIENTIFIC NAMES OF VARIOUS TAXA

The format for writing scientific names of animals and plants is standardized and internationally accepted. "Scientific nomenclature" refers to various names according to a specific field of study. This article is the first in a series on *scientific nomenclature* within specific kingdoms.

Usually, animals & plants are identified by common and scientific names.

Taxonomists have established several "codes" for scientific nomenclature. These codes are universal and are periodically updated by consensus. The protocol for naming species was invented in the 1700s by Swedish botanist Carl Linnaeus. Linnaeus created the system of "binomial nomenclature," which uses only two designations–genus and specific epithet as the species name.
The levels from highest to lowest classification are as follows:

- Domain
- Kingdom
- Phylum
- Class
- Order
- Suborder
- Family
- Genus
- Species
- Subspecies

Using this system, the gray wolf, for example, would be identified as follows:

- Domain: Eukarya.
- Kingdom: Animalia.
- Phylum: Chordata.
- Class: Mammalia.
- Order: Carnivora.
- Suborder: Caniformia.
- Family: Canidae.
- Genus: *Canis.*
- Species: *lupus.*

WRITING SCIENTIFIC NAMES OF ANIMALS

When writing, we use both the scientific name and the "common" name on the first mention. We then choose which to use throughout and make it consistent.

- **Gray wolf (CANIS LUPUS)** is native to North America and Eurasia.

In subsequent references, we can use either the common or scientific name. If we use the scientific name, we need only to use the first letter of the genus followed by a period and the specific epithet. For example:

- In North America, the **gray wolf** was nearly hunted to extinction.
- In North America, **C. LUPUS** was nearly hunted to extinction.

It is also common to refer to several species less than one genus when you want to point out some similar characteristics within a genus. For example:

- All species of **CANIS** are known to be moderate to large and have large skulls.

You could also write this same information another way as follows:

- **CANIS spp.** is known to be moderate to large and have large skulls.

In this case, "spp." is an abbreviation for "several species" ("sp" is the designation for one species) in the genus. Either of the above is acceptable. If you are focusing on a few species in particular, you would refer to the species name of each one.

BLOCK II: EVOLUTION

UNIT 5: LAMARCK & DARWINISM

5.1 Objectives

5.2 Introduction

5.3 Concept & theories of Evolution

5.4 Hardy-Weinberg law of Genetic Equilibrium

5.5 Detailed account of Destabilizing Forces

5.5.1 Natural Selection

5.5.2 Mutation

5.5.3 Genetic Drift

5.5.4 Migration

5.1 OBJECTIVES

We will know about Concept & theories of Evolution & Hardy-Weinberg law of Genetic Equilibrium, Natural Selection, Mutation and Genetic Drift.

5.2 INTRODUCTION

Evolution, theory in biology postulating that the various types of plants, animals, and other living things on Earth have their origin in other preexisting types and that the distinguishable differences are due to modifications in successive generations. The theory of evolution is one of the fundamental keystones of modern biological theory.

The diversity of the living world is staggering. More than 2 million existing species of organisms have been named and described; many more remain to be discovered—from 10 million to 30 million, according to some estimates. What is impressive is not just the numbers but also the incredible heterogeneity in size, shape, and way of life—from lowly bacteria, measuring less than a thousandth of a millimeter in diameter, to stately sequoias, rising 100 meters (300 feet) above the ground and weighing several thousand tons; from bacteria living in hot springs at temperatures near the boiling point of water to fungi and algae thriving on the ice masses of Antarctica and in saline pools at −23 °C (−9 °F); and from giant tube worms discovered living near hydrothermal vents on the dark ocean floor to spiders and larkspur plants existing on the slopes of Mount Everest more than 6,000 meters (19,700 feet) above sea level.

The virtually infinite variations on life are the fruit of the evolutionary process. All living creatures are related by descent from common ancestors. Humans and other mammals descend from shrew like creatures that lived more than 150 million years ago; mammals, birds, reptiles, amphibians, and fishes share as ancestors aquatic worms that lived 600 million years ago; and all plants and animals derive from bacteria-like microorganisms that originated more than 3 billion years ago. Biological evolution is a process of descent with modification. Lineages of organisms change through generations; diversity arises because the lineages that descend from common ancestors diverge through time.

The 19th-century English naturalist Charles Darwin argued that organisms come about by evolution, and he provided a scientific explanation, essentially correct but incomplete, of how evolution occurs and why it is that organisms have features—such as wings, eyes, and kidneys—clearly structured to serve specific functions. Natural selection was the fundamental concept in his explanation. Natural selection occurs because individuals having more-useful traits, such as more-acute vision or swifter legs, survive better and produce more progeny than individuals with less-favorable traits. Genetics, a science born in the 20th century, reveals in detail how natural selection works and led to the development of the modern theory of evolution. Beginning in the 1960s, a related scientific discipline, molecular biology, enormously advanced knowledge of biological evolution and made it possible to investigate detailed problems that had seemed completely out of reach only a short time previously—for example, how similar the genes of humans and chimpanzees might be (they differ in about 1–2 percent of the units that make up the genes).

The evidence for evolution

Darwin and other 19th-century biologists found compelling evidence for biological evolution in the comparative study of living organisms, in their geographic distribution, and in the fossil remains of extinct organisms. Since Darwin’s time, the evidence from these sources has become considerably stronger and more comprehensive, while biological disciplines that emerged more recently—genetics, biochemistry, physiology, ecology, animal behaviour (ethology), and especially molecular biology—have supplied powerful additional evidence and detailed confirmation. The amount of information about evolutionary history stored in the DNA and proteins of living things is virtually unlimited; scientists can reconstruct any detail of the evolutionary history of life by investing sufficient time and laboratory resources.

Evolutionists no longer are concerned with obtaining evidence to support the fact of evolution but rather are concerned with what sorts of knowledge can be obtained from different sources of evidence. The following sections identify the most productive of these sources and illustrate the types of information they have provided.

Paleontologists have recovered and studied the fossil remains of many thousands of organisms that lived in the past. This fossil record shows that many kinds of extinct organisms were very different in form from any now living. It also shows successions of organisms through time, manifesting their transition from one form to another.

When an organism dies, it is usually destroyed by other forms of life and by weathering processes. On rare occasions some body parts—particularly hard ones such as shells, teeth, or bones—are preserved by being buried in mud or protected in some other way from predators and weather. Eventually, they may become petrified and preserved indefinitely with the rocks in which they are embedded. Methods such as radiometric dating—measuring the amounts of natural radioactive atoms that remain in certain minerals to determine the elapsed time since they were constituted—make it possible to estimate the time period when the rocks, and the fossils associated with them, were formed.

Radiometric dating indicates that Earth was formed about 4.5 billion years ago. The earliest fossils resemble microorganisms such as bacteria and cyanobacteria (blue-green algae); the oldest of these fossils appear in rocks 3.5 billion years old. The oldest known animal fossils, about 700 million years old, come from the so-called Ediacara fauna, small wormlike creatures with soft bodies. Numerous fossils belonging to many living phyla and exhibiting mineralized skeletons appear in rocks about 540 million years old. These organisms are different from organisms living now and from those living at intervening times. Some are so radically different that paleontologists have created new phyla in order to classify them. The first vertebrates, animals with backbones, appeared about 400 million years ago; the first mammals, less than 200 million years ago. The history of life recorded by fossils presents compelling evidence of evolution.

The fossil record is incomplete. Of the small proportion of organisms preserved as fossils, only a tiny fraction have been recovered and studied by paleontologists. In some cases the succession of forms over time has been reconstructed in detail. One example is the evolution of the horse. The horse can be traced to an animal the size of a dog having several toes on each foot and teeth appropriate for browsing; this animal, called the dawn horse (genus

Hyracotherium), lived more than 50 million years ago. The most recent form, the modern horse (*Equus*), is much larger in size, is one-toed, and has teeth appropriate for grazing. The transitional forms are well preserved as fossils, as are many other kinds of extinct horses that evolved in different directions and left no living descendants.

Evolution of the horse over the past 55 million years. The present-day Przewalski's horse is believed to be the only remaining example of a wild horse—i.e., the last remaining modern horse to have evolved by natural selection. Numbered bones in the forefoot illustrations trace the gradual transition from a four-toed to a one-toed animal.

Using recovered fossils, paleontologists have reconstructed examples of radical evolutionary transitions in form and function. For example, the lower jaw of reptiles contains several bones, but that of mammals only one. The other bones in the reptile jaw unmistakably evolved into bones now found in the mammalian ear. At first, such a transition would seem unlikely—it is hard to imagine what function such bones could have had during their intermediate stages. Yet paleontologists discovered two transitional forms of mammal-like reptiles, called therapsids, that had a double jaw joint (i.e., two hinge points side by side)—one joint consisting of the bones that persist in the mammalian jaw and the other composed of the quadrate and articular bones, which eventually became the hammer and anvil of the mammalian ear.

For skeptical contemporaries of Darwin, the “missing link”—the absence of any known transitional form between apes and humans—was a battle cry, as it remained for uninformed people afterward. Not one but many creatures intermediate between living apes and humans have since been found as fossils. The oldest known fossil hominins—i.e., primates belonging to the human lineage after it separated from lineages going to the apes—are 6 million to 7 million years old, come from Africa, and are known as *Sahelanthropus* and *Orrorin* (or *Praeanthropus*), which were predominantly bipedal when on the ground but which had very small brains. *Ardipithecus* lived about 4.4 million years ago, also in Africa. Numerous fossil remains from diverse African origins are known of *Australopithecus*, a hominin that appeared between 3 million and 4 million years ago. *Australopithecus* had an upright human stance but a cranial capacity of less than 500 cc (equivalent to a brain weight of about 500 grams), comparable to that of a gorilla or a chimpanzee and about one-third that of humans. Its head displayed a mixture of ape and human characteristics—a low forehead and a long, apelike face but with teeth proportioned like those of humans. Other early hominins partly contemporaneous with *Australopithecus* include *Kenyanthropus* and *Paranthropus*; both had comparatively small brains, although some species of *Paranthropus* had larger bodies.

Paranthropus represents a side branch in the hominin lineage that became extinct. Along with increased cranial capacity, other human characteristics have been found in *Homo habilis*, which lived about 1.5 million to 2 million years ago in Africa and had a cranial capacity of more than 600 cc (brain weight of 600 grams), and in *H. erectus*, which lived between 0.5 million and more than 1.5 million years ago, apparently ranged widely over Africa, Asia, and Europe, and had a cranial capacity of 800 to 1,100 cc (brain weight of 800 to 1,100 grams). The brain sizes of *H. ergaster*, *H. antecessor*, and *H. heidelbergensis* were roughly that of the brain of *H. erectus*, some of which species were partly contemporaneous, though they lived in different regions of the Eastern Hemisphere.

Five hominins—members of the human lineage after it separated at least seven million to six million years ago from lineages going to the apes—are depicted in an artist's interpretation. All but *Homo sapiens*, the species that comprises modern humans, are extinct and have been reconstructed from fossil evidence.

5.3 CONCEPT & THEORIES OF EVOLUTION

(I) Lamarckism or Theory of Inheritance of Acquired characters.

(II) Darwinism or Theory of Natural Selection.

(III) Mutation theory of De - Vries.

(IV) Neo-Darwinism or Modern concept or Synthetic theory of evolution.

I. LAMARCKISM:

It is also called “Theory of inheritance of acquired characters” and was proposed by a great French naturalist, Jean Baptiste de Lamarck (Fig. 7.34) in 1809 A.D. in his famous book “Philosophic Zoologique”. This theory is based on the comparison between the contemporary species of his time to fossil records.

His theory is based on the inheritance of acquired characters which are defined as the changes (variations) developed in the body of an organism from normal characters, in response to the changes in environment, or in the functioning (use and disuse) of organs, in their own life time, to fulfill their new needs. Thus Lamarck stressed on adaptation as means of evolutionary modification.

A. POSTULATES OF LAMARCKISM:

Lamarckism is based on following four postulates:

1. New needs:

Every living organism is found in some kind of environment. The changes in the environmental factors like light, temperature, medium, food, air etc. or migration of animal lead to the origin of new needs in the living organisms, especially animals. To fulfill these new needs, the living organisms have to exert special efforts like the changes in habits or behavior.

2. Use and disuse of organs:

The new habits involve the greater use of certain organs to meet new needs, and the disuse or lesser use of certain other organs which are of no use in new conditions. This use and disuse of organs greatly affect the form, structure and functioning of the organs. Continuous and extra use of organs makes them more efficient while the continued disuse of some other organs lead to their degeneration and ultimate disappearance. So, Lamarckism is also called "Theory of use and disuse of organs." So the organism acquires certain new characters due to direct or indirect environmental effects during its own life span and are called Acquired or adaptive characters.

3. Inheritance of acquired characters:

Lamarck believed that acquired characters are inheritable and are transmitted to the offspring's so that these are born fit to face the changed environmental conditions and the chances of their survival are increased.

4. Speciation:

Lamarck believed that in every generation, new characters are acquired and transmitted to next generation, so that new characters accumulate generation after generation. After a number of generations, a new species is formed.

So according to Lamarck, an existing individual is the sum total of the characters acquired by a number of previous generations and the speciation is a gradual process.

Summary of four postulates of Lamarckism:

1. Living organisms or their component parts tend to increase in size.

2. Production of new organ is resulted from a new need.

3. Continued use of an organ makes it more developed, while disuse of an organ results in degeneration.

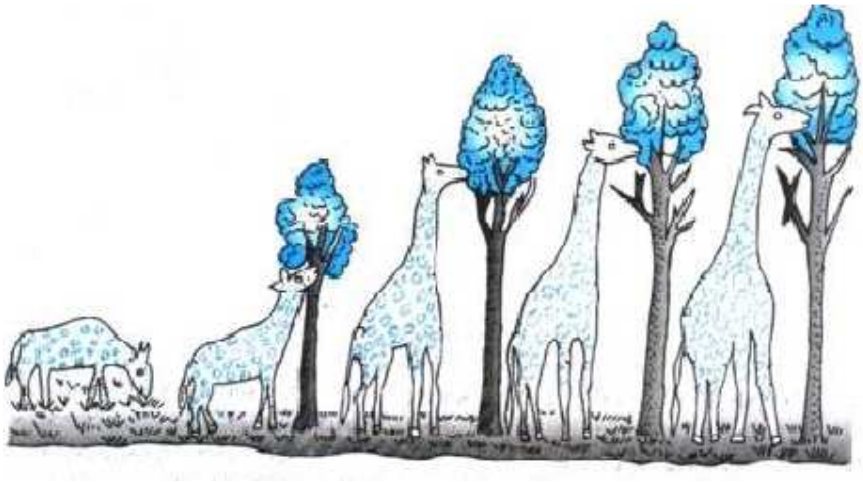
4. Acquired characters (or modifications) developed by individuals during their own lifetime are inheritable and accumulate over a period of time resulting a new species.

B. EVIDENCES IN FAVOUR OF LAMARCKISM:

1. Phylogenetic studies of horse, elephant and other animals show that all these increase in their evolution from simple to complex forms.

2. Giraffe

Development of present day long-necked and long fore-necked giraffe from deer-like ancestor by the gradual elongation of neck and forelimbs in response to deficiency of food on the barren ground in dry deserts of Africa. These body parts were elongated so as to eat the leaves on the tree branches. This is an example of effect of extra use and elongation of certain organs.



Stages in the evolution of present day Giraffe

3. Snakes:

Development of present day limbless snakes with long slender body from the limbed ancestors due to continued disuse of limbs and stretching of their body to suit their creeping mode of locomotion and fossorial mode of living out of fear of larger and more powerful mammals. It is an example of disuse and degeneration of certain organs.

4. Aquatic birds:

Development of aquatic birds like ducks, geese etc. from their terrestrial ancestors by the acquired characters like reduction of wings due to their continued disuse, development of webs between their toes for wading purposes. These changes were induced due to deficiency of food on land and severe competition. It is an example of both extra use (skin between the toes) and disuse (wings) of organs.

5. Flightless birds:

Development of flightless birds like ostrich from flying ancestors due to continued disuse of wings as these were found in well protected areas with plenty of food.

6. Horse:

The ancestors of modem horse (Equus caballus) used to live in the areas with soft ground and were short legged with more number of functional digits (e.g. 4 functional fingers and 3 functional toes in Dawn horse-Eohippus). These gradually took to live in areas with dry ground. This change in habit was accompanied by increase in length of legs and decrease in functional digits for fast running over hard ground.

C. CRITICISM OF LAMARCKISM:

A hard blow to Lamarckism came from a German biologist, August Weismann who proposed the "Theory of continuity of germplasm" in 1892 A.D. This theory states that environmental factors do affect only somatic cells and not the germ cells.

As the link between the generations is only through the germ cells and the somatic cells are not transmitted to the next generation so the acquired characters must be lost with the death of an organism so these should have no role in evolution. He suggested that germplasm is with special particles called "ids" which control the development of parental characters in offsprings.

Weismann mutilated the tails of mice for about 22 generations and allowed them to breed, but tailless mice were never born. Pavlov, a Russian physiologist, trained mice to come for food on hearing a bell. He reported that this training is not inherited and was necessary in every generation. Mendel's laws of inheritance also object the postulate of inheritance of acquired characters of Lamarckism.

Similarly, boring of pinna of external ear and nose in Indian women; tight waist, of European ladies circumcising (removal of prepuce) in certain people; small sized feet of Chinese women etc are not transmitted from one generation to another generator.

Eyes which are being used continuously and constantly develop defects instead of being improved. Similarly, heart size does not increase generation after generation though it is used continuously.

Presence of weak muscles in the son of a wrestler was also not explained by Lamarck. Finally, there are a number of examples in which there is reduction in the size of organs e.g. among Angiosperms, shrubs and herbs have evolved from the trees.

So, Lamarckism was rejected.

D. SIGNIFICANCE:

1. It was first comprehensive theory of biological evolution.
2. It stressed on adaptation to the environment as a primary product of evolution.

Neo-Lamarckism:

Long forgotten Lamarckism has been revived as Neo-Lamarckism, in the light of recent findings in the field of genetics which confirm that environment does affect the form, structure; colour, size etc. and these characters are inheritable.

Main scientists who contributed in the evolution of Neo-Lamarckism are: French Giard, American Cope, T.H. Morgan, Spencer, Packard, Bonner, Tower, Naegali, Mc Dougal, etc. Term neo-Lamarckism was coined by Alphaeus S. Packard.

Neo-Lamarckism states:

1. Germ cells may be formed from the somatic cells indicating similar nature of chromosomes and gene make up in two cell lines e.g.

(a) Regeneration in earthworms.

(b) Vegetative propagation in plants like Bryophyllum (with foliar buds).

(c) A part of zygote (equipotential egg) of human female can develop into a complete baby (Driesch).

2. Effect of environment on germ cells through the somatic cells e.g. Heslop Harrison found that a pale variety of moth, Selenia bilunaria, when fed on manganese coated food, a true breeding melanic variety of moth is produced.

3. Effect of environment directly on germ cells. Tower exposed the young ones of some potato beetles to temperature fluctuation and found that though beetles remained unaffected with no somatic change but next generation had marked changes in body colouration. **Muller confirmed the mutagenic role of X-rays on Drosophila while C. Auerbach et., al. confirmed the chemical mutagens (mustard gas vapours) causing mutation in Drosophila melanogaster, so neo-Lamarckism proved:**

(a) Germ cells are not immune from the effect of environment.

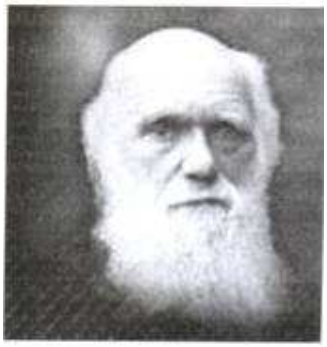
(b) Germ cells can carry somatic changes to next progeny (Harrison's experiment).

(c) Germ cells may be directly affected by the environmental factors (Tower's experiment).

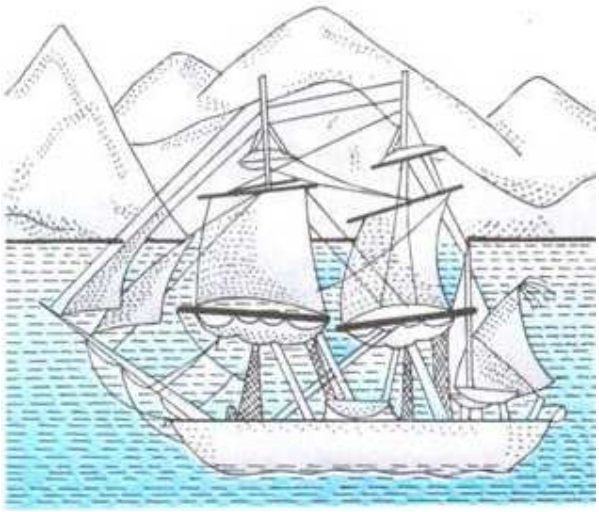
II. DARWINISM (THEORY OF NATURAL SELECTION):

A. INTRODUCTION:

Charles Darwin (1809- 1882 A.D.), an English naturalist, was the most dominant figure among the biologists of the 19th century. He made an extensive study of nature for over 20 years, especially in 1831-1836 when he went on a voyage on the famous ship "H.M.S. Beagle" (Fig. 7.37) and explored South America, the Galapagos Islands and other islands.



Charles Robert Darwin



HMS beagle ship

He collected the observations on animal distribution and the relationship between living and extinct animals. He found that existing living forms share similarities to varying degrees not only among themselves but also with the life forms that existed millions of years ago, some of which have become extinct.

He stated that every population has built in variations in their characters. From the analysis of his data of collection and from Malthus's Essay on Population, he got the idea of struggle for existence within all the populations due to continued reproductive pressure and limited resources and that all organisms, including humans, are modified descendants of previously existing forms of life.

In 1858 A.D., Darwin was highly influenced by a short essay entitled "On the Tendency of Varieties to Depart Indefinitely from the Original Type" written by another naturalist, Alfred Russel Wallace (1812-1913) who studied biodiversity on Malayan archipelago and came to similar conclusions.

Darwin and Wallace's views about evolution were presented in the meeting of Linnaean Society of London by Lyell and Hooker on July 1, 1858. Darwin's and Wallace's work was jointly published in "Proceedings of Linnean Society of London" in 1859. So it is also called Darwin-Wallace theory.

Darwin explained his theory of evolution in a book entitled "On the Origin of Species by means of Natural Selection". It was published on 24th Nov., 1859. In this theory, Charles Darwin proposed the concept of natural selection as the mechanism of evolution.

B. Postulates of Darwinism:

Main postulates of Darwinism are:

1. Geometric increase.

2. Limited food and space.

3. Struggle for existence.

4. Variations.

5. Natural selection or Survival of the fittest.

6. Inheritance of useful variations.

7. Speciation.

1. Geometric increase:

According to Darwinism, the populations tend to multiply geometrically and the reproductive powers of living organisms (biotic potential) are much more than required to maintain their number e.g.,

Paramecium divides three times by binary fission in 24 hours during favorable conditions. At this rate, a Paramecium can produce a clone of about 280 million Paramecia in just one month and in five years, can produce Paramecia having mass equal to 10,000 times than the size of the earth.

Other rapidly multiplying organisms are: Cod (one million eggs per year); Oyster (114 million eggs in one spawning); Ascaris (70, 00,000 eggs in 24 hours); housefly (120 eggs in one laying and laying eggs six times in a summer season); a rabbit (produces 6 young ones in a litter and four litters in a year and young ones start breeding at the age of six months).

Similarly, the plants also reproduce very rapidly e.g., a single evening primrose plant produces about 1, 18,000 seeds and single fern plant produces a few million spores.

Even slow breeding organisms reproduce at a rate which is much higher than required e.g., an elephant becomes sexually mature at 30 years of age and during its life span of 90 years, produces only six offspring's. At this rate, if all elephants survive then a single pair of elephants can produce about 19 million elephants in 750 years.

These examples confirm that every species can increase manifold within a few generations and occupy all the available space on the earth, provided all survive and repeat the process. So the number of a species will be much more than can be supported on the earth.

2. Limited food and space:

Darwinism states that though a population tends to increase geometrically, the food increases only arithmetically. So two main limiting factors on the tremendous increase of a population are: limited food and space which together form the major part of carrying capacity of environment. These do not allow a population to grow indefinitely which are nearly stable in size except for seasonal fluctuation.

3. Struggle for existence:

Due to rapid multiplication of populations but limited food and space, there starts an everlasting competition between individuals having similar requirements. In this competition, every living organism desires to have an upper hand over others.

This competition between living organisms for the basic needs of life like food, space, mate etc., is called struggle for existence which is of three types:

(a) Intraspecific:

Between the members of same species e.g. two dogs struggling for a piece of meat.

(b) Interspecific:

Between the members of different species e.g. between predator and prey.

(c) Environmental or Extra specific:

Between living organisms and adverse environmental factors like heat, cold, drought, flood, earthquakes, light etc.

Out of these three forms of struggle, the intraspecific struggle is the strongest type of struggle as the needs of the individuals of same species are most similar e.g., sexual selection in which a cock with a more beautiful comb and plumage has better chances to win a hen than a cock with less developed comb.

Similarly, cannabilism is another example of intraspecific competition as in this; individuals eat upon the members of same species.

In this death and life struggle, the majority of individuals die before reaching the sexual maturity and only a few individuals survive and reach the reproductive stage. So struggle for existence acts as an effective check on an ever-increasing population of each species.

The nature appears saying, "They are weighed in the balance and are found wanting." So the number of offspring's of each species remains nearly constant over long period of time.

4. Variations:

Variation is the law of nature. According to this law of nature, no two individuals except identical (monozygotic) twins are identical. This everlasting competition among the organisms has compelled them to change according to the conditions to utilize the natural resources and can survive successfully.

Darwin stated that the variations are generally of two types—continuous variations or fluctuations and discontinuous variations. On the basis of their effect on the survival chances of living organisms, the variations may be neutral, harmful and useful.

Darwin proposed that living organisms tend to adapt to changing environment due to useful continuous variations {e.g., increased speed in the prey; increased water conservation in plants; etc.), as these will have a competitive advantage.

5. Natural selection or Survival of the fittest:

Darwin stated that as many selects the individuals with desired characters in artificial selection; nature selects only those individuals out of the population which are with useful continuous variations and are best adapted to the environment while the less fit or unfit individuals are rejected by it.

Darwin stated that if the man can produce such a large number of new species/varieties with limited resources and in short period of time by artificial selection, then natural selection could account for this large biodiversity by considerable modifications of species with the help of unlimited resources available over long span of time.

Darwin stated that discontinuous variations appear suddenly and will mostly be harmful, so are not selected by nature. He called them "sports". So the natural selection is an automatic and self-going process and keeps a check on the animal population.

This sorting out of the individuals with useful variations from a heterogeneous population by the nature was called Natural selection by Darwin and Survival of the fittest by Wallace. So natural selection acts as a restrictive force and not a creative force.

6. Inheritance of useful variations:

Darwin believed that the selected individuals pass their useful continuous variations to their offspring's so that they are born fit to the changed environment.

7. Speciation:

According to Darwinism, useful variations appear in every generation and are inherited from one generation to another. So the useful variations go on accumulating and after a number of generations, the variations become so prominent that the individual turns into a new species. So according to Darwinism, evolution is a gradual process and speciation occurs by gradual changes in the existing species.

Thus the two key concepts of Darwinian Theory of Evolution are:

1. Branching Descent, and 2. Natural Selection.

C. EVIDENCES IN FAVOUR OF DARWINISM:

1. There is a close parallelism between natural selection and artificial selection.

2. The remarkable cases of resemblance e.g. mimicry and protective coloration can be achieved only by gradual changes occurring simultaneously both in the model and the mimic.

3. Correlation between position of nectarines in the flowers and length of the proboscis of the pollinating insect.

D. EVIDENCES AGAINST DARWINISM:

Darwinism is not able to explain:

1. The inheritance of small variations in those organs which can be of use only when fully formed e.g. wing of a bird. Such organs will be of no use in incipient or underdeveloped stage.

2. Inheritance of vestigial organs.

3. Inheritance of over-specialized organs e.g. antlers in deer and tusks in elephants.

4. Presence of neuter flowers and sterility of hybrids.

5. Did not differentiate between somatic and germinal variations.

6. He did not explain the causes of the variations and the mode of transmission of variations.

7. It was also refuted by Mendel's laws of inheritance which state that inheritance is particulate.

So this theory explains only the survival of the fittest but does not explain the arrival of the fittest so Darwin himself confessed, "natural selection has been main but not the exclusive means of modification."

PRINCIPLE OF NATURAL SELECTION:

It was proposed by Ernst Mayer in 1982. It stems from five important observations and three inferences. This principle demonstrates that natural selection is the differential success in reproduction and enables the organisms to adapt them to their environment by development of small and useful variations.

These favorable Variations accumulate over generation after generation and lead to speciation. So natural selection operates through interactions between the environment and inherent variability in the population.

III. Mutation Theory of Evolution:

The mutation theory of evolution was proposed by a Dutch botanist, Hugo de Vries (1848-1935 A.D.) (Fig. 7.38) in 1901 A.D. in his book entitled "Species and Varieties, Their Origin by Mutation". He worked on evening primrose (Oenothera lamarckiana).

A. EXPERIMENT:

Hugo de Vries cultured O. lamarckiana in botanical gardens at Amsterdam. The plants were, allowed to self-pollinate and next generation was obtained. The plants of next generation were again subjected to self-pollination to obtain second generation. Process was repeated for a number of generations.

B. OBSERVATIONS:

Majority of plants of first generation were found to be like the parental type and showed only minor variations but 837 out of 54,343 members were found to be very different in characters like flower size, shape and arrangement of buds, size of seeds etc. These markedly different plants were called primary or elementary species.

A few plants of second generation were found to be still more different. Finally, a new type, much longer than the original type. He also found the numerical chromosomal changes in the variants (e.g. with chromosome numbers 16, 20, 22, 24, 28 and 30) up to 30 (Normal diploid number is 14).

C. CONCLUSION:

1. The evolution is a discontinuous process and occurs by mutations (L. mutate = to change; sudden and inheritable large differences from the normal and are not connected to normal by intermediate forms). Individuals with mutations are called mutants.

2. Elementary species are produced in large number to increase chances of selection by nature.

3. Mutations are recurring so that the same mutants appear again and again. This increases the chances of their selection by nature.

4. Mutations occur in all directions so may cause gain or loss of any character.

5. Mutability is fundamentally different from fluctuations (small and directional changes).

So according to mutation theory, evolution is a discontinuous and jerky process in which there is a jump from one species to another so that new species arises from pre-existing species in a single generation (macro genesis or saltation) and not a gradual process as proposed by Lamarck and Darwin.

D. EVIDENCES IN FAVOUR OF MUTATION THEORY:

1. Appearance of a short-legged sheep variety, Ancon sheep from long-legged parents in a single generation in 1791 A.D. It was first noticed in a ram (male sheep) by an American farmer, Seth Wright.

Appearance of short legged Ancon Sheep

2. Appearance of polled Hereford cattle from horned parents in a single generation in 1889.

3. De Vries observations have been experimentally confirmed by McDougal and Shull in America and Gates in England.

4. Mutation theory can explain the origin of new varieties or species by a single gene mutation e.g. Cicer gigas, Nuval orange. Red sunflower, hairless cats, double- toed cats, etc.

5. It can explain the inheritance of vestigial and over-specialized organs.

6. It can explain progressive as well as retrogressive evolution.

E. EVIDENCES AGAINST MUTATION THEORY:

1. It is not able to explain the phenomena of mimicry and protective colouration.

2. Rate of mutation is very low, i.e. one per million or one per several million genes.

3. Oenothera lamarckiana is a hybrid plant and contains anamolous type of chromosome behaviour.

4. Chromosomal numerical changes as reported by de Vries are unstable.

5. Mutations are incapable of introducing new genes and alleles into a gene pool.

IV. NEO-DARWINISM OR MODERN CONCEPT OR SYNTHETIC THEORY OF EVOLUTION:

The detailed studies of Lamarckism, Darwinism and Mutation theory of evolution showed that no single theory is fully satisfactory. Neo-Darwinism is a modified version of theory of Natural Selection and is a sort of reconciliation between Darwin's and de Vries theories.

Modern or synthetic theory of evolution was designated by Huxley (1942). It emphasizes the importance of populations as the units of evolution and the central role of natural selection as the most important mechanism of evolution.

The scientists who contributed to the outcome of Neo-Darwinism were: J.S. Huxley, R.A. Fischer and J.B.S. Haldane of England; and S. Wright, Ford, H.J. Muller and T. Dobzhansky of America.

A. POSTULATES OF NEO-DARWINISM:

1. Genetic Variability:

Variability is an opposing force to heredity and is essential for evolution as the variations form the raw material for evolution. The studies showed that the units of both heredity and mutations are genes which are located in a linear manner on the chromosomes.

Various sources of genetic variability in a gene pool are:

(i) Mutations:

These are sudden, large and inheritable changes in the genetic material. On the basis of amount of genetic material involved, mutations are of three types:

(a) Chromosomal aberrations:

These include the morphological changes in the chromosomes without affecting the number of chromosomes. These result changes either in the number of genes (deletion and duplication) or in the position of genes (inversion).

These are of four types:

1. Deletion (Deficiency) involves the loss of a gene block from the chromosome and may be terminal or intercalary.

2. Duplication involves the presence of some genes more than once, called the repeat. It may be tandem or reverse duplication.

3. Translocation involves transfer of a gene block from one chromosome to a non-homologous chromosome and may be simple or reciprocal type.

4. Inversion involves the rotation of an intercalary gene block through 180° and may be Para centric or pericentric.

(b) Numerical chromosomal mutations:

These include changes in the number of chromosomes. These may be euploidy (gain or loss of one or more genomes) or aneuploidy (gain or loss of one or two chromosomes). Euploidy may be haploidy or polyploidy.

Among polyploidy, tetraploidy is most common. Polyploidy provides greater genetic material for mutations and variability. In haploids, recessive genes express in the same generation.

Aneuploidy may be hypoploidy or hyperploidyl Hypoploidy may be monosomy (loss of one chromosome) or nullisomy (loss of two chromosomes). Hyperploidy may be trisomy (gain of one chromosome) or tetrasomy (gain of two chromosomes).

(c) Gene mutations (Point mutations):

These are invisible changes in chemical nature (DNA) of a gene and are of three types:

1. Deletion involves loss of one or more nucleotide pairs.

2. Addition involves gain of one or more nucleotide pairs.

3. Substitution involves replacement of one or more nucleotide pairs by other base pairs. These may be transition or trans version type.

These changes in DNA cause the changes in the sequence of amino acids so changing the nature of proteins and the phenotype.

(ii) Recombination of genes:

Thousands of new combinations of genes are produced due to crossing over, chance arrangement of bivalents at the equator during metaphase – I and chance fusion of gametes during fertilization.

(iii) Hybridization:

It involves the interbreeding of two genetically different individuals to produce 'hybrids'.

(iv) Physical mutagens (e.g. radiations, temperature etc.) and chemical mutagens (e.g. nitrous acid, colchicine, nitrogen mustard etc.).

(v) Genetic drift:

It is the elimination of the genes of some original characteristics of a species by extreme reduction in a population due to epidemics or migration or Sewell Wright effect.

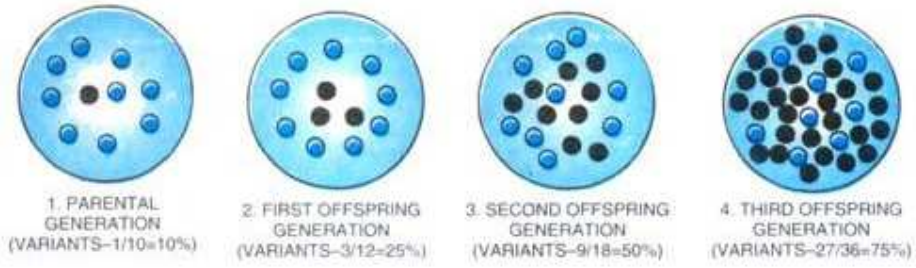
The chances of variations are also increased by non-random mating.

2. Natural Selection:

Natural selection of Neo- Darwinism differs from that of Darwinism that it does not operate through "survival of the fittest" but operates through differential reproduction and comparative reproductive success.

Differential reproduction states that those members, which are best adapted to the environment, reproduce at a higher rate and produce more offsprings than those which are less adapted. So these contribute proportionately greater percentage of genes to the gene pool of next generation while less adapted individuals produce fewer offsprings.

If the differential reproduction continues for a number of generations, then the genes of those individuals which produce more offspring's will become predominant in the gene pool of the population.



Spread of Genetic variability by differential reproduction

Due to sexual communication, there is free flow of genes so that the genetic variability which appears in certain individuals, gradually spreads from one deme to another deme, from deme to population and then on neighboring sister populations and finally on most of the members of a species. So natural selection causes progressive changes in gene frequencies, 'i.e. the frequency of some genes increases while the frequency of some other genes decreases.

Which individuals produce more offspring's?

(i) Mostly those individuals who are best adapted to the environment.

(ii) Whose sum of the positive selection pressure due to useful genetic variability is more than the sum of negative selection pressure due to harmful genetic variability?

(iii) Which have better chances of sexual selection due to development of some bright coloured spots on their body e.g. in many male birds and fish.

(iv) Those who are able to overcome the physical and biological environmental factors to successfully reach the sexual maturity.

So natural selection of Neo-Darwinism acts as a creative force and operates through comparative reproductive success. Accumulation of a number of such variations leads to the origin of a new species.

3. Reproductive isolation:

Any factor which reduces the chances of interbreeding between the related groups of living organisms is called an isolating mechanism. Reproductive isolation is must so as to allow the accumulation of variations leading to speciation by preventing hybridization.

In the absence of reproductive isolation, these variants freely interbreed which lead to intermixing of their genotypes, dilution of their peculiarities and disappearance of differences between them. So, reproductive isolation helps in evolutionary divergence.

5.4 HARDY-WEINBERG LAW OF GENETIC EQUILIBRIUM

This fundamental idea in population genetics was offered by the Englishman G.H. Hardy (a mathematician) and the German W. Weinberg simultaneously in the year 1908. It is known as the Hardy-Weinberg law.

Mendelian genetics were rediscovered in 1900. However, it remained somewhat controversial for several years as it was not then known how it could cause continuous characteristics. Udny Yule (1902) argued against Mendelism because he thought that dominant alleles would increase in the population. The AmericanWilliam E. Castle (1903) showed that without selection, the genotype frequencies would remain stable. Karl Pearson (1903) found one equilibrium position with values of $p = q = 0.5$. Reginald Punnett, unable to counter Yule's point, introduced the problem to G. H. Hardy, a Britishmathematician, with whom he played cricket. Hardy was a pure mathematician and held applied mathematics in some contempt; his view of biologists' use of mathematics comes across in his 1908 paper where he describes this as "very simple".

To the Editor of Science: I am reluctant to intrude in a discussion concerning matters of which I have no expert knowledge, and I should have expected the very simple point which I wish to make to have been familiar to biologists. However, some remarks of Mr. Udny Yule, to which Mr. R. C. Punnett has called my attention, suggest that it may still be worth making...

Suppose that Aa is a pair of Mendelian characters, A being dominant, and that in any given generation the number of pure dominants (AA), heterozygotes (Aa), and pure recessives (aa) are asp:2q:r. Finally, suppose that the numbers are fairly large, so that mating may be regarded as random, that the sexes are evenly distributed among the three varieties, and that all are equally fertile. A little mathematics of the multiplication-table type is enough to show that in the next generation the numbers will be as $(p + q)^2$: 2 $(p + q)(q + r)$:$(q + r)^2$, or as p_1:$2q_1$:r_1, say.

The interesting question is: in what circumstances will this distribution be the same as that in the generation before? It is easy to see that the condition for this is$q^2 = pr$. And since $q_1^2 = p_1 r_1$, whatever the values ofp, q, andrmay be, the distribution will in any case continue unchanged after the second generation

The principle was thus known as *Hardy's law* in the English-speaking world until 1943, when Curt Stern pointed out that it had first been formulated independently in 1908 by the German physician Wilhelm Weinberg. William Castle in 1903 also derived the ratios for the special case of equal allele frequencies, and it is sometimes (but rarely) called the Hardy–Weinberg–Castle Law.

The law forms the foundation of population genetics and of modern evolutionary theory. The law states that: both gene (allelic) frequencies and genotype frequencies will remain constant from generation to generation in an infinitely large interbreeding population in which mating is at random and no selection, migration or mutation occurs. Should a population initially be in disequilibrium, one generation of random mating is sufficient to bring it into genetic equilibrium and thereafter the population will remain in equilibrium (unchanged in gametic and zygotic frequencies) as long as Hardy-Weinberg condition persists.

Hardy-Weinberg law depends on the following kinds of genetic equilibrium for its full attainment.

1. The population is infinitely large and mate at random.

2. No selection is operative.

3. No mutation is operative in alleles.

4. The-population is closed, i.e., no immigration or emigration occurs.

5. Meiosis is normal so that chance is the only factor operative in gametogenesis.

The law describes a theoretical situation in which a population is undergoing no evolutionary change. It explains that if evolutionary forces are absent; the population is large; its individuals have random mating, each parent produces roughly equal number of gametes and the gametes produced by the mating parents combine at random and the gene frequency remains constant; then the genetic equilibrium of the genes in question is maintained and the variability present in the population is preserved. Suppose there is a panmictic population with gene (allele) A and a on one locus, then the frequency of gametes with gene A will be

the same as the frequency of gene A and similarly the frequency of gametes with a will be equal to the frequency of gene a. Let us presume that the numerical proportion of different gene in this population is as follows:

AA- 36%

Aa- 48%

aa -16%

Since AA individuals make up 36% of the total population they will contribute approximately 36% of all the gametes formed in the population. These gametes will possess gene A. Similarly, aa individuals will produce 16% of all the gametes. But the gametes from Aa individuals will be of two types i.e., with gene A and gene a roughly in equal proportion. Since these constitute together 48% of the total population, they will contribute 48% gametes but out of them 24% will possess gene A and the other 24% will have gene a. Hence the overall output of the gametes 'will be as follows:

Parents	Gametes	Parents	Gametes
36% AA	36% A	16% aa	16% a
48% Aa	24% A	48% Aa	24% a
Total	60% A	Total	40% a

If the gametes unite at random, the total number of different genotypes will be :

Sperms	Ova	Gene Frequency	Offspring
A	A	60×60	36% AA
A	a	60×40	24% Aa
a	A	40×60	24% Aa
a	a	40×40	16% aa

If frequency of gene A is represented by p and frequency of gene a is represented by q and there is a random mating of the gametes with allele A arid a at the equilibrium state, the population will contain the following frequencies of the genes A and a, generation after generation.

AA + 2Aa + aa genotype

$p^2 + 2pq + q^2$ gene (allele) frequency

The above results could be explained by relying on the theory of probability. In a population of large size, the probability of receiving the gene A from both parents will be p x p = p^2, similarly, for gene a it will be q x q = q^2 and the probability of being heterozygous will be pq

+ pq = 2pq. The relationship between gene (allele) frequency and genotype frequency can be expressed as

$p^{2+}2pq + q^2 = 1$ or $(p + q)^2 = 1$

This is known as Hardy-Weinberg formula or binomial expression. If the frequency of one of the alleles (e.g., p) is known then the frequency of the other allele (q = 1-p) is known, and the frequencies of the homozygous genotypes (p^2 and q^2) as well as those of the heterozygous genotype (2pq) can be calculated. Or, if the frequency of homozygous recessive individuals in the population (a/a or q^2) is known, then the frequencies of the allele (q) and the A allele (p or 1-q) can be calculated. It is then possible to predict genotypic frequencies in the present and further generations. From this binomial expression, proposed by Hardy and Weinberg, it is clear that in a large random mating population not only gene frequencies but also the genotype frequencies will remain constant.

SALIENT FEATURES OF HARDY-WEINBERG LAW:

1. The gene and genotype frequencies of each gene or allele in a population remain at an equilibrium generation after generation.

2. In a population, the mating is a completely random phenomenon.

3. The equilibrium in the gene and genotype frequencies occurs only in large sized populations. In a small population gene frequencies may be unpredictable.

4. All the genotypes in a population reproduce equally successfully.

5. Particular alleles will neither be differentially added to nor differentially subtracted from a population.

SIGNIFICANCE OF HARDY-WEINBERG LAW:

The law is important primarily because it describes the situation in which there is no evolution, and thus it provides a theoretical baseline for measuring evolutionary change. The equilibrium tendency serves to conserve gains which have been made in the past and also to avoid too rapid changes; in other words, giving a genetic stability to the population.

The Hardy-Weinberg equation describes conditions that are not found in natural population. The function of the Hardy-Weinberg principle, and its equation, is as an experimental control— a prediction of what the allelic and genotypic frequencies should be if nothing acts

to alter the gene pool. Thus, if q is known to be 0.40 then q^2 in the next generation should be 0.16.

If instead it is 0.02, then we know that a change has occurred in the gene pool, the magnitude of that change, and that it was caused by: mutations, genetic drift, gene flow, assertive mating, or natural selection. We can then design experiments to test which of the five agents of change contributed most to the change in allelic and genotypic frequencies.

Deviations from Hardy–Weinberg equilibrium

The seven assumptions underlying Hardy–Weinberg equilibrium are as follows:[3]

- organisms are diploid
- only sexual reproduction occurs
- generations are nonoverlapping
- mating is random
- population size is infinitely large
- allele frequencies are equal in the sexes
- there is no migration, gene flow, admixture, mutation or selection

Violations of the Hardy–Weinberg assumptions can cause deviations from expectation. How this affects the population depends on the assumptions that are violated.

- Random mating. The HWP states the population will have the given genotypic frequencies (called Hardy–Weinberg proportions) after a single generation of random mating within the population. When the random mating assumption is violated, the population will not have Hardy–Weinberg proportions. A common cause of non-random mating is inbreeding, which causes an increase in homozygosis for all genes.

If a population violates one of the following four assumptions, the population may continue to have Hardy–Weinberg proportions each generation, but the allele frequencies will change over time.

- Selection, in general, causes allele frequencies to change, often quite rapidly. While directional selection eventually leads to the loss of all alleles except the favored one (unless one allele is dominant, in which case recessive alleles can survive at low

frequencies), some forms of selection, such as balancing selection, lead to equilibrium without loss of alleles.

- Mutation will have a very subtle effect on allele frequencies. Mutation rates are of the order 10^{-4} to 10^{-8}, and the change in allele frequency will be, at most, the same order. Recurrent mutation will maintain alleles in the population, even if there is strong selection against them.
- Migration genetically links two or more populations together. In general, allele frequencies will become more homogeneous among the populations. Some models for migration inherently include nonrandom mating (Wahlund effect, for example). For those models, the Hardy–Weinberg proportions will normally not be valid.
- Small population size can cause a random change in allele frequencies. This is due to a sampling effect, and is called genetic drift. Sampling effects are most important when the allele is present in a small number of copies.

In real world genotype data, deviations from Hardy-Weinberg Equilibrium may be a sign of genotyping error.

5.5 DETAILED ACCOUNT OF DESTABILIZING FORCES

It's hard for us, with our typical human life spans of less than 100 years, to imagine all the way back, 3.8 billion years ago, to the origins of life. Scientists still study and debate how life came into being and whether it originated on Earth or in some other region of the universe (including some scientists who believe that studying evolution can reveal the complex processes that were set in motion by God or a higher power). What we do know is that a living single-celled organism was present on Earth during the early stages of our planet's existence. This organism had the potential to reproduce by making copies of itself, just like bacteria, many amoebae, and our own living cells today. In fact, with today's genetic and genomic technologies, we can now trace genetic lineages, or phylogenies, and determine the relationships between all of today's living organisms—eukaryotes (animals, plants, fungi, etc.), archaea, and bacteria—on the branches of the phylogenetic tree of life. Looking at the common sequences in modern genomes, we can even make educated guesses about what the genetic sequence of the first organism, or universal ancestor of all living things, would likely have been. Through a wondrous series of mechanisms and events, that first single-celled organism gave rise to the rich diversity of species that fill the lands, seas, and skies of our

planet. This chapter explores the mechanisms by which that amazing transformation occurred and considers some of the crucial scientific experiments that shaped our current understanding of the evolutionary process.

5.5.1 NATURAL SELECTION

(i) Definition:The process by which comparatively better adapted individuals out of a heterogeneous population are favoured by the Nature over the less adapted individuals is called natural selection.

(ii) Mechanism: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's 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's. If differential reproduction continues for a number of generations, then the genes of those individuals which produce more offspring's will become predominant in the gene pool of the population:

Due to sexual communication, there is free flow of genes so that the genetic variability which appears in certain individuals, gradually spreads from one deme to another deme, from deme to population and then on neighboring sister populations and finally on most of the members of a species. So natural selection causes progressive changes in gene frequencies, i.e. the frequency of adaptive genes increases while the frequency of less adaptive genes decreases. So natural selection of Neo-Darwinism acts as a creative force and operates through comparative reproductive success. Accumulation of such variations leads to the origin of a new species.

(iii) Typesof Natural selection:The three different types of natural selections observed are:

1. Stabilizing or balancing selection:It leads to the elimination of organisms having overspecialized characters and maintains homogenous population which is genetically constant. It favours the average or normal phenotypes, while eliminates the individuals with extreme expressions. In this, more individuals acquire mean character value. It reduces variation but does not change the mean value. It results very slow rateof evolution. If we draw a graphical curve of population, it is bell-shaped. The bell-shaped curve narrows due to elimination of extreme variants.

Example:Sickle-cell anaemia in human beings.

2. Directional or Progressive selection: In this selection, the populationchanges towards one particular direction along with change in environment. As environment is undergoing a continuous change, the organisms having acquired new characters survive and others are eliminated gradually. In this, individuals at one extreme (less adapted) are eliminated while individuals at other extreme (more adapted) are favoured. This produces more andmore adapted individuals in the population when such a selection operates for many generations. In this type of selection, more individuals acquire value other than mean character value.

Examples: Industrial melanism: In this, number of the light coloured moths {Biston betularia) decreased gradually while that of the melanic moths (B. carbonaria) increased showing directional selection. DDT-resistant mosquitoes:In this, sensitive mosquitoeswere eliminated and resistant ones increased in number. So the population of resistant mosquitoes increased showing directional selection.

3. Disruptive selection: It is a type of natural selection which favours extreme expressions of certain traits to increase variance in a population. It breaks a homogeneous population into many adaptive forms. It results in balanced polymorphism. In this type of selection, more individuals acquire peripheral character value at both ends of the distribution curve. This kind of selection is rare and eliminates most of the members with mean expression so producing two peaks in the distribution of a trait

Example: In sea, the three types of snails i.e. white coloured; brown coloured and black coloured are present. The white coloured snails are invisible when covered by barnacles. The black coloured snails are invisible when rock is bare. But brown coloured snails are eaten by predators in both the conditions. So these are eliminated gradually

5.5.2 MUTATION

These are characterized by:

(i) These are sudden, large and inheritable changes in the genetic material.

(ii) Mutations are random (indiscriminate) and occur in all directions.

(iii) Most mutations are harmful or neutral. It is estimated that only one out of 1,000 mutations is useful.

(iv) Rate of mutation is very low, i.e. one per million or one per several million genie loci. But rate of mutation is sufficient to produce considerable genetic variability.

(v) Certain mutations are preadaptive and appear even without exposure to a specific environment. These express and become advantageous only when after exposure to new environment which only selects the preadaptive mutations that occurred earlier. Existence of preadaptive mutations in Escherichia coli was experimentally demonstrated by Esther Lederberg (1952) in replica plating experiment (Explained in Neo-Darwinism).

(vi) Onthe basis of amount of genetic material involved, mutations are of three types

(vii) On the basis of their origin, mutations are of two types

Differences between Spontaneous and Induced mutations.			
Characters	Spontaneous mutations	Induced mutations	
Caused by	By natural agents, so also called natural mutations or background mutations.	By man	
Frequency of mutations	Very low (about one per million genes or even more)	Faster	
Causes	Not certain, many cellular products e.g. formaldehyde, nitrous acid, peroxides, etc. act as mutagens	Certain physical {e.g. radiations temperature, etc.) and chemical agents called mutagens	

5.5.3 GENETIC DRIFT

Genetic Drift: It is the random change in the frequency of alleles occurring by chance fluctuations. It is characterized by:

(viii) It is a binomial sampling error of the gene pool, i.e. that alleles which form the gene pool of the next generation are a sample of the alleles of present population.

(ix) Genetic drift always influences frequencies of alleles and is inversely proportional to the size of population. So genetic drift is most important in very small populations in which there are increased chances of inbreeding which increases the frequency of individuals homozygous for recessive alleles, many of which maybe deleterious.

(x) Genetic drift occurs when a small group separates from a larger population and may not have all the alleles or may differ from the parental population in the frequencies of certain genes. This explains for the difference between island populations and mainland population.

(xi) In a small population, a chance event (e.g. snow storm) may increase the frequency of a character having little adaptive value.

(xii) Genetic drift can also operate through founder effect. In this, genetic drift can cause dramatic changes in the allele frequencies in a population derived from small groups of colonizers, called founders, to a new habitat. These founders do not have all of the alleles found in their source population. These founders become quickly different from the parental population and may form a new species, e.g. evolution of Darwin finches on Galapagos Islands which were probably derived from a few initial founders.

(xiii) Population bottleneck: It is reduction in allele frequencies caused by drastic reduction in population size called population crash e.g. decrease in cheetah population in Africa due to over-hunting. As the given gene pool is limited, population bottleneck often prevents the species to reestablish its former richness so new population has a much restricted gene pool than the larger parent population.

5.5.4 MIGRATION

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.

UNIT 6: QUANTIFYING GENETIC VARIABILITY

6.1 Objectives
6.2 Introduction
6.3 Genetic structure of Natural Populations
6.4 Phenotypic Variations
6.4.1 Phenotype & Phenotypic Variation

6.1 OBJECTIVES

We study about Genetic structure of Natural Populations Phenotypic Variations in this topic.

6.2 INTRODUCTION

Population genetics began as a reconciliation of Mendelian inheritance and biostatistics models. Natural selection will only cause evolution if there is enough genetic variation in a population. Before the discovery of Mendelian genetics, one common hypothesis was blending inheritance. But with blending inheritance, genetic variance would be rapidly lost, making evolution by natural or sexual selection implausible. The Hardy–Weinberg principle provides the solution to how variation is maintained in a population with Mendelian inheritance. According to this principle, the frequencies of alleles (variations in a gene) will remain constant in the absence of selection, mutation, migration and genetic drift. The next key step was the work of the British biologist and statistician Ronald Fisher. In a series of papers starting in 1918 and culminating in his 1930 book *The Genetical Theory of Natural Selection*, Fisher showed that the continuous variation measured by the biometricians could be produced by the combined action of many discrete genes, and that natural selection could change allele frequencies in a population, resulting in evolution. In a series of papers beginning in 1924, another British geneticist, J. B. S. Haldane, worked out the mathematics of allele frequency change at a single gene locus under a broad range of conditions. Haldane also applied statistical analysis to real-world examples of natural selection, such as peppered moth evolution and industrial melanism, and showed that selection coefficients could be

larger than Fisher assumed, leading to more rapid adaptive evolution as a camouflage strategy following increased pollution.

6.3 GENETIC STRUCTURE OF NATURAL POPULATIONS

Population genetics is a subfield of genetics that deals with genetic differences within and between populations, and is a part of evolutionary biology. Studies in this branch of biology examine such phenomena as adaptation, speciation, and population structure.

Population genetics was a vital ingredient in the emergence of the modern evolutionary synthesis. Its primary founders were Sewall Wright, J. B. S. Haldane and Ronald Fisher, who also laid the foundations for the related discipline of quantitative genetics. Traditionally a highly mathematical discipline, modern population genetics encompasses theoretical, laboratory, and field work. Population genetic models are used both for statistical inference from DNA sequence data and for proof/disproof of concept.

What sets population genetics apart from newer, more phenotypic approaches to modelling evolution, such as evolutionary game theory and adaptive dynamics, is its emphasis on such genetic phenomena as dominance, epistasis, the degree to which genetic recombination breaks linkage disequilibrium, and the random phenomena of mutation and genetic drift. This makes it appropriate for comparison to population genomics data.

MODERN SYNTHESIS

The mathematics of population genetics were originally developed as the beginning of the modern synthesis. Authors such as Beatty have asserted that population genetics defines the core of the modern synthesis. For the first few decades of the 20th century, most field naturalists continued to believe that Lamarckism and orthogenesis provided the best explanation for the complexity they observed in the living world. During the modern synthesis, these ideas were purged, and only evolutionary causes that could be expressed in the mathematical framework of population genetics were retained. Consensus was reached as to which evolutionary factors might influence evolution, but not as to the relative importance of the various factors.

Theodosius Dobzhansky, a postdoctoral worker in T. H. Morgan's lab, had been influenced by the work on genetic diversity by Russian geneticists such as Sergei Chetverikov. He helped to bridge the divide between the foundations of microevolution developed by the population geneticists and the patterns of macroevolution observed by field biologists, with

his 1937 book *Genetics and the Origin of Species*. Dobzhansky examined the genetic diversity of wild populations and showed that, contrary to the assumptions of the population geneticists, these populations had large amounts of genetic diversity, with marked differences between sub-populations. The book also took the highly mathematical work of the population geneticists and put it into a more accessible form. Many more biologists were influenced by population genetics via Dobzhansky than were able to read the highly mathematical works in the original. In Great Britain E. B. Ford, the pioneer of ecological genetics, continued throughout the 1930s and 1940s to empirically demonstrate the power of selection due to ecological factors including the ability to maintain genetic diversity through genetic polymorphisms such as human blood types. Ford's work, in collaboration with Fisher, contributed to a shift in emphasis during the modern synthesis towards natural selection as the dominant force.

NEUTRAL THEORY AND ORIGIN-FIXATION DYNAMICS

The original, modern synthesis view of population genetics assumes that mutations provide ample raw material, and focuses only on the change in frequency of alleles within populations. The main processes influencing allele frequencies are natural selection, genetic drift, gene flow and recurrent mutation. Fisher and Wright had some fundamental disagreements about the relative roles of selection and drift. The availability of molecular data on all genetic differences led to the neutral theory of molecular evolution. In this view, many mutations are deleterious and so never observed, and most of the remainder are neutral, i.e. are not under selection. With the fate of each neutral mutation left to chance (genetic drift), the direction of evolutionary change is driven by which mutations occur, and so cannot be captured by models of change in the frequency of (existing) alleles alone. The origin-fixation view of population genetics generalizes this approach beyond strictly neutral mutations, and sees the rate at which a particular change happens as the product of the mutation rate and the fixation probability.

FOUR PROCESSES

SELECTION

Natural selection, which includes sexual selection, is the fact that some traits make it more likely for an organism to survive and reproduce. Population genetics describes natural selection by defining fitness as a propensity or probability of survival and reproduction in a particular environment. The fitness is normally given by the symbol **w**=1-**s** where **s** is the

selection coefficient. Natural selection acts on phenotypes, so population genetic models assume relatively simple relationships to predict the phenotype and hence fitness from the allele at one or a small number of loci. In this way, natural selection converts differences in the fitness of individuals with different phenotypes into changes in allele frequency in a population over successive generations.

Before the advent of population genetics, many biologists doubted that small differences in fitness were sufficient to make a large difference to evolution. Population geneticists addressed this concern in part by comparing selection to genetic drift. Selection can overcome genetic drift when **s** is greater than 1 divided by the effective population size. When this criterion is met, the probability that a new advantageous mutant becomes fixed is approximately equal to **2s**.The time until fixation of such an allele depends little on genetic drift, and is approximately proportional to log(sN)/s.

DOMINANCE

Dominance means that the phenotypic and/or fitness effect of one allele at a locus depends on which allele is present in the second copy for that locus. Consider three genotypes at one locus, with the following fitness values

Genotype: A_1A_1 A_1A_2 A_2A_2

Relative fitness: 1 1-hs 1-s

s is the selection coefficient and h is the dominance coefficient. The value of h yields the following information:

h=0 A_1 dominant, A_2 recessive

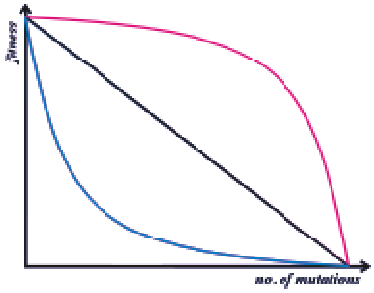
h=1 A_2 dominant, A_1 recessive

0<h<1 incomplete dominance

h<0 overdominance

h>1 Underdominance

EPISTASIS



The logarithm of fitness as a function of the number of deleterious mutations. Synergistic epistasis is represented by the red line - each subsequent deleterious mutation has a larger proportionate effect on the organism's fitness. Antagonistic epistasis is in blue. The black line shows the non-epistatic case, where fitness is the product of the contributions from each of its loci. Epistasis means that the phenotypic and/or fitness effect of an allele at one locus depends on which alleles are present at other loci. Selection does not act on a single locus, but on a phenotype that arises through development from a complete genotype. However, many population genetics models of sexual species are "single locus" models, where the fitness of an individual is calculated as the product of the contributions from each of its loci—effectively assuming no epistasis.

In fact, the genotype to fitness landscape is more complex. Population genetics must either model this complexity in detail, or capture it by some simpler average rule. Empirically, beneficial mutations tend to have a smaller fitness benefit when added to a genetic background that already has high fitness: this is known as diminishing returns epistasis.When deleterious mutations also have a smaller fitness effect on high fitness backgrounds, this is known as "synergistic epistasis". However, the effect of deleterious mutations tends on average to be very close to multiplicative, or can even show the opposite pattern, known as "antagonistic epistasis". Synergistic epistasis is central to some theories of the purging of mutation load and to the evolution of sexual reproduction.

MUTATION

Mutation is the ultimate source of genetic variation in the form of new alleles. In addition, mutation may influence the direction of evolution when there is mutation bias, i.e. different probabilities for different mutations to occur. For example, recurrent mutation that tends to be in the opposite direction to selection can lead to mutation–selection balance. At the molecular level, if mutation from G to A happens more often than mutation from A to G, then

genotypes with A will tend to evolve. Different insertion vs. deletion mutation biases in different taxa can lead to the evolution of different genome sizes. Developmental or mutational biases have also been observed in morphological evolution. For example, according to the phenotype-first theory of evolution, mutations can eventually cause the genetic assimilation of traits that were previously induced by the environment. Mutation bias effects are superimposed on other processes. If selection would favor either one out of two mutations, but there is no extra advantage to having both, then the mutation that occurs the most frequently is the one that is most likely to become fixed in a population.

Drosophila melanogaster

Mutation can have no effect, alter the product of a gene, or prevent the gene from functioning. Studies in the fly *Drosophila melanogaster* suggest that if a mutation changes a protein produced by a gene, this will probably be harmful, with about 70 percent of these mutations having damaging effects, and the remainder being either neutral or weakly beneficial. Most loss of function mutations are selected against. But when selection is weak, mutation bias towards loss of function can affect evolution. For example, pigments are no longer useful when animals live in the darkness of caves, and tend to be lost. This kind of loss of function can occur because of mutation bias, and/or because the function had a cost, and once the benefit of the function disappeared, natural selection leads to the loss. Loss of sporulation ability in a bacterium during laboratory evolution appears to have been caused by mutation bias, rather than natural selection against the cost of maintaining sporulation ability. When there is no selection for loss of function, the speed at which loss evolves depends more on the mutation rate than it does on the effective population size, indicating that it is driven more by mutation bias than by genetic drift. Mutations can involve large sections of DNA becoming duplicated, usually through genetic recombination. This leads to copy-number variation within a population. Duplications are a major source of raw material for evolving

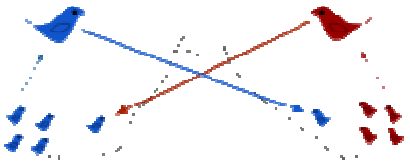
new genes. Other types of mutation occasionally create new genes from previously noncoding DNA.

GENETIC DRIFT

Genetic drift is a change in allele frequencies caused by random sampling. That is, the alleles in the offspring are a random sample of those in the parents. Genetic drift may cause gene variants to disappear completely, and thereby reduce genetic variability. In contrast to natural selection, which makes gene variants more common or less common depending on their reproductive success, the changes due to genetic drift are not driven by environmental or adaptive pressures, and are equally likely to make an allele more common as less common. The effect of genetic drift is larger for alleles present in few copies than when an allele is present in many copies. The population genetics of genetic drift are described using either branching processes or a diffusion equation describing changes in allele frequency. These approaches are usually applied to the Wright-Fisher and Moran models of population genetics. Assuming genetic drift is the only evolutionary force acting on an allele, after t generations in many replicated populations, starting with allele frequencies of p and q, the variance in allele frequency across those populations is

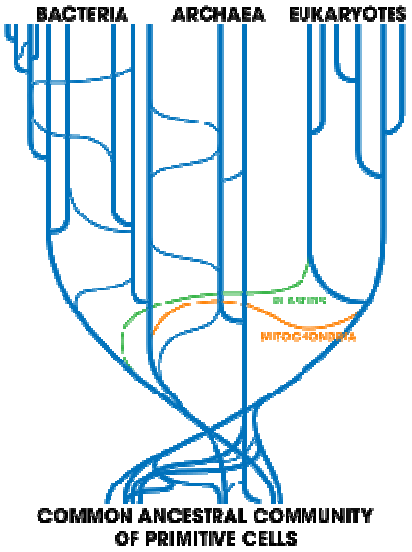
Ronald Fisher held the view that genetic drift plays at the most a minor role in evolution, and this remained the dominant view for several decades. No population genetics perspective has ever given genetic drift a central role by itself, but some have made genetic drift important in combination with another non-selective force. The shifting balance theory of Sewall Wright held that the combination of population structure and genetic drift was important. Motoo Kimura's neutral theory of molecular evolution claims that most genetic differences within and between populations are caused by the combination of neutral mutations and genetic drift. The role of genetic drift by means of sampling error in evolution has been criticized by John H Gillespie and Will Provine, who argue that selection on linked sites is a more important stochastic force, doing the work traditionally ascribed to genetic drift by means of sampling error. The mathematical properties of genetic draft are different from those of genetic drift. The direction of the random change in allele frequency is autocorrelated across generations.

GENE FLOW



Gene flow is the transfer of alleles from one population to another population through immigration of individuals. In this example, one of the birds from population A immigrates to population B, which has fewer of the dominant alleles, and through mating incorporates its alleles into the other. Because of physical barriers to migration, along with the limited tendency for individuals to move or spread (vagility), and tendency to remain or come back to natal place (philopatry), natural populations rarely all interbreed as may be assumed in theoretical random models (panmixy). There is usually a geographic range within which individuals are more closely related to one another than those randomly selected from the general population. This is described as the extent to which a population is genetically structured. Genetic structuring can be caused by migration due to historical climate change, species range expansion or current availability of habitat. Gene flow is hindered by mountain ranges, oceans and deserts or even man-made structures such as the Great Wall of China, which has hindered the flow of plant genes. Gene flow is the exchange of genes between populations or species, breaking down the structure. Examples of gene flow within a species include the migration and then breeding of organisms, or the exchange of pollen. Gene transfer between species includes the formation of hybrid organisms and horizontal gene transfer. Population genetic models can be used to identify which populations show significant genetic isolation from one another, and to reconstruct their history. Subjecting a population to isolation leads to inbreeding depression. Migration into a population can introduce new genetic variants, potentially contributing to evolutionary rescue. If a significant proportion of individuals or gametes migrate, it can also change allele frequencies, e.g. giving rise to migration load. In the presence of gene flow, other barriers to hybridization between two diverging populations of an outcrossing species are required for the populations to become new species.

HORIZONTAL GENE TRANSFER



Current tree of life showing vertical and horizontal gene transfers.

Horizontal gene transfer is the transfer of genetic material from one organism to another organism that is not its offspring; this is most common among prokaryotes. In medicine, this contributes to the spread of antibiotic resistance, as when one bacterium acquires resistance genes it can rapidly transfer them to other species. Horizontal transfer of genes from bacteria to eukaryotes such as the yeast *Saccharomyces cerevisiae* and the adzuki bean beetle *Callosobruchus chinensis* may also have occurred. An example of larger-scale transfers are the eukaryotic bdelloid rotifers, which appear to have received a range of genes from bacteria, fungi, and plants. Viruses can also carry DNA between organisms, allowing transfer of genes even across biological domains. Large-scale gene transfer has also occurred between the ancestors of eukaryotic cells and prokaryotes, during the acquisition of chloroplasts and mitochondria.

LINKAGE

If all genes are in linkage equilibrium, the effect of an allele at one locus can be averaged across the gene pool at other loci. In reality, one allele is frequently found in linkage disequilibrium with genes at other loci, especially with genes located nearby on the same chromosome. Recombination breaks up this linkage disequilibrium too slowly to avoid genetic hitchhiking, where an allele at one locus rises to high frequency because it is linked to an allele under selection at a nearby locus. Linkage also slows down the rate of adaptation, even in sexual populations. The effect of linkage disequilibrium in slowing down the rate of

adaptive evolution arises from a combination of the Hill–Robertson effect (delays in bringing beneficial mutations together) and background selection (delays in separating beneficial mutations from deleterious hitchhikers). Linkage is a problem for population genetic models that treat one gene locus at a time. It can, however, be exploited as a method for detecting the action of natural selection via selective sweeps. In the extreme case of an asexual population, linkage is complete, and population genetic equations can be derived and solved in terms of a travelling wave of genotype frequencies along a simple fitness landscape. Most microbes, such as bacteria, are asexual. The population genetics of their adaptation have two contrasting regimes. When the product of the beneficial mutation rate and population size is small, asexual populations follow a "successional regime" of origin-fixation dynamics, with adaptation rate strongly dependent on this product. When the product is much larger, asexual populations follow a "concurrent mutations" regime with adaptation rate less dependent on the product, characterized by clonal interference and the appearance of a new beneficial mutation before the last one has fixed.

APPLICATIONS

EXPLAINING LEVELS OF GENETIC VARIATION

Neutral theory predicts that the level of nucleotide diversity in a population will be proportional to the product of the population size and the neutral mutation rate. The fact that levels of genetic diversity vary much less than population sizes do is known as the "paradox of variation". While high levels of genetic diversity were one of the original arguments in favor of neutral theory, the paradox of variation has been one of the strongest arguments against neutral theory.

It is clear that levels of genetic diversity vary greatly within a species as a function of local recombination rate, due to both genetic hitchhiking and background selection. Most current solutions to the paradox of variation invoke some level of selection at linked sites. For example, one analysis suggests that larger populations have more selective sweeps, which remove more neutral genetic diversity. A negative correlation between mutation rate and population size may also contribute. Life history affects genetic diversity more than population history does, e.g. r-strategists have more genetic diversity.

DETECTING SELECTION

Population genetics models are used to infer which genes are undergoing selection. One common approach is to look for regions of high linkage disequilibrium and low genetic

variance along the chromosome, to detect recent selective sweeps. A second common approach is the McDonald–Kreitman test. The McDonald–Kreitman test compares the amount of variation within a species (polymorphism) to the divergence between species (substitutions) at two types of sites, one assumed to be neutral. Typically, synonymous sites are assumed to be neutral. Genes undergoing positive selection have an excess of divergent sites relative to polymorphic sites. The test can also be used to obtain a genome-wide estimate of the proportion of substitutions that are fixed by positive selection, α. According to the neutral theory of molecular evolution, this number should be near zero. High numbers have therefore been interpreted as a genome-wide falsification of neutral theory.

DEMOGRAPHIC INFERENCE

The simplest test for population structure in a sexually reproducing, diploid species, is to see whether genotype frequencies follow Hardy-Weinberg proportions as a function of allele frequencies. For example, in the simplest case of a single locus with two alleles denoted **A** and **a** at frequencies p and q, random mating predicts freq(**AA**) = p^2 for the **AA**homozygotes, freq(**aa**) = q^2 for the **aa** homozygotes, and freq(**Aa**) = $2pq$ for the heterozygotes. In the absence of population structure, Hardy-Weinberg proportions are reached within 1-2 generations of random mating. More typically, there is an excess of homozygotes, indicative of population structure. The extent of this excess can be quantified as the inbreeding coefficient, F. Individuals can be clustered into K subpopulations. The degree of population structure can then be calculated using F_{ST}, which is a measure of the proportion of genetic variance that can be explained by population structure. Genetic population structure can then be related to geographic structure, and genetic admixture can be detected.

Coalescent theory relates genetic diversity in a sample to demographic history of the population from which it was taken. It normally assumes neutrality, and so sequences from more neutrally-evolving portions of genomes are therefore selected for such analyses. It can be used to infer the relationships between species (phylogenetics), as well as the population structure, demographic history (e.g. population bottlenecks, population growth), biological dispersal, source–sink dynamics and introgression within a species.

EVOLUTION OF GENETIC SYSTEMS

By assuming that there are loci that control the genetic system itself, population genetic models are created to describe the evolution of dominance and other forms of robustness, the evolution of sexual reproduction and recombination rates, the evolution of mutation rates, the

evolution of evolutionary capacitors, the evolution of costly signalling traits, the evolution of ageing, and the evolution of co-operation. For example, most mutations are deleterious, so the optimal mutation rate for a species may be a trade-off between the damage from a high deleterious mutation rate and the metabolic costs of maintaining systems to reduce the mutation rate, such as DNA repair enzymes.

One important aspect of such models is that selection is only strong enough to purge deleterious mutations and hence overpower mutational bias towards degradation if the selection coefficient s is greater than the inverse of the effective population size. This is known as the drift barrier and is related to the nearly neutral theory of molecular evolution. Drift barrier theory predicts that species with large effective population sizes will have highly streamlined, efficient genetic systems, while those with small population sizes will have bloated and complex genomes containing for example introns and transposable elements. However, somewhat paradoxically, species with large population sizes might be so tolerant to the consequences of certain types of errors that they evolve higher error rates, e.g. in transcription and translation, than small populations.

6.4 PHENOTYPIC VARIATIONS

Phenotypes are traits or characteristics of an organism that we can observe, such as size, color, shape, capabilities, behaviors, etc. Not all phenotypes can actually be seen. For example, blood types are phenotypes that we can only observe using laboratory techniques. Phenotypes can be caused by genes, environmental factors, or a combination of both.

Phenotypic variation, then, is the variability in phenotypes that exists in a population. For example, people come in all shapes and sizes: height, weight, and body shape are phenotypes that vary. Hair, eye color, and the ability to roll your tongue are variable phenotypes, too. What about other organisms? All organisms can have phenotypic variation. In plants, flower color and leaf shape are examples of variable phenotypes. In bacteria, resistance to antibiotics is a variable phenotype: some bacteria are resistant and survive antibiotic treatment, while others are susceptible and die when antibiotics are given.

In genetics, the **phenotype** (from Greek φαινο- *(faino-)* 'showing', and τύπος *(túpos)* 'type') is the set of observable characteristics or traits of an organism.The term covers the organism's morphology or physical form and structure, its developmental processes, its biochemical and

physiological properties, its behavior, and the products of behavior. An organism's phenotype results from two basic factors: the expression of an organism's genetic code, or its genotype, and the influence of environmental factors. Both factors may interact, further affecting phenotype. When two or more clearly different phenotypes exist in the same population of a species, the species is called polymorphic. A well-documented example of polymorphism is Labrador Retriever coloring; while the coat color depends on many genes, it is clearly seen in the environment as yellow, black, and brown. Richard Dawkins in 1978 and then again in his 1982 book *The Extended Phenotype* suggested that one can regard bird nests and other built structures such as caddis-fly larvae cases and beaver dams as "extended phenotypes". Wilhelm Johannsen proposed the genotype-phenotype distinction in 1911 to make clear the difference between an organism's heredity and what that heredity produces. The distinction resembles that proposed by August Weismann (1834–1914), who distinguished between germ plasm (heredity) and somatic cells (the body). The genotype-phenotype distinction should not be confused with Francis Crick's central dogma of molecular biology, a statement about the directionality of molecular sequential information flowing from DNA to protein, and not the reverse.

6.4.1 PHENOTYPE AND PHENOTYPIC VARIATION

The word **phenotype** refers to the observable characters or attributes of individual organisms, including their morphology, physiology, behavior, and other traits. The phenotype of an organism is limited by the boundaries of its specific genetic **complement** (**genotype**), but is also influenced by environmental factors that impact the expression of genetic potential.

All organisms have unique genetic information, which is embodied in the particular nucleotide sequences of their **DNA** (**deoxyribonucleic acid**), the genetic biochemical of almost all organisms, except for **viruses** and **bacteria** that utilize **RNA** as their genetic material. The genotype is fixed within an individual organism but is subject to change (**mutations**) from one generation to the next due to low rates of natural or spontaneous mutation. However, there is a certain degree of developmental flexibility in the phenotype, which is the actual or outward expression of the genetic information in terms of anatomy, behavior, and **biochemistry**. This flexibility can occur because the expression of genetic potential is affected by environmental conditions and other circumstances.

Consider, for example, genetically identical bacterial cells, with a fixed complement of genetic each plated on different gels. If one bacterium is colonized under ideal conditions, it

can grow and colonize its full genetic potential. However, if a genetically identical bacterium is exposed to improper nutrients or is otherwise grown under adverse conditions, colony formation may be stunted. Such varying growth patterns of the same genotype are referred to as phenotypic plasticity. Some traits of organisms, however, are fixed genetically, and their expression is not affected by environmental conditions. Moreover, the ability of species to exhibit phenotypically plastic responses to environmental variations is itself, to a substantial degree, genetically determined. Therefore, phenotypic plasticity reflects both genetic capability and varying expression of that capability, depending on circumstances.

Phenotypic variation is essential for **evolution**. Without a discernable difference among individuals in a population there are no genetic **selection** pressures acting to alter the variety and types of alleles (forms of genes) present in a population. Accordingly, genetic mutations that do not result in phenotypic change are essentially masked from evolutionary mechanisms. Phenetic similarity results when phenotypic differences among individuals are slight. In such cases, it may take a significant alteration in environmental conditions to produce significant selection pressure that results in more dramatic phenotypic differences. Phenotypic differences lead to differences in fitness and affect adaptation.

Phenotypes are traits or characteristics of an organism that we can observe, such as size, color, shape, capabilities, behaviors, etc. Not all phenotypes can actually be seen. For example, blood types are phenotypes that we can only observe using laboratory techniques. Phenotypes can be caused by genes, environmental factors, or a combination of both. **Phenotypic variation**, then, is the variability in phenotypes that exists in a population. For example, people come in all shapes and sizes: height, weight, and body shape are phenotypes that vary. Hair, eye color, and the ability to roll your tongue are variable phenotypes, too. What about other organisms? All organisms can have phenotypic variation. In plants, flower color and leaf shape are examples of variable phenotypes. In bacteria, resistance to antibiotics is a variable phenotype: some bacteria are resistant and survive antibiotic treatment, while others are susceptible and die when antibiotics are given.

Phenotypic variation is an important adaptive mechanism in rotifers, but has posed difficult problems for systematists. This variation arises by several mechanisms including cyclomorphosis, dietary- and predatorinduced polymorphisms, polymorphisms in hatchlings from resting eggs, and dwarfism. Cyclomorphosis is the seasonal phenotypic change in body size, spine length, pigmentation, or ornamentation found in successive generations of zooplankton. These changes are phenotypic alterations in a single population that are related

to physical, chemical, or biologic features of the environment. Each different morphological form is called a morphotype. Specifically excluded from cyclomorphotic change are seasonal succession of sibling species and clonal replacements of genotypes, both of which are genetic changes in populations.

A striking phenotypic change in morphology that is associated with a dietary polymorphism was described for three *Asplanchna* species (*brightwelli*, *intermedia*, *sieboldi*) by Gilbert (1980a). Diets that include the plant product *a*-tocopherol (vitamin E) induce saccate females, the smallest morphotype, to produce cruciform daughters. Cruciforms have lateral outgrowths of the body wall that protect them from cannibalism by conspecifics by making them larger and, thus, more difficult to ingest if captured. In the presence of *a*-tocopherol and certain prey types, cruciforms can produce a third morphotype called campanulates (more prevalent in *A. sieboldi* and *A. intermedia*). Campanulates are very large females (>2000 μm), which heavily cannibalize saccate females. Female polymorphism is much less pronounced in *A. brightwelli* where there is a 50–60% increase in body size, but no campanulates are produced and body wall outgrowths are slight. Dietary polymorphism in *Asplanchna* (gigantism) may have evolved originally as a generalized growth response to larger prey typical of eutrophic waters (Gilbert, 1980a; Gilbert and Stemberger, 1985c). The tocopherol response probably is adaptive, because it signals the availability of nutritious rotifer and microcrustacean prey.

Another source of phenotypic variation is predator-induced polymorphisms. Spined and unspined forms had been recognized in several rotifer species for many years, but the cause(s) and significance(s) of these variations remained an enigma (Fig. 12). However, Gilbert (1966, 1967) was the first to show that spine production could be induced in the offspring of female *B. calyciflorus* if adults were exposed to culture medium which had previously held the predatory species *Asplanchna*. Gilbert (1967) also demonstrated that such spines were strong deterrents to predation by *Asplanchna* (see Section III.C.4). However, Stemberger (1990) has shown that food concentration can dramatically modify the development of spines in *B. calyciflorus*.

Two additional sources of phenotypic variation are polymorphisms called “aptera generations” in the hatchlings of resting eggs and dwarfism, both of which have been reported in rotifers of some tropical crater lakes (Green, 1977). Aptera morphotypes were initially thought to be different species of *Polyarthra*, but later were shown to be forms lacking the paddles that are characteristic of this genus. Only the generation hatching from resting eggs lacks paddles; their parthenogenetic offspring develop into typical morphotypes.

Similar polymorphisms between resting egg hatchlings and parthenogenetic generations were described for *Keratella quadrata* and are suspected for *Notholca acuminata* (Amrén, 1964). Dwarfism in *Brachionus caudatus* in Cameroon crater lakes was described by Green (1977) and is characterized by reduced body size and spination as compared to normal morphotypes. Green speculated that high temperature combined with reduced food supply may cause this condition.

DIFFICULTIES IN DEFINITION

Despite its seemingly straightforward definition, the concept of the phenotype has hidden subtleties. It may seem that anything dependent on the genotype is a phenotype, including molecules such as RNA and proteins. Most molecules and structures coded by the genetic material are not visible in the appearance of an organism, yet they are observable (for example by Western blotting) and are thus part of the phenotype; human blood groups are an example. It may seem that this goes beyond the original intentions of the concept with its focus on the (living) organism in itself. Either way, the term phenotype includes inherent traits or characteristics that are observable or traits that can be made visible by some technical procedure. A notable extension to this idea is the presence of "organic molecules" or metabolites that are generated by organisms from chemical reactions of enzymes. The term "phenotype" has sometimes been incorrectly used as a shorthand for phenotypic difference from wild type, yielding the statement that a "mutation has no phenotype". Another extension adds behavior to the phenotype, since behaviors are observable characteristics. **Behavioral phenotypes** include cognitive, personality, and behavioral patterns. Some behavioral phenotypes may characterize psychiatric disorders or syndromes.

PHENOTYPIC VARIATION

Phenotypic variation (due to underlying heritable genetic variation) is a fundamental prerequisite for evolution by natural selection. It is the living organism as a whole that contributes (or not) to the next generation, so natural selection affects the genetic structure of a population indirectly via the contribution of phenotypes. Without phenotypic variation, there would be no evolution by natural selection.

The interaction between genotype and phenotype has often been conceptualized by the following relationship:

$$\text{genotype (G)} + \text{environment (E)} \rightarrow \text{phenotype (P)}$$

A more nuanced version of the relationship is:

> genotype (G) + environment (E) + genotype & environment interactions (GE) → phenotype (P)

Genotypes often have much flexibility in the modification and expression of phenotypes; in many organisms these phenotypes are very different under varying environmental conditions (see ecophenotypic variation). The plant *Hieracium umbellatum* is found growing in two different habitats in Sweden. One habitat is rocky, sea-side cliffs, where the plants are bushy with broad leaves and expanded inflorescences; the other is among sand dunes where the plants grow prostrate with narrow leaves and compact inflorescences. These habitats alternate along the coast of Sweden and the habitat that the seeds of *Hieracium umbellatum* land in, determine the phenotype that grows. An example of random variation in *Drosophila* flies is the number of ommatidia, which may vary (randomly) between left and right eyes in a single individual as much as they do between different genotypes overall, or between clones raised in different environments.

The concept of phenotype can be extended to variations below the level of the gene that affect an organism's fitness. For example, silent mutations that do not change the corresponding amino acid sequence of a gene may change the frequency of guanine-cytosine base pairs (GC content). These base pairs have a higher thermal stability (*melting point*) than adenine-thymine, a property that might convey, among organisms living in high-temperature environments, a selective advantage on variants enriched in GC content.

THE EXTENDED PHENOTYPE

Richard Dawkins described a phenotype that included all effects that a gene has on its surroundings, including other organisms, as an extended phenotype, arguing that "An animal's behavior tends to maximize the survival of the genes 'for' that behavior, whether or not those genes happen to be in the body of the particular animal performing it." For instance, an organism such as a beaver modifies its environment by building a beaver dam; this can be considered an expression of its genes, just as its incisor teeth are—which it uses to modify its environment. Similarly, when a bird feeds a brood parasite such as a cuckoo, it is unwittingly extending its phenotype; and when genes in an orchid affect orchid bee behavior to increase pollination, or when genes in a peacock affect the copulatory decisions of peahens, again, the phenotype is being extended. Genes are, in Dawkins's view, selected by their phenotypic effects. Other biologists broadly agree that the extended phenotype concept is relevant, but

consider that its role is largely explanatory, rather than assisting in the design of experimental tests.

PHENOME AND PHENOMICS

Although a phenotype is the ensemble of observable characteristics displayed by an organism, the word *phenome* is sometimes used to refer to a collection of traits, while the simultaneous study of such a collection is referred to as *phenomics*. Phenomics is an important field of study because it can be used to figure out which genomic variants affect phenotypes which then can be used to explain things like health, disease, and evolutionary fitness. Phenomics has widespread applications in the agricultural industry. With an exponentially growing population and inconsistent weather patterns due to global warming, it has become increasingly difficult to cultivate enough crops to support the world's population. Advantageous genomic variations, such as drought and heat resistance, can be identified through phenomics to create more durable GMOs. Phenomics may be a stepping stone towards personalized medicine, particularly drug therapy. Once the phenomic database has acquired more data, a person's phonemic information can be used to select specific drugs tail

The RNA world is the hypothesized pre-cellular stage in the evolutionary history of life on earth, in which self-replicating RNA molecules proliferated prior to the evolution of DNA and proteins. The folded three-dimensional physical structure of the first RNA molecule that possessed ribozyme activity promoting replication while avoiding destruction would have been the first phenotype, and the nucleotide sequence of the first self-replicating RNA molecule would have been the original genotype.

UNIT 7: GENETICS OF SPECIATION

7.1 OBJECTIVES

- Study of Species
- Study of Speciation
- How do we study speciation?
- Study of Phylogenetic, Biological and other Concepts of Species

7.2 INTRODUCTION

Speciation has occurred, is occurring and will occur. These are undeniable facts. The problem is: **How do we study speciation?** There is no single approach since there is no single mechanism by which species spectate. Some approaches used in the past:

Study patterns of morphological **change in the fossil record** in a well-defined lineage of organisms. Success depends on many unknowns: stratigraphic resolution (will you "see" the speciation event); distinguishing geographic variants from true species (all you have is morphology.

Comparisons of **closely related species**. These have speciated recently (assuming closely related ~ short time since speciation) so careful studies of their biology may identify important features that contribute to reproductive isolation.

Study **intraspecific variation**. Look for evidence of incipient barriers to gene exchange. Perform crosses between individuals from different regions; look for differences in genital morphology, secondary sexual characteristics. These may show some bimodal distribution suggestive of early steps in evolution. Must ask: what might we expect to find? This depends entirely on the **model** of speciation that might apply to the organism under study. Looking within a large species range for signs of variation may be fruitless if the speciation mode is peripatric with genetic revolutions?

Laboratory populations might serve as model systems. One can establish the conditions of the specific model under question and ask if the predicted divergence is observed. **Mathematical models** can address specific predictions about modes of speciation. Both of these "artificial" methods are important since they can **identify what is possible**. Knowing

what's possible might spur one on to looking for it in unexpected contexts in natural populations.

With the use of molecular tools the comparisons of intraspecific and interspecific genetic variation has been studied in some detail. Aim is to identify **genetic changes during speciation**. These data show us that genetic change is associated with speciation. We want to be able to describe the **genetics of speciation** and the **genetics of species differences**. To do so we need to **distinguish** genetic changes that **cause speciation** from those that **accompany speciation**. These will differ a lot from one group of organisms to the next and will depend on the **genetic architecture of speciation.** Best data on both of these issues have come from the many species of Drosophila

Coyne and Orr (1989, Evolution vol. 43, pg. 362-381) take Ayala's approach one step further and attempt to correlate genetic distance (Nei's D) with amounts of prezygotic and postzygotic isolation. In the literature there are many reports of the amount of genetic distance between closely related species of Drosophila and the amount of reproductive isolation between many of the species for which genetic distance has been measured (**premating or prezygotic isolation** is measured as [1-(proportion of heterotypic matings/proportion of homotypic matings)] which ranges from - infinity for all heterotypic (between species) matings to 0 for random mating to +1 for all homotypic matings. Rarely do two species prefer to mate with the wrong type so the index effectively ranges from 0 to 1).

Post zygotic or postmating isolation can be measured as in the following example. Consider two species, A and B. These can be crossed two ways (reciprocally) to produce **hybrid offspring**. We can also examine the viability or fertility of the two sexes of these hybrid offspring, hence four contexts are examined to score post zygotic isolation:

Case	Female Parent	Male parent	Offspring	In viable or sterile?	
1.	Species A	Species B	Male	No = 0	Yes = 1
2.	Species A	Species B	Male	No = 0	No = 0
3.	Species B	Species A	Female	No = 0	No = 0
4.	Species B	Species A	Female	No = 0	No = 0
				I = 0	I = 0.25

In any particular case one could choose to score isolation in terms of the presence or absence of either isolation or sterility. Normally hybrid sterility evolves before hybrid in viability (mules are sterile but viable). Hence an index based on sterility would have higher values than an index based only on evidence for in viable hybrid offspring.

Coyne and Orr extracted these two types of data from the literature and tested some important ideas about the genetics of speciation. The general idea is that **genetic distance (D) is positively related to time** (the molecular clock hypothesis) and thus species pairs showing different degrees of genetic distance should be at different degrees of completion of the speciation process (be aware that many organisms are in the process of spectating as you read these notes). Coyne and Orr show that there is a significant relationship between genetic

Distance and both premating and post mating isolation two interesting additional points: **sympatric** species show **greater prezygotic isolation** than allopatric species pairs. This pattern is consistent with the **reinforcement** hypothesis and suggests that reinforcement can act. A second observation: less genetic distance **between species pairs** that produce **sterile or inviable males** than **between species pairs** that produce **sterile or inviable females** ($D_{(A\text{-}B)\text{sterile males}} < D_{(A\text{-}B)\text{sterile females}}$).

This observation confirmed a well-documented pattern known as **Haldane's Rule** stating that when hybrid crosses produce sterile or in viable offspring, the sex that exhibits this is most likely the **heterogametic sex** (the sex with two different sex chromosomes, e.g. X and Y in male humans and Drosophila; in birds and butterflies the female is heterogametic with Z and

W). Another "rule" of speciation is that **genes affecting reproductive isolation** are typically **found on the X chromosome** (where X is the "female" chromosome; see another paper by Coyne and Orr: "Two Rules of Speciation", in Speciation and its Consequences, 1989, D. Otte & J. Endler, editors, Sinauer Associates).

The current belief about the large "X effect" is that advantageous mutations are more likely to accumulate on the X since it is **homozygous** in males, so half of the time recessive advantageous mutations will be expressed. Similar mutations occurring on autosomes will be less likely to be expressed because autosomes are always paired and an advantageous mutation would have to be dominant to be "visible" to selection. Thus **diverging populations** (incipient species) will tend to accumulate **different mutations on their respective X chromosomes**. When individuals are crossed between these divergent populations, there will deleterious pleiotropic interaction effects between these new alleles on the X and other genes throughout the genome. The new mutations certainly **were not deleterious when they arose** within each separated population, but when paired with autosomes from a diverged population these mutations do not function properly, thus one would **only see the effect in a hybrid cross.**

Attempts to identify genes that keep species isolated go back to Dobzhansky in the 1930's: crosses between *D. pseudoobscura* and *D. persimilis* produce sterile males and fertile females as F1 hybrids. These F1 females can be backcrossed to males of either species, so the backcrossed offspring can have all combinations of chromosomes. With four chromosome pairs in each species, the F1 hybrid will have **four heterokaryotypicpairs** of chromosomes. The two possible backcrosses (one in each direction) can result in **16 possible combinations of chromosomes**. Frequently find that the offspring with nonmotile sperm (= sterile) are the ones with **sex chromosomes from each species**. Deleterious interactions between sex chromosomes and/or between sex chromosomes and autosomes are implied, but the details are the topic of a lot of current research. These types of experiments, coupled with molecular biology may someday allow us to identify the genes and the types of changes that can lead to speciation. Again, we would like to know the **genetic architecture** of speciation: how many genes involved? what sorts of mutations at each gene? What sorts of interactions among genes? Etc.

7.3 PHYLOGENETIC, BIOLOGICAL AND OTHER CONCEPTS OF SPECIES

The concept of a species as an irreducible group whose members are descended from a common ancestor and who all possess a combination of certain defining, or derived traits. Hence, this concept defines a species as a group having a shared and unique evolutionary history. It is less restrictive than the biological species concept, in that breeding between members of different species does not pose a problem. Also, it permits successive species to be defined even if they have evolved in an unbroken line of descent, with continuity of sexual fertility. However, because slight differences can be found among virtually any group of organisms, the concept tends to encourage extreme division of species into ever-smaller groups.

A new population that results from a speciation event is called a species. But although species result from a simple process, recognizing species in nature can be complicated. Biologists cannot travel in time to observe the speciation's that resulted in today's diversity of life, so they must observe the reproduction of living organisms to determine the makeup of species. Paleontologists can find the fossil evidence of the ancestors of today's species, but they cannot observe whether those fossil organisms could reproduce with each other. Because scientists have different kinds of evidence about organisms, they use different concepts of species when testing hypotheses about their evolution.

BIOLOGICAL SPECIES

The most obvious property that helps to define species is reproductive isolation. Biologists studying living animals often use the biological species concept, which envisions a species as a "group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1942). It is the biological species concept that primatologists use to grapple with whether chimpanzees and bonobos are different species, for example, by observing the differences in their reproductive behaviors and the strength of geographic isolation between their populations.

The biological species concept has some important limitations for paleontology. Making use of the concept depends on observing the mating behavior and interbreeding patterns of animals in their natural environments, which is not possible with fossils of organisms that lived in the past. Other kinds of observations that paleontologists might gather, such as

morphological differences between fossils, have no necessary value under this concept. Another limitation is that the biological species concept does not incorporate any idea of how species may change over time. Paleontologists study fossils that may be separated by hundreds of thousands of years of time. It is difficult to imagine such widely separated individuals as part of the same reproductive community, even if they were very similar to each other. Over such time periods, evolution can transform populations substantially. The biological species concept recognizes the genetic continuity within a species caused by gene flow, but it does not incorporate a view of species existing over evolutionary time. For these reasons, paleontology requires a different kind of species concept.

PHYLOGENETIC SPECIES CONCEPT

The phylogenetic species concept is an attempt to define species by their relationships to other species. Instead of trying to determine the reproductive boundaries of populations, scientists using the phylogenetic species concept attempt to uncover their genealogical relationships. A group of individuals that includes all the descendants of one common ancestor, leaving no descendants out, is called a monophyletic group.

Paleontologists Niles Eldredge and Joel Cracraft devised a species concept called the "Phylogenetic Species Concept," intended to apply to circumstances in which reproduction or isolation among organisms could not be observed. Under this concept, a species is "a diagnosable cluster of individuals within which there is a parental pattern of ancestry and escent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind" (Eldredge and Cracraft 1980:92).

Key to the phylogenetic species concept is the idea that species must be "diagnosable." In other words, members of the species should share a combination of characteristics that other species lack. To look for the unique features that define a phylogenetic species, paleontologists must perform systematic comparisons with other related fossils or living species. These aspects of the concept make it widely applicable in paleontology.

But the phylogenetic species concept is not without its problems. Because the concept defines species based on morphology, without explicitly referring to populations or reproductive boundaries, it does not apply well to cases where morphologically different populations are connected by gene flow. Morphological variation among populations is not uncommon within living species. Humans today are a species with substantial morphological variation from continent to continent. Humans on different continents are not reproductively isolated,

and their variation is largely distributed as clines over large geographic distances. Yet a paleontologist who had only a few fragmentary specimens from each continent would not necessarily know the pattern of variation and many features of his specimens would appear to be unique. What would the paleontologist make of the high nose of a European specimen, the forward-facing cheeks of an Asian fossil, or the strong brow ridge above the eye orbits of an Australian, each taken randomly from their variable populations? By applying the phylogenetic species concept, a paleontologist would probably conclude that the different continents were homes to different human species.

Thus, because the phylogenetic species concept does not identify species based on the reproductive boundaries between them, it may have the effect of identifying populations connected by gene flow as different species. For this reason, a phylogenetic species as defined by a paleontologist may not correspond to a real prehistoric population that was the product of a speciation. Some paleontologists do not view this potential conflict as a problem, because identifying species based on unique characteristics will create as full as possible a systematization of the evolution of new features. Assuming that the number of ancient species was very large, and the number of fossils representing each of them is very small, then paleontologists can hardly hope to identify every speciation event in the past. The phylogenetic species concept may therefore provide a better approximation of the number and diversity of species that existed than other alternatives.

On the other hand, identifying populations connected by gene flow as different species can be a significant problem for paleontologists who take a greater interest in the processes of evolution than in the diversity of species in the past. Gene flow is a significant force shaping evolutionary change within populations. Moreover, evolution may cause a single species to change over time, possibly acquiring new unique features without any division of a species into separate reproductively isolated populations. Some paleontologists approach these difficulties by altering their view of the evolutionary process. If speciation's can happen as a transformation of a single population in addition to the appearance of reproductive boundaries between populations, then a single evolving population may over time comprise several phylogenetic species. Or if most evolutionary change happened at the time of speciation, as asserted by the concept of punctuated equilibrium, then the phylogenetic species concept might more closely approximate the actual pattern of speciation's in the past. But without such assumptions, the phylogenetic species concept's problems sometimes create

a stumbling block for some paleontologists in attempting to understand the evolutionary process.

EVOLUTIONARY SPECIES

The evolutionary species concept combines the genealogical basis of the phylogenetic species concept with the genetic basis of the biological species concept. An evolutionary species is a lineage of interbreeding organisms, reproductively isolated from other lineages that have a beginning, an end, and a distinct evolutionary trajectory (Wiley 1978). The beginning of a species' existence is a speciation, as a population becomes reproductively isolated from a parent population. The end of a species occurs either with extinction or with the branching of the species into one or more descendants.

Central to the evolutionary species concept is the idea of an evolutionary trajectory. The trajectory of a species is the evolutionary pattern of its characteristics over time. For example, one of the earliest species in the story of human evolution, *Australopithecus afarensis*, is represented by dozens of fossil teeth and mandibles, as well as other remains. Paleontologists hypothesize that these fossils, from several sites in East Africa, are members of a single species because of their many morphological resemblances. No very similar fossils have ever been found before 3.6 million or after 3 million years ago, dates that appear to indicate the beginning and the end of the species.

Nevertheless, the fossils do show some differences that appear over time. Although the molar teeth of the fossils do not change over time, the mandibles are thicker and more massive in more recent fossils than in the most ancient ones. As far as paleontologists can test, the mandibles form a single series evolving over time toward greater size and thickness. The evolutionary species concept infers that the fossils represent a species, beginning 3.6 million years ago and ending 3 million years ago, with an evolutionary trajectory that includes the evolution of greater mandibular thickness, without apparent changes in molar sizes.

The strength of the evolutionary species concept is that it allows paleontologists to focus on the causes of evolutionary change, whether they occur during speciation’s or at other times. Regarding *A. afarensis*, the observation that mandibles increased in size during the existence of the species may be explained by different evolutionary forces and conditions than if all the change occurred with the reproductive isolation of a new population. Although the greater mandibular thickness of later mandibles might be a unique feature, attempting to establish a new phylogenetic species for the later fossils might detract from an explanation of the overall evolutionary pattern.

Phylogenetic species vs. evolutionary species concepts

But the evolutionary species concept also has its problems. Because it uses several different criteria, much more information may be necessary to define an evolutionary species. Some scientists do not view this as a drawback, since even if a scientific view of the species that once existed and their boundaries and relationships proves a challenge, it may nevertheless add to our understanding of the evolutionary process.

Yet for many paleontologists, the need to amass great numbers of fossils from different times makes the evolutionary species concept nearly impossible to implement. At the same time, if scientists always hold out the possibility that two different fossils were actually connected by gene flow, it may impede an understanding of evolutionary changes that accompany the appearance of new reproductively isolated species. If we want to have a scientific, meaning falsificationist, view of the species that have existed and their boundaries and relationships to each other, we must accept that the process will in many cases be difficult. Simply making up many species hypotheses cannot add to our knowledge and in many cases it may detract. What is important is that we realize that our record of past species is incomplete, and our failure to substantiate the existence of many species in the past does not constitute evidence that they did not exist.

TESTING SPECIES HYPOTHESES

However species are defined, whenever scientists identify a species, they actually are stating a hypothesis about the relationships among individual organisms. Such a hypothesis may be tested using morphological, genetic, or behavioral evidence. Discovering real species that existed in the past involves predicting the morphological variability of populations, including variation that occurs among populations connected by gene flow. In the relatively small fossil samples available to paleontologists, determining the number of species in a sample is a significant problem. Researchers use a number of techniques to test species hypotheses with limited morphological samples.

Two fossil hominids: different species or not?

1. What is the level of morphological difference between two or more specimens? Using a living species for comparison, scientists can determine the likelihood of sampling similar variability as the fossil sample (Miller 2000).
2. What are the relative frequencies of characteristics in two samples of fossils? Statistical comparison with the differences between different populations within a living species can determine whether the differences in frequencies observed in the

fossils would be likely to occur within the comparison species. Such comparisons can be extended to the differences between the sexes of a living species to test whether sexual dimorphism accounts for differences between fossils (Lee 1999).

3. If one fossil sample has a high incidence of several features that are absent or at low frequency in another sample, this supports the hypothesis that the two samples represent different species. With samples of sufficient size, say, 10 individuals or more, paleontologists can even estimate the maximum level of gene flow consistent with the morphological differences, and thereby frame a test of the hypothesis of different species in solid evolutionary terms (Hawks and Wolpoff 2001).
4. Do samples represent change over time? Sometimes paleontologists can use different populations from living species to evaluate likelihood that certain kinds of changes might occur over time. The best comparisons are with large samples of fossils that represent long spans of time, however. Although the evolutionary process is in ways unique for each species, analyses of the rate and level of changes in other species provide the most powerful tests of species hypotheses available in studying the past.

7.4 ISOLATION

The reproductive characteristics which prevent species from fusing. Isolating mechanisms are particularly important in the *biological species concept*, in which species of sexual organisms are defined by *reproductive isolation*, i.e. a lack of gene mixture. Two broad kinds of isolating mechanisms between species are typically distinguished, together with a number of sub-types (modified from Mayr 1970):

1) *Pre-mating isolating mechanisms*. Factors which cause species to mate with their own kind (*assortative mating*).

a) *Temporal isolation*. Individuals of different species do not mate because they are active at different times of day or in different seasons.
b) *Ecological isolation*. Individuals mate in their preferred habitat, and therefore do not meet individuals of other species with different ecological preferences.
c) *Behavioral isolation*. Potential mates meet, but choose members of their own species.
d) *Mechanical isolation*. Copulation is attempted, but transfer of sperm does not take place.

2) *Post-mating isolating mechanisms*. Genomic incompatibility, hybrid inviability or sterility.

a) *Gametic incompatibility*. Sperm transfer takes place, but egg is not fertilized.
b) *Zygotic mortality*. Egg is fertilized, but zygote does not develop.
c) *Hybrid inviability*. Hybrid embryo forms, but of reduced viability.
d) *Hybrid sterility*. Hybrid is viable, but resulting adult is sterile.
e) *Hybrid breakdown*. First generation (F1) hybrids are viable and fertile, but further hybrid generations (F2 and backcrosses) may be inviable or sterile.

An alternative classification of isolating mechanisms contrasts *pre-zygotic isolation* (items 1+ 2a above) with *post-zygoticisolation* (items 2b-e above). As an example of the application of isolating mechanisms, the apple-feeding *host race* of the tephritid fruit fly (*Rhagoletis pomonella*) differs from the hawthorn-feeding race in that the apple race emerges earlier in the year (1a), and each *host race* preferentially chooses to rest, lay eggs and mate on its own host plant (1b). On the other hand, laboratory experiments show that there is little behavioral, mechanical, or post-mating isolation (1c,d; 2a-e).

The term isolating mechanisms was introduced by T. Dobzhansky in the 1930s, and has been popularized in a number of books by E Mayr. Both authors originally proposed that isolating mechanisms were group traits beneficial at the level of the species; today, this is generally disbelieved. Recent authors have pointed out that the word "mechanism" is particularly misleading as *pre-mating* and *post-mating isolation* are likely to evolve as a by-product of natural selection or genetic drift within species, rather than as a direct result of their utility as barriers to fertilization and gene mixing between species (a process known as *reinforcement*). A leading critic of the *biological species concept* and of the term isolating mechanisms is HEH Paterson, who argues that species are cohesive wholes as a result of *pre-zygotic* sexual signalling within species, rather than due to isolating mechanisms between species. Paterson therefore introduced a competing idea of species, the *recognition concept* of species, in which isolating mechanisms were replaced by *specific mate recognition systems* as an alternative. Unfortunately, the word "system" has as many group-benefit connotations as "mechanism", and the *recognition concept* of species has not gained universal acceptance.

There is also the terminological problem that *reproductive isolation* combines traits that reduce *gene flow*, such as mate choice or fertilization barriers, with traits that select against genes that have flowed, such as hybrid incompatibility. Lumping these two antagonistic features is confusing, since they are unrelated and evolve in very different ways. For instance, whereas it is conceivable that *reinforcement* might evolve to reduce an individual's tendency to mate with another species and produce inviable offspring, it is almost impossible to

imagine that hybrid in viability itself would evolve as an adaptation. This *reproductive isolation* terminology leads also to a muddled use of the term *gene flow* as the opposite of *reproductive isolation*; in other words, *gene flow* comes to include not only the flow of genes, but also the effects of any natural selection on the frequency of such genes within each population.

Perhaps the most fundamental problem with isolating mechanisms (and *specific mate recognition systems*) is that species are implied to be qualitatively different from subspecies, races, or forms by their possession of these traits. Races cannot, in theory, differ in either type of trait because only species are defined by their possession. Arguably, by making species seem qualitatively different from races, these terms have spawned a number of special models of speciation where *geographic isolation*, also known as *allopatry*, or sudden bursts of evolution in small founder populations (*founder events* or *punctuated equilibria*) play important roles. Only such unusual conditions were thought to be able to give rise to new species that differ in isolating mechanisms (or *specific mate recognition systems*). In reality, there is little to distinguish *mate choice* and *disruptive natural selection* commonly observed within species from *pre-mating* and *post-mating isolation* between species; and, indeed, it is hard to distinguish species from races in many actual organisms. There are five types of isolation that biologically prevent species that might otherwise interbreed to produce hybrid offspring. These are ecological, temporal, behavioral, mechanical/chemical and geographical.

ECOLOGICAL ISOLATION

Ecological, or habitat, isolation occurs when two species that could interbreed do not because the species live in different areas. For example, in India both the lion and tiger exist and are capable of interbreeding; however, the lion lives in the grasslands and the tiger lives in the forest. The two species live in different habitats and will not encounter one another: each is isolated from the other species.

TEMPORAL ISOLATION

Temporal isolation is when species that could interbreed do not because the different species breed at different times. This temporal difference could occur at difference times of day, different times of the year, or anything in between. For example, the field crickets Gryllus pennsylvanicus and G. veleti become sexually mature at different seasons, one in the spring and the other in the autumn.

BEHAVIORAL ISOLATION

Behavioral isolation refers to the fact that many species perform different mating rituals. This is a common barrier between animals. For example, certain species of crickets will only mate with males that produce a particular mating song. Other species rituals may include a mating dance or emitting a scent. These clues are ignored by species not accustomed to the ritual.

MECHANICAL OR CHEMICAL ISOLATION

Mechanical isolation is caused by structures or chemical barriers that keep species isolated from one another. For example, in flowering plants, the shape of the flower will tend to match up with a natural pollinator. Plants that do not have the correct shape for the pollinator will not receive a pollen transfer. Likewise, certain chemical barriers prevent gametes from forming. These chemical barriers will only allow sperm from the correct species to fertilize the egg.

GEOGRAPHICAL ISOLATION

Geographical isolation refers to the physical barriers that exist that keep two species from mating. For example, a species of monkey that is located on an island cannot breed with another species of monkey on the mainland. The water and distance between the two species keep them isolated from one another and make it impossible for them to breed.

7.5 PATTERNS AND MECHANISMS OF REPRODUCTIVE ISOLATION

The mechanisms of **reproductive isolation** are a collection of evolutionary mechanisms, behaviors and physiological processes critical for speciation. They prevent members of different species from producing offspring, or ensure that any offspring are sterile. These barriers maintain the integrity of a species by reducing gene flow between related species.

The mechanisms of reproductive isolation have been classified in a number of ways. Zoologist Ernst Mayr classified the mechanisms of reproductive isolation in two broad categories: pre-zygotic for those that act before fertilization (or before mating in the case of animals) and post-zygotic for those that act after it. The mechanisms are genetically controlled and can appear in species whose geographic distributions overlap (sympatric speciation) or are separate (allopatric speciation).

PRE-ZYGOTIC ISOLATION

Pre-zygotic isolation mechanisms are the most economic in terms of the natural selection of a population, as resources are not wasted on the production of a descendant that is weak, non-viable or sterile. These mechanisms include physiological or systemic barriers to fertilization.

Temporal or habitat isolation

Any of the factors that prevent potentially fertile individuals from meeting will reproductively isolate the members of distinct species. The types of barriers that can cause this isolation include: different habitats, physical barriers, and a difference in the time of sexual maturity or flowering. An example of the ecological or habitat differences that impede the meeting of potential pairs occurs in two fish species of the family *Gasterosteidae* (sticklebacks). One species lives all year round in fresh water, mainly in small streams. The other species lives in the sea during winter, but in spring and summer individuals migrate to river estuaries to reproduce. The members of the two populations are reproductively isolated due to their adaptations to distinct salt concentrations. An example of reproductive isolation due to differences in the mating season is found in the toad species *Bufo americanus* and *Bufo fowleri*. The members of these species can be successfully crossed in the laboratory producing healthy, fertile hybrids. However, mating does not occur in the wild even though the geographical distribution of the two species overlaps. The reason for the absence of inter-species mating is that *B. americanus* mates in early summer and *B. fowleri* in late summer. Certain plant species, such as *Tradescantia canaliculata* and *T. subaspera*, are sympatric throughout their geographic distribution, yet they are reproductively isolated as they flower at different times of the year. In addition, one species grows in sunny areas and the other in deeply shaded areas.

Behavioral isolation

The different mating rituals of animal species creates extremely powerful reproductive barriers, termed sexual or behavior isolation that isolates apparently similar species in the majority of the groups of the animal kingdom. In dioeciously species, males and females have to search for a partner, be in proximity to each other, carry out the complex mating rituals and finally copulate or release their gametes into the environment in order to breed. Mating dances, the songs of males to attract females or the mutual grooming of pairs, are all examples of typical courtship behavior that allows both recognition and reproductive isolation. This is because each of the stages of courtship depends on the behavior of the partner. The male will only move onto the second stage of the exhibition if the female shows

certain responses in her behavior. He will only pass onto the third stage when she displays a second key behavior. The behaviors of both interlink, are synchronized in time and lead finally to copulation or the liberation of gametes into the environment. No animal that is not physiologically suitable for fertilization can complete this demanding chain of behavior. In fact, the smallest difference in the courting patterns of two species is enough to prevent mating (for example, a specific song pattern acts as an isolation mechanism in distinct species of grasshopper of the genus *Chorthippus*). Even where there are minimal morphological differences between species, differences in behavior can be enough to prevent mating. For example, *Drosophila melanogaster* and *D. simulans* which are considered twin species due to their morphological similarity do not mate even if they are kept together in a laboratory.*Drosophila ananassae* and *D. pallidosa* are twin species from Melanesia. In the wild they rarely produce hybrids, although in the laboratory it is possible to produce fertile offspring. Studies of their sexual behavior show that the males court the females of both species but the females show a marked preference for mating with males of their own species. A different regulator region has been found on Chromosome II of both species that affects the selection behavior of the females. Pheromones play an important role in the sexual isolation of insect species. These compounds serve to identify individuals of the same species and of the same or different sex. Evaporated molecules of volatile pheromones can serve as a wide-reaching chemical signal. In other cases, pheromones may be detected only at a short distance or by contact.

In species of the *melanogaster* group of *Drosophila*, the pheromones of the females are mixtures of different compounds; there is a clear dimorphism in the type and/or quantity of compounds present for each sex. In addition, there are differences in the quantity and quality of constituent compounds between related species; it is assumed that the pheromones serve to distinguish between individuals of each species. An example of the role of pheromones in sexual isolation is found in 'corn borers' in the genus *Ostrinia*. There are two twin species in Europe that occasionally cross. The females of both species produce pheromones that contain a volatile compound which has two isomers, E and Z; 99% of the compound produced by the females of one species is in the E isomer form, while the females of the other produce 99% isomer Z. The production of the compound is controlled by just one locus and the interspecific hybrid produces an equal mix of the two isomers. The males, for their part, almost exclusively detect the isomer emitted by the females of their species, such that the hybridization although possible is scarce. The perception of the males is controlled by one

gene, distinct from the one for the production of isomers; the heterozygous males show a moderate response to the odour of either type. In this case, just 2 'loci' produce the effect of ethological isolation between species that are genetically very similar. Sexual isolation between two species can be asymmetrical. This can happen when the mating that produces descendants only allows one of the two species to function as the female progenitor and the other as the male, while the reciprocal cross does not occur. For instance, half of the wolves tested in the Great Lakes area of America show mitochondrial DNA sequences of coyotes, while mitochondrial DNA from wolves is never found in coyote populations. This probably reflects an asymmetry in inter-species mating due to the difference in size of the two species as male wolves take advantage of their greater size in order to mate with female coyotes, while female wolves and male coyotes do not mate.

Mechanical isolation

Mating pairs may not be able to couple successfully if their genitals are not compatible. The relationship between the reproductive isolation of species and the form of their genital organs was signaled for the first time in 1844 by the French entomologistLéon Dufour. Insects' rigid carapaces act in a manner analogous to a lock and key, as they will only allow mating between individuals with complementary structures, that is, males and females of the same species (termed *co-specifics*). Evolution has led to the development of genital organs with increasingly complex and divergent characteristics, which will cause mechanical isolation between species. Certain characteristics of the genital organs will often have converted them into mechanisms of isolation. However, numerous studies show that organs that are anatomically very different can be functionally compatible, indicating that other factors also determine the form of these complicated structures. Mechanical isolation also occurs in plants and this is related to the adaptation and coevolution of each species in the attraction of a certain type of pollinator (where pollination is zoophilic) through a collection of morphophysiological characteristics of the flowers (called floral syndromes), in such a way that the transport of pollen to other species does not occur.

GAMETIC ISOLATION

The synchronous spawning of many species of coral in marine reefs means that inter-species hybridization can take place as the gametes of hundreds of individuals of tens of species are liberated into the same water at the same time. Approximately a third of all the possible crosses between species are compatible, in the sense that the gametes will fuse and lead to individual hybrids. This hybridization apparently plays a fundamental role in the evolution of

coral species. However, the other two-thirds of possible crosses are incompatible. It has been observed that in sea urchins of the genus *Strongylocentrotus* the concentration of spermatocytes that allow 100% fertilization of the ovules of the same species is only able to fertilize 1.5% of the ovules of other species. This inability to produce hybrid offspring, despite the fact that the gametes are found at the same time and in the same place, is due to a phenomenon known as *gamete incompatibility*, which is often found between marine invertebrates, and whose physiological causes are not fully understood. In some *Drosophila* crosses, the swelling of the female's vagina has been noted following insemination. This has the effect of consequently preventing the fertilization of the ovule by sperm of a different species.

In plants the pollen grains of a species can germinate in the stigma and grow in the style of other species. However, the growth of the pollen tubes may be detained at some point between the stigma and the ovules, in such a way that fertilization does not take place. This mechanism of reproductive isolation is common in the angiosperms and is called *cross-incompatibility* or *incongruence*. A relationship exists between self-incompatibility and the phenomenon of cross-incompatibility. In general crosses between individuals of a self-compatible species (SC) with individuals of a self-incompatible (SI) species give hybrid offspring. On the other hand, a reciprocal cross (SI x SC) will not produce offspring, because the pollen tubes will not reach the ovules. This is known as *unilateral incompatibility*, which also occurs when two SC or two SI species are crossed.

POST-ZYGOTIC ISOLATION

Zygote mortality and non-viability of hybrids

A type of incompatibility that is found as often in plants as in animals occurs when the egg or ovule is fertilized but the zygote does not develop, or it develops and the resulting individual has a reduced viability. This is the case for crosses between species of the frog genus, where widely differing results are observed depending upon the species involved. In some crosses there is no segmentation of the zygote (or it may be that the hybrid is extremely non-viable and changes occur from the first mitosis). In others, normal segmentation occurs in the blastula but gastrulation fails. Finally, in other crosses, the initial stages are normal but errors occur in the final phases of embryo development. This indicates differentiation of the embryo development genes (or gene complexes) in these species and these differences determine the non-viability of the hybrids. Similar results are observed in mosquitoes of the genus *Culex*, but the differences are seen between reciprocal crosses, from which it is concluded that the

same effect occurs in the interaction between the genes of the cell nucleus (inherited from both parents) as occurs in the genes of the cytoplasmic organelles which are inherited solely from the female progenitor through the cytoplasm of the ovule.In Angiosperms, the successful development of the embryo depends on the normal functioning of its endosperm. The failure of endosperm development and its subsequent abortion has been observed in many interploidal crosses (that is, those between populations with a particular degree of intra or interspecific ploidy), and in certain crosses in species with the same level of ploidy. The collapse of the endosperm, and the subsequent abortion of the hybrid embryo is one of the most common post-fertilization reproductive isolation mechanism found in angiosperms.

HYBRID STERILITY

A hybrid may have normal viability but is typically deficient in terms of reproduction or is sterile. This is demonstrated by the mule and in many other well-known hybrids. In all of these cases sterility is due to the interaction between the genes of the two species involved; to chromosomal imbalances due to the different number of chromosomes in the parent species; or to nucleus-cytoplasmic interactions such as in the case of *Culex* described above.

Hinnies and mules are hybrids resulting from a cross between a horse and a donkey or between a mare and a donkey, respectively. These animals are nearly always sterile due to the difference in the number of chromosomes between the two parent species. Both horses and donkeys belong to the genus *Equus*, but *Equus caballus* has 64 chromosomes, while *Equus asinus* only has 62. A cross will produce offspring (mule or hinny) with 63 chromosomes that will not form pairs which means that they do not divide in a balanced manner during meiosis. In the wild, the horses and donkeys ignore each other and do not cross. In order to obtain mules or hinnies it is necessary to train the progenitors to accept copulation between the species or create them through artificial insemination.

The sterility of many interspecific hybrids in angiosperms has been widely recognised and studied. Interspecific sterility of hybrids in plants has multiple possible causes. These may be genetic, related to the genomes, or the interaction between nuclear and cytoplasmic factors, as will be discussed in the corresponding section. Nevertheless, it is important to note that in plants, hybridization is a stimulus for the creation of new species – the contrary to the situation in animals. Although the hybrid may be sterile, it can continue to multiply in the wild by asexual reproduction, whether vegetative propagation or apomixis or the production of seeds. Indeed, interspecific hybridization can be associated with polyploidia and, in this way, the origin of new species that are called allopolyploids. *Rosa canina*, for example, is the

result of multiple hybridizations. or there is a type of wheat that is an allohexaploid that contains the genomes of three different species.

MULTIPLE MECHANISMS

In general, the barriers that separate species do not consist of just one mechanism. The twin species of *Drosophila*, *D. pseudoobscura* and *D. persimilis*, are isolated from each other by habitat (*persimilis* generally lives in colder regions at higher altitudes), by the timing of the mating season (*persimilis* is generally more active in the morning and *pseuoobscura* at night) and by behavior during mating (the females of both species prefer the males of their respective species). In this way, although the distribution of these species overlaps in wide areas of the west of the United States of America, these isolation mechanisms are sufficient to keep the species separated. Such that, only a few fertile females have been found amongst the other species among the thousands that have been analyzed. However, when hybrids are produced between both species, the gene flow between the two will continue to be impeded as the hybrid males are sterile. Also, and in contrast with the great vigor shown by the sterile males, the descendants of the backcrosses of the hybrid females with the parent species are weak and notoriously non-viable. This last mechanism restricts even more the genetic interchange between the two species of fly in the wild.

HYBRID SEX: HALDANE'S RULE

Haldane's rule states that when one of the two sexes is absent in interspecific hybrids between two specific species, and then the sex that is not produced, is rare or is sterile is the heterozygous (or heterogametic) sex. In mammals, at least, there is growing evidence to suggest that this is due to high rates of mutation of the genes determining masculinity in the Y chromosome.

It has been suggested that Haldane's rule simply reflects the fact that the male sex is more sensitive than the female when the sex-determining genes are included in a hybrid genome. But there are also organisms in which the heterozygous sex is the female: birds and butterflies and the law is followed in these organisms. Therefore, it is not a problem related to sexual development, nor with the sex chromosomes. Haldane proposed that the stability of hybrid individual development requires the full gene complement of each parent species, so that the hybrid of the heterozygous sex is unbalanced (i.e. missing at least one chromosome from each of the parental species). For example, the hybrid male obtained by crossing *D.*

melanogaster females with *D. simulans* males, which is non-viable, lacks the X chromosome of *D. simulans*.

GENETICS

Pre-copulatory mechanisms in animals

The genetics of ethological isolation barriers will be discussed first. Pre-copulatory isolation occurs when the genes necessary for the sexual reproduction of one species differ from the equivalent genes of another species, such that if a male of species A and a female of species B are placed together they are unable to copulate. Study of the genetics involved in this reproductive barrier tries to identify the genes that govern distinct sexual behaviors in the two species. The males of *Drosophila melanogaster* and those of *D. simulans* conduct an elaborate courtship with their respective females, which are different for each species, but the differences between the species are more quantitative than qualitative. In fact the *simulans* males are able to hybridize with the *melanogaster* females. Although there are lines of the latter species that can easily cross there are others that are hardly able to. Using this difference, it is possible to assess the minimum number of genes involved in pre-copulatory isolation between the *melanogaster* and *simulans* species and their chromosomal location.

In experiments, flies of the *D. melanogaster* line, which hybridizes readily with *simulans*, were crossed with another line that it does not hybridize with, or rarely. The females of the segregated populations obtained by this cross were placed next to *simulans* males and the percentage of hybridization was recorded, which is a measure of the degree of reproductive isolation. It was concluded from this experiment that 3 of the 8 chromosomes of the haploid complement of *D. melanogaster* carry at least one gene that affects isolation, such that substituting one chromosome from a line of low isolation with another of high isolation reduces the hybridization frequency. In addition, interactions between chromosomes are detected so that certain combinations of the chromosomes have a multiplying effect. Cross incompatibility or incongruence in plants is also determined by major genes that are not associated at the self-incompatibility*S locus*.

Post-copulation or fertilization mechanisms in animals

Reproductive isolation between species appears, in certain cases, a long time after fertilization and the formation of the zygote, as happens – for example – in the twin species *Drosophila pavani* and *D. gaucha*. The hybrids between both species are not sterile, in the sense that they produce viable gametes, ovules and spermatozoa. However, they cannot produce offspring as the sperm of the hybrid male do not survive in the semen receptors of the females, be they hybrids or from the parent lines. In the same way, the sperm of the males of the two parent species do not survive in the reproductive tract of the hybrid female. This type of post-copulatory isolation appears as the most efficient system for maintaining reproductive isolation in many species.

The development of a zygote into an adult is a complex and delicate process of interactions between genes and the environment that must be carried out precisely, and if there is any alteration in the usual process, caused by the absence of a necessary gene or the presence of a different one, it can arrest the normal development causing the non-viability of the hybrid or its sterility. It should be borne in mind that half of the chromosomes and genes of a hybrid are from one species and the other half come from the other. If the two species are genetically different, there is little possibility that the genes from both will act harmoniously in the hybrid. From this perspective, only a few genes would be required in order to bring about post copulatory isolation, as opposed to the situation described previously for pre-copulatory isolation.

In many species where pre-copulatory reproductive isolation does not exist, hybrids are produced but they are of only one sex. This is the case for the hybridization between females of *Drosophila simulans* and *Drosophila melanogaster* males: the hybridized females die early in their development so that only males are seen among the offspring. However, populations of *D. simulans* have been recorded with genes that permit the development of adult hybrid females, that is, the viability of the females is "rescued". It is assumed that the normal activity of these speciation genes is to "inhibit" the expression of the genes that allow the growth of the hybrid. There will also be regulator genes.

A number of these genes have been found in the *melanogaster* species group. The first to be discovered was "Lhr" (Lethal hybrid rescue) located in Chromosome II of *D. simulans*. This dominant allele allows the development of hybrid females from the cross between *simulans* females and *melanogaster* males. A different gene, also located on Chromosome II of *D. simulans* is "Shfr" that also allows the development of female hybrids, its activity being

dependent on the temperature at which development occurs. Other similar genes have been located in distinct populations of species of this group. In short, only a few genes are needed for an effective post copulatory isolation barrier mediated through the non-viability of the hybrids.

As important as identifying an isolation gene is knowing its function. The *Hmr* gene, linked to the X chromosome and implicated in the viability of male hybrids between *D. melanogaster* and *D. simulans*, is a gene from the proto-oncogene family *myb*, that codes for a transcriptional regulator. Two variants of this gene function perfectly well in each separate species, but in the hybrid they do not function correctly, possibly due to the different genetic background of each species. Examination of the allele sequence of the two species shows that change of direction substitutions are more abundant than synonymous substitutions, suggesting that this gene has been subject to intense natural selection.

The Dobzhansky–Muller model proposes that reproductive incompatibilities between species are caused by the interaction of the genes of the respective species. It has been demonstrated recently that *Lhr* has functionally diverged in *D. simulans* and will interact with *Hmr* which, in turn, has functionally diverged in *D. melanogaster* to cause the lethality of the male hybrids. *Lhr* is located in a heterochromatic region of the genome and its sequence has diverged between these two species in a manner consistent with the mechanisms of positive selection. An important unanswered question is whether the genes detected correspond to old genes that initiated the speciation favoring hybrid non-viability, or are modern genes that have appeared post-speciation by mutation, that are not shared by the different populations and that suppress the effect of the primitive non-viability genes. The *OdsH* (abbreviation of *Odysseus*) gene causes partial sterility in the hybrid between *Drosophila simulans* and a related species, *D. mauritiana*, which is only encountered on Mauritius, and is of recent origin. This gene shows monophyly in both species and also has been subject to natural selection. It is thought that it is a gene that intervenes in the initial stages of speciation, while other genes that differentiate the two species show polyphyly. *Odsh* originated by duplication in the genome of *Drosophila* and has evolved at very high rates in *D. mauritania*, while its paralogue, *unc-4*, is nearly identical between the species of the group *melanogaster*. Seemingly, all these cases illustrate the manner in which speciation mechanisms originated in nature, therefore they are collectively known as "speciation genes", or possibly, gene sequences with a normal function within the populations of a species that diverge rapidly in response to positive selection thereby forming reproductive isolation barriers with other

species. In general, all these genes have functions in the transcriptional regulation of other genes.

The *Nup96* gene is another example of the evolution of the genes implicated in post-copulatory isolation. It regulates the production of one of the approximately 30 proteins required to form a nuclear pore. In each of the *simulans* groups of *Drosophila* the protein from this gene interacts with the protein from another, as yet undiscovered, gene on the X chromosome in order to form a functioning pore. However, in a hybrid the pore that is formed is defective and causes sterility. The differences in the sequences of *Nup96* have been subject to adaptive selection, similar to the other examples of *speciation genes* described above.

Post-copulatory isolation can also arise between chromosomally differentiated populations due to chromosomal translocations and inversions. If, for example, a reciprocal translocation is fixed in a population, the hybrid produced between this population and one that does not carry the translocation will not have a complete meiosis. This will result in the production of unequal gametes containing unequal numbers of chromosomes with a reduced fertility. In certain cases, complete translocations exist that involve more than two chromosomes, so that the meiosis of the hybrids is irregular and their fertility is zero or nearly zero. Inversions can also give rise to abnormal gametes in heterozygous individuals but this effect has little importance compared to translocations. An example of chromosomal changes causing sterility in hybrids comes from the study of *Drosophila nasuta* and *D. albomicans* which are twin species from the Indo-Pacific region. There is no sexual isolation between them and the F1 hybrid is fertile. However, the F2 hybrids are relatively infertile and leave few descendants which have a skewed ratio of the sexes. The reason is that the X chromosome of *albomicans* is translocated and linked to an autosome which causes abnormal meiosis in hybrids. Robertsonian translocations are variations in the numbers of chromosomes that arise from either: the fusion of two acrocentric chromosomes into a single chromosome with two arms, causing a reduction in the haploid number, or conversely; or the fission of one chromosome into two acrocentric chromosomes, in this case increasing the haploid number. The hybrids of two populations with differing numbers of chromosomes can experience a certain loss of fertility, and therefore a poor adaptation, because of irregular meiosis.

7.6 MODELS OF SPECIATION

Speciation is a fundamental issue in evolutionary biology, but it is both fascinating and frustrating: we know **it does happen** but it it's an **historical phenomenon** so it is difficult to observe. The two camps of evolutionary biologists best equipped to deal with speciation (in terms of mechanism, population geneticists; in terms of time-frames, paleontologists) are both incapable of "seeing" speciation except in very special situations. We must rely on **strong inference** to properly understand speciation. This inference is in many cases very rigorous and scientific although it is historical, i.e., requires an interpretation of what has gone on in the past.

Defining speciation **depends on one's species concept**. (Recall species concepts: typological, evolutionary, biological, recognition). In its simplest form speciation is **lineage splitting**; the resulting lineages are genetically isolated and ecologically distinct. This implies that something **intrinsic** about the new lineages (an aspect of its biology, e.g., genetics) makes/keeps them distinct. Speciation then must involve the evolution of **intrinsic barriers to gene exchange**. Intrinsic barriers can related in many ways to **extrinsic barriers** to gene exchange (abiotic factors limiting gene flow: rivers, isolated islands, glaciers). A variant of a species could be adapted to live in a particular environment that is spatially distinct from other types of environmental conditions; here an intrinsic component contributes to an extrinsic barrier. The notion of the evolution of barriers to gene exchange applies to virtually all species concepts since unlimited gene exchange between two populations/species would prevent the evolution of the defining principles of a given species concept: 1) true typological differences must have a genetic basis, 2) evolutionary lineages would not have their own "evolutionary tendencies" with homogenization due to gene exchange, 3) reproductive isolation (either pre- or postmating) would not be maintained with unlimited gene flow, and 4) mate recognition systems could not be maintained as distinct with unlimited gene exchange.

Without the evolution of some intrinsic barrier to gene exchange, **fusion** of the two incipient species would be one likely outcome (populations would blend back into one), or **extinction** of one or the other lineages (one population out competed [at the individual level!] the diverged sister population leaving only one population).

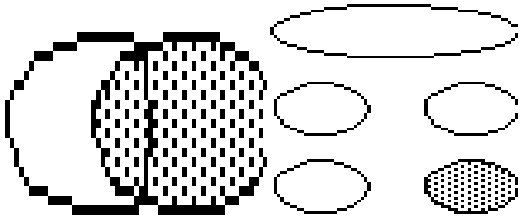
MODELS OF SPECIATION

There are many models which have been proposed that enable barriers to gene exchange to evolve; as argued by Ernst Mayr, geographic isolation provides the most effective barrier. We thus consider the **allopatric model**:

1. Continuous distribution split into two (or more) sub populations

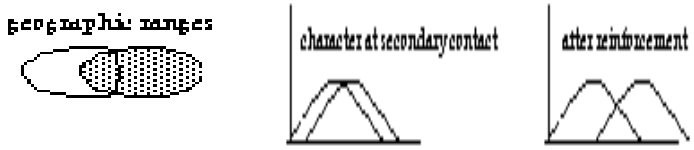
2. Differentiation in allopatric (different selection regimes; not necessarily selection for speciation)

3. if populations come into secondary contact, no gene flow (= speciation complete)



If no gene flow after secondary contact, **speciation was completed in allopatric**. Speciation would then be viewed as a **byproduct of divergence in allopatry**. What happens after secondary contact is a matter of great debate: If the two differentiated forms mix or **hybridize** this may provide the context for **selection for assortative mating** also called **reinforcement of premating isolation** (reinforcement hypothesis). In this case speciation was not completed in allopatry and fate of the two populations depends on the outcome of the interaction upon secondary contact.

Patterns predicted from the action of reinforcement:



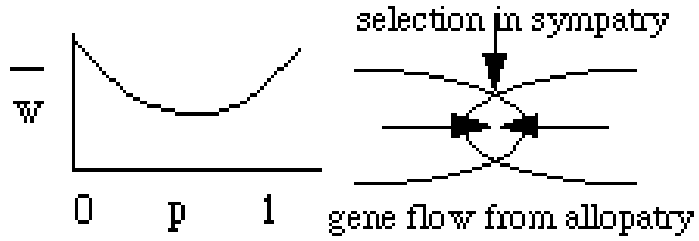
Selection in zone of overlap for increased premating isolation. See artificial demonstration with a selection experiment.

Reinforcement model assumes that hybrids are **less fit** (=means by which selection for further isolation can operate). This assumes that **post mating barriers arise first** and that premating barriers arise **as a result of selection in sympatry;** these assumptions may not hold in all cases. However, if premating barriers evolved first, there might be little hybridization (speciation complete?); if there was no postmating barrier, even with small

amounts of hybridization the two forms would fuse back together because there would be no selection against hybrids!

Reinforcement is actually a special case of **character displacement** which is the accentuation of differences between species (or forms) by selection against the individuals of similar phenotype (reinforcement = reproductive character displacement and is achieved by selection against hybrids). If reinforcement is true, we should expect to see displacement of characters associated with pre-mating barriers to gene exchange in areas of secondary contact. Some cases we do: **calling songs of anurans**; frequently such reproductive character displacement **is not observed**. When "reinforcement-like" patterns are observed, one has to be sure that the phenotypic shift is actually an evolutionary response to the presence of the other incipient species and not to some other clinal variation (e.g., ecological factors that generate parallel clines).

Problems with reinforcement: other possible outcomes: **fusion of the two populations** because differentiation was sufficiently slight that selection against hybrids is weak relative to the gene flow between forms. **Extinction of one or the other** of the two forms. Quite likely when there is selection against heterozygotes. In population genetic terms, equivalent to **heterozygote disadvantage** AA, Aa, aa with fitnesses 1,1-s,1, a **metastable equilibrium**



Selection against hybrids within the zone of secondary contact **only favors displacement in sympatry**; gene flow in from allopatry will swamp the effect. One could view such hybrid zones as **genetic canyons** of lost alleles. Another important question: if selection against hybrids is the driving force for reproductive character displacement, how will the genes for the different components of isolation/recognition sweep through the allopatric regions of the two species ranges where there is no hybridization, hence no selection?

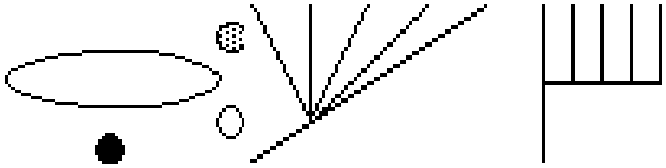
Another allopatric model is the **Peripatric model** referring to populations surrounding the main part of the current species range.

1. Small isolated populations

2. Genetic drift via population bottleneck or **founder event** => new allele frequencies

3. new "genetic environment" => different response to selection than in main population

4. effect is a major genetic change = "**genetic revolution**"



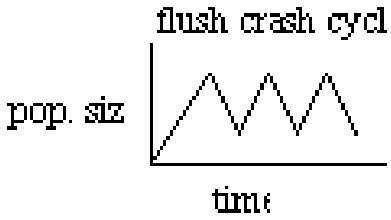
One consequence is that speciation **may not be dichotomous**. Important consequence: **rapid divergence, unlikely to leave fossil intermediates** (these possibilities will come in to play when we discuss "punctuated equilibrium" later).

A variant on this theme proposed by Hampton Carson an influential evolutionary biologist from the University of Hawaii is **Founder-Flush speciation**:

1. population initiated with small number of individuals (founders)

2. flush in population size; relaxed selection during this phase; low fitness recombinants survive

3. crash in population size; selection and drift determine which genotypes survive.



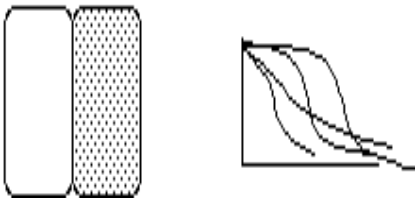
Carson's view: two "parts" to the genome: the "**open** variability system" and the "**closed** variability system" **Open** system has **much variability**, responds rapidly to **selection** (loci encoding allozyme polymorphisms such as enzymes in glycolysis and Krebs cycle, etc.); **closed** system is **resistant to selection; less variable**) loci encoding courtship song, developmental patterns, etc**.)** In Carson's view the **closed system is reorganized** during the flush-crash cycles, leads to a genetic change that contributes to reproductive isolation/mate recognition.

Questions about the founder flush speciation: **how small** is population after crash?, **how long** does population stay at reduced population size? Could retain a large portion of the genetic variation after one crash; extended bottle necks will be more effective in reducing variation.

These questions also could apply to Mayr's peripatric speciation model

Parapatric Model of speciation. Ranges of two differentiated forms are contiguous and non-overlapping. Patterns of discontinuities between differentiated forms/populations may be due

to secondary contact after a period in allopatry, or the discontinuity could be due to **primary differentiation *in situ***. One cause of this might be a steep environmental gradient or habitat boundary. With selection on loci that affect reproductive isolation/mate recognition, populations can become differentiated. Will be apparent in the formation of a **cline**. Can lead to sufficient divergence of reproductive/mating characteristics that barrier to gene flow is established (e.g., plants growing on **mine tailings** have diverged in **flowering time**).



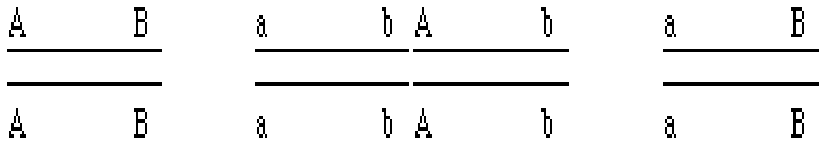
Studies of parapatric distributions are frequently concerned with the **concordance of clines**. Selection acting on one locus/trait can impose a cline on another character if the **two characters/loci are linked.** Are clines superimposed, shifted, different slopes. Slatkin (1973) has shown that the width of a cline is: $\text{width} = \frac{\sigma}{s}$ See fig. 16.9, page 439; text uses different letters for equation). Different loci may have different cline shapes due to different strengths of selection acting on them.

The text is a bit misleading about Parapatric speciation. It might lead one to believe that when a hybrid zone is observed, parapatric speciation is involved. This is not true since the hybrid zone may be the result of secondary contact after allopatry, rather than primary differentiation at the hybrid zone interface. Here again we need to determine the relative importance of the allopatric phase and the parapatric interaction in determining the outcome of speciation (or fusion). The cricket hybrid zone is in fact the result of allopatry followed by secondary contact (my personal knowledge), but Ridley does not let you know this.

Non-allopatric models of speciation are controversial but not impossible. **Sympatric speciation** can be modeled with a two locus polymorphism, one locus (A) affecting fitness (in this case by affecting fitness in terms of survival on one of two alternative hosts/patches), and another locus (B) affecting mate choice which is crucial in the evolution of **assortative mating**, a barrier to gene exchange (proposed by John Maynard-Smith in 1966)

These selective regimes maintain polymorphism at the A locus as in a multiple niche polymorphism considered in the population genetics section. These sets of fitness/mating values will result in the **evolution of associations** (e.g., linkage disequilibria) between the A

and the B locus (e.g., AABB individuals and aabb individuals will be found in the populations with few intermediates.



These have high fitness these have low fitness

The green lacewings (Genus Chrysoperla; formerly Chrysopa) seem to exhibit patterns of host preference and mate choice similar to that presented above (studied by the Taubers, Cornell University). One form is adapted to one host/habitat and a second to another; this habitat preference appears to be controlled by a single locus with other modifying loci (some evolutionists have not accepted the lacewing data as conclusive).

See the other sympatric speciation model that involves variation in a resource base. This model still requires the evolution of associations (e.g., linkage disequilibrium) between fitness genes and behavior genes.

But, if sympatric speciation is, if not common, at least possible, is the model really sympatric?: **is it just microallopatric speciation** (some argue NO if adults come up off their hosts into a mating swarm, but then proceed to mate). Another crucial issue is: what is the **rate of recombination** between these two types of loci since crossing over will break up favorable associations. A model of host preference and assortative mating invoking many genes (polygenic model) make it more difficult to maintain nonrandom associations. A general issue with all of these models is **how much gene flow** is tolerated. Evolution of **barriers to gene exchange** is the issue, gene flow = gene exchange; how much gene flow can take place and still evolve **barriers to** the gene flow?? The answer depends on the **genetic architecture of speciation** (how many genes, how much divergence, etc.; next lecture on genetics of speciation).

Saltatory speciation: Richard Goldschmitt in the Material Basis of Evolution proposed the idea that **Macromutations** (mutations with big effects) would result in major developmental and phenotypic changes in their carriers producing the so-called **hopeful monster**. Ridiculed at the time; recently gained a new readership due to the molecular characterization of genes that cause major phenotypic effects (more later on evolution of development). Big problem remains: who is the hopeful monster going to **mate** with?

Chromosomal speciation: Consider a diploid with 2N = 4 chromosomes. If two such individuals failed to undergo the reduction division of meiosis their gametes would be 2N=4. If these gametes were **used in fertilization** of one another, a new chromosomal number would be established: 4N = 8. If this became stabilized as a new chromosomal type (and this is common in plants), this new type can be reproductively isolated from the original 2N = 4 species. The reproductive isolation would be due to an imbalance of chromosome sets in the new zygote: N = 2 gamete crossed to an N = 4 gamete results chromosomal type of 3N = 6. There can be two consequences with this imbalance: i) inviability due to failure during development or ii) instability during chromosome segregation could result in gametes with an incomplete set of chromosomes (aneuploidy). These consequences could have the effect of a reproductive barrier between the original 2N = 4 and the polyploid 4N = 8 type. Speciation can be nearly instantaneous when such chromosomal events are involved (multiples of even numbered ploidy levels: can produce gametes with some exceptions; multiples of odd numbered ploidy levels: usually cannot produce gametes due to imbalance of haploid complements) => speciation. Thus **polyploid hybrids are frequency genetically isolated from their progenitors**.

The simple inversion model illustrates another way that chromosomal factors might play a role in speciation.

How should we think about speciation events? What are the models of divergence: is speciation like a peak shift in an adaptive landscape, or is speciation a gradual divergence process on a flat adaptive landscape? Main issue is whether the **peak itself shifts** and hence the population shifts with it, or whether the two **alternative peaks already exist** and the problem is shifting between the two alternatives.

Some fundamental issues in thinking about speciation:

1) does speciation require **allopatry** or can speciation occur in **non-allopatric** contexts (sympatric, parapatric) ?;

2) does speciation require changes in **many genes** or can changes in a **few specific genes** lead to speciation?;

3) is speciation itself **adaptive** or does speciation occur as a **byproduct** of adaptive responses to other pressures?;

4) what determines the **rates of speciation**? (some lineages speciate at very different rates).

7.6.1 ALLOPATRIC

Allopatric speciation (from Ancient Greek ἄλλος, *allos*, meaning "other", and πατρίς, *patris*, "fatherland"), also referred to as **geographic speciation**, **vicariant speciation**, or its earlier name, the **dumbbell model**, is a mode of speciation that occurs when biological populations become geographically isolated from each other to an extent that prevents or interferes with gene flow.

Various geographic changes can arise such as the movement of continents, and the formation of mountains, islands, bodies of water, or glaciers. Human activity such as agriculture or developments can also change the distribution of species populations. These factors can substantially alter a region's geography, resulting in the separation of a species population into isolated subpopulations. The vicariant populations then undergo genetic changes as they become subjected to different selective pressures, experience genetic drift, and accumulate different mutations in the separated populations gene pools. The barriers prevent the exchange of genetic information between the two populations leading to reproductive isolation. If the two populations come into contact they will be unable to reproduce—effectively speciating. Other isolating factors such as population dispersal leading to emigration can cause speciation (for instance, the dispersal and isolation of a species on an oceanic island) and is considered a special case of allopatric speciation called peripatric speciation.

Allopatric speciation is typically subdivided into two major models: vicariance and peripatric. Both models differ from one another by virtue of their population sizes and geographic isolating mechanisms. The terms *allopatry* and *vicariance* are often used in biogeography to describe the relationship between organisms whose ranges do not significantly overlap but are immediately adjacent to each other—they do not occur together or only occur within a narrow zone of contact. Historically, the language used to refer to modes of speciation directly reflected biogeographical distributions. As such, allopatry is a geographical distribution opposed to sympatry (speciation within the same area). Furthermore, the terms allopatric, vicariant, and geographical speciation are often used interchangeably in the scientific literature. This article will follow a similar theme, with the exception of special cases such as peripatric, centrifugal, among others.

Observation of nature creates difficulties in witnessing allopatric speciation from "start-to-finish" as it operates as a dynamic process. From this arises a host of various issues in defining species, defining isolating barriers, measuring reproductive isolation, among others.

Nevertheless, verbal and mathematical models, laboratory experiments, and empirical evidence overwhelmingly supports the occurrence of allopatric speciation in nature. Mathematical modeling of the genetic basis of reproductive isolation supports the plausibility of allopatric speciation; whereas laboratory experiments of *Drosophila* and other animal and plant species have confirmed that reproductive isolation evolves as a byproduct of natural selection.

A population becomes separated by a geographic barrier; reproductive isolation develops, resulting in two separate species.

The notion of vicariant evolution was first developed by Leon Croizat in the mid-twentieth century. The Vicariance theory, which showed coherence along with the acceptance of plate tectonics in the 1960s, was developed in the early 1950s by this Venezuelan botanist, who had found an explanation to the existence of American and Africa similar plants, by deducing that they had originally been a single population before the two continents drifted apart.

Currently, speciation by vicariance is widely regarded as the most common form of speciation; and is the primary model of allopatric speciation. Vicariance is a process by which the geographical range of an individual taxon, or a whole biota, is split into discontinuous populations (disjunct distributions) by the formation of an extrinsic barrier to the exchange of genes: that is, a barrier arising externally to a species. These extrinsic barriers often arise from various geologic-caused, topographic changes such as: the formation of mountains (orogeny); the formation of rivers or bodies of water; glaciation; the formation or elimination of land bridges; the movement of continents over time (by tectonic plates); or island formation, including sky islands. Vicariant barriers can change the distribution of species populations. Suitable or unsuitable habitat may be come into existence, expand, contract, or disappear as a result of global climate change or even large scale human activities (for example, agricultural, civil engineering developments, and habitat fragmentation). Such factors can alter a region's geography in substantial ways, resulting in the separation of a species population into isolated subpopulations. The vicariant populations may then undergo genotypic or phenotypic divergence as: (a) different mutations arise in the gene pools of the populations, (b) they become subjected to different selective pressures, and/or (c) they independently undergo genetic drift. The extrinsic barriers prevent the exchange of genetic information between the two populations, potentially leading to differentiation due to the ecologically different habitats they experience; selective pressure then invariably leads to complete reproductive isolation. Furthermore, a species' proclivity to remain in its ecological

niche through changing environmental conditions may also play a role in isolating populations from one another, driving the evolution of new lineages.

Allopatric speciation can be represented as the extreme on a gene flow continuum. As such, the level of gene flow between populations in allopatry would be, where equals the rate of gene exchange. In sympatry (panmixis), while in parapatric speciation, represents the entire continuum, although some scientists argue that a classification scheme based solely on geographic mode does not necessarily reflect the complexity of speciation. Allopatry is often regarded as the default or "null" model of speciation. but this too is debates.

Reproductive isolation

Reproductive isolation acts as the primary mechanism driving genetic divergence in allopatry and can be amplified by divergent selection. Pre-zygotic and post-zygotic isolation are often the most cited mechanisms for allopatric speciation, and as such, it is difficult to determine which form evolved first in an allopatric speciation event. Pre-zygotic simply implies the presence of a barrier prior to any act of fertilization (such as an environmental barrier dividing two populations), while post-zygotic implies the prevention of successful inter-population crossing after fertilization (such as the production of an infertile hybrid). Since species pairs who diverged in allopatry often exhibit pre- and post-zygotic isolation mechanisms, investigation of the earliest stages in the life cycle of the species can indicate whether or not divergence occurred due to a pre-zygotic or post-zygotic factor. However, establishing the specific mechanism may not be accurate, as a species pair continually diverges over time. For example, if a plant experiences a chromosome duplication event, reproduction will occur, but sterile hybrids will result—functioning as a form of post-zygotic isolation. Subsequently, the newly formed species pair may experience pre-zygotic barriers to reproduction as selection, acting on each species independently, will ultimately lead to genetic changes making hybrids impossible. From the researcher's perspective, the current isolating mechanism may not reflect the past isolating mechanism.

Reinforcement

In allopatric speciation, a species population becomes separated by a geographic barrier, whereby reproductive isolation evolves producing two separate species. From this, if a recently separated population comes in contact again, low fitness hybrids may form, but reinforcement acts to complete the speciation process.

Reinforcement has been a contentious factor in speciation. It is more often invoked in sympatric speciation studies, as it requires gene flow between two populations. However,

reinforcement may also play a role in allopatric speciation, whereby the reproductive barrier is removed, reuniting the two previously isolated populations. Upon secondary contact, individuals reproduce, creating low-fitness hybrids. Traits of the hybrids drive individuals to discriminate in mate choice, by which pre-zygotic isolation increases between the populations. Some arguments have been put forth that suggest the hybrids themselves can possibly become their own species. known as hybrid speciation. Reinforcement can play a role in all geographic modes (and other non-geographic modes) of speciation as long as gene flow is present and viable hybrids can be formed. The production of inviable hybrids is a form of reproductive character displacement, under which most definitions is the completion of a speciation event.

Research has well established the fact that interspecific mate discrimination occurs to a greater extent between sympatric populations than it does in purely allopatric populations; however, other factors have been proposed to account for the observed patterns. Reinforcement in allopatry has been shown to occur in nature (evidence for speciation by reinforcement), albeit with less frequency than a classic allopatric speciation event. A major difficulty arises when interpreting reinforcement's role in allopatric speciation, as current phylogenetic patterns may suggest past gene flow. This masks possible initial divergence in allopatry and can indicate a "mixed-mode" speciation event—exhibiting both allopatric and sympatric speciation processes.

Mathematical models

Developed in the context of the genetic basis of reproductive isolation, mathematical scenarios model both prezygotic and postzygotic isolation with respect to the effects of genetic drift, selection, sexual selection, or various combinations of the three. Masatoshi Nei and colleagues were the first to develop a neutral, stochastic model of speciation by genetic drift alone. Both selection and drift can lead to postzygotic isolation, supporting the fact that two geographically separated populations can evolve reproductive isolation—sometimes occurring rapidly. Fisherian sexual selection can also lead to reproductive isolation if there are minor variations in selective pressures (such as predation risks or habitat differences) among each population. Mathematical models concerning reproductive isolation-by distance have shown that populations can experience increasing reproductive isolation that correlates directly with physical, geographical distance. This has been exemplified in models of ring species. however, it has been argued that ring species are a special case, representing

reproductive isolation-by distance, and demonstrate parapatric speciation instead—as parapatric speciation represents speciation occurring along a cline.

Other models

Various alternative models have been developed concerning allopatric speciation. Special cases of vicariant speciation have been studied in great detail, one of which is peripatric speciation, whereby a small subset of a species population becomes isolated geographically; and centrifugal speciation, an alternative model of peripatric speciation concerning expansion and contraction of a species' range. Other minor allopatric models have also been developed are discussed below.

Peripatric

In peripatric speciation, a small, isolated population on the periphery of a central population evolves reproductive isolation due to the reduction or elimination of gene flow between the two.

Peripatric speciation is a mode of speciation in which a new species is formed from an isolated peripheral population. If a small population of a species becomes isolated (*e.g.* a population of birds on an oceanic island), selection can act on the population independent of the parent population. Given both geographic separation and enough time, speciation can result as a byproduct. It can be distinguished from allopatric speciation by three important features: 1) the size of the isolated population, 2) the strong selection imposed by the dispersal and colonization into novel environments, and 3) the potential effects of genetic drift on small populations. However, it can often be difficult for researchers to determine if peripatric speciation occurred as vicariant explanations can be invoked due to the fact that both models posit the absence of gene flow between the populations. The size of the isolated population is important because individuals colonizing a new habitat likely contain only a small sample of the genetic variation of the original population. This promotes divergence due to strong selective pressures, leading to the rapid fixation of an allele within the descendant population. This gives rise to the potential for genetic incompatibilities to evolve. These incompatibilities cause reproductive isolation, giving rise to rapid speciation events. Models of peripatry are supported mostly by species distribution patterns in nature. Oceanic islands and archipelagos provide the strongest empirical evidence that peripatric speciation occurs.

Centrifugal

Centrifugal speciation is a variant, alternative model of peripatric speciation. This model contrasts with peripatric speciation by virtue of the origin of the genetic novelty that leads to reproductive isolation. When a population of a species experiences a period of geographic range expansion and contraction, it may leave small, fragmented, peripherally isolated populations behind. These isolated populations will contain samples of the genetic variation from the larger parent population. This variation leads to a higher likelihood of ecological niche specialization and the evolution of reproductive isolation. Centrifugal speciation has been largely ignored in the scientific literature. Nevertheless, a wealth of evidence has been put forth by researchers in support of the model, much of which has not yet been refuted. One example is the possible center of origin in the Indo-West Pacific.

Microallopatric

Microallopatry refers to allopatric speciation occurring on a small geographic scale. Examples of microallopatric speciation in nature have been described. Rico and Turner found intralacustrine allopatric divergence of *Pseudotropheus callainos* (*Maylandia callainos*) within Lake Malawi separated only by 35 meters. Gustave Paulay found evidence that species in the subfamily Cryptorhynchinae have microallopatrically speciated on Rapa and its surrounding islets. A sympatrically distributed triplet of diving beetle (*Paroster*) species living in aquifers of Australia's Yilgarn region have likely speciated microallopatrically within a 3.5 km^2 area. The term was originally proposed by Hobart M. Smith to describe a level of geographic resolution. A sympatric population may exist in low resolution, whereas viewed with a higher resolution (*i.e.* on a small, localized scale within the population) it is "microallopatric". Ben Fitzpatrick and colleagues contend that this original definition, "is misleading because it confuses geographical and ecological concepts".

Modes with secondary contact

Ecological speciation can occur allopatrically, sympatrically, or parapatrically; the only requirement being that it occurs as a result of adaptation to different ecological or micro-ecological conditions. Ecological allopatry is a reverse-ordered form of allopatric speciation in conjunction with reinforcement. First, divergent selection separates a non-allopatric population emerging from pre-zygotic barriers, from which genetic differences evolve due to the obstruction of complete gene flow. The terms allo-parapatric and allo-sympatric have been used to describe speciation scenarios where divergence occurs in allopatry but

speciation occurs only upon secondary contact. These are effectively models of reinforcement or "mixed-mode" speciation events.

Observational evidence

As allopatric speciation is widely accepted as a common mode of speciation, the scientific literature is abundant with studies documenting its existence. The biologist Ernst Mayr was the first to summarize the contemporary literature of the time in 1942 and 1963. Many of the examples he set forth remain conclusive; however, modern research supports geographic speciation with molecular phylogenetics—adding a level of robustness unavailable to early researchers. The most recent thorough treatment of allopatric speciation (and speciation research in general) is Jerry Coyne and H. Allen Orr's 2004 publication *Speciation*. They list six mainstream arguments that lend support to the concept of vicariant speciation:

- Closely related species pairs, more often than not, reside in geographic ranges adjacent to one another, separated by a geographic or climatic barrier.
- Young species pairs (or sister species) often occur in allopatry, even without a known barrier.
- In occurrences where several pairs of related species share a range, they are distributed in abutting patterns, with borders exhibiting zones of hybridization.
- In regions where geographic isolation is doubtful, species do not exhibit sister pairs.
- Correlation of genetic differences between an array of distantly related species that correspond to known current or historical geographic barriers.
- Measures of reproductive isolation increase with the greater geographic distance of separation between two species pairs.

Endemism

Allopatric speciation has resulted in many of the biogeographic and biodiversity patterns found on Earth: on islands, continents, and even among mountains.

Islands are often home to species endemics—existing only on an island and nowhere else in the world—with nearly all taxa residing on isolated islands sharing common ancestry with a species on the nearest continent. Not without challenge, there is typically a correlation between island endemics and diversity; that is, that the greater the diversity (species richness) of an island, the greater the increase in endemism. Increased diversity effectively drives speciation. Furthermore, the number of endemics on an island is directly correlated with the

relative isolation of the island and its area. In some cases, speciation on islands has occurred rapidly.

Islands are not the only geographic locations that have endemic species. South America has been studied extensively with its areas of endemism representing assemblages of allopatrically distributed species groups. *Charis* butterflies are a primary example, confined to specific regions corresponding to phylogenies of other species of butterflies, amphibians, birds, marsupials, primates, reptiles, and rodents. The pattern indicates repeated vicariant speciation events among these groups. It is thought that rivers may play a role as the geographic barriers to *Charis*, not unlike the river barrier hypothesis used to explain the high rates of diversity in the Amazon basin—though this hypothesis has been disputed. Dispersal-mediated allopatric speciation is also thought to be a significant driver of diversification throughout the Neotropics.

Allopatric speciation can result from mountain topography. Climatic changes can drive species into altitudinal zones—either valleys or peaks. Colored regions indicate distributions. As distributions are modified due to the change in suitable habitats, reproductive isolation can drive the formation of a new species.

Patterns of increased endemism at higher elevations on both islands and continents have been documented on a global level. As topographical elevation increases, species become isolated from one another; often constricted to graded zones. This isolation on "mountain top islands" creates barriers to gene flow, encouraging allopatric speciation, and generating the formation of endemic species. Mountain building (orogeny) is directly correlated with—and directly affects biodiversity. The formation of the Himalayan mountains and the Qinghai–Tibetan Plateau for example have driven the speciation and diversification of numerous plants and animals such as *Lepisorus* ferns; glyptosternoid fishes (Sisoridae); and the *Rana chensinensis* species complex. Uplift has also driven vicariant speciation in *Macowania* daisies in South Africa's Drakensberg mountains, along with *Dendrocincla* woodcreepers in the South American Andes. The Laramide orogeny during the Late Cretaceous even caused vicariant speciation and radiations of dinosaurs in North America. Adaptive radiation, like the Galapagos finches observed by Charles Darwin, is often a consequence of rapid allopatric speciation among populations. However, in the case of the finches of the Galapagos, among other island radiations such as the honeycreepers of Hawaii represent cases of limited geographic separation and were likely driven by ecological speciation.

Isthmus of Panama

A conceptual representation of species populations becoming isolated (blue and green) by the closure of the Isthmus of Panama (red circle). With the closure, North and South America became connected, allowing the exchange of species (purple). Grey arrows indicate the gradual movement of tectonic plates that resulted in the closure.

Geological evidence supports the final closure of the isthmus of Panama approximately 2.7 to 3.5 mya, with some evidence suggesting an earlier transient bridge existing between 13 and 15 mya. Recent evidence increasingly points towards an older and more complex emergence of the Isthmus, with fossil and extant species dispersal (part of the American biotic interchange) occurring in three major pulses, to and from North and South America. Further, the changes in terrestrial biotic distributions of both continents such as with *Eciton* army ants supports an earlier bridge or a series of bridges. Regardless of the exact timing of the isthmus closer, biologists can study the species on the Pacific and Caribbean sides in what has been called, "one of the greatest natural experiments in evolution". Additionally, as with most geologic events, the closure was unlikely to have occurred rapidly, but instead dynamically—a gradual shallowing of sea water over millions of years.

Studies of snapping shrimp in the genus *Alpheus* have provided direct evidence of an allopatric speciation event, as phylogenetic reconstructions support the relationships of 15 pairs of sister species of *Alpheus*, each pair divided across the isthmus and molecular clock dating supports their separation between 3 and 15 million years ago. Recently diverged species live in shallow mangrove waters while older diverged species live in deeper water, correlating with a gradual closure of the isthmus. Support for an allopatric divergence also comes from laboratory experiments on the species pairs showing nearly complete reproductive isolation. Similar patterns of relatedness and distribution across the Pacific and Atlantic sides have been found in other species pairs such as:

- *Diadema antillarum* and *Diadema mexicanum*
- *Echinometra lucunter* and *Echinometra vanbrunti*
- *Echinometra viridis* and *E. vanbrunti*
- *Bathygobius soporator* and *Bathygobius ramosus*
- *B. soporator* and *Bathygobius andrei*
- *Excirolana braziliensis* and variant morphs
-

Refugia

Ice ages have played important roles in facilitating speciation among vertebrate species. This concept of refugia has been applied to numerous groups of species and their biogeographic distributions.

Glaciation and subsequent retreat caused speciation in many boreal forest birds, such as with North American sapsuckers (Yellow-bellied, Red-naped, and Red-breasted); the warblers in the genus *Setophaga* (*S. townsendii*, *S. occidentalis*, and *S. virens*), *Oreothlypis* (*O. virginiae*, *O. ridgwayi*, and *O. ruficapilla*), and *Oporornis* (*O. tolmiei* and *O. philadelphia* now classified in the genus *Geothlypis*); *Fox sparrows* (sub species *P. (i.) unalaschensis*, *P. (i.) megarhyncha*, and *P. (i.) schistacea*); *Vireo* (*V. plumbeus*, *V. cassinii*, and *V. solitarius*); *tyrant flycatchers* (*E. occidentalis* and *E. difficilis*); *chickadees* (*P. rufescens* and *P. hudsonicus*); and *thrushes* (*C. bicknelli* and *C. minimus*).

As a special case of allopatric speciation, peripatric speciation is often invoked for instances of isolation in glaciation refugia as small populations become isolated due to habitat fragmentation such as with North American red (*Picea rubens*) and black (*Picea mariana*) spruce or the prairie dogs *Cynomys mexicanus* and *C. ludovicianus*.

Super species

The red shading indicates the range of the bonobo (*Pan paniscus*). The blue shading indicates the range of the Common chimpanzee (*Pan troglodytes*). This is an example of allopatric speciation because they are divided by a natural barrier (the Congo River) and have no habitat in common. Other *Pan* subspecies are shown as well.

Numerous species pairs or species groups show abutting distribution patterns, that is, reside in geographically distinct regions next to each other. They often share borders, many of which contain hybrid zones. Some examples of abutting species and superspecies (an informal rank referring to a complex of closely related allopatrically distributed species, also called *allospecies*) include:

- Western and Eastern meadowlarks in North America reside in dry western and wet eastern geographic regions with rare occurrences of hybridization, most of which results in infertile offspring.
- Monarch flycatchers endemic to the Solomon Islands; a complex of several species and subspecies (Bougainville, white-capped, and chestnut-bellied monarchs and their related subspecies).

- North American sapsuckers and members of the genus *Setophaga* (the hermit warbler, black-throated green warbler, and Townsend's warbler).
- Sixty-six subspecies in the genus Pachycephala residing on the Melanesian islands.
- Bonobos and chimpanzees.
- *Climacteris* tree creeper birds in Australia.
- Birds-of-paradise in the mountains of New Guinea (genus *Astrapia*).
- Red-shafted and yellow-shafted flickers; black-headed grosbeaks and rose-breasted grosbeaks; Baltimore orioles and Bullock's orioles; and the lazuli and indigo buntings.
- All of these species pairs connect at zones of hybridization that correspond with major geographic barriers.
- *Dugesia* flatworms in Europe, Asia, and the Mediterranean regions.

In birds, some areas are prone to high rates of superspecies formation such as the 105 superspecies in Melanesia, comprising 66 percent of all bird species in the region. Patagonia is home to 17 superspecies of forest birds, while North America has 127 superspecies of both land and freshwater birds. Sub-Saharan Africa has 486 passerine birds grouped into 169 superspecies. Australia has numerous bird superspecies as well, with 34 percent of all bird species grouped into superspecies.

7.6.2 SYMPATRIC

SYMPATRIC

Sympatric speciation is speciation that occurs when two groups of the same species live in the same geographic location, but they evolve differently until they can no longer interbreed and are considered different species. It is different from other types of speciation, which involve the formation of a new species when a population is split into groups via a geographic barrier or migration. Sympatric speciation can be seen in many different types of organisms including bacteria, cichlid fish, and the apple maggot fly, but it can be difficult to tell when sympatric speciation is occurring or has occurred in nature.

To understand sympatric speciation, one must first understand the other types of speciation. There are four types of speciation: sympatric, allopatric, parapatric, and peripatric. The other three types of speciation involve the physical separation of two populations of the same species, while sympatric speciation does not.

- In allopatric speciation, two different species can form when one species is separated into different groups due to population dispersal or a natural geologic event such as a mountain formation. Like all forms of speciation, the process is usually very gradual.
- Parapatric speciation is when speciation occurs in subpopulations of the same species that are mostly isolated from each other, but have a narrow area where their ranges overlap.
- Peripatric speciation occurs when members of a population on the border of that population's habitat separate off from the main group and evolve over many generations to become a different species.

Sympatric speciation is unique because it takes place while two subpopulations of the same species are occupying the same range or in a range that highly overlaps. Even though the territory that the organisms live in is the same, they are able to split into two different groups that eventually become so genetically different from one another that they can no longer breed with each other. When one group can no longer breed with another, it is a separate species.

It can be difficult to tell whether speciation that has taken place is sympatric, another type, or even a mix of both during the speciation process. This has led to much discussion among evolutionary biology researchers as to what species have truly evolved sympatrically. For example, it was originally thought that two closely related stickleback species evolved via sympatric speciation, but further research suggests that the two different species actually colonized the lake independently. The first colonization led to the rise of one species of stickleback, while the other species evolved from the second colonization.

Jerry Coyne and H. Allen Orr have developed four criteria for inferring whether species have arisen sympatrically:

1. The species' ranges must overlap significantly.
2. There must be complete speciation (i.e., the two species cannot interbreed).
3. The species must be sister species (most closely related to each other) or part of a monophyletic group, which includes an ancestor and all its descendants; in other words, all the descendant species have to be included if there are more than two, not just some of them.

4. The history of the species' geographic range and evolution must make allopatry seem very unlikely, as allopatric speciation is much more common than sympatric speciation.

EXAMPLES

In Bacteria

True examples of sympatric speciation have rarely been observed in nature. Sympatric speciation is thought to occur more often in bacteria, because bacteria can exchange genes with other individuals that aren't parent and offspring in a process known as horizontal gene transfer. Sympatric speciation has been observed in BACILLUS and SYNECHOCOCCUS species of bacteria, and in the bacterioplankton VIBRIO SPLENDIDUS, among others. Subgroups of species that are undergoing sympatric speciation will show few differences since they have been diverging for a relatively recent time on the slow timescale at which evolution takes place. It is thought that one important factor in cases of sympatric speciation is adaptation to environmental conditions; if some members are specialized for living in a certain environment, that subgroup may go on to occupy a different environmental niche and eventually evolve into a new species over time.

In Cichlids

Another example of sympatric speciation is found in two species of Midas cichlid fish (AMPHILOPHUS species), which live in Lake Apoyo, a volcanic crater lake in Nicaragua. Researchers analyzed the DNA, appearance, and ecology of these two closely related species. The two species, though overall very similar, do have slight differences in appearance, and they cannot interbreed. All available evidence suggests that one species evolved from the other, which is the species of Midas cichlids that originally colonized the lake. The newer species evolved relatively recently, but in evolutionary terms, this means that it is thought to have evolved less than 10,000 years ago.

In Apple Maggot Flies

An extremely recent example of sympatric speciation may be occurring in the apple maggot fly, RHAGOLETIS POMONELLA. Apple maggot flies used to lay their eggs only on the fruit of hawthorn trees, but less than 200 years ago, some apple maggot flies began to lay their eggs on apples instead. Now there are two groups of apple maggot flies: one that lays eggs on hawthorns and one that lays eggs on apples. Males look for mates on the same type of fruit that they grew on, and females lay their eggs on the same type of fruit that they grew up on. Therefore, flies that grew up on hawthorns will raise offspring on hawthorns, and flies that

grew up on apples will raise offspring on apples. There are already genetic differences between the two groups, and over a long period of time, they could become separate species. This shows how speciation can occur even when different subgroups of the same species have the same geographic range.

7.6.3 PARAPATRIC

In **parapatric speciation**, two subpopulations of a species evolve reproductive isolation from one another while continuing to exchange genes. This mode of speciation has three distinguishing characteristics:

1) Mating occurs non-randomly,

2) Gene flow occurs unequally, and

3) Populations exist in either continuous or discontinuous geographic ranges.

This distribution pattern may be the result of unequal dispersal, incomplete geographical barriers, or divergent expressions of behavior, among other things. Parapatric speciation predicts that hybrid zones will often exist at the junction between the two populations.

In biogeography, the terms **parapatric** and **parapatry** are often used to describe the relationship between organisms whose ranges do not significantly overlap but are immediately adjacent to each other; they do not occur together except in a narrow contact zone. Parapatry is a geographical distribution opposed to sympatry (same area) and allopatry or peripatry (two similar cases of distinct areas). Various "forms" of parapatry have been proposed and are discussed below. Coyne and Orr in *Speciation* categorise these forms into three groups: clinal (environmental gradients), "stepping-stone" (discrete populations), and stasipatric speciation in concordance with most of the parapatric speciation literature. Henceforth, the models are subdivided following a similar format. Charles Darwin was the first to propose this mode of speciation. It was not until 1930 when Ronald Fisher published *The Genetical Theory of Natural Selection* where he outlined a verbal theoretical model of **clinal speciation**. In 1981, Joseph Felsenstein proposed an alternative, "discrete population" model (the "stepping-stone model). Since Darwin, a great deal of research has been conducted on parapatric speciation—concluding that its mechanisms are theoretically plausible, "and has most certainly occurred in nature".

MODELS

Mathematical models, laboratory studies, and observational evidence supports the existence of parapatric speciation's occurrence in nature. The qualities of parapatry imply a partial

extrinsic barrier during divergence; thus leading to a difficulty in determining whether this mode of speciation actually occurred, or if an alternative mode (notably, allopatric speciation) can explain the data. This problem poses the unanswered question as to its overall frequency in nature.

Parapatric speciation can be understood as a level of gene flow between populations wherein allopatry (and peripatry), in sympatry, and midway between the two in parapatry.Intrinsic to this, parapatry covers the entire continuum. Some biologists reject this delineation, advocating the disuse of the term "parapatric" outright, "because many different spatial distributions can result in intermediate levels of gene flow". Others champion this position and suggest the abandonment of geographic classification schemes (geographic modes of speciation) altogether.

Natural selection has been shown to be the primary driver in parapatric speciation (among other modes), and the strength of selection during divergence is often an important factor. Parapatric speciation may also result from reproductive isolation caused by social selection: individuals interacting altruistically.

Environmental gradients

Due to the continuous nature of a parapatric population distribution, population niches will often overlap, producing a continuum in the species' ecological role across an environmental gradient. Whereas in allopatric or peripatric speciation—in which geographically isolated populations may evolve reproductive isolation without gene flow—the reduced gene flow of parapatric speciation will often produce a cline in which a variation in evolutionary pressures causes a change to occur in allele frequencies within the gene pool between populations. This environmental gradient ultimately results in genetically distinct sister species.

Fisher's original conception of clinal speciation relied on (unlike most modern speciation research) the morphological species concept. With this interpretation, his verbal, theoretical model *can* effectively produce a new species; of which was subsequently confirmed mathematically. Further mathematical models have been developed to demonstrate the possibility of clinal speciation with most relying on, what Coyne and Orr assert are, "assumptions that are either restrictive or biologically unrealistic".

A mathematical model for clinal speciation was developed by Caisse and Antonovics that found evidence that, "both genetic divergence and reproductive isolation may therefore occur between populations connected by gene flow". This research supports clinal isolation

comparable to a ring species (discussed below), except that the terminal geographic ends do not meet to form a ring.

Doebeli and Dieckmann developed a mathematical model that suggested that ecological contact is an important factor in parapatric speciation and that, despite gene flow acting as a barrier to divergence in the local population, disruptive selection drives assortative mating; eventually leading to a complete reduction in gene flow. This model resembles reinforcement with the exception that there is never a secondary contact event. The authors conclude that, "spatially localized interactions along environmental gradients can facilitate speciation through frequency-dependent selection and result in patterns of geographical segregation between the emerging species." However, one study by Polechová and Barton disputes these conclusions.

Ring species

In a ring species, individuals are able to successfully reproduce (exchange genes) with members of their own species in adjacent populations occupying a suitable habitat around a geographic barrier. Individuals at the ends of the cline are unable to reproduce when they come into contact.

The concept of a ring species is associated with allopatric speciation as a special case; however, Coyne and Orr argue that Mayr's original conception of a ring species does not describe allopatric speciation, "but speciation occurring through the attenuation of gene flow with distance". They contend that ring species provide evidence of parapatric speciation in a non-conventional sense. They go on to conclude that:

Nevertheless, ring species are more convincing than cases of clinal isolation for showing that gene flow hampers the evolution of reproductive isolation. In clinal isolation, one can argue that reproductive isolation was caused by environmental differences that increase with distance between populations. One cannot make a similar argument for ring species because the most reproductively isolated populations occur in the *same* habitat.

Discrete populations

Referred to as a "stepping-stone" model by Coyne and Orr, it differs by virtue of the species population distribution pattern. Populations in discrete groups undoubtedly speciate more easily than those in a cline due to more limited gene flow. This allows for a population to evolve reproductive isolation as either selection or drift overpower gene flow between the populations. The smaller the discrete population, the species will likely undergo a higher rate of parapatric speciation.

Several mathematical models have been developed to test whether this form of parapatric speciation can occur, providing theoretical possibility and supporting biological plausibility (dependent on the models parameters and their concordance with nature). Joseph Felsenstein was the first to develop a working model. Later, Sergey Gavrilets and colleagues developed numerous analytical and dynamical models of parapatric speciation that have contributed significantly to the quantitative study of speciation.

Para-allopatric speciation

Further concepts developed by Barton and Hewitt in studying 170 hybrid zones, suggested that parapatric speciation can result from the same components that cause allopatric speciation. Called para-allopatric speciation, populations begin diverging parapatrically, fully speciating only after allopatry.

Stasipatric models

One variation of parapatric speciation involves species chromosomal differences. Michael J. D. White developed the stasipatric speciation model when studying Australian morabine grasshoppers (*Vandiemenella*). The chromosomal structure of sub-populations of a widespread species become underdominate; leading to fixation. Subsequently, the sub-populations expand within the species larger range, hybridizing (with sterility of the offspring) in narrow hybrid zones. Futuyama and Mayer contend that this form of parapatric speciation is untenable and that chromosomal rearrangements are unlikely to cause speciation. Nevertheless, data does support that chromosomal rearrangements can possibly lead to reproductive isolation, but it does not mean speciation results as a consequence.

7.7 CO-EVOLUTION AND SEXUAL SELECTION, ALTRUISM

Coevolution, the process of reciprocal evolutionary change that occurs between pairs of species or among groups of species as they interact with one another. The activity of each species that participates in the interaction applies selection pressure on the others. In a predator-prey interaction, for example, the emergence of faster prey may select against individuals in the predatory species who are unable to keep pace. Thus, only fast individuals or those with adaptations allowing them to capture prey using other means will pass their genes to the next generation. Coevolution is one of the primary methods by which biological communities are organized. It can lead to very specialized relationships between species, such as those between pollinator and plant, between predator and prey, and between parasite and host. It may also foster the evolution of new species in cases where individual

populations of interacting species separate themselves from their greater met populations for long periods of time.

How an interaction coevolves between species depends not only on the current genetic makeup of the species involved but also on new mutations that arise, the population characteristics of each species, and the communitycontext in which the interaction takes place. Under some ecological conditions (such as in some predator-prey interactions or between competitors for a resource), an antagonistic interaction between two species can coevolve to enhance the antagonism; the species "build up" methods of defense and attack, much like an evolutionary arms race. Under other ecological conditions (such as in certain parasite-host interactions), however, the antagonism may be lessened.

Coevolution does not necessarily require the presence of antagonism. The interactions or characteristics within groups of unrelated species may converge to allow individual species to exploit valuable resources or enjoy increased protection. Once an interaction evolves between two species, other species within the community may develop traits akin to those integral to the interaction, whereby new species enter into the interaction. This type of convergence of species has occurred commonly in the evolution of mutualistic interactions, including those between pollinators (such as bees) and plants and those between vertebrates (such as birds and bats) and fruits.

Some of the species drawn into mutualistic interactions become co-mutualistic, contributing as well as benefiting from the relationship, whereas others become cheaters that only exploit the relationship. In many interactions between bee pollinators and plants, bees collect the nectar from the reproductive parts of the plant and are often dusted with pollen in the process. When the bees fly to another plant of the same species, they may fertilize the plant by depositing pollen on the plant's stigma. In contrast, some bumblebees, such as those of BOMBUS TERRESTRIS, obtain nectar from the plant without picking up or dropping off pollen. They cheat by cutting through other parts of the plant instead of entering the flower.

In other cases, the behaviour or appearance of several species may converge to enhance their mutual protection. For example, several species of heliconid butterflies that are distasteful to predators have evolved to resemble one another. In addition, one species may evolve to mimic the behaviour or appearance of another to garner some of the same protections enjoyed by the model species. This evolutionary strategy has been successful for nonvenomous snakes, such as the scarletking snake (LAMPROPELTIS TRIANGULUM ELAPSOIDES), whose coloration closely resembles that of coral snakes, which can deliver a poisonous bite.

Coevolution is a complex process that occurs on many levels. It may appear in situations where one species interacts closely with several others, such as the interaction between European cuckoos (CUCULUS CANORUS) and the other species whose nests they parasitize; it may involve many species, as in relationships between fruit-bearing plants and birds; or it may take place in some subgroups of species but not others. It is important to note that human activities often disrupt the process of coevolution by changing the nature and the extent of the interactions between coevolving species. Some examples of harmful human activities include habitat fragmentation, increased hunting pressure, favouritism of one species over another, and the introduction of exotic species into ecosystems that are ill-equipped to handle them

Mutual attraction between the sexes is an important factor in reproduction. The males and females of many animalspecies are similar in size and shape except for the sexual organs and secondary sexual characteristics such as the breasts of female mammals. There are, however, species in which the sexes exhibit striking dimorphism. Particularly in birds and mammals, the males are often larger and stronger, more brightly coloured, or endowed with conspicuous adornments. But bright colours make animals more visible to predators—the long plumage of male peacocks and birds of paradise and the enormous antlers of aged male deer are cumbersome loads in the best of cases. Darwin knew that natural selection could not be expected to favour the evolution of disadvantageous traits, and he was able to offer a solution to this problem. He proposed that such traits arise by "sexual selection," which "depends not on a struggle for existence in relation to other organic beings or to external conditions but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex."

The concept of sexual selection as a special form of natural selection is easily explained. Other things being equal, organisms more proficient in securing mates have higher fitness. There are two general circumstances leading to sexual selection. One is the preference shown by one sex (often the females) for individuals of the other sex that exhibit certain traits. The other is increased strength (usually among the males) that yields greater success in securing mates.

The presence of a particular trait among the members of one sex can make them somehow more attractive to the opposite sex. This type of "sex appeal" has been experimentally demonstrated in all sorts of animals, from vinegar flies to pigeons, mice, dogs, and rhesus monkeys. When, for example, DROSOPHILA flies, some with yellow bodies as a result of

spontaneous mutation and others with the normal yellowish gray pigmentation, are placed together, normal males are preferred over yellow males by females with either body colour.

Sexual selection can also come about because a trait—the antlers of a stag, for example—increases prowess in competition with members of the same sex. Stags, rams, and bulls use antlers or horns in contests of strength; a winning male usually secures more female mates. Therefore, sexual selection may lead to increased size and aggressiveness in males. Male baboons are more than twice as large as females, and the behaviour of the docile females contrasts with that of the aggressive males. A similar dimorphism occurs in the northernsea lion, EUMETOPIAS JUBATA, where males weigh about 1,000 kg (2,200 pounds), about three times as much as females. The males fight fiercely in their competition for females; large, battle-scarred males occupy their own rocky islets, each holding a harem of as many as 20 females. Among many mammals that live in packs, troops, or herds—such as wolves, horses, and buffaloes—there usually is a hierarchy of dominance based on age and strength, with males that rank high in the hierarchy doing most of the mating.

The apparent altruistic behaviour of many animals is, like some manifestations of sexual selection, a trait that at first seems incompatible with the theory of natural selection. Altruism is a form of behaviour that benefits other individuals at the expense of the one that performs the action; the fitness of the altruist is diminished by its behaviour, whereas individuals that act selfishly benefit from it at no cost to themselves. Accordingly, it might be expected that natural selection would foster the development of selfish behaviour and eliminate altruism. This conclusion is not so compelling when it is noticed that the beneficiaries of altruistic behaviour are usually relatives. They all carry the same genes, including the genes that promote altruistic behaviour. Altruism may evolve by kin selection, which is simply a type of natural selection in which relatives are taken into consideration when evaluating an individual’s fitness.

Natural selection favours genes that increase the reproductive success of their carriers, but it is not necessary that all individuals that share a given genotype have higher reproductive success. It suffices that carriers of the genotype reproduce more successfully on the average than those possessing alternative genotypes. A parent shares half of its genes with each progeny, so a gene that promotes parental altruism is favoured by selection if the behaviour’s cost to the parent is less than half of its average benefits to the progeny. Such a gene will be more likely to increase in frequency through the generations than an alternative gene that does not promote altruistic behaviour. Parental care is, therefore, a form of altruism readily

explained by kin selection. The parent spends some energy caring for the progeny because it increases the reproductive success of the parent's genes.

Kin selection extends beyond the relationship between parents and their offspring. It facilitates the development of altruistic behaviour when the energy invested, or the risk incurred, by an individual is compensated in excess by the benefits ensuing to relatives. The closer the relationship between the beneficiaries and the altruist and the greater the number of beneficiaries, the higher the risks and efforts warranted in the altruist. Individuals that live together in a herd or troop usually are related and often behave toward each other in this way. Adult zebras, for instance, will turn toward an attacking predator to protect the young in the herd rather than fleeing to protect themselves.

Altruism also occurs among unrelated individuals when the behaviour is reciprocal and the altruist's costs are smaller than the benefits to the recipient. This reciprocal altruism is found in the mutual grooming of chimpanzees and other primates as they clean each other of lice and other pests. Another example appears in flocks of birds that post sentinels to warn of danger. A crow sitting in a tree watching for predators while the rest of the flock forages incurs a small loss by not feeding, but this loss is well compensated by the protection it receives when it itself forages and others of the flock stand guard.

A particularly valuable contribution of the theory of kin selection is its explanation of the evolution of social behaviour among ants, bees, wasps, and other social insects. In honeybee populations, for example, the female workers build the hive, care for the young, and gather food, but they are sterile; queen bees alone produce progeny. It would seem that the workers' behaviour would in no way be promoted or maintained by natural selection. Any genes causing such behaviour would seem likely to be eliminated from the population, because individuals exhibiting the behaviour increase not their own reproductive success but that of the queen. The situation is, however, more complex.

Queen bees produce some eggs that remain unfertilized and develop into males, or drones, having a mother but no father. Their main role is to engage in the nuptial flight during which one of them fertilizes a new queen. Other eggs laid by queen bees are fertilized and develop into females, the large majority of which are workers. Some social insects, such as the stingless Meliponinae bees, with hundreds of species across the tropics, have only one queen in each colony. The queen typically mates with a single male during her nuptial flight; the male's sperm is stored in the queen's spermatheca, from which it is gradually released as she lays fertilized eggs. All the queen's female progeny therefore have the same father, so that

workers are more closely related to one another and to any new sister queen than they are to the mother queen. The female workers receive one-half of their genes from the mother and one-half from the father, but they share among themselves three-quarters of their genes. The half of the set from the father is the same in every worker, because the father had only one set of genes rather than two to pass on (the male developed from an unfertilized egg, so all his sperm carry the same set of genes). The other half of the workers' genes come from the mother, and on the average half of them are identical in any two sisters. Consequently, with three-quarters of her genes present in her sisters but only half of her genes able to be passed on to a daughter, a worker's genes are transmitted one and a half times more effectively when she raises a sister (whether another worker or a new queen) than if she produces a daughter of her own.

A**ltruism** refers to behaviour by an individual that increases the fitness of another individual while decreasing the fitness of the actor. Altruism in this sense is different from the philosophical concept of altruism, in which an action would only be called "altruistic" if it was done with the conscious intention of helping another. In the behavioural sense, there is no such requirement. As such, it is not evaluated in moral terms—it is the consequences of an action for reproductive fitness that determine whether the action is considered altruistic, not the intentions, if any, with which the action is performed. The term altruism was coined by the French philosopher Auguste Comte in French, as *altruisme*, for an antonym of egoism. He derived it from the Italian *altrui*, which in turn was derived from Latin *alteri*, meaning "other people" or "somebody else".

Altruistic behaviours appear most obviously in kin relationships, such as in parenting, but may also be evident among wider social groups, such as in social insects. They allow an individual to increase the success of its genes by helping relatives that share those genes. Obligate altruism is the permanent loss of direct fitness (with potential for indirect fitness gain). For example, honey bee workers may forage for the colony. Facultative altruism is temporary loss of direct fitness (with potential for indirect fitness gain followed by personal reproduction). For example, a Florida scrub jay may help at the nest, then gain parental territory.

In ethology (the study of behavior), and more generally in the study of social evolution, on occasion, some animals do behave in ways that reduce their individual fitness but increase the fitness of other individuals in the population; this is a functional definition of altruism. Research in evolutionary theory has been applied to social behaviour, including altruism.

Cases of animals helping individuals to whom they are closely related can be explained by kin selection, and are not considered true altruism. Beyond the physical exertions that in some species mothers and in some species fathers undertake to protect their young, extreme examples of sacrifice may occur. One example is matriphagy (the consumption of the mother by her offspring) in the spider *Stegodyphus*; another example is a male spider allowing a female fertilized by him to eat him. Hamilton's rule describes the benefit of such altruism in terms of Wright'scoefficient of relationship to the beneficiary and the benefit granted to the beneficiary minus the cost to the sacrificer. Should this sum be greater than zero a fitness gain will result from the sacrifice.

When apparent altruism is not between kin, it may be based on reciprocity. A monkey will present its back to another monkey, who will pick out parasites; after a time the roles will be reversed. Such reciprocity will pay off, in evolutionary terms, as long as the costs of helping are less than the benefits of being helped and as long as animals will not gain in the long run by "cheating"—that is to say, by receiving favours without returning them. This is elaborated on in evolutionary game theory and specifically the prisoner's dilemma as social theory.

IMPLICATIONS IN EVOLUTIONARY THEORY

The existence of altruism in nature is at first sight puzzling, because altruistic behaviour reduces the likelihood that an individual will reproduce. The idea that *group selection* might explain the evolution of altruism was first broached by Darwin himself in The Descent of Man, and Selection in Relation to Sex, (1871). The concept of group selection has had a chequered and controversial history in evolutionary biology but the uncritical 'good of the species' tradition came to an abrupt halt in the 1960s, due largely to the work of George C. Williams, and John Maynard Smith as well as Richard Dawkins. These evolutionary theorists pointed out that natural selection acts on the individual, and that it is the individual's fitness (number of offspring and grand-offspring produced compared to the rest of the population) that drives evolution. A group advantage (e.g. hunting in a pack) that is disadvantageous to the individual (who might be harmed during the hunt, when it could avoid injury by hanging back from the pack but still share in the spoils) cannot evolve, because the selfish individual will leave, on average, more offspring than those who join the pack and suffer injuries as a result. If the selfishness is hereditary, this will ultimately result in the population consisting entirely of selfish individuals. However, in the 1960s and 1970s an alternative to the "group selection" theory emerged. This was the kin selection theory, due originally to W. D. Hamilton. Kin selection is an instance of inclusive fitness, which is based on the notion that

an individual shares only half its genes with each offspring, but also with each full sib. From an evolutionary genetic point of view it is therefore as advantageous to help with the upbringing of full sibs as it is to produce and raise one's own offspring. The two activities are evolutionarily entirely equivalent. Co-operative breeding (i.e. helping one's parents raise sibs—provided they are full sibs) could thus evolve without the need for group-level selection. This quickly gained prominence among biologists interested in the evolution of social behaviour.

In 1971 Robert Trivers introduced his reciprocal altruism theory to explain the evolution of helping at the nest of an unrelated breeding pair of birds. He argued that an individual might act as a helper if there was a high probabilistic expectation of being helped by the recipients at some later date. If, however, the recipients did not reciprocate when it was possible to do so, the altruistic interaction with these recipients would be permanently terminated. But if the recipients did not cheat then the reciprocal altruism would continue indefinitely to both parties' advantage. This model was considered by many (e.g. West-Eberhard and Dawkins) to be evolutionarily unstable because it is prone to invasion by cheats for the same reason that cooperative hunting can be invaded and replaced by cheats. However, Trivers did make reference to the Prisoner's Dilemma Game which, 10 years later, would restore interest in Trivers' reciprocal altruism theory, but under the title of "tit-for-tat".

In its original form the Prisoner's Dilemma Game (PDG) described two awaiting trial prisoners, A and B, each faced with the choice of betraying the other or remaining silent. The "game" has four possible outcomes: (a) they both betray each other, and are both sentenced to two years in prison; (b) A betrays B, which sets A free and B is sentenced to four years in prison; (c) B betrays A, with the same result as (b) except that it is B who is set free and the other spends four years in jail; (d) both remain silent, resulting in a six-month sentence each. Clearly (d) ("cooperation") is the best mutual strategy, but from the point of view of the individual betrayal is unbeatable (resulting in being set free, or getting only a two-year sentence). Remaining silent results in a four-year or six-month sentence. This is exemplified by a further example of the PDG: two strangers attend a restaurant together and decide to split the bill. The mutually best ploy would be for both parties to order the cheapest items on the menu (mutual cooperation). But if one member of the party exploits the situation by ordering the most expensive items, then it is best for the other member to do likewise. In fact, if the fellow diner's personality is completely unknown, and the two diners are unlikely ever to meet again, it is always in one's own best interests to eat as expensively as possible.

Situations in nature that are subject to the same dynamics (rewards and penalties) as the PDG define cooperative behaviour: it is never in the individual's fitness interests to cooperate, even though mutual cooperation rewards the two contestants (together) more highly than any other strategy. Cooperation cannot evolve under these circumstances.

However, in 1981 Axelrod and Hamilton noted that if the same contestants in the PDG meet repeatedly (the so-called Iterated Prisoner's Dilemma game, IPD) then tit-for-tat (foreshadowed by Robert Triver's reciprocal altruism theory) is a robust strategy which promotes altruism. In "tit-for-tat" both players' opening moves are cooperation. Thereafter each contestant repeats the other player's last move, resulting in a seemingly endless sequence of mutually cooperative moves. However, mistakes severely undermine tit-for-tat's effectiveness, giving rise to prolonged sequences of betrayal, which can only be rectified by another mistake. Since these initial discoveries, all the other possible IPD game strategies have been identified (16 possibilities in all, including, for instance, "generous tit-for-tat", which behaves like "tit-for-tat", except that it cooperates with a small probability when the opponent's last move was "betray".), but all can be outperformed by at least one of the other strategies, should one of the players switch to such a strategy. The result is that none is evolutionarily stable, and any prolonged series of the iterated prisoner's dilemma game, in which alternative strategies arise at random, gives rise to a chaotic sequence of strategy changes that never ends.

There are striking parallels between altruistic acts and exaggerated sexual ornaments displayed by some animals, particularly certain bird species, such as, amongst others, the peacock. Both are costly in fitness terms, and both are generally conspicuous to other members of the population or species. This led Amotz Zahavi to suggest that both might be fitness signals rendered evolutionarily stable by his handicap principle. If a signal is to remain reliable, and generally resistant to falsification, the signal has to be evolutionarily costly. Thus, if a (low fitness) liar were to use the highly costly signal, which seriously eroded its real fitness, it would find it difficult to maintain a semblance or normality.Zahavi borrowed the term "handicap principle" from sports handicapping systems. These systems are aimed at reducing disparities in performance, thereby making the outcome of contests less predictable. In a horse handicap race, provenly faster horses are given heavier weights to carry under their saddles than inherently slower horses. Similarly, in amateur golf, better golfers have fewer strokes subtracted from their raw scores than the less talented players. The handicap therefore correlates with unhandicapped performance, making it possible, if one

knows nothing about the horses, to predict which unhandicapped horse would win an open race. It would be the one handicapped with the greatest weight in the saddle. The handicaps in nature are highly visible, and therefore a peahen, for instance, would be able to deduce the health of a potential mate by comparing its handicap (the size of the peacock's tail) with those of the other males. The loss of the male's fitness caused by the handicap is offset by its increased access to females, which is as much of a fitness concern as is its health. An altruistic act is, by definition, similarly costly. It would therefore also signal fitness, and is probably as attractive to females as a physical handicap. If this is the case altruism is evolutionarily stabilized by sexual selection.

There is an alternate strategy for identifying fit mates which does not rely on one gender having exaggerated sexual ornaments or other handicaps, but is generally applicable to most, if not all sexual creatures. It derives from the concept that the change in appearance and functionality caused by a non-silentmutation will generally stand out in a population. This is because that altered appearance and functionality will be unusual, peculiar, and different from the norm within that population. The norm against which these unusual features are judged is made up of fit attributes that have attained their plurality through natural selection, while less adaptive attributes will be in the minority or frankly rare. Since the overwhelming majority of mutant features are maladaptive, and it is impossible to predict evolution's future direction, sexual creatures would be expected to prefer mates with the fewest unusual or minority features. This will have the effect of a sexual population rapidly shedding peripheral phenotypic features and canalizing the entire outward appearance and behavior so that all the members of that population will begin to look remarkably similar in every detail, as illustrated in the accompanying photograph of the African pygmy kingfisher, *Ispidina picta*. Once a population has become as homogeneous in appearance as is typical of most species, its entire repertoire of behaviors will also be rendered evolutionarily stable, including any altruistic, cooperative and social characteristics. Thus, in the example of the selfish individual who hangs back from the rest of the hunting pack, but who nevertheless joins in the spoils, that individual will be recognized as being different from the norm, and will therefore find it difficult to attract a mate. Its genes will therefore have only a very small probability of being passed on to the next generation, thus evolutionarily stabilizing cooperation and social interactions at whatever level of complexity is the norm in that population.

RECIPROCITY MECHANISMS

Altruism in animals describes a range of behaviors performed by animals that may be to their own disadvantage but which benefit others. The costs and benefits are measured in terms of reproductive fitness, or expected number of offspring. So by behaving altruistically, an organism reduces the number of offspring it is likely to produce itself, but boosts the likelihood that other organisms are to produce offspring. There are other forms of altruism in nature other than risk-taking behavior, such as reciprocal altruism. This biological notion of altruism is not identical to the everyday human concept. For humans, an action would only be called 'altruistic' if it was done with the conscious intention of helping another. Yet in the biological sense there is no such requirement. Instead, until we can communicate directly with other species, an accurate theory to describe altruistic acts between species is Biological Market Theory. Humans and other animals exchange benefits in several ways, known technically as reciprocity mechanism. No matter what the mechanism, the common thread is that benefits find their way back to the original giver.

Symmetry-based

Also known as the "buddy-system", mutual affection between two parties prompts similar behavior in both directions without need to track of daily give-and-take, so long as the overall relationship remains satisfactory. This is one of the most common mechanisms of reciprocity in nature; this kind is present in humans, primates, and many other mammals.

Attitudinal

Also known as, "If you're nice, I'll be nice too." This mechanism of reciprocity is similar to the heuristic of the golden rule, "Treat others how you would like to be treated." Parties mirror one another's attitudes, exchanging favors on the spot. Instant attitudinal reciprocity occurs among monkeys, and people often rely on it with strangers and acquaintances.

Calculated

Also known as, "what have you done for me lately?" Individuals keep track of the benefits they exchange with particular partners, which help them decide to whom to return favors. This mechanism is typical of chimpanzees and very common among human relationships. Yet some opposing experimental research suggests that calculated or contingent reciprocity does not spontaneously arise in laboratory experimental settings, despite patterns of behavior.

UNIT 8: ORIGIN OF HIGHER EVOLUTION

8.1 Objectives

8.2 Introduction

8.3 Phylogenetic Gradualism and Punctured equilibrium

8.4 Major Trends in the Origin of Higher Categories

8.5 Micro, Macro and Mega Evolution

8.6 Evolution of Man

8.1 OBJECTIVES

The Study of Phylogenetic Gradualism and Punctured equilibrium & Micro, Macro and Mega Evolution, We know about the Evolution of Man in this topics.

8.2 INTRODUCTION

The word *phyletic* derives from the Greek*phūletikos*, which conveys the meaning of a line of descent. Phyletic gradualism contrasts with the theory of punctuated equilibrium, which proposes that most evolution occurs isolated in rare episodes of rapid evolution, when a single species splits into two distinct species, followed by a long period of stasis or non-change. These models both contrast with variable-speed evolution ("variable speedism"), which maintains that different species evolve at different rates, and that there is no reason to stress one rate of change over another.

Evolutionary biologistRichard Dawkins argues that constant-rate gradualism is not present in the professional literature; thereby the term serves only as a straw-man for punctuated-equilibrium advocates. In his book *The Blind Watchmaker*, Dawkins observes that Charles Darwin himself was not a constant-rate gradualist, as suggested by Niles Eldredge and Stephen Jay Gould. In the first edition of *On the Origin of Species*, Darwin stated that "Species of different genera and classes have not changed at the same rate, or in the same degree. In the oldest tertiary beds a few living shells may still be found in the midst of a multitude of extinct forms... The Silurian *Lingula* differs but little from the living species of this genus".

Lingula is among the few brachiopods surviving today but also known from fossils over 500 million years old. In the fifth edition of *The Origin of Species*, Darwin wrote that "the periods during which species have undergone modification, though long as measured in years, have probably been short in comparison with the periods during which they retain the same form".

8.3 PHYLOGENETIC GRADUALISM AND PUNCTURED EQUILIBRIUM

Phyletic gradualism is a model of evolution which theorizes that most speciation is slow, uniform and gradual. When evolution occurs in this mode, it is usually by the steady transformation of a whole species into a new one (through a process called anagenesis). In this view no clear line of demarcation exists between an ancestral species and a descendant species, unless splitting occurs. The theory is contrasted with punctuated equilibrium.

PUNCTUATED EQUILIBRIUM

In evolutionary biology, **punctuated equilibrium** (also called **punctuated equilibria**) is a theory that proposes that once a species appears in the fossil record, the population will become stable, showing little evolutionary change for most of its geological history. This state of little or no morphological change is called *stasis*. When significant evolutionary change occurs, the theory proposes that it is generally restricted to rare and geologically rapid events of branching speciation called cladogenesis. Cladogenesis is the process by which a species splits into two distinct species, rather than one species gradually transforming into another. Punctuated equilibrium is commonly contrasted against phyletic gradualism, the idea that evolution generally occurs uniformly and by the steady and gradual transformation of whole lineages (called anagenesis). In this view, evolution is seen as generally smooth and continuous. In 1972, paleontologists Niles Eldredge and Stephen Jay Gould published a landmark paper developing their theory and called it *punctuated equilibria*. Their paper built upon Ernst Mayr's model of geographic speciation, I. Michael Lerner's theories of developmental and genetic homeostasis, and their own empirical research. Eldredge and Gould proposed that the degree of gradualism commonly attributed to Charles Darwin is virtually nonexistent in the fossil record, and that stasis dominates the history of most fossil species.

Punctuated equilibrium originated as a logical consequence of Ernst Mayr's concept of genetic revolutions by allopatric and especially peripatric speciation as applied to the fossil record. Although the sudden appearance of species and its relationship to speciation was

proposed and identified by Mayr in 1954, historians of science generally recognize the 1972 Eldredge and Gould paper as the basis of the new paleobiological research program. Punctuated equilibrium differs from Mayr's ideas mainly in that Eldredge and Gould placed considerably greater emphasis on stasis, whereas Mayr was concerned with explaining the morphological discontinuity (or "sudden jumps") found in the fossil record. Mayr later complimented Eldredge and Gould's paper, stating that evolutionary stasis had been "unexpected by most evolutionary biologists" and that punctuated equilibrium "had a major impact on paleontology and evolutionary biology."

A year before their 1972 Eldredge and Gould paper, Niles Eldredge published a paper in the journal *Evolution* which suggested that gradual evolution was seldom seen in the fossil record and argued that Ernst Mayr's standard mechanism of allopatric speciation might suggest a possible resolution. The Eldredge and Gould paper was presented at the Annual Meeting of the Geological Society of America in 1971. The symposium focused its attention on how modern microevolutionary studies could revitalize various aspects of paleontology and macroevolution. Tom Schopf, who organized that year's meeting, assigned Gould the topic of speciation. Gould recalls that "Eldredge's 1971 publication [on Paleozoictrilobites] had presented the only new and interesting ideas on the paleontological implications of the subject—so I asked Schopf if we could present the paper jointly." According to Gould "the ideas came mostly from Niles, with yours truly acting as a sounding board and eventual scribe. I coined the term *punctuated equilibrium* and wrote most of our 1972 paper, but Niles is the proper first author in our pairing of Eldredge and Gould." In his book *Time Frames* Eldredge recalls that after much discussion the pair "each wrote roughly half. Some of the parts that would seem obviously the work of one of us were actually first penned by the other—I remember for example, writing the section on Gould's snails. Other parts are harder to reconstruct. Gould edited the entire manuscript for better consistency. We sent it in, and Schopf reacted strongly against it—thus signaling the tenor of the reaction it has engendered, though for shifting reasons, down to the present day."

John Wilkins and Gareth Nelson have argued that French architect Pierre Trémaux proposed an "anticipation of the theory of punctuated equilibrium of Gould and Eldredge."

EVIDENCE FROM THE FOSSIL RECORD

The fossil record includes well documented examples of both phyletic gradualism and punctuational evolution. As such, much debate persists over the prominence of stasis in the fossil record. Before punctuated equilibrium, most evolutionists considered stasis to be rare

or unimportant. The paleontologist George Gaylord Simpson, for example, believed that phyletic gradual evolution (called *horotely* in his terminology) comprised 90% of evolution. More modern studies, including a meta-analysis examining 58 published studies on speciation patterns in the fossil record showed that 71% of species exhibited stasis, and 63% were associated with punctuated patterns of evolutionary change. According to Michael Benton, "it seems clear then that stasis is common, and that had not been predicted from modern genetic studies." A paramount example of evolutionary stasis is the fern *Osmunda claytoniana*. Based on paleontological evidence it has remained unchanged, even at the level of fossilized nuclei and chromosomes, for at least 180 million years.

THEORETICAL MECHANISMS

Punctuational change

When Eldredge and Gould published their 1972 paper, allopatric speciation was considered the "standard" model of speciation. This model was popularized by Ernst Mayr in his 1954 paper "Change of genetic environment and evolution," and his classic volume *Animal Species and Evolution* (1963).

Allopatric speciation suggests that species with large central populations are stabilized by their large volume and the process of gene flow. New and even beneficial mutations are diluted by the population's large size and are unable to reach fixation, due to such factors as constantly changing environments. If this is the case, then the transformation of whole lineages should be rare, as the fossil record indicates. Smaller populations on the other hand, which are isolated from the parental stock, are decoupled from the homogenizing effects of gene flow. In addition, pressure from natural selection is especially intense, as peripheral isolated populations exist at the outer edges of ecological tolerance. If most evolution happens in these rare instances of allopatric speciation then evidence of gradual evolution in the fossil record should be rare. This hypothesis was alluded to by Mayr in the closing paragraph of his 1954 paper:

Rapidly evolving peripherally isolated populations may be the place of origin of many evolutionary novelties. Their isolation and comparatively small size may explain phenomena of rapid evolution and lack of documentation in the fossil record, hitherto puzzling to the paleontologist.

Although punctuated equilibrium generally applies to sexually reproducing organisms, some biologists have applied the model to non-sexual species like viruses, which cannot be stabilized by conventional gene flow. As time went on biologists like Gould moved away

from wedding punctuated equilibrium to allopatric speciation, particularly as evidence accumulated in support of other modes of speciation. Gould, for example, was particularly attracted to Douglas Futuyma's work on the importance of reproductive isolating mechanisms.

STASIS

Many hypotheses have been proposed to explain the putative causes of stasis. Gould was initially attracted to I. Michael Lerner's theories of developmental and genetic homeostasis. However this hypothesis was rejected over time, as evidence accumulated against it. Other plausible mechanisms which have been suggested include: habitat tracking, stabilizing selection, the Sternest-Maynard Smith stability hypothesis, constraints imposed by the nature of subdivided populations, normalizing clade selection, and koinophilia. Evidence for stasis has also been corroborated from the genetics of sibling species, species which are morphologically indistinguishable, but whose proteins have diverged sufficiently to suggest they have been separated for millions of years. Fossil evidence of reproductively isolated extant species of sympatric Olive Shells (*Amalda* sp.) also confirms morphological stasis in multiple lineages over three million years. According to Gould, "stasis may emerge as the theory's most important contribution to evolutionary science." Philosopher Kim Sterelny in clarifying the meaning of stasis adds, "In claiming that species typically undergo no further evolutionary change once speciation is complete, they are not claiming that there is no change at all between one generation and the next. Lineages do change. But the change between generations does not accumulate. Instead, over time, the species wobbles about its phenotypic mean. Jonathan Weiner's *The Beak of the Finch* describes this very process."

HIERARCHICAL EVOLUTION

Punctuated equilibrium has also been cited as contributing to the hypothesis that species are Darwinian individuals, and not just classes, thereby providing a stronger framework for a hierarchical theory of evolution.

QUANTUM EVOLUTION

Quantum evolution was a controversial hypothesis advanced by Columbia University paleontologist George Gaylord Simpson, who was regarded by Gould as "the greatest and most biologically astute paleontologist of the twentieth century." Simpson's conjecture was that according to the geological record, on very rare occasions evolution would proceed very rapidly to form entirely new families, orders, and classes of organisms. This hypothesis differs from punctuated equilibrium in several respects. First, punctuated equilibrium was

more modest in scope, in that it was addressing evolution specifically at the species level. Simpson's idea was principally concerned with evolution at higher taxonomic groups. Second, Eldredge and Gould relied upon a different mechanism. Where Simpson relied upon a synergistic interaction between genetic drift and a shift in the adaptive fitness landscape, Eldredge and Gould relied upon ordinary speciation, particularly Ernst Mayr's concept of allopatric speciation. Lastly, and perhaps most significantly, quantum evolution took no position on the issue of stasis. Although Simpson acknowledged the existence of stasis in what he called the bradytelic mode, he considered it (along with rapid evolution) to be unimportant in the larger scope of evolution. In his *Major Features of Evolution* Simpson stated, "Evolutionary change is so nearly the universal rule that a state of motion is, figuratively, normal in evolving populations. The state of rest, as in bradytely, is the exception and it seems that some restraint or force must be required to maintain it." Despite such differences between the two models, earlier critiques—from such eminent commentators as Sewall Wright as well as Simpson himself—have argued that punctuated equilibrium is little more than quantum evolution relabeled.

MULTIPLE MEANINGS OF GRADUALISM

Punctuated equilibrium is often portrayed to oppose the concept of gradualism, when it is actually a form of gradualism. This is because even though evolutionary change appears instantaneous between geological sedimentary layers, change is still occurring incrementally, with no great change from one generation to the next. To this end, Gould later commented that "Most of our paleontological colleagues missed this insight because they had not studied evolutionary theory and either did not know about allopatric speciation or had not considered its translation to geological time. Our evolutionary colleagues also failed to grasp the implication(s), primarily because they did not think at geological scales".

Richard Dawkins dedicated a chapter in *The Blind Watchmaker* to correcting, in his view, the wide confusion regarding *rates of change*. His first point is to argue that phyletic gradualism—understood in the sense that evolution proceeds at a single uniform rate of speed, called "constant speedism" by Dawkins—is a "caricature of Darwinism" and "does not really exist". His second argument, which follows from the first, is that once the caricature of "constant speedism" is dismissed, we are left with one logical alternative, which Dawkins terms "variable speedism". Variable speedism may also be distinguished one of two ways: "*discrete variable* speedism" and "*continuously variable* speedism". Eldredge and Gould, proposing that evolution jumps between stability and relative rapidity, are described as

"discrete variable speediest", and "in this respect they are genuinely radical." They assert that evolution generally proceeds in bursts, or not at all. "Continuously variable speedists", on the other hand, advance that "evolutionary rates fluctuate continuously from very fast to very slow and stop, with all intermediates. They see no particular reason to emphasize certain speeds more than others. In particular, stasis, to them, is just an extreme case of ultra-slow evolution. To a punctuationist, there is something very special about stasis." Dawkins therefore commits himself here to an empirical claim about the geological record, in contrast to his earlier claim that "The paleontological evidence can be argued about, and I am not qualified to judge it." It is this particular commitment that Eldredge and Gould have aimed to overturn.

8.4 MICRO, MACRO AND MEGA EVOLUTION

Based on the degree of change and speed of evolution three stages in evolutionary process can be identified:

1) Origin of small evolutionary differences at sub specific level.

2) Modifications in larger groups of animals, producing species and genera by adaptive radiation.

3) Evolution of new types from their predecessors by large genetic changes, often producing families, orders, classes and phyla.

MICROEVOLUTION

This is also called Sequential evolution, which involves a continuous and gradual change in an interbreeding population, usually giving rise to new subspecies and geographical races. Basic process involves changes in gene frequencies in a population from one generation to the next. Microevolution is produced by stabilizing or normalizing natural selections that operate in stable environmental conditions and in short time span.

Examples: Rowe has discovered several lines of descent in sea urchin, Micraster, where he found gradual change in characters from M. cordovans to that of M. cor-anguinum, mainly in the shape of the test, structure of oral opening and the form of ambulacra. The changes took place in a more or less stable environment. Similarly Fenton has described gradual replacement of one species by another in brachiopod.

MACROEVOLUTION

This may also be called Adaptive radiation, which includes evolutionary changes above the species level that may result in the production of new adaptive types through genetic divergence. The changes are on account of large gene mutations or macromutations and result in the establishment of new genera, families and orders. Macroevolution takes place in individuals that have entered a new environmental zone, which is free of competition. Darwin called such directional changes Orthogenesis.

Examples: Evolution of horse is a perfect example of macroevolution, in which there was an increase in the size of body and legs and in the enlargement of teeth. All body changes were related to life in open grasslands, fast running and feeding on harsh grasses, eventually leading to new adaptive types. Other examples of macroevolution are: adaptive radiation in Darwin's finches, divergence of reptiles and evolution of camel and elephant.

MEGAEVOLUTION

This includes formation of new groups, classes or phyla due to evolution of new types from its predecessors by general adaptation. Mega evolutionary changes are rare and have occurred rarely in the evolutionary history. During mega evolution, organisms of the ancestral stalk attempt to enter a new and very different environmental zone where they face strong natural selection, for which they must possess certain pre-adaptations to enable them to survive in the new zone. Mega evolution is brought about by large genetic changes that are capable of producing different types and disruptive or divergent natural selection that makes the population occupy different types of environmental zones.

Examples: Amphibians were preadapted to live on land for short periods since as fish they already possessed lungs for air breathing and limbs to support body on land. Origin of birds from reptiles included growth of feathers and sudden change in the fore limb to produce wing, which enabled them to invade air and then developed beak, sternal keel and loss of tail as post adaptations.

Origin of mammals can be traced back from series of fossil reptiles (Synapsida) of Triassic period. During evolution, a false palate was formed, teeth became thecodont, and limbs moved under the body for better locomotion. Emergence of bats (Order Chiroptera) from the primitive insectivores has been a sudden event in the beginning of Coenozoic era. Skeletons of early Eocene bats show fully developed wings, much like our modern day species possess. No transitional forms are known; suggesting that bats emerged by a mega evolutionary event. Mega evolution is always followed by micro-and macroevolution.

MOLECULAR EVOLUTION

Changes in the base pair sequences in DNA or RNA molecules and changes in amino acid sequences and their molecular configuration in different proteins, from generation to generation are known as molecular evolution. It is possible to measure differences between these molecules obtained from different organisms (such as humans, apes, monkeys, prosimians etc.) on a unit scale of amino acids or nucleotides and demonstrate their relationships. As the molecular sequences are heritable, their variations produce molecular records that have been transferred from generation to generation during evolution. A triplet made of three pairs of nucleotides is called a codon. A codon will change if one of the three bases changes and it may or may not end up in a change in the amino acid synthesized by it. Majority of these changes are small and inconsequential but accumulate over long periods to bring about large alterations in the gene frequencies in populations. Two kinds of such changes are possible:

Silent site substitution: These are such changes in DNA sequences which do not result in any change in amino acid synthesis and hence composition of proteins is not changed. They are usually changes in the last base pair of the codon. For example in mRNA strand GCA codes for alanine and if adenine is replaced by guanine, the resulting GCG will still code for the same amino acid alanine. Silent site substitutions do not bring about any phenotypic changes.

Replacement substitution: They are changes in the bases of codons that result in synthesis of new amino acids and are capable of altering the structure of proteins that are controlled by them and thus changing the phenotype. Silent site substitutions have much higher rate of change as compared to the replacement substitutions, since the former do not produce changes that can be exposed to natural selection but the latter do. For the same reason genes which are less vital to the cell can undergo rapid changes by replacement substitution without showing harmful effects.Pseudogenes, which are duplicated sequences of bases and do not code for proteins and hence are not exposed to natural selection, are known to undergo higher rate of evolutionary changes.

Sequencing amino acids:

Comparing amino acid sequences in a protein in different species by using biochemical techniques is one of the most popular methods to determine phylogeny. For example, in hemoglobin two pairs of alpha and beta sequences of polypeptide chains form a tetramer that can be distinguished by different amino acid sequences in different species. In vertebrates

different types of globin chains appeared during evolution and in each species they followed their own evolutionary path by changes in the amino acid sequences. They are all variations of a single globin ancestor that is controlled by similar globin genes which are believed to have originated by gene duplication of the original type.

NEUTRAL THEORY OF MOLECULAR EVOLUTION

Moto Kimura (1986) proposed that a vast majority of base substitutions that are preserved in a population are neutral with regards to natural selection. Positive substitutions are so rare that they are inconsequential in molecular evolution, while negative changes are quickly eliminatedby natural selection. Natural selection seems to favour neutral changes which determine the overall rate of sequential evolution. For instance, pseudogenes have the highest substitution rate among the genes but the changes are completely neutral with regard to selection.

The theory was tested by J. McDonald and M. Kreitman (1991) by comparing base sequences of alcohol dehydrogenase gene of Drosophila melanogaster, D. simulans and D. yakuba. Kimura's theory not only contradicts classical Darwinism but also does not explain fixation of various types of alleles in different sizes of population. The theory holds that the rate of fixation of neutral mutations does not depend on population size butthe genes are fixed or eliminated by genetic drift. The neutral theory provides theoretical framework for testing and predicting molecular evolution in the absence of positive selection.

8.5 DIFFERENCE BETWEEN MICRO-EVOLUTION AND MACRO-EVOLUTION

Given below points are the essential one to distinguish between micro-evolution and macro-evolution:

1. The **heritable change** in the gene frequency is called as evolution when the evolution occurs on a small scale and within a single population is **micro-evolution**, while the evolution that occurs on a large and surpasses the level of the single species is **macro-evolution**.
2. Micro-evolution gives rise to changes in the **gene pool**, which results in few changes in the same species also called **Intra-species genetic change**, whereas the macro-evolution results in the formation of new species.
3. The changes in micro-evolution occur over short-time scales, whereas the changes observed in macro-evolution occur over long-time scales.

4. **Genetic information** gets altered or rearranged in micro-evolution, whereas there is the new addition, deletion in the genetic structure, resulting in the formation of new species in macroevolution.
5. **Creationists** support micro-evolution as this process has been experimentally proven and is observed frequently, although there are many barriers in providing experimental proof and so creationists do not support this kind of evolution as it takes a lot of time to occur.
6. **Example** of the micro-evolution is the peppered moth, new strains of flu viruses, Galapagos finch beaks, etc. and Origin of different phyla, development of vertebrates from invertebrates, development of feathers is the examples of macro-evolution.

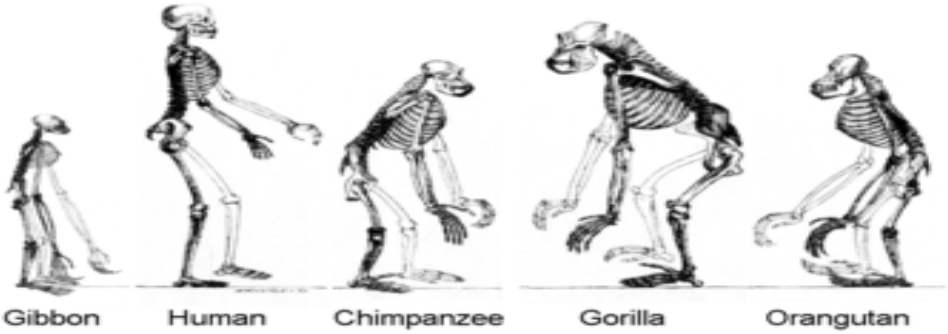
8.6 EVOLUTION OF MAN

Human evolution is the evolutionary process within the history of primates that led to the emergence of *Homo sapiens* as a distinct species of the hominid family, which includes the great apes. This process involved the gradual development of traits such as human bipedalism and language, as well as interbreeding with other hominines, which indicate that human evolution was not linear but a web.

The study of human evolution involves several scientific disciplines, including physical anthropology, primatology, archaeology, paleontology, neurobiology, ethology, linguistics, evolutionary psychology, embryology and genetics. Genetic studies show that primates diverged from other mammals about 85 million years ago, in the Late Cretaceous period, and the earliest fossils appear in the Paleocene, around 55 million years ago.

Within the superfamily Hominoidea, the family Hominidae diverged from the family Hylobatidae some 15–20 million years ago; subfamily Homininae (African apes) diverged from Ponginae (orangutans) about 14 million years ago; the tribe Hominini (including humans, *Australopithecus*, and chimpanzees) parted from the tribe Gorillini (gorillas) between 8–9 million years ago; and, in turn, the subtribes Hominina (humans and extinct biped ancestors) and Panina (chimpanzees) separated 4–7 million years ago.

Anatomical changes



The hominoids are descendants of a common ancestor

Human evolution from its first separation from the last common ancestor of humans and chimpanzees is characterized by a number of morphological, developmental, physiological, and behavioral changes. The most significant of these adaptations are bipedalism, increased brain size, lengthened ontogeny (gestation and infancy), and decreased sexual dimorphism. The relationship between these changes is the subject of ongoing debate. Other significant morphological changes included the evolution of a power and precision grip, a change first occurring in *H. erectus*.

Bipedalism

Bipedalism is the basic adaptation of the hominid and is considered the main cause behind a suite of skeletal changes shared by all bipedal hominids. The earliest hominid, of presumably primitive bipedalism, is considered to be either *Sahelanthropus* or *Orrorin*, both of which arose some 6 to 7 million years ago. The non-bipedal knuckle-walkers, the gorillas and chimpanzees, diverged from the hominin line over a period covering the same time, so either *Sahelanthropus* or *Orrorin* may be our last shared ancestor. *Ardipithecus*, a full biped, arose approximately 5.6 million years ago.

The early bipeds eventually evolved into the australopithecines and still later into the genus *Homo*. There are several theories of the adaptation value of bipedalism. It is possible that bipedalism was favored because it freed the hands for reaching and carrying food, saved energy during locomotion, enabled long-distance running and hunting, provided an enhanced field of vision, and helped avoid hyperthermia by reducing the surface area exposed to direct sun; features all advantageous for thriving in the new savanna and woodland environment created as a result of the East African Rift Valley uplift versus the previous closed forest habitat. A 2007 study provides support for the hypothesis that walking on two legs, or bipedalism, evolved because it used less energy than quadrupedal knuckle-walking. However, recent studies suggest that bipedalism without the ability to use fire would not have

allowed global dispersal. This change in gait saw a lengthening of the legs proportionately when compared to the length of the arms, which were shortened through the removal of the need for brachiating. Another change is the shape of the big toe. Recent studies suggest that australopithecines still lived part of the time in trees as a result of maintaining a grasping big toe. This was progressively lost in habilines.

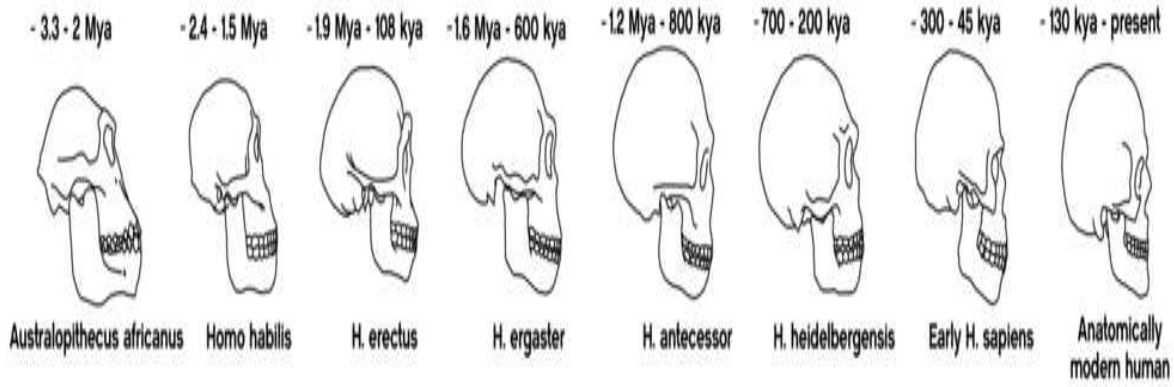
Anatomically, the evolution of bipedalism has been accompanied by a large number of skeletal changes, not just to the legs and pelvis, but also to the vertebral column, feet and ankles, and skull. The femur evolved into a slightly more angular position to move the center of gravity toward the geometric center of the body. The knee and ankle joints became increasingly robust to better support increased weight. To support the increased weight on each vertebra in the upright position, the human vertebral column became S-shaped and the lumbar vertebrae became shorter and wider. In the feet the big toe moved into alignment with the other toes to help in forward locomotion. The arms and forearms shortened relative to the legs making it easier to run. The foramen magnum migrated under the skull and more anterior.

The most significant changes occurred in the pelvic region, where the long downward facing iliac blade was shortened and widened as a requirement for keeping the center of gravity stable while walking; bipedal hominids have a shorter but broader, bowl-like pelvis due to this. A drawback is that the birth canal of bipedal apes is smaller than in knuckle-walking apes, though there has been a widening of it in comparison to that of australopithecine and modern humans, permitting the passage of newborns due to the increase in cranial size but this is limited to the upper portion, since further increase can hinder normal bipedal movement.

The shortening of the pelvis and smaller birth canal evolved as a requirement for bipedalism and had significant effects on the process of human birth which is much more difficult in modern humans than in other primates. During human birth, because of the variation in size of the pelvic region, the fetal head must be in a transverse position (compared to the mother) during entry into the birth canal and rotate about 90 degrees upon exit. The smaller birth canal became a limiting factor to brain size increases in early humans and prompted a shorter gestation period leading to the relative immaturity of human offspring, who are unable to walk much before 12 months and have greater neoteny, compared to other primates, who are mobile at a much earlier age. The increased brain growth after birth and the increased dependency of children on mothers had a major effect upon the female reproductive cycle,

and the more frequent appearance of alloparenting in humans when compared with other hominids. Delayed human sexual maturity also led to the evolution of menopause with one explanation providing that elderly women could better pass on their genes by taking care of their daughter's offspring, as compared to having more children of their own.

Encephalization



Skulls of successive (or near-successive, depending on the source) human evolutionary ancestors, up until 'modern' *Homo sapiens*. The human species eventually developed a much larger brain than that of other primates—typically 1,330 cm^3 (81 cu in) in modern humans, nearly three times the size of a chimpanzee or gorilla brain. After a period of stasis with *Australopithecus anamensis* and *Ardipithecus*, species which had smaller brains as a result of their bipedal locomotion, the pattern of encephalization started with *Homo habilis*, whose 600 cm^3 (37 cu in) brain was slightly larger than that of chimpanzees. This evolution continued in *Homo erectus* with 800–1,100 cm^3 (49–67 cu in), and reached a maximum in Neanderthals with 1,200–1,900 cm^3 (73–116 cu in), larger even than modern *Homo sapiens*. This brain increase manifested during postnatal brain growth, far exceeding that of other apes (heterochrony). It also allowed for extended periods of social learning and language acquisition in juvenile humans, beginning as much as 2 million years ago.

Furthermore, the changes in the structure of human brains may be even more significant than the increase in size. The size and shape of the skull changed over time. The leftmost, and largest, is a replica of a modern human skull. The temporal lobes, which contain centers for language processing, have increased disproportionately, as has the prefrontal cortex, which has been related to complex decision-making and moderating social behavior. Encephalization has been tied to increased meat and starches in the diet, and the development of cooking, and it has been proposed that intelligence increased as a response to an increased necessity for solving social problems as human society became more complex. Changes in

skull morphology, such as smaller mandibles and mandible muscle attachments, allowed more room for the brain to grow.

The increase in volume of the neocortex also included a rapid increase in size of the cerebellum. Its function has traditionally been associated with balance and fine motor control, but more recently with speech and cognition. The great apes, including hominids, had a more pronounced cerebellum relative to the neocortex than other primates. It has been suggested that because of its function of sensory-motor control and learning complex muscular actions, the cerebellum may have underpinned human technological adaptations, including the preconditions of speech.

The immediate survival advantage of cephalization is difficult to discern, as the major brain changes from *Homo erectus* to *Homo heidelbergensis* were not accompanied by major changes in technology. It has been suggested that the changes were mainly social and behavioural, including increased empathic abilities, increases in size of social groups, and increased behavioural plasticity. Encephalization may be due to a dependency on calorie-dense, difficult-to-acquire food.

SEXUAL DIMORPHISM

The reduced degree of sexual dimorphism in humans is visible primarily in the reduction of the male canine tooth relative to other ape species (except gibbons) and reduced brow ridges and general robustness of males. Another important physiological change related to sexuality in humans was the evolution of hidden estrus. Humans are the only hominoids in which the female is fertile year round and in which no special signals of fertility are produced by the body (such as genital swelling or overt changes in proceptivity during estrus).

Nonetheless, humans retain a degree of sexual dimorphism in the distribution of body hair and subcutaneous fat, and in the overall size, males being around 15% larger than females. These changes taken together have been interpreted as a result of an increased emphasis on pair bonding as a possible solution to the requirement for increased parental investment due to the prolonged infancy of offspring.

Ulnar opposition

The ulnar opposition—the contact between the thumb and the tip of the little finger of the same hand—is unique to the genus *Homo*, including Neanderthals, the Sima de los Huesoshominins and anatomically modern humans. In other primates, the thumb is short and unable to touch the little finger. The ulnar opposition facilitates the precision grip and power grip of the human hand, underlying all the skilled manipulations.

Other changes

A number of other changes have also characterized the evolution of humans, among them an increased importance on vision rather than smell; a longer juvenile developmental period and higher infant dependency; a smaller gut; faster basal metabolism; loss of body hair; evolution of sweat glands; a change in the shape of the dental arcade from being u-shaped to being parabolic; development of a chin (found in *Homo sapiens* alone); development of styloid processes; and the development of a descended larynx.

History of study

Before Darwin

The word *homo*, the name of the biological genus to which humans belongs, is Latin for "human". It was chosen originally by Carl Linnaeus in his classification system. The word "human" is from the Latin *humanus*, the adjectival form of *homo*. The Latin "homo" derives from the Indo-European root **dhghem*, or "earth". Linnaeus and other scientists of his time also considered the great apes to be the closest relatives of humans based on morphological and anatomical similarities.

Darwin

The possibility of linking humans with earlier apes by descent became clear only after 1859 with the publication of Charles Darwin's *On the Origin of Species*, in which he argued for the idea of the evolution of new species from earlier ones. Darwin's book did not address the question of human evolution, saying only that "Light will be thrown on the origin of man and his history". The first debates about the nature of human evolution arose between Thomas Henry Huxley and Richard Owen. Huxley argued for human evolution from apes by illustrating many of the similarities and differences between humans and other apes, and did so particularly in his 1863 book *Evidence as to Man's Place in Nature*. Many of Darwin's early supporters (such as Alfred Russel Wallace and Charles Lyell) did not initially agree that the origin of the mental capacities and the moral sensibilities of humans could be explained by natural selection, though this later changed. Darwin applied the theory of evolution and sexual selection to humans in his 1871 book *The Descent of Man, and Selection in Relation to Sex*.

FIRST FOSSILS

A major problem in the 19th century was the lack of fossil intermediaries. Neanderthal remains were discovered in a limestone quarry in 1856, three years before the publication of *On the Origin of Species*, and Neanderthal fossils had been discovered in Gibraltar even earlier, but it was originally claimed that these were the remains of a modern human who had suffered some kind of illness. Despite the 1891 discovery by Eugène Dubois of what is now called *Homo erectus* at Trinil, Java, it was only in the 1920s when such fossils were discovered in Africa, that intermediate species began to accumulate. In 1925, Raymond Dart described *Australopithecus africanus*. The type specimen was the Taung Child, an australopithecine infant which was discovered in a cave. The child's remains were a remarkably well-preserved tiny skull and an endocast of the brain.

Although the brain was small (410 cm^3), its shape was rounded, unlike that of chimpanzees and gorillas, and more like a modern human brain. Also, the specimen showed short canine teeth, and the position of the foramen magnum (the hole in the skull where the spine enters) was evidence of bipedal locomotion. All of these traits convinced Dart that the Taung Child was a bipedal human ancestor, a transitional form between apes and humans.

THE EAST AFRICAN FOSSILS

During the 1960s and 1970s, hundreds of fossils were found in East Africa in the regions of the Olduvai Gorge and Lake Turkana. These searches were carried out by the Leakey family, with Louis Leakey and his wife Mary Leakey, and later their son Richard and daughter-in-law Meave, fossil hunters and paleoanthropologists. From the fossil beds of Olduvai and Lake Turkana they amassed specimens of the early hominins: the australopithecines and *Homo* species, and even *Homo erectus*.

These finds cemented Africa as the cradle of humankind. In the late 1970s and the 1980s, Ethiopia emerged as the new hot spot of paleoanthropology after "Lucy", the most complete fossil member of the species *Australopithecus afarensis*, was found in 1974 by Donald Johanson near Hadar in the desertic Afar Triangle region of northern Ethiopia. Although the specimen had a small brain, the pelvis and leg bones were almost identical in function to those of modern humans, showing with certainty that these hominins had walked erect. Lucy was classified as a new species, *Australopithecus afarensis*, which is thought to be more closely related to the genus *Homo* as a direct ancestor, or as a close relative of an unknown ancestor, than any other known hominid or hominin from this early time range; *see*terms "hominid" and "hominin". (The specimen was nicknamed "Lucy" after the Beatles' song "Lucy in the Sky with Diamonds", which was played loudly and repeatedly in the camp

during the excavations). The Afar Triangle area would later yield discovery of many more hominin fossils, particularly those uncovered or described by teams headed by Tim D. White in the 1990s, including *Ardipithecus ramidus* and *Ardipithecus kadabba*.

In 2013, fossil skeletons of *Homo naledi*, an extinct species of hominin assigned (provisionally) to the genus*Homo*, were found in the Rising Star Cave system, a site in South Africa's Cradle of Humankind region in Gauteng province near Johannesburg. As of September 2015, fossils of at least fifteen individuals, amounting to 1,550 specimens, have been excavated from the cave. The species is characterized by a body mass and stature similar to small-bodied human populations, a smaller endocranial volume similar to *Australopithecus*, and a cranialmorphology (skull shape) similar to early *Homo* species. The skeletal anatomy combines primitive features known from australopithecines with features known from early hominins. The individuals show signs of having been deliberately disposed of within the cave near the time of death. The fossils were dated close to 250,000 years ago, and thus are not a direct ancestor but a contemporary with the first appearance of larger-brained anatomically modern humans.

THE GENETIC REVOLUTION

The genetic revolution in studies of human evolution started when Vincent Sarich and Allan Wilson measured the strength of immunological cross-reactions of blood serumalbumin between pairs of creatures, including humans and African apes (chimpanzees and gorillas). The strength of the reaction could be expressed numerically as an immunological distance, which was in turn proportional to the number of amino acid differences between homologous proteins in different species. By constructing a calibration curve of the ID of species' pairs with known divergence times in the fossil record, the data could be used as a molecular clock to estimate the times of divergence of pairs with poorer or unknown fossil records.

In their seminal 1967 paper in *Science*, Sarich and Wilson estimated the divergence time of humans and apes as four to five million years ago, at a time when standard interpretations of the fossil record gave this divergence as at least 10 to as much as 30 million years. Subsequent fossil discoveries, notably "Lucy", and reinterpretation of older fossil materials, notably *Ramapithecus*, showed the younger estimates to be correct and validated the albumin method.

Progress in DNA sequencing, specifically mitochondrial DNA (mtDNA) and then Y-chromosome DNA (Y-DNA) advanced the understanding of human origins. Application of the molecular clock principle revolutionized the study of molecular evolution.

On the basis of a separation from the orangutan between 10 and 20 million years ago, earlier studies of the molecular clock suggested that there were about 76 mutations per generation that were not inherited by human children from their parents; this evidence supported the divergence time between hominins and chimpanzees noted above. However, a 2012 study in Iceland of 78 children and their parents suggests a mutation rate of only 36 mutations per generation; this datum extends the separation between humans and chimpanzees to an earlier period greater than 7 million years ago (Ma). Additional research with 226 offspring of wild chimpanzee populations in eight locations suggests that chimpanzees reproduce at age 26.5 years on average; which suggests the human divergence from chimpanzees occurred between 7 and 13 million years ago. And these data suggest that *Ardipithecus* (4.5 Ma), *Orrorin* (6 Ma) and *Sahelanthropus* (7 Ma) all may be on the hominid lineage, and even that the separation may have occurred outside the East African Rift region.

Furthermore, analysis of the two species' genes in 2006 provides evidence that after human ancestors had started to diverge from chimpanzees, interspecies mating between "proto-human" and "proto-chimpanzees" nonetheless occurred regularly enough to change certain genes in the new gene pool:

- A new comparison of the human and chimpanzee genomes suggests that after the two lineages separated, they may have begun interbreeding... A principal finding is that the X chromosomes of humans and chimpanzees appear to have diverged about 1.2 million years more recently than the other chromosomes.
- There were in fact two splits between the human and chimpanzee lineages, with the first being followed by interbreeding between the two populations and then a second split. The suggestion of hybridization has startled paleoanthropologists, who nonetheless are treating the new genetic data seriously.

HUMAN DISPERSAL

Anthropologists in the 1980s were divided regarding some details of reproductive barriers and migratory dispersals of the genus *Homo*. Subsequently, genetics has been used to investigate and resolve these issues. According to the Sahara pump theory evidence suggests that the genus *Homo* have migrated out of Africa at least three and possibly four times (e.g. *Homo erectus*, *Homo heidelbergensis* and two or three times for *Homo sapiens*). Recent evidence suggests these dispersals are closely related to fluctuating periods of climate change.

Recent evidence suggests that humans may have left Africa half a million years earlier than previously thought. A joint Franco-Indian team has found human artifacts in the Siwalk Hills north of New Delhi dating back at least 2.6 million years. This is earlier than the previous earliest finding of genus *Homo* at Dmanisi, in Georgia, dating to 1.85 million years. Although controversial, tools found at a Chinese cave strengthen the case that humans used tools as far back as 2.48 million years ago. This suggests that the Asian "Chopper" tool tradition, found in Java and northern China may have left Africa before the appearance of the Acheulian hand axe.

Dispersal of modern *Homo sapiens*

Up until the genetic evidence became available, there were two dominant models for the dispersal of modern humans. The multiregional hypothesis proposed that the genus *Homo* contained only a single interconnected population as it does today (not separate species), and that its evolution took place worldwide continuously over the last couple of million years. This model was proposed in 1988 by Milford H. Wolpoff. In contrast, the "out of Africa" model proposed that modern *H. sapiens*speciated in Africa recently (that is, approximately 200,000 years ago) and the subsequent migration through Eurasia resulted in the nearly complete replacement of other *Homo* species. This model has been developed by Chris B. Stringer and Peter Andrews.

Sequencing mtDNA and Y-DNA sampled from a wide range of indigenous populations revealed ancestral information relating to both male and female genetic heritage, and strengthened the "out of Africa" theory and weakened the views of multiregional evolutionism. Aligned in genetic tree differences were interpreted as supportive of a recent single origin. Analyses have shown a greater diversity of DNA patterns throughout Africa, consistent with the idea that Africa is the ancestral home of mitochondrial Eve and Y-chromosomal Adam, and that modern human dispersal out of Africa has only occurred over the last 55,000 years.

"Out of Africa" has thus gained much support from research using female mitochondrial DNA and the male Y chromosome. After analysing genealogy trees constructed using 133 types of mtDNA, researchers concluded that all were descended from a female African progenitor, dubbed Mitochondrial Eve. "Out of Africa" is also supported by the fact that mitochondrial genetic diversity is highest among African populations.

A broad study of African genetic diversity, headed by Sarah Tishkoff, found the San people had the greatest genetic diversity among the 113 distinct populations sampled, making them

one of 14 "ancestral population clusters". The research also located a possible origin of modern human migration in southwestern Africa, near the coastal border of Namibia and Angola. The fossil evidence was insufficient for archaeologist Richard Leakey to resolve the debate about exactly where in Africa modern humans first appeared. Studies of haplogroups in Y-chromosomal DNA and mitochondrial DNA have largely supported a recent African origin. All the evidence from autosomal DNA also predominantly supports a Recent African origin. However, evidence for archaic admixture in modern humans, both in Africa and later, throughout Eurasia has recently been suggested by a number of studies.

Recent sequencing of Neanderthal and Denisovan genomes shows that some admixture with these populations has occurred. All modern human groups outside Africa have 1–4% or (according to more recent research) about 1.5–2.6% Neanderthal alleles in their genome, and some Melanesians have an additional 4–6% of Denisovan alleles. These new results do not contradict the "out of Africa" model, except in its strictest interpretation, although they make the situation more complex. After recovery from a genetic bottleneck that some researchers speculate might be linked to the Toba supervolcano catastrophe, a fairly small group left Africa and interbred with Neanderthals, probably in the Middle East, on the Eurasian steppe or even in North Africa before their departure. Their still predominantly African descendants spread to populate the world. A fraction in turn interbred with Denisovans, probably in southeastern Asia, before populating Melanesia. HLA haplotypes of Neanderthal and Denisova origin have been identified in modern Eurasian and Oceanian populations. The Denisovan EPAS1 gene has also been found in Tibetan populations. Studies of the human genome using machine learning have identified additional genetic contributions in Eurasians from an "unknown" ancestral population potentially related to the Neanderthal-Denisovan lineage.

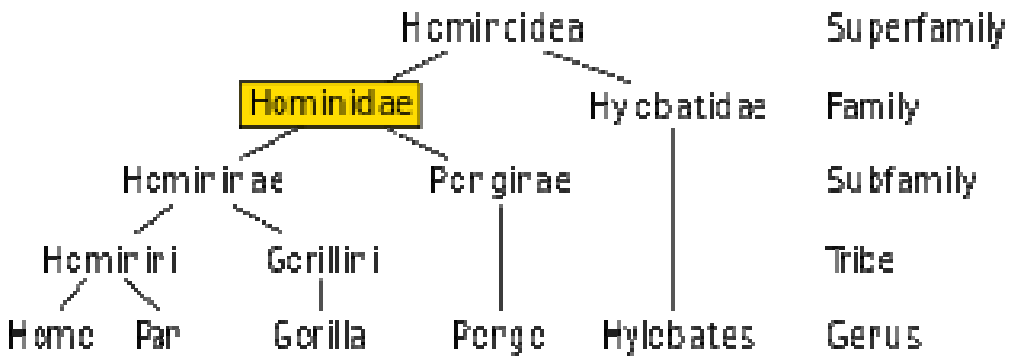
There are still differing theories on whether there was a single exodus from Africa or several. A multiple dispersal model involves the Southern Dispersal theory, which has gained support in recent years from genetic, linguistic and archaeological evidence. In this theory, there was a coastal dispersal of modern humans from the Horn of Africa crossing the Bab el Mandib to Yemen at a lower sea level around 70,000 years ago. This group helped to populate Southeast Asia and Oceania, explaining the discovery of early human sites in these areas much earlier than those in the Levant. This group seems to have been dependent upon marine resources for their survival.

Stephen Oppenheimer has proposed a second wave of humans may have later dispersed through the Persian Gulf oases, and the Zagros mountains into the Middle East. Alternatively it may have come across the Sinai Peninsula into Asia, from shortly after 50,000 yrs BP, resulting in the bulk of the human populations of Eurasia. It has been suggested that this second group possibly possessed a more sophisticated "big game hunting" tool technology and was less dependent on coastal food sources than the original group. Much of the evidence for the first group's expansion would have been destroyed by the rising sea levels at the end of each glacial maximum. The multiple dispersal model is contradicted by studies indicating that the populations of Eurasia and the populations of Southeast Asia and Oceania are all descended from the same mitochondrial DNA L3 lineages, which support a single migration out of Africa that gave rise to all non-African populations. On the basis of the early date of Badoshan Iranian Aurignacian, Oppenheimer suggests that this second dispersal may have occurred with a pluvial period about 50,000 years before the present, with modern human big-game hunting cultures spreading up the Zagros Mountains, carrying modern human genomes from Oman, throughout the Persian Gulf, northward into Armenia and Anatolia, with a variant travelling south into Israel and to Cyrenicia. Recent genetic evidence suggests that all modern non-African populations, including those of Eurasia and Oceania, are descended from a single wave that left Africa between 65,000 and 50,000 years ago.

EVIDENCE

The evidence on which scientific accounts of human evolution are based comes from many fields of natural science. The main source of knowledge about the evolutionary process has traditionally been the fossil record, but since the development of genetics beginning in the 1970s, DNA analysis has come to occupy a place of comparable importance. The studies of ontogeny, phylogeny and especially evolutionary developmental biology of both vertebrates and invertebrates offer considerable insight into the evolution of all life, including how humans evolved. The specific study of the origin and life of humans is anthropology, particularly paleoanthropology which focuses on the study of human prehistory.

Evidence from molecular biology



Family tree showing the extant hominoids: humans (genus *Homo*), chimpanzees and bonobos (genus *Pan*), gorillas (genus *Gorilla*), orangutans (genus *Pongo*), and gibbons (four genera of the family Hylobatidae: *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus*). All except gibbons are hominids.

The closest living relatives of humans are bonobos and chimpanzees (both genus *Pan*) and gorillas (genus *Gorilla*). With the sequencing of both the human and chimpanzee genome, as of 2012 estimates of the similarity between their DNA sequences range between 95% and 99%. By using the technique called the molecular clock which estimates the time required for the number of divergent mutations to accumulate between two lineages, the approximate date for the split between lineages can be calculated.

The gibbons (family Hylobatidae) and then the orangutans (genus *Pongo*) were the first groups to split from the line leading to the hominins, including humans—followed by gorillas (genus *Gorilla*), and, ultimately, by the chimpanzees (genus *Pan*). The splitting date between hominin and chimpanzee lineages is placed by some between 4 to 8million years ago, that is, during the Late Miocene. Speciation, however, appears to have been unusually drawn out. Initial divergence occurred sometime between 7 to 13million years ago, but ongoing hybridization blurred the separation and delayed complete separation during several millions of years. Patterson (2006) dated the final divergence at 5 to 6million years ago.

Genetic evidence has also been employed to resolve the question of whether there was any gene flow between early modern humans and Neanderthals, and to enhance our understanding of the early human migration patterns and splitting dates. By comparing the parts of the genome that are not under natural selection and which therefore accumulate mutations at a fairly steady rate, it is possible to reconstruct a genetic tree incorporating the entire human species since the last shared ancestor.

Each time a certain mutation (single-nucleotide polymorphism) appears in an individual and is passed on to his or her descendants, a haplo group is formed including all of the descendants of the individual who will also carry that mutation. By comparing mitochondrial DNA which is inherited only from the mother, geneticists have concluded that the last female common ancestor whose genetic marker is found in all modern humans, the so-called mitochondrial Eve, must have lived around 200,000 years ago.

GENETICS

Human evolutionary genetics studies how one human genome differs from the other, the evolutionary past that gave rise to it, and its current effects. Differences between genomes have anthropological, medical and forensic implications and applications. Genetic data can provide important insight into human evolution.

EVIDENCE FROM THE FOSSIL RECORD

There is little fossil evidence for the divergence of the gorilla, chimpanzee and hominin lineages. The earliest fossils that have been proposed as members of the hominin lineage are *Sahelanthropus tchadensis* dating from 7 million years ago, *Orrorin tugenensis* dating from 5.7 million years ago, and *Ardipithecus kadabba* dating to 5.6 million years ago. Each of these has been argued to be a bipedal ancestor of later hominins but, in each case, the claims have been contested. It is also possible that one or more of these species are ancestors of another branch of African apes, or that they represent a shared ancestor between hominins and other apes.

The question then of the relationship between these early fossil species and the hominin lineage is still to be resolved. From these early species, the australopithecines arose around 4 million years ago and diverged into robust (also called *Paranthropus*) and gracile branches, one of which (possibly *A. garhi*) probably went on to become ancestors of the genus *Homo*. The australopithecine species that is best represented in the fossil record is *Australopithecus afarensis* with more than 100 fossil individuals represented, found from Northern Ethiopia (such as the famous "Lucy"), to Kenya, and South Africa. Fossils of robust australopithecines such as *Au. robustus* (or alternatively *Paranthropus robustus*) and *Au./P. boisei* are particularly abundant in South Africa at sites such as Kromdraai and Swartkrans, and around Lake Turkana in Kenya.

The earliest member of the genus *Homo* is *Homo habilis* which evolved around 2.8 million years ago. *Homo habilis* is the first species for which we have positive evidence of the use of stone tools. They developed the Oldowan lithic technology, named after the Olduvai Gorge in

which the first specimens were found. Some scientists consider *Homo rudolfensis*, a larger bodied group of fossils with similar morphology to the original *H. habilis* fossils, to be a separate species, while others consider them to be part of *H. habilis*—simply representing intraspecies variation, or perhaps even sexual dimorphism. The brains of these early hominins were about the same size as that of a chimpanzee, and their main adaptation was bipedalism as an adaptation to terrestrial living.

During the next million years, a process of encephalization began and, by the arrival (about 1.9 million years ago) of *Homo erectus* in the fossil record, cranial capacity had doubled. *Homo erectus* was the first of the hominins to emigrate from Africa, and, from 1.8 to 1.3million years ago, this species spread through Africa, Asia, and Europe. One population of *H. erectus*, also sometimes classified as a separate species *Homo ergaster*, remained in Africa and evolved into *Homo sapiens*. It is believed that these species, *H. erectus* and *H. ergaster*, were the first to use fire and complex tools.

The earliest transitional fossils between *H. ergaster/erectus* and archaic *H. sapiens* are from Africa, such as *Homo rhodesiensis*. These descendants of African *H. erectus* spread through Eurasia from ca. 500,000 years ago, evolving into *H. antecessor*, *H. heidelbergensis* and *H. neanderthalensis*. The earliest fossils of anatomically modern humans are from the Middle Paleolithic, about 300–200,000 years ago such as the Herto and Omo remains of Ethiopia, Jebel Irhoud remains of Morocco, and Florisbad remains of South Africa; later fossils from Es Skhul cave in Israel and Southern Europe begin around 90,000 years ago (0.09 million years ago).

As modern humans spread out from Africa, they encountered other hominins such as *Homo neanderthalensis* and the Denisovans, who may have evolved from populations of *Homo erectus* that had left Africa around 2 million years ago. The nature of interaction between early humans and these sister species has been a long-standing source of controversy, the question being whether humans replaced these earlier species or whether they were in fact similar enough to interbreed, in which case these earlier populations may have contributed genetic material to modern humans.

This migration out of Africa is estimated to have begun about 70–50,000 years BP and modern humans subsequently spread globally, replacing earlier hominins either through competition or hybridization. They inhabited Eurasia and Oceania by 40,000 years BP, and the Americas by at least 14,500 years BP.

INTER-SPECIES BREEDING

The hypothesis of interbreeding, also known as hybridization, admixture or hybrid-origin theory, has been discussed ever since the discovery of Neanderthal remains in the 19th century. The linear view of human evolution began to be abandoned in the 1970s as different species of humans were discovered that made the linear concept increasingly unlikely. In the 21st century with the advent of molecular biology techniques and computerization, whole-genome sequencing of Neanderthal and human genome were performed, confirming recent admixture between different human species. In 2010, evidence based on molecular biology was published, revealing unambiguous examples of interbreeding between archaic and modern humans during the Middle Paleolithic and early Upper Paleolithic. It has been demonstrated that interbreeding happened in several independent events that included Neanderthals and Denisovans, as well as several unidentified hominins. Today, approximately 2% of DNA from all non-African populations (including Europeans, Asians, and Oceanians) is Neanderthal, with traces of Denisovan heritage. Also, 4–6% of modern Melanesian genetics are Denisovan. Comparisons of the human genome to the genomes of Neandertals, Denisovans and apes can help identify features that set modern humans apart from other hominin species. In a 2016 comparative genomics study, a Harvard Medical School/UCLA research team made a world map on the distribution and made some predictions about where Denisovan and Neanderthal genes may be impacting modern human biology.

For example, comparative studies in the mid-2010s found several traits related to neurological, immunological, developmental, and metabolic phenotypes that were developed by archaic humans to European and Asian environments and inherited to modern humans through admixture with local hominins.

Although the narratives of human evolution are often contentious, several discoveries since 2010 show that human evolution should not be seen as a simple linear or branched progression, but a mix of related species. In fact, genomic research has shown that hybridization between substantially diverged lineages is the rule, not the exception, in human evolution. Furthermore, it is argued that hybridization was an essential creative force in the emergence of modern humans.

EARLY EVOLUTION OF PRIMATES

The evolutionary history of the primates can be traced back 65 million years. One of the oldest known primate-like mammal species, the *Plesiadapis*, came from North America;

another, *Archicebus*, came from China. Other similar basal primates were widespread in Eurasia and Africa during the tropical conditions of the Paleocene and Eocene.

David R. Begun concluded that early primates flourished in Eurasia and that a lineage leading to the African apes and humans, including to *Dryopithecus*, migrated south from Europe or Western Asia into Africa. The surviving tropical population of primates—which is seen most completely in the Upper Eocene and lowermost Oligocene fossil beds of the Faiyum depression southwest of Cairo—gave rise to all extant primate species, including the lemurs of Madagascar, lorises of Southeast Asia, galagos or "bush babies" of Africa, and to the anthropoids, which are the Platyrrhines or New World monkeys, the Catarrhines or Old World monkeys, and the great apes, including humans and other hominids.

The earliest known catarrhine is *Kamoyapithecus* from uppermost Oligocene at Eragaleit in the northern Great Rift Valley in Kenya, dated to 24 million years ago. Its ancestry is thought to be species related to *Aegyptopithecus*, *Propliopithecus*, and *Parapithecus* from the Faiyum, at around 35 million years ago. In 2010, *Saadanius* was described as a close relative of the last common ancestor of the crown catarrhines, and tentatively dated to 29–28 million years ago, helping to fill an 11-million-year gap in the fossil record.

In the Early Miocene, about 22 million years ago, the many kinds of arboreally adapted primitive catarrhines from East Africa suggest a long history of prior diversification. Fossils at 20 million years ago include fragments attributed to *Victoriapithecus*, the earliest Old World monkey. Among the genera thought to be in the ape lineage leading up to 13 million years ago are *Proconsul*, *Rangwapithecus*, *Dendropithecus*, *Limnopithecus*, *Nacholapithecus*, *Equatorius*, *Nyanzapithecus*, *Afropithecus*, *Heliopithecus*, and *Kenyapithecus*, all from East Africa.

The presence of other generalized non-cercopithecids of Middle Miocene from sites far distant—*Otavipithecus* from cave deposits in Namibia, and *Pierolapithecus* and *Dryopithecus* from France, Spain and Austria—is evidence of a wide diversity of forms across Africa and the Mediterranean basin during the relatively warm and equable climatic regimes of the Early and Middle Miocene. The youngest of the Miocene hominoids, *Oreopithecus*, is from coal beds in Italy that have been dated to 9 million years ago.

Molecular evidence indicates that the lineage of gibbons (family Hylobatidae) diverged from the line of great apes some 18–12 million years ago, and that of orangutans (subfamily Ponginae) diverged from the other great apes at about 12 million years; there are no fossils that clearly document the ancestry of gibbons, which may have originated in a so-far-

unknown Southeast Asian hominoid population, but fossil proto-orangutans may be represented by *Sivapithecus* from India and *Griphopithecus* from Turkey, dated to around 10 million years ago.

DIVERGENCE OF THE HUMAN CLADE FROM OTHER GREAT APES

Species close to the last common ancestor of gorillas, chimpanzees and humans may be represented by *Nakalipithecus* fossils found in Kenya and *Ouranopithecus* found in Greece. Molecular evidence suggests that between 8 and 4 million years ago, first the gorillas, and then the chimpanzees (genus *Pan*) split off from the line leading to the humans. Human DNA is approximately 98.4% identical to that of chimpanzees when comparing single nucleotide polymorphisms. The fossil record, however, of gorillas and chimpanzees is limited; both poor preservation – rain forest soils tend to be acidic and dissolve bone – and sampling bias probably contribute to this problem.

Other hominins probably adapted to the drier environments outside the equatorial belt; and there they encountered antelope, hyenas, dogs, pigs, elephants, horses, and others. The equatorial belt contracted after about 8 million years ago, and there is very little fossil evidence for the split—thought to have occurred around that time—of the hominin lineage from the lineages of gorillas and chimpanzees. The earliest fossils argued by some to belong to the human lineage are *Sahelanthropus tchadensis* (7 Ma) and *Orrorin tugenensis* (6 Ma), followed by *Ardipithecus* (5.5–4.4 Ma), with species *Ar. kadabba* and *Ar. ramidus*.

It has been argued in a study of the life history of *Ar. ramidus* that the species provides evidence for a suite of anatomical and behavioral adaptations in very early hominins unlike any species of extant great ape. This study demonstrated affinities between the skull morphology of *Ar. ramidus* and that of infant and juvenile chimpanzees, suggesting the species evolved a juvenalised or paedomorphic craniofacial morphology via heterochronic dissociation of growth trajectories. It was also argued that the species provides support for the notion that very early hominins, akin to bonobos (*Pan paniscus*) the less aggressive species of the genus *Pan*, may have evolved via the process of self-domestication. Consequently, arguing against the so-called "chimpanzee referential model". The authors suggest it is no longer tenable to use chimpanzee (*Pan troglodytes*) social and mating behaviors in models of early hominin social evolution.

Genus *Australopithecus*

The genus *Australopithecus* evolved in eastern Africa around 4 million years ago before spreading throughout the continent and eventually becoming extinct 2 million years ago.

During this time period various forms of australopiths existed, including *Australopithecus anamensis*, *Au. afarensis*, *Au. sediba*, and *Au. africanus*. There is still some debate among academics whether certain African hominid species of this time, such as *Au. robustus* and *Au. boisei*, constitute members of the same genus; if so, they would be considered to be *Au. robust australopiths* whilst the others would be considered *Au. gracile australopiths*. However, if these species do indeed constitute their own genus, then they may be given their own name, *Paranthropus*.

- *Australopithecus* (4–1.8 Ma), with species *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. bahrelghazali*, *Au. garhi*, and *Au. sediba*;
- *Kenyanthropus* (3–2.7 Ma), with species *K. platyops*;
- *Paranthropus* (3–1.2 Ma), with species *P. aethiopicus*, *P. boisei*, and *P. robustus*

A new proposed species *Australopithecus deyiremeda* is claimed to have been discovered living at the same time period of *Au. afarensis*. There is debate if Au.deyiremeda is a new species or is *Au. afarensis*.*Australopithecus prometheus*, otherwise known as Little Foot has recently been dated at 3.67 million years old through a new dating technique, making the genus *Australopithecus* as old as *afarensis*. Given the opposable big toe found on Little Foot, it seems that he was a good climber, and it is thought given the night predators of the region, he probably, like gorillas and chimpanzees, built a nesting platform at night, in the trees.

Evolution of genus *Homo*

The earliest documented representative of the genus *Homo* is *Homo habilis*, which evolved around 2.8 million years ago, and is arguably the earliest species for which there is positive evidence of the use of stone tools. The brains of these early hominins were about the same size as that of a chimpanzee, although it has been suggested that this was the time in which the human SRGAP2gene doubled, producing a more rapid wiring of the frontal cortex. During the next million years a process of rapid encephalization occurred, and with the arrival of *Homo erectus* and *Homo ergaster* in the fossil record, cranial capacity had doubled to 850 cm^3. (Such an increase in human brain size is equivalent to each generation having 125,000 more neurons than their parents.) It is believed that *Homo erectus* and *Homo ergaster* were the first to use fire and complex tools, and were the first of the hominin line to leave Africa, spreading throughout Africa, Asia, and Europe between 1.3 to 1.8million years ago.

A model of the phylogeny of *H. sapiens* during the Middle Paleolithic. The horizontal axis represents geographic location; the vertical axis represents time in thousands of years ago.

Homo heidelbergensis is shown as diverging into Neanderthals, Denisovans and *H. sapiens*. With the expansion of *H. sapiens* after 200 kya, Neanderthals, Denisovans and unspecified archaic African hominins are shown as again subsumed into the *H. sapiens* lineage. In addition, admixture events in modern African populations are indicated.

According to the recent African origin of modern humans theory, modern humans evolved in Africa possibly from *Homo heidelbergensis*, *Homo rhodesiensis* or *Homo antecessor* and migrated out of the continent some 50,000 to 100,000 years ago, gradually replacing local populations of *Homo erectus*, Denisova hominins, *Homo floresiensis*, *Homo luzonensis* and *Homo neanderthalensis*. Archaic *Homo sapiens*, the forerunner of anatomically modern humans, evolved in the Middle Paleolithic between 400,000 and 250,000 years ago. Recent DNA evidence suggests that several haplotypes of Neanderthal origin are present among all non-African populations, and Neanderthals and other hominins, such as Denisovans, may have contributed up to 6% of their genome to present-day humans, suggestive of a limited interbreeding between these species. The transition to behavioral modernity with the development of symbolic culture, language, and specialized lithic technology happened around 50,000 years ago, according to some anthropologists, although others point to evidence that suggests that a gradual change in behavior took place over a longer time span.

Homo sapiens is the only extant species of its genus, *Homo*. While some (extinct) *Homo* species might have been ancestors of *Homo sapiens*, many, perhaps most, were likely "cousins", having speciated away from the ancestral hominin line. There is yet no consensus as to which of these groups should be considered a separate species and which should be a subspecies; this may be due to the dearth of fossils or to the slight differences used to classify species in the genus *Homo*. The Sahara pump theory (describing an occasionally passable "wet" Sahara desert) provides one possible explanation of the early variation in the genus *Homo*.

Based on archaeological and paleontological evidence, it has been possible to infer, to some extent, the ancient dietary practices of various *Homo* species and to study the role of diet in physical and behavioral evolution within *Homo*.

Some anthropologists and archaeologists subscribe to the Toba catastrophe theory, which posits that the supereruption of Lake Toba on Sumatran island in Indonesia some 70,000 years ago caused global consequences, killing the majority of humans and creating a population bottleneck that affected the genetic inheritance of all humans today. The genetic and archaeological evidence for this remains in question however.

H. habilis and *H. gautengensis*

Homo habilis lived from about 2.8 to 1.4 Ma. The species evolved in South and East Africa in the Late Pliocene or Early Pleistocene, 2.5–2 Ma, when it diverged from the australopithecines. *Homo habilis* had smaller molars and larger brains than the australopithecines, and made tools from stone and perhaps animal bones. One of the first known hominins was nicknamed 'handy man' by discoverer Louis Leakey due to its association with stone tools. Some scientists have proposed moving this species out of *Homo* and into *Australopithecus* due to the morphology of its skeleton being more adapted to living on trees rather than to moving on two legs like *Homo sapiens*.

H. rudolfensis and *H. georgicus*

These are proposed species names for fossils from about 1.9–1.6 Ma, whose relation to *Homo habilis* is not yet clear.

- *Homo rudolfensis* refers to a single, incomplete skull from Kenya. Scientists have suggested that this was another *Homo habilis*, but this has not been confirmed.
- *Homo georgicus*, from Georgia, may be an intermediate form between *Homo habilis* and *Homo erectus*, or a subspecies of *Homo erectus*.

H. ergaster and *H. erectus*

The first fossils of *Homo erectus* were discovered by Dutch physician Eugene Dubois in 1891 on the Indonesian island of Java. He originally named the material *Anthropopithecus erectus* (1892–1893, considered at this point as a chimpanzee-like fossil primate) and *Pithecanthropus erectus* (1893–1894, changing his mind as of based on its morphology, which he considered to be intermediate between that of humans and apes). Years later, in the 20th century, the German physician and paleoanthropologistFranz Weidenreich (1873–1948) compared in detail the characters of Dubois' Java Man, then named *Pithecanthropus erectus*, with the characters of the Peking Man, then named *Sinanthropus pekinensis*. Weidenreich concluded in 1940 that because of their anatomical similarity with modern humans it was necessary to gather all these specimens of Java and China in a single species of the genus *Homo*, the species *Homo erectus*. *Homo erectus* lived from about 1.8 Ma to about 70,000 years ago – which would indicate that they were probably wiped out by the Toba catastrophe; however, nearby *Homo floresiensis* survived it. The early phase of *Homo erectus*, from 1.8 to 1.25 Ma, is considered by some to be a separate species, *Homo ergaster*, or as *Homo erectus ergaster*, a subspecies of *Homo erectus*. In Africa in the Early Pleistocene, 1.5–1 Ma, some populations of *Homo habilis* are thought to have evolved larger brains and to have made

more elaborate stone tools; these differences and others are sufficient for anthropologists to classify them as a new species, *Homo erectus*—in Africa. The evolution of locking knees and the movement of the foramen magnum are thought to be likely drivers of the larger population changes. This species also may have used fire to cook meat. Richard Wrangham suggests that the fact that Homo seems to have been ground dwelling, with reduced intestinal length, smaller dentition, "and swelled our brains to their current, horrendously fuel-inefficient size", suggest that control of fire and releasing increased nutritional value through cooking was the key adaptation that separated Homo from tree-sleeping Australopithecines.

A famous example of *Homo erectus* is Peking Man; others were found in Asia (notably in Indonesia), Africa, and Europe. Many paleoanthropologists now use the term *Homo ergaster* for the non-Asian forms of this group, and reserve *Homo erectus* only for those fossils that are found in Asia and meet certain skeletal and dental requirements which differ slightly from *H. ergaster*.

H. cepranensis* and *H. antecessor

These are proposed as species that may be intermediate between *H. erectus* and *H. heidelbergensis*.

- *H. antecessor* is known from fossils from Spain and England that are dated 1.2 Ma–500 ka.
- *H. cepranensis* refers to a single skull cap from Italy, estimated to be about 800,000 years old.

H. heidelbergensis

H. heidelbergensis ("Heidelberg Man") lived from about 800,000 to about 300,000 years ago. Also proposed as *Homo sapiens heidelbergensis* or *Homo sapiens paleohungaricus*.

***H. rhodesiensis*, and the Gawis cranium**

- *H. rhodesiensis*, estimated to be 300,000–125,000 years old. Most current researchers place Rhodesian Man within the group of *Homo heidelbergensis*, though other designations such as archaic *Homo sapiens* and *Homo sapiens rhodesiensis* have been proposed.
- In February 2006 a fossil, the Gawis cranium, was found which might possibly be a species intermediate between *H. erectus* and *H. sapiens* or one of many evolutionary dead ends. The skull from Gawis, Ethiopia, is believed to be 500,000–250,000 years old. Only summary details are known, and the finders have not yet released a peer-

reviewed study. Gawis man's facial features suggest its being either an intermediate species or an example of a "Bodo man" female.

NEANDERTHAL AND DENISOVAN

Homo neanderthalensis, alternatively designated as *Homo sapiens neanderthalensis*, lived in Europe and Asia from 400,000 to about 28,000 years ago. There are a number of clear anatomical differences between anatomically modern humans (AMH) and Neanderthal populations. Many of these relate to the superior adaptation to cold environments possessed by the Neanderthal populations. Their surface to volume ratio is an extreme version of that found amongst Inuit populations, indicating that they were less inclined to lose body heat than were AMH. From brain Endocasts, Neanderthals also had significantly larger brains. This would seem to indicate that the intellectual superiority of AMH populations may be questionable. More recent research by Eiluned Pearce, Chris Stringer, R.I.M. Dunbar, however, have shown important differences in brain architecture. For example, in both the orbital chamber size and in the size of the occipital lobe, the larger size suggests that the Neanderthal had a better visual acuity than modern humans. This would give a superior vision in the inferior light conditions found in Glacial Europe. It also seems that the higher body mass of Neanderthals had a correspondingly larger brain mass required for body care and control.

The Neanderthal populations seem to have been physically superior to AMH populations. These differences may have been sufficient to give Neanderthal populations an environmental superiority to AMH populations from 75,000 to 45,000 years BP. With these differences, Neanderthal brains show a smaller area was available for social functioning. Plotting group size possible from endocranial volume, suggests that AMH populations (minus occipital lobe size), had a Dunbars number of 144 possible relationships. Neanderthal populations seem to have been limited to about 120 individuals. This would show up in a larger number of possible mates for AMH humans, with increased risks of inbreeding amongst Neanderthal populations. It also suggests that humans had larger trade catchment areas than Neanderthals (confirmed in the distribution of stone tools). With larger populations, social and technological innovations were easier to fix in human populations, which may have all contributed to the fact that modern Homo sapiens replaced the Neanderthal populations by 28,000 BP.

Earlier evidence from sequencing mitochondrial DNA suggested that no significant gene flow occurred between *H. neanderthalensis* and *H. sapiens*, and that the two were separate

species that shared a common ancestor about 660,000 years ago. However, a sequencing of the Neanderthal genome in 2010 indicated that Neanderthals did indeed interbreed with anatomically modern humans *circa* 45,000 to 80,000 years ago (at the approximate time that modern humans migrated out from Africa, but before they dispersed into Europe, Asia and elsewhere). The genetic sequencing of a 40,000-year-old human skeleton from Romania showed that 11% of its genome was Neanderthal, and it was estimated that the individual had a Neanderthal ancestor 4–6 generations previously, in addition to a contribution from earlier interbreeding in the Middle East. Though this interbred Romanian population seems not to have been ancestral to modern humans, the finding indicates that interbreeding happened repeatedly.

All modern non-African humans have about 1% to 4% or, according to more recent data, about 1.5% to 2.6% of their DNA derived from Neanderthal DNA, and this finding is consistent with recent studies indicating that the divergence of some human alleles dates to one Ma, although the interpretation of these studies has been questioned. Neanderthals and *Homo sapiens* could have co-existed in Europe for as long as 10,000 years, during which human populations exploded vastly outnumbering Neanderthals, possibly outcompeting them by sheer numerical strength. In 2008, archaeologists working at the site of Denisova Cave in the Altai Mountains of Siberia uncovered a small bone fragment from the fifth finger of a juvenile member of Denisovans. Artifacts, including a bracelet, excavated in the cave at the same level were carbon dated to around 40,000 BP. As DNA had survived in the fossil fragment due to the cool climate of the Denisova Cave, both mtDNA and nuclear DNA were sequenced.

While the divergence point of the mtDNA was unexpectedly deep in time, the full genomic sequence suggested the Denisovans belonged to the same lineage as Neanderthals, with the two diverging shortly after their line split from the lineage that gave rise to modern humans. Modern humans are known to have overlapped with Neanderthals in Europe and the Near East for possibly more than 40,000 years, and the discovery raises the possibility that Neanderthals, Denisovans, and modern humans may have co-existed and interbred. The existence of this distant branch creates a much more complex picture of humankind during the Late Pleistocene than previously thought. Evidence has also been found that as much as 6% of the DNA of some modern Melanesians derive from Denisovans, indicating limited interbreeding in Southeast Asia.

Alleles thought to have originated in Neanderthals and Denisovans have been identified at several genetic loci in the genomes of modern humans outside of Africa. HLA haplotypes from Denisovans and Neanderthal represent more than half the HLA alleles of modern Eurasians, indicating strong positive selection for these introgressed alleles. Corinne Simoneti at Vanderbilt University, in Nashville and her team have found from medical records of 28,000 people of European descent that the presence of Neanderthal DNA segments may be associated with a likelihood to suffer depression more frequently.

The flow of genes from Neanderthal populations to modern humans was not all one way. Sergi Castellano of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, has in 2016 reported that while Denisovan and Neanderthal genomes are more related to each other than they are to us, Siberian Neanderthal genomes show similarity to the modern human gene pool, more so than to European Neanderthal populations. The evidence suggests that the Neanderthal populations interbred with modern humans possibly 100,000 years ago, probably somewhere in the Near East. Studies of a Neanderthal child at Gibraltar show from brain development and teeth eruption that Neanderthal children may have matured more rapidly than is the case for Homo sapiens.

H. floresiensis

H. floresiensis, which lived from approximately 190,000 to 50,000 years before present (BP), has been nicknamed the *hobbit* for its small size, possibly a result of insular dwarfism. *H. floresiensis* is intriguing both for its size and its age, being an example of a recent species of the genus *Homo* that exhibits derived traits not shared with modern humans. In other words, *H. floresiensis* shares a common ancestor with modern humans, but split from the modern human lineage and followed a distinct evolutionary path. The main find was a skeleton believed to be a woman of about 30 years of age. Found in 2003, it has been dated to approximately 18,000 years old. The living woman was estimated to be one meter in height, with a brain volume of just 380 cm^3 (considered small for a chimpanzee and less than a third of the *H. sapiens* average of 1400 cm^3).

However, there is an ongoing debate over whether *H. floresiensis* is indeed a separate species. Some scientists hold that *H. floresiensis* was a modern *H. sapiens* with pathological dwarfism. This hypothesis is supported in part, because some modern humans who live on Flores, the Indonesian island where the skeleton was found, are pygmies. This, coupled with pathological dwarfism, could have resulted in a significantly diminutive human. The other

major attack on *H. floresiensis* as a separate species is that it was found with tools only associated with *H. sapiens*.

The hypothesis of pathological dwarfism, however, fails to explain additional anatomical features that are unlike those of modern humans (diseased or not) but much like those of ancient members of our genus. Aside from cranial features, these features include the form of bones in the wrist, forearm, shoulder, knees, and feet. Additionally, this hypothesis fails to explain the find of multiple examples of individuals with these same characteristics, indicating they were common to a large population, and not limited to one individual.

H. luzonensis

A small number of specimens from the island of Luzon, dated 50,000 to 67,000 years ago, have recently been assigned by their discoverers, based on dental characteristics, to a novel human species, *H. luzonensis*.

H. sapiens

H. sapiens (the adjective *sapiens* is Latin for "wise" or "intelligent") emerged in Africa around 300,000 years ago, likely derived from *Homo heidelbergensis* or a related lineage. In September 2019, scientists reported the computerized determination, based on 260 CT scans, of a virtual skull shape of the last common human ancestor to modern humans/*H. sapiens*, representative of the earliest modern humans, and suggested that modern humans arose between 260,000 and 350,000 years ago through a merging of populations in East and South Africa. Between 400,000 years ago and the second interglacial period in the Middle Pleistocene, around 250,000 years ago, the trend in intra-cranial volume expansion and the elaboration of stone tool technologies developed, providing evidence for a transition from *H. erectus* to *H. sapiens*. The direct evidence suggests there was a migration of *H. erectus* out of Africa, then a further speciation of *H. sapiens* from *H. erectus* in Africa. A subsequent migration (both within and out of Africa) eventually replaced the earlier dispersed *H. erectus*. This migration and origin theory is usually referred to as the "recent single-origin hypothesis" or "out of Africa" theory. *H. sapiens*interbred with archaic humans both in Africa and in Eurasia, in Eurasia notably with Neanderthals and Denisovans. The Toba catastrophe theory, which postulates a population bottleneck for *H. sapiens* about 70,000 years ago, was controversial from its first proposal in the 1990s and by the 2010s had very little support. Distinctive human genetic variability has arisen as the result of the founder effect, by archaic admixture and by recent evolutionary pressures.

USE OF TOOLS

The use of tools has been interpreted as a sign of intelligence, and it has been theorized that tool use may have stimulated certain aspects of human evolution, especially the continued expansion of the human brain. Paleontology has yet to explain the expansion of this organ over millions of years despite being extremely demanding in terms of energy consumption. The brain of a modern human consumes about 13 watts (260 kilocalories per day), a fifth of the body's resting power consumption. Increased tool use would allow hunting for energy-rich meat products, and would enable processing more energy-rich plant products. Researchers have suggested that early hominins were thus under evolutionary pressure to increase their capacity to create and use tools.

Precisely when early humans started to use tools is difficult to determine, because the more primitive these tools are (for example, sharp-edged stones) the more difficult it is to decide whether they are natural objects or human artifacts. There is some evidence that the australopithecines (4 Ma) may have used broken bones as tools, but this is debated.

Many species make and use tools, but it is the human genus that dominates the areas of making and using more complex tools. The oldest known tools are flakes from West Turkana, Kenya, which date to 3.3 million years ago. The next oldest stone tools are from Gona, Ethiopia, and are considered the beginning of the Oldowan technology. These tools date to about 2.6 million years ago. A *Homo* fossil was found near some Oldowan tools, and its age was noted at 2.3 million years old, suggesting that maybe the *Homo* species did indeed create and use these tools. It is a possibility but does not yet represent solid evidence. The third metacarpal styloid process enables the hand bone to lock into the wrist bones, allowing for greater amounts of pressure to be applied to the wrist and hand from a grasping thumb and fingers. It allows humans the dexterity and strength to make and use complex tools. This unique anatomical feature separates humans from apes and other nonhuman primates, and is not seen in human fossils older than 1.8 million years.

Bernard Wood noted that *Paranthropus* co-existed with the early *Homo* species in the area of the "Oldowan Industrial Complex" over roughly the same span of time. Although there is no direct evidence which identifies *Paranthropus* as the tool makers, their anatomy lends to indirect evidence of their capabilities in this area. Most paleoanthropologists agree that the early *Homo* species were indeed responsible for most of the Oldowan tools found. They argue that when most of the Oldowan tools were found in association with human fossils, *Homo* was always present, but *Paranthropus* was not.

In 1994, Randall Susman used the anatomy of opposable thumbs as the basis for his argument that both the *Homo* and *Paranthropus* species were toolmakers. He compared bones and muscles of human and chimpanzee thumbs, finding that humans have 3 muscles which are lacking in chimpanzees. Humans also have thicker metacarpals with broader heads, allowing more precise grasping than the chimpanzee hand can perform. Susman posited that modern anatomy of the human opposable thumb is an evolutionary response to the requirements associated with making and handling tools and that both species were indeed toolmakers.

STONE TOOLS

Stone tools are first attested around 2.6 million years ago, when hominins in Eastern Africa used so-called core tools, choppers made out of round cores that had been split by simple strikes. This marks the beginning of the Paleolithic, or Old Stone Age; its end is taken to be the end of the last Ice Age, around 10,000 years ago. The Paleolithic is subdivided into the Lower Paleolithic (Early Stone Age), ending around 350,000–300,000 years ago, the Middle Paleolithic (Middle Stone Age), until 50,000–30,000 years ago, and the Upper Paleolithic, (Late Stone Age), 50,000–10,000 years ago.

Archaeologists working in the Great Rift Valley in Kenya have discovered the oldest known stone tools in the world. Dated to around 3.3 million years ago, the implements are some 700,000 years older than stone tools from Ethiopia that previously held this distinction. The period from 700,000 to 300,000 years ago is also known as the Acheulean, when *H. ergaster* (or *erectus*) made large stone hand axes out of flint and quartzite, at first quite rough (Early Acheulian), later "retouched" by additional, more-subtle strikes at the sides of the flakes. After 350,000 BP the more refined so-called Levallois technique was developed, a series of consecutive strikes, by which scrapers, slicers ("racloirs"), needles, and flattened needles were made. Finally, after about 50,000 BP, ever more refined and specialized flint tools were made by the Neanderthals and the immigrant Cro-Magnons (knives, blades, skimmers). Bone tools were also made by *H. sapiens* in Africa by 90–70,000 years ago and are also known from early *H. sapiens* sites in Eurasia by about 50,000 years ago.

TRANSITION TO BEHAVIORAL MODERNITY

Until about 50,000–40,000 years ago, the use of stone tools seems to have progressed stepwise. Each phase (*H. habilis*, *H. ergaster*, *H. neanderthalensis*) started at a higher level than the previous one, but after each phase started, further development was slow. Currently paleoanthropologists are debating whether these *Homo* species possessed some or many of the cultural and behavioral traits associated with modern humans such as language, complex

symbolic thinking, technological creativity etc. It seems that they were culturally conservative maintaining simple technologies and foraging patterns over very long periods.

Around 50,000 BP, modern human culture started to evolve more rapidly. The transition to behavioral modernity has been characterized by some as a "Great Leap Forward", or as the "Upper Palaeolithic Revolution", due to the sudden appearance of distinctive signs of modern behavior and big game hunting in the archaeological record. Evidence of behavioral modernity significantly earlier also exists from Africa, with older evidence of abstract imagery, widened subsistence strategies, more sophisticated tools and weapons, and other "modern" behaviors, and many scholars have recently argued that the transition to modernity occurred sooner than previously believed. Some other scholars consider the transition to have been more gradual, noting that some features had already appeared among archaic African *Homo sapiens* since 300–200,000 years ago. Recent evidence suggests that the Australian Aboriginal population separated from the African population 75,000 years ago, and that they made a sea journey of up to 160 km 60,000 years ago, which may diminish the evidence of the Upper Paleolithic Revolution.

Modern humans started burying their dead, using animal hides to make clothing, hunting with more sophisticated techniques (such as using trapping pits or driving animals off cliffs), and engaging in cave painting. As human culture advanced, different populations of humans introduced novelty to existing technologies: artifacts such as fish hooks, buttons, and bone needles show signs of variation among different populations of humans, something that had not been seen in human cultures prior to 50,000 BP. Typically, *H. neanderthalensis* populations do not vary in their technologies, although the Chatelperronian assemblages have been found to be Neanderthal innovations produced as a result of exposure to the Homo sapiens Aurignacian technologies.

Among concrete examples of modern human behavior, anthropologists include specialization of tools, use of jewellery and images (such as cave drawings), organization of living space, rituals (for example, burials with grave gifts), specialized hunting techniques, exploration of less hospitable geographical areas, and barter trade networks. Debate continues as to whether a "revolution" led to modern humans ("the big bang of human consciousness"), or whether the evolution was more "gradual".

RECENT AND ONGOING HUMAN EVOLUTION

Anatomically modern human populations continue to evolve, as they are affected by both natural selection and genetic drift. Although selection pressure on some traits, such as

resistance to smallpox, has decreased in the modern age, humans are still undergoing natural selection for many other traits. Some of these are due to specific environmental pressures, while others are related to lifestyle changes since the development of agriculture (10,000 years ago), urbanization (5,000), and industrialization (250 years ago). It has been argued that human evolution has accelerated since the development of agriculture 10,000 years ago and civilization some 5,000 years ago, resulting, it is claimed, in substantial genetic differences between different current human populations, and more recent research indicates that for some traits, the developments and innovations of human culture have driven a new form of selection that coexists with, and in some cases has largely replaced, natural selection.

Particularly conspicuous is variation in superficial characteristics, such as Afro-textured hair, or the recent evolution of light skin and blond hair in some populations, which are attributed to differences in climate. Particularly strong selective pressures have resulted in high-altitude adaptation in humans, with different ones in different isolated populations. Studies of the genetic basis show that some developed very recently, with Tibetans evolving over 3,000 years to have high proportions of an allele of EPAS1 that is adaptive to high altitudes.

Other evolution is related to endemic diseases: the presence of malaria selects for sickle cell trait (the heterozygous form of sickle cell gene), while in the absence of malaria, the health effects of sickle-cell anemia select against this trait. For another example, the population at risk of the severe debilitating disease kuru has significant over-representation of an immune variant of the prion protein gene G127V versus non-immune alleles. The frequency of this genetic variant is due to the survival of immune persons. Some reported trends remain unexplained and the subject of ongoing research in the novel field of evolutionary medicine: polycystic ovary syndrome (PCOS) reduces fertility and thus is expected to be subject to extremely strong negative selection, but its relative commonality in human populations suggests a counteracting selection pressure. The identity of that pressure remains the subject of some debate. Recent human evolution related to agriculture includes genetic resistance to infectious disease that has appeared in human populations by crossing the species barrier from domesticated animals, as well as changes in metabolism due to changes in diet, such as lactase persistence.

Culturally-driven evolution can defy the expectations of natural selection: while human populations experience some pressure that drives a selection for producing children at younger ages, the advent of effective contraception, higher education, and changing social norms have driven the observed selection in the opposite direction. However, culturally-

driven selection need not necessarily work counter or in opposition to natural selection: some proposals to explain the high rate of recent human brain expansion indicate a kind of feedback whereupon the brain's increased social learning efficiency encourages cultural developments that in turn encourage more efficiency, which drive more complex cultural developments that demand still-greater efficiency, and so forth. Culturally-driven evolution has an advantage in that in addition to the genetic effects, it can be observed also in the archaeological record: the development of stone tools across the Palaeolithic period connects to culturally-driven cognitive development in the form of skill acquisition supported by the culture and the development of increasingly complex technologies and the cognitive ability to elaborate them.

In contemporary times, since industrialization, some trends have been observed: for instance, menopause is evolving to occur later. Other reported trends appear to include lengthening of the human reproductive period and reduction in cholesterol levels, blood glucose and blood pressure in some populations.